OPHIDIAN FAUNA (REPTILIA, SERPENTES) FROM THE UPPERMOST MIOCENE OF ALGORA (SPAIN)

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ABSTRACT

Fossil snakes from the Uppermost Miocene (NM 13) of Algora (Guadalajara, Spain) are described. The following forms have been recognized: Scolecophidia indet., *Elaphe algorensis* sp. nov. and *Hispanophis coronelloideus* gen. et sp. nov. (Colubridae), *Naja iberica* sp. nov. (Elapidae), Viperidae indet. This faunistic assemblage, being uncomparable with any other snake fauna of Europe, includes both endemic forms (colubrids) as well as close relatives of North African species (*Naja iberica* sp. nov., may be also vipers).

KEY WORDS: Serpentes, Miocene, Iberia, Taxonomy, Biogeography.

RESUMEN

"Fauna de ofidios (Reptilia, Serpentes) del yacimiento finimioceno de Algora (España)".
Se estudian los restos de ofidios del Mioceno terminal (MN 13) de Algora (Guadalajara, España). Se han detectado las siguientes formas. Scolecophidia indet., *Elaphe algorensis* sp. nov. e *Hispanophis coronelloideus* gen. sp. nov. (Colubridae), *Naja iberica* sp. nov. (Elapidae), y Viperidae indet. Esta asociación faunística no es comparable a las restantes faunas de ofidios conocidas de otras localidades europeas, e incluye tanto formas endémicas (Colubridae), como especies evolutivamente emparentadas con formas norteafricanas (*Naja iberica* sp. nov., quizás también las víboras).

PALABRAS CLAVE: Serpentes, Mioceno, Iberia, Taxonomía, Biogeografía.

Introduction

Snakes from the Iberian Neogene are poorly known. The few available reports on these reptiles are either erroneous, inadequate, or based on strongly damaged and thus unidentifiable materials. The first of these papers is presumably that of Navás (1922), dealing with an almost complete articulated ophidian skeleton from the Upper Miocene of Libros (Teruel) that was provisionally classified as *Plymophis sansaniensis* (= *Natrix sansaniensis*). Most likely, the same specimen was afterwards erroneously identified by Piveteau (1927) as belonging to the viperid genus *Bitis*. Remains of Lower Miocene squamates, including boids, viperids and colubrids, coming from Lisboa, were described by Antunes and Rage (1974). Recently, fossil scolecophidians, erycines, elapids and colubrids were reported from the Lower Miocene of Córcoles (Alférez & Brea, 1981). Moreover, badly preserved remains of elapids were described from the Uppermost Miocene of Librilla (Alberdi *et al.*, 1981).

Contrary to previously described fossils, the ophidian material from Algora consists of abundant and perfectly preserved bones, including many cranial elements. Under the circumstances, it has been possible to give a detailed description of some new snake taxa whose taxonomic status documents both Iberian endemisms and zoogeographic relationships between Iberia and Africa.

Data on the location, geology and faunistic list of the fossil karstic breccia from Algora (province of Guadalajara, Spain) has been presented by Hoyos *et al.* (in press). On account of its micromammalian fauna, it has been dated on the Uppermost Miocene, corresponding to Mein's (1975) European Continental biozone NM 13. All the material here analyzed comes from a single rock, roughly pyramidal, of about 35 cm. on its maximal length. It was prepared by B. Sanchíz (Madrid) by a stepwise complete disolution of the matrix with acetic acid. The different elements are thus to be considered as strictly synchronous. All the material belongs to the Museo Nacional de Ciencias Naturales (Madrid) collection.

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Systematic paleontology

Scolecophidia
Scolecophidia indet.
(Fig. 1)

Material: About 50 precaudal vertebrae.

Scolecophidian vertebrae from Algora, preserved in perfect state, belongs to the cervical and thoracic regions of the vertebral column. These small vertebrae with centra not exceeding the length of 1.4 mm, display all the characteristic morphological features of scolecophidian snakes, namely a depressed neural arch devoid of neural spine, paradiapophyses forming a single articular surface, haemal keel lacking, cotyle and condyle dorso-ventrally depressed, paracotylar foramina absent (cf. Rage, 1984). The zygosphenal roof of the trunk vertebrae from Algora is medially notched in dorsal view. Lateral foramina present. Subcentral foramina of variable size. Both pre- and postzygapophyseal articular surfaces strongly elongated antero-posteriorly. Long, conical shaped prezygapophyseal processes.
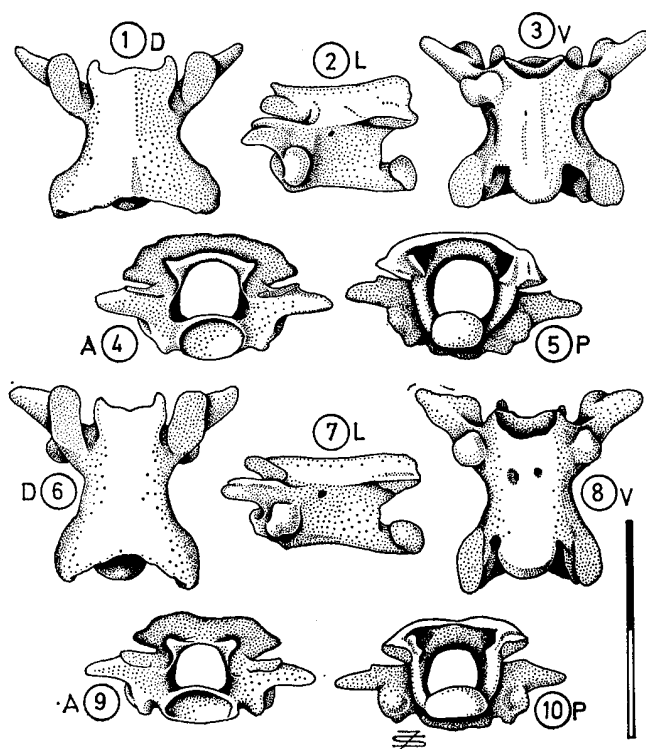

Fig. 1.—Scolecophidia indet. 1-5, cervical vertebra (MNCN, no Alg I - 2); 6-10, trunk vertebra (MNCN, no Alg I - 1). A - anterior, D - dorsal, L - lateral, P - posterior, V - ventral views. Scale equals 2 mm.

Comments

Scolecophidian remains were repeatedly reported from fossil localities, although they are usually neither described in detail nor figured. From the West Palearctic region these snakes are known in the Lo-

wer Eocene of Dormaal, Belgium (Godinot *et al.,* 1978), Upper Eocene of some sites of the Quercy complex, France (Rage, 1974, 1978), Lower Miocene (MN 4) of Dolnice, Czechoslovakia (Szyndlar, in preparation), Lower Miocene (NM 4b) of Córcoles, Spain (Alférez & Brea, 1981) Middle Miocene (MN 7) of Beni Mellal, Morocco (Rage, 1976), Middle Miocene (NM 7-8) of La Grive-Saint-Alban, France (Hoffstetter, 1946), and Upper Pliocene (NM 16) of Çalta, Turkey (Rage & Şen, 1976). The latter locality is situated in the present range area of scolecophidians.

The West Palearctic region is presently inhabited by at least 3 species that belong to the family Leptotyphlopidae and 3 species of the family Typhlopidae. The European range of these snakes is restricted to the Balkan Peninsula, occupied by a member of the latter family, *Typhlops vermicularis.* Due to the inaccessibility of skeletons belonging to the above forms, it has been impossible to give a correct identification of the Algora remains even to familial level. It is obvious that other authors were confronted with similar difficulties alike, including Hoffstetter (1946) that erected *Typhlops grivensis,* the only European fossil scolecophidian identified to specific level (this species differs from the Algora form in having a medial tubercle instead of a notch in its zygosphenal roof). Generic and familial referral of *T. grivensis* was recently questioned by Rage (1984). Identification of the Córcoles scolecophidian as *Typhlops* sp. (Alférez and Brea, 1981) seems to be also baseless.

Alethinophidia
Family Colubridae

Correct identification of colubrid remains from Algora has been somewhat problematic regarding the abundance of disarticulated cranial elements and their dissimilarity to living snakes. Considering that the colubrid vertebrae from the Algora deposit display rather clearly only two homogeneous morphological patterns, the cranial bones have also been attributed to two different forms of snakes, described below as new extinct taxa. Fortunately, these snakes differed considerably from each other by their size, and thus the reference of particular skull bones to one of the two vertebral samples has been usually obvious. There is, however, a number of cranial elements that could indicate the presence of a third colubrid species, perhaps of the genus *Coluber.* These bones are either referred with doubt to the new species described below or placed among indeterminable remains in the hope that the finding of similar remains in other fossil sites could throw some light on their precise taxonomic allocation.

Genus *Elaphe* FITZINGER, 1833
Elaphe algorensis sp. nov.
(Figs. 2-4)

Holotype: A basiparasphenoid, MNCN Alg. I-3.

