

The oldest known Miocene snake fauna from Central Europe: Merkur-North locality, Czech Republic

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The Early Miocene Merkur-North locality (MN 3a) represents the oldest known Miocene ophidian locality in Europe east of Germany. The snake assemblage is characterised by high species diversity and includes the following families: Boidae (*Bavarioboa* sp.), Colubridae (*Coluber dolnicensis*, *Coluber suevicus*, *Coluber caspioides*, cf. *Elaphe* sp., *Natrix merkurensis* sp. nov., *Natrix sansaniensis*), Elapidae (Elapidae gen. et sp. indet.), and Viperidae (*Vipera* sp.—“*Vipera aspis*” complex). Fossils of the extinct species, *Coluber dolnicensis*, *Coluber suevicus*, and *Natrix sansaniensis*, represent their earliest known occurrences. The cranial elements of *C. suevicus* and *N. sansaniensis* are described for the first time. Discoveries of cf. *Elaphe* sp. may represent the earliest fossil member of the genus *Elaphe*. Elapidae gen. et sp. indet. probably represents the oldest known member of the cobras.

Key words: Snakes, Boidae, Colubridae, Elapidae, Viperidae, Early Miocene, Czech Republic.

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Introduction

The Merkur-North locality is situated in the opencast brown coal mine near Tušimice, in the area of the former village Ahníkov, close to Chomutov (northwestern Bohemia) (Fig. 1). The fossiliferous grey calcareous marls were found underlying and at the base of the so called “Main Brown Coal Seam”. This seam was recorded about 1890 in the underground brown coal mines Marianna and Prokopi at Skyřice. Grey marls in the Merkur-North, thought to be reworked volcanic ash, produced a rich fauna of limnic and terrestrial molluscs, plants, mammals (Fejfar and Kvaček 1993; Fejfar, Engesser, and Tomida, 1997; Fejfar, Heizmann, and Major 1997; Fejfar, Rummel, and Tomida 1998), amphibians and reptiles (Vejvalka 1997; Ivanov 1997a). The fossiliferous layer was first recovered in boreholes in the outlying area of Chomutov (Čtyroký, Fejfar, and Holý 1962). Since 1980s the layer was found in several different sections in the opencast mine Merkur-North. In the roof of the grey calcareous marls, layers with a rich fauna of cyprinid fishes was recorded in the Most area (Obrhelová 1970, 1971).

The palaeobotanical investigation indicates a tropical to subtropical climate with a suggested mean annual temperature 15° C and more than 1000 mm of annual precipitation. The stratigraphical age is based on the study of small mammals and corresponds to the Early Miocene (Eggenburgian), early Orleanian, zone MN 3a.

A list of synonyms indicated in the systematic part is restricted to the fossils from Czech Republic. The snake material from Merkur-North was collected by Mr. Z. Dvořák (specimens labelled Ah) and Prof. O. Fejfar (specimens la-

belled 7408/MI) and is stored in the geological collection of the opencast mine Bílina, abbreviated as SGDB (Sbírký geologie, Doly Bílina).

Abbreviations.—n, number of specimens; cl, centrum length; naw, centrum width; or, observed range.

Systematic palaeontology

Suborder Alethinophidia Nopcsa, 1923

Superfamily Booidea Gray, 1825

Family Boidae Gray, 1825

Genus *Bavarioboa* Szyndlar and Schleich, 1993

Bavarioboa sp.

Type species: *Bavarioboa hermi* Szyndlar and Schleich, 1993.

Material.—Four trunk vertebrae (SGDB 7408/MI-1–4), 2 cervical vertebrae (SGDB Ah-1, 2), 7 trunk vertebrae (SGDB Ah-3–9), 1 cloacal vertebra (SGDB Ah-10).

Cervical vertebrae (Fig. 2A₁–A₄).—Fragmentary vertebrae with hypapophyses broken off at their base are typified by a vaulted neural arch. The neural canal is approximately circular with small lateral sinuses. The neural spine is restricted to the posterior half of the vertebral length, its cranial margin is directed posteriorly as is the caudal margin. The paradiapophyses are indistinctly divided and the parapophyseal processes are very short and obtuse. The prezygapophyseal articular facets are oval to subtriangular and the prezygapophyseal processes are very short and hardly visible from

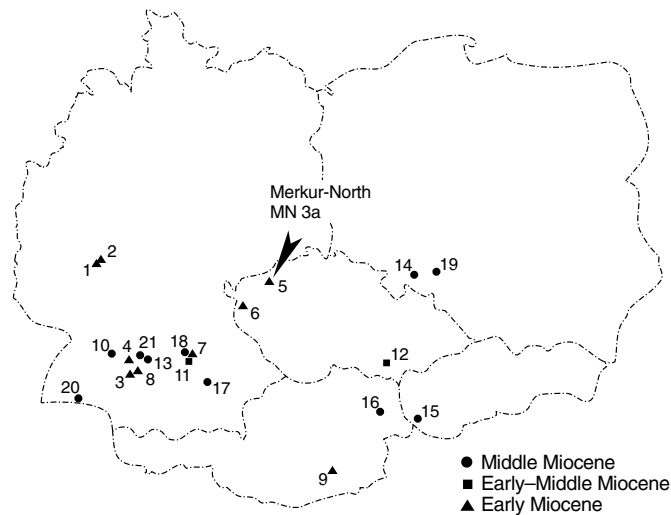


Fig. 1. The distribution of some Early and Middle Miocene ophidian localities in the areas of Germany, Czech Republic, Slovak Republic, Poland and Austria. 1, Weisenau (MN 1); 2, Hessler (MN 1); 3, Ulm-Westtangente (MN 2); 4, Stubersheim 3 (MN 3); 5, Merkur-North (MN 3a); 6, Dolnice (MN 4); 7, Petersbuch 2 (MN 4); 8, Langenau (MN 4); 9, Oberdorf (MN 4); 10, Randecker Maar (MN 5); 11, Eichstätt (MN 4–6); 12, Ivančice (MN ?4–6); 13, Oggenhausen (MN 5/6); 14, Przeworno (MN 5–6); 15, Devínska Nová Ves (MN 6); 16, Vösendorf; 17, Sandelzhausen (MN 6); 18, Rothenstein 13 (MN 6); 19, Opole (MN 7); 20, Öhningen (MN 7+8); 21, Steinheim am Albuch (MN 7+8).

above. In dorsal view, the cranial margin of the zygosphenes bears the distinct lateral lobes and a blunt median lobe.

Trunk vertebrae (Fig. 2B₁–B₅).—In lateral view, the neural spine is about as long as high. The cranial margin of the neural spine overhangs anteriorly and the caudal margin overhangs posteriorly. The dorsal border of the neural spine is markedly thickened. Relatively sharp interzygapophyseal ridges are well developed. Small lateral foramina are visible and are not situated in depressions. Subcentral ridges are marked, relatively short and dorsally arched. The haemal keel is distinct. The paradiapophyses are not distinctly divided and the parapophyses are short and rounded at the ventral margin. Postzygapophyses are tilted upward as seen in caudal view. In dorsal view, the cranial margin of the zygosphenes has distinct lateral lobes and a wide median lobe. The neural spine rises just at the base of zygosphenes and occupies less than half of the vertebral length. The neural spine is thickened dorsally, sometimes with an indistinct bifurcation at its caudal margin. The prezygapophyseal articular facets are subtriangular; the prezygapophyseal processes are very short and hardly visible in dorsal view. Epizygapophyseal ridges are obsolete. In ventral view, the distinct haemal keel is wide at the base but relatively sharp at its ventral margin and sometimes has a small tubercle developed on its cranial margin. The subcentral ridges and grooves are better developed in the cranial portion of the vertebrae. The subcentral foramina are obvious and in one vertebra the right subcentral foramen is doubled. The postzygapophyseal articular facets are either suborbicular or irregularly shaped. In

cranial view, the neural arch is slightly flattened dorso-ventrally and the neural canal is approximately circular with small lateral sinuses. The zygosphenal lip is straight or slightly concave. The prezygapophyses are strongly tilted upward. The paracotylar foramina are missing. Measurements are as follows ($n = 6$): $cl/or = 2.64\text{--}4.56$ mm; $naw/or = 3.14\text{--}5.47$ mm; $cl/naw/or = 0.83\text{--}1.05$, mean 0.90 ± 0.08 .

Cloacal vertebra.—The cranial margin of the dorsally thickened neural spine overhangs anteriorly and the caudal margin overhangs posteriorly. The haemal keel is sharp at its caudal part, resembling a small hypapophysis. The pleurapophyses are broken off at their bases.

Comments.—The described vertebrae, originally identified as belonging to *Boidae A* (Ivanov 1997a: 39, fig. 20), undoubtedly belong to the family Boidae, which is shown by the low ratio cl/naw . Based on morphology and measurements, *Bavarioboa* sp. resembles *Bavarioboa hermi* Szyndlar and Schleich, 1993, the only known species of this genus. This species was described (Szyndlar and Schleich 1993) from the west Bohemian Early Miocene (MN 4) locality at Dolnice (originally identified by Szyndlar 1987, from this site as a possible member of the recent Asiatic ericine genus *Gongylophis*, cf. *Gongylophis* sp.). One cannot exclude the fact that some morphotypes of the family Boidae from the Bavarian localities at Ehrenstein 7 (Late Oligocene) and Rothenstein 13 (Middle Miocene) also belong to the genus *Bavarioboa* (Szyndlar and Schleich 1993). *Bavarioboa* sp. from Merkur-North shares several features with the representatives of *Bavarioboa hermi* reported from the Bavarian type locality at Petersbuch 2, MN 4 (Szyndlar and Schleich 1993) and the differences are only minimal as follows: 1) the cranial margin of the neural spine of *Bavarioboa* sp. overhangs anteriorly in lateral view, while in *Bavarioboa hermi* this cranial margin is vertical or inclined posteriorly; 2) in dorsal view, the thickened dorsal border of the neural spine has the same width along its entire length, while in *Bavarioboa hermi* this border is anteriorly narrow and becomes wider posteriorly; 3) in cranial view, the zygosphenal lip is not always concave in *Bavarioboa* sp., unlike the species *Bavarioboa hermi*.

Superfamily Colubroidea Oppel, 1811

Family Colubridae Oppel, 1811

Subfamily Colubrinae Oppel, 1811

Genus *Coluber* Linnaeus, 1758

Coluber dolnicensis Szyndlar, 1987

Coluber dolnicensis; Szyndlar 1987: 65–66, fig. 8.

Coluber dolnicensis Szyndlar; Szyndlar 1991a: 115, fig. 10.

Coluber dolnicensis Szyndlar; Ivanov 1997a: 45–46, fig. 24.

Material.—One left dentary (SGDB Ah-12), 4 compound bones (3 left + 1 right) (SGDB 7408/MI-9, 10; SGDB Ah-13, 14), 1 cervical vertebra (SGDB Ah-15), 2 cervical vertebrae (SGDB 7408/MI-5, 6), 23 trunk vertebrae (SGDB 7408/MI-7–4; SGDB 7408/MI-92–95; SGDB 7408/MI-101), 19 trunk verte-

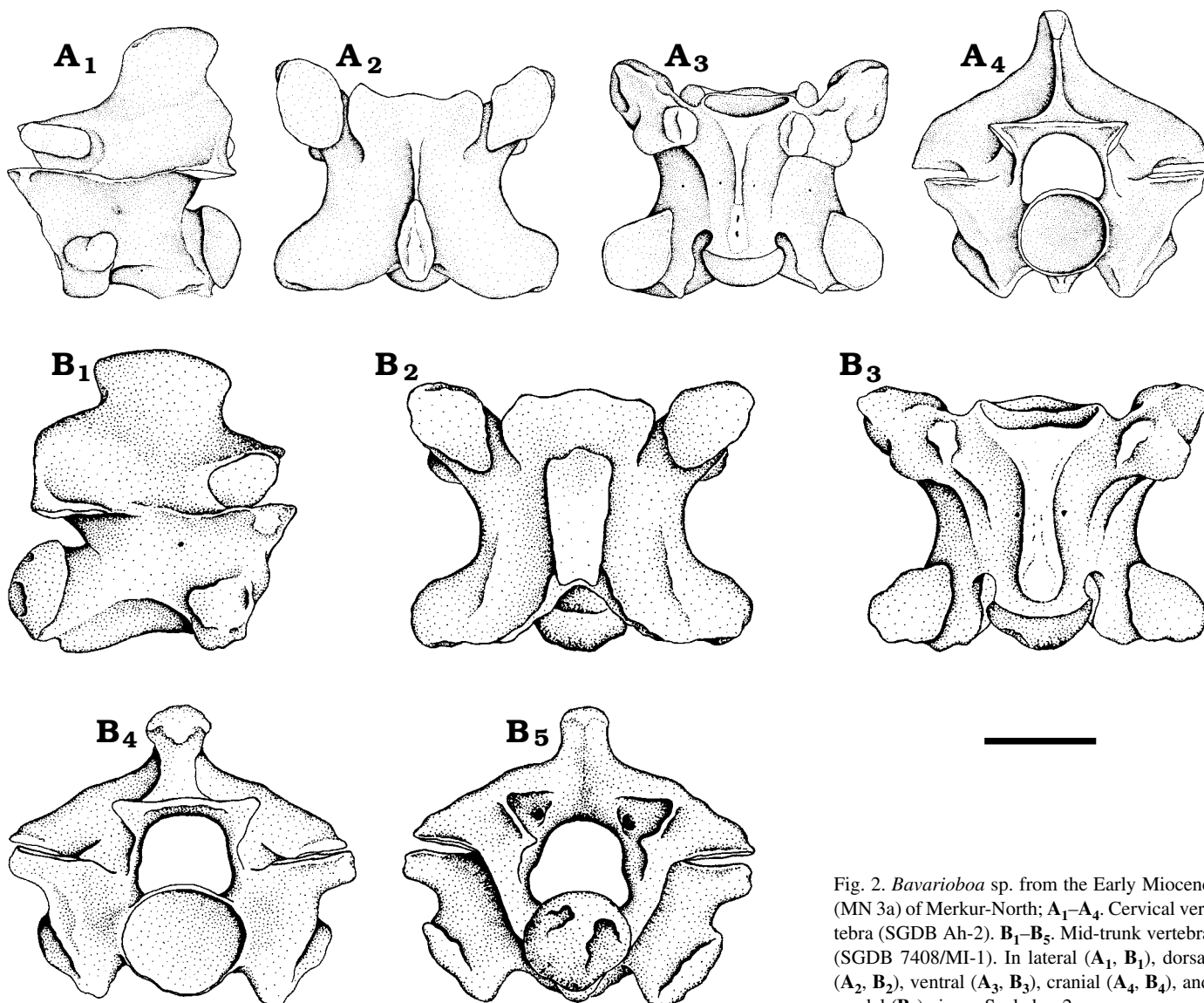


Fig. 2. *Bavarioboa* sp. from the Early Miocene (MN 3a) of Merkur-North; A₁–A₄. Cervical vertebra (SGDB Ah-2). B₁–B₅. Mid-trunk vertebra (SGDB 7408/MI-1). In lateral (A₁, B₁), dorsal (A₂, B₂), ventral (A₃, B₃), cranial (A₄, B₄), and caudal (B₅) views. Scale bar 2 mm.

brae (SGDB Ah-16–32; SGDB Ah-613, 614), 1 caudal vertebra (SGDB 7408/MI-25).

