

Festschrift for Marian Mlynarski

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**The oldest known colubrid snakes. The state of the art**

[With 2 text-figs]

**Najstarsze znane węże z rodziny Colubridae**

**Abstract.** Colubrid snakes have undergone a very important diversification since the Miocene; they infrequently occur in ante-Miocene sediments. Snakes referred to the *Colubridae* were reported from the Eocene; they are reviewed and annotated. It is shown that these so-called eocene *Colubridae* are either non-colubrid snakes or non-eocene fossils (at least quite probably non-eocene). The oldest known unquestionable *Colubridae* are *Coluber cadurci*, *Coluber atavus*, both from the European Oligocene, *Texasophis galbreathi* from the North American Oligocene, and *Natrix mlynarskii* sp. n. that occurred in European ante-Miocene localities that are quite probably Oligocene.

**I. INTRODUCTION**

The *Colubridae* represent one of the more advanced snake families. Today, this enormous cosmopolitan group (about 1550 species, that is two thirds of the living snake species) includes terrestrial, aquatic, arboreal, secretive and more or less fossorial forms. Unfortunately, the colubrid vertebral morphology is very homogeneous, which renders the paleontological study of the group quite difficult. Moreover, taxa of highly doubtful validity were established by non-experts. Only MLYNARSKI (1961) ventured to review fossil snakes referred to this family.

Colubrid snakes have been reported from the Paleogene, but they did not thrive before the Miocene. From time to time, it has been reported that the *Colubridae* are known since the Eocene (DUELLMAN, 1979; BAEZ and GASPARINI, 1979; HOLMAN, 1979; HAUBOLD, 1983). However, it is now established that the supposed eocene *Colubridae* are either non-colubrid snakes or non-eocene fossils. As I am partly involved in this state of affairs (most of the aforementioned reports are based on one of my papers: RAGE, 1974), it seems necessary to restate the question.

This review deals with fossils housed in the collections of the Istituto di Geologia, Paleontologia e Geologia Applicata (IGP), University of Padua, Italy, the Institut für Paläontologie der Universität Bonn (IPBo), West Ger-

many, the Museum national d'Histoire naturelle (MNHN), Paris, France, and Université des Sciences et Techniques du Languedoc (USTL), Montpellier, France.

## II. REVIEW OF THE SO-CALLED EOCENE COLUBRID SNAKES

### *Coluber beggiatoi* DE ZIGNO, 1889

- 1889 *Coluber beggiatoi*: DE ZIGNO, p. 112—113.
- 1939 *Coluber beggiatoi* ZIGNO 1889: KUHN, p. 18.
- 1955 "*Coluber*" *beggiatoi* ZIGNO 1890: HOFFSTETTER, p. 657.
- 1961 *Coluber beggiattoii* ZIGNO: MLYNARSKI, p. 21.
- 1962 "*Coluber*" *beggiatoi* ZIGNO 1890: HOFFSTETTER, p. 270.
- 1963 ? *Coluber beggiatoi* ZIGNO 1890: KUHN, p. 20.
- 1974 *Coluber beggiatoi*: RAGE, p. 293.
- 1984a *Coluber beggiatoi* ZIGNO, 1889: RAGE, p. 52.

Locality and age: Colle di Lonigo, Italy. DE ZIGNO considered this fossil comes from eocene beds, which is questionable (see below).

Comments: This species has been based on a specimen comprising some cranial bones (only the parabasisphenoid is illustrated) and a part of the axial skeleton. The DE ZIGNO's description is cursory. The figures show bones very similar to those of recent *Colubridae*. This quite modern morphology casts doubts on the stratigraphic origin of this fossil that was not embedded in the sediment (HOFFSTETTER, 1955; MLYNARSKI, 1961). These bones might belong to a recent snake that died in a crevice of the eocene beds. The holotype, and only known specimen, being likely destroyed, and the description and figures being inadequate, *C. beggiatoi* is considered a nomen dubium (RAGE, 1984a).

### "*Coluber*" *ombonii* DE ZIGNO, 1889

- 1889 *Coluber ombonii*: DE ZIGNO, p. 113.
- 1939 *Coluber ombonii* ZIGNO 1890: KUHN, p. 19.
- 1961 *Coluber ombonii* ZIGNO: MLYNARSKI, p. 35.
- 1963 *Coluber ombonii* DE ZIGNO 1890: KUHN, p. 21.
- 1974 *Coluber ombonii*: RAGE, p. 293.
- 1984a "*Coluber*" *ombonii* ZIGNO, 1889: RAGE, p. 58.

Locality and age: La Pesciara ("Monte Bolca"), Italy. Late early Eocene.

Comments: DE ZIGNO (1889) tentatively referred a species based on an imprint of the posterior part of a snake (IGP, 8360) to the genus *Coluber*. The outlines of some vertebrae are more or less apparent; the vertebrae are not elongate, their width being similar to their length. Such a morphology is not inconsistent with the colubrid vertebral type, but it very infrequently occurs

in the *Colubridae*. Nothing supports the referral to the *Colubridae*. Moreover, it is not possible to determine the systematic assignment of this fossil on the basis of such a specimen. *Coluber ombonii* is a nomen dubium (RAGE, 1984a).

