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First fossil record of *Vipera Laurenti* 1768 “Oriental vipers complex” (Serpentes: Viperidae) from the Early Pliocene of the western Mediterranean islands

Première mention fossile de Vipera Laurenti 1768 « complexe des vipères orientales » (Serpentes: Viperidae) dans le Pliocène inférieur des îles de l'Ouest méditerranéen

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ABSTRACT

The first fossil record of *Vipera* “Oriental vipers complex” (Serpentes: Viperidae) in the western Mediterranean islands is presented. Two large-sized vertebrae were found in an Early Pliocene karstic deposit located on the eastern coast of Mallorca, close to Caló den Rafelino (Manacor). The centrum length of the trunk vertebra (12.7 mm) represents the largest-sized known specimen of the European vipers belonging to the “Oriental vipers complex” and it suggests a body length close or greater than 200 cm. The arrival of this snake to Mallorca probably took place during the Messinian Salinity Crisis of the Mediterranean Sea (Late Miocene, 5.6–5.32 My ago) and it should be considered as one of the largest predators in Mallorca during the Early Pliocene. Although patterns of body size change in island snakes are unclear, some considerations about the large size of the Caló den Rafelino viper and co-evolution with endothermic preys are proposed.

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RÉSUMÉ

La première mention fossile de *Vipera* « complexe des vipères orientales » dans les îles de l'Ouest de la Méditerranée est ici présentée. Deux vertèbres de grande taille ont été récoltées dans les dépôts karstiques d'âge Pliocène inférieur à l'est de la côte de Majorque, près de Caló den Rafelino (Manacor). La longueur du centrum de la vertèbre troncale (12,7 mm) constitue la plus grande taille connue pour un spécimen de vipère du complexe des vipères orientales en Europe et suggère une longueur corporelle d'environ 200 cm ou plus. L'arrivée de ce serpent à Majorque a probablement eu lieu au cours de la crise de salinité du Messinien de la mer Méditerranée (Miocène supérieur, entre 5,6 et 5,32 Ma). Ce serpent peut être considéré comme le plus grand prédateur de Majorque au Pliocène inférieur. Bien que les

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diagrammes de changement de taille corporelle des serpents dans les îles restent encore incertains, un phénomène de co-évolution lié à la disponibilité des proies endothermes est proposé pour expliquer la grande taille de cette vipère.

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1. Introduction

Until the middle 1990s, the Neogene fossil record of reptiles from the eastern Balearic Islands (or Gymnesics, western Mediterranean) was restricted to lizards of genus *Podarcis* and tortoises of genus *Cheirogaster* (e.g. Alcover et al., 1981, Bate, 1914, Kotsakis, 1981, Pons-Moyà et al., 1981). Several localities of Punta Nati, at the Northwest coast of Menorca, with a tentative Early-Middle Pliocene chronology (Quintana, 1998), have increased this record. Bailon et al., 2002 obtained *Vipera* sp. in Punta Nati 3 and 12, and described *Vipera natiensis* (an endemic species from Menorca, included to the *V. aspis* complex) in Punta Nati 12. Garcia Porta et al., 2002 identified *Blanus* sp. (Amphisbenia) in Punta Nati 12. Finally, Bailon et al., 2005 described remains belonging to an unidentified Gekkonidae from Punta Nati 3 and 12, and to *Coluber* sp. (*C. dolnicensis*-*C. pouchetti* complex) from Punta Nati 12. Additionally, Bailon et al., 2002 reported an undetermined viperid in Punta Nati 2, a Middle Miocene Menorcan site.

It should be noted the viperids, as *Blanus* and “*Coluber*” are absent from the Balearic Islands today.

Although, snakes, tortoises, anguids, crocodyles and varanids have been recorded from several Oligocene localities from Mallorca (Adrover et al., 1977), they are unknown from the post-Messinian deposits of this island. The goal of this article is to describe the first fossil remains of snakes obtained in the Neogene from Mallorca, found in a post-Messinian site.

2. The site

The fossiliferous bone breccia yielding the fossils here studied is located on the East coast of Mallorca, close to Caló den Rafelino, near Cala Morlanda (Manacor; Fig. 1). The breccia consists of hardened red silts of a collapsed cave excavated in the Upper Miocene reef complex (Fornós, 1998, Pomar et al., 1990). This complex has a Late Tortonian-Messinian chronology (Bizon et al., 1973). Although the red silts are filling the whole collapse, the fossils are concentrated in a very small area, about 1 sqm (Fig. 1).

The stratigraphic evidence suggests a very Early Pliocene chronology for the Caló den Rafelino site (Bover et al., 2007, Quintana et al., in press). The fossiliferous breccia is the cemented floor sediment on a cave excavated in the limestones of the Upper Miocene. Up to now, no snakes have been found in the Mallorcan sites containing the mammalian *Myotragus pepgonellae* (attributed to Early or Middle Pliocene [MN14 or MN16; Moyà-Solà and Pons-Moyà, 1982, Pons-Moyà et al., 1979]) and their descendants. Thus, the Caló den Rafelino infilling should have been restricted to a very short period, posterior to the Upper Tortonian-Lower Messinian and previous to

Middle Pliocene (MN16). The mammalian fauna of this deposit (Bover et al., 2007, Quintana et al., in press) suggests that the colonization event occurred during the MSC (5.6–5.32 My ago, according to [Clauzon et al., 1996, Krijgsman et al., 1999]). Consequently, a very Early Pliocene age is suggested for the site.

The whole fauna obtained at this site is currently under study. It includes birds, reptiles (two viperids, one of them described here, a colubrid, a chelonid, two lacertids and an anguid), and mammals (a bovid, a leporid, a glirid, a cricetid and an insectivore) (Bover et al., 2007; Quintana et al., in press).

