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MID-CRETACEOUS (CENOMANIAN) SNAKES FROM WADI ABU HASHIM, SUDAN: THE EARLIEST SNAKE ASSEMBLAGE

by

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ABSTRACT

The Cenomanian (mid-Cretaceous) beds at Wadi Abu Hashim (Sudan) have yielded a snake assemblage that is very rich and diverse for its geological age. It is by far the oldest known snake fauna. As the assignment of the hitherto earliest presumed snake (Barremian) to the Serpentes may now be questioned, this diverse fauna is only slightly younger than the earliest certain appearance of snakes (late Albian). The fauna is a surprising mixture of very primitive and comparatively advanced snakes. It includes two forms belonging to the lapparentophiid-grade of snakes ('lapparentophiid-grade snake A' and 'lapparentophiid-grade snake B'), an indeterminate Madtsoiidae, a possible Palaeophiidae, the aniliid *Coniophis dabiebus* sp. nov., *Coniophis* cf. *C. dabiebus*, the nigerophiid *Nubianophis afaahus* gen. et sp. nov., *Nubianophis* cf. *N. afaahus*, the russellophiid *Krebsophis thobanus* gen. et sp. nov., a Colubroidea *incertae sedis* (indeterminate family), and two indeterminate snakes. In sum, at least nine species, perhaps twelve, are present. They represent at least seven families: at least one family of lapparentophiid-grade (?Lapparentophiidae), Madtsoiidae, ?Palaeophiidae, Aniliidae, Nigerophiidae, Russellophiidae, and an indeterminate colubroid family.

The presence of colubroid snakes (Russellophiidae and an indeterminate family) as early as the mid-Cretaceous is especially unexpected. It may be inferred from phylogenies that the higher taxa of snakes (Anilioidea, Booidea, Acrochordoidea, Colubroidea, and obviously Scolecophidia) were already present during mid-Cretaceous times. The diversity of this fauna, coupled with the presence of advanced forms (colubroids), suggest that the origin of snakes markedly antedates the Cenomanian. Africa played an important role in the early radiation and, probably, in the origin of snakes.

KEYWORDS: Cenomanian, earliest radiation, snakes, Sudan.

INTRODUCTION

Snakes were not very diverse during the early and middle parts of the Cretaceous. But this period is very important in the evolutionary history of snakes: 1) the earliest snake, whatever it may be, is expected from this period of time, and 2) the Cenomanian appears as the first phase of radiation of snakes.

The hitherto earliest presumed snake (an unnamed form) was reported from the Early Cretaceous (Barremian) of Spain (Rage & Richter 1994), but new data on mid-Cretaceous varanoid squamates cast doubt on the referral of this fossil to snakes. The Late Albian of Algeria yielded two or three snakes: two unnamed fossils and perhaps *Lapparentophis defrennei* (the geological age of the latter is not definitively settled) (Cuny *et al.* 1990). Cenomanian beds have hitherto produced several snakes: *Lapparentophis defrennei* from Algeria, if it is not of Late Albian age, *Pouitella pervetus* from France (Rage 1988a), *Pachyrhachis problematicus* (= *Estesius colberti*) from the Middle East (Caldwell & Lee 1997), *Simoliophis* (*S. rochebrunei* from France and Portugal and *Simoliophis* sp. from Egypt; Rage 1984), and several unnamed snakes (seven taxa according to Werner & Rage 1994) from Sudan. Moreover, the Cenomanian has produced some snake-like squamates whose relationships are unknown: *Pachyophis woodwardi* and *Mesophis nopcsai*, both from former Bosnia-Hercegovina, remain poorly known.

In this paper we describe in detail the snakes from the Cenomanian (mid-Cretaceous) of Sudan. Werner & Rage (1994) briefly reported on this fauna in a preliminary paper. At that time, seven unnamed species (from six families) were recognized. The present detailed study has shown that in fact at least nine species are present, representing at least seven families. In other words, this Sudanese fauna is the earliest diverse fauna of snakes known and it is the only diverse snake fauna from the Cretaceous; therefore it represents a very important landmark in the early history of snakes.

GEOLOGICAL, STRATIGRAPHIC AND PALAEONTOLOGICAL CONTEXT

The fossils are derived from the Wadi Milk Formation, which is widely distributed in northern Sudan. The Wadi Milk Formation is subdivided into two members: the Wadi Abu Hashim Member at the base and the Jebel Abu Tuweiqiya Member at the top (Bussert 1998). The Jebel Abu Tuweiqiya Member represents sand-dominated braided to meandering river sediments. The Wadi Abu Hashim Member, although prevailing in subsurface, is exposed exclusively at the plateau-like rim of the source area of the Wadi Abu Hashim, nearly 200 km northwest of Khartoum (Figure 1). It is characterised by very fine-grained sandstone, siltstone and claystone showing such sedimentary features as horizontal- or ripple lamination, calcretes and mottling (Bussert 1993). The depositional environment is interpreted as shallow playa lakes on flood plains near suspended-load meandering rivers (Bussert 1998). The outcropping horizons of the Wadi Abu Hashim Member are 15 m thick, at which a smectite-rich siltstone produces isolated vertebrate remains in abundance.

The age of the Wadi Milk Formation was formerly considered as ranging from Albian to Cenomanian (Schrank & Awad 1990; Schrank 1990; Wycisk 1991). New lithological and biostratigraphic correlation of the surface and subsurface data of the Dongola, Wadi Muqaddam (Schrank 1990) and Khartoum region (Awad 1994) suggests an Albian to Cenomanian age for the Wadi Abu Hashim Member and a Turonian to Santonian age for the Jebel Abu Tuweiqiya Member (Bussert 1998). The presence of the shark *Asteracanthus aegyptiacus* and the lungfish *Protopterus protopteroides*, *Ceratodus humei* and *Ceratodus tuberculatus*, all known from the Cenomanian Bahariya Formation of Egypt, strongly favours a Cenomanian age for the outcropping part of the Wadi Abu Hashim Member (Werner 1994a; Gloy 1997).

Except for one hand-sized leaf of an aquatic plant, all fossils found in the Wadi Abu Hashim Member are isolated vertebrate remains. No articulated skeletons were observed in the field.

The Cenomanian fish fauna of Sudan is highly diverse. Apart from rare elasmobranchs (e.g. one tooth of a new batoid and a few fragments of the freshwater shark *Asteracanthus aegyptiacus*), indeterminable ichthyoliths and most probably teleostean teeth and vertebrae clearly predominate (Werner 1994a). A characiform, osteoglossids and lepisosteids have been recognized (Werner 1994a). Ranging among the oldest records of polypterids, the fourteen polypterid species of the Wadi Abu Hashim Member show an extraordinary diversity (Werner & Gayet 1997; Gayet *et al.* 1997 a,b). As mentioned above, lungfish are represented in the

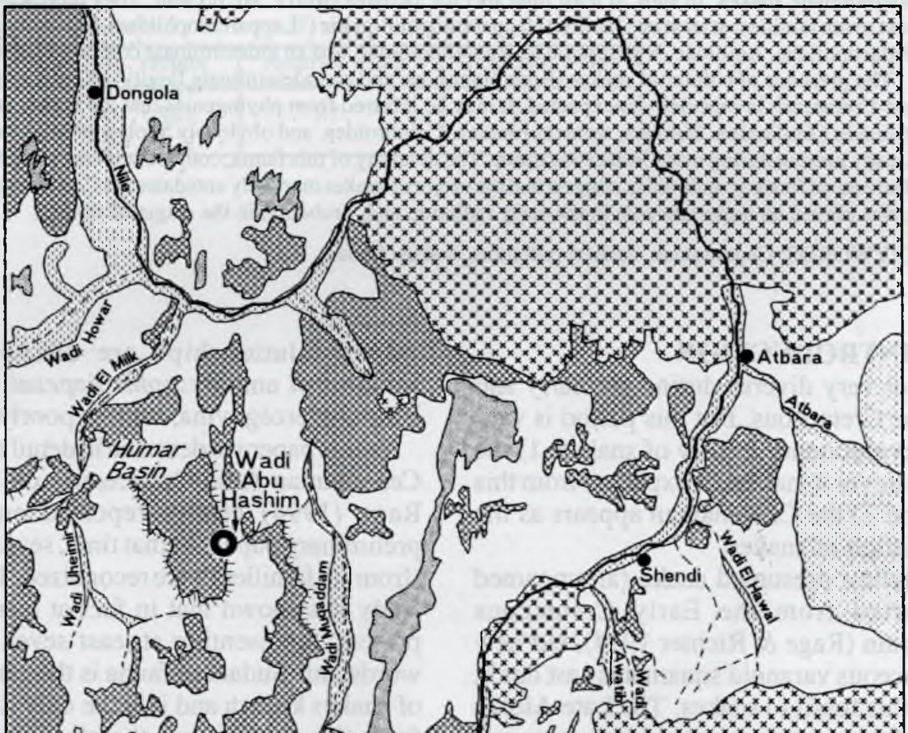


Figure 1. Map of a portion of northern Sudan showing the location of the fossiliferous site.

Cenomanian of Sudan by *Protopterus protopteroides*, *Ceratodus humei*, *Ceratodus tuberculatus*, and a new species of *Protopterus* not yet named (Gloy 1997).

The presence of all three lissamphibian groups in one Cretaceous locality has not previously been reported, but in the Wadi Abu Hashim Member frogs, gymnophionans (Werner 1994 a,b), and salamanders (Evans *et al.* 1996) have been found. Turtle and crocodile remains occur in abundance and have yet to be studied in detail; both groups include three taxa (Werner 1994a). The extraordinary diversity of the dinosaur assemblage is reflected by the occurrence of nine taxa: two titanosaurs, an undefinable other sauropod, two charcharodontosaurs, a questionable hypsilophodontid, *Ouranosaurus*, another indeterminable iguanodontid, and a dromaeosaurid theropod (Rauhut 1999, this volume; Rauhut & Werner 1995). Apart from the snakes studied in this paper, squamates are also represented by several lacertilian osteoscutes.

At present, the disarticulated vertebrate fragments of the Cenomanian Wadi Abu Hashim Member of Sudan, which comprise numerous fish and tetrapod taxa, represent one of the most diverse vertebrate faunas known up to now from Africa.

MATERIALS AND METHODS

A minor proportion of the fossils studied was collected by systematically scanning the weathered surfaces of the vertebrate-bearing layers. In addition, more than seven tons of sediment were collected and screen-washed as already described in detail (Werner 1994a). Inspection of the washing residue yielded the bulk of the snake material.

The terminology for snake vertebral morphology used here is that of Auffenberg (1963) as modified by Gasc (1974), and Rage (1984). The snake material described here is curated at the fossil collection of the Technical University of Berlin - Special Research Project 69 (TUB-SFB69) and bears the following catalogue numbers Vb-662 to Vb-690, Vb-709, Vb-1041 to Vb-1061.

SYSTEMATIC ACCOUNT

According to most recent classifications, living snakes are divided into two groups: the Scolecophidia and Alethinophidia. Nopcsa (1923) erected a third group, the Cholophidia, for old snakes, i.e. the Simoliophiidae. He regarded the Cholophidia as the stem group of both Scolecophidia and Alethinophidia. Other fossil snakes corresponding to an ante-Scolecophidia/Alethinophidia grade are now known (Rage & Prasad 1992; Caldwell & Lee 1997).

There are no scolecophidians at Wadi Abu Hashim. These snakes are generally small and their bones are brittle, and they are very rare in the fossil record. Some of the snakes recovered at Wadi Abu Hashim are perhaps more primitive than the scolecophidians and alethinophidians. Snakes of lapparentophiid grade (i.e. Lapparentophiidae) and the Madtsoiidae were considered as Alethinophidia by Rage (1984, 1987), but such a referral may be questioned today. The recovery of a skull and various skull bones belonging to the Madtsoiidae (Barrie 1990; Scanlon 1996) has shown that this family corresponds to an old lineage (Scanlon 1994, 1996). Madtsoiids have been considered alethinophidians, but this is now being challenged. McDowell (1987) suggested that the Madtsoiidae belong to an ante-Scolecophidia/Alethinophidia radiation. The snakes of lapparentophiid grade are still very poorly known; their relationships cannot be established. However, as they are more primitive than the Madtsoiidae, they might belong to a group more primitive than the Scolecophidia and Alethinophidia. The other taxa found at Wadi Abu Hashim belong to the Alethinophidia.

Lapparentophiid-grade snakes

The Lapparentophiidae are rare mid-Cretaceous snakes known only from isolated vertebrae. The family includes *Lapparentophis defrennei* from the Late Albian or Cenomanian of Algeria (Cuny *et al.* 1990). *Pouitella pervetus* from the Cenomanian of France has been provisionally allocated to this family (Rage 1988a). A possible lapparentophiid from the Late Albian of Algeria was described but not named (Cuny *et al.* 1990). *Simoliophis* (only one valid species named: *S. sauvagei*), which is referred to its own family (Simoliophiidae), is rather frequent in the marine deposits of the Cenomanian. It was regarded as closely related to the Lapparentophiidae (Hoffstetter 1959; Rage 1984); but new material leads to questions about such relationships (Rage, in progress).

The vertebrae of these lapparentophiid-grade snakes are primarily characterized by primitive features, which, coupled with the nature of the fossils, makes it difficult to establish both their interrelationships and relationships with other snakes. These fossils apparently represent a primitive level of evolution within snakes. Two vertebrae from Wadi Abu Hashim represent this level of snake evolution. They probably belong to two distinct taxa.

Lapparentophiid-grade snake A (genus and species new, unnamed)

(Figure 2)

Referred material: one trunk vertebra (Vb-671).

Description.

The vertebra is probably from the mid-trunk region; it lacks the posterior part of the neural arch on the left side, the top of the neural spine, and various salient parts are more or less eroded.

Measurements: length of centrum from cotylar rim to tip of condyle, 6.6 mm; width of interzygapophyseal constriction, 6 mm; width through articular facets of prezygapophyses, 9.4 mm; width of zygosphene, 4.2 mm.

Anterior view: The vertebra is not depressed, nor clearly wide. The articular facets of the prezygapophyses are inclined above the horizontal. The prezygapophyses do not strongly project laterally. Although the lateral tip of both prezygapophyses is damaged, the right side is sufficiently preserved to show that there was no projection which might be considered a prezygapophyseal (or 'accessory') process. This is clearly demonstrated by the regular curvature of the ventro-lateral surface of the right prezygapophysis (Figure 2a, rl). The cross section of the neural canal is rather small. The zygosphene is not very thick; its roof is slightly concave dorsally. The zygosphenal facets define planes which intersect at the zygosphenal centre (= 'centre zygosphénien', Gasc 1974: 53); this centre is situated just below the floor of the neural canal in this taxon. The cotyle appears circular and as wide as the zygosphene; its rim is thick. The two fossae on either side of the cotyle are deep; they appear to lack paracotylar foramina. Parazygosphenal foramina are also lacking. The paradiapophyses are badly damaged; however, it is presumed that they did not project laterally beyond the tip of the prezygapophyses.

Dorsal view: The vertebra is wider than long. Although not deep, the interzygapophyseal constriction is well marked. The bottom of the constriction appears as an obtuse angle which is slightly asymmetric (vertex located somewhat anteriorly). The anterior border of the zygosphene forms a median lobe flanked by two lateral lobes. The prezygapophyseal facets are oval and their major axis is clearly oblique, at about 40° from the vertebral axis. The median notch which indents the posterior border of the neural arch is of moderate depth.

Lateral view. The vertebra appears short and high. The neural spine is restricted to the posterior half of the neural arch; its anterior border rises steeply. The height of the neural spine remains unknown. The facets of the zygosphene are broad and oval. The paradiapophyses were broad, they are rather extended anteroposteriorly. The interzygapophyseal ridge is short, nearly straight, and salient. Lateral foramina are present. The axis of the condyle is oblique.

Ventral view: The centrum appears approximately triangular and poorly delimited by faint subcentral ridges. These ridges are concave posterolaterally. The haemal keel is rather wide and blunt. Anteriorly, it reaches the cotyle rim; it even causes a slight anterior projection of the rim. The keel markedly narrows between the two subcentral foramina.

Posterior view: The neural arch is moderately vaulted. The posterior border of the neural spine and the roof of the zygantrum are thick. The posterior face of the neural arch lacks parazygantral foramina.

Discussion.