Referred material: 3 parietals, 2 supraoccipitals, 2 exoccipitals (1 right, 1 left), 1 basioccipital, 1 left prefrontal, 3
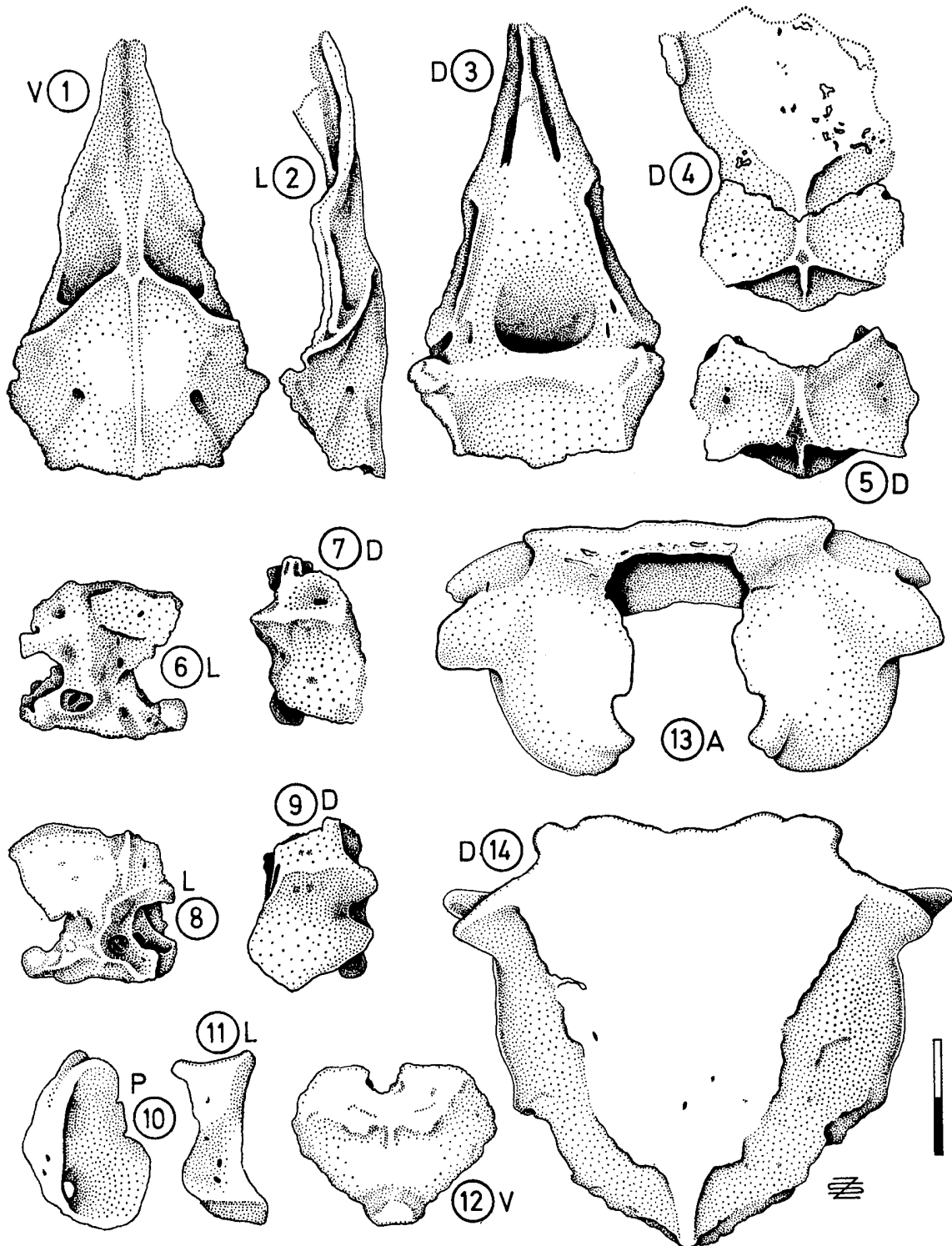
Fig. 2.—*Elaphe algorensis* sp. nov., braincase bones. 1-3, holotype basiparasphenoid (MNCN, nc Alg I - 3); 4, fragmentary parietal and supraoccipital (MNCN, no Alg I - 4); 5, supraoccipital (MNCN, no Alg I - 5); 6, 7, left exoccipital (MNCN, no Alg I - 6); 8, 9, right exoccipital (MNCN, no Alg I - 7); 10, 11, left prefrontal (MNC, no Alg I - 8); 12, basioccipital (MNCN, no Alg I - 9); 13, 14, parietal (MNCN, no Alg I - 10). A - anterior, D - dorsal, L - lateral, P - posterior, V - ventral views. Scale equals 2 mm.

right maxillary fragments, 1 left maxillary fragment, 1 left ectopterygoid, 1 right pterygoid fragment, 1 left palatine fragment, 3 quadrates, 12 compound bones, 5 dentaries, and several hundred vertebrae (125 of them examined in detail). In addition, there are many tiny fragments of cranial bones, presumably belonging to the same species.

Etymology: After Algora, the type locality.

thin and dorso-ventrally elongated paradiapophyses on the trunk vertebrae.

Description of the holotype (fig. 2: 1-3)

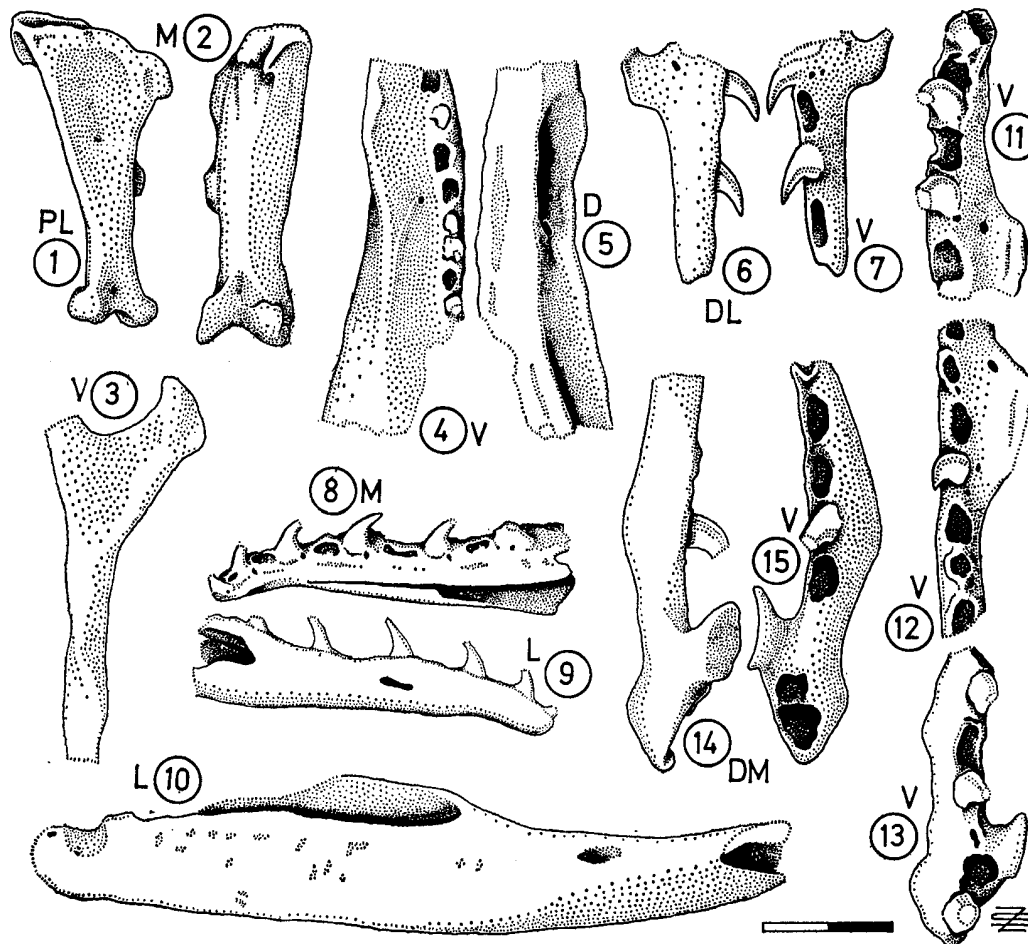A basiparasphenoid, perfectly preserved except for the distal portion of its parasphenoid process, which

Fig. 3.—*Elaphe algorensis* sp. nov., cranial bones. 1, 2, left quadrate (MNC, no Alg I - 11); 3, left ectopterygoid (MNCN, no Alg I - 12); 4, 5, fragmentary right pterygoid (MNCN, no Alg I - 13); 6, 7, posterior fragment of left palatine (MNCN, no Alg I -14); 8, 9, right dentary (MNCN, no Alg I - 15); 10, right compound bone (MNCN, no Alg I - 16)'; 11, posterior fragment of right maxilla (MNCN, no Alg I - 17); 12, middle fragment of right maxilla (MNCN, no Alg I - 18); 13, posterior fragment of right maxilla (MNCN, no Alg I - 19)'; 14, 15, posterior fragment of left maxilla (MNCN, no Alg I - 20). D - dorsal, DL - dorso-lateral, DM - dorso-medial, L - lateral, M - medial, LP - postero-lateral, V - ventral views. Scale equals 2 mm.

Diagnosis: A colubrid snake characterized by a mixture of osteological features found in the larger members of the European genus *Elaphe*. The new species can be differentiated from the other forms in the following particular characters: common foramina located in the middle of the postpterygoid area of the basiparasphenoid; anterior Vidian foramina laterally surrounded by bony collars; large square-shaped postorbitals; doubled vagus-hypoglossal nerve foramen located into a deep concavity; vomerine process of palatine relatively small and very short at its base; slender dentary;

is missing. Shape of the bone triangular, with weakly developed suborbital flanges in ventral view. Basipterygoid processes moderately developed, surmounted by well defined and anteriorly inclined pterygoid crests. Basisphenoid crest well visible, extending from the posterior margin of the bone, anteriorly to the joint of both pterygoid crests. Common foramina (posterior Vidian foramen and

cerebral foramen) large, situated far from the posterior border of the bone. Anterior Vidian foramina located before pterygoid crests, laterally sheltered by bony collars. In lateral view, suborbital flanges bent upwards. Frontal step strongly projecting dorsally (its anterior portion missing). In dorsal view, the anterior abducens nerve foramina and the right sympathetic nerve foramen are well visible. Prominent notches for sympathetic nerves.

Description of remaining material

The parietal (fig. 2: 4, 13, 14) is characterized by a flat dorsal surface, without any medial furrow. Parietal crests sharply approach each other immediately before reaching the posterior end of the bone. Descending parts of the parietal (lateral walls) convex. Distinct postorbitals produced into broad and square-shaped lobes in anterior view. Supraoccipital (fig. 2. 4-5) with strongly reduced posterior area, covered from above with broad occipital crests. Saggital crest, being the continuation of the parietal crests, well developed and extended throughout the supraoccipital. Basioccipital (fig. 2: 12) laterally expanded, with underdeveloped basioccipital tubercles. Basioccipital crest produced into two small lateral lobes, wihout a central basioccipital process. Medial crest absent. Occipitocondylar tubercle relatively small. Exoccipital (fig. 2: 6, 7 and 8, 9) with weakly developed occipital crest; the area posterior to the latter structure extensive, with moderate parotic process. Exoccipital tubercle relatively short. Circumfenestral crest, being the posterior wall of the vestibular window (fenestra ovalis), forms a deep and round-shaped sinus. Vagus-hypoglossal nerve foramen doubled, located into a deep concavity, not accompanied posteriorly by additional foramina. Prootic (fig. 2: 10, 11) with a small-sized lacrimal foramen located near the bone lower margin. Upper border of the prootic forms a distinct posterior extension.

The small maxillar fragments recovered (fig. 3: 11-15) enable, however, a complete bone reconstruction. Teeth isodont, relatively large. Anterior end of the bone slightly curved medially. Prefrontal process much longer than wide, located at the level of the 6-8th teeth. Posterior end of the bone characterized by a dorsal constriction for the ectopterygoid maxillary ramus. Ectopterygoid process infero-anteriorly projected, situated medially to a diastema, the latter followed by two terminal teeth. Ectopterygoid (fig. 3: 3) with well defined rami, distinctly separated from each other. External ramus considerably long, with widening end; internal ramus missing. A single pterygoid (fig. 3: 4-5) preserved in fragmentary state (its anterior and posterior portions remain unknown). The dorsal surface of the fragment shows a distinct crest. Pterygoid flange weakly developed. Palatine (fig. 3: 6, 7) also only known from a single (posterior) fragment. Vomerine process relatively short at its base, square-shaped, followed by three teeth or tooth sockets. Quadrate (fig. 3: 1, 2) with a stout trunk of equal thickness throughout its length in medial view. Stapedial process distinct. Quadrate crest well developed in the upper portion of the bone. Compound bone (fig. 3: 10) with relatively low medial flange. External surface of the lateral flange flat. Retroarticular process unknown. Dentary (fig. 3: 8, 9) slender, presumably isodontic. Meckelian groove closes completely at the 5th tooth. Elongated mental foramen, lying at the level of the 7-8th teeth. Compound notch on the lateral surface usually approaches the 10th tooth. Posteriormost portion of the bone unknown.

