Snakes from Griesbeckerzell (Langhian, Early Badenian), North Alpine Foreland Basin (Germany), with comments on the evolution of snake faunas in Central Europe during the Miocene Climatic Optimum

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ABSTRACT

Two fossil-bearing levels at Griesbeckerzell (the central part of the North Alpine Foreland Basin; Early Badenian, Mittlere Serie of the Upper Freshwater Molasse) have produced a rich reptile fauna that includes a large number of snakes, i.e. Grisbeckerzell 1b (OSM E, 15.0-14.9 Ma): Boidae: *Python* sp.; Colubridae: "*Coluber*" cf. *caspioides*; Viperidae: *Vipera* sp. ("oriental vipers" group) or *Daboia* sp.; Griesbeckerzell 1a (beginning of unit OSM F, 14.77 Ma): Boidae: *Bavarioboa* aff. *hermi*, cf. *Bavarioboa* sp., *Python* sp.; Colubridae: "*Coluber*" cf. *caspioides*, *Coluber hungaricus*, "*Coluber*" sp., *Texasophis* cf. *meini*, *Natrix* sp.; Elapidae: *Micrurus* cf. *gallicus*; Viperidae: *Vipera* sp. ("Oriental vipers" group), *Vipera* sp. ("European vipers" group; "*Vipera aspis* complex"). The Miocene Climatic Optimum (MCO) is documented in central Europe by the presence of highly thermophilous reptile taxa, including *Python* sp., which is the most thermophilous reptile known from the European Neogene. The presence of *Python* sp. in Griesbeckerzell 1a pushes up the last appearance date (LAD) of this large Booidea in central Europe into the early Middle Miocene. The dramatic decrease in temperatures after 14.0 Ma (i.e. below 16°C in mean annual air temperature) was most probably responsible for the extinction of the European non-Erycinae Booidea, regardless of food competition. The genus *Bavarioboa* (*Bavarioboa* aff. *hermi*) and possibly "*Coluber*" *caspioides* ("*Coluber*" cf. *caspioides*) both have their LADs in Griesbeckerzell 1a; *Coluber hungaricus* probably represents the earliest appearance (FAD) of this colubrid snake. Palaeoclimatic analyses of the herpetofauna indicate for both Griesbeckerzell levels humid conditions of between 750 and 1 025 mm mean annual precipitation. Temperature estimates combined with palaeobotanical data indicate a warm, subtropical climate with mean annual temperatures of 18.6 to 20.8°C, cold month temperatures with 12.6 to 13.3°C, and warm month temperatures with 25.1 to 28.1°C.

KEY WORDS
Squamata,
Boidae,
Colubridae,
Elapidae,
Viperidae,
Miocene Climatic Optimum,
North Alpine Foreland Basin,
palaeoclimate.

RÉSUMÉ

Serpents de Griesbeckerzell (Langhien, Badénien inférieur), Bassin de l'avant-pays nord-alpin (Allemagne). Commentaires sur l'évolution des faunes de serpents en Europe centrale pendant l'Optimum Climatique du Miocène.

Deux niveaux fossilifères de Griesbeckerzell (partie centrale du Bassin de la Molasse du Sud de l'Allemagne, Badénien inférieur, Mittlere Serie de la Molasse d'eau douce supérieure) ont livré une riche faune de reptiles qui contient un grand nombre de serpents : Griesbeckerzell 1b (OSME, 15,0-14,9 Ma) : Boidae : *Python* sp. ; Colubridae : « *Coluber* » cf. *caspioides* ; Viperidae : *Vipera* sp. (groupe des « vipères orientales ») ou *Daboia* sp. ; Griesbeckerzell 1a (début de l'unité biostratigraphique OSM F, 14,77 Ma) : Boidae : *Bavarioboa* aff. *hermi*, cf. *Bavarioboa* sp., *Python* sp. ; Colubridae : « *Coluber* » cf. *caspioides*, *Coluber hungaricus*, « *Coluber* » sp., *Texasophis* cf. *meini*, *Natrix* sp. ; Elapidae : *Micrurus* cf. *gallicus* ; Viperidae : *Vipera* sp. (groupe des « vipères orientales »), *Vipera* sp. (groupe des « vipères européennes » ; « complexe *Vipera aspis* »). L'Optimum Climatique du Miocène (Miocene Climatic Optimum) est documenté par la présence de reptiles extrêmement thermophiles, dont *Python* sp., qui est le reptile le plus thermophile du Néogène européen. La présence de *Python* sp. à Griesbeckerzell 1a remonte la date de la dernière occurrence (last appearance date) de ce grand Booidea en Europe centrale au début du Miocène Moyen. La chute dramatique de la température après 14,0 Ma (température moyenne annuelle de l'air inférieure à 16°C) fut probablement responsable de l'extinction des Booidea européens, hors Erycinae, la compétition trophique n'étant pas prise en compte. Le genre *Bavarioboa* (*Bavarioboa* aff. *hermi*) et probablement « *Coluber* » *caspioides* (« *Coluber* » cf. *caspioides*) ont tous deux leur LAD à Griesbeckerzell 1a; *Coluber hungaricus* de ce niveau représente probablement la plus ancienne occurrence (First appearance date) de ce serpent colubridé. Les analyses paléoclimatiques relatives à l'herpétofaune indiquent des conditions humides pour les deux niveaux de Griesbeckerzell (entre 750 et 1025 mm de précipitation annuelle moyenne). Les estimations de températures, associées aux données paléobotaniques, indiquent un climat subtropical chaud avec des températures annuelles comprises entre 18,6 et 20,8°C, des températures du mois le plus froid atteignant 12,6 à 13,3°C et des températures du mois le plus chaud oscillant entre 25,1 et 28,1°C.

MOTS CLÉS
Squamata,
Boidae,
Colubridae,
Elapidae,
Viperidae,
Optimum climatique du Miocène,
bassin d'avant-pays nord-alpin,
paléoclimat.

INTRODUCTION

The Miocene Climatic Optimum (MCO) was initially defined in the oceanic record (Flower & Kennett 1994) and shows also a marked signal in continental biota (Böhme 2003). It represents the temporary return of the (para-)tropical humid climate in central Europe (e.g., Böhme 2003) after the relatively cool (and dry) Oligocene period (Mosbrugger *et al.* 2005). The MCO last from the Early Miocene (~17

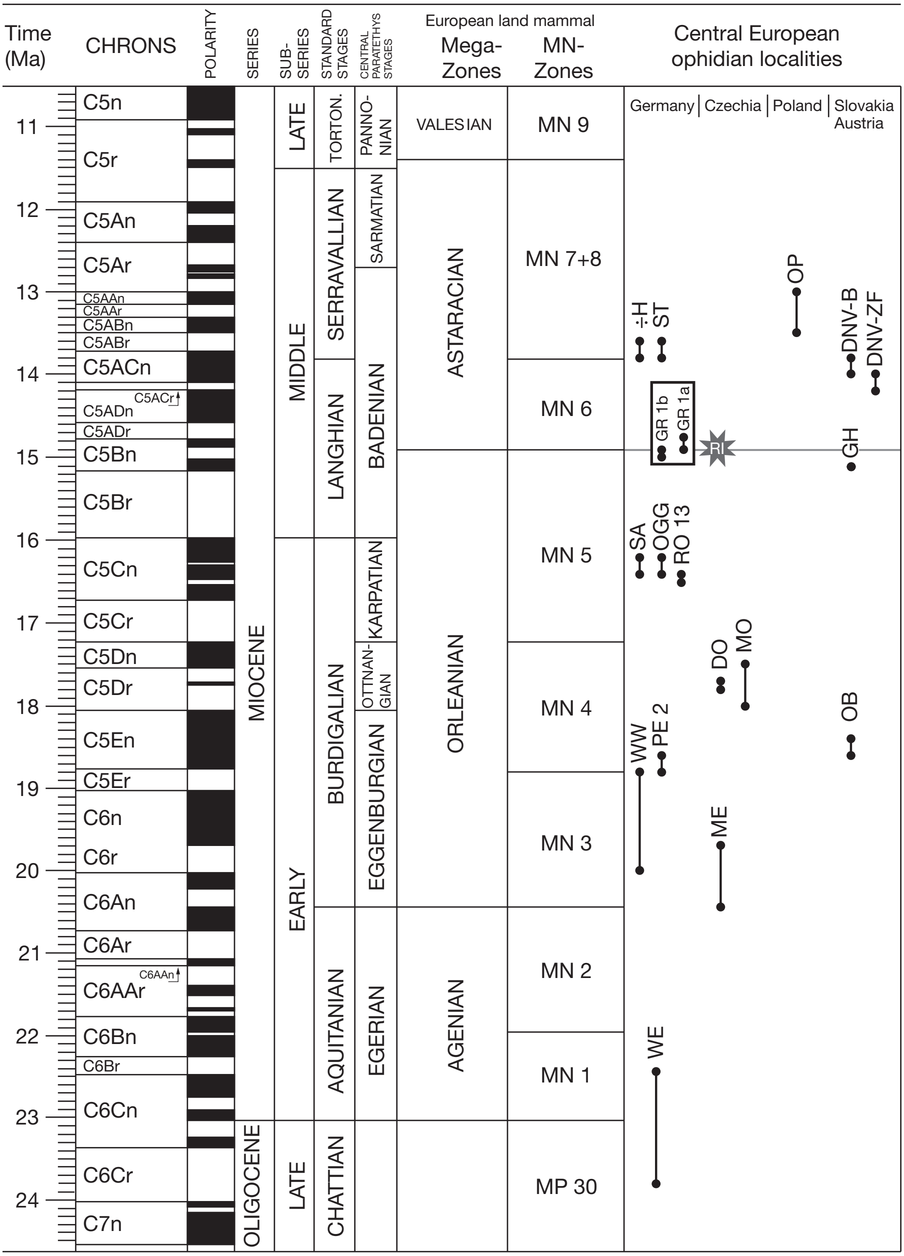

FIG. 1. — Standard chronostratigraphy and biostratigraphy of the European Miocene with the stratigraphical position of the Early and Middle Miocene ophidian localities. Localities: Germany: **WE**, Weisenau; **WW**, Wintershof-West; **PE 2**, Petersbuch 2; **SA**, Sandelzhausen; **RO 13**, Rothenstein 13; **OGG**, Oggenhausen; **GR 1a**, Griesbeckerzell 1a; **GR 1b**, Griesbeckerzell 1b; **ÖH**, Öhningen; **ST**, Steinheim a. Albuch; Czechia: **ME**, Merkur-North; **DO**, Dolnice; **MO**, Mokrá-Western Quarry; Poland: **OP**, Opole 2; Slovakia: **DNV-B**, Devínska Nová Ves-Bonanza; **DNV-ZF**, Devínska Nová Ves-Zapfe Fissures; Austria: **OB**, Oberdorf; **GH**, Grund near Hollabrun. Chronostratigraphy and palaeomagnetism according to Gradstein *et al.* (2008). The ages have been determined based on various sources (e.g., the latest work on the NAFB by Abdul Aziz *et al.* 2009) and reflect the knowledge of the second author. However, the exact age of many localities remains a matter of debate. Abbreviation: **RI** (in asterisk), Ries Impact. Data according to Böhme (2003), Böhme & Ilg (2003), Ivanov (1998, 2002a, 2006, unpublished data), Szyndlar (1987, 1991a, b, 1998, 2009), Szyndlar & Schleich (1993), Szyndlar & Böhme (1993).

Ma) to the early Middle Miocene (~14 Ma) and represents, beside the Miocene Thermal Maximum around 17.8-17.7 Ma (Böhme & Winklhofer 2008), the warmest period of the Neogene (Zachos *et al.* 2001). Most of the central European Paleogene snake groups, especially the Boidae (with the exception of subfamily Erycinae), were extruded by Asiatic immigrants before the end of the MCO (e.g., Rage & Holman 1984; Szyndlar & Schleich 1993; Ivanov 2002a; Szyndlar & Rage 2003). The early Middle Miocene (Langhian, Early Badenian) is believed to represent the last period during which non-Erycinae Boidae occur in central Europe (Szyndlar & Rage 2003). Although the late Early and Middle Miocene herpetofaunas of Germany are generally well documented, snake fossils from this period of time are still nearly unknown with the exception of several well documented localities, including Sandelzhausen (Late Karpatian, latest Burdigalian; Szyndlar 2009), Öhningen (Late Badenian, early Serravallian), and Steinheim a. Albuch (Late Badenian, early Serravallian; Szyndlar & Böhme 1993) (Fig. 1). In this paper, we compare the relatively diversified herpetofauna, especially the snakes, from Griesbeckerzell 1a and 1b with herpetological assemblages from other central European localities.

GEOLOGICAL SETTING AND BIOSTRATIGRAPHY

The abandoned sand pit of Griesbeckerzell is located approximately 6 km ESE of Aichach (14 km NE of Augsburg; coordinates 48°26'36.96"N, 11°2'39.84"E) in the central part of the North Alpine Foreland Basin (NAFB) (Fig. 2). The strata exposed in this sand pit (~480 to ~495 m asl) represent channel fill sediments of the Early Badenian Mittlere Serie of the Upper Freshwater Molasse (Abdul Aziz *et al.* 2008). Lithostratigraphically they can be assigned to the younger part of the Fluviatile Untere Serie lithostratigraphic unit (Fig. 2; Doppler 1989; Abdul Aziz *et al.* 2010). The geologic situation of the region has been described by Fiest (1989) for the areas around Gallenbach and Unterneul, situated 5 km SW of Griesbeckerzell. Fiest (1989) discriminates two main sedimentary units: the unit of Unterneul positioned below the Brock horizon (limestone boulder horizon, originating from the Ries meteoritic impact, for details see Böhme *et al.* 2001), and the unit of Gallenbach above the Brock horizon. The section of Griesbeckerzell belongs to the Unterneul sedimentary unit and terminates with the Brock horizon on top. Two fossil-bearing levels occur within the unit: Griesbeckerzell 1a represents the Brock horizon itself and Griesbeckerzell 1b represents fine-grained sands that occur about six to eight meters below the Brock horizon (sand horizon of the Unterneul unit according to Fiest [1989]). Biostratigraphically the lower fossil layer belongs to the regional unit OSM E that is characterized by the cricetids *Megacricetodon lappi* (Mein, 1958) and *Cricetodon meini* Freudenthal, 1963 (Abdul Aziz *et al.* 2008, 2010; Prieto *et al.* 2009), which is also confirmed by the occurrence of jaw fragments of *Cricetodon* aff. *meini* in Griesbeckerzell 1b. Fossil localities of the Brock horizon lacking fossils of the large-sized lineage of *Megacricetodon* Fahlbusch, 1964 are placed at the beginning of unit OSM F (Heissig 1989, 1997; Böhme *et al.* 2001; Abdul Aziz *et al.* 2008). According to the new palaeomagnetic and radiometric dating of the Ries impact event (Abdul Aziz *et al.* 2008), Griesbeckerzell 1a probably is approximately 14.77 Ma (14.88 ± 0.11 Ma for the Ries impact and chron C5ADr for sediments containing the Brock horizon) in age, whereas the sediments of the unit OSM E correlate to chron C5Bn.1r (Abdul Aziz *et al.* 2008), thus suggesting an age of between 15.0 and 14.9 Ma for Griesbeckerzell 1b (Fig. 3).

FISH- AND HERPETOFAUNA OF GRIESBECKERZELL (TABLE 1)

The channel-fill sands from both Griesbeckerzell levels contain a rich and comparatively diverse fish fauna, represented by abundant teeth, as well as cranial and postcranial bones. Together with other fully aquatic vertebrates they represent the typical association for relatively fast flowing meandering rivers of the Fluviatile Untere Serie lithostratigraphic unit (Prieto *et al.* 2009). The most characteristic elements from both levels include the large-sized *Barbus* s.l. sp. B, *Palaeoleuciscus* sp. A and *Channa* sp. (represented

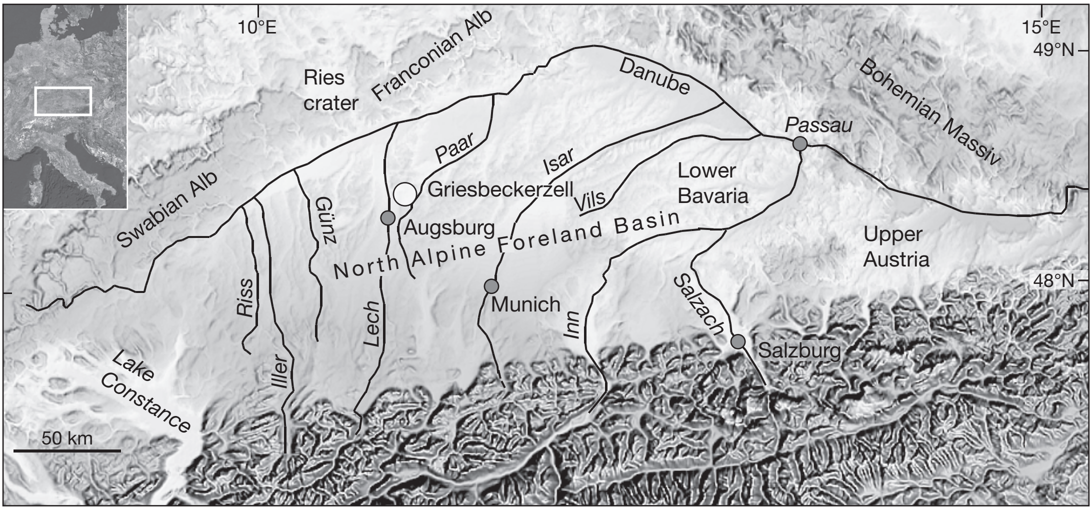

FIG. 2. — Digital elevation model of southern Germany (from Kuhlemann *et al.* 2006), indicating the geographic position of Griesbeckerzell.

probably by several species), as well as *Mioproteus caucasicus* Estes & Darevsky, 1977 and *Trionyx* sp. Another typical fluvial taxon is the seabass *Morone* sp., which frequently enters the rivers of the North Alpine Foreland Basin from the Mediterranean Sea, but may also occur in lacustrine sediments (e.g., localities Pfaffenzell, Unterwohlbach; Böhme & Ilg 2003).

Amphibians are relatively diversified (eight species), but only known from Griesbeckerzell 1a. The association, which includes the genera *Mioproteus* Estes & Darevsky, 1977*, Chelotriton* Pomel, 1853, *Salamandra* Laurenti, 1768*, Pelophylax* Fitzinger, 1843, *Latonia* Meyer, 1843*, Eopelobates* Parker, 1929, *Pelobates* Wagler, 1830*, Bufo* Laurenti, 1768, is regarded as typical for the Upper Freshwater Molasse during the Miocene Climatic Optimum.