Dentary (Fig. 3A₁–A₂).—The bone is very fragmentary, the preserved rostral part is curved medially. The bone originally was probably massive and it is markedly thickened close to the symphysis which can be easily observed, especially in ventral view. The Meckel's groove is completely enclosed at the level of the 6th tooth. The mental foramen occurs at the level of the 9th and 10th teeth. Unfortunately, the caudal part of the dentary is not preserved, therefore it was not possible to determine either the precise position of the rostral termination of the compound notch or the number of tooth spaces.

Compound bone (Fig. 3B₁–B₂, C).—In labial view, the lingual flange of the fossa mandibularis is twice high as the labial flange. The antero-dorsal margin of the lingual flange is distinctly steep. The labial flange is more or less rectilinear

and at the ventral border it is limited by the elongated supraangular crest which extends to the supraangular foramen. The supraangular foramen lies far from the rostral termination of the fossa mandibularis. Caudal parts of the bone with slender retroarticular process are preserved in two specimens. A distinct large foramen occurs at the medial side of the base of the retroarticular process.

Cervical vertebrae (Fig. 3D₁–D₄).—The vertebrae are fragmentary with the neural spines broken off close to their base. The neural arch is slightly vaulted and the neural canal is rounded. The subcentral ridges are well developed and moderately arched dorsally. The paradiapophyses are distinctly divided; the diapophyses are directed postero-laterally, and they are about as large as the parapophyses. The parapophyseal processes are directed antero-ventrally. The lateral lobes of the zygosphenes are well developed in dorsal view,

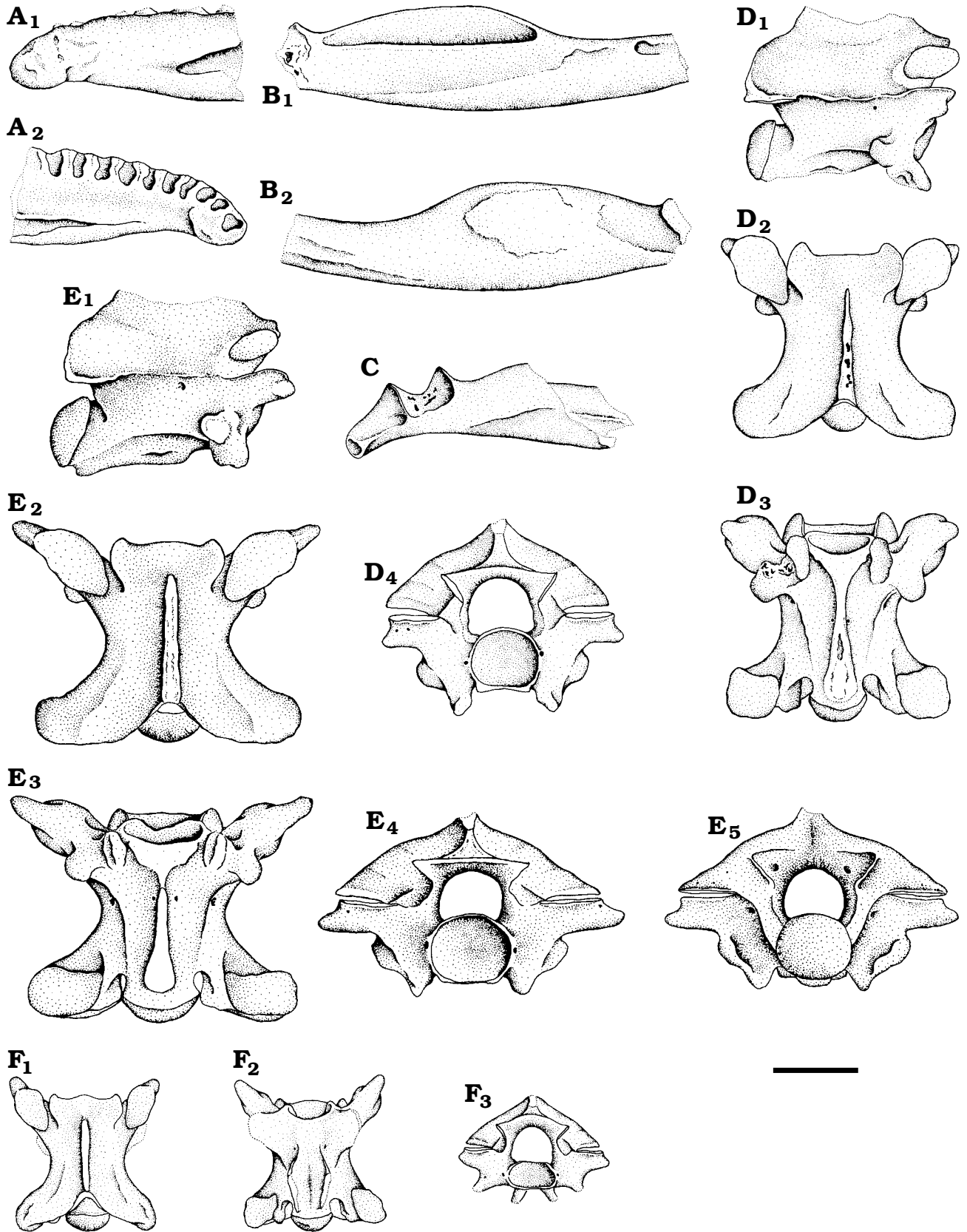


Fig. 3. *Coluber dolnicensis* Szyndlar, 1987 from the Early Miocene (MN 3a) of Merkur-North. **A₁**, **A₂**. Left dentary (SGDB Ah-12). **B₁**, **B₂**. Right compound bone (SGDB Ah-14). **C**. Left compound bone (SGDB 7408/MI-9). **D₁**–**D₄**. Cervical vertebra (SGDB 7408/MI-5). **E₁**–**E₅**. Trunk vertebra (SGDB 7408/MI-7). **F₁**–**F₃**. Caudal vertebra. In labial (**A₁**, **B₁**), lingual (**A₂**, **B₂**, **C**), lateral (**D₁**, **E₁**), dorsal (**D₂**, **E₂**, **F₁**), ventral (**D₃**, **E₃**, **F₂**), cranial (**D₄**, **E₄**, **F₃**), and caudal (**E₅**) views. Scale bar 2 mm.

the median lobe is not produced, thus the margin of the zygosphenal lip is slightly concave. The large prezygapophyseal articular facets are suborbicular to irregularly shaped and the prezygapophyseal processes are very small (about 1/5 of the length of the prezygapophyseal articular facets) and pointed.

Trunk vertebrae (Fig. 3E₁–E₅).—In lateral view, the neural spine is about twice as long as high. The cranial margin of the damaged neural spine was probably vertical or overhanging anteriorly. The caudal margin of the neural spine clearly overhangs posteriorly. The interzygapophyseal ridges are well developed and distinct lateral foramina occur in depressions (which are sometimes relatively deep) slightly ventral to the ridges. Lateral foramina are obvious, especially from latero-ventral view rather than in lateral view. The subcentral ridges are distinct and are straight or slightly arched dorsally. The haemal keel is terminated anteriorly by a distinct step. The parapophyses are separated from diapophyses and the diapophyses are as large as parapophyses or somewhat smaller. The parapophyseal processes are very short and rounded at their ventral margin. In dorsal view, the zygosphenal lip is either straight or convex with distinct lateral lobes. The prezygapophyseal articular facets are widely oval and the prezygapophyseal processes are about two times shorter than the prezygapophyseal articular facets. The epizygapophyseal ridges are underdeveloped. In ventral view, the subcentral grooves are shallow. The haemal keel is separated from the area just posterior to the cotyle by a distinct step. A small subcotylar tubercle is sometimes also developed. In cranial view, the neural arch is moderately vaulted and the neural canal is rounded with small lateral sinuses. The zygosphenal lip is straight to slightly convex. The paracotylar foramina lie in depressions on both sides of the circular cotyle. In caudal view, minute parazygantral foramina occur in some vertebrae just above the postzygapophyseal articular facets. Measurements are as follows (n = 21): cl: or = 4.10–5.40 mm; naw: or = 3.05–4.01 mm; cl/naw: or = 1.20–1.50, mean 1.37±0.09.

Caudal vertebra (Fig. 3F₁–F₃).—A very fragmentary vertebra has its neural spine, the pleurapophyses and the haemapophyses broken off just at their bases. The small lateral foramina occur in depressions just under the interzygapophyseal ridges. In dorsal view, the zygosphenal lip has distinct lateral lobes and a wide median lobe. The prezygapophyseal articular facets are oval and the pointed prezygapophyseal processes are about half the length of the prezygapophyseal articular facets. The paracotylar foramina are small and occur in depressions on both sides of the cotyle which is slightly depressed dorso-ventrally.

Comments.—The dentary of *Coluber dolnicensis* Szyndlar, 1987 is described for the first time here. A fragmentary compound bone was described earlier by Szyndlar (1987).

The fragmentary dentary was probably massive and the mental foramen is relatively long which allowed assignment to the genus *Coluber*. The bone differs from both the recent

and fossil representatives of this genus by its massive structure in the proximity of the symphysis. This element is assigned to the species *C. dolnicensis* but assignment to some other species of the genus *Coluber* cannot be excluded.

The compound bone is referred to *C. dolnicensis* based on the general morphological resemblance to the type material from Dolnice, MN 4 (Szyndlar 1987). The most diagnostic character is the presence of the prominent crest evolved from the elongated supraangular crest. This crest, unlike the material from Dolnice (Szyndlar 1987), extends to the supraangular foramen.

On the basis of vertebrae alone, determination of fossil representatives of the subfamily Colubrinae is very difficult. Therefore, it is not often possible to identify this material to the species or even at the generic level without cranial bones. The absence of the hypapophyses on relatively long and slender vertebrae and the relatively low neural spines allow assignment of this material to the subfamily Colubrinae and to the genus *Coluber*. Fossil representatives of the genus *Coluber* are relatively common in the European Neogene including (Szyndlar and Böhme 1993; Szyndlar and Schleich 1993; Bachmayer and Szyndlar 1985, 1987; Bolckay 1913; Venczel 1994, 1998): cf. “*Coluber*” *cadurci* Rage, 1974 (MN 1), ?*Coluber cadurci* Rage, 1974 (MN 2), *Coluber caspioides* Szyndlar and Schleich, 1993 (MN 3a, this paper – MN 4), *Coluber dolnicensis* Szyndlar, 1987 (MN 3a, this paper – MN 4), *Coluber sansaniensis* Lartet, 1851 (MN 6), *Coluber suevicus* (Fraas, 1870) (MN 3a, this paper – MN 7+8), *Coluber planicarinatus* (Bachmayer and Szyndlar, 1985) (MN 11) and *Coluber hungaricus* (Bolckay, 1913) (MN 13).

The trunk vertebrae from Merkur-North are most similar to the species *C. dolnicensis*. Cervical vertebrae are described in this extinct species for the first time and differ from the cervical vertebrae of other species by the slender parapophyseal processes that project under the vertebral centrum. Very short prezygapophyseal processes in trunk vertebrae are rare in the genus *Coluber*. Trunk vertebrae of *C. dolnicensis* differ from living and extinct members of the genus *Coluber* by the prominent step in anterior part of the haemal keel and by the diapophyses, which are shifted far behind the parapophyses (Szyndlar 1987). The caudal vertebra, although very fragmentary, is assigned to the species *C. dolnicensis* on the basis of the general shape of the zygosphenal lip, the presence of the distinct interzygapophyseal ridges and lateral foramina which are situated in depressions.

Coluber suevicus (Fraas, 1870)

Naja suevica; Fraas 1870: 291.

?*Coluber suevica* (Fraas); Rage 1984: 45.

Coluber suevicus (Fraas); Szyndlar and Böhme 1993: 405, fig. 7.

Coluber suevicus (Fraas); Ivanov 1997a: 48, fig. 25.

Material.—One right quadrate (SGDB Ah-33), 3 cervical vertebrae (SGDB Ah-34–36), 11 trunk vertebrae (SGDB 7408/MI-26–36), 7 trunk vertebrae (SGDB Ah-37–43).

