

The Cenomanian: stage of hindlimbed snakes

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Abstract: Three "snakes with legs" are known: *Pachyrhachis problematicus*, *Haasiophis terrasanctus* and *Eupodophis descouensi*. They have short posterior limbs but lack an anterior girdle and forelimbs. Moreover, *Pachyophis woodwardi*, *Mesophis nopcsai* and *Simoliophis* ssp. appear to be closely related to the hindlimbed taxa; consequently, although the presence of posterior limbs has not been demonstrated for these genera, it is presumed that they too were hindlimbed. All these snakes have been recovered only from the Cenomanian. Moreover, these six genera come from a restricted area (western Europe and northwesternmost Africa to the Middle East). This limited geographic range suggests that snakes might have originated in the "Mediterranean" part of the Tethys, but the restricted stratigraphical range remains unexplained.

Key Words: Cenomanian; Cretaceous; Pachyostosis; Paleogeography; Reptilia; Hindlimbed Snakes

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Résumé : *Le Cénomaniien : étage des serpents bipèdes.*- Trois serpents munis de pattes sont connus : *Pachyrhachis problematicus*, *Haasiophis terrasanctus* et *Eupodophis descouensi*. Ils possèdent des membres et une ceinture postérieurs mais n'ont ni ceinture ni membres antérieurs, c'est-à-dire qu'ils sont bipèdes. De plus, *Pachyophis woodwardi*, *Mesophis nopcsai* et *Simoliophis* ssp. semblent être étroitement apparentés aux serpents bipèdes ; par conséquent, bien que des membres postérieurs n'aient pas été mis en évidence chez eux, il est supposé qu'ils étaient aussi bipèdes. Tous les serpents bipèdes et ceux qui sont supposés l'avoir été ont été trouvés dans le Cénomaniien seulement. De plus, ces six genres proviennent d'une aire géographique réduite (de l'Europe occidentale et Afrique du nord-ouest au Moyen-Orient). Cette répartition géographique limitée suggère que les serpents sont nés dans la partie "méditerranéenne" de la Téthys, mais la distribution stratigraphique restreinte reste inexpliquée.

Mots-Clefs : Cénomaniien ; Crétacé ; Paléogéographie ; Reptiles ; Serpents bipèdes

I - Introduction

That snakes are tetrapods was established long ago. Furthermore, the representatives of most existing families have vestiges of a pelvic girdle and posterior limbs. However, in all modern snakes the pelvic girdle, if indeed present, has lost all bone-to-bone contact with the vertebral column. The limb is but a single very small bone that logically is considered to represent the femur. Thus the Leptotyphlopidae, several anilioids (*Anilius*, *Cylindrophis*, *Anomochilus*), the booid *Loxocemus* and the Boidae have vestiges of a pelvis and a femur. These elements are also present in the Tropicodidae *s.l.*, but only in the male. As for the Typhlopidae, they still have a pelvis but no femur. Note that there is no trace of forelimbs or an anterior girdle in snakes, living or fossil.

One might expect to find fossil snakes with limbs, but it is only recently that such fossils have been recognized or discovered. Three taxa

are unquestionably snakes with hind legs; they are known from articulated and largely complete skeletons. They represent three distinct genera. These snakes are very similar: they all have a pelvic girdle and short but well developed hind legs. Curiously, all were found in strata of Cenomanian age. So they are among the oldest snakes yet found, although some older and problematic remains are considered to be snakes (see below and Fig. 1).

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II - The oldest snakes

The oldest snakes come from the middle Cretaceous. One had been reported but not named from the Barremian of Spain (RAGE & RICHTER, 1994). It was identified on the basis of isolated vertebrae. Afterward, the study of Cretaceous lizards showed that the characters supposedly demonstrating the Spanish fossil to be a snake also exist in some lizards (the presence of a zygosphenal roof, although it is notched; the existence of subcentral ridges reaching the ventral part of the paradiapophyses). Consequently, the Barremian fossil can no longer be regarded as a snake.

The oldest unequivocal snakes known come from the Upper Albian (level C of the "série de Tiout") of Algeria. They are represented only by poorly preserved vertebrae (CUNY *et alii*, 1990) but incontestably they are snakes. The vertebrae represent a possible Lapparentophiidae and a snake *incertae sedis* (Fig. 1). The first was certainly terrestrial, but the second shows possible adaptations to an aquatic life. *Lapparentophis defrennei* (Lapparentophiidae), a terrestrial snake also found in Algeria (HOFFSTETTER, 1959), comes from the "série d'In Akhamil" that may correspond to the Upper Albian or Cenomanian (CUNY *et alii*, 1990). In North America (USA),

Coniophis sp. has been reported from the Upper Albian or Lower Cenomanian (GARDNER & CIFELLI, 1999); this terrestrial snake, probably a burrower, is attributed to the Aniliidae *s.l.*, a family that at least when its fossil representatives are included is probably paraphyletic and is comprised of generally primitive forms. These snakes are known only from isolated vertebrae so it is impossible to determine if they had legs.