Chelonians are represented by the soft-shell turtle *Trionyx* sp. and the pond turtle *Mauremys* sp., the tortoise *Testudo* sp., and the giant tortoise *Geochelone* sp. (only from Griesbeckerzell 1a). Also common are fossils of the small alligatorid *Diplocynodon styriacus* (Hofmann, 1885). Squamate reptiles (except snakes) are dominated (Klembara *et al.* 2010) by *Pseudopus laurillardi* (Lartet, 1851), whereas *Ophisaurus* sp., lacertids, and skinks are relatively rare. Interesting is the presence of a dental and a frontal bone of a possible cordylid lizard. This thermophilous family is quite common in the late Early Miocene (Roček 1984; Böhme 2002, 2010), but was not previously reported from Middle Miocene deposits of Europe.

MATERIAL AND METHODS

The fossils of ophidians from Griesbeckerzell are kept in the collection of the Bayerische Staatssammlung für Geologie und Paläontologie in Munich, Germany. The fossil assemblage is composed exclusively of isolated vertebrae, which are fragmentary and mostly poorly preserved. Identification down to species level therefore remains problematic in many instances. The vertebrae terminology follows Hoffstetter & Gasc (1969) and Szyndlar (1984).

ABBREVIATIONS

BSPG	Bayerische Staatsammlung für Paläontologie und Geologie, Munich;
CMT	annual air temperatures;
FAD	first appearance date;
LAD	last appearance date;
MAT	annual air temperatures;
MCO	Miocene climatic optimum;
WMT	warm month temperature.

Measurements (see Szyndlar 1984)

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

Anatomical abbreviations

cd	condyle;
ct	cotyle;
dia	diapophysis;
es	epizypapophyseal spine;
hae	haemapophysis;
hk	haemal keel;
hy	hypapophysis;
lf	lateral foramen;
na	neural arch;
nc	neural canal;
ns	neural spine;
pa	parapophysis;
pctf	paracotylar foramen;
ple	pleurapophysis;
pr	prezygapophysis;
prf	prezygapophyseal articular facet;
prp	prezygapophyseal process;
po	postzygapophysis;
pof	postzygapophyseal articular facet;
pp	parapophyseal process;
scf	subcentral foramen;
scr	subcentral ridge;
scg	subcentral groove;
syn	synapophysis;
zy	zygosphene;
zyg	zygantrum.

SYSTEMATICS

Infraorder ALETHINOPHIDIA Nopcsa, 1923
Superfamily Booidea Gray, 1825
Family Boidae Gray, 1825

Genus *Bavarioboa* Szyndlar & Schleich, 1993

Type species. — *Bavarioboa hermi* Szyndlar & Schleich, 1993.

Bavarioboa* aff. *hermi
Szyndlar & Schleich, 1993

Material examined. — 2 trunk vertebrae (BSPG 1997 XIII 499, 500); 1 cloacal vertebra (BSPG 1997 XIII 501).

Locality. — Griesbeckerzell 1a.

Description

Trunk vertebrae (Fig. 4A)

In lateral view, the more complete vertebra (BSPG 1997 XIII 499) is slightly higher than long. The neural spine is low and short, occupying about one third of the neural arch length. It was not possible to observe the typical dorsal thickening of the neural spine because the dorsal tip is not preserved, but we assume that at least in one vertebra the dorsal thickening was not developed. The lateral foramina are indistinct. The short interzygapophyseal ridges are sharp. The paradiapophyses are damaged; the subdivision into para- and diapophysis is indistinct. The diapophysis originally was much more smaller than the parapophysis. The relatively straight or slightly dorsally arched subcentral ridges are strongly developed and reach the condylar base. The ventral margin of the haemal keel is arched dorsally.

In dorsal view, the vertebrae are wider than long. The prezygapophyseal articular facets are subtriangular and elongated in lateral direction. Prezygapophyseal processes are not visible from above. The cranial margin of the zygosphene is almost straight; sometimes two small lateral lobes are developed. The base of the neural spine rises at the level of the posterior margin of the prezygapophyseal articular facets. The posterior end of the neural spine is widened. The interzygapophyseal constriction is moderately deep.

In ventral view, the centrum is slightly wider than long. The prominent haemal keel is limited by the deep subcentral grooves. Subcentral foramina are small and situated at the base of the anterior part of the haemal keel. The subtriangular to oval postzygapophyseal articular facets are strongly laterally elongated.

In cranial view, the zygosphene is straight and is either as wide as the cotyle or markedly wider. In one vertebra the zygosphenal lip is thickened. The cotylar rim is circular; paracotylar foramina in deep depressions are absent.

In caudal view, the neural arch is weakly vaulted, and the condyle is rounded and situated on a short neck. Measurements of the larger vertebra are as follows: cl = 5.37 mm; naw = 6.32 mm.; cl/naw = 0.85.

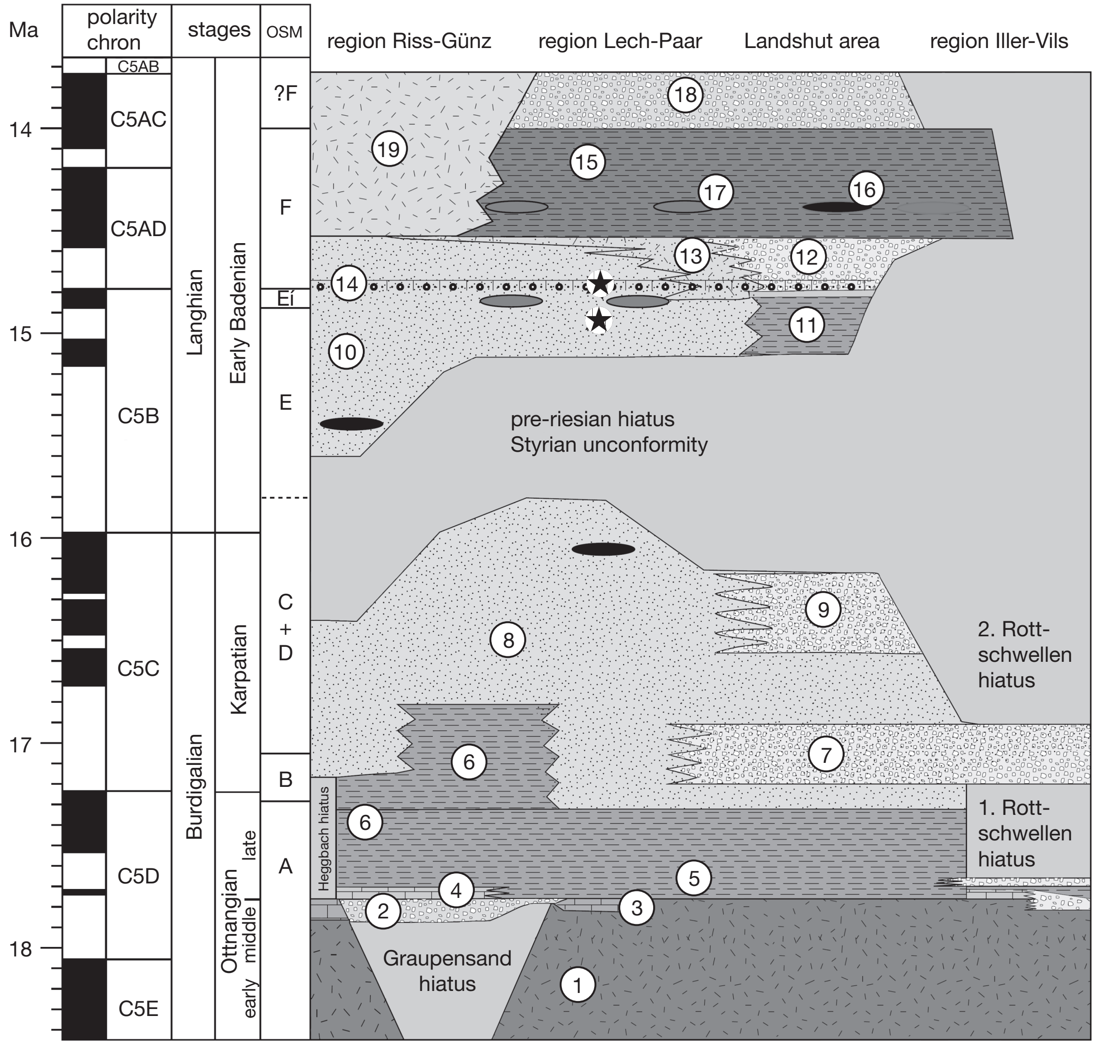

FIG. 3. — Synoptical chart of the chronology for the Early to Middle Miocene lithostratigraphic units in the Bavarian part of the NAFB (modified from Abdul Aziz *et al*. 2010) and stratigraphic position of the Griesbeckerzell localities (★): **1**, Marine Molasse; **2**, Grimmelfingen beds; **3**, Albstein; **4**, Kirchberg Formation; **5**, Sand-Kalkmergel-Serie and untere Bunte Mergel Serie; **6**, Limnische Untere Serie; **7**, Nördlicher Vollschotter, lower part; **8**, Fluviatile Untere Serie; **9**, Nördlicher Vollschotter, upper part; **10**, Fluviatile Untere Serie; **11**, Zwischenmergel; **12**, Nördlicher Vollschotter, upper part; **13**, Geröllsand Serie; **14**, Brock-horizon; **15**, Sand-Mergel-Decke; **16**, dated volcanic ash; **17**, undated volcanic ash; **18**, Lower Laimering Series, Ubergangsschichten; **19**, Steinbalmensande.

Cloacal vertebra (Fig. 4B)

A single fragmentary vertebra is preserved with broken off prezygapophyses. Bases of the incipient haemapophyses occupy unusually anterior position. They are developed at the ventral margin of the haemal keel, which is typical for the cloacal region of the vertebral column.

DISCUSSION

Although paracotylar foramina are absent, the vertebrae can be assigned to the Boinae based on the relatively small dimensions (compared with Miocene Pythoninae Fitzinger, 1826, e.g., *Python europaeus* Szyndlar & Rage, 2003 [cf. Ivanov 2000; Szyndlar & Rage 2003]) and several typical features of the genus

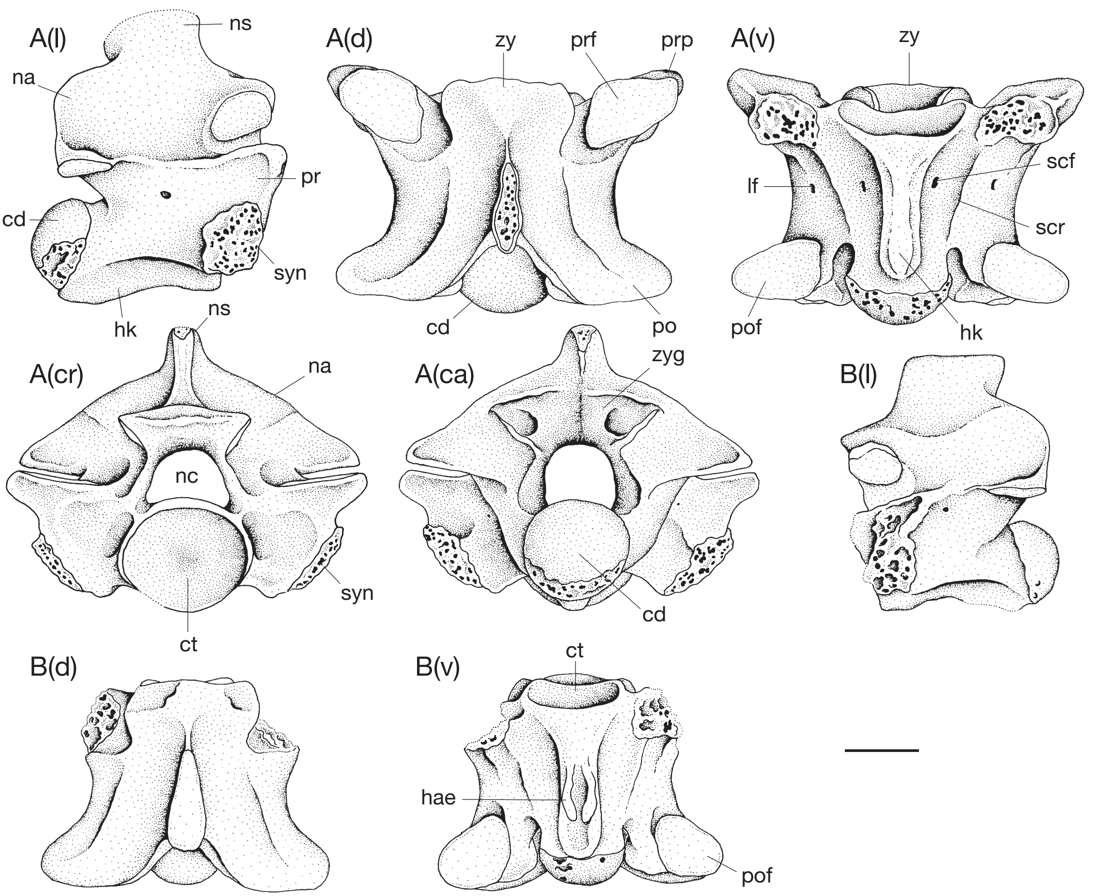

FIG. 4. — *Bavarioboa* aff. *hermi* from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a in lateral (**l**), dorsal (**d**), ventral (**v**), cranial (**cr**), and caudal (**ca**) views: **A**, middle trunk vertebra (BSPG 1997 XIII 499); **B**, cloacal vertebra (BSPG 1997 XIII 501). Abbreviations: **cd**, condyle; **ct**, cotyle; **hae**, haemapophysis; **hk**, haemal keel; **lf**, lateral foramen; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pr**, prezygapophysis; **prf**, prezygapophyseal articular facet; **prp**, prezygapophyseal process; **po**, postzygapophysis; **pof**, postzygapophyseal articular facet; **scf**, subcentral foramen; **scr**, subcentral ridge; **syn**, synapophysis; **zy**, zygosphene; **zyg**, zygantrum. Scale bar: 2 mm.

Bavarioboa. The general morphology concurs with that of *Bavarioboa*, including the absence of dorsal thickening of the neural spine in the middle trunk vertebrae, the straight cranial margin of the zygosphene in cranial view, and the weakly vaulted neural arch (cf. Szyndlar & Rage 2003). Vertebrae of *Bavarioboa* aff. *hermi* resemble those of *Bavarioboa hermi* from the type locality Petersbuch 2, Germany (Early Miocene, late Eggenburgian) in the following features: 1) the cranial margin of the zygosphene is straight and small lateral lobes may occur; 2) the haemal keel is widened posteriorly, especially in one specimen of a posterior precaudal vertebra; and 3) the neural spine of trunk vertebrae is not thickened. However, the trunk vertebrae are somewhat lower compared to those of *Bavarioboa hermi*, but the neural spine is not as low as the neural spine of the late Early Miocene (Karpatian) *Bavarioboa ultima* Szyndlar & Rage, 2003 from Rothenstein 13, Germany (cf. Szyndlar & Rage 2003). Morphologically, vertebrae of *Bavarioboa* aff. *hermi* from Griesbeckerzell 1a seem to occupy an intermediate position between the Early Miocene *Bavarioboa hermi* from Petersbuch 2 (Germany) and Dolnice (Czech Republic; Ottnangian) and the late Early Miocene *Bavarioboa ultima* from Rothenstein 13 (Germany), which has been regarded as the

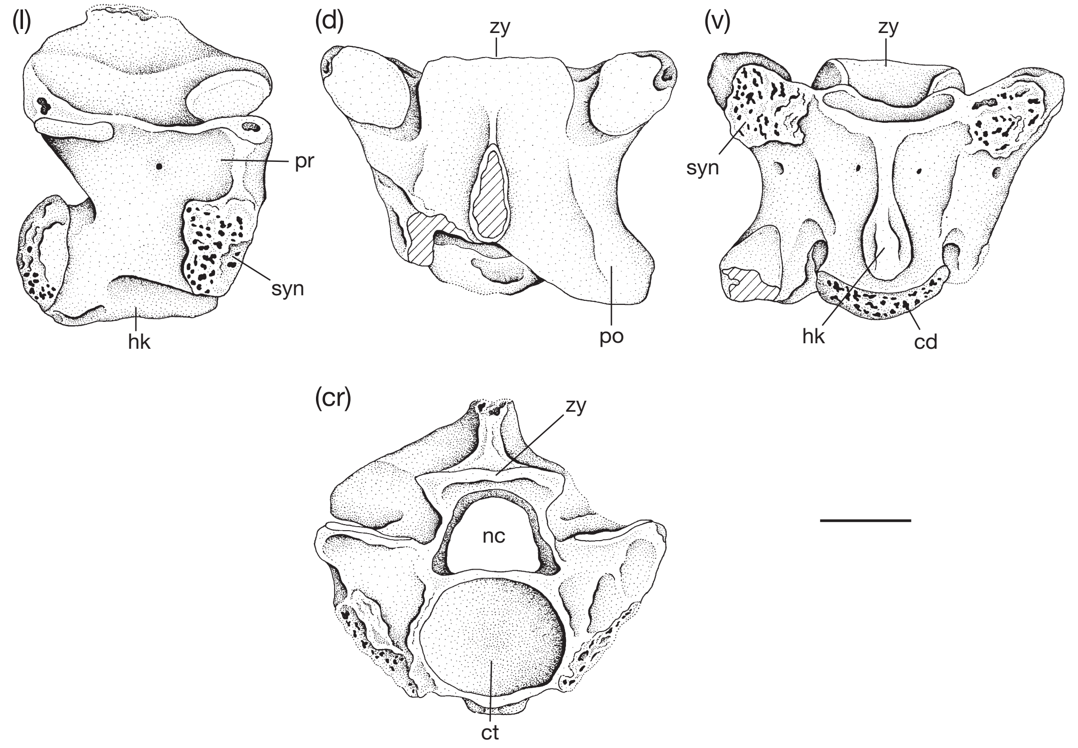

FIG. 5. — cf. *Bavarioboa* sp. from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a. Anterior trunk vertebra (BSPG 1997 XIII 502) in lateral (**l**), dorsal (**d**), ventral (**v**), and cranial (**cr**) views. Abbreviations: see Figure 4. Scale bar: 2 mm.

last representative of the genus *Bavarioboa* in Europe (Szyndlar & Rage 2003).

cf. ***Bavarioboa*** sp.

MATERIAL EXAMINED. — 5 trunk vertebrae (BSPG 1997 XIII 502-506).

LOCALITY. — Griesbeckerzell 1a.

DESCRIPTION

Trunk vertebrae (Fig. 5)

Several fragmentary vertebrae can be assigned to the Boidae with confidence because they display a low cl/naw ratio. Deep subcentral grooves accompanied by distinct and sharp subcentral ridges indicate the presence of posterior trunk vertebrae in the available material. The weakly vaulted neural arch, the slightly dorsally inclined prezygapophyses located clearly above the floor of the neural canal, the absence of paracotylar foramina, and the small dimensions further support affinities with *Bavarioboa* (for the detailed diagnosis of *Bavarioboa* see Szyndlar & Rage 2003). A straight zygosphene, in which the cranial margin is characetrized by distinct lateral lobes, has also been observed in *Bavarioboa hermi*. Unfortunately, the vertebrae are fragmentarily preserved and the neural spines are missing, and thus a more precise determination remains impossible at present. Measurements of the best preserved vertebra are as follows: cl = 4.54 mm; naw = 5.44 mm; cl/naw = 0.83.

