ACTA ZOOL. CRACOV.	31	27	687—706	KRAKÓW, 30. VI. 1988

Festschrift for Marian Młynarski

Zbigniew SZYNDLAR

Two new extinct species of the genera *Malpolon* and *Vipera* (*Reptilia, Serpentes*) from the Pliocene of Layna (Spain)

[With 8 text-figs]

Dwa nowe kopalne gatunki z rodzajów *Malpolon* i *Vipera* (*Reptilia, Serpentes*) z plioceńskiego stanowiska Layna w Hiszpanii

Abstract. Fossil material from the Middle Pliocene (MN 15) of Layna (Province of Soria, Spain) contains remains of at least 5 different snake taxa, belonging to the families *Colubridae*, *Elapidae* and *Viperidae*. Two of them, *Malpolon mlynarskii* sp. n. and *Vipera maxima* sp. n., dominant in the snake fauna, are described in detail. *Malpolon mlynarskii* sp. n. is regarded as a sister species of the living *M. monspessulanus*. *Vipera maxima* sp. n. probably belongs to the '*russelli*' complex of the genus *Vipera*. The composition of the Layna assemblage demonstrates that the extant snake fauna appeared in the Iberian Peninsula later than the Middle Pliocene.

I. INTRODUCTION

The locality of Layna (also known as Cerro Pelado) is situated in the Spanish province of Soria, north-east of Madrid. Numerous remains of terrestrial vertebrates coming from this site have been described in several papers by various authors; these descriptions were summarized in a report by AGUIRRE et al. (1981). The age of the fauna from Layna is Middle Pliocene (Mammalian Unit MN 15). A preliminary report on the snake fauna from Layna was given by JAEN and SANCHÍZ (1985); according to these authors, snakes are represented by four different taxa, namely *Coronella* sp., "... a probably new species of the colubrid genus *Malpolon*", *Naja* cf. *naja*, and *Vipera* sp.

The snake material from Layna consists of about 200 disarticulated precaudal vertebrae (most of them extensively damaged) and an almost complete braincase. Most vertebrae belonged to large snakes; they are referred here to three different genera: *Malpolon* (*Colubridae*), *Vipera* (*Viperidae*), and cf. *Naja* (*Elapidae*). Only the two former snakes are described below in detail.

Vertebral fragments referred to the *Elapidae* are poorly preserved and their correct identification to the specific level is problematic. Two tiny trunk vertebrae present in the material are also not clearly identifiable. One of them (MNCN 10026) resembles vertebrae of *Macroprotodon*, rather than those of *Coronella* as previously suggested, while the other (MNCN 10031) belonged to a small member of the genus *Vipera* (different than the viper described below).

The fossil snake material from Layna is the property of the Museo Nacional de Ciencias Naturales in Madrid.

Abbreviations for museums: GNM — Natural History Museum, Göteborg; MNCN — Museo Nacional de Ciencias Naturales (C. S. I. C.), Madrid; ZFMK — Zoologisches Forschungsinstitut und Museum Alexander KOENIG, Bonn; ZZSiD — Institute of Systematic and Experimental Zoology (Polish Acad. Sci.), Cracow.

Acknowledgements. I am deeply grateful to Dr. Borja SANCHÍZ (Madrid) for loaning the fossil material from Layna as well as to Miss María Jesús JAEN (Salamanca) who preparared the material for study. Snake skeletons used for comparative purposes were kindly provided by Dr. Wolfgang BÖHME (Bonn), Dr. Göran NILSON (Göteborg), and Dr. Borja SANCHÍZ (Madrid). I am indebted to Dr. Brian C. GROOMBRIDGE (Cambridge, UK) who brought his observations on the taxonomic status of *Vipera gedulyi* to my attention. Special thanks are due to the editor of this paper, Dr. Richard ESTES (San Diego), for his helpful comments.

II. SYSTEMATIC PALEONTOLOGY

Family *Colubridae* s. l.

The fossil remains described below are clearly referable to the family *Colubridae* because the posterior foramina of the Vidian canals and the cerebral foramina are confluent and located within the basiparasphenoid. The braincase cannot be referred to the *Viperidae*, which have the posterior orifice of the Vidian canal well separated from the cerebral foramen, and the anterior orifice located between the basiparasphenoid and parietal; it cannot be referred to the *Elapidae*, which have the posterior orifice of the Vidian canal located between the basiparasphenoid and prootic, while the anterior orifice is located between the basiparasphenoid and parietal. Moreover, trunk vertebrae of vipers and elapids have well defined hypapophyses, which are absent in the from Layna. For the same reasons, the fossils cannot be referred to vertebrae the natricine snakes.

Of the West Palearctic colubrine snakes, the fossil remains resemble closely members of the genera *Malpolon*, *Coluber* and *Elaphe*. Other compared genera

(*Eirenis*, *Psammophis*, *Lytorhynchus*, *Spalerosophis*, *Telescopus*, *Macroprotodon*, *Coronella*) display clearly different morphological features; these comparisons are omitted below.

Genus *Malpolon* FITZINGER, 1826

Malpolon mlynarskii sp. n.
(Figs 1 and 2)

Holotype. — A posterior braincase, MNCN 10000.

Referred material. — 27 precaudal vertebrae, MNCN 10001—10025.

Etymology. — Named in honour of Professor Marian MŁYNARSKI.

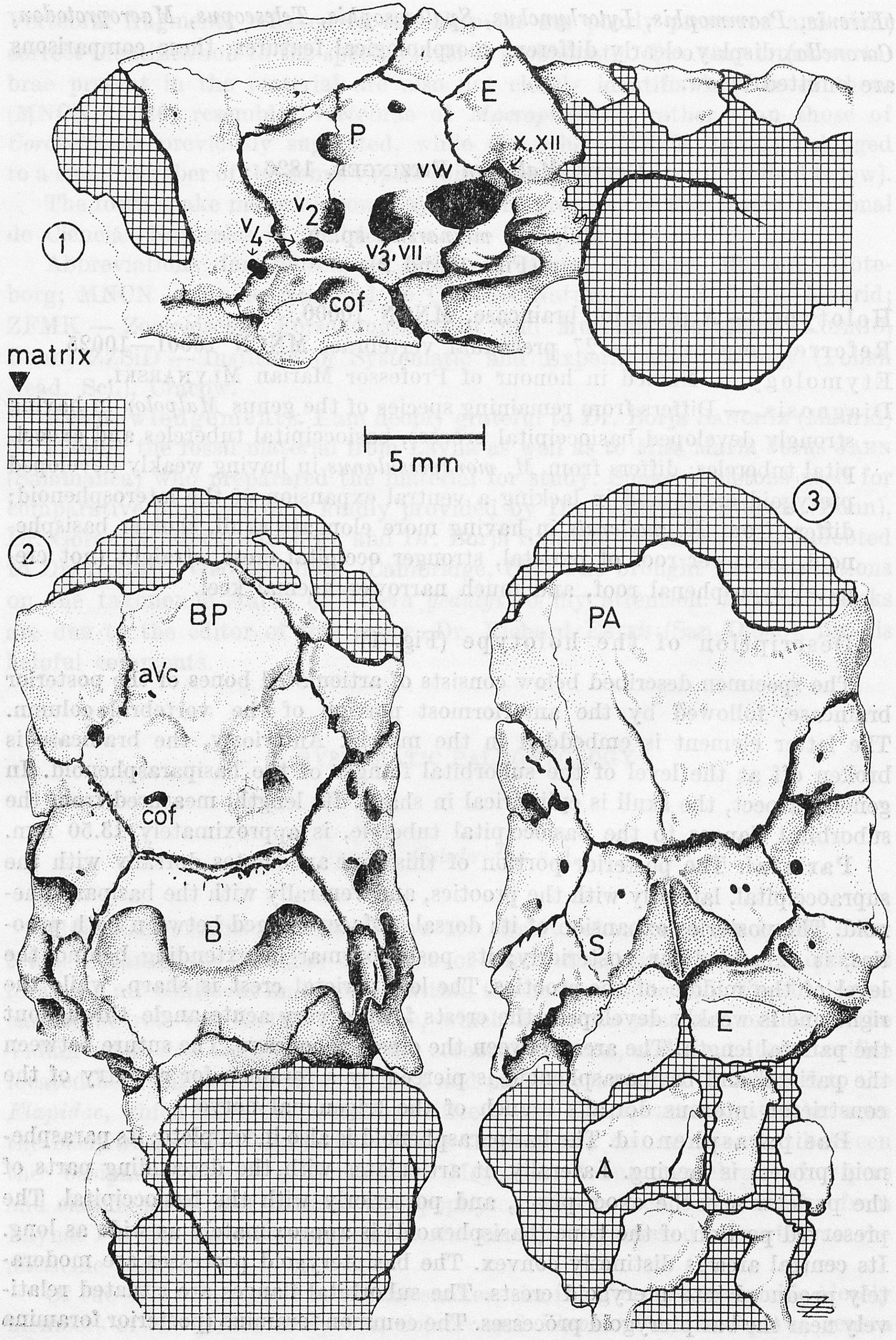
Diagnosis. — Differs from remaining species of the genus *Malpolon* in having strongly developed basioccipital process, basioccipital tubercles and exoccipital tubercles; differs from *M. monspessulanus* in having weakly developed pterygoid crests and in lacking a ventral expansion of the laterosphenoid; differs from *M. moilensis* in having more elongate skull, shorter basisphenoid, narrower roof of parietal, stronger occipital crest, straight (not crenate) zygosphenal roof, and much narrower haemal keel.