The Cenomanian has provided several taxa. Only one of them was terrestrial. This is *Pouitella*, from the Lower Cretaceous of France (RAGE, 1988); represented by only one vertebra, it is impossible to know if it had legs. The others were completely adapted to an aquatic life and all were found in marine sediments. *Pachyrhachis*, *Eupodophis* and *Haasiophis* are three snakes from the Cenomanian of the Middle East with hind legs. *Pachyophis* and *Mesophis* come from the Middle or more probably from the Upper Cenomanian of Bosnia. LEE *et alii* (1999) supposed that *Pachyophis* may have had hind legs (see below). *Mesophis* is very poorly known; the only specimen seems to be lost. Finally, *Simoliophis*, represented by vertebrae and isolated ribs is known from the Lower, Middle, and perhaps Upper Cenomanian of Western Europe and North Africa.

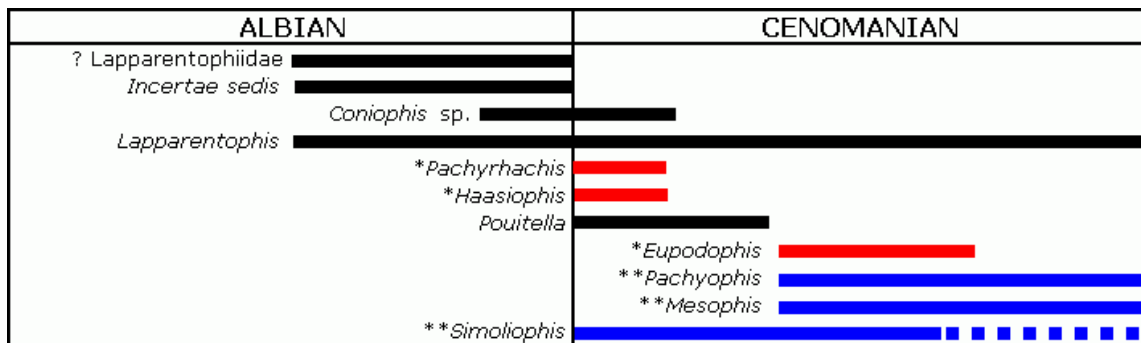


Figure 1: Stratigraphic distribution of the oldest snakes (*unquestionable hindlimbed snakes; **probable hindlimbed snakes). Note: with the exception of *Simoliophis*, each taxon comes from only one locality; so each bar indicates the maximum possible range.

III - Hindlimbed snakes

A - Unquestionable hindlimbed snakes

Pachyrhachis problematicus HAAS, 1979

- 1979 *Pachyrhachis problematicus* : HAAS, p. 51-64, fig. 1-6.
- 1980 *Ophiomorphus colberti* : HAAS, p. 190-192, fig. 10.1-10.6.
- 1984 *Estesius colberti* (HAAS, 1980) : WALLACH, p. 329.

In 1979 HAAS described a fossil under the name *Pachyrhachis problematicus*. This fossil, found in the house of a quarrier, comes from the Cenomanian limestone of Ein Jabrud near Ramallah in Palestine. Its age, earliest

Cenomanian (CHALIFA & TCHERNOV, 1982), is unquestioned. The fossil comprises the skull and a large portion of the vertebral column, but not the posterior part. The skull proved indisputably that the animal was a squamate and the vertebral column showed that it was snake-like. But HAAS, although indicating that the skull had characteristics of a snake, considered the fossil to be a varanoid lizard (Platynota). He was concerned particularly with the primitive characteristics of the skull (that obviously suggested affinities with lizards) and the pachyostosis (*i.e.* thickening) of a part of the vertebrae and ribs. This pachyostosis resembled that of *Simoliophis*, a Cenomanian fossil known only from vertebrae and ribs, and generally considered to be a snake. Based on vertebral morphology, HAAS put *Pachyrhachis* in the same

family as *Simoliophis* (Simoliophiidae) and considered the two genera to be snake-like varanoid lizards.

HAAS remarked on a particularly striking aspect of the skull, its macrostomate (large-mouth) structure (see below: Phyletic Considerations), but did not take it into account in establishing the affinities of *Pachyrhachis*.

