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Iberian snake fauna of the early / middle Miocene transition

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Abstract: The paper reviews ophidian taxa of the Iberian Peninsula during the "MN4-event" at the end of the early Miocene, when the "ancient" snake fauna was replaced, in a rather rapid way, by "modern" one. The replacement was a part of a vast process, occurring simultaneously throughout Europe. Both the "ancient" and "modern" Iberian faunas are closely related to the contemporary faunas inhabiting France and Germany. The following snake taxa, coming from four Spanish and Portuguese localities (Agramón: MN3 or MN3-4, Córcoles: MN4, Quinta das Pedreiras: MN4, and Amor: MN5) were described in brief: Scolecophidia indet., *Eoanilius* sp., cf. *Bavarioboa* sp., cf. *Falseryx* sp., *Eryx* sp., cf. *Eryx* sp., Booidea indet., Natricinae indet., cf. "*Coluber*" *cadurci*, cf. *Coluber* sp., non-natricine Colubridae indet., *Naja* sp., *Vipera* sp. ("*aspis*" complex), *Vipera* sp. ("Oriental viper").
Key words: Early / middle Miocene transition, Iberian Peninsula, serpentes.

Resumen: La fauna de serpientes ibéricas en la transición Mioceno inferior / Mioceno medio. – Se revisan los taxones de ofidios presentes en la Península Ibérica durante el "evento MN4" al final del Mioceno inferior, cuando la "antigua" fauna de serpientes fue reemplazada, de forma bastante rápida, por otra "moderna". Este reemplazo fue parte de un amplio proceso ocurrido simultáneamente en toda Europa y ambas faunas ibéricas, "antigua" y "moderna", se encuentran estrechamente relacionadas con las propias de Francia y Alemania. Se describen los siguientes taxones de serpientes: Scolecophidia indet., *Eoanilius* sp., cf. *Bavarioboa* sp., cf. *Falseryx* sp., *Eryx* sp., cf. *Eryx* sp., Booidea indet., Natricinae indet., cf. "*Coluber*" *cadurci*, cf. *Coluber* sp., Colubridae indet. no natricina, *Naja* sp., *Vipera* sp. ("*aspis*" complex), *Vipera* sp. ("Oriental viper"), procedentes de cuatro localidades españolas y portuguesas (Agramón: MN3 ó MN3-4, Córcoles: MN4, Quinta das Pedreiras: MN4 y Amor: MN5).
Palabras clave: Península Ibérica, serpientes, transición Mioceno inferior / Mioceno medio.

INTRODUCTION

The oldest snakes known from the Iberian Peninsula, represented by poorly preserved fossils, are of Cretaceous age (SAUVAGE, 1896; RAGE, 1981, 1999). The only Paleogene snakes ever reported from Iberia come from the early Eocene of Portugal (RAGE & AUGÉ, 2003) and late Eocene of Spain (SZYNDLAR & SCHLEICH, 1994). There is a long gap in our knowledge on Iberian ophidian faunas, ranging from the late Eocene to the beginning of the Miocene. The oldest Neogene snake fauna known from Iberia is that reported from the Spanish locality of Bardenas Reales de Navarra (biozone MN2b-3; for the definition of MN biozones see STEININGER, 1999) by MURELAGA *et al.* (2002). The fauna described by MURELAGA *et al.* (2002) consists of poorly preserved remains identified as "?*Eryx*" (p. 358, Fig. 9.2) and "Colubridae indéterminés" (p. 359, Fig. 9.3). Another uni-

dentified colubrid snake ("«Colubriné» à vertebres relativement allongées") was mentioned from the Portuguese site of Universidade Católica (MN3) by ANTUNES & RAGE (1974; p. 52). The snake fossils coming from the above two localities have not been examined by the authors of the present paper.

Compared with the older fossils, the snake fauna inhabiting the Iberian Peninsula at the end of the early Miocene, i.e. around the biozone MN4 (between ca. 18 and 17 mya), is rich enough and fairly well documented. This period is of special interest in the history of European snakes, because it was just the early / middle Miocene transition when an ancient ophidian fauna, largely consisting of extinct genera of primitive ophidians, was replaced suddenly by modern immigrants from the East (these newcomers will be termed "MN4-wave" in the farther text). Most of the latter snakes do not differ much, at least at the generic level, from those inhabiting recently the West Palaearctic (but not necessarily Europe). Thus far, most data on the ophidians representing the "MN4-wave" in the Iberian Peninsula were dispersed in literature and in most cases they were restricted to short mentions only or remained unpublished. In the present paper we make an attempt to gather the entire available information and to review briefly what we currently know about the snakes living in Iberia, immediately before and during the time of the great invasion.

MATERIALS

The fossil remains examined in this study come from the following four localities (the ages of the faunas follow the references given in parentheses): Agramón (Albacete, Spain), MN3-4 (BÖHME & ILG, 2003) or MN3 (A.J. van der Meulen, unpublished data); Córcoles (Guadalajara, Spain), MN4b (ALFÉREZ *et al.* 1982); Quinta das Pedreiras (Lisboa, Portugal), MN4 (ANTUNES, 2000); and Amor (Lisboa, Portugal), MN5 (ANTUNES, 2000).

