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by

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Squamate reptiles from the early Miocene of Arrisdrift (Namibia)

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The early Miocene of Arrisdrift (Namibia) has produced a relatively rich fauna of squamates. It comprises the lizard *Varanus* (one or two species), an indeterminate amphisbaenian, and various snakes. The latter include a Boidae (*Python* cf. *P. sebae*), an indeterminate colubrid, an Elapidae (cf. *Naja*), a snake that is either a colubrid or an elapid, and two Viperidae (*Bitis* sp. and either *Vipera* (of the 'oriental group') or Daboia). On the whole, the fauna shows a pattern characteristic of Africa south of the Sahara. However, one of the Viperidae (*Vipera* or *Daboia*) represents a more northern, perhaps non-African, taxon in the fauna.

Version française abrégée

Les squamates du Tertiaire d'Afrique sont peu connus; les gisements sont rares et n'ont livré que peu de spécimens. Toute nouvelle localité fossilifère présente donc un certain intérêt. En Namibie, plusieurs gisements du Miocène ont fourni des faunes de squamates. Ces fossiles constituent un jalon important dans l'histoire du groupe en Afrique. Ici, est étudiée la faune d'Arrisdrift qui est la plus riche et la plus diversifiée de Namibie. Son âge est équivalent de l'Orléanien de la stratigraphie continentale en Europe (Burdigalien en stratigraphie marine). La faune montre un cachet moderne. Les fossiles sont pour la plupart étroitement apparentés, où appartiennent peut-être, à des taxons actuels. Malheureusement, l'ostéologie de la grande majorité des espèces actuelles d'Afrique reste inconnue; le présent travail ne peut donc être que de nature préliminaire.

Liste des taxons

La faune comprend les taxons suivants: Varanidae (*Varanus* indéterminé(s)), Amphisbaenia indéterminé, Lacertilia? indéterminé, Boidae (*Python* cf. *P. sebae*), Colubridae indéterminé, Elapidae (cf. *Naja*), Colubridae où Elapidae (une espèce indéterminée), Viperidae (*Bitis* sp.; *Vipera* du groupe des 'vipères orientales' où *Daboia*).

Commentaires: Seuls le Varanidae, le Boidae et l'un des deux Viperidae méritent des commentaires particuliers.

Varanus indéterminé(s):

Ce taxon est représenté par un maxillaire en mauvais état et par des vertébrés. Le maxillaire porte des dents non aiguës; il s'accorde avec les espèces actuelles *Varanus niloticus* et *V. exanthematicus* d'Afrique, *V. olivaceus* d'Asie, ainsi qu'àvec les espèces fossiles *V. rusingensis*, du Miocène inférieur du Kenya, et *V. hooijeri* du Pléistocène d'Indonésie. Les vertébrés posent un problème. En effet, si elles montrent toutes la morphologie globale caractéristique de *Varanus*, la constriction précondylaire se présente sous deux formes différentes. Sur certaines vertébrés, elle est bien marquée et située nettement en avant du condyle. Il s'agit là de la condition qui apparaît chez toutes les espèces connues, actuelles où fossiles. Sur les autres vertébrés, la constriction est peu profonde et elle se situé contre le condyle; elle peut même être absente. La question qui se pose alors est de savoir si il y a une où deux espèces.

Si ces vertébrés correspondent à une seule espèce, les variations intracolumnaires dépassént largement celles qui sont connues chez les autres *Varanus*. Le fossile d'Arrisdrift représenterait une espèce nouvelle (peut-être même un genre nouveau).

Si deux espèces sont présentes, le maxillaire (qui ne diffère pas de celui d'espèces actuelles) peut être associé aux vertébrés 'normâles'. Ces dernières s'accordent bien avec *V. griseus* et *V. exanthematicus* qui vivent aujourd'hui en Afrique. Mais, *V. griseus* dont les dents sont aiguës, doit être écarté. Cette forme d'Arrisdrift pourrait donc être rapportée à l'actuel *V. exanthematicus*. Toutefois, le maxillaire d'Arrisdrift ne diffère pas de celui de *V. rusingensis* du Miocène inférieur du Kenya. Les vertébrés de ce dernier se distinguent de celles d'Arrisdrift par leur constriction un peu moins profonde. Si on admet que la profondeur un peu plus grande de la constriction entre dans les variations intraspécifiques, ce varan d'Arrisdrift pourrait être attribué à *V. rusengensis*. Quoi qu'il en soit, *V. exanthematicus*, *V. rusingensis* et ce varan d'Arrisdrift sont morphologiquement proches. En plus de ce varan, à Arrisdrift, les vertébrés sans constriction où à constriction faible située contre le condyle représenteraient une seconde espèce, nouvelle, où même un genre distinct.

Python cf. *P. sebae*:

Le python d'Arrisdrift, comme quelques autres fossiles d'Afrique, est étroitement apparenté à l'actuel *P. sebae*; il pourrait même s'agir de cette dernière espèce. La 'lignée' qui conduit à *P. sebae* se trouvait donc en Afrique dès le Miocène inférieur.

