

# Snakes of the lower/middle Miocene transition at Vieux Collonges (Rhône, France), with comments on the colonisation of western Europe by colubroids

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## ABSTRACT

The diverse snake assemblage of the lower/middle Miocene (MN 4/5) site Vieux Collonges (France) includes Boidae (*Python* sp., *Eryx* sp., Boidae B & C), Colubridae (*Texasophis* sp., *Neonatrix* cf. *europaea*, *Natrix* aff. *sansaniensis*, Natricinae A, B, C & D), Elapidae (*Micrurus* aff. *gallicus*, *Naja* cf. *romani*, *Naja* sp. 1, Elapidae A & B) and Viperidae (Viperinae A, *Vipera* [“Oriental vipers”] or *Daboia*). The Boidae represent an “ancient” component of the snake fauna which was displaced from Europe by “modern” Asiatic and North American immigrants during the lower and the middle Miocene. Although the representatives of the family Boidae were still common in West Europe at the lower/middle Miocene transition (Vieux Collonges), the representatives of the Colubridae were predominant in Central Europe (Merkur, Dolnice, Petersbuch 2) already during the lower Miocene. It may be possible that the first Colubridae have immigrated into the Central European areas across the Mazury-Mazowsze continental bridge (Poland) in the lower Oligocene and then penetrated into West Europe across the Rhine Graben in several waves of dispersal. The small representatives of family Elapidae appeared in Europe most probably slightly earlier (MN 3a) than the large representatives of the genus *Naja* commonly present at Vieux Collonges. Similarly, for the oldest European viperids are typical small vipers, the large “Oriental” vipers appeared later (MN 3) in Europe. Concerning Vieux Collonges, the representatives of the Viperidae are relatively rare.

## KEY WORDS

Snakes,  
Boidae,  
Colubridae,  
Elapidae,  
Viperidae,  
lower/middle Miocene transition,  
dispersals,  
France.

## RÉSUMÉ

*Serpents du Miocène inférieur/moyen à Vieux Collonges (Rhône, France), avec les commentaires sur la colonisation de l'Europe de l'Ouest par des colubroïdes.*

L'ensemble des serpents du Miocène moyen/inférieur à Vieux Collonges est très diversifié : il inclut des Boidae (*Python* sp., *Eryx* sp., Boidae B & C), Colubridae (*Texasophis* sp., *Neonatrix* cf. *europaea*, *Natrix* aff. *sansaniensis*, Natricinae A, B, C & D), Elapidae (*Micrurus* aff. *gallicus*, *Naja* cf. *romani*, *Naja* sp. 1, Elapidae A & B) et Viperidae (Viperinae A, *Vipera* [« Oriental vipers »] ou *Daboia*). Les Boidae représentent une faune ancienne de serpents qui fut refoulée de l'Europe par les immigrants modernes asiatiques et nord-américains pendant le Miocène inférieur et moyen. Bien que les représentants des Boidae soient toujours communs, dans l'Europe de l'Ouest, à la frontière du Miocène inférieur et moyen, les représentants des Colubridae prédominent en Europe centrale (Merkur, Dolnice, Petersbuch 2) dès le Miocène inférieur. Les premiers Colubridae immigrèrent en Europe centrale grâce au « pont continental » Mazury-Mazowsze (Pologne) dès l'Oligocène inférieur et pénétrèrent ensuite en Europe de l'Ouest à travers le fossé rhénan en plusieurs vagues de dispersion. En ce qui concerne les Elapidae, les petits représentants de cette famille apparurent en Europe (MN 3a), le plus probablement un peu avant les grands représentants du genre *Naja* généralement présents à Vieux Collonges. De façon analogue, les Viperidae européens les plus anciens sont représentés par de petites vipères, les grandes vipères « orientales » apparaissent plus tard (MN 3) en Europe. En ce qui concerne Vieux Collonges, les représentants de la famille des Viperidae sont relativement rares.

## MOTS CLÉS

Serpents,  
Boidae,  
Colubridae,  
Elapidae,  
Viperidae,  
Miocène inférieur/moyen,  
migration,  
France.

## INTRODUCTION

Vieux Collonges, former “Mont Ceindre” (part of the village of Collonges at the Mont-d’Or) is located in southeastern France, about 2 km North of the northern border of Lyon and 2 km from the right bank of the Saône river. The fossiliferous site is a fissure within the Jurassic limestone which is filled with Miocene sediments. These sediments contain a rich fauna of vertebrates. The mammalian fauna has been investigated by Mein (1958) and Guérin & Mein (1971). Vieux Collonges is a significant locality (Fig. 1) of the lower/middle Miocene transition (MN 4/5) (Bruijn *et al.* 1992) (Ottangian/Karpatian [Orleanian] *sensu* Steininger *et al.* [1996]). Miocene fauna of snakes indicating relations between Europe and North America have been investigated by Rage & Holman (1984). The snake assemblage from Vieux Collonges is considerably diverse, with representatives of the “ancient” (Boidae) and the

“modern” (Colubridae, Elapidae, Viperidae) snake fauna. The latter mentioned group is represented mostly by Asiatic immigrants.

In the systematic part, the “synonymes” include the references to the material studied.

The fossil material of snakes from Vieux Collonges is stored in the Centre des Sciences de la Terre, Université Claude-Bernard, Lyon (collected by P. Mein) and in the Laboratoire de Paléontologie, Muséum national d’Histoire naturelle, Paris.

## ABBREVIATIONS

VCO	Vieux Collonges, France;
MNHN	Laboratoire de Paléontologie, Muséum national d’Histoire naturelle, Paris;
FSL	Faculté des Sciences de Lyon, Lyon;
ZZSiD	Instytut systematyki i ewolucji zwierząt PAN, Kraków;
n	number of specimens;
cl	centrum length;
naw	centrum width;
or	observed range.

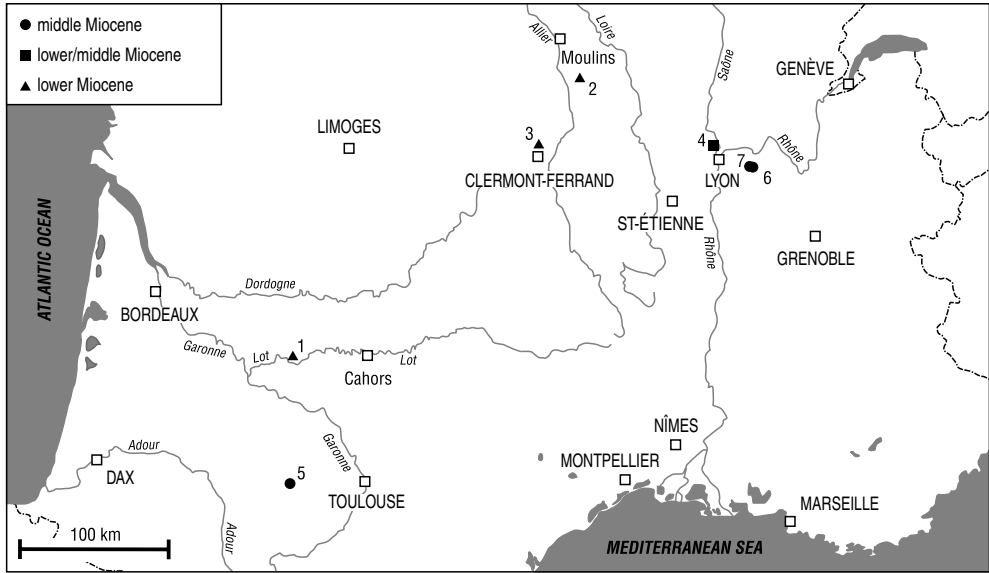


FIG. 1. — Distribution of some French lower and middle Miocene ophidian localities; 1, Paulhiac (MN 1); 2, "Saint-Gérard-le-Puy" (MN 2); 3, Marcoin (MN 2); 4, Vieux Collonges (MN 4/5); 5, Sansan (MN 6); 6, La Grive M, L7, L5, L3 (MN 7+8); 7, Isle d'Abeau (MN 7/8).

## SYSTEMATIC PALEONTOLOGY

Suborder ALETHINOPHIDIA Nopcsa, 1923  
 Superfamily BOOIDEA Gray, 1825  
 Family BOIDAE Gray, 1825  
 Subfamily PYTHONINAE Fitzinger, 1826  
 Genus *Python* Daudin, 1803

### *Python* sp.

"unnamed species of *Python*" – Rage in Thomas *et al.* 1982: 117.

"assez gros Boïné" – Rage in Demarcq *et al.* 1983: 256.

*Python* sp. – Ivanov 1997a: 35-36, fig. 18.

MATERIAL EXAMINED. — 1 palatine (FSL 368001), 37 cervical vertebrae (MNHN; VCO 5-VCO 9; FSL 368002-FSL 368032, FSL 368033), 321 trunk vertebrae (MNHN; VCO 10-VCO 29; FSL 368034-368334), 2 caudal vertebrae (FSL 368335, FSL 368336).

## DESCRIPTION

### Palatine (Fig. 2A)

The complete maxillary process and the base of the vomerine process are preserved. Both the rostral and the caudal parts of the bone are broken

off. The maxillary process is relatively short, a distinct foramen for maxillary nerve penetrates its base. The vomerine process was directed anteriorly, however its distal end is broken off. The teeth are not preserved, with the exception of the base of one tooth.

### Cervical vertebrae (Fig. 2B-D)

The vertebrae are massively built. In lateral view, the neural spine is as long as high or somewhat higher. The anterior cervical vertebrae possess caudally shifted neural spine; both the cranial and caudal margins of the neural spine are inclined posteriorly. In posterior cervical vertebrae, the cranial margin of the neural spine is almost vertical. The interzygapophyseal ridges are considerably developed and they are anteroventrally directed. Generally, the lateral foramina are very small and indistinct. The hypapophyses are broken off nearby their base. The subcentral ridges are arched slightly dorsally, in some cases they are straight. The indistinctly divided paradiapophyses are mostly heavy damaged. In dorsal view, the zygosphenal lip is almost straight with

indistinct median lobe, or it is even slightly concave. The neural spine can be slightly thickened postero-dorsally, however its cranial margin is always sharp. The prezygapophyseal articular surfaces are irregular – originally, they could be subtriangular. In ventral view, both the subcentral ridges and grooves are mostly distinct, especially in the cranial part of vertebrae. The subcentral foramina are distinct. The postzygapophyseal articular surfaces are shaped irregularly. In cranial view, the neural arch is considerably arched, the neural canal is suborbicular. The zygosphenal lip is straight to slightly convex dorsally. The parapophyseal processes are short and rounded ventrally. The cotyle is rounded to slightly flattened dorso-ventrally. The paracotylar foramina are lacking.

#### *Trunk vertebrae (Fig. 2E-I)*

All vertebrae are damaged. In lateral view, the neural spines are broken off mostly at the base. The cranial margin of the neural spine is almost vertical, rarely it overhangs anteriorly. The caudal margin overhangs posteriorly. The sharp interzygapophyseal ridges are markedly directed antero-ventrally. The lateral foramina are distinct, they are not situated in any depressions. The aliform processes can project behind the postzygapophyseal articular surfaces. Paradiapophyses are indistinctly divided. The subcentral ridges are arched dorsally. In dorsal view, the neural spine is thick, especially its caudal part. The cranial margin is sharp. The prezygapophyseal articular surfaces are subtriangular. The zygosphenal lip is wide with variable shape – it may be straight with well-developed lateral lobes, but sometimes the wide median lobe is present. The prezygapophyseal processes are very short. In ventral view, the haemal keel is wide, especially in large vertebrae. In some cases, a cranial expansion of the haemal keel is observed just behind the cotyle. The haemal keel is better developed in posterior trunk vertebrae where it becomes more pronounced because of deeper subcentral grooves and more distinct subcentral ridges. The subcentral ridges extend from the parapophyses to almost the base of the condyle. The subcentral foramina are well-

perceptible. Laterally expanded postzygapophyseal articular surfaces are irregular. In cranial view, the margin of the massive zygosphenon is straight, rarely concave. The neural arch is vaulted, the neural canal is about subtriangular with distinct lateral sinuses. The prezygapophyses are slightly turned up. The cotyle is almost rounded, rarely flattened dorso-ventrally. The paracotylar foramina are missing. In caudal view, is seen the massively build zygantrum. Metrical measurements are as follows ( $n = 24$ ): cl: or = 6.04-10.11; naw: or = 7.08-13.42; cl/naw: or = 0.71-0.89, mean  $0.79 + 0.04$ .

#### *Caudal vertebrae*

Both the pleurapophyses and haemapophyses are broken off at the base. In lateral view, the neural spine is short, somewhat longer than high. The interzygapophyseal ridges are distinct, the lateral foramina are very small. In dorsal view, the zygosphenal lip is straight or concave, lateral lobes are turned up dorsally in cranial view. The prezygapophyseal articular surfaces are expanded antero-laterally. They are irregularly, subtriangularly shaped. In cranial view, the neural arch is considerably vaulted, the cotyle is flattened dorso-ventrally and the paracotylar foramina are lacking.

