The snakes (Reptilia, Serpentes) of the Miocene of Portugal

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ABSTRACT

Key-words: Snakes (Reptilia); Boidae; Colubridae; Oriental vipers; Miocene; Portugal.

The ophidian fauna coming from the Miocene of Amor (MN 5), Quinta das Pedreiras and Quinta do Pombeiro (both MN4) (Portugal) consists of the following taxa: cf. Bavarioboa sp. (Boidae); cf. Coluber sp. (Colubridae); two unidentified Colubridae; Vipera sp. ("Oriental vipers" complex) (Viperidae). The assemblage is characteristic for the lower/middle Miocene transition and it resembles snake faunas known from other European localities of similar age.

RESUMO

Palavras chave: Serpentes (Reptilia; Bódeos; Colubrídios; vipers orientais; Miocênico; Portugal.

As faunas de ofideos do Miocénico de Amor (MN5), Quinta das Pedreiras e Quinta do Pombeiro (ambas MN4), em Portugal, consistem nos seguintes taxa: cf. Bavarioboa sp. (Boidae); cf. Coluber sp. (Colubridae); dois colubrídios indeterminados; Vipera sp. (complexo de "vipers orientais") (Viperidae). A associação é característica da transição do Miocénico inferior para o Miocénico médio; assemelha-se às faunas de ofideos europeias de idade similar.

INTRODUCTION

The first presence of snakes in Portugal has been reported from the Cretaceous period. These ophidians, represented by poorly preserved fossils, were the marine Simoliophis (Sauvage, 1896) and an unidentified terrestrial boid (Rage, 1981). Thus far, the only Paleogene terrestrial snakes reported from Portugal are a late Paleocene or Lowermost Eocene Boid from Silveirinha (Antunes, 1981; Antunes & Russell, 1981). The oldest subsequent fossil record of Portuguese ophidian comes from the Miocene. The present paper discusses the taxonomic position of the latter snakes.

The snake remains from the Portuguese Miocene available for study have been found in three localities: Amor, Quinta das Pedreiras, and Quinta do Pombeiro (biozone MN 5: Antunes & Mein, 1981; M.T.Antunes, pers. comm.; Antunes, this volume). The material is consisted of several trunk vertebrae, usually in bad state of preservation; no cranial elements have been found.

The entire material from the Portuguese Miocene, except for two vertebrae, was previously described by Antunes & Rage (1974). Antunes & Rage identified the ophidian fossils to the family level only: Boidae, Colubridae, and Viperidae. No doubt, more precise identification of the remains was impossible at those times, mainly due to the fact that lower/middle Miocene snake faunas of Europe were poorly recognized in the early 1970s. In the meantime, our knowledge on snakes inhabiting the western Palaeartic in the early Neogene has considerably grown, especially during the last two decades. Thanks to that, it is now possible to identify most of the fossils originally described by Antunes & Rage to the generic level.

The ophidian remains from the Portuguese sites were compared with fossils coming from a number of European localities, in particular those of similar geological age (i.e., lower/middle Miocene transition). These localities are following (papers describing snake faunas are given in parentheses): Córcoles in Spain (MN 4) (Alférrez & Brea 1981); Agramon in Spain (MN 4) (unpublished observations); Dolnice in Czechia (MN 4) (Szyndlar 1987); Petersbuch 2 in Germany (MN 4) (Szyndlar & Schleich, 1993); Oberdorf in Austria (MN 4) (Szyndlar 1998); Vieux Collonges in France (MN 4/5) (Ivanov 1997, Szyndlar & Rage 1999).
DESCRIPTION OF THE MATERIAL

Family BOIDAE

Cf. Bavarioboia sp.
(Fig. 1)

1974 - Boidae: Boidé indét. Antunes & Rage, Table I (p. 59).

Material
Two mid-trunk vertebrae from Quinta das Pedreiras, Va2 local unit, MN4.

One vertebra was described and figured by Antunes & Rage (1974: 53, fig. 3) (Fig. 1 A-E in the present paper); the other vertebra, partly damaged (Fig. 1 F-G), was previously not studied.

Both vertebrae display features characteristic for the Booidae (= family Boidae s.l.), among others they are strongly built and possess relatively very short centra and reduced prezygapophyseal processes. By their overall morphology, the vertebrae are most similar to those of the extinct European genus Bavarioboia. Close similarities can be observed in relatively large absolute dimensions of the vertebrae (when compared with the Erycinae, another lineage of boid snakes widespread in the European Neogene), stout morphology of the entire vertebral body, weakly marked indentation between pre- and postzygapophyses, vaulted neural arch, and strongly built haemal keel (Szyndlar & Schleich, 1993). Precise taxonomic allocation of the vertebrae from Quinta das Pedreiras is however not fully possible, first of all because of the scantiness of the material; on account of that the generic name is preceded by the particle “cf.”

