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SQUAMATES FROM THE EARLY MIOCENE (AQUITANIAN) OF WEIßENBURG 6 (BAVARIA, GERMANY)

ŠUPINATÍ ZE SPODNÍHO MIOCÉNU (AKVITÁN) LOKALITY WEIßENBURG 6 (BAVORSKO, NĚMECKO)

VÁCLAV PACLÍK, MARTIN IVANOV

Abstract

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Squamates from the early Miocene (Aquitanian) of Weißenburg 6 (Bavaria, Germany)

Squamate assemblages of the earliest Miocene (Aquitanian) are extremely rare in Europe due to the lack of well-documented (or dated) localities. We describe a small collection of squamates from the early Miocene (MN 1–2?) locality of Weißenburg 6, Germany. The community consists of four squamate taxa including Lacertidae indet., cf. *Eoanilius* sp., 'Colubridae' gen. et sp. indet. and Viperidae gen. et sp. indet. The presence of *Eoanilius* indicates that thermophilic 'anilioid', whose extant relatives occur under the tropical humid climate, might have survived locally the global decrease in temperatures around the Oligocene/Miocene transition (23.03 Ma). The 'colubrid' snake from Weißenburg 6 differs from known late Palaeogene and earliest Miocene Colubroidea (Colubridae + Natricidae). Although colubroids were apparently common in Europe since the earliest Miocene (Aquitanian), the first significant post-Oligocene dispersal of Colubroidea from Asia and/or North Africa into Europe, accompanied by a quick dispersal of Viperidae (both 'European' and 'Oriental' vipers) and small Elapoidea, can be dated to the early Budrigalian (MN 3). The indeterminate viperid from Weißenburg 6 is among the oldest known fossil record of Viperidae.

Key words: Lacertidae, 'Anilioidea', Colubridae, Viperidae, early Miocene, Germany.

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1. INTRODUCTION

The late early Miocene (MN 4 and early MN 5) squamate assemblages are well-documented in Central Europe including numerous localities in Germany (e.g. Szyndlar and Schleich 1993; Szyndlar and Böhme 1993; Szyndlar and Rage 2003; Szyndlar 2009; Ivanov and Böhme 2011) and several localities in Czech Republic (e.g. Roček 1984; Szyndlar 1987; Čerňanský 2010a, 2010b; Ivanov *et al.* 2020) and Austria (Szyndlar 1998, Čerňanský 2016). Although Aquitanian and early Burdigalian (MN 1 – MN 3) squamates are still poorly known in Europe (Georgalis and Scheyer 2021), at least four Central European localities provided rather diversified communities including the German localities Amöneburg (MN 2; Čerňanský *et al.* 2015), Ulm-Westtangente (MN 2; Čerňanský *et al.* 2016; Klembara *et al.* 2019) and Wintershof-West (MN 3; Ivanov 2015; Paclík *et al.* 2018) and the Czech locality of Merkur-North (MN 3a; e.g. Ivanov 2002; Klembara 2008, 2015; Klembara and Rummel 2018).

As regards snakes, the late Oligocene to early Miocene (Chattian to Burdigalian; MP 28–early MN 5) period is characterized by a strong retreat of Constrictores (usually small forms) and 'anilioids' (MP 28–MN 2), which were common during the Oligocene, followed by an increase in diversity of Colubriformes (sensu Zaher *et al.* 2019) including Viperidae, Elapoidea and Colubroidea [Colubridae + Natricidae + perhaps also Dipsadidae (Georgalis – pers. comm.)] during the early Miocene (Szyndlar and Schleich 1993; Ivanov *et al.* 2000; Szyndlar and Rage 2003; Szyndlar 2012). Traditionally it is presupposed that this change was completed by the massive dispersal of 'modern' snake families (Viperidae, Elapidae, 'Colubridae', Natricidae) into Europe from Asia and/or North Africa during the Miocene Climatic Optimum, MCO (Szyndlar and Schleich 1993; Ivanov 2001; Szyndlar and Rage 2003). However, recent research on European early Miocene snake assemblages (Ivanov 2002, 2015; Paclík *et al.* 2018; Georgalis *et al.* 2019a) indicate that this change in composition of European snake fauna was largely finished as early as the early Burdigalian (Eggenburgian, MN 3), i.e., before the onset of the MCO.

Squamate assemblages of the Oligocene/Miocene transition are almost unknown due to the lack of well-documented MP 30 and MN 2 localities (Szyndlar and Böhme 1996; Szyndlar and Rage 2003; Szyndlar 2012; Georgalis and Scheyer 2021). With the exception of Amöneburg (MN 2; Čerňanský *et al.* 2015), the only diversified earliest Miocene locality is the German locality of Weisenau, MN 1–2 (Villa *et al.* 2021), where two snake taxa from the old collection (MN 2) have their first occurrence including well-documented *Falseryx petersbuchi* (Tropidophiidae) and several trunk vertebrae of *Zamenis kohfidischi* (Colubridae).

In present paper we discuss a small collection of squamates from the German early Miocene locality of Weißenburg 6 (MN 1 – MN 2?). Although the presence of Anguidae and erycid genus *Bransateryx* have been mentioned by Böhme (2003) squamates have never been described in detail. This paper is the first actual documentation of fossil squamates from this locality.

2. LOCALITY AND MATERIAL

The Weißenburg 6 locality was discovered in a limestone quarry, situated about 4 km SW of the Weißenburg town (Bavaria) during the field research conducted by prof. R. Dehm in 1961. The fossil material comes from unstratified deposits of the karstic fissure developed in the Upper-Jurassic limestones of the Swabian Mountains. This fissure provided a diversified fauna of amphibians including Albanerpetontidae (Gardner and Böhme 2008), Salamandridae, Alytidae, Bombinatoridae (Sanchíz and Schleich 1986; Sanchíz 1998; Rage and Roček 2003; Roček 2013), Palaeobatrachidae, Pelobatidae, Pelodytidae and Ranidae (Böhme 2003) but with exception of Albanerpetontidae and Bombinatoridae all remaining amphibians are still undescribed. Turtles are represented by the genus *Ptychogaster* (Geoemydidae; Schäfer 2013), for squamates see above. The age of the karstic filling corresponds to the early Miocene (Aquitanian) of the Lower Freshwater Molasse (fig. 1; Werner 1994). However, a more precise age based on the diversified small mammal community including Eomyidae, Gliridae, Dimylidae and Muridae (Müller 1967; Fahlbusch 1968; Mayr 1979; Ziegler 2006; Prieto and Böhme 2007; Mörs and Flink 2017) is still a matter of debate (MN 1 – MN 2?).