*Coluber papyraceus* TROSCHER, 1854

- 1854 *Coluber papyraceus*: TROSCHER, p. 19.  
 1859 *Morelia papyracea*: TROSCHER, p. 237.  
 1861 *Morelia papyracea*: TROSCHER, p. 353 and 357.  
 1961 *Coluber papyraceus* FISCHER?: MLYNARSKI, p. 37.  
 1961 *Morelia papyracea* TROSCHER?: MLYNARSKI, p. 37.  
 1963 *Coluber papyraceus* FISCHER 1858: KUHN, p. 21.  
 1984a *Coluber papyraceus* TROSCHER, 1854: RAGE, p. 60.

Locality and age: Rott, West Germany, Latest Oligocene.

Comments: The name *Coluber papyraceus* first appeared in the TROSCHER's article (1854) without comments or illustrations. Later (1859, 1861) TROSCHER inadequately and cursorily described the species and he referred it to the genus *Morelia* (that is an extant Australian python!). The type material is unknown. *Coluber papyraceus* is a nomen nudum (see below: *Coluber atavus*).

*Coluber lafonti* FILHOL, 1877

- 1877 *Coluber lafonti*: FILHOL, p. 558.  
 1963 ? *Coluber lafonti* FILHOL 1877: KUHN, p. 21.

Locality and age: unknown locality from the Phosphorites du Quercy, France. Precise age unknown, the Phosphorites span the late Eocene and the Oligocene.

Comments: The name *Coluber lafonti* does not appear in the FILHOL's text but only in the captions; besides, in the captions, the numbering is erroneous: *Coluber lafonti* corresponds to figures 413—418, not to figures 414—419 as printed in the FILHOL's work. Moreover, the cursory description of this species appears only as the last paragraph of the description of *Python cadurcensis*! This species was based on four "mummified" portions of trunk that are the syntypes. It is not demonstrated that these specimens all belong to the same species. Moreover, only one specimen (MNHN, QU 16342) permits the recognition of the family because some attached vertebrae are observable (fig. 413—414 in FILHOL). The other specimens are unsuitable for purposes of identification. FILHOL considered that *Coluber lafonti* is not very different from the living Aesculapian colubrid, that is *Elaphe longissima*. DE ROCHEBRUNE (1880) coined the taxon *Scytalophis lafonti* based on five articulated vertebrae (specimen lost) from the Phosphorites which were not known by FILHOL. DE ROCHEBRUNE also referred to *S. lafonti* the only syntype of *C. lafonti* whose vertebrae are apparent (MNHN, QU 16342). This species is not a new species erected by



DE ROCHEBRUNE, it is the FILHOL's species transferred to the genus *Scytalophis* erected by DE ROCHEBRUNE. Therefore, although DE ROCHEBRUNE based *Scytalophis lafonti* on the above mentioned five articulated vertebrae, the type of the latter species is the trunk fragment QU 16342 referred to *C. lafonti* by FILHOL. DE ROCHEBRUNE rightly considered that *Scytalophis* is not a colubrid snake; but he wrongly referred it to the *Tortricides* (= *Aniliidae*). The two specimens referred to *Scytalophis* by DE ROCHEBRUNE do not belong to the same species but both actually belong to the *Boidae*. *Scytalophis* DE ROCHEBRUNE is a junior synonym of *Scytalophis* KAUP (an eel), therefore WALLACH (1986) replaced this generic name by the new name *Rageophis*.

The specimen QU 16338 referred to *Coluber lafonti* by FILHOL was assigned to a new genus and species (*Palaelaphis antiquus*) by DE ROCHEBRUNE (see below). The other two specimens referred to *C. lafonti* are lost; anyhow, such specimens afford no useful information.

### *Palaelaphis antiquus* DE ROCHEBRUNE, 1884

- 1884 *Palaelaphis antiquus*: DE ROCHEBRUNE, p. 156—157.
- 1905 *Elaphis antiquus* DE ROCHEBRUNE sp.: DE STEFANO, p. 40.
- 1939 *Elaphis antiquus* ROCHEBR. 1884 sp.: KUHN, p. 20.
- 1939 *Palaelaphis antiquus* ROCHEBRUNE: HOFFSTETTER, p. 67.
- 1961 "*Elaphis*" *antiqua* ROCHEBRUNE: MLYNARSKI, p. 38.
- 1963 *Palaelaphis antiquus* ROCHEBR. 1884: KUHN, p. 14.
- 1974 *Palaelaphis antiquus*: RAGE, p. 277.
- 1984a *Palaelaphis antiquus* ROCHEBRUNE 1884: RAGE, p. 32.

Locality and age: As for *Coluber lafonti* (see above).

Comments: DE ROCHEBRUNE (1884) erected the genus *Palaelaphis* for the reception of two new species from the Phosphorites du Quercy: *Palaelaphis antiquus*, the type-species, and *P. robustus*. DE ROCHEBRUNE believed that *Palaelaphis* is close to the living colubrid genus *Elaphe* and subsequently DE STEFANO (1905) erroneously synonymized *Palaelaphis* with this latter genus.