The fossil materials belong to the collections housed in the Universidad Complutense in Madrid (UCM), Museo Nacional de Ciencias Naturales in Madrid (MNCN / CSIC), and Universidade Nova in Lisboa (UNL) (Table 1).

The present paper is based in part on previously reported remains as well as on those undescribed yet. Table 1 (below) summarizes the entire published (descriptions, faunistic lists or short mentions) and unpublished fossil record.

REVIEW OF SNAKE TAXA

Scolecophidia indet.

The oldest scolecophidians appeared in Europe in the early Eocene (GODINOT, *et al.* 1978) and disappeared prior to the "Grande Coupure" events at the Eocene / Oligocene boundary (e.g. RAGE, 1974, 1978).

There is no fossil record of scolecophidians from the European Oligocene and the beginning of the Miocene. These snakes re-appeared in Spain (the locality of Córcoles) (ALFÉREZ & BREA, 1981) and Czechia (SZYNDLAR, 1987) at the end of the early Miocene, perhaps as members of the "MN4-wave" coming from the East. Scolecophidians survived in southeastern Europe until now. They inhabited Spain until at least the end of the Miocene (SZYNDLAR & SCHLEICH, 1994).

The most probable generic allocation of the European fossil scolecophidians is in the genus *Typhlops* (family Typhlopidae), the only living representative of this group in the European continent. Unfortunately, because of the very simple vertebral morphology of these snakes, it is impossible to identify their

TABLE 1. Material examined, indicating taxonomic position, localities and references.
TABLA 1. Material examinado, detallando posición taxonómica, localidad de procedencia y referencias.

Taxon	Locality	Original systematic allocation & Reference
Scolecophidia indet.	Córcoles	*Typhlops*: ALFÉREZ & BREA (1981; p. 12, pl. I10)
Eoanilius sp.	Agramón	*Eoanilius* sp.: SZYNDLAR & RAGE (2003; p. 15); this paper (Fig. 1A-E)
cf. *Bavarioboa* sp.	Quinta das Pedreiras	boidé indét.: ANTUNES & RAGE (1974; p. 59, Fig. 3); cf. *Bavarioboa* sp.: SZYNDLAR (2000; p. 311, Fig. 1); cf. *Bavarioboa* sp.: SZYNDLAR & RAGE (2003; p. 45, Fig. 17)
Falseryx sp.	Agramón	cf. *Falseryx* sp.: SZYNDLAR & RAGE (2003; p. 65, Fig. 29)
Eryx sp.	Córcoles	Erycinae gén. & sp. indet.: ALFÉREZ & BREA (1981; p. 15, pl. I11); *Eryx*: SZYNDLAR & SCHLEICH (1994; p. 236); this paper (Fig. 2A-I)
cf. *Eryx* sp.	Agramón	this paper (Fig. 1F-G)
Booidea indet.	Córcoles	subfamily Boinae: SZYNDLAR (1985; p. 463); Booidea indet.: SZYNDLAR & RAGE (2003; p. 89)
Natricinae indet.	Agramón	*Natrix* sp.: SZYNDLAR & RAGE (2003; p. 15); this paper (Fig. 2H-I)
cf. "*Coluber*" *cadurci*	Agramón	this paper (Fig. 1J-L)
cf. *Coluber* sp.	Amor	cf. *Coluber* sp.: SZYNDLAR (2000; p. 312, Fig. 2)
cf. *Coluber* sp.	Córcoles	this paper
non-natricine Colubridae indet.	Quinta das Pedreiras	Colubridae indet.: SZYNDLAR (2000; p. 312)
non-natricine Colubridae indet.	Córcoles	Colubrinae gén. & sp. indet.: ALFÉREZ & BREA (1981; p. 14, pl. I9)
non-natricine Colubridae indet.	Agramón	unidentified non-natricine Colubridae: SZYNDLAR & RAGE (2003; p. 15)
Naja sp.	Córcoles	*Palaeonaja* sp.: ALFÉREZ & BREA (1981; p. 13, Fig. 5, pl. I13); *Naja* sp.: SZYNDLAR & RAGE (1990; p. 387)
Vipera sp. ("*aspis* complex")	Agramón	*Vipera* ('*V. aspis*' complex): SZYNDLAR & RAGE (1999; p. 15, Fig. 7.10)
Vipera sp. ("Oriental viper")	Quinta das Pedreiras	Vipéridé indét.: ANTUNES & RAGE (1974; p. 59, Fig. 4); *Vipera* sp. ("Oriental vipers" complex): SZYNDLAR (2000; p. 313)
Vipera sp. ("Oriental viper")	Córcoles	this paper (Fig. 2J-K)

vertebrae (the only known fossil remains) even to the family level.