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3. Systematic paleontology

Order Serpentes Linné, 1758.

Family Viperidae Laurenti, 1768.

Genus *Vipera* Laurenti, 1768.

***Vipera* sp. “Oriental vipers complex”.**

Material: Middle trunk vertebra (IMEDEA 90113) and a cervical vertebra (IMEDEA 90116).

Age: Tentatively very Early Pliocene.

3.1. Description

IMEDEA 90113: Middle trunk vertebra of a large-sized snake (Fig. 2a–e). **Measurements.** Centrum Length (CL)=12.7 mm; Minimum Interzygapophyseal Constriction (MIC)=13.7 mm; Maximum Length between anterior edge of prezygapophyseal facet and posterior edge of postzygapophyseal facet (ML)=16.6 mm; Maximum Width between lateral edges of prezygapophyseal facets (PR-PR)=22.44 mm; Maximum Width between lateral edges of postzygapophyseal facets (PO-PO)=20.84 mm; Total Height (TH)=18.4 mm; Zygosphene Width (ZW)=10.32 mm; Cotyle Width (CTW)=8.28 mm; Cotyle Height (CTH)=7.42 mm; Condyle Width (CDW)=7.3 mm.

In dorsal view, the vertebra is slightly wider than long (ML/PR-PR ratio=0.74). The MIC is shallow and slightly displaced to the posterior half of the vertebra. The right prezygapophyseal articular facet has a subrectangular shape, but the left articular facet is eroded. The main axis of these two facets is slightly inclined in an antero-lateral direction. The central notch of the posterior edge in the neural arch is moderately deep and the posterior neural wings (= aliform process) are well developed, and apparently lack of the epizygapophyseal spine. The anterior edge of the zygosphene is slightly eroded, but it has a small central lobe whose dorsal surface is slightly concave. The neural spine is long, relatively thin, and anteriorly lengthened on the zygosphene. The neural arch and both sides of

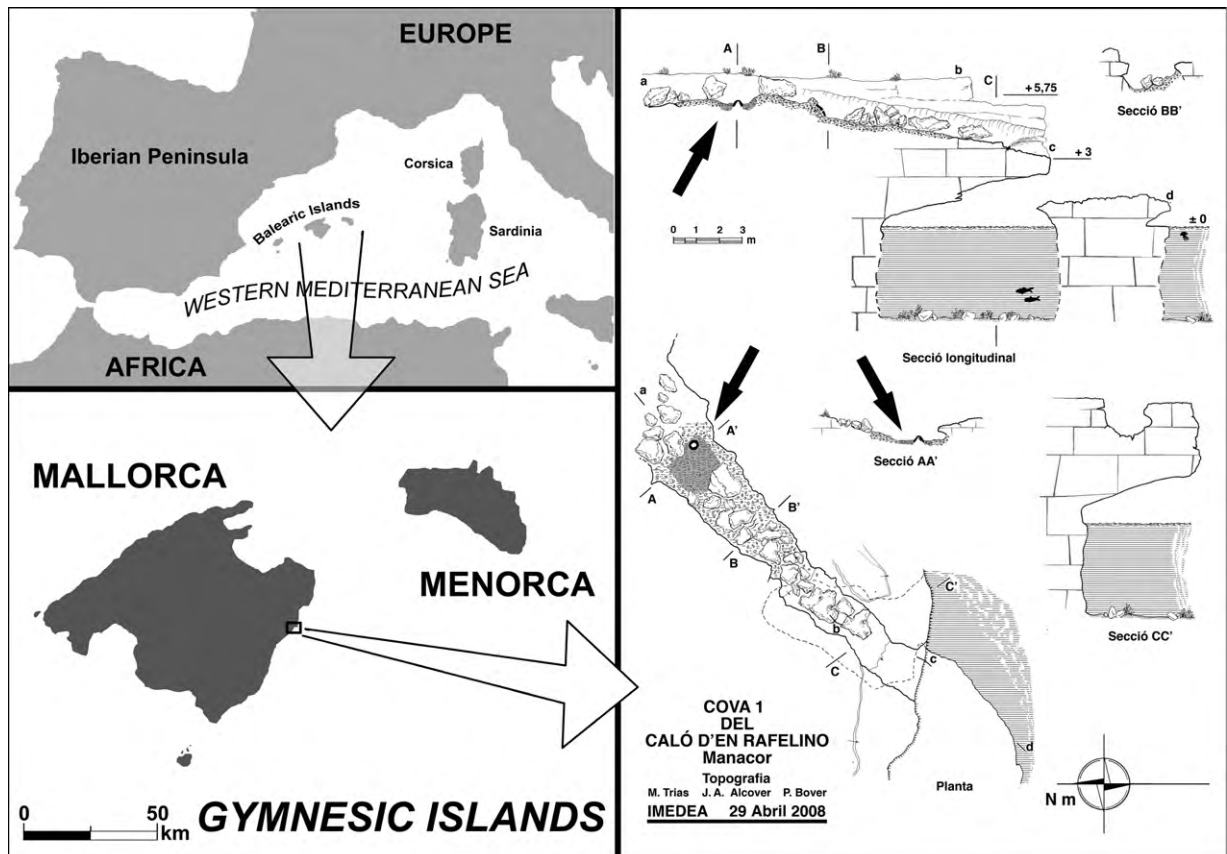


Fig. 1. Location map (left) and topographic survey (right) of the palaeontological deposit from Caló den Rafelino. Arrows and grey colour indicate the exact location of the fossiliferous breccia. Translation, “secció” = cross-section, “planta” = plan.

Fig. 1. Localisation (gauche) et topographie (droite) du dépôt paléontologique de Caló den Rafelino. Les flèches et la couleur grise indiquent la localisation exacte de la brèche fossilifère. Traduction, « secció » = section, « planta » = plan.

the neural spine display clearly marked impressions for the dorsal muscles. These impressions are anteriorly limited by a tenuous bone keel extending from each side, between the anterior end of the neural spine and the posterior limit of the prezygapophyseal facets.