The absence of any trace of prezygapophyseal processes represents one of the most noticeable feature of this vertebra. In various aquatic extinct and living snakes, a dorsoventral keel which runs along the prezygapophyseal buttress supersedes the true prezygapophyseal process. Vb-671 has neither a ridge nor a prezygapophyseal process. The lack of any trace of a prezygapophyseal salient characterizes the vertebrae of *Lapparentophis*, *Pouitella*, the Madtsoiidae, *Simoliophis,* and nearly all lizards (Rage 1988a). *Lapparentophis*, *Pouitella*, and *Simoliophis* occur only in the middle part of the Cretaceous, whereas madtsoiids range from the mid-Cretaceous to the Pleistocene (see below). The vertebrae of *Lapparentophis* are very different from that of Vb-671: they are more heavily built, their prezygapophyseal facets are very strongly inclined (the level of their lateral tip lies slightly above the roof of the neural arch), their zygosphene is very narrow and its anterolateral corners are truncated, the zygosphenal centre lies clearly more ventrally (at about the centre of the cotyle), the posterior part of their neural arch clearly slopes anteriorly, their paradiapophyses are elongate dorsoventrally, and paracotylar foramina are present. The vertebrae of *Simoliophis* are very peculiar; a heavy pachyostosis strongly alters their morphology. The overall morphology of Vb-671 is consistent with that of the madtsoiid vertebrae, but it lacks parazygantral foramina, which is the most important vertebral character of this family. Moreover, the lack of paracotylar foramina also argues against a referral to the Madtsoiidae. Finally, the closest resemblance of Vb-671 seems to be with *Pouitella pervetus*, a possible Lapparentophiidae, from the Cenomanian of France. However, it clearly differs from *Pouitella* in lacking parazygosphenal foramina and in having a markedly lower neural spine.

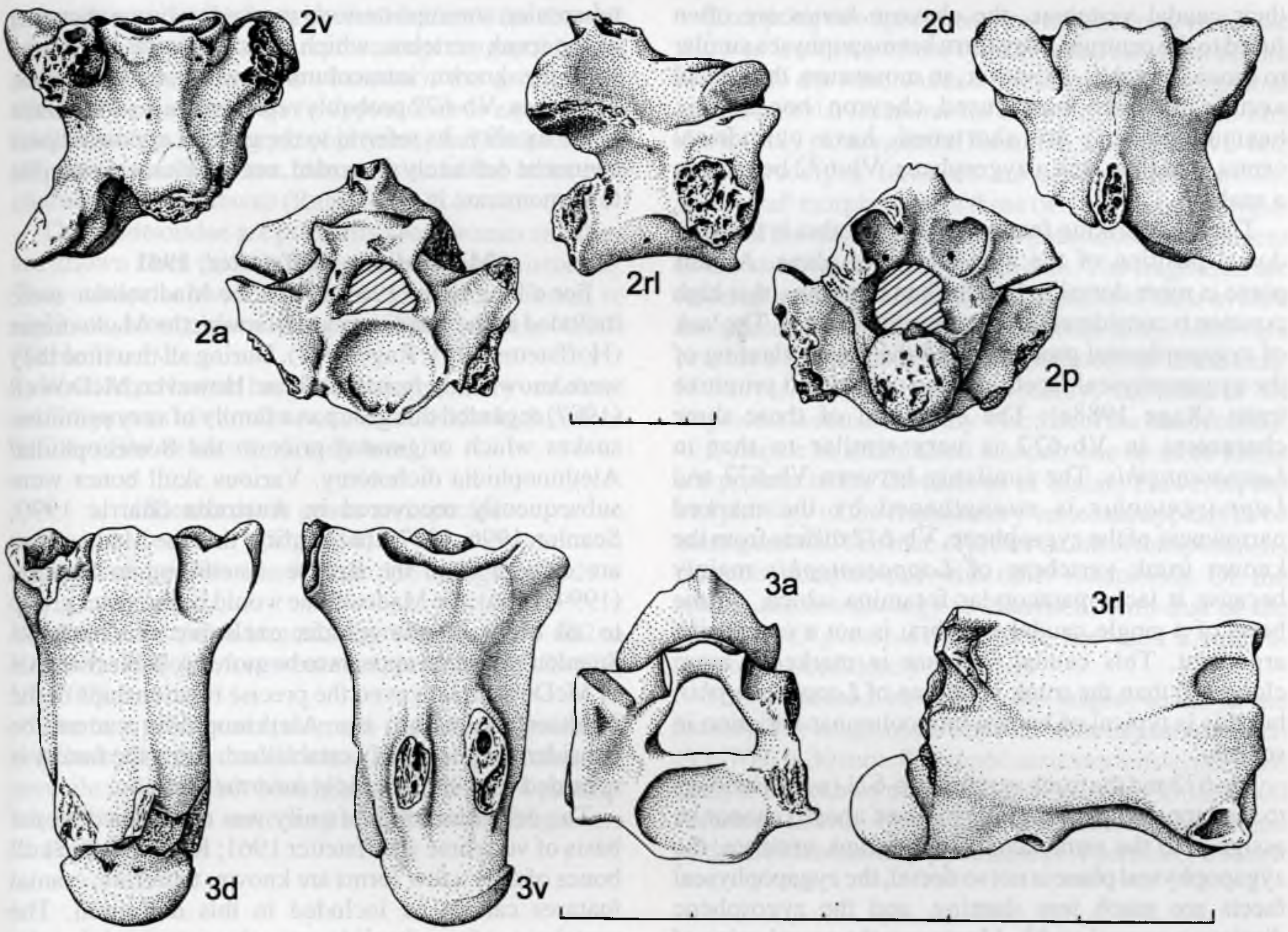
The absence of prezygapophyseal processes, the slanting of the prezygapophyseal facets, and the lack of parazygantral foramina indicate a lapparentophiid level of evolution, but the precise systematic assignment of Vb-671 remains unknown. It might belong to the Lapparentophiidae but this cannot be demonstrated. This vertebra surely represents a new genus and new species, but the single specimen in hand is not complete enough to be a name-bearer of a new taxon. Therefore, we leave this taxon unnamed.

Lapparentophiid-grade snake B (indeterminate snake)
(Figure 3)

Referred material: one caudal vertebra (Vb-672).

Description.

This small caudal vertebra is incomplete: the posterior part of the neural arch, the neural spine, the pleurapophyses (or lymphapophyses), the left prezygapophysis, and the haemapophyses are broken off.



Figures 2-3. Lapparentophiid-grade snakes. 2: Lapparentophiid-grade snake A, trunk vertebra (Vb-671). 3: Lapparentophiid-grade snake B, caudal vertebra (Vb-672). Anterior (a), dorsal (d), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 5 mm.

Measurements: length of centrum from cotyle to tip of condyle, 2.7 mm; width of interzygapophyseal constriction, 1.3 mm; width of zygosphene, 0.6 mm; horizontal diameter of cotyle, 1 mm.

Anterior view: The zygosphene is very narrow, comparatively thick, and arched dorsally. The orientation of the zygosphenal facets is nearly vertical; as a result, the zygosphenal centre lies far beyond the ventral surface of the centrum. The transverse section of the neural canal is triangular and wider than the zygosphene. The cotyle is depressed and wider than the neural canal. The zygapophyseal plane lies at a very high level: the level of the medio-ventral limit of the zygapophyseal articular facets is situated just below the ventral limit of the zygosphenal facets. The zygapophyseal facets slant prominently. The zygapophyseal process is absent. The zygapophyseal buttress is strongly compressed; it forms a thick vertical lamina. The vertebra lacks paracotylar foramina.

Dorsal view: The vertebra is very elongate. The anterior border of the zygosphene is somewhat distorted; it apparently formed small lateral lobes and a rather pointed median lobe. The prezygapophyseal facet is elongate and oblique, with its long axis at about 29° to the vertebral axis. The neural spine probably comprised a posterior tubercle, the height of which cannot be estimated, anteriorly prolonged by a faint keel which does not reach the zygosphene.

Lateral view: The neural arch rises moderately posteriorly. The zygosphenal facets are anteroposteriorly short. The vertebra lacks marked interzygapophyseal ridges, but the subcentral ridges are well marked. The axis of the condyle appears to be horizontal or subhorizontal. Lateral foramina cannot be detected.

Ventral view: Subcentral ridges clearly bound the ventral face of the centrum. This surface is narrow, elongate, and its median area forms an elongate anteroposterior bulge; between the bulge and the subcentral ridges the surface is nearly flat. The bases of the haemapophyses are located rather anteriorly, far from the condyle. The subcentral foramina are very tiny.

As Vb-672 lacks the posterior part of the neural arch, the posterior aspect of the vertebra is not informative.

Discussion.

The narrowness of the zygosphene may suggest that this vertebra belongs to mosasaurs. These lizards have generally well-shaped zygosphenes; moreover, on their caudal vertebrae, the chevron bones are often fused to the centrum, they form haemapophyses similar to those in snakes. However, in mosasaurs, the caudal vertebrae which bear fused chevron bones (i.e., haemapophyses) are shortened, have cylindrical centra, and they lack a zygosphene. Vb-672 belongs to a snake.

The most striking feature of this vertebra is the very dorsal position of the zygapophyseal plane. As this plane is more dorsal in lizards than in snakes, this high position is considered to be a primitive feature. The lack of zygapophyseal processes and the strong slanting of the zygapophyseal facets are also considered primitive traits (Rage 1988a). The condition of these three characters in Vb-672 is very similar to that in *Lapparentophis*. The similarity between Vb-672 and *Lapparentophis* is strengthened by the marked narrowness of the zygosphene. Vb-672 differs from the known trunk vertebrae of *Lapparentophis* mainly because it lacks paracotylar foramina which, on the basis of a single caudal vertebra, is not a conclusive argument. This caudal vertebra is markedly more elongated than the trunk vertebrae of *Lapparentophis*, but this is typical of known intracolumnar variation in snakes.

Vb-672 and the trunk vertebra Vb-671 (which belongs to the lapparentophiid grade too; see above) cannot be assigned to the same taxon. In the trunk vertebra, the zygapophyseal plane is not so dorsal, the zygapophyseal facets are much less slanting, and the zygosphene displays a normal width. Moreover, the neural spine of the caudal vertebra (i.e., Vb-672) was probably tubercular, anteroposteriorly markedly shorter than that of the trunk vertebra, which does not seem consistent with the known intracolumnar variation in snakes. Therefore, Vb-672 probably represents a distinct snake in the locality. Its referral to the genus *Lapparentophis* cannot be definitely discarded, nor does it seem possible to demonstrate it.

Madtsoiidae Hoffstetter, 1961

For a long time (1961-1987), the Madtsoiidae were included in the Boidae as a subfamily, the Madtsoiinae (Hoffstetter 1961; Rage 1987). During all that time they were known only from vertebrae. However, McDowell (1987) regarded this group as a family of very primitive snakes which originated prior to the Scolecophidia/Alethinophidia dichotomy. Various skull bones were subsequently recovered in Australia (Barrie 1990; Scanlon 1996, 1997) that confirm that the Madtsoiidae are distinct from the Boidae. According to Scanlon (1994, 1996), the Madtsoiidae would be the sister group to all other Alethinophidia exclusive of *Dinilysia*. Scanlon's opinion appears to be more probable than that of McDowell; however, the precise relationships of the Madtsoiidae within the Alethinophidia cannot be considered as definitely established. Here, the family is regarded as Alethinophidia *incertae sedis*.

The definition of the family was established on the basis of vertebrae (Hoffstetter 1961; Rage 1984). Skull bones of only a few forms are known; therefore, cranial features cannot be included in this definition. The vertebrae of madtsoiids are characterized by the combination of the following characters: presence of

TABLE 1.
List of all known Madtsoiidae

Taxa	Geological Ages	Gondwanan areas	Laurasian
Indeterminate genus and species (this paper)	Cenomanian	Sudan	
Madtsoia aff. *madagascariensis*	Coniacian or Santonian	Niger	
Madtsoia madagascariensis	Santonian or Campanian	Madagascar	
Madtsoia laurasiae	Late Campanian or Early Maastrichtian		Spain
Herensugea caristiorum	Late Campanian or Early Maastrichtian		Spain
Alamitophis argentinus	Campanian or Maastrichtian	Argentina	
Patagoniophis parvus	Campanian or Maastrichtian	Argentina	
?Madtsoiid: *Rionegrophis madtsoioides*	Campanian or Maastrichtian	Argentina	
?Madtsoiid	Maastrichtian	India	
?Madtsoiid	Early Palaeocene	Bolivia	
Madtsoia camposi	Middle Palaeocene	Brazil	
Madtsoia cf. *M. bai*	Middle or Late Palaeocene	Argentina	
Indeterminate genus and species	Late Palaeocene	Morocco	
Madtsoia bai	Early Eocene	Argentina	
Patagoniophis cf. *P. parvus*	?Early Eocene	Australia	
Alamitophis cf. *A. argentinus*	?Early Eocene	Australia	
Gigantophis garstini	Late Eocene	Egypt, Libya	
Yurlunggur sp.	Oligo-Miocene	Australia	
Wonambi sp.	Oligo-Miocene	Australia	
Nanowana godthelpi	Early Miocene	Australia	
Nanowana schrenki	Early Miocene	Australia	
Yurlunggur camfieldensis	Middle Miocene	Australia	
Wonambi cf. *W. naracoortensis*	Pliocene	Australia	
Yurlunggur sp.	Pliocene	Australia	
Yurlunggur sp.	Pleistocene	Australia	
Wonambi naracoortensis	Pleistocene	Australia	

parazygantral foramina (a derived feature), the absence of any salient which could represent a prezygapophyseal process (a plesiomorphic character), the great width through the diapophyses (it approaches or exceeds the width through the prezygapophyses), and the presence of paracotylar foramina (the polarity of the latter two characters is unknown) (Rage, 1998).

The Madtsoiidae are primarily Gondwanan and they are known from the late Cretaceous to the Pleistocene. They comprise twelve or thirteen species referred to eight or nine genera (Rage, 1998; Scanlon 1997) (Table 1).

Wadi Abu Hashim has yielded fragmentary vertebrae and fragments of vertebrae of a madtsoiid which cannot be identified below the family level.

Indeterminate genus and species
(Figure 4)

Madtsoiidae: Werner & Rage 1994, Figures 1, 2.

Referred material: 8 fragmentary vertebrae (Vb-662 to Vb-669) and 34 fragments of vertebrae (Vb-670, Vb-709).

The best preserved specimens (i.e., the fragmentary vertebrae) are the smaller ones (including vertebrae of juvenile individuals). Nearly all fragments are parts of large to very large vertebrae; all but one are fragments of centra.

Excepting two specimens, the fragmentary vertebrae show at least two of the typical features which secure referral to the Madtsoiidae (presence of parazygantral and paracotylar foramina; for example, Vb-668). Vb-665 shows only parazygantral foramina whereas in Vb-662 only paracotylar foramina are observable. However, the overall morphology of these two vertebrae is similar to that of the remainder of the sample and their assignment to the same family is beyond doubt. The fragments are referred to the Madtsoiidae on the basis of their overall morphology and, when areas adjacent to the cotyle are preserved, the presence of paracotylar foramina. Moreover, throughout this locality, the size of all fragments is consistent only with that of the Madtsoiidae.

It cannot be established whether one or more forms are present in the Cretaceous of Sudan. However, the morphology of the fragmentary vertebrae appears to be homogeneous. The state of preservation of the specimens prevents comparisons with other madtsoiids. On the whole, the morphology is consistent with that of the *Madtsoia-Gigantophis* complex, but such a referral cannot be confidently proposed.

This madtsoiid is, by far, the largest snake in the locality. The length of the centrum of the largest specimen (Vb-709) is 30 mm. *Wonambi naracoortensis*, the most completely known madtsoiid, had between 350 and 400 vertebrae (Barrie 1990). This number is similar to that of the Boidae (mainly pythonines). Therefore, a rough

Figures 4-5. 4: Madtsoiidae, indeterminate genus and species, juvenile individual, trunk vertebra (Vb-668). 5: ? Palaeophiidae, indeterminate genus and species, centrum of trunk vertebra (Vb-688). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 5 mm.

comparison with pythons indicates that the largest specimen from Wadi Abu Hashim represents a snake probably 6 to 7 m long, perhaps more.

?Palaeophiidae Lydekker, 1888

A possible Palaeophiidae is present at Wadi Abu Hashim. It was not identified in the preliminary article (Werner & Rage 1994). The Palaeophiidae are an extinct family of snakes highly adapted to aquatic life. The family comprises two subfamilies, the Palaeophiinae and the Archaeophiinae. The Palaeophiinae are known only by isolated vertebrae; they include two phenotypic genera: *Palaeophis* (Maastrichtian-Lutetian, perhaps early Bartonian) and *Pterosphenus* (late Lutetian-late Eocene); a third genus, *Vialovophis*, from the late Palaeocene or early Eocene (Nessov & Udovitschenko 1984), is apparently a synonym of *Palaeophis* (Rage 1987). The Archaeophiinae are represented by two articulated specimens from the early Eocene. They belong to two different taxa. *Archaeophis proavus* was redescribed by Janensch (1906); it probably corresponds to a juvenile individual. The second specimen was referred to as *Archaeophis turkmenicus* by Tatarinov (1963); however, it probably belongs to a distinct genus (Rage 1984). Tatarinov (1963) assigned *Archaeophis* to the Palaeophiidae because the vertebrae of *A. turkmenicus* have well developed pterapophyses. The skull of archaeophiines is known (Janensch 1906; Tatarinov 1988); unfortunately, that of the palaeophiines remains unknown, which makes the referral of both groups to the same family uncertain. Here, we follow Tatarinov's concept of the Palaeophiidae (i.e., archaeophiines included) because it remains the best established opinion.

