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RESEARCH **Open Access**

A unique snake assemblage from the Early Miocene locality of Wintershof-West, Germany, with comments on the transitional period in the evolution of European snake fauna

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Abstract

The early Burdigalian (20.4–18.2 Ma) ophidian localities are rare in the European fossil record and with exception of Merkur-North (Ahníkov I), Czechia (early MN 3) our knowledge on the evolution of snake communities before the Early Ottnangian Cooling (EOC; 18.1–17.8 Ma) event are still strongly restricted. Here we present the unusually diversified snake community from the German Early Miocene (early Burdigalian, early MN 3) Wintershof-West locality based on the detailed comparative osteological studies with a special focus on the intracolumnar variability. The following snake taxa have been reported from Wintershof-West: Alethinophidia *incertae sedis* (cf. *Falseryx* sp.), Booidea (*Bavarioboa wintershofensis* sp. nov., Booidea indet.), Viperidae (Viperinae indet. – 'Oriental vipers', *Vipera* sp. ['*V. aspis*' complex]), Elapidae (*'Micrurus' gallicus*, Elapidae indet., type 1), Natricidae (*Natrix* cf. *sansaniensis*, *Wintershofia robusta* gen. et sp. nov., *Palaeonatrix* aff. *lehmani*, Natricidae indet., type 1, Natricidae indet.), 'Colubridae' (*'Coluber'* aff. *caspioides*, 'Colubridae' indet., type 1, 2, and 3, 'Colubridae' indet.), and Colubroidea indet.

The snake community from Wintershof-West documents the first return of the genus *Bavarioboa* (*B. wintershofensis* sp. nov.) into Europe after its temporal demise from European region during the latest Oligocene climatic deterioration. Colubriform snakes became diversified in Central Europe during the onset of the early Burdigalian ~20 Mya. Viperid snakes from Wintershof-West comprise the earliest known distinct appearance of 'Oriental vipers'. Several other colubriform taxa display their first documented appearance including *Palaeonatrix* aff. *lehmani* and *'Coluber'* aff. *caspioides* which might represent the evolutionary older members of the *'C.' caspioides* and *P. lehmani* lineages. The unusual diversification of snake taxa resulted from the onset of the warm early Burdigalian climate, which we refer here as the Eggenburgian Climatic Optimum (ECO). The presence of several thermophilic taxa in Wintershof-West including cf. *Falseryx* sp., *Bavarioboa wintershofensis* sp. nov., *'Micrurus' gallicus* and another indeterminate coral snake, and 'Oriental vipers', point to a relatively major warming before the onset of the EOC event. However, the absence of highly thermophilic true cobras of the genus *Naja* as well as Pythonoidea in Central European MN 3 localities demonstrates mean annual temperatures did not reach their maximum, as during the Miocene Thermal Maximum (MTM, MN 4) of the middle and late Ottnangian. The karstic environment around the Wintershof-West locality corresponds to the semi-arid hydroclimate which fits with the numerous small booidea and 'Oriental vipers'. Wintershof-West is the best documented early Burdigalian (early MN 3, Eggenburgian) ophidian locality in Europe which substantially

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increases our knowledge of the evolution of European snake fauna during its transitional period of the early Burdigalian.

Keywords Booidea, Colubriformes, Climatic evolution, Burdigalian, Palaeobiogeography, Bavaria

Introduction

The fossil record of Miocene snakes is generally well-documented in Europe with a number of localities distributed across the whole continent (Ivanov, 2022; Rage, 2013; Szyndlar & Rage, 1999, 2002; Szyndlar, 1991a, 1991b, 2012). The Early Miocene localities (Fig. 1a) comprising diverse snake communities have been reported mainly from France (Ivanov, 2000; Rage & Bailon, 2005; Szyndlar & Rage, 2003), Germany (Čerňanský et al., 2015; Szyndlar, 2009; Szyndlar & Böhme, 1993; Szyndlar & Rage, 2003; Szyndlar & Schleich, 1993; Villa et al., 2021), and Czech Republic (Ivanov et al., 2020; Ivanov, 2002a; Szyndlar, 1987). Further to the south/southeast (Fig. 1a), our knowledge on the Early Miocene snakes is strongly restricted because of total absence of ophidian localities of appropriate age with exception of the Middle Burdigalian (Ottnangian, MN 4; MN - Mammal Neogene zone) locality of Oberdorf, Austria (Szyndlar, 1998) and the coeval Greek localities of Aliveri and Karydia, whose snake remains are poorly preserved (Georgalis et al., 2019a), and the possibly somewhat older Kymi locality (MN 3/4) from where the first European Miocene occurrence of a pythonoid snake has been reported (Roemer 1870; Szyndlar & Rage, 2003).

Although European earliest Miocene (Aquitanian, MN 1–MN 2) snake communities contain several colubriform (sensu Zaher et al., 2019) taxa including the first known viperid snakes (Kuch et al., 2006; Paclík & Ivanov, 2022; Szyndlar & Rage, 2002; Villa et al., 2021), the presupposed first massive dispersal event of Colubriformes is dated to the early Burdigalian MN 3 (Ivanov, 2002a; Rage, 2013), as well-documented only in the early Burdigalian (early MN 3) locality of Merkur-North (Ahníkov I), Czech Republic, where Colubroidea ('Colubridae' and Natricidae) strongly outnumber rarely occurring representatives of non-erycid Booidea (Ivanov, 2002a). The presence of small-sized *Bavarioboa* in Merkur-North, different from its Oligocene relatives (Rage, 2013), as well as minute elapoids reminiscent of extant coral snakes (Ivanov, 2002a), agrees with increased temperatures and humidity during the early Burdigalian (Böhme, 2003; Mosbrugger et al., 2005). However, no other comparable MN 3 locality with diversified snake community have been studied in detail and therefore, appropriate conclusions concerning early to middle Burdigalian (MN 3–4; ~20.4–16.4 Ma) transitional period in the evolution of European snake fauna (Rage, 2013) need to be further supported.

The German Wintershof-West locality, which is coeval or slightly older than Merkur-North (Ahníkov I) (Fig. 1b; Bonilla-Salomón et al., 2022), yielded unusually rich snake community, that is even more diversified than that known from the Czech locality. The main aims of our study are as follows: (1) the detailed description of snake material (isolated vertebrae) from Wintershof-West, with a special focus on the intracolumnar variability; and (2) to increase our knowledge of early Burdigalian (~20.4–18.2 Ma) snake evolution in Central Europe in the context of its palaeoclimatic and palaeogeographic evolution.

Material and methods

Locality and material

The Wintershof-West locality was discovered in 1937 in a now inactive Otto Neumeyer's Quarry (Dehm, 1937), situated about 1 km west of the Wintershof village near Eichstätt (Bavaria, Germany). There, karst fissures have been uncovered within the Upper Jurassic lithographic plattenkalk limestone (Altmühltal Formation) of the Franconian Alb (Dehm, 1950a; Koenigswald, 1970). The partially stratified fissure-filling provided an extensive number of fossils accumulated mainly in the western part of the locality. The top layer of the karstic filling was formed by the fossiliferous 1.5 m thick layer of a brown mudstone with eroded limestone and larger fossils. Underneath, layers of yellowish and greenish clay alternated without any distinct

(See figure on next page.)

Fig. 1 Distribution map of the Early and Early/Middle Miocene ophidian localities in Europe (**A**); Early Miocene timescale and biostratigraphy with stratigraphical positions of European snake localities (**B**). 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 (Ivanov, 2022, modified)

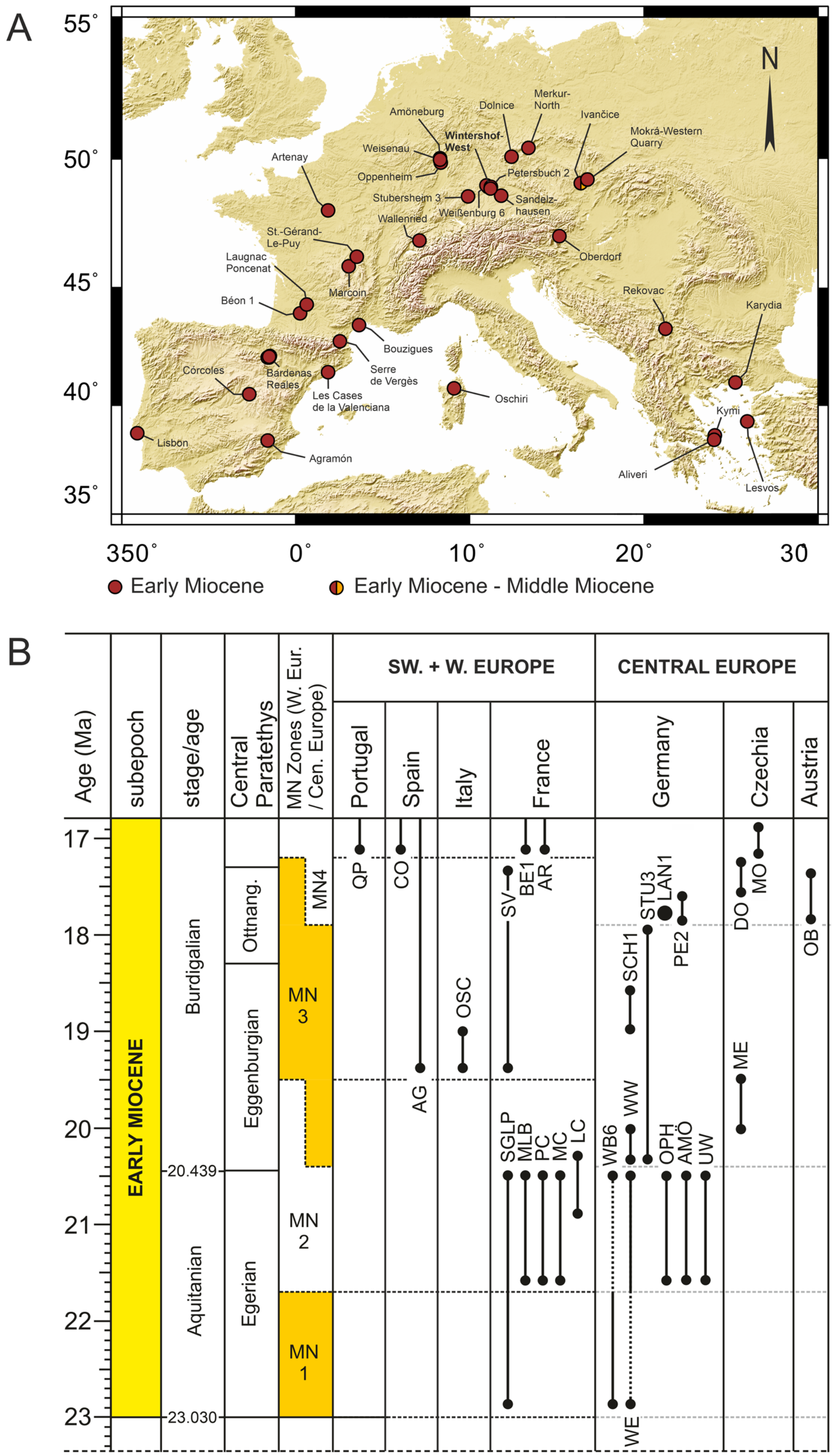

Fig. 1 (See legend on previous page.)

boundaries. From the upper to the deepest part of the filling, there were white and brownish pieces and limestone beds with numerous cavities rich in fossil vertebrates including amphibians and reptiles (Böhme, 2003), birds (Ballmann, 1969) and mammals. Mammal taxa are highly diversified in Wintershof-West including all main groups, e.g., Eulipotyphla (Doben-Florin, 1964; Müller, 1967; Ziegler, 1985, 1989, 1990, 1994, 2006; Ziegler et al., 2005), Rodentia (Dehm, 1950b; Fahlbusch, 1970; Hrubesch, 1957; Mayr, 1979; Wu, 1993), Carnivora (Dehm, 1950a), Perissodactyla (Ginsburg & Guérin, 1979; Heissig, 1969), and Artiodactyla (Obergfell, 1957). The age of the fissure-filling corresponds to the lower Burdigalian of the Upper Marine Molasse and more precisely Wintershof -West, which is a reference locality of the MN 3 Zone (de Bruijn et al., 1992; Mein, 1975), corresponds to the early MN 3 (Aguilar et al., 2003; Bonilla-Salomón et al., 2022). In an extension of the main fissure, approximately 14 m east of it, a sandy mud containing shell material of the testudinoid turtle *Ptychogaster* cf. *boettgeri* has been reported (Dehm, 1950a; Schäfer, 2013). All other turtle remains have been destroyed during the Second World War (Dehm, 1950a).

The studied material, consisting of more than 2000 isolated snake vertebrae, is housed in the Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich under the collection numbers SNSB-BSPG 1937 II 23343 to SNSB-BSPG 1937 II 25383.

Methods

The anatomical terminology and descriptions are primarily based on Szyndlar (1984), Szyndlar and Rage (2003) and Ikeda (2007). All depicted vertebrae were cleaned with the Ulsonix Proclean 0.7D ultrasonic cleaner and then documented by the LEICA MZ-16 stereomicroscope equipped with the digital camera LEICA DMC 5400 (20 mpx). The metrical measurements (Appendix 1 and 2) follow Szyndlar (1984) and Villa et al. (2024): CL, centrum length; NAW, neural arch width; NAH, neural arch height, i.e., the height of the roof of the zygantrum to the mid-point of the PO-PO line (hPO-PO); PR-PR, the length of the line connecting the outer edges of the prezygapophyses; PO-PO, the length of the line connecting the outer edges of the postzygapophyses; PR-PO, the length of the line connecting the anterior edge of the prezygapophysis and posterior edge of the postzygapophysis; ZW, zygosphene width; CTH, cotyle height; CTW, cotyle width. Measurements were performed by using measurement module of the LAS X software. The degree of vaulting of the neural arch, expressed as the "vaulting ratio" (VR), follows Georgalis et al. (2021b): VR = NAH to hPO-PO. The complete measurements were performed only on the type material, i.e. holotypes + paratypes (see Appendix 2).

The comparative osteological studies are based on published sources as well as skeletal collections of extant snakes housed in the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków (Poland), Muséum national d'Histoire naturelle, Paris (France), Národní museum, Praha (Czech Republic), Zoologisches Forschungsinstitut und Museum Alexander König, Bonn (Germany), and Florida Museum of Natural History, Gainesville (Florida, USA). The μCT scan data of natricid snake skeletons (Appendix 3) were accessed from the Morphosource repository (Duke University; https://www.morphosource.org). 3D-models for comparative studies were processed by the Dragonfly software (Object Research System), version 2022.2.0.1399.

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the official registry of zoological nomenclature for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'https://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:267B2B79-2E17-4013-8BDC-5E741F019962. The LSIDs for the taxa appear in the respective entries below.

Systematic palaeontology

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Alethinophidia *incertae sedis* (sensu Smith & Georgalis, 2022)

Falseryx Szyndlar & Rage, 2003

cf. *Falseryx* sp.

Material. – Two anterior trunk vertebrae (SNSB-BSPG 1937 II 23343–23344), 57 middle and posterior trunk vertebrae (SNSB-BSPG 1937 II 23345–23401).

Anterior trunk vertebra (Fig. 2a–e): The only preserved anterior trunk vertebra is partially fragmentary with damaged right prezygapophyseal process, posterodorsal termination of the neural spine and eroded synapophyses. In lateral view, the low neural spine rises behind the zygosphene. Its anterior and posterior margins are inclined posteriorly. The short subcentral ridge occurs only close behind the synapophysis base and posteriorly becomes indistinct. The short hypapophysis is shallow with rounded termination reaching the condylar base which indicates the position of vertebra close to the anterior/middle trunk transition. In dorsal view, there is a distinct interzygapophyseal constriction with large widely oval prezygapophyseal articular facets and very short prezygapophyseal processes. The zygosphene is almost straight with short lateral lobes and moderately developed central lobe. The caudal notch is shallow. In ventral view, there are large subcentral foramina situated at the hypapophyseal base. Subcentral groves are slightly developed only in the anterior half of the centrum. In cranial view, the neural canal is rounded with short and narrow lateral sinuses. The zygosphenal lip is straight. There are depressions situated laterally from the circular cotylar rim but paracotylar foramina are absent. In caudal view, the neural arch is depressed dorsoventrally and the zygantrum is wide. Parazygantral foramina are present but only the left foramen is well-visible.

Middle and posterior trunk vertebrae (Fig. 2f–y): The vertebrae, which are slightly longer than high, are small with the centrum length of the largest specimen 3.63 mm (SNSB-BSPG 1937 II 23396; Fig. 2k–o; see Appendix 1). In lateral view, the low neural spine is twice longer than high and rises at the posterior border of the oval zygosphenal facet. Its cranial margin slightly inclines posteriorly, while the caudal margin is inclined anteriorly, or may be vertical. The small lateral foramen is situated posteriorly to the prezygapophysis and under the sharp interzygapophyseal ridge. The craniocaudally elongated parapophysis is slightly larger than the diapophysis. The short subcentral ridge, which is better developed only in the anterior half of the centrum, is slightly arched dorsally. It diminishes towards the markedly short condylar neck. There is a prominent furrow on the condylar neck demarcating the base of the large condyle. In dorsal view, the vertebrae are characterised by the prominent interzygapophyseal constriction. The three-lobed zygosphenal lip is well-developed, with rounded lateral lobes and equally sized medial lobe. Prezygapophyseal articular facets are oval in outline, with their long axes directed anteriorly rather than anterolaterally. The markedly short prezygapophyseal processes, about five times shorter than prezygapophyseal articular facets, are directed anterolaterally. The cranial margin of the neural spine is thin but becomes wider towards its caudal termination. The caudal notch is moderately deep. The epizygapophyseal ridges are absent or indistinctly developed. In ventral view, the centrum is triangular and lateroventrally delimited by the slightly concave subcentral ridges. The subcentral grooves are deeper with the more posterior position of the vertebra within the vertebral column. The noticeable subcentral foramina are situated approximately in the middle of the centrum length, at the constricted base of the otherwise wide haemal keel. The laterally elongated postzygapophyseal articular facets are subtriangular in outline. In cranial view, the neural canal is rounded with short lateral sinuses. The zygosphenal lip is straight, with thin lateral lobes directed dorsolaterally. Prezygapophyses are tilted up, with articular facets situated high above the base of the neural canal. There are depressions on either side of the subcircular cotylar rim but paracotylar foramina are absent except of the posterior trunk vertebrae. In caudal view, the neural arch is depressed dorsoventrally, with a vaulting ratio ranging from 0.17 to 0.27. The zygantrum with large zygantral foramina is wide and tiny parazygantral foramina occur in posterior border of the neural arch. The condyle is suborbicular, or it has a slightly depressed its ventral margin.

Remarks: The genus *Falseryx,* whose uncertain assignation to extant dwarf boas ('Tropidophiidae' sensu Szyndlar et al., 2008) was discussed in the context of a distant phylogenetic position of Ungaliophiinae and Tropidophiinae confirmed by both morphological and molecular studies (Vidal & David, 2004; Vidal & Hedges, 2002; Wilcox et al., 2002; Zaher, 1994), is currently considered an Alethinophidia *incertae sedis* (Smith & Georgalis, 2022). The identification of isolated trunk vertebrae of non-'erycid' *Falseryx* is complicated if no caudal vertebrae are present because the only difference between *Falseryx* and the 'erycid' monotypic genus *Bransateryx* Hoffstetter & Rage, 1972 (species *Bransateryx vireti* Hoffstetter & Rage, 1972) is the complex structure of caudal vertebrae in the latter (Čerňanský et al., 2015; Szyndlar & Rage, 2003; Szyndlar et al., 2008). Therefore, most of the recently described occurrences of *Falseryx* lack a distinct genus allocation, excepting of *Falseryx* cf. *neervelpensis* from the early Oligocene (MP 23–24) of Suceag 1, Romania (Venczel et al., 2025) and *Falseryx* sp. from the Anatolian latest Oligocene-earliest Miocene localities of Kargi 2 (MP 30–MN 1; Georgalis et al., 2021a) and Kılçak (MN 1; Syromyatnikova et al., 2019). The uncertain allocation

(See figure on next page.)

Fig. 2 cf. *Falseryx* sp. from Wintershof-West. **a**–**e**, anterior trunk vertebra (SNSB-BSPG 1937 II 23344) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**i**, anterior middle trunk vertebra (SNSB-BSPG 1937 II 23400) in right lateral (**f**), dorsal (**g**), ventral (**h**), and cranial (**i**) views; **j**, middle trunk vertebra in dorsal view (SNSB-BSPG 1937 II 23395); **k**–**o**, middle trunk vertebra (SNSB-BSPG 1937 II 23396) in left lateral (**k**), dorsal (**l**), ventral (**m**), cranial (**n**), and caudal (**o**) views; **p**–**t**, middle trunk vertebra (SNSB-BSPG 1937 II 23398) in left lateral (**p**), dorsal (**q**), ventral (**r**), cranial (**s**) and caudal (**t**) views; **u**–**y**, posterior trunk vertebra (SNSB-BSPG 1937 II 23401) in right lateral (**u**), dorsal (**v**), ventral (**w**), cranial (**x**), and caudal (**y**) views. cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scf, subcentral foramen; scg, subcentral groove; scr, subcentral ridge; tub, tubercle; zy, zygosphene

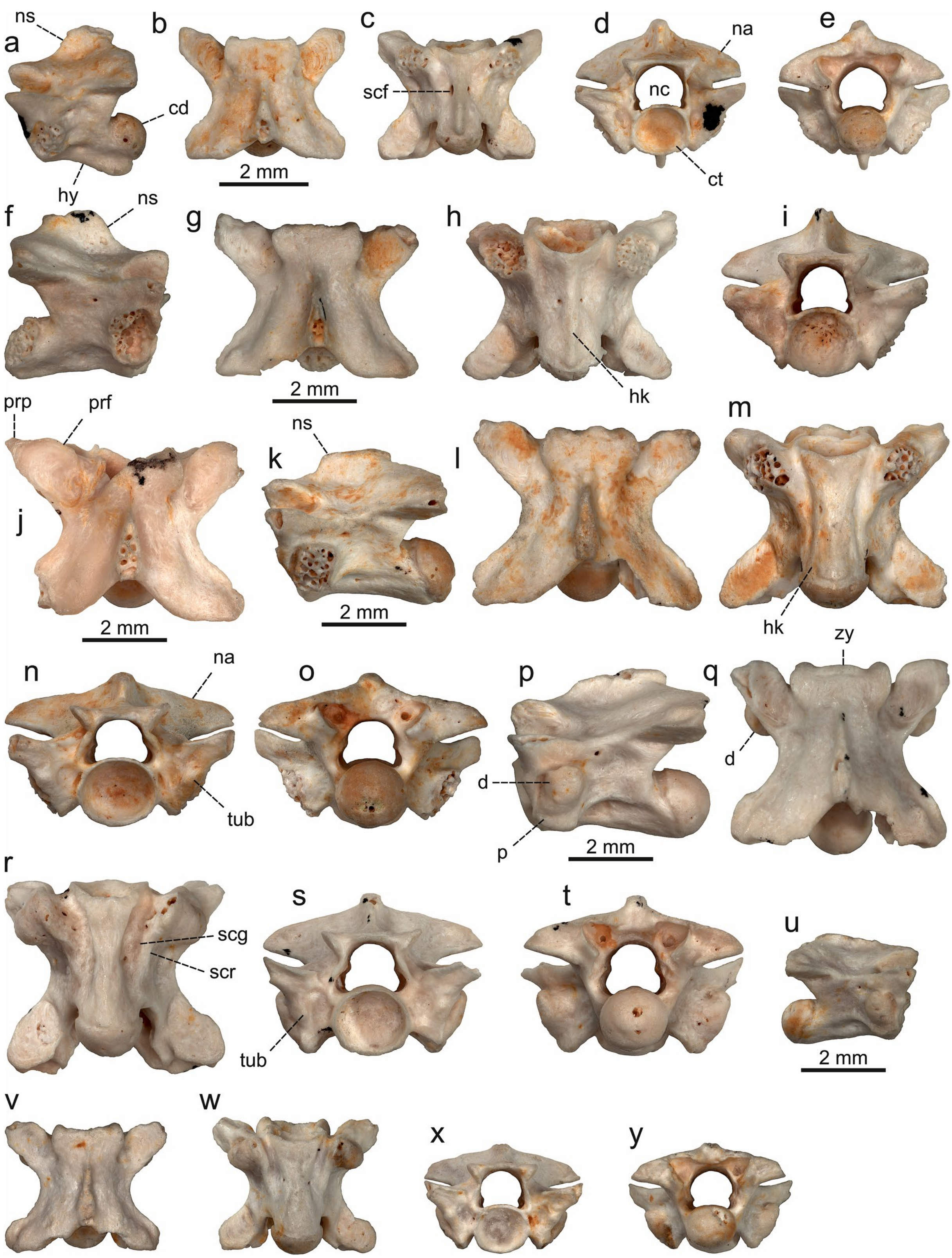

Fig. 2 (See legend on previous page.)

is true for German occurrences of cf. *Falseryx* sp. from Amöneburg (MN 2a; ?*Falseryx* sp. sensu Čerňanský et al., 2015), Hambach (MN 5; Čerňanský et al., 2017) and Steinheim am Albuch (MN 7 + 8; (?) *Falseryx* sp. sensu Szyndlar & Rage, 2003) as well as the only Iberian occurrence of cf. *Falseryx* sp. from Agramón, Spain (MN 4; Szyndlar & Rage, 2003; Szyndlar & Alférez, 2005).

The middle trunk vertebrae from Wintershof-West share the following combination of features with those of the genus *Falseryx* (Szyndlar & Rage, 2003; Szyndlar et al., 2008): (1) in lateral view, the vertebrae are somewhat longer that high; (2) the neural arch is strongly depressed; (3) the neural spine is low, extending over approximately one third of the neural arch length; (4) the interzygapophyseal constriction is well-developed; (5) the caudal notch situated at the posterior border of the neural arch is not deep; (6) the centrum is slightly longer than wide; (7) the haemal keel is wide and becomes wider and flat in posterior direction; (8) the zygosphene is three-lobed in dorsal view and straight in cranial view; (9) prezygapophyses are situated clearly above the base of the neural canal; (10) paracotylar foramina are absent**.**

There are only two distinct species of the genus *Falseryx*, i.e., *Falseryx petersbuchi* Szyndlar & Rage, 2003 and *Falseryx neervelpensis* Szyndlar, Smith & Rage, 2008. The oldest occurrence of the genus, attributed to *Falseryx neervelpensis*, is documented in the earliest Oligocene (MP 21) locality of Boutersem TGV, Belgium (Szyndlar et al., 2008). *Falseryx petersbuchi* is well-documented (a single caudal vertebra was actually referred) only in the late Early Miocene (MN 4) type locality of Petersbuch 2 (Szyndlar & Rage, 2003; Szyndlar & Schleich, 1993). The remaining two occurrences of *F. petersbuchi*, one from the Early Miocene of Weisenau, Germany (old collection, MN 2; Villa et al., 2021), the other from Dolnice, Czechia, MN 4 (Szyndlar, 1987; Szyndlar & Rage, 2003) are based on the description of isolated trunk vertebrae. Vertebrae of cf. *Falseryx* sp. from Wintershof-West differ from those of *F. neervelpensis* in having a more gracile structure, a deeper interzygapophyseal constriction, smaller vertebral foramina, a more prominent neural spine lacking dorsal thickening, a well-developed medial lobe of the zygosphene, larger synapophyses, and less distinct tubercles on the prezygapophyseal buttresses (Szyndlar et al., 2008). The middle trunk vertebrae of cf. *Falseryx* sp. differ from those of *F. petersbuchi* (Szyndlar & Rage, 2003) by the posteriorly inclined cranial margin of the neural spine, the slightly deeper caudal notch of the neural arch and the presence of parazygantral foramina. Although we consider these slight differences to be the intraspecific variability and vertebrae could be probably identified as belonging to *Falseryx petersbuchi*, we avoid a species or even definite genus-level attribution because of the absence of highly important caudal vertebrae (Szyndlar & Rage, 2003; Szyndlar et al., 2008).

Constrictores Oppel, 1811a (sensu Georgalis & Smith, 2020)
Booidea Gray, 1825 (sensu Pyron et al., 2014)
Bavarioboa Szyndlar & Schleich, 1993
Bavarioboa wintershofensis **sp. nov.**

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Descriptive diagnosis. *Bavarioboa wintershofensis* sp. nov. share the following features with those of the genus *Bavarioboa*: (1) the middle trunk vertebrae are higher than long in lateral view and shorter than wide in dorsal/ventral aspects; (2) the interzygapophyseal constriction is well expressed; (3) the neural arch is depressed; (4) the neural spine is as high as long; (5) the haemal keel is prominent and wide; (6) prezygapophyses are dorsally inclined, with articular facets located above the neural canal floor in anterior view; (7) prezygapophyseal processes are weakly developed; (8) paracotylar foramina are absent in most of trunk vertebrae. *B. wintershofensis* sp. nov. differs from all known *Bavarioboa* species by the unique combination of characters reported in the middle trunk vertebrae: (1) the depressed neural arch is upswept posterodorsally forming bulbous bumps in dorsal view; (2) the neural spine rises behind or close to the posterior border of the zygosphenal articular facets; its anterodorsal portion usually forms a thin straight lamina inclined posterodorsally; (3) neural spine foramina usually occur on either side of the neural spine base; (4) the zygosphene is three-lobed with the central lobe forming the dorsally arched and slightly downwards shifted thin lamina in anterior view; (5) the wide haemal keel is constricted at the level of the subcentral foramina, with its ventral surface expanding in the caudal direction; (6) paracotylar foramina are present in some trunk vertebrae.

Etymology. Species name derived from the name of the German type locality: Wintershof-West.

Type locality. Wintershof-West, Bavaria, Southern Germany.

Distribution and age. Known only from the type locality, Wintershof-West, Bavaria, Southern Germany. The age corresponds to the Early Miocene, Burdigalian, lower part of the MN 3 Zone (MN 3a; Aguilar et al., 2003; Bonilla-Salomón et al., 2022).

Holotype. Specimen SNSB-BSPG 1937 II 23804, a middle trunk vertebra (Fig. 3).

Paratypes. Specimen SNSB-BSPG 1937 II 23478 (an anterior trunk vertebra, Fig. 4d–h); SNSB-BSPG 1937 II

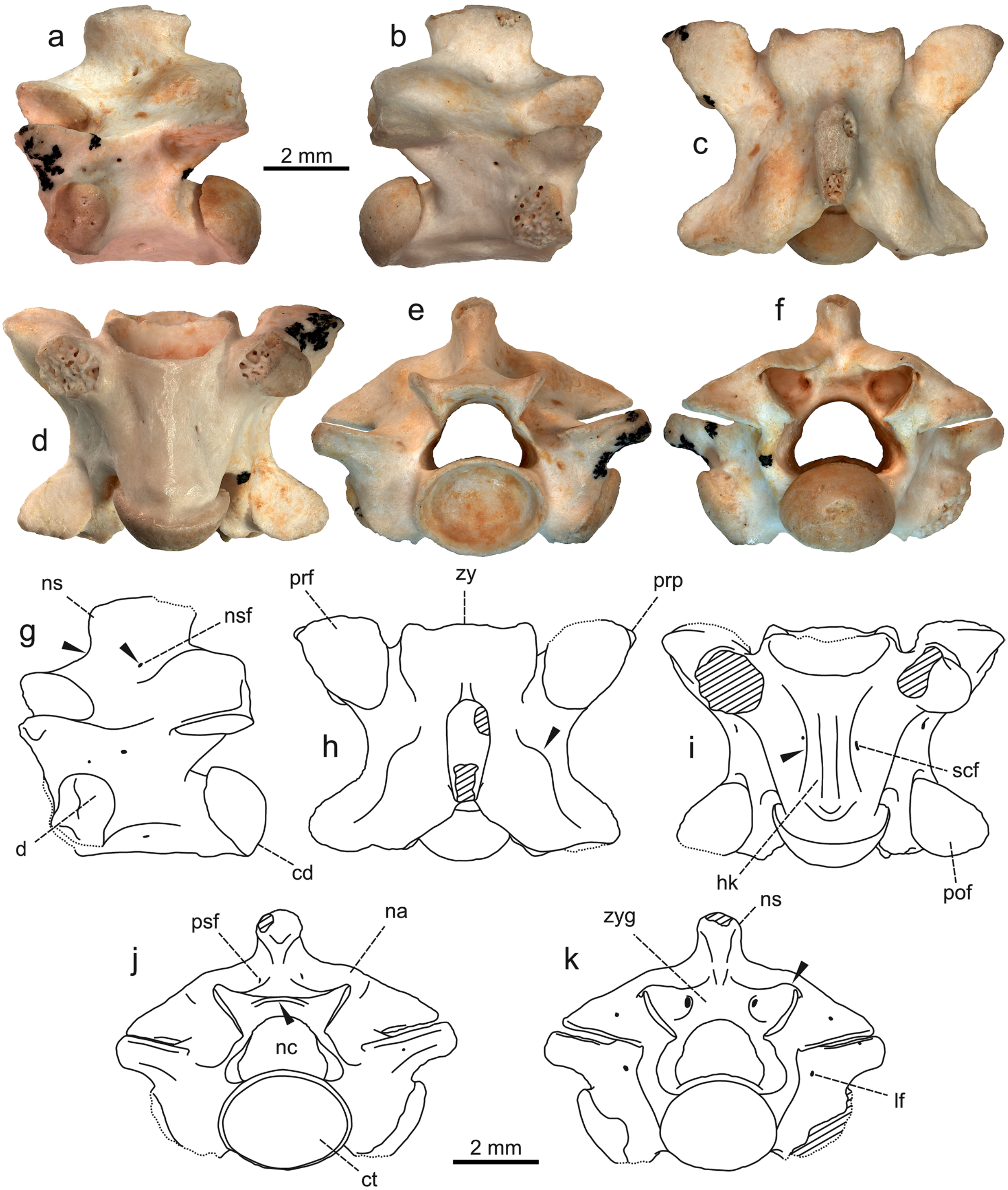

Fig. 3 *Bavarioboa wintershofensis* sp. nov. from Wintershof-West. **a**–**f**, middle trunk vertebra, holotype (SNSB-BSPG 1937 II 23804) in left lateral (**a**), right lateral (**b**), dorsal (**c**), ventral (**d**), cranial (**e**), and caudal (**f**) views; **g**–**k**, the same holotype vertebra (SNSB-BSPG 1937 II 23804), important anatomical structures are highlighted. cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; lf, lateral foramen; na, neural arch; nc, neural canal; ns, neural spine; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; nsf, neural spine foramen; scf, subcentral foramen; zy, zygosphene; zyg, zygantrum. Arrows indicate important features

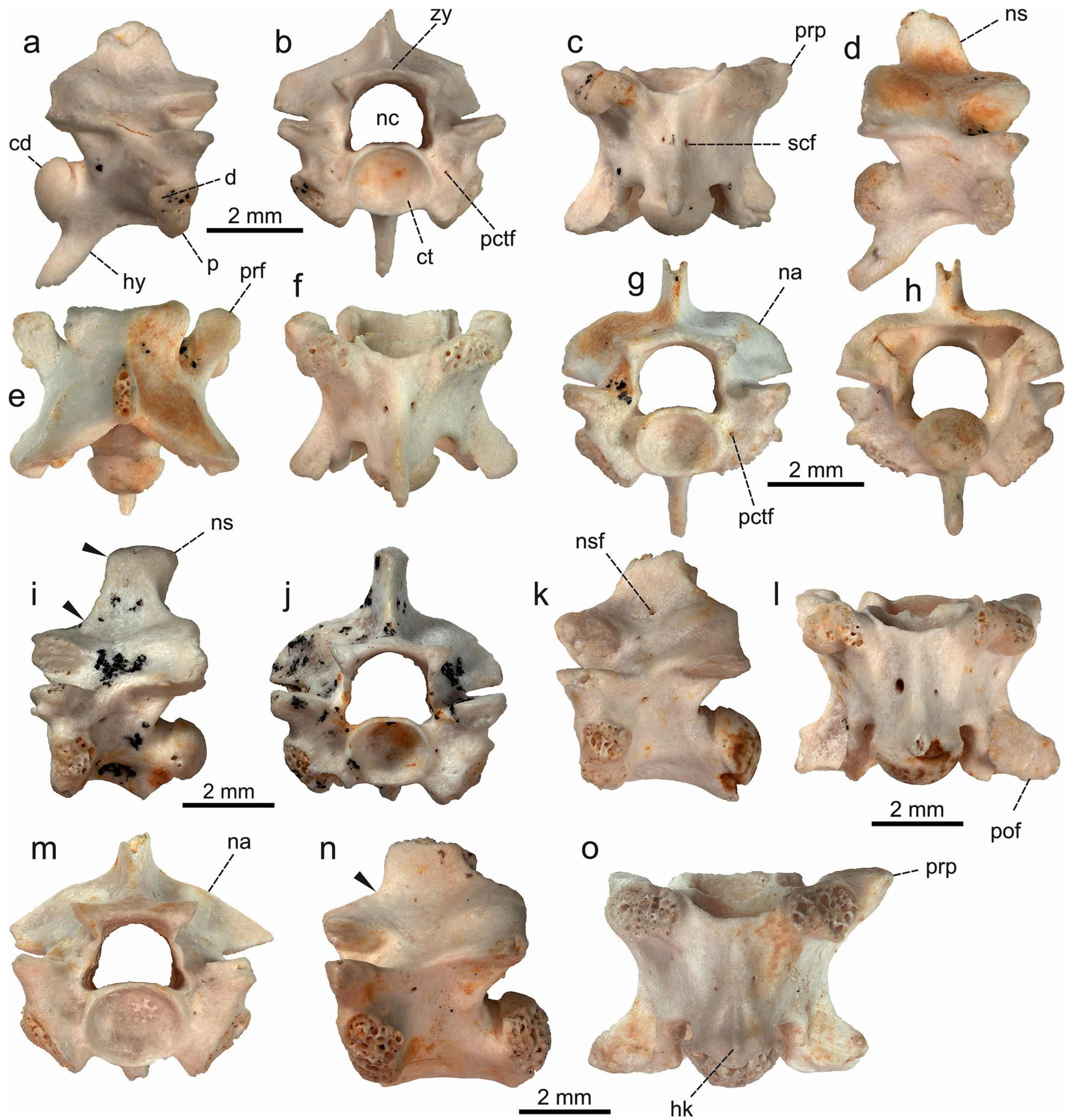

Fig. 4 *Bavarioboa wintershofensis* sp. nov. from Wintershof-West. **a**–**c**, anterior trunk vertebra (SNSB-BSPG 1937 II 23474) in right lateral (**a**), cranial (**b**), and ventral (**c**) views; **d**–**h**, paratype anterior trunk vertebra (SNSB-BSPG 1937 II 23478) in right lateral (**d**), dorsal (**e**), ventral (**f**), cranial (**g**), and caudal (**h**) views; **i**–**j**, anterior trunk vertebra (SNSB-BSPG 1937 II 23477) in left lateral (**i**), and cranial (**j**) views; **k**–**m**, trunk vertebra close to anterior/middle trunk transition (SNSB-BSPG 1937 II 23476) in left lateral (**k**), ventral (**l**), and cranial (**m**), views; **n**, **o**, middle trunk vertebra (SNSB-BSPG 1937 II 23796) in left lateral (**n**) and ventral (**o**) views. cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; nsf, neural spine foramen; scf, subcentral foramen; zy, zygosphene. Arrows indicate important features