#### DISCUSSION

The palatine of representatives of the subfamily Pythoninae is characterised by the distinct foramen at the base of the maxillary process (Underwood 1967). The discovered palatine is very fragmentary, however, because of the dimensions of the bone it may be assumed that it likely belongs to an adult representative of the genus *Python*. The vertebrae are massively built with a very low ratio cl/naw, which is apparently lower than 1.00. Moreover, the paracotylar foramina are absent. Therefore, it can be assumed that the discovered vertebrae belong to the Boidae. The allocation to the subfamily Pythoninae and the genus *Python* is based on the presence of well-preserved palatine. The fossil material could be compared only with the recent species *Python reticulatus* (Schneider, 1801)

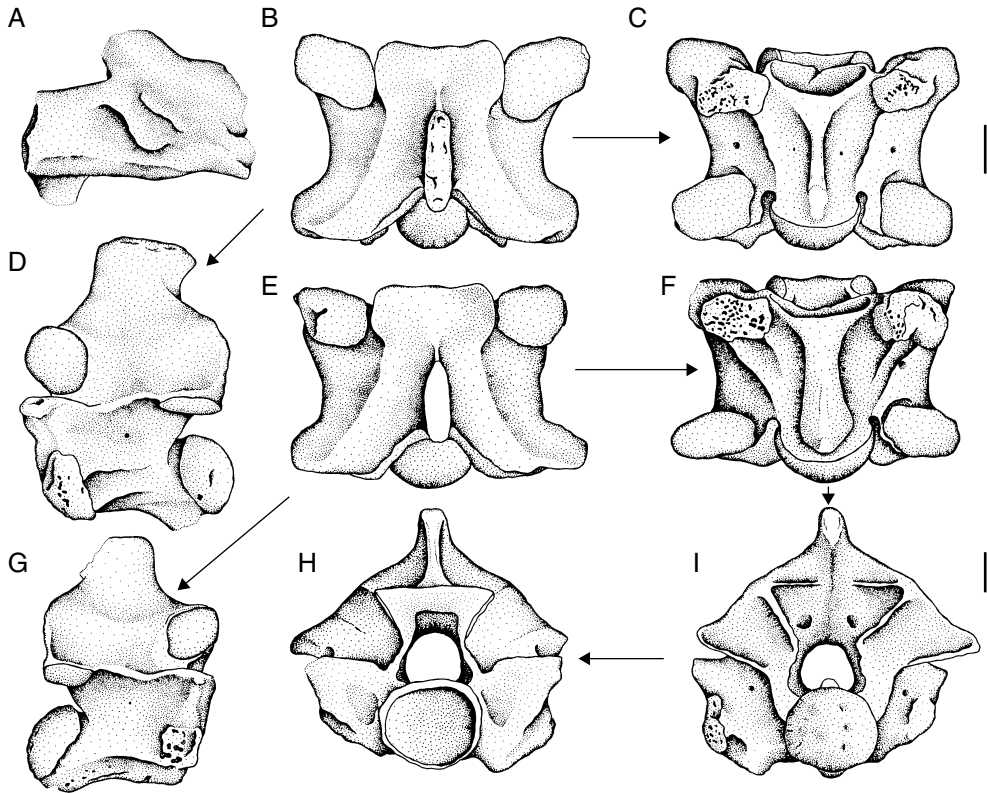


FIG. 2. — *Python* sp. from the lower/middle (MN 4/5) Miocene of Vieux Collonges; A, left palatine (FSL 368001), labial view; B-D, cervical vertebra (FSL 368002); B, dorsal view; C, ventral view; D, lateral view; E-I, trunk vertebra (FSL 368039); E, dorsal view; F, ventral view; G, lateral view; H, cranial view; I, caudal view. Scale bars: 2 mm.

(ZZSiD 436 juv., ZZSiD 437 juv.) and *Python molurus* (Linnaeus, 1758) (ZZSiD 460) – however, because of the scantiness of cranial bones a more precise determination was not possible. The vertebrae of *Python* sp. differ from the morphotypes Boidae B & C (see below) in: 1) the much more vaulted neural arch; 2) the shape of the massive zygospheal lip.

At present, the available material represents the only known representative of the subfamily Pythoninae from the European Neogene. Another unquestionable Pythoninae comes from the German locality Messel (middle Eocene) where a great number of cranial bones, still articulated (including maxilla and palatine with taxonomically important features), have been discovered (Szyndlar & Böhme 1993). However, the axial

skeleton was not precisely studied (Szyndlar & Böhme 1993). The extinct species *Palaeopython sardus* Portis, 1901 (= ?*Python sardus* [Rage, 1984]) belongs most likely also to the subfamily Pythoninae. Both last mentioned constrictors were characterised by considerable diameters.

Subfamily ERYCINAE Bonaparte, 1831  
Genus *Eryx* Daudin, 1803

*Eryx* sp.

*Bransateryx* sp. – Hoffstetter & Rage 1972: 102, pl. II, fig. 11. — Ivanov 1997a: 36-37, fig. 19.

MATERIAL EXAMINED. — 4 trunk vertebrae (FSL 368337-FSL 368340), 2 caudal vertebrae (FSL 368341, FSL 368342).

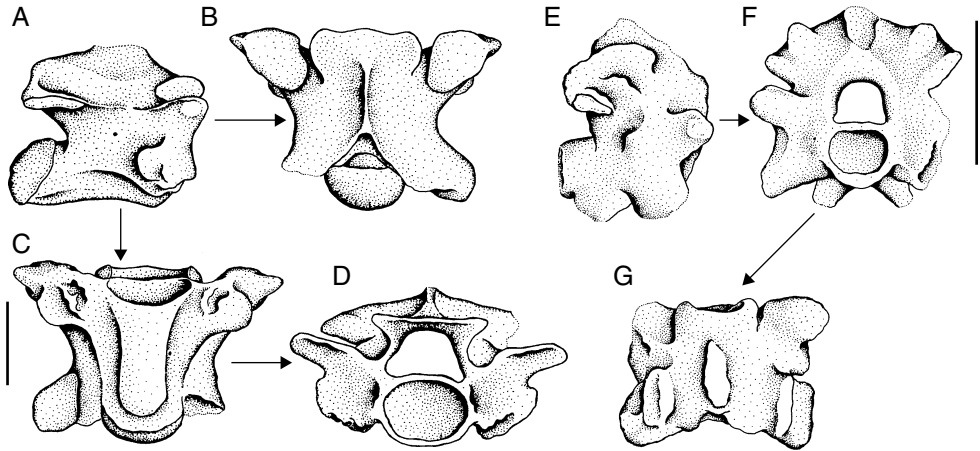


FIG. 3. — *Eryx* sp. from the lower/middle (MN 4/5) Miocene of Vieux Collonges; **A-D**, trunk vertebra (FSL 368339); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E-G**, posterior caudal vertebra (FSL 368341); **E**, lateral view; **F**, cranial view; **G**, dorsal view. Scale bars: 2 mm.

#### DESCRIPTION

##### *Trunk vertebrae* (Fig. 3A-D)

In lateral view, the bases of broken off neural spines are shifted caudally. Short interzygapophyseal ridges are sharp. The caudal part of the neural arch is turned up dorsally. The slightly dorsally arched subcentral ridges extend from the distinctly cranially situated synapophyses to the basis of the condyle. The paradiapophyses are not distinctly divided, the diapophyseal area is larger than the parapophyseal one. The lateral foramina are relatively large and well-visible. In dorsal view, the cranial margin of the zygosphene has prominent lateral lobes and the median lobe is wide. The neural spine is narrow. The prezygapophyseal articular surfaces are subtriangular, well-visible prezygapophyseal processes are very short and pointed. In ventral view, the haemal keel is very wide. It extends from the base of the cotyle to the base of the condyle. In the cranial part of vertebrae the haemal keel can be strikingly expanded. The haemal keel is very distinct in posterior trunk vertebrae. In the case of anterior trunk vertebrae, the haemal keel is indistinct as well as the short subcentral ridges and the shallow subcentral grooves. In all vertebrae, both the subcentral grooves and ridges are more distinct in their cranial part. The subcentral foramina are

very small and hardly perceptible. In cranial view, the neural arch is conspicuously flattened, the neural canal is approximately circular with distinct lateral sinuses. The cranial margin of the gracile zygosphene is straight. The prezygapophyses are distinctly tilted upward. The cotyle is flattened dorso-ventrally, the paracotylar foramina are lacking. Metrical measurements are as follows ( $n = 4$ ): cl: or = 1.65-3.41; naw: or = 1.88-3.52; cl/naw: or = 0.74-0.97, mean  $0.84 \pm 0.11$ .

##### *Caudal vertebrae* (Fig. 3E-G)

Both the zygosphene and the zygantrum are absent, which proves that these specimens are posterior caudal vertebrae. In lateral view, the vertebrae are high with short vertebral centrum. On the more complete vertebra the right pleurapophysis is broken off near its base (the left pleurapophysis is completely missing like the left prezygapophysis). The neural spine, broken off at the base, is accompanied laterally with prominent pterapophyses which project cranially into a distinct process. The caudal extension is less perceptible. The pleurapophysis projects distally into a process where the prezygapophysis of the subsequent vertebra is wedged between this process and the postzygapophysis. In dorsal view, the damaged right prezygapophyseal artic-

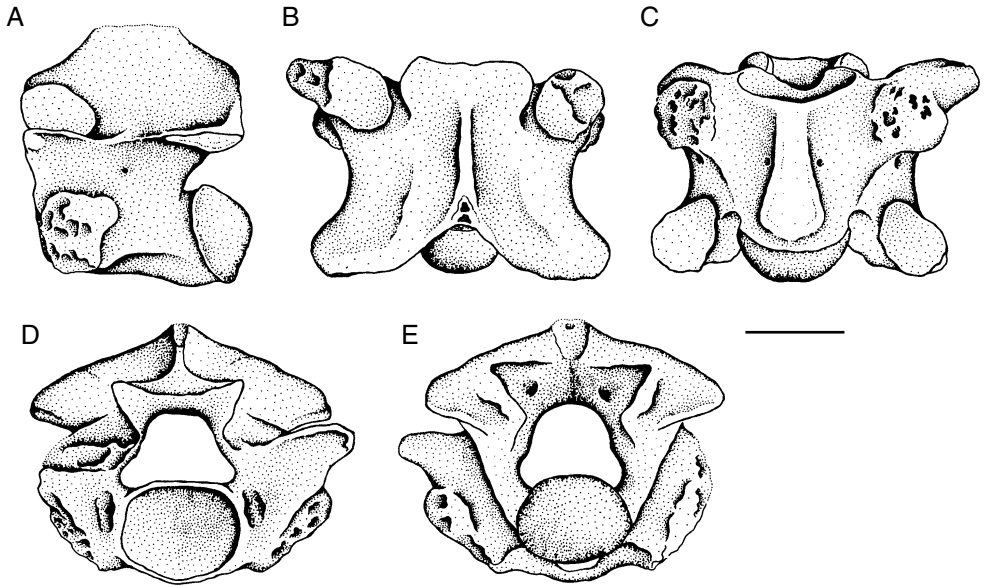


FIG. 4. — Boidae B from the lower/middle (MN 4/5) Miocene of Vieux Collonges, mid-trunk vertebra (FSL 368343); A, lateral view; B, dorsal view; C, ventral view; D, cranial view; E, caudal view. Scale bar: 2 mm.

ular surface is irregular, the pterapophyses are relatively wide. In cranial view, the neural arch is approximately rounded with lateral sinuses, the prezygapophyses are tilted upward and the prezygapophyseal processes are very short and obtuse. The cotyle is approximately rounded, its ventral margin is thickened. The haemapophyses are directed latero-ventrally, their distal ends are broken off.

#### DISCUSSION

The assignment to the subfamily Erycinae and to the genus *Eryx* is based on the presence of caudal vertebrae with complicated structure. The discovered vertebrae belong most probably to the genus *Eryx* – the remaining material of 25 caudal and 70 trunk vertebrae of this genus, discovered at Vieux Collonges, have recently been investigated by Szyndlar & Rage (in prep.). The morphology of the caudal vertebrae is very complicated in the subfamily Erycinae and the problems connected with the determination of such vertebrae will be widely discussed (Szyndlar & Rage in prep.).

#### Subfamily indeterminate

#### Boidae B

Boidae B – Ivanov 1997a: 41, fig. 21.

MATERIAL EXAMINED. — 2 trunk vertebrae (FSL 368343, FSL 368344).

#### DESCRIPTION

##### *Trunk vertebrae* (Fig. 4)

In lateral view, the basis of the neural spine is shifted anteriorly. Although the neural spine is incompletely preserved, it may be assumed that its cranial margin is vertical or slightly inclined posteriorly like the caudal margin. The neural arch is turned up caudally, the interzygapophyseal ridges are distinct and sharp. The lateral foramina are large and distinct, situated in shallow depressions. The subcentral ridges are indistinct and short. The synapophyses are very damaged. In dorsal view, the zygosphenal lip is clearly concave. The obovate (?subtriangular) prezygapophyseal articular surfaces are damaged, the prezygapophyseal processes are very short,

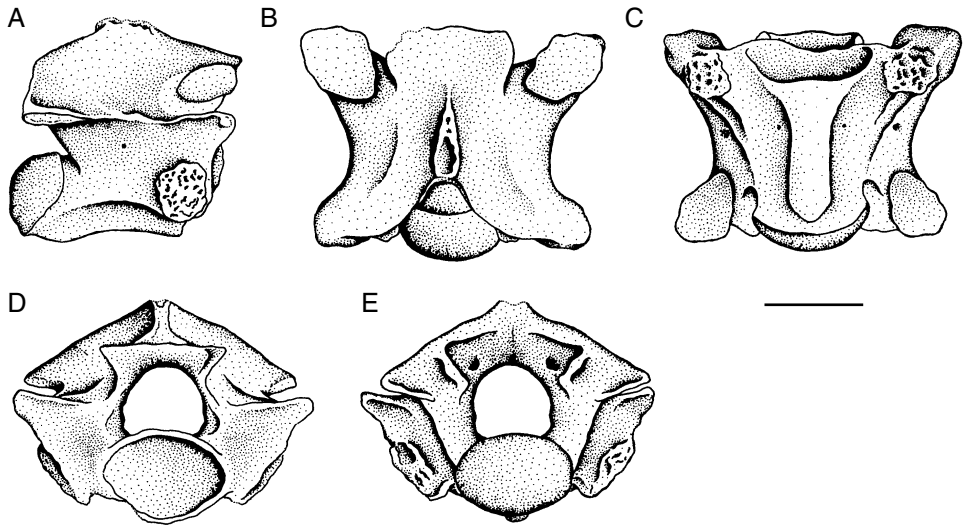


FIG. 5. — Boidae C from the lower/middle (MN 4/5) Miocene of Vieux Collonges, mid-trunk vertebra (FSL 368346); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E**, caudal view. Scale bar: 2 mm.

however, they are well-perceptible from the dorsal view. Epizygapophyseal spines are lacking. In ventral view, both the subcentral ridges and wide subcentral grooves are relatively indistinct, the subcentral foramina are large and situated close to the distinct haemal keel. The haemal keel may be wide or relatively narrow. The postzygapophyseal articular surfaces are approximately oval. In cranial view, the neural arch is slightly vaulted, the neural canal is subcircular with distinct lateral sinuses. The massive zygosphenal lip is straight to slightly concave. The prezygapophyses are strongly tilted upward. Wide depressions are situated on either side of the rounded cotyle, the paracotylar foramina are lacking. Metrical measurements: larger vertebra:  $cl = 3.72$ ;  $naw = 4.51$ ;  $cl/naw = 0.82$ ; smaller vertebra:  $cl = 3.52$ ;  $naw = 3.99$ ;  $cl/naw = 0.88$ .