On account of overall vertebral morphology, the Palaeophiidae were regarded as related to the Boidae or to the Booidea (Hoffstetter 1955; Rage 1984). But McDowell (1987) referred them to his Acrochordoidea and Rage (1988a) questioned their booid affinities. The relationships of the Palaeophiidae cannot be settled on the base of the currently available evidence. They are here considered as Alethinophidia *incertae sedis*.

Indeterminate genus and species
(Figure 5)

Referred material: one centrum of a trunk vertebra (Vb-688).

Description.

One centrum appears very peculiar within this snake fauna. It is elongate and narrow. The subcentral ridges are faint and very short; they originate from the posteroventral corner of the paradiapophyses and they vanish at about mid-length of the centrum. Subcentral foramina are present. Ventrally, the centrum bears a deep and sharp sagittal keel. Posteriorly, the keel projects ventrally, thus forming a short hypapophysis. Anteriorly, below the cotyle, it also slightly projects ventrally. As a result of the lack of subcentral ridges, the transverse section of the posterior half of the centrum is approximately triangular. The cotyle is nearly circular, but the dorsalmost part of its rim is somewhat straight; similarly, the dorsal part of the codyle is slightly flattened. In lateral view, the axis of the condyle is nearly horizontal or perhaps horizontal (because of the shape of the outline of the condyle, the orientation of the axis is difficult to estimate).

Discussion.

The overall morphology of this centrum is clearly reminiscent of the Palaeophiidae and Nigerophiidae. The very faint subcentral ridges are consistent with both families. However, the deep sagittal keel and short hypapophysis suggest only the Palaeophiidae. A referral to the Palaeophiidae is also supported by the presence of the slight ventral projection of the anterior part of the sagittal keel (it is sometimes called an 'anterior hypapophysis'). Such an anterior ventral process is present in species of *Palaeophis* interpreted as 'advanced species' by Rage (1984) and in *Pterosphenus*. On the other hand, the morphology of the cotyle and condyle, the dorsal part of which is slightly truncated, also occurs in various species of *Palaeophis*; it is unknown in other snakes. The peculiar orientation of the condyle (axis horizontal or nearly horizontal) is also characteristic of the Palaeophiidae; this condition is approached by the Nigerophiidae and Russellophiidae.

Therefore, several peculiar characters clearly argue for an assignment to the Palaeophiidae, which is consistent with the overall morphology of this fragment of vertebra. Within Palaeophiidae, an assignment to the Archaeophiinae may be apparently discarded because of the marked elongation of the centrum. But, it is not possible to refer so poorly preserved a specimen to any taxon without reservation. Vb-688 is only tentatively referred to the Palaeophiidae.

If this specimen really belongs to the Palaeophiidae, then it is the oldest member of the family. A palaeophiid snake was briefly reported, but not described, by Sereno *et al.* (1996) from the Cenomanian of Morocco, but examination of the fauna has shown that palaeophiids are lacking. Hitherto, the earliest certain palaeophiid is an indeterminate *Palaeophis* from the Maastrichtian of Morocco (Rage & Wouters 1979).

It should be noted that within *Palaeophis*, species with massive and short vertebrae (i.e. booid-like) were considered as more primitive, whereas those with more elongate and less massive vertebrae were regarded as advanced (Rage 1984). This opinion was based on the fact that the Palaeophiidae were regarded as booid snakes, which may be questioned (McDowell 1987; Rage 1988a). The presumed primitive morphology characterizes species from the early and middle Eocene, whereas the presumed derived morphology occurs in clearly older geological levels: Maastrichtian of Morocco (Rage & Wouters, 1979), Palaeocene of Morocco (unpublished), and even Cenomanian if Vb-688 really represents a Palaeophiidae. Obviously, stratigraphic distribution should not be taken into account in the polarization of characters. However, in the present case, it casts doubts on the previous interpretation.

Anilioidea Fitzinger, 1826

The Anilioidea are an assemblage of primitive alethinophidian snakes that is probably paraphyletic (Cundall *et al.* 1993). They likely form the stem group of the other alethinophidians, i.e., the Macrostomata (Rage 1997). The relationships within the Anilioidea cannot be considered as settled. Traditionally, two families (Aniliidae and Uropeltidae) were recognized within this assemblage. McDowell (1975, 1987) included the Xenopeltidae and Loxocemidae in the Anilioidea, but these two families appear to be closer to the Booidea (Rage, 1998). The Uropeltidae *s.s.* (= Uropeltinae of McDowell 1987), i.e., Cylindrophiinae excluded, unquestionably form a monophyletic group, but the remaining Anilioidea (i.e., the traditional Aniliidae) probably make up a paraphyletic assemblage. Cundall *et al.* (1993) recognized three monophyletic lineages within these non-uropeltid anilioids: each living genus (*Anilius*, *Cylindrophis*, *Anomochilus*) represents one lineage. In order to avoid paraphyletic taxa, they elevated each of these lineages to family rank. But, since it cannot be definitely considered that the traditional Aniliidae are paraphyletic, and because the relationships within this group are not definitely demonstrated, it seems premature to adopt a new classification for non-uropeltid anilioids. It seems preferable to provisionally hold the traditional Aniliidae (which may be labelled 'Aniliidae *s.l.*'), keeping in mind that they are probably, but not certainly, paraphyletic (Rage, 1998).

No fossil was referred to the Uropeltidae, but some fossil taxa are referred to the Aniliidae *s.l.*

Aniliidae Fitzinger, 1826

As indicated above, the Aniliidae, as they are accepted here (= Aniliidae *s.l.*), include the non-uropeltid Anilioidea. They comprise the living genera *Anilius* (South America), *Cylindrophis* and *Anomochilus* (both from Southern Asia), and various fossils. Two extinct species may be referred to the Aniliidae *s.l.* without reservation: *Colombophis portai* from the Miocene of South America (Hoffstetter & Rage 1977) and *Michauxophis occitanus* from the Pliocene of western Europe (Bailon 1988). The genus *Coniophis* (mid-Cretaceous to late Eocene; see below) is tentatively referred to the Aniliidae *s.l.* The genus *Eoanilius* (late Eocene to early Miocene) includes two species: *E. europae* and *E. oligocenicus* (Rage 1984; Szyndlar 1994). It was assigned to the Aniliidae *s.l.* (Rage 1974); this referral has been more or less accepted by McDowell (1987), who considered it as a member of his Cylindrophiinae, and by Cundall *et al.* (1993). Szyndlar (1994) and Szyndlar & Schleich (1993) referred *Eoanilius* to the Aniliidae *s.s.*, that is, to a family which includes only one living genus, *Anilius*.

Vertebrae belonging to *Coniophis* were recovered at Wadi Abu Hashim.

Coniophis Marsh, 1892

Coniophis is known only from vertebrae that are characterized by their comparatively massive construction, their relatively depressed neural arch that does not rise markedly above the zygapophyseal plane, their prezygapophyseal processes that are either very short or lacking, the lack of a median notch in the posterior border of the neural arch (a shallow embayment is often present), their centrum which only slightly widens anteriorly, the more or less oblique long axis of their prezygapophyseal facets, their much reduced neural spine, and their haemal keel generally distinct in at least a part of the vertebral column (Rage, 1998).

The relationships of *Coniophis* are controversial. *Coniophis* was first considered as a snake without a more precise assignment (Marsh 1892; Gilmore 1938). Hoffstetter (1955) erected the family Coniophiidae for the reception of *Coniophis precedens*, the only species known at that time. Hecht (1959) allocated *Coniophis* to the Aniliidae *s.l.* and he considered that its closest relative might be the living *Cylindrophis*. Later, Hecht (1982) suggested that *Coniophis* might be closely related to *Dinilysia* from the late Cretaceous (?Campanian). Subsequently, McDowell (1987) placed *Coniophis* in the Dinilysiidae. The features which characterize the vertebrae of *Coniophis* are either primitive or non-polarizable, which accounts for this uncertainty. *Coniophis* probably represents a paraphyletic assemblage. The vertebral morphology of *Coniophis* corresponds either to that of very primitive Alethinophidia (i.e., to that of Aniliidae *s.l.*) or, perhaps, to an intermediate between scolecophidians and alethinophidians (Rage 1984, 1987). As *Coniophis* is probably a very primitive alethinophidian, we tentatively retain it in the anilioids, and as it cannot be referred to the very peculiar uropeltids, it is tentatively referred to the Aniliidae *s.l.*

On the other hand, two main morphologies may be recognized within *Coniophis*: the Cretaceous species appear to be rather different from the Eocene ones (see below). However, we provisionally maintain *Coniophis* as a valid genus, it being understood that it probably represents a paraphyletic assemblage. At present, neither the relationships within this assemblage nor relationships with other aniliids can be established.

Four species have been described: *C. cosgriffi* from the late Campanian (Edmontonian) (Armstrong-Ziegler 1978), *C. precedens* from the late Maastrichtian (Lancian) (Marsh 1892), and *C. carinatus* and *C. platycarinatus*, both from the late early or early middle Eocene (Bridgerian) (Hecht 1959). These four species are known only from North America. *Coniophis* cf. *C. precedens* was reported from the early Campanian (Aquilan) of Canada (Fox 1975) and from the middle Palaeocene of Brazil (Albino 1990; Rage 1998). Other *Coniophis*, referred to as *Coniophis* sp., occur in the late Albian/earliest Cenomanian (Gardner & Cifelli, 1999), the middle/late Campanian (Judithian) (Breithaupt 1985), the middle Paleocene (Torrejonian) (Estes 1976), the late Eocene (Uintan) (Holman 1979) of the USA, the late Eocene of France (Rage 1988b), the late Palaeocene (Gheerbrant *et al.* 1993) and early Eocene (unpublished) of Morocco, and the early Eocene of Algeria (unpublished). Moreover, *Coniophis* is perhaps present in a Peruvian locality the geological age of which is either latest Cretaceous or earliest Palaeocene (Rage 1991).

Wadi Abu Hashim has yielded seven vertebrae which correspond to the 'definition' of *Coniophis*. Whatever the precise status of the genus, this fossil represents a new species.

Coniophis dabiebus sp. nov.

(Figures 6, 7, 8)

Holotype: one mid-trunk vertebra (Vb-673).

Type locality: Wadi Abu Hashim, Sudan.

Horizon: Wadi Abu Hashim Member of Wadi Milk Formation; Cenomanian.

Etymology: from Al Dabieb, a local Sudanese name for snakes.

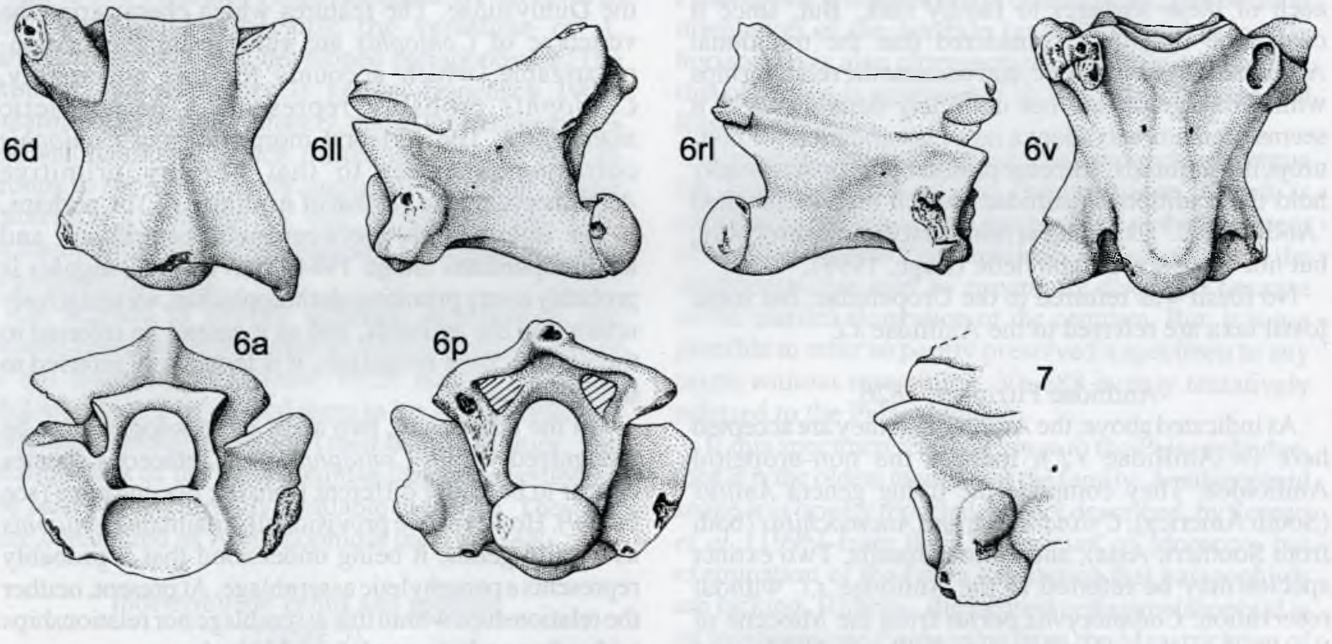
Referred material: 6 trunk vertebrae (Vb-674 to Vb-679).

Diagnosis: *Coniophis dabiebus* differs from the other species of *Coniophis* by its more elongate vertebrae. It is distinguished from *C. precedens*, *C. carinatus*, and *C. platycarinatus* by its less deep interzygapophyseal constriction. It differs from *C. carinatus*, *C. platycarinatus*, and *C. cosgriffi* by its clearly less prominent neural spine. It differs from *C. carinatus* and *C. platycarinatus* by the lack of any indication of prezygapophyseal processes, by its laterally less projecting prezygapophyses, and by its more elongate prezygapophyseal articular facets.

Description of the holotype.

The holotype is a nearly complete mid-trunk vertebra which lacks only the extremities of the left prezygapophysis and the left postzygapophysis.

Measurements: length of centrum from cotylar rim to tip of condyle, 1.9 mm; width of zygosphene, 1 mm; width of interzygapophyseal constriction, 1.3 mm; horizontal diameter of cotyle, 0.9 mm.



Figures 6-8. Aniliidae, *Coniophis dabiebus* sp. nov. 6: mid-trunk vertebra, Holotype (Vb-673). 7: anterior portion of a trunk vertebra showing a well-preserved paradiapophysis, left lateral view (Vb- 674). 8: posterior trunk vertebra (Vb-679); anterior border of zygosphene reconstructed on the basis of Vb-678. Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bar represents 5 mm.

Anterior view. The vertebra appears rather high and narrow, not massive. The neural canal is ovoid and high. The lateral walls of the canal are thin. The zygosphene is as wide as the cotyle and slightly wider than the neural canal; its roof is thin and slightly arched dorsally. The zygosphenal centre is located in the dorsal part of the cotyle. The cotyle is dorso-ventrally depressed; the dorsal part of its rim is nearly straight. The prezygapophyseal body is high and narrow and the prezygapophyses do not strongly project laterally. The prezygapophyseal facets clearly slant; they lie at a high level, i.e. between two thirds and three quarters of the height of the neural canal. Although the tip of each prezygapophysis is broken off, it may be inferred that the prezygapophyseal processes are absent. The paradiapophyses do not markedly project laterally. The depressions between the cotyle and prezygapophyses do not form well-delimited fossae; they lack paracotylar foramina.

Dorsal view: The vertebra shows a squarish outline. The interzygapophyseal constriction is rather deep and almost symmetrical: its maximum depth occurs at about mid-length of the vertebra. The zygosphene is moderately wide; its anterior border is straight and it forms two small lateral lobes, as a result it appears concave. The articular facets are oval and their major axis is oblique (about 40° to the vertebral axis). No prezygapophyseal process projects beyond the facet. The posterior half of the neural arch gradually slopes anteriorly; the neural arch appears to be somewhat saddle-shaped. The neural spine is a low tubercle (the tip of which is broken) on the posteriormost part of the neural arch; it extends anteriorly as a faint ridge that vanishes in the middle part of the neural arch. The posterior border of the neural arch forms a shallow concavity lacking a median notch. The right postzygapophysis (the only preserved one) markedly projects posteriorly, which is unusual.

Lateral view. The vertebra is moderately elongate. The posterior half of the neural arch clearly rises posteriorly. The neural spine does not appear clearly marked off from the neural arch. The zygosphenal facet is elongate and its long axis is slightly inclined above the horizontal. The paradiapophysis does not markedly extend dorso-ventrally (however, its ventral border is broken). The parapophyseal part is broader than the diapophyseal one. The interzygapophyseal and subcentral ridges are not well-marked. The lateral foramen occupies a low position. The haemal keel is not deep.