One specimen (MNHN, QU 16338) referred to *Coluber lafonti* by FILHOL (fig. 415 in FILHOL, 1877) was assigned to *Palaelaphis antiquus* by DE ROCHEBRUNE (Pl. I, fig. 3, 3a in DE ROCHEBRUNE, 1884) along with several specimens unknown by FILHOL (one anterior trunk vertebra: MNHN, QU 16339 = the lectotype of *P. antiquus*; one caudal vertebra: MNHN, QU 16340; another mummified trunk portion: MNHN, QU 16337; one left dentary: MNHN, QU 16336).

None of these specimens referred to *P. antiquus* may be assigned to the *Colubridae*. The "mummies" provide no taxonomic information below the suborder (*Alethinophidia*) level. The vertebrae and the dentary belong to the *Boidae*, but it is not established that they belong to the same species. Anterior



trunk vertebrae are the worst for purposes of identification, therefore the taxonomic status below familial level cannot be inferred from the lectotype; hence, *Palaelaphis antiquus* is a nomen dubium (RAGE, 1984a).

*Palaelaphis robustus* DE ROCHEBRUNE, 1884

- 1884 *Palaelaphis robustus*: DE ROCHEBRUNE, p. 156.  
 1939 *Palaelaphis robustus* ROCHEBRUNE: HOFFSTETTER, p. 67.  
 1963 *Palaelaphis robustus* ROCHEBR. 1884: KUHN, p. 14.  
 1974 *Palaelaphis robustus*: RAGE, p. 277.  
 1984a *Palaelaphis robustus* ROCHEBRUNE, 1884: RAGE, p. 32.

Locality and age: As for *Coluber lafonti* (see above).

Comments: The holotype (MNHN, QU 16341) is a fragmentary maxilla that belongs to the *Boidae*. This fossil gives no information below the family level; consequently, *P. robustus* is a nomen dubium (RAGE, 1984a).

"*Elaphis*" *boulei* DE STEFANO, 1905

- 1905 *Elaphis boulei*: DE STEFANO, p. 41—42.  
 1939 *Elaphis boulei* DE STEFANO 1905: KUHN, p. 20.  
 1939 *Elaphis boulei* STEFANO: HOFFSTETTER, p. 68.  
 1961 *Elaphis boulei* (STEFANO): MEYNARSKI, p. 38.  
 1963 *Elaphis boulei* DE STEFANO 1905: KUHN, p. 24.  
 1984a "*Elaphis*" *boulei* STEFANO, 1905: RAGE, p. 33.

Locality and age: As for *Coluber lafonti* (see above).

Comments: The type material, that is one dentary and several vertebrae, is lost. DE STEFANO assigned this species to the extant genus *Elaphis* (= *Elaphe*). Nothing demonstrates these specimens all belong to the same species. The DE STEFANO's figures clearly show that these specimens belong to the *Boidae* (HOFFSTETTER, 1939). Moreover, only the anterior and posterior faces of one vertebra are portrayed which is not sufficient for the determination of taxonomic assignment within *Boidae*; the dentary affords no information below the family level. *Elaphe boulei* is a nomen dubium (RAGE, 1984a).

*Tachyophis nitidus* DE ROCHEBRUNE, 1884

- 1884 *Tachyophis nitidus*: DE ROCHEBRUNE, p. 159.  
 1905 *Tachyophis nitidus* DE ROCHEBRUNE: DE STEFANO, p. 42—43.  
 1939 *Tachyophis nitidus* DE ROCHEBR. 1884: KUHN, p. 26.  
 1939 *Tachyophis nitidus* ROCHEBRUNE: HOFFSTETTER, p. 68.  
 1963 *Tachyophis nitidus* ROCHEBRUNE 1884: KUHN, p. 16.  
 1974 *Tachyophis nitidus*: RAGE, p. 277.  
 1984a *Tachyophis nitidus* ROCHEBRUNE, 1884: RAGE, p. 32—33.

Locality and age: As for *Coluber lafonti* (see above).

Comments: DE ROCHEBRUNE based this species on four articulated vertebrae (MNHN, QU 16331: the lectotype; RAGE, 1984a), one mummified trunk portion (MNHN, QU 16329) and one pterygoid (MNHN, QU 16330). DE ROCHEBRUNE did not prove these specimens all belong to the same species. He considered that the genus *Tachyophis* is closely related to the recent colubrid genus *Zamenis* (that is *Coluber*). Astonishingly, KUHN (1939) referred *Tachyophis* to the *Elapidae* [*Elypidae* (sic!) in KUHN] without clarification. In reality, it is only possible to indicate that the pterygoid and vertebrae belong to the *Boidae* (HOFFSTETTER, 1939) and that the "mummy" belongs to an alethinophidian snake. The vertebrae display characteristics of a juvenile individual and they are unsuitable for a precise assignment. The pterygoid is useless below the family level. *Tachyophis nitidus* is considered a nomen dubium (RAGE, 1984a). DE STEFANO (1905) referred one pterygoid and three articulated vertebrae to *T. nitidus*. He did not describe the pterygoid but he illustrated the vertebrae; these vertebrae display the morphology of boid anterior trunk vertebrae.