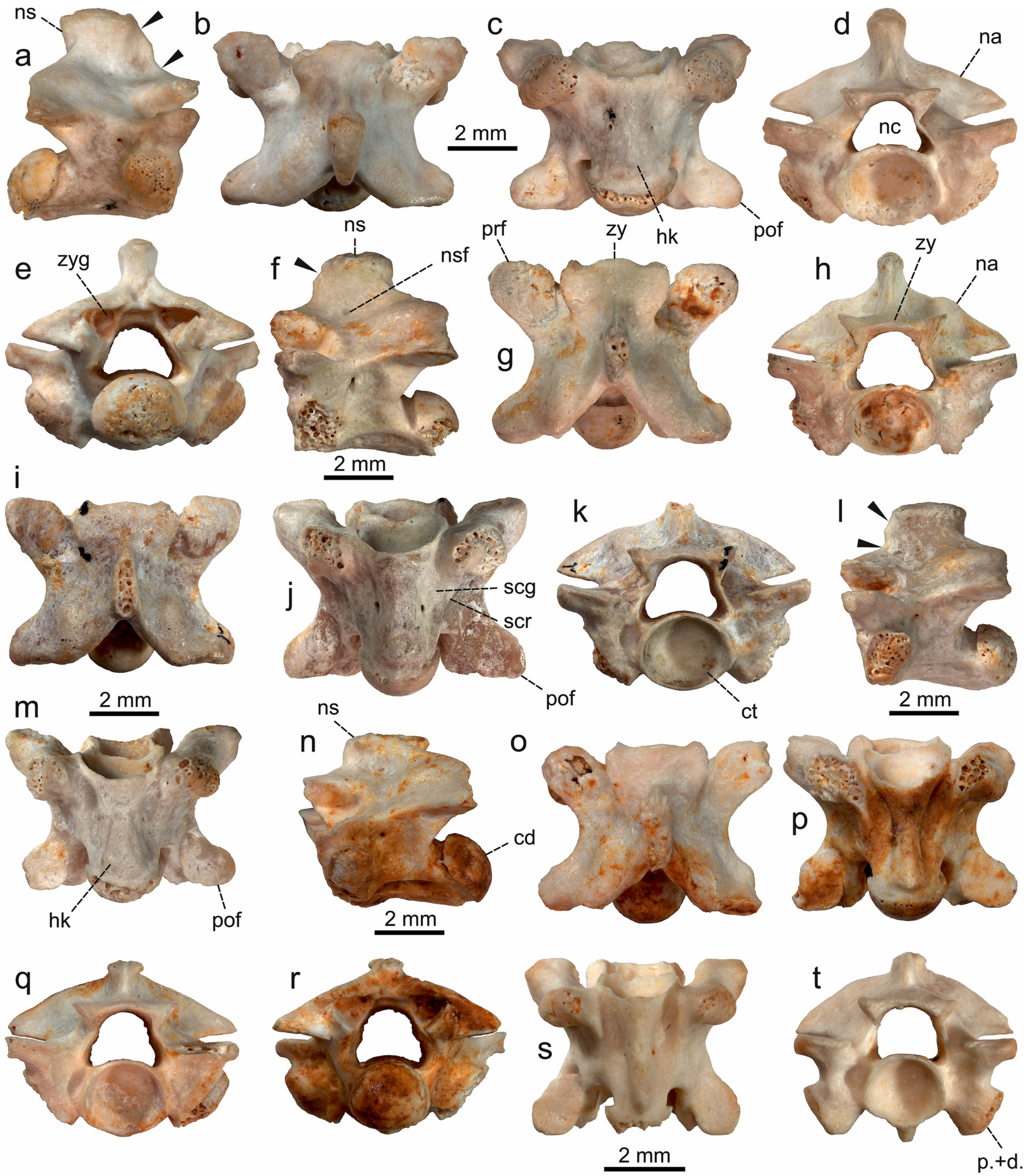

Fig. 5 *Bavarioboa wintershofensis* sp. nov. from Wintershof-West. **a**–**e**, paratype middle trunk vertebra (SNSB-BSPG 1937 II 23803) in right lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views. **f**–**h**, middle trunk vertebra (SNSB-BSPG 1937 II 23788) in left lateral (**f**), dorsal (**g**), and cranial (**h**) views; **i**–**k**, middle trunk vertebra (SNSB-BSPG 1937 II 23795) in dorsal (**i**), ventral (**j**), and cranial (**k**) views; **l**, **m**, middle trunk vertebra (SNSB-BSPG 1937 II 23789) in left lateral (**l**) and ventral (**m**) views; **n**–**r**, paratype posterior trunk vertebra (SNSB-BSPG 1937 II 23791) in left lateral (**n**), dorsal (**o**), ventral (**p**), cranial (**q**), and caudal (**r**) views; **s**, **t**, posterior trunk vertebra (SNSB-BSPG 1937 II 23781) in ventral (**s**) and cranial (**t**) views. cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; na, neural arch; nc, neural canal; ns, neural spine; nsf, neural spine foramen; p, parapophysis; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene; zyg, zygantrum. Arrows indicate important features

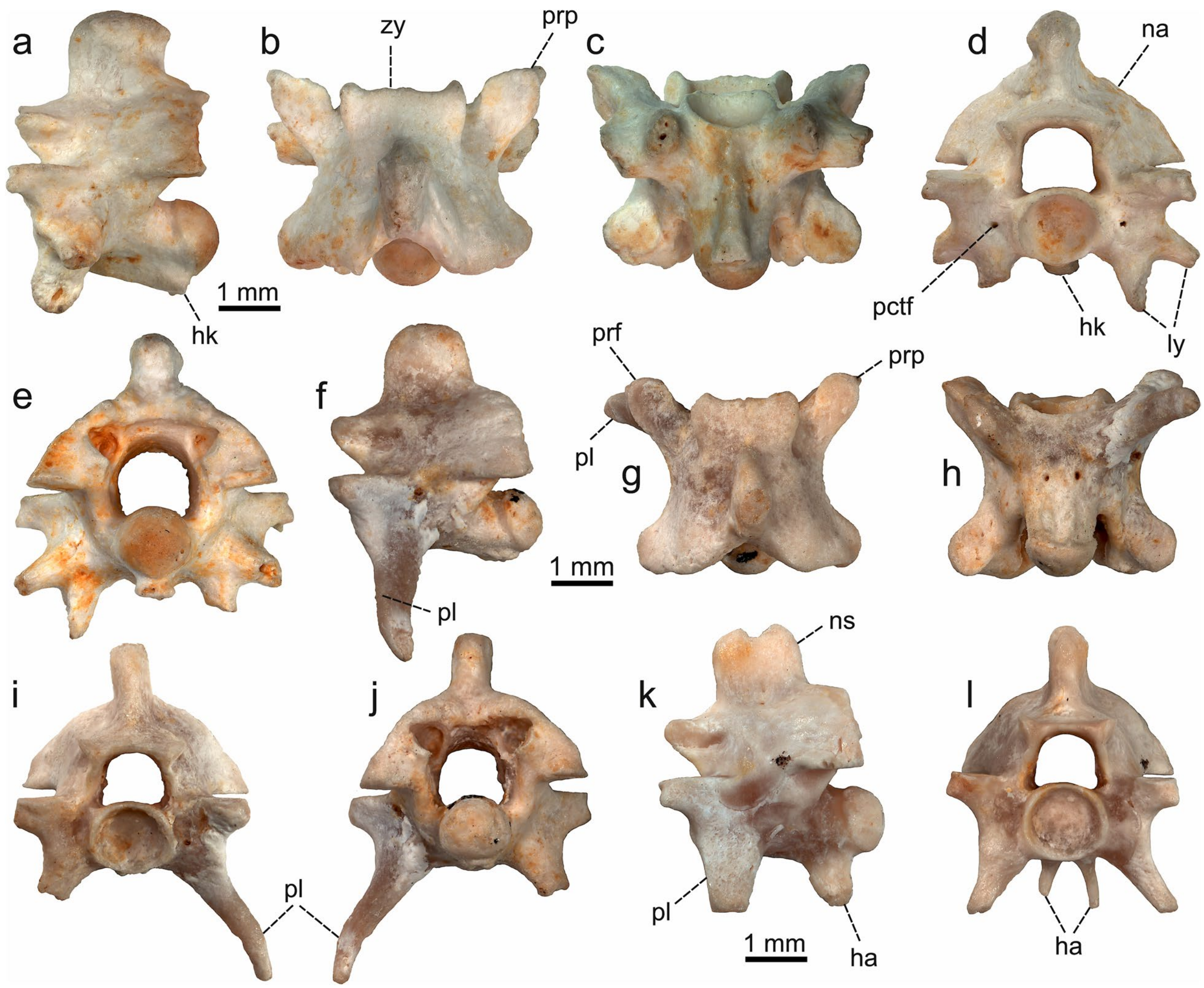

Fig. 6 *Bavarioboa wintershofensis* sp. nov. from Wintershof-West. **a**–**e**, paratype cloacal vertebra (SNSB-BSPG 1937 II 23805) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**j**, paratype anterior caudal vertebra (SNSB-BSPG 1937 II 23857) in left lateral (**f**), dorsal (**g**), ventral (**h**), cranial (**i**), and caudal (**j**) views; **k**, **l**, caudal vertebra (SNSB-BSPG 1937 II 23856) in left lateral (**k**) and cranial (**l**) views. ha, haemapophysis; hk, haemal keel; ly, lymphapophysis; na, neural arch; ns, neural spine; pctf, paracotylar foramen; pl, pleurapophysis; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; zy, zygosphene. Arrows indicate important features

23803 (a middle trunk vertebra, Fig. 5a–e); SNSB-BSPG 1937 II 23791 (a posterior trunk vertebra, Fig. 5n–r), SNSB-BSPG 1937 II 23805 (a cloacal vertebra, Fig. 6a–e); SNSB-BSPG 1937 II 23857 (a caudal vertebra, Fig. 6f–j).

Referred material. – 79 anterior trunk vertebrae (73 + 6 articulated (2 + 2 + 2) vertebrae (SNSB-BSPG 1937 II 23402–23477), 325 middle and posterior trunk vertebrae (SNSB-BSPG 1937 II 23479–23802), 10 cloacal vertebrae (SNSB-BSPG 1937 II 23806–23815), 41 caudal vertebrae (SNSB-BSPG 1937 II 23816–23856).

Description of the holotype (Fig. 3): The nearly completely preserved middle trunk vertebra with broken-off right paradiapophysis and left parapophysis. The CL is 4.38 mm, and NAW is 4.62 mm with CL/NAW = 0.95 (for complete measurements see Appendix 2). In lateral view (Fig. 3a, b, g), the vertebra is higher than long. The neural spine rises at the posterior margin of the zygosphenal facets. Its cranial margin is roughly vertical whereas caudal margin is slightly inclined posteriorly. The neural arch is slightly upswept dorsally. The lateral foramina are situated at the base of prezygapophyses and below the short and rather sharp interzygapophyseal ridges. The only preserved left diapophysis is slightly elongated dorsally. The dorsally arched subcentral ridges diminish in posterior half of the vertebra and disappear completely at the base of the short condylar neck. In dorsal view (Fig. 3c, h), the zygosphenal lip is three-lobed with pointed lateral lobes and wide central lobe. Prezygapophyseal articular facets are subtriangular and prezygapophyseal processes are rather short but well seen in dorsal aspect. The neural spine is thick with its anterior margin wider compared to the posterior one. The distinct nutrient foramina, neural spine foramina sensu Georgalis and Scheyer (2019), are placed on either side of the neural spine base. The neural arch is markedly swollen close behind the neural spine foramina. The caudal notch is deep, extending to condylar neck/condyle transition. In ventral view (Fig. 3d, i), the centrum is triangular. The blunt subcentral ridges are almost straight and shallow subcentral grooves extend along the base of the haemal keel to small subcentral foramina situated in the middle of the centrum length. The haemal keel is wide with constriction at the level of subcentral foramina. The postzygapophyseal articular facets are sub-triangular in outline. In cranial view (Fig. 3e, j), the neural canal is rounded with prominent lateral sinuses. The zygosphenal articular facets extend clearly above the zygosphenal roof. The central lobe of the zygosphene forms a dorsally vaulted thin lamina which is shifted slightly below the zygosphenal roof. Prezygapophyses are distinctly tilted up dorsally with prezygapophyseal articular facets situated high above the dorsal margin of the dorsoventrally depressed cotyle. A small nutrient foramen occurs below the left prezygapophyseal facet. The slightly eroded parapophyseal portion of the paradiapophysis likely did not extend beyond the ventral margin of the cotylar rim. Paracotylar foramina are absent. In caudal view (Fig. 3f, k), the neural arch is depressed, with a vaulting ratio 0.27, and the "pagoda"-like roof of the deep zygantrum corresponds to the shape of the zygosphenal lip. The condyle is slightly depressed dorsoventrally.

Description of paratypes and referred material–intracolumnar variation

Anterior trunk vertebrae (Fig. 4a–m): Most of the anterior trunk vertebrae are fragmentary, usually with strongly damaged neural spine and broken-off hypapophysis. In lateral view, both the cranial and caudal margins of the high neural spine are clearly inclined posteriorly (Fig. 4d, i, k). The dorsal termination of the only complete neural spine (Fig. 4i) is slightly vaulted dorsally. The zygapophyseal facets are large and oval. Small lateral foramina are situated below short and massively built interzygapophyseal ridges. The diapophyses are slightly larger than the parapophyses. The condyle is developed on the short neck. Two almost complete hypapophyses with broken-off their distal terminations indicate that the vertebra with the more anterior position (Fig. 4a) has developed straight hypapophysis inclined posteroventrally, whereas the vertebra positioned more posteriorly has slender hypapophysis bent more caudally and extended behind the caudal border of the condyle (Fig. 4d). Vertebrae positioned around the anterior/middle trunk section are distinctly higher than long with high neural spine and vestigial ventrally directed hypapophysis. In dorsal view, the wide zygosphenal roof has developed short and distally pointed lateral lobes whereas the central lobe is wide and blunt. The large prezygapophyseal articular facets are widely subtriangular and elongated anteriorly rather than anterolaterally. Prezygapophyseal processes are short. The posterodorsal portion of the neural arch is "swollen". The caudal notch is shallow. The interzygapophyseal constriction is well-developed. In ventral view, the centrum is triangular, with short subcentral ridges and wide subcentral grooves developed only in the anterior half of the centrum. Subcentral foramina are usually large (Fig. 4c, f, l). The hypapophysis is narrow, with its anterior keel extending up to the cotylar rim. However, in the vertebrae placed close to the anterior/middle trunk section, the base of the short hypapophysis is attached to the markedly wide base that transforms into the haemal keel in the middle trunk vertebrae (Fig. 7a). Postzygapophyseal articular facets are roughly oval to subtriangular and elongated laterally. In cranial view, the neural arch is depressed. The zygosphene is lightly build, with a distinct dorsally arched (sometimes almost straight) lamina of the central lobe. Prezygapophyses are inclined dorsally but sometimes are nearly horizontal (Fig. 4g). Small paracotylar foramina occur sometimes on one or both sides of the dorsoventrally slightly depressed cotyle.

Middle and posterior trunk vertebrae (Figs. 4n, o and 5a–t): The morphology of the middle and posterior trunk vertebrae largely corresponds to that of the holotype, although there is a high intracolumnar variability especially in the shape of the neural spine and the haemal keel. The posteriorly shifted neural spine, which usually rises behind the zygosphenal roof or close to the posterior border of the zygosphenal articular facets (Fig. 7), displays a peculiar shape of its cranial margin. In lateral view, the basal third of the neural spine height is vertical or even slightly inclined anteriorly but the distinctly straight and blade-like lamina, best visible in anterior view, continues posterodorsally up to the horizontal slightly dorsally arched distal termination of the neural spine. This lamina is present in the largest middle trunk vertebrae (Figs. 5a, f, l), except of the holotype (Fig. 3a), which undoubtedly comes from the anterior/middle trunk section as documented by the low haemal keel and rather shallow and short subcentral grooves. The neural spine of the posterior trunk vertebrae is low, its anterodorsal lamina is short and the caudal margin sometimes forms a short but distinct posteriorly directed spur (Figs. 5n and 7e). The zygosphene is three-lobed, with well-developed lateral lobes in dorsal view, and the wide central lobe contributing to the thin lamina, best visible in anterior aspect. The bulbous posterodorsal portion of the neural arch occurs in all vertebrae. The neural spine foramina, usually situated on either side of the neural spine base, occur in most vertebrae. The morphology of the haemal keel is variable within the vertebral column. In ventral view, the narrow haemal keel, which is rounded ventrally or with moderately developed ventral ridge, occurs in the anteriorly positioned vertebrae (close to the anterior/middle trunk transition; Figs. 4n, o and 7a). However, in the largest middle trunk vertebrae, the haemal keel is markedly wide with almost flat its expanding ventral surface situated behind the constriction at the level of subcentral foramina (Figs. 5c and 7c, d). In posterior trunk vertebrae, the prominent haemal keel is roughly biconcave (Figs. 5p and 7e). Subcentral ridges of anteriorly positioned middle trunk vertebrae are blunt and separated from the haemal keel by narrow subcentral grooves but in the posterior trunk vertebrae the ridges are rather narrow and usually with prominent subcentral grooves developed in anterior half of the centrum. In cranial view, the cotylar rim is widely oval, with no paracotylar foramina within depressions on either side of the cotyle. In caudal view, the neural arch is depressed dorsoventrally, with a vaulting ratio ranging from 0.24 to 0.36. The zygantrum is wide, with its laterodorsal extensions usually lifted dorsolaterally to fit raised lateral lobes of the zygosphene. The condyle is slightly depressed dorsolaterally in anteriorly positioned vertebrae but in posterior trunk vertebrae the condyle is moderately depressed dorsoventrally.

Cloacal vertebrae (Fig. 6a–e): Vertebrae from the cloacal portion of the column are clearly higher than long and differ from posteriormost trunk vertebrae by the presence of lymphapophyses instead of paradiapophyses. In lateral view, the neural spine of the most complete vertebra is as high as long, its anterior and posterior margins are vertical with rounded anterodorsal termination. The haemal keel protrudes posteriorly into the small hypapophysis. In dorsal view, the zygosphenal lip has two distinct lateral lobes but medial lobe is underdeveloped. Prezygapophyseal articular facets are elongated anterolaterally and prezygapophyseal processes are small but well perceptible. The dorsal margin of the neural spine is thickened and sometimes this lateral expansion is remarkable although pathological development cannot be ruled out. In ventral view, the postzygapophyseal articular facets are circular or widely drop-like in outline. Small subcentral foramina occur at the base of the posteriorly expanding haemal keel/hypapophysis. In cranial view, prezygapophyses are horizontal, with articular facets situated high above the base of the neural canal. The dorsal branch of lymphapophyses is directed lateroventrally, whereas their ventral branch is directed ventrally rather than laterally. Paracotylar foramina occur

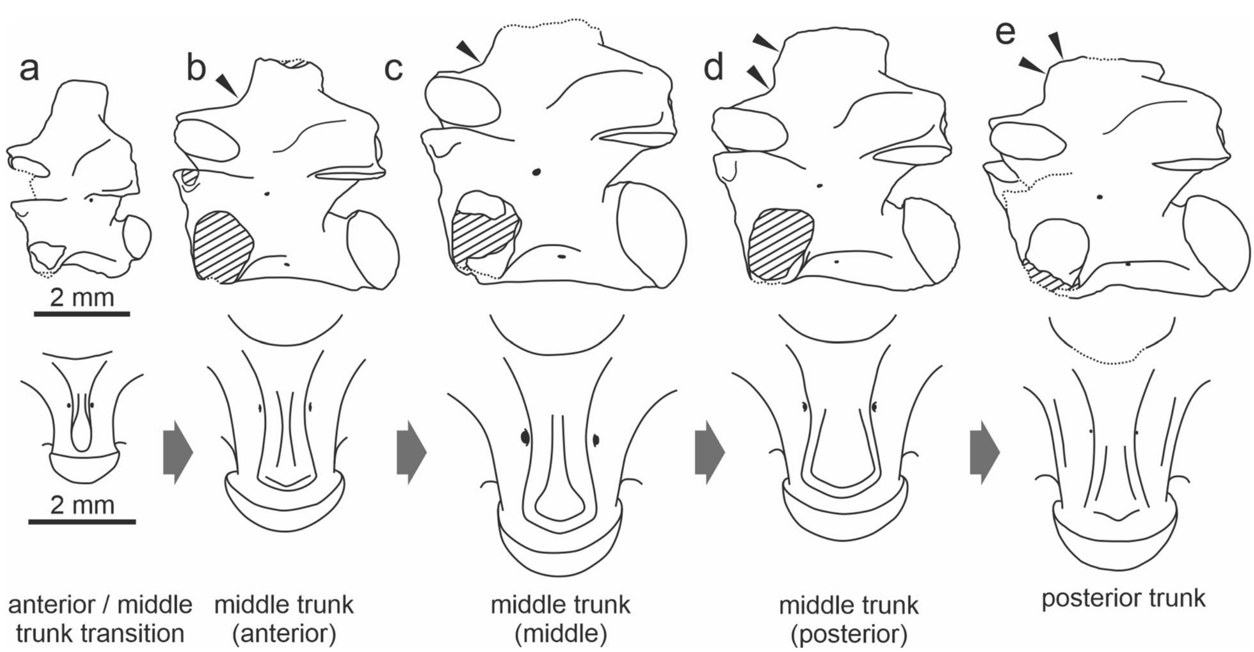

Fig. 7 *Bavarioboa wintershofensis* sp. nov. from Wintershof-West. **a**–**e**, intracolumnar variability through the middle trunk section of the vertebral column in *Bavarioboa wintershofensis*. **a**, SNSB-BSPG 1937 II 23471; **b**, SNSB-BSPG 1937 II 23793; **c**, SNSB-BSPG 1937 II 23795; **d**, SNSB-BSPG 1937 II 23789; **e**, SNSB-BSPG 1937 II 23791. Arrows indicate important features

on either side of the cotylar rim. In caudal view, the neural arch is distinctly vaulted.

Caudal vertebrae (Fig. 6f–l): These fragmentary vertebrae provided with pleurapophyses are rather small. In lateral view, the one of the best-preserved vertebrae has a right pleurapophysis and an almost complete neural spine, which is slightly inclined posteriorly. The pleurapophysis had a wide base with a weak anterior protrusion. The narrowing distal termination of the pleurapophysis is directed ventrally. The paired haemapophyses form small bulges rather than distinctly developed structures. However, they can be partially eroded. In cranial view, the neural arch is vaulted, and the neural canal is subsquare. Prezygapophyses are horizontal. The straight right pleurapophysis is directed lateroventrally. Paracotylar foramina occur on either side of the slightly dorsoventrally depressed cotyle. In caudal view, the neural arch is vaulted.

Remark on the trunk/caudal transition

The morphology of snake vertebrae is strongly affected by their position within the vertebral column (e.g., Georgalis et al., 2021b; Hoffstetter & Gasc, 1969; Szyndlar, 1984; Szyndlar & Georgalis, 2023; Szyndlar & Rage, 2003). The trunk/caudal transition displays a characteristic sequence of subcentral structures in most snake lineages (Szyndlar & Georgalis, 2023; Szyndlar & Rage, 2003). The abundant and relatively well-preserved material of *Bavarioboa wintershofensis* sp. nov. enabled the most detailed view on the posterior trunk—cloacal—anterior caudal transition in *Bavarioboa* (Fig. 8).

In the posteriormost trunk vertebrae of *Bavarioboa wintershofensis* sp. nov., short hypapophysis is developed. The neural spine is low in lateral view and wide (not thickened) in dorsal/cranial views. We presuppose that the cloacal region included a succession of at least three

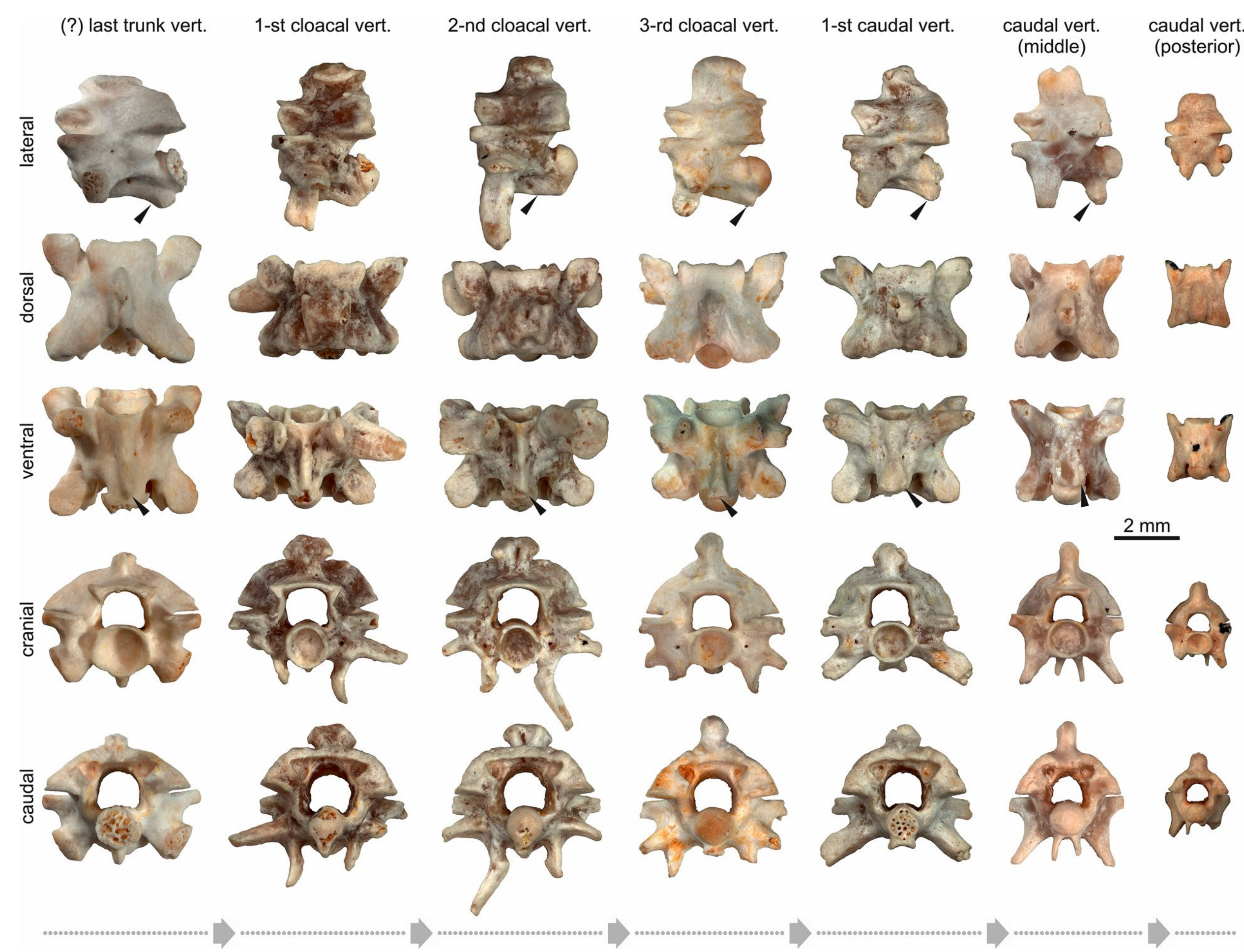

Fig. 8 Trunk/caudal transition in *Bavarioboa wintershofensis* sp. nov. from Wintershof-West. (?) last trunk vertebra (SNSB-BSPG 1937 II 23781); cloacal: 1-st (SNSB-BSPG 1937 II 23815), 2-nd (SNSB-BSPG 1937 II 23810), 3-rd (SNSB-BSPG 1937 II 23805), and caudal vertebrae: (?) 1-st (SNSB-BSPG 1937 II 23817), middle (SNSB-BSPG 1937 II 23856), and posterior (SNSB-BSPG 1937 II 23816). Short hypapophysis-like haemal keel occurs in posteriormost (?) trunk vertebra, haemal keel slightly bifurcated in cloacal/caudal transition, middle and posterior caudal vertebrae with prominent ventrally projected haemapophyses

vertebrae which agrees with most of Booidea (Szyndlar & Georgalis, 2023). In the first cloacal vertebra, the hypapophysis is reduced to rather thin haemal keel provided posteroventrally by a small bulge. The neural spine is strongly thickened dorsally. In the second cloacal vertebra, the haemal keel is straight in lateral view and slightly broader compared to the 1st cloacal vertebra in ventral view. The dorsal portion of the neural spine is strongly thickened. The last cloacal vertebra is provided with haemal keel, whose posteroventral termination displays initial bifurcation. The neural spine is less thickened dorsally. The dorsal and ventral branches of lymphapophyses form a more acute angle compared to more anteriorly positioned cloacal vertebrae. The lymphapophysis upper branch of the 3rd cloacal vertebra is directed lateroventrally instead of laterally directed upper branch of the 1st and 2nd cloacal vertebrae. The most anterior (? 1st) caudal vertebra displays posteriorly bifurcated haemal keel rather than distinct haemapophyses. Pleurapophyses are strongly built, with distinct bumps developed on their dorsal base. These bumps represent most probably reduced dorsal branches of lymphapophyses.

Comparison and discussion

Seven species of the extinct genus *Bavarioboa* — *Bavarioboa bachensis* Szyndlar & Rage, 2003, *Bavarioboa vaylatsae* Szyndlar & Rage, 2003, *Bavarioboa crocheti* Szyndlar & Rage, 2003, *Bavarioboa minuta* Szyndlar & Rage, 2003, *Bavarioboa herrlingensis* Szyndlar & Rage, 2003, *Bavarioboa hermi* Szyndlar & Böhme, 1993, and *Bavarioboa ultima* Szyndlar & Rage, 2003 — are known from the middle Oligocene (MP 26) to early Middle Miocene of Europe (Szyndlar & Rage, 2003; Szyndlar & Schleich, 1993). Most of them are known only from their type localities except of *B. crocheti* reported from the late Oligocene (MP 28) of Pech-Desse and Pech-du-Fraysse, France (Szyndlar & Rage, 2003) and *B. hermi* reported from the Early Miocene (MN 4) of Petersbuch 2, Germany (Szyndlar & Schleich, 1993), Dolnice and possibly Mokrá-Western Quarry, Czech Republic (Ivanov et al., 2020; Szyndlar & Rage, 2003) and uncertainly from the early Middle Miocene (MN 5) of Griesbeckerzell 1a, Germany (Ivanov & Böhme, 2011). *Bavarioboa wintershofensis* sp. nov. differs from all known species by the following unique combination of characters reported in middle trunk vertebrae:

(1) the dorsoventrally depressed neural arch is upswept posterodorsally forming bulbous bumps in dorsal view

Remarks: The neural arch is depressed in anterior view in all species of *Bavarioboa* except *Bavarioboa herrlingensis* (Szyndlar & Rage, 2003). The distinctly bulbous posterior dorsal portion of the neural arch is absent in *B. bachensis*, *B. minuta*, *B. hermi*, and *B. ultima* (Szyndlar & Schleich, 1993; Fig. 2; Szyndlar & Rage, 2003; figs. 5, 14, 19–22, 24). Moreover, *B. bachensis* differs from all other congeners by the straight posterodorsal laminae of the neural arch in caudal view. Although upswept posterodorsal portion of the neural arch may occur in *B. vaylatsae*, *B. crocheti* and *B. herrlingensis* (Szyndlar & Rage, 2003: figs. 6, 8–13, 15–16), it is never so markedly developed as it is in *B. wintershofensis* sp. nov. The development of this structure does not depend on the position of vertebra within the vertebral column as documented by its presence in cervical as well as cloacal and caudal vertebrae.

(2) the neural spine rises behind or close to the posterior border of the zygosphenal articular facets; its anterodorsal portion often forms a thin straight lamina inclined posterodorsally

Remarks: The only *Bavarioboa* with the neural spine placed behind the zygosphene is *Bavarioboa minuta* (see Szyndlar & Rage, 2003). *B. wintershofensis* differs from *B. minuta* by the thicker neural spine and further by the larger absolute size, dorsally inclined prezygapophyses and clearly wider haemal keel in the middle trunk vertebrae. Although a blad-like lamina may occur on the anterior/anterodorsal margin of the neural spine in *B. vaylatsae*, *B. crocheti*, *B. herrlingensis* and *B. hermi* all three Oligocene species differ from *B. wintershofensis* sp. nov. by the distinctly rounded anterodorsal margin of the neural spine in lateral view (Szyndlar & Rage, 2003; figs. 6, 8, 9, 11, 12, 15, 16). Most middle trunk vertebrae of *B. hermi* differ from those of *B. wintershofensis* by the more anterior position of the cranial margin of neural spine. Moreover, the three-lobed zygosphene is not developed in *B. hermi*. The holotype of a posterior trunk vertebra of *B. bachensis* differs from posterior trunk vertebrae of *B. wintershofensis* by the straight posterodorsal laminae of the neural arch in caudal view. *B. ultima* differs from *B. wintershofensis* by the lower neural spine which is not laterally expanded in its anterior portion (Szyndlar & Rage, 2003) unlike anteriorly wide neural spine in *B. wintershofensis* sp. nov.

(3) neural spine foramina usually occur on either side of the neural spine base

Remarks: The paired neural spine foramina occur frequently in trunk vertebrae of *Bavarioboa wintershofensis* sp. nov. These nutrient foramina have been depicted rarely in some extant Booidea (*Sanzinia* Gray, 1834, *Epicrates* Wagler, 1830, *Eunectes* Wagler, 1830, *Candoia* Gray, 1842a) and Pythonoidea (*Bothrochilus* Fitzinger, 1843) (see Szyndlar & Georgalis, 2023), as well as the extinct booids cf. *Bavarioboa* sp.

from the early late Oligocene (MP 25) of Rigal Jouet, France and *Bavarioboa crocheti* from the late Oligocene (MP 28) of Pech-Desse, France (Szyndlar & Rage, 2003: figs. 4, 8 and 9), but also Eocene constrictors, such as *Palaeopython helveticus* Georgalis & Scheyer, 2019 (see Georgalis & Scheyer, 2019: figs. 6, 9). These foramina, well-documented in mammals, are probably the entry points for the posterior dorsal branches of segmental arteries (e.g., Etz et al., 2011; Oshina et al., 2018). However, during the vertebrae formation, dorsal segmental arteries may obliterate and as a consequence, there are usually no traces of those dorsally positioned nutrient foramina in postembryonic snakes. As the origin of these foramina are related to the early ontogenetic stages, we can speculate that in *Bavarioboa wintershofensis* sp. nov. these foramina for the posterior dorsal branches of segmental arteries persisted up to adult postembryonic stage and throughout the whole vertebral column.

(4) the zygosphene is three-lobed with the central lobe forming the dorsally arched and slightly downwards shifted thin lamina in anterior view

Remarks: The presence of three-lobated zygosphene does not occur in known Miocene species of *Bavarioboa*. The zygosphene of *Bavarioboa hermi* lacks the central lobe and *B. ultima* possesses convex zygosphene with minute lateral lobes (Szyndlar & Rage, 2003). The central lobe occurs in all Oligocene *Bavarioboa*, except of *B. bachensis* holotype which represents a posterior trunk vertebra (Szyndlar & Rage, 2003). *Bavarioboa bachensis* differs from *B. wintershofensis* sp. nov. by the straight posterodorsal laminae of the neural arch as well as craniocaudally distinctly broaden prezygapophyses. *Bavarioboa minuta* differs from *Bavarioboa wintershofensis* sp. nov. by the straight lamina of the zygosphene which is not shifted downwards. *Bavarioboa herrlingensis* differs from *B. wintershofensis* sp. nov. by the straight and sometimes thick zygosphene in anterior aspect and the absence of a thin lamina of the central lobe. The only *Bavarioboa* with central lobe of the zygosphene distinctly shifted downwards are *B. vaylatsae* and *B. crocheti*. However, both last-mentioned species differ from *B. wintershofensis* by the more anterior position of the cranial margin of the neural spine whose anterodorsal termination is distinctly rounded in lateral view. Moreover, the zygosphene of *B. wintershofensis* sp. nov. is never thick unlike that of *B. crocheti* (Szyndlar & Rage, 2003).