In 1980, HAAS described (as *Ophiomorphus colberti*) a second serpentiform squamate acquired under the same conditions and from the same locality as *Pachyrhachis*. The fossil consists of a vertebral column (a part of its anterior region and the posterior part of the tail are missing), a pelvic girdle and short hind legs. In addition there is a poorly preserved skull under the vertebral column. The vertebrae and ribs are pachyostotic, but less so than in *Pachyrhachis*. HAAS interpreted this fossil as an intermediate between varanoid lizards and snakes.

WALLACH (1984) thereafter proposed the genus name *Estesius* to replace *Ophiomorphus*, which was preoccupied.

McDOWELL (1987) was the first to consider forthrightly that *Pachyrhachis* is a snake; on the other hand he removed *Ophiomorphus* (*i.e.* *Estesius*) from this group.

In 1997, CALDWELL & LEE showed that

1) the specimen described as *Pachyrhachis problematicus* is indeed a snake, and

2) that the specimen corresponding to *Estesius colberti* belongs to *Pachyrhachis problematicus*, the difference in pachyostosis being ontogenetic.

Therefore, *Pachyrhachis problematicus* was a snake with hind legs! Some doubt might still exist because the skull that demonstrates its serpenthood is on one specimen while the legs are on the other specimen (the skull of the latter specimen is present but it is crushed under the ribs). But subsequently the discovery of *Eupodophis descouensi* and *Haasiophis terrasanctus* proved that CALDWELL & LEE (1997) were right to put the two specimens in one taxon.

The anatomy of *Pachyrhachis problematicus* was revised in detail by LEE & CALDWELL (1998). In particular it shows that *Pachyrhachis* was truly macrostomate. *Pachyrhachis* is the largest of the hindlimbed snakes, but its length is difficult to estimate (more than 1.5 meters).

Eupodophis descouensi (RAGE & ESCUILLIÉ, 2000)

- 2000 *Podophis descouensi*: RAGE & ESCUILLIÉ, p. 513-520, fig. 1-2.
- 2002 *Eupodophis descouensi*: RAGE & ESCUILLIÉ, p. 232-233.

This taxon is represented by a specimen found in the Middle Cenomanian of Al Nammoura in Lebanon (Fig. 2-3). The specimen includes the skull, the vertebral column (a part is missing in the posterior third), the pelvic girdle and the hind limb. The skull is less well-preserved than that of *Pachyrhachis* but it confirms the macrostomate condition of hindlimbed snakes. Most presacral vertebrae and ribs are thickened and pachyostotic. One of the most interesting points is the excellent preservation of the posterior portion of the vertebral column which shows that the tail was astonishingly short (Fig. 4). While the total length of the animal is estimated at 85 cm, the leg is located only 5 cm from the end of the tail. The leg is about 2 cm long. In the tail the chevron bones are articulated with the vertebrae, not united to them; this is a plesiomorphic (*i.e.* primitive) character important in phylogenetic analysis.

Eupodophis differs from *Pachyrhachis* in the more pointed form of the skull, by its quadrate bone that is much less drawn out anteroposteriorly and by the presence of special dorsal tubercles on the vertebrae (RAGE & ESCUILLIÉ, 2000). In addition, the body seems to be more flattened laterally than in *Pachyrhachis*.

Haasiophis terrasanctus TCHERNOV *et alii*, 2000

This taxon too is represented by only one specimen; it is almost complete and undoubtedly the best preserved of all the specimens of hindlimbed snakes. It comes from the same site as *P. problematicus* and therefore is dated earliest Cenomanian. Its size is close to that of *Eupodophis*. The published description is rather brief and concerns mainly the skull; in particular the caudal region is poorly described and the description must be completed in its entirety before its characteristics can be fully known. It was flattened laterally but the degree of flattening has not been determined. Judged by its principal characteristics it is very similar to the two other taxa. It is distinct in its very much reduced coronoid and a much less marked macrostomate condition.



Figure 2: *Eupodophis descouensi*. Al Nammoura, Lebanon, Cenomanian. Ventral view. The animal has been broken and the posterior portion is fossilized near the head. The total length is about 85 cm.



Figure 3: *Eupodophis descouensi*. Al Nammoura, Lebanon, Cenomanian. Sacral and caudal regions and the back leg; the leg includes the femur, the tibia and the fibula, plus some more distal bones.

In addition it differs from *Pachyrhachis* in its anteroposteriorly narrow quadrate and from *Eupodophis* in the absence of dorsal tubercles on the vertebrae. The position of the leg in relation to the caudal extremity is unknown. Furthermore, the presence of haemapophyses in the tail reported by TCHERNOV *et alii* (2000),

poses a problem: does it concern haemapophyses in a strict sense (united to the centrum) or are they chevrons (articulated to the centrum)? The presence of true haemapophyses in *Haasiophis*, while *Eupodophis* has articulated chevrons, would be surprising.