In ventral view, the vertebral centrum is slightly shorter than wide (LC/MIC ratio = 0.93). It is robust, triangular, with well-defined ventral margins and a flat ventral surface. The basis of hypapophysis is slightly wide and it extends anteriorly in the form of a haemal keel, gradually becoming wider until it reaches the base of the cotyle. Only a small subcotylar tubercle on the right side is preserved. The parapophyseal process on the same side is also preserved, but its anterior tip is missing. A deep and narrow groove separates this parapophyseal process from the cotyle. The left parapophyseal process is broken at the base. The postzygapophyseal articular facets are rectangular and well developed. The prezygapophyseal processes are broken and the diapophysis and parapophysis are strongly eroded.

In lateral view the vertebra is slightly higher than long. The dorsal border of the neural spine is eroded, but it does not seem to be broken; thus, this structure was likely longer than high. Its anterior border originates at the anterior third of the zygosphenal roof and it is slightly inclined. The diapophysis and parapophysis are heavily eroded, although

they can be clearly identified. The parapophyseal process is robust, and it is antero-ventrally inclined and broken at the anterior top margin. The lateral foramen is located in a deep longitudinal depression. The subcentral ridge is clearly visible, but it does not reach posteriorly the base of the condyle. The hypapophysis is broken at the base, but it can be definitively observed that it is posterior-ventrally directed. The condyle has a short neck and it is ventrally attached to the hypapophysis basis.

In anterior view, the articular facets of the prezygapophyses are inclined upward. The zygosphene is robust, slightly wider than the cotyle, with developed articular facets and its dorsal edge is slightly concave dorsally. The paracotylar foramina are clearly visible and the neural canal is narrow.

In posterior view, the neural arch is depressed. The postzygapophyses are inclined upwards. The zygantrum is deep and it displays well-developed articular facets. The condyle is large and slightly wider than high.

IMEDEA 90116. Cervical vertebra (Fig. 2f–g). A fragment of cervical vertebra has been also recovered from Caló den Rafelino. Only the centrum and a lateral right portion of the vertebra (including the lateral wall of the vertebra, prezygapophysis, diapophysis and parapophysis) are preserved. In ventral view, the centrum is robust, with a CL