Among the numerous vertebrae attributed to this snake, unfortunately there is no representation of the anteriormost elements. Cervical vertebrae (fig. 4: 13), preserved in the material, show relatively long and slender hypapophysis, postero-ventrally directed, as well as a relatively low neural spine, longer than higher.

Mid-trunk vertebrae (fig. 4: 1-10) have centra relatively short, reaching the length of 4.5 mm in the biggest bones. Haemal keel very distinct, relatively high in lateral view, in ventral view spatulate or lanceolate-shaped posteriorly, narrowing near the subcentral foramina. Subcentral ridges fairly well developed when posterior to the parapophyses, but diminishing posteriorly before the base of the condyle. Neural arch vaulted. Neural spine somewhat longer than higher, slightly overhanging anteriorly. Zygosphene of larger vertebrae straight from above, with two small lateral lobes; smaller vertebrae show crenate zygosphenes. Prezygapophyses slightly tilted upwards, with slender and acuminate prezygapophyseal processes. Prezygapophyseal articular surfaces oval. Postzygapophyses postero-laterally expanded, with their articular surfaces obovate. Moderately developed interzygapophyseal ridges. Lateral foramina well marked. Paradiapophyses relatively short and high in lateral view. Parapophyseal and diapophyseal portions are not clearly distinct from each other. Cotyle and condyle depressed dorso-ventrally. Paracotylar foramina well defined. Mid-trunk vertebrae belonging to smaller individuals (fig. 4: 6-10) characterized, as typical for snakes, by relatively longer centrum, wider and higher neural canal, strongly defined lobes of zygosphenal roof, and some other minor features.

The posterior trunk vertebrae (fig. 4: 11, 12) differ distinctly from those of the mid-thoracic region in several features: Less vaulted neural arch which protrudes posteriorly behind the condyle. Neural spine lower. Very deep haemal keel, strongly flattened posteriorly. Paradiapophyses low and stout. Caudal vertebrae (fig. 4: 14, 15) with relatively short pleurapophyses, projecting ventrally, or even slightly postero-ventrally, in the anterior caudal region, antero-ventrally in the posterior region. The haemapophyses of the examined vertebrae were broken off.

Comparisons and Comments

The basiparasphenoid, in the general shape and morphology of its pterygoid crests resembles *Elaphe longissima* and *E. scalaris,* but differs significantly from these, and remaining species, in the location of the Vidian canal orifices, which are diagnostic characters. The parietal, though also similarly built as in both mentioned species, can be differentiated by the shape of the postfrontals fused with it unparalleled among European colubrids. The supraoccipital is similar to that of *E. quatuorlineata.* The basioccipital, owing to its shape, lack of medial crest and weakly defined basioccipital crest, resembles *Coluber hippocrepis* but no species of *Elaphe.* The exoccipital, taking into consideration the relatively large size of its postero-dorsal portion and weakly developed ocipital crest, resembles that of *Elaphe longissima;* however, the disposition of the vagus-hypoglossal nerve foramina is a distinct feature of the Algora snake (in the other colubrids here discussed the orifice of this nerve is formed by a single large foramen posteriorly accompanied by additional tiny foramina).

The elements of the jaw apparatus bear lower taxonomic information than the braincase bones do. The morphology of the anterior portion of the maxi-

lla is characteristic for several other species, while the shape of the ectopterygoid process, projected into a spur-like anterior extension, is only observed in two species of the genus *Coluber*, namely *C. jugularis* and *C. viridiflavus* (but no species of *Elaphe*). Also the ectopterygoid (with an articular surface closely corresponding with the dorsal constriction of the maxilla) is comparable only with these two species of *Coluber*, regarding especially the relative length of its external ramus. There is therefore not clear whether just this «*Coluber*-like» maxilla, together with the corresponding ectopterygoid, or another one-*Elaphe*-like maxilla (see Serpentes indet., fig. 11: 4, 5) should be referred to *Elaphe algorensis*. Nevertheless, considering the distinction of the Algora species in comparison with the living members of the genus *Elaphe*, as well as the fact that many cranial features are parallel in *Coluber* and *Elaphe*, a definitive taxonomic identification of these elements should remain as an open question.
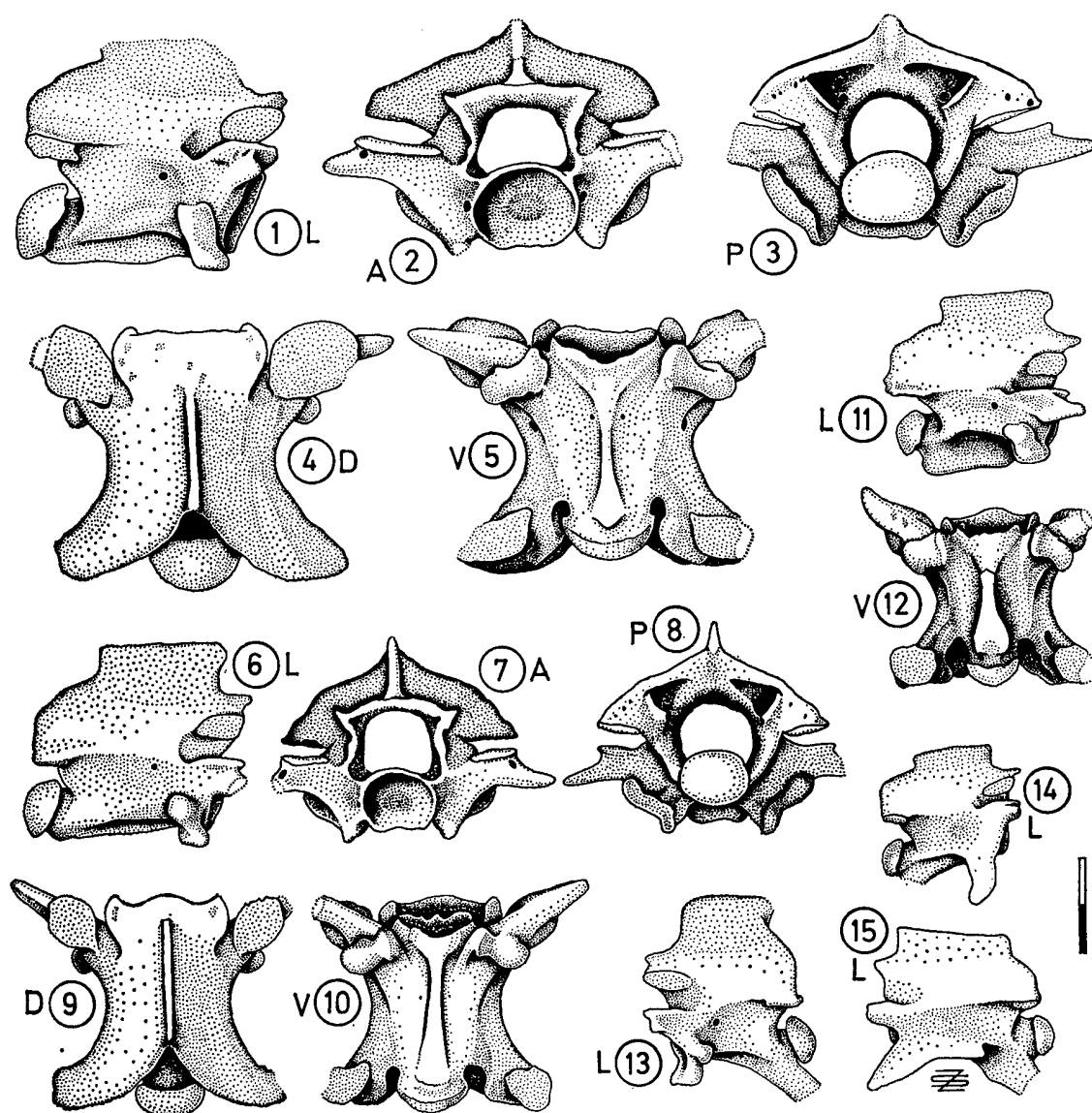

Fig. 4.—*Elaphe algorensis* sp. nov., vertebrae. 1-5, mid-trunk vertebra (MNCN, no Alg I - 21); 6-10, mid-trunk vertebra of a subadult individual (MNCN, no Alg I - 22); 11, 12, posterior trunk vertebra (MNCN, no Alg I - 23); 13, cervical vertebra (MNCN, no Alg I - 24); 14, anterior caudal vertebra (MNCN, no Alg I - 25); 15, posterior caudal vertebra (MNCN, no Alg I - 26). A - anterior, D - dorsal, L - lateral, P - posterior, V - ventral views. Scale equals 2 mm.

The palatine, although fragmentary, is distinct among other colubrids by having a shorter base of its much smaller vomerine process. The quadrate, also doubtfully referred to this form, is identical to that of *Elaphe quatuorlineata*. The dentary, regarding the Meckelian groove closure location, compound notch and mental foramen towards the dentition, closely resembles that of *E. scalaris*, but this element is much more slender in the Algora snake.

The cervical vertebrate, with relatively low neural spine, are comparable with two fossil species from the Central European Neogene: *Elaphe paralongissima* Szyndlar, 1984, and *E. kohfidischi* Bachmayer and Szyndlar, 1985; living forms have always higher spines. In the morphology of the trunk vertebrae the snake from Algora most resembles *E. longissima*. Nevertheless, *Elaphe algorensis*, by having very thin paradiapophyses and some other minor features, is well differentiated from other forms. Caudal vertebrae mostly resemble those of the extinct *E. kohfidischi*.

From the above comparisons results that the newly described species shows, besides its distinct features, also a mixture of various characters observed in most of the large snakes of the genus *Elaphe*, as well as (although to much lesser degree) characters of *Coluber* snakes. Therefore, there is no clear indication of close relationship between the Algora *Elaphe* species with any particular species of Iberian or European colubrids. Since also the fossil evidence of the genus *Elaphe*, although scanty in Europe and lacking in North Africa, does not confirm a wider distribution for similar forms, the Algora snake should be regarded —at least temporarily— as an extinct Iberian endemism.

Hispanophis gen. nov.

Type species: Hispanophis coronelloideus sp. nov.

Etymology: From Hispania, Latin name of the Iberian peninsula, and οφις, Greek, a snake.

Diagnosis: As for type species below.

Hispanophis coronelloideus sp. nov.

(Fig. 5)

Holotype: A basiparasphenoid, MNCN Alg. I-27.

Paratype: A basiparasphenoid, MNCN Alg. I-28.

Referred material: A left quadrate; 4 trunk vertebrae.

Etymology: From the generic taxonomic name *Coronella*, and τόειδος, Greek, shape or aspect.

Diagnosis: A minute snake differing from other small species of European Colubridae in having a peculiar basiparasphenoid, with extremely short Vidian canals with their orifices located near the lateral borders of the bone. Trunk vertebrae similar to those of the living genus *Coronella*, but differing from them in having a vaulted neural arch as well as better defined and wider haemal keel.