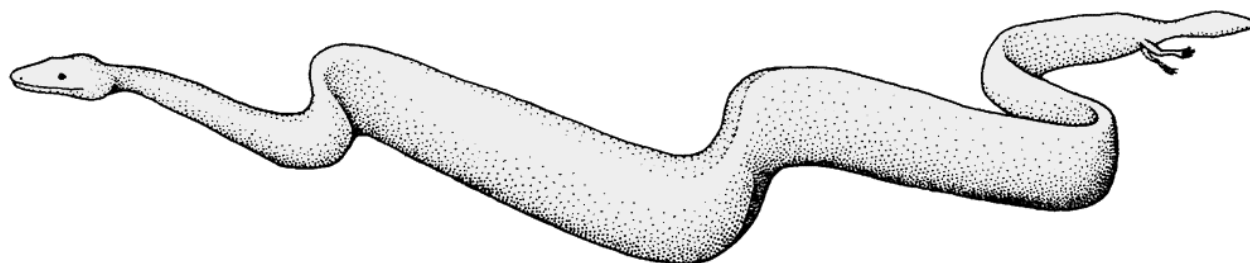


Figure 4: Reconstruction of *Eupodophis descouensi* (note the size and position of the limbs).

B - Possible hindlimbed snakes

(RAGE & ESCUILLIÉ, 2000).

Pachyophis woodwardi NOPCSA, 1923

Mesophis nopcsai BOLKAY, 1925

This snake too is represented by only one specimen. It comes from a quarry near Bileca in Bosnia-Herzegovina. At first considered as early Cretaceous (Neocomian) it is now dated as middle or probably late Cretaceous (SLISKOVIĆ, 1970).

This taxon is represented by an almost complete specimen in which the caudal portion is poorly preserved and perhaps incomplete. Apparently the specimen is lost so this snake is known only from BOLKAY's (1925) description which is not complete enough to establish its relations to the other taxa. It was found in the same site as *Pachyophis*. It is flattened laterally but the degree of flattening could not be determined. A part of the vertebrae are pachyostotic while the ribs are not at all or but weakly affected by pachyostosis. Because it is clearly smaller than *Pachyophis* (approximately half its size) it is possible that the difference is ontogenetic and as the two taxa come from the same site it is possible to suppose, as did NOPCSA (1931: 30), that *Mesophis* is a young *Pachyophis*.

A little smaller than *Eupodophis*, it must have reached some sixty centimeters. The specimen includes the dentition, some fragments of skull bones and the vertebral column (vertebrae and ribs) but the caudal portion is hidden under another part of the column (LEE *et alii*, 1999). The vertebrae and ribs are strongly pachyostotic; the ribs, very thickened, form an almost continuous "wall". The lateral flattening of the body must have been comparable to that in *Eupodophis*. It is difficult to compare *Pachyophis* to the other taxa because it is known only from its dorsal side and the cranial bones are very incomplete. However it can be noted that pachyostosis is stronger than that in the other taxa, although the animal is smaller. So the difference in the degree of pachyostosis cannot be attributed to ontogeny, but represents a valid characteristic of this genus.

Whatever the case, one can only conjecture as long as the specimen is not found again. It might well be another hindlimbed snake.

Simoliophis SAUVAGE, 1880

LEE *et alii* (1999), noting the similarities between *Pachyophis* and *Pachyrhachis* (the only hindlimbed taxon known when this work was published) concluded that *Pachyophis* might also have hind legs. If they are present, which is quite possible or even probable, they must be hidden under the medial portion of the vertebral column.

In contrast with the genera discussed previously, *Simoliophis* comprises several species. On the other hand it is represented by disarticulated specimens consisting only of vertebrae and ribs.

LEE *et alii* (1999) considered that *Pachyophis* and *Pachyrhachis* form a clade and put them in the same family, the Pachyophiidae. Based on the available material, it does not seem possible to confirm this point of view; the possibility that hindlimbed snakes form a paraphyletic assemblage cannot be set aside definitively