*"Pylmophis" gracilis* DE ROCHEBRUNE, 1884

- 1884 *Pylmophis gracilis*: DE ROCHEBRUNE, p. 158.
- 1905 *Pylmophis gracilis* DE ROCHEBRUNE: DE STEFANO, p. 38.
- 1939 *Pylmophis gracilis* ROCHEBR. 1884: KUHN, p. 26.
- 1939 *Pylmophis gracilis* ROCHEBRUNE: HOFFSTETTER, p. 68.
- 1955 "*Pylmophis*" *gracilis*: HOFFSTETTER, p. 656.
- 1961 *Pylmophis gracilis* ROCHEBRUNE: MLYNARSKI, p. 39.
- 1963 *Pylmophis gracilis* ROCHEBRUNE 1884: KUHN, p. 29.
- 1974 *Pylmophis gracilis*: RAGE, p. 277.
- 1984a "*Pylmophis*" *gracilis* ROCHEBRUNE, 1884: RAGE, p. 33.

Locality and age: As for *Coluber lafonti* (see above).

Comments: DE ROCHEBRUNE (1880) erected the genus *Pylmophis* for the Miocene colubrid snake *Coluber sansaniensis* LARTET, 1851. Later, DE ROCHEBRUNE (1884) assigned a new species (*Pylmophis gracilis*) from the Phosphorites du Quercy to this genus. This latter species was based on two articulated trunk vertebrae (MNHN, QU 16335: the lectotype), one dentary (MNHN, QU 16334) and one "mummy" (MNHN, QU 16333). The type-species of the genus, that is the Miocene *Pylmophis sansaniensis*, is now referred to the recent genus *Natrix* (RAGE, 1981); therefore, *Pylmophis* is a junior synonym of *Natrix*. None of the specimens referred to the species from the Phosphorites belongs to the *Colubridae*, consequently it is not possible to assign it to *Natrix*. Surprisingly, KUHN (1939) included *Pylmophis* in the *Elapidae* [*Elypidae* (sic!) in KUHN] without any comment. As usual, the "mummy" gives no useful information. On the other hand, the dentary actually belongs to a lizard (HOFFSTETTER, 1939). The vertebrae (= lectotype) are boid ones; but they are posteriormost trunk vertebrae which prevents a more precise taxonomic assignment. "*Pylmophis*" *gracilis* is a nomen dubium (RAGE, 1984a). A fragmentary maxilla and

several vertebrae from the Phosphorites du Quercy were attributed to "*Pylmophis*" *gracilis* by DE STEFANO (1905). These fossils are lost; the DE STEFANO's description is cursory and the fossils are not illustrated.

*Tropidonotus elongatus* TROSCHEL, 1854

- 1854 *Tropidonotus elongatus*: TROSCHEL, p. 19.  
 1939 *Elaphis elongatus* TROSCHEL 1858: KUHN, p. 20.  
 1961 *Coluber elongatus* TROSCHEL: MLYNARSKI, p. 34.  
 1963 "*Elaphis*" *elongatus* TROSCHEL 1858: KUHN, p. 24.  
 1984a *Tropidonotus elongatus* TROSCHEL, 1854: RAGE, p. 60.

Locality and age: Rott, West Germany, Latest Oligocene.

Comments: This name appears in the TROSCHEL's article without any description. The material is unknown. *Tropidonotus elongatus* is a nomen nudum. Nevertheless, Rott has yielded a colubrid snake (see below: *Coluber atavus*).

*Cheilophis huerfanoensis* GILMORE, 1938

- 1938 *Cheilophis huerfanoensis*: GILMORE, p. 79—80.  
 1955 *Cheilophis huerfanoensis* GILMORE: MILLER, p. 910.  
 1963 *Cheilophis huerfanoensis* GILMORE 1938: KUHN, p. 15.  
 1979 *Cheilophis huerfanoensis* GILMORE 1938: HOLMAN, p. 210.  
 1984a *Cheilophis huerfanoensis* GILMORE, 1938: RAGE, p. 17—18.  
 1984b *Cheilophis huerfanoensis* GILMORE, 1938: RAGE, p. 219—222.

Locality and age: Unnamed site near Gardner, Colorado, USA. Early middle Eocene.

Comments: GILMORE (1938) regarded this fossil as a snake incertae sedis. MILLER (1955), with some reservation but without any comment, placed it in the *Colubridae*. *C. huerfanoensis* is actually a boid snake (RAGE, 1984b).

Eocene colubrid snakes, in RAGE, 1974

I reported (RAGE, 1974: 293—294) the presence of *Colubridae* in the oldest known locality of the Phosphorites du Quercy (Le Breton: middle late Eocene). I indicated that both "colubrine" and "natricine" snakes are present in the locality. I assigned two fragmentary vertebrae to the "natricine" snakes because their centrum is very reminiscent of this group. But the subsequent discovery of *Russellophis* has demonstrated that primitive colubroid snakes display a vertebral morphology resembling that of the *Colubridae* (RAGE, 1975); more especially, the vertebrae of *Russellophidae* somewhat look like those of natricine snakes. Now, I refer these two vertebrae (USTL, BRT 1372 and 1373) to the *Russellophidae* because they lack prezygapophysial processes.