Description of the holotype (fig. 5: 1-3)

A small-sized basiparasphenoid, with its parasphenoid process missing. Ventral surface of the bone convex and smooth, devoid of any distinct crests. Basipterygoid processes weakly developed. On the right side of the bone the posterior Vidian foramen and the cerebral foramen are located separately; on the left side both orifices form a common foramen. Anterior Vidian foramina situated near the lateral borders or the bone, close to the posterior foramina. On the dorsal side of the bone, sympathetic nerve foramina and anterior abducens nerve foramina situated closely each other. Deep notches for sympathetic nerves.

Description of the paratype (fig. 5: 4-6)

A basiparasphenoid closely resembling the holotype, but of somewhat smaller size. Common foramina and anterior Vidian foramina large-sized, located nearer each other than those of the holotype.

Description of the remaining material

A single quadrate (fig. 5: 7, 8), referred with doubt to this snake, is characterized by a slender form and lack of a distintict quadrate crest. Stapedial process moderately developed and dorso-ventrally elongated.

Four minute vertebrae (fig. 5: 9-13) come from the middle of the column. Centrum moderately long (reaching 2 mm), cylindrical. Haemal keel indistinct, broad and flattened, cuneate-shaped. Subcentral ridges underdeveloped. Subcentral grooves weakly defined. Subcentral foramina minute. Interzygapophyseal ridges moderate, parallel to the centrum axis. Neural canal moderately broad and high, somewhat narrower than the circular with a truncated ventral part cotyle. Lateral foramina well marked. Neural arch moderately vaulted. Neural spine long and very low. Crenate zygosphenal roof in dorsal view. Paradiapophyses well separated into two articular facets. Parapophysis stout, twice longer than orbicular diapophysis. Short, strongly built prezygapophyseal processes. Prezygapophyseal articular facets oval, distinctly elongated. Postzygapophyseal articular facets orbicular or obovate. Posterior walls of postzygapophyseal rami present large foramina. Also well marked paracotylar foramina. Condyle oblique, located on a moderately long neck.

Comparisons and Comments

Although hardly comparable with other snakes, identification of the above described basiparasphe-
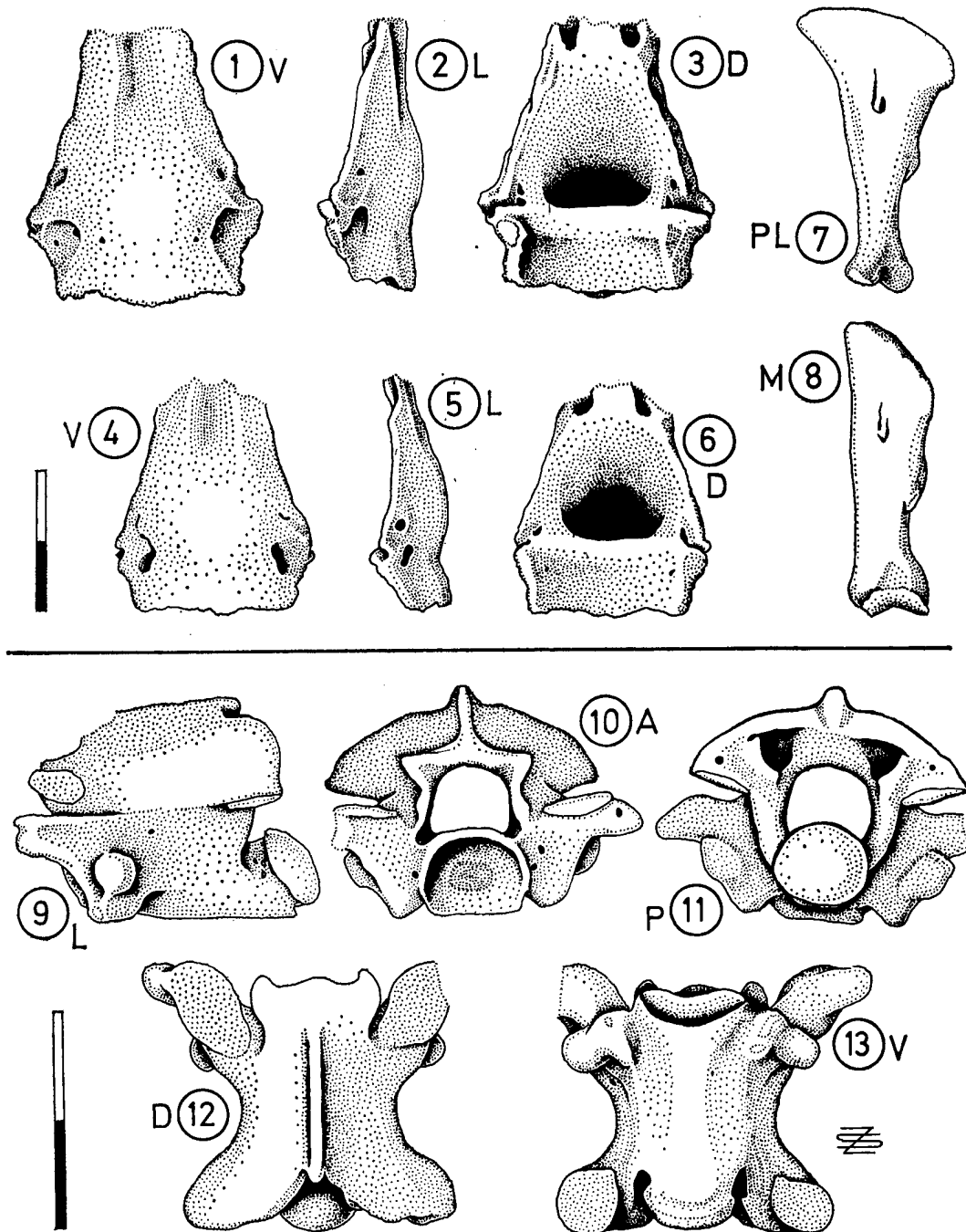
Fig. 5.—*Hispanophis coronelloideus* gen. sp. nov. 1-3, holotype basiparasphenoid (MNCN, no Alg I - 27); 4-6, paratype basiparasphenoid (MNCN, no Alg I - 28); 7, 8, left quadrate (MNCN, no Alg I - 29); 9-13, mid-trunk vertebra (MNCN, no Alg I - 30). A - anterior, D - dorsal, L - lateral, M - medial, P - posterior, PL - postero-lateral, V - ventral views. Scale equals 2 mm.

noids and vertebrae as belonging to the same species is reasonable, if we consider the small size of both elements. The quadrate is referred to this form with some doubt, on account that this bone must have belonged to a considerably larger individual, while the previously mentioned remains represented clearly adult specimen(s). The basiparasphenoid of *Hispanophis* poorly resembles those of other colubrids, especially in the shortness of its Vidian canals. Among European snakes, only *Coluber gemonensis*

phis. In the light of these facts, *Hispanophis,* as *Elaphe algorensis,* is also considered an Iberian endemic taxon.

Family Elapidae

Elapid remains, majority of the Algora ophidian fauna, are described below as a new extinct species clearly differentiated from other West Palearctic cobras. The newly named species has been compared with the living forms
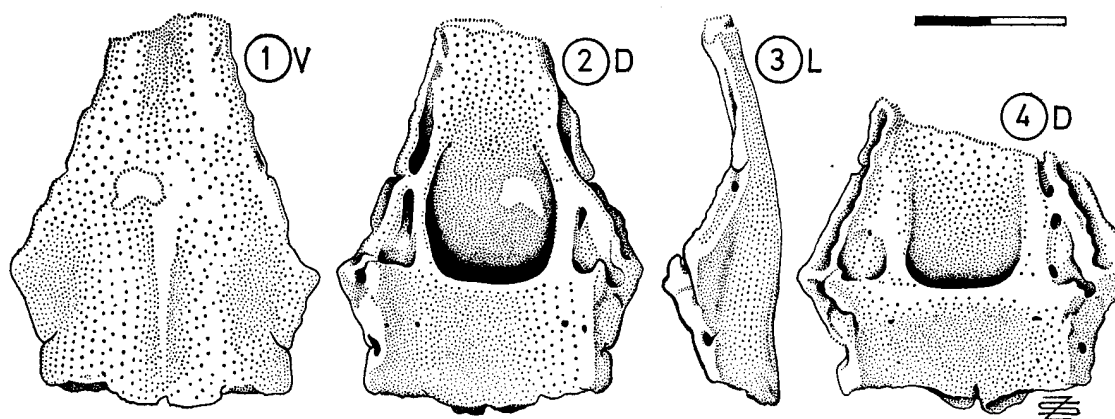

Fig. 6.—*Naja iberica* sp. nov. 1-3, holotype basiparasphenoid (MNCN. no Alg I - 31); 4, paratype basiparasphenoid (MNCN, no Alg I - 32). D - dorsal, L - lateral, V - ventral views. Scale equals 2 mm.

has its Vidian canals shortened to a similar degree, but their orifices are situated much closer to the middle of the bone; moreover, general shape and other features of basiparasphenoids of both forms are completely different. The quadrate resembles those of *Macroprotodon cucullatus* and *Coronella girondica.* The vertebrae most resemble those of the genus *Coronella* (especially *C. austriaca,* regarding the similar form of the paradiapophyses), but differ in having a much more vaulted neural arch, as well as a better defined and wider haemal keel. The latter features are similarly developed in *Coluber najadum* (especially its subspecies *C. n. rubriceps,* recently also regarded as a distinct species), but vertebrae of this snake are lightly built and show distinct subcentral ridges as well as long and slender prezygapophyseal processes, unlike *Hispanophis.*

The morphological dissimilarity of *Hispanophis* to other colubrid genera is rather obvious, but its taxonomic position is much more obscure than in the case of *Elaphe algorensis.* Contrary to larger snakes, the remains of small-sized Colubridae have not been known, until quite lately, from European Neogene sites. The only tiny colubrids described from an adjacent area, recognized as members of genera previously reported from North America (Rage and Holman, 1984), differ significantly from *Hispano-*

presently inhabiting this region (Asiatic *Naja naja* and North African *N. haje* and *N. nigricollis*) as well as with fossil forms included in the genera *Naja* and *Palaeonaja.* The fossil cobras from the discussed area belong to the following species: *Palaeonaja romani* from the Lower Miocene of Vieux-Collonges (= Mont Ceindre; MN 4) and the Middle Miocene (NM 7-8) of La Grive-Saint-Alban, *P. crassa* from the same site, and *P. depereti* from the Middle Pliocene (NM 15) of Perpignan, all these French species described by Hoffstetter (1939); moreover, *Naja antiqua* Rage, 1976, from the Middle Miocene (NM 7) of Beni Mellal, Morocco, and *N. austriaca* Bachmayer & Szyndlar, 1985, from the Upper Miocene (NM 11) of Kohfidisch, Austria. Observations made by all these authors are widely employed in the following description. Comparisons of the Spanish form with other elapid genera, due to the clear differences between the latter and the members of *Naja* and *Palaeonaja,* are omitted.