Subfamily PYTHONINAE Fitzinger, 1826

Genus *Python* Daudin, 1803

TYPE SPECIES. — *Python molurus* (Linnaeus, 1758).

Python sp.

MATERIAL EXAMINED. — Griesbeckerzell 1a: 2 cervical vertebrae (BSPG 1997 XIII 507, 508); 2 trunk vertebrae (BSPG 1997 XIII 509, 510); 2 caudal vertebrae (BSPG 1997 XIII 511, 512). — Griesbeckerzell 1b: 1 trunk vertebra (BSPG 1997 XIII 513).

LOCALITY. — Griesbeckerzell 1a, 1b.

DESCRIPTION

Cervical vertebrae (Fig. 6A)

The vertebrae are markedly wider than long. In lateral view, the better preserved specimens are characterized by a high neural spine that is inclined posteriorly. The neural spine is about two times higher than long, although the distal tip of the spine is slightly damaged. The interzygapophyseal ridges are sharp and slightly upraised in caudal direction. Lateral foramina are large and may be situated in depressions. The straight or slightly dorsally vaulted subcentral ridges are short. The hypapophysis in one of the specimens is short, and its blunt distal tip indicates that the hypapophysis was inclined ventrally rather than postero-ventrally. Synapophyses are weakly divided into para- and diapophyses.

In dorsal view, the prezygapophyseal articular facets are subtriangular to oval and the prezygapophyseal processes are very short. The cranial margin of the zygosphene possesses an indistinct median lobe and small lateral lobes. The anterior base of the neural spine is situated at the base of the zygosphene. The interzygapophyseal constriction is weakly developed.

In ventral view, the centrum is triangular in shape with shallow subcentral grooves and short subcentral ridges. Subcentral foramina are small and situated close to the anterior ventral border of the cotylar rim.

In anterior view, the prezygapophyses are slightly tilted upwards. The neural arch is strongly arched and the neural canal is rounded. The cranial margin of the zygosphene is massive and straight. Deep depressions occur on both sides of the large cotyle of circular shape. Paracotylar foramina are absent.

In caudal view, the neural arch is strongly vaulted; the zygantral area is massive. Parazygantral foramina are absent.

Trunk vertebrae (Fig. 6B, C)

Vertebrae are characterized by a very low cl/naw ratio. In lateral view, the largest vertebra (BSPG 1997 XIII 509) is short and very high, although the neural spine is broken off at the base. The base of the synapophysis is large, but the distal tip is severely damaged. The synapophysis is well preserved in one smaller specimen (BSPG 1997 XIII 510), oblong in shape and indistinctively divided into a para- and diapophysis. The lateral foramina are large (or extremely large in one specimen) and situated in indistinct depressions. The interzygapophyseal ridges are conspicuous and their posterior portion bent in upward direction. The subcentral ridges are short and slightly dorsally vaulted.

In dorsal view, the interzygapophyseal constriction is only weakly expressed. The prezygapophyseal articular facets are triangular and the prezygapophyseal processes are not visible from above. The base of the neural spine begins to rise just at the level of the posterior margin of the prezygapophyseal facets. The posterior part of the neural arch is strongly vaulted and triangularly widened in caudal direction. The cranial margin of the zygosphene is nearly straight.

In ventral view, the centrum of the vertebrae is widely triangular in shape, with shallow subcentral grooves and blunt subcentral ridges. The subcentral foramina are large, may be enlarged antero-posteriorly, and are situated at the base of the wide haemal keel. The postero-ventral margin of the haemal keel may be relatively sharp. The damaged postzygapophyseal articular facets were most probably subtriangular.

In cranial view, the prezygapophyses are upraised and the cranial margin of the zygosphene is extremely thick. The neural arch is strongly vaulted. The neural canal is rounded with shallow lateral sinuses. Deep depressions occur at both dorsolateral sides of the circular cotylar rim. Paracotylar foramina are absent.

In caudal view, the zygantrum is massive; parazygantral foramina have not been observed. Measurements of the larger vertebra from Griesbeckerzell 1a (BSPG 1997 XIII 509) are as follows: cl = 9.32 mm; naw = 12.93 mm; cl/naw = 0.72. Measurements of the vertebra from Griesbeckerzell 1b (BSPG 1997 XIII 513): cl = 6.00 mm; naw = 8.62 mm; cl/naw = 0.70.

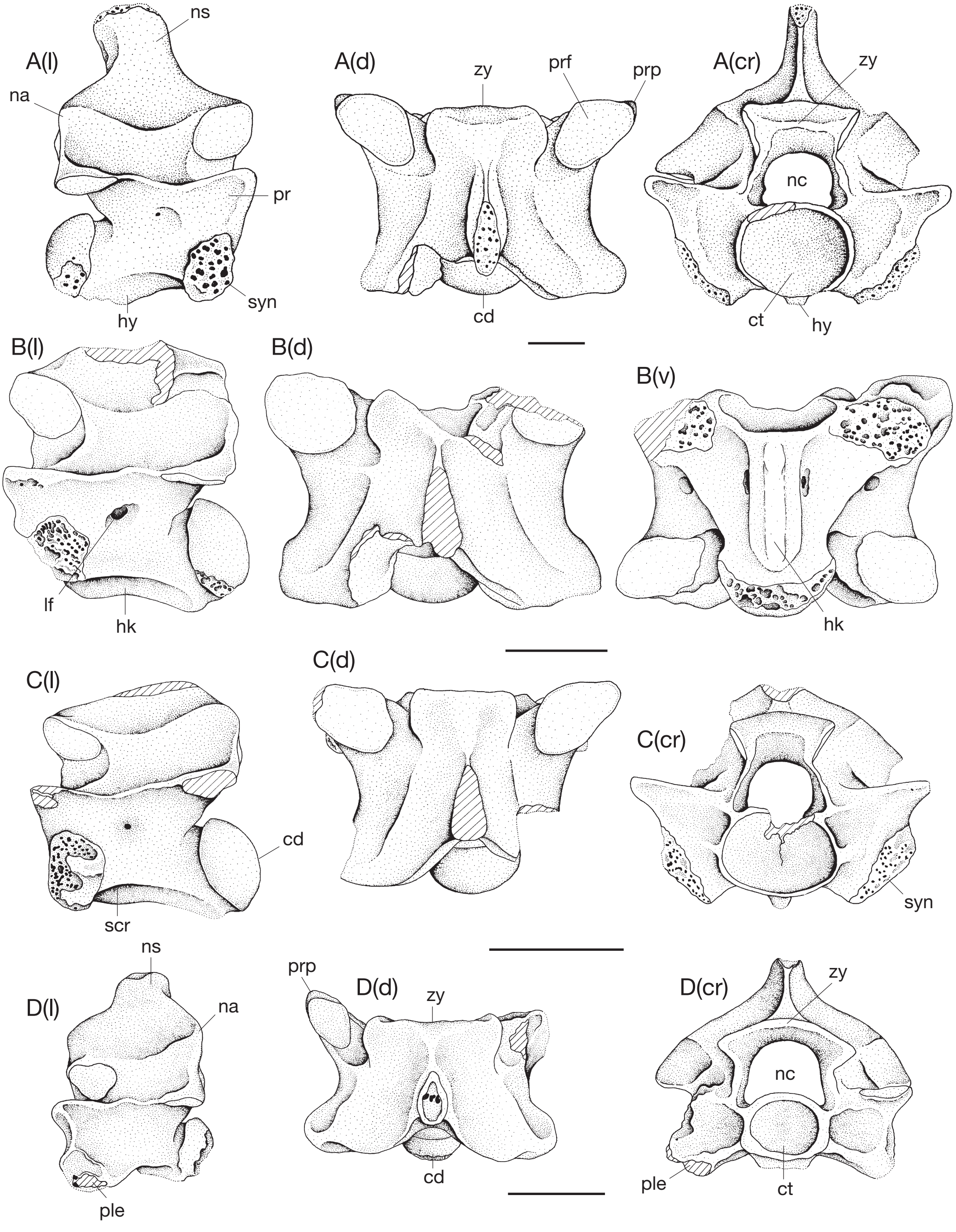

FIG. 6. — *Python* sp. from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a in lateral (**l**), dorsal (**d**), ventral (**v**) and cranial (**cr**) views: **A**, cervical vertebra (BSPG 1997 XIII 507); **B**, middle trunk vertebra (BSPG 1997 XIII 509); **C**, trunk vertebra (BSPG 1997 XIII 510); **D**, caudal vertebra (BSPG 1997 XIII 511). Abbreviations: **hy**, hypapophysis; **ple**, pleurapophysis; for other abbreviations, see Figure 4. Scale bars: A, 2 mm; B, 5 mm; C, 5 mm; D, 2 mm.

Caudal vertebrae (Fig. 6D)

Two of the vertebrae come from the anteriormost section of the caudal region. In lateral view, the vertebral centrum is quite short. The neural spine lacks a dorsal thickening and is shifted to the posterior half of the neural arch. In dorsal view, the anterior margin of the zygosphene is almost straight or slightly concave. Prezygapophyseal articular facets are oval; prezygapophyseal processes are not visible. In ventral view, the bases of the broken off pleurapophyses are directed more or less in anterolateral direction. Haemapophyses are minute in one vertebra (BSPG 1997 XIII 512); the other vertebra (BSPG 1997 XIII 511) possesses an indistinct, wide haemal keel instead of haemapophyses. This suggests that the vertebra occurred in a very anterior (?anteriormost) position within the caudal region. The postzygapophyseal articular facets are damaged; they were probably subsquare in shape. In cranial view, the neural arch is vaulted. Deep depressions occur on both sides of the dorsoventrally slightly depressed cotylar rim. Paracotylar foramina are missing.

Discussion

The absence of paracotylar foramina and large dimensions (see above) are typical features of the vertebrae of pythonine snakes. Although the absence of paracotylar foramina does also occur in boine snakes (Szyndlar & Rage 2003), none of the Boinae reported from the European Miocene reaches the same dimensions as the snake from Griesbeckerzell. Assignment to the genus *Python* is further supported by the general correspondence in morphology of the massive vertebrae with vertebrae of other representatives of that genus. There is no substantial difference between the vertebrae of *Python europaeus* from the French localities Béon 1 (Early Miocene, Burdigalian, MN 4) (Rage & Bailon 2005) and Vieux Collonges (early Middle Miocene, early Langhian, MN 5) (Ivanov 2000; Szyndlar & Rage 2003) and the specimens from Griesbeckerzell (cf. Rage & Bailon 2005). In *Python* from these three sites: 1) the haemal keel is well defined by subcentral grooves that reach the cotyle; 2) the neural arch is markedly vaulted and upswept above the zygantrum; 3) the zygapophyseal facets are weakly inclined; and 4) paracotylar foramina are absent. Minor differences are present with regard to the synapophyses, which are oblong rather than subsquare in *Python* sp. from Griesbeckerzell 1a and 1b and more distinctly shifted anteriorly than the synapophyses of *Python europaeus* from Vieux-Collonges. Moreover, *Python* sp. from Griesbeckerzell lacks a pointed small median projection of the zygosphene. The neural spine, which is an important feature with regard to the assignment to *Python europaeus* (it is lower than the neural spine of any other species of *Python*, cf. Szyndlar & Rage 2003) is broken off at the base. However, the base of the neural spine in one specimen from Griesbeckerzell 1b (BSPG 1997 XIII 513) indicates that this structure was relatively low. The fossil caudal vertebrae resemble those of *Python europaeus* with respect to the position and shape of the neural spine (Szyndlar & Rage 2003). Although the fossil *Python* sp. from Griesbeckerzell 1a and 1b probably belongs to *Python europaeus*, the limited number of damaged vertebrae does not allow for more than identification at genus level.

BOIDAE gen. et sp. indet.

MATERIAL EXAMINED. — 3 cervical vertebrae (BSPG 1997 XIII 514-516); 2 trunk vertebrae (BSPG 1997 XIII 517, 518).

LOCALITY. — Griesbeckerzell 1a.

Description

Cervical and trunk vertebrae

Vertebrae are too fragmentarily preserved to allow for a more precise determination. The gracile cranial margin of the zygosphene in one trunk vertebra may suggest affinities with *Bavarioboa*.

Superfamily COLUBROIDEA Oppel, 1811
Family COLUBRIDAE Oppel, 1811
Subfamily COLUBRINAE Oppel, 1811

Genus *Coluber* (s.l.) Linnaeus, 1758

TYPE SPECIES. — *Coluber constrictor* Linnaeus, 1758.

"*Coluber*" cf. *caspioides* Szyndlar & Schleich, 1993

Material examined. — Griesbeckerzell 1a: 2 cervical vertebrae (BSPG 1997 XIII 519, 520); 19 trunk vertebrae (BSPG 1997 XIII 521-539). — Griesbeckerzell 1b: 1 trunk vertebra (BSPG 1997 XIII 540).

Locality. — Griesbeckerzell 1a, 1b.

Description

Cervical vertebrae (Fig. 7A)

The vertebrae come from the anterior trunk portion because of the presence of hypapophyses, which unfortunately are broken off close to their bases. In lateral view, the neural spine is almost as long as high and its caudal margin overhangs posteriorly. The strongly protruding and postero-laterally directed diapophysis is clearly separated from the somewhat shorter parapophysis. The distal tip of the short parapophyseal processes is directed anteriorly. The preserved base of the hypapophysis indicates a postero-ventral direction. The small lateral foramina are situated close below the prominent interzygapophyseal ridges.

In dorsal view, the vertebra displays a wide zygosphene. The cranial margin of the zygosphene is somewhat convex and possesses distinct lateral lobes (BSPG 1997 XIII 519), or is concave with a wide median notch (Fig. 7A). Prezygapophyseal articular facets are broadly oval. Prezygapophyseal processes are short (less than ½ of the prezygapophyseal facets length) with a pointed tip.

In ventral view, the distal end of the parapophyseal processes is blunt. Small but distinct subcotylar tubercles occur at the sides of the base of the cotylar rim. Subcentral foramina are small. The postzygapophyseal articular facets are subsquare in shape and somewhat enlarged laterally.

In cranial view, the neural arch is vaulted and the neural canal large and rounded with shallow lateral sinuses. The cranial margin of the zygosphenal rim is slightly dorsally arched; however, the middle portion is slightly bent in ventral direction. Prezygapophyses are horizontal. Paracotylar foramina are developed within deep depressions at both sides of the rounded cotyle. A shallow paracotylar notch between parapophyseal process and cotylar rim occurs on both sides of the rounded cotyle.

In caudal view, the zygantral area is large. The condyle is rounded.

Trunk vertebrae (Fig. 7B)

All vertebrae are very fragmentary. In lateral view, the largest vertebra (cl = 7.32 mm; naw = 6.27 mm; cl/naw = 1.17) has distinct lateral foramina situated just below the prominent interzygapophyseal ridges. The synapophyses (strongly damaged in all specimens) are clearly divided into para- and diapophysis. The anterior end of the haemal keel is not steeply terminated. Although the neural spine is broken off in most specimens, the completely preserved neural spine of one posterior trunk vertebra of a subadult specimen documents that the anterior border was inclined anteriorly and the posterior border inclined posteriorly.

In dorsal view, the zygosphenal lip of the largest vertebrae shows a distinct and wide median notch that is less well expressed in one fragmentary specimen. In posterior trunk vertebrae a small indistinct median lobe may be present on the zygosphene instead of a notch. Prezygapophyseal articular facets are oval and elongated. Although the long prezygapophyseal processes are damaged in most specimens, the fragmentary right prezygapophyseal process of the largest vertebra most probably was long.

In ventral view, distinct subcotylar tubercles may be present on both sides of the ventral margin of the cotylar rim. Deep paracotylar notches occur between the subcotylar tubercles and the base of parapophyseal processes. The subcentral grooves are shallow in mid trunk vertebrae, but the subcentral grooves of posterior trunk vertebrae are deep and narrow. Subcentral foramina are usually very small; they may even be absent in some specimens. The ventral margin of the haemal keel is usually sharp and possesses a cuneate caudal tip; however, in the largest specimen the haemal keel is widened in caudal direction and very flat, and thus this specimen probably represents a posterior trunk vertebra. The postzygapophyseal articular facets are subsquarish in shape.

In cranial view, the neural arch is moderately vaulted and the neural canal is rounded with small lateral sinuses. The cranial margin of the zygosphene is dorsally arched; in the largest specimen the zygosphenal lip is roof-like. The distinct shallow paracotylar notches are visible between the subcotylar tubercles and parapophyseal processes. Tiny paracotylar foramina are situated in very deep narrow depressions on both sides of the cotyle. The ventral margin of the cotylar rim is nearly straight.

In caudal view, the zygantral area is large; a small left parazygantral foramen has been observed only in the largest specimen. The rounded condyle is ventrally slightly depressed. Measurements are as follows (n = 6): cl: or = 4.82-7.32 mm; naw: or = 3.19-6.27 mm; cl/naw: or = 1.17-1.51, mean 1.35 ± 0.13.