Description of the holotype (Fig. 1)

The specimen described below consists of articulated bones of the posterior braincase, followed by the anteriormost portion of the vertebral column. The latter element is embedded in the matrix. Anteriorly, the braincase is broken off at the level of the suborbital flanges of the basiparasphenoid. In general aspect, the skull is cylindrical in shape. Its length, measured from the suborbital flanges to the basioccipital tubercle, is approximately 13.50 mm.

Parietal. The posterior portion of this bone articulates dorsally with the supraoccipital, laterally with the prootics, and ventrally with the basiparasphenoid. The posterior expansion of its dorsal surface, wedged between both prootics, is expanded far posteriorly; its posterior margin extending behind the level of the middle of the prootics. The left parietal crest is sharp, while the right one is weakly developed; the crests form a very acute angle throughout the parietal length. The area between the crests is concave. The suture between the parietal and basiparasphenoid is pierced by a foramen for re-entry of the constrictor internus dorsalis branch of the trigeminal nerve.

Basiparasphenoid. The basiparasphenoid is also incomplete; its parasphenoid process is lacking. Laterally, it articulates with the descending parts of the parietal and the exoccipitals, and posteriorly with the basioccipital. The preserved portion of the bone (basisphenoid) is approximately as wide as long. Its central area is distinctly convex. The basipterygoid processes are moderately produced into pterygoid crests. The suborbital flanges are situated relatively near the basipterygoid processes. The common foramina (posterior foramina


1
P
E
X, XII
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V3, VII
cof
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of Vidian canals + cerebral foramina) are distinct and situated at some distance from the postero-lateral corners of the bone. The anterior foramen of the right Vidian canal is small and is situated near the lateral border of the bone; the left foramen is not visible. The posterior border of the bone is not provided with a medial process.

Prootic. Anteriorly, at its articulation with the parietal, the prootic forms a strong expansion. Posteriorly, at its articulation with the exoccipital, the bone is provided with a deep sinus, the latter forming the anterior wall of the vestibular window. A cavity for the maxillary branch of the trigeminal nerve (anterior) is somewhat smaller than that for the mandibular branch of the trigeminal nerve and for the facial nerve (posterior). The former cavity is accompanied ventrally by a foramen for the constrictor internus dorsalis branch of the trigeminal nerve. Immediately above these foramina, the prootic (especially that on the right side of the cranium) is produced into a crest, accompanied dorsally by a series of distinct cavities.

Exoccipital. Anteriorly, this bone is provided with a deep sinus, forming the posterior wall of the vestibular window. Small fragments of the feet of the columellae (in both exoccipitals) cover foramina for the vagus-hypoglossal nerves. The occipital crest is strongly developed (in the right exoccipital it is missing). The exoccipital tubercles (jointed with the basioccipital tubercles) are missing in great part, but most likely they were relatively long.

Basioccipital. The basioccipital is characterized by a very long basioccipital tubercle (the right tubercle is broken off). The basioccipital process is exceptionally strongly developed; although its distal portion is missing, the remnants indicate that this structure was very long.

Supraoccipital. This bone is somewhat wider than long. The sagittal and occipital crests are well developed; the latter are at an acute angle to each other.

Description of vertebrae (Fig. 2)

All the vertebrae referred here to *Malpolon* come from the middle of the column. Most of them belonged to large snake(s); the centrum length of the largest vertebra is approximately 9.50 mm.

The vertebrae have moderately elongate centra, provided with a thin, sharp, and prominent haemal keel. The posterior end of the keel is usually pro-

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Fig. 1. Braincase of *Malpolon mlynarskii* sp. n. (holotype, MNCN 10000). 1 — lateral view, 2 — ventral view, 3 — dorsal view. Abbreviations: A — axis, aVc — anterior orifice of Vidian canal, B — basioccipital, BP — basiparasphenoid, cof — common foramen (posterior foramen of Vidian canal and cerebral foramen), E — exoccipital, P — prootic, PA — parietal, S — supraoccipital, vw — vestibular window, V_2 — foramen for maxillary branch of trigeminal nerve (anterior prootic foramen), V_3 — foramen for mandibular branch of trigeminal nerve (posterior prootic foramen), V_4 — foramina for constictor internus dorsal branch of trigeminal nerve, VII — foramen for facial nerve, X, XII — foramen for vagus-hypoglossal nerve