Comments
Present studies (partly unpublished) indicate that the genus Bavarioboia may have been widespread in Europe in the period between the late Oligocene (MP 27) and the middle Miocene (MN 6) (Szyndlar & Schleich, 1993; Szyndlar, 1998; Rage & Szyndlar, in prep.). The type species (and the only described species), Bavarioboia hermi, was originally reported from the lower Miocene of Petersbuch 2 in Germany (Szyndlar & Schleich, 1993).

Snakes coming from other European localities differ slightly from the type material.
Bavarioboia represents the family Boidae s.s. (= subfamily Booinae or boid) as indicated by the presence of paracotylar foramina in a part of vertebrae coming from the type locality. Occurrence of boas in the lower and middle Miocene of Europe is astonishing, particularly considering the distributional pattern of their living relatives (today occupying the tropical America, Madagascar, and some West Pacific islands). Considering that Bavarioboia was a relatively large and certainly non-burrowing snake, its possible ancestry among European autochthonous Eocene Booidae and, in consequence, its survival despite the severe conditions of the Oligocene is little probable (apart from lacking fossil evidence of such a possibility). This snake is therefore supposed an immigrant that appeared in Europe perhaps yet in the Late Oligocene immediately after improvement of the climatic conditions (Szyndlar & Schleich 1993; Szyndlar & Böhme 1993).

Family COLUBRIDAЕ

Cf. Coluber sp.
(Fig. 2)

Material
One mid-trunk vertebra from Amor (Leiria), MN5.

The vertebra was not studied by Antunes & Rage (1974). Owing to the presence of a haemal keel (instead of hypapophysis), the vertebra is characteristic of the “non-natricine” Colubridae. The vertebra belonged to a large snake; although its condyle is partly damaged and therefore precise measurements are impossible, the centrum length most likely reached the value of 7 mm approximately. Despite the poor preservation of the vertebra, its morphology (in particular the shape of the haemal keel and moderately elongate centrum) along with the relatively large size indicate that it may have represented the living genus Coluber. For the same reasons as in the case of Bavarioboia the generic allocation of the discussed colubrid vertebra cannot be fully demonstrated; on account of that its generic name is preceded by the particle “cf.”

Comments
The snake from Amor is most similar to Coluber dolmicensis and C. caspioides, both extinct species described from the lower Miocene of Dolnice (Szyndlar, 1987) and Petersbuch 2 (Szyndlar & Schleich, 1993), respectively. These two fossil taxa, reported later also from other older and coeval localities (among others in Czechia and Austria: Ivanov 1997; Szyndlar 1998), may have actually represented a single species. Both were probably closely related to C. caspius, inhabiting today southeastern Europe, and may have represented an evolutionary lineage leading to the recent species.

Colubridae indet.

Material
One mid-trunk vertebra from Quinta das Pedreiras; one mid-trunk vertebra from Quinta do Pombeiro, Va2 local unit; MN4.

Antunes & Rage (1974: 56) mentioned that “deux vertèbres de Caenophidiens ne peuvent être déterminées avec précision”. Of these two elements, coming from Quinta das Pedreiras, only one vertebral fragment, consisting of a lower portion of the centrum, was available to study. The presence of a haemal keel (and not hypapophysis) indicates clearly that the vertebra belonged to a “non-natricine” Colubridae.
Two small vertebrae from Quinta do Pombeiro were described by Antunes & Rage (1974, p. 57) as follows: “deux très petites vertèbres appartiennent aux serpents, elles ne sont pas déterminables”. Both bones are strongly damaged and on account of that one of them is indeed unidentifiable. The other vertebra however represented no doubt a member of the family Colubridae. The presence of a haemal keel suggests a “non-natricine” Colubridae.

The vertebra from Quinta das Pedreiras was characterized by a relatively elongate centrum, whereas that from Quinta do Pombeiro was provided with a relatively short centrum. Most likely, both fossils represented two different species.

A single vertebra of an unidentified Colubridae from Universidade Católica (MN 3) “Colubrine à vertèbres relativement allongées”, according to Antunes & Rage (1974, p. 52) was not available to the present study.

Family VIPERIDAE

Vipera sp.

1974 - Viperidae: Vipérid ô indé t. Antunes & Rage, Table I (p. 59).

Material

One mid-trunk vertebra from Quinta das Pedreiras.