Naja Laurenti, 1768
Naja iberica sp. nov.
(Figs. 6-9)

Holotype: A basiparasphenoid, MNCN Alg. I-31.

Paratype: A basiparasphenoid, NMCN Alg. I-32.

Referred material: Maxillae (4 right, 5 left), 5 isolated venom fangs, 1 left septomaxilla, palatines (1 right, 1 left), 1 right pterygoid fragment, compound

bones (2 right, 1 left), dentaries (3 right, 2 left), 2 left quadrates, 1 (left ?) squamosal, 1 right frontal, 2 parietal fragments, 6 basioccipitals, 1 left prootic, 2 left exoccipitals, 1 supraoccipital, 25 ribs, several hundred vertebrae.

Etymology: From *ibericus,* Latin adjective, after the Iberian Peninsula.

Diagnosis: Typical *Naja,* without pterygoid crests on its basiparasphenoid, Vidian canal leaving the basiparasphenoid on its internal side; vestibular window located between prootic and exoccipital, occipital crest not reaching parotic process, and a maxilla that bears two non-venomous teeth. In cranial morphology this form mostly resembles *Naja haje* and *N. antiqua. N. iberica* differs from other species of the genera *Naja* and *Palaeonaja* in the following individual characters: strong grooves accompanying the anterior Vidian foramina; presence of square-shaped lamella after the ascendens nasal pro-
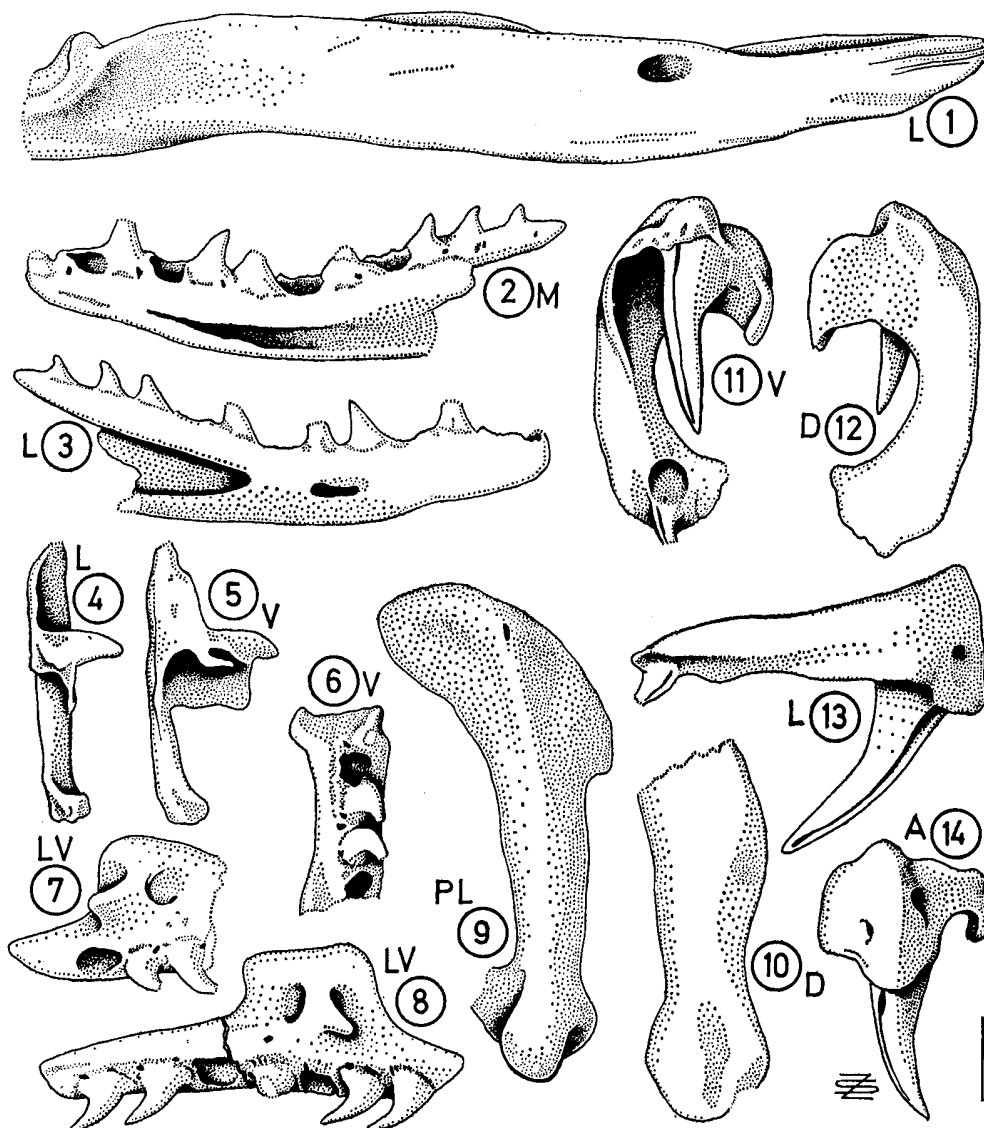

Fig. 7.—*Naja iberica* sp. nov., cranial bones. 1, right compound bone (MNCN, no Alg I - 33); 2, 3, right dentary (MNCN, no Alg I - 34); 4, 5, left septomaxilla (MNCN, no Alg I - 35); 6, anterior fragment of right pterygoid (MNCN, no Alg I - 36); 7, anterior fragment of right palatine (MNCN, no Alg I - 37); 8, left palatine (MNCN, no Alg I - 38); 9, left quadrate (MNCN, no Alg I - 39); 10, squamosal (MNCN, no Alg I - 40); 11-14, right maxilla (MNCN, no Alg I - 41). A - anterior, D - dorsal, L - lateral, LV - latero-ventral, M - medial, P - posterior, PL - postero-lateral, V - ventral views. Scale equals 2 mm.

cess of the septomaxilla; square-shaped vomerine process on the palatine; prootic lacks a dorsal extension above the supraoccipital crest; occipital crest of the exoccipital divided into two distinct but small processes; axis with its neural arch laterally depressed and with a strongly expanded antero-posteriorly neural spine.

Description of the holotype (fig. 6: 1-3)

A basiparasphenoid belonging to a subadult of distinctly smaller size than most individuals from this site. Parasphenoid process missing. In lateral view the bone is distinctly arched. Basipterygoid processes rather well developed, pterygoid crests absent. Basisphenoid crest weakly defined. Central lobe on the posterior border of the bone small, but distinctly split medially. Common foramen located on the lateral margin of the bone, between its postero-lateral corner and the basipterygoid process. On the dorsal side of the bone, sympathetic nerve foramina and anterior orifices of abducens nerves located in a common deep depression aside the pituitary fossa. Right notch for sympathetic nerve dorsally opened, the left one entirely closed. Anterior orifice of the Vidian canal opens into a deep groove situated on the dorsal side of the bone. The role of a foramen located on the right lateral border of the bone at the level of the anterior Vidian foramen, remains unknown.

Description of the paratype (fig. 6: 4)

Basiparasphenoid of similar size as the holotype, not differing essentially from the latter, also with its parasphenoid process broken off. Similarly to the holotype, the left notch for the sympathetic nerve is also well closed and the right one remains distinctly opened. It could be an indication that such an assymetry is a specific feature of this snake.

Description of the remaining material

Maxilla (fig. 7: 11-14) relatively slender, with its anterior part pyramidal-shaped in lateral view. Venom fangs in part with distinct sutures, between entrance lumen and discharge orifice; in some of them, nevertheless, the venom canal is completely closed and no suture is visible. Posteriorly, the bone has two non-venomous teeth. Prefrontal and ectopterygoid processes similarly developed as in other cobras. A single left septomaxilla (fig. 7: 4, 5), preserved in perfect condition, anteriorly presents a long and relatively narrow process. Behind the wing-like ascendens nasal process, a distinct square-shaped lamella is present. Palatine (fig. 7: 7, 8) bears 7 teeth; its vomerine process is distinctly square in shape from a lateral view. Maxillary process, placed between foramina for the maxillary nerve, is relatively short. A single anterior fragment of the right pterygoid (fig. 7: 6) bears almost no taxonomic information and has been iden-

tified as belonging to Naja on the basis of its relatively large size. Dentary (fig. 7: 2, 3) with relatively large teeth, becoming gradually smaller in the posterior direction. Meckelian groove completely closed by the level of the 4th tooth. Compound notch approaches by the 8th tooth. Posteriormost portion of the bone unknown. Compound bone (fig. 7: 1), with lateral and medial flanges of equal height, resembles those of other cobras. Posterior end of the bone (retroarticular process) unknown. The quadrate (fig. 7: 9) has a relatively slender stem and a strongly inclined posteriorly dorsal margin. Squamosal (fig. 7: 10) characterized by a distinct widening of its distal end.

The frontal (fig. 8: 6, 7) is almost twice longer than wide, with a frontal aperture obovate in section and dorso-ventrally depressed. Internal premaxillary process moderately developed, septomaxillary process missing. Anterior border of the bone oblique, with an even margin in dorsal view. Parietal fragments, a posterior portion of the bone (fig. 8: 10) and a right lateral wall (descending part of the parietal), characteristic for the genus Naja, but because of their fragmentary nature they give no relevant taxonomic information. The supraoccipital (fig. 8: 11) shows a strongly developed saggittal crest as well as occipital crests, the latter antero-laterally bordering a trapezium-like posterior area of the bone. A single prootic (fig. 8: 1), belonging to a rather small snake, is clearly referable to Elapidae due to the presence of a distinct notch on its ventral border; this notch, together with a similar structure on the postero-lateral border of the basiparasphenoid, formed a common foramen for the carotid artery and the palatine branch of the cerebral nerve. Foramina for the maxillary branch (anterior) and mandibular branch (posterior) of the trigeminal nerves, located in deep concavities, the latter of them accompanied by the facial nerve foramen. Below the orifice for the maxillary branch of the trigeminal nerve a relatively large foramen for the trigeminal branch innervating the constrictor internus dorsalis muscles pierces the bone. A small orifice located above the common foramen probably contained another branch of the same nerve. Supraoccipital crest moderately developed. The posterior border of the bone forms a shallow concavity, being the anterior wall of the vestibular window, the structure located between prootic and exoccipital. The exoccipial (fig. 8: 2-4) forms the posterior wall of the vestibular window. Elongated vagus-hypoglossal nerve foramen, situated after the vestibular window, accompanied by two other distinct foramina. Occipital crest divided into two separate processes. Basioccipital tubercle relatively short. Basioccipital (fig. 8: 5, 8, 9) characterized by a moderate development of the basioccipital crest, consisting on two separate lobes. Basioccipital tubercles or relatively equal length as (jointed with them in the braincase) the exoccipital tubercles of the exoccipital bone.