Quadrate (Fig. 4A).—In postero-lateral view, this massive bone expands toward the dorsal crest. The dorsal crest is mark-

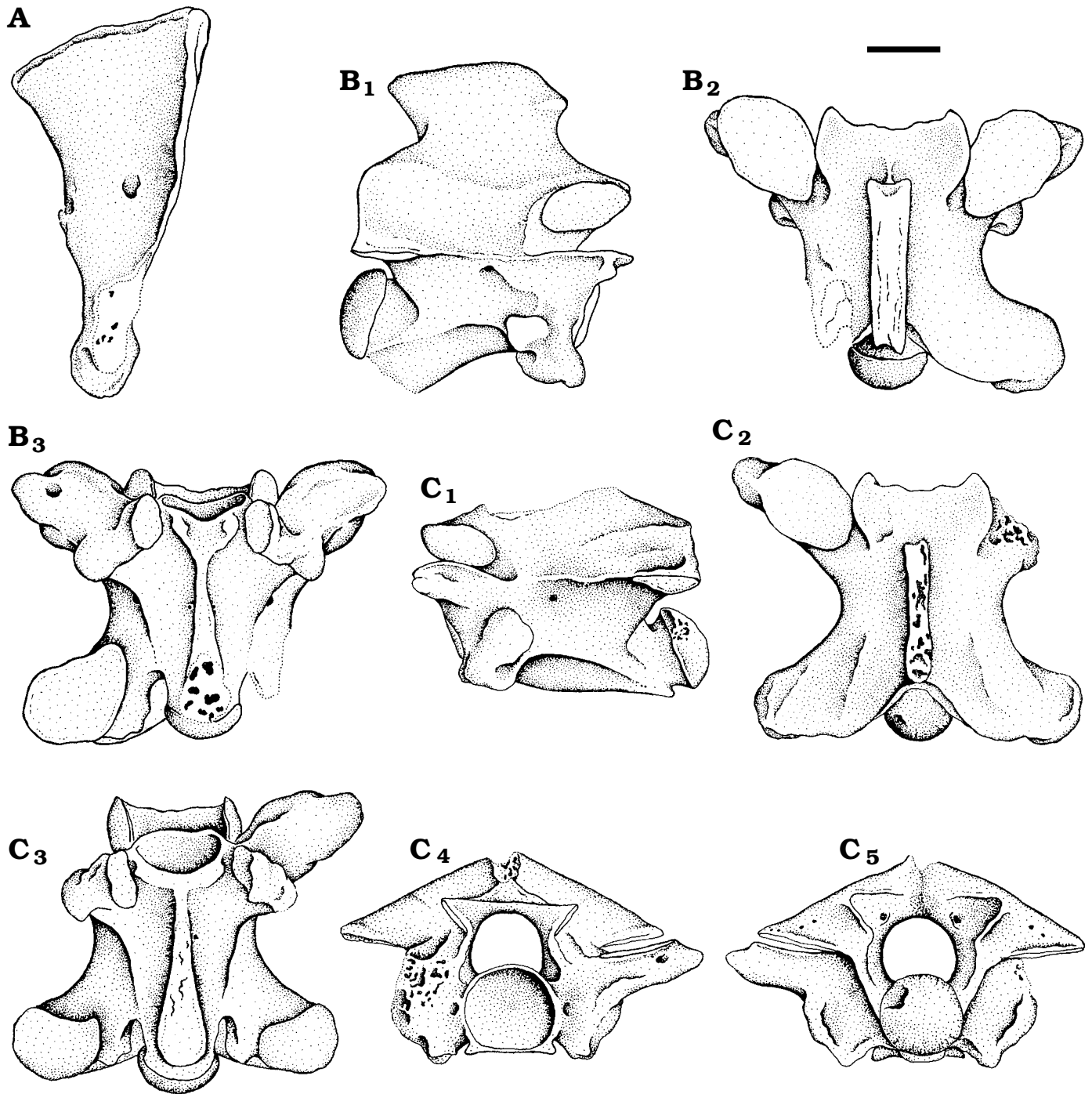


Fig. 4. *Coluber suevicus* (Fraas, 1870) from the Early Miocene (MN 3a) of Merkur-North. A. Right quadrate (SGDB-Ah-33). B₁–B₃. Cervical vertebra (SGDB-Ah-36). C₁–C₅. Trunk vertebra (SGDB 7408/MI-26). In postero-lateral (A), lateral (B₁, C₁), dorsal (B₂, C₂), ventral (B₃, C₃), cranial (C₄), and caudal (C₅) views. Scale bar 2 mm.

edly thickened on its entire length. A small distinct and ventrally directed process occurs on the antero-medial margin of the dorsal crest. The distinct quadrate crest is high and sharp, its distal termination missing as well as a part of trochlea quadrati. The stapedial process is strongly damaged.

Cervical vertebrae (Fig. 4B₁–B₃).—These vertebrae are fragmentary with hypapophyses broken off close to their

base. The neural arch is weakly vaulted, the neural canal is rounded. The dorsally thickened neural spine is about as long as high and both its cranial and caudal margins are bifurcated. The cranial margin of the neural spine slightly overhangs anteriorly and the caudal margin overhangs posteriorly. The parapophyses are as large as the diapophyses or somewhat smaller and the parapophyseal processes are short and directed anteriorly. The zygosphenes have lateral lobes; the me-

dian lobe is short and wide and sometimes it is absent. The hypapophysis extends proximally up to the ventral margin of cotyle where the prominent subcotylar tubercles are situated.

Trunk vertebrae (Fig. 4C₁–C₅).—In lateral view, the neural spine is often broken off; if preserved, it is about twice as long as high and its cranial margin distinctly overhangs anteriorly and caudal margin overhangs posteriorly. In the largest vertebrae, a dorsal thickening of the neural spine may develop. The sharp interzygapophyseal ridges are prominent. The lateral foramina are distinct and they occur in deep depressions just ventral to the interzygapophyseal ridges. The subcentral ridges are short (especially in the largest vertebrae) and arched dorsally. The paradiapophyses are indistinctly divided and the parapophyses are longer than the postero-laterally directed diapophyses. In dorsal view, the zygosphenes are straight or concave with distinct lateral lobes. The prezygapophyseal articular facets are conspicuously broad in the largest vertebrae, are oval or irregularly shaped and the prezygapophyseal processes of the largest vertebrae are very short (about three times the length of the prezygapophyseal articular facets) and obtuse. In smaller vertebrae the prezygapophyseal facets are smaller than the blunt prezygapophyseal processes which are longer. The epizygapophyseal spines are moderately developed. In ventral view, the distinct blunt haemal keel expands posteriorly and its ventral margin is more or less flattened. The haemal keel continues anteriorly toward the base of the cotyle. The distinct subcotylar tubercles are developed at the cotylar base of the largest vertebrae. Subcentral foramina are obvious and they occur just at the base or close to the base of the haemal keel. The postzygapophyseal articular facets of the largest vertebrae are enlarged laterally. In cranial view, the neural arch is moderately vaulted. The neural canal is rounded and has short distinct lateral sinuses. Sometimes prominent nerve foramina occur at the base of the prezygapophyseal processes just below the articular facets. The paracotylar foramina are situated in deep depressions on both sides of the rounded or laterally slightly depressed cotyle. The parapophyseal processes are very short and their ventral margins are slightly below the level of subcotylar tubercles. Measurements are as follows (n = 9): cl: or = 4.14–6.44 mm; naw: or = 3.01–4.66 mm; cl/naw: or = 1.31–1.42, mean 1.36±0.03.

Comments.—The quadrate undoubtedly represents the genus *Coluber* based on the expanding body of the bone, the prominent dorsal crest and the small stapedial process. Unlike the recent and fossil representatives, including *Coluber caspioides* Szyndlar and Schleich, 1993, the area of the dorsal crest is markedly thickened and the bone is much more massively built. The quadrate is identified as belonging to *Coluber suevicus* (Fraas, 1870) based on its large size on the basis that vertebrae of this species belong to the largest colubrine snakes discovered at Merkur-North.

These vertebrae (cervical vertebrae are reported for the first time) certainly belong to a large snake of the genus

Coluber; the material of trunk vertebrae especially resembles *C. suevicus* that was known only from the German Middle Miocene (MN 7+8) type locality at Steinheim (Rage 1984; Szyndlar and Böhme 1993: 407, fig. 7). Trunk vertebrae from Merkur-North do not essentially differ in morphology from the German discoveries of *C. suevicus*, although the prezygapophyseal processes figured by Szyndlar and Böhme (1993) seem to be more pointed. *C. suevicus* from Merkur-North resembles the German specimens of this species mainly by having: 1, the same shape and relative size of the pre- and postzygapophyseal articular facets; 2, the same development of the haemal keel; 3, the presence of distinct subcotylar tubercles; 4, the very short parapophyseal processes whose ventral margin extends only slightly below the level of the subcotylar tubercles. The shape and location of the parapophyseal processes differentiates *C. suevicus* from other known fossil and recent representatives of the genus *Coluber*.

Coluber caspioides Szyndlar and Schleich, 1993

Coluber caspioides; Szyndlar and Schleich 1993: 23–26, fig. 6.

Material.—One left frontal (SGDB Ah-44), 1 right pterygoid (SGDB Ah-45), 1 right palatine (SGDB Ah-46), 1 right quadrate (SGDB Ah-11), 2 (left + right) dentaries (SGDB Ah-47, 48), 2 right compound bones (SGDB Ah-49, 50), 8 cervical vertebrae (SGDB Ah-51–58), 14 trunk vertebrae (SGDB 7408/MI-37–50), 110 trunk vertebrae (SGDB Ah-59–166; SGDB Ah-615, 616), 1 cloacal vertebra (SGDB Ah-167).

Frontal (Fig. 5A₁–A₂).—The bone is very fragmentary and only the dorsal part of the bone is preserved. In dorsal view, the rostral part of the bone expands laterally and the orbital margin is slightly turned up. Both the external and internal premaxillary processes are of equal size and the external process is more rounded than the internal one. In rostral view, the distal end of the distinct internal premaxillary process is markedly rounded.

Palatine (Fig. 5B).—This fragmentary palatine has the complete maxillary process with its wide base preserved. The maxillary process lies at the level of the 5th–6th teeth. The vomerine process is broken off. The postero-labially directed maxillary process has a large maxillary nerve foramen at its base. Because the material is incomplete it is not possible to estimate the number of teeth; only two caudally directed teeth are preserved.

Pterygoid (Fig. 5C₁–C₂).—The fragmentary right pterygoid lacks rostral and caudal parts. In dorsal view, the distinct pterygoid crest can be seen and the pterygoid flange is prominent at the caudal end of the ectopterygoid process. Unfortunately, the rostral part of the ectopterygoid process is damaged. On the ventral side, the bone retains fragmentary tooth row with 5 tooth sockets (only three sockets are complete).

Quadratum (Fig. 5D).—In postero-lateral aspect, this gracile bone becomes wider toward the dorsal crest. The distinct quadrate crest extends from the dorsal crest to the proximity of

the trochlea quadrati. The dorsal crest is only moderately thickened at its antero-medial part. The stapedial process is small and only indistinctly separated from the body of the bone.

Dentary (Fig. 5E).—These bones are fragmentary and their caudal parts are broken off. The rostral part becomes thinner distally just anterior the mental foramen and is curved medially. Meckel's groove is completely enclosed at the level of the 5th tooth. The mental foramen is long and occurs at the level of the 9th (in one bone ?10th) – 11th tooth. From the mental foramen a marked groove extends in rostral direction. The notch for the rostral termination of the compound groove is relatively sharp and is situated at the level of the 15th tooth. The precise number of the teeth (or teeth sockets) remains unknown.

Compound bone (Fig. 5F₁, F₂).—The rostral part of this fragmentary bone is missing and the retroarticular process is broken off at its distal end. In labial view, the labial flange of the mandibular fossa is about 1.5–2 times lower than the lingual flange. The labial flange is concave dorsally and the ventral margin of this concavity forms an enlarged ridge extending from the well developed supraangular crest. This ridge terminates close to the distinct supraangular foramen that lies far from the rostral end of the mandibular fossa. A low but distinct crest occurs on the lingual side of the bone and extends from the base of the retroarticular process to the proximity of the dorsal margin of the lingual flange of the mandibular fossa.

Cervical vertebrae (Fig. 5G₁–G₅).—The neural arch is vaulted and the neural canal is rounded with shallow lateral sinuses. The neural spine is somewhat longer than high with indistinct dorsal thickening and the neural spine overhangs slightly anteriorly, more distinctively posteriorly. The paradiaepophyses are well divided, the diapophyses are longer than the parapophyses and the gracile parapophyseal processes are directed anteriorly. The pointed distal end of the hypapophysis is directed postero-caudally. The subcentral ridges are long and moderately arched dorsally. The zygosphenes have well developed lateral lobes and the median lobe is wide, indistinct, or missing. The prezygapophyseal articular facets are rounded to oval and the prezygapophyseal processes are very short and pointed. The small paracotylar foramina occur in depressions on both sides of the rounded cotyle.

Trunk vertebrae (Fig. 5H₁, H₂, I₁–I₅).—In lateral view, the neural spine is about 1.5 times longer than high, its cranial margin slightly overhangs anteriorly and the caudal margin overhangs caudally. The interzygapophyseal ridges are well developed and the lateral foramina are conspicuous and situated in shallow depressions. The dorsally slightly arched subcentral ridges are well developed and do not reach the cotylar rim. The haemal keel is relatively deep and gradually decreases at about 1/3 of the bone length towards the cotyle. The parapophyses are not distinctly separated from the

diapophyses and the diapophyses are somewhat smaller than the parapophyses. The parapophyses are rounded on the ventral side. In dorsal view, the zygosphenal lip has distinct lateral lobes. Although usually distinct, the median lobe can be either underdeveloped or absent and has a shallow median incision. The prezygapophyseal articular facets are subtriangular to oval, the prezygapophyseal processes are somewhat shorter than the prezygapophyseal facets and they are directed antero-laterally. The epizygapophyseal spines are missing. In ventral view, the blunt subcentral ridges are relatively well developed and the subcentral grooves are wide and shallow. The conspicuous subcentral foramina lie close to the base of the haemal keel. The postzygapophyseal articular facets are irregularly shaped. In cranial view, the neural arch is moderately vaulted and the neural canal is rounded with shallow lateral sinuses and the zygosphenal lip is convex or straight. Nerve foramina occur at the bases of the prezygapophyseal processes. The paracotylar processes occur in depressions on both sides of the rounded cotyle. In caudal view, minute parazygantral foramina are present. Measurements are as follows (n = 26): cl: or = 3.10–5.57 mm; naw: or = 2.20–4.11 mm; cl/naw: or = 1.13–1.76, mean 1.39±0.12.

Cloacal vertebra.—The vertebra is very damaged, the caudal margin of the neural spine overhangs posteriorly and the cranial margin is unpreserved. The lymphapophyses are broken off at their bases. A suggestion of the division of the haemal keel into the haemapophyses can be observed. In dorsal view, the zygosphenes have distinct lateral lobes and the wide and blunt median lobe is obvious. The zygosphenal lip is convex in cranial view.