The report of a "colubrine" snake was founded on a single vertebra that actually belongs to this group. The vertebra is of a very modern type which poses a problem similar to the question raised by *Coluber beggiatoi* (see above). I have been informed that, during sorting of fossils, materials from several localities (including Le Bretou) and various ages were mixed. Therefore, now I am not sure that Le Bretou yielded this vertebra and, because of its quite modern morphology, I am markedly disposed to think that it comes from a clearly younger (non-eocene) locality.

### III. THE OLDEST KNOWN UNQUESTIONABLE COLUBRID SNAKES

Four unquestionable colubrid species are known prior to the Miocene: *Coluber cadurci*, *Coluber atavus*, *Texasophis galbreathi*, from the Oligocene and a new species that probably comes from Oligocene localities, too.

*Natrix mlynarskii* sp. n.

(Fig. 1)

Holotype. — One mid-trunk vertebra (MNHN, QU 17181).

Type-locality. — Unknown locality from the Phosphorites du Quercy, France.

Age. — The holotype has been found in the "old collections" from the Phosphorites du Quercy, therefore the precise locality and age are unknown. The Phosphorites span the late Eocene and the Oligocene. However, because of one vertebra from Mas-de-Got, it is supposed that the age is Oligocene (see below).

Name derivation. — Named in honour of Professor Marian MLYNARSKI for his contribution to the knowledge of paleoherpetology.

Referred material. — One mid-trunk vertebra (MNHN, QU 17182) from the "old collections" of the Phosphorites, and probably one anterior trunk vertebra (USTL, MGT 3508) from the Oligocene of Mas-de-Got, Phosphorites du Quercy, France.

Diagnosis. — Natricine snake whose trunk vertebrae resemble those of living and fossil *Natrix*. *N. mlynarskii* differs from the other *Natrix* species in the following combination of characters: 1) mid-trunk vertebrae rather elongate, 2) neural spine not low, 3) narrowing between pre- and postzygapophyses not deep, 4) ventral face of centrum long, narrow, flattened or even slightly concave, 5) subcentral ridges very strong and sharp, approximately straight in lateral view, slightly arched laterally in ventral view, 6) basis of hypapophysis forming a salient anterior keel that widens into a triangular and protruding area below the cotyle.

