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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Squamate reptiles from the Lower Miocene of the Sperrgebiet, Namibia

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The Lower Miocene of the Sperrgebiet (southwestern Namibia) has produced squamate reptiles. The fossils come from four localities: Grillental area, Langental, Elisabethfeld, and E-Bay. Lizards are represented by a gekkonid and an amphisbaenian that are both indeterminate, and two indeterminate lacertilians. Snakes are more diverse; they include one scolecophidian, two boids (cf. *Python* sp. A and cf. *Python* sp. B), two colubrids (one natricine and one 'colubrine'), one viperid (either one *Vipera* of the oriental complex or *Daboia*), and one indeterminate colubroid (either a colubrid or a viperid). The early Miocene might have been an important period for the diversification of pythonine boids in Africa. The composition of these faunas appears to be less advanced than the Arrisdrift assemblage that is slightly younger.

Version française abrégée

Les squamates ont été trouvés dans le Miocène inférieur du 'Sperrgebiet' (sud-ouest de la Namibie). Ils proviennent de quatre gisements : Grillental (qui comprend plusieurs sites), Langental, Elisabethfeld et E-Bay. Elisabethfeld, E-Bay et les sites de Grillental sont un peu plus anciens (ca 20 Ma) que Langental (ca 19 Ma). Les gisements sont stratigraphiquement proches de la limite entre Aquitanien et Burdigalien.

La faune

Lacertiliens

Les lézards comprennent un gekkonidé et un amphisbaenien, indéterminables au niveau familial, et deux autres lacertiliens inidentifiables.

Serpents
Scolecophidiens

Une unique vertèbre appartient à ce groupe mais l'identification n'est pas discutable. Il s'agit de l'un des très rares représentants fossiles des scolecophidiens en Afrique.

Boidae

La famille est représentée par deux espèces, cf. *Python* sp. A et cf. *Python* sp. B. Elles ne peuvent pas être rapportées au genre *Python* en raison de la faible hauteur de leurs neurépines et de la trop faible épaisseur de leur zygosphène. Le gisement namibien d'Arrisdrift, légèrement plus récent (ca 17 Ma) a fourni un boïdé attribuable à *Python*. cf. *Python* sp. A et cf. *Python* sp. B se distinguent par la hauteur de la neurépine, plus basse chez cf. *Python* sp. A, et la largeur du zygosphène, plus large chez cf. *Python* sp. B.

Colubridae

Deux taxons sont rapportés à cette famille: un natriciné indéterminé et un non-natriciné dont la morphologie vertébrale est de type 'colubriné'; mais l'at-tribution de ce dernier à une sous-famille précise est impossible.

Viperidae

Une seule vertèbre montre la présence d'un viperidé qui appartient soit à *Daboia*, soit à une *Vipera* du complexe oriental. Actuellement, l'aire de répartition des *Vipera* du complexe oriental n'atteint l'Afrique que dans son extrême nord tandis que *Daboia* est absente du continent.

Colubroidea indéterminé

Ce colubroïde montre un ensemble de caractères qui évoque à la fois les viperidés et les colubridés.

Conclusions

La présence de trois pythoninés distincts dans le Miocène inférieur de Namibie (deux dans la présente étude et un à Arrisdrift) suggère que cette période a été importante pour la diversification des pythons en Afrique. Il faut aussi noter que le seul viperidé présent (que ce soit une *Vipera* du complexe oriental ou *Daboia*) se situe géographiquement très loin de son aire de répartition actuelle. Une différence assez nette apparaît entre les compositions des faunes du Sperrgebiet et celle d'Arrisdrift qui est un peu plus récente. *Varanus* (Varanidae), *Naja*? (Elapidae), *Bitis* (Viperidae) et probablement *Python* (Boidae), présents à Arrisdrift, manquent dans les gisements du Sperrgebiet. Arrisdrift apparaît ainsi plus proche de la faune actuelle du sud de l'Afrique. Il faudrait pouvoir établir s'il s'agit d'un changement réel ou d'un biais. Amphisbaeniens et scolecophidiens sont des fouisseurs actifs mais les autres taxons n'apportent pas d'informations claires sur l'environnement.

Introduction

The squamates studied in the present article were recovered from four localities in the northern Sperrgebiet, southwestern Namibia. The localities are Langental, Elisabethfeld, E-Bay, and the Grillental

area. Langental, Elisabethfeld, and E-Bay correspond to one site each, but Grillental includes several sites (Pickford and Senut, 1999). Two sites of the Grillental area (GT 6 and GT Quarry) have produced squamates; however, the detailed source of a part of the fossils from the Grillental area is unknown.

These four localities are of Early Miocene age. The sites of the Grillental area, E-Bay, and Elisabethfeld have been dated at about 20 Ma; Langental is slightly younger (19 Ma) (Pickford and Senut, 1999, 2003). The age of the localities is therefore close to the limit between the Aquitanian and Burdigalian.

Squamates from the Early Miocene of Namibia have been already reported (Rage, 2003); they come from Arrisdrift, the geological age of which (ca 17 Ma) is younger than that of the above four localities (Pickford and Senut, 1999).

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

Systematic descriptions
Lacertilia Owen, 1842

Lizards are not numerous. Within the available lacertilians, only gekkonids and amphisbaenians are identifiable (at high taxonomic level only).

Gekkonidae Gray, 1825
Unidentified genus and species

Provenance: Elisabethfeld
Referred material: 1 fragment of dentary (EF 20'05a).

Description and discussion:
The sulcus meckeli is closed, no suture being apparent. The preserved teeth are tall, narrow, closely spaced, and unicuspid. This assemblage of characters clearly points to the Gekkonidae, but identification below family level is not possible.