Viperid snakes can be easily distinguished from other ophidians bearing hypapophyses throughout the thoracic portion of the column on the basis of several features, among others by having straight hypapophyses, ventrally directed parapophyseal processes, and posteriorly depressed neural arches. The vertebra from Quinta das Pedreiras (cf. Antunes & Rage, 1974, fig. 4), although devoid of parapophyseal processes and hypapophysis, is clearly referable to vipers based on the strong flattening of its neural arch. It displays well several characteristic features of the “Oriental vipers” complex of the living genus Vipera: of them, the most important are large absolute dimensions and relative shortness of the vertebral centrum (Szyndlar & Rage, 1999). The centrum of the discussed vertebra is 7.5 mm long and it is as long as wide. Vertebral centra of members of two other complexes of the genus Vipera (“aspis” and “berus” groups) are smaller and relatively more elongate.

Comments

Large members of the genus Vipera (“Oriental vipers” complex) first appeared in Europe at the end of lower Miocene (MN 4) and since then they belonged to commonest European snakes in a considerable part of the continent. At the turn of the Pliocene the “Oriental vipers” became extinct almost entirely within their European range, mainly because of the climatic deterioration. Today, these snakes inhabit principally Middle East and northern Africa, whereas in Europe they occur in southeasternmost skirts of the continent only.

CONCLUSIONS

Compared with other European faunas of similar age, the Portuguese snakes form an assemblage highly characteristic for the lower/middle Miocene transition. The ophidian fauna from Portugal is not as diverse as the faunas described from coeval localities of other European countries, in particular France, Germany, and Czechia, but this impoverishment no doubt results from the scantiness of the available material rather than from any other reasons. Interestingly, the snake assemblage from Portugal least resembles faunas coming from the nearest localities: Córcoles and Agramon in Spain and Vieux Collonges in France (cf. Table).

The lower/middle Miocene transition (MN 4/5) is a distinct “border line” in the composition of snake faunas in Europe (Szyndlar & Schleich, 1993; Szyndlar & Böhme,

**TABLE**

Comparison of the occurrence of Bavarioboa, Coluber (cf. C. dolnicensis or cf. C. caspioides), and Vipera (“Oriental vipers” complex) in the Portuguese and other European localities in the lower/middle Miocene transition period.

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<th>Bavarioboa</th>
<th>Coluber</th>
<th>Vipera</th>
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<td>Amor</td>
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<td>Q. das Pedreiras</td>
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<td>Córcoles</td>
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<td>Agramon</td>
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<td>Dolnice</td>
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<td>Petersbuch</td>
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<td>Oberdorf</td>
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<tr>
<td>Vieux Collonges</td>
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361
Fig. 1 - Two vertebrae (A-E and F-G) of *Bavarioboa* sp. from Quinta das Pedreiras. A - left lateral view; F - right lateral view; B - dorsal view; C, G - ventral views; D - anterior view; E - posterior view.
Fig. 2. A vertebra of cf. Cetotherium sp. from Anmor. A - right lateral view, B - anterior view, C - posterior view, D - dorsal view, E - ventral view.
1993). Although a number of (usually small-sized) members of the families Colubridae and Viperidae were present in Europe already in the Oligocene and lowermost Miocene, respectively, the ophidian fauna was still dominated by primitive snakes, mainly boas.

At the end of the lower Miocene, a considerable number of new ophidian taxa invaded Europe. The most characteristic (and at the same time most common) elements of the migrations were large-sized snakes belonging to three most advanced ophidian families: *Coluber* (family Colubridae), “Oriental vipers” (Viperidae), and cobras of the genus *Naja* (Elapidae), the latter absent in the Portuguese materials. The invasions of “Oriental vipers” and cobras as well as other thermophilous snakes (in particular *Python*) may have been correlated with the thermal maximum observed in the European climate around the lower/middle Miocene transition (Rage in Demarçq et al., 1983).

Following the arrival of new snakes at the end of the lower Miocene, “archaic” components of the European snake fauna (mainly boas, including *Bavarioboa*) became rare in fossil materials and subsequently disappeared completely in the middle Miocene. Interestingly, an overwhelming majority of “modern” elements of the European snake fauna, inhabiting Europe from the middle Miocene onward, were closely related to species living recently, although not necessarily in the European continent.

ACKNOWLEDGMENTS

I am deeply grateful to Professor Miguel Telles Antunes (Universidade Nova de Lisboa) for the loan of the material to study as well as for his great hospitality during my visit in Portugal in May 1999. The study was supported by the grant 6 P04C 073 14 of the Committee of Scientific Research of Poland.

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