Pachyostosis affects the vertebrae of the middle and posterior trunk portions as well as the ribs that probably came from the same regions. Vertebral morphology is very similar to that of *Eupodophis*, the only unquestionable hindlimbed snake of which a disarticulated vertebra is known. The vertebrae of *Simoliophis* are distinguished from those of *Eupodophis* by the absence of the dorsal tubercles that characterize the neural arch of that genus. On the other hand, what is known about *Pachyrhachis* and *Haasiophis* does not allow a

distinction between the vertebrae of these two genera and those of *Simoliophis*, unless the reconstructions of *Pachyrhachis* vertebrae as proposed by LEE & CALDWELL (1998) are exact. If that be the case, *Pachyrhachis*'s vertebrae would be quite different from those of *Eupodophis* and *Simoliophis*. As reconstructed, the vertebrae of *Pachyrhachis* differ from those of the two other genera mainly in having by far less pachyostotic and more cylindrical centra, more elongated prezygapophyses, less protruding paradiapophyses, and larger condyles and cotyles. Whatever may be determined, the vertebrae of *Eupodophis* and *Simoliophis* (and probably those of *Pachyrhachis* and *Haasiophis*) are very similar and are markedly different from those of non-hindlimbed snakes. For this reason one may postulate that these taxa are either closely related or at least at a similar grade, and therefore the existence of hind legs in *Simoliophis* can be inferred with some confidence.

Simoliophis has been found only in strata of Cenomanian age (see below).

Two valid species have been described, *S. rochebrunei* and *S. libycus*. In addition, specimens of *Simoliophis* from the Cenomanian of Baharija (Egypt), referred to *S. rochebrunei* by NOPCSA (1925), represent a third, unnamed species.

Simoliophis rochebrunei SAUVAGE, 1880

- 1898 *Simoliophis delgadoi* : SAUVAGE, p. 23-24, pl. 2 : fig. 12-14.

S. rochebrunei, the type species of the genus, has been found in the Cenomanian of the central west and southwest of France as well as in Portugal, near Lisbon (JONET, 1981; RAGE, 1984). The species has been recovered from a dozen localities that with two exceptions are dated either Early or Middle Cenomanian. The exact level of the Cenomanian present at Sillac and Basseau, two localities in the Charente now lost, is not known. Consequently it may be that *S. rochebrunei* occurs in the Late Cenomanian.

Simoliophis libycus NESSOV, ZHEGALLO & AVERIANOV, 1998

This species was found in Libya at Draa Ubari. According to Nessonov *et alii* (1998), it is distinguishable from *S. rochebrunei* by a

narrower centrum, a lower neural spine on the anterior vertebrae, the smaller anteroposterior length of the neural spine, and less well developed paradiapophyses. As the species was based on a small amount of material and is smaller than *S. rochebrunei*, it remains to be determined whether or not these differences are only ontogenetic and/or are related to the position of the vertebrae in the vertebral column.

NESSOV *et alii* (1998) considered the age of the outcrops at Draa Ubari as Santonian-Campanian, but all of the stratigraphically significant taxa found at the site are of Cenomanian age, and some may be older (RAGE & CAPPETTA, 2002); the exact age within the Cenomanian cannot be established

The other *Simoliophis*

NOPCSA (1925) described a series of vertebrae and ribs from the Cenomanian of Baharija, Egypt. He attributed these fossils to *S. rochebrunei*, the only species then known. In fact, in reconstructing the vertebral column, NOPCSA probably mixed the vertebrae of two snakes. Some of them, middle and posterior trunk vertebrae, are truly *Simoliophis* but those considered anterior trunk may belong to another distinct genus (opinion based on as yet unpublished specimens of *Simoliophis*). In addition, the vertebrae of *Simoliophis* belong neither to *S. rochebrunei* nor to *S. libycus*, but to another, unnamed species as shown by the marked groove on the base of the anterior edge of the neural spine.

There is no agreement on the precise age of the Baharija locality within the Cenomanian: For some, Early Cenomanian (LAPPARENT DE BROIN, 2000), for others Late Cenomanian (WERNER, 1989). However, on the basis of ammonites DOMINIK (1985) proposed a Late Cenomanian age for at least a part of the Baharija Formation.

Several localities in the Kem Kem (Morocco) have also furnished *Simoliophis* vertebrae that resemble those of *S. libycus* (work in progress). The Kem Kem beds are mainly of Cenomanian age but it is not impossible that the lowermost levels are of Late Albian age. However, all of the levels that furnished specimens of *Simoliophis* are dated Cenomanian (SERENO *et alii*, 1996).