Amphisbaenia Gray, 1844
Unidentified family

Provenance: Grillental area.
Referred material: GT 6, 6 incomplete trunk vertebrae (GT 56'00c; GT 63'00k); GT-precise site unknown, 2 incomplete trunk vertebrae (GT 36'97o).

Description and discussion :
These vertebrae are depressed and they lack a zygosphene. The centrum has a flat ventral surface that is limited by parallel subcentral ridges. The neural spine is very low or absent. The prezygapophyseal facets are strongly inclined on the horizontal. The paradiapophyses are globular and undivided. This morphology is typical of amphisbaenians but these vertebrae do not permit further identification.

Amphisbaenians are frequent components of Tertiary faunas. In Africa, they have been reported from the Upper Palaeocene, Lower and Middle Miocene (Rage, 2003), and Upper Pliocene (Bailon, 2000). Amphisbaenians are elongate burrowers that sometimes enter termitaries and anthills.

Lacertilians indeterminate

Unidentified genus and species 1

Provenance: Grillental area, Langental, and Elisabethfeld.
Referred material: Langental, 1 fragment of bone bearing teeth (LT 120'00).- Grillental area: GT-precise site unknown, 1 fragment of bone bearing teeth (GT 36'97m).- Elisabethfeld, 1 fragment of bone bearing teeth (EF 165'01).

Description and discussion :
All fragments of bones bear similar teeth. The latter are pleurodont, elongate and relatively pointed, without accessory cusps. They do not show peculiar features that may help identification within pleurodont lizards.

Unidentified genus and species 2

Provenance: Elisabethfeld.
Referred material: 1 fragment of maxilla (EF 20'05b).

Description and discussion:
As in the above indeterminate lizard, the teeth are pleurodont. But they are shorter and thicker, their tip is bevelled and shows an incipient bicuspid condition. The family cannot be identified.

Unidentified vertebrae

Provenance: Grillental area.
Referred material: GT 6, 1 trunk (GT 63'00i) and 1 caudal (GT 63'00j) vertebrae; GT-precise site unknown, 1 trunk vertebra (GT 36'97n).

Discussion:
These vertebrae do not belong to gekkonids or amphisbaenians, but further identification is not possible. They may belong to one of, or to the two above reported unidentified genera and species.

Serpentes Linnaeus, 1758

Scolecophidia Duméril and Bibron, 1844
Family indeterminate

Provenance: Grillental area.
Referred material: GT-precise site unknown, 1 trunk vertebra (GT 36'97p).

Description and discussion:

This incomplete, tiny vertebra (centrum length = 0.75 mm) displays a combination of characters that is typical of scolecophidians: ventral surface of centrum flat and limited laterally by parallel subcentral ridges, absence of any trace of haemal keel, absence of neural spine, presence of a zygosphene, cotyle and condyle strongly depressed.

The vertebral morphology being very homogenous within the group, identification is not possible, even at family level. Scolecophidians are rare as fossils. In Africa, they have been reported from two localities only: the Upper Palaeocene of Adrar Mgorn (Gheerbrant *et al.*, 1993; Augé and Rage, in progress) and the Middle Miocene of Beni Mellal (Rage, 1976),

both localities in Morocco. All scolecophidians are fossorial.

Alethinophidia Nopcsa, 1923
Boidae Gray, 1825

Nearly all fossil snakes from Africa that belong to non-erycine Boidae have been assigned to the genus *Python* (Table 1). Thus far, the only exception is a snake from the Lower Pliocene of Libya identified as an indeterminate Boidae by Hecht (1987); however, it might belong to *Python* (Szyndlar and Rage, 2003). Moreover, the Upper Palaeocene of Morocco yielded one incomplete vertebra that probably belongs to a Boidae, but this cannot be definitely confirmed (Szyndlar and Rage, 2003; Augé and Rage, in pro-

Table 1: List of extinct non-erycine Boidae reported from Africa.

Geological ages	Localities	Taxa	References
Middle Pleistocene	Oliduvai, Bed IV (Tanzania)	*Python sebae*	Rage 1973
Lower or lower Middle Pleistocene	Buia (Eritrea)	*Python* gr. *P. sebae*	Delfino *et al.* 2004
Lower Pleistocene	Olduvai, Bed II (Tanzania)	*Python sebae*	Rage 1973
Pliocene/Pleistocene transition	Olduvai, Bed I (Tanzania)	*Python* aff. *P. sebae*	Rage 1973
Plio-Pleistocene (bed unknown)	Omo (Ethiopia)	*Python* sp.	Rage 1979
Plio-Pleistocene (bed unknown)	Hadar (Ethiopia)	*Python* sp. (? P. sebae)	Rage 1979
Upper Pliocene	Laetoli (Tanzania)	*Python sebae*	Meylan 1987
Middle Pliocene	Warwire Fm, Loc. NK 93 (Uganda)	*Python* sp.	Bailon & Rage 1994
Miocene/Pliocene transition	Sahabi (Libya)	Boidae indet. (? *Python*)	Hecht 1987; Szyndlar & Rage 2003
Miocene/Pliocene transition	Nkondo Fm, Loc. NK 43 (Uganda)	*Python* sp.	Bailon & Rage 1994
Miocene/Pliocene transition	Kossom Bougoudi (Chad)	*Python* aff. *P. sebae*	Brunet *et al.* 2000
Uppermost Miocene	Toros Menalla (Chad)	*Python* cf. *P. sebae*	Vignaud *et al.* 2002
Uppermost Miocene	Nkondo Fm, Loc. NK 33 (Uganda)	*Python sebae*	Bailon & Rage 1994
Uppermost Miocene	Nkondo Fm, Loc. NK 11 (Uganda)	*Python* cf. *P. sebae*	Bailon & Rage 1994
Middle Miocene	Beni Mellal (Morocco)	*Python maurus*	Rage 1976
Lower Miocene	Arrisdrift (Namibia)	*Python* cf. *P. sebae*	Rage 2003
Lower Miocene	Langental (Namibia)	cf. *Python* sp. B	This article
Lower Miocene	Napak (Kenya)	Probably *Python*	Unpublished (= '...Lower Miocene of East Africa perhaps … *Python*' in Rage 1984; 21)
Lower Miocene	E-Bay (Namibia)	? cf. *Python* sp. A	This article
Lower Miocene	Elisabethfeld (Namibia)	*Python* sp.	This article
Lower Miocene	Grillental (Namibia)	cf. *Python* sp. A	This article
Upper Palaeocene	Adrar Mgorn 1 (Morocco)	Probable Boidae	Szyndlar & Rage 2003; Augé & Rage, 2006