DISCUSSION

Vertebrae of colubrine snakes are relatively uniform in structure, and thus identification of fragmented specimens often remains problematic. The largest trunk vertebra from Griesbeckerzell 1a belong to a relatively large animal. In total four different large-sized extinct species have been documented from the European Early and Middle Miocene: *Coluber suevicus* (Fraas, 1870), *Coluber dolnicensis* Szyndlar, 1987, *Coluber caspioides* Szyndlar & Schleich, 1993, and *Coluber pouchetii* (Rochebrune, 1880). Large-sized colubrines of the *suevicus-dolnicensis-caspioides-pouchetii* fossil group may be assigned (see Szyndlar 2009: 58) to the genus *Hierophis* Fitzinger, 1834 (*sensu* Schätti & Utiger 2001); we therefore agree with Szyndlar (2009) who proposed to use the traditional generic name "*Coluber*" in quotation marks. The type material of *Coluber suevicus* from the German Middle Miocene (Late Badenian) Steinheim a. Albuch site (Rage 1984a; Szyndlar & Böhme 1993) is poorly understood, and was only briefly described by Rage (1984a) and figured by Szyndlar & Böhme (1993). Colubrines from the Early Miocene (early Eggenburgian) of Merkur-North have been interpreted (Ivanov 2002a) as belonging to "*Coluber*" *suevicus* based on a comparison with two specimens figured by Szyndlar (Szyndlar & Böhme 1993; Fig. 7), but the remarkable interzygapophyseal constriction of vertebrae with a relatively narrow vertebral centre, together with a short and blunt prezygapophyseal processes in the Bohemian material, suggest that they may belong to a different genus (Ivanov pers. obs.). Large colubrines from Griesbeckerzell 1a and 1b differ from "*Coluber*" *suevicus* in having distinctly larger prezygapophyseal processes and a distinct median notch on the cranial margin of the zygosphene (the incipient notch is also visible in one cervical vertebra; BSPG 1997 XIII 520) instead of a straight zygosphenal lip in dorsal view. The large colubrines from Griesbeckerzell 1a and 1b most probably belong to "*Coluber*" *caspioides* (type locality Petersbuch 2, Germany); they resemble the above mentioned species in having: 1, a similar length of the prezygapophyseal processes; 2, a moderately vaulted neural arch of the trunk vertebrae; 3, a median notch on the zygosphene in most of the vertebrae; 4, the same shape of the neural spine and the same postero-ventral direction of the hypapophysis in cervical vertebrae. However, all vertebrae are fragmentary and specific assignment therefore remains provisional. The possible synonymy of "*Coluber*" *caspioides* with "*Coluber*" *dolnicensis* has been discussed by Szyndlar (1998, 2005). The most characteristic morphological feature of the "*Coluber*" *dolnicensis* vertebrae is the distinct "step in the anterior portion of haemal keel" in trunk vertebrae (according to Szyndlar 1987: fig. 8B). Moreover, the cranial margin of the zygosphene is usually straight or convex in dorsal view (Szyndlar 1987: fig. 8C; Ivanov 2002a: fig. $3E_2$), which is unlike to the more or less straight zygosphenal lip that is frequently accompanied by a distinct median notch in "*Coluber*" *caspioides* (Szyndlar & Schleich 1993: fig. 6E; Ivanov 2002a: fig. 5H). Although "*Coluber*" *dolnicensis* was originally established based on only two precaudal vertebrae, the more abundant material of vertebrae from the Early Miocene (early Eggenburgian) of Merkur-North, Czech Republic (42 trunk vertebrae) (Ivanov 2002a) and the late Middle Miocene (Serravallian, MN 7+8) of La Grive M, France (9 trunk vertebrae) (Ivanov 2002b; pers. obs.) show the same morphology as the type material from Dolnice (early Ottnangian, Szyndlar 1987). As a result, we regard "*Coluber*" *dolnicensis* and "*Coluber*" *caspioides* as two separate species.

The distinction of "*Coluber*" *caspioides* from "*Coluber*" *pouchetii* (type locality Sansan, Badenian, France) is complicated by the morphology of the trunk vertebrae, and thus remains unresolved.

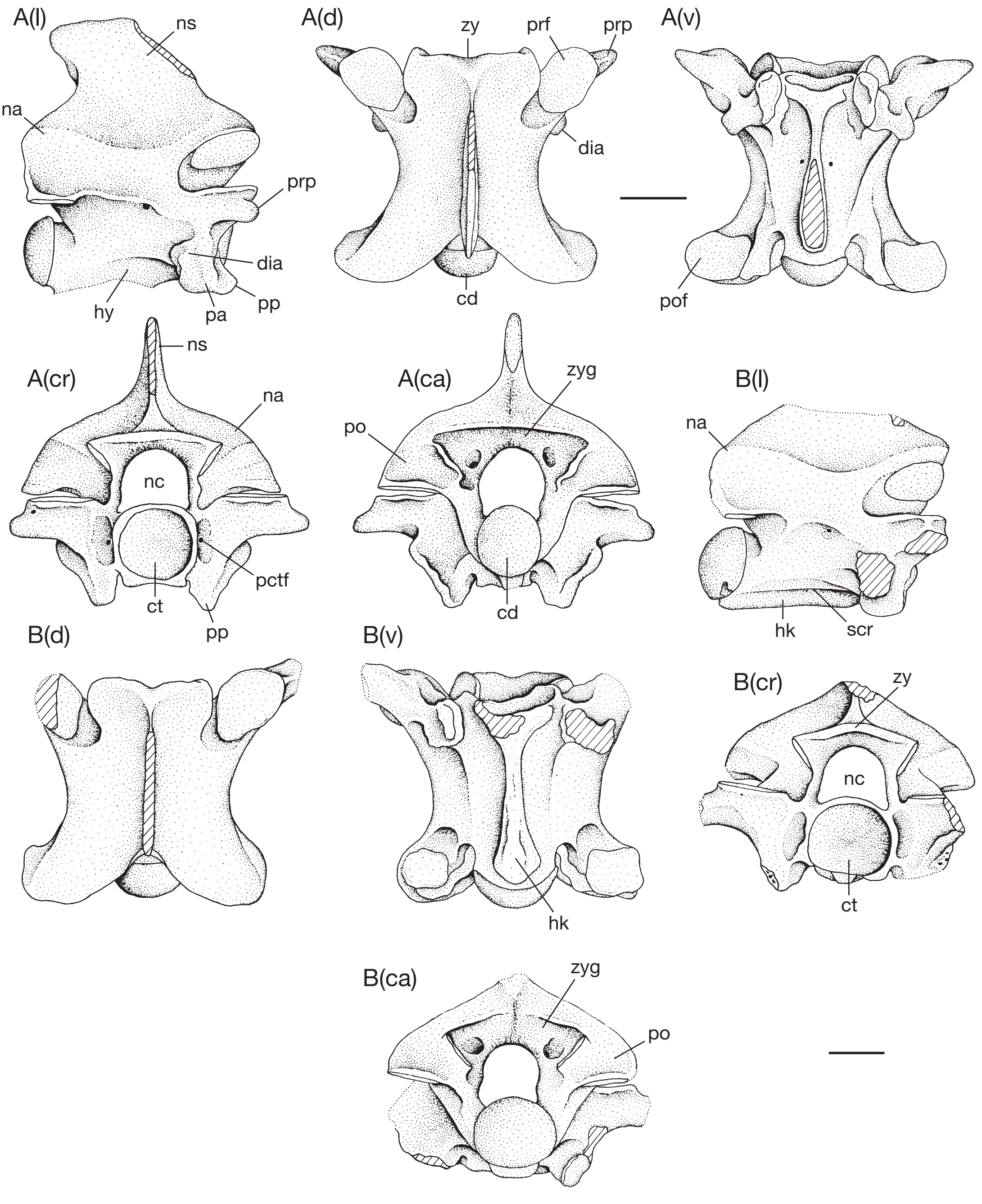

FIG. 7. — "*Coluber*" cf. *caspioides* from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a in lateral (**l**), dorsal (**d**), ventral (**v**), cranial (**cr**) and caudal (**ca**) views: **A**, cervical vertebra (BSPG 1997 XIII 520); **B**, middle trunk vertebra (BSPG 1997 XIII 533). Abbreviations: **dia**, diapophysis; **pa**, parapophysis; **pctf**, paracotylar foramen; **pp**, parapophyseal process; for other abbreviations, and see Figures 4 & 6. Scale bars: 2 mm.

Although Augé & Rage (2000) have defined three vertebral characters of "*Coluber*" *pouchetii* (i.e. 1) weak convexity of the posterior margin of the neural arch, being almost straight; 2) the lateral compression of the cotyle in numerous vertebrae; and 3) the presence of a small median notch of zygosphene in numerous vertebrae), two of these features (i.e. 1 and 3) also occur in "*Coluber*" *caspioides*. Moreover, recent studies of the Late Miocene (early Pannonian) cf. "*Coluber*" *pouchetii* from Rudabánya, Hungary (Szyndlar 2005) indicate that a dorso-ventral compression of the cotyle may be present (Szyndlar 2005) instead of a lateral compression, which was mentioned by Augé & Rage (2000). Therefore, the two features suitable to safely distinguishing the trunk vertebrae of "*Coluber*" *pouchetii* from "*Coluber*" *caspioides* are: 1) the almost vertical anterior and posterior margins of the high neural spine; and 2) the diapophysis, which is as large as the parapophysis or somewhat larger.

Coluber hungaricus (Bolkay, 1913)

Zamenis hungaricus Bolkay, 1913: 223, 224, pl. XXII, fig. 3. — Kuhn 1939: 28.

Zamenis cf. *Dahli* – Szunyoghy 1932: 10 + 49.

Coluber cf. *najadum* – Młynarski 1961: 23.

Coluber hungaricus – Kuhn 1963: 20. — Rage 1984a: 44. — Szyndlar 1991a: 115; 2005: 35, 36, fig. 3. — Venczel 1994: 2-7, figs 1, 2; 2001: 85, fig. 5f-i.

Coluber hungaricus [part] – Venczel 1998: 2-6, figs 1-3.

MATERIAL. — 1 cervical vertebra (BSPG 1997 XIII 541); 9 trunk vertebrae (BSPG 1997 XIII 542-550).

LOCALITY. — Griesbeckerzell 1a.

DESCRIPTION

Cervical vertebra (Fig. 8A)

The only preserved cervical vertebra comes from the posterior part of the cervical region as indicated by the short postero-ventrally directed hypapophysis in lateral view. The diapophysis is as large as the parapophysis and the parapophyseal process is short. The dorsally arched subcentral ridges are blunt but well developed. The neural spine is broken off at the base. Lateral foramina are distinct.

In dorsal view, the vertebra is short and the cranial margin of the zygosphene has a distinct median lobe as well as lateral lobes. Prezygapophyseal articular facets are broadly oval; the left prezygapophyseal process is slender and possesses a pointed distal tip. The process is directed antero-laterally.

In ventral view, the subcentral foramina are small but distinct. The only preserved left postzygapophyseal articular facet is subsquarish.

In cranial view, the neural arch is arched and the neural canal is subsquare and has short and wide lateral sinuses. The zygosphenal lip is dorsally arched. Paracotylar foramina occur in deep depressions on both sides of the dorso-ventrally depressed cotyle.

Trunk vertebrae (Fig. 8B, C)

Vertebrae are typical because of their small dimensions. In lateral view, the neural spine of the posterior trunk vertebra (BSPG 1997 XIII 549) indicates posterior inclination of the caudal margin; the cranial margin was inclined anteriorly. The interzygapophyseal ridges are short and only weakly developed. Lateral foramina are small but distinct, and situated in depressions just beneath the interzygapophyseal ridges. Subcentral ridges are well developed and may run to the vicinity of the condyle. In anterior trunk vertebrae the subcentral ridges are blunt while they are more distinct in the only preserved posterior trunk vertebra. Synapophyses are partially damaged, but it is obvious that the parapophyses were as large as the diapophyses.

In dorsal view, the cranial margin of the zygosphene displays a wide median and well developed lateral lobes. The anterior base of the neural spine arises from the middle of the zygosphene. Prezygapophyseal articular facets are oval and somewhat enlarged; the only preserved right prezygapophyseal process is short and acute, reaching about half of the prezygapophyseal facet length. The incision in the caudal margin of the neural arch is relatively deep.

In ventral view, the triangular centrum is elongated and the haemal keel is well developed, sharp

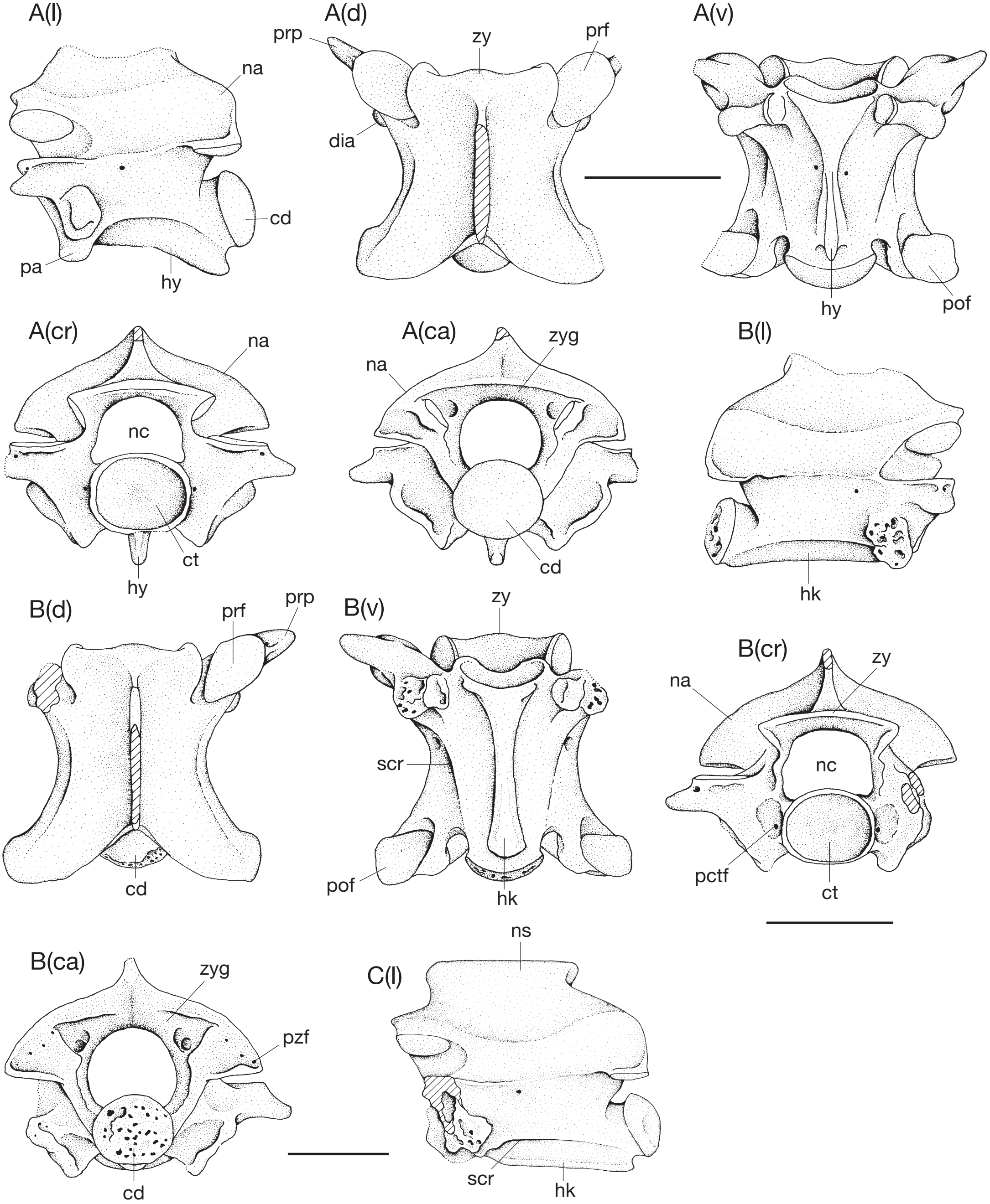

FIG. 8. — *Coluber hungaricus* (Bolkay, 1913) from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a, in lateral (**l**), dorsal (**d**), ventral (**v**), cranial (**cr**) and caudal (**ca**) views: **A**, posterior cervical vertebra (BSPG 1997 XIII 541); **B**, middle trunk vertebra (BSPG 1997 XIII 547); **C**, posterior trunk vertebra (BSPG 1997 XIII 549). Abbreviations: see Figures 4, 6 & 7. Scale bars: 2 mm.

in the middle, and becoming more spatula-shaped towards the tips. The subcentral grooves are shallow and the subcentral ridges are strong and rounded with the only exception of one posterior trunk vertebra in which the subcentral ridges are more distinct, especially in their anterior part. Parapophyseal processes are very short. Postzygapophyseal articular facets are subsquare or subquadrate in shape. Subcentral foramina are very small and usually indistinct.

In cranial view, the neural arch is moderately vaulted and the neural canal is rounded or quadrate-shaped with small and relatively narrow lateral sinuses. The zygosphenal lip is either dorsally arched or almost straight. The large paracotylar foramina are situated in deep depressions on both sides of the dorso-ventrally slightly depressed cotyle.

In caudal view, the zygantral area is distinctly widened. The condyle is damaged in most vertebrae and dorso-ventrally slightly depressed. Measurements are as follows (n = 5): cl: or = 2.95-4.37 mm; naw: or = 2.27-3.01 mm; cl/naw: or = 1.14-1.45, mean 1.30 ± 0.11.

Discussion

Coluber hungaricus belongs to an assemblage that has been labelled small colubrine snakes and it differs from the extant *Coluber gemonensis* (Laurenti, 1768) (*Hierophis gemonensis sensu* Schätti & Utiger 2001) by the longer and distally pointed prezygapophyseal processes (Venczel 1994). This snake from Griesbeckerzell 1a resembles *Coluber hungaricus*, which has been reported from the several Hungarian localities (e.g., Rudabánya [early Pannonian]; Polgárdi 2, 4, 5 [late Pontian]; and Osztramos 1 [early Dacian]; Venczel 1994, 1998; Szyndlar 2005), especially with regard to the following features: 1) shape and length of prezygapophyseal processes if compared with the material from Polgárdi 4 (Venczel 1994); however, middle-trunk vertebrae of *Coluber hungaricus* from Rudabánya possess somewhat shorter prezygapophyseal processes (Szyndlar 2005); 2) shape of the zygosphenal lip; 3) presence of blunt subcentral ridges and shallow subcentral grooves; and 4) length of the parapophyses and diapophyses.

"*Coluber*" sp.

Material examined. — 3 trunk vertebrae (BSPG 1997 XIII 551-553).

Locality. — Griesbeckerzell 1a.

Description

Trunk vertebrae (Fig. 9)

In lateral view, the best preserved vertebra (BSPG 1997 XIII 551) shows distinct and sharp interzygapophyseal ridges. The cranial margin of partially preserved neural spine originates in the middle of the zygosphene length. The neural spine extends to the posterior border of the neural arch. Small but distinct processes (well visible also in cranial view) are developed at bases of the lateral facets of the zygosphene. Large lateral foramina are distinct and situated close to the prezygapophysis and below the interzygapophyseal ridges. The haemal keel is deep, subcentral ridges are prominent and extend as far as to the vicinity of the anterior border of the condyle. The condyle is positioned on a relatively long neck. Para- and diapophyses are damaged; the left synapophysis of the best preserved vertebra shows that the diapophysis was somewhat dorsoventrally longer than the parapophysis.

In dorsal view, the prezygapophysis is separated from the postzygapophysis by a distinct constriction; as a result, the vertebra is X-shaped. The right prezygapophysis of the best preserved vertebra (BSPG 1997 XIII 551) is characterized by a prezygapophyseal articular facet that is subtriangular to roughly sigmoid in shape; the prezygapophyseal process reaches about ½ of the prezygapophyseal facet length. The zygosphene is convex and has distinct lateral lobes.