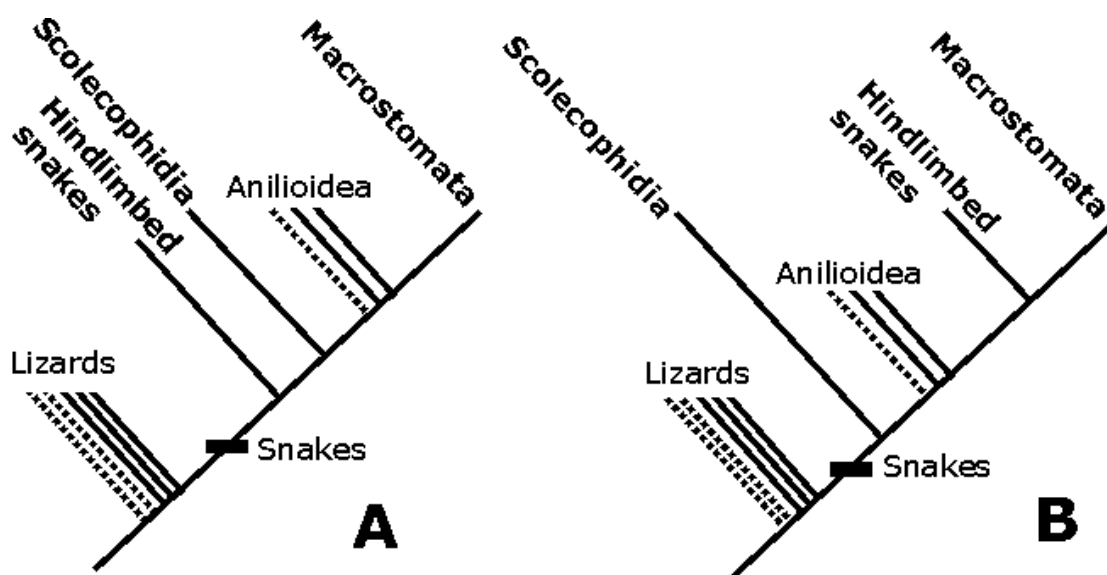


Figure 5: Relationships of the hindlimbed snakes. They may be "primitive" (A) or "advanced" (B).

Summary and conclusions

It is incontestable that three snakes have hind limbs: *Pachyrhachis problematicus* and *Haasiophis terrasanctus* of the earliest Cenomanian, along with *Eupodophis descouensi* of the Middle Cenomanian. All three were found in the Middle East. Three other genera may possess such limbs: *Pachyophis* (unique species: *P. woodwardi*), *Mesophis* (unique species: *M. nopcsai*), both from the Middle, or more probably the Late Cenomanian, and *Simoliophis* (three species: *S. rochebrunei*, *S. libycus* and an unnamed species) from the Early, Middle and perhaps Late, Cenomanian.

It is not impossible that either *Pachyrhachis* or *Haasiophis* is a synonym of *Simoliophis*, for the latter is known only from vertebrae and isolated ribs. The dorsal tubercles on the vertebrae of *Eupodophis* make it impossible for that genus to be a synonym of *Simoliophis*.

IV - Phyletic considerations

It is difficult here not to touch on the question of the relationships of "snakes with legs" even though their phylogenetic aspects are not the main topics of this article. We shall discuss only the three species that are unquestionably hindlimbed.

The phylogenetic position of the hindlimbed taxa in snake classification has led to much debate. Two main facts must be kept in mind:

- 1) these three taxa have hind legs, small but perfectly formed; logically, in snakes this is a plesiomorphic characteristic;
 - 2) the three hindlimbed snakes have a macrostomate skull;
- but in existing snakes this character appears only in forms considered to be the most "advanced", the Macrostromata; *a priori*, this

structure should be derived.

The name macrostomate is given to a structural plan that allows the buccal opening to enlarge. This enlargement is due mainly to a posterior elongation of the supratemporal bone that shifts the quadrate posteriorly, and the dorsoventral elongation of the quadrate. A macrostomate structure permits the ingestion of very large prey, sometimes greater in diameter than the predatory snake itself.

The association of these two characters, the presence of hind legs and a macrostomate structure, poses a serious problem.

Several phyletic analyses have led to diametrically opposite results: snakes with legs may be either

- 1) primitive snakes, sister group to all the other snakes (CALDWELL & LEE, 1997; LEE & CALDWELL, 1998; RAGE & ESCUILLIÉ, 2000; SCANLON & LEE, 2000; LEE & SCANLON, 2002), or
- 2) "advanced" snakes (in spite of the presence of legs), sister group to modern Macrostromata (ZAHER & RIEPPEL, 1999; TCHERNOV *et alii*, 2000; RIEPPEL & ZAHER, 2000; ZAHER & RIEPPEL, 2000).

The first hypothesis (hindlimbed snakes are "primitive"; Fig. 5A) proposes either that the macrostomate structure appeared twice by convergence (in hindlimbed snakes first and in the Macrostromata again) or, more probably, that the macrostomate structure is plesiomorphic (*i.e.* primitive) among snakes (contrary to what was believed) and that in non-macrostromate snakes it was lost because of the adoption of a burrowing habitat (RAGE & ESCUILLIÉ, 2000); in fact, all non-macrostromate snakes are burrowers, a mode of life that entails a reduction in the size of the mouth in vertebrates.

