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RESEARCH PAPER

Snake fauna (Reptilia: Serpentes) from the Early/Middle Miocene of Sandelzhausen and Rothenstein 13 (Germany)

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Abstract The Early/Middle Miocene (European Land Mammal Zone MN5) localities of Sandelzhausen and Rothenstein 13 in southern Germany have yielded remains of about 13 ophidian taxa: *Eoanilius* sp. (Aniliidae), *Bavarioboa ultima* (Boidae), "*Coluber*" sp., ?*Telescopus* sp., *Natrix* sp., cf. *Natrix* sp., cf. "*Neonatrix*" sp., unidentified "colubrines" and "natricines" (Colubridae), *Naja* sp., an unidentified elapid (Elapidae), *Vipera* sp. ("Oriental viper"), *Vipera* sp. ("*aspis* complex") (Viperidae). Both faunas document a transitional phase from those reported from several late Early and Middle Miocene sites of Central and Western Europe. The climates of Sandelzhausen and Rothenstein 13, as indicated by ophidian fossils, were warm, although not tropical or subtropical.

Keywords Reptilia · Serpentes · Miocene · Germany · Taxonomic description · Faunal composition · Palaeoecology

Kurzfassung Aus den unter-/mittelmiozänen (Europäische Landsäuger Zone MN5) Fossilfundstellen Sandelzhausen und Rothenstein 13 in Süddeutschland sind Reste von 13 Schlangentaxa überliefert: *Eoanilius* sp. (Aniliidae), *Bavarioboa ultima* (Boidae), "*Coluber*" sp., ?*Telescopus* sp., *Natrix* sp., cf. *Natrix* sp., cf. "*Neonatrix*" sp., nicht näher identifizierte "colubrine" und "natricine" Schlangen (Colubridae), *Naja* sp., ein nicht näher identifizierter Vertreter der Elapidae, *Vipera* sp. ("Orientalische Viper"), *Vipera* sp. ("*aspis*-Komplex") (Viperidae). Beide Faunen repräsentieren ein Übergangsstadium zwischen Vergesellschaftungen anderer mittel- und westeuropäischer Fundstellen aus dem späten Unter- und Mittelmiozän. Die Schlangenfossilien zeigen für Sandelzhausen und Rothenstein13 ein warmes, aber nicht tropisches oder subtropisches Klima an.

Schlüsselwörter Reptilia · Serpentes · Miozän · Deutschland · Taxonomische Beschreibung · Faunenzusammensetzung · Paläoökologie

Introduction

The end of the Early Miocene (European Land Mammal Zone MN4), when "archaic" snakes were replaced by their "modern" successors, was a turning point in the history of the European ophidian faunas (Szyndlar and Schleich 1993; Szyndlar and Rage 2003; Rage and Szyndlar 2005). The composition of snake assemblages representing MN4 has been fairly well studied in the last decade, but those inhabiting Europe in the latest Early/early Middle Miocene (MN5) have not attracted much attention to date. Thus far, most of our knowledge of the MN5 snakes has been derived from extrapolations of the content of the old levels of the French locality La Grive (MN7 + 8) (e.g. Szyndlar and Rage 2003). In this context, the fossil remains of Sandelzhausen representing the European Land Mammal Zone MN5 (Heissig 1997; Rössner 1997; Fahlbusch 2003; Hokkanen and Evans 2006; Moser et al. 2009 this volume) are of special importance for the knowledge of the history of European ophidian faunas. Although the preservation of the specimens is too poor to provide detailed information, the snake fossils found in both sites give evidence for the faunal turnover in European snakes.

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The snake assemblage from Sandelzhausen is presented here along with that from Rothenstein 13 because of close taxonomical similarities at genus level (unfortunately, most fossil remains cannot be identified to the species level) in both faunas. Rothenstein 13 is a karstic site located at the Franconian Alb in southern Germany north of the Molasse Basin (48°97′N, 11°06′E) with micromammal remains indicating a biostratigraphic age of MN5 (E.P.J. Heizmann, personal communication). So far, several genera of amphibians and reptiles found in the latter locality have been reported (Böhme and Ilg 2003; Szyndlar and Schleich 1993; Szyndlar and Rage 2003).

Up to now, except for *Bavarioboa ultima* (Szyndlar and Rage 2003), snake remains from the aforementioned localities have not been described. The presence of a few ophidian taxa in both sites was mentioned by Szyndlar and Schleich (1993) and Szyndlar and Böhme (1993) (at that time estimated to be of MN6 age). Szyndlar and Rage (2003) listed the snake fauna of Rothenstein 13.

Materials and methods

The entire collection of fossil snake material from Sandelzhausen available for study belongs to the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSPG). Most of the fossils used in the present study, loaned by Prof. Volker Fahlbusch and Dr. Gertrud Rössner in September 2003, are vertebral fragments. Due to the poor state of preservation, identification of the material was impossible below the generic level. Of 346 ophidian fossils available for study, 145 vertebrae and venomous fangs were identified as belonging to the following genera: *Eoanilius* sp. (family Aniliidae), "*Coluber*" sp. and ?*Telescopus* sp. (family Colubridae, subfamily "Colubrinae"), *Natrix* sp., cf. *Natrix* sp. and cf. "*Neonatrix*" sp. (family Colubridae, subfamily "Natricinae"); *Naja* sp. (family Elapidae); *Vipera* sp. ("Oriental viper") (family Viperidae). A further 67 fragmentary vertebrae and 4 fragments of toothed bones were identified to the (sub-) family level only ("Colubrinae" indet., "Natricinae" indet., Elapidae indet.); 130 caudal vertebrae were not identified.

In addition to the above, 48 ophidian fragmentary trunk vertebrae from Sandelzhausen were studied by Szyndlar and Schleich at the end of 1991 and mentioned in their joint paper published in 1993. The remains were identified as *Coluber* sp., *Naja* sp., and *Vipera* sp. ("Oriental viper"). The material from Rothenstein 13 belongs to the collection of the Staatliches Museum für Naturkunde in Stuttgart (SMNS). It consists of 143 (mainly fragmentary) vertebrae and 3 fragments of cranial bones. Of them, 73 vertebrae and 1 compound were identified as belonging to the following snakes: *Bavarioboa ultima* (family Boidae); *Natrix* sp. and cf. "*Neonatrix*" sp. (family Colubridae, subfamily "Natricinae"); *Naja* sp. (family Elapidae); *Vipera* sp. ("*aspis* complex") (family Viperidae). In addition, nine fragmentary vertebrae were identified to the (sub-) family level only ("Colubrinae" indet. and Elapidae indet.); 64 bony elements were not identified.