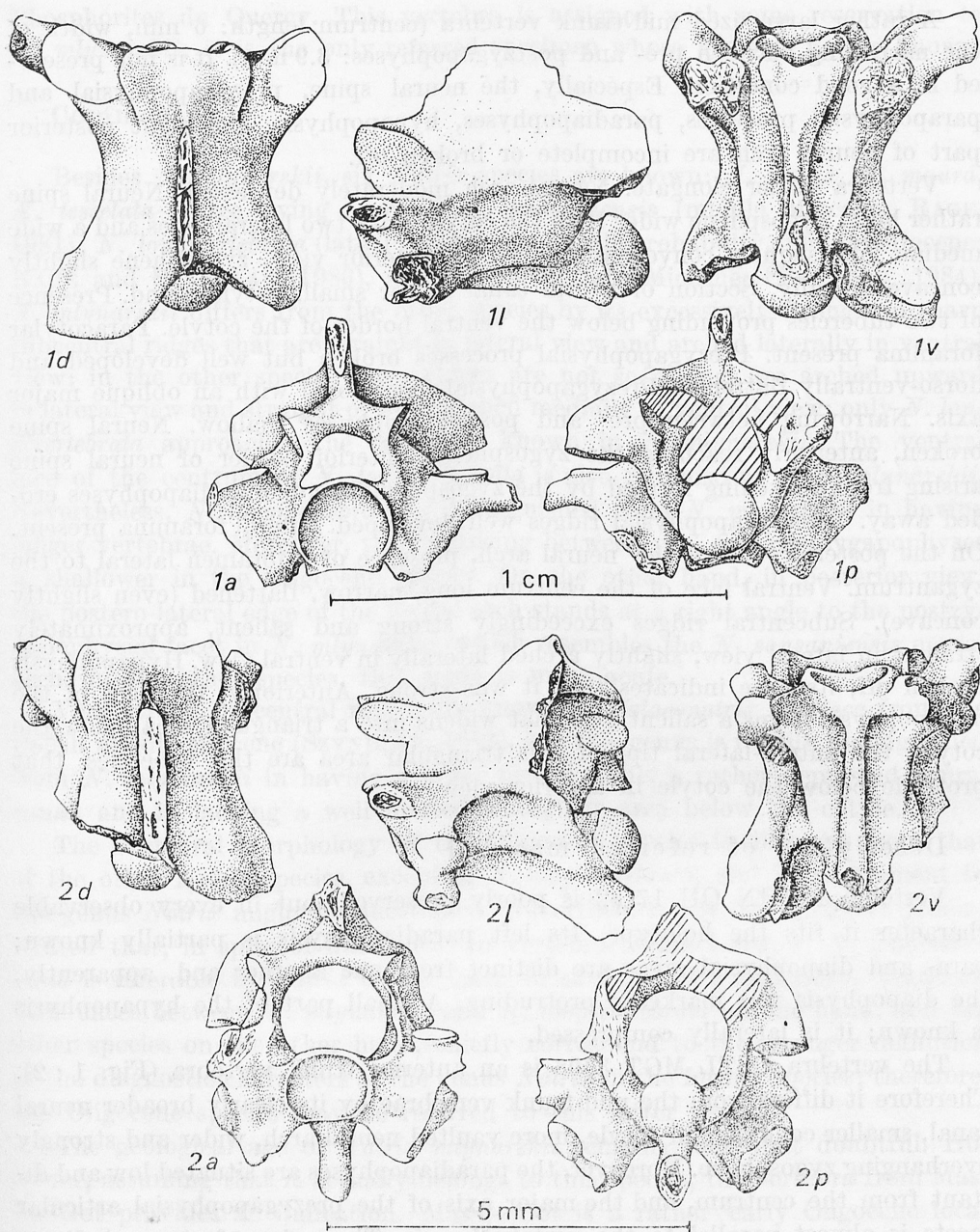


Fig. 1. *Natrix mlynarskii* sp. n. 1 — mid-trunk vertebra (holotype, MNHN, QU 17181); Phosphorites du Quercy, unknown locality, France; ante-Miocene, probably Oligocene. 2 — anterior trunk vertebra (USTL, MGT 3508); Mas-de-Got, Phosphorites du Quercy, France; early Oligocene. Hatched areas = matrix. Views: a — anterior, d — dorsal, l — lateral, p — posterior, v — ventral

## Description of the holotype (Fig. 1:1)

A rather large-sized mid-trunk vertebra (centrum length: 6 mm, width of the narrowing between pre- and postzygapophyses: 3.9 mm). It is not preserved in a good condition. Especially, the neural spine, prezygapophysial and parapophysial processes, paradiapophyses, hypapophysis, and right posterior part of neural arch are incomplete or broken off.

Vertebra rather elongate. Neural arch moderately depressed. Neural spine rather high. Zygosphenes wider than the cotyle, with two lateral lobes and a wide median lobe slightly convex anteriorly. In anterior view, zygosphenes slightly concave dorsally. Section of neural canal rather small. Cotyle round. Presence of two tubercles protruding below the ventral border of the cotyle. Paracotylar foramina present. Prezygapophysial processes broken but well developed and dorso-ventrally flattened. Prezygapophysial facets oval with an oblique major axis. Narrowing between pre- and postzygapophyses shallow. Neural spine broken, anteriorly reaching the zygosphenes; anterior border of neural spine arising from a swelling formed by the zygosphenial roof. Paradiapophyses eroded away. Interzygapophysial ridges well developed. Lateral foramina present. On the posterior wall of the neural arch, presence of a foramen lateral to the zygantrum. Ventral face of the centrum long, narrow, flattened (even slightly concave). Subcentral ridges exceedingly strong and salient, approximately straight in lateral view, slightly arched laterally in ventral view. Hypapophysis broken off, its base indicates that it was strong. Anteriorly, the base of the hypapophysis forms a salient keel that widens into a triangular area below the cotyle; the antero-lateral tips of this triangular area are the tubercles that protrude below the cotyle in anterior view.

## Description of referred material

Vertebra MNHN QU 17182 is poorly preserved, but in every observable character it fits the holotype. Its left paradiapophysis is partially known; para- and diapophysial areas are distinct from one another and, apparently, the diapophysis was markedly protruding. A small part of the hypapophysis is known; it is laterally compressed.

The vertebra USTL MGT 3508 is an anterior trunk vertebra (Fig. 1:2). Therefore it differs from the mid-trunk vertebrae by its clearly broader neural canal, smaller condyle and cotyle, more vaulted neural arch, wider and strongly overhanging zygosphenes. Moreover, the paradiapophyses are situated low and distant from the centrum, and the major axis of the prezygapophysial articular facets is almost parallel to the vertebral axis. These two features indicate that this vertebra is a very anterior one; however, contrary to the usual morphology of very anterior vertebrae, it is rather elongate which is one of the characteristics of *N. mlynarskii* mid-trunk vertebrae. Moreover, a foramen opens laterally to the zygantrum in the posterior wall of the neural arch. This latter character, quite frequent in natricine vertebrae, is known in the mid-



-trunk vertebrae of *N. mlynarskii*, the only known natricine snake from the Phosphorites du Quercy. This vertebra is assigned with some reservation to *N. mlynarskii*; it is the only referred specimen whose geologic age is known.

### Comments

Besides *N. mlynarskii*, six *Natrix* species are known: *N. natrix*, *N. maura*, *N. tessellata* (three living species), *N. sansaniensis* (middle Miocene; RAGE, 1981), *N. longivertebrata* (late Pliocene and, in all probability, middle Miocene; RAGE and SZYNDLAR, 1986), and *N. parva* (late Miocene; SZYNDLAR, 1984). *N. mlynarskii* differs from the other species by its excessively strong and sharp subcentral ridges that are straight in lateral view and arched laterally in ventral view; in the other species these ridges are not so strong, are arched upward in lateral view and straight or even arched medially in ventral view; only *N. longivertebrata* approaches the condition known in *N. mlynarskii*. The ventral face of the centrum of *N. longivertebrata* is also reminiscent of *N. mlynarskii*. Nevertheless, *N. longivertebrata* is distinguished from *N. mlynarskii* in having longer vertebrae. Moreover, the narrowing between pre- and postzygapophyses is shallower in the Oligocene species. On the other hand, in posterior view, the postero-lateral edge of the neural arch stands at a right angle to the postzygapophysial facet in *N. mlynarskii*, which resembles the *N. sansaniensis* neural arch; in the other species, this angle is more acute.