Comments.—Cranial elements are assigned to *Coluber caspioides* Szyndlar and Schleich, 1993 for the first time but we cannot exclude a doubtful assignment of some cranial bones, not only because of the fragmentary condition of the fossil material, but also because several species of the genus *Coluber* occur in the locality. A considerable number of the fossil vertebrae of the genus *Coluber* most likely belong to *C. caspioides*.

The assignment of the frontal to the genus *Coluber* is based on the presence of the prominent internal and external premaxillary processes and also on the general shape of the bone which has a wide rostral area. The long internal premaxillary process is markedly rounded in both dorsal and rostral views, which distinguishes *C. caspioides* from remaining known recent and fossil species of the genus *Coluber*.

The palatine is assigned to the genus *Coluber* based on the presence of a prominent pointed maxillary process with a wide base. The bone is very similar to the palatine of the extant species *C. caspius* based on the conspicuous maxillary nerve foramen.

A very fragmentary pterygoid bone is assigned to the genus *Coluber* based on the presence of a distinct pterygoid crest and ectopterygoid process. The bone especially resembles the pterygoid of the living species *C. viridiflavus* as both

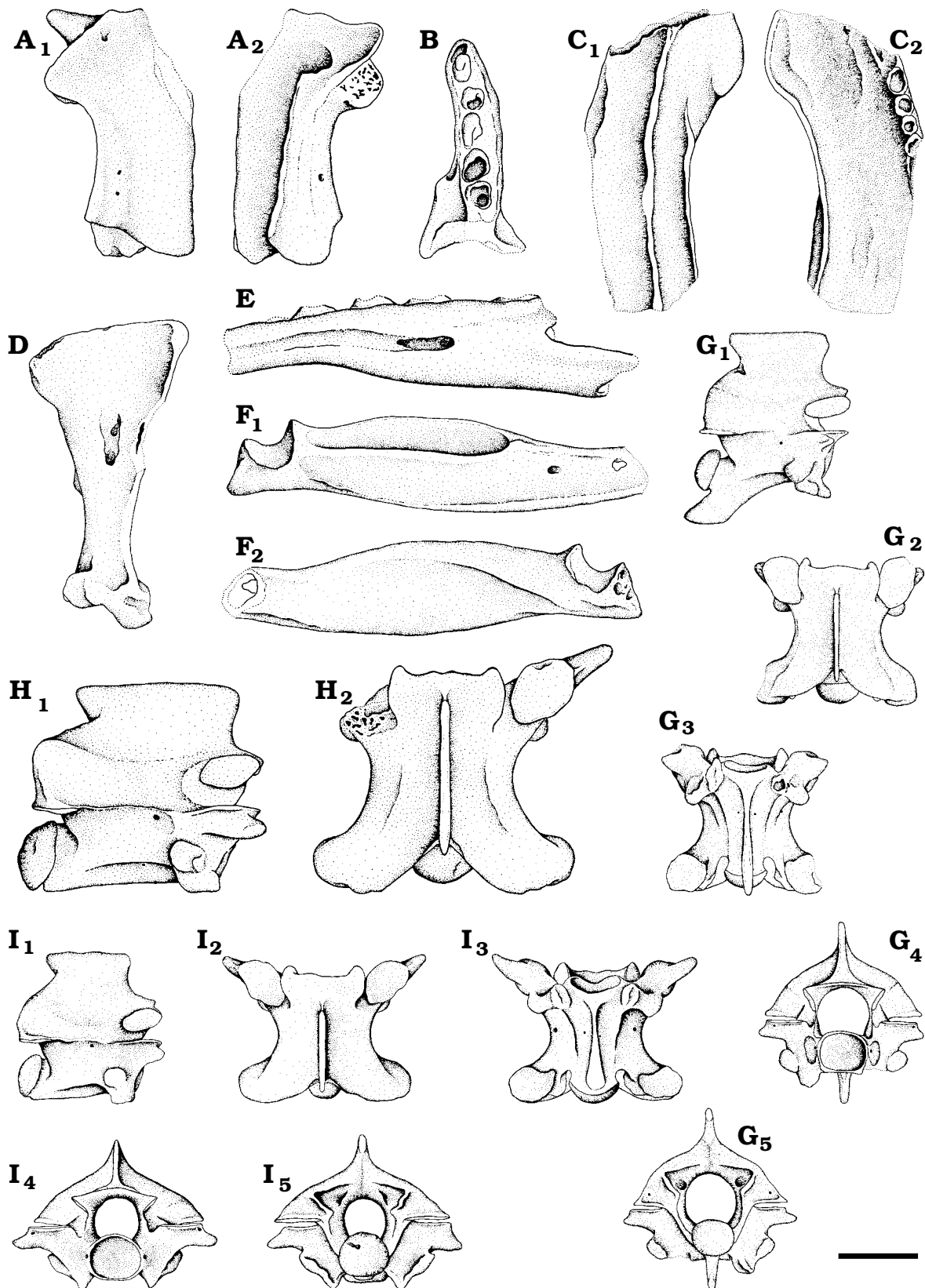


Fig. 5. *Coluber caspioides* Szyndlar and Schleich, 1993 from the Early Miocene (MN 3a) of Merkur-North. **A₁, A₂**, Left frontal (SGDB Ah-44). **B**, Right palatine (SGDB Ah-46). **C₁, C₂**, Right pterygoid (SGDB Ah-45). **D**, Right quadrate (SGDB Ah-1 1). **E**, Left dentary (SGDB Ah-48). **F₁, F₂**, Right compound bone (SGDB Ah-49). **G₁–G₅**, Cervical vertebra (SGDB Ah-51). **H₁, H₂**, Mid-trunk vertebra (SGDB Ah-615). **I₁–I₅**, Posterior trunk vertebra (SGDB 7408/MI-37). In dorsal (**A₁, C₁, G₂, H₂, I₂**), ventral (**A₂, B, C₂, G₃, I₃**), postero-lateral (**D**), labial (**E, F₁**), lingual (**F₂**), lateral (**G₁, H₁, I₁**), cranial (**G₄, I₄**), and caudal (**G₅, I₅**) views. Scale bar 2 mm.

the pterygoid crest and short pterygoid flange are more distinctive in *C. caspioides*.

The quadrate bone is typical of the genus *Coluber* based on its enlarged body near the dorsal crest and the small stapedial process. Unlike the recent representatives, the bone is somewhat shorter and wider. The trochlea quadrati is massively built and is less twisted against the dorsal crest unlike the recent and the known fossil representatives. Unfortunately, we cannot exclude assignment of the quadrate to another member of the genus *Coluber*.

The dentary resembles the genus *Coluber* on the basis of the shape and the position of the mental foramen and the level of enclosure of the Meckel's groove. *C. caspioides* differs from all known recent and fossil representatives based on the distinct groove extending from the mental foramen to the rostral end of the bone.

The compound bone is assigned to the genus *Coluber* on the presence of the distinct supraangular crest and concave labial flange of the mandibular fossa. The labial flange is comparatively high as in the living *C. caspius*. It was not possible to see the orientation of the broken off retroarticular process, therefore, a more precise comparison with other representatives of this genus is not possible. The presence of a low but distinct crest on the lingual side of the bone distinguishes the extinct species *C. caspioides* from other members of the genus *Coluber*.

The assignment of vertebrae to *C. caspioides*, reported originally from the Early Miocene (MN 4) type locality at Petersbuch 2 (Germany), is based on the morphological resemblance to this species (Szyndlar and Schleich 1993). Vertebrae from Merkur-North, originally identified as belonging to Colubrinae A (Ivanov 1997a: 94, fig. 41), resemble the material from Petersbuch 2 especially on the shape of the neural spine and the haemal keel. However, there are several differences: the vertebrae from Merkur-North are smaller and the cranial margin of the zygosphenes is crenate from above and convex in cranial view. On the other hand, the zygosphenes of *C. caspioides* from Petersbuch 2 is straight with a shallow incision in dorsal view and also straight in cranial view. These differences are probably only a result of intraspecific morphological variability because the largest vertebrae of *C. caspioides* from Merkur-North are quite similar to the material from Petersbuch 2.

According to Szyndlar and Schleich (1993), *C. caspioides* could be a member of the lineage leading to the recent species *C. caspius*, however, most of the reported cranial bones of the extinct *C. caspioides* differ significantly from the living representatives of the genus *Coluber* (including *C. caspius*). Therefore, assuming that the referral of cranial bones to the species is accurate, it seems to be more probable that *C. caspioides* is a member of a different, perhaps separate, lineage.

Genus *Elaphe* Fitzinger, 1833

cf. *Elaphe* sp.

Type species: *Elaphe parreyssii* Fitzinger, 1833 = *Elaphe quatuorlineata sauromates* (Pallas, 1811).

Material.—One left dentary (SGDB Ah-168), 50 trunk vertebrae (SGDB Ah-169–215; SGDB Ah-617–619).

Dentary (Fig. 6A₁, A₂).—The caudal part of this gracile, fragmentary bone is broken off. The rostral part is markedly curved medially. The Meckel's groove is completely enclosed at the level of the 4th and 5th teeth. The rostral termination of the notch for the compound bone occurs at the level of the 13th tooth. Because of the fragmentary condition of the bone, it is not possible to determine the number of the teeth.

Trunk vertebrae (Fig. 6B₁–B₅).—In lateral view, the neural spine of the largest vertebra is about 1.5–2 times longer than high and the dorsal margin is not thickened. The cranial margin of the neural spine slightly overhangs anteriorly and the caudal margin overhangs posteriorly. The interzygapophyseal ridges are sharp. The conspicuous lateral foramina are not in depressions. The subcentral ridges are indistinct and slightly arched dorsally. The condyle is situated on a very short neck. The paradiapophyses are distinctly divided and the ventral margin of the parapophyses is rounded with short parapophyseal processes. In dorsal view, the cranial margin of the zygosphenes has distinct lateral lobes, a wide median lobe is also prominent in smaller vertebrae and in the largest vertebrae the median lobe can be absent. The prezygapophyseal articular facets are oval to subtriangular and the prezygapophyseal processes are clearly shorter than the prezygapophyseal facets. The epizygapophyseal spines are well developed. In ventral view, the indistinct subcentral grooves are shallow and the subcentral foramina are very small. The haemal keel expands near the cotylar rim and the paracotylar tubercles are lacking. The rounded subrectangular postzygapophyseal articular facets are enlarged laterally. In cranial view, the neural arch is moderately vaulted and the neural canal is approximately circular with short lateral sinuses. The zygosphenal lip is straight to slightly convex. Paracotylar foramina occur on both sides of the rounded cotyle. Measurements are as follows (n = 20): cl: or = 2.90–4.18 mm; naw: or = 2.31–3.15 mm; cl/naw: or = 1.17–1.43, mean 1.32±0.08.

Comments.—The very fragmentary dentary is identified as probably belonging to the genus *Elaphe* based on the position of the rostral closure of Meckel's groove and the position of the rostral termination of the notch for the compound bone. The mental foramen is very short which is typical for some small representatives of the genus *Elaphe*. Because of the fragmentary condition of the bone, it is not possible to estimate the precise number of teeth in the ramus, thus the identification remains disputable.

The vertebrae have a relatively long neural spine overhanging both anteriorly and posteriorly, pointed prezygapophyseal processes and a crenate zygosphenes (that is convex in cranial view). All of these features are typical for some small extant representatives of the genus *Elaphe*, especially *E. situla*. Vertebrae of cf. *Elaphe* sp. from Merkur-North differ from the majority of the European representatives of the

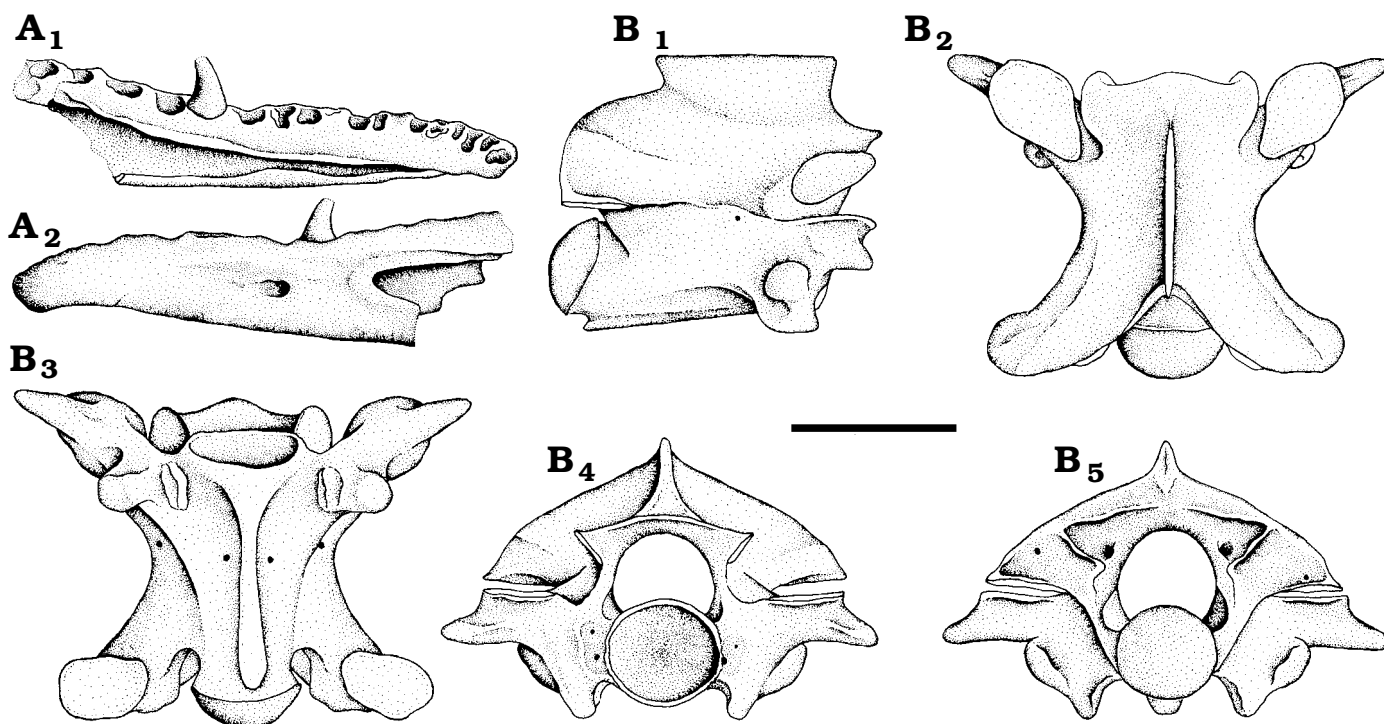


Fig. 6. cf. *Elaphe* sp. from the Early Miocene (MN 3a) of Merkur-North. **A₁**, **A₂**. Left dentary (SGDB Ah-168). **B₁–B₅**. Mid-trunk vertebra (SGDB Ah-215). In lingual (**A₁**), labial (**A₂**), lateral (**B₁**), dorsal (**B₂**), ventral (**B₃**), cranial (**B₄**), and caudal (**B₅**) views. Scale bar 2 mm.

genus *Elaphe* by having well developed epizygapophyseal spines. The precise determination of small representatives of the subfamily Colubrinae is often very difficult without cranial bones (see above). If the vertebrae actually belong to the genus *Elaphe*, then this fossil represents the oldest known record of this genus. At present, the oldest probable representative of *Elaphe* is known from the German Middle Miocene (MN 5/6) Oggenhausen site ("cf. *Elaphe* sp." by Szyndlar and Schleich 1993). The oldest known certain occurrence of the genus *Elaphe*, *Elaphe kansensis* (Gilmore, 1938) is reported from the Middle Miocene of Nebraska (Gilmore 1938; Holman 1964, 2000).