(5) the wide haemal keel is constricted at the level of the subcentral foramina, with its ventral surface expanding in the caudal direction

Remarks: The wide haemal keel in *Bavarioboa wintershofensis* sp. nov., constricted at the level of subcentral foramina and spatulate in caudal direction, is reminiscent that of *B. crocheti* which is the only *Bavarioboa* with a biconcave haemal keel (Szyndlar & Rage, 2003: Fig. 9). However, the haemal keel is often wider and less distinct in *B. wintershofensis* sp. nov. *Bavarioboa winterfofensis* sp. nov. further differs from *B. crocheti* by the more posteriorly situated neural spine with absence of rounded its anterodorsal margin. *B. vaylatsae* and *B. ultima* differ from *B. wintershofensis* by the haemal keel uniform in width along its entire length. The haemal keel in *B. minuta*, *B. herrlingensis*, and *B. hermi* is narrower compared to *B. wintershofensis* sp. nov. (Szyndlar & Rage, 2003; Szyndlar & Schleich, 1993).

(6) paracotylar foramina are present in some trunk vertebrae.

Remarks: Paracotylar foramina have been documented in vertebrae along the entire vertebral column. Paracotylar foramina are usually absent in trunk vertebrae in *Bavarioboa* except for *B. hermi* and *B. ultima* (Szyndlar & Rage, 2003), while they can be occasionally present in some extant booid taxa (Szyndlar & Georgalis, 2023).

Booidea indet.

Material. – 18 anterior trunk vertebrae (SNSB-BSPG 1937 II 23858–23875), 131 middle and posterior trunk vertebrae (SNSB-BSPG 1937 II 23876–24006), five caudal vertebrae (SNSB-BSPG 1937 II 24007–24011).

Trunk and caudal vertebrae: All the preserved anterior, middle and posterior trunk vertebrae are rather fragmentary with broken-off neural spine, damaged paradiapophyses and incomplete pre- and/or postzygapophyses. The trunk vertebrae, typical by the CL/NAW ratio < 1, weakly vaulted neural arch, the neural spine occupying more than half of the neural arch length, the well-developed haemal keel in the middle trunk vertebrae and the absence of paracotylar foramina support attribution to Booidea (Szyndlar & Georgalis, 2023; Szyndlar & Rage, 2003). It is possible that most of rather fragmentary vertebrae might have belonged to the genus *Bavarioboa* but the absence of a thin lamina on the cranial margin of the zygosphene and absence of the distinct bumps in the posterior portion of the neural arch precludes attribution to the new species.

Caenophidia Hoffstetter, 1939
Colubroides Zaher, Grazziotin, Cadle, Murphy, Moura-Leite & Bonatto, 2009
Colubriformes Günther, 1864 (sensu Zaher et al., 2009)
Viperidae Oppel, 1811b

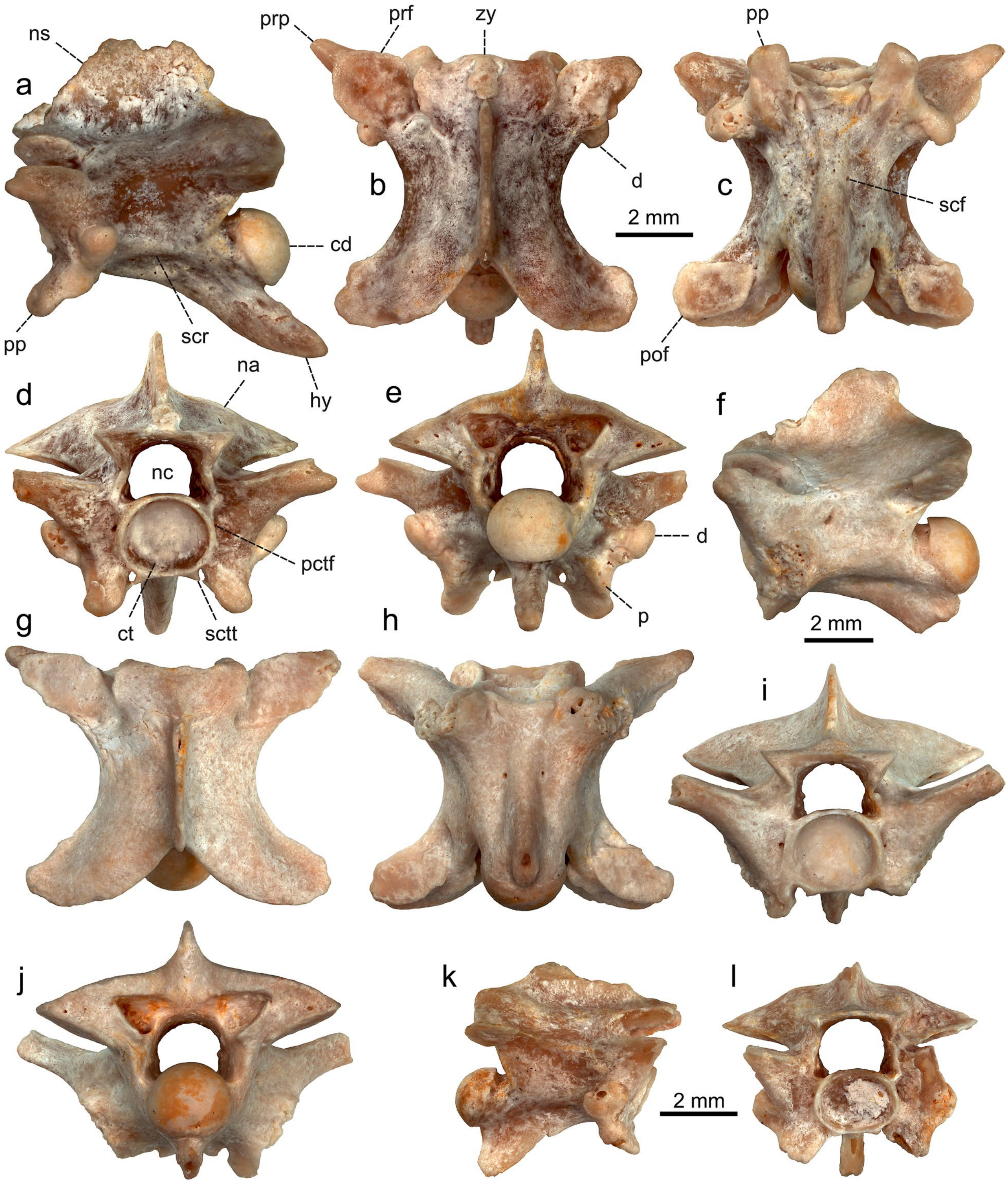

Fig. 9 Viperinae indet. – 'Oriental vipers' from Wintershof-West. **a**–**e**, trunk vertebra (SNSB-BSPG 1937 II 24104) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**j**, middle trunk vertebra (SNSB-BSPG 1937 II 24105) in right lateral (**f**), dorsal (**g**), ventral (**h**), cranial (**i**), and caudal (**j**) views; **k**, **l**, posterior trunk vertebra (SNSB-BSPG 1937 II 24103) in right lateral (**k**), and cranial (**l**) views. cd, condyle; ct, cotyle; d, diapophysis; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; pp, parapophyseal process; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scf, subcentral foramen; scr, subcentral ridge; sctt, subcotylar tubercle; zy, zygosphene

Viperinae Oppel, 1811b

Viperinae indet. – 'Oriental vipers' (sensu Szyndlar & Rage, 1999)

Material. – 99 trunk vertebrae (SNSB-BSPG 1937 II 24012–24110).

Trunk vertebrae (Fig. 9): All preserved vertebrae are at least partially damaged, mostly with incomplete neural spine and hypapophysis and eroded para- and diapophyses. In lateral view, the high neural spine, although with broken-off dorsal termination, is about as high as long, with anterior margin vertical or slightly inclined caudally. The zygosphenal facets are oval in outline. The interzygapophyseal ridges are short and usually blunt. Small lateral foramina are situated close below these ridges just at the posterior base of the prezygapophyses. The diapophyses are about as large as parapophyses. Parapophyseal processes are massively built and directed anteroventrally. Their rarely preserved distal termination is blunt in lateral and cranial views (Fig. 9a, d). Subcentral ridges are slightly arched dorsally. The strongly built hypapophysis, directed posteroventrally, is acute towards its distal termination and extends posterior to the caudal termination of the condyle. The condyle is developed on the very short condylar neck. In dorsal view, the vertebrae are elongated with laterally expanded zygapophyses. The zygosphene has well-developed median lobe and distinct but short lateral lobes. The median lobe is usually wide, but in the largest specimens (Fig. 9g) this lobe is rather small, and the cranial margin of the zygosphene is straight or slightly concave. The large prezygapophyseal articular facets are oval with the long axis directed anterolaterally; however, in more anteriorly positioned vertebrae, these facets are subcircular in outline. The distally slightly pointed prezygapophyseal processes are short reaching about one fourth or one fifth of the prezygapophyseal facets length. The epizygapophyseal spines are absent. The caudal notch at the posterior border of the neural arch is shallow in the largest middle trunk vertebrae. In ventral view, the centrum is triangular, with well-developed, straight subcentral ridges. Subcentral ridges are blunt in the largest middle trunk vertebrae but in more anteriorly positioned vertebrae these ridges are rather sharp (Fig. 9a, c). Subcentral grooves are wide and shallow, with small subcentral foramina usually situated at the base of the massive hypapophysis. The hypapophysis extends anteriorly towards the cotylar rim. In posteriormost trunk vertebrae, the distal tip of the hypapophysis has indication of a slight bifurcation. There are distinct subcotylar tubercles at the base of the cotylar rim. In some vertebrae, their distal termination reaches the medial extension of the parapophyseal base to form a short canal for passage of the circulatory system. The distal termination of the parapophyseal processes is subsquare. The subrectangular postzygapophyseal articular facets are elongated laterally. In cranial view, prezygapophyses are clearly tilted dorsally. The zygosphene is straight. The neural canal is rounded with mostly narrow lateral sinuses. The parapophyses are well-divided from diapophyses. Parapophyseal processes markedly extend ventrally below the circular cotylar rim of the large diameter. Small paracotylar foramina are situated in deep depressions on either side of the cotyle. In caudal view, the neural arch is markedly dorsoventrally compressed, with the postzygapophyses tilted up, and a vaulting ratio ranges from 0.12 to 0.21. One or two distinct parazygantral foramina occur on either side of the wide zygantral area. The condyle is orbicular.

Remarks: The preserved vertebrae can be attributed to 'Oriental vipers' based on (Szyndlar & Rage, 1999): their relatively large dimensions with CL of the largest vertebra 6.74 mm and NAW 4.71 mm; see Appendix 1), strongly depressed neural arch, high neural spine which is about as high as long or slightly higher, clearly tilted zygapophyses, anteroventrally projecting parapophyseal processes, and strongly built hypapophysis with slightly obtuse distal tip directed caudally. The only distinct species of 'Oriental vipers' from the European Early Miocene is *'Vipera' platyspondyla* Szyndlar, 1987 reported from late Early Miocene of Dolnice (MN 4), Czechia (Szyndlar, 1987) and Petersbuch 2 (MN 4a), Germany (Szyndlar & Schleich, 1993). 'Oriental vipers' from Wintershof-West differ significantly from *'V.' platyspondyla* by the distally curved hypapophysis instead of straight hypapophysis reported in extinct species, more elongated vertebrae as well as smaller dimensions (Szyndlar, 1987; Szyndlar & Schleich, 1993). The viperid from Wintershof-West partially shares its vertebral morphology with extant *Macrovipera lebetina* (Linnaeus, 1758) as documented by the wide base of the hypapophysis in middle trunk vertebrae in lateral view which becomes triangular and bifurcated in the posteriormost trunk vertebrae (Szyndlar & Rage, 1999).

'*Vipera aspis*' complex (sensu Szyndlar, 1987)

Vipera Laurenti, 1768

***Vipera* sp.**

Material. – 47 trunk vertebrae (SNSB-BSPG 1937 II 24111–24157).

Trunk vertebrae (Fig. 10): The vertebrae, typical for their small dimensions (the CL of the largest one is 4.63 mm; see Appendix 1), are fragmentary usually with damaged neural spine, hypapophysis and paradiapophyses. In lateral view, the neural spine of the most complete anterior/middle trunk vertebra (Fig. 10a–c) is about twice to three times longer than high. The base

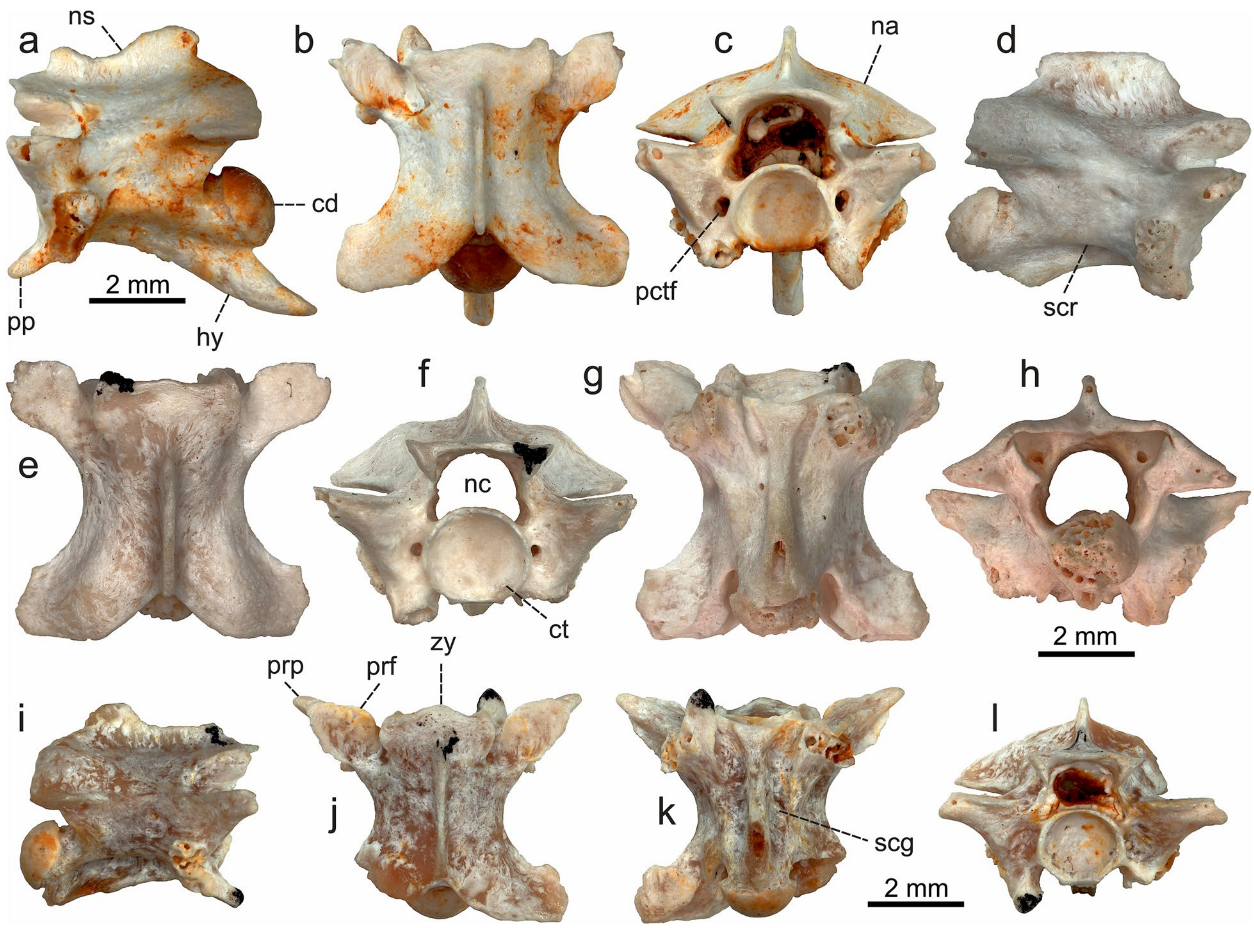

Fig. 10 *Vipera* sp. (*'V. aspis'* complex) from Wintershof-West. **a**–**c**, trunk vertebra (SNSB-BSPG 1937 II 24155) in left lateral (**a**), dorsal (**b**), and ventral (**c**), views; **d**–**h**, middle trunk vertebra (SNSB-BSPG 1937 II 24156) in right lateral (**d**), dorsal (**e**), cranial (**f**), ventral (**g**), and caudal (**h**) views; **i-l**, posterior trunk vertebra (SNSB-BSPG 1937 II 24157) in right lateral (**i**), dorsal (**j**), ventral (**k**), and cranial (**l**) views. cd, condyle; ct, cotyle; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; pctf, paracotylar foramen; pp, parapophyseal process; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene

of its cranial margin is vertical, and the caudal margin is slightly inclined posteriorly. The well-developed interzygapophyseal ridge is short and moderately sharp. The lateral foramen is situated well-below the interzygapophyseal ridge. The slightly eroded right diapophysis is somewhat larger than the parapophysis from which the conspicuously long and slender parapophyseal process projects anteroventrally. The clearly developed subcentral ridge is weakly arched dorsally and extends posteriorly to the base of the short condylar neck. The acute distal tip of the deep posteroventrally projected hypapophysis is directed caudally. In dorsal view, the vertebrae are wide and short. The zygosphenal lip is crenate, with wide medial lobe and distinct lateral lobes. In posteriorly positioned vertebrae (Fig. 10i–l), the triangularly shaped medial lobe clearly projects anteriorly. Prezygapophyseal articular facets are oval with long axis directed anterolaterally. The rarely preserved prezygapophyseal processes are short and acute. Epizygapophyseal spines are either absent or indistinctly developed. In ventral view, the triangular base of the centrum is short and laterally delimited by distinct straight subcentral ridges. Subcentral grooves are shallow and relatively wide in anteriorly positioned vertebrae; however, in posterior trunk vertebrae, these grooves are narrow and deep (Fig. 10k). A narrow sulcus is often present between the anterior keel of the strongly built hypapophysis and the parapophyseal bases. Subcentral foramina, situated at the base of the hypapophysis, are clearly visible. The small subcotylar tubercles usually occur at the base of the cotylar rim. The weakly pointed parapophyseal processes are directed anteriorly. The damaged postzygapophyseal articular facets are either subtriangular or rectangular shaped. In cranial view, the neural canal is rounded to subsquare, with deep lateral sinuses. Prezygapophyses are only slightly tilted up or they can be almost horizontal. The cranial margin of the zygosphene is either slightly arched dorsally, in anteriorly positioned vertebrae, or straight. Conspicuously large paracotylar foramina occur in depressions on either side of the large rounded cotyle. In caudal view, the neural arch is depressed, although weakly vaulted neural arch occasionally occurs (Fig. 10h), with a vaulting ratio ranging from 0.24 to 0.33. The multiple parazygantral foramina are visible. The condyle is orbicular to suborbicular.

Remarks: The vertebrae belong to the family Viperidae as documented by the dorsoventrally strongly flattened neural arch and anteroventrally directed long parapophyseal processes. The small dimensions with the slightly elongated centrum, and the relatively low neural spine (compared to 'Oriental vipers') point to the affiliation to the 'European vipers' informal group of the *'Vipera aspis'* complex (sensu Szyndlar & Schleich, 1993; see also Szyndlar, 1984, 1991b; Szyndlar & Rage, 1999). The only distinct Early Miocene species of 'European vipers' is *Vipera antiqua* Szyndlar, 1987 reported from the earliest Miocene of Weisenau, Germany (MN 1–? MN 2) (Villa et al., 2021; *V.* cf. *V. antiqua* sensu Szyndlar & Böhme, 1993; Szyndlar & Rage, 1999) and two coeval late Early Miocene localities of Petersbuch 2 (MN 4a), Germany (Szyndlar & Schleich, 1993) and Dolnice (MN 4), Czechia (Szyndlar, 1987). Unlike the vertebral morphology of *V. antiqua* which closely resembles that of extant *Vipera ammodytes* (Linnaeus, 1758) by the straight hypapophysis in all precloacal vertebrae (Szyndlar & Schleich, 1993), *Vipera* from Wintershof-West is typical by the caudally curved hypapophysis in posterior trunk vertebrae. The acute distal tip of the hypapophysis corresponds to that of the extant *Vipera latastei* Bosca, 1878 rather than that of *Vipera aspis* (Linnaeus, 1758) possessing distally blunt hypapophysis (see Szyndlar & Schleich, 1993; Szyndlar & Rage, 1999).

Viperidae indet.

Material. – 96 trunk vertebrae (SNSB-BSPG 1937 II 24158–24253).

Remarks: All small to medium sized vertebrae are rather fragmentary with broken-off neural spine and/or hypapophysis close to their bases. The hypapophysis bearing vertebrae are typical by the neural arch, which is strongly depressed dorsoventrally, prezygapophyses inclined dorsally and parapophyseal processes, if preserved, clearly directed anteroventrally. Moreover, the cotyle is distinctly large, with its diameter usually exceeding that of the neural canal. Therefore, vertebrae undoubtedly belong to Viperidae. However, the identification of vertebrae as belonging either to 'Oriental vipers' or 'European vipers' (sensu Szyndlar, 1987) is not possible.

Elapoidea Boie, 1827
Elapidae Boie, 1827
Micrurus Wagler, 1824
'Micrurus' gallicus Rage & Holman, 1984

Material. – 32 trunk vertebrae (28 + 4 articulated (2 + 2) vertebrae) (SNSB-BSPG 1937 II 24254–24283), one cloacal vertebra (SNSB-BSPG 1937 II 24284), one caudal vertebra (SNSB-BSPG 1937 II 24285).

Trunk vertebrae (Fig. 11a–l): The small sized vertebrae are usually fragmentary but two middle trunk vertebrae are nearly complete. In lateral view, the cranial margin of the markedly low neural spine, rising about in the half of the zygosphene length, is vertical or very slightly inclined anteriorly and the caudal margin is inclined posteriorly. The zygosphenal facets are relatively narrow and oval. The blunt interzygapophyseal ridges are moderately developed. The distinct lateral foramina are situated close below these ridges at the anterodorsal border of the wide depression delimited ventrally by the strongly developed subcentral ridges. The almost straight or slightly dorsally arched subcentral ridges extend posteriorly to the close vicinity of the condyle. The para- and diapophyses are roughly equally sized. The parapophysis is rectangular and slightly craniocaudally elongated, with a small but distinct parapophyseal process directed anteriorly. The diapophysis is elongated dorsoventrally. The hypapophysis is moderately deep, with its outer margin forming a very acute angle relative to the main axis of the vertebral body. The ventral margin of the hypapophysis is straight and horizontal, although it slopes toward the cotylar rim in half of the centrum length. The acute caudal tip of the hypapophysis is slightly eroded but it projected at the posterior border or behind the condyle. In dorsal view, the cranial margin of the zygosphene has developed wide and blunt medial lobe and small lateral lobes (Fig. 11g). Prezygapophyseal articular facets are oval, with their long axis directed anterolaterally. The damaged prezygapophyseal processes were probably rather short reaching less than half of the prezygapophyseal facets length. The epizygapophyseal ridges are absent. In ventral view, the ventral surface of the centrum is narrowly triangular and delimited laterally by straight subcentral ridges. Subcentral grooves are wide and shallow. Small subcentral foramina are situated in anterior half of the centrum. The thin hypapophysis extends anteriorly into a low triangular keel reaching the cotylar rim with distinct subcotylar tubercles. Postzygapophyseal articular facets are subcircular in outline. In cranial view, prezygapophyses are oriented horizontally and the neural canal is rounded, with wide and shallow lateral sinuses. The zygosphenal roof is slightly arched dorsally. Distinct paracotylar foramina occur on either side of the rounded cotyle whose ventral

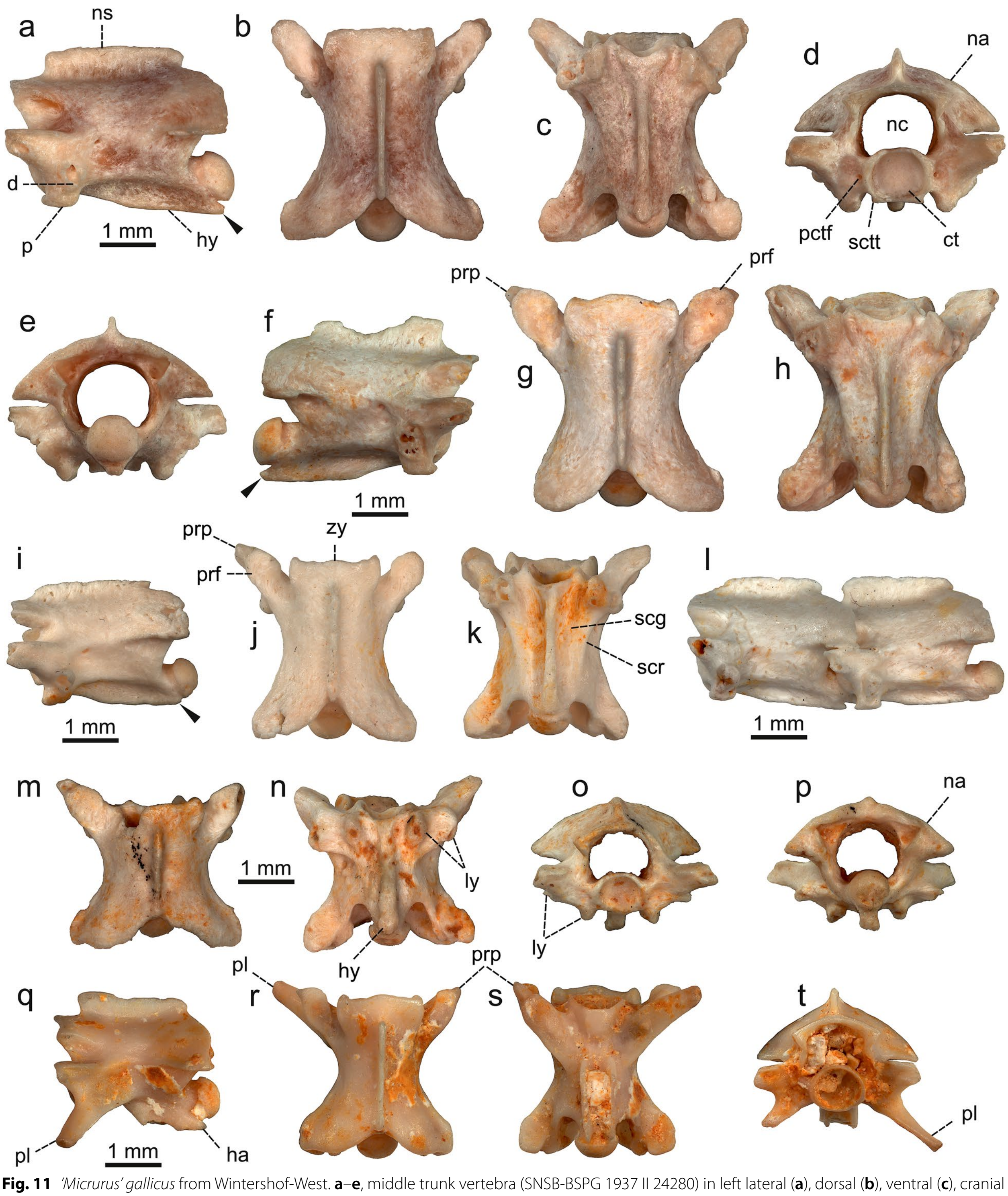

Fig. 11 *'Micrurus' gallicus* from Wintershof-West. **a**–**e**, middle trunk vertebra (SNSB-BSPG 1937 II 24280) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**h**, middle trunk vertebra (SNSB-BSPG 1937 II 24281) in right lateral (**f**), dorsal (**g**), and ventral (**h**) views; **i**–**k**, middle trunk vertebra (SNSB-BSPG 1937 II 24282) in left lateral (**i**), dorsal (**j**), and ventral (**k**) views; **l**, two articulated posterior trunk vertebrae (SNSB-BSPG 1937 II 24283) in left lateral view; **m**–**p**, cloacal vertebra (SNSB-BSPG 1937 II 24284) in dorsal (**m**), ventral (**n**), cranial (**o**), and caudal (**p**) views; **q**–**t**, caudal vertebra (SNSB-BSPG 1937 II 24285) in left lateral (**q**), dorsal (**r**), ventral (s), and cranial (**t**) views. ct, cotyle; d, diapophysis; ha, haemapophysis; hy, hypapophysis; ly, lymphapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pl, pleurapophysis; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; sctt, subcotylar tubercle; zy, zygosphene. Arrows indicate important features

rim with subcotylar tubercles is flattened. In caudal view, the neural arch is regularly vaulted (VR ranging from 0.40 to 0.47), and the suborbicular condyle is rather small.

Cloacal vertebra (Fig. 11m–p): The only preserved fragmentary cloacal vertebra has lymphapophyses broken-off close to their base. Although the dorsal portion of the neural spine is slightly eroded, it was most probably very low. The neural arch is moderately vaulted. Prezygapophyses are not inclined dorsally, prezygapophyseal processes were short reaching at most half the length of prezygapophyseal facets. The well-developed short hypapophysis is present. Epizygapophyseal ridges/spines are not developed. Paracotylar foramina are present on either side of the damaged cotylar rim.

Caudal vertebra (Fig. 11q–t): A fragmentary single caudal vertebra is preserved with broken-off right pleurapophysis and ventral portions of both haemapophyses. The neural spine is low. The left pleurapophysis is slender and directed anteroventrally in lateral and ventrolaterally in cranial views. Epizygapophyseal ridges/spines are absent.

Remarks: The trunk vertebrae, typical by their small dimensions (with centrum length < 4 mm; see Appendix 1) are referable to the small extinct elapid species *'Micrurus' gallicus* Rage & Holman, 1984 reported first from the French Middle Miocene (MN 7) locality of La Grive M (*Micrurus gallicus* sensu Rage & Holman, 1984). The elapid from Wintershof-West is further identical to *'Micrurus' gallicus* reported from the Early Miocene (MN 4a) locality of Petersbuch 2, Germany (Szyndlar & Schleich, 1993: 30, Fig. 8) by the following combination of features (see Szyndlar & Schleich, 1993): (1) the vertebrae are strongly elongated with ventrally flat centrum and prominent subcentral ridges; (2) the neural spine is distinctly low, though not vestigial, and exhibits a vertical cranial margin; (4) the distal tip of hypapophysis is acute and directed posteriorly; (5) the zygosphene possesses wide medial lobe; (6) prezygapophyseal articular facets are oval and postzygapophyseal facets are subcircular in outline.

We provide the first description of cloacal and caudal vertebrae of *'Micrurus' gallicus*. The vertebrae are attributed to *'M.' gallicus* by the same dimensions, the same development of the neural arch, similar shape and length of prezygapophyseal processes, and similar morphology of the zygosphene.

The vertebral morphology of *'Micrurus' gallicus* from the type locality of La Grive M (MN 7) was originally compared only to extant *Micrurus fulvius* Linnaeus, 1766 (see Rage & Holman, 1984). Authors distinguished the extinct species by the less distinct subcentral ridges ('margines inferiores' sensu Rage & Holman, 1984), the shorter hypapophysis, longer prezygapophyseal processes, and less distinct subcentral grooves. Moreover, in several extant species of *Micrurus*, including *M. fulvius*, *Micrurus corallinus* (Merrem, 1820), and *Micrurus lemniscatus* (Linnaeus, 1758) (Holman, 2000; Onary et al., 2018; Fig. 7; Zaher et al., 2019: s2 appendix, fig. F), the hypapophyseal base, laterally delimited by conspicuous subcentral grooves, is strongly built and parapophyses are large compared to extinct *'M.' gallicus* with small parapophyses and minute parapophyseal processes. Although *'M.' gallicus* could be a member of a lineage separate from the well-recognized *Micrurus* clade, the vertebral morphology of diversified Asian clade of extant coral snakes is still poorly known. Therefore, we consider the current generic allocation of *'M.' gallicus* ambiguous and use quotation marks in generic name. In any case, a more detailed comparison with other extant coral snakes will be necessary in future.

Extant coral snakes are geographically divided into Old World coral snakes, comprising three genera *Calliophis* Gray, 1834, *Hemibungarus* Peters, 1862 and *Sinomicrurus* Slowinski, Boundy & Lawson, 2001, and New World coral snakes comprising two genera *Micrurus* and *Micruroides* Schmidt, 1928 (Slowinski et al., 2001). Combined molecular/morphological analyses of Slowinski et al. (2001) and Castoe et al. (2007) as well as a comprehensive analysis of Zaher et al. (2019) recognized Asiatic monophyletic *Sinomicrurus* as a sister clade to the strongly supported New World monophyletic *Micrurus* clade and monotypic *Micruroides*. However, a successive sistership of *Sinomicrurus*, *Micruroides* and *Micrurus* is only ambiguously supported (Zaher et al., 2019). The monophyly of Old World *Calliophis* clade, which is considered a sister-group to all remaining elapids (Figueroa et al., 2016; Pyron et al., 2013; Zaher et al., 2019) was not retrieved because of the currently unambiguous phylogenetic position of *Calliophis bivirgata* (Boie, 1827) nested outside the otherwise strongly supported *Calliophis* clade (Zaher et al., 2019). Rage and Holman (1984) considered *'M.' gallicus* a North American newcomer during the Early/Middle Miocene, but an Asiatic origin of this species is equally probable.

Elapidae indet., type 1

Material. – 22 trunk vertebrae (20 + 2 articulated) vertebrae (SNSB-BSPG 1937 II 24286–24306).

Trunk vertebrae (Fig. 12): The preserved vertebrae are very small with the centrum length of the largest middle trunk vertebra 3.02 mm (SNSB-BSPG 1937 II 24305). In lateral view, the neural spine of the best-preserved vertebra (SNSB-BSPG 1937 II 24306; Fig. 12) is markedly low, approximately six times longer than high, with roughly vertical its cranial and caudal margins. The small and

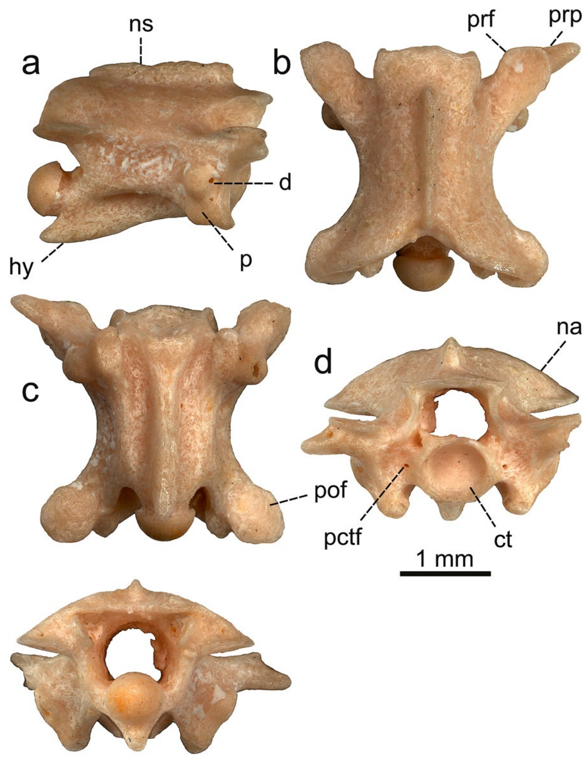

Fig. 12 Elapidae indet., type 1 from Wintershof-West. **a**–**e**, middle trunk vertebra (SNSB-BSPG 1937 II 24306) in right lateral (**a**), dorsal (**b**), ventral (**c**), and cranial (**d**) views. ct, cotyle; d, diapophysis; hy, hypapophysis; na, neural arch; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process

hardly visible lateral foramen is situated below the well-developed interzygapophyseal ridge and posterodorsally to the diapophysis. The parapophysis is slightly longer than the diapophysis, with rather short parapophyseal process. The strongly developed subcentral ridge is arched dorsally and diminishes before reaching condylar neck. The hypapophysis is short, with pointed distal tip at the level of the cranial condylar base. In dorsal view, the zygosphene has short and distally pointed lateral lobes, the medial lobe is wide. The prezygapophyseal articular facets are wide and suboval, with the only preserved right prezygapophyseal process directed anterolaterally. The distal termination of the process is slightly pointed. The diapophysis is directed posterolaterally. Epizygapophyseal ridges and spines are absent. The caudal notch is rather deep. In ventral view, the hypapophysis is wide and anteriorly it is separated from parapophyses by the deep furrows. Small subcentral foramina are situated at the base of the hypapophysis and faced laterally rather than ventrally. The subcentral grooves are wide and deep. The more complete left postzygapophyseal articular facet is subsquare. In cranial view, the neural canal is subsquare with distinct lateral sinuses. The zygosphenal roof is moderately arched. Prezygapophyses are almost horizontal. Paracotylar foramina are located on each side of the rounded cotyle. Subcotylar tubercles are absent; however, tiny tubercles are visible in several other specimens. In caudal view, the neural arch is slightly depressed.

Remarks: The vertebrae are typical for their small size (usually < 3 mm). They differ from *'Micrurus' gallicus* by smaller dimensions and the more prominent hypapophysis which is wide in ventral view unlike thin hypapophysis of *'M.' gallicus* (see above; Rage & Holman, 1984; Szyndlar & Schleich, 1993). The morphology of trunk vertebrae is basically identical with that of indeterminate Elapidae from the Early Miocene (MN 3a) of Merkur-North (Ahníkov I), Czechia (Ivanov, 2002a) and early Middle Miocene (MN 5; Ivanov, 2022) of Vieux-Collonges, France (Ivanov, 2000), and to some degree also to the small vertebrae of the elapid from Spilia 4, Greece (Georgalis et al., 2024: Fig. 59).

Colubroidea Oppel, 1811a, 1811b (sensu Zaher et al., 2009)
Natricidae Bonaparte, 1838a
Natrix Laurenti, 1768
Natrix sansaniensis (Lartet, 1851)
Natrix* cf. *sansaniensis

Material. – 30 trunk vertebrae (SNSB-BSPG 1937 II 24307–24336).