Very strong subcentral ridges are known in *Palaeonatrix silesiaca* from the Polish middle Miocene (SZYNDLAR, 1982), but this genus is readily distinguished from *N. mlynarskii* in having a lower neural spine, a rather depressed neural canal, and in lacking a well limited triangular area below the cotyle.

The vertebral morphology of the Oligocene species is different from that of the other *Natrix* species, excepting *N. longivertebrata*, and its assignment to the genus *Natrix* might be questioned. Nevertheless, SZYNDLAR (1984) demonstrated that, in spite of differences in vertebral characteristics, *N. longivertebrata* is referable to *Natrix* on the basis of skull bones morphology. Vertebral differences between *N. mlynarskii* and *N. longivertebrata* on one hand, and the other species on the other hand, chiefly correspond to the stronger definition of the diagnostic characters of the genus *Natrix* in the former species; therefore, the Oligocene species may be referred to this latter genus.

The geological age of *Natrix mlynarskii* remains somewhat doubtful. However, assuming that it actually belongs to this species, the vertebra from Mas-de-Got provides an indication. Mas-de-Got is a rather early Oligocene locality (Villebramar reference locality; see Fig. 2). Besides, at least in Western Europe, most Eocene reptiles died out by the Eocene-Oligocene transition (RAGE, 1984c, 1986), therefore it may be supposed that *N. mlynarskii* does not come from Eocene localities of the "old collections". Moreover, localities from the late Oligocene being very rich and lacking *N. mlynarskii*, it is supposed that this species occurred during the early and/or middle Oligocene.

*Coluber cadurci* RAGE, 1974

- 1973 "Colubrinae A": DE BONIS et al., tabl. 2 (5).  
 1974 *Coluber cadurci* nov. sp.: RAGE, p. 295—297.  
 1984a *Coluber cadurci*: HOLMAN, p. 225.  
 1984a *Coluber cadurci* RAGE, 1974: RAGE, p. 44.  
 1987 *Coluber cadurci*: RAGE, p. 37.

Stratigraphic and geographic distribution: *C. cadurci* has been reported from the French Oligocene only, from the level of the Villebramar reference locality to that of the Coderet reference locality (see Fig. 2).

Comments: Only vertebrae of *Coluber cadurci* are known. They display a typical colubrid morphology: vertebrae elongate and lightly-built, neural canal broad, zygosphenes wide and thin, neural spine well developed and long (anteriorly reaching the zygosphenes), prezygapophysial processes well developed and strongly projecting, para- and diapophysial areas distinct from one another, paracotylar foramina present, centrum narrow, anterior trunk vertebrae with a hypapophysis, middle and posterior trunk vertebrae with a narrow haemal keel extending nearly the entire length of the ventral face of the centrum. The vertebrae of *C. cadurci* closely resemble those of a group of colubrid snakes that includes the genus *Coluber*. Within this group, vertebrae are exceedingly difficult to identify at the generic level. It is not possible to demonstrate that this fossil snake actually belongs to the genus *Coluber* nor does it seem possible to falsify this assignment. Therefore I only tentatively and symbolically referred the species to *Coluber*.

*C. cadurci* appears abruptly in stratigraphic beds (Villebramar reference locality) that may be labelled early Oligocene (see Fig. 2) and it is known up to the end of the Oligocene. *C. cadurci* perhaps still occurred in the early Miocene.

*Coluber atavus* (MEYER, 1855)

- 1855 *Tropidonotus atavus*: MEYER, p. 336—337.  
 1860 *Coluber (Tropidonotus?) atavus*: MEYER, p. 232.  
 1880 *Elaphis atavus*, MEYER: DE ROCHEBRUNE, p. 291.  
 1888 *Elaphis atavus* (MEYER): LYDEKKER, p. 251.  
 1905 *Tropidonotus atavus*: DE STEFANO, p. 39.  
 1939 *Elaphis atavus* H. v. MEYER: KUHN, p. 20.  
 1961 *Elaphe atavus* (H. v. MEYER): MLYNARSKI, p. 37—38.  
 1963 ?*Coluber atavus* H. v. MEYER 1859: KUHN, p. 20.  
 1984a *Coluber atavus* (MEYER, 1855): RAGE, p. 44.

Stratigraphic and geographic distribution: *C. atavus* is known from Rott, West Germany. Latest Oligocene. According to MEYER (1860), the species could be present in the Weisenau early Miocene (West Germany).