gress). If this vertebra from the Palaeocene actually belongs to the Boidae, then it represents the earliest member of the family in Africa. No other boid is known from the African Plate before the Lower Miocene, except an Erycinae from the Lower Oligocene of the Arabian Peninsula (Thomas *et al.*, 1991).

The earliest confirmed non-erycine Boidae from Africa come from the Namibian localities Arrisdrift (Rage, 2003), Grillental, Langental, Elisabethfeld, and E-Bay (see below), and from the Ugandan locality Napak that yielded a rather large boid (Table 1). While *Python* was reported from Arrisdrift and was perhaps present at Napak, the boids from Grillental, Langental, Elisabethfeld, and E-Bay cannot be securely referred to a genus.

? *Python* Daudin, 1803
cf. *Python* sp. A
(Fig. 1)

Provenance: Grillental area and perhaps E-Bay.
Referred material: Grillental area, GT 6, 1 incomplete compound bone (GT 18'97c), 2 anterior trunk vertebrae (GT 18'97d, e), 2 mid-trunk vertebrae (GT 18'97f, g), 1 posterior trunk vertebra (GT 18'97h), 6 incomplete trunk vertebrae (GT 18'97i-n), fragments of vertebrae (GT 18'97o), and fragmentary ribs (GT 18'97p, q) that probably all belong to one single individual.- E-Bay, perhaps three incomplete vertebrae (107 EPa-c).
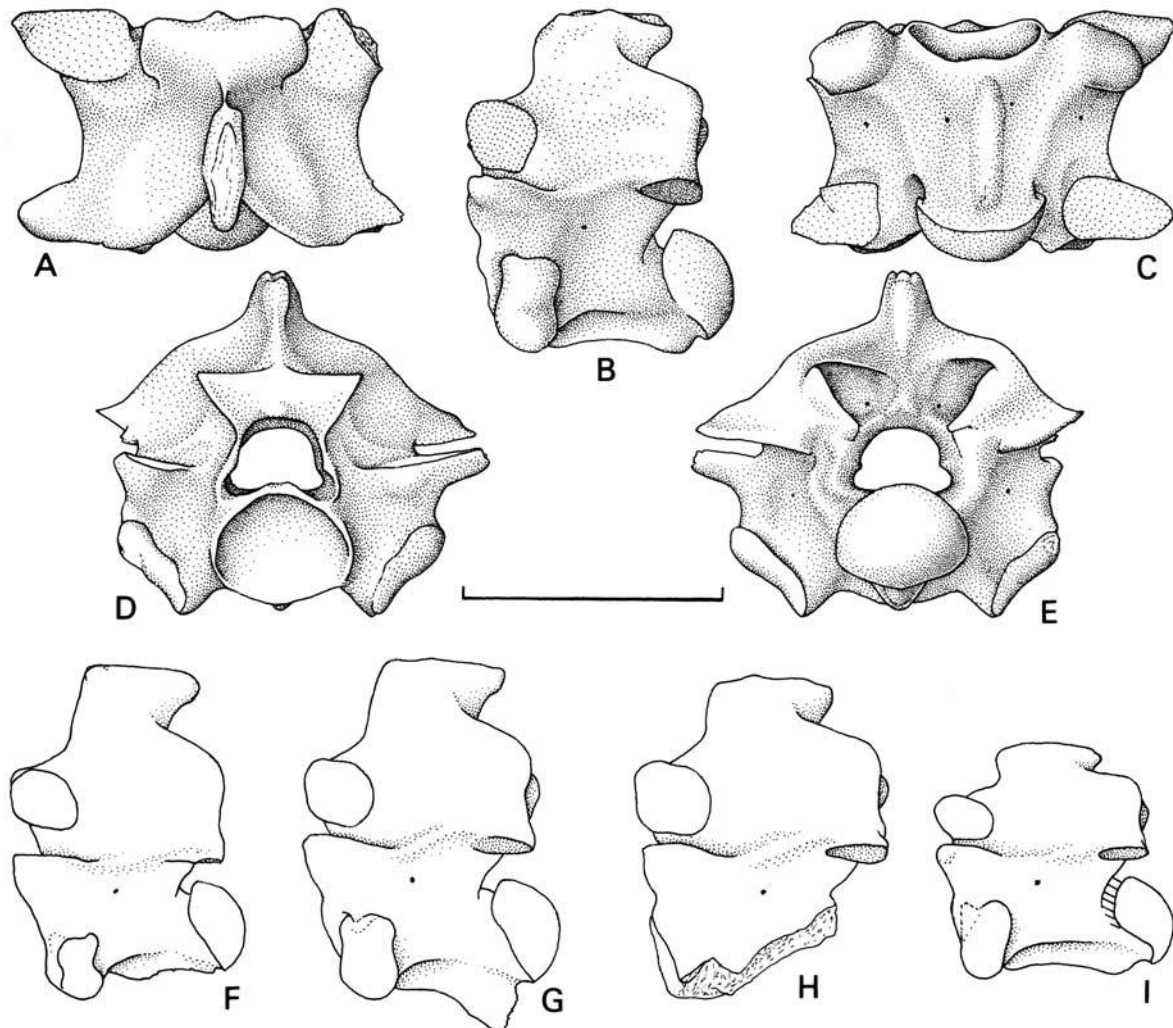