The studied material is housed in the Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich (BSPG) under the collection numbers BSPG-1961 XII 636/1–7.

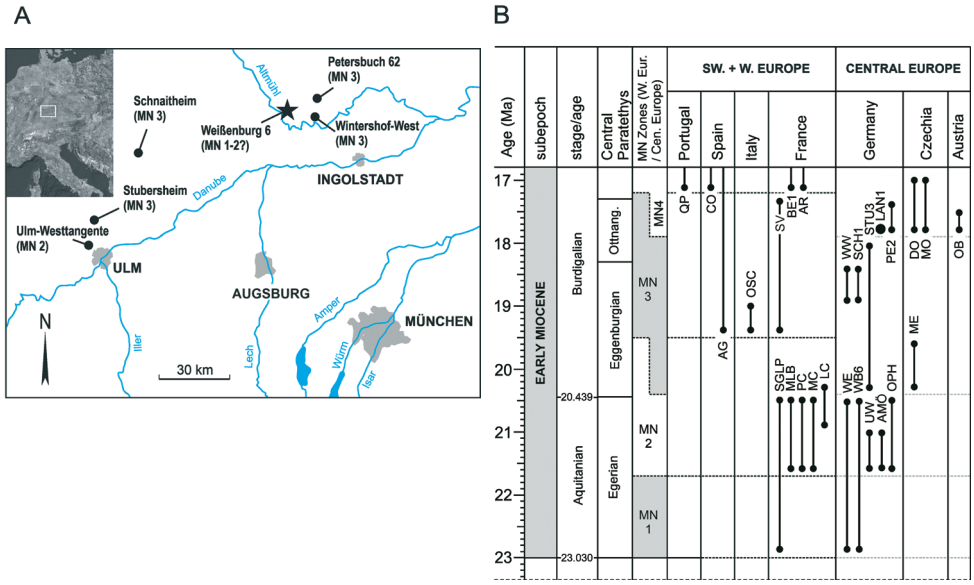

Fig. 1. (A) Map of southern Germany with topographical position of important MN1 – MN 3 squamate localities in Ingolstadt and Ulm region (map based on SCHLEICH 1985, modified); (B) Miocene time scale and biostratigraphy (black dashed lines = Western Europe; grey dashed lines = Central Europe) with stratigraphical positions of Western (SW. + W.) and Central European MN 1 – MN 4 squamate localities. Portugal: **QP**, Quinta das Pedreiras (Lisbon). Spain: **AG**, Agramón; **CO**, Córcoles. Italy: **OSC**, Oschiri. France: **SGLP**, St.-Gérand-le-Puy; **MLB**, Montaigu-le-Blin; **PC**, Poncenat; **MC**, Marcoin; **LC**, Laugnac; **SV**, Serre de Verges; **BE1**, Béon 1; **AR**, Artenay. Germany: **WE**, Weisenau; **WB6**, Weißenburg 6; **AMÖ**, Amöneburg; **UW**, Ulm-Westtangente; **OPH**, Oppenheim/Nierstein; **WW**, Wintershof-West; **STU3**, Stubersheim 3; **SCH1**, Schnaitheim 1; **PE2**, Petersbuch 2; **LAN1**, Langenau 1. Czechia: **ME**, Merkur-North; **DO**, Dolnice; **MO**, Mokrá-Western Quarry. Austria: **OB**, Oberdorf. Miocene time scale and biostratigraphy based on International Chronostratigraphic Chart (COHEN *et al.* 2020), Central Paratethys boundaries follow KOVÁČ *et al.* (2018), modified MN-zonations for Western (left) and Central (right) Europe follow HILGEN *et al.* (2012) and STEININGER (1999). Stratigraphic position of localities modified from IVANOV (2022).

Obr. 1. (A) Mapa jižního Německa s topografickým vyznačením důležitých lokalit (MN1 – MN 3) s faunou šupinatých v oblasti Ingolstadtu a Ulmu (mapa dle SCHLEICH 1985, upraveno); (B) Stratigrafie a biostratigrafie miocénu (černě přerušované linie = západní Evropa; šedě přerušované linie = střední Evropa) se stratigrafickým umístněním lokalit západní (SW. + W.) a střední Evropy s faunou šupinatých (MN 1 – MN 4). Portugalsko: **QP**, Quinta das Pedreiras (Lisabon). Španělsko: **AG**, Agramón; **CO**, Córcoles. Itálie: **OSC**, Oschiri. Francie: **SGLP**, St.-Gérand-le-Puy; **MLB**, Montaigu-le-Blin; **PC**, Poncenat; **MC**, Marcoin; **LC**, Laugnac; **SV**, Serre de Verges; **BE1**, Béon 1; **AR**, Artenay. Německo: **WE**, Weisenau; **WB6**, Weißenburg 6; **AMÖ**, Amöneburg; **UW**, Ulm-Westtangente; **OPH**, Oppenheim/Nierstein; **WW**, Wintershof-West; **STU3**, Stubersheim 3; **SCH1**, Schnaitheim 1; **PE2**, Petersbuch 2; **LAN1**, Langenau 1. Česká republika: **ME**, Merkur-North; **DO**, Dolnice; **MO**, Mokrá-Western Quarry. Rakousko: **OB**, Oberdorf. Stratigrafické a biostratigrafické členění miocénu vychází z mezinárodní chronostratigrafické škály (COHEN *et al.* 2020), členění v oblasti centrální Paratethydy dle KOVÁČ *et al.* (2018), upravená MN-zonace pro západní (vlevo) a střední (vpravo) Evropu podle HILGEN *et al.* (2012) a STEININGER (1999). Stratigrafická pozice lokalit byla upravená dle IVANOV (2022).

3. METHODS

Seven highly fragmentary lizard and snake vertebrae have been preserved. The anatomical terminology for snake vertebrae is based on Szyndlar (1984) and Szyndlar and Rage (2003), the terminology for lizard vertebrae is based on Tschopp (2016) and Čerňanský *et al.* (2019). The material was cleaned with the ultrasonic cleaner Ulsonix Proclean 0.7D and then studied and documented with the Leica MZ-16 stereomicroscope equipped with the digital camera Leica DMC 5400 (20 mpx).

4. SYSTEMATIC PALAEONTOLOGY

Squamata Oppel, 1811
Lacertiformes Estes, Queiroz & Gauthier, 1988
Lacertidae Oppel, 1811
Lacertidae indet.

Material. One posterior presacral vertebra (BSPG-1961 XII 636/1), one anterior caudal vertebra (BSPG-1961 XII 636/2).