***Eoanilius* sp.**

Eoanilius, an extinct genus of the family Aniliidae (with the recent distribution restricted to tropical America) was present in Europe since the late Eocene (RAGE, 1974; MILNER *et al.*, 1982). Remains of aniliid snakes were also found in the late Eocene (MP17) of Sossís in Spain (Z. Szyndlar, unpublished data). Unlike most Eocene ophidians, *Eoanilius* survived the "Grande Coupure" events at the Eocene / Oligocene boundary and occurred in Europe yet in the early Miocene. Interestingly, this snake may have been a dominant in ophidian assemblages of southern Germany in the middle early Miocene (MN2 and 3) (SZYNDLAR & SCHLEICH, 1993; SZYNDLAR & RAGE, 2003).

In Iberia, tiny vertebrae of *Eoanilius* were found in Agramón (Fig. 1A-E).

The genus *Eoanilius* was a typical representative of the ancient fauna; it became extinct in the European continent in the beginning of the middle Miocene (MN5, Sandelzhausen in Germany) (Z. Szyndlar, unpublished data). Interestingly, the Aniliidae (represented by another extinct member, *Michauxophis*) re-appeared (and immediately disappeared) in the European continent in the late Pliocene of France (BAILON, 1988).

cf. *Bavarioboa* sp.

The Booidea (in Europe represented mainly by snakes referred to the family Boidae) dominated in all ophidian assemblages throughout the Paleogene. The extinct genus *Bavarioboa*, a member of the boid subfamily Boinae, was first described from the early Miocene (MN4) of German locality of Petersbuch 2 (SZYNDLAR & SCHLEICH, 1993). Up to now as many as seven species of the genus have been reported from Germany and France (SZYNDLAR & RAGE, 2003). *Bransateryx* was the most common European snake in the middle / late (but not latest) Oligocene. Although it became extinct before the end of the Oligocene, *Bransateryx* re-appeared in Europe as a member of the "MN4-wave".

In Iberia, badly preserved vertebrae of this snake were reported (as cf. *Bavarioboa* sp.) from the Portuguese locality of Quinta das Pedreiras (SZYNDLAR, 2000). According to Scanlon (cited in SZYNDLAR & RAGE, 2003), these vertebrae may have belonged to a juvenile *Python* rather than to *Bavarioboa*. The latter opinion is not improbable, considering that the presence of the living genus *Python* (subfamily Pythoninae) in the Mediterranean area is fairly well documented for the early / middle Miocene transition (MN4 and 5) (SZYNDLAR & RAGE, 2003, and references therein). Unfortunately, the question whether the Portuguese remains represented *Bavarioboa* or *Python* cannot be resolved with certainty because of the very limited (two damaged vertebrae only) fossil record.

cf. *Falseryx* sp.

Falseryx, a peculiar extinct genus of uncertain familial allocation (perhaps Boidae or Tropidophiidae), was described from the early Miocene (MN4) of Petersbuch 2 in Germany (SZYNDLAR & RAGE, 2003); *Falseryx* is probably the last non-erycine booid snake that survived in Europe until the end of the Miocene (MN7-8). A "miniature" of *Falseryx* was found among ophidian vertebrae coming from Agramón. Considering some morphological differences between the Spanish remains and the type material as well as the scarcity of the former, the snake from Agramón was only tentatively compared with the genus *Falseryx*. Any further considerations