It is worth adding that, in the case of a few snake taxa from Sandelzhausen, a striking disproportion in the number of various skeletal elements can be observed. For instance, the ophidian material contains more than 50 isolated venomous fangs of adult individuals of *Vipera* sp., but there are only a dozen vertebrae referred to the same genus. It is clear that 50 fangs must have belonged to 25–50 individuals, so it is surprising that the fangs are accompanied by so few vertebrae. It is difficult to hypothesise what mechanisms may have been behind this disproportionate number of some fossil remains. It seems, however, that the disproportions may have resulted from the applied excavation procedure rather than from the influence of taphonomic processes. The anatomical terminology used is according to Szyndlar and Rage (2003); see Fig. 1 for details.

Systematic palaeontology

Class Reptilia Laurenti, 1768.
Order Squamata Oppel, 1811.
Suborder Serpentes Linnaeus, 1758.
Infraorder Alethinophidia Nopcsa, 1923.
Family Aniliidae Fitzinger, 1826.
Genus *Eoanilius* (Rage 1974).
Type species: *Eoanilius europae* (Rage 1974).

***Eoanilius* sp.**

Figure 1.

Material:

Ten trunk vertebrae from Sandelzhausen.

Description:

The vertebrae are characterized by very small dimensions and relatively simple morphology. In the largest (incomplete) vertebra the centrum length is 2.6 mm; in remaining vertebrae it ranges between 1.8 and 2.1 mm.

Most vertebrae come from the middle trunk portion of the vertebral column. The centrum is as wide as long, and cylindrical. The haemal keel is very indistinct (though broad), accompanied by very shallow subcentral grooves. The neural arch is strongly depressed. The neural spine is extremely low; it occupies one-third the neural arch length. The pre- and postzygapophyseal articular facets are relatively large, oval-shaped and elongated. The prezygapophyseal processes are very short and hardly visible in dorsal view. The zygosphenal roof is either three-lobed in dorsal view or is devoid of the central lobe. The cotyle and

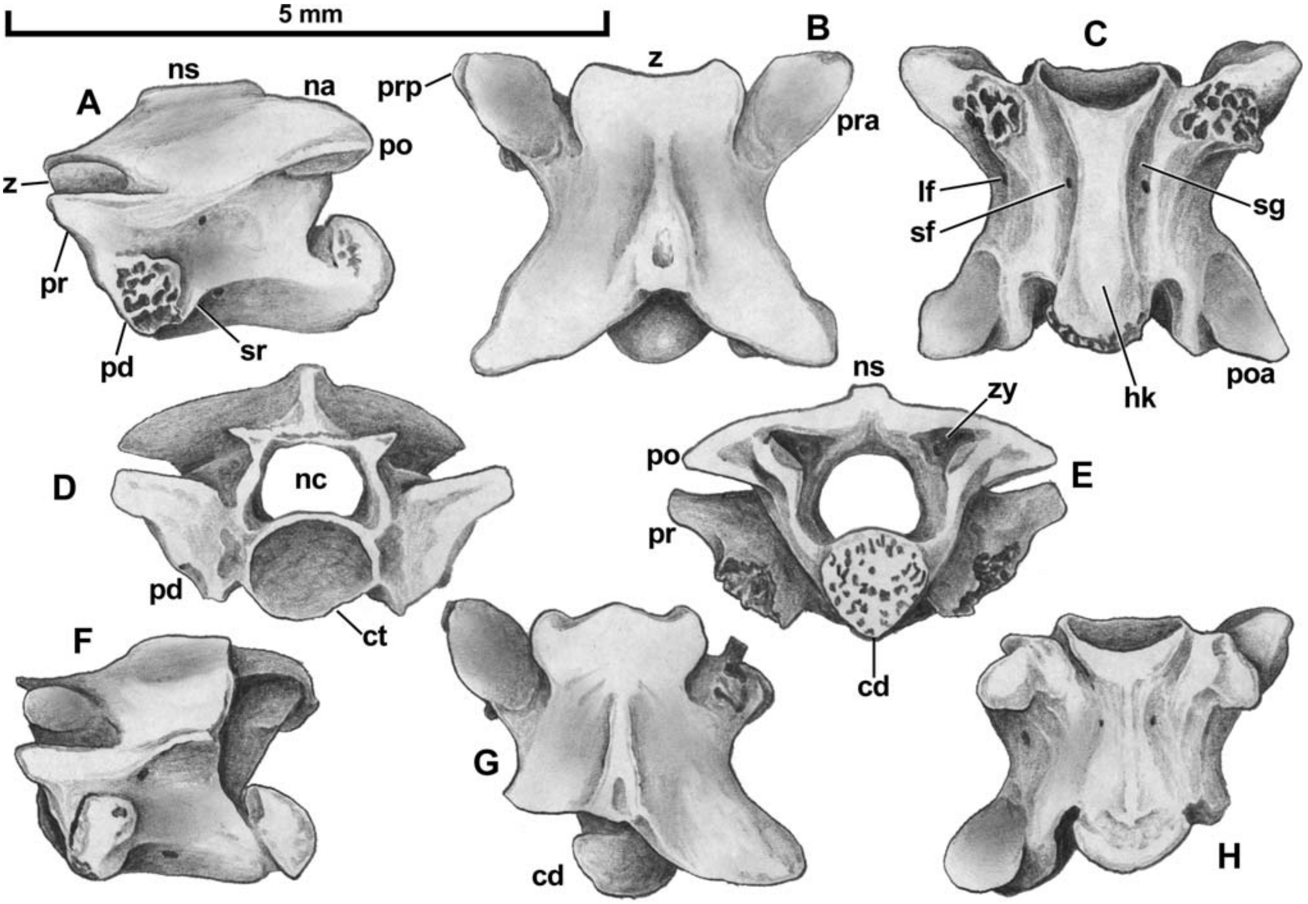

Fig. 1 Two trunk vertebrae (**a–e** BSPG 1959 II 15967; **f–h** BSPG 1959 II 15966) of *Eoanilius* sp. from Sandelzhausen. cd: condyle; ct: cotyle; hk: haemal keel; lf: lateral foramen; na: neural arch; nc: neural canal; ns: neural spine; pd: paradiapophysis; po: postzygapophysis; poa: postzygapophyseal articular surface; pr: prezygapophysis; pra: prezygapophyseal articular surface; prp: prezygapophyseal process; sf: subcentral foramen; sg: subcentral groove; sr: subcentral ridge; z: zygosphene; zy: zygantrum. **a**, **f** left lateral views; **b**, **g** dorsal views; **c**, **h** ventral views; **d** anterior view; **e** posterior view

condyle are suborbicular or flattened dorso-ventrally. The paradiapophyses are relatively large, with no clear division into para- and diapophyseal portions. The lateral and subcentral foramina are distinct; the paracotylar foramina are absent.