Presacral vertebra (fig. 2, A–E): The vertebra is procoelous and rather fragmentary with broken-off left postzygapophysis, condyle, dorsal portion of the neural spine and distal terminations of synapophyses. In lateral view, the neural spine rises anteriorly at the level of the posterior third of prezygapophysis. The base of the neural spine is wide, its cranial margin is inclined posteriorly and damaged posterior margin of the neural spine indicates its extension behind the caudal margin of the neural arch. A short postzygoprezygapophyseal lamina occurs between the pre- and postzygapophysis. A small lateral foramen is situated rather close to the ventral margin of this lamina. The other foramen is situated close to the spinopostzygapophyseal lamina. The ventral margin of the centrum is arched dorsally. In dorsal view, the vertebra is rather wide with shallow interzygapophyseal constriction. The prespinal lamina extends anteriorly to a close vicinity of the slightly eroded anterior edge of the neural arch. This edge (centroprezygapophyseal lamina) is rather wide and roughly straight; it forms a weakly developed pseudozygosphene with small articular facets inclined laterally rather than dorsolaterally. The slightly damaged prezygapophyseal articular facets are widely oval in outline. The preserved portion of the right synapophysis is somewhat prolonged craniolaterally. The neural spine becomes wide towards its caudal termination. In ventral view, a low and wide sagittal ridge extends posteriorly from the cotylar rim. There is a shallow groove in the midline of this ridge. The blunt centrosynapophyseal laminae are concave. A small subcentral foramen occurs left to the sagittal ridge close behind the cotylar rim. In cranial view, prezygapophyses are strongly tilted dorsally. The rather high neural canal is subtriangularly shaped. The oval cotyle is slightly faced ventrally.

Caudal vertebra (fig. 2, F–J): The slightly fragmentary vertebra, with incomplete neural spine and broken-off pleurapophyses, is narrower and more elongated than the presacral vertebra. In lateral view, the neural spine with wide base is high and inclined caudally. A preserved portion of the left pleurapophysis is directed posteroventrally (laterally in dorsal aspect). In dorsal view, the prespinal lamina extends anteriorly and meets the strongly damaged anterior edge of the neural arch. The rising portion of the neural spine becomes wider and exceeds the median notch but not behind the caudal margin of the condyle. Prezygapophyses, with articular facets widely oval, are oriented anterolaterally. In ventral view, paired sagittal ridge (haemapophysis) extends from the ventral margin of the cotylar rim as far as the condylar base but the haemal arch is not preserved. Postzygapophyses with roughly circular articular facets are directed posterolaterally. In cranial view, pre- and post-

zygapophyses are strongly tilted dorsally. The neural canal is subtriangular in outline; it is smaller than the slightly dorsally depressed cotyle. The left pleurapophysis is directed ventrolaterally. In caudal view, the condyle is suborbicular, with well observable haemapophyseal bases underneath.

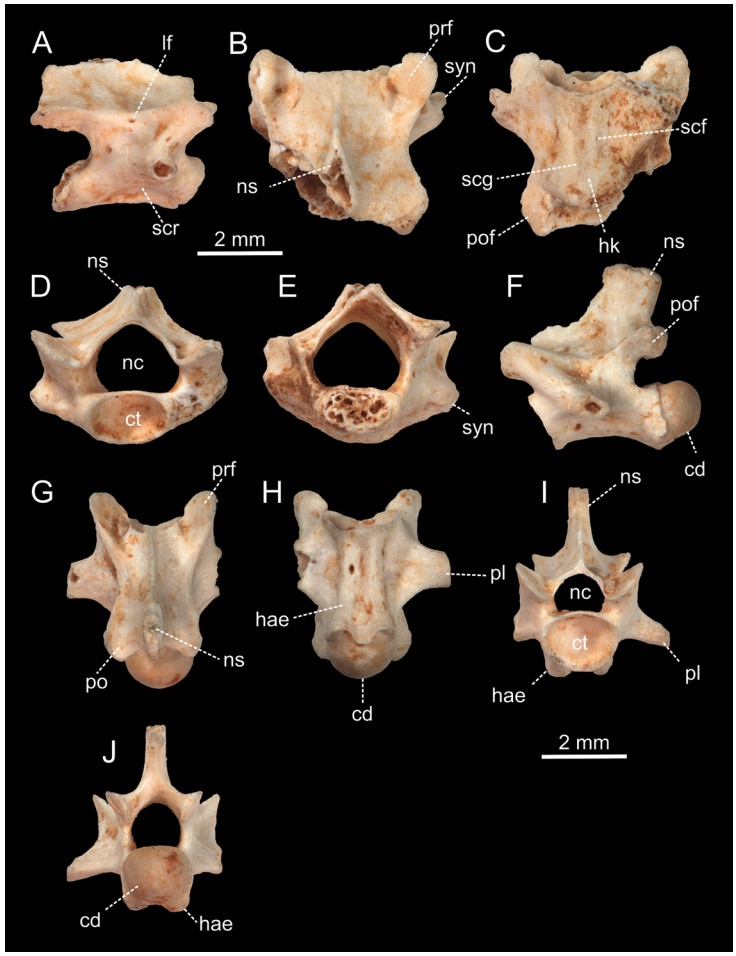

Fig. 2. Lacertidae indet. from the early Miocene (MN 1 – MN2?) of Weißenburg 6. Presacral vertebra (BSPG-1961 XII 636/1) in right lateral (A), dorsal (B), ventral (C), cranial (D) and caudal (E) views. Anterior caudal vertebra (BSPG-1961 XII 636/2) in left lateral (F), dorsal (G), ventral (H), cranial (I) and caudal (J) views. Abbreviations: **cd**, condyle; **ct**, cotyle; **hae**, haemapophysis; **hk**, haemal keel; **lf**, lateral foramen; **nc**, neural canal; **ns**, neural spine; **pl**, pleurapophysis; **po**, postzygapophysis; **pof**, postzygapophyseal articular facet; **prf**, prezygapophyseal articular facet; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **syn**, synapophysis.

Obr. 2. (Lacertidae indet. ze spodního miocénu (MN 1 – MN2?) lokality Weißenburg 6. Presakrální obratel (BSPG-1961 XII 636/1) z pravé laterální (A), dorzální (B), ventrální (C), kraniální (D) a kaudální (E) strany. Přední ocasní obratel (BSPG-1961 XII 636/2) z levé laterální (F), dorzální (G), ventrální (H), kraniální (I) a kaudální (J) strany. Zkratky: **cd**, kondyl; **ct**, kotyl; **hae**, hemapofýza; **hk**, hemální kýl; **lf**, laterální otvor; **nc**, neurální kanálek; **ns**, trnový výběžek; **pl**, pleurapofýza; **po**, postzygapofýza; **pof**, postzygapofyzální artikulární plošká; **prf**, prezygapofyzální artikulární plošká; **scf**, subcentrální otvor; **scg**, subcentrální žlábek; **scr**, subcentrální hřbet; **syn**, synapofýza.