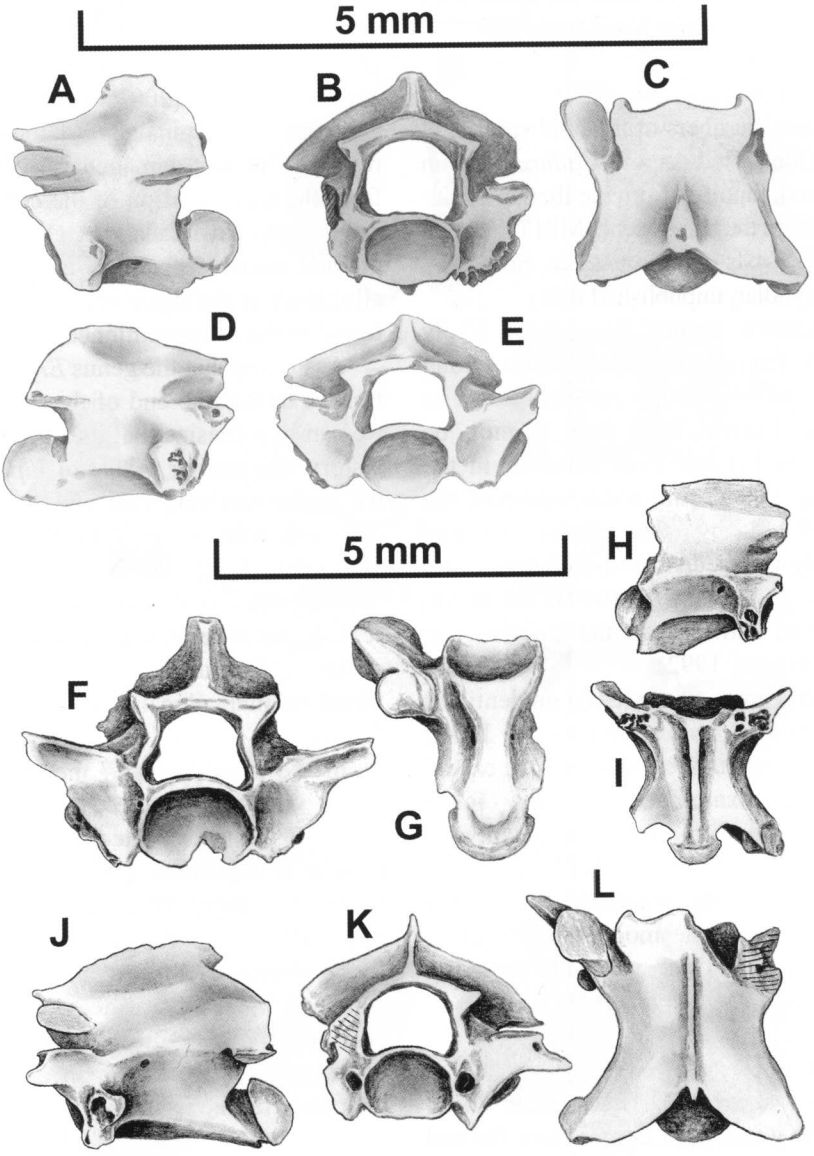

FIGURE 1. Snakes from Agramón, representative of the "ancient" fauna. (A-C and D-E) Anterior trunk and middle trunk vertebrae of *Eoanilius* sp. (F-G) Trunk vertebra of cf. *Eryx* sp. (H-I) Trunk vertebra of Natricinae indet. (J-L) Trunk vertebra of cf. "*Coluber*" *cadurci*. (A, J) Left lateral views. (D, H) Right lateral views. (C, L) Dorsal views. (G, I) Ventral views. (B, E, F, K) Anterior views. The illustrated fossils are property of the Museo Nacional de Ciencias Naturales (CSIC) in Madrid.

FIGURA 1. Serpientes de Agramón representativas de la fauna "antigua". (A-C y D-E) Tronco vertebral anterior y tronco vertebral medio de *Eoanilius* sp. (F-G) Tronco vertebral de cf. *Eryx* sp. (H-I) Tronco vertebral de Natricinae indet. (J-L) Tronco vertebral de cf. "*Coluber*" *cadurci*. (A, J) Visión lateral izquierda. (D, H) Visión lateral derecha. (C, L) Visión dorsal. (G, I) Visión ventral. (B, E, F, K) Visión anterior. Los fósiles ilustrados son propiedad del Museo Nacional de Ciencias Naturales de Madrid (CSIC).

on the Spanish *Falseryx* must be necessarily based on more abundant fossil materials.

***Eryx* sp.**

The oldest members of the boid subfamily Erycinae (identified as cf. *Cadurceryx*, an extinct genus), reported from the Iberian Peninsula, come from the late Eocene (MP17) Spanish locality of Sossís (SZYNDLAR & SCHLEICH, 1994; Z. Szyndlar, unpublished data).

The modern genus *Eryx* most likely appeared in Europe, including Iberia, along with the "MN4-wave"; nevertheless, its appearance before that date cannot be excluded (see below). *Eryx* survived in the European continent until today, however, the area inhabited by this snake became considerably reduced in post-Neogene times (SZYNDLAR & SCHLEICH, 1994). In Spain, *Eryx* survived until at least the middle / late Pliocene (BAILON, 1992).

The first report of *Eryx* (as an unidentified Erycinae) from Córcoles (ALFÉREZ & BREA, 1981) was based on one trunk and one caudal vertebra. The examination of new fossil remains coming from the same locality, in particular the highly complex caudal vertebrae (Fig. 2A-I), reveals that the snake represented indeed the modern genus *Eryx*. Most likely, it was closely related to the living European species, *E. jaculus*.

cf. *Eryx* sp.

As noted above, the first certain fossil record of the genus *Eryx* comes from the end of the early Miocene. Nevertheless, we cannot exclude the possibility that the first appearance of *Eryx* in Europe took place in an earlier phase of the Miocene than postulated in the preceding paragraph. This supposition is based on the presence of "*Eryx*-like" trunk vertebrae in the early Miocene (MN2 and 3) of France and Germany (HOFFSTETTER & RAGE, 1972; SZYNDLAR & SCHLEICH, 1993; SZYNDLAR & RAGE, 2003). Similarly, several vertebrae reported from the Spanish locality of Bardenas Reales de Navarra (MN2b-3) by MURELAGA *et al.* (2002) were also identified as ?*Eryx*. Unfortunately, all these finds are restricted to few damaged vertebrae coming from the trunk portion of the column. At the same time, no caudal vertebrae that could provide decisive evidence about the generic allocation of the discussed snakes have been found in the aforementioned fossil sites.

Assuming that the genus *Eryx* did occur in Europe before the end of the early Miocene, we can hypothesize that its earliest European history was similar to that of *Vipera*, i.e. that the snake was very rare and never played a dominant role in ophidian assemblages (cf. SZYNDLAR & RAGE, 2003). Following the "MN4-event", both *Eryx* and *Vipera* rapidly settled vast areas of Europe and became very common, as indicated by abundant remains found in many localities yielding ophidian fossils.