Daboia où *Vipera* du complexe des 'vipères orientales':

Cette grosse vipère est représentée par deux vertébrés seulement. Malheureusement, la neurépine est cassée sur les deux spécimens ce qui ne permet pas d'établir s'il s'agit du genre *Daboia* où d'une *Vipera* du groupe des 'vipères orientales'. Quels que soient le genre et l'espèce précis, elle représente un taxon 'nordique' dans la faune d'Arrisdrift.

Conclusion

Le python, *Bitis*, et l'une des espèces de varan du gisement (si deux espèces sont présentes) sont des représentants typiquement africains. Ils sont plus particulièrement caractéristiques de l'Afrique au sud du Sahara. En revanche, la grosse vipère, quel que soit le taxon précis, ne vit plus au sud du Sahara. Les 'vipères orientales', s'il s'agit de l'un des représentants du groupe, se rencontrent aujourd'hui dans le nord de l'Afrique, le sud-est de l'Europe et en Asie (du Moyen-Orient à l'Inde). Elles étaient fréquentes en Europe au Néogène. *Daboia*, s'il s'agit de ce genre, est un vipéridé asiatique connu aujourd'hui du Pakistan à l'Indonésie; le genre a atteint la péninsule ibérique au Pliocène.

Cette faune ne fournit pas d'information notable sur le paléoenvironnement

Introduction

The record of squamate reptiles from the Tertiary of Africa is extremely poor both in terms of number of specimens and localities. The Miocene of Namibia has yielded a comparatively rich fauna of squamates which, therefore, represents an interesting landmark in the history of the group in Africa.

This Miocene fauna clearly shows a 'modern' pattern; most taxa, perhaps all, are probably closely related or identical to extant ones. Unfortunately, the osteology of most living African species is unknown; this is especially true for various families of lizards and colubrid snakes. Consequently, the present study can only be of a provisional nature.

Among Namibian localities, Arrisdrift has yielded the richest and most diverse fauna. In terms of European stratigraphy, Arrisdrift may be considered Orleanian in age (i.e. Burdigalian in marine stratigraphy).

Squamata Merrem, 1820
Lacertilia Owen, 1842
Varanidae Gray, 1827

Today the Varanidae are represented only by the genus *Varanus* (However, Pregill *et al.*, 1986, suggested that its sister taxon, i.e. *Lanthanotus* from Sarawak, should be included in the same family). *Varanus* inhabits Africa (but not Madagascar), southern Asia, and Australasia. During the Neogene, *Varanus* was present in Europe, Africa, and Asia (Estes, 1983). Only two other varanid genera occurred during the Neogene: *Iberovaranus* was restricted to the Neogene of the Iberian Peninsula (Hoffstetter, 1968; Antunes & Rage, 1974) whereas *Megalania*, a gigantic lizard, was recovered from the Pliocene and Pleistocene of Australia (Molnar, 1991).