Trunk vertebrae (Fig. 13): In lateral view, the neural spine of the most anteriorly positioned vertebrae is as high as long. The anterodorsal margin of the only completely preserved neural spine is inclined anteriorly but does not overhang its base whereas the caudal margin of the neural spine clearly overhangs posteriorly. In more posterior middle and posterior trunk vertebrae, the neural spine, although still rather high, is slightly lower. In the most complete vertebra, the oval zygosphenal facet is markedly narrow. The small but well-visible lateral foramen is situated close below the sharp interzygapophyseal ridge. The damaged paradiapophyses display roughly orbicular diapophysis situated above the base of the eroded parapophysis. Parapophyseal processes are broken-off but rarely preserved parapophyseal processes of other specimens indicate they were very short. The distinct but blunt subcentral ridge is clearly arched dorsally. The hypapophysis is variable in morphology through the vertebral column. In the more anteriorly positioned vertebrae (Fig. 13a), the anterior keel of the hypapophysis is markedly deep, although its distal termination is not preserved. The only large middle trunk vertebra with preserved hypapophysis displays its non-angular anteroventral curvature and

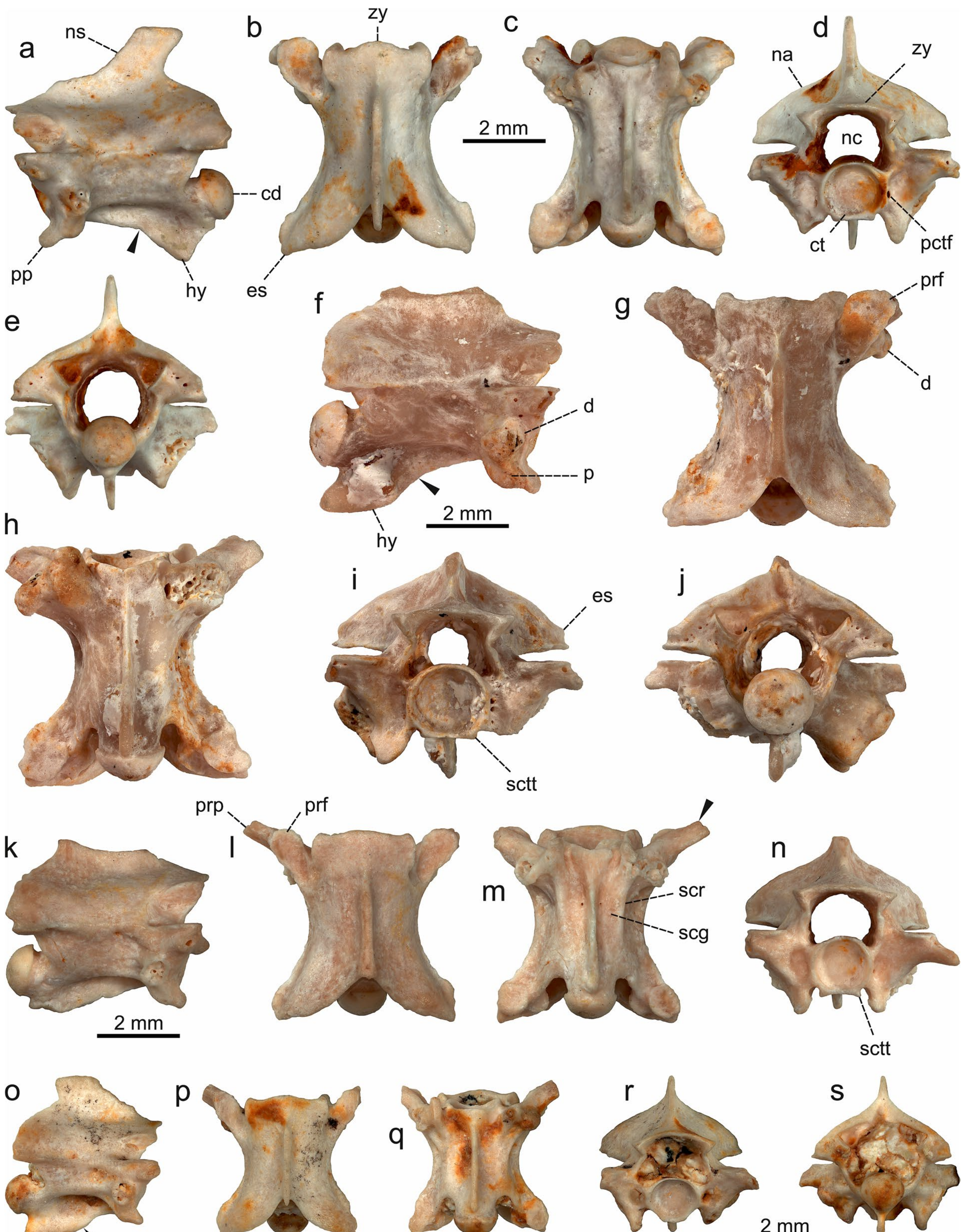

Fig. 13 (See legend on next page.)

(See figure on previous page.)

Fig. 13 *Natrix* cf. *sansaniensis* from Wintershof-West. **a**–**e**, trunk vertebra (SNSB-BSPG 1937 II 24333) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**j**, middle trunk vertebra (SNSB-BSPG 1937 II 24334) in right lateral (**f**), dorsal (**g**), ventral (**h**), cranial (**i**), and caudal (**j**) views; **k**–**n**, posterior trunk vertebra (SNSB-BSPG 1937 II 24335) in right lateral (**k**), dorsal (**l**), ventral (**m**), and cranial (**n**) views; **o**–**s**, posterior trunk vertebra (SNSB-BSPG 1937 II 24336) in right lateral (**o**), dorsal (**p**), ventral (**q**), cranial (**r**), and caudal (**s**) views. cd, condyle; ct, cotyle; d, diapophysis; es, epizygapophyseal spine; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pp, parapophyseal process; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; sctt, subcotylar tubercle; zy, zygosphene. Arrows indicate important features

slightly pointed distal tip (Fig. 13f). In the posterior trunk vertebrae, the straight hypapophysis is lower towards its distal termination reaching at most the base of the short condylar neck (Fig. 13o). In dorsal view, the vertebrae are slightly elongated. The zygosphene is wide, with acute lateral lobes and widely triangular medial lobe. The medial lobe can be notched or even reduced. The ovoid prezygapophyseal articular facets are narrow, with long axis directed anterolaterally. Prezygapophyseal processes, usually broken-off close to their base, were almost as long as prezygapophyseal facets in one specimen (SNSB-BSPG 1937 II 24330), but they were probably much shorter in most other vertebrae. The epizygapophyseal spines are either short or underdeveloped but their erosion during fossilization is also possible. The caudal notch is deep. In ventral view, the centrum is narrow, with subcentral ridges extending parallel to the thin hypapophyseal base. The anterior keel of the hypapophysis, almost reaching the cotylar base, is weakly triangular. The small subcentral foramina are situated in relatively wide subcentral grooves. The partially eroded postzygapophyseal articular facets are irregularly shaped. In cranial view, the neural canal is roughly rounded with short lateral sinuses. The thin zygosphenal lip is convex. Paracotylar foramina occur in wide depressions on either side of the moderately dorsoventrally depressed cotyle. In caudal view, the neural arch is vaulted, with VR ranging from 0.38 to 0.48. The zygantral area is markedly wide, with zygantral articular facets forming an acute angle with postzygapophyseal facets. The condyle is moderately depressed dorsoventrally.

Remarks: The overall small dimensions of this colubroid snake (with the CL usually < 5 mm; see Appendix 1) possessing high neural spine, prominent hypapophysis, vaulted neural arch as well as moderately long prezygapophyseal processes indicate attribution to a small representative of Natricidae. The very high neural spine inclined both anteriorly and posteriorly, prominent anterior keel of the hypapophysis, markedly short parapophyseal processes of the parapophysis, blunt subcentral ridges, and small dimensions enable identification of vertebrae as belonging to *Natrix sansaniensis* (Augé & Rage, 2000; Ivanov, 2002a; Rage, 1981). Prezygapophyseal articular facets are elongated unlike the lectotype from Sansan, France (MNHN, No. SA 9873; Rage, 1981). However, their partial erosion is apparent. The hypapophysis is incomplete in the middle trunk vertebrae except of one large middle trunk vertebra. However, the species identification of this probably oversized specimen is uncertain. Therefore, we avoid of indisputable species level attribution.

Natrix sansaniensis closely resembles extinct *Natrix merkurensis* Ivanov, 2002a by the height and shape of the neural spine but differs from the latter species by the pointed instead of obtuse distal tip of the hypapophysis, shorter parapophyseal processes and larger prezygapophyseal articular facets (see Table 1; Ivanov, 2002a; Szyndlar, 2005; Rage & Bailon, 2005). Among the extant representatives, *N. sansaniensis* is reminiscent of *Natrix tessellata* (Laurenti, 1768) by the pointed distal termination of the hypapophysis (Ivanov, 2002a), but its anteroventral keel is rather deep and non-angled in extinct species unlike distinctly sigmoid hypapophysis with less deep anteroventral keel observed in *N. tessellata* (Augé & Rage, 2000; MI, pers. observ.).

***Wintershofia* gen. nov.**

LSID: urn:lsid:zoobank.org:act:E59200F4-2F88-4D35-B7CB-2E4B54EBB206.

Type species. *Wintershofia robusta* gen. et sp. nov. (by monotypy)

Etymology. The genus name derived from the name of the German type locality – Wintershof (Wintershof-West).

Gender. Gender of the genus *Wintershofia* gen. nov. is feminine.

Diagnosis. As for type and only known species.

***Wintershofia robusta* gen. et sp. nov.**

LSID: urn:lsid:zoobank.org:act:3D55A9C8-C6A8-4F45-A0E4-974B92BB373B

Descriptive diagnosis. The middle trunk vertebrae of *Wintershofia robusta* gen. et sp. nov. share the following features clearly referring this snake to medium-sized Natricidae: (1) the vertebrae are robust with elongated centrum and moderately depressed neural arch; (2) the well-developed neural spine is inclined both anteriorly and posteriorly; (3) prezygapophyseal processes are well-developed; (4) parapophyseal processes are long; (5) the deep hypapophysis, developed throughout the whole precaudal section, is long, with distinct anterior keel extending to the cotylar rim. *Wintershofia robusta* gen. et sp. nov. differs from all known representatives of Natricidae by the following unique combination of features: (1) the neural spine is low, about three times longer than high, with its cranial margin noticeably shifted anteriorly; (2) prezygapophyses with large sub-rhomboid prezygapophyseal articular facets and massively built short and distally slightly pointed prezygapophyseal processes; (3) the large rhomboid zygosphenal facets are only slightly inclined laterally from the parasagittal plane of vertebrae; (4) the slender parapophyseal processes are very long; (5) the hypapophysis with pointed distal tip extending far beyond the caudal termination of the condyle; (6) the prominent and sharp subcentral ridges are long and markedly straight in lateral view; (7) the circular cotylar rim is of small diameter.

Etymology. Species name derived from the Latin term "*robustus*" referring to the robust vertebrae with strongly built prezygapophyseal processes.

Type locality. Wintershof-West, Bavaria, southern Germany.

Distribution and age. Known only from the type locality, Wintershof-West, Bavaria, Southern Germany. The age corresponds to the Early Miocene, Burdigalian, lower part of the MN 3 Zone (MN 3a; Aguilar et al., 2003; Bonilla-Salomón et al., 2022).

Holotype. SNSB-BSPG 1937 II 24388 (a middle trunk vertebra, Fig. 14).

Paratypes. SNSB-BSPG 1937 II 24382 (an anterior/middle trunk vertebra, Fig. 15a–e); SNSB-BSPG 1937 II 24384 (a middle trunk vertebra, Fig. 15f–j); SNSB-BSPG 1937 II 24378 (a middle trunk vertebra, Fig. 15l–p); SNSB-BSPG 1937 II 24381 (posterior trunk vertebra, Fig. 16a–e); SNSB-BSPG 1937 II 24390 (a cloacal vertebra, Fig. 16f–j); SNSB-BSPG 1937 II 24403 (a caudal vertebra, Fig. 16k–o).

Referred material.– 50 trunk vertebrae (SNSB-BSPG 1937 II 24337–24364; SNSB-BSPG 1937 II 24365–24372; two articulated vertebrae SNSB-BSPG 1937 II 24373; two articulated vertebrae SNSB-BSPG 1937 II 24374; two articulated vertebrae SNSB-BSPG 1937 II 24375; SNSB-BSPG 1937 II 24376–24377; SNSB-BSPG 1937 II 24379–24380; SNSB-BSPG 1937 II 24383; SNSB-BSPG 1937 II 24385–24387), one cloacal vertebra (SNSB-BSPG 1937 II 24389), 9 caudal vertebrae (SNSB-BSPG 1937 II 24391–24399), 8 articulated (2 + 3 + 3) caudal vertebrae (SNSB-BSPG 1937 II 24400–24402).

Description of the holotype (Fig. 14): The middle trunk vertebra of the medium sized specimen (CL = 4.69 mm, NAW = 3.18 mm; CL/NAW = 1.47; for complete measurements see Appendix 2) has broken-off right parapophyseal process, eroded left diapophysis, unpreserved distal tip of the hypapophysis and posterodorsal extension of the neural spine. In lateral view (Fig. 14a, b, g), the neural spine rises in the middle of the zygosphenal facet length and is twice longer than high. Its anterodorsal protrusion slightly overhangs the anterior base of the neural spine, while damaged caudal margin was most probably clearly inclined posteriorly. The caudal portion of the neural arch is upswept dorsally. The large lateral foramen is situated close to the anterodorsal margin of a wide and rather deep depression delimited dorsally by the short interzygapophyseal ridge and ventrally by the prominent subcentral ridge. The roughly suborbicular right diapophysis, situated above the same sized articular facet of the parapophysis, is slightly extended posteriorly. The prominent left parapophyseal process, directed cranially rather than cranioventrally, is long and slender, with rounded distal termination in lateral and bevelled in ventral views. The subcentral ridge is straight extending as far as the base of the short condylar neck. The condylar base is well separated from the neck. In dorsal view (Fig. 14c, h), the almost straight zygosphenal lip consists of the wide, indistinct median lobe and two short lateral lobes pointed cranially. The large prezygapophyseal articular facets are widely sub-rhombic in outline. The massively built prezygapophyseal processes are about three times shorter than the long axis of prezygapophyseal articular facets and directed anterolaterally, with slightly pointed their distal terminations. There is no dorsal thickening of the neural spine, although an indistinct bifurcation is developed on its anterodorsal margin. The caudal notch is deep and narrow. The only preserved right epizygapophyseal spine is rather short, but epizygapophyseal ridges occur on either side of the postzygapophysis. In ventral view (Fig. 14d, i), the triangular centrum is delimited by prominent straight subcentral ridges. Subcentral grooves are wide and shallow, extending towards the cotyle. The small subcentral foramina are situated in the half the subcentral grooves length and close to the hypapophyseal base. The hypapophysis is thin, with a thickened posteroventral portion. Although the distal termination of the hypapophysis did not preserve, it undoubtedly projected behind the posterior border of the condyle. The almost completely preserved right postzygapophyseal articular facet is subsquare in outline. In cranial view (Fig. 14e, j), the neural canal is rounded, with shallow and rather wide lateral sinuses. The zygosphenal lip is thin and straight, with lateral lobes slightly protruding upwards. The large

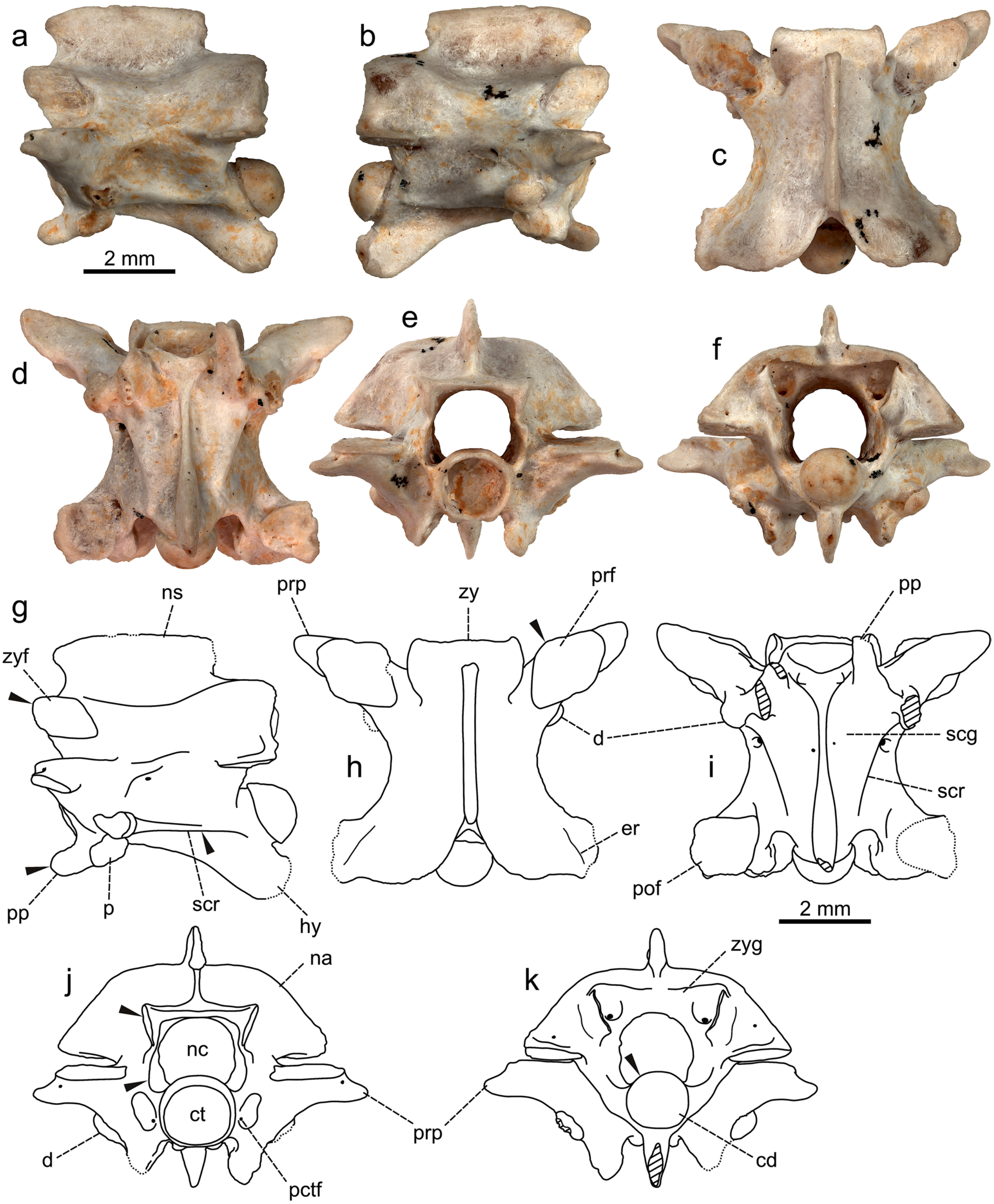

Fig. 14 *Wintershofia robusta* gen. et sp. nov. from Wintershof-West. **a**–**f**, middle trunk vertebra, holotype (SNSB-BSPG 1937 II 24388) in left lateral (**a**), right lateral (**b**), dorsal (**c**), ventral (**d**), cranial (**e**), and caudal (**f**) views; **g**–**k**, the same holotype vertebra (SNSB-BSPG 1937 II 24388), important anatomical structures are highlighted. cd, condyle; ct, cotyle; d, diapophysis; er, epizygapophyseal ridge; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; pp, parapophyseal process; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene; zyf, zygosphenal facet; zyg, zygantrum. Arrows indicate important features

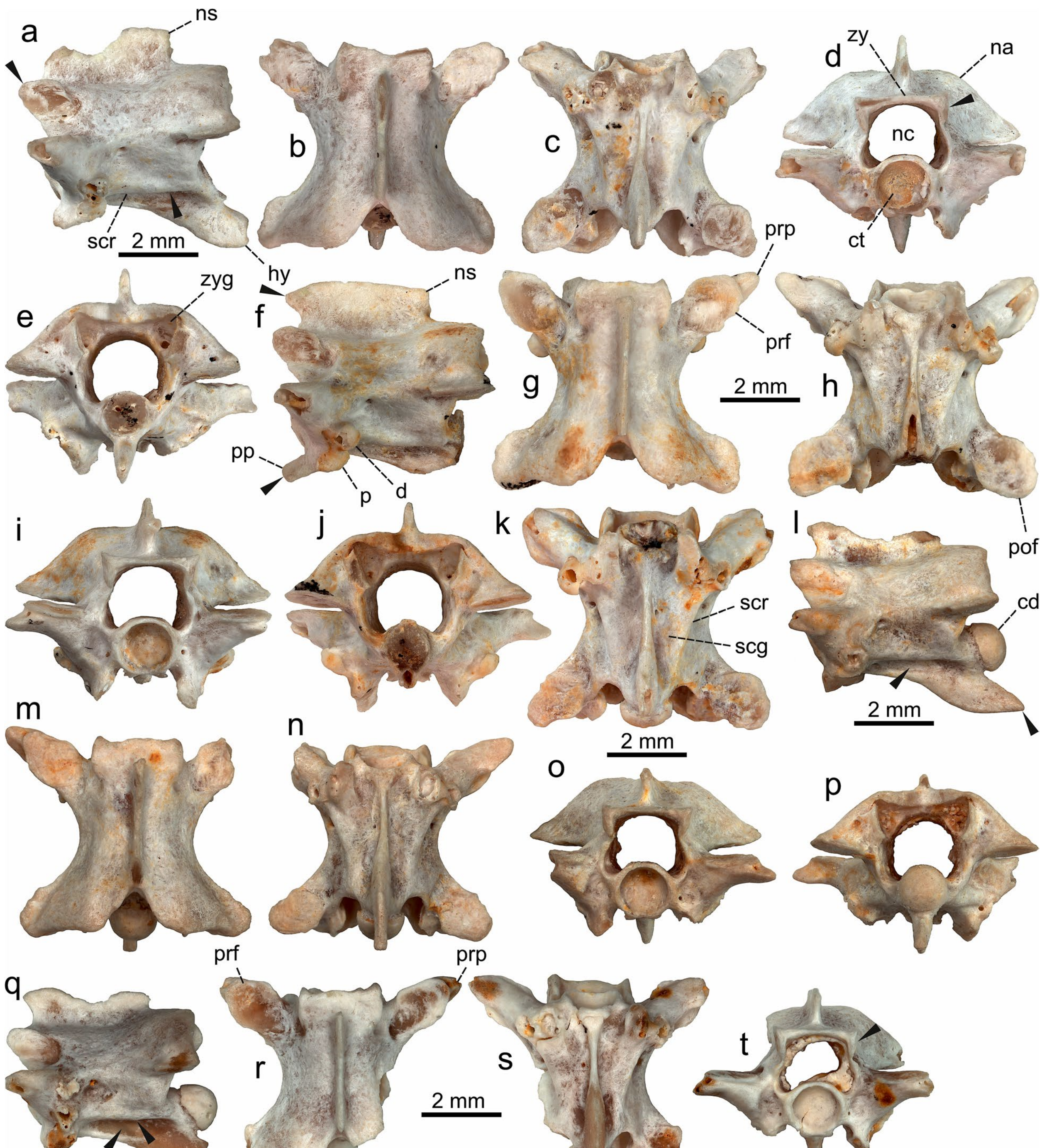

Fig. 15 *Wintershofia robusta* gen. et sp. nov. from Wintershof-West. **a**–**e**, paratype anterior/middle trunk vertebra (SNSB-BSPG 1937 II 24382) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**j**, paratype middle trunk vertebra (SNSB-BSPG 1937 II 24384) in left lateral (**f**), dorsal (**g**), ventral (**h**), cranial (**i**), and caudal (**j**) views; **k**, middle trunk vertebra (SNSB-BSPG 1937 II 24385) in ventral view; **l**–**p**, paratype middle trunk vertebra (SNSB-BSPG 1937 II 24378) in left lateral (**l**), dorsal (**m**), ventral (**n**), cranial (**o**), and caudal (**p**) views; **q**–**t**, posterior trunk vertebra (SNSB-BSPG 1937 II 24383) in left lateral (**q**), dorsal (**r**), ventral (**s**), and cranial (**t**) views. cd, condyle; ct, cotyle; d, diapophysis; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pp, parapophyseal process; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene; zyg, zygantrum. Arrows indicate important features

zygosphenal facets, sub-rhomboid in lateral view, are only slightly (20°) inclined laterally from the medial plane. Prezygapophyses are horizontal, with prezygapophyseal facets situated at the level of the neural canal base. Distinct foramina occur on the bases of prezygapophyseal processes. The cotyle of small diameter (Appendix 2) is circular in outline, with short subcotylar tubercles situated at the base of the cotylar rim. The small paracotylar foramina are situated within depressions on either side of the cotyle. In caudal view (Fig. 14f, k), the posterodorsal lamina of the vaulted neural arch (VR = 0.52), being horizontal above the zygantrum, slopes markedly towards the lateral margins of both postzygapophyses. The small parazygantral foramina occur above the postzygapophyseal facets. The condyle of small diameter is orbicular.

Description of paratypes and referred material

Trunk vertebrae (Figs. 15 and 16a–e): All trunk vertebrae are fragmentary, usually with broken-off hypapophysis and strongly damaged neural spine. The morphology of vertebrae closely resembles that of the holotype. In lateral view, the neural spine is generally low being two times longer than high in more anteriorly positioned vertebrae and three to four times longer than high in vertebrae from the posterior precloacal section of the vertebral column (Figs. 15a, f, l, q and 16a). The anterodorsal protrusion of the thin neural spine is inclined anteriorly but sometimes strongly overhangs the neural spine base (Fig. 15f). Although the posterior portion of the neural spine is broken-off in all specimens, it was likely only slightly inclined posteriorly. Lateral foramina occur in wide depression delimited dorsally by distinct interzygapophyseal ridges and prominent subcentral ridges. The articular facets of paradiapophyses are relatively small but parapophyseal processes are long and slender with rectangular or bevelled distal termination. Prominent subcentral ridges are straight throughout the whole precloacal section. The occasionally preserved distal tip of the hypapophysis is caudally directed, it is acute and usually exceeds caudally beyond the posterior border of the condyle (Fig. 15l). In ventral view, the low anterior edge of the hypapophysis is blade-like, and the markedly narrow hypapophyseal base extends along its entire craniocaudal length, so that a wide groove is visible laterally above the thickened posteroventral portion of the hypapophysis.. In dorsal view, the cranial margin of the zygosphene is straight, with short and acute lateral lobes; however, moderately developed wide medial lobe can be present in some middle and posterior trunk vertebrae (Fig. 15m, r). Prezygapophyseal articular facets are usually sub-rhombic in outline, but they can be nearly suboval in posteriorly positioned vertebrae. The short prezygapophyseal processes reaching about one-third of the prezygapophyseal facets long axis length are always strongly built, with moderately pointed their distal termination (Fig. 15g, m, r). The small sized diapophysis is directed posterolaterally. Although epizygapophyseal ridges are usually well-developed, epizygapophyseal spines are largely absent. In ventral view, the elongated centrum of vertebra is widely triangular delimited by straight and sharp subcentral ridges. Subcentral grooves are wide and shallow in anteriorly positioned vertebrae, whereas in posterior trunk vertebrae these wide grooves become deeper. In the posteriormost trunk vertebrae, the strongly developed subcentral ridges contribute to the lateral border of prominent subcentral grooves, which are equally wide along their entire length. Subcentral foramina are usually situated within subcentral grooves and far from the hypapophyseal base. The anterior keel of the hypapophysis is narrowly triangular close to the base of the cotylar rim where short subcotylar tubercles protrude in lateral direction. The dorsally facing lateral foramina are rather large. Postzygapophyseal articular facets are large and subsquare in outline. In cranial view, the thin zygosphenal lip is straight and zygosphenal articular facets usually form an angle of only 11–15° with the medial plane. The cotyle diameter is clearly smaller than the diameter of the neural canal. In caudal view, the vaulted neural arch is slightly flattened around its posterodorsal portion, with VR ranging from 0.40 to 0.52. Zygantral facets form an angle around 66–68° with postzygapophyseal articular facets. Parazygantral foramina are usually rather small. The rounded condyle is of a small diameter.

Cloacal vertebrae (Fig. 16f–j): All vertebrae are fragmentary, with the neural spine, hypapophysis and lymphapophyses broken-off. In lateral view, the neural spine rises at half the length of the widely oval zygosphenal facet. The preserved base of the upper ramus of lymphapophysis is horizontal. The relatively narrow base of the ventral ramus of lymphapophysis continues in caudal direction in the form of prominent subcentral ridge. The preserved distal portion of the ventral ramus is expanded and slopes in posteroventral direction. The hypapophysis is deep but its posteroventral margin is eroded. In dorsal view, the zygosphene is straight, with distinct lateral lobes. Prezygapophyseal articular facets are subtriangular in outline, with long axis directed anterolaterally. Prezygapophyseal processes are short. The base of the dorsal ramus of lymphapophysis is directed laterally. In ventral view, the preserved basal portion of the hypapophysis is thin extending from the close vicinity of the cotylar rim caudally to the base of the small condyle. In cranial view, the zygosphene is moderately dorsally arched, with zygosphenal facets

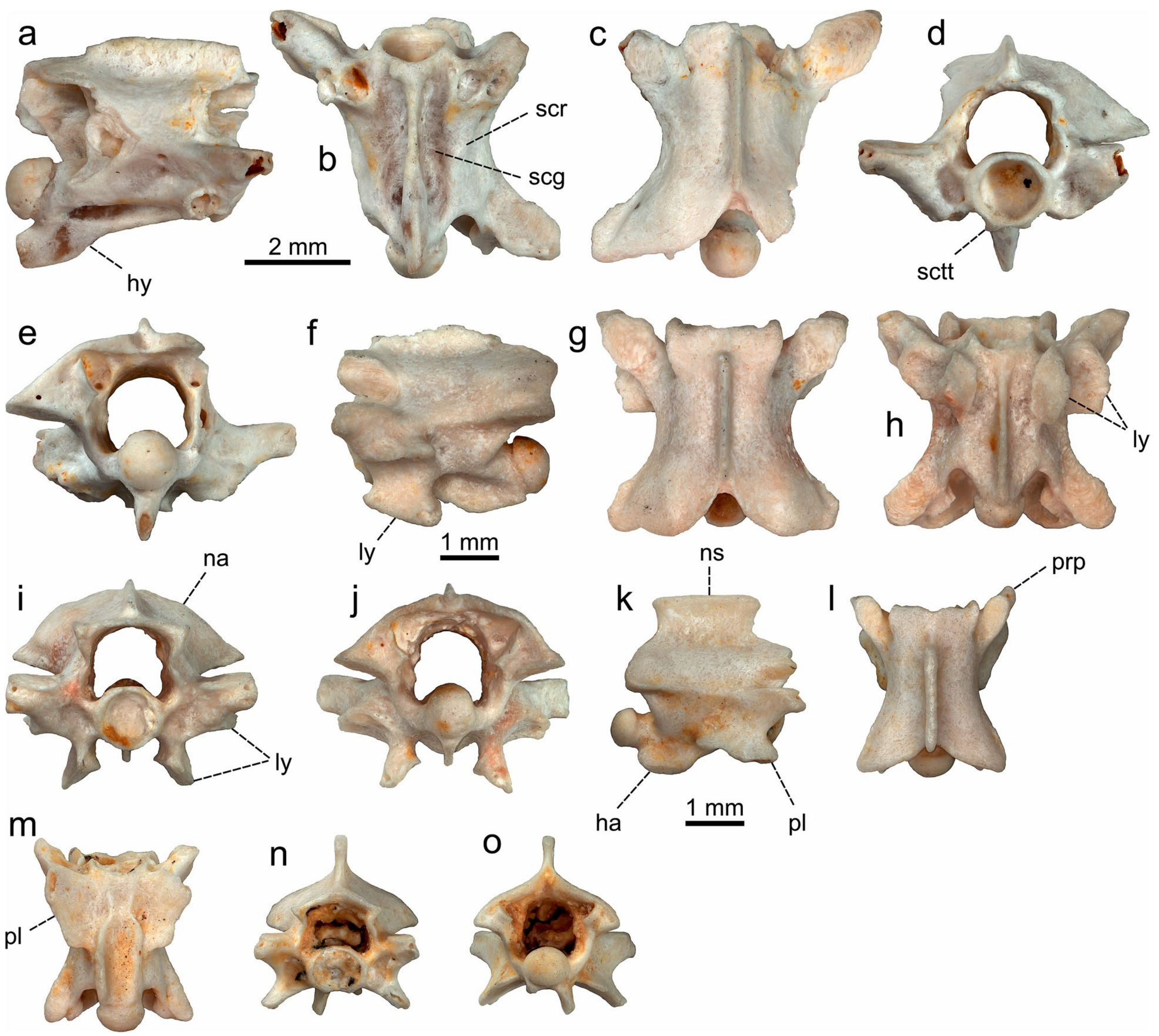

Fig. 16 *Wintershofia robusta* gen. et sp. nov. from Wintershof-West. **a**–**e**, paratype posterior trunk vertebra (SNSB-BSPG 1937 II 24381) in right lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**j**, paratype cloacal vertebra (SNSB-BSPG 1937 II 24390) in left lateral (**f**) and dorsal (**g**), ventral (**h**), cranial (**i**), and caudal (**j**) views; **k**–**o**, paratype caudal vertebra (SNSB-BSPG 1937 II 24403) in right lateral (**k**), dorsal (**l**), ventral (**m**), cranial (**n**), and caudal (**o**) views. ha, haemapophysis; hy, hypapophysis; ly, lymphapophysis; na, neural arch; ns, neural spine; pl, pleurapophysis; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; sctt, subcotylar tubercle. Arrows indicate important features

slightly inclined laterally from the parasagittal plane of the vertebra. The base of the dorsal ramus of the lymphapophysis is roughly perpendicular to its ventral ramus. There is a distinct craniocaudally elongated crest developed on the medial side of the ventral ramus of both lymphapophyses. The cotylar rim is small in diameter compared to rounded neural canal, which has well-developed wide lateral sinuses. Subcotylar tubercles are absent.

Caudal vertebrae (Fig. 16k–o): In lateral view, the most complete vertebra which comes from the mid-caudal section of the vertebral column, is rather short. The neural spine is twice longer than high, with its cranial margin inclined anteriorly and caudal one slightly posteriorly. The distal tip of the wide pleurapophysis is broken-off but it was directed anteroventrally in lateral and anterolaterally in ventral views. The small condyle is developed on the relatively long neck. In dorsal view, the only preserved right lateral lobe of the zygosphene is rather long. Prezygapophyseal articular facets are narrowly oval, with long axis directed anteriorly rather than anterolaterally. The right prezygapophyseal process is short and slightly pointed. In ventral view, haemapophyseal bases are long extending from the mid-length of the pleurapophyseal base caudally to the base of the condylar neck. The oval postzygapophyseal articular facets are narrow and elongated posteriorly. In cranial view, the zygosphene is arched dorsally, with small zygosphenal facets inclined about 45° from the parasagittal plane of vertebra. Pleurapophyseal bases are directed lateroventrally and the right incomplete haemapophysis is directed ventrally. The cotylar rim of small diameter is moderately depressed dorsoventrally.

Comparison and discussion

The Natricidae clade is highly diversified, currently comprising 37 extant genera and 268 species (Sindaco et al. 2013; Deepak et al. 2021). However, the fossil record of this group is restricted only to three extinct genera *Micronatrix* Parmley & Hunter, 2010, *Neonatrix* Holman, 1973, and *Palaeonatrix* Szyndlar in Młynarski et al., 1982 (Holman, 1973, 2000; Parmley & Holman, 1995; Parmley & Hunter, 2010; Szyndlar, 1987) and 11 extant genera *Hebius* Thompson, 1913, *Liodytes* Cope, 1885, *Natrix* Laurenti, 1768, *Nerodia* Baird & Girard, 1853, *Regina* Baird & Girard, 1853, *Rhabdophis* Fitzinger, 1843, *Seminatrix* Cope, 1875, *Storeria* Baird & Girard, 1853, *Thamnophis* Fitzinger, 1843, *Tropidoclonion* Cope, 1860, and *Virginia* Baird & Girard, 1853. *Wintershofia robusta* gen. et sp. nov., unlike *Palaeonatrix lehmani* (Rage & Roček, 1983) described from the Early Miocene (MN 4) of Dolnice, Czechia (Rage & Roček, 1983; Szyndlar, 1987), Petersbuch 2, Germany (Szyndlar & Schleich, 1993) and Béon 1, France (Rage & Bailon, 2005) and *Palaeonatrix silesiaca* Szyndlar in Młynarski et al., 1982 reported from the Middle Miocene (MN 6, see Harzhauser & Neubauer, 2018; Ivanov, 2022) of Opole, Poland (Szyndlar in Młynarski et al., 1982), has less elongated vertebrae craniocaudally, the hypapophysis extending far beyond the caudal condylar tip, much longer parapophyseal processes and distinctly smaller cotyle diameter. *Wintershofia robusta* gen. et sp. nov. differs from North American *Micronatrix juliescottae* Parmley & Hunter, 2010 reported from the Late Miocene (late Clarendonian, 10.5–9.5 Ma) of Pratt Slide, Nebraska (Parmley & Hunter, 2010) and *Neonatrix* (*Neonatrix elongata*, *N. magna*, *N. infera*; Holman, 1973, 1982, 1996, 2000) reported form the Early Miocene (Hemingfordian) of Black Bear Quarry II, South Dakota up to Late Miocene (middle Hemphillian) of Lemoyne Quarry, Nebraska (Holman, 1973, 2000; Parmley & Holman, 1995) by the larger dimensions, prominent deep hypapophysis, very long parapophyseal processes and distinctly smaller diameter of the cotyle related to the neural canal.