Ventral view: The centrum is narrow; it moderately widens anteriorly. Its ventral surface is poorly delimited by weakly defined subcentral ridges. The haemal keel is rather wide and blunt. It is poorly differentiated from the centrum, mainly in the posterior part where its limits become obscure (except its posterior limit which is close to the condyle). Anteriorly, where the haemal keel is defined, the ventral face of the centrum is concave on either side of the keel. Subcentral foramina are present.

Posterior view: The neural arch is very depressed. The neural spine appears low and thick. The roof of the zygantrum and the lateral walls of the neural canal are relatively thin. Parazygantral foramina are absent.

Vertebral variation.

Only mid- and posterior trunk vertebrae are available. Some mid-trunk vertebrae have perfectly preserved prezygapophyses and paradiapophyses. They confirm that the prezygapophyses are without any indication of prezygapophyseal processes (Figure 7, 8a). In the largest vertebrae, the paradiapophyses comprise a hemispherical diapophysis and a broader and rather flat parapophysis (Figure 7). All other features exhibited by these mid-trunk vertebrae are identical to those of the holotype. Two poorly preserved vertebrae are regarded as being from the posterior trunk. They appear more elongate and slightly more depressed than mid-trunk vertebrae. The prezygapophyseal bodies seem less narrow in anterior view. The paradiapophyses are more protruding laterally, they reach the level of the prezygapophyseal tip. The anterior border of the zygosphene forms three lobes. The ventral face of their centrum is even more poorly delimited than in the mid-trunk vertebrae. The haemal keel is hardly distinct. However, if these vertebrae are really from the posterior trunk, it should be noted that they lack the depressions that occur on either side of the haemal keel in the posterior trunk region of most snakes.

Unfortunately, none of these trunk vertebrae retains preserved postzygapophyses. Therefore, it is not possible to establish whether the peculiar posterior projection of the only preserved postzygapophysis in the holotype (Figure 6d, right side) is a specific character or only a peculiarity of this specimen.

Discussion.

The characters exhibited by the *Coniophis* from Sudan clearly show that it represents a distinct species. Apart from the primitive nature of the *Coniophis* features, the most serious problem in the study of this genus is that too many fossils have been referred to as *Coniophis* sp. and remain undescribed. It seems necessary to describe and to name the Sudanese *Coniophis*; the seven available vertebrae permit this.

The vertebrae of *Coniophis dabiebus* are more elongate than those of all other species of the genus. They are narrower and less depressed than those of *C. precedens* and *C. carinatus*. The interzygapophyseal constriction is shallower than that of *C. precedens*, *C. carinatus*, and *C. platycarinatus*. The neural spine does not form a sagittal ridge clearly marked off from the neural arch; by this character, *C. dabiebus* differs from *C. carinatus*, *C. platycarinatus*, and *C. cosgriffi*. Besides, *C. dabiebus* differs markedly from *C. carinatus* and *C. platycarinatus* in lacking any salient which could represent a prezygapophyseal process, in having prezygapophyses less projecting laterally, and articular facets of the prezygapophyses more elongate.

Phenetically, *C. dabiebus* appears to be closer to the other Cretaceous species (*C. precedens* and *C. cosgriffi*) than to the Eocene ones (*C. carinatus* and *C. platycarinatus*). In *C. patycarinatus* and mainly *C. carinatus*, the prezygapophyses stretch markedly laterally and, at their lateral tip, a very short prezygapophyseal process projects slightly beyond the articular facet. This morphology of the prezygapophyses in *C. carinatus* and *C. platycarinatus* is reminiscent of the living Aniliidae (at least *Anilius* and *Cylindrophis*). *C. dabiebus*, *C. precedens*, and *C. cosgriffi* make up an assemblage which is phenetically more distinct from the living forms.

Coniophis cf. *C. dabiebus*

(Figure 9)

Referred material: one vertebra (Vb-680).

A single vertebra displays characters of *C. dabiebus,* but it is shorter than all the vertebrae referred to this species. Such shortness suggests that it might be a very anterior trunk vertebra of *C. dabiebus*. Unfortunately, the posterior part of the centrum is lacking, that is, the presence of a hypapophysis or of a deep haemal keel (which would confirm that the vertebra is an anterior one) cannot be ascertained. On the other hand, the neural arch is not more vaulted and the neural spine is not higher than in the mid-trunk vertebrae, which is not consistent with the usual intracolumnar variation if this vertebra is really a very anterior one. Moreover, the neural spine seems somewhat unusual. It is only a slight thickening of the posterior border of the neural arch which stretches posterodorsally. In lateral view, this thickening resembles a tubercular neural spine (but it is not tubercular); in dorsal view, it projects slightly posteriorly. This vertebra belongs to a juvenile individual as shown by its size and the very depressed cotyle. But this probably cannot account for the differences which distinguish this vertebra from *Coniophis dabiebus*. This specimen cannot be confidently referred to the latter species.

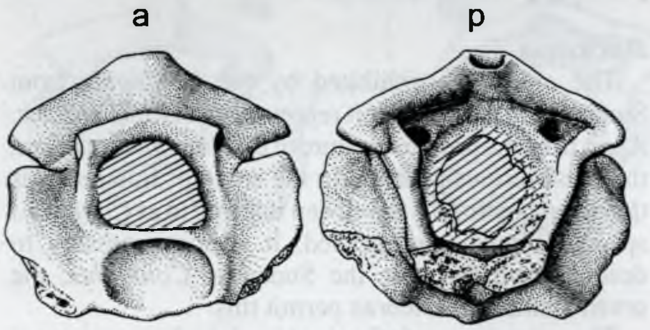


Figure 9. Aniliidae, *Coniophis* cf. *C. dabiebus*. Trunk vertebra (Vb-680). Anterior (a), dorsal (d), left lateral (ll), and posterior (p) views. Scale bar represents 1 mm.

Acrochordoidea Bonaparte, 1838

The Acrochordoidea include the living Acrochordidae and the extinct Nigerophiidae. They are all aquatic snakes. McDowell (1987) assigned the extinct Palaeophiidae to the Acrochordoidea, but they are here considered as Alethinophidia *incertae sedis* (see above).

Nigerophiidae Rage, 1975

The family Nigerophiidae was erected for the single species *Nigerophis mirus* from the Palaeocene of Niger (Rage 1975a). This snake is easily characterized by the overall morphology of its vertebrae which appear to be quite peculiar within snakes. The middle portion of the vertebrae is more or less cylindrical whereas the posterior part is deep. The cylindrical aspect of the middle portion results from the lack, or the weakness, of the interzygapophyseal and subcentral ridges. The vertebrae are posteriorly deep, relative to the anterior and middle parts, because the neural spine (which occupies only the posterior part of the neural arch) is rather high and because the posterior part of the haemal keel is ventrally deflected. This combination of these features is unique within snakes.

Woutersophis novus from the middle Eocene of Belgium (Rage 1980) and *Indophis sahnii* from the latest Cretaceous of India (Rage & Prasad 1992) were tentatively referred to the Nigerophiidae. The vertebrae of *Woutersophis* are reminiscent of both the Nigerophiidae and Palaeophiidae. This genus was referred, with reservation, to the Nigerophiidae because it lacks pterapophyses while these additional apophyses are developed in the Palaeophiidae. *Indophis* shows a rather close phenetic resemblance to *Nigerophis*. However, in *Indophis*, as in *Woutersophis*, the interzygapophyseal and subcentral ridges are clearly defined and the posterior part of the haemal keel is not deflected ventrally. Moreover, in *Indophis*, parazygantral foramina are irregularly present. Therefore, these two snakes cannot be assigned to the Nigerophiidae without reservation.

Wadi Abu Hashim has yielded a snake which appears to be very close to *Nigerophis*. It represents a new genus and species and it may be confidently referred to the Nigerophiidae.

Nubianophis gen. nov.

Type species: *Nubianophis afaahus* sp. nov.

Etymology: from Nubia, the region in which the fossiliferous locality is situated.

Diagnosis: as for the type species and only known species.

Nubianophis afaahus sp. nov.

(Figure 10-12, 13-14)

Holotype: one mid-trunk vertebra (Vb-1041).

Type locality: Wadi Abu Hashim, Sudan.

Horizon: Wadi Abu Hashim Member of Wadi Milk Formation; Cenomanian.

Etymology: from Al Afaa, classical Arabic name for all snakes.

Referred material: 12 trunk vertebrae (Vb-1042 to Vb-1053) and one caudal vertebra (Vb-1054).

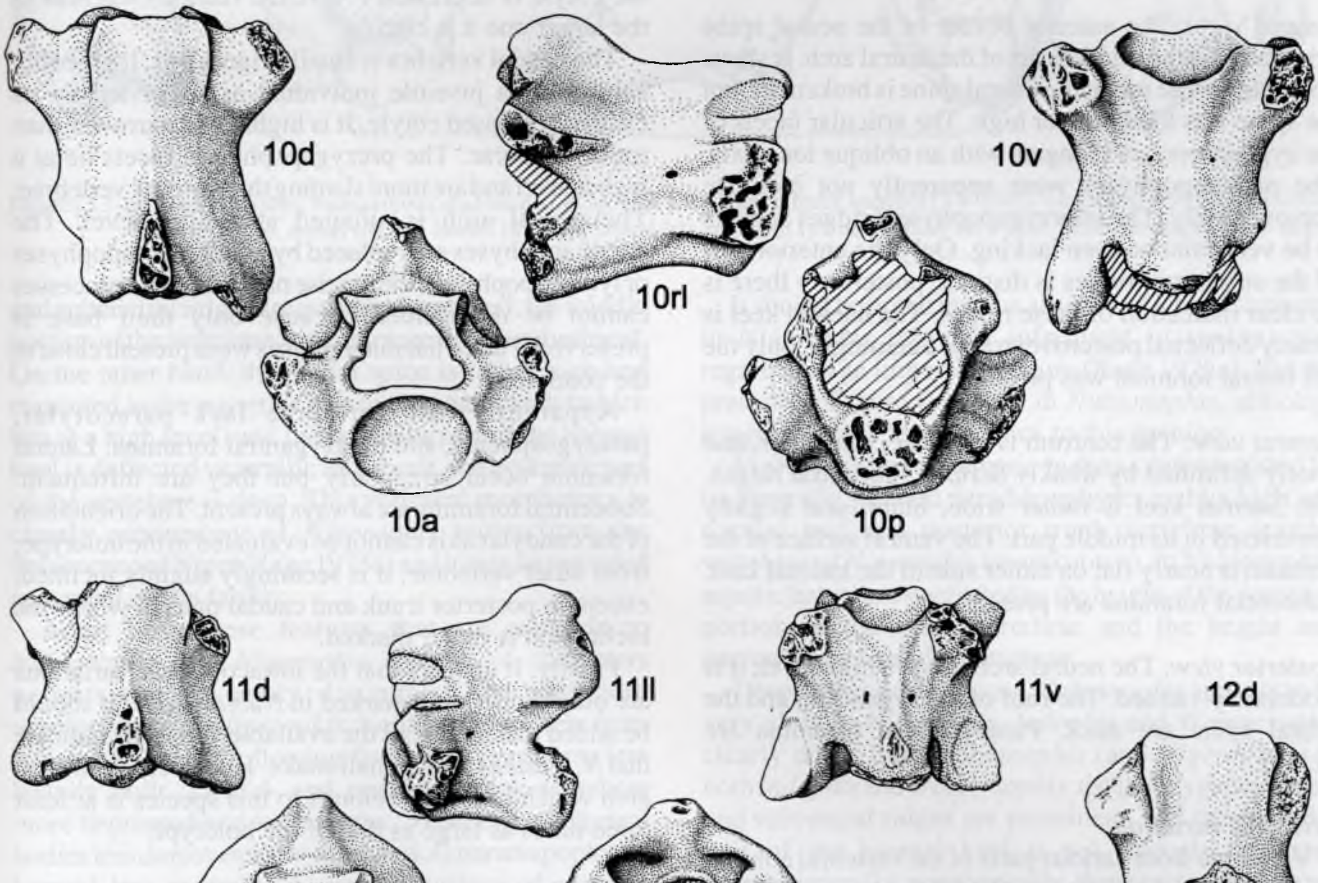
Diagnosis: Snake displaying the unique combination of vertebral features found in *Nigerophis mirus*: interzygapophyseal ridges faint or lacking, subcentral ridges weak, neural spine rather high and restricted to the posterior part of the neural arch, posterior part of the haemal keel deflected ventrally, neural arch lying at a high level. It differs from *N. mirus*, the only other certain nigerophiid, by the following characters: vertebrae more lightly constructed, more depressed and less narrow; prezygapophyseal body less extended dorsoventrally; paradiapophyses situated more dorsally; section of centrum non-subtriangular; ventral surface of centrum weakly bounded laterally; lateral foramina sometimes present; absence of any trace of keel above the postzygapophyses of anterior vertebrae.

Description of the holotype.

The holotype is a mid-trunk vertebra which lacks the tip of each prezygapophysis, the left postzygapophysis, the top of the neural spine, and in which the paradiapophyses and the condyle are eroded. Within the set of available vertebrae, it ranks among the medium-sized ones.

Measurements: width of zygosphene, 1.7 mm; width of interzygapophyseal constriction, 2.4 mm; horizontal diameter of cotyle, 1.5 mm.

Anterior view. The vertebra appears moderately high and narrow. The zygosphene is wide and thin; its anterior edge is nearly straight but its roof bulges slightly dorsally. The zygosphenal centre lies in the



Figures 10-12. Nigerophiidae, *Nubianophis afaahus* gen. et sp. nov. 10: mid-trunk vertebra, Holotype (Vb-1041). 11: anterior trunk vertebra (Vb-1042). 12: mid-trunk vertebra showing a complete zygosphene, dorsal view (Vb-1044). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bar represents 5 mm.

ventral part of the cotyle, close to the ventral border. The section of the neural canal is broad, nearly as wide as the zygosphene, and trifoliate. The cotyle is depressed and as wide as the neural canal. The zygapophyseal facets are inclined above the horizontal; the level of the facets lies above the floor of the neural canal (at about one quarter or one third of the height of the canal). The depressions between the cotyle and each prezygapophysis are rather deep; they lack paracotylar foramina.

Dorsal view: The vertebra is elongate. The interzygapophyseal constriction is rather shallow and asymmetrical (its maximun depth is shifted anteriorly). The roof of the zygosphene is rather wide; its anterior border appears to be sinuous, caused by erosion. None of the prezygapophyseal facets is fully preserved. They were apparently narrow and their long axis was oblique, at approximately 55° to the vertebral axis. The neural spine occupies only the posterior half of the neural arch; it is thick posteriorly. The posterior edge of the neural spine fills a narrow median notch in the posterior border of the neural arch; as a result, the vertebra appears to lack such a notch.

Lateral view: The anterior border of the neural spine originates on the middle part of the neural arch. It slants posteriorly. The top of the neural spine is broken off, but the spine was likely rather high. The articular facets of the zygosphene are elongate with an oblique long axis. The paradiapophyses were apparently not elongate dorsoventrally. The interzygapophyseal ridges appears to be very faint or even lacking. Only the anterior part of the subcentral ridges is distinct; posteriorly there is no clear indication of these ridges. The haemal keel is clearly deflected posteroventrally. Seemingly, only the left lateral foramen was present.

Ventral view: The centrum is elongate, triangular, and poorly delimited by weakly defined subcentral ridges. The haemal keel is rather wide, blunt, and slightly constricted in its middle part. The ventral surface of the centrum is nearly flat on either side of the haemal keel. Subcentral foramina are present.

Posterior view: The neural arch lies at a high level; it is moderately vaulted. The roof of the zygantrum and the neural spine are thick. Parazygantral foramina are lacking.

Vertebral variation.

Vertebrae from various parts of the vertebral column are known. Two anterior trunk vertebrae are available. The most anterior one (Vb-1042) is clearly shorter than those of the mid-trunk region (the latter are exemplified by the holotype); it also appears to be slightly higher and narrower. The neural arch is more vaulted than that of mid-trunk vertebrae. The condyle is circular. The zygapophyseal level and the slant of the zygapophyseal facets are similar to those in the mid-trunk region. The neural spine is broken and its height cannot be evaluated; as in the middle part of the trunk, it is restricted to the posterior area of the neural arch. The centrum is markedly shorter than that of mid-trunk vertebrae. A rather deep haemal keel extends from the cotyle to the condyle; its posterior part is broken off; a hypapophysis may have been present.

The other anterior trunk vertebra (Vb-1043) is only slightly shorter than those from the mid-trunk region. The haemal keel is deflected posteroventrally and its posterior part projects markedly ventrally, but it does not form a hypapophysis. The other characteristics of this vertebra are similar to those of Vb-1042.