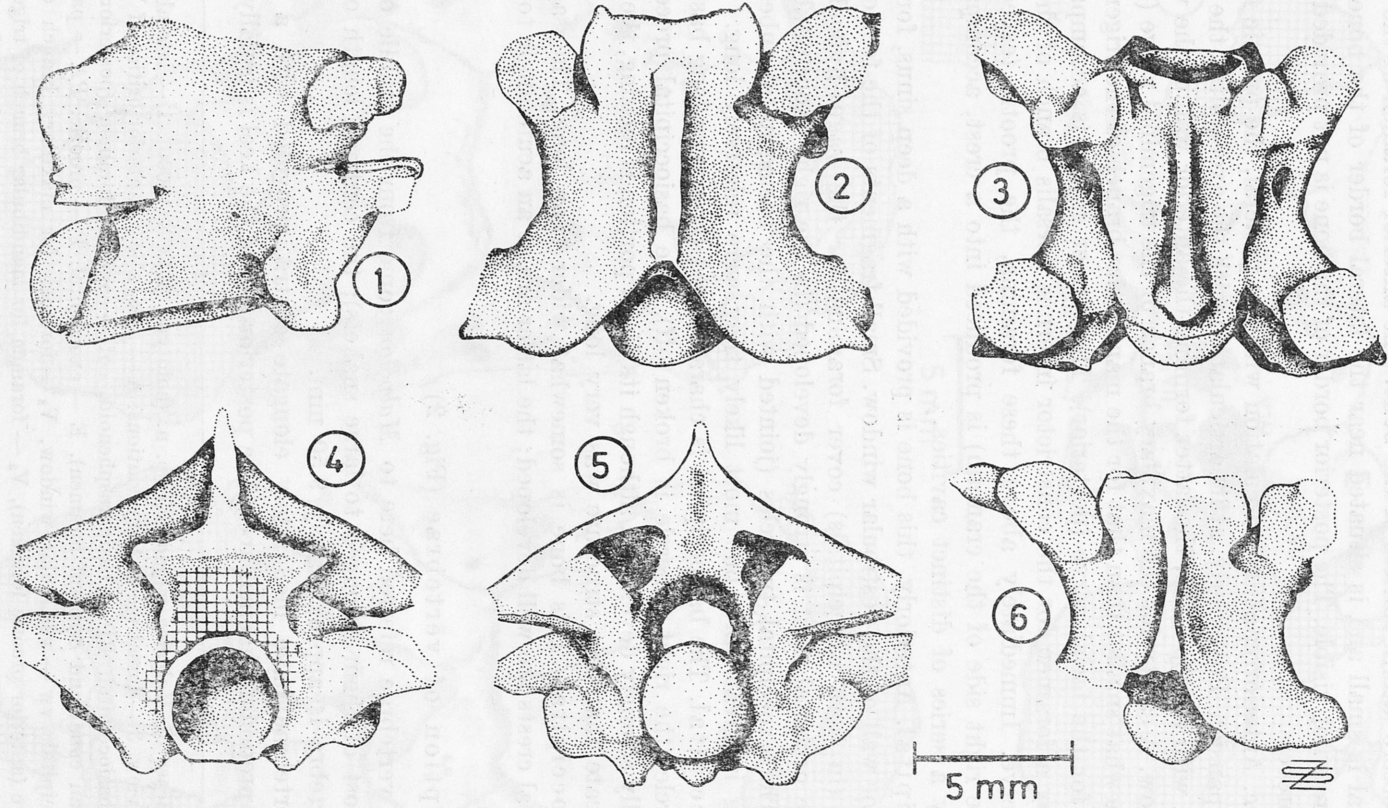


Fig. 2. Three trunk vertebrae of *Malpolon mlynarskii* sp. n. (1—3 — MNCN 10001; 4, 5 — MNCN 10003; 6 — MNCN 10004). 1 — lateral, 2 and 6 — dorsal, 3 — ventral, 4 — anterior, 5 — posterior views

duced into an acute tip. The subcentral ridges are usually moderately developed. The subcentral grooves are shallow. The neural arch is vaulted; its posterior borders are usually straight (not convex) in anterior or posterior view. The epizygapophyseal spines are small. The neural spines are missing from all the material; these structures were probably relatively long, beginning from above the zygosphenal roof. The zygosphenes are straight or weakly concave, in dorsal view. The zygapophyseal articular facets are usually ovaloid. No vertebra has complete prezygapophyseal processes preserved, but, based on their remnants, these structures were probably relatively long. The parapophyses are subquadrate and usually are distinctly longer than the diapophyses. The cotyle and condyle are rounded. The vertebral foramina are very small.

Comparisons

As noted above, the discussed fossils display morphological features of the genus *Malpolon*, but also, although to a lesser degree, these of the genera *Coluber* and *Elaphe*. Osteologically, the genera *Malpolon*, *Coluber* and *Elaphe* can be distinguished easily from one another on the basis of the morphology of the toothed bones, but these elements are lacking in the material from Layna. Unfortunately, intergeneric differences observed in braincase bones are less clear. More attention must be therefore paid to comparisons among braincases of these three genera.

The genus *Malpolon* consists of two living species: *M. moilensis*, inhabiting North Africa, and *M. monspessulanus*, inhabiting both European and African coasts of the Mediterranean Sea. The latter species includes two different subspecies, *M. m. monspessulanus*, from the West Mediterranean including Spain, and *M. m. insignitus*, from the East Mediterranean. Braincase bones of both species of the genus *Malpolon* differ much from each other. Some minor differences are also observed between both subspecies of *M. monspessulanus* (Fig. 3). The only fossil species of this genus, *M. laurenti*, was described on the basis of several vertebrae by Depéret (1890) from the Middle Pliocene (MN 15; same age as Layna) of the Roussillon Basin. Some other finds from the European Neogene referred to this genus are doubtful (cf. Szyndlar, 1984).

Malpolon mlynarskii sp. n. most closely resembles the living *M. monspessulanus*. The most important features found in both these forms and not observed in the genera *Coluber* and *Elaphe* are as follows: considerable posterior expansion of the parietal, a very acute angle between the parietal crests throughout the bone, relatively very short basisphenoid portion of the basiparasphenoid, ventral expansion of the middle of the basisphenoid, elongation of the vertebrae, a thin and sharp haemal keel, and straight posterior margins of the neural arch. In large members of the genera *Coluber* and *Elaphe*, the parietals are less expanded posteriorly and the parietal crests diverge laterally (except for *Coluber jugularis*). The basisphenoids are much more elongate and the pterygoid crests (in *Malpolon monspessulanus* inclined posteriorly, in *M. mlynarskii*