Colubrinae gen. et sp. indet.

Material.—11 trunk vertebrae (SGDB 7408/MI-51–61), 75 precaudal vertebrae (SGDB Ah-216–290).

Trunk vertebrae.—The preserved vertebrae are very fragmentary, mostly with neural spines broken off at their bases and damaged zygapophyses. The hypapophyses of cervical vertebrae are also broken off. Therefore, a more precise determination was not possible.

Subfamily Natricinae Bonaparte, 1838

Genus *Natrix* Laurenti, 1768

Natrix sansaniensis (Lartet, 1851)

(part) *Coluber Sansaniensis*; Lartet 1851: 40.

Pylmophis sansaniensis Lartet; Rochebrune 1880: 282–283, pl. XII: 11.

Pilemophis sansaniensis Rochebrune; Lydekker 1888: 251.

Pylmophis sansaniensis Rochebrune nec Lartet; Mlynarski 1961: 33.

Pylmophis sansaniensis Rochebrune; Kuhn 1963: 29.

Natrix sansaniensis (Lartet); Rage 1981: 538–540, fig. 1A.

Natrix sansaniensis (Lartet); Rage 1984: 48–49, fig. 30A.

Material.—Six compound bones (3 left + 3 right) (SGDB Ah-291–295; SGDB Ah-620), 1 trunk vertebra (SGDB 7408/MI-84), 19 trunk vertebrae (SGDB Ah-296–311; SGDB Ah-621–623).

Compound bone (Fig. 7A₁–A₃, B).—The left compound bone is fragmentary and its rostral part and the retroarticular process are broken off. The labial flange of the comparatively deep mandibular fossa is almost as high as the lingual flange. The labial flange is concave through its entire length and is bordered ventrally by a distinct ridge that extends from distinct supraangular crest to the proximity of the large supraangular foramen. This foramen is situated far from the rostral end of the markedly enlarged mandibular fossa that is narrow in its rostral part. A distinct groove continues anteriorly from the rostral termination of the mandibular fossa. This groove is formed by a connection of the labial and the lingual flange. A low but obvious crest extending from the base of the retroarticular process to the proximity of the rostral end of the mandibular fossa occurs on the inner side of the lingual flange. This crest never reaches the dorsal margin of the lingual flange.

Trunk vertebrae (Fig. 7C₁–C₅).—In lateral view, the neural spine is about 2–3 times longer than high; its cranial margin overhangs anteriorly and the caudal margin overhangs poste-

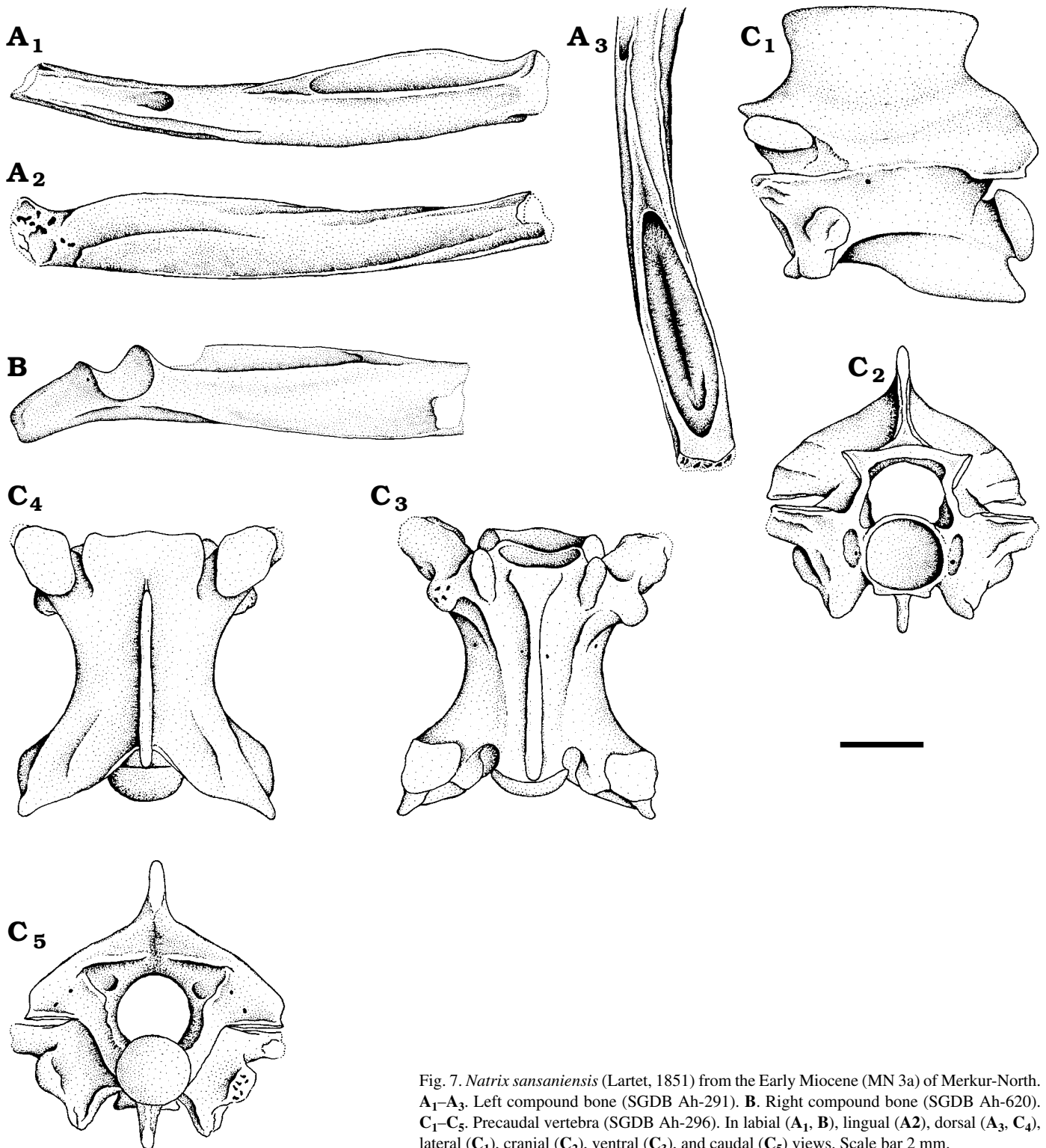


Fig. 7. *Natrix sansaniensis* (Lartet, 1851) from the Early Miocene (MN 3a) of Merkur-North. A₁–A₃. Left compound bone (SGDB Ah-291). B. Right compound bone (SGDB Ah-620). C₁–C₅. Precaudal vertebra (SGDB Ah-296). In labial (A₁, B), lingual (A₂), dorsal (A₃, C₄), lateral (C₁), cranial (C₂), ventral (C₃), and caudal (C₅) views. Scale bar 2 mm.

riorly. The interzygapophyseal ridges are distinct. The lateral foramina are minute and hardly visible and occur in shallow depressions. The paradiapophyses are indistinctly divided and the diapophyses are directed postero-laterally. The parapophyseal processes are short. The subcentral ridges are prominent especially in posterior trunk vertebrae and they

are straight and extend to the short neck on which the rounded condyle occurs. The hypapophysis has a distinct anterior keel, the border of which, slopes postero-ventrally. The distal tip of the hypapophysis is directed caudally. In dorsal view, the zygosphene has distinct lateral lobes and the median lobe is wide and rounded. The enlarged prezygapo-

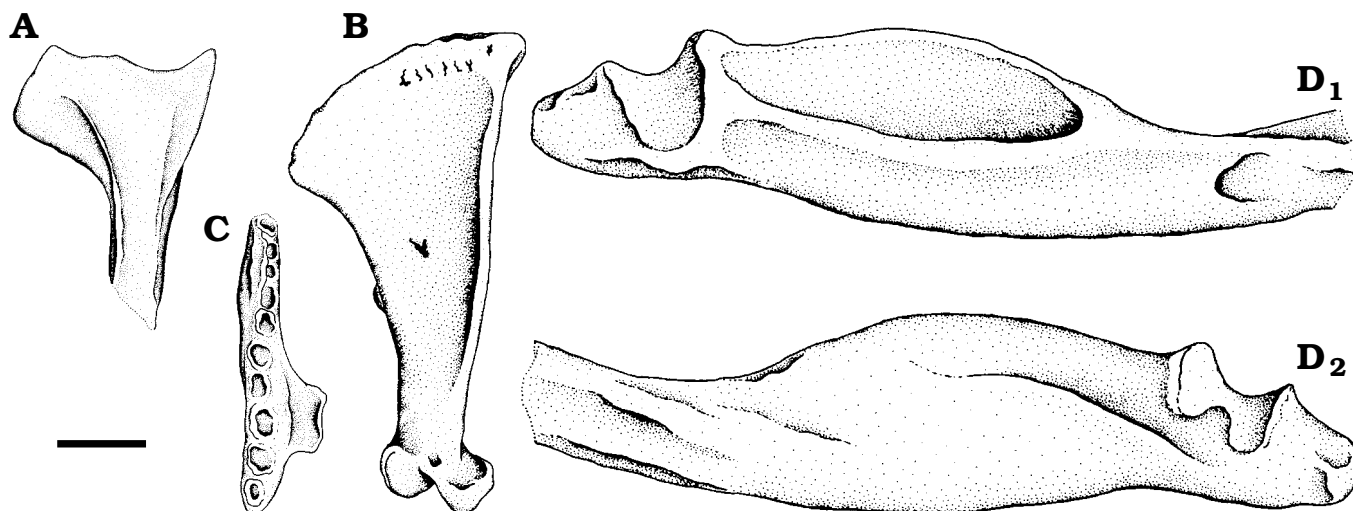


Fig. 8. *Natrix merkuriensis* sp. nov. from the Early Miocene (MN 3a) of Merkur-North. **A**. Left ectopterygoid (SGDB Ah-313, paratype). **B**. Right quadrate (SGDB Ah-312). **C**. Right maxillary (SGDB Ah-314). **D₁**, **D₂**. Right compound bone (SGDB Ah-315, holotype). In dorsal (**A**), postero-lateral (**B**), ventral (**C**), labial (**D₁**), and lingual (**D₂**) views. Scale bar 2 mm.

physeal articular facets are oval to subtriangular and the slender prezygapophyseal processes are obtuse and may be as long or shorter than the prezygapophyseal facets. The epizygapophyseal spines are well developed. In ventral view, the anterior keel of the hypapophysis is triangular anteriorly and the small but distinct subcotylar tubercles are situated at the base of the cotyle. The tiny and hardly visible subcentral foramina occur at the base of the hypapophysis. The laterally slightly enlarged and irregularly shaped postzygapophyseal articular facets are damaged in most vertebrae. In cranial view, the neural arch is moderately vaulted and the neural canal is rounded with distinct lateral sinuses. The cotyle is rounded and distinct paracotylar foramina occur on either side of the cotyle in conspicuous (but sometimes also shallow) depressions. Measurements are as follow ($n = 12$): cl: or = 4.21–5.82 mm; naw: or = 2.52–3.58 mm; cl/naw: or = 1.39–1.80, mean 1.64 ± 0.11 .

Comments.—*Natrix sansaniensis* (Lartet, 1851) represents an extinct species of a small natricine snake. A diagnosis of this taxon including precise description of vertebrae was proposed by Augé and Rage (2000). Extinct species of the genus *Natrix* have not been defined on the basis of cranial bones but only by the structure of vertebrae (with the exception of *Natrix longivertebra* Szyndlar, 1984 and now also of *N. sansaniensis* and *N. merkurensis* sp. nov.). The compound bone resembles especially that of *N. natrix* but there are several differences: 1, the rostral part of the bone is flattened unlike *N. natrix*; 2, the mandibular fossa of *N. sansaniensis* is comparatively longer, narrower and deeper than it is in *N. natrix*; moreover, it markedly narrows in anterior direction in *N. sansaniensis*; 3, the labial flange is higher in *N. sansaniensis* than it is in *N. natrix*; 4, a distinct groove extends from the rostral termination of the mandibular fossa in *N. sansaniensis*; this groove is absent in all living and fossil representatives of *N. natrix*.

The vertebrae (one vertebra was originally assigned to Natricinae C, Ivanov 1997a: 120, fig. 54) are very similar to those of the recent representatives of the genus *Natrix*. The vertebral centra are elongated and the neural spines are very high and overhanging in both anterior and posterior directions. *N. sansaniensis* resembles the recent species *N. tessellata* in having the sigmoid hypapophysis with a pointed distal tip but the prezygapophyseal articular facets are not elongated in *N. sansaniensis*. Vertebrae of *N. sansaniensis* differ from those of the extinct species *N. merkurensis* sp. nov. in having a pointed distal termination of the hypapophysis while in *N. merkurensis* sp. nov. this termination is obtuse. Vertebrae of the extinct species *N. longivertebra* are more elongated, the parapophyseal processes are longer and the hypapophysis extends behind the caudal margin of the condyle. It is possible that *N. sansaniensis* is closely related to the living species *N. natrix*. This is documented not only by the vertebral structure but also by the very similar structure of the compound bone.