No noticeable variation occurs among mid-trunk vertebrae. Their morphology corresponds to that of the holotype. In only one of them, the anterior border of the zygosphene is well preserved (while it is eroded in the holotype). It forms three lobes which protrude only slightly anteriorly (Figure 12).

In the two known posterior trunk vertebrae, the haemal keel is more clearly outlined and more salient than in mid-trunk vertebrae (Figure 13v). The neural arch is approximately as depressed as that of mid-trunk vertebrae. It should be noted that in the smaller vertebra the cotyle is depressed (?juvenile feature) whereas in the larger one it is circular.

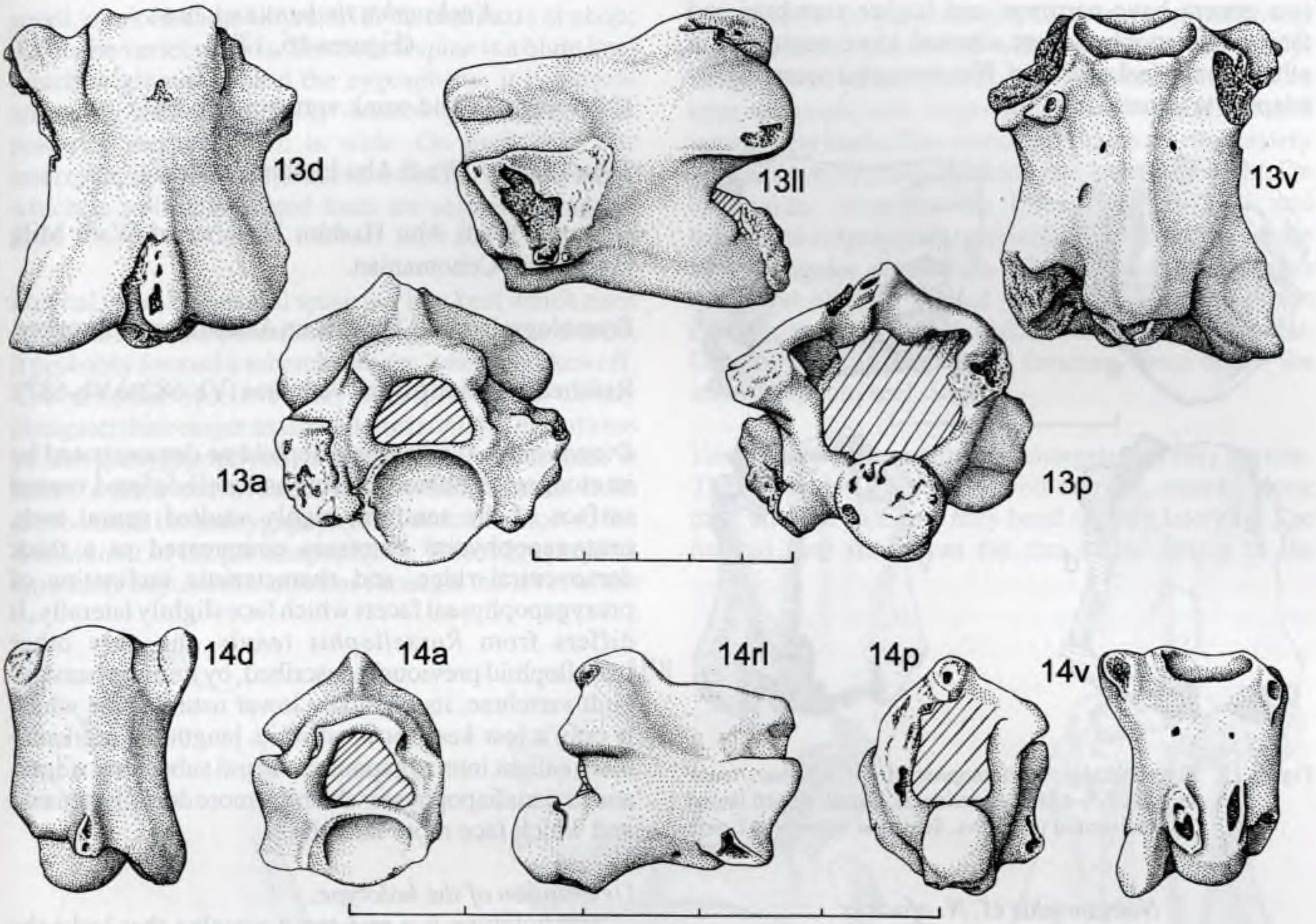
The caudal vertebra is small (Figure 14). It probably belongs to a juvenile individual as suggested by its clearly depressed cotyle. It is higher and narrower than trunk vertebrae. The prezygapophyseal facets lie at a higher level and are more slanting than in trunk vertebrae. The neural arch is situated at a high level. The paradiapophyses are replaced by either pleurapophyses or lymphapophyses; the precise nature of these processes cannot be determined because only their base is preserved. Paired haemapophyses were present close to the condyle.

Apparently, all vertebrae lack paracotylar, parazygosphenal, and parazygantral foramina. Lateral foramina occur irregularly but they are infrequent. Subcentral foramina are always present. The orientation of the condylar axis cannot be evaluated in the holotype; from other vertebrae, it is seemingly slightly inclined, except in posterior trunk and caudal ones in which the inclination is rather marked.

Finally, it appears that the intracolumnar variations are only moderately marked in *Nubianophis*. It should be added that nearly all the available vertebrae indicate that *N. afaahus* was a small snake. However, one neural arch which probably belongs to this species is at least three times as large as that of the holotype.

Discussion.

The vertebrae of *Nubianophis afaahus* display a very peculiar morphology: they are elongate, the interzygapophyseal ridges are faint or absent, the subcentral ridges are weak, the neural spine is restricted to the posterior part of the neural arch, the haemal keel is markedly deflected posteroventrally, and the neural arch is situated at a high level. As the interzygapophyseal



Figures 13-14. Nigerophiidae, *Nubianophis afaahus* gen. et sp. nov. 13: posterior trunk vertebra (Vb-1045). 14: caudal vertebra (Vb-1054). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 5 mm.

and subcentral ridges are not clearly marked, the middle portion of the vertebrae appears more or less cylindrical. On the other hand, the neural spine is rather high and restricted to the posterior part of the neural arch (which lies at a high level) and the posterior part of the haemal keel is deflected ventrally; as a result, the posterior part of the vertebrae is deep. This vertebral morphology is clearly reminiscent of *Nigerophis mirus* from the Palaeocene of Niger (Rage 1975a) and it may be regarded as typical of the family.

Apart from these features that are common to *Nubianophis* and *Nigerophis*, a suite of characters permits one to easily distinguish the Sudanese nigerophiid from *Nigerophis*. *Nubianophis* differs from *Nigerophis* by the following features: 1) vertebrae less heavily built, 2) mid- and posterior trunk vertebrae more depressed and less narrow, 3) prezygapophyseal bodies less dorsoventrally extended, 4) paradiapophyses located less ventrally, 5) ventral surface of centrum better delimited laterally (although poorly delimited), 6) section of centrum not subtriangular, 7) lateral foramina irregularly present, 8) incipient pterapophyses (= weak keels) absent above postzygapophyses of anterior vertebrae, and 9) posterior trunk vertebrae not markedly compressed laterally.

It should be noted that the absence of lateral foramina in *Nigerophis* (absence infrequent in snakes) was regarded as an important feature (Rage 1975a). But the presence of these foramina in *Nubianophis*, although irregular, lends less credence to this opinion.

Nigerophis was an aquatic snake as demonstrated by its ventrally situated paradiapophyses and its high and narrow mid and posterior trunk vertebrae (caudal vertebrae of *Nigerophis* are unknown). In *Nubianophis*, aquatic habits are suggested by the height of the posterior portion of the trunk vertebrae and the height and narrowness of caudal vertebrae.

Despite these differences, *Nubianophis* appears to be very close to *Nigerophis*. *Indophis* and *Woutersophis* clearly differ from *Nubianophis* (and *Nigerophis*). In both *Indophis* and *Woutersophis*, the interzygapophyseal and subcentral ridges are prominent, and the posterior part of the haemal keel is not strongly deflected posteroventrally; consequently, these two snakes do not display the morphology that is so characteristic of *Nubianophis* and *Nigerophis*, and which is characteristic of the Nigerophiidae. Apart from these features, which are perhaps significant at the family level, other characters markedly distinguish *Nubianophis* from *Indophis* and *Woutersophis*. More specifically, the latter two genera have narrower and higher vertebrae and their paradiapophyses are situated more ventrally; in other words *Indophis* and *Woutersophis* were highly adapted to aquatic life.

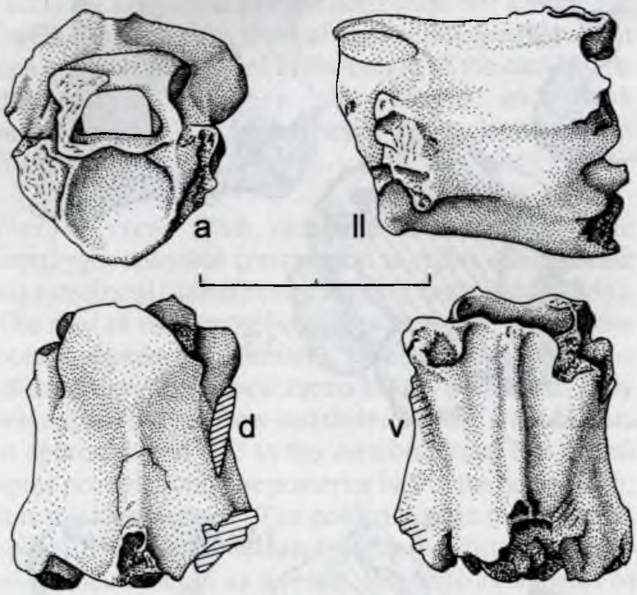


Figure 15. Nigerophiidae, *Nubianophis* cf. *N. afaahus*, trunk vertebra (Vb-1055). Anterior (a), dorsal (d), left lateral (ll), and ventral (v) views. Scale bar represents 2 mm.

Nubianophis cf. *N. afaahus*
(Figure 15)

Referred material: one vertebra (Vb-1055).

One vertebra is fairly similar to those of *Nubianophis afaahus*, but its interzygapophyseal ridges appear to be more prominent, its condyle and cotyle are wider, and its neural canal is smaller than in typical vertebrae of this species. This specimen cannot be confidently referred to *N. afaahus*.

Colubroidea Oppel, 1811

The Colubroidea are considered to be the most advanced snakes. Extant colubroids comprise the Colubridae, Atractaspididae, Elapidae, and Viperidae. Two extinct families, the Anomalophiidae and Russellophiidae, belong to the Colubroidea.

Russellophiidae Rage, 1978

The Russellophiidae, a small family, were hitherto known only in the Palaeogene. They are represented at Wadi Abu Hashim by a new taxon.

Krebsophis gen. nov.

Type species: *Krebsophis thobanus* sp. nov.

Etymology: named in honor of Prof. Dr. Bernard Krebs, Free University of Berlin.

Diagnosis: as for the type species and only known species.

Krebsophis thobanus sp. nov.
(Figures 16, 17)

Holotype: one mid-trunk vertebra (Vb-681).

Type locality: Wadi Abu Hashim, Sudan.

Horizon: Wadi Abu Hashim Member of Wadi Milk Formation; Cenomanian.

Etymology: from Al Thoban, an Arabic name for snakes.

Referred material: 6 trunk vertebrae (Vb-682 to Vb-687).

Diagnosis: A typical russellophiid as demonstrated by its elongate vertebrae, narrow and well-defined ventral surface of the centrum, highly vaulted neural arch, prezygapophyseal butresses compressed as a thick dorsoventral ridge, and characteristic inclination of prezygapophyseal facets which face slightly laterally. It differs from *Russellophis tenuis*, the only other russellophiid previously described, by its more heavily-built vertebrae, its markedly lower neural spine which is only a low keel for most of its length, its markedly more salient interzygapophyseal and subcentral ridges, and its paradiapophyses which are more dorsally situated and which face more laterally.

Description of the holotype.

The holotype is a mid-trunk vertebra that lacks the right prezygapophysis, the left postzygapophysis, and the top of the neural spine. The vertebra is small and elongate.

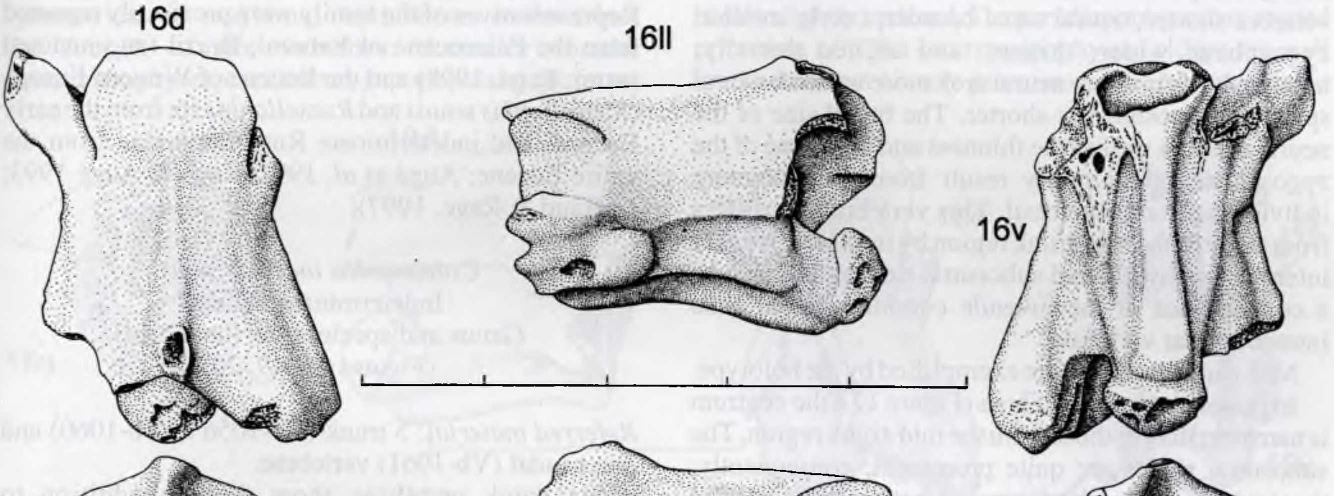
Measurements: length of centrum from rim of cotyle to tip of condyle, 2.7 mm; width of zygosphene, 1.4 mm; width of interzygapophyseal constriction, 1.7 mm; horizontal diameter of condyle, 0.9 mm.

Anterior view: The section of the neural canal is semicircular; as it is rather small, the vertebra does not appear to be lightly-built. The zygosphene is not very thick and it is dorsally flat. It is slightly wider than the cotyle, which is wider than the neural canal. The zygosphenal centre is close to the centre of the cotyle. The cotyle is circular and its rim is thick. The prezygapophyseal articular facet is slightly inclined: it faces somewhat dorsolaterally. The medial border of the facet is approximately level with the floor of the neural canal. The prezygapophysis lacks a prezygapophyseal process. The fossa between the cotyle and the remaining prezygapophysis is deep; it lacks a paracotylar foramen.

Dorsal view: The interzygapophyseal constriction is strongly asymmetrical; its maximum depth is situated quite anteriorly. The zygosphene is broad; its anterior border is convex anteriorly but this shape apparently results from the erosion of small lateral lobes. The articular facet of the remaining prezygapophysis is small, ovaloid and oblique, with its main axis at about 32° to the vertebral axis. The neural spine is a blunt keel which originates behind the zygosphene; it is narrow anteriorly and it gradually widens posteriorly. The posterior median notch is wide. On each side, the interzygapophyseal ridge forms a flat and narrow stripe which is well demarcated from the rest of the neural arch.

Lateral view: The neural spine is a low keel which rises posteriorly; in the posteriormost part of the neural arch, it probably formed a tubercle but the latter is broken off. The articular facets of the zygosphene are clearly elongate; their major axis is subhorizontal. The buttress of the prezygapophysis is somewhat compressed; it forms a thick dorsoventral ridge which extends from just beneath the prezygapophyseal articular facet to the dorsal limit of the paradiapophysis. This ridge projects anteriorly beyond the articular facet. At the level of the dorsal part of the paradiapophysis, the prezygapophyseal buttress forms a tubercle which protrudes anteriorly. The paradiapophyses are broken off. The interzygapophyseal ridges appear as well-defined and very salient keels. The subcentral ridges are moderately arched dorsally; they are thick and laterally salient. On each side, between the interzygapophyseal and subcentral ridges, the lateral wall of the vertebra appears as a triangular depression. The haemal keel is rather deep and slightly arched dorsally. The axis of the condyle appears to be horizontal or nearly horizontal. On either side, a tiny lateral foramen opens below the interzygapophyseal ridge.