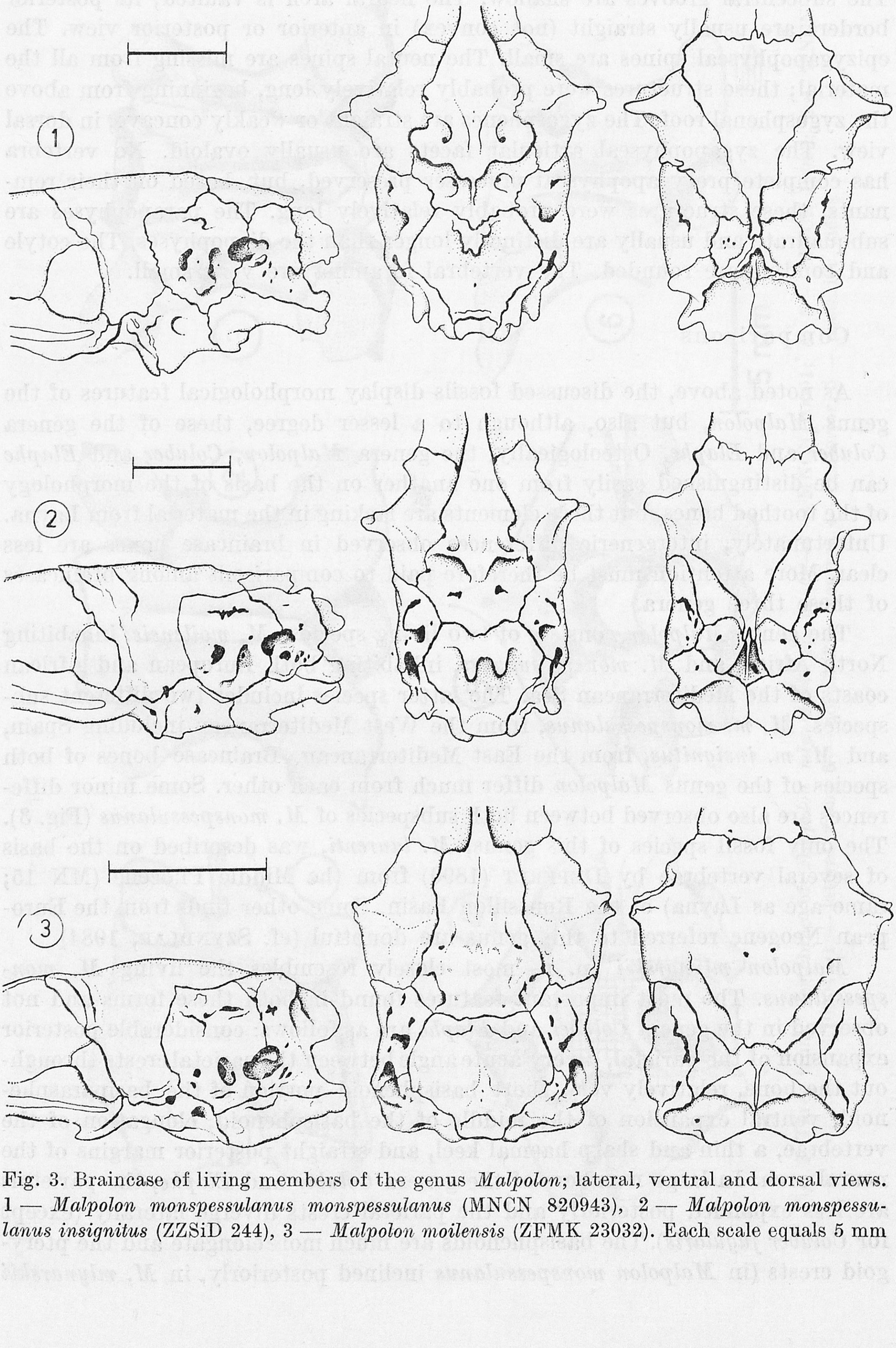


Fig. 3. Braincase of living members of the genus *Malpolon*; lateral, ventral and dorsal views. 1 — *Malpolon monspessulanus monspessulanus* (MNCN 820943), 2 — *Malpolon monspessulanus insignitus* (ZZSiD 244), 3 — *Malpolon moilensis* (ZFMK 23032). Each scale equals 5 mm

sp. n. protruding downwards) are inclined anteriorly (except for *Coluber jugularis*). The vertebrae are relatively shorter, and provided with distinctly convex posterior borders of the neural arch.

The remaining bones largely share some common features with *Malpolon monspessulanus*, but also with several members of *Coluber* and *Elaphe*.

The supraoccipital of *Malpolon mlynarskii* sp. n. is very similar to those of *M. monspessulanus*, especially to an example of *M. m. insignitus* (ZZSiD 333). Some variability is observed in the available sample of *M. m. monspessulanus*; the supraoccipital of the specimen MNCN 820944 is twice as wide as long and its occipital crests are parallel with the posterior border of the bone. The supraoccipital of *M. mlynarskii* sp. n. is also very similar to those of *Elaphe*. In *Coluber viridiflavus* and *C. jugularis*, the occipital crests are expanded far outside the bone and the posterior area is much reduced; in remaining members of the genus *Coluber* the sagittal and occipital crests are weakly defined.

The prootic of *Malpolon mlynarskii* sp. n. is most similar to that of *M. moilensis*. In *M. monspessulanus* the laterosphenoid (= bar dividing the foramina for the trigeminal nerves) is usually produced into as expansion, protruding downwards (except for *M. m. insignitus* ZZSiD 333). In *Elaphe*, the anterior foramen is distinctly smaller than the posterior one, the laterosphenoid is strongly expanded posteriorly, and the supraoccipital crest is underdeveloped. In *Coluber*, the anterior and posterior foramina are of equal size, the laterosphenoid is not expanded posteriorly, and the supraoccipital crest is distint.

The exoccipital resembles that of *Malpolon monspessulanus* in having a strongly expanded occipital crest, but differs in the presence of distinct exoccipital tubercles. Both these structures are present in the genus *Coluber*. Members of the genus *Elaphe* have weakly developed occipital crests and lack occipital tubercles (the latter feature is absent in *E. scalaris* and *E. quatuorlineata*).

The most interesting element in the cranium of *Malpolon mlynarskii* sp. n. is the basioccipital, because of the presence of long basioccipital tubercles and a huge basioccipital process. The relative size of these structures is unparalleled in any West Palearctic colubrid snakes. In the living species of *Malpolon*, the basioccipital tubercles are either absent or, exceptionally (*M. m. monspessulanus*, MMCN 820944), moderately developed. The morphology of the basioccipital process varies in *M. monspessulanus*; in *M. m. monspessulanus* it has always a shape of a strong spur, while in *M. m. insignitus* if forms two separated processes (ZZSiD 244; Fig.3: 2) or is reduced to two indistinct callosities (ZZSiD 333), as in *M. moilensis* (Fig. 3: 3). In *Elaphe*, the basioccipital tubercles are absent or weakly developed, and the basioccipital process is absent, as in most species of *Coluber*. In *Coluber jugularis* and *C. viridiflavus*, the basioccipital is provided with distinct basioccipital tubercles and a strong basioccipital process, but the latter structure is always accompanied laterally by two smaller, although distinct, lobes. The only West Palearctic snakes with basioccipital processes similar to those of *Malpolon mlynarskii* sp. n. are not colubrids,but include the largest members of the genus *Vipera*. These comparisons demonstrate that the morphology of the basioccipital is the most important diagnostic feature differentiating *Malpolon mlynarskii* sp. n. from other species of the *Colubridae*.

Discussion

Based on the criteria for derivativeness (considering also external morphology) proposed by MARX and RABB (1972) and other authors, *Malpolon monspessulanus* apparently seems to be a more advanced species than *M. moilensis*. Outgroup comparison with *Elaphe* and *Coronella*, the conservative genera of the family *Colubridae* (fide UNDERWOOD, 1967) reveals that *M. monspessulanus* and *M. mlynarskii* sp. n. share several derived states in the braincase (of which the most important are: suborbital flanges of the basiparasphenoid shifted far backwards; occipital crest very strong; basioccipital process present and well developed), unlike *M. moilensis*. It is possible that *moilensis* should be removed from the genus *Malpolon*.

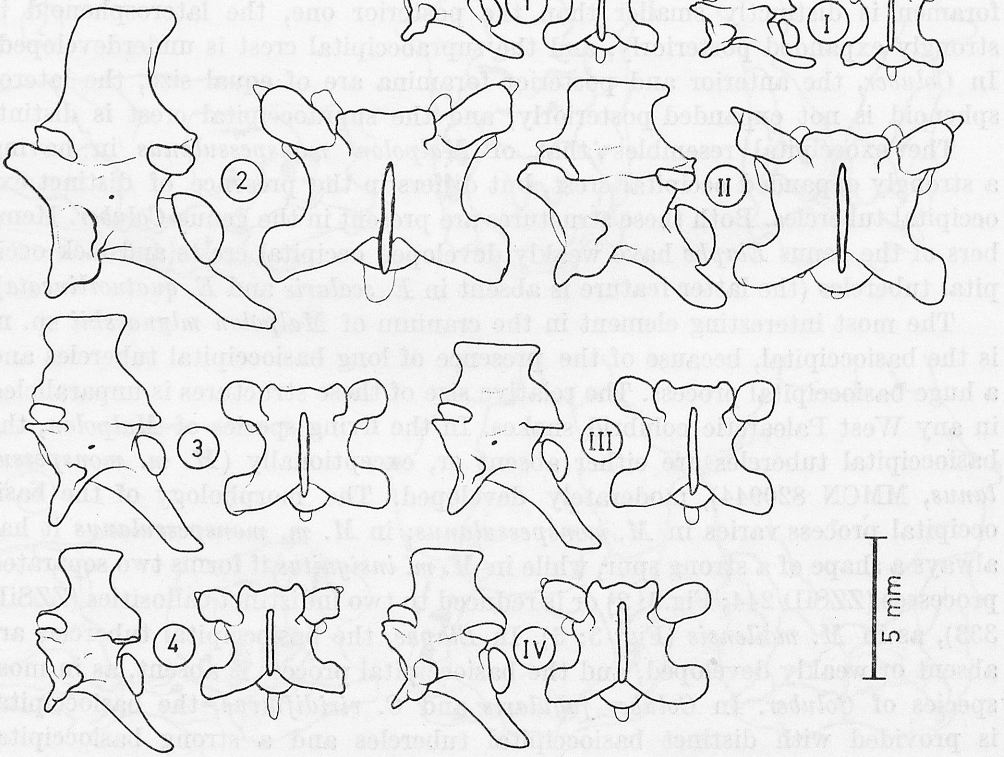


Fig. 4. 60th vertebrae (Arabic numerals) and 100th vertebrae (Roman numerals) of several viperine genera other than the "Oriental vipers"; lateral and dorsal views. 1/I — *Vipera latastei* (MNCN 820971), 2/II — *Bitis arietans* (ZZSiD 355), 3/III — *Cerastes cerastes* (ZZSiD 361), 4/IV — *Echis colorata* (ZZSiD 402)