Remarks. The elongated synapophyses and medial groove occurring on sagittal ridge indicate that the specimen BSPG-1961 XII 636/1 comes probably from the posterior presacral region of the vertebral column. The precaudal vertebra can be attributed to indeterminate Lacertidae on the following combination of features (Čerňanský and Augé 2013; Čerňanský *et al.* 2015, 2019): 1, the vertebra is broad in dorsal view with weak interzygapophyseal constriction; 2, the sagittal ridge occurs on the ventral surface of the vertebra; 3, the pseudozygosphene is developed; 4, the neural arch is vaulted and thin centropostzygapophyseal lamina forms the caudal margin of the neural arch. The autotomy septum is absent in preserved caudal vertebra. This non-autotomy occurs in anterior caudal vertebrae in many lizard families including Lacertidae (Etheridge 1967; Barbadillo *et al.* 1995; Gauthier *et al.* 2012; Čerňanský and Augé 2013). Therefore, we presuppose that the position of the vertebra within vertebral column corresponds to the anterior caudal region.

Serpentes Linnaeus, 1758
'Anilioidea' Fitzinger, 1826 (sensu Smith and Georgalis 2022)
cf. *Eoanilius* sp.

Material. Two trunk vertebrae (BSPG-1961 XII 636/3; BSPG-1961 XII 636/4).

Trunk vertebrae (fig. 3, A–K): Both preserved vertebrae are of small dimensions and rather fragmentary. The more complete middle trunk vertebra (BSPG-1961 XII 636/3) has broken-off both synapophyses, the right prezygapophysis and the left postzygapophysis. The condyle is broken-off in both specimens. In lateral view, the partially damaged neural spine rises far behind the zygosphenal facets in the posterior one-third of the flat neural arch. Its steep cranial margin is inclined posteriorly. In more posterior vertebra (BSPG-1961 XII 636/4) the neural spine was rather low despite the fact that its distal tip is eroded. The zygosphenal facets are roughly rhomboid in outline. Interzygapophyseal ridges are well-developed and steeply rise dorsally in caudal direction. The large lateral foramina are situated close below the ridges. The dorsally vaulted subcentral ridges are rather short but they are indistinct in BSPG-1961 XII 636/4. In dorsal view, the zygosphene has two small cranially pointed lateral lobes and rather wide median lobe. The slightly eroded oval left prezygapophyseal articular facet is preserved only in BSPG-1961 XII 636/4. The caudal notch is deep in BSPG-1961 XII 636/3 but more shallow in BSPG-1961 XII 636/4. In ventral view, the wide haemal keel becomes wider towards the condylar neck. Subcentral grooves are weakly developed and large subcentral foramina occur in mid-length of the haemal keel base. Postzygapophyseal articular facets are strongly damaged. In cranial view, the neural arch is strongly flattened in both specimens and the neural canal is rounded with wide lateral sinuses. The relatively thin zygosphenal lip is straight (it is not preserved in BSPG-1961 XII 636/4). The left prezygapophysis is slightly inclined dorsolaterally, with prezygapophyseal articular facet situated above the base of the neural canal in BSPG-1961 XII 636/3; however, prezygapophyses are horizontal in BSPG-1961 XII 636/4. The cotylar rim is roughly circular and no paracotylar foramina are present in BSPG-1961 XII 636/3 (the cotyle is damaged in second specimen). In caudal view, the zygantrum is wide.

Remarks. Although the vertebra is rather poorly preserved, it can be attributed to 'anilioids' on the basis of the following combination of features (Szyndlar 1994, 2009; Szyndlar and Rage 2003): 1, the vertebra is noticeably low; 2, the neural arch is strongly flattened; 3, the very low neural spine is developed in the posterior third of the neural arch far behind the posterior extension of the zygosphene; 4, synapophyses were large; 5, the haemal keel is moderately developed, wide and arched dorsally; 6, paracotylar foramina are absent. The vertebra comes most probably from the posterior part of the precloacal region

as documented by strongly posteriorly situated neural spine and moderately developed haemal keel. The vertebra most probably belongs to the genus *Eoanilius* which is considered a survivor behind the Eocene-Oligocene transition and strongly resembles *Eoanilius* sp. from the late early Miocene (MN 5) of Sandelzhausen, Germany (Szyndlar 2009). The only *Eoanilius* species from the European Oligocene and Miocene is *Eoanilius oligocenicus* Szyndlar, 1994, first reported from the late Oligocene (MP 28) of Herrlingen 8, Germany