The vertebrae interpreted as coming from the posterior trunk portion of the column are distinctly longer than those from the middle trunk portion; they have more distinct haemal keels and deeper subcentral grooves.

Comments:

The vertebrae are clearly referable to the extinct *Eoanilius*, a member of the family Aniliidae, the present-day distribution of which is restricted to tropical America.

The oldest remains of the extinct genus *Eoanilius*, represented by the type-species *E. europae* (Rage 1974), come from the late Eocene of France (Rage 1974), Britain (Milner et al. 1982) and Spain (Szyndlar and Alférez 2005). *Eoanilius* is considered the only ophidian genus that survived the “Grande Coupure” events at the Eocene/Oligocene boundary in Europe. Geologically younger remains of this snake, usually referred to the species *E. oligocenicus* (Szyndlar 1994), were reported from several German and French localities, dated from the Early Oligocene to Early Miocene (see Szyndlar and Rage 2003, and references therein). Additional remains of *Eoanilius*, not included in the list by Szyndlar and Rage, were also found in two French Oligocene localities, Lebratières 14 and La Colombière (Rage and Szyndlar, unpublished), as well as in the Early Miocene (MN3 or 3–4) of Agramón in Spain (Szyndlar and Alférez 2005).

Interestingly, *Eoanilius* was a dominant element in middle Early Miocene (MN2 and 3) snake assemblages of southern Germany (Szyndlar and Schleich 1993). The vertebrae from Sandelzhausen are morphologically and metrically very similar to those of *Eoanilius* sp. reported from the locality of Petersbuch 2 (MN4) (Szyndlar and Schleich 1993).

Sandelzhausen is the geologically youngest fossil site yielding remains of *Eoanilius*.

Family Boidae Gray, 1825.

Genus *Bavarioboa* Szyndlar and Schleich, 1993.

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

Bavarioboa ultima Szyndlar and Rage, 2003.

Material:

Twenty-two trunk vertebrae, one cloacal vertebra, and one caudal vertebra from Rothenstein 13.

Comments:

Szyndlar and Schleich (1993), who erected the extinct boid genus *Bavarioboa*, considered the snake from Rothenstein 13 a member of the type (then the only known) species, i.e. *Bavarioboa hermi* from Petersbuch 2. Szyndlar and Rage (2003) described the remains from Rothenstein 13 as a distinct species, named *Bavarioboa ultima*. They based their description on 18 trunk vertebrae. In addition, the ophidian material from Rothenstein 13 contains four other trunk vertebrae, one cloacal (sacral) vertebra and one caudal vertebra referable to this snake. See Szyndlar and Rage (2003) for detailed generic and specific diagnoses of this snake.

Representatives of the ophidian superfamily Booidea (mainly members of the family Boidae) were dominant elements in snake faunas throughout the Paleogene, in Europe and elsewhere. Members of the extinct genus *Bavarioboa*, along with the erycine *Bransateryx*, were the most common European snakes in the Middle and Late Oligocene; *Bavarioboa* disappeared from Europe at the end of the Oligocene, but it reappeared in the continent at the end of the Early Miocene (Szyndlar and Rage 2003; Rage and Szyndlar 2005). *Bavarioboa ultima* from Rothenstein 13, along with *Bavarioboa* sp. from the French locality Isle d'Abeau, is the geologically youngest representative of the genus (Szyndlar and Rage 2003). Most European boid snakes became extinct before the end of the Middle Miocene (MN7 + 8); the only representatives of the family that survived until today in the southeastern part of the European continent are small sand boas (genus *Eryx*).

Family Colubridae Oppel, 1811.

Subfamily "Colubrinae".

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

Type species: *Coluber constrictor* Linnaeus, 1758.

"*Coluber*" sp.

Figure 2.

Material:

Sixty-five trunk vertebrae and one maxillary fragment from Sandelzhausen.

Description:

The discussed vertebrae, all preserved in more or less fragmentary state, come from the middle trunk portion of the column. They belonged to large-sized snakes; the centrum length of the largest vertebra (Fig. 2a) is 9.7 mm. The vertebrae are relatively high and short in lateral view. The centrum is triangular in ventral view and it is slightly longer than wide. The subcentral ridges are well developed. The haemal keel is distinct and cuneate-shaped. The neural arch is moderately vaulted, not accompanied by epizygapophyseal spines. The neural spine (almost completely preserved in one vertebra only; Fig. 2j) is approximately as high as long; the posterior margin of the spine slightly overhangs. The zygosphene (completely preserved in few vertebrae) is roughly straight. The prezygapophyseal articular facets are oval. The prezygapophyseal processes (preserved in three vertebrae) are either as long as the articular facet and obtuse (Fig. 2h) or somewhat shorter than the facet and acute (Fig. 2i). The paradiapophyses are moderately well developed, with the dia- and parapophyseal portions of roughly equal length. The cotyle and condyle are slightly depressed dorso-ventrally. The lateral, subcentral and paracotylar foramina are distinct.

Comments:

In its vertebral morphology, the snake from Sandelzhausen most approaches the conditions observed in the vertebrae of four large-sized (and perhaps closely related) fossil species, namely *Coluber dolnicensis*, *C. caspioides*, *C. suevicus* and *C. pouchetii*. A single maxillary fragment, owing to the presence of a completely preserved "*Coluber*-like" ectopterygoid process, is also temporarily referred to the same snake. All the ophidian species mentioned in the preceding paragraph are referred to the informal subfamily "Colubrinae" (or "colubrines"), characterized by the absence of hypapophyses in their middle trunk vertebrae. It is worth adding that, in the recent past, the generic name *Coluber* encompassed as many as nine species of living European "colubrines", today classified in the genera *Hemorrhois*, *Hierophis* and *Platyceps*. The most likely allocation of the fossil group *dolnicensis–caspioides–suevicus–pouchetii* is in the genus *Hierophis*. In this paper I use the traditional name "*Coluber*", mainly because this name is still in use in the European paleontological literature. However, I put the generic name in quotation marks.

Rage and Bailon (2005) listed vertebral characteristics enabling to distinguish remains of the above four fossil species. Unfortunately, regarding the snake from Sandelzhausen, the fragmentary nature of its vertebrae does not enable to identify it to the specific level.