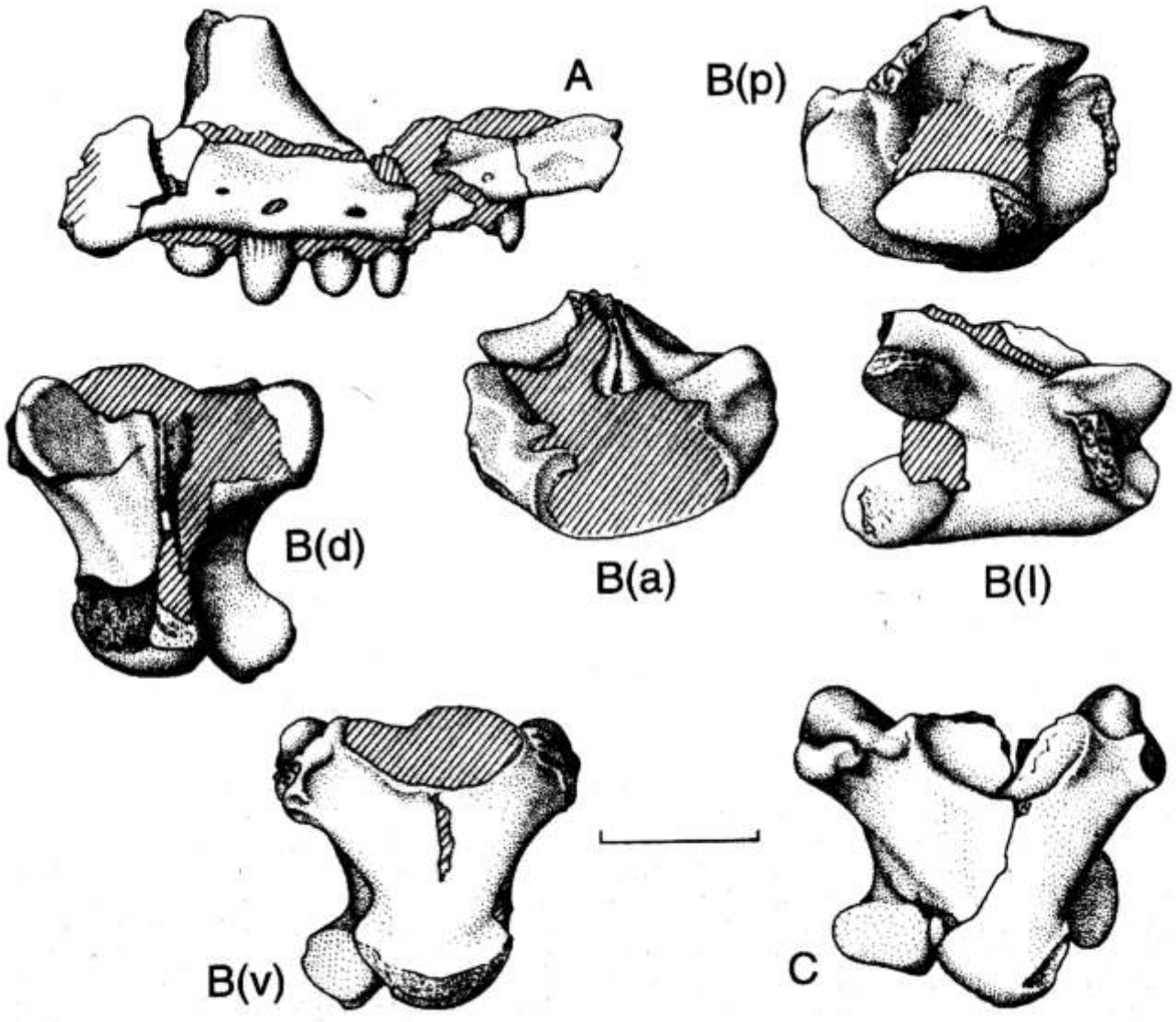

Figure 1: *Varanus*. A: left maxilla (AD 38'99), lateral view. B: trunk vertebra with typical precondylar constriction (PQ AD 3372), in anterior (a), dorsal (d), right lateral (l), posterior (p), and ventral (v) views. C: trunk vertebra with almost lacking precondylar constriction (AD 500'00), ventral view. Hatched areas = matrix. Scale bar represents 1 cm.

Varanus Merrem, 1820

Fossils from the early Miocene (Burdigalian) represent the earliest record of *Varanus*: *V. rusingensis* from Rusinga Island (Kenya), *V. rusingensis* or another species from Songhor (Kenya) (Clos, 1995), and a form close to *V. hofmanni* from Artenay (France) (Hoffstetter, 1968). Up to now, *V. rusingensis* and the form from Songhor, both from the early Miocene of Kenya, and *Varanus* sp. from the late Miocene of Uganda (Bailon & Rage, 1994) have been the only varanids reported from the Cainozoic of Africa.

Indeterminate *Varanus*

Referred material: (Fig. 1). One maxilla (AD 38'99), 9 trunk vertebrae (AD 561'97, AD 466'98, PQ AD 3372, AD 224'94, AD 299'00, AD 500'00, AD 223'94, AD 441'95, PQ AD 3157), 5 caudal vertebrae (AD 239'96, AD 240'96, 502'00, PQ AD 2266, an unnumbered vertebra from the old collection).

Description: Maxilla. The maxilla is incomplete and somewhat distorted (Fig. 1, A). Its prefrontal process rises steeply but this feature apparently displays broad intraspecific variation within the genus. Unfortunately, the prefrontal process of *V. rusingensis* is unknown. The posterior teeth are blunt and bulbous as in adults of the living African *V. niloticus, V. exanthematicus*, and the living Asian *V. olivaceus*. Such teeth are also known in the extinct *V. hooijeri* from the Pleistocene of Indonesia (Brongersma, 1958) and in *V. rusingensis*. The most anterior preserved tooth is more pointed than the posterior ones; however, it is not acute. Blunt teeth suggest that this lizard was primarily molluscivorous.

Vertebrae. On the whole, trunk vertebrae display the typical morphology of *Varanus*. The cotyle and condyle are markedly depressed. The cotyle faces anteroventrally (i.e., it is clearly visible in ventral aspect) while the axis of the condyle is directed posterodorsally. The neural arch slopes anteriorly; its anterior most part forms a distinct area, the *pars tectiformis*, above the anterior most part of the neural canal. There is no pseudozygosphene or zygosphene. Just posterior to the *pars tectiformis* and prezygapophyseal facets, a depression occurs on either side of the neural spine. The deepest part of the interzygapophyseal constriction is shifted posteriorly, just anterior to the postzygapophyses. The neural spine occupied the whole length of the neural arch.

In *Varanus*, the centrum is constricted anterior to the condyle. The constriction is located clearly before the condyle; posterior to the constriction, i.e. between the constriction and the condyle, the centrum widens. This feature also occurs in the varanids *Iberovaranus* and *Megalania*. But the vertebrae of *Iberovaranus* differ from those of *Varanus* in having a more elongate, narrower neural arch, with a shallower interzygapophyseal constriction. *Megalania* displays characteristics of overgrown individuals: vertebrae wide and short, neural canal very small, centrum strongly widening anteriorly.

Among the specimens from Arrisdrift, only two vertebrae (AD 466'98, PQ AD 3372) show the constriction that is typical of *Varanus* (Fig. 1, Bv). In the other specimens, the constriction is very shallow or even almost lacking (Figs. 1, C). Moreover, if present, the constriction occurs against the condyle; in other words, the centrum does not widen between the constriction and condyle. Apart from this difference, all vertebrae from the locality are similar.