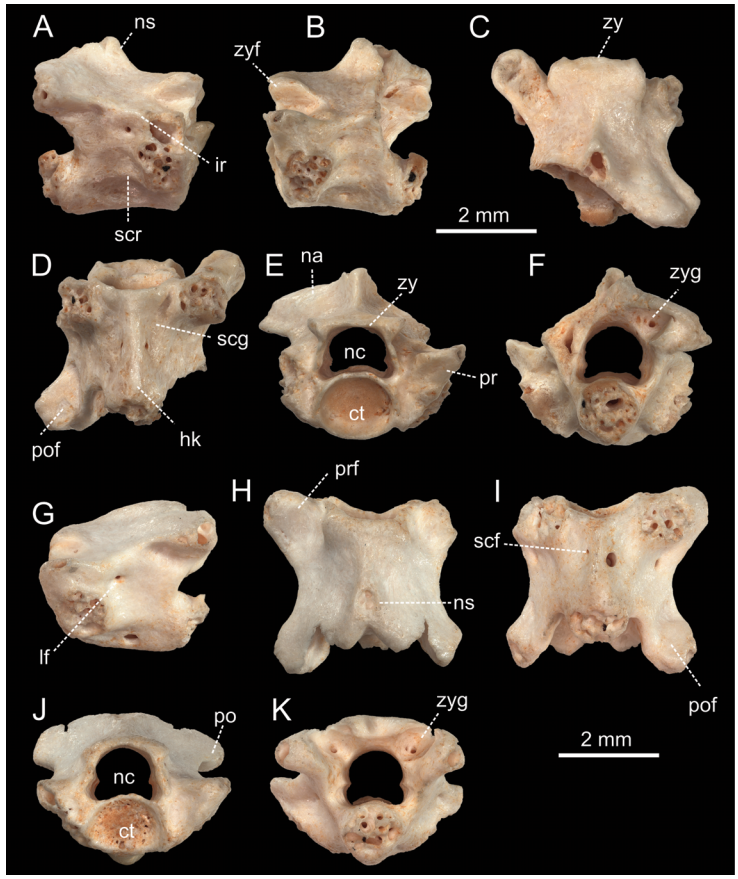

Fig. 3. cf. *Eoanilius* sp. from the early Miocene (MN 1 – MN 2?) of Weißenburg 6. Trunk vertebra (BSPG-1961 XII 636/3) in right lateral (A), left lateral (B), dorsal (C), ventral (D), cranial (E) and caudal (F) views. Posterior trunk vertebra (BSPG-1961 XII 636/4) in left lateral (G), dorsal (H), ventral (I), cranial (J) and caudal (K) views. Abbreviations: **ct**, cotyle; **hk**, haemal keel; **ir**, interzygapophyseal ridge; **lf**, lateral foramen; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **po**, postzygapophysis; **pof**, postzygapophyseal articular facet; **pr**, prezygapophysis; **prf**, prezygapophyseal articular facet; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyf**, zygosphenal facet; **zyg**, zygantrum.

Obr. 3. cf. *Eoanilius* sp. ze spodního miocénu (MN 1 – MN2?) lokality Weißenburg 6. Trupový obratel (BSPG-1961 XII 636/3) z pravé laterální (A), levé laterální (B), dorzální (C), ventrální (D), kraniální (E) a kaudální (F) strany. Zadní trupový obratel (BSPG-1961 XII 636/4) z levé laterální (G), dorzální (H), ventrální (I), kraniální (J) a kaudální (K) strany. Zkratky: **ct**, kotyl; **hk**, hemální kýl; **ir**, interzygapofyzální hřbet; **lf**, laterální otvor; **na**, neurální oblouk; **nc**, neurální kanálek; **ns**, trnový výběžek; **po**, postzygapofýza; **pof**, postzygapofyzální artikulární plošká; **pr**, prezygapofýza; **prf**, prezygapofyzální artikulární plošká; **scf**, subcentrální otvor; **scg**, subcentrální žlábek; **scr**, subcentrální hřbet; **zy**, zygosfén; **zyf**, zygosfenální plošká; **zyg**, zygantrum.

(Szyndlar 1994), with the last occurrence known from early Miocene of Oschiri, Italy (MN 3, Mennecart *et al.* 2018), which has, however, never been figured (Venczel and Sanchíz 2006). Weißenburg 6 specimen differs from *E. oligocenicus* posterior trunk vertebrae by the less distinct haemal keel (see Szyndlar 1994).

Colubroides Zaher, Grazziotin, Cadle, Murphy, Moura-Leite & Bonatto, 2009
Colubroidea Oppel, 1811 (sensu Zaher *et al.* 2009)
'Colubridae' Oppel, 1811
'Colubridae' gen. et sp. indet.

Material. Two trunk vertebrae (BSPG-1961 XII 636/5; BSPG-1961 XII 636/6).

Trunk vertebrae (fig. 4, A–J): Both vertebrae are rather fragmentary. In lateral view, the better preserved vertebra (BSPG-1961 XII 636/5) has an incomplete, but long neural spine, whose cranial margin rises at the level of the posterior border of the zygosphenal facet. The conspicuous lateral foramen occurs within a wide circular depression which is situated under the strongly built interzygapophyseal ridge at the level of the prezygapophyseal base. The subcentral ridges are straight. In dorsal view, the zygosphene possesses pointed lateral lobes, the medial lobe was probably absent despite the fact that zygosphenal lamina is partially eroded. The long axes of elongated oval prezygapophyseal articular facets (subtriangular in BSPG-1961 XII 636/6) are directed anterolaterally. Distinct growing lines are visible under their partially eroded surface. The only preserved right prezygapophyseal process with rounded distal tip is relatively short reaching about a quarter of the prezygapophyseal facet length. In ventral view, the centrum is elongated. The prominent haemal keel is rather thin with large subcentral foramina situated at its base. The anterior keel is triangular with no subcentral tubercles at the base of the cotylar rim. The subcentral grooves are deep. Subcentral ridges are blunt and straight. The partially weathered postzygapophyseal articular facets were probably subrectangular in outline. In cranial view, the neural arch is vaulted and without any visible epizygapophyseal ridges. The neural canal is rounded with prominent lateral sinuses. The zygosphene is moderately vaulted dorsally. Prezygapophyses are oriented horizontally with articular facets above the base of the neural canal. The distal tip of the prezygapophyseal process is clearly bent ventrally. A large foramen occurs at the base of the process. The large paracotylar foramina occur within funnel-like depressions on either side of the circular cotylar rim. In caudal view, zygantrum is wide, with a significant foramen inside and two parazygantral foramina on each side.

Remarks. The light structure of vertebrae together with the elongated centrum, the well-developed prezygapophyseal processes and the presence of paracotylar foramina enable assignation to Colubroidea (e.g. Rage 1984). The vertebrae, which most probably represent a single species, can be identified as belonging to 'Colubridae' on the basis of the following combination of features (Rage 1984; Szyndlar 1984, 1991a, 1991b): 1, the vaulted neural arch; 2, possibly the relatively high neural spine; 3, the absence of epizygapophyseal ridges; 4, short parapophyses with ventral border situated close below the cotylar rim and 5, the presence of haemal keel in mid-trunk vertebrae. The presence of the haemal keel instead of hypapophysis in middle trunk vertebrae have been used for a long time to distinguish fossil 'colubrines' from natricines within the colubrid clade (e.g. Szyndlar 1984; Ivanov 2000, 2002; Georgalis *et al.* 2019b). However, because of the absence of hypapophysis in middle and posterior trunk vertebrae reported in some Dipsadidae and Elapidae, Szyndlar (2012) recommended to use a quotation marks for isolated vertebrae of colubrine snakes ('Colubrinae'). In accordance with recent combined morphological and mole-