The second hypothesis (hindlimbed snakes are "advanced"; Fig. 5B) leads to the supposition either that several groups of snakes (five?) independently lost their hind legs or that hind legs *reappeared* in hindlimbed snakes. Although theoretically not entirely impossible, this last possibility seems most unlikely.

These divergences of opinion concerning the phyletic position of hindlimbed fossils are not without influence on our conceptions of the origin of snakes. It being understood that the lizards are the stem group from which snakes evolved, it was thought for a long time that snakes evolved after a burrowing or semi-fossorial phase (RAGE, 1987). But as hindlimbed snakes are marine, if they are really the sister of or stem group to other taxa, the snakes may

have originated in a marine environment. This hypothesis is clearly supported by the fact that the Mosasauroidea, Cretaceous lizards also markedly adapted to a marine life, are widely recognized as the group most closely related to the snakes (e.g. LEE, 1997; CALDWELL, 1999; LEE & CALDWELL, 2000; see, however, the divergent views of RIEPPEL & ZAHER, 2000). On the other hand, if hindlimbed snakes are "advanced", which seems most unlikely, the origin of snakes subsequent to a burrowing or sub-burrowing phase remains plausible.

A remaining question is whether the hindlimbed snakes form a clade or are a paraphyletic group. This question, raised by RAGE & ESCUILLIÉ (2000), has not yet been answered.