In the present paper, the snake remains (trunk vertebrae) referred with doubt to the genus *Eryx* are reported from the Spanish locality of Agramón (Fig. 1F-G). The reason for which more precise identification is impossible is the fragmentary nature of the fossil bones as well as the lack of caudal vertebrae. A surprising feature of one trunk vertebra from Agramón is the presence of a distinct paracotylar foramen on one side of the cotyle unlike in the genus *Eryx*.

Booidea indet.

The presence of a member "of the subfamily Boinae" in Córcoles (SZYNDLAR, 1985; p. 463), was based on the observation, made in 1983, of a single relatively large boid trunk vertebra belonging to the UCM collection. A more recent examination of the same collection (in October 2003) did not confirm the presence of any non-erycine Boidae.

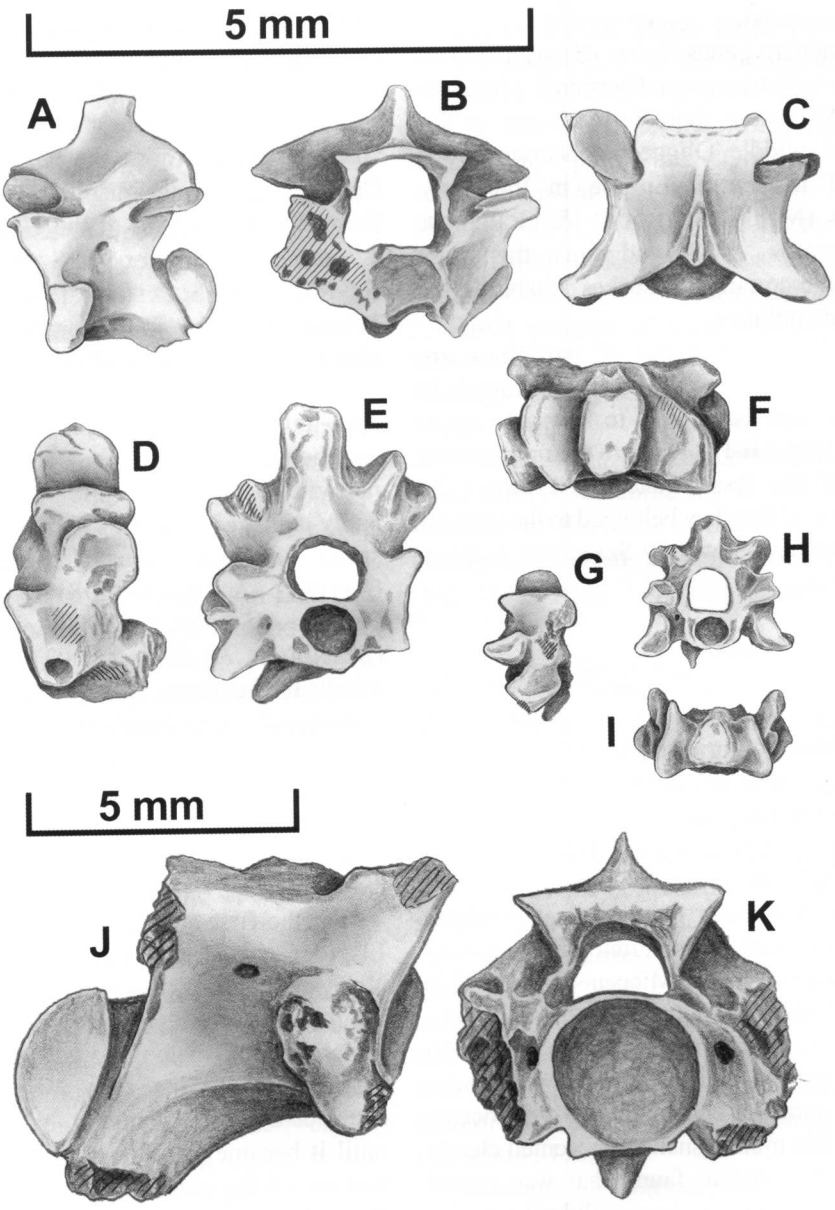

FIGURE 2. Snakes from Córcoles, representative of the "modern" fauna. (A-C) Trunk vertebra of *Eryx* sp. (D-F and G-I) Two caudal vertebrae of *Eryx* sp. (J-K) Trunk vertebra of *Vipera* sp. ("Oriental viper"). (A, D, G) Left lateral views. (J) Right lateral view. (C, F, I) Dorsal views. (B, E, H, K) Anterior views. The illustrated fossils are property of the Universidad Complutense in Madrid.

FIGURA 2. Serpientes de Córcoles representativas de la fauna "moderna". (A-C) Tronco vertebral de *Eryx* sp. (D-F y G-I) Dos vértebras caudales de *Eryx* sp. (J-K) Tronco vertebral de *Vipera* sp. ("Oriental viper"). (A, D, G) Visión lateral izquierda. (J) Visión lateral derecha. (C, F, I) Visión dorsal. (B, E, H, K) Visión anterior. Los fósiles ilustrados son propiedad de la Universidad Complutense de Madrid.