Natrix merkurensis sp. nov.

Derivation of the name: merkurensis, from Merkur (name of the type locality).

Type locality: Merkur-North—opencast brown coal mine near Tušimice, Czech Republic.

Stratum typicum: Orleanian (MN 3a). Early Miocene.

Holotype: Fragmentary right compound bone (SGDB Ah-315).

Paratype: 1 left ectopterygoid (SGDB Ah-313), 1 anterior precaudal vertebra (SGDB 7408/MI-62).

Remaining material.—Two (left + right) quadrate (SGDB Ah-312; SGDB Ah-624), 2 right maxillaries (SGDB 7408/MI-102; SGDB Ah-314), 3 (1 left + 2 right) compound bones (SGDB Ah-315–317), 213 precaudal vertebrae (SGDB 7408/MI-63–83; SGDB 7408/MI-96–98; SGDB Ah-318–504; SGDB Ah-625), 8 caudal vertebrae (SGDB Ah-505–511; SGDB Ah-626).

Diagnosis.—A large natricine snake assigned to the genus *Natrix* on the basis of: 1, the presence of a distinct crest on the dorsal surface of the external ramus; 2, the relatively low flanges of the mandibular fossa; 3, the supraangular foramen situated far from the rostral end of the mandibular fossa; 4, the morphology of vertebrae that are closely similar to the recent representatives of this genus. The compound bone most resembles that of the recent *N. natrix* but it differs by a more massive structure and the higher labial flange of the mandibular fossa. It differs from all recent and fossil (*N. longivertebra*, *N. sansaniensis*) species in having very prominent crest on the inner side of the lingual flange of the mandibular fossa. The vertebrae are similar to those of *N. longivertebra* and *N. natrix* but *N. merkurensis* sp. nov. differs from all recent and fossil members of the genus *Natrix* in having a much more higher neural spine (with exception of *N. sansaniensis*). *N. merkurensis* sp. nov. differs from *N. sansaniensis* on the basis of: 1, the larger size; 2, the rounded distal tip of the hypapophysis; 3, the enlarged prezygapophyseal articular facets in precaudal vertebrae.

Description of the holotype

Right compound bone (Fig. 8D₁, D₂).—The rostral part is broken off. The labial flange of the mandibular fossa is comparatively low and the border of this flange is concave in the proximity of the facet for articulation with the quadrate. The supraangular crest is distinct and long. The lingual flange is about 1.5 times higher than the labial one. The retroarticular process is strong and its pointed distal end is curved medially. The supraangular foramen occurs far from the rostral termination of the mandibular fossa. In lingual view, a very distinct and prominent crest occurs on the lingual flange; this crest extends from the ventral margin of the retroarticular process to the proximity of the antero-dorsal termination of the lingual flange.

Description of paratypes

Ectopterygoid (Fig. 8A).—The bone is fragmentary and its caudal part is lacking. The external ramus of the maxillary articulation is convex and rectangular. A distinct crest is developed on the dorsal surface of the external ramus and this crest turns and extends along the outer side of the bone body. The internal ramus forms about a right angle with the external ramus.

Anterior precaudal vertebra (Fig. 9A₁–A₅).—The vertebra is fragmentary with broken off hypapophysis, the right prezygapophyseal process, and the right parapophyseal process. In lateral view, the neural spine is almost as long as high. Its cranial margin overhangs anteriorly and the caudal margin overhangs posteriorly. Interzygapophyseal ridges are distinct. The distinct lateral foramina occur in shallow depressions. The subcentral ridges are prominent and are arched dorsally. The parapophyses and diapophyses are distinctly separated from each other and the diapophyses are about as large as the parapophyses. The diapophyses are directed lat-

erally in dorsal view. The left parapophyseal process is directed anteriorly. The distinct and deep hypapophysis is broken off near its base. In dorsal view, the cranial margin of the crenate zygosphenon has expanded median lobe. The left prezygapophyseal articular facet is widely oval, the right facet is partially fragmentary. The antero-laterally directed left prezygapophyseal process is longer than the prezygapophyseal facet. The epizygapophyseal spines are prominent. In ventral view, the subcentral grooves are shallow. The subcentral foramina are minute. The anterior keel of the hypapophysis is triangularly expanded and the very distinct subcotylar tubercles are developed at the ventral side of the cotylar rim. The postzygapophyseal articular facets are irregularly shaped. In cranial view, the neural arch is moderately vaulted and the neural canal is rounded and the zygosphenon is straight. The small paracotylar foramina lie in depressions on either side of the rounded cotyle.

Description of the remaining material

Quadrate (Fig. 8B).—In postero-lateral view, the bone is wide and flat. The bone body is wide in the proximity of the trochlea quadrati and it expands towards the dorsal crest. The dorsal crest is thin and lacks dorso-ventral widening. The quadrate crest is prominent especially in the middle of the bone length. The stapedial process is distinct but it is not well demarcated from the bone.

Maxillary (Fig. 8C).—In the more complete bone, the rostral part, including the prefrontal process is broken off. The ectopterygoid process is distinct, as long as wide, is directed medially and its medial part is curved ventrally. The teeth are not preserved; 9 tooth sockets occur on the fragmentary row. The last 2–3 tooth sockets are markedly larger and a gap in the tooth row is lacking.

Compound bone.—The bones are fragmentary and their rostral and caudal terminations are broken off. They do not differ from the holotype.

Precaudal vertebrae (Fig. 9B₁–B₅).—It is difficult to distinguish between cervical and trunk vertebrae in the subfamily Natricinae. Therefore, both are discussed under the heading of “precaudal vertebrae”. Precaudal vertebrae do not differ significantly from the paratype. The vertebrae from the anterior part of the column differ from the posterior precaudal vertebrae generally by the higher neural spine and the deeper hypapophysis. The dorsal margin of the neural spine is usually distinctly thickened and both its cranial and caudal extremities may be slightly bifurcate. However, most of neural spines and all hypapophyses are broken off. The zygosphenon is straight to slightly convex in cranial view. In caudal view, the small (often paired) parazygantral foramina may be visible. Measurements are as follow (n = 25): cl: or = 5.05–6.86 mm; naw: or = 2.98–4.25 mm; cl/naw: or = 1.53–2.00, mean 1.67±0.11.

Caudal vertebrae (Fig. 9C₁–C₄).—All vertebrae are dam-

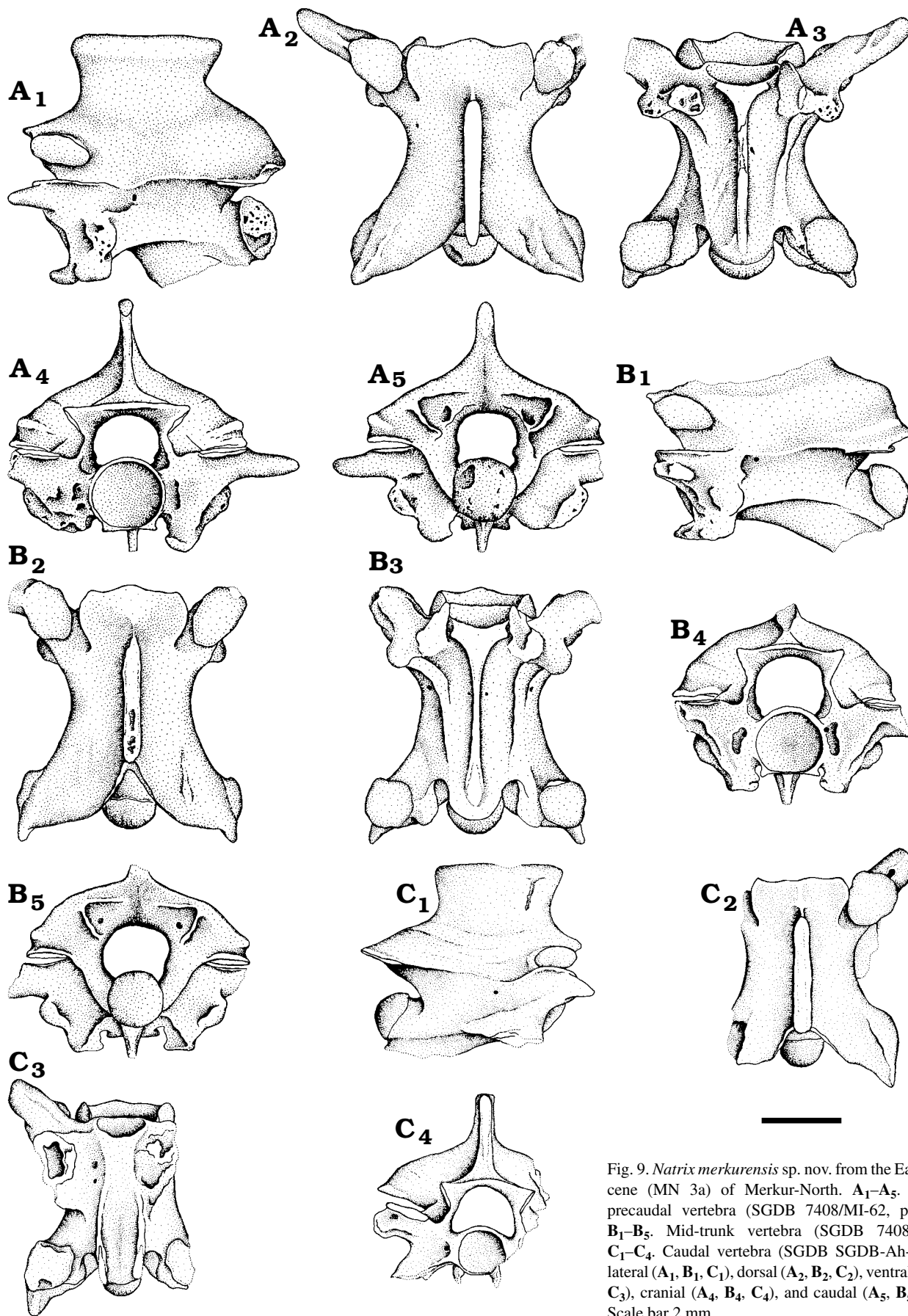


Fig. 9. *Natrix merkurensis* sp. nov. from the Early Miocene (MN 3a) of Merkur-North. A₁–A₅. Anterior pre-caudal vertebra (SGDB 7408/MI-62, paratype). B₁–B₅. Mid-trunk vertebra (SGDB 7408/MI-75). C₁–C₄. Caudal vertebra (SGDB SGDB-Ah-505). In lateral (A₁, B₁, C₁), dorsal (A₂, B₂, C₂), ventral (A₃, B₃, C₃), cranial (A₄, B₄, C₄), and caudal (A₅, B₅) views. Scale bar 2 mm.

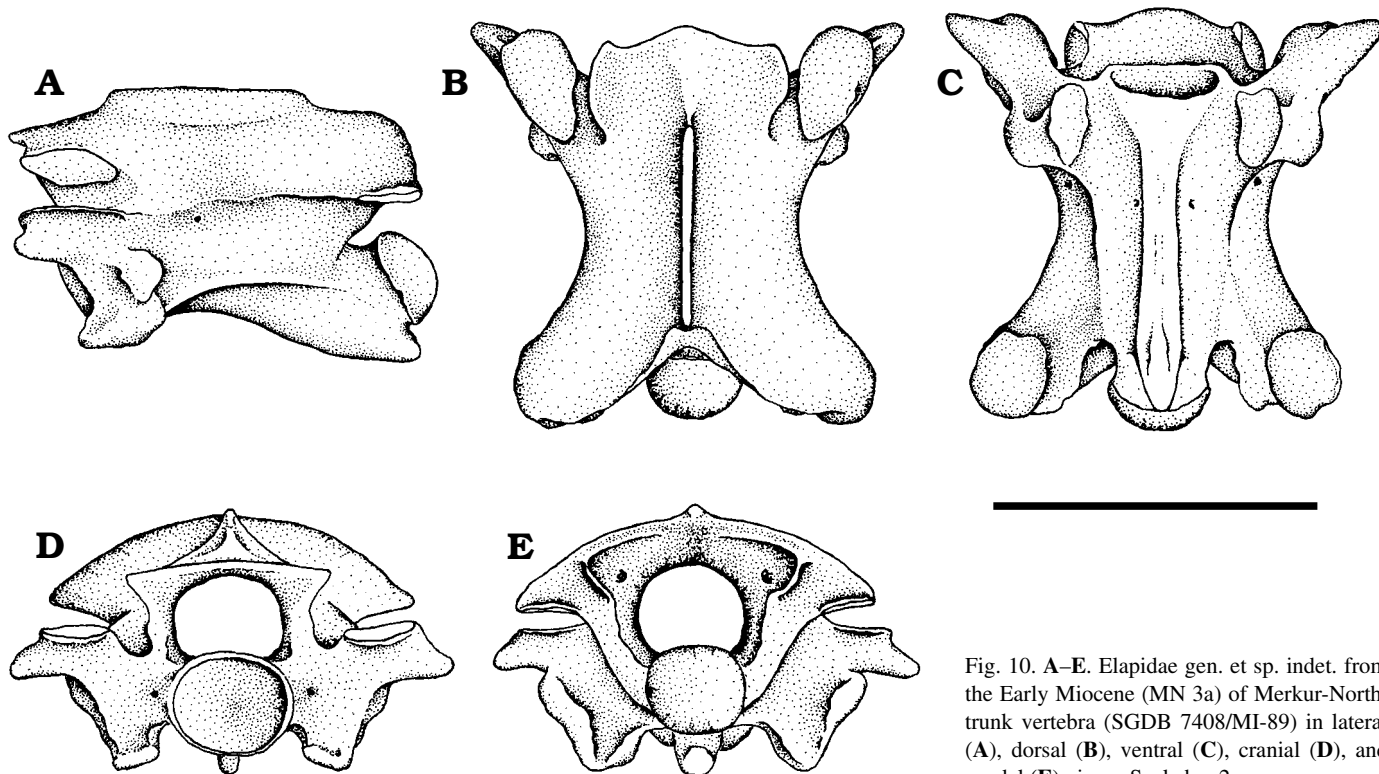


Fig. 10. A–E. Elapidae gen. et sp. indet. from the Early Miocene (MN 3a) of Merkur-North; trunk vertebra (SGDB 7408/MI-89) in lateral (A), dorsal (B), ventral (C), cranial (D), and caudal (E) views. Scale bar 2 mm.

aged and both haemapophyses and lymphapophyses are broken off at their bases. The rarely preserved prezygapophyseal processes are about as long as the widely oval prezygapophyseal articular facets. The cranial margin of the zygosphenon in anterior caudal vertebrae has distinct lateral lobes and the medial lobe is usually indistinct. In posterior caudal vertebrae, the zygosphenal lip is straight.