Figure 1: cf. *Python* sp. A, Grillental (GT6). A-E, mid-trunk vertebra (GT 18'97g) in dorsal (A), left lateral (B), ventral (C), anterior (D), and posterior (E) views. F-I, variation of the height of the neural spine, left lateral views: F, anterior-most available vertebra (GT 18'97e); G, anterior trunk vertebra (GT 18'97d); H, mid-trunk vertebra (GT 18'97f); I, posterior trunk vertebra (GT 18'97h). Scale bar: 1 cm.

Description:

Vertebrae:

The vertebrae belong to a medium sized boid snake. In the largest vertebra (GT 18'97e), the maximum width across the prezygapophyseal processes is 17 mm; therefore, this snake was probably between about 2.20 m and 2.60 m in total length.

The vertebrae show the typical morphology of the Boidae; they are massively built, short and wide; their paradiapophyses are weakly subdivided into para- and diapophyseal surfaces, and their prezygapophyseal processes are very short.

In anterior view, the zygosphene is slightly wider than the cotyle and moderately thick in anterior and mid-trunk, and it is as wide as the cotyle and thinner in posterior trunk vertebrae. The roof of the zygosphene is flat in anterior trunk, whereas it becomes slightly and clearly concave dorsally in mid- and posterior trunks respectively. The median lobe is a thin salient that protrudes from the ventral part of the zygosphene. The cotyle is practically circular in all vertebrae. There is no paracotylar foramina. The articular facets of the zygapophyses are inclined only slightly on the horizontal. In posterior trunk vertebrae, the paradiapophyses are more distant from the centrum than they are in more anterior ones, which is a usual variation in snakes.

In dorsal aspect, the prezygapophyseal facets of anterior and mid-trunk vertebrae are elongate and clearly directed laterally. In posterior trunk vertebrae, they are less elongate, more or less oval, and their main axis is slightly oblique. Whatever the orientation of prezygapophyseal facets, the interzygapophyseal constriction is shallow. The zygosphene forms three lobes that project weakly anteriorly. The median notch in the posterior border of the neural arch is deep.

In lateral view, the neural spine is low for non-erycine standard. In posterior trunk vertebrae, it is relatively long anteroposteriorly and especially low, being about three times longer than high (Fig. 1I). In all vertebrae, its anterior border originates approximately on the posterior limit of the zygosphene and it rises steeply; it is weakly inclined posteriorly in anterior trunk, approximately vertical in mid-trunk, and overhanging anteriorly in posterior trunk vertebrae. In all vertebrae, the posterior border of the neural spine clearly overhangs posteriorly. In several vertebrae, the posterodorsal corner of the neural spine slightly projects posteriorly. The interzygapophyseal ridges are prominent and sharp. The paradiapophyses are comprised of a globulous and salient diapophysis and a nearly flat parapophysis; in posterior trunk vertebrae, the diapophyseal part is clearly larger than the parapophyseal one. The haemal keel projects ventrally in the posterior part of the centrum.

In ventral view, the centrum is relatively narrow and well-limited by subcentral ridges; it does not markedly widen anteriorly. A hypapophysis is present in anterior trunks, but it is replaced by a haemal keel in more posterior vertebrae. The haemal keel is clearly limited laterally by subcentral grooves that extend anteriorly up to the cotylar rim.

In posterior view, the neural arch is relatively vaulted and markedly upswept above the zygantrum in anterior and mid-trunk vertebrae; these traits are less prominent in the posterior trunk region. Parazygantral foramina are absent.

Compound bone:

One incomplete compound bone was found along with the vertebrae described above. Since it belongs to the Boidae and its size is consistent with the vertebrae, it is referred to the same taxon (it probably belongs to the same individual as the vertebrae). It lacks the anteroventral part and the surangular (i.e. lateral) lamina. The articular surface for the quadrate is well-limited anteriorly and posteriorly. The retroarticular process is short, stout, and directed posteromedially. The prearticular (i.e. medial) lamina is low; anteriorly, it gently stretches down and grades into the anterior shaft.

Ribs:

The ribs were found with the above described specimens; moreover, the size of all these elements is consistent. The proximal extremity of ribs shows the typical morphology of boids. The articular surface is reniform and subdivided into two facets; the dorsal facet is concave while the ventral one appears to be more or less flat. The *tuber costae* is short, robust, and compressed anteroposteriorly.

Discussion:

Several features of the vertebrae are consistent with pythonine boids: zygapophyseal facets inclined only slightly on the horizontal, anterior border of the neural spine rising steeply, neural spine overhanging posteriorly, paracotylar foramina absent, haemal keel well-defined by subcentral grooves that reach the cotylar rim, haemal keel projecting ventrally only in the posterior part of each vertebra (Scanlon and Mackness, 2002). In addition, the vaulted neural arch that is upswept above the zygantrum compares favourably with pythons.