Natricinae indet.

The modern genus *Natrix* (RAGE, 1988) as well as a "«Natriciné» indéterminé" (AUGÉ & RAGE, 1995) were sporadic in Europe in the early and middle Oligocene. Natricines re-appeared in central Europe in the early Miocene (MN3) (SZYNDLAR & SCHLEICH, 1993; IVANOV, 2002) and since then they became the commonest snakes inhabiting the European continent.

The Iberian remains of natricines are represented by a few vertebrae found in Agramón and belonging to a rather small snake(s) (Fig. 1H-I). Owing to the fragmentary nature of the fossil material, it cannot be demonstrated that they belonged to the modern genus *Natrix*, as noted by SZYNDLAR & RAGE (2003).

cf. "*Coluber*" *cadurci*

Coluber cadurci, first described from the early Oligocene of France (RAGE, 1974), is one of two oldest colubrid species of Europe. The snake may have not belonged to the living genus *Coluber* and that is why its generic name is put in quotation marks. The snake was widespread in France throughout the Oligocene and it (or another closely related form) still existed in both France and Germany in the beginning of the Miocene (MN1 and 2) (RAGE, 1988; SZYNDLAR & SCHLEICH, 1993).

The fossil remains found in Agramón indicate that "*Coluber*" *cadurci* may have survived until the end of the early Miocene. Anyway, this minute snake represented clearly the ancient ophidian fauna that was ousted from Europe by modern colubrid species belonging to the "MN4-wave". Owing to the fragmentary nature of the vertebrae from Agramón, their allocation in the fossil species "*C.*" *cadurci* cannot be fully demonstrated (Fig. 1J-L).

cf. *Coluber* sp.

This snake (perhaps two or more species) was recorded from the localities of Córcoles and Amor (SZYNDLAR, 2000). The remains differ substantially from the minute "*Coluber*" *cadurci*. Apart from much larger absolute dimensions, the vertebrae from Córcoles and Amor display morphological features characteristic of the *C. dolnicensis-C. caspioides* complex (cf. SZYNDLAR, 1987; SZYNDLAR & SCHLEICH, 1993), the latter belonging to the most common and most characteristic elements of the "MN4-wave".

Non-natricine Colubridae indet.

The snakes named here collectively "non-natricine Colubridae" are represented by badly damaged (and thus hardly identifiable) small vertebrae reported from Córcoles (ALFÉREZ & BREA, 1981), Quinta das Pedreiras (SZYNDLAR, 2000) and Agramón (SZYNDLAR & RAGE, 2003). In paleontological literature, these snakes are often considered members of the so-called subfamily "Colubrinae *sensu lato*", owing to the absence of hypapophyses on most of their trunk vertebrae.

***Naja* sp.**

For the first time, members of the family Elapidae arrived in Europe (including Iberia) along with the "MN4-wave". These oldest immigrants were represented (among others) by large cobras belonging to the genus *Naja* (= *Palaeonaja*). Since then, *Naja* was widely distributed in the southern half of Europe until it became totally extinct in the eastern portion of the continent around the middle Pleistocene (SZYNDLAR & RAGE, 1990).

The oldest Iberian elapid remains, reported from Córcoles by ALFÉREZ & BREA (1981), were restricted to isolated fangs only. ALFÉREZ & BREA (1981) observed that it is difficult to differentiate fangs of the living *Naja* from those of the fossil *Palaeonaja*, but identified the fossils as belonging to the latter genus, thus following the views of

HOFFSTETTER (1939) that all European extinct cobras are members of *Palaeonaja*. Later, in their revision of the European cobras, SZYNDLAR & RAGE (1990) synonymized the extinct genus *Palaeonaja* with the living *Naja*. In Iberia, *Naja* survived until at least the late Pliocene of Spain (Bailon, cited in SZYNDLAR & RAGE, 1990).

***Vipera* sp. ("*aspis* complex")**

The first vipers that invaded Europe in the beginning of the Miocene (MN1) belonged to the "*Vipera aspis* complex" (SZYNDLAR & RAGE, 1999). Although *V. aspis*-like snakes were present in Europe in all following phases of the early Miocene, they were relatively very rare (SZYNDLAR & RAGE, 2003).

In fact, the first great European radiation of these snakes took place at the end of the early Miocene (MN4) (SZYNDLAR & SCHLEICH, 1993; SZYNDLAR & RAGE, 1999). It is difficult (if possible at all) to ascertain whether these vipers were represented by new species belonging to the "MN4-wave" or they were descendants of earliest Miocene invaders. In the Iberian Peninsula, the oldest remains of *Vipera aspis*-like snakes come from Agramón.

The recent distribution of snakes belonging to the "*Vipera aspis* complex" is restricted almost exclusively to Europe. Today, the "*V. aspis* complex" is represented in Portugal and Spain by *Vipera latasti*. Fossil relatives of these snakes were widespread in the Iberian Peninsula, among others in the late Miocene and Pliocene (e.g. SZYNDLAR, 1985; BAILON, 1991).