Discussion: On the basis of vertebrae, it may be entertained whether two or only one taxa are present.

i) Assuming that two taxa are present, the maxilla and vertebrae AD 466'98 and PQ AD 3372 may be associated. The precondylar constriction of these vertebrae from Arrisdrift appears to be shallower than that of the living African *V. niloticus*; it is similar to that of the living African *V. griseus* and *V. exanthematicus*. The constriction seems slightly deeper than in the extinct African *V. rusingensis*. The incomplete and distorted maxilla does not permit precise comparisons, but it cannot be assigned to *V. griseus* the teeth of which are acute. Therefore, this *Varanus* from Arrisdrift might be referred to the living species *V. exanthematicus* or, assuming that the small difference in the depth of the precondylar constriction is only an intraspecific variation, to the Miocene *V. rusingensis*.

In such a case, the vertebrae in which the precondylar constriction is very shallow or lacking would represent another, unknown, species or perhaps even genus.

ii) If all the specimens from Arrisdrift belong to a single species, then the intracolumnar variations in this fossil overstep, by far, those observed in other varanid species. Therefore, the fossil would represent a new taxon (at species, or perhaps genus level).

Consequently, whatever the number of varanid species at Arrisdrift (one or two), a new taxon is present. Unfortunately, on the basis of the available material, this taxon cannot be defined and described. Besides, if there are two species in the locality, one of them may be either the living *V. exanthematicus* or the extinct *V. rusingensis*.

Amphisbaenia Gray, 1844

One vertebra only represents the amphisbaenians. Vertebrae of that taxon display a very distinctive morphology that generally easily distinguish them from other squamates. But, apart from a few exceptions, they do not permit identification within the Amphisbaenia.

Indeterminate amphisbaenian

Referred material: 1 trunk vertebra (AD 523'95a).

Description: The vertebra is small (centrum length = 2.05 mm), short, and markedly depressed. The interzygapophyseal constriction is shallow. The small prezygapophyseal facets markedly slant above the horizontal. The cotyle and condyle are strongly depressed dorso-ventrally. The paradiapophyses form an undivided and small articular surface. The neural spine is broken away; it was apparently low. The centrum hardly widens anteriorly; it bears a thin haemal keel. The presence of the latter keel shows that this vertebra is an anterior trunk one, which accounts for the slight anterior divergence of the lateral limits of the centrum. In mid- and posterior trunk vertebrae, the lateral limits of the centrum are parallel.

Discussion: The morphology of this vertebra unquestionably demonstrates that it belongs to an amphisbaenian. More especially, the depressed condyle and cotyle, strongly inclined

zygapophyseal facets, and the almost parallel lateral limits of the centrum are characteristic of the group. Identification at family level is not possible on the basis of this specimen. In Africa, the earliest amphisbanian was recovered from the late Palaeocene (Thanetian) of Morocco (Gheerbrant *et al.*, 1993). As far as the Miocene is concerned, amphisbaenians were reported from the early Miocene of Kenya (Estes, 1983) and middle Miocene of Morocco (Rage, 1976).

Indeterminate ? Lacertilia

Referred material: 1 trunk vertebra (AD 523'95b).

Description: The vertebra is embedded in matrix and only the centrum, paradiapophyses, and parts of the anterior face and neural arch are exposed. The vertebra is elongate, narrow, and not depressed. The prezygapophyseal facets appear to be elongate in anterior aspect; they are strongly inclined on the horizontal. The cotyle is small and only slightly depressed dorso-ventrally. The centrum is elongate and narrow; its lateral limits diverge slightly anteriorly. The sagittal area of the ventral surface is hardly prominent as a very low haemal keel. The paradiapophyses are small and they form single articular surfaces. The neural arch is apparently depressed; the neural spine was probably comparatively high.

Discussion: The centrum, in ventral aspect, is reminiscent of various colubroid snakes. But this specimen does not belong to a snake. The prezygapophyses, in anterior view, look more or less like those of amphisbaenians, but the small, non clearly depressed cotyle differs from that of observed members of that group. On the whole, the vertebral morphology is consistent with that of lizards. However, it should be noted that the specimen cannot be assigned to the Varanidae (vertebra elongate, narrow and relatively high). In summary, this vertebra appears to be referable to a non-varanid lizard, but the possibility that is represents an anterior trunk vertebra of an amphisbaenian cannot be definitely ruled out.

Serpentes Linnaeus, 1758
Boidae Gray, 1825
***Python* Daudin, 1803**
***Python* cf. *P. sebae* (Gmelin, 1789)**

Referred material: 3 trunk vertebrae (AD 20'97, AD 228'99, AD 32'00).

Description: Three poorly preserved vertebrae represent the genus Python. They are mainly characterized by their shortness, their highly vaulted neural arch, the shallowness of the interzygapophyseal constriction, and their comparatively low neural spine. Moreover, the neural spine is antero-posteriorly short, it does not extend on the zygosphenal roof. There is no vertical ridge on either side of the neural spine. The interzygapophyseal constriction is asymmetrical. Its bottom is located posteriorly; as a result, the ridges that form the anterolateral border of the constriction diverge anteriorly. The haemal keel is strongly prominent, but its ventral border is not trenchant. The zygosphene is thick and slightly wider than the cotyle. Its anterior border formed three lobes.