Ventral view: The centrum is elongate and very narrow. The subcentral ridges are well-marked, mainly along their anterior half, and they bend slightly laterally. The haemal keel runs from the rim of the cotyle to the



Figures 16-17. Russellophiidae, *Krebsophis thobanus* gen. et sp. nov. 16: mid-trunk vertebra, Holotype (Vb-681). 17: posterior trunk vertebra (Vb-682). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 5 mm.

condyle. It is blunt, relatively wide, and clearly set off from the centrum. It is slightly constricted along its middle part. Between the haemal keel and the subcentral ridges, the surface of the centrum is depressed. The subcentral foramina cannot be confidently detected.

Posterior view: The neural arch is strongly vaulted. The posterior border of the neural arch lacks parazygantral foramina. The roof of the zygantrum and the lateral walls of the neural canal are comparatively thick.

Vertebral variation.

Anterior, mid- and posterior trunk vertebrae are known but no caudal vertebra is available.

Only one anterior trunk vertebra was found (Vb-687). It probably belongs to a juvenile individual as shown by its small size and depressed cotyle. Its prezygapophyses, paradiapophyses, and neural spine are broken off. This vertebra differs from mid-trunk vertebrae by characters that correspond to known intracolumnar variation: vertebra shorter; neural canal broader; cotyle smaller; zygosphene wider, thinner, and arched dorsally; hypapophysis present; neural arch more vaulted; neural spine anteroposteriorly shorter. The broad size of the neural canal as well as the thinness and the shape of the zygosphene might partly result from the immature individual age of this fossil. This vertebra also differs from those of the mid-trunk region by its clearly weaker interzygapophyseal and subcentral ridges; this may be a consequence of the juvenile condition rather than intracolumnar variation.

Mid-trunk vertebrae are exemplified by the holotype.

In posterior trunk vertebrae (Figure 17), the centrum is narrower than in those from the mid-trunk region. The subcentral ridges are quite prominent; consequently, the centrum is clearly depressed between the haemal keel and each subcentral ridge. The haemal keel is narrow. Between the interzygapophyseal and subcentral ridges, the lateral wall of the vertebrae appears as a deep and elongate depression.

None of the available vertebrae has a well preserved neural spine, paradiapophyses, or a zygosphene. The anterior border of the zygosphene apparently formed three lobes (a broad median lobe and two small lateral ones) but this cannot be confirmed. Two vertebrae confirm that *K. thobanus* lacks paracotylar foramina. Tiny subcentral foramina are apparently present.

Discussion.

The referral of *Krebsophis thobanus* to the Russellophiidae is clearly demonstrated by the combination of the following features: elongate vertebral form, very vaulted neural arch, peculiar slanting of the prezygapophyseal facets (facing slightly toward the outside), compression of the prezygapophyseal buttresses, narrow and well delimited ventral face of centrum. Previously, *Russellophis tenuis* was the only named species allocated to this family (Rage 1975b, 1984).

The vertebral morphology diagnosing the Russellophiidae from other snakes is distinctive. However, within this family, *Krebsophis* may be easily distinguished from *Russellophis*. *Krebsophis* is more heavily-built: the zygosphene, the cotylar rim, the lateral walls of the vertebrae, and the roof of the zygosphene are thicker than in the Eocene taxon. The cotyle and condyle are larger than in *Russellophis*. On the other hand, in *Russellophis* the neural spine is a rather high lamina, while in *Krebsophis* it is a low keel for most of its length. Although the paradiapophyses are not preserved in *Krebsophis*, it may be inferred from the remaining parts that they were more dorsally placed and that they faced less ventrally than in *Russellophis*. The interzygapophyseal and subcentral ridges are markedly less prominent in the latter genus. These differences in vertebral morphology lead to the placement of the Sudanese species in a separate genus.

Krebsophis is the earliest Russellophiidae. Representatives of the family were previously reported from the Palaeocene of Itaboraí, Brazil (an unnamed taxon; Rage, 1998) and the Eocene of Western Europe (*Russellophis tenuis* and *Russellophis* sp. from the early Eocene, and indeterminate Russellophiidae from the entire Eocene; Augé *et al.* 1997; Rage & Augé 1993; Duffaud & Rage, 1997).

Colubroidea incertae sedis
Indeterminate family
Genus and species new (unnamed)

(Figures 18, 19, 20)

Referred material: 5 trunk (Vb-1056 to Vb-1060) and one caudal (Vb-1061) vertebrae.

Six trunk vertebrae show that, in addition to *Krebsophis thobanus*, a second colubroid snake is present. Unfortunately, these vertebrae are all incomplete. This snake represents a new taxon, but it does not seem possible to erect a new genus and species on the basis of these very poorly preserved specimens.

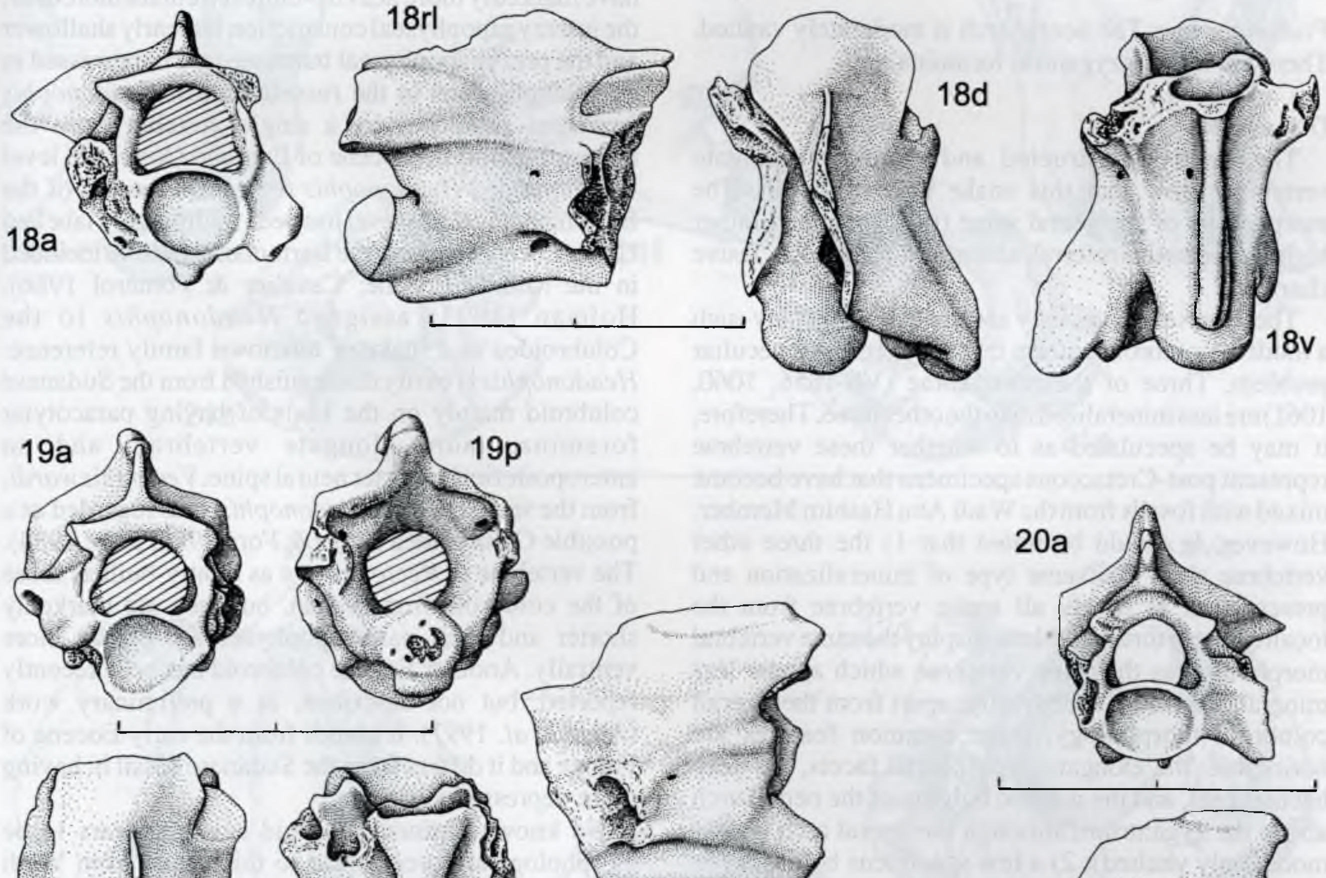
Description.

The vertebrae are lightly-built: the section of the neural canal is broad, the lateral walls of the vertebrae, the zygosphene, and the zygantral roof are thin. They are small: the width of the interzygapophyseal constriction ranges from 1.1 to 1.8 mm (the length of the centrum, from the cotylar rim to the tip of condyle, can be measured on only one vertebra: 1.8 mm).

Anterior view. The most striking feature is the size of the neural canal: its cross-section is broad or, as shown by two vertebrae, very broad as in certain modern colubroids. The zygosphene is thin. It is wider than the cotyle (clearly wider in the most anterior vertebrae, slightly wider in posterior ones). Its roof slightly arches dorsally (it is more convex in the caudal vertebra). The cotyle is circular to slightly depressed, small in the most anterior vertebra, broader in the other specimens. None of the specimens retains a fully preserved prezygapophysis. On the most complete prezygapophysis (Vb-1056), the small preserved part of the articular facet is hardly inclined above the horizontal (Figure 19a); the inclination, if any, is different from that in the Russellophiidae: the facet would face slightly dorsomedially as in practically all snakes in which the facets are not horizontal. The level of the facet lies above the floor of the neural canal, at about one-third of the height of the canal. The precise shape of the prezygapophyseal buttress cannot be determined; however, the remaining parts of the buttress (observable on two vertebrae) show that it was probably not compressed. The paradiapophyses faced ventrolaterally. In the caudal vertebra, the paradiapophyses are replaced by either lymphapophyses or pleurapophyses (Figure 20). Paracotylar foramina are lacking.

Dorsal view. The vertebrae appear elongate. The interzygapophyseal constriction is well-marked and symmetrical; its maximum depth occurs at about half the length of the vertebra. Anterior to the postzygapophyses, each interzygapophyseal ridge forms a narrow and flat area; anteriorly, this flat area reaches only the bottom of the interzygapophyseal constriction, whereas in *Krebsophis* it reaches the posterior limit of the prezygapophysis. The zygosphene is broad; its anterior border forms a very wide central lobe and two small lateral lobes. On the most anterior vertebra available (Vb-1057; Figure 18d), the central lobe strongly protrudes anteriorly. The neural arch swells markedly above the zygantrum. The neural spine is a thin and rather high lamina which extends from the posterior part of the zygosphenal roof to the posterior border of the neural arch. In the only posterior trunk vertebra (Vb-1056), its dorsal edge is slightly thickened; this thickening is very weak in the caudal vertebra. The median notch in the posterior border of the neural arch is shallow. The posterior part of the neural spine overhangs the notch.

Lateral view: The neural spine is comparatively high. Its anterior and posterior borders are inclined posteriorly. The zygosphenal facets are elongate and their long axis is only slightly inclined. The paradiapophyses are eroded or broken off. The interzygapophyseal ridges are well marked but not clearly prominent. The haemal keel is



Figures 18-20. Colubroidea *incertae sedis,* indeterminate family, unnamed new genus and species. 18: relatively anterior trunk vertebra (Vb-1057). 19: posterior trunk vertebra (Vb-1056). 20: caudal vertebra (Vb-1061). Anterior (a), dorsal (d), left lateral (ll), right lateral (rl), posterior (p), and ventral (v) views. Scale bars represent 2 mm.

deep; its ventral border is almost straight. In the most anterior vertebra (Vb-1057), the keel is deep even beneath the cotyle rim where it projects prominently ventrally. In the caudal vertebra, the haemal keel is replaced by paired haemapophyses. The lateral foramina occupy a rather anterior position.

Ventral view: The centrum is elongate, narrow, and rather well delimited by subcentral ridges; however, these ridges are not salient. The haemal keel is well marked off from the centrum and narrow, except in the posterior trunk vertebrae in which it is rather wide and spatulate (as defined by Auffenberg 1963). Anteriorly, the haemal keel reaches the rim of the cotyle and posteriorly it approaches the condyle. The ventral surface of the centrum is approximately flat between the haemal keel and the subcentral ridges, except in the posterior trunk vertebrae in which it is concave and forms a depression on either side of the keel. On the caudal vertebra, paired haemapophyses were present far anteriorly from the condyle (Figure 20 ll). Subcentral foramina are present but they are not visible on all vertebrae.

Posterior view: The neural arch is moderately vaulted. There are no parazygantral foramina.

Discussion.

The lightly constructed and relatively elongate vertebrae show that this snake is a colubroid. The morphology of the neural spine (thin, long, and rather high) supports this referral, although it is not a conclusive character.

These vertebrae, as they are preserved, display such a modern colubroid pattern that they present a peculiar problem. Three of these vertebrae (Vb-1056, 1060, 1061) are less mineralized than the other three. Therefore, it may be speculated as to whether these vertebrae represent post-Cretaceous specimens that have become mixed with fossils from the Wadi Abu Hashim Member. However, it should be noted that 1) the three other vertebrae show the same type of mineralization and preservation as nearly all snake vertebrae from the locality; these three vertebrae display the same vertebral morphology as the three vertebrae which appear less mineralized (more specifically, apart from the overall colubroid morphology, three common features are noticeable: the elongate zygosphenal facets, the deep haemal keel, and the marked bulging of the neural arch above the zygantrum, although the neural arch is only moderately vaulted); 2) a few specimens belonging to other taxa also show a mineralization similar to that of Vb-1056, 1060, 1061; 3) the lack of paracotylar foramina demonstrates that these six vertebrae do not belong to a modern colubroid. Therefore, it is concluded that the six vertebrae belong to the same Cenomanian form.

The lack of well preserved prezygapophyses prevents comparisons with all colubroid taxa. For example, the overall morphology of this fossil is clearly reminiscent of the Colubridae: as the specimens are preserved, only the absence of paracotylar foramina argues against their referral to this family. The Colubridae range from the late Eocene to the Present (Rage *et al.* 1992). The presence of Colubridae in the middle part of the Cretaceous would be very surprising. Only vertebrae with well-preserved prezygapophyses might permit identification at family level of this colubroid from Sudan.

This snake from Wadi Abu Hashim may be also compared with other extinct Colubroidea: Anomalophiidae, Russellophiidae, *Headonophis*, *Vectophis*. Except the russellophiid *Krebsophis,* all these colubroids come from the Eocene. Although it was indicated in the preliminary report that this colubroid from Sudan might be referred to the Russellophiidae (Werner & Rage 1994: 250), such an assignment should be discarded. This colubroid from Wadi Abu Hashim clearly differs from the Russellophiidae by its notably less vaulted neural arch, normal inclination of prezygapophyseal facets, and probably non-compressed prezygapophyseal buttresses. The Anomalophiidae, represented only by *Anomalophis bolcensis* from the early Eocene of Italy (Auffenberg 1959; Rage 1984), have markedly more heavily-built vertebrae; moreover, the interzygapophyseal constriction is clearly shallower and the prezygapophyseal buttresses are compressed in anomalophiids as in the russellophiids. *Headonophis harrisoni* is known by a single vertebra from the uppermost Middle Eocene of England (*Note:* the level which yielded *Headonophis* represents the top of the Bartonian stage; this level has been traditionally labelled Upper Eocene, but now the Bartonian should be included in the Middle Eocene; Cavelier & Pomerol 1986). Holman (1993) assigned *Headonophis* to the Colubroidea as a snake of unknown family reference. *Headonophis* is easily distinguished from the Sudanese colubroid mainly on the basis of having paracotylar foramina, more elongate vertebrae, and an anteroposteriorly shorter neural spine. *Vectophis wardi*, from the same beds as *Headonophis*, was regarded as a possible Colubroidea (Rage & Ford 1980; Rage 1984). The vertebrae of *Vectophis* are as lightly-built as those of the colubroid from Sudan, but they are markedly shorter and their paradiapophyses are placed more ventrally. Another Eocene colubroid has been recently reported, but not described, in a preliminary work (Augé *et al.* 1997). It comes from the early Eocene of France and it differs from the Sudanese fossil in having more depressed vertebrae.

No known extinct colubroid snake appears to be morphologically very close to this snake from Wadi Abu Hashim. On the other hand, a precise conclusion about its relationships within the Colubroidea cannot be reached.

This snake represents a new genus and new species, but none of the vertebrae referred to it is complete enough to be the type-specimen of a new species; as indicated above, in the present case, the absence of well-preserved prezygapophyses is especially incompatible with the erection of a new taxon. It is therefore appropriate to leave this new genus and species unnamed for the present.

Indeterminate snakes

Indeterminate snake A

(Figure 21)

Referred material: one mid-trunk vertebra (Vb-689).