The oldest fossil record of snakes belonging to the discussed group comes from the Czech locality of Merkur-North (MN3) from which Ivanov (2002) reported the presence of three species of the complex (*Coluber dolnicensis*, *C. caspioide* , *C. pouchetii*) altogether. In the final Early and Middle Miocene these species became widespread in the European continent (e.g. Szyndlar and Schleich 1993; Augé and Rage 2000; Ivanov 2000; Rage and Bailon 2005). The geologically youngest record is that of cf. *C. pouchetii* from the early Late Miocene (MN9) of

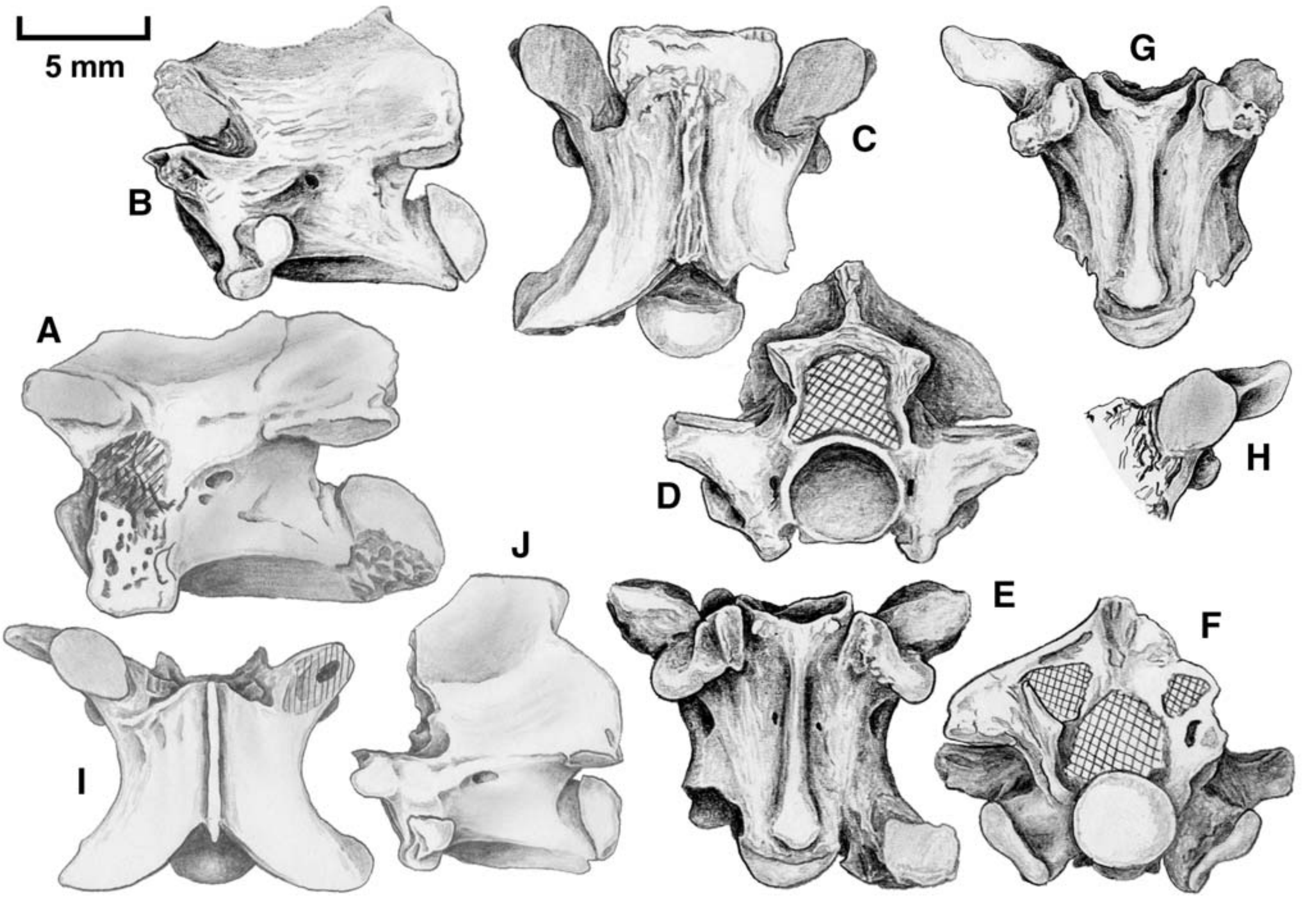

Fig. 2 Four trunk vertebrae (**a** BSPG 1959 II 8094; **b**–**f** BSPG 1952 II 16092; **g**, **h** BSPG 1959 II 16093; **i**, **j** BSPG 1959 II 16131) of *Coluber* sp. from Sandelzhausen. **a**, **b**, **j** left lateral views; **c**, **h**, **i** dorsal views; **d** anterior view; **e**, **g** ventral views; **f** posterior view

the Hungarian locality of Rudabánya (Szyndlar 2005). The alleged closest living relative of the Miocene "*Coluber*" is *Hierophis* (formerly *Coluber*) *caspius*, inhabiting today the southeastern parts of the European continent.

Genus *Telescopus* Wagler, 1830.

Type species: *Telescopus obtusus* Reuss, 1834.

***?Telescopus* sp.**

Material:

Two trunk vertebrae from Sandelzhausen.

Description:

The vertebrae display a number of peculiarities characteristic of the living genus *Telescopus*, among others its parapophyses are distinctly longer than diapophyses, the neural spine is extremely low, and the prezygapophyseal processes are short and obtuse. Unfortunately, exact generic allocation based on such material (two poorly preserved and fragmentary vertebrae only) is not possible.

Comments:

The living genus *Telescopus* is widely distributed in Eurasia and Africa; one species, *T. fallax*, inhabits today southeastern Europe. Fossil remains of *Telescopus* were reported from several localities of eastern and central Europe, ranging in age from the Early Miocene (MN4) to the Pleistocene (for details see Szyndlar 2005, and references therein).

"Colubrinae" indet.

Material:

Ten trunk vertebrae and two maxillary fragments from Sandelzhausen; seven trunk vertebrae from Rothenstein 13.

Comments:

These fragmentary vertebrae represented tiny snakes (with vertebral centra approximately 3 mm long), are morphologically different from the large-sized "*Coluber*" and ?*Telescopus* found in Sandelzhausen.

The vertebrae belonged to at least two different taxa. One vertebra from Sandelzhausen has a broad haemal keel in ventral view; the remaining vertebrae, coming from both sites, have very thin keels. All vertebrae are poorly preserved and devoid of protruding structures, so it is difficult to ascertain whether the snakes from Sandelzhausen and Rothenstein 13 represented different species or not.

Two small maxillary fragments from Sandelzhausen, with partly preserved prefrontal processes, are only temporarily classified as belonging to "colubrines".

Subfamily "Natricinae".

Genus *Natrix* Laurenti, 1768.

Type species: *Coluber natrix* Linnaeus, 1758.

***Natrix* sp.**

Material:

Thirty-two trunk vertebrae from Sandelzhausen and ten trunk vertebrae from Rothenstein 13.