Discussion: Today, three species of Python inhabit Africa: *P. sebae*, *P. regius*, and the very rare *P. anchietae*. Only one extinct species was described in Africa: *P. maurus* from the middle Miocene of Beni Mellal, Morocco (Rage, 1976). In addition, pythons were also reported from the latest Miocene of Uganda (*P. sebae* or a related form; Bailon & Rage, 1994), the Pliocene of Tanzania (*P. sebae*; Meylan, 1987), Ethiopia (*Python* sp. and a form close to *P. sebae*; Rage, 1979), and the latest Pliocene/early Pleistocene of Tanzania (*P.* aff. *sebae*; Rage, 1973).

The fossil from Arrisdrift differs from *Python regius* by its clearly lower neural spine that is antero-posteriorly shorter, its more vaulted neural arch, and its ventrally blunter haemal keel. The vertebrae of *P. anchietae* are unknown; therefore, no comparison with the latter species was possible. However, the largest vertebra from Arrisdrift suggest that the python from the locality reached a length of about 3 m, whereas *P. anchietae* rarely reaches 2 m. *P. maurus* is distinguished from the Arrisdrift fossil in having slightly shorter vertebrae, a higher neural spine, a shallower interzygapophyseal constriction, parallel interzygapophyseal ridges in the bottom of the constriction, and diapophyses that extend more posteriorly.

Finally, the vertebrae from Arrisdrift compare rather closely with those of *P. sebae*. Only one feature distinguishes the fossil from the living species: the neural spine of the fossil is clearly lower than that of the observed extant individuals. However, in *P. sebae*, important variations affect the neural spine. Consequently, the vertebrae from Arrisdrift might fall within the intraspecific range of variation. Besides, since only three incomplete vertebrae are available, the fossil is referred to as *Python* cf. *P. sebae*.

Python sebae or closely related fossils have already been reported from the Neogene and Pleistocene of Africa (see above). One of these fossils is worth mentioning. It was recovered from the latest Pliocene/early Pleistocene 'Bed I' of Olduvai (Tanzania) and was referred to as *Python* aff. *P. sebae* (Rage, 1973). It differs from the extant *P. sebae* in having a pronounced, generally sharp, vertical ridge on each side of the neural spine. Similar ridges occur in *P. maurus*. Moreover, in the fossil (close to *P. sebae*) from the Pliocene of Hadar (Ethiopia) such ridges are present in juvenile specimens but adults lack them. The significance of these ridges is unknown. At Arrisdrift, the neural spine is fully preserved on one vertebra only; its lacks vertical ridges.

Whatever the precise assignment of these fossils may be at species level, the fossil record suggests that the *P. sebae* lineage existed as early as the Miocene and was perhaps thriving as early as the Pliocene.

Colubridae Oppel, 1811

It is generally easy to assign an isolated vertebra to the family Colubridae, although it is sometimes difficult or even impossible to identify a species within Colubridae on the basis of such specimens. However, in some cases, the distinction between isolated vertebrae of Colubridae and Elapidae is problematic.

On the other hand, about three-quarters of the recent species of the World are recognized as belonging to the Colubridae, that is this family includes well over than 1,500 species. They are numerous in Africa and skeletons of only a few of

them are available for comparison. Only one vertebra from Arrisdrift appears to be referrable without reservation to the Colubridae.

Indeterminate Colubridae

Referred material: one trunk vertebra (PQ-AD 3280).

Description: This vertebra belonged to a mid-sized colubrid (centrum length = 5 mm). The neural spine, right prezygapophysis, and paradiapophyses are broken off. The centrum is damaged. The vertebra is elongate and its interzygapophyseal constriction is shallow. The preserved prezygapophyseal facet is markedly oblique in dorsal view; it is slightly inclined above horizontal. The anterior border of the wide zygosphene forms three lobes (a rather wide median lobe and two small and acute lateral ones). The neural arch is moderately vaulted. The centrum is narrow and poorly delimited laterally. It is not possible to determine whether a hypapohysis was present.

Discussion: The presence of only one vertebra belonging to the Colubridae in a Miocene locality of Africa appears to be somewhat surprising. Since the beginning of the Miocene, the Colubridae have been the ruling group within snakes (Rage, 1987) at least in Europe and North America where the fossil herpetofaunas are well known. The situation was apparently similar in Africa (Rage, 1976, 1979). It may be entertained whether this paucity in colubrids really reflects the composition of the snake fauna from Arrisdrift.

Elapidae Boie, 1827

As mentioned above, distinction between disarticulated vertebrae of Elapidae and Colubridae, two very closely related families, is not always easy. Vertebrae of Elapidae can resemble those of natricines and various other colubrids. However, within elapids, snakes belonging to the *Naja* complex are generally distinctive. As in all Elapidae, every trunk vertebra of the '*Naja* group' bears a hypapophysis. The centrum is characteristic: it is clearly limited laterally by prominent subcentral ridges and its ventral surface is flat or even slightly concave. In large forms, the centrum is short and wide. The neural arch is moderately vaulted and the neural spine is comparatively low, longer than high. Parapophyseal processes are present, strong and directed anteriorly. In mid-trunk vertebrae, the border of the zygosphene is almost straight between two small lateral lobes. Only one vertebra from Arrisdrift may be unquestionably referred to the Elapidae. It belongs to a species of the '*Naja* group', probably to the genus *Naja*.

cf. *Naja* Laurenti, 1768

Referred material: one mid-trunk vertebra (AD 181'94).