In ventral view, the synapophysis is indistinctly divided into a dia- and parapophysis, but this may be also a result of surface damage. The parapophyses are short. The haemal keel is sharp; its ventral margin is flattened in one of the posterior trunk vertebrae. The subcentral ridges are well developed, especially in the anterior part of the vertebra, and the subcentral grooves are relatively short. The large subcentral foramina are situated in the anterior half of the vertebral centrum, roughly at the level

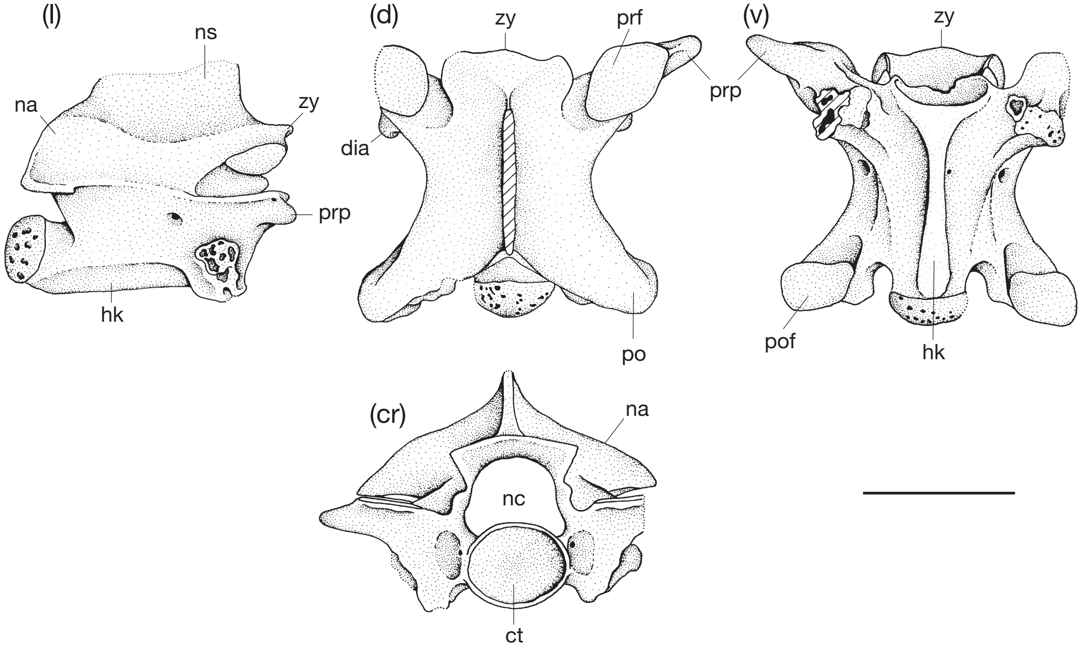

Fig. 9.— "*Coluber*" sp. from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a; middle trunk vertebra (BSPG 1997 XIII 551) in lateral (**l**), dorsal (**d**), ventral (**v**), and cranial (**cr**) views. Abbreviations: see Figures 4 & 7. Scale bar: 2 mm.

of the maximum of interzygapophyseal constriction. Postzygapophyseal articular facets, irregular in shape, originally were laterally enlarged.

In cranial view, the neural arch is weakly vaulted and the neural canal is rounded. The preserved right prezygapophysis is slightly tilted up dorsally. Paracotylar foramina are situated at both sides of the slightly dorsoventrally depressed cotyle.

In caudal view, the zygantral area is gracile and the neural arch is weakly vaulted. Both postzygapophyseal articular facets are tilted up dorsally. Two parazygantral foramina on the left side, as well as the one on the right side, are positioned close to the dorsal margin of the neural arch. The condyle is rounded. Measurements are as follows (n = 3): cl: or = 3.00-3.27 mm; naw: or = 2.33-2.88 mm; cl/naw: or = 1.14-1.29, mean 1.23 ± 0.08.

Discussion

The presence of paracotylar foramina and a haemal keel in trunk vertebrae, together with the small dimensions, indicates that the material belongs to a small colubrine snake. The vertebrae resemble *Coluber hungaricus* reported from the Late Miocene (Venczel 1994, 1998; Szyndlar 2005) and Early Pliocene (Venczel 2001) of Hungary and from the Middle Miocene of Germany in: 1) the shape of the zygosphenal lip; and 2) the shape of the distally pointed prezygapophyseal processes. These features correspond to those seen in the extant *Coluber gemonensis* (*Hierophis gemonensis sensu* Schätti & Utiger 2001), with the exception of the distal tips of the prezygapophyseal processes, which are not pointed in *Coluber gemonensis* according to Venczel (1994). However, "*Coluber*" sp. from Griesbeckerzell 1a differs from both *Coluber gemonensis* and *Coluber hungaricus* in: 1) the shape of the postzygapophyseal articular facets that are strongly enlarged in lateral direction; 2) the shallow indentation of the posterior margin of the neural arch in dorsal view; 3) the prominent subcentral ridges (at least in anterior half of the vertebrae); 4) the presence of small but distinct tubercles at the base of the zygosphenal facets. The relative length of the vertebral centrum depends on the position of the vertebra in the vertebral column – the shortest vertebrae typically occur in the posterior-most trunk section, immediately before the cloacal section (Hoffstetter & Gasc 1969; Szyndlar 1984). The above mentioned features suggest that the fossils represent a new and distinct species; however, the limited number of vertebrae does not allow for studies of the intracolumnar variations among the small colubrines from Griesbeckerzell 1a and 1b.

Genus *Texasophis* Holman, 1977

TYPE SPECIES. — *Texasophis fossilis* Holman, 1977.

Texasophis cf. ***meini*** Rage & Holman, 1984

MATERIAL EXAMINED. — 1 trunk vertebra (BSPG 1997 XIII 554).

LOCALITY. — Griesbeckerzell 1a.

DESCRIPTION

Trunk vertebra (Fig. 10)

In lateral view, the vertebra is elongated. The base of the missing neural spine indicates that this structure was originally very low. Interzygapophyseal ridges are moderately developed. The lateral foramina are large and do not occur in depressions. The condyle is situated on a relatively long neck. The dorsally arched subcentral ridges are indistinct, but this may also be due to the partial corrosion of the vertebra. Synapophyses are strongly damaged.

In dorsal view, the cranial margin of the zygosphene possesses a distinct median and two lateral lobes. The damaged left prezygapophyseal articular facet was originally oval in shape.

In ventral view, the centrum is elongated. Both the wide and flat haemal keel and subcentral ridges are partially corroded. Subcentral foramina are very small and indistinct. The ventral margin of the cotylar rim lacks subcotylar tubercles. The left postzygapophyseal articular facet is irregularly circular in shape.

In cranial view, the neural arch is slightly vaulted and the neural canal is rounded with large lateral sinuses. The zygosphenal lip is straight. Paracotylar foramina are situated in wide depressions on both sides of the slightly dorso-ventrally depressed cotyle.

In caudal view, the zygantral area is wide; the damaged condyle is slightly dorso-ventrally depressed. Measurements of the vertebra are as follows: cl = 3.83 mm; naw = 2.48 mm; cl/naw = 1.54.

DISCUSSION

Texasophis represents a small-sized colubrine snake. Four of five characteristics (Holman 1977, 2000) of the genus *Texasophis* have been observed in the trunk vertebra from Griesbeckerzell 1a: 1) an elongated form of the vertebrae; 2) a moderately vaulted neural arch; 3) a low neural spine; 4) a robust haemal keel; and 5) distinct subcentral grooves and ridges. The subcentral ridges of *Texasophis* cf. *meini* from Griesbeckerzell 1a are blunt and indistinct, which is due probably to partial abrasion. The ventrally flattened haemal keel, which becomes slightly narrower in cranial direction, and a distinct median lobe with well developed lateral lobes of the zygosphene are features that have also been described from the type material of *Texasophis meini* from the French late Middle Miocene of La Grive M (Rage & Holman 1984). The poorly preserved holotype of *Texasophis fossilis* from the Middle Miocene (Early Barstovian) of Texas (Holman 1977; 2000: 192, fig. 122) closely resembles *Texasophis meini* with regard to the wide haemal keel. However, it differs from *Texasophis meini* by the presence of a distinctly shallower notch in the posterior border of the neural arch (cf. Holman 1977, 1979, 2000). The variable width of the haemal keel observed in antero-posterior direction of the holotype of *Texasophis fossilis* is probably a result of the poor state of preservation, but intracolumnar variability may also have existed with regard to this feature (Ivanov, personal observation of *Texasophis meini* from La Grive L7 and M).

COLUBRINAE gen. et sp. indet.

MATERIAL EXAMINED. — Griesbeckerzell 1a: 14 precaudal vertebrae (BSPG 1997 XIII 555-568); Griesbeckerzell 1b: 1 precaudal vertebra (BSPG 1997 XIII 569).

LOCALITY. — Griesbeckerzell 1a, 1b.

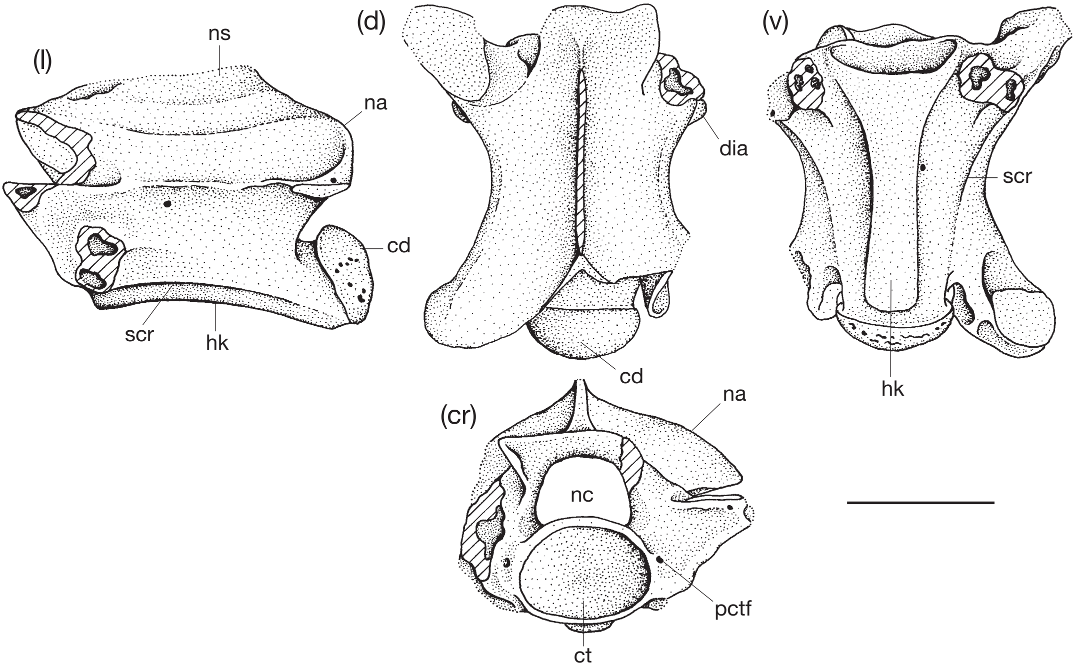

Fig. 10. — *Texasophis* cf. *meini* from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a; middle trunk vertebra (BSPG 1997 XIII 554), in lateral (**l**), dorsal (**d**), ventral (**v**), and cranial (**cr**) views. Abbreviations: see Figures 4 & 7. Scale bar: 2 mm.

Description

Precaudal vertebrae

Preserved precaudal vertebrae (mostly trunk vertebrae determined based on the presence of a haemal keel) are strongly damaged. The cl/naw ratio (>1), presence of paracotylar foramina in deep depressions on both sides of the rounded cotylar rim, a vaulted neural arch, and the absence of hypapophysis indicate that these fossils belong to the subfamily Colubrinae. Remains of the largest vertebrae probably represent middle trunk vertebrae of "*Coluber*" *caspioides*. A distinct step in the anterior portion of the haemal keel resembles that observed in "*Coluber*" *dolnicensis*, although the anterior step of the haemal keel of "*Coluber*" *dolnicensis* extends more vertically (cf. Szyndlar 1987: 64, fig. 8B).

Subfamily Natricinae Bonaparte, 1838

Genus *Natrix* Laurenti, 1768

Type species. — *Coluber natrix* Linnaeus, 1758.

Natrix sp.

Material examined. — 28 precaudal vertebrae (BSPG 1997 XIII 570-597); 2 caudal vertebrae (BSPG 1997 XIII 598, 599).

Locality. — Griesbeckerzell 1a.

Description

Precaudal vertebrae (Fig. 11)

In lateral view, the neural spine, dorsally thickened in one specimen, is high, approximately 2 times longer than high. The cranial margin is inclined anteriorly and the caudal margin inclines posteriorly. The interzygapophyseal ridges are well developed. The lateral foramina are small but distinct and situated in shallow depressions. Synapophyses, usually damaged, are faintly separated into para- and diapophyses of about the same length. The straight or very slightly dorsally vaulted subcentral ridges are prominent, even in anterior precaudal vertebrae. The hypapophysis possesses a well developed anterior keel that usually is triangular in the anterior part.

In dorsal view, the cranial margin of the zygosphene usually has a distinct and wide median lobe; a small distinct median notch in the zygosphenal lip is present in the largest fragmentary vertebra. Short and blunt epizygapophyseal ridges are usually developed in the posterior part of the neural arch. The prezygapophyseal articular facets are broadly oval. Prezygapophyseal processes are sometimes preserved, they reach half the length of the prezygapophyseal facet.

In ventral view, the centrum is elongated and the hypapophysis is narrow. Distinct subcotylar tubercles are consistently present on the ventrolateral margins of the cotylar rim. The parapophyseal processes are distinct and their distal tip (usually broken off) is obtuse. The subcentral ridges are well developed and extend almost to the anterior margin of the condyle in posterior precaudal vertebrae. Subcentral grooves are wide and shallow, and are deeper in posterior precaudal vertebrae. The subcentral foramina are minute. The postzygapophyseal articular facets are irregularly shaped or subtriangular.

In cranial view, the neural arch is moderately vaulted; the neural canal is rounded with small lateral sinuses. The zygosphenal lip is straight or slightly vaulted dorsally. Paracotylar foramina occur on either side of the rounded cotyle.

In caudal view, the neural arch is gracile and vaulted; the zygantral area is wide. A single parazygantral foramen usually occurs on either side of the posterior wall of the neural arch. The condyle is rounded or slightly depressed laterally. Measurements are as follows (n = 15): cl: or = 3.53-5.34 mm; naw: or = 2.28-3.22 mm; cl/naw: or = 1.40-1.71, mean 1.57 ± 0.09.

Caudal vertebrae

The only preserved two posterior caudal vertebrae lack the pleurapophyses and haemapophyses due to breakage close to their bases. The neural spine is high with the cranial margin inclined anteriorly and caudal margin inclined posteriorly.

DISCUSSION

The vertebrae can be assigned to the genus *Natrix* with confidence – the cylindrical vertebral centra are elongated, the neural spines are high and inclined in both anterior (cranial margin) and posterior (caudal margin) direction, subcentral ridges are marked, hypapophysis is narrow, and subcotylar tubercles are well-developed. However, the neural spine in the fossils is generally lower than that documented for *Natrix sansaniensis* (Lartet, 1851) and *N. merkurensis* (Ivanov, 2002), two species from the Miocene (Szyndlar & Schleich 1993; Ivanov 2002a). Although the precaudal vertebrae are similar to those of *Natrix rudabanyaensis* Szyndlar, 2005 reported from the early Late Miocene of Rudabánya, Hungary (Szyndlar 2005) with regard to the shape and height of the neural spine, the prezygapophyseal processes are clearly shorter, extending only to about ½ of the prezygapophyseal articular facets length. Moreover, the parapophyseal processes are not as long as those of the type material of *Natrix rudabanyaensis* (cf. Szyndlar 2005: 39, fig. 5C). A more precise determination was impossible because of the poor preservation of all vertebrae.

NATRICINAE gen. et sp. indet.

MATERIAL EXAMINED. — 16 precaudal vertebrae (BSPG 1997 XIII 600-615).

LOCALITY. — Griesbeckerzell 1a.

DESCRIPTION

The presence of a cylindrical vertebral centrum, epizygapophyseal spines and hypapophyses (although broken off at base) permits assignment of these otherwise highly fragmented vertebrae to small natricines.

COLUBRIDAE gen. et sp. indet.

MATERIAL EXAMINED. — 17 precaudal vertebrae (BSPG 1997 XIII 616-632), 9 caudal vertebrae (BSPG 1997 XIII 633-641).

LOCALITY. — Griesbeckerzell 1a.

DESCRIPTION

The gracile overall morphology of the heavily damaged vertebrae, together with the presence of a vaulted neural arch and paracotylar foramina, allows identification at the family level only.

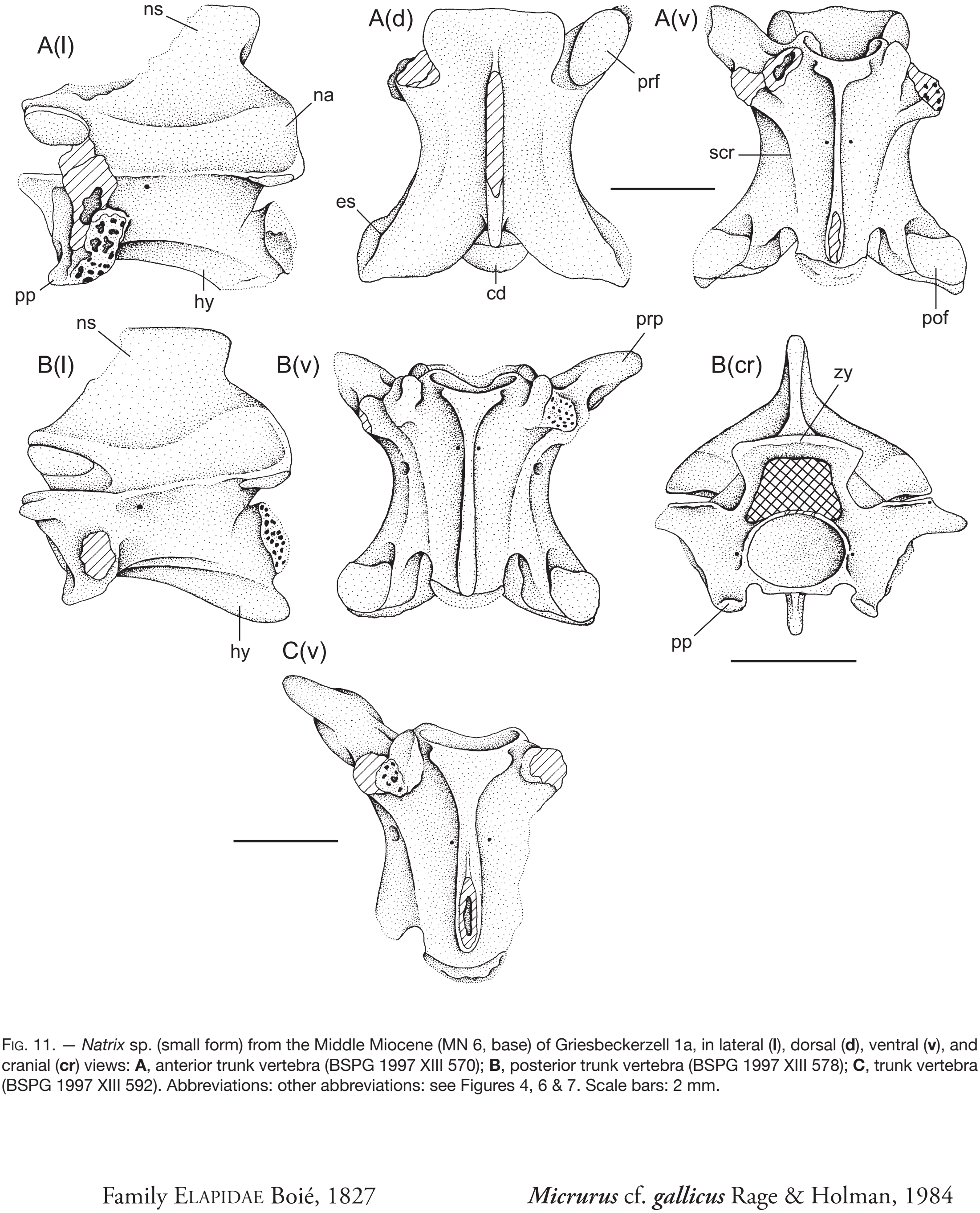

FIG. 11. — *Natrix* sp. (small form) from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a, in lateral (**l**), dorsal (**d**), ventral (**v**), and cranial (**cr**) views: **A**, anterior trunk vertebra (BSPG 1997 XIII 570); **B**, posterior trunk vertebra (BSPG 1997 XIII 578); **C**, trunk vertebra (BSPG 1997 XIII 592). Abbreviations: other abbreviations: see Figures 4, 6 & 7. Scale bars: 2 mm.