Comments: MEYER based the species on a specimen comprising the skull and a part of the axial skeleton embedded in the matrix (IPBo, H. v. MEYER

Nr 9). He first named the species without a description (1855) and he described and illustrated this specimen later (1860, p. 235—236, Pl. 25, fig. 2, 3). MEYER (1860) referred two other specimens to this species. According to the MEYER's figures, mid and posterior trunk vertebrae lack hypapophyses; therefore the species cannot be referred to the genus *Tropidonotus* (= *Natrix*). DE ROCHEBRUNE (1880) assigned this fossil species to the genus *Elaphis* (that is *Elaphe*); LYDEKKER (1888), KUHN (1939, 1963) and MLYNARSKI (1961) endorsed this latter opinion. The articulated nature of the fossils referred to *C. atavus* makes comparisons with species represented by isolated vertebrae impossible. It is not possible to infer a precise referral from the MEYER's article and the assignment to *Coluber* (MEYER, 1860) seems provisionally preferable. This taxon is in need of revision.

According to TROSCHER (1859, 1861), MEYER would have founded *C. atavus* on the material on which *Coluber papyraceus* TROSCHER, 1854, from the same locality, was based (see above). Therefore, *C. atavus* would be a junior synonym of the latter species. In fact, TROSCHER and MEYER did probably not study the same specimens (MLYNARSKI, 1961); anyhow, *Coluber papyraceus* is a nomen nudum (RAGE, 1984a).

The age of Rott, the sole locality that yielded *C. atavus*, has been recently considered early Miocene (BÖHME et al., 1982). This is probably the result of the fact that, in his stratigraphic sequence of the Neogene, MEIN (1975) defined a stratigraphic unit "MN O" below "MN 1". Although termed "MN" (= Neogene Mammals), MN O represents the latest Oligocene, whereas MN 1 is the earliest Miocene horizon.

### *Texasophis galbreathi* HOLMAN, 1984

1984a *Texasophis galbreathi*: HOLMAN, p. 223—225.

1987 *Texasophis galbreathi*: RAGE, p. 37.

Stratigraphic and geographic distribution: *T. galbreathi* is known only from Flats, the type-locality (Colorado, USA). Scenic Member of Brule Formation; age not precisely known: Orellan or Whitneyan; middle or late Oligocene (HOLMAN, 1984b).

Comments: *Texasophis galbreathi* is known only by one trunk vertebra. Although this vertebra is rather poorly preserved, colubrid characteristics are clearly apparent. The vertebra is lightly-built and elongate. The neural canal displays a broad section and the zygosphenes are wide and thin. The neural spine is well developed and long; anteriorly, it reaches the zygosphenial roof. The prezygapophysial processes are broken off but they were well developed although perhaps short. The paradiapophyses are divided into para- and diapophysial parts. The elongate and narrow ventral face of the centrum bears a long and narrow haemal keel whose bottom is flattened. Presence or absence of paracotylar foramina cannot be determined.



		EUROPE		NORTH AMERICA	
million years 23/23.5		reference localities	oligocene colubrid snakes	snakes	mammal ages
OLIGOCENE	Arvernian	Coderet	Coluber cadurci	Coluber atavus	Arikareean
		La Milloque			
		Boningen			
		Mas de Pauffié			Whitneyan
		Antoingt			
	Suevian	Heimersheim	Natrix mlynarskii	Texasophis galbreathi	Orellan
		Les Chapelins			Chadronian
		Montalban			
		Villebramar			
		Hoogbutsei			
34/36					

Fig. 2. Stratigraphic occurrence of the Oligocene *Colubridae*. The stratigraphic distribution of *Natrix mlynarskii* is somewhat doubtful; it is based on one vertebra referred, with some reservations, to this species; the precise stratigraphic origin of the other referred specimens is unknown. *Texasophis galbreathi* is known by only one specimen that comes from one locality that is either Orellan or Whitneyan

#### IV. CONCLUSIONS

Most of the eocene snakes referred to the *Colubridae* actually belong to the *Boidae*. The geological age of the other supposed eocene *Colubridae* is highly questionable. At the present time, unquestionable colubrid snakes are unknown from the Eocene.

Unquestionable *Colubridae* occur in the Oligocene. *Coluber cadurci* and *Natrix mlynarskii* are the oldest known species, they appeared in the European early Oligocene. *Coluber atavus* is a still poorly known colubrid snake from the European latest Oligocene. *Texasophis galbreathi* is the only ante-Miocene colubrid snake reported from North America; it comes from a middle or late Oligocene locality.

It should be noted that both colubrine and natricine vertebral morphology occurred as early as the early Oligocene.

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## STRESZCZENIE

Bujny rozwój węży z rodziny *Colubridae* datuje się od miocenu; w stanowiskach przedmiocénskich węże te są rzadkością. Niniejsza praca zawiera krytyczny przegląd wszystkich doniesień o *Colubridae* z paleogenu. Najstarsze znane węże z rodziny *Colubridae* miały pochodzić z eocenu; w pracy dowiedziono, że tzw. eocénskie *Colubridae* albo nie reprezentują tej rodziny węży, albo że



są one geologicznie młodsze. Najstarszymi niekwestionowanymi przedstawicielami *Colubridae* są *Coluber cadurci* i *Coluber atavus*, oba z oligocenu Europy, *Texasophis galbreathi* z oligocenu Ameryki Północnej oraz *Natrix mlynarskii* sp. n. z przedmioceni, najprawdopodobniej oligoceni, stanowisk europejskich.