#### DISCUSSION

Both the low ratio  $cl/naw$  (lower than 1.00) and the massive structure of vertebrae point to the affiliation to the family Boidae. The morphotype Boidae B does most probably not belong to the subfamily Erycinae because the neural arch is not clearly flattened dorso-ventrally, which is a char-

acteristic of erycine snakes. The vertebrae of the morphotype Boidae B belong most likely to a small representative of the Boinae or Pythoninae. The Boidae B differs from *Python* sp. in: 1) the less vaulted neural arch; 2) the prezygapophyses which are tilted upward. Based on the limited material, a more precise determination was not possible.

#### Subfamily indeterminate

#### Boidae C

Boidae C – Ivanov 1997a: 41-42, fig. 22.

MATERIAL EXAMINED. — 4 trunk vertebrae (FSL 368345-FSL 368348).

#### DESCRIPTION

##### *Trunk vertebrae* (Fig. 5)

In lateral view, the cranial margin of the neural spine is located at the anterior third of the vertebral length. The cranial margin of the only preserved, but very damaged, neural spine is vertical, the caudal margin is broken off. The interzygapophyseal ridges are distinct and sharp.



The large lateral foramina are not situated in depressions. The subcentral ridges are distinct and vaulted dorsally, extending from strongly damaged synapophyses to the base of the condyle. In dorsal view, the zygosphenal lip is characterised by distinct lateral lobes, the median lobe is wide and blunt. The prezygapophyseal articular surfaces are subtriangular, the prezygapophyseal processes are very short and invisible from the dorsal view. Epizygapophyseal spines are lacking. In ventral view, the subcentral ridges and grooves, as well as the deep haemal keel are distinct; the keel expands near the cotyle. The ventral margin of the haemal keel is rounded in the cranial part of vertebrae but, in the caudal part, it is relatively sharp. The subcentral foramina are distinct and large, they open close to the haemal keel. The postzygapophyseal articular surfaces are expanded laterally. In cranial view, the neural arch is arched, the neural canal is subcircular with small lateral sinuses, and the gracile zygosphenal lip is straight. The prezygapophyses are tilted upward. Deep depressions are situated on the both sides of the dorsoventrally flattened cotyle, paracotylar foramina are absent. The metrical measurements are as follows ( $n = 3$ ):  $cl: or = 3.49-4.16$ ;  $naw: or = 3.99-4.93$ ;  $cl/naw: or = 0.84-0.87$ , mean  $0.86 + 0.02$ .

#### DISCUSSION

The vertebrae belong undoubtedly to the family Boidae based on the massive structure and the low ratio  $cl/naw$  (lower than 1.00). A distinctly vaulted neural arch excludes the affiliation to the subfamily Erycinae. The absence of the paracotylar foramina is insufficient for distinction between subfamilies Boinae and Pythoninae (Szyndlar 1994). The morphotype Boidae C differs from the Boidae B on the basis of the following features: 1) the basis of the neural spine is located on the anterior third of the vertebral length; 2) the zygosphenal lip is not so massively built; 3) the lateral sinuses of the neural canal are small. The Boidae C differs from *Python* sp. mainly in: 1) the less vaulted neural arch; 2) the much more gracile zygosphenal lip.

Superfamily COLUBROIDEA Oppel, 1811  
 Family COLUBRIDAE Oppel, 1811  
 Subfamily COLUBRINAE Oppel, 1811  
 Genus *Texasophis* Holman, 1977

*Texasophis* sp.

Colubrinae C – Ivanov 1997a: 96-97, fig. 43.

MATERIAL EXAMINED. — 7 trunk vertebrae (FSL 368349-FSL 368355).

#### DESCRIPTION

*Trunk vertebrae* (Fig. 6)

In lateral view, the neural spine is broken off at the base. The interzygapophyseal ridges are well-developed, the lateral foramina are small, situated closely below the interzygapophyseal ridges. Both the para- and diapophyses are small, indistinctly separated; the parapophyses are smaller than the diapophyses. The subcentral ridges are well-perceptible, they are long and straight. The neck of the condyle is relatively long. In dorsal view, the zygosphenal lip possesses an unusually projecting median lobe, the lateral lobes are smaller. The prezygapophyseal articular surfaces are oval, the prezygapophyseal processes are very short (about one-fifth of the length of the prezygapophyseal surfaces) and blunt. Epizygapophyseal ridges are missing. In ventral view, the shallow subcentral grooves are visible. Very small subcentral foramina are situated near the limit of the shallow haemal keel. The haemal keel expands close to the cotyle; on the ventral side small and indistinct subcotylar tubercles may be observed. The postzygapophyseal articular surfaces are irregularly shaped. In cranial view, the neural arch is clearly vaulted, the neural canal is large with small lateral sinuses. The zygosphenal lip is slightly convex; the paracotylar foramina are minute and situated in shallow depressions on either side of the rounded cotyle. In caudal view, the zygantral area is gracile, parazygantral foramina may occur. The metrical measurements are as follows ( $n = 4$ ):  $cl: or = 3.25-3.97$ ;  $naw: or = 2.14-.2.32$ ;  $cl/naw: or = 1.52-1.71$ , mean  $1.62 + 0.08$ .

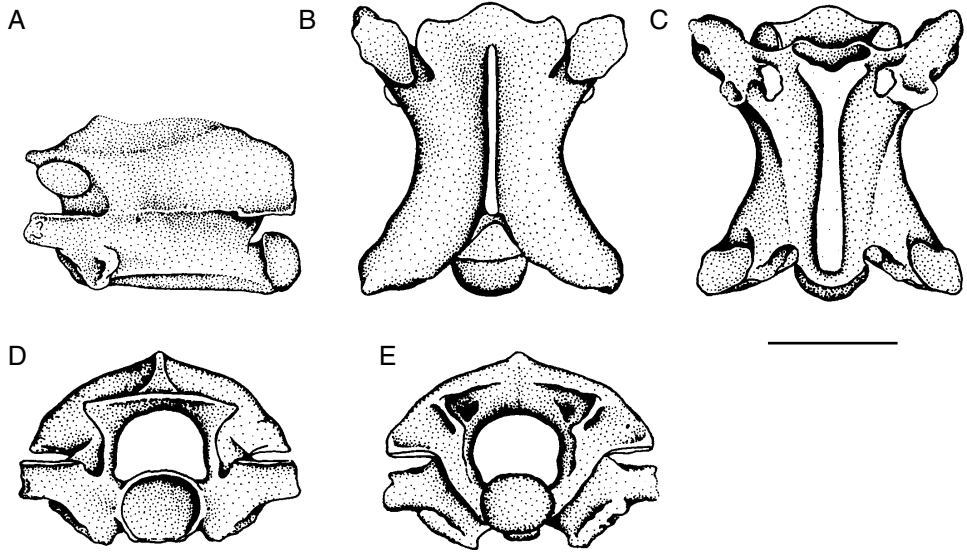


FIG. 6. — *Texasophis* sp. from the lower/middle (MN 4/5) Miocene of Vieux Collonges, mid-trunk vertebra (FSL 368353); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E**, caudal view. Scale bar: 2 mm.

#### DISCUSSION

The fossil material is closely related to the extinct genus *Texasophis* because of the following features: 1) the vaulted neural arch; 2) the shape of the zygosphenal lip with two distinct lateral lobes and the prominent median lobe; 3) the very short prezygapophyseal processes; 4) the flat haemal keel. The only difference from the extinct genus *Texasophis* is the presence of the subcotylar tubercles in some cases. Two species of the genus *Texasophis* have been reported from the European Miocene: *Texasophis meini* Rage & Holman, 1984 from the middle Miocene (MN 7+8) of La Grive M (Rage & Holman 1984) and *Texasophis bohemiacus* Szyndlar, 1987 from the lower Miocene (MN 4) of Dolnice (Szyndlar 1987). *Texasophis* sp. from Vieux Collonges resembles *Texasophis meini* in the shape of the zygosphenal lip. On the other hand, the relatively narrow haemal keel and straight (in lateral view) subcentral ridges are characteristics of the species *Texasophis bohemiacus*.

Subfamily NATRICINAE Bonaparte, 1838  
Genus *Neonatrix* Holman, 1977

#### *Neonatrix* cf. *europaea* Rage & Holman, 1984

*Neonatrix* cf. *europaea* – Rage & Holman 1984: 99. — Ivanov 1997a: 99, fig. 45.

MATERIAL EXAMINED. — 7 trunk vertebrae (FSL 368823-FSL 368829).

#### DESCRIPTION

##### *Trunk vertebrae* (Fig. 7)

In lateral view, the neural spine is about two times longer than high; its cranial margin is vertical or slightly overhangs anteriorly, the caudal margin overhangs posteriorly. The interzygapophyseal ridges are well-developed, however they are not very sharp. Epizygapophyseal spines are lacking. The subcentral ridges are approximately straight and reach the vicinity of the proximal margin of the condyle. The lateral foramina are well-perceptible, they are situated in wide and shallow (rarely deeper) depressions. The para- and diapophyses are clearly separated, the parapophyses are as long as the diapophyses, the antero-ventrally directed parapophyseal processes are relatively short. Mostly broken off hypapophyses were probably very short. In dor-

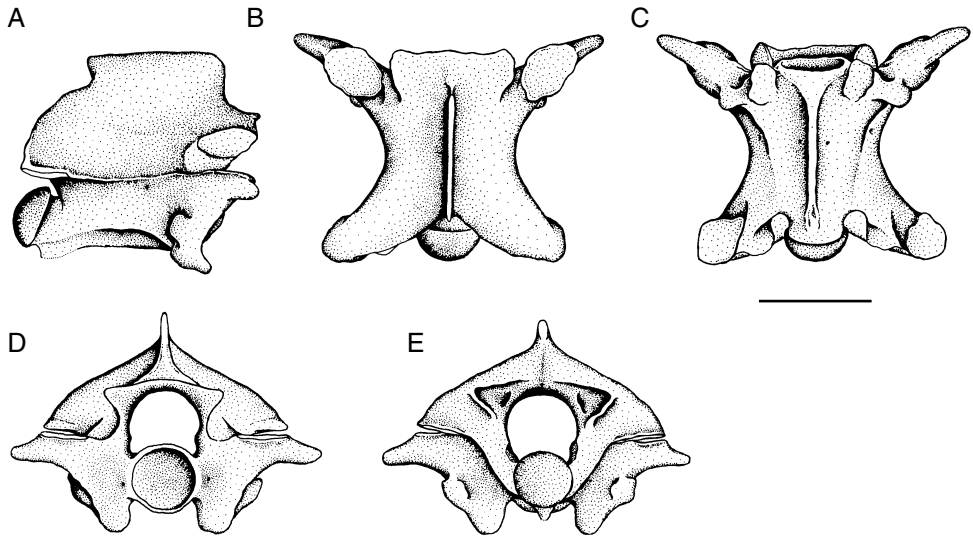


FIG. 7. — *Neonatrix* cf. *europaea* Rage & Holman, 1984 from the lower/middle (MN 4/5) Miocene of Vieux Collonges, trunk vertebra (FSL 368827); A, lateral view; B, dorsal view; C, ventral view; D, cranial view; E, caudal view. Scale bar: 2 mm.

sal view, the zygosphenal lip possesses well-developed lateral lobes, the median lobe is wide, thus, the cranial margin of the zygosphenon seems convex. In some cases, the median lobe is lacking and, therefore, the shape of the zygosphenal lip is variable. The prezygapophyseal articular surfaces are oval; the thin and pointed prezygapophyseal processes reach about half of the length of the prezygapophyseal surfaces. The neural spine is sharp. In ventral view, both the subcentral ridges and grooves are well-developed, they are distinct especially in the cranial part of vertebrae. In posterior trunk vertebrae these structures extend considerably caudally. The hypapophysis is distinct, narrow and short, the anterior keel expands triangularly in the cranial direction. The subcentral foramina are minute and situated mostly at the base of the hypapophysis. The postzygapophyseal articular surfaces are irregular or approximately drop-like. In cranial view, the neural arch is clearly vaulted, the neural canal is circular like the cotyle. The zygosphenal lip is slightly convex. Relatively deep depressions occur on each side of the cotyle, the small paracotylar foramina are situated in these depressions. The parapophyseal

processes are separated from the lateral margins of the cotyle by deep notches.

#### DISCUSSION

The genus *Neonatrix* represents a common representative of the subfamily Natricinae in the European Tertiary. At Vieux Collonges, the determination is very difficult because of the limited number of specimens; therefore, a secure assignment at species level is impossible. Recent investigations (Szyndlar unpubl.; see also Discussion about the morphotype Elapidae B) showed that a great amount of representatives of the family Elapidae, closely similar to small natricine snakes, appeared during the Neogene. The only distinguishing character is the relatively high neural spine in natricines. Unfortunately, the neural spine is often broken off at the base, therefore the assignment at the subfamilial level may be problematical. Therefore, some ophidian paleoherpetologists recommend (Szyndlar pers. comm. 1996) a denotation Natricinae indet. which is less precise but more accurate.

The vertebrae of the genus *Neonatrix* are characterised by the small dimensions and the short hypapophysis which does not reach the caudal

margin of the condyle. Three species of this genus have been discovered in the European Tertiary: *Neonatrix europaea* Rage & Holman, 1984, *N. crassa* Rage & Holman, 1984 (Rage & Holman 1984) and *N. nova* Szyndlar, 1987 (Szyndlar 1987). Remaining three species, *Neonatrix elongata* Holman, 1973, *N. magna* Holman, 1982 and *N. inferna* Holman, 1996 were discovered in the middle and the upper Miocene of Nebraska, Texas and South Dakota (Holman 1979, 1982, 1996). *N. cf. europaea* differs from *N. nova* in its smaller dimensions and the marked median lobe at the zygosphenal lip. Szyndlar (1987) also considers as distinguishing features the less vaulted neural arch and the rounded cotyle in *N. nova*. However, it is suggested that such features may also be seen in *N. europaea*. *N. cf. europaea* differs from *N. crassa* in the cranial margin of the zygosphenon which is convex in the first mentioned species. Contrary to the North American species *N. elongata* and *N. magna*, *N. cf. europaea* has a more developed hypapophysis and longer prezygapophyseal processes (Rage & Holman 1984). *N. inferna* differs from *N. cf. europaea* in the elongate vertebrae and the much more lower neural spine.