The presence of a pythonine snake in Africa suggests the genus *Python*, but two features are not consistent with assignment to this genus: the neural spine is unusually low and the zygosphene is not thick. A low neural spine occurs in some living Australasian pythonines (Szyndlar, pers. comm.). In the genus *Python*, this character is known only in *P. europaeus* from the Lower Miocene of France (Szyndlar and Rage, 2003; Rage and Bailon, 2005), but the neural spine of the Namibian fossil is even lower than that of the European species. On the other hand, a neural spine approximately as low as that of the Namibian python has been observed on an incomplete vertebral column of *Python molurus* (an extant species from southern Asia) in the Paris Museum (MNHN) collec-
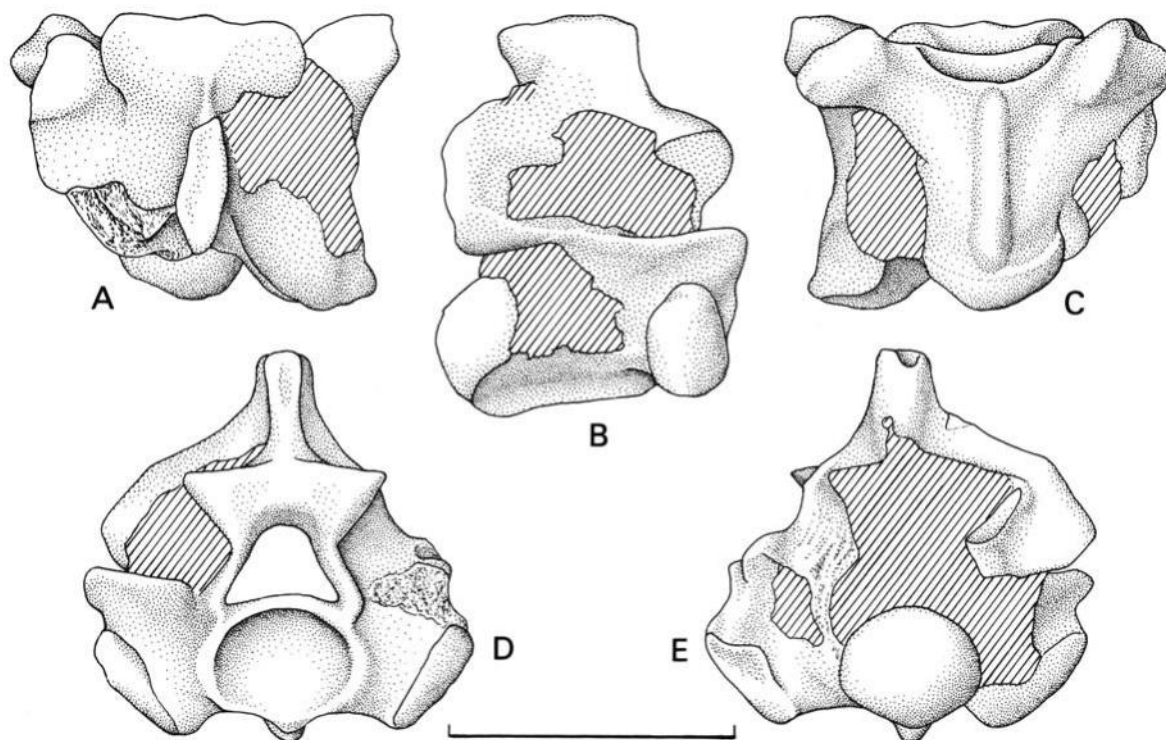
Figure 2: cf. *Python* sp. B, Langental. Mid-trunk vertebra (LT 177'96a) in dorsal (A), right lateral (B), ventral (C), anterior (D), and posterior (E) views. Scale bar: 1 cm.

tions (unnumbered). The morphology of the neural spine in this specimen of *P. molurus* appears as an extreme variation within the species, since, as noted by Szyndlar and Rage (2003: 72), the other skeletons of *P. molurus* examined have markedly higher neural spines. In addition, the zygosphene of the Namibian boid does not reach the thickness that is typical for *Python*. However, this distinctive character is not so striking as the low neural spine.

Consequently, the morphology of these vertebrae differs from that of all other species of *Python*, the closest species morphologically being *P. europaeus* from the Lower Miocene of Europe. These vertebrae from Namibia might be regarded as extreme variants within *Python*, but a referral to this genus cannot be made without reservation. Unfortunately, the poorly preserved compound bone is of no help for identification. Therefore, this snake is only referred to as cf. *Python*. Because of the presence of another problematic pythonine in the Lower Miocene, at Langental (see below), it is more exactly referred to as cf. *Python* sp. A.

cf. *Python* sp. B
(Fig. 2)

Provenance: Langental.

Referred material: 5 trunk vertebrae (LT 177'96a-d; LT 57'99a).

Description:

Only four mid- and one posterior trunk vertebrae from Langental are well-preserved. They mainly differ from the vertebrae of cf. *Python* sp. A in having higher neural spines (except in LT 177'96d) and wider zygosphenes (except in LT 177'96d and LT 57'99a). As far as the size is concerned, no measurement can be used for comparison with cf. *Python* sp. A, but the boid from Langental appears to have been slightly longer than the latter.

Apart from its height, the neural spine does not differ much from that of cf. *Python* sp. A. The anterior border rises steeply from the posterior limit of the zygosphene. It is approximately vertical in mid-trunk vertebrae and, contrary to cf. *Python* sp. A, also in the posterior one (LT 177'96c). As in cf. *Python* sp. A, the posterior border of the neural spine overhangs posteriorly. As far as the height of the neural spine is concerned, the difference between 'sp. B' and 'sp. A' is rather conspicuous in mid-trunk, but it is less prominent in posterior trunk vertebrae. However, LT 177'96d (a mid-trunk vertebra) has a relatively low neural spine that is similar to that of cf. *Python* sp. A.