***Vipera* sp. ("Oriental viper")**

The so called "Oriental vipers" (in modern herpetological literature most often classified as species of the genera *Macrovipera* and *Montivipera*) first appeared in Europe as members of the "MN4-wave" (e.g. SZYNDLAR, 1987; SZYNDLAR & SCHLEICH, 1993). These large vipers were widely distributed in the southern part of Europe in the remaining portion of Miocene and in the Pliocene (SZYNDLAR & RAGE, 1999). In Spain, the "Oriental vipers" survived until at least the end of the Pliocene (BAILON, 1991). Today, except for a few isolated sites in the easternmost skirts of the continent, they do not occur in Europe.

Fossil remains of these snakes are also known from the end of the early Miocene of Portugal and Spain. A vertebra of an "Oriental viper" was reported from Quinta das Pedreiras (SZYNDLAR, 2000) and a few fragmentary vertebrae of a viper clearly referable to the same complex were found among new fossil remains from Córcoles (Fig. 2J-K).

FINAL REMARKS

As evidenced by fossil mammals, in the beginning of the Miocene only an inner–Eurasian continental faunal exchange was possible, whereas a faunal exchange between Africa and Eurasia became possible for the first time between 18 and 19 mya (i.e. around the MN4) (RÖGL, 1999). Similarly to snakes, the earliest Miocene mammalian faunas are not well known. The first faunal exchanges on massive scale between Europe and Africa started at the beginning of MN3 and took place exclusively through south-eastern part of the European continent (VAN DER MADE, 1999).

Although the migratory corridors used by mammals and reptiles were probably the same, however, migratory movements of both groups were subject to different environmental factors. More specifically, the most important factor behind migrations of reptiles, being thermophilous animals (or physiologically dependent on external sources of heat), is the increase of environmental temperatures. BÖHME (2003)

postulated the existence of two waves of non-ophidian reptiles invading Europe: the first group of immigrants of African origin that arrived 20 mya as well as the second group of Asiatic origin that arrived in Europe 18 mya. The latter group may be clearly correlated with the "MN4-wave" of snakes.

Prior to the end of the early Miocene, the European snake faunas were dominated by representatives of the Booidea, in particular Boidae. Although first colubrids appeared in Europe as early as the beginning of the Oligocene (RAGE, 1988), during the subsequent ten million years they were living in the shadow of boid snakes (SZYNDLAR & RAGE, 2003). In the early Miocene (except for its final phase, the zone MN4), the ophidian faunas known from west European localities (France and Germany) were very poor and dominated by Erycinae and Aniliidae. As observed by SZYNDLAR & SCHLEICH (1993), the "snake fauna was subject to rather slow changes in this period" (p. 40). SZYNDLAR & RAGE (2003) coined the term "Dark Period" for this peculiar chapter in the history of the European snakes. Interestingly, although most representatives of the Oligocene Booidea became extinct and at the same time a number of colubrid and viperid species were already present in western Europe, by no means can the "Dark Period" be regarded as the beginning of the domination of colubroid snakes.

After the prolonged stasis characteristic of the "Dark Period", drastic changes in the composition of the West European snake faunas took place at the end of the lower Miocene (MN4). The changes resulted from the competition of new waves of eastern invaders, composed principally of modern colubroids. This phenomenon was first observed with reference to fossil snakes from southern Germany by SZYNDLAR & SCHLEICH (1993) who stated that "the end of the Lower Miocene ... was one of the most important turning points in the history of the German ophidian faunas" (p. 39). As demonstrated by later studies, the "MN4-wave" was a universal phenomenon that touched also other places in Europe.

In the course of the "MN4-event", the poor "ancient" or "archaic" ophidian fauna was literally flooded by eastern immigrants, principally representatives of the colubroid families Colubridae, Elapidae, and Viperidae (but also Scolecophidia and Boidae). The concept of IVANOV (2000, 2001) that the ancient European snake fauna was "gradually" replaced by modern snakes is not supported by the existing fossil record. Instead, the replacement was a rapid and drastic event (SZYNDLAR & SCHLEICH, 1993; SZYNDLAR & RAGE, 2003).

Interestingly, exactly the same phenomena must have taken place also in the westernmost skirts of the European continent or in the Iberian Peninsula, where the "MN4-wave" coming from the East replaced the ancient snake fauna characteristic of the earliest phases of the Miocene. In Iberia, the ancient fauna, represented by *Eoanilius*, presumed *Eryx*, cf. *Falseryx*, cf. "*Coluber*" *cadurci*, and perhaps the other minute colubrine(s), does not differ considerably from the contemporary faunas known from France and Germany (SZYNDLAR & RAGE, 2003). Also, there are no significant differences between the modern fauna of the Iberian Peninsula and those established in the aforementioned countries. The Iberian modern fauna (or immigrants belonging to the "MN4-wave") consists of Scolecophidia (perhaps *Typhlops*), *Bavarioboa* and / or *Python*, *Eryx*, cf. *Coluber*, *Naja*, and *Vipera* ("Oriental viper").