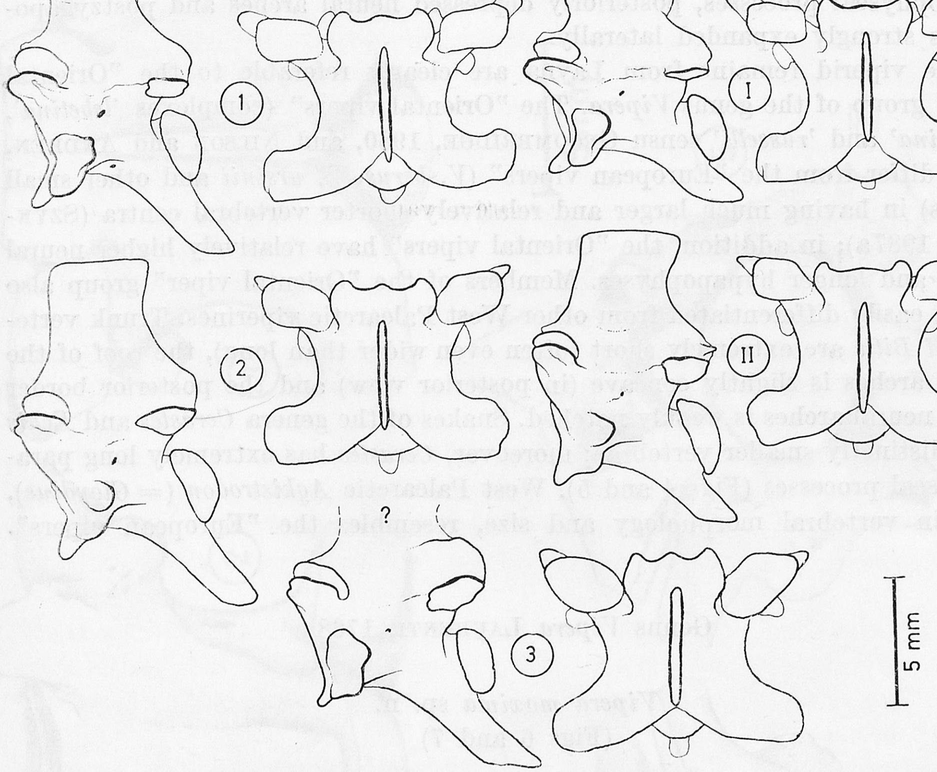


Fig. 5. 60th vertebrae (Arabic anumerals) and 100th vertebrae (Roman numerals) of three representatives of "Oriental vipers"; lateral and dorsal views. 1/I — *Vipera mauritanica* (GNM 10637), 2/II — *Vipera russelli* (ZZSiD 362), 3 — mid-trunk vertebra of *Vipera platyspondyla* from the Czech Miocene (after SZYNDLAR, 1987a; slightly reconstructed)

M. mlynarskii sp. n. cannot be regarded as an ancestral form of *M. monspessulanus* because of the presence of some derived states absent in the latter (exoccipital tubercles and basioccipital tubercles very long; basioccipital process exceptionally large). It suggests that *M. monspessulanus* and *M. mlynarskii* sp. n. may form sister groups. The taxonomic position of *M. laurenti* is uncertain; according to HOFFSTETTER (1939), the vertebrae of this Pliocene snake are comparable, perhaps identical, with those of *M. monspessulanus*.

Family *Viperidae*

The vertebrae referred to the *Viperidae* are quite different from those of other hypapophysis-bearing snakes. They differ from those of the *Natricinae* in having straight (not sigmoid) hypapophyses, posteriorly depressed neural arches (SZYNDLAR, 1984), distinctly longer parapophyseal processes,, and much shorter vertebral centra; they differ from the West Palearctic *Elapidae* (the

Naja group) in having longer neural spines and hypapophyses, distinctly longer parapophyseal processes, posteriorly depressed neural arches and postzygapophyses strongly expanded laterally.

The viperid remains from Layna are clearly referable to the "Oriental viper" group of the genus *Vipera*. The "Oriental vipers" (complexes *'lebetina'*, *'xanthina'* and *'russelli'* sensu GROOMBRIDGE, 1980, and NILSON and ANDRÉN, 1986) differ from the "European vipers" (*V. berus*, *V. ursinii* and other small species) in having much larger and relatively shorter vertebral centra (SZYNDLAR, 1987a); in addition, the "Oriental vipers" have relatively higher neural spines and longer hypapophyses. Members of the "Oriental viper" group also can be easily differentiated from other West Palearctic viperines. Trunk vertebrae of *Bitis* are extremely short (often even wider than long), the roof of the neural arches is slightly concave (in posterior view) and the posterior border of the neural arches is weakly notched. Snakes of the genera *Cerastes* and *Echis* have distinctly smaller vertebrae; moreover, *Cerastes* has extremely long parapophyseal processes (Figs 4 and 5). West Palearctic *Agkistrodon* (= *Gloydius*), both in vertebral morphology and size, resembles the "European vipers".

Genus *Vipera* LAURENTI, 1768

Vipera maxima sp. n.
(Figs 6 and 7)

Holotype. — A trunk vertebra, MNCM 10032.
Referred material. — 19 predaudal vertebrae, MNCN 10033—10048.
Etymology. — From Latin *maximus*, superlative of *magnus* — large.
Diagnosis. — Differs from all living and extinct members of the "Oriental viper" group of the genus *Vipera* in having distinctly larger size and strongly depressed cotyle and condyle; differs from all the "Oriental vipers" except for *V. russelli* in having higher neural spine of posterior trunk vertebrae; differs from *V. xanthina* and *V. platyspondyla* in having a rectangular shape of the prezygapophyseal articular facets.

Description of the holotype (Fig. 6)

The vertebra comes from the mid-trunk region of the column of a very large snake. The basic measurements of the holotype vertebra are as follows: centrum length 11.80 mm; centrum width 10.32 mm; length from the anterior edge of prezygapophyseal articular surface to the posterior edge of postzygapophyseal articular surface 13.43 mm; zygospohene width 7.53 mm; cotyle height 5.88 mm; cotyle width 7.18 mm.