Middle trunk vertebrae of *Wintershofia robusta* gen. et sp. nov. differ from those of extant small-sized New World natricid *Clonophis kirtlandii* (Kennikott, 1856), *Seminatrix pygaea* (Cope, 1871), *Storeria dekayi* (Holbrook, 1839), *Storeria occipitomaculata* (Storer, 1839), *Tropidoclonion lineatum* (Hallowell, 1856), *Virginia striatula* (Linnaeus, 1766), and *Virginia valeriae* Baird & Girard, 1853 by the larger size, higher neural spine and distal tip of the hypapophysis protruding more posteriorly beyond the condyle (see Auffenberg, 1963; Malnate, 1972; Holman, 2000; Parmley et al., 2020). *Wintershofia robusta* gen. et sp. nov. differs from the extant New World mid- to large-sized *Liodytes alleni* (Garman, 1874), *Liodytes rigida* (Say, 1825), *Nerodia clarkii* (Baird & Girard, 1853), *Nerodia cyclopion* (Duméril, Bibron & Duméril, 1854), *Nerodia erythrogaster* (Forster, 1771), *Nerodia fasciata* (Linnaeus, 1766), *Nerodia floridana* (Goff, 1936), *Nerodia rhombifer* (Hallowell, 1852), *Nerodia sipedon* (Linnaeus, 1758), *Nerodia taxispilota* (Holbrook, 1838), *Regina grahamii* Baird & Girard, 1853, and *Regina septemvittata* Say, 1823 by the lower neural spine, clearly longer parapophyseal processes directed anteriorly, and smaller diameter of the rounded cotyle (Auffenberg, 1963; Holman, 1968, 2000; Mead & Steadman, 2017; Meylan, 1982). The extinct *Nerodia hibbardi* Holman, 1968 reported from the Pliocene (Blancan III, 4.1−3.0 Ma; Repenning, 1988; Rook et al., 2019) of Idaho (Holman, 1968), *Nerodia hillmani* (Wilson, 1968) reported from the Late Miocene (late Clarendonian; Tedford et al., 2004) of Kansas (Holman, 1975, 2000; Wilson, 1968) and Nebraska (Parmley & Hunter, 2010), and *Regina intermedia* Meylan, 1982 reported from the Early Pleistocene of Florida (Meylan, 1982), differ from *W. robusta* gen. et sp. nov. by the relatively higher neural spine, less extended hypapophysis posteriorly, and shorter parapophyseal processes. Several species of the diversified genus *Thamnophis*, e.g., *Thamnophis elegans* (Baird & Girard, 1853), *Thamnophis proximus* (Say in James, 1823), *Thamnophis radix* (Baird & Girard, 1853), *Thamnophis rufipunctatus* (Cope, 1875), *Thamnophis saurita* (Linnaeus, 1766), *Thamnophis scaliger* (Jan, 1863) and *Thamnophis sirtalis* (Linnaeus, 1758), are reminiscent of *Wintershofia robusta* gen. et sp. nov. by the relatively strongly built and distally pointed prezygapophyseal processes and long hypapophysis (Bullock & Tanner, 1966; Holman, 2000; LaDuke, 1991; MI, pers. observ.). However, the cranio-caudally elongated neural spine of *Wintershofia* is lower, parapophyseal processes are much slender and longer and the cotyle diameter is smaller compared to *Thamnophis*.

Wintershofia robusta gen. et sp. nov. differs from the extant Indo-Malayan *Fowlea piscator* (Schneider, 1799), *Xenochrophis cerasogaster* (Cantor, 1839) and *Atretium* *schistosum* (Daudin, 1803a) by the more massively built prezygapophyseal processes, longer parapophyseal processes and relatively smaller cotyle diameter (Ikeda et al., 2019; Malnate & Minton, 1965; MI, pers. observ.). The new natricid from Wintershof-West differs from the small-sized *Hebius vibakari* (Boie, 1826) by the larger dimensions, cranial margin of the neural spine inclined anteriorly, strongly built prezygapophyseal processes, longer parapophyseal processes and much longer hypapophysis (Ikeda, 2007). It further differs from *Hebius pryeri* (Boulenger, 1887) by having more robustly developed prezygapophyseal processes, longer parapophyseal processes, and relatively smaller cotyle dimensions (Nakamura et al., 2013). *Wintershofia robusta* gen. et sp. nov. differs from extant *Blythia reticulata* (Blyth, 1854) by the clearly elongated middle trunk vertebrae, the higher neural spine whose cranial margin is shifted anteriorly, the presence of prominent subcentral ridges much longer parapophyseal processes. It differs from extant *Aspidura brachyorrhos* (Boie, 1827) by the more anteriorly shifted cranial margin of the neural spine, the presence of prominent sharp and straight subcentral ridges and by the long parapophyseal processes. The extant mid-sized Indo-Malayan *Rhabdophis flaviceps* (Duméril, Bibron & Duméril, 1854), *Rhabdophis subminiatus* (Schlegel, 1837), *Rhabdophis helleri* (Schmidt, 1925), and *Rhabdophis tigrinus* (Boie, 1826), whose fossil occurrences of *R.* cf. *helleri* and *R.* cf. *tigrinus* have recently been reported from the Early Pliocene of Queshan, China and the Early Pleistocene of Shanyangzhai Cave, Hebei (Chen et al., 2021; Shi et al., 2023), differ from *Wintershofia robusta* gen. et sp. nov. by the more elongated and narrower centrum of vertebra in ventral view, the longer prezygapophyseal processes, the shorter parapophyseal processes and cotyle diameter at least as large as the diameter of the neural canal (Chen, 2020; Chen et al., 2021; MI, pers. observ.). *Wintershofia robusta* gen. et sp. nov. differs from *Pseudagkistrodon rudis* (Boulenger, 1906) and *Trimerodytes annularis* (Hallowell, 1856) by the lower neural spine, longer parapophyseal processes and cotyle of small diameter (Chen, 2020). *Wintershofia robusta* gen. et sp. nov. differs from *Amphiesmoides ornaticeps* (Werner, 1924) in having less elongate middle trunk vertebrae, massively built prezygapophyseal processes, the distinct hypapophysis rather than the prominent haemal keel, and long parapophyseal processes instead of markedly short or underdeveloped ones.

As concerns African natricids, *Wintershofia robusta* gen. et sp. nov. differs from the small-sized *Natriciteres olivacea* (Peters, 1854) by the less elongate vertebrae, more anteriorly shifted cranial margin of the neural spine, much wider zygosphenal facets, and much longer prezygapophyseal processes (Zaher et al., 2019: s2 appendix, fig. F). *Hydraethiops melanogaster* Günther, 1872 differs from *Wintershofia robusta* gen. et sp. nov. by much higher neural spine positioned more posteriorly compared to new extinct genus, more ventrally inclined hypapophysis, distinctly shorter and anteroventrally inclined parapophyseal processes. However, we could not compare a new fossil natricid with the genus *Afronatrix*, whose only studied specimen (CAS:HERP:230205, ID 000063851; Appendix 3) contains only the skull and anteriormost trunk vertebrae.

The trunk vertebrae of *Wintershofia robusta* gen. et sp. nov. particularly resemble those of the extant Old-World genus *Natrix* recently widely distributed in Eurasia and extending to North/Northwest Africa (Sindaco et al., 2013). The genus *Natrix* is the only among Natricidae whose rich fossil record is known across the whole Europe, and it is by far the best documented colubroid in European Cenozoic (e.g., Augé & Rage, 2000; Georgalis et al., 2019b, 2024; Ivanov et al., 2020; Ivanov, 2002a; Rage & Szyndlar, 1986; Szyndlar & Schleich, 1993; Szyndlar, 1984, 1991b, 1991c, 2005; Venczel, 2000). The genus *Natrix* includes in total five extinct species known from the European Early Oligocene to the Late Pliocene: *'Natrix' mlynarskii* Rage, 1988, *Natrix merkurensis* Ivanov, 2002a, and *Natrix sansaniensis* (Lartet, 1851), *Natrix rudabanyaensis* Szyndlar, 2005, *Natrix longivertebrata* Szyndlar, 1984, and *'Natrix' natricoides* (Augé & Rage, 2000) (e.g., Augé & Rage, 2000; Ivanov, 2002a, 2022; Rage, 1988; Szyndlar, 1984, 1991b, 2005, 2012).

The holotype of *'Natrix' mlynarskii*, a middle trunk vertebra (MNHN.F.QU17181) from the "Quercy old collection", comes from an unknown locality of Phosphorites du Quercy and its true age is unknown. A fragmentary anterior trunk vertebra (UM-MGT 3508) from the early Oligocene of Mas-de-Got, Prosphorites du Quercy, France (Rage, 1988) attributed with some reservation to *N. mlynarskii* (Rage, 1988: 467), indicates that *'N.' mlynarskii* biostratigraphic age likely corresponds to around the MP 22 (?MP 22 sensu Szyndlar, 2012). Rage (1988) based his identification on the unusually significant elongation of this vertebra, which he considered positioned very anteriorly in the column, and linked with elongated middle trunk vertebrae of the *'N.' mlynarskii* holotype. However, the neural spine of the UM-MGT 3508 specimen rises very anteriorly above the zygosphenal facet in the lateral aspect which would be unusual for the anteriormost trunk vertebrae of *Natrix* positioned just posteriorly to the atlas-axis complex. In *Natrix*, the neural spine of the anteriormost trunk vertebrae rises close to posterior base or behind the zygosphene (MI, pers. observ.). Moreover, the preserved portion of the hypapophysis is directed clearly posteroventrally instead of more ventrally directed hypapophysis in anteriormost trunk vertebrae known in *Natrix*. The "*N.*" *mlynarskii* (sensu Rage, 1988) anterior trunk vertebra differs from the genus *Natrix* by the absence of distinct parapophyseal processes which are not preserved in the type specimen of *'N.' mlynarskii* (Rage, 1988: Fig. 2; see also Smith & Georgalis, 2022: appendix 4.S1). Although the presence/absence of subcotylar tubercles can be variable even in a single skeleton, the UM-MGT 3508 specimen differs from the holotype vertebra of *'N.' mlynarskii* by the absence of a triangular anterior keel and wide instead of narrow lateral sinuses of the neural canal. Following the above discussion, we consider the "*N.*" *mlynarskii* (sensu Rage, 1988) anterior trunk vertebra (UM-MGT 3508) of different taxonomic assignation. Small dimensions together with the vaulted neural arch, narrowly oval zygosphenal facets with long axis directed anteriorly rather than anterodorsally, the wide lateral sinuses of the rounded neural canal, and apparently the very short parapophyseal processes directed anteriorly are reminiscent of small elapoid snakes rather than Natricidae but the presence of other colubriform snake cannot be excluded because the height of the neural spine is unknown. Therefore, we avoid even superfamily assignation and consider the UM-MGT 3508 specimen Colubriformes indet. In the *'Natrix' mlynarskii* holotype, the middle trunk vertebra (MNHN.F.QU17181), only the hypapophyseal base including triangular anterior keel is preserved and parapophyses are completely damaged. Therefore, we consider the generic allocation of *'N.' mlynarskii* to be provisional and write the generic name in quotation marks, an approach followed by other recent workers (e.g., Smith & Georgalis, 2022).

The Early Miocene representatives of *Natrix* are represented by two distinct species. The first, *Natrix merkurensis*, is known from the early Burdigalian (MN 3a) of Merkur-North, Czechia (Ivanov, 2002a) and possibly from the middle or late Burdigalian (MN 4) of Béon 1, France (*N.* aff. *merkurensis*; Rage & Bailon, 2005). The second species, *Natrix sansaniensis*, first appeared in Merkur-North (MN 3a; Ivanov, 2002a) but became widely distributed since the late Early Miocene as documented by its occurrences in Petersbuch 2, Germany, MN 4 (*Natrix* aff. *sansaniensis*; Szyndlar & Schleich, 1993), French localities Béon 1, MN 4 (Rage & Bailon, 2005), Vieux-Collonges, MN 5 (*N.* aff. *sansaniensis*; Ivanov, 2000), Sansan, MN 6 (Augé & Rage, 2000) and La Grive M, MN 7 + 8 (*N.* cf. *sansaniensis*; Ivanov, 2002b), and from Hungarian locality of Mátraszőlős, MN 6 or MN 7–8 (*N.* cf. *sansaniensis*; Gál et al., 1999). *Natrix rudabanyaensis* was first described from the Late Miocene (MN 9) type locality of Rudabánya, Hungary (Szyndlar, 2005) but uncertain occurrences of this species (*N.* cf. *rudabanyaensis*) have been reported from the Middle Miocene of Hungary (MN 6 to MN 7 + 8; Venczel, 2011) and Romania (MN 7 + 8; Venczel & Ştiucă, 2008) as well as Late Miocene/Early Pliocene of Maramena, Greece (*N.* aff. *rudabanyaensis*; Georgalis et al., 2019b) and the Early Pliocene of the localities of Spilia 0, Spilia 1, Spilia 4, and Vevi in Greece (*N.* aff. *rudabanyaensis*; Georgalis et al., 2024). *Natrix longivertebrata*, which was first described from the Late Pliocene (MN 16) type locality of Rębielice Królewskie 1A, Poland (Szyndlar, 1984), has commonly reported from the European Miocene to Late Pliocene, although a definite species attribution is uncertain in most localities (Ivanov, 2022; Szyndlar, 1991b, 2012), including *N.* aff. *longivertebrata* from French localities Béon 1, France (MN 4; Rage & Bailon, 2005), Sansan (MN 6; Augé & Rage, 2000), and La Grive L3 and L7 (MN 7 + 8; Rage & Szyndlar, 1986) or *N.* cf. *longivertebrata* from the earliest Late Miocene of Gritsev, Ukraine (MN 7 + 8 to MN 9 base; Zerova, 1993; Ivanov), Late Miocene of Cherevichnoie, Ukraine (MN 12; Szyndlar & Zerova, 1992), and Polgárdi 2, 4 and 5, Hungary (MN 13; Venczel, 1994, 1998). *'Natrix' natricoides*, originally described from the Middle Miocene (MN 6) of Sansan, France, as belonging to the genus *Neonatrix* (see Augé & Rage, 2000) was later allocated to the genus *Natrix* by Szyndlar (2005, 2012). However, the hypapophysis is rather reduced (Augé & Rage, 2000: figs. 24 and 25) compared to other known *Natrix* species. Therefore, Ivanov (2022) assumed that the generic allocation is not sure and treated the genus into quotation marks, i.e., *'Natrix' natricoides*.

There are six extant species of the genus *Natrix* including *Natrix maura* (Linnaeus, 1758), *Natrix tessellata* (Laurenti, 1768), *Natrix natrix* (Linnaeus, 1758), *Natrix helvetica* (Lacépède, 1789), and *Natrix astreptophora* (Seoane, 1885) (Pokrant et al., 2016). *Natrix maura* has been reported from Western European Pliocene and Pleistocene localities (Agustí et al., 2010; Bailon, 1991; Blain & Bailon, 2006; Blain et al., 2011) e.g., Sète, France (MN 15; *N.* cf. *N. maura* sensu Bailon, 1991), Cova Bonica, Spain (MN 16; *N.* cf. *maura*; Blain & Bailon, 2006; Blain, 2009), and Grotte de la Carrière, France (Late Pleistocene; Bailon, 1991). The fossil record of *Natrix tessellata* is restricted mainly to Quaternary of Central and Eastern Europe (e.g., Holman, 1998; Ivanov, 1997, 2007; Szyndlar, 1991b; Venczel, 2000), with its earliest occurrence in the Late Pliocene (MN 16) of Kotlovina, Ukraine (Ratnikov, 2002, 2009; Ratnikov & Mebert, 2011). The most abundant fossil record belongs to *Natrix natrix* which is widely distributed throughout the Europe since the beginning of Pleistocene (e.g., Bailon, 1991; Blain & Bailon, 2006; Holman, 1998; Ivanov, 2007, 2015; Szyndlar, 1991b). No other extant species of *Natrix* has a fossil record.

Wintershofia robusta gen. et sp. nov. differs from those of other known extinct and extant natricids by the unique combination of characters (see Diagnosis). Below we discuss those characters in detail to differentiate *W. robusta* gen. et sp. nov. from all extinct and extant representatives of the genus *Natrix*:

(1) the neural spine is low, about three times longer than high, with its cranial margin noticeably shifted anteriorly

Remarks: The neural spine of *Wintershofia robusta* gen. et sp. nov. is about two and half to three times longer than high in lateral view. The neural spine is higher in most of extinct *Natrix* species including *'Natrix' mlynarskii* (despite incomplete neural spine; Rage, 1988, Fig. 1), *N. sansaniensis* (Augé & Rage, 2000: Fig. 21), *N. merkurensis* (Ivanov, 2002a: Fig. 7C) and *N. rudabanyaensis* (Szyndlar, 2005: Fig. 5H and O). The similarly low neural spine has been reported only in *N. longivertebrata*; however, this species differs from *W. robusta* gen. et sp. nov. by the much higher CL/NAW ratio (1.92 ± 0.12, $n = 27$; Szyndlar, 1984), the dorsally arched subcentral grooves in lateral view and prezygapophyseal processes wide and obtuse in dorsal and flattened in cranial views (Rage & Szyndlar, 1986; Szyndlar, 1984; Fig. 16). In extant *N. astreptophora* (MNCN 16422, MNCN 16425), *N. helvetica* (ZFMK 68430, ZFMK 71685), and *N. tessellata* (ZFMK 24680) the neural spine is higher compared to *W. robusta* gen. et sp. nov. In *Natrix natrix*, the relative height of the neural spine in middle trunk vertebrae is variable with Early and Early/Middle Pleistocene specimens possessing somewhat lower neural spine compared to stratigraphically younger specimens from the Polish Quaternary localities (Szyndlar, 1984).

(2) prezygapophyses with large sub-rhomboid prezygapophyseal articular facets and massively built short and distally slightly pointed prezygapophyseal processes

Remarks: The large sub-rhomboid prezygapophyseal articular facets, reported in middle trunk vertebrae of *Wintershofia robusta* gen. et sp. nov., are unknown in *Natrix*. All extant species of *Natrix* display more or less elongated prezygapophyseal articular facets of oval outline (e.g., Markert, 1975; Ratnikov & Mebert, 2011; Szyndlar, 1984, 1991b; MI, pers. observ.). The markedly elongated prezygapophyseal facets of oval to sub-triangular outline occur in extinct *Natrix longivertebrata* (Rage & Szyndlar, 1986; Szyndlar, 1984). Oval prezygapophyseal facets occur in *N. sansaniensis* (Augé & Rage, 2000; Ivanov, 2002a; Rage, 1981) whereas widely oval to subcircular prezygapophyseal facets of rather small diameter have been reported in *N. merkurensis* (Ivanov, 2002a). The holotype of *'N.' mlynarskii* displays a widely oval prezygapophyseal facet (Rage, 1988). Prezygapophyseal processes of middle trunk vertebrae in *W. robusta* are shorter than those of *N. sansaniensis*, *N. merkurensis* and *N. rudabanyaensis* (Augé & Rage, 2000; Ivanov, 2002a; Szyndlar, 2005). Although the distal termination of the left prezygapophyseal process did not preserve in *'N.' mlynarskii* (Rage, 1988, Fig. 1), *W. robusta* gen. et sp. nov. differs from this species by the shorter and more pointed prezygapophyseal processes as well as by the lower neural spine and the cotyle of smaller diameter.

(3) the large rhomboid zygosphenal facets are only slightly inclined laterally from the parasagittal plane of vertebrae

Remarks: The zygosphenal facets are, unlike those of *Wintershofia robusta* gen. et sp. nov., oval in most of *Natrix* species including extinct *'N.' mlynarskii* (Rage, 1988), *N. merkurensis* (Ivanov, 2002a), *N. sansaniensis* (Augé & Rage, 2000; Ivanov, 2002a; Rage, 1981), *N. rudabanyaensis* (Szyndlar, 2005) and *N. longivertebrata* (Rage & Szyndlar, 1986; Szyndlar, 1984, 1991b). Oval zygosphenal facets occur in all extant species except of *N. tessellata* (Ratnikov & Mebert, 2011: Fig. 2C; MI, pers. observ.). The slight inclination of zygosphenal facets from the parasagittal plane (about 11–15°) reported in *W. robusta* gen. et sp. nov. is unusual in *Natrix* but this development has been documented in *N.* cf. *longivertebrata* reported from the Polish Pliocene localities Węże I, II and Rębielice Królewskie II (Szyndlar, 1984, 1991b).

(4) the slender parapophyseal processes are very long

Remarks: The long parapophyseal processes reported in *Wintershofia robusta* gen. et sp. nov. is feature shared with several species of the genus *Natrix*. In lateral view, anteriorly rather than anteroventrally directed parapophyseal processes are longer than those reported in most *Natrix* species except *N. longivertebrata* and *N. rudabanyaensis*. Contrary to both extinct *Natrix* species (Rage & Szyndlar, 1986; Fig. 16; Szyndlar, 2005), parapophyseal processes are noticeably slender in *W. robusta* gen. et sp. nov. *Wintershofia robusta* gen. et sp. nov. further differs from *N. longivertebrata* and *N. rudabanyaensis* by the straight subcentral ridges, shorter prezygapophyseal processes as well as by the presence of sub-rhomboid prezygapophyseal and zygapophyseal articular facets.

(5) the hypapophysis with pointed distal tip extending far beyond the caudal termination of the condyle

Remarks: The hypapophysis of *Wintershofia robusta* gen. et sp. nov. is sigmoid in lateral view. Its pointed distal termination extends behind the caudal margin of the condyle (Fig. 14k). The hypapophysis of *W. robusta* is elongated more caudally compared to this reported in

Natrix sansaniensis (Augé & Rage, 2000; Ivanov, 2002a). The preserved base of the incomplete hypapophysis in *N. merkurensis* (Ivanov, 2002a: Fig. 9A) indicates that its anterior portion is clearly deeper compared to *W. robusta*. The hypapophysis of *W. robusta* is extended more caudally compared to this of *'Natrix' natricoides* (Augé & Rage, 2000, Fig. 24 and 25), *Natrix natrix* (Szyndlar, 1984, 1991b), *Natrix maura* (Blain et al., 2011, Fig. 6.2.), *N. helvetica* (ZFMK 68430, ZFMK 71685) and *Natrix astreptophora* (MNCN 16422, MNCN 16425). The middle trunk vertebrae of *W. robusta* differ from those of extinct *N. longivertebrata* (Rage & Szyndlar, 1986; Szyndlar, 1984) and *N. rudabanyaensis* (Szyndlar, 2005) by pointed distal termination of the hypapophysis which is rounded in two last mentioned species.

(6) prominent and sharp subcentral ridges are long and markedly straight in lateral view

Remarks: The strongly developed subcentral ridges occur in *'Natrix' mlynarskii* and *N. longivertebrata* (Rage, 1988; Szyndlar, 1984, 2005). Although subcentral ridges are "sharp, approximately straight in lateral view" in *'N.' mlynarskii* according to (Rage, 1988), *W. robusta* differs from the first mentioned species by the clearly longer, and completely straight subcentral ridges in both lateral and ventral views. Moreover, the neural spine was lower in *W. robusta* compared to uncomplete neural spine in *'N.' mlynarskii* and prezygapophyseal processes are slightly shorter and more pointed distally unlike moderately long and obtuse prezygapophyseal processes reported in holotype of *'N.' mlynarskii* (see Rage, 1988, Fig. 1). *N. longivertebrata* differs from *W. robusta* by the clearly dorsally arched subcentral ridges in lateral view (Rage & Szyndlar, 1986; Szyndlar, 1984).

(7) the circular cotylar rim is of small diameter

Remarks: In *Wintershofia robusta* gen. et sp. nov., the diameter of the cotylar rim is clearly smaller than the diameter of the neural canal. Although the neural canal diameter is strongly affected by the ontogenetic stage with the large diameter observed in neonates/juveniles (Georgalis & Scheyer, 2019; Scanlon et al., 2003; Szyndlar, 1984; Xing et al., 2018), the relatively large dimensions indicate that trunk vertebrae of *W. robusta* belonged to an adult individual(s). A similarly small cotyle has not been reported in other representatives of *Natrix*.

Palaeonatrix Szyndlar in Młynarski et al., 1982
Palaeonatrix lehmani (Rage & Roček, 1983)

Palaeonatrix aff. lehmani

Material. – 26 trunk vertebrae (SNSB-BSPG 1937 II 24404–24429), two caudal vertebrae (SNSB-BSPG 1937 II 24430–24431).

Trunk vertebrae (Fig. 17a–t): All preserved vertebrae are at least partially fragmentary, mostly with damaged or broken-off neural spine, hypapophysis and prezygapophyseal processes. The vertebrae are typical of their relatively large dimensions and strong craniocaudal elongation of the centrum of vertebra (measurements of the largest vertebra: CL = 7.04 mm, NAW = 3.48 mm, CL/NAW = 1.99 mm; see Appendix 1). In lateral view, the neural spine of the middle trunk vertebrae is about three times longer than high. The cranial margin of the neural spine, damaged in all specimens, was most probably vertical or very slightly inclined anteriorly, the caudal margin is clearly inclined posteriorly. In more anteriorly positioned vertebrae, including those from the anterior precaudal section, the neural spine is about twice longer than high. The interzygapophyseal ridges are distinct and sharp. The lateral foramina are situated very close to the interzygapophyseal ridge base and in one specimen (Fig. 17k) the right foramen is doubled. There is usually a distinct furrow which extends at the base of the prezygapophysis between the lateral foramen and posterodorsal border of the diapophysis (Fig. 17a, f, k). The para- and diapophyses are well separated, with diapophysis situated clearly behind the parapophysis. The articular facet of the diapophysis, usually unpreserved, is small compared to parapophyseal facet and placed on the broad diapophyseal base as best visible in dorsal view. The strong subcentral ridges are slightly arched dorsally in anterior and middle trunk vertebrae but it is straight in posterior trunk vertebrae. The morphology of the hypapophysis is considerably variable in the vertebral column. In anterior trunk vertebrae, the anterior portion of the hypapophysis, close behind the cotyle, is relatively deep and

(See figure on next page.)
Fig. 17 *Palaeonatrix* aff. *lehmani* from Wintershof-West. **a**–**e**, anterior trunk vertebra (SNSB-BSPG 1937 II 24405) in right lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**j**, anterior/middle trunk vertebra (SNSB-BSPG 1937 II 24427) in left lateral (**f**), dorsal (**g**), ventral (**h**), cranial (**i**), and caudal (**j**) views; **k**–**o**, middle trunk vertebra (SNSB-BSPG 1937 II 24428) in right lateral (**k**), dorsal (**l**), ventral (**m**), cranial (**n**), and caudal (**o**) views; **p**–**t**, posterior trunk vertebra (SNSB-BSPG 1937 II 24429) in left lateral (**p**) and dorsal (**q**), ventral (**r**), cranial (**s**), and caudal (**t**) views; **u**, **v**, anterior caudal vertebra (SNSB-BSPG 1937 II 24431) in right lateral (**u**), and cranial (**v**) views. cd, condyle; ct, cotyle; d, diapophysis; es, epizygapophyseal spine; ha, haemapophysis; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pl, pleurapophysis; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; sctt, subcotylar tubercle; zy, zygosphene. Arrows indicate important features

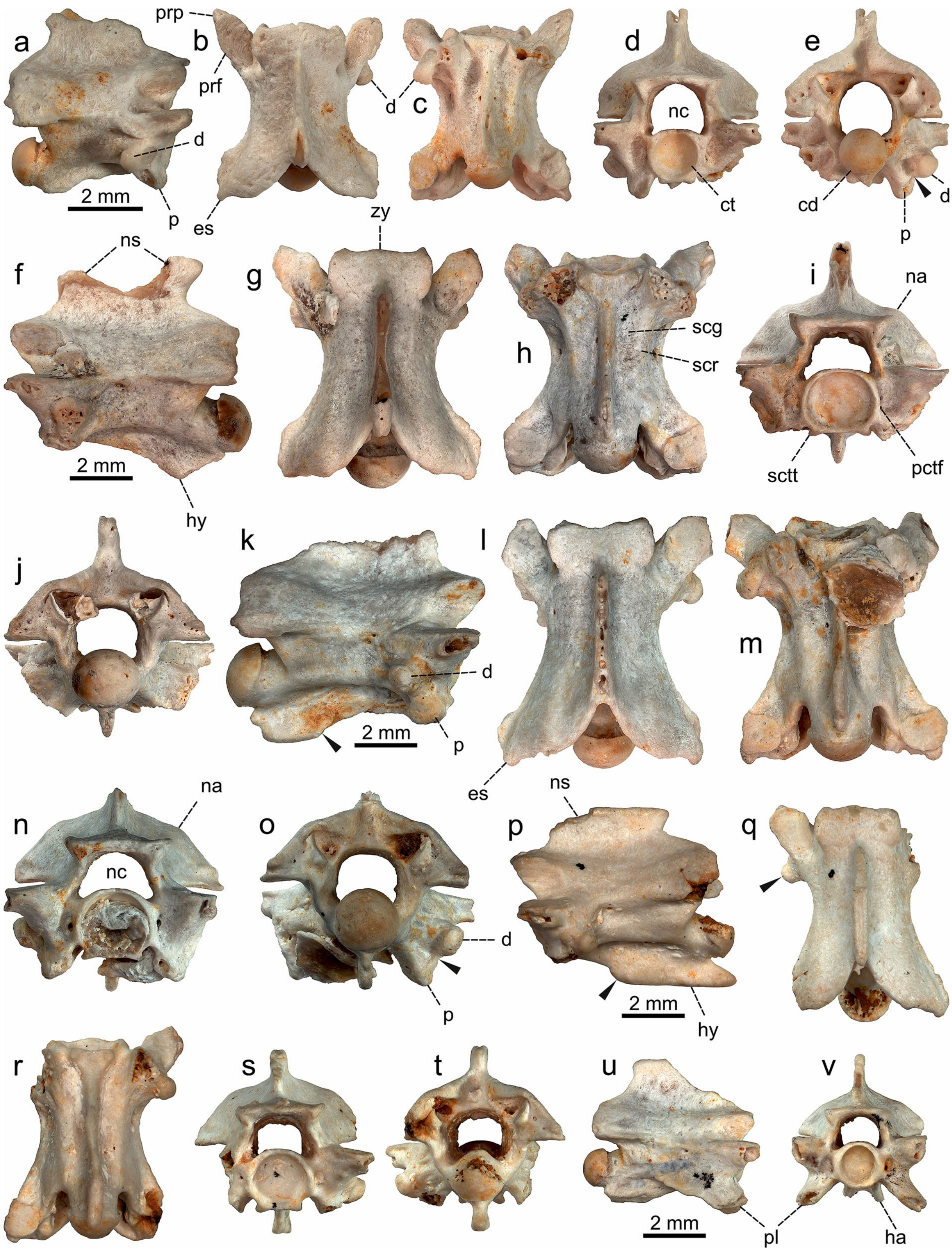

Fig. 17 (See legend on previous page.)

its ventral margin slightly curves ventrally roughly in the half of the centrum length (Fig. 17f). Although the distal termination of the hypapophysis is unknown, the middle and probably also posterior trunk vertebrae (Fig. 17k, p) clearly show that hypapophysis was deep, with the distinct "step" close behind the posterior border of the diapophysis and followed by the straight ventral margin of the hypapophysis. This straight portion of the ventral margin of the hypapophysis is parallel to the main axis of vertebra. The distal tip of the hypapophysis is acute as documented by the only complete hypapophysis of the middle/posterior trunk vertebra (Fig. 17p). The craniocaudally short condyle is developed on the long neck. In dorsal view, the maximum of the interzygapophyseal constriction occurs close behind the base of the diapophysis. The zygosphenal lip has wide medial and short lateral lobes. In anterior trunk vertebrae, the cranial margin of the zygosphene is convex and lateral lobes small. Prezygapophyseal articular facets are elongated and oval with long axis directed anterolaterally. Prezygapophyseal processes are very short in anterior trunk vertebrae but those of middle trunk vertebrae are unknown. The distal tip of the diapophysis, which occurs on its wide base, protrudes in caudal direction. The caudal notch of the neural arch is deep and narrow. Epizygapophyseal spines are prominent and usually accompanied by distinct ridges extending on the postzygapophyseal surface. In ventral view, prominent subcentral ridges are blunt and extend caudally almost parallel to the hypapophysis. Subcentral grooves are noticeably narrow and rather deep. Postzygapophyseal articular facets are small and subrectangular. The paired subcentral foramina are usually distinct but sometimes (Fig. 17h) only one is present. In cranial view, the neural canal is rounded or subrectangular with distinct, sometimes prominent, lateral sinuses. The zygosphene is straight. Paracotylar foramina occur within deep depressions on either side of the rounded cotyle. There are distinct subcotylar tubercles on the ventral margin of the cotylar rim. In caudal view, the neural arch is strongly vaulted, with VR ranging from 0.47 to 0.53; the zygantrum is rather wide and the condyle is suborbicular. Multiple parazygantral foramina occur on the posterior wall of the neural arch.

Caudal vertebrae (Fig. 17u, v): In lateral view, the more anteriorly positioned fragmentary caudal vertebra (SNSB-BSPG 1937 II 24431) is elongated with the neural spine about two times longer than high. Its cranial margin is not preserved, and the caudal one is vertical. The bases of incomplete pleurapophyses are markedly wide. Pleurapophyses with broken-off distal terminations are directed anteroventrally in lateral and ventrolaterally in anterior views. Haemapophyses are broken-off close to their base in SNSB-BSPG 1937 II 24431 but in smaller and more posteriorly positioned caudal vertebra (SNSB-BSPG 1937 II 24430) the preserved portions of haemapophyses are inclined posteroventrally. The condyle is developed on the relatively short neck. In dorsal view, the zygosphene is three lobate with short lateral and wide medial lobe. Prezygapophyseal articular facets are oval and the only complete right prezygapophyseal process preserved in SNSB-BSPG 1937 II 24430 is short and directed anteriorly rather than anterolaterally. Prezygapophyseal articular facets are narrowly oval, with long axis directed anteriorly rather than anterolaterally. In ventral view, haemapophyseal bases are long extending from the distinct subcentral foramina but low crests continue anteriorly to the cotylar rim. The slightly eroded postzygapophyseal articular facets are sub-rhomboid, with long axis directed posterolaterally. In cranial view, the zygosphene is only slightly arched dorsally. Haemapophyses are directed ventrally which is well visible only in SNSB-BSPG 1937 II 24430. The circular cotylar rim is of the same diameter as the rounded neural canal.

Remarks: The elongated centrum of cylindrical vertebrae together with moderately high neural spine, well developed hypapophysis in the middle trunk vertebrae, distinct prezygapophyseal processes, as well as the presence of prominent epizygapophyseal spines indicate attribution to Natricidae (Head et al., 2016; Rage, 1984; Szyndlar, 1984, 1991b). The peculiar shape of the plate-like hypapophysis with prominent anterior keel distinguishes natricid from Wintershof-West from all known representatives of the genus *Natrix* and clearly refer to the genus *Palaeonatrix* (Szyndlar in Młynarski et al., 1982; Szyndlar, 1987). The attribution to the genus *Palaeonatrix* is based on the following combination of features (Szyndlar in Augé & Rage, 2000; Młynarski et al., 1982; Szyndlar, 1987; Szyndlar & Schleich, 1993): (1) the centrum of vertebrae is strongly elongated; (2) subcentral ridges are conspicuously developed; (3) the plate-like hypapophysis is not deep, there is a prominent anterior keel which forms a distinct "step" towards the cotyle; (4) parapophyses project clearly below the ventral limit of the centrum. There are two species of *Palaeonatrix* in European Miocene—*Palaeonatrix silesiaca* Szyndlar in Młynarski et al., (1982) from the Middle Miocene (MN 6) of Opole, Poland (Szyndlar in Młynarski et al., 1982; Szyndlar, 1984) and *Palaeonatrix lehmani* (Rage & Roček, 1983) from the Czech Early Miocene locality of Dolnice, MN 4 (Szyndlar, 1987), originally attributed by Rage and Roček (1983) to the genus *Dolniceophis* Rage & Roček, 1983. *Palaeonatrix silesiaca* has been described based on a rather fragmentary material and the most distinctive structure, the hypapophysis, is known only on its basal portion. Unlike *Palaeonatrix* from Wintershof-West, *P. silesiaca* lacks epizygapophyseal spines. There is no substantial difference between *P.* aff. *lehmani* from Wintershof-West and *P. lehmani* reported by Szyndlar and Schleich (1993: Fig. 5) from Petersbuch 2. However, there are at least two differences which enable distinction of above-mentioned snakes from the type material originally reported by Rage and Roček (1983) from Dolnice: (1) the diameter of the cotyle relative to the diameter of the neural canal is not small and (2) the diapophyseal base is wide and clearly protrudes posterolaterally as best visible in ventral (and even dorsal) view. Moreover, in the type vertebra of *P. lehmani* (DP FNSP 3920) the triangular delimitation of the centrum by subcentral ridges is wider compared to markedly narrow ventral surface of the centrum with subcentral ridges extending parallel or almost parallel to the long axis of the vertebra. Therefore, we consider *P.* aff. *lehmani* morphotype from Wintershof-West together with *P. lehmani* from Petersbuch 2 (Szyndlar & Schleich, 1993) taxon different from the type material reported from Dolnice (Rage & Roček, 1983). The caudal vertebrae have been tentatively attributed to *Palaeonatrix* on the basis of the low neural spine and large diameter of the cotyle.

The taxonomic distinctiveness of the genus *Palaeonatrix* is uncertain according to Szyndlar and Schleich (1993). The shape of the hypapophysis is rather peculiar within Natricidae as results from the comparison of *Palaeonatrix* with most of extant genera, including e.g., *Natrix*, *Nerodia*, *Xenochrophis* Günther, 1864, *Natriciteres* Loveridge, 1953, *Thamnophis*, and *Rhabdophis*.

Natricidae indet., type 1

Material. – 16 trunk vertebrae (SNSB-BSPG 1937 II 24432–24447).