Family ELAPIDAE Boié, 1827

Genus *Micrurus* Wagler, 1824

TYPE SPECIES. — *Micrurus spixi* Wagler, 1824.

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

MATERIAL EXAMINED. — 1 precaudal vertebra (BSPG 1997 XIII 642).

LOCALITY. — Griesbeckerzell 1a.

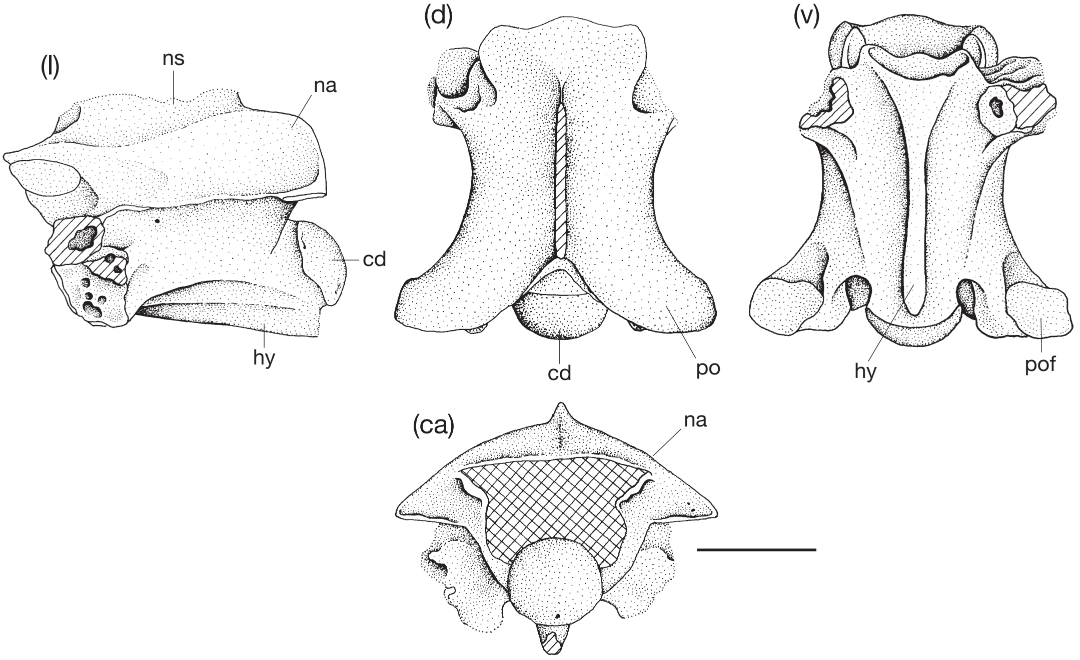

FIG. 12. — *Micrurus* cf. *gallicus* from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a; trunk vertebra (BSPG 1997 XIII 642), in lateral (**l**), dorsal (**d**), ventral (**v**), and caudal (**ca**) views. Abbreviations: see Figures 4 & 6.

DESCRIPTION

Precaudal vertebra (Fig. 12)

In lateral view, the vertebra is elongated. The neural spine is low; the cranial margin was most probably vertical or inclined caudally. The interzygapophyseal ridges are moderately well developed. The lateral foramina are small and not situated in depressions. The subcentral ridges are blunt but well developed, and extend from the heavily damaged synapophyses to the proximal margin of the condyle; they are slightly bent in dorsal direction. The distal tip of the straight and probably short hypapophysis is broken off.

In dorsal view, the zygosphenal lip shows a wide median and two distinct lateral lobes. The prezygapophyses are broken off. Epizygapophyseal spines are missing.

In ventral view, the hypapophysis extends cranially as far as the smooth cotylar rim. Blunt subcentral ridges are separated from the hypapophysis by wide and shallow subcentral grooves. The subcentral foramina are extremely small and barely visible at the base of the hypapophysis. The postzygapophyseal articular facets are subrectangular.

In cranial view, the neural arch is moderately and regularly vaulted; the neural canal (filled with firm sediment) displays wide lateral sinuses. The zygosphenal lip is almost straight, it is wide in comparison to the rounded cotyle.

In caudal view, the postzygapophyseal articular facets are horizontal and the zygantral area (also filled with firm sediment) is relatively wide. The condyle is rounded. Measurements of the vertebra are as follows: cl = 4.55 mm; naw = 3.02 mm; cl/naw = 1.51.

DISCUSSION

The vertebra represents an adult individual with a neural canal that is characterized by a large diameter in comparison with the cotyle. Relatively small dimensions of the vertebra, together with an elongated vertebral centrum, short hypapophysis directed more posteriorly than ventrally, low neural

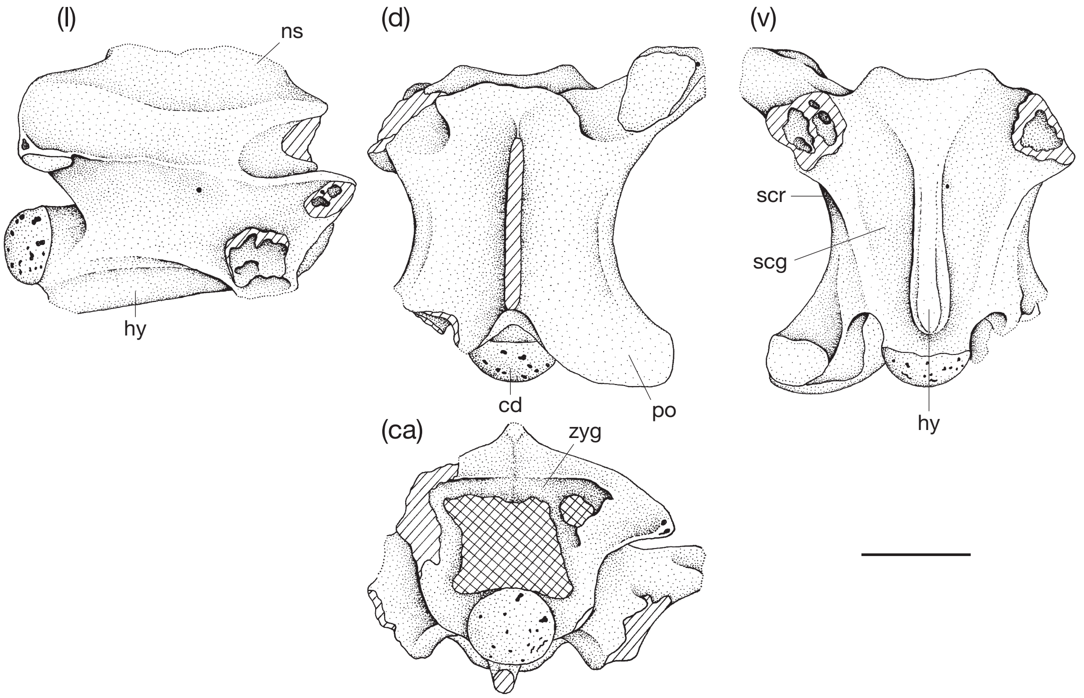

FIG. 13. — Elapidae indet. from the Middle Miocene (MN 6, base) of Griesbeckerzell 1a; trunk vertebra (BSPG 1997 XIII 643) in lateral (**l**), dorsal (**d**), ventral (**v**), and caudal (**ca**) views. Abbreviations: **scg**, subcentral groove; other abbreviations: see Figure 4.

spine, and small cotyle and condyle are typical for the genus *Micrurus*. The vertebra does not differ from that of *Micrurus gallicus* reported originally from the French late Middle Miocene locality La Grive M (Rage & Holman 1984). However, the material does not allow for a safe species identification.

ELAPIDAE indet.

MATERIAL EXAMINED. — 3 precaudal vertebrae (BSPG 1997 XIII 643-645).

LOCALITY. — Griesbeckerzell 1a.

DESCRIPTION

Precaudal vertebrae (Fig. 13)

In lateral view, the neural spine is very low, although the distal tip is not preserved in all specimens. In one specimen (BSPG 1997 XIII 643), the base of the neural spine indicates that the cranial and caudal margins were not inclined. The interzygapophyseal ridges are well developed and the epizygapophyseal ridges are generally missing. Lateral foramina are situated in shallow depressions. The diapophysis is larger than the anteriorly situated parapophysis (both structures are strongly damaged in the largest specimen). The parapophyseal process is very short. The straight subcentral ridges are distinct and extend as far as the postero-ventral tip of the lateral wall of neural arch. The hypapophysis is straight; the tip is not preserved, but was directed postero-ventrally.

In dorsal view, the largest vertebrae are relatively short and wide. The prezygapophyseal articular facets are broadly oval to subtriangular; the only preserved fragmentary prezygapophyseal process is short and reaches approximately ⅓ to ½ of the prezygapophyseal facet length. The zygosphene possesses a wide median and two distinct lateral lobes. A median notch occurs in the zygosphenal lip in two of the specimens (BSPG 1997 XIII 644, 645).

In ventral view, the anterior base of the hypapophysis is triangularly widened. The triangular ventral surface of the anterior keel is rounded. In middle trunk vertebrae the narrow part of the hypapophysis begins at about ⅓ of the centrum length. Subcotylar tubercles are absent. Subcentral ridges are prominent, relatively sharp, and more prominently expressed in posterior precaudal vertebrae. Subcentral grooves are indistinct in anterior trunk vertebrae, and thus the centrum is triangular in shape and flat. On the other hand, the subcentral grooves are distinct and relatively deep in posterior precaudal vertebrae. The fragmentary postzygapophyseal articular facets are irregular and somewhat enlarged laterally.

In cranial view, the neural arch is moderately vaulted and the neural canal is rounded with wide lateral sinuses. The paracotylar foramina are large and situated in wide bowl-like depression on either side of the rounded cotyle. The ventral base of the cotylar rim is flat.

In caudal view, the neural arch is moderately vaulted; the ventral portion of the lateral walls of neural arch is clearly bent medially. The condyle is rounded. Measurements of the best preserved vertebra are as follows: cl = 5.12 mm; naw = 3.56 mm; cl/naw = 1.44.

DISCUSSION

The trunk vertebrae show the typical features of elapid snakes: 1) low neural spine (although usually not preserved); 2) presence of a short hypapophysis; and 3) weakly developed or absent epizygapophyseal spines. The largest vertebra (BSPG 1997 XIII 643) has a slightly enlarged vertebral centrum, contrary to that of *Naja romani* (Hoffstetter, 1939), which is almost identical to that seen in the morphotype Elapidae B from the French early Middle Miocene of Vieux-Collonges (Ivanov 2000). It appears that the Griesbeckerzell vertebra belongs to the genus *Naja* Laurenti, 1768 based mainly on the larger dimensions and low cl/naw in comparison to *Micrurus* (precise measurements were impossible due to poor preservation). Furthermore, this vertebra may be related to certain extant Asiatic members of the genus *Naja* as suggested by Ivanov (2000). It is possible that the two smaller vertebrae belong to the genus *Micrurus*.

Family VIPERIDAE Oppel, 1811
Subfamily VIPERINAE Oppel, 1811
Genus indeterminate

Vipera sp. (“Oriental vipers” group) or ***Daboia*** sp.

MATERIAL. — Griesbeckerzell 1b: 3 precaudal vertebrae (BSPG 1997 XIII 646-648).

LOCALITY. — Griesbeckerzell 1b.

DESCRIPTION

Precaudal vertebrae (Fig. 14A)

The low cl/naw and large dimensions characterize these vertebrae. The neural spine is broken off, and thus it cannot be determined if it originally was high or low. The short interzygapophyseal ridges are either blunt or sharp. The diapophysis is large and clearly separated from the somewhat smaller parapophysis. The single preserved right parapophyseal process is directed antero-ventrally. Subcentral ridges are blunt. Lateral foramina are large and occur in shallow depressions. The hypapophysis is massive and its postero-ventral tip is rounded. The condyle occurs on a very short neck.

In dorsal view, the cranial margin of the zygosphenal lip of one specimen (BSPG 1997 XIII 647) bears a small and pointed median lobe that is as large as the widely separated lateral lobes. The prezygapophyseal articular facets are roughly oval, and the distal tips of the prezygapophyseal processes are not preserved, but were probably small (i.e. approximately half of the prezygapophyseal facet length). Epizygapophyseal spines are absent.

In ventral view, the hypapophysis is massive; the anterior keel is triangularly widened. The largest vertebrae bear small but distinct subcotylar tubercles on the ventral margin of the cotylar rim. The parapophyseal process is large and wide, and has an obtuse distal tip. The subcentral ridges are blunt and subcentral grooves are wide and very shallow. The subcentral foramina are usually very small and situated at the base of the wide hypapophysis. Postzygapophyseal articular facets are laterally enlarged.

In cranial view, the neural arch is dorso-ventrally flattened. The neural canal is rounded with short

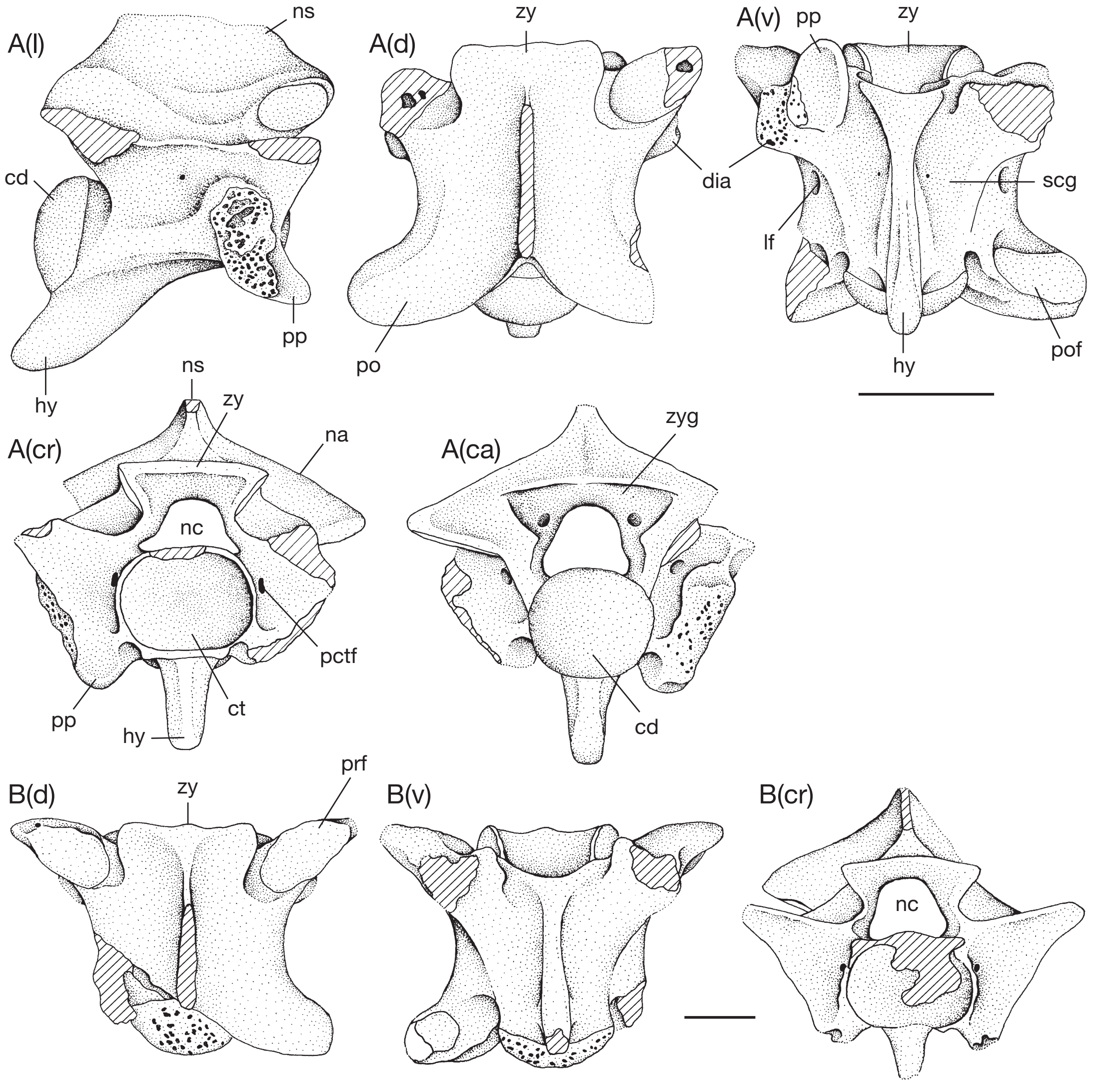

FIG. 14. — **A**, *Vipera* sp. ("Oriental vipers" group) or *Daboia* sp. from the Middle Miocene (late MN 5) of Griesbeckerzell 1b; trunk vertebra (BSPG 1997 XIII 646) in lateral (**l**), dorsal (**d**), ventral (**v**), cranial (**cr**), and caudal (**ca**) views; **B**, *Vipera* sp. ("Oriental vipers" group) from the Middle Miocene (MN 6, base) of the Griesbeckerzell 1a; trunk vertebra (BSPG 1997 XIII 656) in dorsal (**d**) ventral (**v**), and cranial (**cr**) views. Abbreviations: see Figures 4, 6, 7 & 13.

and very narrow lateral sinuses. The cotyle is slightly depressed dorso-ventrally; in the largest vertebrae, the diameter of this structure reaches almost two times that of the neural canal. Prezygapophyses are tilted up dorsally. The distal tips of the parapophyseal processes are directed medio-ventrally. Paracotylar foramina occur in depressions on both sides of the cotyle, and are shifted somewhat dorsally from the middle horizontal line. Small subcotylar tubercles are directed ventro-laterally.