Description and discussion: The vertebra is poorly preserved. Only its centrum, zygosphene, and neural arch are observable. Their morphology matches that of observed snakes of the *Naja* group (see above), more especially of the genus *Naja*. This vertebra belonged to a mid-sized individual.

Today, snakes of the *Naja* group inhabit southern Asia and most of Africa. Fossils referred to the genus *Naja* were reported from the Neogene of Africa and Europe (Szyndlar & Rage, 1990). In Africa, two species were described: *Naja antiqua* from the middle Miocene of Morocco (Rage, 1976) and *Naja robusta* from the Pliocene of Tanzania (Meylan, 1987). Undescribed members of the *Naja* group are perhaps present in the lower Miocene of the Rift Valley (Rage, 1979). Moreover, a form close to the living *Naja nigricollis* was reported from the latest Pliocene/early Pleistocene of Tanzania (Rage, 1973).

Colubridae or Elapidae

Referred material: 4 trunk vertebrae (AD 479'94, AD 113'97, AD 423'00, AD 735'00).

Four vertebrae belong to the Colubroidea. They do not pertain to the Viperidae or Atractaspididae, but it is not possible to determine whether they represent elapid or colubrid snakes.

Description and discussion: These vertebrae are not markedly different from AD 181'94 which is referred to the Elapidae, but they are more elongate and less massively built. The centrum is narrower, it widens only slightly anteriorly. These vertebrae look like lightened vertebrae of snakes belonging to the *Naja* group. These differences do not justify exclusion from the Elapidae, and even from the *Naja* group. However, such a morphology approaches that of various Colubridae (natricines among others). Consequently, they cannot be referred to the Elapidae without reservation.

Viperidae Oppel, 1811
Vipera Laurenti, 1768

The systematics of the assemblage of living species that makes up the genus *Vipera* s.l. has been recently subjected to various changes. It has been subdivided into several complexes of species or into distinct genera (*Vipera* s.s., Pelias, *Macrovipera*, *Daboia*) (see a review in Szyndlar & Zerova 1992, and Szyndlar & Rage, 1999). Most changes are based on biochemical characteristics and opinions about presumed relationships within the *Vipera* s.l. complex are generally contradictory (Herrmann *et al.*, 1992; Joger *et al.*, 1999; Lenk *et al.*, 2001). These subdivisions of *Vipera* s.l. do not fit osteological data. The osteology of living forms shows that four complexes may be distinguished within *Vipera* s.l. (Szyndlar & Rage, 1999). One of them corresponds to the living species *V. russelii* which is removed from the genus *Vipera* and allocated to *Daboia* as the only living species of the genus. The three other complexes represent informal assemblages which are retained in *Vipera* s.s.: '*Vipera berus* complex', '*Vipera aspis* complex', and 'Oriental vipers'. One vertebra from Arrisdrift represents *Vipera* s.l.

'Oriental viper' or *Daboia*

Referred material: (Fig. 2a) two trunk vertebra (AD 467'98, AD 900'97).

Description: The vertebrae are comparatively large and well preserved. However, the neural spine and hypapophysis are broken away in both specimens. The vertebrae are short, not depressed, and their interzygapophyseal constriction is deep.

The articular facets of the prezygapophyses are elongate and they are clearly inclined above horizontal; their major axis is perpendicular to the vertebral axis (AD 467'98) or slightly oblique (AD 900'97) in dorsal view. The postzygapophyses extend markedly laterally. The zygosphene is relatively wide and thin and its anterior border is almost straight. Small lateral lobes are preserved in AD 900'97. The cotyle was apparently as wide as the zygosphene and slightly depressed dorsoventrally. The posterior median notch in the neural arch appears rather obtuse and shallow.

The base of the neural spine occupies about half the length of the neural arch. The articular surfaces of the paradiapophyses are damaged. A parapophyseal process is preserved in AD 900'97; it is strong, antero-posteriorly compressed, and it projects anteroventrally. The centrum is relatively narrow; it does not widen strongly anteriorly. The base of the hypapophysis is thick and it extends anteriorly as a prominent keel. The hypapophysis was directed posteroventrally. The neural arch is strongly depressed; its dorsoposterior borders are straight in posterior aspect. The roof of the zygantrum is thick. The condyle is large and slightly depressed dorsoventrally.

Discussion: These vertebrae differ from those of species included in the *V. berus* and *V. aspis* complexes in being larger and clearly shorter. They display the overall morphology of 'oriental vipers' and *Daboia*. Unfortunately, the distinction between the two latter taxa rests on skull bones and, as far as vertebrae are concerned, the height of the neural spine. Since the neural spine is broken off in the vertebrae from Arrisdrift, it is not possible to determine whether these fossils belong to the 'oriental vipers' group or to *Daboia*.