Atlas unknown. A single axis (fig. 9: 1, 2) characterized by a laterally depressed neural arch and a strong extension of the neural spine; the structure anteriorly reaching the level of the odontoid process. These features are not known among other cobras. However, on account of the large size of the bone, it could belong to no Algora snake species but Naja. Transverse processes, posterior intercentrum (hypapophysis) and spinal process of the axis missing. Except the axis, no other anteriormost vertebrae are known; those coming from the immediately further part of the column (fig. 9: 3) do not differ distinctly from the mid-trunk vertebrae except for heir zygosphenal roof, crenate in dorsal view.

Mid-trunk vertebrae (fig. 9: 4-8) have relatively short centra, with a concave ventral surface, laterally limited by prominent subcentral ridges. Neural arch moderately vaulted. Neural spine moderately developed, somewhat longer than higher. Hypapophysis distally rounded and postero-laterally directed. Paradiapophyses well developed; parapophyseal process usually directed forwards. Zygapophyseal articular facets slightly oval in shape. Zygosphene in mid-trunk vertebrae usually straight in dorsal view and with two lateral

tiny lobes, although the latter are sometimes absent. Cotyle of moderate development, slightly depressed dorsoventrally.

The posterior trunk vertebrae (fig. 9: 9) have a strongly depressed neural arch, very low neural spine and very short hypapophyses. Zygosphene crenate in dorsal view, as in cervical vertebrae. It seems that a crenate form of the zygosphene is characteristic for all precaudal vertebrae belonging to younger snakes, regardless from which columnar region they come. Among caudal vertebrae, only some bones coming from the anterior caudal region (fig. 9: 10) have been provisionally classified as belonging to *Naja*. This de-

termination is based rather on their relatively large size than on morphology, as the vertebrae are usually preserved in fragmentary state (haemapophyses and pleurapophyses damaged.) Some other vertebrae from the cloacal and posterior caudal regions of the column, belonging perhaps to this snake, are placed among indeterminate snake remains (fig. 11: 6-8).

The ribs, coming from the mid-trunk region of the vertebral column, generally resemble those of other cobras, although their articular facet is less robust.
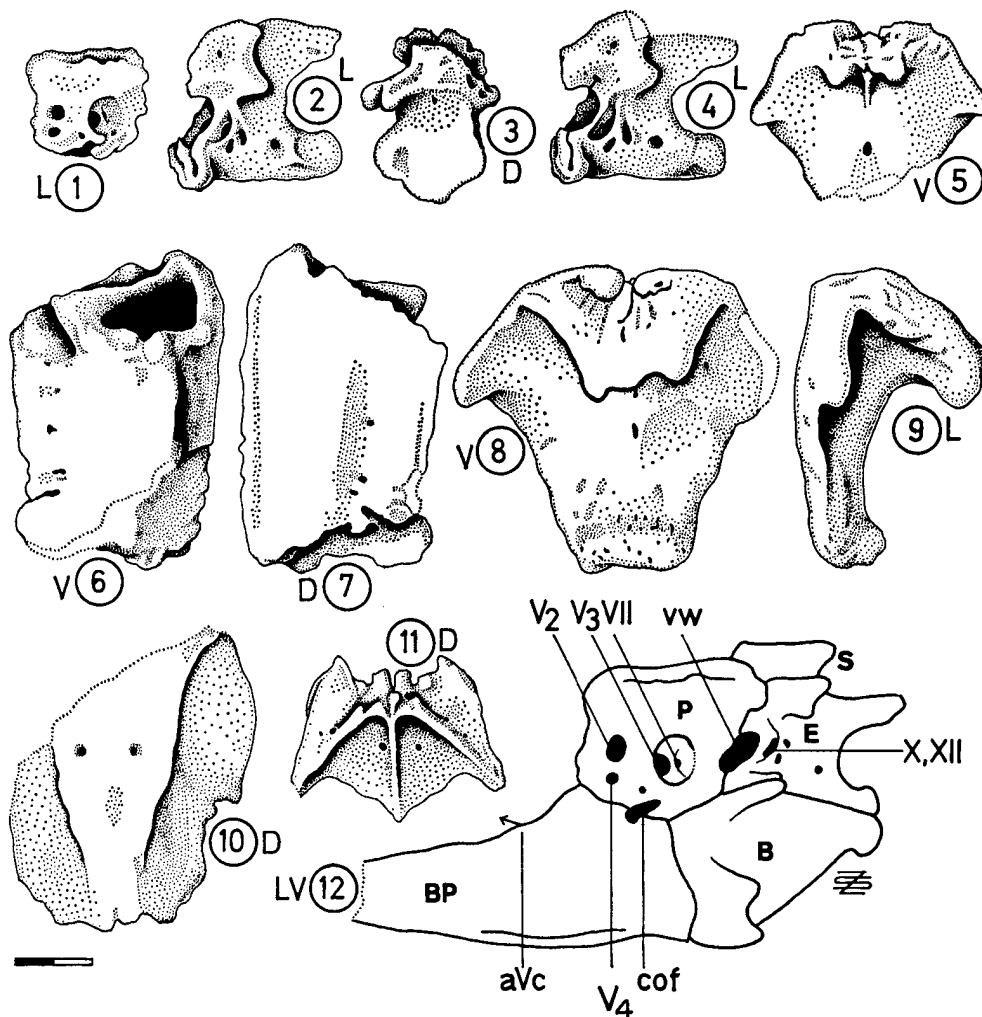

Fig. 8.—*Naja iberica* sp. nov., braincase bones. 1, left prootic (MNCN, no Alg I - 42); 2, 3, left exoccipital (MNCN, no Alg I - 43); 4, left exoccipital (MNCN, no Alg I - 44); 5, basioccipital (MNCN, no Alg I - 45); 6, 7, right frontal (MNCN, no Alg I - 46); 8, 9, basioccipital (MNCN, no Alg I - 47); 10, posterior parietal fragment (MNCN, no Alg I - 48); 11, supraoccipital (MNCN, no Alg I - 49); 12, reconstruction of posterior braincase. Abbreviations: aVc - anterior orifice of Vidian canal, B - basioccipital, BP - basiparasphenoid, cof - common foramen, E - exoccipital, P - prootic, S - supraoccipital, vw - vestibular window, V_2 - foramen for maxillary branch of trigeminal nerve, V_3 - foramen for mandibular branch of trigeminal nerve, V_4 - foramen for trigeminal branch innervating constrictor internus dorsalis muscles, VII - facial nerve foramen, X, XII - vagus hypoglossal nerve foramen. D - dorsal, L - lateral, LV - latero-ventral, V - ventral views. Scale equals 2 mm; figure 12 not to scale.

Comparisons and Comments

In the shape of its basiparasphenoid the Algora elapid is similar to the North African species (recent *Naja haje* and *N. nigricollis*, fossil *N. antiqua*). The lack of pterygoid crests surmounting the basipterygoid processes distinguishes this snake from the Euroasiatic forms (Recent *N. Naja*, fossil *Palaeonaja*
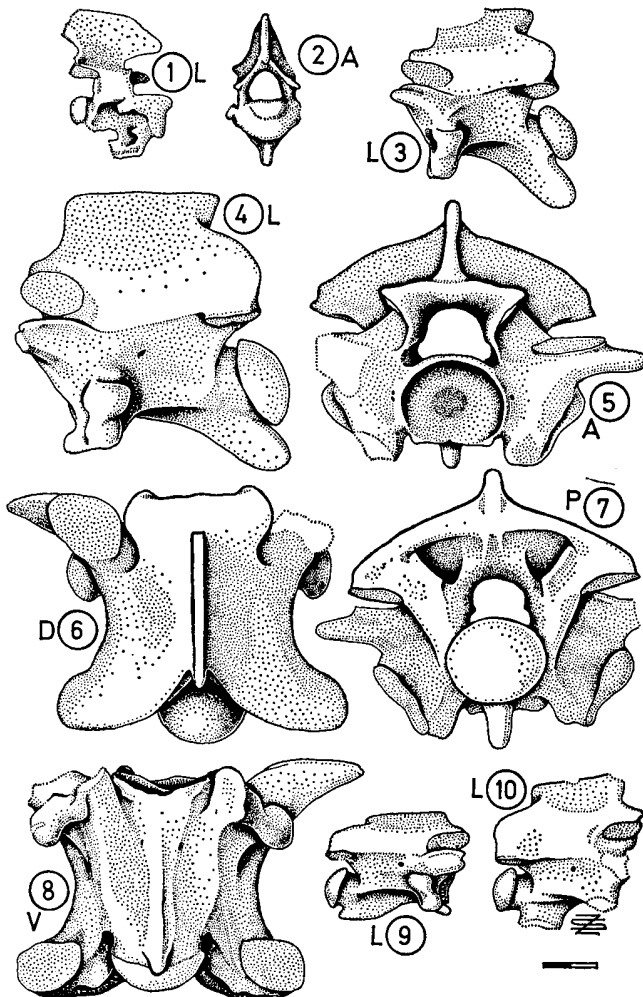

Fig. 9.—*Naja iberica* sp. nov., vertebrae. 1, 2, axis (MNCN, no Alg I - 50); 3, cervical vertebra (MNCN, no Alg I - 51); 4-8, mid-trunk vertebra (MNCN, no Alg I - 52); 9, posterior trunk vertebra (MNCN, no Alg I - 53); 10, anterior caudal vertebra (MNCN, no Alg I - 54). A - anterior, D - dorsal, L - lateral, P - posterior, V - ventral views. Scale equals 2 mm.

romani and *Naja austriaca*). In the disposition of the foramina on the dorsal side of the bone it resembles other cobras except *N. austriaca*, but the deep grooves accompanying the anterior Vidian foramina are stronger in the Spanish fossil than in other species.

By having two non-venomous teeth on the posterior end of its maxilla, the Algora cobra resembles living African *Naja* and the fossil European species (*Palaeonaja romani* and *Naja austriaca*), but differs from *N. naja*, as the latter presents either a toothless maxilla devoid of solid teeth or provided with one tooth. The Spanish fossil can be distinguished from *N. haje* by having a convex lateral border of this bone in dorsal view (in *N. haje* the maxilla is distinctly concave in the middle of its lenght); maxillae of European species are much more robust and present relatively shorter venom fangs.

In the morphology of the anterior portion of its septomaxilla, *Naja iberica* resembles *N. haje* (in *N. naja* the anterior portion conforms into a rather broad sheet), but differs in having a square-shaped lamella behind the ascendens nasal process, a structure not observed in *N. haje*.

The palatine, although generally resembles those of *Naja naja*, *N. haje* and *N. nigricollis* (palatines of fossil species unknown), contrary to them has a square-shaped, not triangular, vomerine process. The maxillary process is somewhat shorter than in other cobras. As in other species, the bone bears 7 teeth. The characteristic features of the dentaries from Algora are identically developed as in the mentioned living species. In two fossil species (*Palaeonaja romani* and *Naja austriaca*) the mental foramen is located somewhat closer to the compound notch. The remaining characteristic features are developed just as in both living and fossil species. In the compound bone, the posteriormost part of its lateral flange is not inclined aside in dorsal view, a situation observed in *Naja naja* and *Palaeonaja romani*. The quadrate is very similar to that of *Naja naja* (in *Palaeonaja romani* it is relatively shorter and its stem is proximally widened), but differs in having a distinct dorsal crest with a posterior part shifted backwards. Squamosal, in having a distinctly widened distal end, resembles that of *P. romani* and differs from *Naja*.