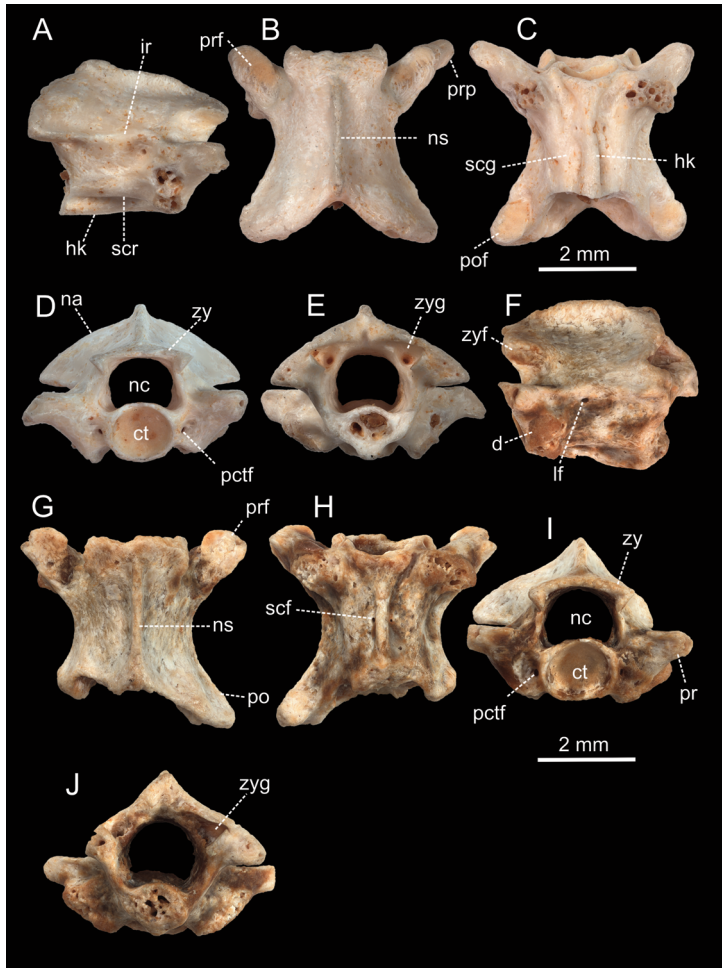

Fig. 4. ‘Colubridae’ gen. et sp. indet. from the early Miocene (MN 1 – MN 2?) of Weißenburg 6. Trunk vertebra (BSPG-1961 XII 636/5) in right lateral (A), dorsal (B), ventral (C), cranial (D) and caudal (E) views. Trunk vertebra (BSPG-1961 XII 636/6) in left lateral (F), dorsal (G), ventral (H), cranial (I) and caudal (J) views. Abbreviations: **ct**, cotyle; **d**, diapophysis; **hk**, haemal keel; **ir**, interzygapophyseal ridge; **lf**, lateral foramen; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pctf**, paracotylar foramen; **po**, postzygapophysis; **pof**, postzygapophyseal articular facet; **pr**, prezygapophysis; prf, prezygapophyseal articular facet; **prp**, prezygapophyseal process; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyf**, zygosphenal facet; **zyg**, zygantrum.

Obr. 4. ‘Colubridae’ gen. et sp. indet. ze spodního miocénu (MN 1 – MN2?) lokality Weißenburg 6. Trupový obratel (BSPG-1961 XII 636/5) z pravé laterální (A), dorzální (B), ventrální (C), kraniální (D) a kaudální (E) strany. Trupový obratel (BSPG-1961 XII 636/6) z levé laterální (F), dorzální (G), ventrální (H), kraniální (I) a kaudální (J) strany. Zkratky: **ct**, kotyl; **d**, diapofýza; **hk**, hemální kýl; **ir**, interzygapofyzální hřbet; **lf**, laterální otvor; **na**, neurální oblouk; **nc**, neurální kanálek; **ns**, trnový výběžek; **pctf**, parakotylární otvor; **po**, postzygapofýza; **pof**, postzygapofyzální artikulární plošku; **pr**, prezygapofýza; **prf**, prezygapofyzální artikulární plošku; **prp**, prezygapofyzální výběžek; **scf**, subcentrální otvor; **scg**, subcentrální žlábek; **scr**, subcentrální hřbet; **zy**, zygosfén; **zyf**, zygosfenální plošku; **zyg**, zygantrum.

cular studies (Zaher *et al.* 2019), Colubridae, Natricidae and Dipsadidae form separate families within the colubroidean clade. Similarly, psammophiids, which were once lumped into 'colubrines', but are now considered to be elapoids instead, also most usually lack hypapophyses, and this applies to all European extinct and extant forms (Georgalis and Szyndlar 2022). Therefore, we use quotation marks (see Ivanov 2022) for isolated vertebrae of 'Colubridae' whose taxonomically important cranial elements are unknown.

There are only few 'colubrid' species reported from the European Oligocene and earliest Miocene including *'Coluber' cadurci* Rage, 1974 (appeared first in the earliest Oligocene, MP 21, France; Rage 1974), *Texasophis bohemiacus* Szyndlar, 1987 (appeared first in the early Oligocene, MP 22, Germany; Szyndlar 1994) and *Zamenis kohfidischi* (Bachmayer & Szyndlar, 1985) (the first record from the earliest Miocene of Weisenau (old collection, MN 2; Villa *et al.* 2021). 'Colubridae' gen. et sp. indet. from Weißenburg 6 is different from above mentioned species. It differs from *'Coluber' cadurci* (Rage 1974, 1988) by 1, the shorter prezygapophyseal processes; 2, the absence of epizygapophyseal ridges and 3, subcentral ridges diverging anteriorly. 'Colubridae' gen. et sp. indet. further differs from *Zamenis kohfidischi* (Bachmayer and Szyndlar 1985; Villa *et al.* 2021) by 1, the blunt subcentral ridges; 2, ventrally bent prezygapophyseal processes; 3, lateral foramen situated within funnel-like depression; 4, shorter parapophysis compared to *Z. kohfidischi. Texasophis* strongly differs from the Weißenburg 6 'colubrid' by the rather low neural spine and flat ventral margin of the haemal keel (Szyndlar 1987, 1994). A more precise comparison is impossible because of poor preservation of material.

Viperidae OPPEL, 1811
Viperidae gen. et sp. indet.

Material. One trunk vertebra (BSPG-1961 XII 636/7).