The composition of the snake assemblage from Agramón, consisting of a few "ancient" elements (in particular, *Eoanilius*) and devoid of any apparently "modern" elements, indicates that the age of the fauna may have been MN3 rather than MN4. In such a case

the natricine (perhaps *Natrix*) and *Vipera* (a member of the "*V. aspis* complex") from Agramón would have represented the autochthonous ancient fauna and not modern immigrants.

Of special interest is the arrival, along with the "MN4-wave", of *Bavarioboa* and / or *Python*. The appearance (re-appearance in the case of *Bavarioboa*) of the non-erycine boids was a short episode probably connected with improvement of the climate observed around the early / middle Miocene transition (SZYNDLAR & RAGE, 2003). As indicated by the fossil record coming from a few European countries (in particular Germany), the European boids (except for the Erycinae) were ousted by colubroids yet during the middle Miocene.

Although, as it was demonstrated above, the ophidian fauna inhabiting Iberia around the early / middle Miocene transition is fairly well recognized, our knowledge about succeeding snake faunas inhabiting the Iberian Peninsula in the middle and late (but not latest) Miocene is again very poor, in particular if we consider published data. To our best knowledge, there exist only three publications covering the latter period: NAVÁS (1922), describing fossil vertebrates from the late Miocene (MN9-10) of Libros (Teruel); CRUSAFONT PAIRÓ & VILLALTA (1952), dealing with the end of the middle Miocene (MN7+8) of Sant Quirze de Galliners and Hostalets de Pierola (lower) in the Vallès-Penedès basin in Catalonia; LÓPEZ-MARTÍNEZ & SANCHÍZ (1982), reviewing microvertebrates from the Duero basin. NAVÁS (1922) described briefly an almost complete ophidian skeleton, identifying it as the fossil colubrid *Pylmophis sansaniensis* (= *Natrix sansaniensis*); most likely the same skeleton (SZYNDLAR, 1985) was later identified as the viper *Bitis* sp. by PIVETEAU (1927); finally Hoffstetter (cited in MARX & RABB, 1965) reconsidered the fossil as a member of the family Colubridae. CRUSAFONT PAIRÓ & VILLALTA (1952; pp. 215-217) mentioned the presence of vertebrae of "Colúbridos del grupo de los Coronélidos" and *Vipera* sp. in both localities and one vertebra of a boid snake ("un Bóido") from Hostalets de Pierola; LÓPEZ-MARTÍNEZ & SANCHÍZ (1982) listed and draw in their Fig. 2 remains of *Natrix* sp. from Torrem 4 and Ampudia 9 (MN9) and of "Colubridae" from several Astaracian to Vallesian (MN6 to MN10) sites. Except for PIVETEAU (1927), no detailed descriptions or figures of the fossils reported in the aforementioned publications are available. However, we know quite a lot about ophidians coming from the Spanish latest Miocene (ALBERDI *et al.*, 1981; SZYNDLAR, 1985) and subsequent phases of the Pliocene (SZYNDLAR, 1988; BAILON, 1991, 1992; SZYNDLAR & SCHLEICH, 1994).

Despite the gap in literature, there still exist undescribed middle and late Miocene ophidians collected in several localities, mainly in Catalonia and the Duero River basin, among others: Las Planas (MN6), Manchones (MN6 or 7 + 8), Can Almirall, Castell de Barberà, Hostalets de Pierola (lower), and Simancas (MN7+8), Ampudia and Can Ponsic (MN9), Hostalets de Pierola (upper) (MN9), Casa del Acero (MN12), Los Mansuetos (MN12). Unfortunately these collections are scarce and badly preserved; the snake remains belonged to unidentified Colubridae, *Naja* and two forms of *Vipera* ("Oriental vipers" and "*V. aspis*-complex") (Z. Szyndlar & H.H. Schleich, unpublished data).

Therefore, what do we know exactly about snakes inhabiting the Iberian Peninsula in the long period between the "MN4-event" and the latest Miocene (MN13)? Unfortunately, our knowledge is imperfect. Although inferring from negative evidence may be often misleading in systematic paleontology, we can be certain that since the latest Miocene onward no ancient snakes occurred

in the Iberian faunas. Unfortunately, we cannot have such a certainty with reference to middle / late Miocene snakes, owing to the scarcity of the available fossil record. We can speculate that, similarly to other European regions (especially Germany and France), the ancient elements of the Iberian snake fauna did not survive beyond the early / middle Miocene boundary or, if survived, they became extinct during the middle Miocene. Although, as stated in the preceding paragraph, the presence of cobras and vipers is quite well documented in the Spanish middle and late Miocene, unfortunately we cannot detect minor changes in the successions of ophidian faunas because of the lack of identified colubrid species. In particular, we cannot recognize whether middle and late Miocene Colubridae were represented by extinct or extant genera. As indicated by the fossil record from the Hungarian locality Rudabánya, the extinction of fossil colubrid genera was a phenomenon characteristic of the beginning of the late Miocene (MN9) (SZYNDLAR, 2005); it is possible (but not demonstrated) that similar changes may have taken place also in the Iberian Peninsula.

However, the ultimate proof can be provided only in the case when new (hopefully abundant and well preserved!) fossil materials coming from the middle and late Miocene of the Iberian Peninsula become available for study.

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