The frontal of the Algora species is similar to that of *Naja haje*, although the latter differs from the fossil in having a sinuous shape on its anterior border. The supraoccipital resembles closely those of *N. haje* and *N. antiqua*. The only notorious difference appears on two prominent tubercles lying in the middle of the anterior border of the *N. iberica* bone (junction with the parietal), being this feature absent in the remaining species. In *N. naja*, contrary to the above mentioned cobras, the posterior area of the supraoccipital is reduced and its anterior portion (before occipital crests) strongly extended. Dorsal portion of prootic, unlike other cobras, is not projected upwards into a wing-like expansion. The location of the common foramen between basiparasphenoid and prootic, as observed in *N. iberica*, is characteristic for other cobras except *N. antiqua*

(and perhaps *Palaeonaja romani*), where the foramen pierces the latter bone. The location of the vestibular window between prootic and exoccipital is characteristic for African species (recent *N. haje* and *N. nigricollis*, fossil *N. antiqua*), while in Euroasiatic species (recent *N. naja,* fossil *Palaeonaja romani*) a circumfenestral crest, surrounding the vestibular window, is entirely enclosed within the exoccipital. Exoccipitals of the form from Algora resemble that of *Naja naja* in the morphology of the occipital crest, with two separate processes, but in the latter snake the processes are much longer. In African cobras (*Naja haje, N. antiqua*) and *Palaeonaja romani* the occipital crest reaches the parotic

process, a situation not observed in *Naja iberica.* In the moderate development of the basioccipital crest and the basioccipital tubercles, *N. iberica* resembles *N. haje.* In other recent and fossil cobras these structures are much stronger. The vertebral characters of the Algora form represent a mixture of features visible among other cobras, however, its vertebrae resemble least those of *N. haje* and *N. antiqua* in spite of the similarities based on their cranial bones. The morphology of the axis is different from that of other cobras. Concerning trunk vertebrae, their centra are relatively longer than in the fosil species *Palaeonaja crassa, P. depereti* and *Naja austriaca.* The neural spine is of comparable
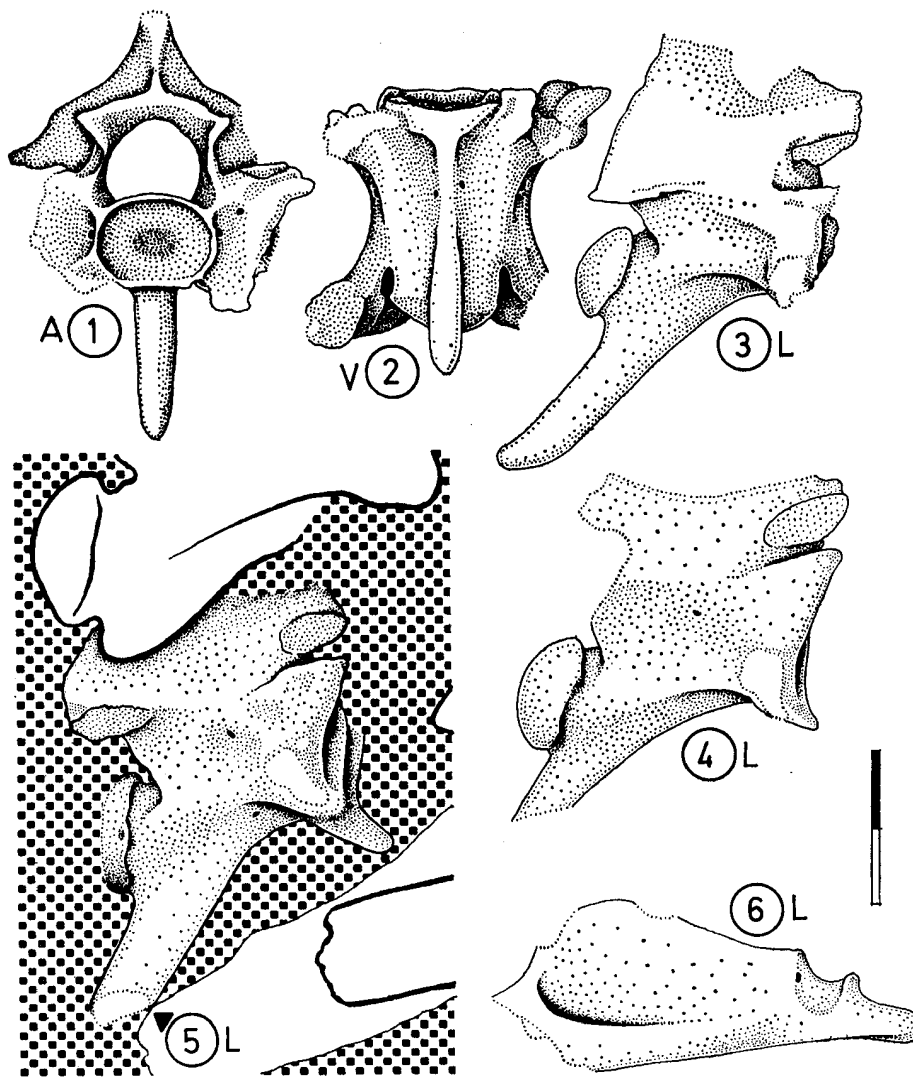

Fig. 10.—Viperidae indet. 1-3, cervical vertebra (MNCN, no Alg I - 55); 4, posterior trunk vertebra (MNCN, no Alg I - 56); 5, mid-trunk vertebra (in matrix: MNCN, no Alg I - 58); 6, left compound bone (MNCN, no Alg I - 57). A - anterior, L - lateral, V - ventral views. Scale equals 2 mm.

height with other species, except North African forms. Hypapophyses similar to those of *P. romani*. The lenght of the prezygapophyseal processes is only comparable with those of *P. romani* and *N. austriaca*; however, in the latter forms the processes are more obtuse. In the zygosphenal form of the mid-trunk vertebrae *N. iberica* resembles *Palaeonaja romani* and *N. austriaca*. Intracolumnar variability of the zygosphene is similar to that of *Palaeonaja romani*.

férez and Brea, 1981) enables identification to familial level at most; ophidian material from Córcoles contains additionally two undescribed elapid vertebrae, but, unfortunately, their bad state of preservation makes more precise identification impossible (Szyndlar, personal observation). Identification of elapid remains (strongly damaged trunk vertebrae) from Librilla (Alberdi *et al.*, 1981) as belonging to *Palaeonaja* aff. *depereti* is also uncertain on account of its preservation. Fossil elapids
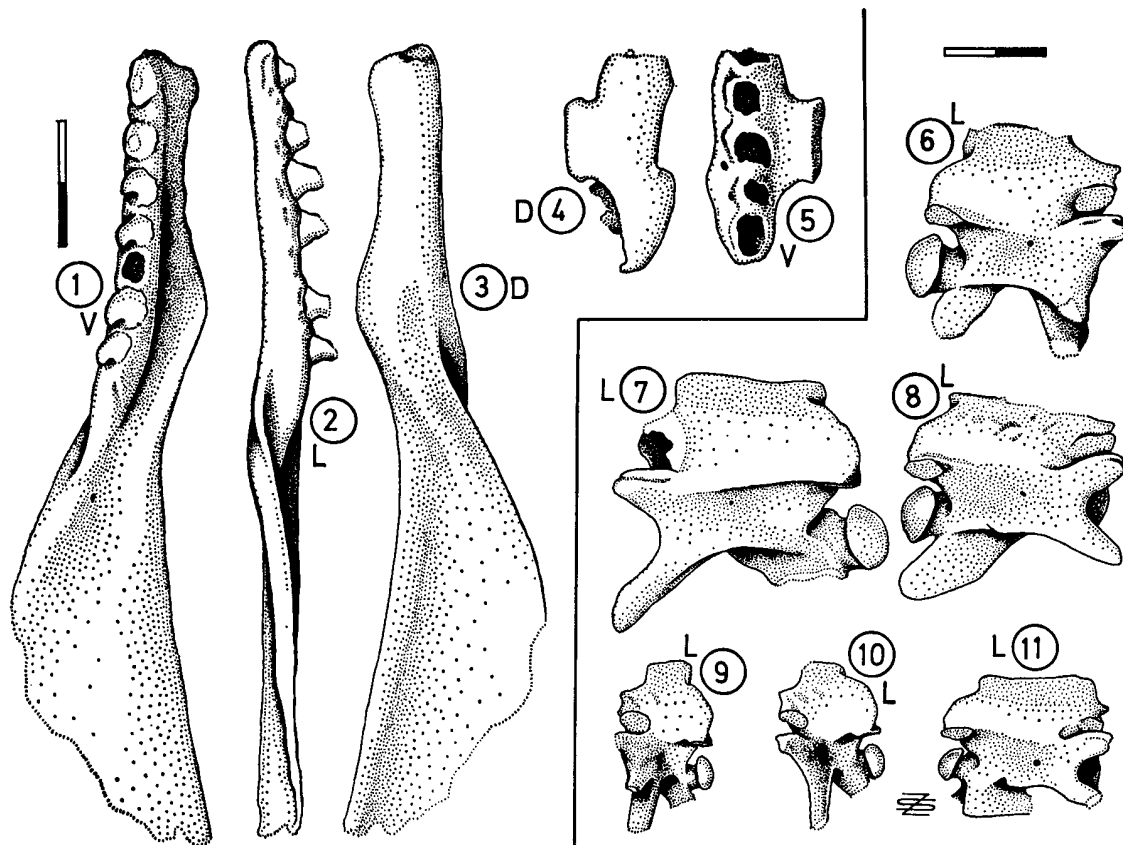

Fig. 11.—Serpentes indet. 1-3, left pterygoid (MNCN, no Alg I - 59); 4, 5, posterior fragment of right maxilla (MNCN, no Alg I - 60); 6, cloacal vertebra (MNCN, no Alg I - 61); 7, mid-caudal vertebra (MNCN, no Alg I - 62); 8, posterior caudal vertebra (MNCN, no Alg I - 63); 9, cloacal vertebra (MNCN, no Alg I - 64); 10, anterior caudal vertebra (MNCN, no Alg I - 65); 11, posterior caudal vertebra (MNCN, no Alg I - 66). D - dorsal, L - lateral, V - ventral views. Scale equals 2 mm.

Elapid remains previously reported from the Iberian Peninsula were classified as belonging to the genus *Palaeonaja*. These finds come from the Lower Miocene, NM 4b, of Córcoles (Alférez and Brea, 1981), and from the Uppermost Miocene (NM 13) of Librilla (Alberdi *et al.*, 1981). Attribution of the elapids from the former locality to the genus *Palaeonaja* was too hasty, because the solitary venom fangs on which the description was based (Al-

were furthermore reported from another Spanish locality of the same age (NM 13), Venta del Moro (Alberdi *et al.*, 1981) but no detailed description of these remains is available.