In lateral view, the vertebra is relatively short and high. The neural arch is strongly depressed and tilted in the postzygapophyseal region. The neural spine begins above the zygosphenal articular facets and occupies two-thirds

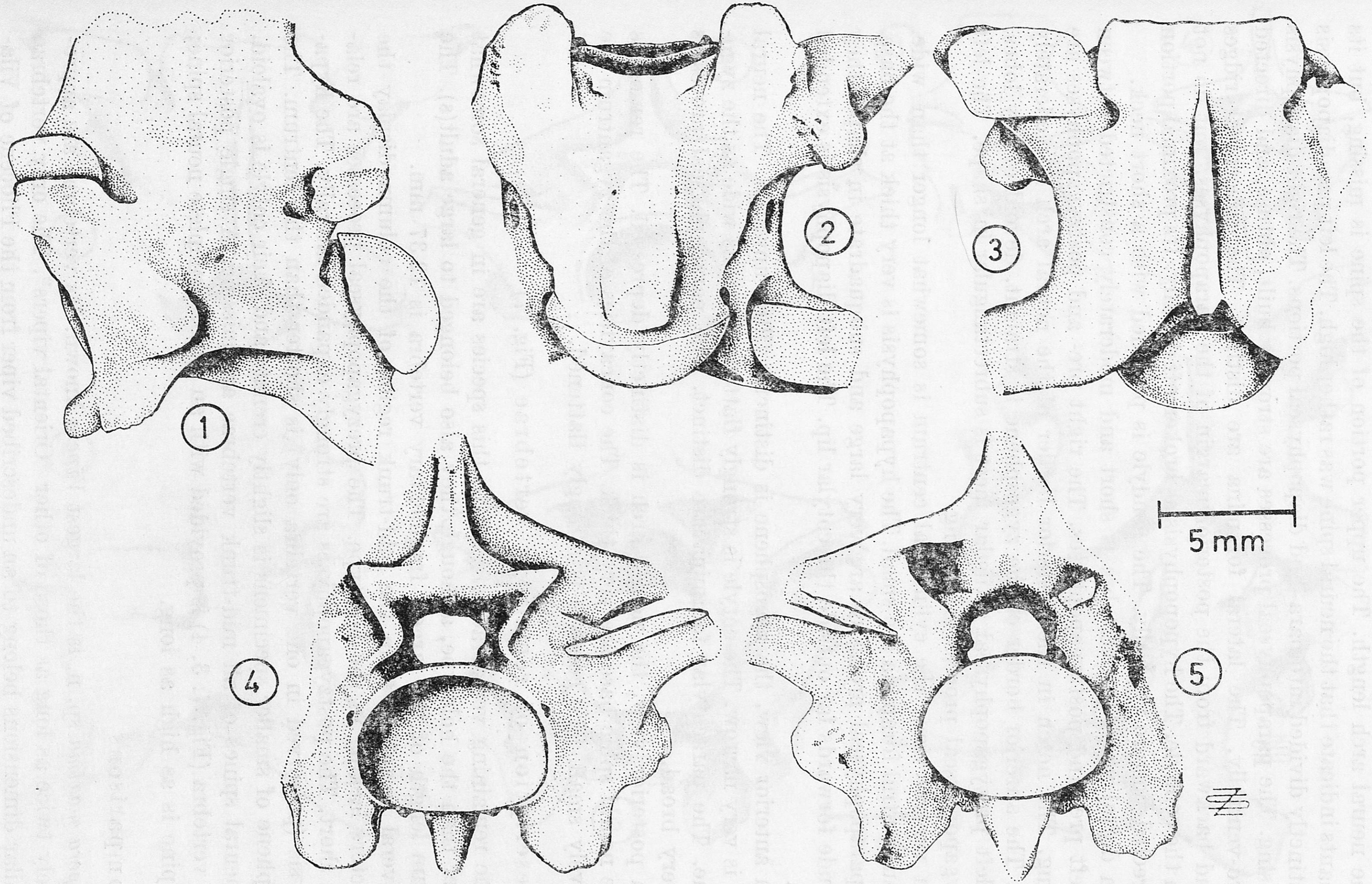


Fig. 6. Trunk vertebra of *Vipera maxima* sp. n. (holotype, MNCN 10032). 1 — lateral, 2 — ventral, 3 — dorsal, 4 — anterior, 5 — posterior views

of the neural arch length. The upper portion of the spine is missing, but its remnants indicate that the neural spine was rather high. The left paradiapophysis is distinctly divided into para- and diapophyseal portions. The right diapophysis is mising. The parapophyseal processes are strongly built, obtuse, and directed antero-ventrally. The lateral foramina are distinct. The subcentral ridges extend backward from the posterior margin of the parapophyses, but do not reach the condyle. The hypopophysis is broken off distally. Its proximal portion is directed postero-ventrally. The condyle is provided with a short neck.

In dorsal view, the vertebra is short and moderately constricted between the left pre- and postzygapophyses. The right pre- and postzygapophyses are missing. The notch in the posterior border of the neural arch is moderately deep. The anterior border of the zygosphene is straight, devoid of any lobes. The left prezygapophyseal articular facet is subrectangular in shape. The left prezygapophyseal process is missing.

In ventral view, the cylindrical centrum is somewhat longer than wide. The subcentral foramina are small. The hypapophysis is very thick at the base. The parapophyseal processes are very large and subquadrate in shape; they protrude forwards far outside the cotylar lip. The left diapophysis is extended aside.

In anterior view, the zygosphene is distinctly tilted upwards. The neural canal is very narrow. The cotyle is strongly flattened; it is as wide as the zygosphene. The paracotylar foramina are distinct. The parapophyseal processes are very broad.

In posterior view, the neural arch is distinctly depressed. The remnants of the neural spine base are very thick. The concavities of the zygantrum are relatively small. The condyle is strongly flattened.

Description of remaining vertebrae (Fig. 7)

The remaining vertebrae referred to this species are in general somewhat smaller than the holotype, although they also belonged to large adult(s). The centrum length of the largest fragmentary vertebra is 12.37 mm.

Several vertebrae from the mid-trunk region of the column display the characters lacking in the holotype. The prezygapophyseal processes are relatively short. The postzygapophyses are strongly expanded laterally. The hypapophysis (preserved in one vertebra only) is shorter than the centrum. The zygosphene of smaller specimens is slightly crenate and their cotyle is ovaloid. The neural spines of all mid-trunk vertebrae are missing. A single posterior trunk vertebra (Fig. 7: 3, 4) is provided with an almost complete neural spine; this spine is as high as long.

Comparisons

Vipera maxima sp. n. is the largest *Vipera* known. Its vertebrae are approximately twice as long as those of other "Oriental vipers". The only vertebrae of similar dimensions belong to an undescribed viper from the Pliocene of Vila-