Trunk vertebrae (Fig. 18): All preserved vertebrae, typical of their small dimensions, are at least partially fragmentary with the incomplete prezygapophyseal processes and damaged para-diapophyses. In lateral view, the incomplete neural spine of one vertebra positioned around the anterior/middle trunk transition is about 1.5 times longer than high (Fig. 18a). The cranial margin of the neural spine is absent, and the damaged caudal margin was inclined posteriorly. In vertebrae from the middle trunk section of the column (Fig. 18f–j) the neural spine is moderately high, about two times longer than high, with cranial margin inclined anteriorly and caudal margin overhanging posteriorly. The small lateral foramina are situated close below the well-developed interzygapophyseal ridges. The usually heavily damaged para- and diapophyses are well separated with diapophysis situated roughly above the parapophysis. The subcentral ridges are arched dorsally. The hypapophysis is noticeably shallow and short in middle trunk vertebrae, with distal tip reaching at most the condylar base. In posterior trunk vertebrae the hypapophysis is strongly reduced reminiscent of the high haemal keel with straight ventral margin.

In dorsal view, the zygosphenal lip has wide medial and short lateral lobes. In posterior trunk vertebrae, the medial lobe is narrower, and lateral lobes are less distinct. Prezygapophyseal articular facets are elongated and oval, with long axis directed anterolaterally. Prezygapophyseal processes are of unknown length. The epizygapophyseal spines are absent. In ventral view, subcentral ridges are distinct but better developed on the anterior half of the centrum. Subcentral grooves are narrow and shallow. The partially eroded postzygapophyseal articular facets are small and subrectangular in outline. The paired subcentral foramina occur at the base of the narrow hypapophysis. In cranial view, the neural canal is rounded with shallow lateral sinuses. The zygosphene is arched dorsally. Paracotylar foramina occur within deep depressions on either side of the rounded or dorsoventrally slightly depressed cotyle. The subcotylar tubercles are only indistinctly developed at the base of the cotylar rim. In caudal view, the neural arch is vaulted, with VR ranging from 0.40 to 0.52, and zygantrum is rather wide. Up to three parazygantral foramina occur on either side of the posterior wall of the neural arch.

Remarks: This small-sized natricid snake (CL of the largest specimen is 3.79 mm; Appendix 1), whose posterior tip of the short and reduced hypapophysis does not extend behind the anteroventral base of the condyle, is reminiscent of the extinct genus *Neonatrix* first reported from the Middle Miocene of Nebraska (Holman, 1973, 2000). In total three species of the genus *Neonatrix* have been reported from North America: *Neonatrix elongata* Holman, 1973 (the type species), *Neonatrix magna* Holman, 1982, and *Neonatrix infera* Holman, 1996 (Holman 1973, 1982, 1996, 2000). In addition, other three *'Neonatrix'* species (for the use of parentheses in European species, see Szyndlar & Schleich, 1993; Szyndlar, 2005) have been reported from France, *'Neonatrix' europaea* Rage & Holman, 1984, *'Neonatrix' crassa* Rage & Holman, 1984, and *'Neonatrix' natricoides* Augé & Rage, 2000 (Augé & Rage, 2000; Ivanov, 2000; Rage & Bailon, 2005; Rage & Holman, 1984) with the latter species reassigned to the genus *Natrix* by Szyndlar (2005). *'Neonatrix' nova* Szyndlar, 1987, known only from its type late Early Miocene (MN 4) locality of Dolnice, Czech Republic (Szyndlar, 1987), is the only distinct *'Neonatrix'* species reported outside France despite the fact that indeterminate *'Neonatrix'*, often of uncertain generic attribution, have been reported from several other localities in Central and southeastern Europe covering the time span from the Early Miocene (MN 2) up to the Early

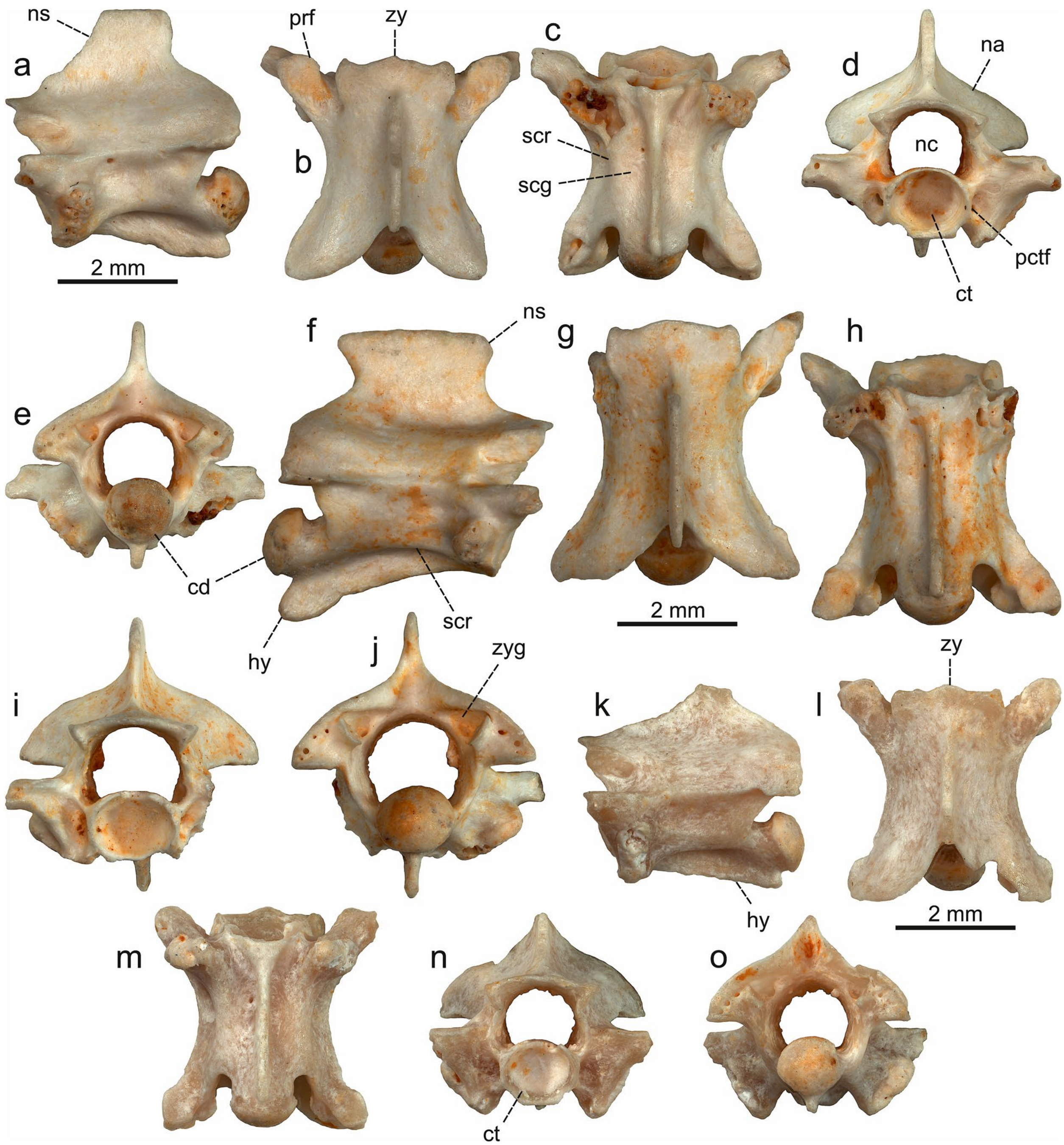

Fig. 18 Natricidae indet., type 1 from Wintershof-West, Germany. **a**–**e**, anterior/middle trunk vertebra (SNSB-BSPG 1937 II 24432) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**j**, middle trunk vertebra (SNSB-BSPG 1937 II 24446) in right lateral (**f**), dorsal (**g**), ventral (**h**), cranial (**i**), and caudal (**j**) views; **k**–**o**, posterior trunk vertebra (SNSB-BSPG 1937 II 24447) in right lateral (**k**), dorsal (**l**), ventral (**m**), cranial (**n**), and caudal (**o**) views. cd, condyle; ct, cotyle; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; pctf, paracotylar foramen; prf, prezygapophyseal articular facet; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene; zyg, zygantrum

Pliocene (MN 14) (Čerňanský et al., 2015; Ivanov, 1998; Szyndlar, 1998, 2005, 2009; Szyndlar & Schleich, 1993).

The genus *Neonatrix* was originally diagnosed as a "natricine genus with distinctly smaller hypapophyses of the lumbar vertebrae (i.e., trunk vertebrae) than any known natricine genus" (Holman, 1973: 130). The revised diagnosis of this genus presented by Rage and Holman (1984) diagnosed *Neonatrix* as a small-sized natricine snake with weakly developed hypapophysis and the low neural spine. However, additional new material attributed to *N. magna* (MSUVP 1087; Holman, 1987: Fig. 6) and description of another species originally attributed to *Neonatrix natricoides* (see Augé & Rage, 2000), whose neural spine is high, resulted in restricted emended diagnosis of the genus *Neonatrix* where the presence of the low neural spine was omitted (Augé & Rage, 2000; Holman, 2000). However, the MSUVP 1087 specimen of *N. magna* is, unlike other representatives of this genus, about as wide as long with moderately developed subcentral ridges and shallow subcentral grooves. The attribution of MSUVP 1087 specimen to a different genus or even a non-natricid vertebra positioned around the anterior/middle trunk transition seems more plausible. Therefore, we consider original Rage and Holman's (1984) diagnosis of *Neonatrix* to be more appropriate, although still insufficient (see below).

Szyndlar and Schleich (1993) were the first who emphasized that North American *Neonatrix* possesses apparently less developed hypapophysis unlike European *'Neonatrix'* species described by Rage and Holman (1984) where short hypapophysis is reduced but not 'vestigial' and restricted to the posterior half of centrum. Szyndlar and Schleich (1993), therefore, considered European *'Neonatrix'* the genus (or genera) different from North American *Neonatrix*. Holman subsequently (2000), considering the results of Augé and Rage (2000), revised his diagnoses of all North American *Neonatrix* species as natricids with "the hypapophysis very poorly developed and mainly confined to the posterior part of the centrum".

'Neonatrix' europaea and *'Neonatrix' nova* are the only European natricid species with a relatively low neural spine and reduced (but not 'vestigial') hypapophysis. The height of the neural spine is unknown in *'N.' crassa* reported only from the Middle Miocene (MN 7 + 8) type locality of Sansan, France (Rage & Holman, 1984); however, the well-preserved middle trunk vertebra of the natricid from Wintershof-West, closely resembling the holotype specimen (UCBL 285012) of *'N.' crassa* (Rage & Holman, 1984: Fig. 5), retains the high neural spine. The only difference is the less protruding diapophyses posterolaterally compared to *'N.' crassa*. The high neural spine would be unusual in *'Neonatrix'* and therefore, we do not attribute the natricid from Wintershof-West to *'Neonatrix'*. The reduced hypapophysis does not allow attribution to most of the extant natricid genera characterized by the usually deep hypapophysis including *Amphiesma* Duméril et al., 1854, *Atretium* Cope, 1861, *Hydraethiops* Günther, 1872, *Lycognathophis* Boulenger, 1893, *Lyodytes* Cope, 1885, *Natriciteres*, *Natrix*, *Nerodia*, *Regina*, and *Thamnophis* (see Malnate, 1972; Szyndlar, 1984, 1987, 1991b; Holman, 2000; Zaher et al., 2019). The very low hypapophysis reported in trunk vertebrae of *Storeria*, *Tropidoclonion*, and *Virginia* Baird & Girard, 1853 (see Malnate, 1972; Holman, 2000) is pointed caudally reaching the caudal tip of the condyle unlike short rounded hypapophysis terminated at the condylar base of natricid from Wintershof-West. Although the Wintershof-West morphotype could represent a distinct or even a new genus of Natricidae, we avoid of a more precise identification because of the so far unknown axial skeleton of many representatives of this diversified clade. As regards *'N.' crassa*, we consider the genus attribution of the incomplete holotype vertebra (see Rage & Holman, 1984) to be uncertain. If the vertebrae of Natricidae indet., type 1 from Wintershof-West and those of *'N.' crassa* eventually represent the same taxon, we consider the attribution to *'Neonatrix'* weakly supported and suggest the assignment to a separate/new genus.

Natricidae indet.

Material. – 77 trunk vertebrae (SNSB-BSPG 1937 II 24448–24524).

Trunk vertebrae: All vertebrae are highly fragmentary, usually exhibiting eroded paradiapophyses, damaged zygosphenes and neural spines, and hypapophyses broken-off close to their bases. Several fragments indicate that the uncomplete neural spine was high and hypapophysis was most probably deep. The presence of high neural spine, deep hypapophysis with triangular its anterior keel, the presence of epizygapophyseal spines as well as slender structure of elongated cylindrical vertebrae indicates attribution to Natricidae (Head et al., 2016; Rage, 1984; Szyndlar, 1984, 1991b). The presence of the deep hypapophysis excludes attribution to the genus *Neonatrix* (see Holman, 1973, 2000; Rage & Holman, 1984; Szyndlar, 1991b). The vertebrae most likely belong to the genus *Natrix* but different from the above described *Wintershofia robusta* gen. et sp. nov. However, attribution to other natricids, e.g., *Palaeonatrix* Szyndlar in Młynarski et al., (1982), could also be possible.

'Colubridae' Oppel, 1811b (sensu Ivanov, 2022)
Coluber (s.l.) Linnaeus, 1758
'Coluber' caspioides Szyndlar & Schleich, 1993
'Coluber' aff. caspioides

Material. – Nine anterior trunk vertebrae (SNSB-BSPG 1937 II 24525–24533), 118 middle and posterior trunk vertebrae (SNSB-BSPG 1937 II 24534–24651), one cloacal vertebra (SNSB-BSPG 1937 II 24652), and six caudal vertebrae (SNSB-BSPG 1937 II 24653–24658).

Anterior trunk vertebrae (Fig. 19a–e): The most complete vertebra has broken-off neural spine and hypapophysis close to their bases. In general, their morphology clearly refers to middle trunk vertebrae. The neural spine was most probably high. However, inclination of its anterior and posterior margin cannot be assessed in lateral view. The zygosphenal facet is oval. The large lateral foramen is situated at the posterior base of the prezygapophysis. The almost completely preserved paradiapophysis has anteriorly enlarged parapophysis, with short parapophyseal process slightly larger than the diapophysis. The short subcentral ridge is arched dorsally. The hypapophysis with high anterior keel extending to the cotylar base was inclined posteroventrally. In dorsal view, the zygosphene has a wide median lobe and distinct lateral lobes (only the right one is preserved). The right prezygapophyseal articular facet is oval, with long axis directed anterolaterally. The slender prezygapophyseal process, with its obtuse distal termination, is about half the prezygapophyseal facet length. In ventral view, the elongated centrum is delimited by straight subcentral ridges. Large subcentral foramina occur at the base of thin hypapophysis. In cranial view, the neural canal has developed prominent lateral sinuses. The zygosphenal lip is flat. The right prezygapophysis is horizontal. The only visible left paracotylar foramen is situated in deep depression close to the circular cotylar rim. The well-developed subcotylar tubercles occur at the cotylar base. In caudal view, the neural arch is moderately vaulted, with an almost straight posterodorsal lamina. Large paired parazygantral foramina occur on posterior wall of the neural arch.

Middle and posterior trunk vertebrae (Figs. 19f–w and 20a–i): The small to medium-sized vertebrae (Appendix 1) are at least partially fragmentary, usually with damaged neural spine, para-diapophyses and broken-off prezygapophyseal processes. However, several specimens are almost complete and enable observation of intracolumnar variability. In lateral view, the neural spine, which rises in the mid-length of the zygosphenal facet, is usually somewhat longer than high with its cranial margin inclined anteriorly and caudal one posteriorly. However, in the largest middle trunk vertebra (SNSB-BSPG 1937 II 24646) the neural spine is as high as long and its anterodorsal portion is tilted (Fig. 19f). The neural spine of more posteriorly positioned vertebrae is about 2–2.5 times longer than high. The short but strongly built interzygapophyseal ridge continues posteriorly as a thin lamina delimiting anterolaterally the postzygapophyseal portion of the vertebra. The large lateral foramen, situated close below the interzygapophyseal ridge, is faced lateroventrally. In large specimens, lateral foramina can be partially covered by the laterally expanding base of the prezygapophyses. The diapophysis is situated above the posterior half of the clearly larger parapophysis whose ventral base is elongated craniocaudally. The strong subcentral ridge is arched dorsally and extends as far as the posterior third of the centrum length. However, in the posterior trunk vertebrae, the subcentral ridge continues as far as the short condylar neck (Fig. 20a, f). The condyle is developed on a short condylar neck, which dorsally forms a deep furrow separating condylar base from the centrum of vertebra. The distinct haemal keel is roughly straight along its entire length in the anteriormost middle trunk vertebrae, but in the more posteriorly positioned vertebrae, the anterior third of the haemal keel slopes slightly towards the cotylar base. In the posterior trunk vertebrae, a distinct and sometimes prominent step may occur just behind the posterior margin of the diapophysis (Fig. 20a, f). The haemal keel is markedly reduced in front of the condylar neck. In dorsal view, the zygosphene is always three-lobate with two pointed lateral lobes and wide, blunt central lobe. Prezygapophyseal articular facets are oval to elongated subtriangular in outline, with long axes directed anterolaterally. The anterolaterally directed prezygapophyseal processes are moderately long reaching no more than half the prezygapophyseal facets length. Their distal termination is either moderately pointed in anteriorly positioned vertebrae or acute in posterior trunk vertebrae. The proximal bases of the prezygapophyseal processes are usually strongly flattened and tilted posteroventrally. The epizygapophyseal spines are usually absent but the largest specimens have developed prominent epizygapophyseal ridges. In ventral view, the elongated centrum of vertebra is triangular and delimited lateroventrally by the straight subcentral ridges. The subcentral grooves are shallow and wide, with subcentral foramina usually situated at the base of the haemal keel. Additional left subcentral foramen is present in several specimens (e.g., SNSB-BSPG 1937 II 24649;

(See figure on next page.)

Fig. 19 *'Coluber'* aff. *caspioides* from Wintershof-West, Germany. **a**–**e**, anterior trunk vertebra (SNSB-BSPG 1937 II 24533) in right lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**i**, middle trunk vertebra (SNSB-BSPG 1937 II 24646) in left lateral (**f**), dorsal (**g**), ventral (**h**), and cranial (**i**) views; **j**–**n**, middle trunk vertebra (SNSB-BSPG 1937 II 24647) in right lateral (**j**), dorsal (**k**), ventral (**l**), cranial (**m**), and caudal (**n**) views; **o**–**s**, middle trunk vertebra (SNSB-BSPG 1937 II 24648) in left lateral (**o**) and dorsal (**p**), ventral (**q**), cranial (**r**), and caudal (**s**) views; **t**–**w**, middle/posterior trunk vertebra (SNSB-BSPG 1937 II 24649) in right lateral (**t**), ventral (**u**), cranial (**v**), and caudal (**w**) views. cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scf, subcentral foramen; scg, subcentral groove; scr, subcentral ridge; sctt, subcotylar tubercle; zy, zygosphene. Arrows indicate important features

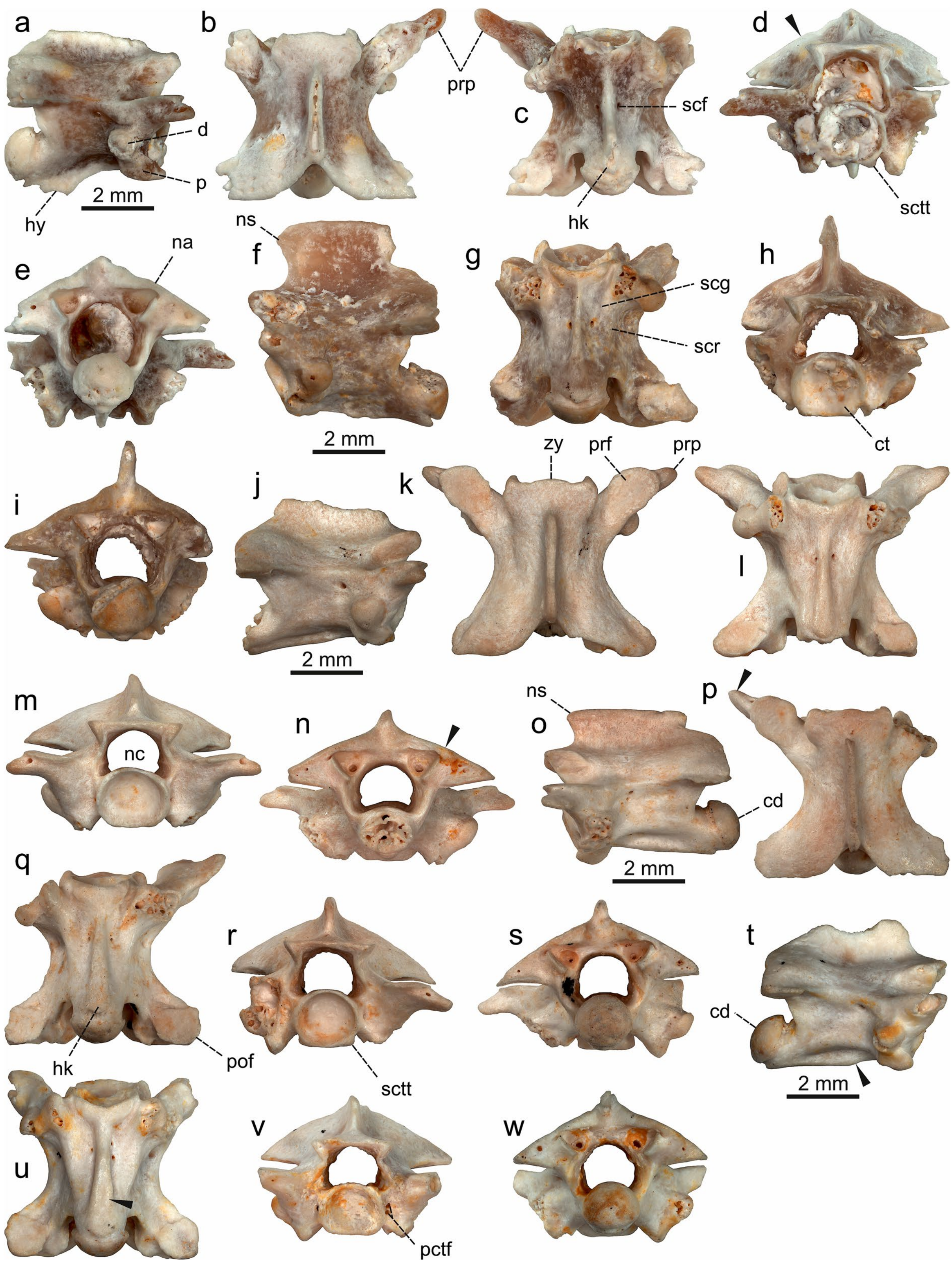

Fig. 19 (See legend on previous page.)

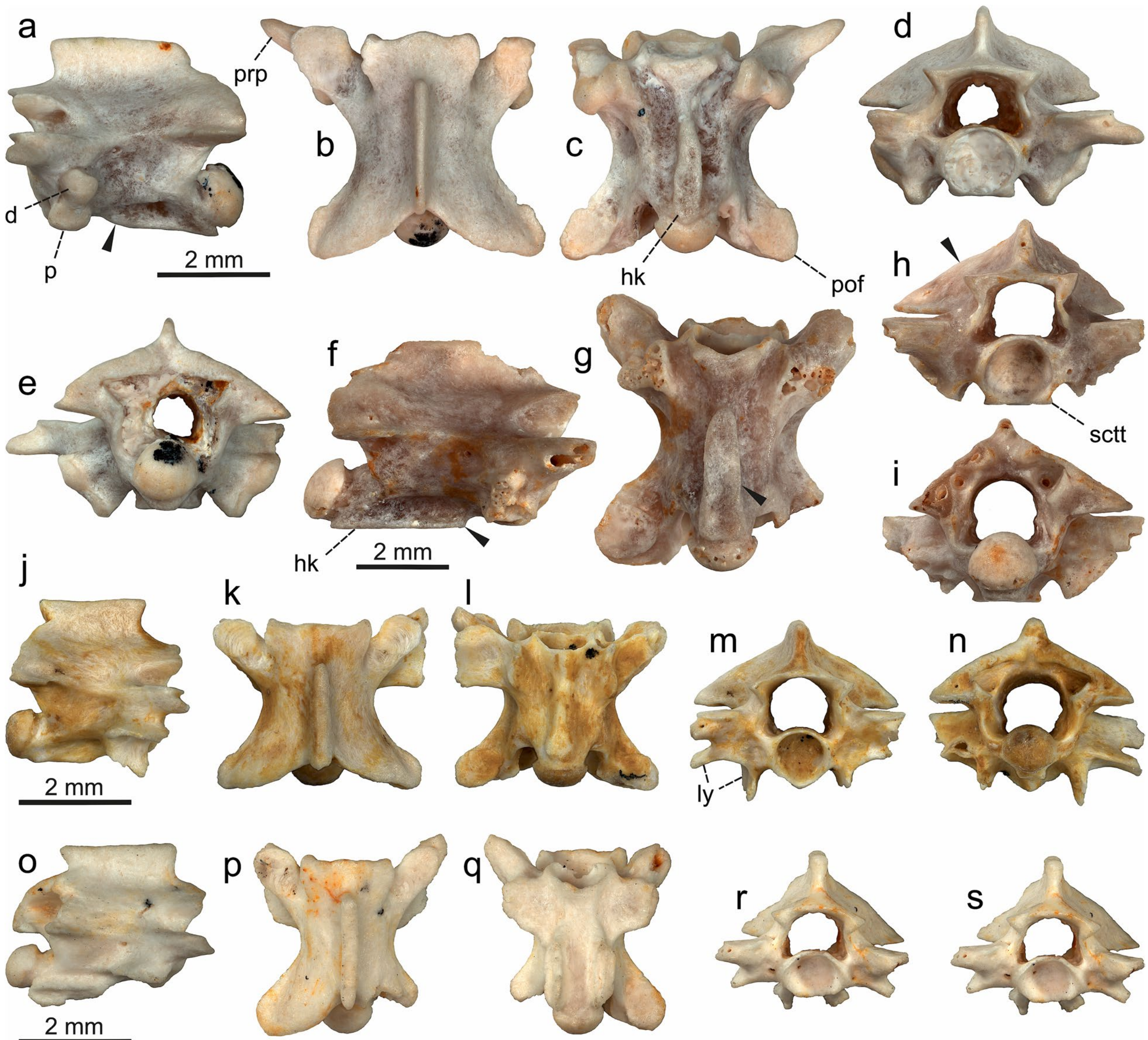

Fig. 20 *'Coluber'* aff. *caspioides* from Wintershof-West, Germany. **a**–**e**, posterior trunk vertebra (SNSB-BSPG 1937 II 24650) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**i**, posterior trunk vertebra (SNSB-BSPG 1937 II 24651) in right lateral (**f**), ventral (**g**), and cranial (**h**), and caudal (**i**) views; **j**–**n**, cloacal vertebra (SNSB-BSPG 1937 II 24652) in right lateral (**j**), dorsal (**k**), ventral (**l**), cranial (**m**), and caudal (**n**) views; **o**–**s**, caudal vertebra (SNSB-BSPG 1937 II 24658) in right lateral, dorsal ventral, and cranial views. d, diapophysis; hk, haemal keel; ly, lympapophysis; p, parapophysis; pof, postzygapophyseal articular facet; prp, prezygapophyseal process; sctt, subcotylar tubercle. Arrows indicate important features

Fig. 19u). The haemal keel is narrow in vertebrae from the anterior middle trunk section, with flattened and lanceolate caudal termination. However, in the more posteriorly positioned vertebrae, the haemal keel becomes flat with ventral surface expanded laterally. In the posterior trunk vertebrae, this lateral expansion, which begins roughly at the level or close behind the subcentral foramina, is prominent and contributes to the medioventral cover of the narrow subcentral grooves (Fig. 20c, g). The postzygapophyseal articular facets are sub-square in outline but the almost complete left facet of the largest specimen is strongly elongated laterally. In cranial view, the neural canal is rounded or sub-square, with prominent lateral sinuses. The zygosphenal lip is arched dorsally in smaller specimens but in large vertebrae, the zygosphenal lip is almost straight or with central lobe slightly shifted ventrally. Prezygapophyses are horizontal with prezygapophyseal processes either horizontal or slightly bent ventrally. There is a distinct and sometimes rather large foramen at the base of the prezygapophyseal processes. The paracotylar foramina occur within depressions on either side of the circular cotylar rim. The ventrolaterally directed subcotylar tubercles occur usually at the base of the cotylar rim thus the ventral border of the cotyle can be almost straight. In caudal view, the weakly vaulted posterodorsal lamina of the neural arch, with VR ranging from 0.20 to 0.39, is slightly convex or nearly straight. The zygantrum is wide. Multiple parazygantral foramina of variable dimensions usually occur on the posterior wall of the of neural arch between the zygantral and postzygapophyseal articular facets. Sometimes, these foramina can be rather large. The condyle is suborbicular with flat ventral base.

Cloacal vertebra (Fig. 20j–n): In lateral view, the fragmentary cloacal vertebra has neural spine twice longer than high with its anterior margin inclined anteriorly and posterior one posteriorly. Anteriorly, the neural spine rises at the zygosphenal base. The haemal keel distinctly slopes anteriorly behind the lymphapophyseal base. The condyle, developed on the short neck, is separated from the centrum by the furrow. In dorsal view, the zygosphene has wide and moderately developed median lobe and long, distally pointed lateral lobes. The only preserved right parapophyseal processes with slightly eroded its distal termination is short. In ventral view, the bases of lymphapophyses are wide and directed laterally. The haemal keel is flat in its caudal portion. In cranial view, the base of ventral branch of the lymphapophysis is directed ventrally in right angle to the horizontal plane. The base of the dorsal branch of the lymphapophysis is directed laterally rather than lateroventrally. In caudal view, the condyle diameter is smaller than this of neural canal.

Caudal vertebrae (Fig. 20o–s): All preserved caudal vertebrae are fragmentary with incomplete pleurapophyses and broken-off haemapophyses. In lateral view, the most complete anterior caudal vertebra possesses the neural spine which is about 2–3 times longer than high, with its cranial margin slightly inclined anteriorly and the caudal one inclined posteriorly. The zygosphenal facet is oval and narrow. The small lateral foramen is placed close below the short but distinct interzygapophyseal ridge. The condyle is developed on the short condylar neck. In dorsal view, small but well visible lateral lobes are developed on the slightly convex zygosphenal lip. Prezygapophyseal articular facets are oval, with long axis directed anterolaterally. The only preserved right prezygapophyseal process is short reaching a length of less than half the length of the prezygapophyseal facet. In ventral view, preserved bases of pleurapophyses are directed laterally the left postzygapophyseal articular facet is widely oval. In cranial view, the neural arch is markedly vaulted. The zygosphene is convex. Pleurapophyseal are directed laterally rather than ventrolaterally. The distinct paracotylar foramina occur on either side of the dorsoventrally depressed cotyle.

Remarks: The lightly built trunk vertebrae can be identified as belonging to 'Colubridae' based on the elongated centrum with CL/NAW ratio > 1, the presence of paracotylar foramina, the well-developed thin neural spine, the haemal keel developed in middle trunk vertebrae, and the presence of well-developed prezygapophyseal processes. The attribution of the middle trunk vertebrae to the genus '*Coluber*' (for further discussion concerning taxonomy of fossil representatives see Szyndlar, 2009, 2012) is further supported by the strong craniocaudal elongation of the centrum, the vaulted (though weakly) neural arch, the narrow but prominent haemal keel in middle trunk vertebrae and long prezygapophyseal processes. 'Colubrines' referred to the genus *'Coluber'* have been reported from numerous European Neogene localities (e.g., Ivanov & Böhme, 2011; Ivanov, 2002a, 2002b, 2022; Rage & Bailon, 2005; Szyndlar & Schleich, 1993; Szyndlar, 1991a, 2005, 2009, 2012; Venczel, 1994, 1998, 2001). There are three large-sized and probably closely related *'Coluber'* species (Szyndlar, 2005) in the European Miocene including *'Coluber' dolnicensis* Szyndlar, 1987 (de Rochebrune, 1880) (MN 3a–4), *'Coluber' caspioides* (MN 3a–?MN 6), and *'Coluber' pouchetii*(MN 4–9). The taxonomic position of *'C.' dolnicensis* and *'C.' caspioides* as two separate species has been disputed by Szyndlar (1998) who stated that *'C.' dolnicensis* have been established on the basis of two vertebrae only (Szyndlar, 1987) and the degree of intraspecific variability had therefore not been assessed. The comparison of both these latter species from the locality of Merkur-North, Czechia (MN 3a) uncovered that *'C.' dolnicensis* differed from *'C.' caspioides* by the presence of a distinct 'step' formed by the haemal keel in the anterior part of centrum through the middle and posterior trunk section as well as by the diapophysis shifted posteriorly with regard to the parapophysis (Ivanov, 2002a; Szyndlar, 1987). Alternatively, a possible close relation of *'C.' dolnicensis* and *'C.' pouchetii* has been considered (Rage & Bailon, 2005) by the same development of the paradiapophysis and similar morphology of the haemal keel. However, in *'C.' pouchetii*, a 'step' forming haemal keel occurs only in posterior trunk vertebrae (Rage & Bailon, 2005).

The 'colubrid' snake from Wintershof-West cannot be attributed to *'Coluber' pouchetii* because the morphology of its trunk vertebrae is different from that known in the latter species (Augé & Rage, 2000; Rage, 1981; Rage & Bailon, 2005; Szyndlar, 2005): (1) the ventral centrum of vertebrae delimited by strongly developed subcentral ridges is elongated and narrow instead of relatively wide centrum reported in *'C.' pouchetii*; (2) the zygosphenal lip is always distinctly three-lobed in dorsal view unlike straight or weakly convex zygosphene, sometimes with an indistinct medial notch reported in *'C.' pouchetii*; (3) the diapophysis is not positioned behind the parapophysis; (4) cotyle is circular instead of laterally depressed cotyle in *'C.' pouchetii*; (5) incomplete hypapophyses of the anterior trunk vertebrae display posterior inclination instead of vertical or anteriorly inclined hypapophysis reported in *'C.' pouchetii* from France and Hungary (Augé & Rage, 2000; Rage & Bailon, 2005; Szyndlar, 2005).

Trunk vertebrae of *'Coluber'* aff. *caspioides* from Wintershof-West particularly resemble those of *'C.' caspioides* reported from the Early Miocene (MN 4a) type locality of Petersbuch 2, Germany (Szyndlar & Schleich, 1993) by the following combination of characters: (1) the centrum is elongated craniocaudally; (2) the posterodorsal lamina of the neural arch is usually weakly vaulted, nearly straight or straight in caudal view; (3) the neural spine of the middle trunk vertebrae is high, with cranial margin inclined anteriorly and caudal one posteriorly (the anterodorsal portion of the neural spine can be is tilted in the largest specimen; (4) the haemal keel is prominent, thin and enlarged (cuneate shaped) posteriorly or with flat posterior ventral surface in middle trunk vertebrae. The haemal keel is variable within the vertebral column with sloping anterior keel in vertebrae positioned in the posterior trunk section. Moreover, the largest (overgrown) specimen of the posterior trunk vertebra (SNSB-BSPG 1937 II 24641; Fig. 20f–i) displays rather wide ventral surface of the haemal keel with shallow but distinct medial furrow restricted mainly in its posterior portion (Fig. 20g). However, *'C.'* aff. *caspioides* differs from *'C.' caspioides* by the (1) clearly three-lobed zygosphene in dorsal view in all precaudal vertebrae instead of mostly straight and medially slightly notched zygosphenal roof with moderately developed lateral lobes in the latter species; (2) shorter prezygapophyseal processes; (3) smaller dimensions. Because of close morphological similarity of *'C.'* aff. *caspioides* with *'C.' caspioides* reported from Petersbuch 2 (MN 4) we hypothesise that *'C.'* aff. *caspioides* morphotype could represent a member of the lineage ancestral to the later species. The caudal vertebrae have been attributed to *'C.'* aff. *caspioides* based on the shape of the neural spine and the nearly straight posterodorsal lamina of the neural arch. However, identification of fragmentary caudal vertebrae of colubroid snakes is usually problematic and therefore, this identification is only tentative.

'Colubridae' indet., type 1

Material. – 43 trunk vertebrae (SNSB-BSPG 1937 II 24659–24701).