Daboia includes a single living species (*D. russelii*) which inhabits southern Asia from Pakistan to Indonesia (Golay *et al.*, 1993). Only one extinct species is referred to the genus: *D. maxima* from the Pliocene of Spain (Szyndlar, 1988). The 'oriental vipers' group includes six living species (*V. deserti, V. lebetina, V. mauritanica, V. palestinae, V. schweizeri, V. xanthina*). The range of these species extends from northwestern most Africa (Morocco) and southeasternmost Europe (Greece) to India, through Middle East and Central Asia. Moreover, six or seven extinct species are assigned to the 'oriental vipers' complex: *Vipera burgenlandica* (Miocene of Austria; Bachmayer & Szyndlar, 1987), *V. gedulyi* (Miocene of Hungary; Venczel, 1998), *V. platyspondyla* (Miocene of the Czech Republic; Szyndlar, 1987), *V. sarmatica* (Miocene of Moldova; Chkhikvadze & Lungu, 1987), *V. ukrainica* (Miocene of Ukraine; Zerova, 1992), *V. kuchurganica* (Pliocene of Ukraine; Zerova, 1987), and perhaps *V. aegertica* (Miocene of France; Augé & Rage, 2000). Therefore, all these extinct species were found in the Neogene of Europe. However, indeterminate species of 'oriental vipers' were reported from the Neogene of Africa (from Morocco only); they come from the latest Pliocene (reported as *Macrovipera* sp.; Bailon, 2000) and the Pliocene/Pleistocene limit (Szyndlar & Rage, in press). Consequently, whatever the precise identification ('oriental viper' or *Daboia*), this extinct viper represents a taxon of northern, perhaps European or Asian, affinity in the fauna from Arrisdrift.

Bitis Gray, 1842
Bitis sp.

Referred material: (Fig. 2b) one trunk vertebra (PQ AD 1110).

Description: Only one poorly preserved specimen represents the genus. This vertebra belongs to a mid-sized individual. The neural spine, hypapophysis, and prezygapophyses are broken off. The vertebra is short and its interzygapophyseal constriction is shallow. The zygosphene is thin, not very wide, and its anterior border is nearly straight; small lateral lobes are present. The cotyle is circular and comparatively broad, but slightly narrower than the zygosphene. The posterior median notch in the neural arch is very shallow. The neural spine was antero-posteriorly long; its anterior border arose from the roof of the zygosphene. The centrum is short, it clearly widens anteriorly. The hypapohysis was strong; a blunt keels prolongs it anteriorly. The neural arch is depressed, but slightly upswept above the zygantrum. The condyle is circular.

Discussion: The overall morphology, the shallowness of the interzygapophyseal constriction, and the anteroposterior length of the neural spine of the vertebra point to the genus *Bitis*. In mid- and posterior trunk vertebrae of *Bitis*, the neural arch is strongly depressed; its dorsoposterior borders are straight and even slightly concave in posterior view. In the specimen from Arrisdrift, these borders are slightly convex dorsally, which means that this vertebra comes from the anterior trunk region. Usually, in *Bitis*, the interzygapophyseal ridges which form the bottom of the interzygapophyseal constriction are more or less straight. In this vertebra, the ridges are concave laterally; this appears to be a variation that is not inconsistent with the referral of this specimen to the genus *Bitis*.

Today, *Bitis* includes 13 living species according to Golay *et al.*, (1993). The genus occupies Africa, except the northernmost part of the continent (approximately south of a line South Morocco-Ethiopia). It also inhabits southern Arabia. Reports of extinct *Bitis* are rare. Only one extinct species was reported: *Bitis olduvaiensis* from the latest Pliocene/early Pleistocene of Tanzania (Rage, 1973). Meylan (1987) reported the latter species or the living *B. arietans* from the Pliocene of Tanzania. *Bitis* sp. was recovered from the latest Pliocene of Morocco, north of the range of living species (Bailon, 2000). The fossil from Arrisdrift documents the earliest fossil record of the genus *Bitis*.

? Indeterminate Viperidae

Referred material: one trunk vertebra (AD 294'96).

A poorly preserved vertebra is assigned to the Viperidae, based on its broad cotyle, slanting prezygapophyseal facets, and non-prominent subcentral ridges. A referral within the family is not possible.

Indeterminate snake

Referred material: one trunk vertebra (PQ AD 707).

A poorly preserved, worn vertebra unquestionably belongs to a snake, but no assignment at family level can be made.