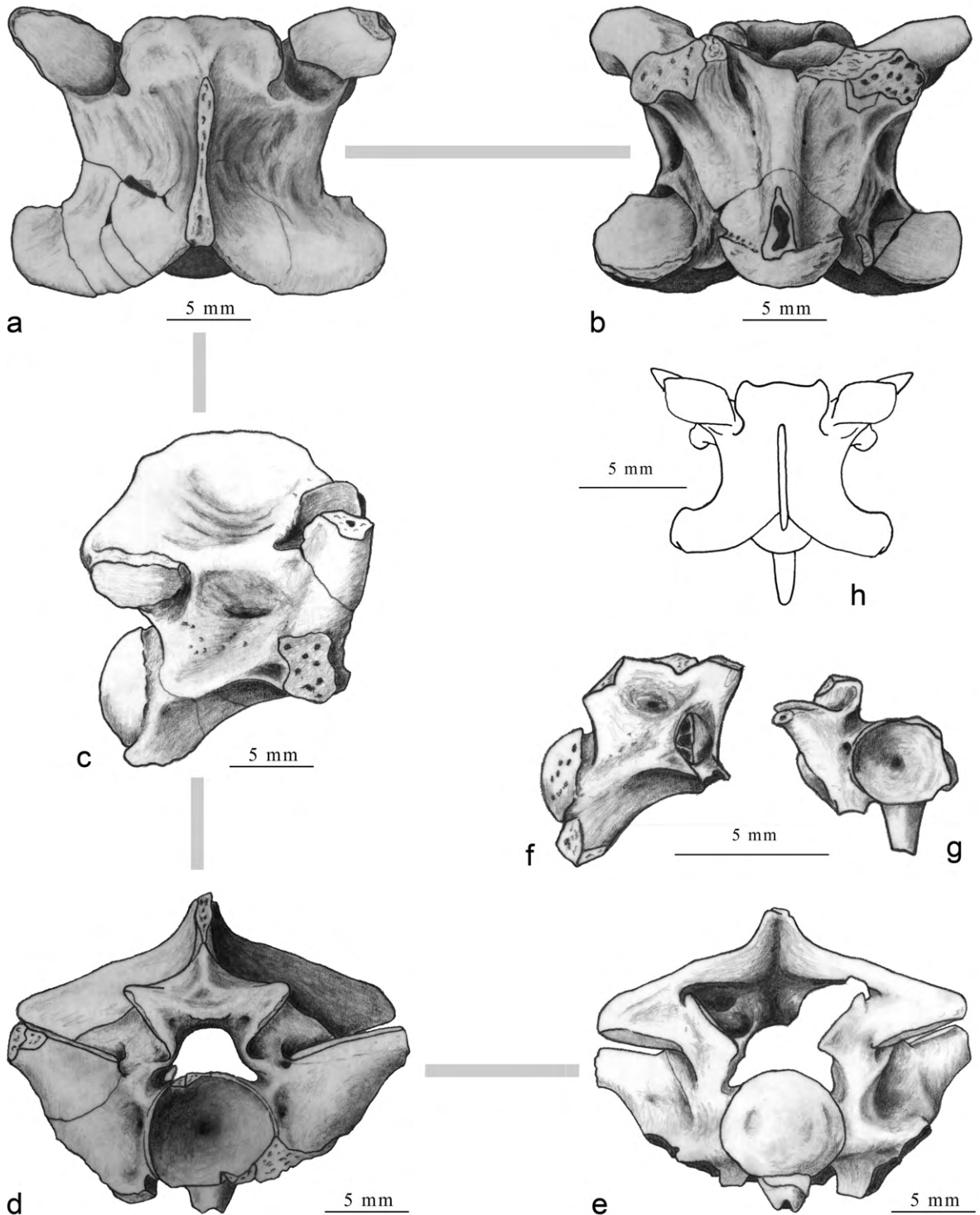


Fig. 2. Comparison of the vertebrae of *Vipera* sp. (Oriental vipers complex) from Caló den Rafelino (Manacor, Mallorca), with a trunk vertebra of a *Vipera lebetina* of a body length of 1 meter. Middle trunk vertebra IMEDEA 90113: **a**: dorsal; **b**: ventral; **c**: right lateral; **d**: anterior view; **e**: posterior views. Cervical vertebra IMEDEA 90116: **f**: right lateral; **g**: anterior views. **h**: Trunk vertebra of *Vipera lebetina* (dorsal view).

Fig. 2. Comparaison de la vertèbre de *Vipera* sp. (complexe des vipères orientales) de Caló den Rafelino (Manacor, Majorque), avec une vertèbre de *Vipera lebetina* d'un mètre de longueur du corps. Vertèbre troncale moyenne IMEDEA 90113, vues : **a** : dorsale ; **b** : ventrale ; **c** : latérale droite ; **d** : antérieure ; **e** : postérieure. Vertèbre cervicale IMEDEA 90116 vues : **f** : latérale droite ; **g** : antérieure. **h** : Vertèbre troncale moyenne de *Vipera lebetina* (vue dorsale).

of 5.5 mm. It displays a flat ventral surface in its anterior half and the marked subcentral ridges clearly diverge anteriorly. In lateral view, this fragment seems to be part of a vertebra markedly higher than long (a diagnostic character of cervical vertebrae). The lateral foramen is located in a deep longitudinal depression. The subcentral ridge is slightly arched and it reaches the posterior two thirds of the centrum. The diapophysis is quite eroded and has an oval outline whose main axis is perpendicular to the longitudinal axis of the vertebra. The parapophysis is broken in the distal part and it is antero-ventrally inclined. Although the parapophyseal and hypapophyseal processes are also broken, and their complete morphology cannot be described, the hypapophysis seems to be a robust structure postero-ventrally directed. It is extended anteriorly to the base of the cotyle through a high haemal keel. In dorsal view, the prezygapophysis is highly eroded and its morphology cannot be observed. The prezygapophyseal process is also broken. Cotyle and condyle are well developed.

3.2. Systematics affinities

The fossil vertebrae from Caló den Rafelino can be clearly attributed to the family Viperidae. This taxonomic assignment is suggested by the presence of the following combination of characters (Fig. 2): vertebrae with:

- (1) straight hypapophysis;
- (2) posteriorly depressed neural arches;
- (3) zygapophyseal articular facets dorsally inclined;
- (4) parapophyseal processes antero-ventrally directed;
- (5) developed condyles and cotyles;
- (6) relatively short centrum;
- (7) condyle ventrally attached to the hypapophysis basis (see [Bailon, 1991, Szyndlar, 1991, Szyndlar and Rage, 1999]).

Several papers on Viperidae systematics, taxonomy and phylogeny have been published during the last years. All of them caused remarkable, and controversial, changes. On the basis of morphological data (Ashe and Marx, 1988, Groombridge, 1986, Nilson and Andrén, 1997, Nilson et al., 1999, Obst, 1983, Saint Girons, 1978), immunological distances of proteins (Herrmann et al., 1992a, Herrmann et al., 1992b) and mitochondrial DNA analyses (Garrigues et al., 2005, Lenk et al., 2001) the genus *Vipera* (sensu lato) has been divided in different complexes: *Vipera* (s.s.), *Vipera* 1, *Vipera* 2, *Pelias*, *Montivipera*, *Macrovipera*, and *Daboia*. Unfortunately, these complexes do not display outstanding osteological diagnostic differences to clarify relationships between fossil material, mainly composed by vertebrae, and extant taxa (Szyndlar, 1991, Szyndlar and Rage, 1999, Szyndlar and Rage, 2002). Thus, in this article we use the subdivision of the genus *Vipera* s.l. into complexes suggested by Szyndlar and Rage, 1999, on the basis of morphological differences in the Viperinae trunk vertebrae:

- 1- *Vipera* “*Vipera berus* complex” (= *Pelias* in [Nilson and Andrén, 1997]), in which the trunk vertebrae have a small size (CL < 5 mm). They are relatively long, with a short neural spine, and a short hypapophysis;
- 2- *Vipera* “*Vipera aspis* complex” (= *Vipera* 1 in [Nilson and Andrén, 1997]), in which trunk vertebrae show an intermediate morphology and size between the “*V. berus* complex” and the “Oriental vipers complex”;
- 3- *Vipera* “Oriental vipers complex”, except *Daboia* (= *Vipera* 2 + *Macrovipera* in [Nilson and Andrén, 1997]), characterized by larger and more robust vertebrae (CL > 5 mm), with a short centrum, generally well limited laterally, and displaying well developed neural spine and hypapophysis;
- 4- *Daboia*, in which the recent *D. russelii* (Obst, 1983) and the fossil *D. maxima* of MN15 from the Iberian Peninsula (Szyndlar, 1988) are included. The trunk vertebrae of this group differ from the previous group by their great development of the neural spine, which is higher than long.