Description:

All vertebrae are fragmentary and most of their protruding elements are lacking. For instance, only one vertebra has fully preserved hypapophysis, whereas only two vertebrae have preserved prezygapophyseal processes (on one side only). The vertebral centra are considerably elongated, with flat ventral surface delimited laterally with usually strongly developed subcentral ridges. The centrum length ranges between 3.0 and 4.0 mm. The hypapophysis (preserved only in one vertebra from Sandelzhausen) is rather straight (and not sigmoid-shaped) in lateral view and its distal tip is obtuse. The neural arch is weakly vaulted. The neural spine (present partly in three vertebrae) is somewhat lower than long, distinctly overhanging posteriorly (anterior portions of all spines are broken). The paradiapophyses are strongly built, provided with prominent parapophyseal processes, obtuse in shape and directed anteriorly; the diapophyses are usually as long as parapophyses. The zygosphenal roof is usually slightly convex in dorsal view. The prezygapophyseal articular facets are oval-shaped and elongate. Few postzygapophyseal articular facets are preserved; they are small and subsquare. The prezygapophyseal processes (missing in most vertebrae) are as long as the prezygapophyseal articular facets and slender. The cotyle and condyle are orbicular. The subcentral, lateral and paracotylar foramina are distinct, though rather small.

Comments:

The morphological characteristics of the discussed vertebrae are typical of the living genus *Natrix*. One of the most important diagnostic features is the shape of the hypapophysis, in our case unfortunately preserved in one vertebra only. Although the hypapophysis is not sigmoid-shaped (as characteristic of most vertebrae of members of the genus *Natrix*), straight-shaped hypapophyses are also not uncommon in trunk vertebrae of *Natrix* (especially in those located in more anterior portions of the column). Identification of *Natrix* from Sandelzhausen and Rothenstein 13 to the specific level, owing to the poor preservation of the vertebrae, is not possible.

Members of the genus *Natrix* were present in Europe since the Early Oligocene (Rage 1988), but the great bloom of these snakes in the European continent began in the second half of the Early Miocene (MN3) (Ivanov 2002). Along with "colubrines", "natricines" (represented by at least three different genera) were the most diverse and most widespread ophidian group in the period between the late Early and early Late Miocene (MN4 to 9). The genus *Natrix* was represented in the aforementioned period by six extinct species. See Rage and Bailon (2005) and Szyndlar (2005) for up-to-date reviews of the fossil record of Miocene *Natrix*.

cf. *Natrix* sp. (large form).

Material:

Three trunk vertebrae from Sandelzhausen.

Comments:

Morphologically, these vertebrae do not differ considerably from those referred above to *Natrix* sp., but they must have belonged to (a) specimen(s) of distinctly larger dimensions, perhaps representing a distinct species. The centrum length measured in two vertebrae is 7.4 mm. The bones are badly damaged.

Genus *Neonatrix* Holman, 1973.

Type species: *Neonatrix elongata* Holman, 1973.

cf. "*Neonatrix*" sp.

Material:

Four trunk vertebrae from Sandelzhausen and ten trunk vertebrae from Rothenstein 13.

Description:

These vertebrae are relatively small, with the centrum length 2.7 mm or shorter. The bones are poorly preserved; however, most of them have retained complete (or almost complete) neural spines and hypapophyses. The spines are extremely low, whereas the hypapophyses are very short.

Comments:

Both these characteristics were considered the most important diagnostic features of the extinct genus *Neonatrix* (cf. Rage and Holman 1984). Later, however, in the emended generic diagnosis of this genus, Augé and Rage (2000) redefined *Neonatrix* as "a small »natricine« with a short hypapophysis" (whereas the significance of a low neural spine was ignored), an action criticised by Szyndlar (2005) (cf. also Szyndlar and Schleich 1993).

In the opinion of Szyndlar and Schleich (1993), this genus may be an artificial, polyphyletic taxon; for this reason, the generic name *Neonatrix* is presented in quotation marks.

Snakes classified in the genus *Neonatrix*, originally described from the Miocene of North America, were widespread in the European continent in the period between the late Early Miocene (MN4) (Szyndlar 1987; Szyndlar and Schleich 1993; Rage and Bailon 2005) and the beginning of the Pliocene (MN14) (cf. *Neonatrix*; Venczel 2001). See Holman (2000) for the review of the North American record of the genus.

"Natricinae" indet.

Material:

Fifty trunk vertebrae from Sandelzhausen.

Comments:

These vertebrae cannot be identified owing to their strong damage. Probably they belonged to the aforementioned natricine snakes.

Family Elapidae Boie, 1827.

Genus *Naja* Laurenti, 1768.

Type species: *Coluber naja* Linnaeus, 1758.

***Naja* sp.**

Figure 3.

Material:

Six trunk vertebrae from Sandelzhausen and (possibly) eight trunk vertebrae from Rothenstein 13.

Description:

The vertebrae from Sandelzhausen come from the middle and posterior portions of the trunk region of the column. The largest and best preserved middle trunk vertebra (Fig. 3a–d) is incomplete; its protruding parts are lacking. It is relatively very short, with rather weakly developed indentation between the pre- and postzygapophyses. The centrum length is 7.7 mm, centrum width is 6.5 mm; it is triangular in ventral view, with almost flat ventral surface. The subcentral ridges are well developed. The hypapophysis and neural spine remain unknown. The neural arch is weakly vaulted. The paradiapophyses are well developed; the parapophyseal processes are projected anteriorly and obtuse in shape. The zygosphenal roof is roughly straight in dorsal view, laterally provided with two indistinct lobes. The prezygapophyseal articular facet (preserved in another mid-trunk vertebra: Fig. 3e) is oval-shaped. The prezygapophyseal process is well developed, somewhat shorter than the articular facet a, having moderately obtuse tip; it is directed laterally. The cotyle and condyle are orbicular. The subcentral, lateral and paracotylar foramina are distinct.