Genus *Natrix* Laurenti, 1768

*Natrix* aff. *sansaniensis* (Lartet, 1851)

*Natrix* aff. *sansaniensis*. — Ivanov 1997a: 102, fig. 47.

MATERIAL EXAMINED. — 2 trunk vertebrae (FSL 368830, FSL 368831).

#### DESCRIPTION

##### *Trunk vertebrae*

In lateral view, the neural spine is unusually high, almost as high as long. Its cranial margin overhangs anteriorly and the caudal margin overhangs caudally. The relatively sharp interzygapophyseal ridges are strikingly developed. The conspicuous lateral foramina are situated in shallow depressions. The subcentral ridges are considerably marked and they are arched dorsally. The para- and diapophyses are well-separated, the posterolaterally directed

diapophyses are about as large as the parapophyses. The parapophyseal processes are directed anteriorly. The broken off hypapophyses were distinct and deep. In dorsal view, the zygosphenal lip has distinct lateral lobes and a prominent median lobe, in anterior (rarely in posterior) trunk vertebrae the median lobe may be laterally expanded, thus the zygosphenal lip is almost convex. The prezygapophyseal articular surfaces are circular to oval, the antero-laterally directed prezygapophyseal processes are very long – at least as long as the prezygapophyseal surfaces. The dorsal border of the neural spine is usually expanded. The epizygapophyseal spines are prominent. In ventral view, the subcentral ridges are distinct, however the subcentral grooves are shallow. The subcentral foramina are minute and hardly visible. The anterior keel of the hypapophysis is triangular; very distinct subcotylar tubercles are developed at the ventral margin of the cotyle. The postzygapophyseal articular surfaces are irregularly shaped. In cranial view, the neural arch is weakly vaulted, the neural canal is circular and the zygosphenal lip is straight to slightly convex. The small paracotylar foramina are situated in prominent depressions on both sides of the rounded cotyle.

#### DISCUSSION

The described shape of the neural spine is characteristic for the genus *Natrix*. *N. sansaniensis* differs from all other *Natrix* species, living and extinct, in its very high neural spine (Szyndlar & Schleich 1993). The following extinct species of the genus *Natrix* have been reported: *Natrix mlynarskii* Rage, 1988 (MP 22) (Rage 1988), *Natrix sansaniensis* (Lartet, 1851) (?MN 4-MN 6) (Rage 1981; Szyndlar & Schleich 1993), *Natrix longivertebra* Szyndlar, 1984 (?MN 7+8-MN 16) (Szyndlar 1984, 1991a, b), *Natrix parva* Szyndlar, 1984 (Szyndlar 1984). The described species is closely related to “*Natrix* aff. *N. sansaniensis* (Lartet, 1851)” reported from the German lower Miocene (MN 4) locality Petersbuch 2 (Szyndlar & Schleich 1993). A denotation “aff.” has been used because of some morphological resemblance with the extinct species *N. mlynarskii* Rage, 1988 (Szyndlar & Schleich 1993).

## Natricinae A

Natricinae A – Ivanov 1997a: 117-119, fig. 52.

MATERIAL EXAMINED. — 3 cervical vertebrae (FSL 368832-FSL 368834), 32 trunk vertebrae (FSL 368835-FSL 368837; FSL 368838-FSL 368866).

## DESCRIPTION

*Cervical vertebrae (Fig. 8A-E)*

All preserved vertebrae are very fragmentary. Most likely, the broken off neural spines were originally high. In lateral view, the interzygapophyseal ridges are distinct and the epizygapophyseal spines are under-developed. The lateral foramina are small, but generally well visible and they are situated in shallow depressions. The subcentral ridges are distinct, long and slightly arched dorsally. The bases of the hypapophyses are wide; the hypapophyses were most probably relatively long, which is demonstrated by the long hypapophyses of trunk vertebrae. In dorsal view, the cranial margin of the fragmentary zygosphenes possesses distinct lateral lobes and a wide median lobe. The prezygapophyseal articular surfaces were originally oval; the prezygapophyseal processes are broken off. In ventral view, both the subcentral ridges and the wide subcentral grooves are well-developed, the subcentral foramina are minute and hardly visible. The hypapophysis is narrow and the anterior keel expands in the vicinity of the ventral margin of the cotyle. The small subcotylar tubercles are very distinct. The postzygapophyseal articular surfaces are irregular. In cranial view, the neural arch is prominently vaulted, the neural canal is circular (a large calibre documents subadult specimen) and the zygosphenal lip is convex. The minute paracotylar foramina occur in depressions on both sides of the rounded cotyle.

*Trunk vertebrae (Fig. 8F-J)*

In lateral view, the neural spine is about two times longer than high. The cranial margin of the neural spine clearly overhangs anteriorly, the caudal margin overhangs posteriorly. A dorsal expansion of the neural spine does not occur. The interzygapophyseal ridges are mostly well-

developed, however, they are not sharp. The epizygapophyseal spines are usually very indistinctly developed. Mostly well-visible lateral foramina are situated in shallow depressions. Both the subcentral ridges and grooves are less developed in anterior trunk vertebrae; in lateral view, they are almost straight. The hypapophysis is relatively long, straight and directed postero-ventrally. Its caudally directed distal tip is slightly rounded to pointed. Mostly damaged para- and diapophyses are well-separated from each other; the parapophyseal processes are short and directed antero-ventrally or anteriorly. In dorsal view, the lateral lobes of the zygosphenal lip are developed better than the wide median lobe which is often missing. Thus, the cranial margin of the zygosphenes may be concave. The prezygapophyseal articular surfaces are oval, rarely preserved prezygapophyseal processes are thin and pointed. In ventral view, both the subcentral ridges and the relatively wide subcentral grooves are well-developed. The subcentral foramina are often very small. The anterior keel of the hypapophysis expands clearly in cranial direction, the distinct subcotylar tubercles are developed under the ventral margin of the cotyle. In cranial view, the neural arch is vaulted, the neural canal is approximately circular with distinct lateral sinuses and the zygosphenal lip is straight or convex. The notches between parapophyseal processes and the lateral margins of cotyle are not deep, the paracotylar foramina occur on both sides of the cotyle in more or less developed depressions. The metrical measurements are as follows ( $n = 15$ ):  $cl: or = 3.83-4.95$ ;  $naw: or = 2.80-3.47$ ;  $cl/naw: or = 1.37-1.59$ , mean  $1.46 + 0.07$ .

## DISCUSSION

The presence of a high neural spine whose cranial margin is anteriorly overhanging, the distinct haemal keel and the lateral foramina situated in shallow depressions, support the assignment to the subfamily Natricinae. The distinct hypapophyses extending often behind the distal end of the condyle and the relatively large dimensions of the vertebrae exclude the assignment to the

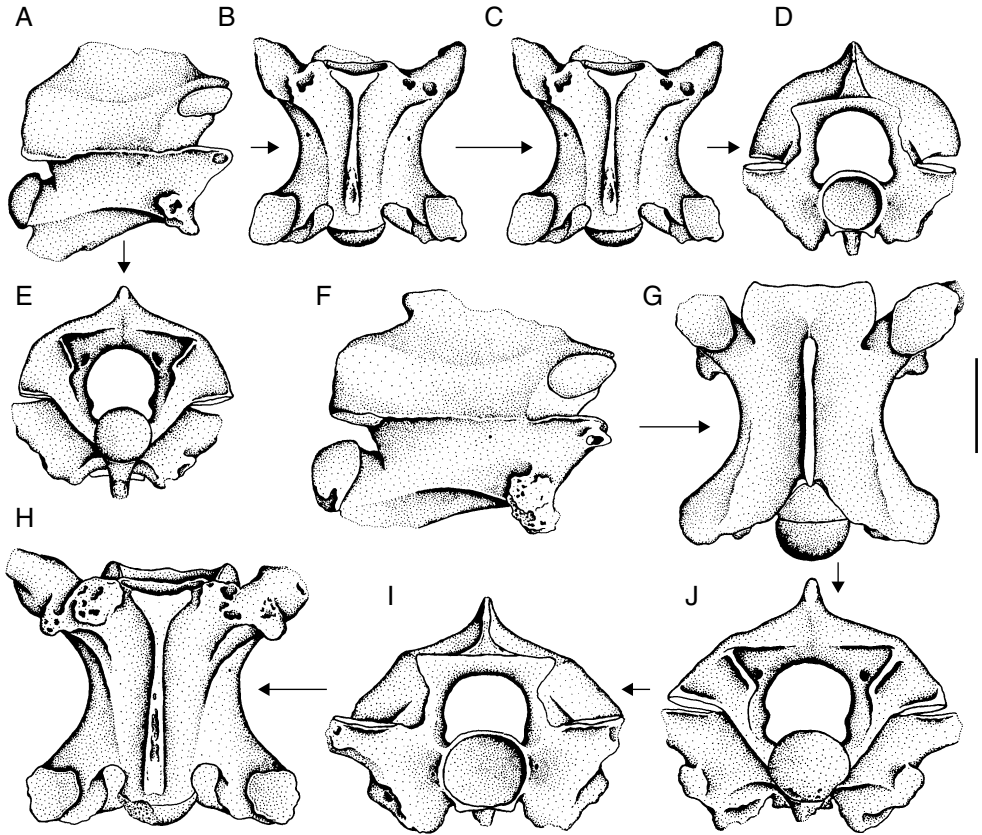


FIG. 8. — Natricinae A from the lower/middle (MN 4/5) Miocene of Vieux Collonges; **A-E**, cervical vertebra (FSL 368834); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E**, caudal view; **F-J**, trunk vertebra (FSL 368855); **F**, lateral view; **G**, dorsal view; **H**, ventral view; **I**, cranial view; **J**, caudal view. Scale bar: 2 mm.

genus *Neonatrix*. The shape of the relatively high neural spine and the shallow triangular anterior keel exclude the referral to the genus *Palaeonatrix* (Szyndlar in Młynarski *et al.* 1982; Szyndlar 1987). The morphotype Natricinae A most probably belongs to the genus *Natrix*, which is supported by the shape of the neural spine and the hypapophysis and by the dimensions of the vertebrae. The morphotype Natricinae A differs from the oldest representative – *Natrix młynarskii* Rage, 1988 (MP 22) – especially in the shape of the subcentral ridges which are straight in lateral view and slightly medially bent in ventral view (Rage 1988). It differs from *Natrix sansaniensis* (Lartet, 1851) in the lower neural spine and absence of blunt ridges extending from

the base of the neural spine to each prezygapophysis (Rage 1981). Rage (1984) assumes that the above mentioned ridges occur also in some living taxa. Szyndlar & Schleich (1993) consider the height of the neural spine as the crucial character for the affiliation to the extinct *Natrix sansaniensis* (Lartet, 1851). The morphotype Natricinae A differs from *Natrix longivertebrata* Szyndlar, 1984 in smaller dimensions, the lower ratio  $cl/naw$ , and pointed distal tip of the hypapophysis.

#### Natricinae B

Natricinae B – Ivanov 1997a : 119-120, fig. 53.

MATERIAL EXAMINED. — 2 trunk vertebrae (FSL 368867, FSL 368868).

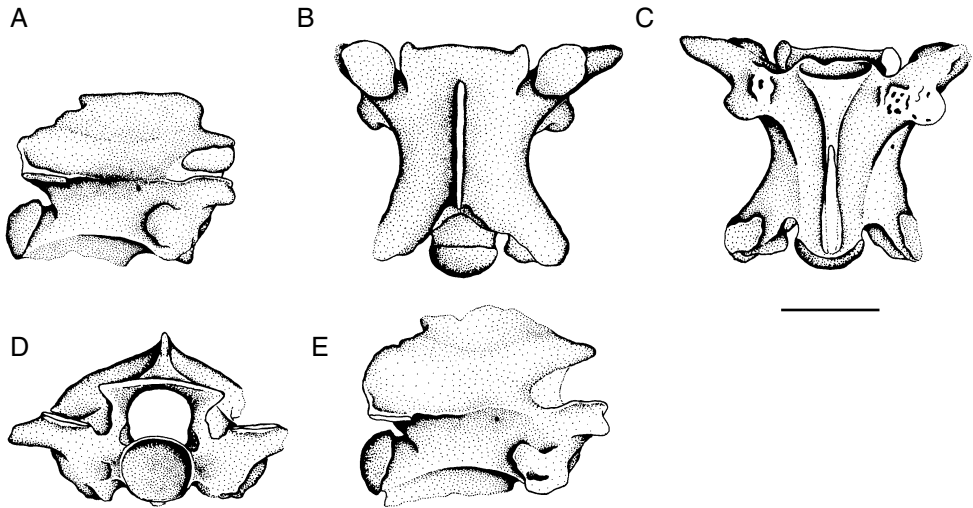


FIG. 9. — *Natricinae* B from the lower/middle (MN 4/5) Miocene of Vieux Collonges; **A-D**, posterior trunk vertebra (FSL 368867); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E**, posterior trunk vertebra (FSL 368868), lateral view. Scale bar: 2 mm.

#### DESCRIPTION

##### *Trunk vertebrae* (Fig. 9)

In lateral view, the neural spine is relatively low (the distinct subcentral ridges and grooves show that this specimen is most probably a posterior trunk vertebrae), its cranial margin overhangs anteriorly and the caudal margin overhangs caudally. The blunt interzygapophyseal ridges are well-developed. The subcentral ridges are long, only slightly arched dorsally. The hypapophysis is broken off in the vicinity of its base which is unusually wide in lateral view. The lateral foramina are distinct and large, in one vertebra the foramina occur in wide depressions. The para- and diapophyses are indistinctly separated, the damaged diapophyses were probably larger than the parapophyses. The damaged parapophyses were shifted under the vertebral centrum, the parapophyseal processes were most likely short. The aliform processes extend behind the caudal margin of the postzygapophyseal surfaces. In dorsal view, the vertebrae are characterised by the long and relatively narrow vertebral constriction. The zygosphenal lip possesses distinct lateral lobes, the median lobe does not protrude strikingly and is very wide. The prezygapophyseal articular surfaces are oval to subtriangular, the

prezygapophyseal processes reach about two-thirds of the length of the prezygapophyseal surfaces, they are pointed but relatively massively built. Epizygapophyseal spines are lacking. The diapophyses are directed clearly postero-laterally. In ventral view, the subcentral ridges are sharp, the subcentral grooves are prominently wide. The small subcentral foramina occur at the base of the hypapophysis. The hypapophysis is expanded proximally into a triangular anterior keel which is inclined antero-ventrally. The anterior keel is separated from the remaining hypapophysis by a prominent furrow. In cranial view, the neural arch is slightly vaulted, the neural canal is approximately circular and the zygosphenal lip is convex. The distinct paracotylar foramina are situated in deep depressions on either side of the rounded cotyle. The deep grooves between damaged parapophyseal processes and the margin of cotyle are separated from the depressions with paracotylar foramina by peculiar sharp bony bar. The subcotylar tubercles are lacking or very slightly developed. Metrical measurements: larger vertebra:  $cl = 4.72$ ;  $naw = 3.04$ ;  $cl/naw = 1.55$ ; smaller vertebra:  $cl = 4.37$ ;  $naw = 2.92$ ;  $cl/naw = 1.50$ .