Although the size of the vertebrae does not clearly differ from that of cf. *Python* sp. A, the zygosphene is clearly wider in sp. B, except in LT 57'99a and LT 177'96d. In 'sp. B', the ratio width of zygosphene/ width of cotyle reaches 1.37 in mid-trunk and 1.45 in posterior trunk vertebrae, whereas it is 1.21 and 1.07

respectively in 'sp. A'. However, in LT 177'96d and LT 57'99a the ratios (1.16 and 1.15 respectively) are smaller and fall within the range of variation shown by 'sp. A'. Another difference is shown by the roof of the zygosphene: it is weakly convex dorsally is 'sp. B', except in LT 57'99a in which it is flat, whereas in 'sp. A' the roof is either flat or concave. As in 'sp. A', the anterior border of the zygosphene forms three lobes. In 'sp. B', the lobes are hardly perceivable in some vertebrae; this is probably an artifact because vertebrae from Langental are slightly worn. As in 'sp. A', the zygosphene is not as thick as in typical *Python*.

Discussion:

Three vertebrae from Langental have a relatively high neural spine and a wide zygosphene, which strongly suggests that this snake represents a taxon distinct from cf. *Python* sp. A. However, two other vertebrae from Langental show morphological traits known in 'sp. A': LT 57'99a and LT 177'96d have a zygosphene as narrow as that of 'sp. A' and the latter vertebra has also a neural spine nearly as low as that of 'sp. A'. Finally, LT 177'96d differs from 'sp. A' only in having a dorsally convex roof of the zygosphene; however, this vertebra is put into the same taxon as the other vertebrae from Langental because the small sample from this locality shows important morphological variation.

The neural spines of the form from Langental are higher (except in one specimen) than those of the vertebrae from Grillental, i.e. cf. *Python* sp. A, and are therefore more consistent with *Python*. But the wide and relatively thin zygosphene does not permit a secure assignment to that genus. Therefore, the specimens from Langental are referred to as cf. *Python* sp. B.

Boidae indeterminate

Some poorly preserved vertebrae or vertebrae of juvenile individuals cannot be identified below family level. Moreover, a few snake teeth are referred to the Boidae on the basis of their size.

Provenance: Langental, Grillental area, Elisabethfeld, and E-Bay.
Referred material: <u>Langental</u>, about fifteen fragmentary vertebrae (LT 177'96e; LT 57'99b; LT 70'03; LT 160'03).- <u>Grillental area: GT 6</u>, 3 teeth (GT 56'00c; GT 63'00-l), 3 incomplete vertebrae (GT 66'96), 1 caudal vertebra (GT 63'00q); <u>GT-precise site unknown</u>, 4 teeth (GT 36'97n), 3 vertebrae of juveniles (GT 36'97m), 1 caudal vertebra (GT 36'97t).- <u>Elisabethfeld</u>, 1 tooth (EF 237'01a), 1 vertebra (EF 108'01), 7 vertebrae of a juvenile individual (EF 20'05c).- <u>E-Bay</u>, 2 fragments of vertebrae (107 EPd, e).

Remarks on the pythonine Boidae from the Lower Miocene of Namibia

As a preliminary remark, it should be noted that Broadley (1999) rised the living subspecies *Python sebae natalensis* to species status. But, the osteological differences between *P. sebae* and *P. natalensis*, if any, are still unknown. Therefore, it should be understood that, in the present article as well as in the previous palaeontological studies, *P. sebae* corresponds to the former acceptance of the species, i.e. *P. sebae* including *P. natalensis*.

Rage (2003) reported *Python* cf. *P. sebae* from the Lower Miocene of Arrisdrift (Namibia). According to Pickford and Senut (1999), Arrisdrift is younger than Langental (slightly less than 2 million years younger) and Grillental (slightly less than 3 m.y. younger). The fossil from Arrisdrift is represented by three poorly preserved vertebrae, including a rather large one; on the latter vertebra, the width of the zygosphene (the only possible common measurement) is 9.6 mm, whereas it is 6.4 mm and 7.2 mm on the largest vertebrae from Grillental and Langental respectively. Based on the largest vertebra, the *Python* from Arrisdrift was referred to *Python* cf. *P. sebae* because its overall vertebral morphology clearly differs from that of African pythons except that of the living *P. sebae*. However, it differs from the latter by its lower neural spine. Although low, the neural spine of the Arrisdrift python is higher than that of cf. *Python* sp. A from Grillental; the height is approximately similar in the python from Arrisdrift and cf. *Python* sp. B, but comparison is difficult because of the important difference in size. The low neural spine of the Arrisdrift python was interpreted as a possible variant within *P. sebae*, the neural spine of which is affected by variation. Moreover, the zygosphene of the Arrisdrift python shows the typical morphology of *Python* in being thick, contrary to those of the Grillental and Langental forms.

Vertebrae referred to both cf. *Python* sp. A and sp. B, although smaller than those of *Python* cf. *P. sebae* from Arrisdrift, do not belong to juvenile individuals. Differences noted between 'sp. A.' and 'sp. B' on the one hand, and the larger *Python* from Arrisdrift on the other, cannot be of ontogenetic nature, i.e. size-related. Therefore, three distinct pythonine taxa are present in the Lower Miocene of Namibia. The early Miocene may have been a key period in the diversification of pythonines in Africa.

Colubridae s.l. Oppel, 1811

The systematics and phylogeny of colubrids has been long debated and no satisfaying solution has been reached. Colubrids are here understood in their broadest acceptation. Colubrid species and genera are numerous today, more specifically in Africa. The vertebral morphology of most living forms is unknown. Consequently, the identification of the colu-

brids from the Miocene of Namibia is not possible at genus, or even subfamily levels.

Natricinae Bonaparte, 1838
Unidentified genus and species

Provenance: Grillental area.
Referred material: <u>GT Quarry</u>, 1 trunk vertebra (GT 139'04).