The large size of the vertebrae from Caló den Rafelino (CL = 5.7 mm for the cervical vertebra and 12.7 mm for the trunk vertebra), together with the robustness and the presence of a short and laterally well marked centrum, with a flat ventral surface, are typical characters displayed by the viperines of complexes 3 and 4 (*Vipera* “Oriental vipers complex” and *Daboia*, respectively). However, the possible presence of a neural spine longer than high in the fossil trunk vertebra allows us to identify the fossil as belonging to the *Vipera* “Oriental vipers complex” and differentiate it from *Daboia*, which displays a higher neural spine (Szyndlar, 1988, Szyndlar and Rage, 1999).

The main feature of the Caló den Rafelino snake is its large size. The trunk vertebra is the largest one so far described in Europe for *Vipera* “Oriental vipers complex” (CL = 12.7 mm). Among the different known fossil and extant species, only the Pliocene *D. maxima* (*Daboia* complex) from Layna (Spain) has a similar vertebral size (CL of the holotype = 11.8 mm; [Szyndlar, 1988]), while within the “Oriental vipers complex”, the maximum size is displayed by the putatively assigned specimens from Langenau, Germany (Lower Miocene, MN4, maximum CL = 10.5 mm, [Szyndlar and Rage, 1999]), Vieux-Collonges, France (*Vipera* “Oriental Vipers complex” or *Daboia*; Lower/Middle Miocene, MN4/5; CL = 10.2 mm, [Szyndlar and Rage, 1999]) and the specimen from Aetokremnos, Cyprus (Xth millennium BC, *Vipera lebetina*, maximum CL = 10.07 mm, [Bailon, 1999]). In this sense, the direct comparison of the Mallorcan fossil trunk vertebra with same vertebra from a specimen of *V. lebetina obtusa* of 103.5 cm of total body length (maximum CL = 6.32 mm), suggests that the Mallorcan specimen could have reached a body length close or greater than 200 cm.

The rest of characters displayed by the fossil vertebra, such as the limited depth of the interzygapophyseal constriction, considerable development of the aliform process, morphology of the zygosphenes with a small central lobe and whose roof is slightly concave dorsally, strong muscle impressions observed on the vertebra, and the robustness of the vertebra, are within the morphological variability recorded in fossils (and more frequently in the large vertebrae) attributed to this complex of snakes. All these characters are almost certainly related to its large body size.

4. Paleobiogeography and origin of the fossil from Caló den Rafelino

The earliest representative of the “Oriental vipers complex” in Europe comes from the early Miocene (MN4) from Lisboa (Antunes and Rage, 1974). From the MN4 to the MN16 this complex had a wide distribution in central and southern Europe (Czech Republic, France, Germany, Russia, Hungary, Italy, Moldova, Austria, Ukraine, Iberian Peninsula, Greece). Szyndlar and Rage, 2002 published a complete record and chronology of deposits with *Vipera* “Oriental vipers complex”, while Bailon and Blain, 2007 mentioned the last representative of the complex in western Europe (MN16 from Cova Bonica, Iberian Peninsula). However, no representative of the group had been found on islands of the western Mediterranean. In island context, the only fossil records attributed to the “Oriental vipers complex” come from the Middle Pleistocene of Chios, where a Viperidae with a similar morphology to the extant forms *V. palestina*–*V. lebetina* has been obtained (Schneider, 1975), and from the Holocene (Pre-Neolithic) of Cyprus (*V. lebetina*, [Bailon, 1999]). Currently, *V. schweizeri*, previously considered as a subspecies of *V. lebetina*, is found on Chios, while *V. lebetina* is present in Cyprus.

The initial separation of the Balearic block from continent occurred likely during the end of the Oligocene, c. 25 My ago (e.g. de Bruijn et al., 1979). Although Adrover et al., 1977 recorded varanids, anguids and snakes in the Balearic Islands Oligocene, no description of this material has been published yet. Otherwise, the earliest known chronology for the “Oriental Vipers complex” is the MN4, between 18 and 20 My ago. Thus, it seems reasonable to suggest that the snake from Caló den Rafelino cannot be considered as a relict taxon of the fauna that accompanied the Balearic block during its first separation from the European continent, and the colonization of Mallorca by this viperid should have been a more recent event. It probably occurred during some posterior connection between mainland and the island or by overseas colonization. In this sense, several episodes of faunal colonization of the Balearic Islands (and more specifically for Mallorca and Menorca) have been proposed according to the mammalian fossil succession (e.g. Bover et al., 2008, Quintana, 1998). A first colonization event occurred during the Langhian-Serravallian regression (Middle Miocene, c. 14.2 My ago), as documented by the faunal assemblage from Sant Llorenç and Santa Margalida in Mallorca (Adrover et al., 1985, Mein and Adrover, 1982) and Punta Nati 2 in Menorca (Quintana, 1998, Quintana and Agustí, 2007). In this Menorcan site, a viperid fang displays a morphology and size similar to those of the small European vipers has been attributed to *Vipera* sp. by Bailon et al., 2002.

During the Messinian Salinity Crisis (MSC) (Upper Miocene, between 5.6 and 5.32 My ago), the Mediterranean sea level dropped about 1500 m (Clauzon et al., 1996, Gautier et al., 1994, Krijgsman et al., 1999), establishing new connection between the mainland and the Balearic Islands and a second colonization event. A Messinian chronology has been proposed for the colonization of the Balearic Islands by *Podarcis lilfordi* and *P. pityusensis* (Alcover and Mayol, 1981, Alcover and Mayol, 1982,

Kotsakis, 1981). Bover et al., 2007 suggested that the arrival to Mallorca of the fauna found in the Caló den Rafelino took place during the main regressive episode of the Messinian. No relationship between the faunal assemblage of the Middle Miocene from Mallorca (Adrover et al., 1985, Mein and Adrover, 1982) and the fauna from Caló den Rafelino apparently exists.

5. The viperid from Caló den Rafelino and the island context

Island faunas furnish relevant documentation for ecologic and evolutionary studies. Body size changes (gigantism or dwarfism) are among the most remarkable features displayed by insular species.