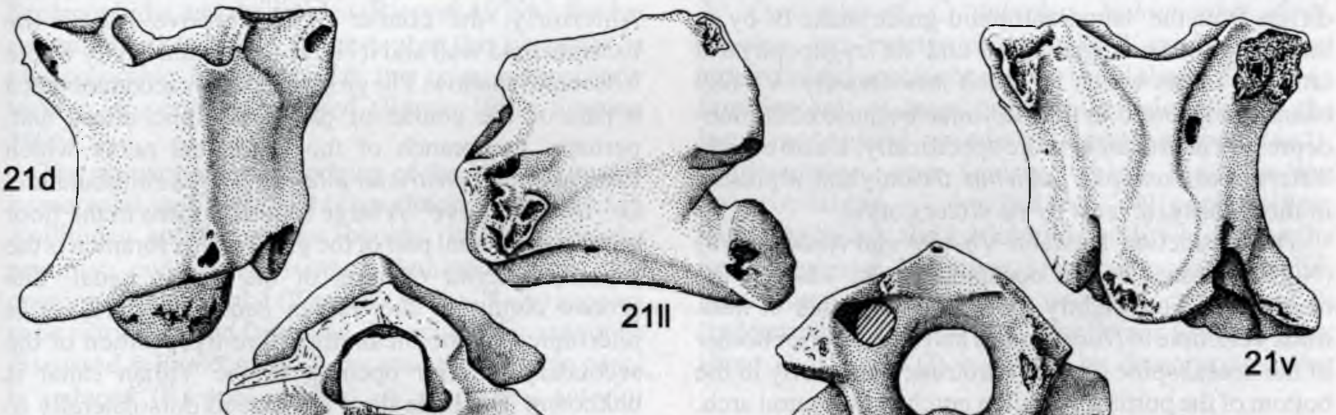
One poorly preserved vertebra cannot be identified. Because of its depressed cotyle and condyle, poorly marked interzygapophyseal and subcentral ridges, and poorly developed postzygapophyseal articular facets, it probably represents a juvenile individual.

Description.

The vertebra lacks the zygosphene, both prezygapophyses, and the right postzygapophysis. The paradiapophyses are eroded.

Measurements: length of centrum from cotylar rim to tip of condyle, 2.5 mm; width of interzygapophyseal constriction, 2.1 mm; horizontal diameter of cotyle, 1.3 mm.

The vertebra is somewhat elongate and, despite its probable juvenile stage, it is rather heavily-built. The depressed cotyle is wider than the neural canal. The size of the zygantrum suggests that the zygosphene was wider than the cotyle. On the anterior face, the depressions, on either side of the cotyle, apparently lack paracotylar foramina. The interzygapophyseal constriction is shallow. The neural spine consists of a long, low and blunt anterior keel with a shorter and higher posterior part (the full height of the latter part remains unknown). The median notch in the posterior border of the neural arch appears as a shallow and wide embayment. The interzygapophyseal and subcentral ridges are rather weak. The axis of the condyle is clearly inclined. Tiny lateral foramina are perhaps present. The



Figures 21-22. Indeterminate snakes. 21: indeterminate snake A, trunk vertebra (Vb-689). 22: Indeterminate snake B, fragmentary basiparasphenoid (Vb-690). Anterior (a), dorsal (d), left lateral (ll), posterior (p), and ventral (v) views. af: *abducens* nerve foramen, aVc: primary anterior opening of Vidian canal, dhf: dorsal hypophysial foramen, ic: internal carotid foramen, pVc: posterior opening of Vidian canal, vhf: ventral hypophysial foramen. Scale bars represent 5 mm.

ventral face of the centrum does not markedly widen anteriorly; it bears a wide and blunt haemal keel which is strongly constricted at mid-length. A very large subcentral foramen opens on the left side; the right foramen cannot be detected. The neural arch is clearly, but not strongly, vaulted. The posterior border of the neural arch lacks parazygantral foramina.

Discussion

Because of the state of preservation of Vb-689, full comparisons cannot be made. This vertebra is comparatively heavily-built, therefore it cannot be referred to the Colubroidea. The vertebrae of the Palaeophiidae display a very peculiar morphology (more specifically, presence of pterapophyses) that differs markedly from that of Vb-689. The absence of parazygantral foramina, as well as the probable lack of paracotylar foramina, are not consistent with the Madtsoiidae. Vb-689 cannot be referred to the 'lapparentophiid-grade snake A' because of the morphology of the neural spine and the shallowness of the posterior median notch in the neural arch. It clearly differs from the 'lapparentophiid-grade snake B' by its markedly wider zygosphene and its zygapophyseal articular facets which lie much less dorsally. Vb-689 cannot be referred to the Aniliidae because of its non-depressed neural arch; more specifically, it also clearly differs from *Coniophis dabiebus*, the only aniliid present in the locality, at least by its wider cotyle.

The distinction between Vb-689 and *Nubianophis* (Nigerophiidae) is less conspicuous. In Vb-689, the neural arch lies slightly more ventrally than in mid-trunk vertebrae of *Nubianophis* and the posterior border of the neural spine does not protrude posteriorly in the bottom of the posterior median notch of the neural arch. Moreover, in Vb-689 the cotyle is clearly wider and the posterior part of the haemal keel is not so deflected ventrally. The interzygapophyseal and subcentral ridges of Vb-689 are hardly more apparent than those of *Nubianophis*; but this likely results from the fact that Vb-689 probably belongs to a juvenile individual (in adults, the ridges are more marked).

Finally, vertebra Vb-689 cannot be referred to one of the above taxa identified at Wadi Abu Hashim. It represents an indeterminate snake. The presence of a unilateral very large subcentral foramen is reminiscent of the Scolecophidia, but this vertebra unquestionably belongs to the Alethinophidia as demonstrated by its overall morphology (vertebra not depressed, neural spine present, axis of zygapophyseal facets oblique...).

Indeterminate snake B
(Figure 22)

Referred material: one fragmentary basiparasphenoid (Vb-690).

This specimen is the only skull bone from the locality belonging to a snake. It is impossible to decide the proper association of this bone with the fossils described above.

Description.

Vb-690 corresponds to the posterior part of a basiparasphenoid, i.e., approximately the basisphenoid part of the bone. Anteriorly, it is missing the cultriform process. The remnant is almost hexagonal.

The dorsal face bears a deep, circular, and well defined *sella turcica* (= hypophyseal, or pituitary, fossa). The wall of the *sella turcica* is subvertical and higher along the posterior half of this fossa than along the anterior half. Posteriorly, this wall is pierced by two foramina for the internal carotids (= cerebral carotids). Anteriorly, a sagittal foramen opens at the base of the wall; this foramen is the hypophysial foramen (Scanlon 1996), awkwardly named cerebral foramen by Barrie (1990) (this foramen is not the cerebral foramen of Underwood 1967: 17). There is no *crista sellaris* posterior to the *sella turcica*. The anterolateral borders of the fragment are very thick; they form the uneven sutural edge for the posteroventral edges of the parietal. Each of these two thick edges is hollowed by a deep longitudinal groove that is open dorsally. The groove is located approximately dorsal to the Vidian canal. Anteriorly, the course of the groove leaves the basisphenoid wall and it enters the cranial cavity where it becomes shallow. The groove probably accommodated a part of the course of the ophthalmic artery and, perhaps, the branch of the trigeminal nerve which innervates the *constrictor internus dorsalis* musculature, i.e., the 'cid nerve'. A large foramen opens in the floor of the intracranial part of the groove; this foramen is the primary anterior opening of the Vidian canal. The groove continues the Vidian canal anteriorly; it is interrupted by the break, therefore the position of the secondary anterior opening of the Vidian canal is unknown. The bone does not extend dorsolaterally to the Vidian canal and groove, that is to say, it lacks the 'lateral wing' (= 'triangular wing'; McDowell 1967) that characterizes the living Alethinophidia (McDowell 1987). On each side, posterolaterally to the *sella turcica*, is a foramen that corresponds to the posterior opening for the *abducens* nerve; these two foramina occupy a position that is typical in snakes. Each anterior foramen for *n. abducens* is apparently located in the above-mentioned groove, i.e. posterior to the primary anterior opening of the Vidian canal.

On the ventral face, a thin sagittal keel is present. Anteriorly, just behind the level of the break, the keel widens and forms a small triangular area which extended on the missing part. A tiny foramen opens in this triangular area. As shown by the madtsoiid *Wonambi naracoortensis* (Barrie 1990), this foramen probably communicates with the hypophysial foramen of the dorsal face; here, these two foramina are labelled ventral and dorsal hypophysial foramina respectively (Figure 22v, d). In the posterior half of the remainder, two large foramina represent the posterior openings of the Vidian canals. The two Vidian canals show similar diameters. As a result of the position of these openings, the Vidian canals are not short. None of the basipterygoid processes is preserved. Obviously, the anterior part of the bone is broken off, but there is no indication of prominences anteriorly; therefore, it may be questioned whether these processes were present. On each side, a broad corrugated surface extends between the anterior border of the bone and the posterior opening of the Vidian canal. These surfaces probably correspond to the areas of insertion for *m. protractor pterygoidei.*

Discussion.

Vb-690 clearly differs from the basisphenoid of scolecophidians. In these snakes, the *sella turcica* is very close to the posterior limit of the bone and the Vidian canal is a groove (Rieppel 1979a). On the other hand, the lack of lateral wings is a feature known only in scolecophidians (McDowell 1967), Madtsoiidae (Scanlon 1996) and the late Cretaceous *Dinilysia* (Estes *et al.* 1970). According to Rieppel (1979a), it is difficult to demonstrate whether the absence of the wings is a plesiomorphic or derived character; but the above-mentioned systematic distribution argues for a primitive condition.

The absence of a *crista sellaris* characterizes the Scolecophidia and Anilioidea (Rieppel 1979b). Such a systematic distribution suggests that this character is plesiomorphic. In Madtsoiidae, this *crista* is apparently lacking or poorly developed (Barrie 1990; Scanlon 1996).

The primary anterior opening of the Vidian canal is intracranial in Vb-690. This condition is observed in Anilioidea and in various booids; it would be the primitive condition. In other alethinophidians, this opening is extracranial (Rieppel 1979b). It also appears to be extracranial in *Dinilysia.* This character cannot be discussed in Scolecophidia, because their Vidian canal is reduced (Rieppel, 1979a). A secondary anterior opening of the Vidian canal was necessarily present in Vb-690, although its location remains unknown (see above). *Dinilysia* lacks a secondary opening whereas the presence of this foramen appears to be variable in Madtsoiidae (Scanlon 1996).

The presence of hypophysial foramina was reported only in Madtsoiidae (Barrie 1990; Scanlon 1996). However, Barrie (1990) also noted the presence of such foramina in the living *Trachyboa* (Tropidophiidae), but we cannot confirm Barrie's observation; these foramina are perhaps not constant in this genus. The strong muscular insertions on the ventral surface of Vb-690 are unknown in other snakes.

This set of characters does not permit an assignment within snakes, especially given that the polarity of features exhibited by the basiparasphenoid cannot be considered as well established.

Among the snakes present in the locality, the size of Vb-690 is consistent only with that of the Madtsoiidae and 'lapparentophiid-grade snake A'. The presence of hypophysial foramina might argue for a referral to the Madtsoiidae. But differences between Vb-690 and the known madtsoiid basiparasphenoids are marked: the specimen from Sudan has broad muscular insertions on the ventral face and it perhaps lacks basipterygoid processes; however, a referral to this family cannot be definitively ruled out. On the other hand, snakes of the lapparentophiid-grade are known only by vertebrae, therefore we cannot discuss the possible referral of this basiparasphenoid to this assemblage. As a result, Vb-690 may belong to the Madtsoiidae, to a lapparentophiid-grade family, or to a still unknown family.

CONCLUSION

The Cenomanian of Wadi Abu Hashim has yielded a snake fauna that is an amazing mixture of advanced and very primitive forms (Table 2). It comprises at least nine species (perhaps 12), representing at least seven families (perhaps ten). The nine species are: 'lapparentophiid-grade snake A', 'lapparentophiid-grade snake B', an indeterminate genus and species of Madtsoiidae, an indeterminate genus and species presumably belonging to the Palaeophiidae, *Coniophis dabiebus* sp. nov. (Aniliidae), *Nubianophis afaahus* gen. et sp. nov. (Nigerophiidae), *Krebsophis thobanus* gen. et sp. nov. (Russellophiidae), an unnamed colubroid gen. et sp. nov. (indeterminate family), and 'indeterminate snake A'. *Coniophis* cf. *C. dabiebus*, *Nubianophis* cf. *N. afaahus*, and 'indeterminate snake B' might represent either distinct species or species listed above. The seven families are: at least one family belonging to the lapparentophiid grade (Lapparentophiidae?), Madtsoiidae, one family which may be the Palaeophiidae, Aniliidae, Nigerophiidae, Russellophiidae, and a colubroid family which is not the Russellophiidae. Moreover, 1) the two lapparentophiid-grade forms may belong to two distinct families, 2) 'indeterminate snake A' may also belong to a family not listed above, and 3) it cannot be demonstrated that

TABLE 2.
List of snakes from the Cenomanian of Wadi Abu Hashim, Sudan.

- Lapparentophiid-grade snakes
  - Lapparentophiid-grade snake A
  - Lapparentophiid-grade snake B
- Madtsoiidae Hoffstetter, 1961
  - Indeterminate genus and species
- ?Palaeophiidae Lydekker, 1888
  - Indeterminate genus and species
- Aniliidae Fitzinger, 1826
  - *Coniophis* Marsh, 1892
    - *Coniophis dabiebus* sp. nov.
    - *Coniophis* cf. *C. dabiebus*
- Nigerophiidae Rage, 1975
  - *Nubianophis* gen. nov.
    - *Nubianophis afaahus* sp. nov.
    - *Nubianophis* cf. *N. afaahus*
- Russellophiidae Rage, 1978
  - *Krebsophis* gen. nov.
    - *Krebsophis thobanus* sp. nov.
- Colubroidea *incertae sedis*
  - Genus and species new (unnamed)
- Indeterminate snakes
  - Indeterminate snake A
  - Indeterminate snake B

'indeterminate snake B', i.e. the basiparasphenoid, belongs to one of the above-mentioned families.

Wadi Abu Hashim has produced the earliest Madtsoiidae, Nigerophiidae, Russellophiidae, and Palaeophiidae – if the identification of the latter family proves correct. The presence of Colubroidea (Russellophiidae and an indeterminate family) was particularly unexpected. Previously, the oldest colubroids were reported from the early Eocene. However, on the basis of molecular and palaeontological data, combined with biogeography, Cadle (1988) presumed that some extant lineages of Colubroidea may have originated during the Cretaceous (without more precision) or earliest Tertiary. The presence of extinct colubroid lineages in the Cenomanian might corroborate Cadle's estimate.

The fauna includes aquatic forms (*Nubianophis afaahus* and the presumed Palaeophiidae), which is consistent with the palaeoenvironment (Bussert, 1998; see above). *Coniophis* was either fossorial or secretive. The other taxa do not show morphological traits which could indicate a peculiar mode of life.

The fossils from Wadi Abu Hashim rank among the oldest known snakes. If the fossil from the Barremian of Spain (Rage & Richter 1994) is not a snake (see above), then the oldest snake remains are only slightly older (late Albian) than those from Sudan. Astonishingly, these Sudanese snakes make up a fauna which is very rich and diverse having regard to its geological age. It is by far the earliest known snake fauna. Apart from Wadi Abu Hashim, other Cretaceous localities yielded at most three taxa represented by rare specimens (e.g., Campanian or Maastrichtian of Cerro Cuadrado, Argentina; Albino 1986). Faunas remain poor and rare in Palaeocene beds. The only rich and diverse faunas from the Palaeocene are those from Itaboraí (Middle Palaeocene, Brazil; Rage 1998) and, to a lesser degree, Adrar Mgorn (Late Palaeocene, Morocco; Gheerbrant *et al.* 1993). Rich and diverse snake faunas are relatively frequent only from the Early Eocene onwards.

From the diversity of the fauna from Wadi Abu Hashim it can be inferred that snakes have had a pre-Cenomanian history, perhaps a rather long one, in Africa. This continent played an important role in the early radiation of snakes. Moreover, if the fossil from the Barremian of Spain is not a snake, the fauna from Sudan may also suggest that Africa is the cradle of snakes, although a snake has been recently recovered from the mid-Cretaceous of North America (Gardner & Cifelli, 1999).

Three of the four higher taxa ('superfamilies') of extant Alethinophidia (Anilioidea, Acrochordoidea, Colubroidea) were therefore present as early as the Cenomanian. But the presence at that time of the fourth 'superfamily', namely the Booidea, and of the sister group of the Alethinophidia, that is the Scolecophidia, may be extrapolated from the recognized phylogenies (Rieppel 1988; Kluge 1991; Cundall *et al.* 1993; Rage 1997). Therefore, the major lineages of living snakes were individualized as early as the mid-Cretaceous. The snake fauna from the Cenomanian of Wadi Abu Hashim documents several of these lineages and thus represents a very important landmark in the history of snakes.