Description and discussion:

The vertebra comes from the mid-trunk region. It is mainly characterized by the presence of a short, laterally compressed hypapophysis. The ventral surface of the centrum is flat and clearly limited by subcentral ridges; it is relatively narrow and elongate. The thin zygosphene is clearly wider than the cotyle. The neural canal is broad and high. The neural arch is moderately vaulted and, in posterior view, it is obtusely angled above each zygantral fossa. The relatively high neural spine overhangs anteriorly; its posterior border is broken off.

The lateral compression of the hypapophysis and the morphology of the ventral face of the centrum point to the Natricinae. This referral is supported also by the overhanging anterior border of the neural spine and the morphology of the neural arch in posterior view. Identification below the subfamily level is not possible.

'Colubrines'
Unidentified genus and species

Provenance: Grillental area, Langental, and Elisabethfeld.
Referred material: <u>Grillental area: GT 6</u>, 1 nearly complete and 2 fragmentary trunk vertebrae (GT 63'00m-o); <u>GT-precise site unknown</u>, 1 trunk vertebra (GT 36'97s).- <u>Langental</u>, 1 incomplete trunk vertebra (LT 199'99).- <u>Elisabethfeld</u>, 13 trunk vertebra (EF 237'01b; EF 20'05d), 3 larger trunk vertebrae (EF 20'05e), and perhaps 7 partly articulated trunk vertebrae in matrix (EF 21'97).

Description and discussion:

Apparently, all vertebrae referred to the 'colubrines' represent a single morph. They are relatively elongate, not markedly depressed and, in those from the mid- and posterior trunk regions, a haemal keel replaces the hypapophysis, i.e. they belong to the 'colubrine' type. This does not mean that they belong to the subfamily Colubrinae. Within this morphological type, the main characteristics displayed by these vertebrae include the markedly three-lobed zygosphene, relatively depressed neural arch, short prezygapophyseal processes and, in mid-trunk vertebrae, the thin and clear-cut haemal keel.

Colubridae indeterminate

Specimens (caudal and two poorly preserved trunk vertebrae) that cannot be compared to the above colubrids are listed here.

Provenance: Grillental area and Elisabethfeld.
Referred material: <u>Grillental area: GT 6</u>, 1 caudal vertebra (GT 56'00e), 1 caudal vertebra and 1 fragmentary trunk vertebra (GT 63'00p).- <u>Elisabethfeld</u>, 1 fragmentary trunk vertebra (EF 41'00).

Viperidae Oppel, 1811
Unidentified genus and species

Provenance: Elisabethfeld.
Referred material: 1 trunk vertebra (EF 56'01).

Description and discussion:

The vertebra is incomplete but it may be securely referred to the Viperidae on the basis of the following characters: vertebra short and massive; section of neural canal small, narrower than cotyle; cotyle and condyle large; prezygapophyseal facets slightly inclined on the horizontal; neural arch strongly depressed; posterodorsal borders of neural arch straight in posterior view.

The general proportions of the specimen are reminiscent of *Bitis*, *Daboia*, and large *Vipera* of the 'oriental complex'. The comparatively deep interzygapophyseal constriction suggests *Daboia* or the oriental complex of *Vipera*. Today, *Daboia* is absent from Africa while the range of the oriental complex of *Vipera* encroaches only the northernmost part of the continent. The Lower Miocene of Arrisdrift (Namibia), that is slightly younger than Elisabethfeld (Pickford and Senut, 1999), already yielded a large viper that belongs to one of these two taxa (Rage, 2003). It would be of interest to identify which genus is present in the Lower Miocene of Namibia, unfortunately the distinction between these two taxa on the basis of vertebrae is difficult and requires well-preserved specimens (Szyndlar and Rage, 1999, 2002).

Colubroidea indeterminate
Unidentified genus and species
(Fig. 3)

Provenance: Elisabethfeld.
Referred material: 2 incomplete trunk vertebrae (EF 71'94a; EF 20'05f) and perhaps 5 articulated vertebrae embedded in matrix (EF 16'94) and two incomplete vertebrae (EF 71'94b; EF 13'97).

Description :

EF 71'94a, which is relatively well-preserved although incomplete, is not massively built. It is high and moderately elongate. The neural canal is broad, nearly as wide as the cotyle, and high. One paracoty-
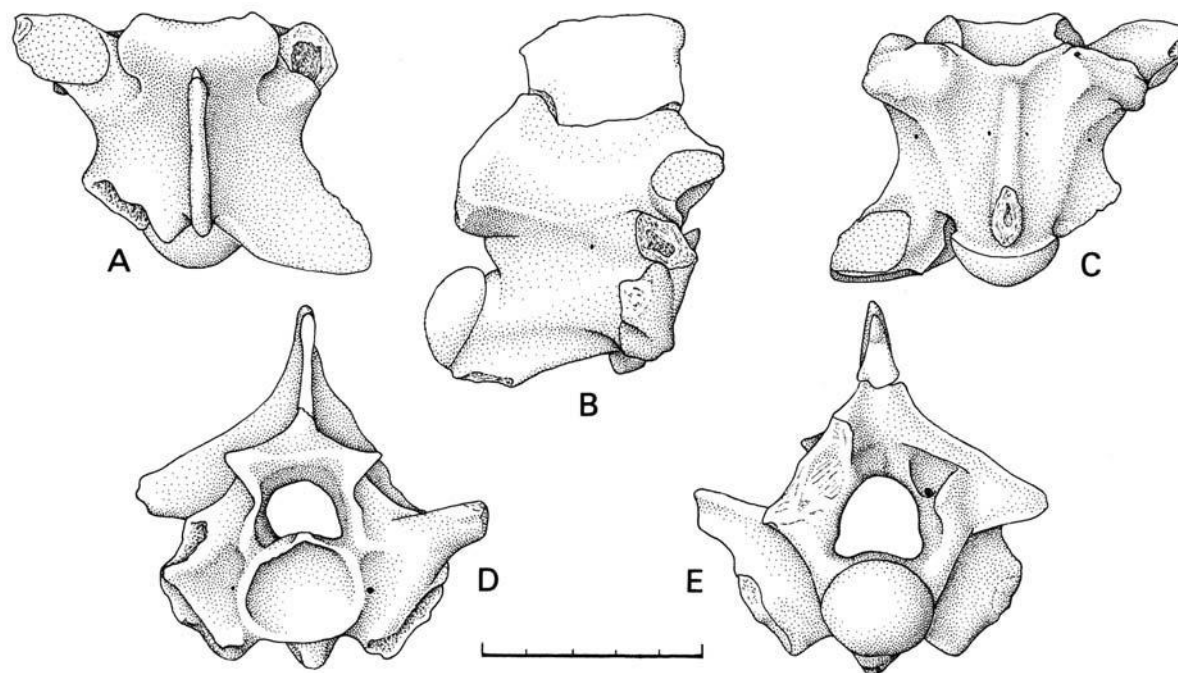
Figure 3: Colubroidea indeterminate, Elisabethfeld. Trunk vertebra (EF 71'94a) in dorsal (A), right lateral (B), ventral (C), anterior (D), and posterior (E) views. Scale bar: 5 mm.