Trunk vertebrae (Fig. 21): All preserved vertebrae of this small-sized snake (CL of the largest specimen is 4.31 mm; see Appendix 1) are at least partially fragmentary. In lateral view, the neural spine of the middle trunk vertebrae rises roughly in mid-length of the zygosphene. It is almost three times longer than high and its cranial margin is vertical or slightly inclined anteriorly and the caudal one overhangs posteriorly. The zygosphenal facet is usually narrow and oval-shaped, with its long axis oriented distinctly anteriorly. The lateral foramen is situated close below the well-developed interzygapophyseal ridge. The distal contact surface of the diapophysis and the short parapophysis are equally sized. The ventral border of the parapophysis extends below the cotyle. The blunt but strongly developed subcentral ridge is either moderately or more distinctly arched dorsally. The haemal keel is prominent, with anterior keel sloping towards the cotylar rim in the posterior trunk vertebrae. The condyle is developed on the short neck. In dorsal view, the zygosphene is usually three lobed, with median lobe blunt and wider than pointed lateral lobes, but in the largest vertebrae, the cranial margin can be almost convex or straight, with short lateral lobes. Prezygapophyseal articular facets are large and subtriangular in outline. Prezygapophyseal processes are rather short, usually reaching less than half the prezygapophyseal facet length, with blunt their distal termination. The specimen SNSB-BSPG 1937 II 24676 with distally pointed prezygapophyseal processes is the only exception (Fig. 21g–k). The prezygapophyseal processes are strongly flattened at their base, which is inclined posteroventrally, as best visible in lateral aspect. The diapophysis is directed laterally rather than posterolaterally. The epizygapophyseal ridges are absent. The caudal notch is deep. In ventral view, deep and relatively wide notches occur between parapophyseal bases and the ventral margin of the cotylar rim. The straight subcentral ridges are short disappearing far from the posterior lamina of the pedicle. The subcentral grooves are wide, but in more posteriorly positioned vertebrae, they become deeper and narrower. In the largest middle trunk vertebrae (Fig. 21f), the thin haemal keel with rounded ventral surface is of equal width along its entire length; however, in more posteriorly positioned (Fig. 21n, s) vertebrae, the haemal keel slightly expands towards its caudal termination. Postzygapophyseal articular facets are subtriangular to subsquare. In cranial view, the neural canal is rounded with wide lateral sinuses. The zygosphenal roof is vaulted dorsally. Prezygapophyses are directed horizontally with large foramina situated at the bases of the prezygapophyseal processes. There are deep depressions occurring on either side of the cotyle, with paracotylar foramen

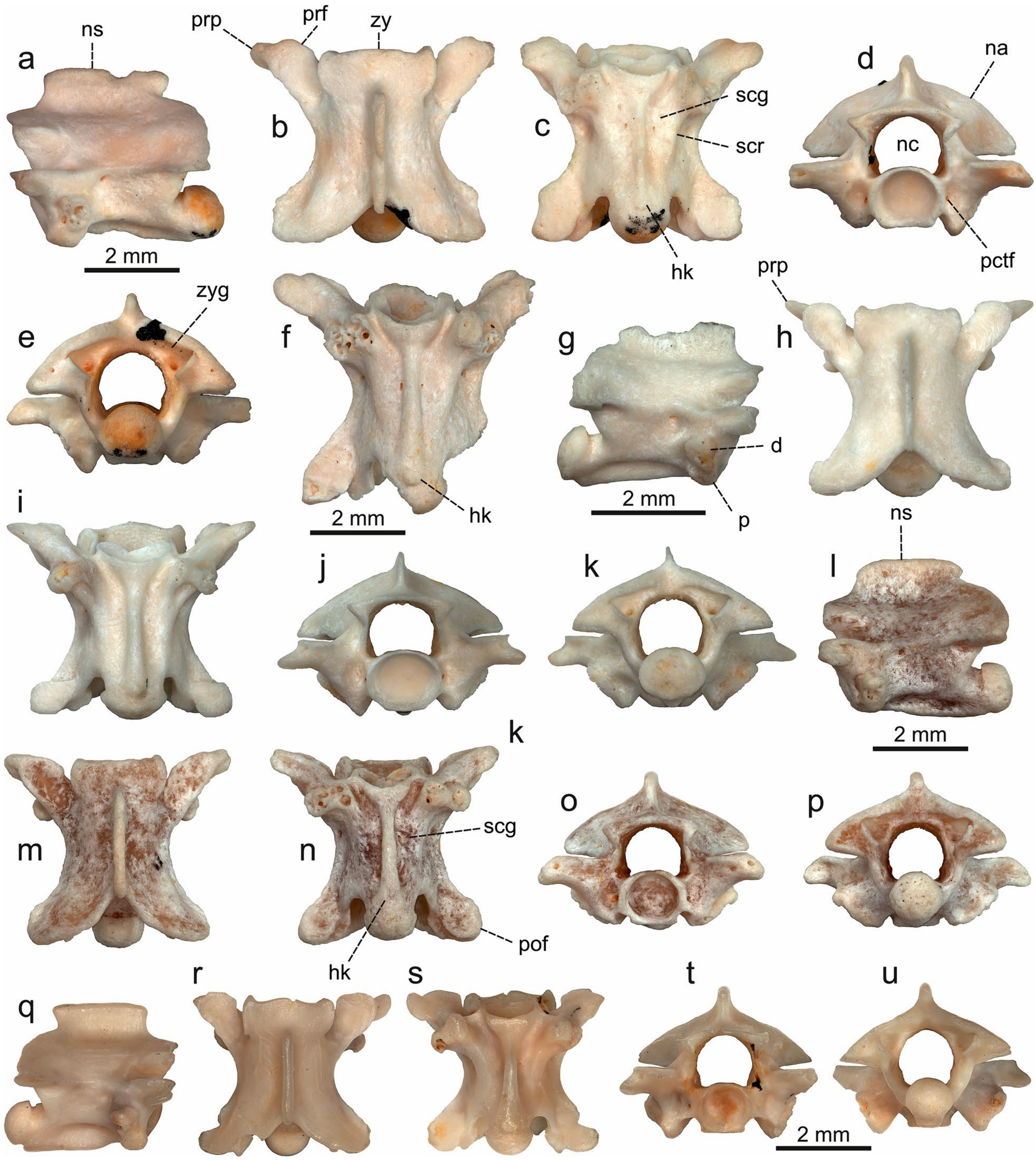

Fig. 21 'Colubridae' indet., type 1 from Wintershof-West, Germany. **a**–**e**, anterior middle trunk vertebra (SNSB-BSPG 1937 II 24674) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**, middle trunk vertebra (SNSB-BSPG 1937 II 24675) in ventral view; **g**–**k**, middle trunk vertebra (SNSB-BSPG 1937 II 24676) in right lateral (**g**), dorsal (**h**), ventral (**i**), cranial (**j**), and caudal (**k**) views; **l**–**p**, middle/posterior trunk vertebra (SNSB-BSPG 1937 II 24677) in left lateral (**l**), dorsal (**m**), ventral (**n**), cranial (**o**), and caudal (**p**) views; **q**–**u**, posterior trunk vertebra (SNSB-BSPG 1937 II 24678) in right lateral (**q**), dorsal (**r**), ventral (**s**), cranial (**t**), and caudal (**u**) views. d, diapophysis; hk, haemal keel; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene; zyg, zygantrum

situated close to the slightly dorsoventrally depressed cotylar rim. Small subcotylar tubercles are present. In caudal view, the neural arch is vaulted, with VR ranging from 0.34 to 0.45; the zygantral area is wide, with parazygantral foramina situated between the zygantral and postzygapophyseal facets. The small condyle is rounded and usually with slightly compressed its ventral border.

Remarks: The middle trunk vertebrae unquestionably belong to colubroids as documented by the presence of paracotylar foramina, elongated centrum, the vaulted neural arch, the well-developed thin neural spine and the horizontal prezygapophyses with distinct prezygapophyseal processes (Rage, 1984; Szyndlar, 1984, 1991a; Zaher et al., 2019). The unambiguous attribution of isolated fossil snake vertebrae to Colubridae is often complicated because similar vertebral features shared in multiple clades are most likely a result of homoplasy (e.g., Head, 2005; McCartney, 2015). The absence of hypapophysis in middle trunk vertebrae excludes attribution to Asiatic Pseudoxenodontidae, Sibynophiidae and almost all Old and New World Natricidae except for *Amphiesma* (Ikeda, 2007; Zaher et al., 2019), although possible absence of hypapophysis in other natricids has been also considered (McDowell, 1961). 'Colubrid' morphotype 1 from Wintershof-West differs from South Asiatic *Oreocalamus hanitschi* Boulenger, 1899 (Calamariidae) by the less elongated centrum, the more anteriorly placed anterior margin of the neural spine, absence of long and acute prezygapophyseal processes and well-developed subcentral ridges instead of blunt subcentral ridges in calamariids (Zaher et al., 2019). It differs from African *Grayia* Günther, 1858 (Grayiidae) by the less vaulted neural arch with shallower caudal notch, caudal lamina of the neural arch not extending behind the postzygapophyseal articular facets, less elongated centrum, obtuse distal tip of prezygapophyseal processes and ventrally rounded instead of flat haemal keel (Zaher et al., 2019). The distinction of 'Colubridae' indet., type 1 from the highly diversified Dipsadidae (more than 800 species; Grazziotin et al., 2012; Serrano et al., 2024) is complicated as vertebral morphology of most of dipsadids is still unknown. However, almost all members of this group, except for the basal *Thermophis* Malnate, 1953 which is endemic to China (He et al., 2009; Huang et al., 2009), are restricted to the New World, mainly in Central and South America (Grazziotin et al., 2012; Serrano et al., 2024). The North American clade of dipsadids comprises only five extant species including *Carphophis* Gervais in Orbigny, 1843; *Contia* Baird & Girard, 1853, *Diadophis* Baird & Girard, 1853, *Farancia* Gray, 1842b, and *Heterodon* Latreille in Sonnini and Latreille, 1801 Pinou et al., (2004) and three extinct genera including *Dryinoides* Auffenberg, 1958, probably closely related to *Heterodon*, *Paleoheterodon* Holman, 1964, and *Paleofarancia* Auffenberg, 1963 of indistinct taxonomic status (Holman, 2000). 'Colubridae' indet., type 1 from Wintershof-West differs from above mentioned extant and fossil North American dipsadids by the following combination of characters in middle trunk vertebrae: (1) the centrum is elongated; (2) prezygapophyseal processes are short and obtuse; (3) the neural spine is moderately low and without protrusion behind its anterior base; (4) the haemal keel is not wide. We consider attribution to Colubridae as the most plausible. The short and distally obtuse prezygapophyseal processes together with the neural spine which does not overhang anteriorly and clearly protrudes posteriorly, as well as narrow haemal keel indicate a possible attribution to the genus *Elaphe*. We found only minor differences from the extant Asiatic *Elaphe*, mainly *Elaphe dione* (Pallas, 1773). 'Colubrid' from Wintershof-West differs from the latter species by (1) the zygosphene which is straight to crenate in dorsal aspect and arched dorsally in anterior aspect instead of crenate and straight zygosphene in *E. dione*; (2) obtuse prezygapophyseal processes instead of usually more acute prezygapophyseal processes reported in *E. dione* (Ratnikov, 2004, 2022). We consider 'colubrid' from Wintershof-West a distinct morphotype; however, we avoid a more precise taxonomic identification.

'Colubridae' indet., type 2

Material. – 16 trunk vertebrae (SNSB-BSPG 1937 II 24702–24717).

Trunk vertebrae (Fig. 22) The vertebrae are mostly fragmentary, with damaged neural spine, prezygapophyseal processes and incomplete paradiapophyses. The vertebrae are small with centrum length of the largest vertebra (SNSB-BSPG 1937 II 24717; Fig. 22k, l) < 4 mm (Appendix 1). In lateral view, the neural spine is about twice longer than high. The cranial margin of the neural spine, which rises at the level of the mid-length of the oval zygapophyseal facet, is nearly vertical and its caudal margin is inclined posteriorly. The small lateral foramen is situated below the well-developed interzygapophyseal ridge, which is blunt at the level of the narrowest interzygapophyseal constriction. The rather small diapophysis is well-separated from the equally sized or slightly larger parapophysis. The blunt subcentral ridges are almost straight of slightly arched dorsally. The ventral margin of the shallow haemal keel is straight. The relatively short condyle is developed on the distinct condylar neck. In dorsal view, the zygosphenal lip possesses well-developed and distally pointed lateral lobes, while the medial lobe is wide and usually less distinct. The large prezygapophyseal articular facets are sub-rhomboid in the most complete vertebra (Fig. 22b) with long axes directed anterolaterally.

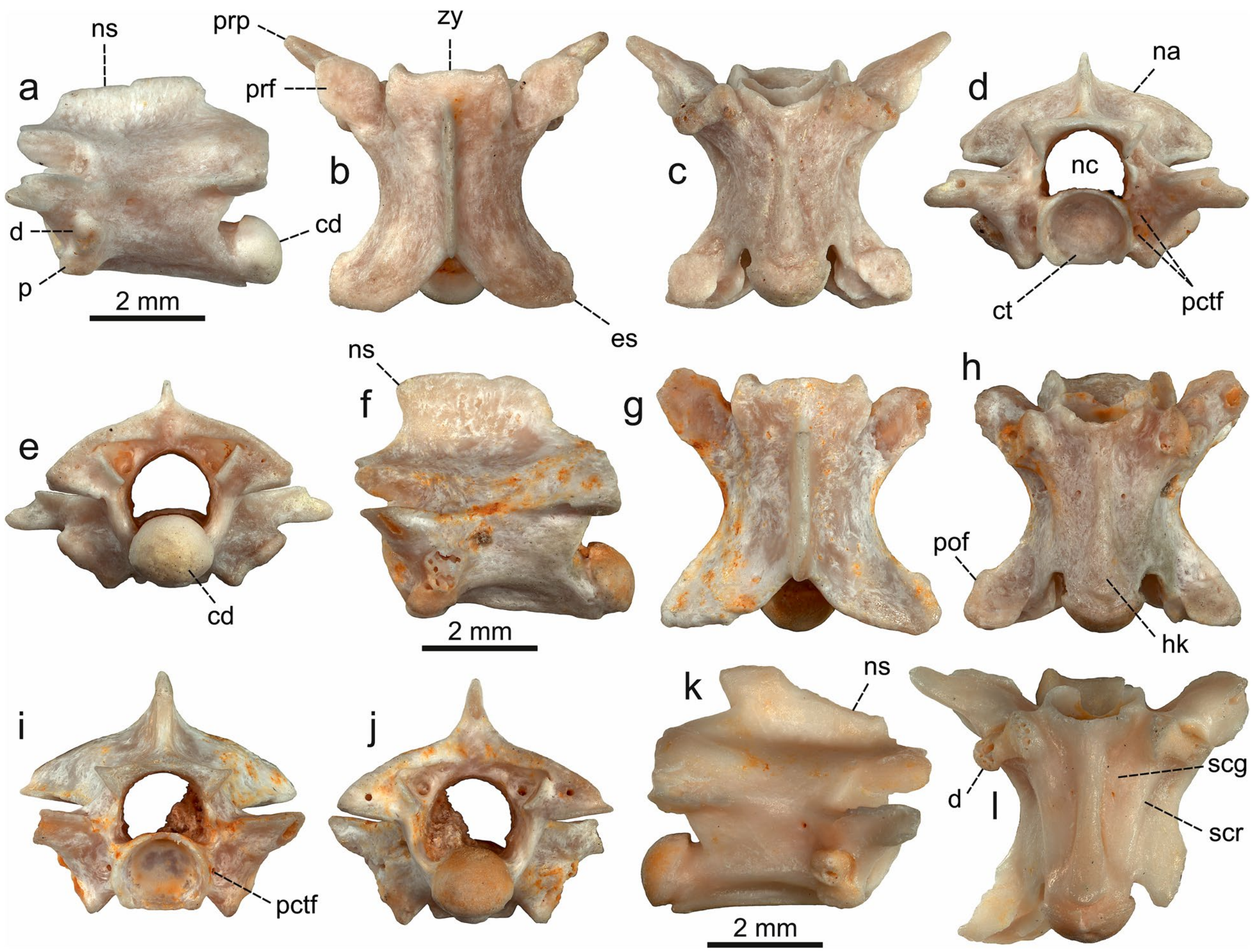

Fig. 22 'Colubridae' indet., type 2 from Wintershof-West, Germany. **a**–**e**, middle trunk vertebra (SNSB-BSPG 1937 II 24715) in left lateral (**a**), dorsal (**b**), ventral (**c**), cranial (**d**), and caudal (**e**) views; **f**–**j**, middle trunk vertebra (SNSB-BSPG 1937 II 24716) in right lateral (**f**), dorsal (**g**), cranial (**h**), ventral (**i**), and caudal (**j**) views; **k**, **l**, posterior trunk vertebra (SNSB-BSPG 1937 II 24717) in right lateral (**k**) and ventral (**l**) views. cd, condyle; ct, cotyle; d, diapophysis; es, epizygapophyseal spine; hk, haemal keel; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene

The anterolaterally directed prezygapophyseal processes reach half the prezygapophyseal articular facets length. They are slender, with their distal termination pointed or moderately rounded. There is no thickening of the neural spine. The epizygapophyseal spines are either absent or present as minute projections visible at the caudal margin of the postzygapophyses. The caudal notch is deep. In ventral view, the centrum ventral base is narrow and delimited by straight to medially slightly curved subcentral ridges. The subcentral ridges are blunt and subcentral grooves are shallow in the middle trunk vertebrae; however, in the posterior trunk vertebrae, the subcentral ridges are sharper and separated from the haemal keel by the deep subcentral grooves. The ventral surface of the cuneate haemal keel is rounded, with slightly flattened its caudal portion in the middle trunk vertebrae. In the posterior trunk vertebrae, the prominent haemal keel is straighter along its entire length. The subcotylar tubercles are absent. The postzygapophyseal articular facets are subsquare to subrectangular in outline. In cranial view, the neural canal is rounded with short lateral sinuses. The thin zygosphenal lip is moderately arched dorsally. Prezygapophyseal articular facets are placed above the dorsal margin of the cotylar rim. They are horizontal with large foramina situated at the base of the prezygapophyseal processes. Paracotylar foramina, sometimes doubled, occur within deep depressions on either side of the dorsoventrally flattened cotyle with straight its ventral margin. In caudal view, the neural arch is vaulted, with VR ranging from 0.31 to 0.41, and the zygantrum is wide. The irregularly spaced parazygantral foramina occur between the zygantral and postzygapophyseal facets. The condyle is rounded, with its ventral border slightly flattened.

Remarks: The middle trunk vertebrae are typical by the elongated centrum, well-developed prezygapophyseal processes, moderately high neural spine, vaulted neural arch and the presence of prominent cuneate haemal keel which enables attribution to a small-sized 'colubrid' snake. The vertebrae of 'Colubridae' indet., type 2 differ from those of 'Colubridae' indet., type 1 by much straight, slender, longer and distally pointed or moderately rounded prezygapophyseal processes. 'Colubridae' indet., type 2 differs from the genus *Eirenis* Jan, 1863 by larger dimensions and more slender prezygapophyseal processes (Szyndlar, 1991a). The morphotype differs from all representatives of the genus *Elaphe*, including small to medium-sized *Elaphe dione* and *Elaphe quadrivirgata* (Boie, 1826), as well as *Zamenis* Wagler, 1830, including the small to medium-sized *Zamenis scalaris* (Schinz, 1822) and *Zamenis situla* (Linnaeus, 1758) by the more elongated centrum of the middle trunk vertebrae, longer and more slender prezygapophyseal processes directed anterolaterally and smaller para- and diapophyses (Chen, 2020; Ikeda, 2007; Ratnikov, 2004, 2022; Szyndlar, 1984, 1991a). The morphotype differs from *Hemorrhois hippocrepis* (Linnaeus, 1758) by the more depressed neural arch, the more anteriorly directed prezygapophyseal processes and cuneate instead of sharp haemal keel (Bailon, 1986), it differs from *Hemorrhois ravergieri* (Ménétriés, 1832) and *Hemorrhois nummifer* (Reuss, 1834) by its more depressed neural arch and further from *H. nummifer* by the higher ratio of the centrum length to the prezygapophyseal articular facets outer edges width (0.75 vs. 0.63–0.71; Schätti, 1987; Deepak et al., 2021b). It differs from *Platyceps najadum* (Eichwald, 1831) by larger prezygapophyseal articular facets and extinct *Platyceps planicarinatus* (Bachmayer & Szyndlar, 1985) by the longer prezygapophyseal processes, much narrower haemal keel, and flattened cotyle (Bachmayer & Szyndlar, 1987). The 'colubrid' morphotype 2 from Wintershof-West differs from *Telescopus fallax* Fleischmann, 1831 and the extinct *Telescopus bolkayi* Szyndlar, 2005 by the less depressed neural arch, less distinct medial lobe of the zygosphene, and spatulate haemal keel (Szyndlar, 2005; Venczel, 2000). The trunk vertebrae of 'Colubridae' indet., type 2 resemble those of small-sized colubrids of genus *Hierophis* including extinct *Hierophis hungaricus* (Bolkay, 1913) reported from the early Middle Miocene of Germany (Ivanov & Böhme, 2011) up to the Early Pliocene of Hungary (Venczel, 2001). The 'colubrid' morphotype 2 from Wintershof-West shares vertebral morphology with *H. hungaricus* by the same length of prezygapophyseal processes, the moderately dorsally vaulted zygosphene which is wider than cotyle having wide medial and short lateral lobes, the blunt subcentral ridges, and cuneate ventrally rounded to flat haemal keel (Venczel, 1994, 1998, 2011; Szyndlar, 2005; Venczel & Ştiucă 2008). However, prezygapophyseal articular facets of the middle trunk vertebrae of 'Colubridae' indet., type 2 are wider and sub-rhomboid in outline, prezygapophyseal processes are more slender, and cotyle is flattened dorsoventrally unlike those reported in *H. hungaricus* (Venczel, 1994, 1998). The vertebral morphology is rather homogeneous within small-sized 'colubrids' and it is even difficult to distinguish different genera like *Hierophis*, *Platyceps*, *Eirenis* or *Hemorrhois* (e.g., Georgalis et al., 2019b, 2024; Szyndlar, 1991a, 2012). Therefore, we avoid of identification to the generic level.

'Colubridae' indet., type 3

Material. – 24 middle trunk vertebrae (SNSB-BSPG 1937 II 24718−24741).

Trunk vertebrae (Fig. 23): In lateral view, the small-sized vertebrae are all fragmentary, with partially damaged neural spine, broken-off prezygapophyseal processes close to their base, and usually damaged paradiapophyses. In lateral view, the neural spine is moderately high and about 2.5 times longer than high. Its cranial margin is vertical whereas caudal one is slightly inclined posteriorly. The zygosphenal facet is oval. The prominent lateral foramen is situated in no depression and close below the distinct interzygapophyseal ridge. The para- and diapophyses are equally sized. The parapophysis only slightly extends below the cotylar base, which is best seen in anterior view. The blunt subcentral ridge is moderately arched dorsally. The haemal keel is markedly low and usually slightly arched dorsally. The condyle is developed on the short neck. In dorsal view, the vertebrae are elongated craniocaudally, with distinct interzygapophyseal constriction. The zygosphene is convex with short lateral lobes. The long axis of oval prezygapophyseal articular facets is directed anterolaterally, however, their exact outline cannot be judged due to their partial damage. The epizygapophyseal ridges/spines are absent. The caudal notch is deep. In ventral view, the centrum ventral base is triangular and delimited laterally by the slightly medially arched subcentral ridges. The subcentral foramina are situated at the base of the flat haemal keel. The haemal keel becomes slightly wider and spatulate toward its caudal termination. Subcentral grooves are very shallow and developed only in the anterior half of the centrum. In the more posteriorly positioned vertebrae the subcentral ridges and grooves are more noticeable. The postzygapophyseal articular facets are subsquare (Fig. 23f). In cranial view, the neural canal is rounded with short lateral

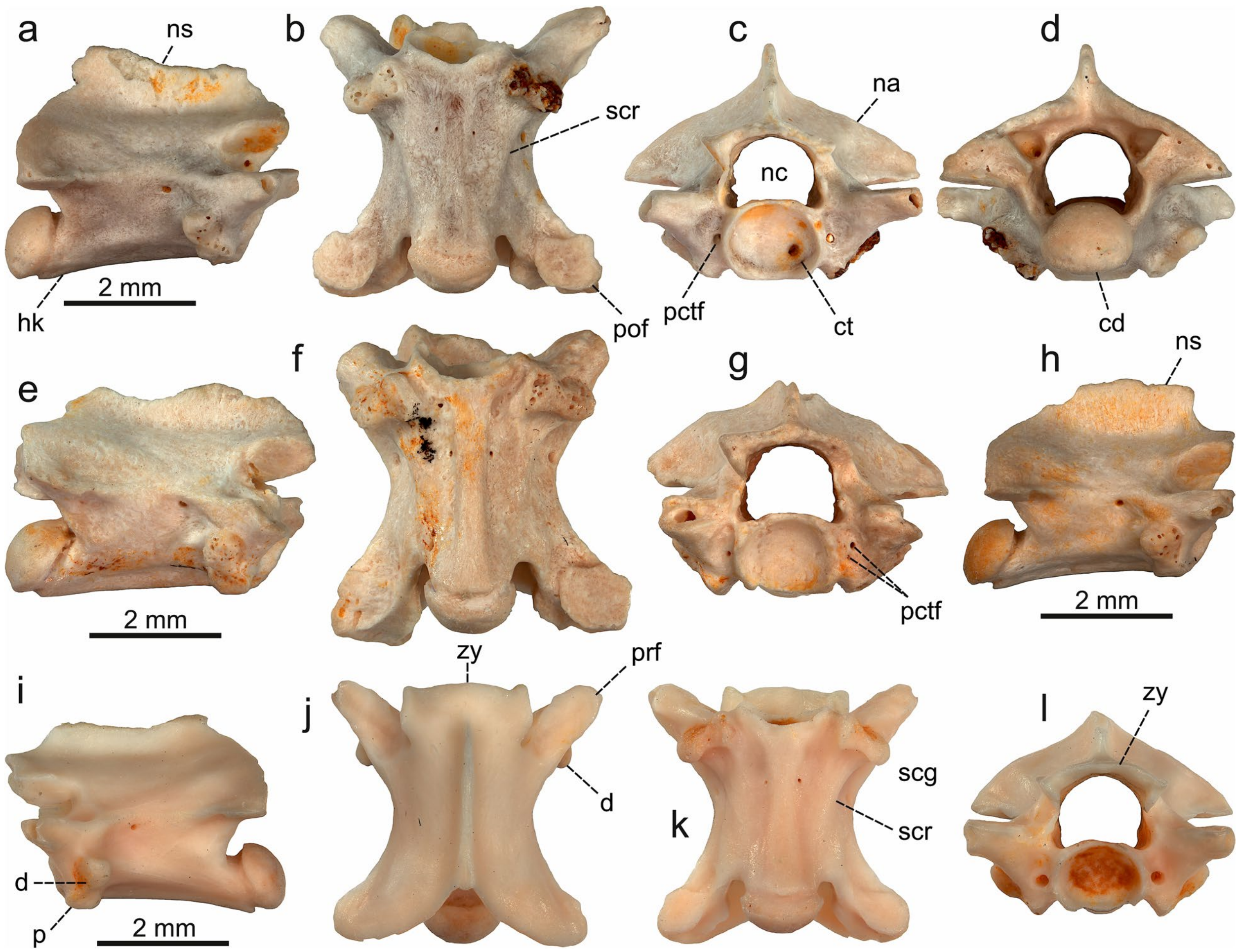

Fig. 23 'Colubridae' indet., type 3 from Wintershof-West, Germany. **a**–**d**, middle trunk vertebra (SNSB-BSPG 1937 II 24738) in right lateral (**a**), ventral (**b**), cranial (**c**), and caudal (**d**) views; **e**–**g**, middle trunk vertebra (SNSB-BSPG 1937 II 24739) in right lateral (**e**), ventral (**f**), and cranial (**g**) views; **h**, middle trunk vertebra (SNSB-BSPG 1937 II 24740) in right lateral view; **i**–**l**, middle/posterior trunk vertebra (SNSB-BSPG 1937 II 24741) in left lateral (**i**), dorsal (**j**), ventral (**k**), and cranial (**l**) views. cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene

sinuses. The zygosphenal lip is arched dorsally. Prezygapophyses are horizontal with prezygapophyseal articular facets developed at the level of the dorsal margin of the slightly dorsoventrally depressed cotylar rim. Paracotylar foramina are prominent and occur on either side of the cotylar rim. Sometimes, paracotylar foramina are doubled (Fig. 23g). In caudal view, the posterodorsal lamina of the neural arch is vaulted, with VR ranging from 0.38 to 0.46. The zygantrum is wide. Multiple parazygantral foramina usually occur on the posterior wall of the neural arch.

Remarks: The small-sized fragmentary vertebrae (see Appendix 1) display typical colubrid morphology including an elongated centrum, the moderately high neural spine, the moderately arched neural arch, horizontal prezygapophyses in cranial view, the presence of well-developed prezygapophyseal processes, the presence of distinct haemal keel in middle trunk vertebrae, and the presence of paracotylar foramina. 'Colubridae' indet., type 3 differs from other two Wintershof-West morphotypes ('Colubridae' indet., type 1 and 2) by the haemal keel being markedly flat and spatulate posteriorly in ventral view and low and slightly dorsally arched in lateral view. 'Colubridae' indet., type 1 further differs from 'Colubridae' indet., type 3 by the presence of smaller paracotylar foramina and parapophyses protruding more ventrally below the cotyle. The elongated centrum, the moderately arched neural arch, the moderately high neural spine whose cranial margin is vertical and caudal one inclined posteriorly, and the flat haemal keel reported in 'Colubridae' indet., type 3 are features reminiscent of European colubrids of the *Hierophis* clade and especially *Hierophis viridiflavus* (Lacépède, 1789) (e.g., Szyndlar, 1991a; Venczel, 2000). However, 'Colubridae' indet., type 3 differs from the extant species by the less ventrally protruding parapophyses in anterior view and larger paracotylar foramina. The fragmentary state of preserved vertebrae does not allow a more precise identification.

'Colubridae' indet.

Material. – 18 anterior trunk vertebrae (SNSB-BSPG 1937 II 24742–24759), 292 middle and posterior trunk vertebrae (SNSB-BSPG 1937 II 24760–25051), five articulated (3 + 2) trunk vertebrae (SNSB-BSPG 1937 II 25052–25053), four articulated (2 + 2) trunk vertebrae (SNSB-BSPG 1937 II 25054–25055), four articulated (2 + 2) trunk vertebrae (SNSB-BSPG 1937 II 25056–25057), one cloacal vertebra (SNSB-BSPG 1937 II 25058), and two caudal vertebrae (SNSB-BSPG 1937 II 25059–25060).

Remarks: All vertebrae are fragmentary, usually exhibiting broken-off neural spines, incomplete prezygapophyseal processes and eroded paradiapophyses. The presence of paracotylar foramina, well developed prezygapophyseal processes (although their distal termination did not preserve), the vaulted neural arch and elongated centrum with well-developed haemal keel in the middle trunk vertebrae enable attribution to 'Colubridae' (Szyndlar, 1984, 1991a). The moderately developed interzygapophyseal ridges which are blunt rather than sharp, the posteriorly spatulate haemal keel and lateral foramina well-visible in lateral view are reminiscent of *Hierophis hungaricus* reported from the Late Miocene of Hungary, MN 13 (see below; Venczel, 1994, 1998). However, the poor preservation of vertebrae does not allow a closer identification, and it cannot be even ruled out that several distinct taxa might occur within the indeterminate 'colubrid' assemblage.

Colubriformes indet.

Material. – Seven anterior trunk vertebrae (SNSB-BSPG 1937 II 25061–25067), 36 middle and posterior trunk vertebrae (SNSB-BSPG 1937 II 25068–25103), 6 articulated (2 + 2 + 2) trunk vertebrae (SNSB-BSPG 1937 II 25104–25106), and 277 cloacal and caudal vertebrae (SNSB-BSPG 1937 II 25107–25383).

Remarks: All preserved vertebrae are very fragmentary with broken-off or eroded neural spine and hypapophysis in anterior trunk vertebrae, the damaged neural spine, paradiapophyses and prezygapophyses in the middle trunk vertebrae, and lymphapophyses or pleurapophyses and haemapophyses in cloacal and caudal vertebrae. The elongated centrum in the middle trunk vertebrae, the presence of paracotylar foramina, well-developed neural spine and subcentral structures and well-developed prezygapophyseal processes indicate that fragmentary vertebrae belonged to indeterminate colubriform snakes.

Discussion

The fissure filling Wintershof-West is one of the most exceptional Miocene fossil sites in Central Europe in terms of mammalian abundance and diversity. From the original excavation in 1937, two metric tons of sedimentary fissure infill were collected, yielding 100.000 vertebrate specimens (Dehm, 1961), of which approximately 50.000 survived the Second World War (Dehm, 1950a). From the 85 documented mammal taxa (e.g., Dehm, 1950a, 1950b; Hrubesch, 1957; Ginsburg & Guérin, 1979; Ziegler 2005, Ziegler et al., 2005), 30 carnivoran species are described, deriving from nearly 2000 specimens (Dehm, 1950a). This represents the highest observed carnivore diversity from a single fissure filling, respectively site (Kargopoulos et al., 2024). Cranial and dental material of rodents enumerate 10,000 specimens (Dehm, 1950b). The most frequent rodent species are the eomyid *Ligerimys lophidens* (MNI = 778), the glirid *Prodryomys gregarius* (MNI = 729), and the tree squirrel *Palaeosciurus fissurae* (MNI = 213) (Dehm, 1950b).

Although the highly diversified vertebrates from Wintershof-West include also amphibians, reptiles, and birds, only albanerpetontids (Gardner & Böhme, 2008), geoemydid turtles of the genus *Ptychogaster* (Schäfer, 2013), chamaeleonids (Moody & Roček, 1980), and birds (Ballmann, 1969; Göhlich, 2017; Mlíkovský, 2002; Mlíkovský & Göhlich, 2000) have been studied in detail.

In the following paragraphs we discuss the evolutionary, environmental, and palaeoclimatic implications, based on the taxonomic results of the diverse ophidian fauna of Wintershof-West, representing 14 species out of 2000 isolated vertebrae.

Aquitanian—the final stage of the 'Dark Period' for European booid snakes

The European fossil snake record is generally well-known for the Paleogene and Neogene (e.g., Ivanov, 2007, 2022; Smith & Georgalis, 2022; Szyndlar & Rage, 2003; Szyndlar, 1991a, 1991b, 2012). However, our knowledge of snakes from the latest Oligocene (MP 29–30; e.g., Rage, 1987; Böhme, 2008; Szyndlar & Böhme, 1996; Szyndlar & Rage, 2003) and earliest Miocene (MN 1–2; see below) is still very restricted. The early Aquitanian decrease of temperatures in Central Europe with mean annual temperature (MAT) ~16 °C and cold month mean temperature (CMMT) ~5.5 °C (Mosbrugger et al., 2005) which continued towards the Western Asia with MAT ~14–16 °C and CMMT ~2–5 °C (Kayseri-Özer, 2013) contributed to the decrease of European snake diversity within the time span from MP 29 to MN 2. This decrease, sometimes called the 'Dark Period' for booid snakes (Rage & Szyndlar, 2005; Szyndlar & Rage, 2003), is particularly remarkable in comparison with the relatively rich MP 28 communities known mainly from France and Germany (Szyndlar & Rage, 2003). The distribution of Booidea was affected by this climatic change and most Oligocene thermophilic Booidea and alethinophidians of currently uncertain taxonomic allocation (Alethinophidia *incertae sedis* sensu Smith & Georgalis, 2022; see also Szyndlar & Georgalis, 2023) such as *Rottophis* Szyndlar & Böhme, 1996, *Platyspondylia* Rage, 1974 and possibly *Falseryx* (Rage, 1974; Szyndlar & Böhme, 1996; Szyndlar & Rage, 2003) did not survive the Oligocene/Miocene transition in Western and Central Europe. However, it is likely that *Falseryx* could have survived continuously in the southeastern part of Europe until the Miocene, as evidenced by its occurrence in the lowermost Miocene of Anatolia (Syromyatnikova et al., 2019).

Aquitanian (MN 1–2) vertebrate localities are rare in Central Europe, with most known ophidian sites located in Germany, including Weisenau (MN 1–2; Szyndlar & Rage, 2002; Villa et al., 2021), Weißenburg 6 (MN 1–2?; Paclík & Ivanov, 2022; Ivanov, 2022; Figs. 1 and 24), Oppenheim/Nierstein (MN 2; Kuch et al., 2006), Ulm-Westtangente (MN 2; Szyndlar & Rage, 2003), Hessler (MN 2; Kinkelin, 1892; Szyndlar & Böhme, 1993), and Amöneburg (MN 2a; Čerňanský et al., 2015). We know only several snake taxa inhabiting Central Europe during this period including cf. *Eoanilius* sp., *Falseryx petersbuchi*, cf. *Falseryx* sp., *Bransateryx* cf. *vireti*, *Vipera antiqua*, *Vipera* sp. ('*V. aspis*' complex), *Natrix* sp., *Neonatrix* sp., *'Coluber' cadurci*, *'Coluber'* sp., and *Zamenis kohfidischi* (Čerňanský et al., 2015; Ivanov, 2022; Paclík & Ivanov, 2022; Szyndlar & Rage, 2002; Villa et al., 2021). Most Aquitanian snake taxa reported from Central and Western Europe are considered Miocene newcomers whose dispersal from Asia/North America into broader parts of Europe may have been facilitated by the disappearance of the highly thermophilic taxa from Europe (Ivanov et al., 2000; Ivanov, 2000, 2001a; Szyndlar & Schleich, 1993). The only exceptions are *Eoanilius*, *Bransateryx*, and *'Coluber' cadurci*, considered survivors across the Oligocene/Miocene transition (Ivanov, 2022; Szyndlar, 1994, 2012).

There are two events impacting the composition of snake assemblages associated with the palaeobiogeographic and palaeoclimatic evolution of the European area during the earliest Miocene. The first one is the disappearance of 'erycids' of the monotypic genus *Bransateryx* (with the only currently valid species *B. vireti*; Hoffstetter & Rage, 1972) from the European fossil record since the onset of Burdigalian, with its last occurrences in two German localities, Weisenau — old collection, MN 2 (caudal vertebrae are missing; Szyndlar & Böhme, 1993) and Weißenburg 6, MN 1–2? (MI, unpublished) and three localities in France: Paulhiac, MN 1, Saint-Gérand-le-Puy, MN 2, and Poncenat, MN 2 (Georgalis & Scheyer, 2021; Hoffstetter & Rage, 1972; Müller, 1998). However, the absence of caudal vertebrae in Weisenau renders attribution of the available specimens to *Bransateryx* doubtful (Čerňanský et al., 2015). The disappearance of *Bransateryx* from the fossil record might be explained by lower temperatures and increased humidity in Central and Western Europe and lack of arid or semi-arid environments. The extant genus *Eryx* whose uncertain occurrence have been reported in the Spanish Early Miocene locality of Agramón, MN 3/4 (cf. *Eryx* sp.; Szyndlar & Alférez, 2005: Fig. 1F, G) replaced *Bransateryx* in southern Europe. In fact, that figured trunk vertebra from Agramón is heavily damaged and its identification as Booidea indet. would be more plausible. Therefore, the first European *Eryx*, identified on the basis of caudal vertebrae, comes only from the late Early Miocene, MN 4 of Córcoles, Spain (Szyndlar & Alférez, 2005: fig. D-I). The genus *Eryx* is most likely of Asian origin as supported by its earliest appearance in Ayakoz, Kazakhstan (MN 1–2, for updated age see Vasilyan et al., 2017; Malakhov, 2005; Ivanov, 2022: Fig. 5.5).