## DISCUSSION

The morphotype Natricinae B is defined by the shape of the hypapophysis with prominent anterior keel, which is separated from the remaining hypapophysis by a considerable furrow. The hypapophysis was well-developed and probably relatively deep. This feature helps to distinguish the morphotype Natricinae B from the genus *Neonatrix*. However, it is impossible to recognize unambiguously whether Natricinae B belongs to *Palaeonatrix* or *Natrix*. The morphotype Natricinae B possesses the following features which are characteristic of the genus *Palaeonatrix*: 1) the hypapophysis markedly extend anteriorly as a keel; 2) the subcentral ridges are prominent (especially in one vertebra). Szyndlar (*in* Młynarski *et al.* 1982; Szyndlar 1987) mentioned that the neural spine of the genus *Palaeonatrix* is low, however, the study at the locality Petersbuch 2 (Szyndlar & Schleich 1993) showed that also high neural spines may occur in this genus. The morphotype Natricinae B is most similar to the species *Palaeonatrix silesiaca* Szyndlar, 1982 which is only known (Szyndlar *in* Młynarski *et al.* 1982) from the type locality Opole 2, Poland (MN 7). The morphotype Natricinae B differs from the extinct species of *Natrix* in the prominent anterior keel; thus, the Natricinae B differs from *Natrix longivertebrata* Szyndlar, 1984. From the species *Natrix mlynarskii* Rage, 1988 the morphotype Natricinae B differs also in the considerably narrow constriction between the prezygapophyses and the postzygapophyses. The Natricinae B differs from *Natrix sansaniensis* (Lartet, 1851) in the much more lower neural spine – it is about two to three times longer than high. The morphotype Natricinae B differs from the Natricinae A in indistinct subcotylar tubercles. The anterior keel of the hypapophysis is separated from the remaining hypapophysis by a considerable furrow – this feature makes the Natricinae B distinguishable from all remaining morphotypes (Natricinae A, C & D).

## Natricinae C

Natricinae C – Ivanov 1997a: 120, fig. 54.

MATERIAL EXAMINED. — 24 trunk vertebrae (FSL 368869-FSL 368891).

## DESCRIPTION

*Trunk vertebrae*

In lateral view, the neural spine is about two times longer than high, its cranial margin overhangs slightly anteriorly, the posterior overhanging is considerable. The largest vertebrae have the top of neural spine very slightly expanded laterally. The interzygapophyseal ridges are distinct but blunt. Well-perceptible lateral foramina are situated within wide and deep depressions. The subcentral ridges are straight to arched slightly dorsally. The ventral margin of the peculiar hypapophysis is not straight (Ivanov 1997a: fig. 54A), the distal end of the hypapophysis is rounded and directed caudally. The para- and diapophyses are well-separated from each other, the parapophyses are nearly as large as the diapophyses. The parapophyseal processes are short and directed anteriorly rather than antero-ventrally. In dorsal view, the cranial margin of the zygosphene is mostly concave to straight, rarely a wide median lobe may occur. The prezygapophyseal articular surfaces are obovate, the prezygapophyseal processes are not preserved. The epizygapophyseal spines are slightly developed. In ventral view, both the subcentral ridges and grooves are well-developed only in the posterior trunk vertebrae, in the middle trunk vertebrae these structures are not so distinct. The subcentral foramina, situated at the base of the gracile hypapophysis, are minute and hardly perceptible. Subcotylar tubercles often occur on the ventral margin of the cotyle. The postzygapophyseal articular surfaces are irregular. In cranial view, the neural arch is more or less vaulted and the neural canal is rounded with small lateral sinuses. The zygosphenal lip is convex. The parapophyseal processes are separated from the cotyle by shallow furrows. The paracotylar foramina are situated in deep or shallow depressions. The metrical measurements are as follows ( $n = 8$ ): cl/or = 3.54-4.90; naw/or = 2.25-3.40; cl/naw/or = 1.38-1.63, mean 1.50 + 0.10.

## DISCUSSION

Although low (rarely high) neural spine of most vertebrae is broken off at the base, it may be observed that its cranial margin overhangs ante-



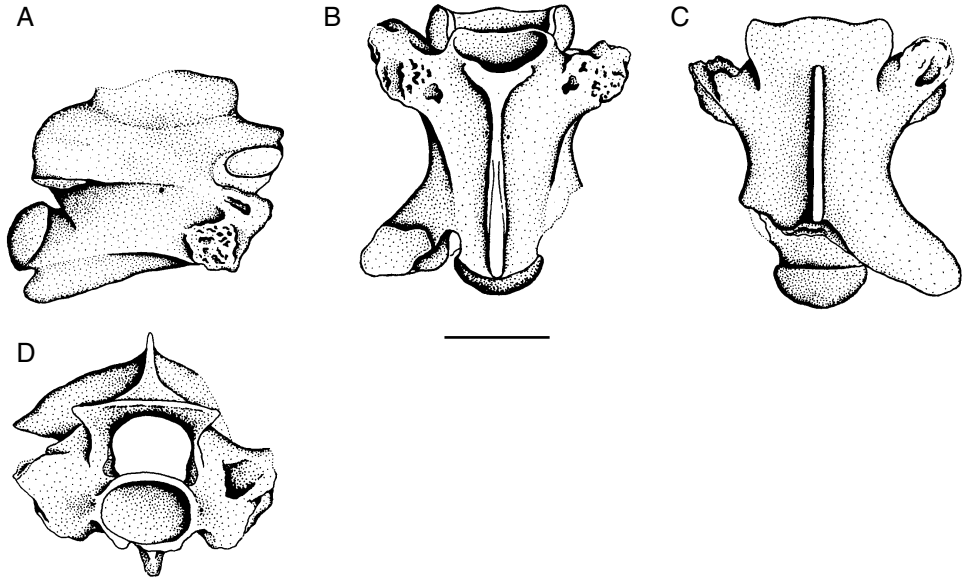


FIG. 10. — Natricinae D from the lower/middle (MN 4/5) Miocene of Vieux Collonges, trunk vertebra (FSL 368894); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view. Scale bar: 2 mm.

riorly, the caudal margin overhangs posteriorly. This is the most important criterion for the affiliation to the subfamily Natricinae. Based on the height of the neural spine, it is assumed that the Natricinae C may belong to the genus *Natrix*. However, a peculiar shape of the hypapophysis distinguishes the morphotype Natricinae C from all known representatives of the genus *Natrix*. Regarding the extinct genus *Neonatrix*, the morphotype Natricinae C somewhat resembles the new species of this genus from the middle Miocene (MN 6) of the French locality Sansan (Rage pers. comm. 1996; Augé & Rage 2000). However, the shape of the hypapophysis is similar to only one vertebra (Augé & Rage 2000: fig. 25A), while the other vertebrae differ considerably in the shape of the hypapophysis. Moreover, the vertebrae of the new species of *Neonatrix* (Augé & Rage 2000) are smaller than those of Natricinae C. The Natricinae C differs from the Natricinae A in the following features: 1) the hypapophysis is not straight; 2) the lateral sinuses of the neural canal are small and indistinct. Due to the quite different shape of the hypapophysis, without furrow separating

the anterior keel from the remaining hypapophysis, the Natricinae C differs from the Natricinae B.

#### Natricinae D

Natricinae D – Ivanov 1997a: 122, fig. 55.

MATERIAL EXAMINED. — 4 trunk vertebrae (FSL 368892-FSL 368895).

#### DESCRIPTION

##### *Trunk vertebrae* (Fig. 10)

In lateral view, the neural spine is about four times longer than high; its cranial margin overhangs anteriorly, the caudal margin is broken off in all vertebrae. The interzygapophyseal ridges are slightly developed; the small lateral foramina do not open in depressions. The subcentral ridges are straight to weakly arched dorsally. The relatively straight and short hypapophysis is directed caudally; its distal termination is pointed or slightly rounded. The synapophyses are very damaged, the para- and diapophyses were most likely well-separated from each other. The anteriorly directed parapophyseal processes are short. The condyle is situ-

ated on a short neck. In dorsal view, the zygosphenal lip generally possesses distinct lateral lobes and the wide median lobe is slightly developed. The prezygapophyseal articular surfaces are obovate to subtriangular, the prezygapophyseal processes are relatively short, heavily built and pointed. The epizygapophyseal spines are underdeveloped. In ventral view, the hypapophysis is sharp, its anterior keel expands anteriorly. The blunt subcentral ridges are well developed; the subcentral grooves are wide and more distinct in the cranial part of vertebrae. The subcotylar tubercles are absent or very slightly developed. The subcentral foramina are very small. In cranial view, the neural arch is slightly vaulted, the neural canal is subcircular and the zygosphenal lip is convex. The parapophyseal processes are separated from the cotyle by relatively deep furrows. The conspicuous paracotylar foramina are situated on both sides of the rounded to dorso-ventrally slightly flattened cotyle. The measurements of vertebrae are as follows ( $n = 4$ ):  $cl/or = 3.33-4.37$ ;  $naw/or = 2.32-2.80$ ;  $cl/naw/or = 1.42-1.56$ , mean  $1.48 \pm 0.06$ .

#### DISCUSSION

The vertebrae of the morphotype *Natricinae D* are characterised by both the relatively high neural spine and straight as well as short hypapophysis. The *Natricinae D* resembles especially some representatives of the genus *Neonatrix*. The *Natricinae D* differs from the morphotypes *Natricinae A, B & C* in the straight and short hypapophysis. A more precise determination was not possible because of damaged neural spines, synapophyses and broken off prezygapophyseal processes.

Family ELAPIDAE Boié, 1827  
Genus *Micrurus* Wagler, 1824

*Micrurus* aff. *gallicus* Rage & Holman, 1984

*Micrurus* cf. *gallicus* – Rage & Holman 1984: 99.  
*Micrurus* aff. *gallicus* – Ivanov 1997a: 129, fig. 59.

MATERIAL EXAMINED. — 1 trunk vertebra (FSL 369450).

#### DESCRIPTION

##### *Trunk vertebra (Fig. 11)*

In lateral view, the neural spine is low, both the cranial and caudal margins overhang caudally. The interzygapophyseal ridges are slightly developed. The lateral foramina are small and not situated in depressions. The subcentral ridges are prominent, extending from the synapophyses to the proximal margin of the condyle. Both the para- and diapophyses are broken off at the base. The hypapophysis is damaged, without its distal tip. In dorsal view, the zygosphenal lip is very wide, thus, the zygosphenal lip is more convex than crenate. The prezygapophyseal articular surfaces are oval, the prezygapophyseal processes are broken off at the base. Epizygapophyseal spines are missing. In ventral view, the hypapophysis extends cranially to the basis of the cotyle where it forms a small and wide tubercle. Both the subcentral ridges and wide subcentral grooves are distinct. The subcentral foramina are very small, located at the base of the hypapophysis. The postzygapophyseal articular surfaces are roughly rounded to irregularly shaped. In cranial view, the neural arch is moderately and regularly vaulted; the neural canal is circular with wide lateral sinuses. The zygosphenal lip is convex. On both sides of the rounded cotyle are situated paracotylar foramina in wide depressions. In caudal view, the postzygapophyseal articular surfaces are tilted upward, the zygantral area is relatively wide. The relatively small condyle is rounded. Small parazygantral foramina are situated above the postzygapophyseal surfaces. The measurements of vertebra are as follows:  $cl = 3.02$ ;  $naw = 2.05$ ; width between prezygapophyses ( $pr-pr$ ) = 3.57; width between postzygapophyses ( $po-po$ ) = 3.40; distance between pre- a postzygapophyses ( $pr-po$ ) = 3.47; zygosphenal width ( $zw$ ) = 1.73; height of cotyle ( $cth$ ) = 1.09; width of cotyle ( $ctw$ ) = 1.23.

#### DISCUSSION

The vertebra was originally referred to as *Micrurus* cf. *gallicus* by Rage & Holman (1984),

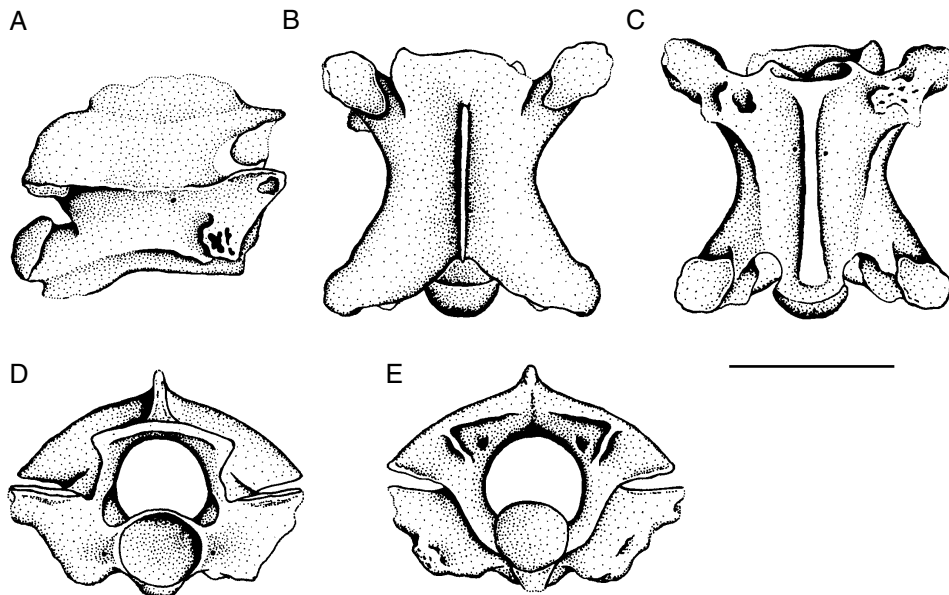


FIG. 11. — *Micrurus* aff. *gallicus* Rage & Holman, 1984 from the lower/middle (MN 4/5) Miocene of Vieux Collonges, trunk vertebra (FSL 369450); A, lateral view; B, dorsal view; C, ventral view; D, cranial view; E, caudal view. Scale bar: 2 mm.

however, without precise description and depiction. The vertebra belongs most probably to a small representative of the family Elapidae on the basis of the low neural spine overhanging posteriorly and the presence of a hypapophysis. Most likely, it represents an adult individual having small dimensions – small diameter of the neural canal, which is as wide as the cotyle (without lateral sinuses). Therefore, the vertebra is assigned to the genus *Micrurus*. The vertebra is very similar to the extinct species *Micrurus gallicus* reported originally from the French locality La Grive M (MN 7) (Rage & Holman 1984). *M. aff. gallicus* from Vieux Collonges differs from *M. gallicus* in the following features: 1) the subcentral ridges are better developed in *M. aff. gallicus* but this character may be explained by the fact that this vertebra is a posterior trunk one; 2) in cranial view, the zygospheal lip of *M. aff. gallicus* is convex while in known representatives of *M. gallicus* it is straight; 3) *M. aff. gallicus* has a small distinct tubercle developed on the ventral margin of the cotyle. In case of *M. gallicus* this tubercle is absent. A denotation “aff.” reflected small mor-

phological differences between *M. aff. gallicus* and *M. gallicus*.