lar foramen opens on either side of the cotyle. The thin zygosphene is slightly wider than the cotyle. The zygapophyseal articular facets are only weakly inclined on the horizontal. Prezygapophyseal processes were present and, as judged from the only remaining base, relatively long. The neural spine is high and long; anteriorly, it approaches the anterior border of the zygosphene; the latter border forms a shallow anterior concavity in dorsal aspect. The interzygapophyseal constriction is moderately deep. The neural arch is relatively depressed and the only preserved posterodorsal border is straight in porterior aspect. A hypapophysis was present (it is broken off on all specimens); its base suggests that it was slightly compressed laterally. The ventral face of the centrum is flat and well delimited by marked subcentral ridges.

Discussion:

The combination of features displayed by this snake is confusing. As shown by its relatively light structure and elongation and by the presence of well-developed prezygapophyseal processes, we are dealing with a colubroid. But identification at family level is difficult. On the one hand, the depressed neural arch with straight (in posterior aspect) posterodorsal borders and the high neural spine are really viperid-like. On the other hand, the probably long prezygapophyseal process, marked subcentral ridges, flat ventral surface of the centrum, and lateral compression of the hypapophysis do not appear to be consistent with the Viperidae. The height of the neural spine leads me to eliminate the Elapidae, while the

height of the vertebra and the presence of a hypapophysis is not consistent with the Atractaspididae. Finally, no character argues against assignment to the Colubridae; but I have never come upon such a vertebral morphology among the colubrids I have seen.

Viperid genera are not numerous and none of them matches the vertebral morphology of the Namibian fossil. However, the above viperid-like features are striking and referral to the Viperidae cannot be definitely ruled out. On the other hand, colubrid taxa are so numerous that one may expect this morphology to exist within this group. Obviously, this is not a sound argument to assign this snake to the Colubridae. Consequently, EF 71'94a is referred to as Colubroidea indeterminate.

Indeterminate snakes

Provenance: Grillental area and Elisabethfeld.
Referred material: <u>Grillental area</u>: GT6, 1 incomplete trunk vertebra (GT 63'00r).- <u>Elisabethfeld</u>, 11 incomplete trunk and caudal vertebrae (EF 20'05g).

Conclusions

The faunas of squamates yielded by the Lower Miocene deposits of Langental, Elisabethfeld, E-Bay and the Grillental area (Sperrgebiet, Namibia) include several taxa of lizards and snakes.

The lizard assemblage is comprised of one indeterminate gecko, one indeterminate amphisbaenian and two indeterminate lacertilians. The snakes in-

clude one indeterminate scolecophidian, two Boidae, one natricine and one 'colubrine' Colubridae, one Viperidae, and one indeterminate Colubroidea.

The Boidae represent the dominant taxa; they comprise two medium sized species that cannot be securely assigned to the extant genus *Python*. They are referred to as cf. *Python* sp. A (from Grillental area and perhaps E-Bay) and cf. *Python* sp. B (from Langental). They both differ from the boid from the slightly younger locality of Arrisdrift (Namibia) that was referred to *Python* (*Python* cf. *P. sebae*; Rage, 2003). This diversity suggests that the early Miocene might have been an important period for the evolution of pythonines in Africa. The viperid belongs to either *Daboia* or to the oriental complex of *Vipera*. Today, African *Vipera* of the oriental complex are present only in the northernmost part of the continent, whereas *Daboia* is absent from Africa.

The main differences between the assemblages from the northern Sperrgebiet on the one hand, and Arrisdrift (Rage, 2003) on the other, are the absences, from the former area, of the extant genera *Varanus* (Varanidae), *Naja* ? (Elapidae), *Bitis* (Viperidae), and probably *Python* (Boidae). Consequently, the faunas from the northern Sperrgebiet appear to be less advanced, which is consistent with the younger age of Arrisdrift (about 2 million years separate Langental, the youngest site of Sperrgebiet, from Arrisdrift according to Pickford and Senut, 2003). Therefore, it might be inferred that the above genera arrived in southern Africa between the level of the fossiliferous sites of Sperrgebiet and that of Arrisdrift. But it is certainly premature to regard such a conclusion as well-established, it is only a working hypothesis.

From a palaeoenvironmental point of view, this fauna does not provide clear information. The amphisbaenian and scolecophidian were fossorial. None of the taxa displays prominent adaptation to aquatic life, but the natricine was probably more or less aquatic as are all members of this group. No significant stratigraphical information can be drawn from this fauna.

Acknowledgements

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