One vertebra coming from the posterior (but not posteriormost) trunk portion of the column (Fig. 3f–g) is much more elongate than the mid-trunk vertebrae. The hypapophysis is very short, triangular-shaped, with the distal tip acute and projecting posteriorly. The neural spine is very low. It does not differ substantially from the posterior trunk

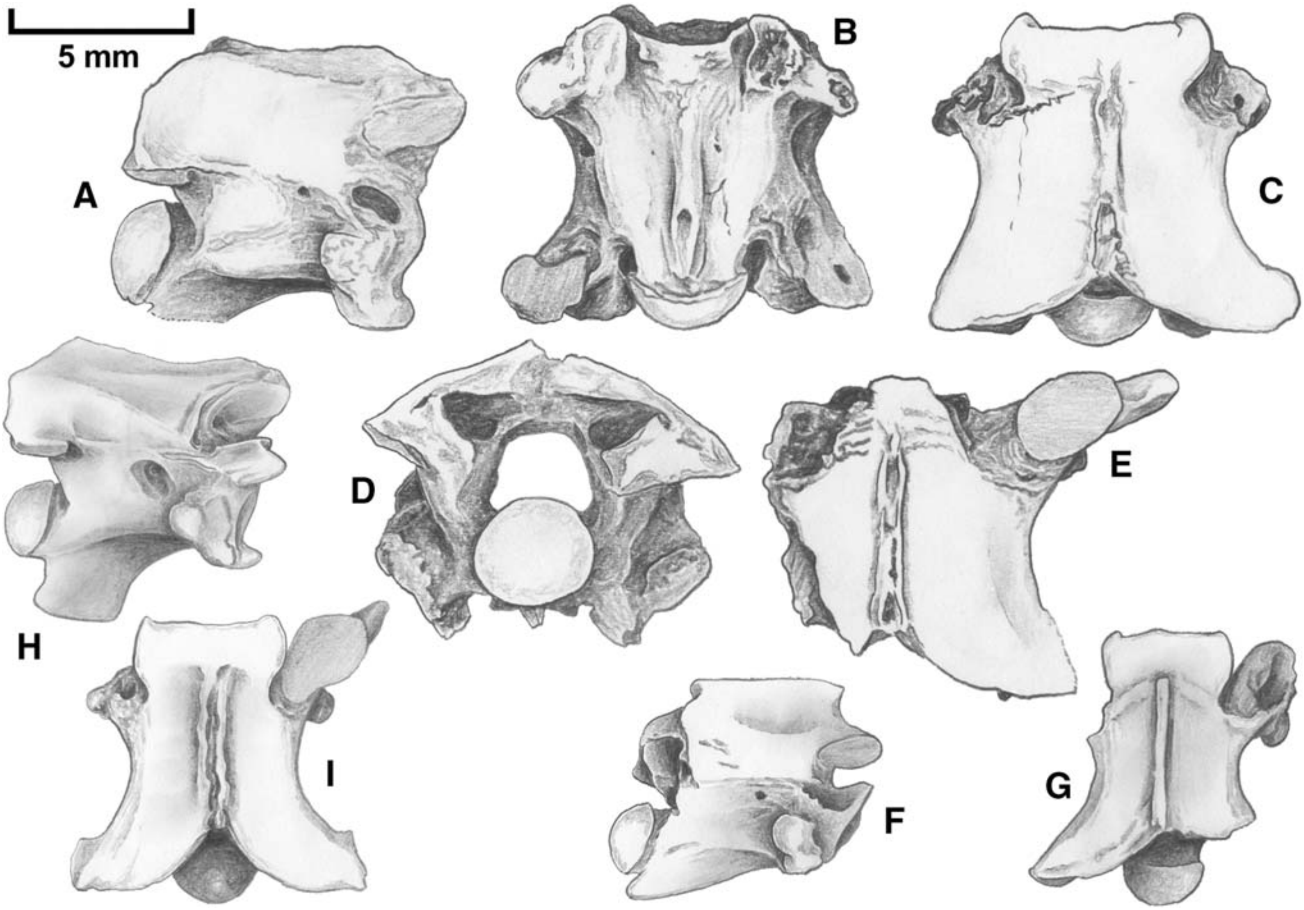

Fig. 3 Four trunk vertebrae (**a–d** BSPG 1959 II 16096; **e** BSPG 1959 II 16097; **f**, **g** BSPG 1959 II 16018); **h**, **i** BSPG 1959 II 15958) of *Naja* sp. from Sandelzhausen. **a**, **f**, **h** right lateral views; **b** ventral view; **c**, **e**, **g**, **i** dorsal views; **d** posterior view

vertebrae of *Naja romani* from the French Middle Miocene depicted by Hoffstetter (1939, pl. II Fig. 8; originally described as *Palaeonaja romani*).

Another vertebra from Sandelzhausen (Fig. 3h–i) may have been the last trunk vertebra (or one of a few last trunk vertebrae). It lacks the neural spine and left prezygapophysis, but besides it is perfectly preserved. The centrum length is 6.1 mm and centrum width is 4.5 mm. Its most striking feature is the shape of the hypapophysis: in lateral view, it looks like a subsquare-shaped plate.

The vertebrae from Rothenstein 13, belonging to (a) smaller individual(s), are badly damaged and their assignment to the genus cannot be fully demonstrated.

Comments:

The vertebrae are similar to those of *Naja romani*, the elapid widespread in Europe from the Early (MN4) to the Late (MN11) Miocene (Szyndlar and Rage 1990), and perhaps they actually belong to this species. However, considering the poor preservation of the material (in particular the mid-trunk vertebrae), this cannot be stated with certainty. The bone interpreted as the last trunk vertebra (Fig. 3h–i) is strikingly similar to that of *N. romani* reported recently (Szyndlar 2005) from the Hungarian locality of Rudabánya. Szyndlar made attempts to reconstruct the morphology of the posterior trunk portion of the vertebral column of *N. romani*, pointing out similarities between this fossil species and its living relative, *N. naja* from southern Asia. It is not certain, however, whether the middle trunk and posterior trunk vertebrae from Sandelzhausen belonged to the same species of cobra. The snake from which the posteriormost vertebra originates must have possessed much larger mid-trunk vertebrae than those found in Sandelzhausen. Also the cobra from Rothenstein 13 may have represented another species, characterized by smaller dimensions.

For the full account of the fossil record of the genus *Naja* in Europe see Szyndlar and Rage (1990); for recent updates see Szyndlar (2005).

Elapidae indet.

Material:

Six trunk vertebrae from Sandelzhausen and two trunk vertebrae from Rothenstein 13.

Description:

These fragmentary vertebrae, belonging to relatively small snakes, are characterized by elongated centra and very short (vestigial) hypapophyses. The latter structures, completely preserved in most vertebrae, are the only protruded elements in the discussed remains. The centrum length of most vertebrae found in both localities ranges between 3.0 and 4.0 mm. In one vertebra from Sandelzhausen (belonging to an adult snake) the centrum length is 1.5 mm only. It is possible that the vertebrae belonged to two or more different species.

Comments:

The systematic allocation of these vertebrae is unclear. Most likely they belonged to elapid snakes, but their allocation in the colubrid subfamily “Natricinae” is also possible.