Comments.—The quadrate is assigned to the genus *Natrix* on the basis of the presence of the thin dorsal crest and the small stapedial process that is indistinctly demarcated from the bone. The quadrate of *Natrix merkurensis* sp. nov. differs from that of the recent representatives (*N. natrix*, *N. tessellata*, *N. maura*) and the extinct *N. longivertebra* on the basis of the trochlea quadrati which is slightly bent ventrally. The bone is massively built thus is assigned to *N. merkurensis* rather than to *N. sansaniensis*.

The ectopterygoid, whose widely rectangular external ramus and pointed internal ramus of the maxillary articulation form an obtuse angle, is generally similar to the ectopterygoid of the recent genus *Natrix*. The ectopterygoid of *N. merkurensis* differs from all recent representatives and *N. longivertebra* in having a distinct crest on the dorsal surface of the external ramus. The bone is massive and relatively large and therefore it can be assigned rather to *N. merkurensis* than to *N. sansaniensis*.

The very fragmentary maxillary with a preserved ectopterygoid process especially resembles that of the recent species of the genus *Natrix*. It cannot be excluded the assignment of this bone to the extinct species *N. sansaniensis*. For the as-

signation of the compound bone to *N. merkurensis* see “Diagnosis”.

Precaudal vertebrae, originally assigned to *Natrix* aff. *sansaniensis* (Ivanov 1997a: 102, fig. 47), are identified as belonging to the genus *Natrix* on the basis of the presence of hypapophyses and the shape of the neural spine whose cranial margin overhangs anteriorly and the caudal margin which overhangs posteriorly. *N. merkurensis* has strongly elongated vertebral centra with prominent subcentral ridges and it differs from all recent and fossil representatives of this genus (with the exception of *N. sansaniensis*) on the basis of the very high neural spine. Vertebrae of *N. merkurensis* are practically identical to the vertebrae of “*Natrix* aff. *N. sansaniensis*” reported from Petersbuch 2 (Szyndlar and Schleich 1993). Therefore, it may be reasonably assumed that *N. merkurensis* sp. nov. from Merkur-North and “*Natrix* aff. *N. sansaniensis*” from Petersbuch 2 represent a single species.

Several fossil representatives of the genus *Natrix* were reported from the European Cenozoic: *Natrix mlynarskii* Rage, 1988 (MP 22) (Rage 1988), *Natrix sansaniensis* (Lartet, 1851) (MN 4–MN 6) (Rage 1981; Szyndlar and Schleich 1993; Augé and Rage 2000), *Natrix longivertebra* Szyndlar, 1984 (MN 7+8–MN16) (Szyndlar 1984, 1991b, c), and *Natrix parva* Szyndlar, 1984 (Szyndlar 1984). New discoveries at Merkur-North indicate that a part of the material from Merkur-North belongs to the new species *N. merkurensis* and that the remaining determinable material probably belongs to *N. sansaniensis*. A single lineage *N. mlynarskii*–*N. sansaniensis* and *N. longivertebra* (Szyndlar and Schleich 1993)

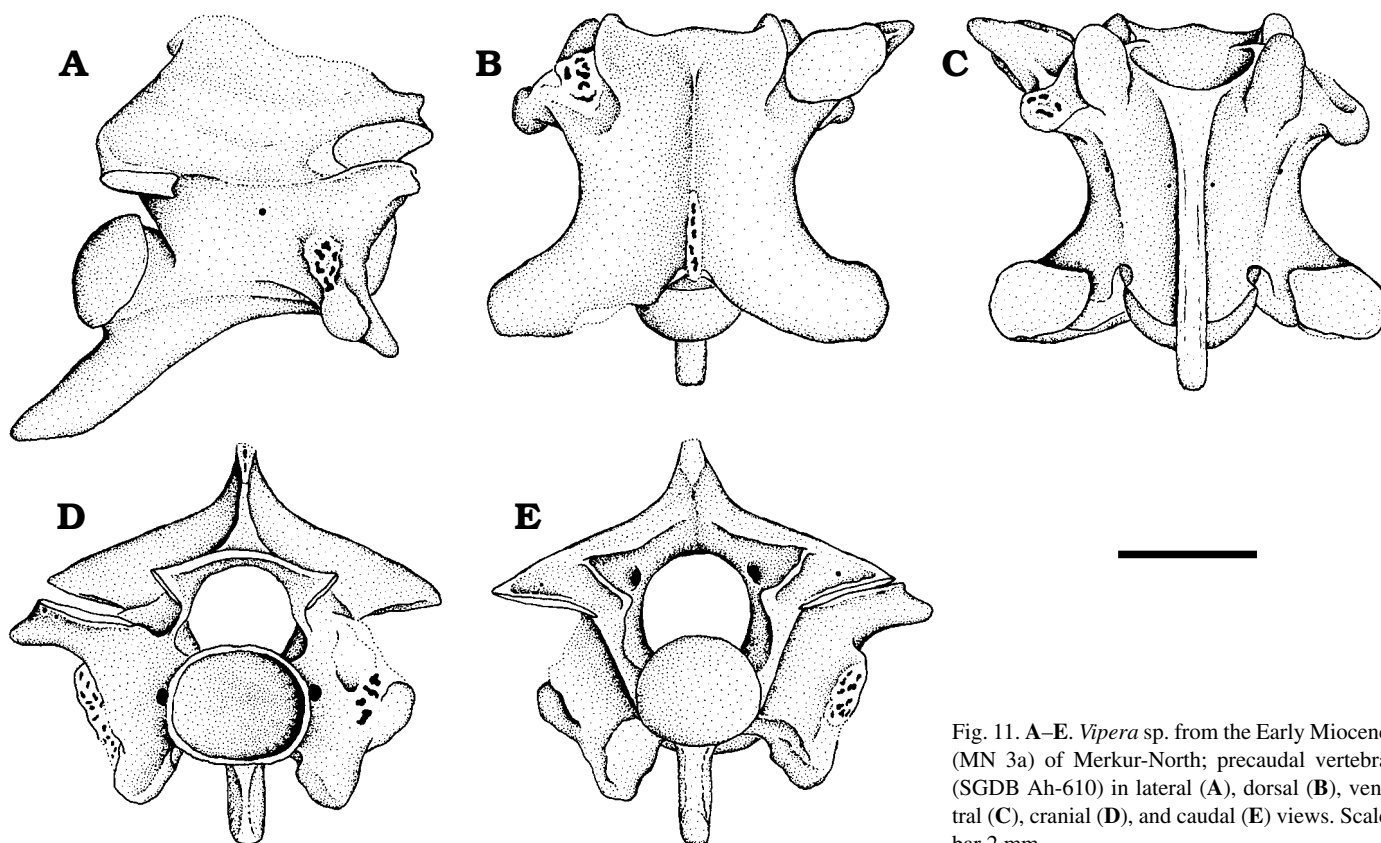


Fig. 11. A–E. *Vipera* sp. from the Early Miocene (MN 3a) of Merkur-North; precaudal vertebra (SGDB Ah-610) in lateral (A), dorsal (B), ventral (C), cranial (D), and caudal (E) views. Scale bar 2 mm.

can be neither supported nor excluded. The discovery of *N. merkurensis* complicates this situation. The compound bone of the new described species differs markedly from remaining representatives of the genus *Natrix*, thus it can be suggested that *N. merkurensis* represents an evolutionary side branch.

Natricinae gen. et sp. indet.

Material.—83 precaudal vertebrae (SGDB 7408/MI-85–88; SGDB Ah-512–580; SGDB Ah-627–636).

Precaudal vertebrae.—The material is fragmentary and all taxonomically important structures are completely missing or heavily damaged. The assignment to the subfamily Natricinae is based on both the presence of hypapophyses in precaudal vertebrae and the triangularly expanded anterior keel.

Colubridae gen. et sp. indet.

Material.—17 precaudal vertebrae (SGDB Ah-581–597), 9 caudal vertebrae (SGDB Ah-598–603; SGDB 7408/MI-103–105).

Precaudal and caudal vertebrae.—All vertebrae are fragmentary and a more precise determination was not possible.

Family Elapidae Boie, 1827

Elapidae gen. et sp. indet.

Material.—Three trunk vertebrae (SGDB 7408/MI-89–91), 6 trunk vertebrae (SGDB Ah-604–609).

Trunk vertebrae (Fig. 10A–E).—In lateral view, the neural spine is very low and does not overhang either anteriorly nor posteriorly. The interzygapophyseal ridges are strongly developed and the lateral foramina usually occur in depressions (with exception of posterior trunk vertebrae). The paradiapophyses are clearly divided and the diapophysis is much more smaller than the parapophysis. The parapophyseal processes are short. The subcentral ridges are very short and arched dorsally and in posterior trunk vertebrae are longer and strongly developed. The hypapophysis is very short and its distal tip is situated close to the anterior margin of the condyle. The condyle has a short neck. In dorsal view, the cranial margin of the zygosphenal lip has distinct lateral lobes and the prominent median lobe is wide. The prezygapophyseal articular surfaces are obovate and the prezygapophyseal processes are short and pointed. The epizygapophyseal spines are missing. In ventral view, the subcentral ridges of the anterior trunk vertebrae are indistinct and the subcentral grooves are underdeveloped. In posterior trunk vertebrae, both the subcentral ridges and subcentral grooves are strongly developed. The subcentral foramina are shifted anteriorly and occur at the base of the wide hypapophysis. The hypapophysis distinctly deepens toward the condyle and the anterior keel is not triangularly expanded. The post-

zygapophyseal articular surfaces are obovate. In cranial view, the neural arch is slightly regularly vaulted, the neural canal is approximately circular with lateral sinuses, and the zygosphenal lip is convex. Distinct foramina occur at the base of the prezygapophyseal processes. The large paracotylar foramina occur in depressions on either side of the circular cotylar rim. In posterior trunk vertebrae the depressions for paracotylar foramina become deeper. Measurements are as follows ($n = 6$): cl: or = 2.21–3.01 mm; naw: or = 1.57–2.21 mm; cl/naw: or = 1.34–1.59, mean 1.47 ± 0.09 .

Comments.—The vertebrae are very small. The assignment to Elapidae gen. et sp. indet. (morphotype Elapidae A *sensu* Ivanov 1997a: 134–135, fig. 62) is based on the presence of hypapophyses in trunk vertebrae, very low neural spines, vaulted neural arches, and anteriorly directed parapophyseal processes. Therefore, the vertebrae probably belong to small cobra taxa. Several small elapids are reported from the German and French Early and Middle Miocene localities: *Micrurus gallicus* Rage and Holman, 1984, “*Micrurus gallicus* Rage and Holman, 1984”, Elapidae A (Rage and Holman 1984; Szyndlar and Schleich 1993; Ivanov 2000a). *Micrurus* sp. is reported from the Middle Miocene of Nebraska and the Late Miocene of Florida (Holman 1977b, 2000). Representatives of the recent species *M. fulvius* are known from many Pleistocene localities in Florida and Texas (Holman 1981b, 1995, 2000). Elapidae gen. et sp. indet. (very similar to the morphotype Elapidae A, reported from the French Early/Middle Miocene, MN 4/5 locality at Vieux-Collonges, Ivanov 2000a) resembles extinct species *M. gallicus* in having elongated vertebral centra, the shape of the zygosphenal lip, and the relatively deep caudal notch. The hypapophysis is directed caudally but in *M. gallicus* the hypapophysis is shorter. Elapidae gen. et sp. indet. differs from *M. gallicus* especially by its very low and indistinct neural spine and shorter prezygapophyseal processes (see also Ivanov 2000a). The vertebrae of Elapidae gen. et sp. indet. are most similar to the vertebrae of Elapidae indet. from the German Early Miocene (MN 4) locality at Petersbuch 2 compared to the genera *Micrurus* and *Maticora* (Szyndlar and Schleich 1993; Szyndlar unpubl. data). Therefore, we can agree with assumption of Szyndlar and Schleich (1993) that the vertebrae from Petersbuch 2 (and now also from Merkur-North) belong to small “euproteroglyphous” elapids—i.e., subfamilies Calliophinae, Maticorinae or Elapinae. A more precise evaluation of taxonomic status of Elapidae gen. et sp. indet. cannot presently be made because of the lack of recent comparative material. Elapidae gen. et sp. indet. from Merkur-North (MN 3a) represents the oldest known member of this family.

Family Viperidae Oppel, 1811
 Subfamily Viperinae Oppel, 1811
 Genus *Vipera* Laurenti, 1768
Vipera sp.
 (“*Vipera aspis* complex”)

Type species: Vipera Francisci Redi Laurenti, 1768 = *Vipera aspis* (Linnaeus, 1758).

Material.—Three precaudal vertebrae (SGDB Ah-610–612).

Precaudal vertebrae (Fig. 11A–E).—All vertebrae are damaged and the neural spine is always broken off at the base. In lateral view, the distinct long hypapophysis is directed postero-ventrally. The interzygapophyseal ridges are indistinct and blunt as are the subcentral ridges. The well visible lateral foramina are small and do not lie in depressions. The paradiapophyses are distinctly divided and the parapophyses are situated anterior to the diapophyses. The slender parapophyseal processes are directed antero-ventrally. The condyle has a very short neck. In dorsal view, the cranial margin of the zygosphenal lip has distinct lateral lobes and the median lobe is also distinct. The prezygapophyseal articular surfaces are irregularly shaped and the prezygapophyseal processes are short and pointed. The epizygapophyseal spines are absent. In ventral view, the minute and nearly indiscernible subcentral foramina occur at the base of the hypapophysis. The subcentral grooves are underdeveloped. The postzygapophyseal articular surfaces are irregularly tetragonal and enlarged laterally. In cranial view, the neural arch is flattened and the neural canal is rounded with shallow lateral sinuses. The cranial margin of the zygosphenal lip is convex. The relatively large paracotylar foramina occur in depressions on both sides of the rounded cotyle. The paracotylar tubercles are missing or underdeveloped. Measurements of the two most complete vertebrae are as follows: smaller vertebra: cl = 3.69 mm; naw = 2.93 mm. The metrical measurements of the larger vertebra are as follows: cl = 3.95 mm; naw = 3.20 mm.