The second event is the first appearance of endoglyptodont clades Viperidae and Elapoidea. The indeterminate viperid from the earliest Miocene of Weiβenburg 6, Germany (MN 1–?2; Paclík & Ivanov, 2022) together with *Vipera* of the '*V. aspis*' complex from St.-Gérand-le-Puy, France (MN 1 or MN 2a) (Szyndlar & Rage, 2002; Szyndlar & Schleich, 1993) and *Vipera antiqua*, also attributed to the '*V. aspis*' complex (Szyndlar, 1987; Szyndlar & Rage, 2002; Szyndlar & Schleich, 1993) and recently described from Weisenau, Germany (MN 2 — old collection; Villa et al., 2021), are among the oldest known viperids. The first stratigraphically unquestionable records of Viperidae represent isolated fangs from MN 2 of Oppenheim/Nierstein, Germany corresponding in size to fangs of the '*V. aspis*' complex (Kuch et al., 2006). The same locality yielded fangs of elapoid snakes, morphologically reminiscent of *Naja* spp. and the extant Asian genus *Bungarus* Daudin, 1803b (Kuch et al., 2006), but the presence of immature viperids (for ontogenetic development of fangs see Zahradnicek et al., 2008) cannot be ruled out (Rage, 2013). However, still undescribed vertebrae closely similar to those of natricids and non-*Naja* elapoids indicate that elapoids were indeed present in MN 2 of Central Europe (Kuch et al., 2006).

Early Burdigalian (Eggenburgian)—a complete renewal of the European snake fauna

The early Burdigalian (Eggenburgian, ~late MN 2 and most of MN 3; 20.4–18.2 Ma) warming associated with increase in mean annual air temperature (MAT) from 16 °C potentially up to over 20 °C, as evidenced by Böhme (2003) by the first occurrence of large-sized chamaeleonids [*Chamaeleo caroliquarti* Moody & Roček, 1980 reported from the Early and Middle Miocene of Czech Repiblic and Germany (Moody & Roček 1980; Böhme, 2003) is currently considered a nomen dubium (Čerňanský, 2010)] and gavialoids (*Gavialosuchus eggenburgensis* Toula & Kail, 1885). Because this very warm period coincides with the Paratethyan regional stage Eggenburgian, we name it here Eggenburgian Climatic Optimum (ECO; Fig. 25). The ECO was a period of significant changes in the composition of Eurasian snakes including massive dispersal of colubriform snakes in Europe (Ivanov, 2015, 2022; this paper, Figs. 24, 25). Although it cannot be entirely ruled out that the first European Miocene *Falseryx*, *F. petersbuchi*, from the Aquitanian of Weisenau (old collection, MN 2), Germany, was a European survivor from the Oligocene (Villa et al., 2021), it appears more plausible that *Falseryx* entered Central Europe from Southeastern Europe, as supported by its presence in the latest Oligocene–earliest Miocene of Anatolia (Georgalis et al., 2021a; Syromyatnikova et al., 2019). *Falseryx* became widespread in Central Europe during the early Burdigalian as documented by its presence at German localities Bissingen 1, MN 3a (*F. petersbuchi*; Ivanov, MI, pers. observ.) and Wintershof-West, MN 3a (cf. *Falseryx* sp.; see the Systematic Part). The Miocene dispersal of *Falseryx* in Central Europe apparently preceded that of booid genus *Bavarioboa* (Čerňanský et al., 2015; Ivanov, 2022; Villa et al., 2021).

The ECO is followed by the Early Ottnangian Cooling (EOC) event (18.1–17.8 Ma; Grunert et al., 2014). In the Western Paratethys (alkenone-based) Sea Surface Temperature (SST) drop significantly by ~4 °C near the end of the lower Ottnangian stage, from > 28.2 to 24.1 °C, possibly associated with the Mi1b Antarctic glaciation (Grunert et al., 2014).

This intermitted early Ottnangian cooler period was followed by the warmest interval during the Neogene, called Miocene Thermal Maximum (MTM) by Böhme and Winklhofer (2008), dated between 17.7 and 17.2 Ma [the age assignments in Böhme and Winklhofer (2008) are updated in Kováč et al. (2018)]. Fossils from continental sediments attributed to the middle and beginning of late Ottnangian suggest MAT between 22.2 and 24.2 °C. Among these bio-indicators are the highest crocodile diversity with three sympatric species (Baltringen locality, 17.7 Ma), the largest body-size recorded in European crocodiles (Eggingen-Mittelhart locality, 17.5 Ma) and aquatic turtles (Langenau locality, 17.2 Ma), and a paratropical evergreen forest from the Ortenburger Gravel xyloflora (17.2 Ma; Böhme et al., 2007). The very warm atmospheric temperatures are corroborated by tropical SST in the middle and late Ottnangian Paratethys Sea (Grunert et al., 2014).

For the latest Ottnangian and the following Karpathian stage (late Burdigalian) fossil ectotherms and xyloflora point to subtropical temperatures, with MAT between 18.6 and 20.5 °C (Böhme, 2003; Böhme et al., 2007; Ivanov & Böhme, 2011), pointing to a slightly warmer climate than that of the Eggenburgian. This climatic period represents the Miocene Climatic Optimum and lasts till the latest Langhian stage (Fig. 25).

Constrictores (Booidea and Pythonoidea)

Bavarioboa wintershofensis sp. nov., together with *Bavarioboa* sp. from Merkur-North (or Ahníkov I), Czechia (MN 3a; Ivanov, 2002a) and the slightly younger locality of Schnaitheim 1, Germany (MN 3; MI, pers. observ.; for age see Bonilla-Salomón et al., 2022) represent the first European occurrences of the genus *Bavarioboa* since its almost 5 million years lasting disappearance from European fossil record in the late Oligocene about 25 Ma (Szyndlar & Rage, 2003). The Early Miocene reappearance of *Bavarioboa* in Central Europe resulted from its dispersal from Asia as supported by the presence of this genus in Oligo-Miocene Anatolian localities of Kurucan (MP 30–MN 1; Szyndlar & Hoşgör, 2012) and Kilçak (MN 1; Syromyatnikova et al., 2019). *Bavarioboa wintershofensis* sp. nov. differs from its late Oligocene congeners and late Early Miocene (MN 4) *B. hermi* among others by its clearly smaller dimensions. This development reported in early Burdigalian Wintershof-West locality is most likely related to somewhat lower MATs before the onset of the EOC compared to the Miocene Climatic Optimum (MCO, ~17–14.5 Ma; Böhme, 2003; Zachos et al., 2008) whose thermal maximum in western Central Europe (NAFB, North Alpine Foreland Basin) indicates paratropical environment and MAT ~22–24 °C with coldest month temperature above 16 °C (Böhme, 2003). This post-EOC warm climate favoured the dispersal of the largest European Booidea and Pythonoidea (Rage & Szyndlar, 2005), though the first Miocene large constrictor, *Python euboicus* Roemer, 1870 from the Early Miocene, MN 3/4 of Kymi, Greece (Roemer 1870; Szyndlar & Rage, 2003) inhabited Southern Europe as a result of its dispersal either from Asia or Africa via the '*Gomphotherium* land bridge' ~19 Ma (Georgalis et al., 2020a; Harzhauser et al., 2007; Rögl, 1999); this is further supported by the presence of a form reminiscent of *Python euboicus* from the 'nearby' western Anatolian early Middle Miocene (late MN 5) locality of Paşalar (Georgalis et al., 2020b).

Viperidae

Colubriform snakes are represented in the European Early Miocene record by Viperidae, Elapoidea, and Colubroidea clades and became widely distributed in Europe, although the early Burdigalian (MN 3) snakes are well-known only from Merkur-North (Ahníkov), Czechia and Wintershof-West, Germany (Ivanov, 2002a, 2022; Fig. 24). Viperid snakes, being common in Wintershof-West and roughly coeval Schnaitheim 1 locality (MI, pers. observ.), document the oldest distinct appearances of 'Oriental vipers' whose generic status is uncertain because of rather uniform morphology of isolated precaudal vertebrae (e.g., Szyndlar & Rage, 1999). The early Burdigalian appearance of 'Oriental vipers' agrees with time-calibrated tree of vipers, which place the split of *Daboia* + *Vipera* clade from 'Oriental vipers' of the *Macrovipera* + *Montivipera* clade to the earliest Miocene (Šmíd & Tolley, 2019).

Elapoidea

Elapoid snakes from Wintershof-West are represented by the earliest occurrence of *'Micrurus' gallicus*, a coral snake previously reported since the late Early Miocene (MN 4) of France and Germany (Rage & Bailon, 2005; Szyndlar & Schleich, 1993), as well as by another indeterminate elapid, also attributed to coral snakes, which is virtually identical to the small elapid reported from Merkur-North (Ahníkov I), MN 3a, Czechia (Ivanov, 2002a). The fossil record of European pre-EOC elapoids consists only of small-sized snakes reminiscent of recent Asian coral snakes such the as Old World *Calliophis* (Ivanov, 2002a) or attributed to the New World genus *Micrurus* (Paclík et al., 2018). An Asian origin of coral snakes, as revealed by recent molecular studies, displays a sister-group position of the well-supported *Calliophis* clade (excluding *C. bivirgata*; Zaher et al., 2019; Burbrink et al., 2020) to all remaining Elapidae (Burbrink et al., 2020; Das et al., 2023, 2024; Figueroa et al., 2016; Weinell et al., 2024). The vertebral morphology of the diversified Asian clade of extant coral snakes is still largely unknown and the fossil record of Asian coral snakes is missing (Ivanov, 2022). Therefore, it cannot be excluded that European *'Micrurus'*, originally considered the North American newcomer across the 'Bering land bridge' (Rage & Holman, 1984), represents a member of the Asian clade separate from the New World *Micrurus* (Georgalis et al., 2024; Ivanov, 2022; Szyndlar, 2005; Szyndlar & Schleich, 1993; Zaher et al., 2019). Several morphologically different types of coral snakes likely occurred in Europe since MN 2 (Augé & Rage, 2000; Ivanov & Böhme, 2011; Ivanov, 2000, 2002a; Kuch et al., 2006; Rage & Bailon, 2005; Rage & Holman, 1984; Szyndlar & Schleich, 1993) up to the Early Pliocene (Georgalis et al., 2019b, 2024). However, large elapoids, such as the true cobra genus *Naja*, appeared at mid-latitudes in Western or Central Europe somewhat later (Ivanov, 2000, 2001a, 2002a; Villa et al., 2024) and specifically with the onset of the Miocene Climatic Optimum (MCO) because *Naja* is more thermophilic than most 'Oriental vipers' (Ivanov, 2000; Rage & Bailon, 2005; Szyndlar, 2005; Szyndlar & Schleich, 1993).

Colubroidea

Although rather limited occurrences of Colubroidea have been reported in Aquitanian localities, the presence of two morphotypes of 'colubrids' (*Coluber* s.l. 1 and *Coluber* s.l. 2) and three natricids (cf. *Natrix* sp., cf. *Neonatrix* sp., and *?Neonatrix* sp.) in Amöneburg, Germany (MN 2; Čerňanský et al., 2015) as well as the earliest occurrence of *Zamenis kohfidischi* (Bachmayer & Szyndlar, 1985) in Weisenau, Germany (Villa et al., 2021) indicate that colubroids were already relatively diversified in Central Europe during this time. However, only the highly diversified communities of colubroid snakes reported from the early Burdigalian (MN 3) Wintershof-West and Merkur-North (Ahníkov I), Czechia (Ivanov, 2002a; Paclík et al., 2018) localities document their massive dispersal at the beginning of the ECO. As many as seven colubroid taxa make their first appearance during the early Burdigalian (MN 3): 'Colubridae': *'Coluber' dolnicensis*, *'C.' suevicus*, *'C.' caspioides*; Natricidae: *Natrix merkurensis*, *N. sansaniensis*, *Wintershofia robusta* gen. et sp. nov. and possibly *Palaeonatrix lehmani* (*P.* aff. *lehmani*). Moreover, four other distinct colubroid morphotypes occur in Wintershof-West including Natricidae indet., type 1 and 'Colubridae' indet., type 1, 2, and 3. Such sudden increase in colubroid diversity resulted most likely from the existence of a mosaic of variable biotopes which were developed in Central Europe with the onset of warming and increased humidity before the EOC (Mosbrugger et al., 2005). *'C.'* aff. *caspioides* and *P.* aff. *lehmani* also represent distinct morphotypes and might belong to the evolutionary older members of *'C.' caspioides* and *P. lehmani* lineages.

The early Burdigalian 'colubrid' snakes currently attributed to the genus *'Coluber'* (or *Coluber* s.l.), as well as several 'colubrid' morphotypes reported from Wintershof-West, indicate their close similarity with extant relatives. Based exclusively on the vertebrae morphology, *'C.'* aff. *caspioides* is closely related to *'C.' caspioides* reported from coeval Merkur North (Ahníkov I) locality (Ivanov, 2002a). Isolated trunk vertebrae of *'C.' caspioides* from the late Early Miocene (MN 4a) type locality of Petersbuch

2, Germany are almost indistinguishable from those of extant *Dolichophis caspius* (Gmelin, 1789) as stated by Szyndlar and Schleich (1993): "The fossil age of the species from Petersbuch 2 counted on our decision to create a new species rather than to identify it as a living species." Although the axial skeleton displays close similarity with *Dolichophis* (formerly *Coluber*; see Szyndlar & Schleich, 1993), the attribution to extant *Dolichophis* is still not unambiguously supported by cranial bones, which have been identified only at Merkur-North (Ahníkov I), where several cranial elements attributed to *'C.' caspioides* resemble those of extant *Hierophis* (Ivanov, 2002a).

According to recent molecular studies, a split of the *Dolichophis* clade from the *Hierophis-Eirenis* clade is dated back to the late Middle Miocene (~13.5 Ma, early Serravallian) and quickly followed by the split of the *Hierophis* and *Eirenis* clades around ~ 12.5 (Mezzasalma et al., 2015: Fig. 3). The occurrence of a *'C.'* aff. *caspioides* morphotype at Wintershof-West is consistent with the split of whip snakes around the Early Miocene, about 20–19 Ma ago, which agrees with Nagy et al. (2004), who proposed the early splitting of *Hierophis* (including later established *Dolichophis-Eirenis* clade) about 20–18 Ma.

The coeval Wintershof-West and Merkur-North (Ahníkov I) localities display the diversified fauna of Natricidae including at least three extinct species: *Natrix merkurensis*, *N. sansaniensis*, and *Wintershofia robusta* gen. et sp. nov. Although isolated cranial bones (compound bone, quadrate, ectopterygoid, and maxilla) have rarely been described in *N. merkurensis* and *N. sansaniensis* (Ivanov, 2002a), braincase elements, being of crucial importance for the genus level allocation (e.g., Head et al., 2016; Rage & Szyndlar, 1986; Szyndlar, 1984), are absent. The oldest indisputable representative of the *Natrix* lineage comes from the Early Miocene (MN 4) of Echzell, Germany based on an incomplete basisphenoid portion of the parabasisphenoid. Although that well-described basisphenoid was attributed to extinct *Natrix longivertebrata* Szyndlar, 1984 (Vasilyan et al., 2022), there are significant differences between the basisphenoid from Echzell and the referred material from the Late Pliocene (MN 16) type locality of Rębielice Królewskie 1A, Poland (ISEA FR/RK I-10003–10007; Szyndlar, 1984): (1) posterior orifices of the Vidian canal (poVc) are not placed close to the posterior border of the bone in Echzell specimen unlike *N. longivertebrata* from the type locality, whose poVc are situated far behind the caudal termination of the hypophyseal fossa and very close to the posterior border of the bone (see also Rage & Szyndlar, 1986: figs. 5–8 for *N.* aff. *longivertebrata*); (2) there is a low but distinct basisphenoid crest in the Echzell basisphenoid, which can be seen in the photograph but not in the drawing (Vasilyan et al., 2022: Fig. 19A–B). Although this basisphenoid displays morphology known in the grass snake lineage, we consider its attribution to *N. longivertebrata* to be doubtful. The *Natrix* aff. *longivertebrata* morphotype from the Middle Miocene (MN 7 + 8) locality of La Grive L7, France, exhibiting postcranial morphology different from *N. longivertebrata* (Rage & Szyndlar, 1986), most likely represents a separate species, thought to be very closely related to *N. longivertebrata* (Ivanov, 2001a, 2001b; MI, pers. observ.).

Recent molecular studies indicate that the stem *Natrix* lineage diverged from the outgroup (*Thamnophis*) already during the late Eocene (~35.8 Ma, 95% confidence interval [CI]: 52.1–28.8 Ma; Schöneberg et al., 2023). The onset of *Natrix* diversification begun by the splitting off *Natrix maura* in the Early Miocene (21.5 Ma, CI 31.3–17.3 Ma), quickly followed by *N. tessellata* (18.8 Ma, CI 27.2–15.1 Ma) (Schöneberg et al., 2023). *N. natrix* diverged as the most basal grass snake species in the Middle Miocene (13.7 Ma, CI 20.0–11.1 Ma; Schöneberg et al., 2023). The simultaneous appearance of two extinct *Natrix* species, i.e., *N. merkurensis* and *N. sansaniensis*, in the early Burdigalian (MN 3) of Central Europe supports the assumption of a rapid diversification of the genus *Natrix* during the Early Miocene ~20–18 Ma (Fig. 24).

Palaeoenvironment

The non-ophidian herpetofauna from the Early Miocene (early MN 3) Wintershof-West provides 14 taxa, belonging to albanerpetontids, newts, salamanders, frogs, chamaeleons, glass lizards, other lizards, turtles, and crocodiles (see Appendix 4). In contrast to mammals and snakes, the finds are not numerous and count to less than 200 specimens. In terms of Minimal Numbers of Individuals (MNI) the collection is dominated by the parsley frog *Pelodytes*, and a yet undescribed species of crocodile newt *Chelotriton* Pomel, 1853, whereas all other taxa are rare. The majority of faunal elements point to the presence of at least temporary water bodies, especially the very abundant *Pelodytes* Bonaparte, 1838b. It is possible that perennial waters (e.g., a karstic lake) have existed nearby, but the indicative taxa like the water frog (*Pelophylax* Fitzinger, 1843) and the crocodile (non-*Diplocynodon*) were rare (Appendix 4). Similarly rare are the heliophobic newts *Ichthyosaura wintershofi* (Lunau, 1950), originally attributed to the genus *Triturus* Rafinesque, 1815, later considered *incertae sedis* within *Triturus* (s.l.) (see Estes, 1981), which were assigned to *Ichthyosaura* (Sonnini de Manoncourt & Latreille, 1801) by Martín et al. (2012), as well as the salamander *Salamandra sansaniensis* Lartet, 1851, suggesting a trend to open landscapes with some bigger trees inhabited by the large-sized chamaeleonids in the vicinity of the fissure. An estimate of palaeo-humidity according to

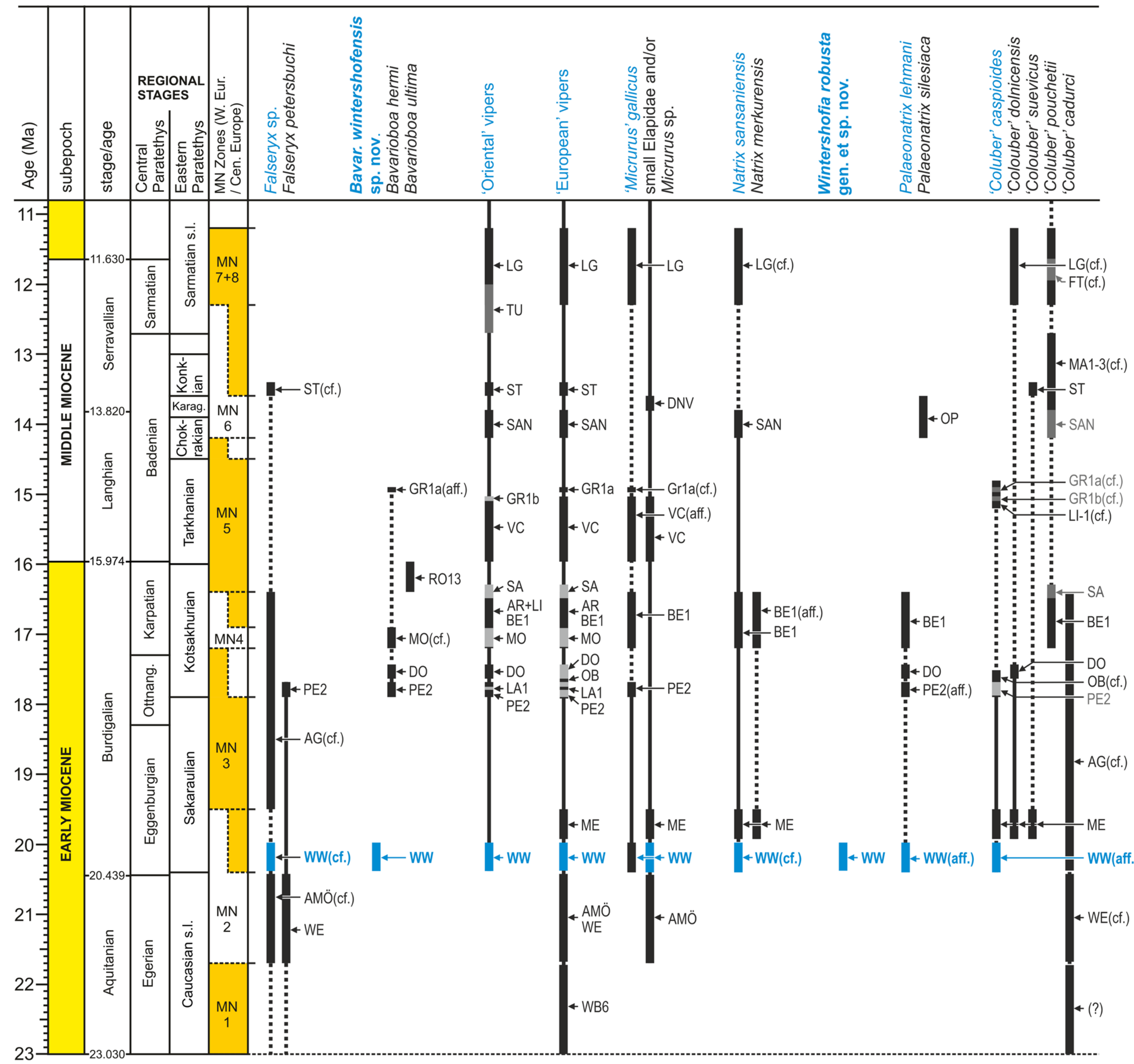

Fig. 24 Stratigraphic ranges of *Falseryx*, *Bavarioboa*, 'Oriental vipers', 'European' vipers of the *'V. aspis'* complex, *Natrix*, *Wintershofia* gen. nov., *Palaeonatrix*, and *'Coluber'* reported from the early Burdigalian of Wintershof-West and other significant Central and Western European localities. Portugal: LI, Lisboa. Spain: AG, Agramón. France: (?), unknown MN 1 locality; BE1, Béon 1; AR, Artenay; VC, Vieux-Collonges; SAN, Sansan; LG, La Grive L5, L7, and M. Germany: WB6, Weißenburg 6; WE, Weisenau; AMÖ, Amöneburg; WW, Wintershof-West; PE2, Petersbuch 2; LA1, Langenau 1; SA, Sandelzhausen; RO13, Rothenstein 13; GR1a and GR1b, Griesbeckerzell 1a and Griesbeckerzell 1b; ST, Steinheim a. Albuch. Poland: OP, Opole. Czech Republic: ME, Merkur-North; MO, Mokrá-Western Quarry; DO, Dolnice. Slovakia: DNV, Devínska Nová Ves. Austria: OB, Oberdorf. Hungary: LI-1, Litke 1; MA1–3, Mátraszőlős 1–3; FT, Felsőtárkány. Romania: TU, Tauţ. Thick lines, stratigraphic ranges of localities; thin lines, confirmed occurrences of taxa; dotted lines, unconfirmed occurrences. Chronostratigraphy and MN zonation according to Ivanov, (2022) (modified). Data compiled from Antunes and Rage (1974), Augé and Rage (2000), Čerňanský et al. (2015), Ivanov (1998, 2002a, 2002b, 2022), Ivanov and Böhme (2011), Ivanov et al. (2020), Paclík and Ivanov (2022), Rage and Bailon (2005), Szyndlar (1987, 2009, 2012), Szyndlar and Alférez (2005), Szyndlar in Młynarski et al. (1982), Szyndlar and Schleich (1993), Szyndlar and Rage (2002, 2003), Venczel (2011), Venczel and Hír (2015), and Venczel and Ştiucă (2008)

the method described by Böhme et al. (2006) results in 500–600 mm rainfall per year. These values are rather an upper estimate, because the faunal composition is biased, at least for the otherwise in fissure-fillings common land tortoises, since practically all recovered chelonian remains have been lost during bombardments of Munich during the Second World War (Dehm, 1950a; the few pieces described by Schäfer, 2013 derive from the

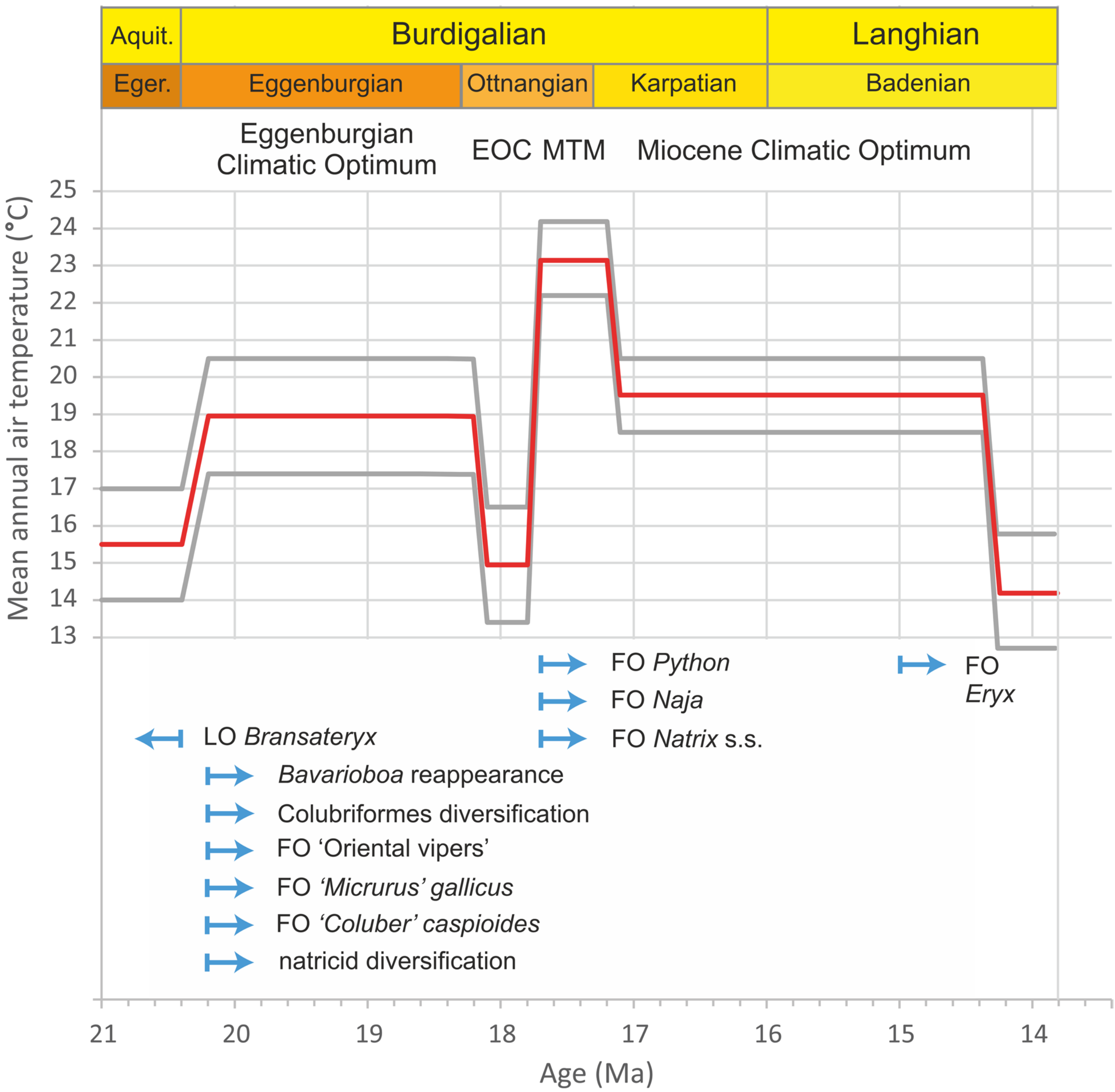

Fig. 25 Ophidian dispersal and diversification events during the Burdigalian and the inferred terrestrial temperatures in Central Europe based on ectotherms and xyloflora evidence (Böhme, 2003; Böhme & Winklhofer, 2008; Böhme et al., 2007; Ivanov & Böhme, 2011). The position and the magnitude of the Early Ottnangian Cooling (EOC), a short-term drop in Paratethyan SST, is according Grunert et al. (2014). The Miocene Thermal Maximum (MTM) is according Böhme and Winklhofer (2008). The chronostratigraphy according to Kováč et al. (2018)

Senckenberg collection in Frankfurt). Keeping in mind the warm subtropical temperatures estimated for the early Burdigalian (Fig. 25), the potential evapotranspiration should be substantial, resulting very probably in a semi-arid hydroclimate for Wintershof-West.

The highly diversified ophidians from the Early Miocene (early MN 3) Wintershof-West locality point to a predominance of heliophile taxa inhabiting various terrestrial environments (Appendix 4): Alethinophidia incertae sedis (cf. *Falseryx* sp.), Booidea (*Bavarioboa wintershofensis* sp. nov.), Viperidae (Viperinae indet. – 'Oriental vipers', *Vipera* sp. '*V. aspis*' complex), Natricidae (*Natrix* cf. *sansaniensis*, *Wintershofia robusta* gen. et sp. nov., *Palaeonatrix* aff. *lehmani*), Colubridae ('*Coluber*' aff. *caspioides*, 'Colubridae' indet., type 1, 'Colubridae' indet., type 2, 'Colubridae' indet, type 3). Fossorial snakes are significantly less represented with only coral snakes ('*Micrurus*' *gallicus* and another, indeterminate, small elapid different from *'M.' gallicus*), whose extant relatives occupy mostly tropical or subtropical habitats with dense vegetation. Thermophilic snakes such as booids (*B. wintershofensis*), elapoids (*'Micrurus' gallicus*, Elapidae indet., type 1) and viperids attributed to 'Oriental vipers' indicate warm climatic conditions. This assumption is also supported by the occurrence of chamaeleonids (Böhme, 2003; Čerňanský, 2010; Moody & Roček, 1980) indicating MAT ≥ 17.4 °C, the mean CMT ~10.8 °C, and mean WMT ~25.1 °C (Böhme, 2003). However, the presence of paratropical climate can be excluded because of the absence of pythonoids (*Python*), the most thermophilic taxon in the Miocene of Europe (Ivanov & Böhme, 2011; Ivanov et al., 2020) and the fact that the only booid from Wintershof-West, *B. wintershofensis*, is comparatively small unlike large *Bavarioboa* reported in Central Europe after the EOC during the thermal maximum of the MCO (Ivanov & Böhme, 2011; Rage & Szyndlar, 2005). Moreover, highly thermophilic true cobras of the genus *Naja*, which first appeared in Europe in middle Burdigalian (Ottnangian, MN 4; Szyndlar & Schleich, 1993), are absent.

The presence of mainly semi-aquatic natricids (*Natrix* cf. *sansaniensis* and possibly *Wintershofia robusta* gen. et sp. nov. and *Palaeonatrix* aff. *lehmani*) indicate small water reservoirs, such as ponds or small lakes, whose shores were frequently occupied by these snakes (e.g., Gruschwitz et al., 1999; Rossman et al., 1996; Schätti, 1999).

The open dry shrubby environment with xerothermic habitats, inhabited by heliophile snakes (*'C.'* aff. *caspioides*, Colubridae indet., type 1, Colubridae indet., type 2), alternated with dense shrub and tree vegetation, inhabited by fossorial coral snakes (*'M.' gallicus*, Elapidae indet., type 1) and further *Falseryx*, booids (*B. wintershofensis*) and arboreal taxa such as chamaeleonids.

Although the Wintershof-West snake community shares several taxa known from the coeval north Bohemian locality of Merkur-North (Ahníkov I) (Ivanov, 2002a), the karstic environment occurring around Wintershof-West, corresponding to the semi-arid hydroclimate, was completely different from extensive swamps and marshy environment reported from north Bohemia (Kvaček et al., 2004). This is best documented by the numerous remains of Booidea and Viperidae (especially 'Oriental vipers) in Wintershof-West, whereas in Merkur North (Ahníkov I) both booids and viperids belong to the extremely rarely occurring taxa (Ivanov, 2002a).

Conclusions

The snake community reported from the Early Miocene (early MN 3) of Wintershof-West, Germany is unusually diversified comprising at least two taxa of alethinophidians and twelve taxa of caenophidians of which two of them represent new extinct species including one new extinct genus. The following snake taxa currently occur at Wintershof-West locality: **Alethinophidia incertae sedis:** cf. *Falseryx* sp.; **Booidea:** *Bavarioboa wintershofensis*, sp. nov., Booidea indet.; **Viperidae:** Viperinae indet. – 'Oriental' vipers, *Vipera* sp. (*'V. aspis'* complex); **Elapidae:** *'Micrurus' gallicus*, Elapidae indet., type 1; **Natricidae:** *Natrix* cf. *sansaniensis*, *Wintershofia robusta* gen. et sp. nov., *Palaeonatrix* aff. *lehmani*, Natricidae indet., type 1, Natricidae indet.; **'Colubridae':** *'Coluber'* aff. *caspioides*, 'Colubridae' indet., type 1, 2, and 3, 'Colubridae' indet., Colubroidea indet.

Bavarioboa wintershofensis sp. nov. is among the first Miocene occurrences of *Bavarioboa* in Europe after its temporal demise during the late Oligocene. The snake community from Wintershof-West indicates that Colubriformes became highly diversified in Central Europe during the onset of the early Burdigalian ~20 Mya. Viperinae 'Oriental vipers' are among the earliest known distinct occurrences of 'Oriental vipers'. Colubroideans display roughly equal diversification of Natricidae and 'Colubridae', with *Palaeonatrix* aff. *lehmani* and *'Coluber'* aff. *caspioides* which might represent the evolutionary older members of *'C.' caspioides* and *P. lehmani* lineages. This diversification resulted from onset of the warm early Burdigalian (20.4–18.2 Ma) climate (Eggenburgian Climatic Optimum, ECO). The presence of several thermophilic taxa in Wintershof-West, i.e., cf. *Falseryx* sp., *B. wintershofensis*, *'Micrurus' gallicus* and other indeterminate coral snake, and 'Oriental vipers', point to a relatively rapid warming before the onset of Early Ottnangian Cooling (EOC, 18.1–17.8 Ma). However, the absence of highly thermophilic true cobras (the genus *Naja*) and especially Pythonoidea in Central European MN 3 localities demonstrate mean annual temperatures lower compared to the Miocene Thermal Maximum (MTM, MN 4, middle and early late Ottnangian), preceeding the Miocene Climatic Optimum (MCO). Wintershof-West currently represents the best documented early Burdigalian (Eggenburgian; early MN 3) ophidian locality in Europe.

Appendix 1

Basic measurements (CL, NAW) of the largest trunk vertebrae of all snake taxa described from Wintershof-West (A), and vaulting ratios (VR) of the figured specimens (B). All measurement are in [mm]. Additional file 1.

Appendix 2

Complete metrical measurements of the type specimens of *Bavarioboa wintershofensis* sp. nov. and *Wintershofia robustra* gen. et sp. nov. All measurement are in [mm]. Additional file 2.

Appendix 3

List of the μCT scan data of natricid skeletons accessed by the Morphosource repository (Duke University; https://www.Morphosource.org). Additional file 3.

Appendix 4

Faunal list and suspected ecology of the herpetofauna from Wintershof-West (MN 3). The non-ophidian herpetofauna, Minimum Numbers of Individuals (MNI) and ecology after Böhme (2003), Böhme et al. (2006), Gardner and Böhme (2008), and Schäfer (2013). The ecology of ophidian fauna according to Ivanov et al. (2020). Additional file 4.

Abbreviations

SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander König, Bonn (Germany)
MNHN	Muséum national d'Histoire naturelle, Paris
UM (formerly abbreviated as USTL)	Institut des Sciences de l 'Évolution, Université de Montpellier, Montpellier, France
UCBL	Université Claude Bernard Lyon 1, Lyon
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
DP FNSP	Department of Palaeontology, Faculty of Natural Sciences, Charles University, Prague
ISEA	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków
MSUVP	Michigan State University Vertebrate Paleontology Division
CAS	California Academy of Sciences, San Francisco

Supplementary Information

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Additional file 1.

Additional file 2.

Additional file 3.

Additional file 4.

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Author contributions

MI, VP, ÀHL, and MB wrote the manuscript text; MI, VP and MB took the photographs and prepared the Figures. All authors read and approved the final manuscript.

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Data availability

All fossil specimen described in this article are available in the Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich under the collection numbers SNSB-BSPG 1937 II 23343 to SNSB-BSPG 1937 II 25383. All data generated or analysed during this study are included in this published artice [and its supplementary information files–Appendix 1, Appendix 2, Appendix 4]. The supporting μCT scan data were accessed by the Morphosource repository, Duke University; [https://www.Morphosource.org] (https:/www.Morphosource.org) (Appendix 3).

Declarations

Competing interests

The authors declare no competing interests.

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