The discussed vertebrae resemble those of a number of small elapids reported from several Miocene localities of Europe. Of them, the only snake identified to the specific level is *Micrurus gallicus* (Rage and Holman 1984), a fossil member of the extant North American genus reported from several Early and Middle (MN4 to MN7 + 8) Miocene sites (see Rage and Bailon 2005, and references therein). However, the vertebrae from Sandelzhausen and Rothenstein 13 seem to be morphologically closer to the remains of another tiny alleged elapid snake first reported from the Early Miocene (MN4) of Petersbuch 2 by Szyndlar and Schleich 1993 (termed “Elapidae indet.”); these authors compared the snake from Petersbuch 2 with the Asiatic living genus *Maticora* (now synonymised with *Calliophis*). Similar small elapids are known from Europe from the period ranging in age from the Early (MN3) (Ivanov 2000) to Late (MN9) Miocene (Szyndlar 2005), but their taxonomic status and possible relationships with other fossil and living snakes remain unknown.

McDowell (1987) once suggested close similarities between New World (*Micrurus*) and Asian Coral snakes (*Calliophis*). However, Slowinski et al. (2001) demonstrated that Asian coral snakes (*Calliophis*) are paraphyletic relatives to New World coral snakes (*Micrurus*). They proposed that the origin of New World coral snakes was Asian; hence, New World coral snakes derived from an ancestor which arrived into the Americas via Bering Land Bridge.

Family Viperidae Oppel, 1811.

Genus *Vipera* Laurenti, 1768.

Type species: *Coluber aspis* Linnaeus, 1758.

***Vipera* sp. (“*aspis* complex”).**

Material:

Twenty trunk vertebrae and one right compound bone from Rothenstein 13.

Description and comments:

Members of the living genus *Vipera* referred to the so-called *aspis* complex were present in Europe, including Germany, since the beginning of the Miocene (MN1) (Szyndlar and Böhme 1993). Since the end of the Early Miocene (MN4), in most fossil assemblages these reptiles were usually accompanied by members of another complex of the genus *Vipera*, namely “Oriental vipers” (Szyndlar and Rage 2002). Specific identification of viperid fossils is very difficult, but distinguishing the two complexes based on vertebrae is a relatively easy task. Vertebrae of the “Oriental vipers” are relatively very large and short, having high neural spines, whereas those of the “*aspis* complex" are smaller and more elongate, having lower neural spines.

The viperid vertebrae from Rothenstein 13, although strongly damaged, display clearly the conditions characteristic of the latter group. The centrum length of the largest vertebral fragment is 6.0 mm; the remaining vertebrae have smaller dimensions.

A small posterior fragment of a compound bone (without number in the collection of the SMNS) is identifiable as belonging to *Vipera* based on its relatively high medial flange.

Fossil remains of *Vipera* belonging to the "*aspis* complex" were fairly common in Miocene and Pliocene sites. Today the range of the distribution of these vipers is restricted almost exclusively to southern Europe (south of the Alps). See Szyndlar and Rage (2002) for more information on the past distribution of "*aspis*-like" vipers and other members of the genus *Vipera* (s.l.).

***Vipera* sp. ("Oriental viper").**

Figure 4.

Material:

Eighteen trunk vertebrae, one cloacal vertebra and >50 isolated venomous fangs from Sandelzhausen.

Description and comments:

The presence of the "Oriental vipers" in Sandelzhausen was first reported by Szyndlar and Schleich (1993). Most vertebrae, coming from the middle trunk portion of the column, although badly damaged, display clearly characteristic of the "Oriental vipers". The centrum length of the largest vertebra is 9.2 mm; centrum width is 8.5 mm; centrum length/centrum width ratio <1.1.

The centrum of the trunk vertebrae is distinctly triangular-shaped in ventral view. The subcentral ridges and subcentral grooves are distinct in the anterior portion of the centrum. The hypapophyses are missing in all vertebrae, but the remnants indicate that the structure was very strong and thick. The neural arch is strongly depressed and tilted in the postzygapophyseal area, devoid of epizygapophyseal spines. The neural spine is lacking in all vertebrae. The zygosphene is very thick in anterior view and straight in dorsal view. The prezygapophyseal articular facet, preserved on one side in one vertebra only, is rectangular-shaped, strongly elongated laterally. Prezygapophyseal processes, parapophyses and parapophyseal processes are either lacking or eroded in all available vertebrae. The cotyle and condyle are (usually strongly)