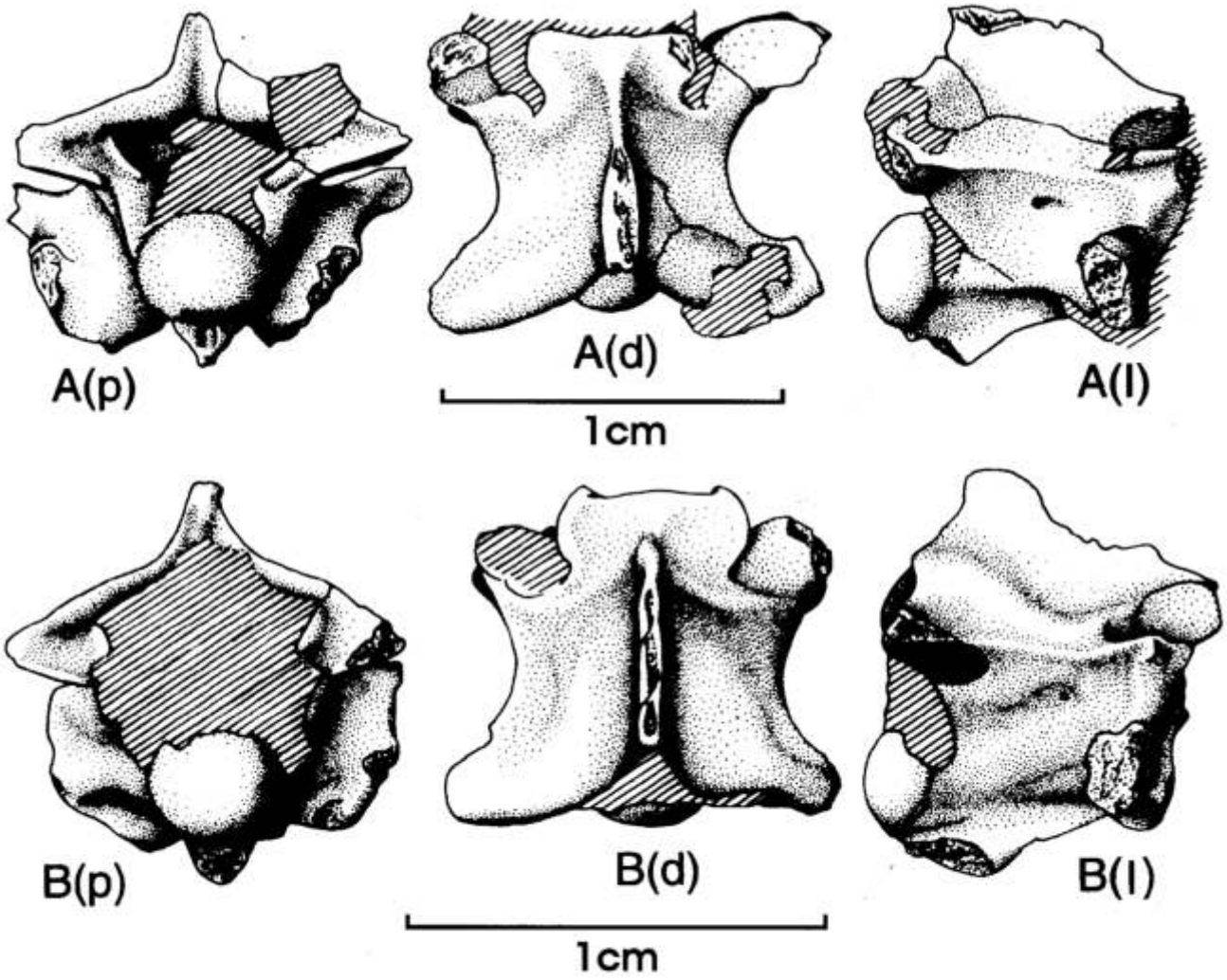

Figure 2: Viperidae. A: 'Oriental viper' or *Daboia*, trunk vertebra (AD 467'98). B: *Bitis* sp.: trunk vertebra (PQ AD 1110). (d: dorsal view, l: right lateral view, p: posterior view). Hatched areas = matrix. Scale bars represent 1 cm.

Conclusion

The fauna of early Middle Miocene (Burdigalian) squamates from Arrisdrift (Namibia) is comparatively rich and diverse. The fauna comprises one lizard (an indeterminate *Varanus*, with perhaps two species), an indeterminate amphisbaenian, and several snakes. The latter include a Boidae (*Python* cf. *P. sebae*), an ascertained Colubridae (indeterminate genus), an Elapidae (cf. *Naja*), a colubroid snake that represents either a colubrid or an elapid, and two Viperidae (*Bitis* sp. and another genus that is either *Vipera* (of the 'oriental complex') or *Daboia*).

Varanus poses a peculiar problem. It is difficult to assess whether it is represented by one or two species. Assuming that two species are present, then one of them is a new one while the other might be either the living *V. exanthematicus* or the extinct *V. rusingensis* (known from the early Miocene of Kenya). If there is only one species, then it represents a new taxon. It cannot be definitely ruled out that, in both possibilities, the new taxon represents a distinct genus although this appears to be unlikely.

The python, *Bitis*, and *Varanus* (if *V. exanthematicus* or *V. rusingensis* is present) are typical African taxa. Today, Python occurs south of the Sahara whereas *Bitis* and *Varanus* reach North Africa but are markedly more frequent and diverse south of the Sahara. The large viperid ('oriental viper' or *Daboia*) represents a taxon with more northern affinities in the fauna of the locality. Today 'oriental vipers' are present in northernmost Africa, in southeasternmost Europe and southern Asia; *Daboia* does not reach Africa, it occurs in southern Asia (living species) and in southern most Europe (an extinct species).

This fauna does not provide information about the local palaeoenvironment.

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