Genus *Naja* Laurenti, 1768

*Naja* cf. *romani* (Hoffstetter, 1939)

Part – *Palaeonaja romani*. — Rage 1984: 54.  
Part – *Naja* cf. *N. romani* (Hoffstetter, 1939). — Szyndlar & Rage 1990: 387, fig. 1.  
*Naja* sp. 1 – Ivanov 1997a: 130-131, fig. 60.

MATERIAL EXAMINED. — 2 cervical vertebrae (FSL 369104, FSL 369105), 35 trunk vertebrae (FSL 369106-FSL 369115, FSL 369116-FSL 369140).

#### DESCRIPTION

##### *Cervical vertebrae* (Fig. 12A-D)

The vertebrae have short and wide vertebral centra. In lateral view, the neural spine is lower than long, its cranial margin is almost vertical or overhangs slightly posteriorly, the caudal margin overhangs posteriorly. The interzygapophyseal ridges are prominent, the distinct lateral foramina are situated in deep depressions below the

interzygapophyseal ridges. The subcentral ridges are considerably developed, extending from the synapophyses to the proximal margin of the condyle. The heavily built hypapophysis is long and directed postero-ventrally. Unfortunately, its distal tip is broken off. The para- and diapophyses are well-separated from each other, the postero-laterally directed diapophyses are approximately as large as the parapophyses. The parapophyseal processes are short, directed anteriorly rather than antero-ventrally. In dorsal view, the zygosphenal lip is concave or straight (however, it may be possible that the cranial margin of the zygosphenon was most likely damaged). The damaged prezygapophyseal articular surfaces were probably suborbicular, the prezygapophyseal processes are broken off at the base. Epizygapophyseal spines are indistinct. In ventral view, subcotylar tubercles occur on the ventral margin of the cotyle. Both the subcentral ridges and wide subcentral grooves are well developed, the subcentral foramina are small. The postzygapophyseal articular surfaces are roughly rounded. In cranial view, the neural arch is vaulted and the subcircular neural canal has distinct lateral sinuses. The zygosphenal lip is slightly convex. The paracotylar foramina are situated in deep and wide depressions on both sides of the rounded cotyle.

#### *Trunk vertebrae (Fig. 12E-I)*

The vertebrae are characterised by the relatively short and wide centra, which is a typical feature of the large colubrids. In lateral view, the neural spine is somewhat lower than long. The cranial margin of the neural spine is almost vertical, the caudal margin overhangs posteriorly. The interzygapophyseal ridges are prominent. The lateral foramina are distinct and situated in deep wide depressions. The subcentral ridges are straight or weakly arched dorsally. Epizygapophyseal spines are under-developed. The para- and diapophyses are not distinct from each other, the parapophyses are as large as the diapophyses or somewhat larger. The parapophyseal processes are relatively long and directed anteriorly rather than antero-ventrally. The hypapophyses are broken off at the base. In dorsal view, the zygosphenal lip is concave to

straight (in many vertebrae a mechanical damage is possible), the prezygapophyseal articular surfaces are wide and oval to suborbicular, the fragmentary prezygapophyseal processes are heavily built and relatively long. Dorsal expansion of the neural spine has not been noticed. In ventral view, the prominent subcentral ridges and the deep subcentral grooves are visible. Both structures are best developed in posterior trunk vertebrae. The subcentral foramina are small and difficult to recognise. The parapophyseal processes are obtuse. The hypapophysis is gracile, the anterior keel expands near the ventral margin of the cotyle. The subcotylar tubercles are often developed. The postzygapophyseal articular surfaces are irregularly shaped. In cranial view, the neural arch is moderately arched, the neural canal is circular with short lateral sinuses, the zygosphenal lip is straight to concave. The shallow furrows separating the parapophyseal processes from the rounded cotyle are narrowed by the subcotylar tubercles. The paracotylar foramina are situated at the inner margins of deep depressions on both sides of the cotyle. The metrical measurements are as follows ( $n = 11$ ):  $cl: or = 6.21-8.75$ ;  $naw: or = 5.09-8.25$ ;  $cl/naw: or = 1.01-1.28$ , mean  $1.13 \pm 0.09$ .

#### DISCUSSION

The discovered vertebrae belong to a typical representative of the family Elapidae. The vertebrae are relatively large with a low ratio  $cl/naw$  and have a flattened and wide vertebral centra. Therefore, the vertebrae are assigned to the genus *Naja*. Three species of large cobras have been discovered in the European Cenozoic: *Naja romani* (Hoffstetter, 1939), *Naja iberica* Szyndlar, 1985 and "*Naja* (?) *depereti* (Hoffstetter, 1939)". The last known species – *Naja antiqua* Rage, 1976 has been reported from the middle Miocene (MN 7) of Beni Mellal in Morocco (Rage 1976). The vertebrae of *Naja* cf. *romani* are most similar to the species *N. romani* and especially to the material from the Austrian locality Kohfidisch (MN 11) originally (Bachmayer & Szyndlar 1985) assigned to the extinct species *Naja austriaca*. The species *Naja austriaca* was established especially because of the

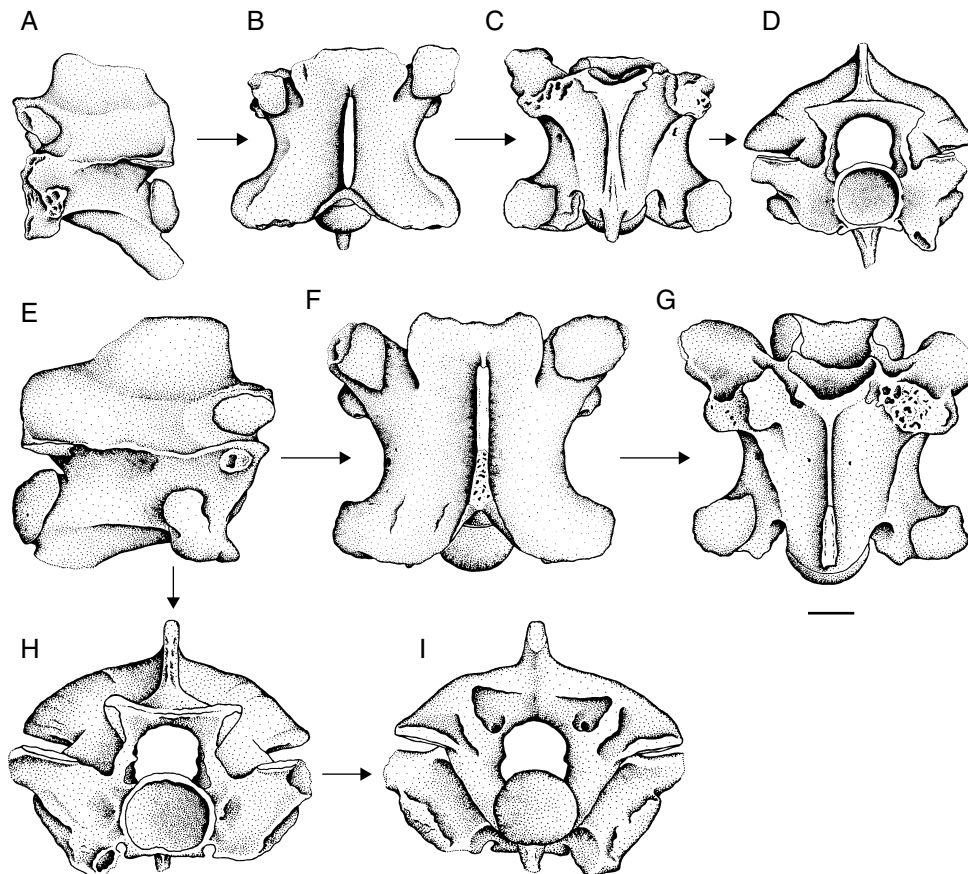


FIG. 12. — *Naja* cf. *romani* from the lower/middle (MN 4/5) Miocene of Vieux Collonges; **A-D**, cervical vertebra (FSL 369105); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E-I**, trunk vertebra (FSL 369113); **E**, lateral view; **F**, dorsal view; **G**, ventral view; **H**, cranial view; **I**, caudal view. Scale bar: 2 mm.

shape of the zygosphenal lip which is concave (cervical and trunk vertebrae) to crenate with three distinct lobes (posterior trunk vertebrae). The study of some East European localities (including Gritsev, Ukraine) showed that intraspecific variability has existed within the described snakes; therefore, *N. austriaca* was synonymised with *N. romani* (Szyndlar & Zerova 1990). The vertebrae of *Naja* cf. *romani* resemble *Naja romani* from Kohfidisch not only in the shape of the zygosphenal lip but also in the vertical cranial margin of the neural spine. *N. cf. romani* differs from the recent representatives of the Asiatic cobras — *N. naja* (Linnaeus, 1758) (ZZSiD 358), *N. spu-*

*atrix* (Boié, 1827) (ZZSiD 470) and *N. oxiana* (Eichwald, 1831) (ZZSiD 474) — in the lower neural spine and the longer prezygapophyseal processes (Szyndlar 1991a).

#### *Naja* sp. 1

Part — *Palaeonaja romani* Hoffstetter, 1939. — Rage 1984: 54.

Part — *Naja* cf. *N. romani* (Hoffstetter, 1939). — Szyndlar & Rage 1990: 387, fig. 1.

*Naja* sp. 2 — Ivanov 1997a: 132-134, fig. 61.

MATERIAL EXAMINED. — 4 cervical vertebrae (FSL 369141-FSL 369144), 52 trunk vertebrae (FSL 369145-FSL 369177, FSL 369178-FSL 369196).

## DESCRIPTION

*Cervical vertebrae (Fig. 13A-D)*

In lateral view, the neural spine is lower than long, both its cranial and caudal margins are inclined posteriorly. A dorsal expansion of the neural spine is not observed. The distal tip of the hypapophyses is broken off; fragmentary hypapophyses are directed postero-ventrally. The interzygapophyseal ridges are short but distinct. The lateral foramina situated in relatively deep depressions are well visible. In dorsal view, the vertebral centrum is narrow, the cranial margin of the damaged zygosphenes exhibits originally weakly developed lateral lobes and the median lobe. The prezygapophyseal articular surfaces are oval to subtriangular. Epizygapophyseal spines are well-developed. In ventral view, both the subcentral ridges and grooves are relatively well-developed, the subcentral foramina are distinct. The postzygapophyseal articular surfaces are irregularly shaped. In cranial view, the zygosphenal lip is considerably convex, the neural canal is circular with small lateral sinuses. Small subcotylar tubercles occur under the ventral margin of the cotyle. The paracotylar foramina, situated in marked depressions, are distinct and close to the lateral margins of the cotyle. In caudal view, the zygantral area is gracile, the condyle is rounded.

*Trunk vertebrae (Fig. 14E-I)*

The vertebrae are characterised by the relatively short and wide vertebral centra, similar features exhibit representatives of the large colubrids. In lateral view, the neural spine is about two to three times lower than long. The cranial margin of the neural spine overhangs anteriorly, the caudal margin is inclined posteriorly. The interzygapophyseal ridges are mostly well-developed. The lateral foramina occur in wide and sometimes deep depressions, the subcentral ridges are distinct, rounded and often almost straight. The para- and diapophyses are well-separated from each other, the relatively long parapophyseal processes are directed anteriorly. The parapophyses and postero-laterally directed diapophyses are comparative in size. In dorsal

view, the zygosphenal lip has prominent lateral lobes, while the median lobe is wide. The prezygapophyseal articular surfaces are roughly oval, the prezygapophyseal processes are long and weakly pointed. Epizygapophyseal spines are missing or under-developed. In ventral view, the subcentral ridges are rounded, the subcentral grooves are distinct (in the posterior trunk vertebrae they are very deep). The subcentral foramina are minute and hardly visible. The anterior keel of the hypapophysis expands in the vicinity of the ventral margin of the cotyle, occasionally it can be developed as distinct subcotylar tubercles. The postzygapophyseal articular surfaces are damaged. In cranial view, the neural arch is often weakly vaulted, the neural canal is subcircular with short lateral sinuses. The parapophyseal processes are separated from the lateral margins of the cotyle by narrow furrows. The paracotylar foramina are situated mostly in deep depressions. The metrical measurements are as follows ( $n = 10$ ):  $cl/or = 5.87-7.32$ ;  $naw/or = 4.37-6.25$ ;  $cl/naw/or = 1.04-1.49$ , mean  $1.29 \pm 0.13$ .