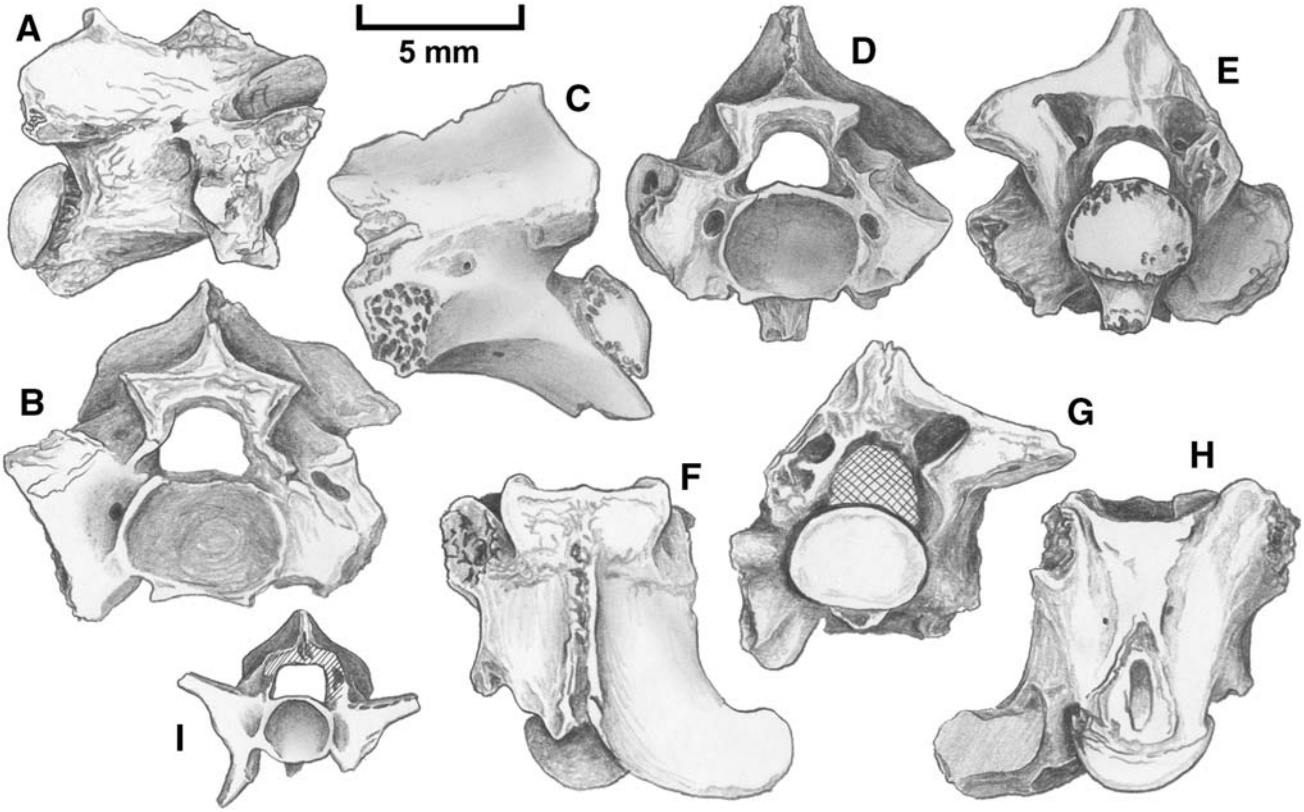

Fig. 4 Four trunk vertebrae (**a** BSPG 1952 II 16090; **b** BSPG 1952 II 16091; **c–e** BSPG 1959 II 16010; **f–h** BSPG 1959 II 16095) and a cloacal vertebra (**i** BSPG 1959 II 15976) of *Vipera* sp. ("Oriental viper") from Sandelzhausen. **a** right lateral view; **b**, **d**, **i** anterior views; **c** left lateral view; **e**, **g** posterior views; **f** dorsal view; **h** ventral views

flattened dorso-ventrally. All vertebral foramina are distinct.

Today "Oriental vipers" (in recent herpetological literature usually classified in the genera *Macrovipera* and *Montivipera*) are distributed in Asia and northern Africa; in Europe, their distribution is restricted to southeastern outskirts of the continent. However, in the Neogene they inhabited vast areas of Europe (at least its southern half) and belonged to the commonest elements of fossil snake assemblages. See Szyndlar and Rage (2002) for more information on the past distribution of these vipers.

Serpentes indet.

Material:

One hundred and thirty caudal vertebrae, 2 dentary fragments and 1 fragment of an unidentified toothed bone from Sandelzhausen; 46 trunk vertebrae, 13 caudal vertebrae and 2 ?pterygoid fragments from Rothenstein 13.

Comments:

The bones likely belonged to the above described taxa, but this cannot be demonstrated owing to the poor preservation of the remains. A small fragment of an unidentified toothed bone (bearing two teeth) and two fragmentary dentaries may have belonged to colubrids.

Discussion

The overall composition of the assemblages from Sandelzhausen and Rothenstein 13 is roughly the same as those reported from two late Early Miocene (MN4) localities situated nearby: Dolnice in western Czechia (Szyndlar 1987) and Petersbuch 2 in southern Germany (Szyndlar and Schleich 1993). Unfortunately, owing to the poor preservation of the fossils from Sandelzhausen and Rothenstein 13, most faunal elements cannot be compared precisely at the specific level. At the generic level, the fossils do not differ substantially from those found in a number of European sites representing European Land Mammal Zones MN4 and MN6 (cf. Ivanov 2000, fig. 16; Rage and Bailon 2005, tab. 1).

The snake assemblage from Sandelzhausen differs from that of Rothenstein 13 by the presence of *Eoanilius*, *Telescopus* and "Oriental viper". In contrast, the assemblage from Sandelzhausen lacks *Bavarioboa* and the "*aspis*-like" *Vipera*, which are represented in Rothenstein 13. These differences in the faunal compositions might indicate the ecologically different habitats (wet Molasse Basin and dry karstic area of the Franconian Alb) (Kaiser and Rössner 2007) or ecologically differently adapted species. The main ecological difference of both habitats are seasonally dry conditions in the Molasse Basin compared with year-round dry edaphic conditions and missing open water in the karstic area. On the other hand, the different faunal composition might be due to taphonomical effects, where a higher specimen number supports the probability of a record of a higher taxonomical diversity. However, the fossil remains are too scarce and too fragmentary to give answers on these questions. But, since differences in the habitat conditions are indisputable, possible differences in the adaptations of single taxa have to be considered, especially in creeping reptiles, for which this study might be an initial suggestion.

The most interesting component of the discussed snake faunas is the extinct aniliid genus *Eoanilius*: Sandelzhausen is the geologically youngest site yielding this Eocene survivor. Similarly, the extinct boid *Bavarioboa* from Rothenstein 13 (along with a related snake from the coeval locality of Isle d'Abeau in France) is the geologically youngest representative of the genus (Szyndlar and Rage 2003).

Fossil snakes do not seem to be a useful tool for reconstructing most factors of palaeoecosystems; nevertheless, they are commonly considered very good indicators of past climates, in particular environmental temperatures. This property results directly from their physiological dependence on external sources of heat. Although the reduction in diversity from lower to higher latitudes can be observed in virtually all groups of animals and plants worldwide, among terrestrial vertebrates reptiles (including snakes) are particularly sensitive to cold. In other words, their south-to-north geographical distribution is largely determined by available heat energy. The composition of the snake fauna from Sandelzhausen and Rothenstein 13, similarly to the older (MN4) faunas coming from several nearby localities, indicates that air temperatures in the area must have been distinctly higher that today. However, the climate in Central Europe must have been less favourable for highly thermophilous reptiles than in the case of more southern parts of Europe. The most obvious indicator of lower temperatures in southern Germany compared with southern Europe in the Miocene is the absence of the genus *Python* successfully invading Mediterranean coasts at the Early/Middle Miocene transition (Szyndlar and Rage 2003). Other obvious candidates for highly thermophilous forms could be cobras of the genus *Naja*. Unfortunately, our knowledge about possible relationships between the extinct cobras from Sandelzhausen and Rothenstein 13 and their living relatives from Asia is limited, again due to poor preservation of the fossil remains. Most living members of the genus *Naja* inhabiting the Asiatic continent today are highly thermophilous; *N. oxiana*, however, distributed relatively closely to the European eastern outskirts and reaching the elevations of almost 2,000 m (Joger 1984), is apparently an animal adapted to more severe climatic conditions.

Conclusion

The ophidian faunas from Sandelzhausen and Rothenstein 13 fill a gap in knowledge between MN4 and MN6, which were expected to document a turnover from still archaic influenced to completely modern composed communities. In fact, the hitherto youngest known occurrences of the last archaic elements *Eoanilius* and *Bavarioboa* could be identified, demonstrating a successive modernisation of Central European ophidian faunas from the late Early to the early Middle Miocene.

Based on the ophidian fossils, the climates of Sandelzhausen and Rothenstein 13, although warm, cannot be considered as tropical or subtropical.

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