Trunk vertebra (fig. 5, A–E): The vertebra is rather fragmentary with weathered surface. It has broken-off hypapophysis, the left postzygapophysis, prezygapophyseal processes, para-diapophyses and incomplete neural spine. In lateral view, the cranial margin of the neural spine rises above the zygosphenal facets of widely oval outline. Interzygapophyseal ridges are rather sharp. The markedly large lateral foramen is situated below this ridge. Subcentral ridges are slightly vaulted and better developed in anterior half of the centrum. The preserved portion of hypapophysis indicates that its distal elongation was directed posteroventrally. The diapophysis was large and preserved base of the right parapophysis indicates that parapophyseal process was inclined anteroventrally. The large condyle is situated on the short neck. In dorsal view, the vertebra is short and wide. The partially damaged zygosphene possesses small and wide left lateral lobe. The interzygapophyseal constriction is well-developed, although it is shallow. Prezygapophyseal articular facets are oval in outline. In ventral view, the ventral margin of the hypapophysis is thin and its anterior keel is triangular. Subcentral grooves are wide and shallow and subcentral foramina occur roughly in the mid-length between the cotylar rim and the base of the condyle. Subcentral ridges are straight and widely expand in cranial direction. Postzygapophyseal articular facets are incomplete. In cranial view, the neural arch is depressed dorsoventrally and the neural canal is rounded with prominent lateral sinuses. The zygosphenal roof is slightly vaulted dorsally. Prezygapophyses are tilted up, with articular facets situated above the base of the neural canal. The cotylar rim is circular with short subcotylar tubercles beneath. Paracotylar foramina occur within depressions which are situated on either side of the cotyle. In caudal view, the zygantrum is rather wide. The partially eroded condyle is incomplete, most probably orbicular in shape.

Remarks. The vertebra is assigned to Viperidae on the basis of the dorsoventrally flattened neural arch, the presence of hypapophysis, the dorsally inclined prezygapophyses and the base of right parapophyseal process which indicates its anteroventral inclination (e.g. Szyndlar 1991b, Szyndlar and Rage 2002). Although it seems probable, that the fragmentary vertebra belonged to the 'European vipers' group represented in Europe by the genus *Vipera* since the early Miocene (Aquitanian), the absence of dorsal portion of the neural spine and distal termination of the hypapophysis prevent a more precise comparison with

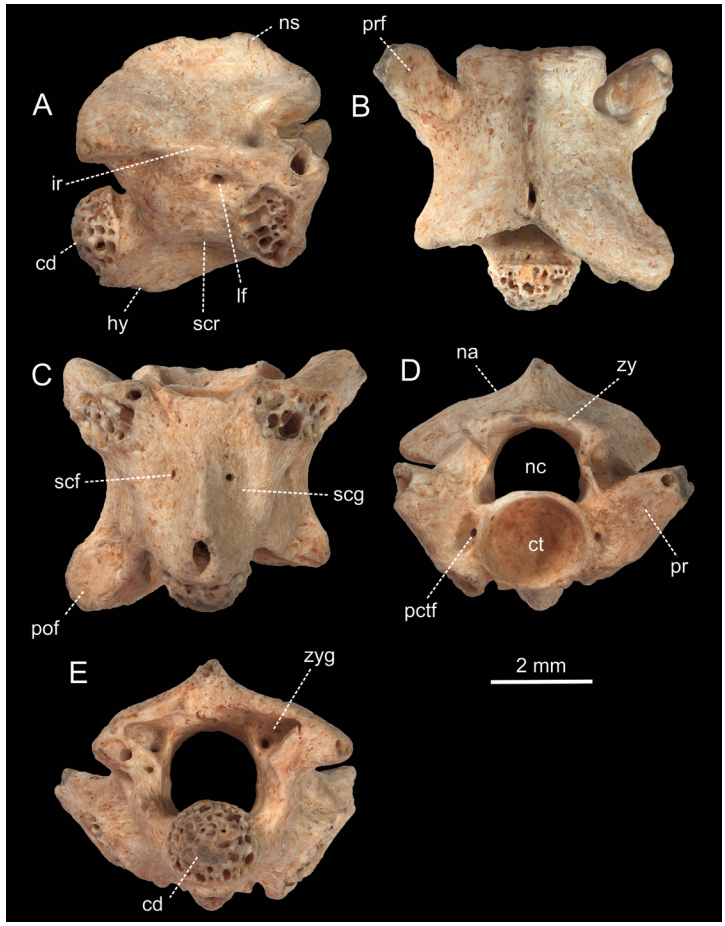

Fig. 5. Viperidae gen. et sp. indet. from the early Miocene (MN 1 – MN 2?) of Weißenburg 6. Trunk vertebra (BSPG-1961 XII 636/7) in right lateral (A), dorsal (B), ventral (C), cranial (D) and caudal (E) views. Abbreviations: **cd**, condyle; **ct**, cotyle; **hy**, hypapophysis; **ir**, interzygapophyseal ridge; **lf**, lateral foramen; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pctf**, paracotylar foramen; **pof**, postzygapophyseal articular facet; **pr**, prezygapophysis; **prf**, prezygapophyseal articular facet; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyg**, zygantrum.

Obr. 5. Viperidae gen. et sp. indet. ze spodního miocénu (MN 1 – MN2?) lokality Weißenburg 6. Trupový obratel (BSPG-1961 XII 636/7) z pravé laterální (A), dorzální (B), ventrální (C), kraniální (D) a kaudální (E) strany. Zkratky: **cd**, kondyl; **ct**, kotyl; **hy**, hypapofýza; **ir**, interzygapofyzální hřbet; **lf**, laterální otvor; **na**, neurální oblouk; **nc**, neurální kanálek; **ns**, trnový výběžek; **pctf**, parakotylární otvor; **pof**, postzygapofyzální artikulární plošká; **pr**, prezygapofýza; **prf**, prezygapofyzální artikulární plošká; **scf**, subcentrální otvor; **scg**, subcentrální žlábek; **scr**, subcentrální hřbet; **zy**, zygosfén; **zyg**, zygantrum.

other viperids including *Vipera* cf. '*aspis* complex' from Amöneburg (Čerňanský *et al.* 2015) and still oldest known distinct viperid species, *Vipera antiqua* Szyndlar, 1987 reported from Weisenau (MN 2; Szyndlar and Böhme 1993; Villa *et al.* 2021). Although assignation to 'Oriental vipers' group cannot be completely ruled out, their occurrence in Central Europe since Aquitanian stage is less probable because climatic conditions shortly after the Oligocene-Miocene transition did not favour this rather thermophile group which first appeared in Central Europe during the early Burdigalian (MN 3; Ivanov 2015; Paclík *et al.* 2018).

5. DISCUSSION

Diversified amphibian and reptile assemblage has been reported from Weißenburg 6 including Albanerpetontidae, Salamandridae, Alytidae, Bombinatoridae, Palaeobatrachidae, Pelobatidae, Pelodytidae, Ranidae, Geoemydidae, Anguidae and Erycidae (Böhme 2003 – Supplementary files). Our research which was based on several isolated vertebrae uncovered surprisingly high diversity of Squamata, though rather fragmentary material could be mostly attributed only to indeterminate families: Lacertidae, 'anilioids' (cf. *Eoanilius* sp.), 'Colubridae' and Viperidae.