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REFERENCES

ALBINO, A.M. 1986. Nuevos Boidae Madtsoiinae en el Cretacico tardio de Patagonia (Formacion Los Alamitos, Rio Negro, Argentina). *Actas IV Congr. Argentino Paleontol. y Bioestratigr., Mendoza* **2,** 15-21.

-------- 1990. Las serpientes de São José de Itaboraí (Edad Itaboraiense, Paleoceno medio), Brasil. *Ameghiniana* **27,** 337-342.

ARMSTRONG-ZIEGLER, G. 1978. An aniliid snake and associated vertebrates from the Campanian of New Mexico. *J. Paleont.* **52,** 480-483.

AUFFENBERG, W. 1959. *Anomalophis bolcensis* (Massalongo), a new genus of fossil snake from the Italian Eocene. *Breviora* **114,** 1-16.

-------- 1963. The fossil snakes of Florida. *Tulane Stud. Zool.* **10,** 131-216.

AUGE, M., DUFFAUD, S., LAPPARENT de BROIN, F. de, RAGE, J.C. & VASSE, D. 1997. Les amphibiens et les reptiles de Prémontré (Cuisien, Bassin parisien): une herpétofaune de référence pour l'Eocène inférieur. *Géologie de la France* **1,** 23-33.

AWAD, M.Z. 1994. Stratigraphic, palynological and paleoecological studies in the East-Central Sudan (Khartoum and Kosti Basins), Late Jurassic to mid-Tertiary. *Berliner geowiss. Abh.,* A **161,** 1-163.

BAILON, S. 1988. Un Aniliidé (Reptilia, Serpentes) dans le Pliocène supérieur européen. *C. R. Acad. Sci. Paris,* II **306,** 1255-1258.

BARRIE, J. 1990. Skull elements and additional remains of the Pleistocene boid snake *Wonambi naracoortensis. Mem. Queensland. Mus.* **28,** 139-151.

BREITHAUPT, B.H. 1985. Nonmammalian vertebrate faunas from the late Cretaceous of Wyoming. *Wyoming Geol. Assoc. 36th Annual Field Conf. Guidebook,* 159-175.

BUSSERT, R. 1993. Evolution of Cretaceous continental basins in northern Sudan. **In:** Thorweihe, U. & Schandelmeier, H., Eds, *Geoscientific Research in Northeast Africa* 407-414. Rotterdam, Balkema.

-------- 1998. Die Entwicklung intrakratonaler Becken im Nordsudan. *Berliner geowiss. Abh.,* A **196,** 1-329.

CADLE, J.E. 1988. Phylogenetic relationships among advanced snakes. A molecular perspective. *Univ. California Publ. Zool.* **119,** 1-77.

CALDWELL, M.W. & LEE, M.S.Y. 1997. A snake with legs from the marine Cretaceous of the Middle East. *Nature* **386,** 705-709.

CAVELIER, C. & POMEROL, C. 1986. Stratigraphy of the Paleogene. *Bull. Soc. géol. Fr.* **2,** 255-265.

CUNDALL, D., WALLACH, V. & ROSSMAN, D.A. 1993. The systematic relationships of the snake genus *Anomochilus. Zool. J. Linn. Soc.* **109,** 275-299.

CUNY, G., JAEGER, J.J., MAHBOUBI, M. & RAGE, J.C. 1990. Les plus anciens Serpents (Reptilia, Squamata) connus. Mise au point sur l'âge géologiques des Serpents de la partie moyenne du Crétacé. *C. R. Acad. Sci. Paris,* II **311,** 1267-1272.

DUFFAUD, S. & RAGE, J.C. 1997. Les remplissages karstiques polyphasés (Eocène, Oligocène, Pliocène) de Saint-Maximin (Phosphorites du Gard) et leur apport à la connaissance des faunes européennes, notamment pour l'Eocène moyen (MP 13). 2.- Systématique: Amphibiens et Reptiles. **In:** Aguilar, J.P., Legendre, S. & Michaux, J., Eds, *Actes du Congrès BiochroM'97. Mém. Trav. E.P.H.E., Inst. Montpellier* **21,** 729-735.

ESTES, R. 1976. Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana. *J. Paleontol.* **50,** 500-520.

--------, FRAZZETTA, T.H. & WILLIAMS, E.E. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward: Part I. Cranial morphology. *Bull. Mus. Comp. Zool.* **140,** 25-73.

EVANS, S.E., MILNER, A.R. & WERNER, C. 1996. Sirenid salamanders and a gymnophionan amphibian from the Cretaceous of the Sudan. *Palaeontology* **39,** 77-95.

FOX, R. 1975. Fossil snakes from the Upper Milk River Formation (Upper Cretaceous), Alberta. *Canadian J. Earth Sci.* **12,** 1557-1563.

GARDNER, J.D. & CIFELLI, R.L. (1999). A primitive snake from the Cretaceous of Utah. *Special papers in Palaeontology* **60,** 87-100

GASC, J.P. 1974. L'interprétation fonctionnelle de l'appareil musculo-squelettique de l'axe vertébral chez les serpents (Reptilia). *Mém. Mus. natn. Hist. nat.*, A **83,** 1-182.

GAYET, M., MEUNIER, F.J. & WERNER, C. 1997a. Strange polypteriforms from the Cretaceous of In Becetem (Niger) and Wadi Milk Formation (Sudan). *Geobios* **20,** 249-255.

-------- , --------- , & --------- . 1997b. Maastrichtian Polypteriformes of South America and their African affinities. *Gaea heidelbergensis* **3,** 141.

GHEERBRANT, E., CAPPETTA, H., FEIST, M., JAEGER, J.J., SUDRE, J., VIANEY-LIAUD, M. & SIGÉ, B. 1993. La succession des faunes de vertébrés d'âge paléocène supérieur et éocène inférieur dans le bassin d'Ouarzazate, Maroc. Contexte géologique, portée biostratigraphique et paléogéographique. *Newsl. Stratigr.* **28,** 35-58.

GILMORE, C.W. 1938. Fossil snakes of North America. *Geol. Soc. Amer.*, special paper **9,** 1-96.

GLOY, U. 1997. *Eine Dipnoifauna aus der unteren Oberkreide des Sudan.* Unpublished dipl.thesis, Dept. of Palaeontology, Free University, Berlin.

HECHT, M.K. 1959. Amphibians and Reptiles. **In:** McGrew, P.O., Ed., *the Geology and Paleontology of the Elk Mountain and Tabernacle Butte Area, Wyoming. Bull. Amer. Mus. nat. Hist.* **117,** 130-146.

-------- 1982. The vertebral morphology of the Cretaceous snake, *Dinilysia patagonica* Woodward. *N. Jb. Geol. Paläont. Mh.* **9,** 523-532.

HOFFSTETTER, R. 1955. Squamates de type moderne. **In:** Piveteau, J., Ed., *Traité de Paléontologie* **5,** 606-662. Paris, Masson.

-------- 1959. Un serpent terrestre dans le Crétacé inférieur du Sahara. *Bull. Soc. géol. Fr.* **1,** 897-902.

-------- 1961. Nouveaux restes d'un serpent boïdé (*Madtsoia madagascariensis* nov. sp.) dans le Crétacé supérieur de Madagascar. *Bull. Mus. natn. Hist. nat.* **33,** 152-160.

-------- & RAGE, J.C. 1977. Le gisement de vertébrés miocènes de La Venta (Colombie) et sa faune de serpents. *Ann. Paléontol.* **63,** 161-190.

HOLMAN, J.A. 1979. Paleontology and geology of the Badwater Creek area, Central Wyoming. Part 17. The late Eocene snakes. *Ann. Carnegie Mus.* **48,** 103-110.

-------- 1993. A new genus of primitive colubroid snake from the Upper Eocene, Isle of Wight, England. *Tertiary Research* **14,** 151-154.

JANENSCH, W. 1906. Über *Archaeophis proavus* Mass., eine Schlange aus dem Eocän des Monte Bolca. *Beitr. Pal. Oster.-Ungarns* **19,** 1-33.

KLUGE, A.G. 1991. Boine snake phylogeny and research cycles. *Misc. Publ., Mus. Zool., Univ. Michigan* **178,** 1-58.

MARSH, O.C. 1892. Notice of new reptiles from the Laramie formation. *Amer. J. Sci.*, ser. 3 **43,** 449-453.

McDOWELL, S.B. 1967. Osteology of the Typhlopidae and Leptotyphlopidae: a critical review. *Copeia* 1967, 686-692.

-------- 1975. A catalogue of the snakes of New Guinea and the Solomons ... Part II. Anilioidea and Pythoninae. *J. Herpetol.* **9,** 1-80.

-------- 1987. Systematics. **In:** Seigel, R.A., Collins, J.T. & Novak, S.S., Eds., *Snakes. Ecology, and Evolutionary Biology*, 3-50. New York, McMillan.

NESSOV, L.A. & UDOVITSCHENKO, N.I. 1984. Sea snakes and cartilaginous fishes of the Paleogene of South Kazakhstan. *Paleont. Sbornik* **21,** 69-74 (in Russian).

NOPCSA, F. 1923. Die Familien der Reptilien. *Fortsch. Geol. Palaeont.* **2,** 1-210.

RAGE, J.C. 1974. Les serpents des Phosphorites du Quercy. *Palaeovertebrata* **6,** 274-303.

-------- 1975a. Un serpent du Paléocène du Niger. Etude préliminaire sur l'origine des Caenophidiens (Reptilia, Serpentes). *C. R. Acad. Sci. Paris*, D **281,** 515-518.

-------- 1975b. Un Caenophidien primitif (Reptilia, Serpentes) dans l'Eocène inférieur. *C. R. som. Soc. géol. Fr.* **2,** 46-47.

-------- 1980. Un serpent marin nouveau de l'Eocène de Belgique. Le problème des serpents marins du Paléogène. *C. R. Acad. Sci. Paris* D **291,** 469-471.

-------- 1984. Serpentes. *Encyclopedia of Paleoherpetology*, part 11. Stuttgart, Gustav Fischer Verlag.

-------- 1987. Fossil History. **In:** Seigel, R.A., Collins, J.T. & Novak, S.S., Eds, *Snakes: Ecology, and Evolutionary Biology* 51-76. New York, McMillan.

-------- 1988a. Un serpent primitif (Reptilia, Squamata) dans le Cénomanien (base du Crétacé supérieur). *C. R. Acad. Sci. Paris*, II **307,** 1027-1032.

-------- 1988b. Le gisement du Bretou (phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de Vertébrés de l'Eocène supérieur. I. Amphibiens et Reptiles. *Palaeontographica* A **205,** 3-27.

-------- 1991. Squamate reptiles from the early Paleocene of Tiupampa area (Santa Lucía Formation), Bolivia. **In:** Suarez-Soruco, R., Ed., *Fosiles y Facies de Bolivia. vol. I. Vertebrados. Rev. Técnica YPFB* **12,** 503-508.

-------- 1997. Phylogeny and origin of snakes. **In:** Rocek, Z. & Scott, H., Eds, *Herpetology' 97, 3rd World Congress of Herpetology*, 167. Prague, Abstract Volume.

-------- 1998. Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part I. Madtsoiidae, Aniliidae. *Palaeovertebrata* **27,** 109-144.

-------- & AUGE, M. 1993. Squamates from the Cainozoic of the Western part of Europe. A review. *Rev. Paléobiol.*, vol. sp. **7,** 199-216.

--------, BUFFETAUT, E., BUFFETAUT-TONG, H., CHAIMANEE, Y., DUCROCQ, S., JAEGER, J.J. & SUTEETHORN, V. 1992. A colubrid snake in the late Eocene of Thailand: The oldest known Colubridae (Reptilia, Serpentes). *C. R. Acad. Sci. Paris*, II **314,** 1085-1089.

-------- & FORD, R.L.E. 1980. Amphibians and squamates from the Upper Eocene of the Isle of Wight. *Tertiary Research* **3,** 47-60.

-------- & PRASAD, G.V.R. 1992. New snakes from the late Cretaceous (Maastrichtian) of Naskal, India. *N. Jb. Geol. Paläont. Abh.* **187,** 83-97.

-------- & RICHTER, A. 1994. A snake from the Lower Cretaceous (Barremian) of Spain: The oldest known snake. *N. Jb. Geol. Paläont. Mh.* 1994, 561-565.

-------- & WOUTERS, G. 1979. Découverte du plus ancien Palaeopheidé (Reptilia, Serpentes) dans le Maestrichtien du Maroc. *Geobios* **12,** 293-296.

RAUHUT O.W.M. 1995. *Eine Dinosaurierfauna aus der mittleren Kreide (Alb-Cenoman) des nördlichen Sudan.* Unpublished dipl. thesis. Dept. of Palaeontology, Free University, Berlin.

-------- (1999). A dinosaur fauna from the upper Cretaceous (Cenomanian) of Northern Sudan. *Palaeontologia africana* **35,** 61-84.

-------- & WERNER, C. 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläont. Z.* **69,** 475-489.

RIEPPEL, O. 1979a. The braincase of *Typhlops* and *Leptotyphlops* (Reptilia: Serpentes). *Zool. J. Lin. Soc.* **65,** 161-176.

-------- 1979b. The evolution of the basicranium in the Henophidia (Reptilia: Serpentes). *Zool. J. Lin. Soc.* **66,** 411-431.

-------- 1988. A review of the origin of snakes. **In:** Hecht, M.K., Wallace, B. & Prance, G.T., Eds, *Evolutionary Biology* **22,** 37-130. New York, Plenum Press.

SCANLON, J.D. 1994. The phylogenetic position of the Madtsoiidae (Serpentes). *2nd World Congr. Herpetology* 230-231. Adelaide, Abstract vol..

-------- 1996. *Studies in the palaeontology and systematics of Australian snakes.* Unpublished PhD thesis, University of New South Wales, Sydney.

-------- 1997. *Nanowana* gen. nov., small madtsoiid snakes from the Miocene of Riversleigh: sympatric species with divergently specialised dentition. *Mem. Queensland Mus.* **41,** 393-412.

SCHRANK, E. 1990. Palynology of the clastic Cretaceous sediments between Dongola and and Wadi Muqaddam, Northern Sudan. *Berliner geowiss. Abh.* A **120.1,** 149-168.

-------- & AWAD, M.Z. 1990. Palynological evidence for the age and depositional environment of the Cretaceous Omdurman Formation in the Khartoum area, Sudan. *Berliner geowiss. Abh.* A **120.1,** 169-182.

SERENO, P.C., DUTHEIL, D.B., IAROCHENE, M., LARSSON, H.C.E., LYON, G.H., MAGWENE, P.M., SIDOR, C.A., VARRICHIO, D.J. & WILSON, J.A. 1996. Predatory dinosaurs from the Sahara and late Cretaceous fauna differentiation. *Science* **272,** 986-991.

SZYNDLAR, Z. 1994. Oligocene snakes of southern Germany. *J. Vertebr. Paleontol.* **14,** 24-37.

-------- & SCHLEICH, H.H. 1993. Description of Miocene snakes from Peterbuch 2 with comments on the Lower and Middle Miocene ophidian faunas of southern Germany. *Stuttgarter Beitr. Naturk.*, B **192,** 1-47.

TATARINOV, L.P. 1963. The first occurrence in the USSR of ancient sea snakes. *Paleont. Zh.* **2,** 109-115 (in Russian).

-------- 1988. The cranial structure of the lower Eocene sea snake "*Archaeophis*" *turkmenicus* from Turkmenia. *Paleont. Journ.* (translation of *Paleont. Zhurn.*) **22,** 73-79.

UNDERWOOD, G. 1967. *A Contribution to the Classification of Snakes.* London, Brit. Mus. (N.H.), publ. n° 653.

WERNER, C. 1994a. Die kontinentale Wirbeltierfauna aus der unteren Oberkreide des Sudan (Wadi Milk Formation). *Berliner geowiss. Abh,* E **13,** 221-249.

-------- 1994b. Der erste Nachweis von Gymnophionen (Amphibia) in der Kreide (Wadi Milk Formation, Sudan). *N. Jb. Geol. Paläont. Mh.* 1994, 633-640.

-------- & GAYET, M. 1997. New fossil polypterids from the Cenomanian of Sudan. An evidence of their high diversity in the early Late Cretaceous. *Cybium* **21,** 67-81.

-------- & RAGE, J.C. 1994. Mid-Cretaceous snakes from Sudan. A preliminary report on an unexpectedly diverse snake fauna. *C. R. Acad. Sci.* II **319,** 247-252.

WYCISK, P. 1991. Stratigraphic update of the nonmarine Cretaceous from SW Egypt and NW Sudan. *Cretaceous Research* **12,** 185-200.