The large size observed in the viperid from Caló den Rafelino suggests a putative case of island gigantism. Nevertheless, in the case of snakes, some further considerations should be taken into account. First, most of the reptilian species have a continuous (though increasingly slow) growth once sexual maturity is reached (Andrews, 1982). Second, snakes display a wide range of adult body size, even within the same population and among different populations, as a consequence of the ectothermic metabolism (avoiding the constraints promoted by the maintenance of a constant body temperature, as is the case in endothermic animals) (Pough, 1980). Third, in the fossil record for this group of vipers it can be found examples of continental populations of large size, although slightly smaller than the snake from Caló den Rafelino (Szyndlar and Rage, 1999). Currently, the maximum body size known for a continental *V. lebetina* (“Oriental vipers complex”) is 214 cm, with a high variability among different populations, while the insular subspecies *V. lebetina lebetina* from Cyprus and *V. schweizeri* from the Cyclades Islands are generally much smaller (Mallow et al., 2003).

Patterns of body size change in island snakes are unclear. Case, 1978 described a trend towards decreasing body size (dwarfism) in island snake populations, attributed to changes in food availability. Other papers described an opposite scenario, i.e., snake populations with larger body size on islands than on mainland (Forsman, 1991, Mori, 1994, Rodriguez and Drummond, 2000, Schwaner and Sarre, 1988). All these authors related the size of the snakes to the size of the consumed preys, the latter being different on islands from that consumed on mainland (“diet alteration hypothesis” [Boback, 2003]).

Boback, 2003 studied the body size of 30 snake species and he suggested that body size changes in snakes are bimodal and mainly influenced by the size of the available preys, whereas none of the physiographic or phylogenetic history variables seem to be key factors to determine the recorded size trends. The distribution of populations of giant or dwarf snakes differs significantly between the families Colubridae and Viperidae (Boback, 2003): while in viperids a reduction of size in island populations is frequently observed, the foraging style of colubrids (nest-robbing behaviour) may promote the increase of body size in island populations. However, almost all viperids studied by Boback, 2003 belong to the genus *Crotalus*, and it cannot definitively be established if the reduction in body

size on islands affects all Viperidae genera or just species of *Crotalus*. According to Boback, 2003, island populations of *Vipera schweizeri* (*V. lebetina* in the Boback paper) from Cyclades Islands, the only representative of the “Oriental vipers complex” considered by this author, displays a remarkable decrease in body size. However, Boback and Guyer, 2003 proposed an empirical model that suggests a trend for snakes to acquire an optimal body size. In the case of snakes with continental and island populations, these authors noted that the species of small body size become larger in the islands, while the large species on the continents are smaller in the islands.

Several papers suggested that populations of snakes that reach a large body size live on islands with abundant endothermic preys, while the body size is ostensibly reduced in populations living on islands with only ectothermic animals (Aubret and Shine, 2007, Bonnet et al., 2002, Case, 1978, Hasegawa, 2003, Schwaner and Sarre, 1988).

With an unknown mainland ancestor, the interpretation of the large size of the Caló den Rafelino snake is controversial. Its size is close to the maximum end of the body size range known for the “Oriental vipers complex”, suggesting that an insular body size decrease should be excluded. In this sense, the emerging trend of body size change does not agree with the snake general model of Case, 1978 and Boback and Guyer, 2003, or of Boback, 2003 model for the Viperidae. According to these models, the viperid from Mallorca should have displayed a smaller size than its mainland ancestors.

In our view, the isolation of a viperid on Mallorca after the MSC, should have produced adaptations to a new diet, consuming preys of larger size, mainly endothermic vertebrates (birds and mammals), whose size and probably abundance have been increased through their insular evolution (at least for some of them, as evidenced by the existence in the deposit of rodents of large size). The great phenotypic plasticity of this group of snakes should have selected phenotypes successively adapted to the change of body size of the preys. A co-evolution process between the island populations of this group of vipers and endothermic preys existing in the island could have been the key factor to explain the large body size displayed by this fossil viper.

This process was probably favoured, although to a lesser degree, by the existence of favourable ecological conditions, such as the existence of a warm-temperate climate and perhaps a relatively dry and open landscape. Due to its large body size, the snake from Caló den Rafelino can be considered as one of the largest predators in Mallorca during the Early Pliocene.