Mean annual temperatures (MAT) estimated on the basis of palaeobotanical record ranged from ~15°C up to ~17°C in the North Alpine Foreland Basin (NAFB) during the Aquitanian stage (Mosbrugger *et al.* 2005). Those climatic conditions with relatively high temperatures and high humidity (mean annual precipitation ~900–1350 mm; Mosbrugger *et al.* 2005) were unsuitable for erycids which is documented by their temporal decline and extinction of Oligocene *Bransateryx* during the earliest Miocene (Hoffsttetter and Rage 1972; Georgalis and Scheyer 2021; Ivanov 2022). On the other hand, *Eoanilius*, which disappeared from European Oligocene fossil record for ~5 My, appeared in Central Europe (Germany) during the late Oligocene (Szyndlar 1994; Szyndlar & Rage 2003). *Eoanilius* most probably survived locally the deterioration of climate around the late Oligocene/early Miocene transition as documented by its presence in Weißenburg 6 (MN 1 – MN 2?) and several other early Miocene localities across a relatively broad geographic distribution in Europe and southwestern Asia (Syromyatnikova *et al.* 2019), with its last occurrence in late early Miocene of Sandelzhausen, Germany (Szyndlar and Rage 2003; Szyndlar 2009). Although relatively warm climatic conditions during Aquitanian stage favoured occurrence of other thermophilic snakes such as Tropidophiidae, recently reported by *Falseryx petersbuchi* Szyndlar & Rage, 2003 from the early Miocene (MN 2) of Weisenau, Germany (Villa *et al.* 2021), the first distinct early Miocene dispersal of highly thermophilic snakes (large Booidea) occurred since the Burdigalian (MN 3) when increase in MAT persisted > 16 °C and the coldest monthly mean temperature (CMMT) was ~6 °C in Central Europe (Mosbrugger *et al.* 2005).

Colubroid snakes which first appeared in Europe during the earliest Oligocene (MP 21) are still poorly known from the European earliest Miocene. Although 'Colubridae' gen. et sp. indet. from Weißenburg 6 differs from other contemporary 'colubrids', still rarely reported from the European Oligocene and earliest (MN 1–2) Miocene (Čerňanský *et al.* 2015; Villa *et al.* 2021), the first distinct dispersal of Colubroidea (Colubridae + Natricidae) is documented from early Burdigalian (MN 3) as reported by diversified communities from Merkur-North, Czech Republic (MN 3a; Ivanov 2002) and Wintershof-West (MN 3; Ivanov 2015; Paclík *et al.* 2018).

The indeterminate viperid is among the oldest known fossil record of Viperidae in Germany together with viperid from Hessler (MN 2), Oppenheim/Nierstein (MN 2), *Vipera* '*aspis* complex' from Amöneburg (MN 2) and *Vipera antiqua* reported from the old collection (MN 2) of Weisenau (Szyndlar 1997; Szyndlar and Rage 1999, 2002; Kuch *et al.* 2006; Čerňanský *et al.* 2015; Villa *et al.* 2021). However, if Weißenburg 6 corresponds with MN 1 (e.g. Ziegler 2006; Prieto and Böhme 2007) then indeterminate vipe-

rids from this locality and Saint-Gérand-le-Puy (MN 1 and/or MN 2; Szyndlar and Rage 2002) could represent the oldest known fossil records of Viperidae.

Palaeoecology: The generally poor preservation of squamate material with distinct signs of abrasion in all studied samples indicates most probably allochthonous origin of small vertebrates community in this locality. Nevertheless, amphibian and reptile taxa reported from Weißenburg 6, together with palaeobotanical record from the NAFB (Böhme 2003; Mosbrugger *et al.* 2005), indicate relatively warm and rather humid climatic conditions around this karstic locality during Aquitanian stage. This is in accordance with diversified amphibian assemblage including *Albanerpeton* (Allocaudata), who preferred stable moist conditions with water reservoirs in densely forested karstic environment (Gardner and Böhme 2008). This environment was fully suitable for the fossorial *Eoanilius* ('anilioids') whose supposed extant relative (*Anilius scytale*) inhabits warm tropical regions of Central and South America (Uetz *et al.* 2022). Although semi-aquatic *Ptychogaster* has also been reported in Weißenburg 6 (Schäfer 2013), the presence of non-fossorial 'colubrid' (with a relatively high neural spine) and viperid snakes indicate a mosaic of more open biotopes with low vegetation in nearby surroundings.

6. CONCLUSION

The early Miocene squamate community, reported from Weißenburg 6 by only 7 isolated vertebrae, is surprisingly diverse. The following taxa have been identified: Lacertidae indet, cf. *Eoanilius* sp., 'Colubridae' gen. et sp. indet. and Viperidae gen. et sp. indet. The presence of tiny 'anilioids' (cf. *Eoanilius* sp.) in Aguitanian (MN 1 – MN 2?) supports the presumption that *Eoanilius*, reported in Central Europe from the German late Oligocene might have survived locally the global decrease in temperatures around the Oligocene/Miocene transition (23.03 Ma). Although colubroid snakes appeared in Europe at the beginning of Oligocene, they are still poorly known from the earliest Miocene (Aquitanian). The first significant post-Oligocene dispersal of Colubroidea (Colubridae + Natricidae) from Asia and/or North Africa into Europe can be dated to the early Budrigalian. Colubroidea became a dominant snake group in European early Miocene since MN 3. However, this assumption needs to be supported by the studies from other localities. The indeterminate viperid from Weißenburg 6 is among the oldest known fossil record of Viperidae.

SOUHRN

Fosilní nálezy šupinatých plazů z období nejspodnějšího miocénu (akvitán, MN 1–2) jsou ve střední Evropě poměrně vzácné, jedná se vesměs o lokality ležící na území dnešního Německa (Weisenau, Amöneburg, Ulm-Westtangente). Přestože některé publikace poskytují zmínku o výskytu konkrétních taxonů, jen několik málo z nich přináší ucelenou dokumentaci s detailním popisem a diskuzí daného materiálu. Tento článek přináší první popis fauny šupinatých z bavorské lokality Weißenburg 6 spodnomiocenního stáří (akvitán, MN 1–2?). Ze sbírky obsahující malé množství fragmentárního fosilního materiálu bylo zjištěno relativně diverzifikované společenstvo šupinatých plazů zahrnující Lacertidae indet., cf. *Eoanilius* sp., 'Colubridae' gen. et sp. indet. a Viperidae gen. et sp. indet. Přítomnost posledního taxonu představuje jeden z nejstarších jasně doložených výskytů čeledi Viperidae. Výsledky studia tak doplňují naše znalosti týkající se paleobiogeografického a paleoklimatického vývoje v oblasti střední Evropy během spodního miocénu.

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