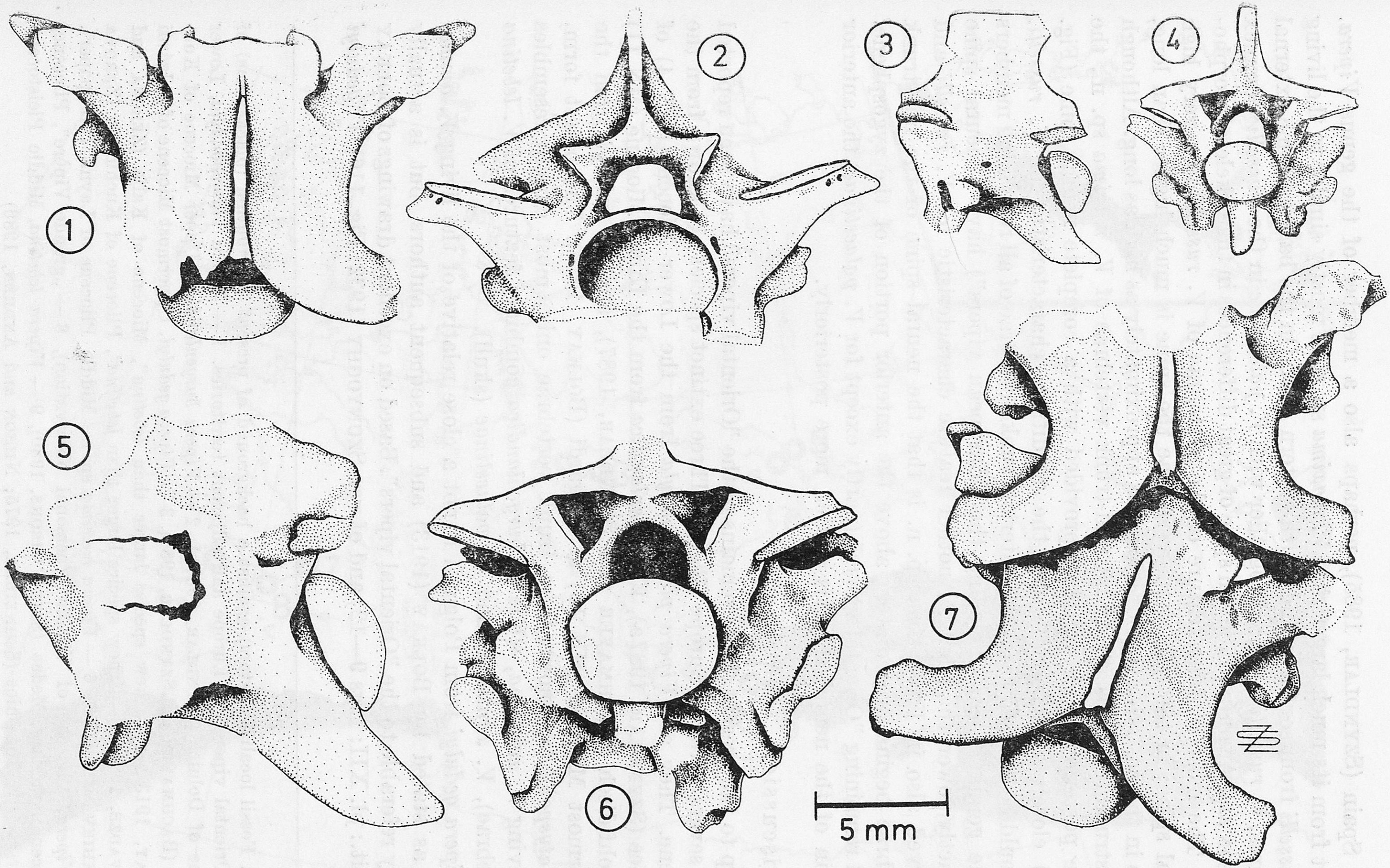


Fig. 7. Mid-trunk vertebrae (1, 2 — MNCN 10033; 5 — MNCN 10034; 6, 7 — MNCN 10035) and posterior trunk vertebra (3, 4 — MNCN 10036) of *Vipera maxima* sp. n. 1 and 7 — dorsal, 2 — anterior, 3 and 5 — lateral, 4 and 6 — posterior views

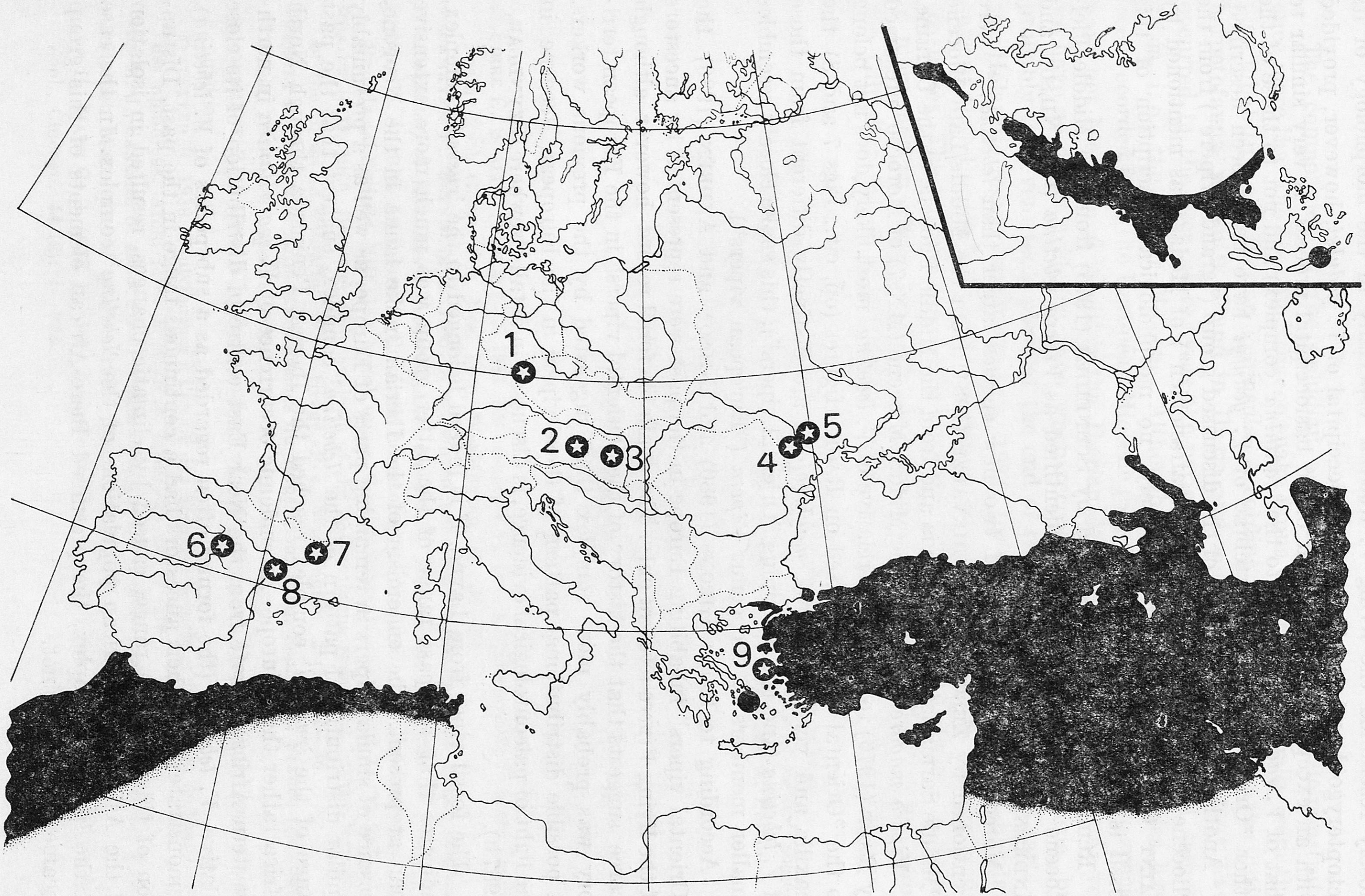
fant, Spain (Szyndlar, 1985), perhaps also a member of the genus *Vipera*. Apart from its much larger size, *V. maxima* sp. n. is mostly similar to the living *V. russelli* from southern and south-eastern Asia. On the basis of some external features, *V. russelli* is placed together with *V. palaestine* in the '*russelli*' complex (Nilson and Andrén, 1986), in spite of great differences in their skeletal morphology. The most striking feature of the vertebrae of *V. russelli* is a very high neural spine; in the mid-trunk vertebrae the spine is much higher than long, while in the posterior trunk region it is approximately as high as long. Although this structure is missing in all mid-trunk vertebrae of *V. maxima* sp. n., the single posterior trunk vertebra provided with a complete neural spine (Fig. 7: 3) closely corresponds with the conditions characteristic for *V. russelli*. It should be stressed that the posterior trunk vertebrae of all remaining members of the genus *Vipera* (including the "European vipers") have a neural spine distinctly lower than long. Another feature characteristic for *V. russelli* and observed also in *V. maxima* sp. n. is that the neural spine of the mid-trunk vertebrae begins immediately above the anterior portion of the zygosphene. In all remaining "Oriental vipers" (partly except for *V. palaestinae*) the anterior margin of the neural spine is shifted more posteriorly.