In caudal view, the neural arch is strongly depressed and the zygantral area is massive. The condyle is slightly depressed dorso-ventrally. No parazygantral foramina have been observed. Measurements of the two well-preserved vertebrae are as follows: cl = 8.34 mm; naw = 7.99 mm; cl/naw = 1.04 (BSPG 1997 XIII 646) and cl = 7.76 mm; naw = 6.89 mm; cl/naw = 1.13 (BSPG 1997 XIII 647).

DISCUSSION

Precaudal vertebrae of *Vipera* sp. ("Oriental vipers" group) or *Daboia* sp. are very large by viperid standards (see above) and massive, and characterized by the large diameter of the cotyle. Unfortunately, the neural spine is not preserved in any of the specimens, and thus cannot be compared to the relatively high neural spines seen in members of the genus *Daboia* Gray, 1842 or lower ones in *Vipera* Laurenti, 1768 (Szyndlar & Rage 1999). The shape of the parapophyseal process is almost identical with that of the short parapophyseal processes recorded for *Daboia maxima* (Szyndlar, 1988) from the Early Pliocene (late MN 15) of Layna, Spain (Szyndlar 1988).

Genus *Vipera* Laurenti, 1768

TYPE SPECIES. — *Vipera aspis* (Linnaeus, 1758).

Vipera sp. ("Oriental vipers" group)

MATERIAL EXAMINED. — 10 precaudal vertebrae (BSPG 1997 XIII 649-658).

LOCALITY. — Griesbeckerzell 1a.

DESCRIPTION

Precaudal vertebrae (Fig. 14B)

The neural spine is broken off at its base. In lateral view, the interzygapophyseal ridges are short; the lateral foramina are situated below the cranial part of the these ridges in depressions. Synapophyses are divided into dia- and parapophysis. The diapophysis is about as large as the parapophysis. If preserved, the narrow and long parapophyseal processes are directed antero-ventrally. The hypapophysis is massive and directed postero-ventrally. The distal tip of the hypapophysis is broken off.

In dorsal view, the vertebrae are relatively short. Prezygapophyseal articular facets are roughly oval and the prezygapophyseal processes are short and blunt. However, in one specimen, the distal tip of the left prezygapophyseal process (BSPG 1997 XIII 656) is pointed. The cranial margin of the zygosphenal lip is characterized by a small median lobe; the lateral lobes are prominent. The neural spine arises from the mid part of the zygosphene.

In ventral view, small (and sometimes indistinct) subcotylar tubercles are visible at the base of the cotylar rim. Subcentral ridges are blunt; they are visible only in the anterior half of the vertebral length in a similar way as the shallow and wide subcentral grooves. Subcentral foramina are small and situated at the base of the wide hypapophysis. Diapophyses are directed postero-laterally. Postzygapophyseal articular facets are subtriangular and slightly expanded laterally.

In cranial view, the prezygapophyses are tilted dorsally. The neural arch is usually depressed, but weakly vaulted in the best preserved vertebra. The neural canal is rounded with large and wide lateral sinuses. The cotyle is only slightly larger than the diameter of the neural canal. The cranial margin of the zygosphenal lip is slightly dorsally vaulted. The distal tip of the parapophyses is narrow, but they are blunt and directed ventrally or ventrolaterally, rather than medially. Distinct paracotylar foramina are situated in depressions on both sides of the rounded cotyle.

DISCUSSION

The vertebrae are relatively short, with a low cl/naw, but only two of the specimens have been measured: BSPG 1997 XIII 655: cl = 7.51 mm; naw = 7.38 mm; cl/naw = 1.02; BSPG 1997 XIII 656: cl = 4.91 mm; naw = 4.29 mm; cl/naw = 1.14). The massive structure of the vertebrae and the strong hypapophysis represent a typical complement of features for the "Oriental vipers" group. The cranial margin of the zygosphene, with the distinct lateral lobes and a small median lobe is similar to the zygosphene of the extant *Vipera lebetina* Linnaeus, 1758 (*Macrovipera lebetina sensu* Hermann *et al.* 1992) reported by Szyndlar & Rage (1999: 10, fig. 1). However, a precise distinction between *V. lebetina* and *V. xantina* (Gray, 1849) (*Montivipera xanthina sensu* Nilson *et al.* 1999) based exclusively on vertebral morphology is problematic (Szyndlar & Rage 1999).

Vipera sp.
("European vipers" group; "*Vipera aspis* complex")

MATERIAL. — 1 precaudal vertebra (BSPG 1997 XIII 659).

LOCALITY. — Griesbeckerzell 1a.

DESCRIPTION

Precaudal vertebra

The only preserved vertebra is very fragmentary. The neural spine was probably low, although only the base is preserved. The interzygapophyseal ridges are narrow and short. Synapophyses are heavily damaged, but the base of the parapophysis indicates that the parapophyseal processes were directed antero-ventrally. The subcentral ridges are distinct, long, and straight. The preserved base of the hypapophysis shows that its distal tip was directed postero-ventrally. Lateral foramina are small and indistinct.

In dorsal view, the vertebra is relatively short. The preserved left prezygapophysis possesses a prezygapophyseal articular facet that is roughly oval in shape. The epizygapophyseal ridges are underdeveloped.

In ventral view, the subcentral ridges are blunt and the subcentral grooves are well developed only in the anterior half of the vertebral length. Subcentral foramina are tiny and indistinct.

In cranial view, the neural arch is depressed and the neural canal is rounded with wide lateral sinuses. The cotylar rim was probably slightly depressed dorso-ventrally. Its diameter was originally somewhat larger than the diameter of the neural canal. The preserved left prezygapophysis is tilted dorsally. Paracotylar foramina are developed in deep depressions on both sides of the cotyle.

DISCUSSION

The vertebra is typical of viperids as shown by the dorso-ventrally depressed neural arch, tilted up prezygapophyses, and the presence of hypapophysis in precaudal vertebrae. A relatively high cl/naw (cl = 3.88 mm; naw = 2.80 mm; cl/naw = 1.39) and the postero-ventrally rather than posteriorly directed hypapophysis indicate assignation of the fossil vertebra to the "European vipers" group. Postero-ventral direction of hypapophysis in precaudal vertebrae is typical for "*Vipera aspis* complex" (e.g., Szyndlar 1984; 1991b), but a more precise affiliation is impossible because of the preservation of the vertebra.

PALAEOCLIMATIC ANALYSIS OF THE GRIESBECKERZELL 1A AND 1B ASSEMBLAGES

The amphibian and reptile assemblages from both Griesbeckerzell levels (Table 1) can be used in palaeo-temperature and -precipitation estimates according to the methods outlined in Böhme (2003) and Böhme *et al.* (2006). Table 2 summarizes the minimum temperature requirements of the most thermophilous reptiles based on their nearest living relatives. The fossils from both Griesbeckerzell levels are indicative of warm subtropical conditions with mean annual air temperatures (MAT) >18.6°C, mean cold month air temperatures (CMT) >12.6 °C, and mean warm month air temperatures (WMT) >25.1°C.

Palaeo-precipitation estimates (Table 1) are based on 7 (Griesbeckerzell 1b) and 21 (Griesbeckerzell 1a) species and resulted in humid climates with MAP (Mean Annual Precipitation) 1025 ± 258 mm for Griesbeckerzell 1b and 750 ± 253 mm for Griesbeckerzell 1a. Due to taphonomical or sampling reasons (i.e. lack of amphibians), the value for Griesbeckerzell 1b may be slightly overestimated.

These results are in good agreement with estimates based on the Coexistence Approach (fossil plant taxa have similar climatic requirements as their nearest living relatives) of the fossil wood flora from the Bavarian part of the North Alpine Foreland Basin (Böhme *et al.* 2007), which have produced the following values for sediments just below and just above the Brock horizon (e.g., Gallenbach sands and gravel): MAT 15.7-20.8°C, CMT 4.8-13.3°C, WMT 20.2-28.1°C, and MAP 828-1 362 mm.

If these results are combined with the herpetofaunal approach we may characterize the climate in

TABLE 1. — Fishes, amphibians, crocodilians, turtles, and squamate reptiles from Griesbeckerzell 1a and 1b, supposed ecophysiological groups, and calculation details for the estimation of palaeo-precipitation (according to Böhme *et al.* 2006). Abbreviations: **G1a**, Griesbeckerzell 1a; **G1b**, Griesbeckerzell 1b.

Order	Family	Taxon	G1b	G1a	Ecophysiologic group	Index
Cypriniformes	Cyprinidae	*Palaeoleuciscus* sp. A		+	none	
		Barbus s.l. sp. B	+	+	none	
Channiformes	Channidae	*Channa* sp. (? div. sp.)	+	+	none	
Perciformes	Moronidae	*Morone* sp.	+	+	none	
Proteoidea	Proteidae	*Mioproteus caucasicus*		+	full aquatic	1
Salamandroidea	Salamandridae	*Chelotriton* sp.		+	peri-aquatic	0.3918
		Salamandra sansaniensis		+	peri-aquatic	0.3918
Anura	Discoglossidae	*Latonia gigantea*		+	peri-aquatic	0.3918
	Pelobatidae	*Pelobates* sp.		+	fossorial	0.0917
		Eopelobates sp.		+	peri-aquatic	0.3918
	Bufonidae	*Bufo* cf. *viridis*		+	heliophil	0
	Ranidae	*Pelophylax* sp.		+	semi-aquatic	0.513
Chelonia	Trionychidae	*Trionyx* sp.	+	+	full aquatic	1
	Emydidae	*Mauremys* sp.	+	+	full aquatic	1
	Testudinidae	*Testudo* sp.	+	+	heliophil	0
		Geochelone sp.		+	woodland	0.513
Crocodilia	Alligatoridae	*Diplocynodon styriacus*	+	+	full aquatic	1
Squamata	Chamaeleontidae	*Chamaeleo caroliquarti*	+		arboricol	0.0917
	Lacertidae	*Lacerta* s.l. sp.	+	+	heliophil	0
		Edlartetia sansaniensis		+	heliophil	0
	Scincidae	Scincidae gen. et sp. indet.		+	heliophil	0
	Cordylidae	?Cordylidae indet.		+	heliophil	0
	Anguidae	*Pseudopus laurillardi*	+	+	heliophil	0
		Ophisaurus sp.		+	heliophil	0
	Boidae	*Bavarioboa* aff. *hermi*		+	none	
		Python sp.	+	+	none	
	Colubridae	*Coluber* cf. *caspioides*	+	+	none	
		Coluber hungaricus		+	none	
		“*Coluber*” sp.		+	none	
		Texasophis cf. *meini*		+	fossorial	0.0917
		Colubrinae gen. et sp. indet.	+	+	none	
		Natrix sp.		+	none	
	Elapidae	*Micrurus* cf. *gallicus*		+	fossorial	0.0917
		Elapidae indet.		+	none	
	Viperidae	*Vipera* sp. (“Oriental vipers” group) or *Daboia* sp.	+		none	
		Vipera sp. (“Oriental vipers” group)		+	none	
		Vipera sp. (“European vipers” group; *V. aspis* complex)		+	none	
		ecophysiologic index	0.4417	0.3271		
		mean annual precipitation (in mm)	1025	750		
		95% prediction interval (in mm)	258	253		

the North Alpine Foreland Basin around the Ries meteoritic impact as wet and warm-subtropical, with MAT between 18.6 and 20.8°C, CMT between 12.6 and 13.3°C, and WMT between 25.1 and 28.1°C, quite similar to the latest Early Miocene (Böhme 2010).

TABLE 2. — The most thermophilous reptiles from Griesbeckerzell, their assumed nearest living relatives (NLR) and minimum temperature requirements (in °C). Abbreviations: **CMT**, mean cold month temperature; **MAT**, mean annual air temperature; **WMT**, mean warm month temperature). Data according to Böhme (2003, 2010) and this paper.

Thermophilous taxon	NLR	MAT	CMT	WMT
Diplocynodon styriacus	Crocodylia	14.2	5.5	~16
Python sp.	*Python* sp.	18.6	8.1	24.9
?Cordylidae indet.	Cordylidae	17.0	12.6	21.5
Chamaeleo caroliquarti	Chamaeleonidae	17.4	10.8	25.1
Geochelone sp.	*Geochelone*	17.0	12.6	21.5

THE PALAEOCLIMATIC SIGNIFICANCE OF LARGE BOID SNAKES, ESPECIALLY THE GENUS *PYTHON*

Large boid snakes of the genus *Python* (subfamily Pythoninae) today are distributed in tropical and subtropical regions of South and Southeast Asia and in Africa South of the Sahara (Zug *et al.* 2001). The Burmese Python (*P. molurus bivittatus* Kuhl, 1820) is the species with the largest extra-tropical distribution in Asia. Its northern geographic limits in China reach the subtropical evergreen broadleaf forests of Nanping (Fujian Province, 26.5°N) in the north-east and the Sichuan Basin (Sichuan Province, 30°N) in the north (Barker & Barker 2008). In both subtropical monsoon climates, the MAT reaches 19.3 and 18.6°C respectively (Guo *et al.* 2009; Müller & Hennings 2009). In Chongqing (Sichuan Basin), the CMT is 8.1°C and the WMT 28.8°C (Müller & Hennings 2009).

With regard to the African *Python* species, *P. natalensis* Smith, 1840 exhibits the most southern distribution. This taxon thrives in moist savannahs and moist coastal forests in the coastal region of Kwazulu-Natal (South Africa, 30°S; O'Shea 2007). In this warm-subtropical area the MAT reaches 21.4°C, whereas CMT and WMT are 17.9°C and 24.9°C respectively (climate station Durban; Müller & Hennings 2009).

Summarizing these results, and according to the actualistic approach, fossil large boid snakes of the genus *Python* are indicative of at least warm-subtropical climate conditions with a minimal temperature regime of 18.6°C in the annual mean and 8.1°C in the coldest month. Pythons are therefore the single most thermophilous reptiles of the European Neogene (Table 2), followed by water skinks of the genus *Tropidophorus* Duméril & Bibron, 1839, chamaeleonids, cordylid lizards and giant tortoises (Böhme 2003, 2010).

PALAEOENVIRONMENT OF GRIESBECKERZELL

The snake fossils from Griesbeckerzell 1a and 1b come from fine-grained deposits (fine sands, Gallenbach sand) of fluvial origin (meandering rivers), an environment that was also inhabited by a diverse fish fauna. Fossil wood from the Gallenbach sand and the slightly younger Gallenbach gravel in the vicinity of Griesbeckerzell is suggestive of a dry deciduous forest with a few evergreen elements (Böhme *et al.* 2007).

The herpetological assemblage of Griesbeckerzell 1b is relatively poor in taxa (Table 1). The predominance of terrestrial representatives (Table 1), including *Chamaeleo caroliquarti* Moody & Roček, 1980, *Pseudopus laurillardi*, "*Coluber*" cf. *caspioides*, and *Vipera* sp. ("Oriental vipers" group) or *Daboia* sp., is typical. Amphibians are lacking, due probably to taphonomic or sampling reasons. The only herpetofaunal members typical for freshwater environments are the alligatorid *Diplocynodon styriacus*, the softshell turtle *Trionyx* sp. and the pond turtle *Mauremys* sp. However, several extant pythonine species may also occur near river streams, at least during the subadult stage of their development (Manthey & Grossmann 1997; Kocián 2000). Occurrences of dry, shrubby vegetation cover at Griesbeckerzell 1b is supported by the presence of the arboreal *Chamaeleo caroliquarti*, the colubrid snake "*Coluber*" cf. *caspioides* (probably closely related [Szyndlar & Schleich 1993] to *Coluber* (= *Hierophis*) *caspius* of the similar habitat), and the viperid snake *Vipera* sp. ("Oriental vipers" group) or *Daboia* sp. The genus *Python* also frequently occurs in open areas such as grasslands, savannahs and open forests (including semiarboreal forms); however, pythons are usually dependent (e.g., Manthey & Grossmann 1997; McDiarmid *et al.* 1999; Barker & Barker 2008) on the existence of freshwater sources in the vicinity.

The herpetological assemblage from Griesbeckerzell 1a is much more diversified compared to Griesbeckerzell 1b (Table 1). It is also dominated by typical terrestrial forms, including squamates and certain turtles: i.e. *Lacerta* sp., *Edlartetia sansaniensis* (Lartet, 1851), Scincidae indet., ?Cordylidae, *Ophisaurus* sp., *Pseudopus laurillardi*, *Testudo* sp., *Geochelone* sp., *Bavarioboa* aff. *hermi*, cf. *Bavarioboa* sp., "*Coluber*" cf. *caspioides*, *Coluber hungaricus*, "*Coluber*" sp., *Micrurus* cf. *gallicus*, *Vipera* sp. ("Oriental vipers" group), and *Vipera* sp. ("European vipers" group; "*Vipera aspis* complex"). Small dimensions and the presence of a low neural spine in *Texasophis* (*Texasophis* cf. *meini*) indicate a fossorial or semi-fossorial habitat (cf. Szyndlar 1994). *Natrix* sp. may either be a terrestrial or semi-aquatic snake. *Chelotriton* and *Pelobates* are adapted to dry environments (Böhme 2002; Ivanov *et al.* 2006). Moreover, the presence of *Pelobates*, which usually prefers sandy soil substrates (e.g., Baruš *et al.* 1992), exhibits a spawning behavior that is induced by precipitation, and this documents an increase in seasonality (Böhme 2002, 2010). This assumption is in accordance with other investigations and palaeobotanical results (Böhme 2003; Böhme *et al.* 2007).

The presence of *Salamandra sansaniensis* is particularly interesting. For this species, Böhme (2010) suggested a rheophilic larval stage similar to that of the recent *S. salamandra* that required oligotrophic, fish-free brooks for their development. Due to an increased topographic relief (Böhme *et al.* 2007) as a result of a slight uplift in the eastern NAFB (Prieto *et al.* 2009) after the extrusion of the Eastern Alps, such brooks may have existed independently from the main discharge system.

As indicated in Table 1, inhabitants of the later system are fishes and fully-aquatic herpetofaunal elements (*Barbus* s.l. sp. B, *Palaeoleuciscus* sp. A, *Channa* sp., *Morone* sp., *Mioproteus caucasicus*, *Trionyx* sp., *Diplocynodon styriacus*), which represent the typical association for relatively fast flowing meandering rivers of the Fluviatile Untere Serie lithostratigraphic unit (Prieto *et al.* 2009).

GRIESBECKERZELL 1A AND 1B ASSEMBLAGES AND THE MIDDLE MIOCENE EVOLUTION OF SNAKE FAUNA IN NAFB

Most of the snakes reported from the German Middle Miocene occurred as early as the Early Miocene; there are only minor differences in composition of the snake assemblages between the Early and the Middle Miocene (Szyndlar & Schleich 1993).