Hoffstetter's (1939) most important diagnostic features of the genus *Palaeonaja*, i. e. prefrontal relatively lower and dentary shorter than in *Naja* (cf. Rage, 1984) cannot be employed here because of absence of the former bone among the Algora

material and lack of a dentary fused with the compound bone. Comparison of individual cranial features, however, clearly indicates the similarity of the snake from Algora to the African members of the genus *Naja* and its dissimilarity to the extinct genus *Palaeonaja*.

This is not an aim of this paper to revise the taxonomic status of the European elapids, but it should be mentioned that recent finds of the family in the territory of Europe (including the recently described *Naja austriaca*) involves new taxonomic problems and the necessity of a future detailed re-examination of the West Palearctic cobras as a whole. More satisfactory generic description of the extinct *Palaeonaja* than that given by Hoffstetter (1939) is needed as well, since new fossil data impair to some extent the taxonomic distinction of this snake. Regarding living species, no description of their comparative osteology is available, as Bogert's (1943) classical work devoted to Elapidae deals with dentition and only infinitesimally with other cranial elements. There are also apparent differences in skull morphology among living members of *Naja*, and a review of this genus, based on their osteology, should be done.

In my opinion, taking into consideration such an important cranial feature as the location of the vestibular window (either between prootic and exoccipital or within the latter bone), West Palearctic cobras should be divided into two separate groups: (1) Ibero-North African group, including recent *Naja haje* and *N. nigricollis* as well as fossil *N. antiqua* and *N. iberica;* (2) Euroasiatic group, consisting of recent *Naja naja* and fossil *Palaeonaja romani* and *Naja austriaca*. Albeit location of the vestibular window on *N. austriaca* remains unknown, other features such as the development of distinct pterygoid crests, are indicative of its attachment to the Euroasiatic stock. In this way, the proposed partition disagrees with the generic subdivision of Palearctic cobras into *Naja* and *Palaeonaja*.

Family Viperidae

Viperidae indet.

(Fig. 10)

Material: A left compound bone and 4 precaudal vertebrae.

The viperid material is badly preserved. The bones belonged to small but adult snake(s).

The compound bone (fig. 10: 6), with its anterior portion missing, is characterized by a strongly dorsally expanded medial flange, three times higher than the lateral flange, and with a very steep anterior margin. The retroarticular process is posteriorly directed in lateral view.

The vertebrae, though not numerous, represent however the three main precaudal regions of the column, i. e. cervical (fig. 10: 1-3), mid-trunk (fig. 10: 5) and posterior trunk

(fig. 10: 4) regions. Vertebral centra moderately long, with relatively long (short on the posterior trunk region) hypapophyses, directed postero-ventrally. Subcentral ridges present only immediately behind parapophyses. Neural spine unknown. Paradiapophyses damaged in all vertebrae. Parapophyseal processes of cervical vertebrae unknown, those of mid-trunk vertebrae prominent, antero-ventrally directed, the processes of the posterior trunk vertebrae reduced. Cotyle slightly flattened. Condyle of the cervical vertebrae relatively small, those of the trunk vertebrate much larger. All vertebral foramina well marked.

Comparisons and Comments

The territory of the Iberian Peninsula is presently inhabited by three species of the genus *Vipera*: *V. aspis, V. seoanei* and *V. latasti*. The latter species also occurs in the adjacent area of north-western Africa, together with members of other viperid genera [*Bitis, Cerastes* and *Daboia* (*)]. Although these genera are well differentiated on the basis of skeletal characters, a correct identification of the viperid remains from Algora, due to the scarcity of the material and its bad preservation, is probably not possible below familial level.

The Algora viperid resembles, in its rather small size, the three recent Iberian species, but morphologically it considerably differs from *Vipera aspis* and *V. seoanei*. The compound bone of the Algora fossil, regarding the height of its medial flange and especially the steepness of the anterior margin of the latter structure, most resembles those of *Cerastes* and *Bitis*, but differs from them in having a straight retroarticular process in lateral view, this structure being strongly curved downwards in African forms.

The vertebrae distinctly differs from those of *Cerastes*, which has extremely long parapophyseal processes and relatively short hypapophyses, whereas there are no significant differences between the Algora viper on one hand, *Bitis, Daboia* and *Vipera latasti* on the other hand, in their vertebral morphology. The neural spine, a structure useful for the differentiation among European vipers, is unfortunately missing in all vertebrae from Algora. Thus, the taxonomic status of the Viperidae from this locality remains an open question.

Vipers were reported from numerous fossil sites in Europe (cf. Szyndlar, 1984, and references therein), but their remains were rarely identified to specific level. Fossil Viperidae from Iberia are also poorly known, although their presence in the peninsula is documented since almost the beginning of the Neogene. Viperid remains have been reported from the Lower Miocene (NM 3) of Lisboa (Antunes and Rage, 1974); strongly damaged vertebrae,

(*) *Daboia* GRAY is a generic name recently proposed for *Vipera mauretanica* (see Obst, 1983). The generic distinction of this snake is also well confirmed by the morphology of its skeleton (personal observation).

presumably belonging to this group, are present in the sample from the Lower Miocene (NM 4b) of Córcoles (Szyndlar, personal observation). Vertebrae of a Viperidae of enormous size are also contained in an undescribed material from the Pliocene of Vilafant (Szyndlar, personal observation). The only fossil identified to generic level was that from the Upper Miocene of Libros (Teruel), referred by Piveteau (1927) to *Bitis* sp.; in opinion of Robert Hoffstetter (see Marx and Rabb, 1965) these remains belong actually to Colubridae and not to Viperidae.

Serpentes indet.

(Fig. 11)

Several bones, including two cranial elements and many post-thoracic vertebrae, are hardly referrable to any of the previously described snakes.

A pterygoid (fig. 11: 1-3), almost completely preserved, is characterized by a short but distinct tooth-ramus, including 7 stout teeth, as well as by a peculiar crest on the medial border of the bone. This element, morphologically different from that referred to *Elaphe algorensis*, most resembles those of the genus *Elaphe* (but not *Coluber*), especially regarding its shape and relative shortness of the tooth-ramus. Nevertheless, the form of the medial crest as well as the low number of teeth, are not observed on these snakes. Because of its size, the bone could not belong to *Hispanophis*. The bone can be referred neither to *Naja*, a form with a tooth-ramus occupying at least two thirds of the total bone length, nor to Viperidae, characterized by a much more slender pterygoid with long and thin teeth.

A porterior maxillary fragment (fig. 11: 4-5) belong to a colubrid snake. It differs morphologically from maxillae referred to *Elaphe algorensis* (vide infra). The bone was most likely too large to be referred to *Hispanophis*.

Since there are only unclear indications that the Algora material contains rests of more than two colubrid species, these two cranial bones remain unidentified. Contrary to the cranial elements, unidentified vertebrae most likely belonged to the previously described forms, but their correct referring to particular taxa is at present uncertain.

The larger vertebrae from the cloacal (fig. 11: 6), mid-caudal (fig. 11: 7) and posterior caudal (fig. 11: 8) regions, because of their size, presumably belonged to *Naja iberica*, although some features, among others the overgrowth of the haemapophyses in comparison with the pleurapophyses in the posterior caudal vertebrae, are not observed in living *Naja*.

Cloacal (fig. 11: 9) and anterior caudal vertebrae (fig. 11: 10), belonging to a small snake, are antero-posteriorly shortened to a degree that is not observed on living European species. They might have belonged to *Hispanophis*.

Porsterior caudal vertebrae (fig. 11: 11), characterized by strongly expanded anteriorly haemapophyses, are also dissimilar to living species. Only *Coronella girondica* and *Vipera latasti* have somewhat similar haemapophyses. Since these vertebrae are too large to be referrable to *Hispanophis*, they might have belonged to the Viperidae.

Discussion

Since ophidian faunas from the Uppermost Miocene are either unknown or their descriptions inadequate, no fruitful comparisons with the Spanish faunal assemblage are possible. The only European fossil site dated similarly as Algora (NM 13), from which a snake fauna was described, is Polgárdi in Hungary. The taxonomic status of the snakes from this locality is unfortunately uncertain. The ophidian fossils from Polgárdi were suspected, either in part (Bolkay, 1913) or even all but one (Szunyoghy, 1932), to represent living species, whereas paleontological evidence derived from all the remaining Holarctic sites indicates that the recent snakes did not appear before the Middle Pliocene (see Szyndlar, 1984, for discussion). In order to explain these questions the material from Polgárdi should be re-examined. In the author's opinion, the Polgárdi material was probably mixed and the snake remains (if they indeed belong to presently living species) may come from geologically younger layers.

Similarities of the ophidian faunas from Algora and some other slightly older or younger sites are observed at most at the generic level. Nevertheless, the dissimilarities at the specific level are not surprising phenomena if we consider that our knowledge of Neogene snakes (especially colubroids) and their European distribution is still highly limited. As a consequence, the overwhelming majority of the extinct snake species are unknown beyond their type localities. On the other hand, an intense endemism is characteristic for the Iberian faunas, a phenomenon also observed within presently living snakes, and thus the ophidians from Algora could represent endemic forms as well.

There are, however, clear differences between the fauna from Algora, mostly composed of advanced snakes, and the Lower Miocene ophidian faunas, characterized by the presence of some archaic elements. The latter are represented by members of the subfamily Boinae, also observed in Lower Miocene sites of the Iberian Peninsula, i. e. Lisboa (Antunes and Rage, 1974) and Córcoles (Szyndlar, personal observation). In Europe, these reptiles are unknown from the period following the Middle Miocene (cf. Rage, 1984). It is not unlikely that European Boinae became extinct before the end of the Miocene. Other boid snakes, the Erycinae, widespread in the older half of the European Neogene, were also reported from the Lower Miocene of Córcoles (Alférez and Brea, 1981). Their absence in the Algora material obviously is not an evidence of their absence in Iberia at the end of the Miocene, as they have been recovered in Salobreña, a Mio-Pliocene site in Southern Spain (B. Sanchíz, personal communication), and were present in southern France as recently as the Upper Pliocene (NM 16: Hoffstetter and Rage, 1972). Nevertheless, assuming that the European range of these snakes was diminishing gradually from West to East (the present range of Erycinae in Europe is restricted to its southeastern part), it is possible that the extinction of

Iberian erycines preceded their disappearance in more eastern areas. On the other hand, Algora is now the youngest among West European fossil sites containing remains of scolecophidians, a group inhabiting presently the same area as erycines.

For paleozoogeographical considerations, the most interesting are the close affinities of the elapid that dominates the Algora assemblage with cobras from Africa. The faunal exchange in this region at the Miocene/Pliocene boundary was previously evidenced for several groups of mammals (Brandy and Jaeger, 1980; Geraads, 1982; Jaeger *et al.*, 1977; Thomas *et al.*, 1982). In our case we receive also a direct evidence of the African origin of the Iberian snake fauna, according to expectations by Szyndlar (1984). The end of the Miocene was an especially favorable period for the migrations between Africa and Iberia owing to the appearance of a land bridge linking both continents.

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