Discussion

Up to the present, fossil remains of the "Oriental vipers" have been reported from several sites in Europe (Fig. 8). Three extinct species are known from the Miocene. They are *Vipera platyspondyla* from the Lower Miocene (MN 4) of Dolnice (Szyndlar, 1987a), *V. burgenlandica* from the Upper Miocene (MN 11) of Kohfidisch (Bachmayer and Szyndlar, 1987), and *V. gedulyi* from the Uppermost Miocene (MN 13) of Polgárdi (Bolkay, 1913). The oldest form, *V. platyspondyla*, known from trunk vertebrae only, most closely resembles the living *V. xanthina*, while *V. burgenlandica* combines features of *V. lebetina* (vertebrae), *V. xanthina*, and *V. palaestinae* (skull).

Vipera gedulyi from Polgardi is not a close relative of the living *V. ammodytes* as stated by Bolkay (1913) and subsequent authors but is actually clearly referable to the "Oriental vipers". Based on excellent drawings of Bolkay (op. cit.: pl. XII: Figs 9—12) and of von Szunyoghy (1932: Fig. 116) *V. gedulyi*

Fig. 8. Fossil localities (stars) against a background of present distribution (black areas) of the "Oriental vipers" in Europe and adjacent territories. 1 — *Vipera platyspondyla*, Lower Miocene of Dolnice (Szyndlar, 1987a), 2 — *Vipera burgenlandica*, Upper Miocene of Kohfidisch (Bachmayer and Szyndlar, 1987), 3 — *Vipera gedulyi*, Uppermost Miocene of Polgárdi (Bolkay, 1913), 4 — „new species larger than *lebetina*", Miocene of Kalfa (Zerova and Ckhikvadze, 1984), 5 — „new species larger than *lebetina*", Pliocene of Kuchurgan (Zerova and Ckhikvadze, 1984), 6 — *Vipera maxima* sp. n., Middle Pliocene of Layna (this paper), 7 — ?*Vipera*, Pliocene of Vilafant (personal observation), 8 — „grande Vipère", Pliocene/Pleistocene boundary, Medas (Saint Girons, 1980), 9 — *Vipera lebetina*, Middle Pleistocene of Chios (Schneider, 1975; Nilson and Andrén, 1986)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closely resembled the living *V. lebetina* especially in the morphology of its ectopterygoid and maxilla. The basioccipital of *V. gedulyi*, however, provided with an exceptionally long and broad basioccipital process is very similar to that of *V. raddei* (belonging to the '*xanthina*' complex) and not to those of the other "Oriental vipers"; vertebrae of *V. gedulyi* have never been described.

Another possible member of the discussed group ("grande vipère") from the Pliocene/Pleistocene boundary ("Villafranchien") of Medas was mentioned by SAINT GIRONS (1980); unfortunately no morphological description of this fossil is available.

Remains of a viper described by SCHNEIDER (1975) from the Middle Pleistocene of Chios were recently identified as *Vipera lebetina* (fide NILSON and ANDRÉN, 1986).

Moreover "... vertebrae of two new species larger than *lebetina*..." were mentioned by ZEROVA and CKHIKVADZE (1984) from the Middle/Late Miocene ("Middle Sarmatian") of Moldavia and from the Middle Pliocene of the Ukraine.

Vipera maghrebiana from the Middle Miocene (MN 7) of Morocco presumed by RAGE (1976) to be a close relative of *V. lebetina* most likely does not belong to the "Oriental vipers". Based on RAGE's figures (op. cit.: Figs 7 and 8) the maxilla and vertebrae of *V. maghrebiana* are distinctly different from those of *V. lebetina* (and the remaining "Oriental vipers"); this snake closely resembles smaller members of the genus *Vipera* ("European vipers").

According to SAINT GIRONS (1980) and NILSON and ANDRÉN (1986) the "Oriental vipers" inhabiting Europe in the past were represented by ancestors of the living *Vipera lebetina* only. The available fossil record however although scarce suggests that the history of the "Oriental vipers" in the European territory was probably more complex than suggested by the previous workers. A possible distributional pattern of these vipers in the European Neogene in the light of paleontological evidence, is discussed in detail elsewhere (SZYNDLAR, 1987b).

The fossil viper from Layna, if it indeed belonged to the '*russelli*' complex, indicates that the past range of the latter group was much more extensive than at present. The endemism of the Iberian snake fauna in the Neogene, absence of similar vipers in remaining parts of Europe, as well as a presumably similar distributional pattern of the '*lebetina*' complex, suggest that the past range of the '*russelli*' complex reached the Iberian Peninsula through North Africa rather than Europe. An endemic occurrence of *V. mauritanica* in north-western Africa, remote from the Near East centre of distribution of its close relative, *V. lebetina* (the former often regarded as a subspecies of *V. lebetina*), demonstrates that their ancestors had a continuous range in the past. Disruption of this common range, caused by climatic changes, resulted in isolation of the Asiatic and African populations of the '*lebetina*' complex. In the case of the '*russelli*' complex, the presumed Ibero-African elements of this group became totally extinct.

III. CONCLUDING REMARKS

The composition of the ophidian assemblage from Layna demonstrates once more that the Iberian Neogene snake fauna differs substantially from that now inhabiting the Iberian Peninsula. According to Busack (1986), the entire herpetofauna presently found in Iberia and north-western Africa may have occurred in the area as early as the period preceding the Messinian salinity crisis, i. e., the Upper Miocene. Although some living anuran species have been recorded from the European Miocene (Sanchíz, 1983), extant snake species have not been found in either the Iberian Miocene or anywhere else. As yet, we have no direct evidence as to when recent snakes appeared in Iberia, but probably this event took place at the end of the Pliocene, as in other parts of the Holarctic region (see Szyndlar, 1984, for discussion). The available data suggest that Busack's hypothesis cannot be accepted, at least with reference to snakes. The recent snake fauna arrived in the Iberian Peninsula certainly in more modern times, probably as a result of invasion(s) from Africa across the Gibraltar Strait, as previously suggested by Szyndlar (1984, 1985).

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STRESZCZENIE

Praca opisuje dwa nowe gatunki węży, *Malpolon mlynarskii* sp. n. i *Vipera maxima* sp. n., pochodzące ze środkowoplioceńskiego stanowiska Layna w prowincji Soria w Hiszpanii. *Malpolon mlynarskii* sp. n. został określony jako gatunek siostrzany współczesnego *M. monspessulanus*, zamieszkującego wybrzeża Morza Śródziemnego. *Vipera maxima* sp. n., rozmiarami znacznie przewyższająca gatunki współczesne i poznane dotąd gatunki kopalne, należała prawdopodobnie do kompleksu *russelli*, którego przedstawiciele (*V. russelli* i *V. palaestinae*) zamieszkują współcześnie południową Azję. Pracę uzupełnia krytyczny przegląd opisanych dotychczas kopalnych szczątków wielkich żmij z rodzaju *Vipera* (tzw. „żmije orientalne"). Wyniki niniejszej pracy negują pogląd, jakoby herpetofauna spotykana współcześnie na Płw. Iberyjskim i w Afryce płn.-zach. miała zamieszkiwać te obszary już w górnym miocenie.

Special Editor for this paper: Dr. R. Estes