BOIDAE

Boid snakes from Griesbeckerzell are represented by at least two taxa (Table 1), *Bavarioboa* aff. *hermi* (Griesbeckerzell 1a; OSM F, 14.8 Ma) and *Python* sp. (Griesbeckerzell 1b, OSM E; Griesbeckerzell 1a, OSM F). Seven species of the genus *Bavarioboa* are known to date (Szyndlar & Rage 2003), but only two are still known to have survived in the Miocene. *Bavarioboa* aff. *hermi* probably represents the only occurrence of *Bavarioboa hermi* (still unquestionably known only from the Early Miocene of Petersbuch 2 [Szyndlar & Schleich 1993; Szyndlar & Rage 2003]) from the European Middle Miocene. *Bavarioboa* aff. *hermi* from Griesbeckerzell 1a also represents the youngest occurrence of the genus *Bavarioboa* in Europe (Fig. 15). It is presupposed that *Bavarioboa hermi* is an Asiatic immigrant that reached Europe together with colubroids during the Early Miocene (Szyndlar & Rage 2003). However, minor differences between the fossils from Griesbeckerzell 1a and the type material from Petersbuch 2, Germany (Szyndlar & Schleich 1993) may suggest that the genus *Bavarioboa* in the central European late Early and Middle Miocene consisted of several different but similarly sized species. The only known latest Early Miocene *Bavarioboa* from central Europe is *Bavarioboa ultima* from Rothenstein 13, Germany; this fissure filling corresponds to the late Karpatian according to the evolutionary level of *Megacricetodon* aff. *bavaricus* Fahlbusch, 1964 (Abdul Aziz *et al.* 2008: supplementary materials). Apart from differences in morphology (Szyndlar & Rage 2003), *Bavarioboa ultima* was smaller than *Bavarioboa hermi*.

The largest boid vertebrae from Griesbeckerzell 1a and 1b most probably belong to pythonine snakes, i.e. the genus *Python*. Pythonine snakes have rarely been reported from the European Miocene, but numerous remains are known from the French Early Miocene of Béon 1 (Rage & Bailon 2005), the Early Miocene (Ottnangian) of Ivančice, Czech Republic (Ivanov 1996), early Middle Miocene of Vieux-Collonges (Ivanov 2000; Szyndlar & Rage 2003), and early Middle Miocene (old level) of La Grive P and B (Rage & Szyndlar 2005). The presence of pythonine snakes in Griesbeckerzell 1a and 1b pushes the LAD of large boid snakes (*Python* sp.) to about 14.7 Ma (Fig. 15). It seems reasonable to conclude that Miocene pythonine snakes from European localities do not represent survivors from the Eocene (Szyndlar & Rage 2003) because these highly thermophilous snakes (for extant relatives see Haller-Probst [1997]) did not survive the Grande Coupure characterized by a drop in temperature and humidity (Rage 1984a, b; 1987). The extinction of the Eocene pythonine snakes in Europe is supported by the fact that no remains of this group have been reported from the European Oligocene. It is difficult to elucidate the origin of European Miocene pythonine snakes. However, based on the spatial and temporal distribution of pythonine snakes in the early Middle Miocene of France (Szyndlar & Rage 2003) and late Middle Miocene of Morocco (Rage 1976) it seems possible that the European Miocene pythonine snakes are of African rather than Asiatic origin.

Body length of snakes is believed to represent a good proxy indicator for temperature (Head *et al.* 2009). Interesting is a progressive decrease in length of the *Python* middle trunk vertebrae. The largest vertebra of *Python europaeus* (11.1 mm) has been reported from the Early Miocene of Béon 1, France (Rage & Szyndlar 2005), while the largest vertebra from Griesbeckerzell 1a is 9.3 mm long. Although the only measured vertebra of *Python* sp. from Griesbeckerzell 1a is statistically inconclusive, the progressive decrease in vertebral centre length in vertebrae from Béon 1 (middle Burdigalian) and La Grive P and B (late Burdigalian to early Langhian) may correspond with the decrease in MAT during the late Early and early Middle Miocene in western Europe. The presence of the largest *Python europaeus* in Béon 1 corresponds with measurements of the body length of the largest *Tomistoma* Müller, 1846 (Crocodylidae), *Chelydropsis* Peters, 1868 (Chelydridae), and *Trionyx* (Trionychidae) reported from the Middle to Late Ottnangian (17.9-17.8 Ma) of NAFB (Böhme & Winklhofer 2008). Although no other occurrences of large Boidae are known from the Middle Miocene that are younger than 14.7 Ma, it is very probable that large Boidae, including pythons, temporarily survived in central Europe throughout the Early Badenian. Increasing competition with highly dominant colubroids was an important factor contributing to the local extinction of large boids in Europe (Szyndlar & Rage 2003). On the other hand, the dramatic decrease in temperature shortly after 14.0 Ma below 16°C in MAT (Böhme 2003) may also have critically affected the geographic distribution of the large Booidea (Haller-Probst 1997). These snakes probably would have become extinct at the end of the Miocene Climatic Optimum anyway, regardless of food competition.

COLUBROIDEA

Colubroid snakes from Griesbeckerzell 1a and 1b are represented by three "modern" families: Colubridae, Elapidae and Viperidae:

Colubridae

The presence of Asiatic/North American immigrants (see Rage & Holman 1984) in Griesbeckerzell 1a is evidenced only by the fossils of *Texasophis*. Although the oldest known European *Texasophis* (*Texasophis bohemiacus*) that has been reported from the German Early Oligocene (Ehrenstein 12, MP 22) is of Asiatic/North American origin (Szyndlar 1994), it remains inconclusive as to whether the German Middle Miocene representatives of *Texasophis meini* were survivors from the Oligocene or Early Miocene eastern immigrants.

"*Coluber*" cf. *caspioides* from Griesbeckerzell 1a and 1b perhaps represents the last occurrence of this species. The oldest known representatives of "*Coluber*" *caspioides* come form the Early Miocene (early Eggenburgian) of the Czech Republic, Merkur-North site (Ivanov 2002a). According to Szyndlar & Schleich (1993), "*Coluber*" *caspioides* is closely related to the extant *Coluber* (= *Hierophis*) *caspius*. However, trunk vertebrae of "*Coluber*" cf. *caspioides* are also very similar to those of "*Coluber*" *pouchetii* (cf. Szyndlar 2005), and cranial morphology (Ivanov 2002a) is somewhat different to that seen in *Coluber* (= *Hierophis*) *caspius*.

Although *Coluber hungaricus* was originally reported from the latest Miocene of Polgárdi 2, 4 ("Lower" and "Upper" fissure fillings) and doubtfully (cf. Szyndlar 2005) from Polgárdi 5, Hungary (Bolkay 1913; Venczel 1994, 1998), the presence of this species in the early Late Miocene of Rudabánya (Szyndlar 2005) and perhaps in the Middle Miocene of Mátraszőlős (*Coluber* sp. – small colubrine snake similar to e.g., *Coluber hungaricus* – cf. Gál *et al.* 1999), as well as in the Early Pliocene of Osztramos 1 (Venczel 2001), indicates a wider temporal distribution of this species. Possible occurrence of *Coluber hungaricus* in the latest Miocene/Early Pliocene of Maramena, Greece (Szyndlar 1995, 2005), and the new discoveries from Griesbeckerzell 1a indicate that *Coluber hungaricus* was probably widely distributed, at least throughout the central and possibly also the eastern part of Europe.

Natricine snakes have been reported only as *Natrix* sp. from Griesbeckerzell 1a. *Natrix* sp. from Griesbeckerzell 1a is morphologically similar to the modern European natricine snakes, including the extinct *Natrix rudabanyaensis* from the early Late Miocene of Rudabánya, Hungary (Szyndlar 2005), and *Natrix longivertebrata* from the Pliocene of numerous localities, including the Polish type locality of Rebięlice Królewskie 1A (Szyndlar 1984, 1991b), as well as several extant relatives. In general, Middle Miocene natricine snakes from Griesbeckerzell 1a differ from the natricine assemblages reported from the Early Miocene of Petersbuch 2, Germany (Szyndlar & Schleich 1993), and Merkur-North, Czech Republic (Ivanov 2002a) by the absence of two extinct species *Natrix merkurensis* and *Natrix sansaniensis*. These two species (especially *Natrix merkurensis*) differ from the other European natricine snakes with regard to vertebral morphology (cf. Ivanov 2002a), which appears to be intermediate between the Palearctic *Natrix* and extant North American water snake of the genus *Nerodia* Baird & Girard, 1853. Adding support to this assumption is the co-occurrence of very long prezygapophyseal processes, a moderately to strongly flattened neural arch, a conspicuously high neural spine and prominent epizygapophyseal spines in *Natrix merkurensis* and several species of *Nerodia* (*N. fasciata* (Linnaeus, 1766), *N. sipedon* (Linnaeus, 1758) a *N. floridiana* Goff, 1936) (Ivanov pers. obs.; see Holman 2000: 200-208). Although the natricine snakes from Griesbeckerzell 1a are probably of Asiatic origin, they undoubtedly belong to an immigration wave different from that to which belong snakes from the above mentioned Early Miocene localities.

Elapidae

The only elapid from Griesbeckerzell 1a has been identified as belonging to *Micrurus* cf. *gallicus*. *Micrurus gallicus* is the only fossil representative of the extant New World coral snake genus *Micrurus*. Although Rage & Holman (1984) interpereted the European fossil *Micrurus* as North American invaders, a relatively recent study indicated that the origin of this genus is Asiatic rather than New World (Slowinski *et al.* 2001). Fossil representatives of *Micrurus gallicus*, originally reported from the French late Middle Miocene of La Grive M (Rage & Holman 1984), are known from several Early and Middle Miocene localities in France and Germany (Szyndlar & Schleich 1993; Ivanov 2000, 2002b; Rage & Bailon 2005).

European Miocene large cobras include the endemic *Naja iberica* from the latest Miocene of Spain (Szyndlar 1985) and *Naja romani*, which was reported from the Early to the Late Miocene (Bachmayer & Szyndlar 1985; Szyndlar & Rage 1990; Szyndlar & Böhme 1993; Szyndlar & Schleich 1993). Although the fragmentary vertebrae (for the largest one the cl = 5.12 mm) from Griesbeckerzell 1a cannot be attributed to any species or genus with confidence, the elongated centre and vertebral morphology is quite similar to that seen in the Elapidae B morphotype from the French Early Middle Miocene

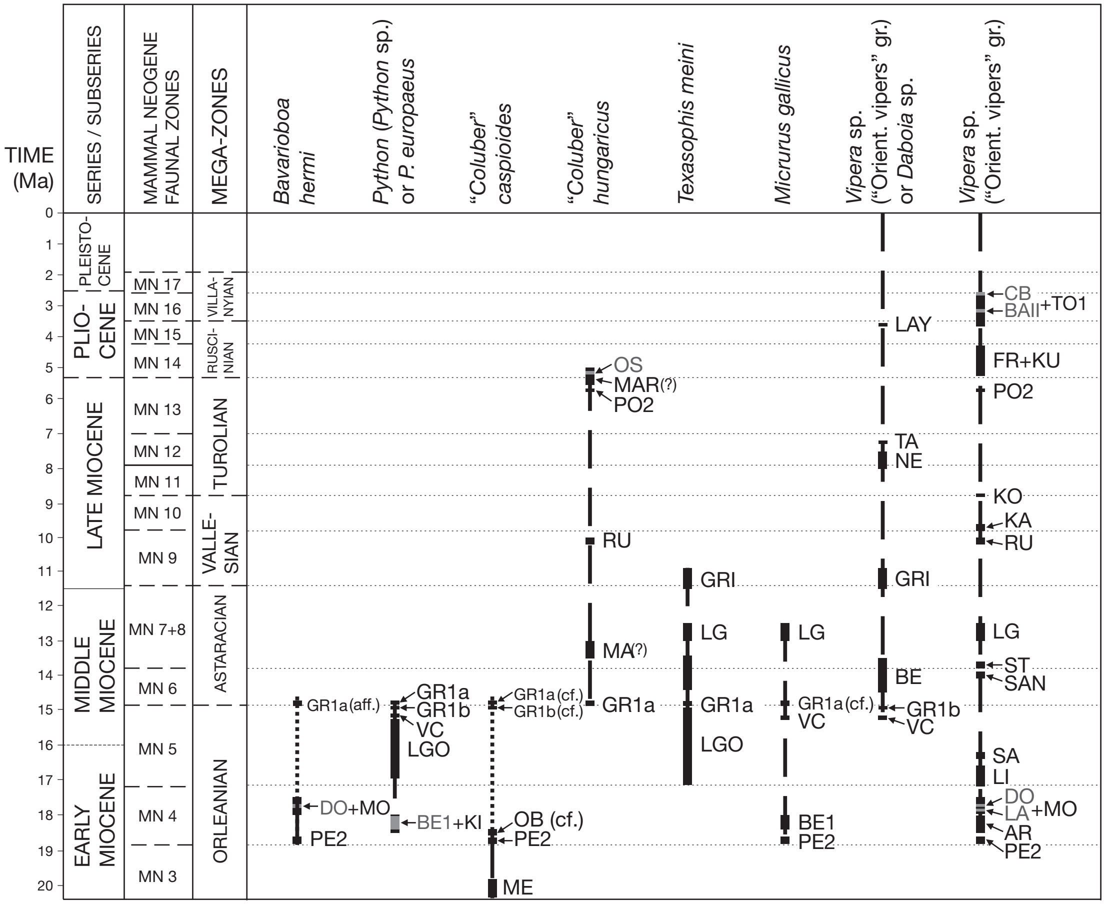

FIG. 15. — Stratigraphic ranges of significant ophidian taxa from the Middle Miocene of Griesbeckerzell 1a and 1b. Abbreviations: Germany: **PE2**, Petersbuch 2; **SA**, Sandelzhausen; **LA**, Langenau; **GR1a** and **GR1b**, Griesbeckerzell 1a and Griesbeckerzell 1b; **ST**, Steinheim a. Albuch. France: **BE1**, Béon 1; **AR**, Artenay; **VC**, Vieux-Collonges; **LGO**, La Grive (old level); **SAN**, Sansan; **LG**, La Grive L5, L7, and M; **BAII**, Balaruc 2. Czech Republic: **ME**, Merkur-North; **MO**, Mokrá-Western Quarry; **DO**, Dolnice. Austria: **OB**, Oberdorf; **KO**, Kohfidisch. Hungary: **MA**, Mátraszőlős; **RU**, Rudabánya; **TA**, Tardosbánya; **PO2**, Polgárdi 2; **OS**, Osztramos. Moldova: **KA**, Kalfa. Ukraine: **GRI**, Gritsev; **NE**, Novoelizabetovka (lower layer); **FR**, Frunzovka-2; **KU**, Kuchurgan; Russia: **BE**, Belomechetskaya. Greece: **KI**, Kimi; **MAR**, Maramena; **TO1**, Tourkobounia 1. Spain: **LAY**, Layna; **CB**, Cova Bonica. Portugal: **LI**, Lisboa. **Thick lines**, stratigraphic ranges of significant localities; **thin lines**, confirmed occurrences of significant taxa; **dotted lines**, unconfirmed occurrences. For equivalence between Mega-Zones and stages, see Figure 1. Data compiled from Szyndlar (1991a, b, 1998, 2005, 2009), Venczel (1994, 1998, 2001), Ivanov (1997, 2000, 2002b), Antunes & Rage (1974), Szyndlar & Schleich (1993), Szyndlar & Rage (1999, 2002, 2003), Rage & Bailon (2005), Böhme *et al.* (2008), Abdul Aziz *et al.* (2010).

of Vieux-Collonges (Ivanov 2000). The relatively high neural spine, if compared with small cobras (*Micrurus* or *Maticora*/*Calliophis*), suggests affinities with the genus *Naja*. Large cobras from Griesbeckerzell 1a with elongated centra are believed to have originated in Asia rather than Africa based on the similarity with extant Asiatic representatives, e.g., *Naja sputatrix* (Ivanov 2000; Ivanov pers. obs.).

The earliest European elapid fossils come from the early Early Miocene of the Oppenheim/Nierstein Quarry in Germany (Kuch *et al.* 2006). Although the fangs generally show a *Naja* spp. or *Bungarus sindanus* morphology (cf. Kuch *et al.* 2006), the vertebrae are "morphologically closest to natricine and non-*Naja* elapid vertebrae as described by Ivanov" (Kuch *et al.* 2006). The earliest distinct European elapids known on isolated vertebrae are all individuals with small body sizes. Small elapids – similar to *Micrurus* or *Maticora* Gray, 1834 (the latter recently synonymised with *Calliophis* Gray, 1834) – have been reported from the middle Early Miocene of Merkur-North, Czech Republic (Ivanov 2002a), and Wintershof-West, Germany (Ivanov unpubl. data). The middle Early Miocene dominance of small elapids was terminated during the late Early Miocene when the large elapid genus *Naja* appeared in Europe (Alférez Delgado & Brea López 1981; Szyndlar & Schleich 1993; Ivanov 2000). The increased abundance of large cobras is probably connected to the Miocene Climatic Optimum (MCO), because most *Naja* species are highly thermophilous, with occurrence ranges from MAT 13.4°C to 28.1°C (Haller-Probst 1997). This assumption is supported by the dominance of the genus *Naja* among the elapids on several late Early and Middle Miocene localities in France and Germany (Ivanov 2002b; Szyndlar 2005).

Viperidae

The oldest known true viper, *Vipera* cf. *antiqua* ("European vipers" group; "*V. aspis* complex"), has been recorded for the earliest Miocene of Weisenau, Germany (Szyndlar & Böhme 1993; Szyndlar & Schleich 1993). The oldest European large "Oriental vipers" appeared, and immediately became widespread, in the late Early Miocene. These forms include the central European *Vipera platyspondyla* from the late Early Miocene (late Ottnangian) of Dolnice, Czech Republic, and Petersbuch 2, Germany (Szyndlar 1987; Szyndlar & Schleich 1993) and *Vipera* sp. ("Oriental vipers" group) from the Mokrá-Western Quarry, Czech Republic (Ivanov *et al.* 2006). With the exception of the large "Oriental vipers" from the Middle Miocene of western Europe, e.g., *Vipera aegertica* from the Middle Miocene of Sansan, France (Augé & Rage 2000) and *Vipera* sp. ("Oriental vipers" group) from the late Middle Miocene of La Grive L7 and M (Ivanov 2002b), these snakes thrived in central Europe throughout the Middle Miocene (Germany: Edelbeuren-Mauerkopf, Griesbeckerzell 1a and 1b, Petersbuch 39, Steinheim a. Albuch) untill the latest Miocene, with the last occurrence recorded from Polgárdi in Hungary (Venczel 1994, 1998; Szyndlar & Rage 2002).

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