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References

- Adrover, R., Huguency, M., Mein, P., 1977. Fauna africana oligocena y nuevas formas endémicas entre los micromamíferos de Mallorca (Nota preliminar). *Boll. Soc. Hist. Nat. Balears* 22, 137–149.
- Adrover, R., Agustí, J., Moyà, S.S., Pons, J., 1985. Nueva localidad de micromamíferos insulares del Mioceno Medio en las proximidades de San Lorenzo en la isla de Mallorca. *Paleontologia i Evolució* 18, 121–129.
- Alcover, J.A., Mayol, J., 1981. Espècies reliquies d'amfibis i de rèptils a les Balears i Pitiüses. *Boll. Soc. Hist. Nat. Balears* 25, 151–167.
- Alcover, J.A., Mayol, J., 1982. Espècies relictuelles d'amphibiens et de reptiles des Îles Baléares et Pityuses : une extension des résultats. *B. Soc. Herp. Fr.* 22, 69–73.
- Alcover, J.A., Moyà-Solà, S., Pons-Moyà, J., 1981. Les quimeres del passat. Els vertebrats fòssils del Plio-Quaternari de les Balears i Pitiüses, Ed. Moll, Palma, 260.
- Andrews, R.M., 1982. Patterns of growth in reptiles. In: Gans, G., Pough, F.H. (Eds.), *Biology of the Reptilia*, vol. 13. Academic Press, New York, pp. 273–320.
- Antunes, M.T., Rage, J.C., 1974. Notes sur la géologie et la paléontologie du Miocène de Lisbonne. XIV Quelques Squamata (Reptilia). *B. Soc. Geol. Port.* 19, 47–60.
- Ashe, J.S., Marx, H., 1988. Phylogeny of the viperine snakes (Viperinae): part II. Cladistic analysis and major lineages. *Fieldiana: Zool.* 52, 1–23.
- Aubret, F., Shine, R., 2007. Rapid prey-induced shift in body size in an isolated snake population (*Notechis scutatus*, Elapidae). *Austral Ecol.* 32, 889–899.
- Bailon, S., 1991. Les amphibiens et les reptiles du Pliocène et du Quaternaire de France et d'Espagne : mise en place et évolution des faunes, PhD. Thesis, Université de Paris-7, Paris, 499 p.
- Bailon, S., 1999. Toad and snake. In: Simmons, A.H. (Ed.), *Faunal extinction in an island society*. Kluwer Academic/Plenum Publishers, New York, pp. 182–186.
- Bailon, S., Blain, H.A., 2007. Faunes de reptiles et changements climatiques en Europe occidentale autour de la limite Plio-Pléistocène. *Quaternaire* 18, 55–63.
- Bailon, S., Garcia Porta, J., Quintana, J., 2002. Première découverte de Viperidae (Reptilia, Serpentes) dans les Îles Baléares (Espagne) en el Pliocène de Neogène de Minorque. Description d'une nouvelle espèce du Pliocène. *C. R. Palevol* 1, 227–234.
- Bailon, S., Quintana, J., Garcia Porta, J., 2005. Primer registro fósil de las familias Gekkonidae (Lacertilia) y Colubridae (Serpentes) en el Plioceno de Punta Nati (Menorca, Islas Baleares). In: Alcover, J.A., Bover, P. (Eds.), *Proceedings of the International Symposium “Insular Vertebrate Evolution: the Palaeontological Approach”*. *Mon. Soc. Hist. Nat. Balears* 12, pp. 27–32.
- Bate, D.M.A., 1914. A gigantic land tortoise from the Pleistocene of Menorca. *Geol. Mag.* 6, 100–107.
- Bizon, G., Bizon, J.J., Bourrouilh, R., Massa, D., 1973. Présence aux îles Baléares (Méd. occ.) de sédiments “messiniens” déposés dans une mer ouverte, à salinité normale. *C. R. Acad. Sci. Paris, Ser. D* 277, 985–988.
- Boback, S.M., 2003. Body size evolution in snakes: evidence from island populations. *Copeia* 2003, 81–94.
- Boback, S.M., Guyer, C., 2003. Empirical evidence for an optimal body size in snakes. *Evolution* 57, 345–351.
- Bonnet, X., Pearson, D., Ladyman, M., Lourdais, O., Bradshaw, S.D., 2002. “Heaven” for serpents? A mark-recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. *Austral Ecol.* 27, 442–450.
- Bover, P., Quintana, J., Agustí, J., Bailon, S., Alcover, J.A., 2007. Caló den Rafelino: an early Pliocene site in Mallorca, Western Mediterranean, in: *Libro de resúmenes del VII Simposio Internacional de Zoología. Topes de Collantes (Sancti Spiritus, Cuba)*, 119 p.
- Bover, P., Quintana, J., Alcover, J.A., 2008. Three islands, three worlds: paleogeography and evolution of the vertebrate fauna from the Balearic Islands. *Quatern Int.* 182, 135–144.
- Case, T.J., 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59, 1–18.
- Clauzon, G., Suc, J.-P., Gautier, F., Berger, A., Loutre, M.F., 1996. Alternate interpretation of the Messinian salinity crisis: controversy resolved? *Geology* 24, 363–366.
- de Bruijn, H., Sondaar, P.Y., Sanders, E.A.C., 1979. On a new species of *Pseudodolomys* (Theridomyidae, Rodentia) from the Paleogene of Mallorca. *P. K. Ned. Akad. Wetensch.* 82, 1–10.
- Fornós, J.J., 1998. Karts collapse phenomena in the Upper Miocene of Mallorca (Balearic Islands, Western Mediterranean). *Acta Geol. Hung.* 42, 237–250.