## DISCUSSION

The vertebrae belong to large representatives of the family Elapidae. The vertebrae have low ratio  $cl/naw$  and the trunk vertebrae have low neural spine which distinguishes *Naja* sp. 1 from the recent representatives of the genus *Naja*. Moreover, the lateral foramina occur in deep and wide depressions. *Naja* sp. 1 resembles *N. romani* from Kohfidisch (Bachmayer & Szyndlar 1985: fig. 5) in the shape and the length of the prezygapophyseal processes and resembles *N. romani* from Petersbuch 2 (Szyndlar & Schleich 1993: fig. 7F) in the shape of the zygosphenal lip; in *N. depereti* the lateral lobes of the zygosphenes are under-developed (Bachmayer & Szyndlar 1985). *Naja* sp. 1 resembles *N. iberica* in the ratio  $cl/naw$  (in *N. iberica* the vertebrae are relatively narrower than in *N. romani* [Szyndlar 1985]) and the length of the prezygapophyseal processes; however, the processes in *Naja* sp. 1 seem to be somewhat longer. *Naja* sp. 1 differs from *Naja romani* in the following features: 1) the relatively narrow-

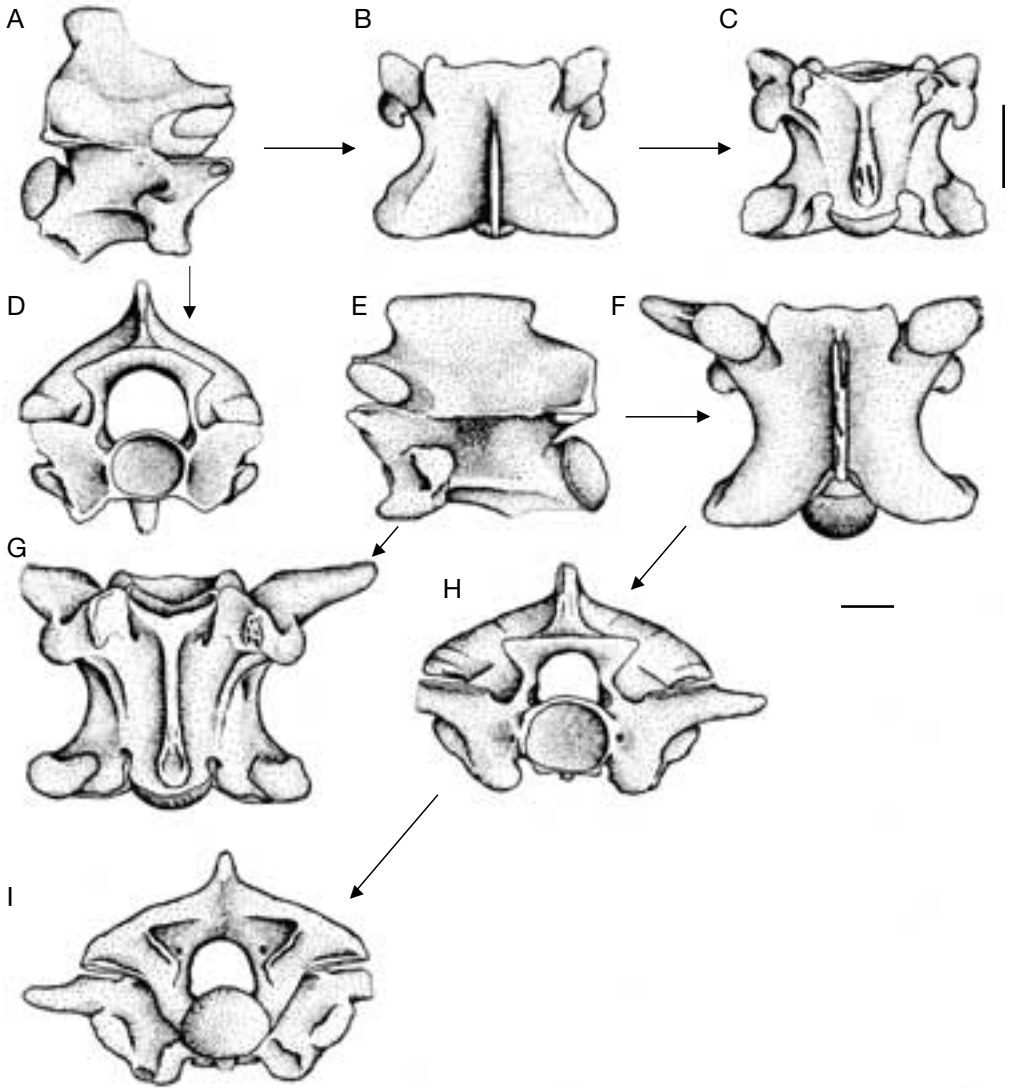


FIG. 13. — *Naja* sp. 1 from the lower/middle (MN 4/5) Miocene of Vieux Collonges; **A-D**, cervical vertebra (FSL 369144); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E-I**, trunk vertebra (FSL 369178); **E**, lateral view; **F**, dorsal view; **G**, ventral view; **H**, cranial view; **I**, caudal view. Scale bars: 2 mm.

er vertebrae in *Naja* sp. 1; 2) the anterior margin of the neural spine is clearly inclined anteriorly in *Naja* sp. 1 while in *Naja romani* it is almost vertical. Concerning the recent representatives of the genus *Naja*, the Asiatic members of this genus are characterised by the relatively narrower vertebral centres, especially *N. sputatrix* (ZZSiD 470), in contrast to the African members – *N. haje*

(Linnaeus, 1758) (ZZSiD 491) and *N. nigricollis* Reinhardt, 1843 (ZZSiD 492).

#### Elapidae A

Elapidae A – Ivanov 1997a: 134-135, fig. 62.

MATERIAL EXAMINED. — 2 trunk vertebrae (FSL 369197, FSL 369198).

## DESCRIPTION

*Trunk vertebrae*

In lateral view, the neural spine is very low with vertical margins. The interzygapophyseal ridges are prominently developed, the lateral foramina are situated in deep depressions. The para- and the diapophyses are clearly separated, the diapophysis is strikingly smaller than the parapophysis. The parapophyseal processes are short. The subcentral ridges are strongly developed and arched dorsally. The hypapophysis is very short, its distal tip is situated closely near the proximal margin of the condyle; in the posteriormost vertebrae the hypapophysis can be bifurcated (FSL 369198). The condyle is borne by a short neck. In dorsal view, the cranial margin of the zygosphenon has distinct lateral lobes, the strongly damaged median lobe was originally distinct and wide. The prezygapophyseal articular surfaces are obovate, the short prezygapophyseal processes are pointed. Epizygapophyseal spines are missing. In ventral view, both the subcentral ridges and grooves are noticeably developed. The subcentral foramina are shifted anteriorly at the basis of wide hypapophysis. The minute subcotylar tubercles are developed in one vertebra (FSL 369197). The postzygapophyseal articular surfaces are obovate. In cranial view, the neural arch is vaulted, the neural canal is circular with lateral sinuses at the ventral margin; the zygosphenal lip is convex. Distinct nerve foramina may be seen at the bases of the prezygapophyseal processes. The large paracotylar foramina are situated in depressions on either side of the rounded cotyle.

## DISCUSSION

The vertebrae of the morphotype Elapidae A are characterised by the following features: 1) the very small dimensions; 2) the very low neural spine; 3) the vaulted neural arch; 4) short parapophyseal processes directed anteriorly. The vertebrae belong most likely to small representatives of cobras. The morphotype Elapidae A resembles extinct species *Micrurus gallicus* Rage & Holman, 1984 because of the elongated centra of vertebrae, the shape of the zygosphenon and the rela-

tively shallow caudal notch. The hypapophysis is directed caudally, however, in *M. gallicus* the hypapophysis is shorter. The most visible difference is the very low and indistinct neural spine in the morphotype Elapidae A; in the case of *M. gallicus* the low neural spine is distinctly developed (Szyndlar & Schleich 1993). Moreover, Elapidae A is characterised by shorter prezygapophyseal processes.

## Elapidae B

Elapidae B – Ivanov 1997a: 135-137, fig. 63.

MATERIAL EXAMINED. — 17 trunk vertebrae (FSL 369199-FSL 369208, FSL 369209-FSL 369215).

## DESCRIPTION

*Trunk vertebrae (Fig. 14)*

In lateral view, the neural spine is very low, the cranial margin of the neural spine does not overhang anteriorly, the caudal margin is vertical. The interzygapophyseal ridges are mostly well-developed, the small lateral foramina are not situated in depressions. The distinct subcentral ridges are clearly arched dorsally. The relatively straight and very short hypapophysis is directed caudally. Its distal tip is pointed or slightly rounded. The para- and diapophyses are well-separated from each other and the diapophyses are about as large as the parapophyses. Viewing dorsally, the diapophyses are directed posterolaterally. The parapophyseal processes are short and directed anteriorly. The condyle is situated on a short neck. In dorsal view, the zygosphenal lip exhibits distinct lateral lobes, the wide median lobe is often damaged. The damaged prezygapophyseal articular surfaces were originally most probably oval, the broken off prezygapophyseal processes were probably short. Epizygapophyseal spines are lacking. In ventral view, the hypapophysis is sharp and its anterior keel expands near the cotyle. The rounded subcentral ridges are often prominent, the subcentral grooves are wide and deep only in the cranial part of vertebrae. The small subcotylar tubercles are present. The subcentral foramina are minute. In cranial view, the neural arch is



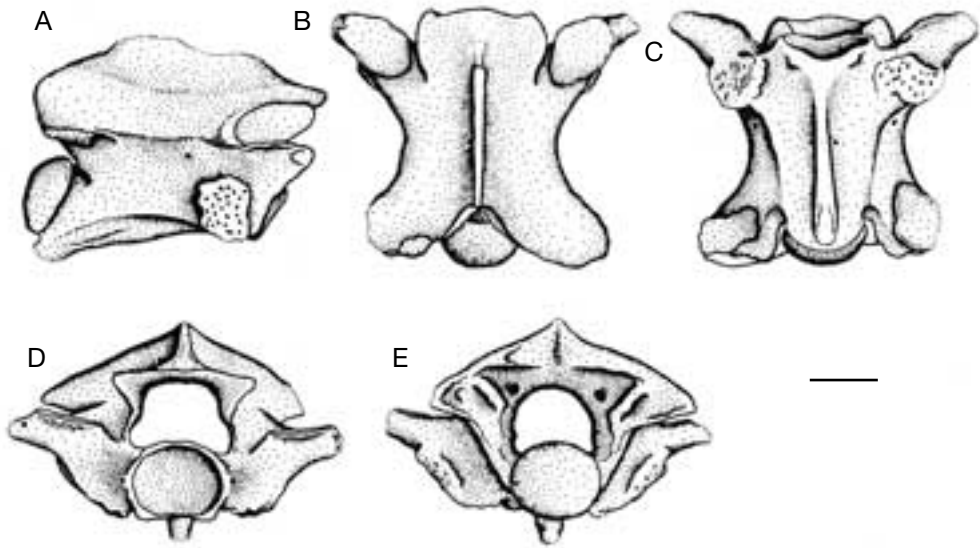


FIG. 14. — Elapidae B from the lower/middle (MN 4/5) Miocene of Vieux Collonges, trunk vertebra (FSL 369214); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E**, caudal view. Scale bar: 2 mm.

more or less vaulted with the circular neural canal and the convex zygosphenal lip. The parapophyseal processes are separated from the cotyle by relatively shallow furrows. The prominent paracotylar foramina occur within deep depressions at both sides of the cotyle which is rounded to weakly flattened dorso-ventrally. The measurements of the largest vertebrae are as follows ( $n = 8$ ):  $cl: or = 4.35-6.71$ ;  $naw: or = 2.98-4.53$ ;  $cl/naw: or = 1.42-1.50$ , mean  $1.47 + 0.03$ .

#### DISCUSSION

The vertebrae have considerably elongated vertebral centra, thus at the first sight, they may suggest representatives of the subfamily Natricinae, especially *Natrix* or *Neonatrix*, rather than elapids. However, these two genera are characterised by the markedly higher neural spine and smaller dimensions (*Neonatrix*). The vertebrae of the morphotype Elapidae B are relatively large. They are assigned to the family Elapidae on the basis of the occurrence of hypapophyses in trunk vertebrae and as well as on the basis of the low neural spine. Based on the shape of the

neural spine, the vertebrae belong most probably to the genus *Naja*. Because of the high ratio  $cl/naw$ , it is assumed that the vertebrae probably belong to the representatives of the Asiatic rather than African cobras. The morphotype Elapidae B differs from the Elapidae A in: 1) the larger dimensions of vertebrae; 2) the higher neural spine.

Family VIPERIDAE Oppel, 1811  
Subfamily VIPERINAE Oppel, 1811

“European vipers” group  
“*aspis* complex”

Viperinae A

Viperinae A – Ivanov 1997a: 147, fig. 68.

MATERIAL EXAMINED. — 12 trunk vertebrae (FSL 369451-FSL 369462).

#### DESCRIPTION

*Trunk vertebrae* (Fig. 15)

All vertebrae are fragmentary. In lateral view, the neural spine is relatively low (about three times longer than high). Both its cranial and caudal

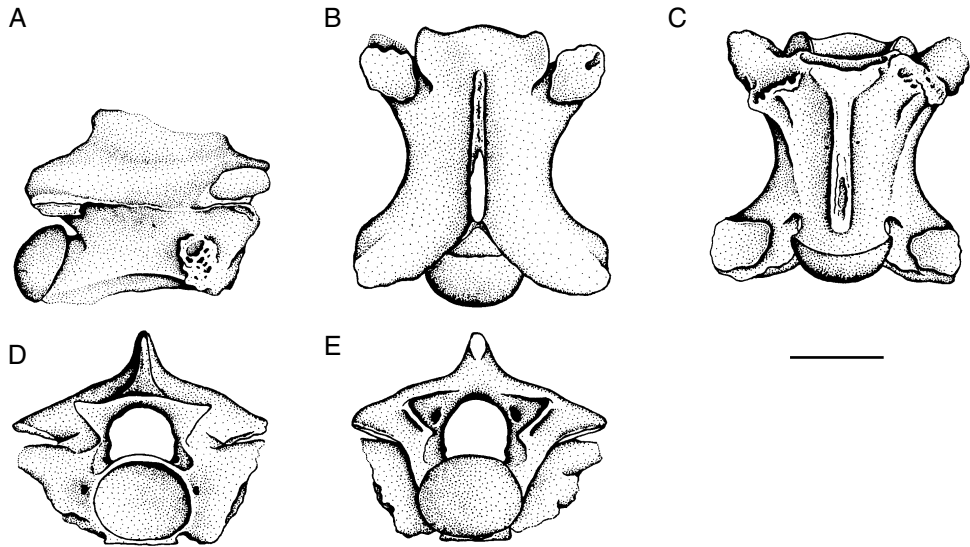


FIG. 15. — *Viperinae A* from the lower/middle (MN 4/5) Miocene of Vieux Collonges, trunk vertebra (FSL 369457); **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, cranial view; **E**, caudal view. Scale bar: 2 mm.

margins are inclined caudally. The interzygapophyseal ridges are conspicuous. Small but distinct lateral foramina may occur in shallow depressions. The subcentral ridges are well-developed. The para- and diapophyses, mostly broken off, are well-separated from each other. The parapophyseal processes are directed distinctly antero-ventrally. The hypapophyses are broken off at the base. In dorsal view, the zygosphenal lip is generally crenate with distinct lateral and median lobes, the zygosphenon is not usually straight. The damaged prezygapophyseal articular surfaces were most probably oval, the prezygapophyseal processes are always broken off at the base. Epizygapophyseal spines are lacking. The condyle is considerably large. In ventral view, the anterior keel of the hypapophysis expands triangularly, distinct subcotylar tubercles occur below the ventral margin of the cotyle in some cases. The subcentral ridges are mostly not prominent, the subcentral grooves are wide and very shallow. The subcentral foramina are well-visible and situated at the base of the hypapophysis. In cranial view, the neural arch is strongly flattened dorso-ventrally, the neural canal is subcircular with lateral sinuses. The zygosphenal lip is convex. The

prezygapophyses are tilted upward. Very large paracotylar foramina occur in depressions on both sides of the rounded to slightly dorso-ventrally flattened cotyle. The metrical measurements of the largest vertebrae are as follows ( $n = 5$ ):  $cl/or = 3.34-4.51$ ;  $naw/or = 2.30-3.05$ ;  $cl/naw/or = 1.32-1.51$ , mean  $1.43 \pm 0.07$ .