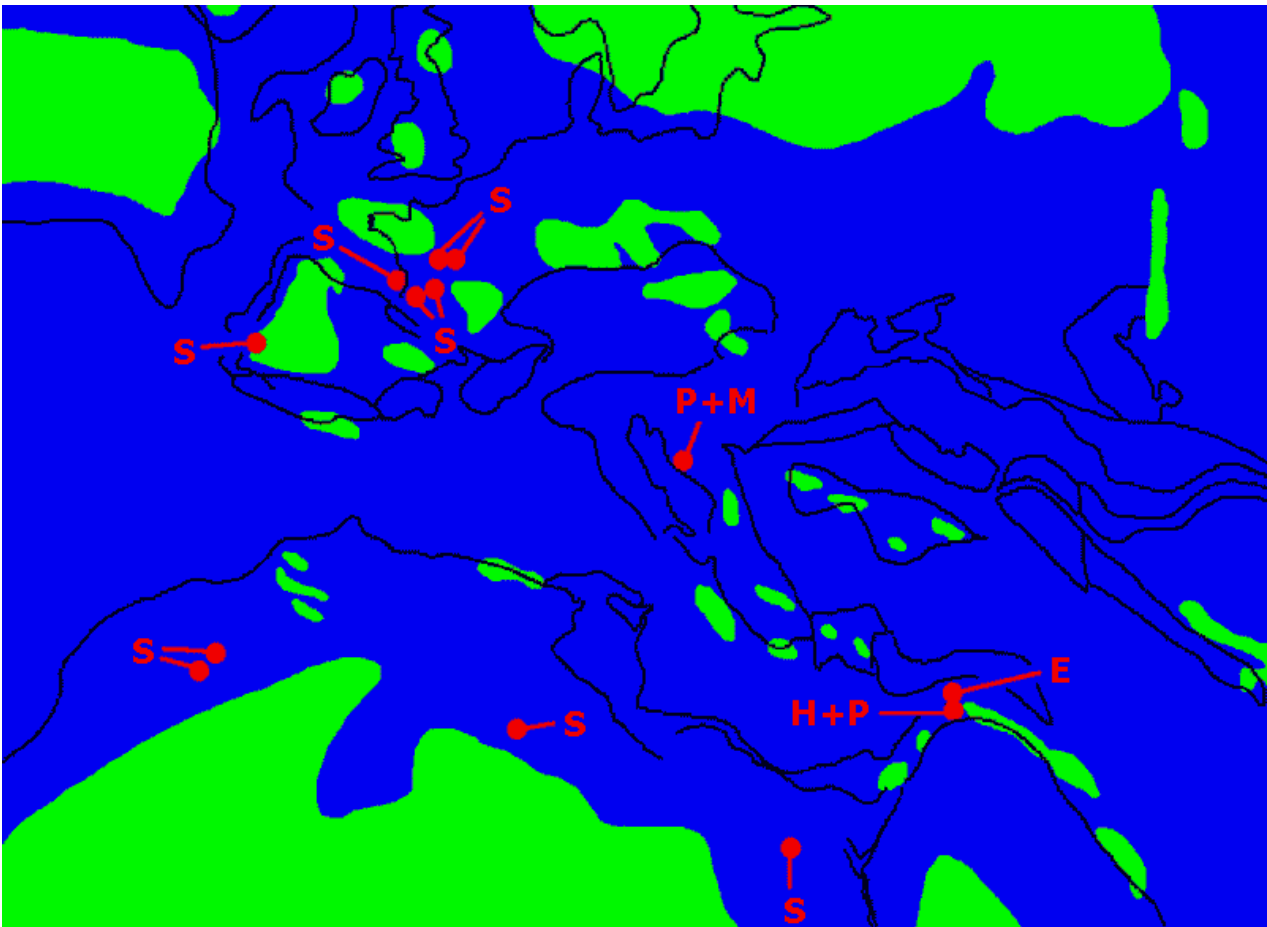


Figure 6: Geographic distribution of hindlimbed and presumed hindlimbed snakes. Paleogeography of the Mediterranean region during the Cenomanian (from VOIGT, 1996, simplified). **E:** *Eupodophis*; **H+P:** *Haasiophis* and *Pachyrhachis*; **P+M:** *Pachyophis* and *Mesophis*; **S:** *Simoliophis* (because of their proximity, all the localities with *Simoliophis* in France, Portugal and Morocco are not shown).

V - Hindlimbed snakes and the Cenomanian

The fact that all snakes confirmed or inferred to be limbed are of Cenomanian age is striking. It is true, too, that the rare fossils found in older beds (Upper Albian), are all in the form of poorly preserved isolated vertebrae so that it is not possible to determine whether or not they had legs. Whatever may be the case, it must be

stated that legged snakes and those supposed to have had them have vertebrae of a very special morphology that distinguishes them from all other snakes. But this type of vertebra has been found only in the Cenomanian. Consequently, one may assume that legged snakes occur only in strata assigned this stage.

In addition, these snakes have a very restricted geographic distribution. All occur in the "Mediterranean" area of the Tethys or in its

immediate vicinity: the north, east and south margins of the existing Mediterranean and its extension as far as the transitional area between the Aquitaine and Paris basins (Fig. 6).

If hindlimbed snakes really belong to a basal group (sister group to all other snakes) as we uphold, and as did CALDWELL & LEE (1997) and SCANLON & LEE (2000), then their range that is very restricted in both time and space deserves attention. As a consequence, snakes would have originated in an aquatic, marine environment (NOPCSA, 1923; CALDWELL, 1999; RAGE, 2000), although Lee *et alii* (1999) did not reject the possibility that legged snakes were only secondarily aquatic. If snakes really originated in a marine environment, the "Mediterranean" part of the Tethys might be regarded as the cradle of the whole group. As far as their very limited stratigraphic range (Cenomanian only) is concerned, no explanation can be brought forward, although a taphonomic bias cannot be definitely ruled out.

VI - Why pachyostosis?

One of the traits that most clearly distinguish the legged snakes is pachyostosis, that is a non-pathologic "thickening" of the bones of a large portion of the vertebral column. HOFFSTETTER (1955) presented two hypotheses to explain the advantages to the animal of pachyostosis:

- a) an increase in the amount of tissues that make erythrocytes, thus an augmentation of respiratory capacity;
- b) as ballast to improve the animal's swimming capabilities.

No one else has followed up on HOFFSTETTER's hypothesis concerning erythrocytes (which does not mean that it is erroneous), but BUFFRÉNIL & RAGE (1993) and SCANLON *et alii* (1999) support the idea that pachyostosis played a hydrostatic role. Indeed, the area in which the bones are pachyostotic and could serve as ballast is situated in the region of the lungs; consequently pachyostosis may have helped in buoyancy control. More precisely, according to SCANLON *et alii* (1999), thanks to pachyostosis, the mean density of the animal was probably close to that of water and its center of gravity must have been near that of buoyancy. From a study of *Pachyrhachis*, they concluded that the animal was not a surface dweller and that pachyostosis probably allowed it to remain at depth.

BUFFRÉNIL & RAGE (1993), based on a study of *Simoliophis* (the existence of legs in some snakes was not known at the time) and SCANLON *et alii* (1999) from *Pachyrhachis*, reached very similar conclusions concerning the habitat of these snakes. These animals lived in shallow water among reefs, in lagoons, and could not have been deep divers. They were slow, not very mobile, and probably ate slow-moving prey, or cornered faster prey in burrows or

crevices. According to SCANLON *et alii* (1999), they were able to hunt through ambush, as do modern sea snakes.

The major characteristics of the anatomy of all the legged snakes is so homogenous that the major points regarding their way of life derived from *Pachyrhachis* and *Simoliophis* should be applicable to all of them.

Finally and inevitably is the question of the function of the back legs in these snakes. Very much reduced, they could not have really aided locomotion. It has been suggested that they may have served as a way to anchor the body in fissures, or as aids to mating (SCANLON *et alii*, 1999). But as they were simply limbs in the process of total regression perhaps they had no function.

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