Comments.—Based on the dorso-ventrally strongly depressed neural arch, antero-ventrally directed prezygapophyseal processes and the long slender hypapophysis the vertebrae were assigned to the living genus *Vipera*. The vertebrae are small with low ratio cl/naw; therefore, they were assigned to the “*Vipera aspis* complex” (the informal name *sensu* Groombridge 1986). *Vipera* sp. from Merkur-North resembles especially the extinct species *Vipera antiqua* Szyndlar, 1987 from the Bohemian locality at Dolnice (MN 4) and the German locality at Petersbuch 2 (MN 4) (Szyndlar 1987; Szyndlar and Schleich 1993). The oldest unquestionable record of the genus *Vipera* from the German lowermost Miocene (MN 1) locality of Weisenau most probably belongs to *V. antiqua* (“*Vipera* cf. *V. antiqua*”, cf. Szyndlar and Schleich 1993) (Szyndlar and Rage 1999).

Composition of the Central European snake fauna during the Early Miocene

The Merkur-North locality is of interest mainly because of the relatively high diversity of its snakes (Table 1). The Euro-

Table 1. Representatives of the families Boidae, Colubridae (Colubrinae + Natricinae), Elapidae and Viperidae from Merkur-North and some other Miocene localities of Czech Republic, Germany and France. Data concerning localities Dolnice, Petersbuch 2, and Vieux Collonges according to Szyndlar (1987), Szyndlar and Schleich (1993), and Ivanov (2000a).

		Merkur (MN 3a)	Dolnice near Cheb (MN 4)	Petersbuch 2 (MN 4)	Vieux Collonges (MN 4/5)
BOIDAE	<i>Python</i> sp.	-	-	-	361
	<i>Bavarioboa hermi</i>	-	14	275	-
	<i>Bavarioboa</i> sp.	14	-	-	-
	<i>Bransat. septentrionalis</i>	-	7	434	-
	<i>Eryx</i> sp.	-	-	-	6
	Boidae B	-	-	-	2
	Boidae C	-	-	-	4
Boidae indet.	-	-	3	-	
COLUBRINAE	<i>Coluber dolnicensis</i>	52	3	-	-
	<i>Coluber suevicus</i>	22	-	-	-
	<i>Coluber caspioides</i>	140	-	675	-
	<i>Texasophis bohemicus</i>	-	3	-	-
	<i>Texasophis</i> sp.	-	-	-	7
	cf. <i>Elaphe</i> sp.	51	-	-	-
	Colubrinae gen. et sp. indet.	11	-	-	444
NATRICINAE	<i>Palaeonatrix lehmani</i>	-	14	19	-
	<i>Neonatrix nova</i>	-	63	-	-
	<i>Neonatrix</i> cf. <i>europaea</i>	-	-	-	7
	cf. " <i>Neonatrix</i> " sp.	-	-	63	-
	<i>Natrix sansaniensis</i>	26	-	-	-
	<i>Natrix</i> aff. <i>sansaniensis</i>	-	-	158	2
	<i>Natrix merkurensis</i> sp. nov.	229	-	-	-
	Natricinae A	-	-	-	35
	Natricinae B	-	-	-	2
	Natricinae C	-	-	-	24
	Natricinae D	-	-	-	4
	Natricinae gen. et sp. indet.	83	-	-	147
	Natricinae indet.	-	-	461	-
ELAPIDAE	<i>Micrurus gallicus</i>	-	-	27	-
	<i>Micrurus</i> aff. <i>gallicus</i>	-	-	-	1
	<i>Naja romani</i>	-	-	642	-
	<i>Naja</i> cf. <i>romani</i>	-	-	-	37
	<i>Naja</i> sp. 1	-	-	-	56
	Elapidae A	-	-	-	2
	Elapidae B	-	-	-	17
	Elapidae gen. et sp. indet.	9	-	-	235
Elapidae indet.	-	-	16	-	
VIPERINAE	<i>Vipera platyspondyla</i>	-	8	872	-
	<i>Vipera antiqua</i>	-	6	794	-
	<i>Vipera</i> sp.	3	-	-	-
	Viperinae A	-	-	-	12
	Viperinae B	-	-	-	2

pean snake fauna underwent a massive adaptive radiation in the Early Miocene as a result of optimal climatic conditions and this is especially the case in family Colubridae (Ivanov et al. 2000). The Miocene snake radiation strongly contrasts with that of the Oligocene period, when the relatively cool climate prevailed and small representatives of the family Boidae (especially the subfamily Erycinae) predominated (Rage 1987, 1988; Szyndlar 1994). Nevertheless, the Oligocene is considered an important period in the evolution of the modern European snake fauna because the first repre-

sentatives of Colubridae immigrated into Central Europe (most probably through the Mazury-Mazowsze continental barrier) and West Europe (across the Rhine Graben) as early as the Early Oligocene (MP 22) (Ivanov 1997a, b, 2000b). Subsequently, the representatives of the family Colubridae gradually replaced the ancient snake fauna (especially of Boidae) in Europe. The Early Miocene collision between Eurasia and Africa allowed the exchange of faunas with West Europe (Rage and Augé 1993) and similarly the modern Asiatic taxa gradually colonized East European areas. The erycine snakes, represented in the Miocene by the genera *Eryx*, *Bransateryx*, and *Albaneryx* are the most common representatives of the family Boidae. The taxonomic position of non-erycine boids remains unknown in most cases with exception of *Bavarioboa hermi* (subfamily Boinae) from the Bohemian locality of Dolnice and some German localities (Szyndlar and Schleich 1993) and the genus *Python* sp. from the French Vieux Collonges locality (Ivanov 2000a). The vertebrae of *Bavarioboa* sp. from the Merkur-North locality most resemble the only member of this genus *Bavarioboa hermi* which were reported first from the German Early Miocene (MN 4) type locality at Petersbuch 2 (Szyndlar and Schleich 1993). *Bavarioboa* sp. from Merkur-North represents the earliest distinct occurrence of this genus (Fig. 12). Several morphotypes reported from Germany (Boinae B & C from Ehrenstein 7—MP 27) are regarded as belonging to cf. *Bavarioboa* sp. (Szyndlar and Schleich 1993).

Discoveries of representatives of the family Colubridae are relatively scarce in stages MN 1—MN 3 (cf. "*Coluber cadurci*" from Germany, MN 1, and ?*Coluber cadurci* from France, MN 2) (cf. Szyndlar and Schleich 1993).

The first appearance of a rich colubrid fauna have been reported from the Early Miocene (MN 4) localities at Dolnice and Petersbuch 2 (Szyndlar 1987; Szyndlar and Schleich 1993). The study at the Bohemian Early Miocene Merkur-North locality (MN 3a), which is the oldest known Miocene ophidian locality in Central and East Europe, shows a considerable representation of the family Colubridae (compared with the family Boidae—cf. Rage 1987) as early as the stage MN 3a (Table 1). The snake assemblage at Merkur-North especially resembles the assemblages of the Early Miocene (MN 4) localities at Dolnice and Petersbuch 2. This is supported by the presence of the genus *Bavarioboa*, the species *Coluber dolnicensis*, *Coluber caspioides*, *Natrix sansaniensis* and the species *Natrix merkurensis* sp. nov. Surprisingly, there is a considerable representation of colubrids in comparison with other snake families together, especially rare vipers (Table 1). Szyndlar and Schleich (1993) generally considered the Early Miocene colubrids very similar to the recent species. However, the colubrids from Merkur-North differ from the living species which is especially true for *Coluber caspioides* that was known only from the type locality at Petersbuch 2 (Szyndlar and Böhme 1993) and *Natrix merkurensis* sp. nov. Both mentioned species probably represent the side evolutionary lineages in the evolution leading to the extant representatives of Colubridae.

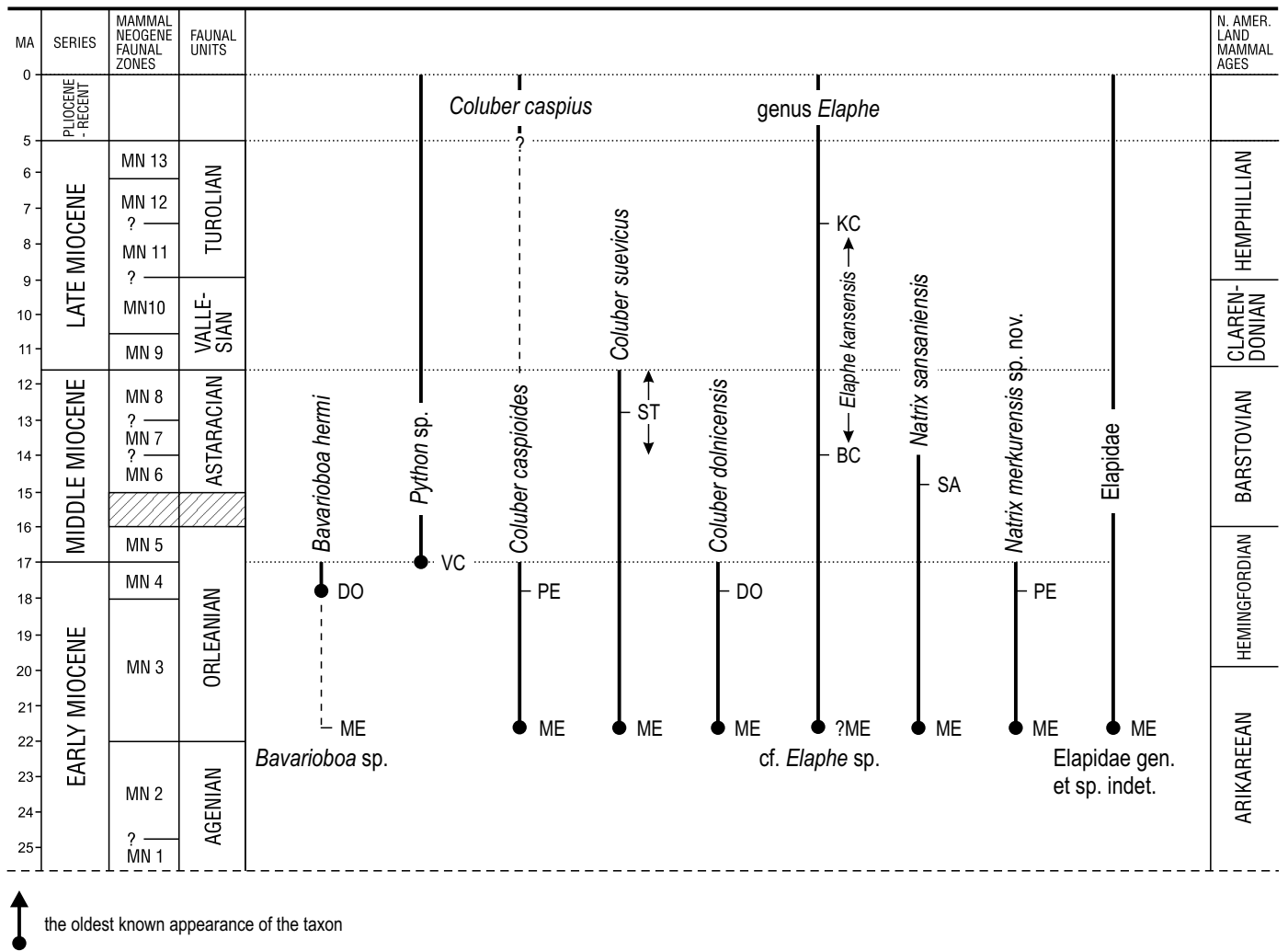


Fig. 12. Stratigraphic range of some representatives of families Boidae, Colubridae, and Elapidae. Abbreviations: ME, Merkur-North; DO, Dolnice; PE, Petersbuch 2; VC, Vieux Collonges; SA, Sansan; ST, Steinheim am Albuch; BC, Brown County (Nebraska, USA); KC, Keith County (Nebraska, USA). Several taxa appeared first (FAD, first appearances date) at Merkur-North: *Coluber caspioides*, *Coluber suevicus*, *Coluber dolnicensis*, probably the genus *Elaphe* (cf. *Elaphe* sp.), *Natrix sansaniensis*, *Natrix merkurensis* sp. nov., and family Elapidae. “*Natrix* aff. *N. sansaniensis*” from Petersbuch 2 (MN 4) (Szyndlar and Schleich 1993) probably represents *N. merkurensis* sp. nov. Data according to Szyndlar (1987), Szyndlar and Schleich (1993), Ivanov (2000a, 2001), Augé and Rage (2000) and Holman (2000). Stratigraphic correlations according to Steininger et al. (1996) and Kelly (1998).

The oldest known representatives of the family Elapidae have been reported from the European Early Miocene, Germany: *Naja romani*, *Micrurus gallicus* (Szyndlar and Schleich 1993); Spain: *Naja* sp. (Alfárez and Brea 1981). Elapidae gen. et sp. indet. from the Bohemian Merkur-North locality (MN 3a) (Table 1) probably represents the oldest known representative of the family Elapidae (Fig. 12). Elapidae gen. et sp. indet. most resembles the diversified genus *Micrurus* (inhabiting today the area of North and South America) and less diversified genus *Maticora* (inhabiting today the area of South-Eastern Asia). Because of the absence of large cobras (genus *Naja*) at Merkur-North, it is possible to suggest that small elapids appeared in Europe somewhat earlier than large elapids.

Remains of *Vipera* sp. from Merkur-North are comparable with *Vipera antiqua*; this species represents most proba-

bly the oldest known member of the genus *Vipera* (Szyndlar and Böhme 1993). Based on the fossil record, representatives of the “*Vipera aspis* complex” appeared in Europe somewhat earlier (MN 1) than the “Oriental vipers” group (informal name *sensu* Groombridge 1986) (MN 4) (Antunes and Rage 1974; Szyndlar and Rage 1999).

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