- Forsman, A., 1991. Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *J. Anim. Ecol.* 60, 253–267.
- García Porta, J., Quintana, J., Bailon, S., 2002. Primer hallazgo de *Blanus* sp (Amphisbaenia, Reptilia) en el Neógeno balear. *Rev. Esp. Herp.* 16, 19–28.
- Garrigues, T., Dauga, C., Ferquel, E., Choumet, B., Failloux, A.-B., 2005. Molecular phylogeny of *Vipera Laurenti*. 1768 and the related genera *Macrovipera* (Reuss, 1927) and *Daboia* (Gray, 1842), with comments about neurotoxic *Vipera aspis aspis* populations. *Mol. Phylogenet. Evol.* 35, 35–47.
- Gautier, F., Clauzon, G., Suc, J.-P., Cravatte, J., Violantini, D., 1994. Âge et durée de la crise de salinité messinienne. *C. R. Acad. Sci. Ser. II* 318, 1103–1109.
- Groombridge, B., 1986. Phyletic relationships among viperine snakes. In: *Proceedings of the Third European Herpetological Meeting*, Charles University, Prague, pp. 11–17.
- Hasegawa, M., 2003. Ecological diversification of insular terrestrial reptiles: a review of the studies on the lizard and snakes of the Izu Islands. *Global Environ. Res.* 7, 59–67.
- Herrmann, H.-W., Joger, U., Nilson, G., 1992a. Molecular phylogeny and systematics of viperine snakes I. General phylogeny of European vipers (*Vipera sensu stricto*). In: Korsós, Z., Kiss, I. (Eds.), *Proceedings of the Sixth Ordinary General Meeting of the Societas Europaea Herpetologica*. Hungarian Natural History Museum, Budapest, pp. 219–224.
- Herrmann, H.-W., Joger, U., Nilson, G., 1992b. Phylogeny and systematics of viperine snakes. III: resurrection of the genus *Macrovipera* (Reuss, 1927) as suggested by biochemical evidence. *Amphibia-Reptilia* 13, 375–392.
- Kotsakis, T., 1981. La lucertole (Lacertidae, Squamata) del Pliocene, Pleistocene e Olocene delle Baleari. *Boll. Soc. Hist. Nat. Balears* 25, 135–150.
- Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J., Wilson, D.S., 1999. Chronology, causes and progression of the Messinian salinity crisis. *Nature* 400, 652–655.
- Lenk, P., Kalyabina, S., Wink, M., Joger, U., 2001. Evolutionary relationships among the true vipers (Reptilia: Viperidae) inferred from mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* 19, 94–104.
- Mallow, D., Ludwig, D., Nilson, G., 2003. *True vipers. Natural history and toxinology of Old World vipers*. Krieger Publishing Company, Florida, 359 p.
- Mein, P., Adrover, R., 1982. Une faunule de mammifères insulaires dans le Miocène moyen de Majorque (Îles Baléares). *Geobios mem. spec.* 6, 451–463.
- Mori, A., 1994. Ecological and morphological characteristics of the Japanese rat snake, *Elaphe climacophora*, on Kammuri-jima Island: a possible case of insular gigantism. *The Snake* 26, 11–18.
- Moyà-Solà, S., Pons-Moyà, J., 1982. *Myotragus peponellae* nov. sp., un primitivo representante del género *Myotragus* Bate, 1909 (Bovidae, Mammalia) en la isla de Mallorca. *Acta Geol. Hisp.* 17, 77–87.
- Nilson, G., Andrén, C., (1997). Evolution, systematics and biogeography of Palaearctic vipers, In: R.S. Thorpe, W. Wüster, A. Malhotra (Eds.), *Venomous snakes: ecology, evolution and snakebite*, Symp. Zool. Soc. London 70:31–42.
- Nilson, G., Tuniyev, B., Andrén, C., Orlov, N.L., 1999. Vipers of Caucasus: taxonomic considerations. In: Joger, U. (Ed.), *Kaupia. Phylogeny and Systematics of the Viperidae*. Hessisches Landesmuseum Darmstadt/Technische, Darmstadt, pp. 103–106.
- Obst, F.J., 1983. Zur Kenntnis der Schlangengattung *Vipera* (Reptilia, Serpentes, Viperidae). *Zool. Abh.* 38, 229–235.
- Pomar, L., Rodríguez-Perea, A., Sabat, F., Fornós, J.J., 1990. Neogene stratigraphy of Mallorca Island. *Paleontología i Evolució* 2, 271–320.
- Pons-Moyà, J., Moyà-Solà, S., Kopper, S., 1979. La fauna de mamíferos de la Cova de Canet y su cronología. *Endins* 5–6, 55–56.
- Pons-Moyà, J., Moyà-Solà, S., Agustí, J., Alcover, J.A., 1981. La fauna de mamíferos de los yacimientos menorquines con *Geochelone gymnesica* (Bate 1914). Nota preliminar. *Acta Geol. Hisp.* 16, 129–130.
- Pough, F.H., 1980. The advantages of ectothermy for tetrapods. *Amer. Nat.* 115, 92–112.
- Quintana, J., 1998. Aproximación a los yacimientos de vertebrados del Mio-Plioceno de la isla de Menorca. *Boll. Soc. Hist. Nat. Balears* 41, 101–117.
- Quintana, J., Agustí, J., 2007. Los mamíferos insulares del Mioceno medio y superior de Menorca (Islas Baleares, Mediterráneo occidental). *Geobios* 40, 677–687.
- Quintana, J., Bover, P., Alcover, J.A., Agustí, J., Bailon, S., in press. Presence of *Hypolagus* Dice, 1917 (Lagomorpha, Leporidae, Archaeolaginae) in the Neogene of the Balearic Islands (Western Mediterranean). Description of *Hypolagus balearicus* sp. nov., *Geobios*.
- Rodríguez, C., Drummond, H., 2000. Exploitation of avian nestlings and lizards by insular milk snakes, *Lampropeltis triangulum*. *J. Herpetol.* 34, 139–142.
- Saint Girons, H., 1978. Morphologie externe comparée et systématique des vipères d'Europe (Reptilia, Viperidae). *Rev. Suisse Zool.* 85, 565–595.
- Schneider, B., 1975. Eine Mittelpleistozäne Herpetofauna von der Insel Chios, Ägäis. *Senck. Biol.* 56, 191–198.
- Schwane, T.D., Sarre, S.D., 1988. Body size of tiger snakes in southern Australia, with particular reference to *Notechisater serventyi* (Elapidae) on Chappell Island. *J. Herpetol.* 22, 24–33.
- Szyndlar, Z., 1988. Two new extinct species of the genera *Malpolon* and *Vipera* (Reptilia, Serpentes) from the Pliocene of Layna Spain. *Acta Zool. Cracov.* 31, 687–706.
- Szyndlar, Z., 1991. A review of Neogene and Quaternary snakes of central and eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios Geol.* 47, 237–266.
- Szyndlar, Z., Rage, J.-C., 1999. Oldest fossil vipers (Serpentes: Viperidae) from the old World. *Kaupia* 8, 9–20.
- Szyndlar, Z., Rage, J.-C., 2002. The fossil record of true vipers. In: Schuett, G.W., Höggren, M., Greene, H.W. (Eds.), *Biology of the vipers*. Eagle Mountain Publishers, pp. 419–444.