#### DISCUSSION

The vertebrae belong to the family Viperidae and to the subfamily Viperinae which is demonstrated by the dorso-ventrally strongly flattened neural arch and antero-ventrally directed parapophyseal processes. The vertebrae have relatively high ratio  $cl/naw$  and the low neural spine which represents the basic criterion for the affiliation to the “European vipers” group. The neural spine is not so extremely low as it is in case of representatives of the complex “*berus*”, therefore, it is assumed that these vertebrae belong to the representatives of the complex “*aspis*” (Szyndlar 1991a). This is also supported by the fact that the ratio  $cl/naw$  is lower, in case of the representatives of the complex “*aspis*”, in comparison with the representatives of the complex “*berus*” where the ratio is higher. Thus, the presupposed (Szyndlar

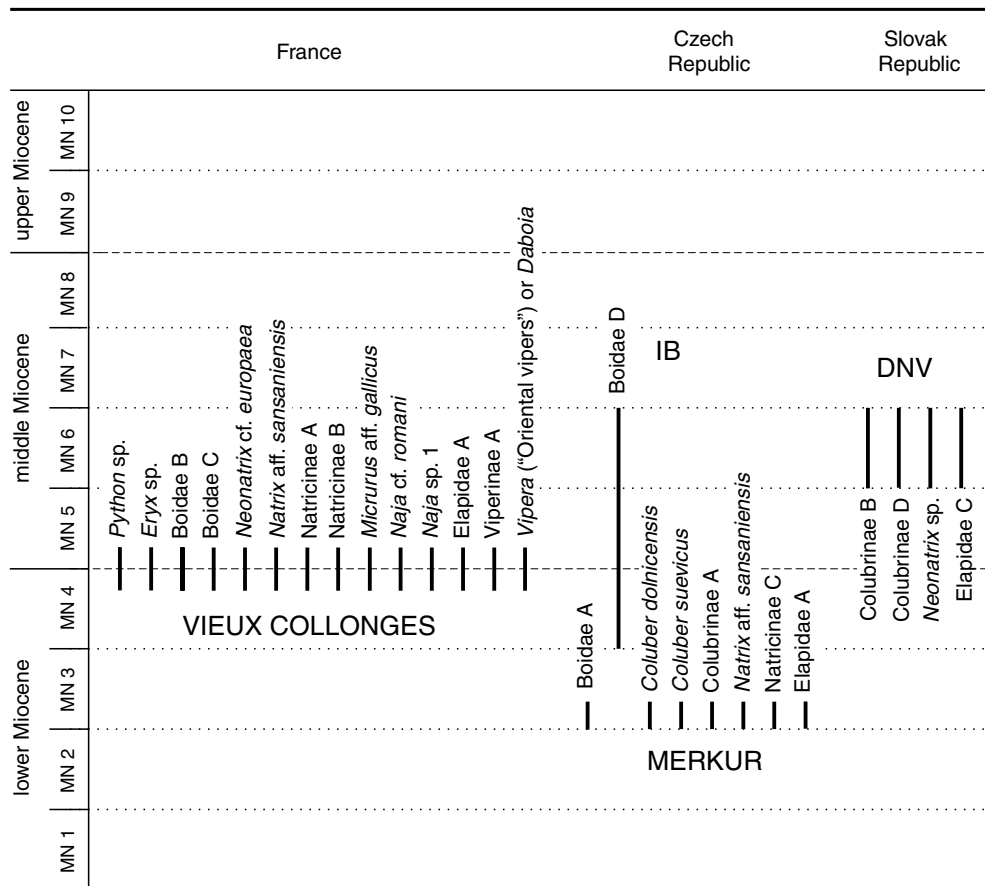


FIG. 16. — Stratigraphic range of the Miocene snake taxa recently reported from some West- and Central European localities. Abbreviations: IB, Ivančice near Brno; DNV, Devínska Nová Ves ("Bonanza").

& Rage 1999) occurrence of the "aspis" group at Vieux Collonges is supported.

#### "Oriental vipers" group

##### *Vipera* ("Oriental vipers") or *Daboia*

Viperinae B – Ivanov 1997a: 153, fig. 69.

MATERIAL EXAMINED. — 2 trunk vertebrae (FSL 369463, FSL 369464).

#### DESCRIPTION

A great number of viperine vertebrae from Vieux Collonges (233 trunk vertebrae), belonging actually to "*Vipera* ('Oriental vipers') or *Daboia*", has

recently been reported by Szyndlar & Rage (1999: fig. 9).

#### CONCLUSION

Vieux Collonges is a significant locality of the lower/middle Miocene (MN 4/5) transition which has exhibited a very diverse snake assemblage. This fauna includes the families Boidae (*Python* sp., *Eryx* sp., Boidae B & C), Colubridae (*Texasophis* sp., *Neonatrix* cf. *europaea*, *Natrix* aff. *sansaniensis*, Natricinae A, B, C & D), Elapidae (*Micrurus* aff. *gallicus*, *Naja* cf. *romani*, *Naja* sp. 1, Elapidae A & B), and Viperidae (Viperinae A,

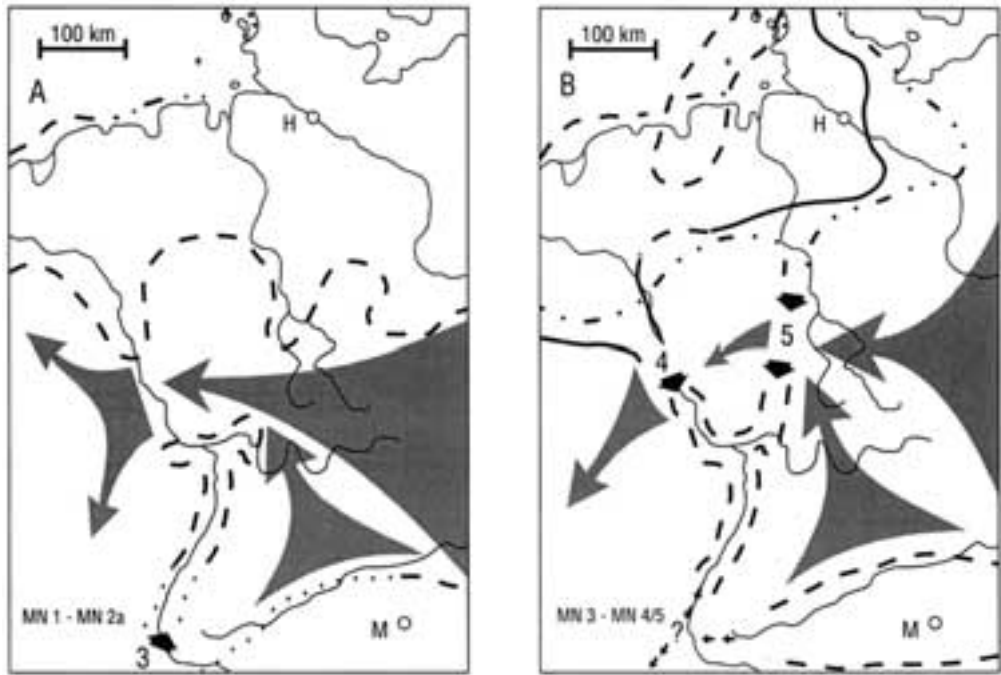


FIG. 17. — Approximate coastlines in Central Europe during the earliest Miocene (MN 1-MN 2a); **A**, till the lower-lower/middle Miocene (MN 3-MN 4/5); **B**, numbered arrows indicate source of incursions 3 to 5 (*sensu* Martini 1990). Other possible connections between the Upper Rhine Graben system and the North Sea Basin and/or Paratethys are marked with arrows and a question mark. Abbreviations: **H**, Hamburg; **M**, München (Martini 1990). Grey arrows indicate single dispersal waves of terrestrial vertebrates with snakes of the family Colubridae.

*Vipera* [“Oriental vipers”] or *Daboia*). The Boidae represent members of an “ancient” snake fauna which were displaced from Europe by “modern” Asiatic and North American immigrants during the lower and the middle Miocene. Although representatives of Boidae are still common in West Europe by the lower/middle Miocene transition (Vieux Collonges), representatives of Colubridae are predominant in Central Europe (Mercur, Dolnice, Petersbuch 2) already during the lower Miocene (Figs 16; 18). The last Central and East European representative of large Boidae (Boinae or Pythoninae) – i.e. the Boidae D – has been reported (Ivanov 1996) from the lower/middle Miocene transition (MN ?4-6) of Ivančice near Brno (Czech Republic, South Moravia). The first Colubridae might have immigrated into Central European areas probably across the Mazury-Mazowsze continental bridge in the lower Oligocene (MP 22) and subsequently penetrated

into West Europe across the Rhine Graben in several waves of dispersal (Ivanov 1997b). During the marine incursion 3 (MN 1-MN 2a) (*sensu* Martini 1990) the connection of the Rhine Graben with the northern Sea Basin was interrupted and the representatives of the oldest Miocene colubrids might have dispersed into West Europe for about two to three million years (Fig. 17A). The dispersal wave of the eastern colubrid immigrants, closely preceding the incursion 4 (MN 3-MN 4) (*sensu* Martini 1990), participated in the last displacement of the Boidae in Europe (Fig. 17B). As for the Elapidae, the small representatives of this family appeared in Europe most probably somewhat earlier than the large representatives of the genus *Naja* commonly present at Vieux Collonges. Similarly, the oldest European viperids are represented by small vipers, the large “Oriental vipers” appeared later (MN 3) in Europe. At Vieux Collonges, the representatives of the Viperidae are

		Merkur (MN 3a)	Dolnice (MN 4)	Petersbuch 2 (MN 4)	Vieux Collonges (MN 4/5)	Ivančice near Brno (MN 24-6)			Merkur (MN 3a)	Dolnice (MN 4)	Petersbuch 2 (MN 4)	Vieux Collonges (MN 4/5)	Ivančice near Brno (MN 24-6)
BOIDAE	<i>Python</i> sp.	-	-	-	361	-	NATRICINAE	<i>Palaeonatrix lehmani</i>	-	14	19	-	-
	<i>Bavarioboa hermi</i>	-	14	275	-	-		<i>Neonatrix nova</i>	-	63	-	-	-
	<i>Bransat. septentrionalis</i>	-	7	434	-	-		<i>Neonatrix cf. europaea</i>	-	-	-	7	-
	<i>Eryx</i> sp.	-	-	-	6	-		cf. « <i>Neonatrix</i> » sp.	-	-	63	-	-
	Boidae A	4	-	-	-	-		<i>Natrix aff. sansaniensis</i>	25	-	158	2	-
	Boidae B	-	-	-	2	-		Natricinae A	-	-	-	35	-
	Boidae C	-	-	-	4	-		Natricinae B	-	-	-	2	-
	Boidae D	-	-	-	-	1		Natricinae C	1	-	-	24	-
Boidae indet.	-	-	3	-	-	Natricinae D	-	-	-	4	-		
COLUBRINAE	<i>Coluber dolnicensis</i>	25	3	-	-	-	Natricinae g. et s. indet.	4	-	-	147	-	
	<i>Coluber suevicus</i>	11	-	-	-	-	Natricinae indet.	-	-	461	-	-	
	<i>Coluber caspioides</i>	-	-	675	-	-	ELAPIDAE	<i>Micrurus gallicus</i>	-	-	27	-	-
	<i>Texasophis bohemiacus</i>	-	3	-	-	-		<i>Micrurus aff. gallicus</i>	-	-	-	1	-
	<i>Texasophis</i> sp.	-	-	-	7	-		<i>Naja romani</i>	-	-	642	-	-
	Colubrinae A	14	-	-	-	-		<i>Naja cf. romani</i>	-	-	-	37	-
	Colubrinae g. et s. indet.	11	-	-	444	-		<i>Naja</i> sp. 1	-	-	-	56	-
								Elapidae A	3	-	-	2	-
						Elapidae B		-	-	-	17	-	
						Elapidae g. et s. indet.		-	-	-	235	-	
						Elapidae indet.	-	-	16	-	-		
						VIPERINAE	<i>Vipera platyspondyla</i>	-	8	872	-	-	
							<i>Vipera antiqua</i>	-	6	794	-	-	
							Viperinae A	-	-	-	12	-	
							<i>Vipera</i> or <i>Daboia</i>	-	-	-	2	-	

FIG. 18. — Representatives of the families Boidae, Colubridae (Colubrinae + Natricinae), Elapidae and Viperidae reported from the Miocene localities of France, Germany and Czech Republic. Numbers in the table represent the numbers of specimens.

relatively common, including both the “European” (Viperinae A) and “Oriental” (*Vipera* [“Oriental vipers”] or *Daboia*) vipers.

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