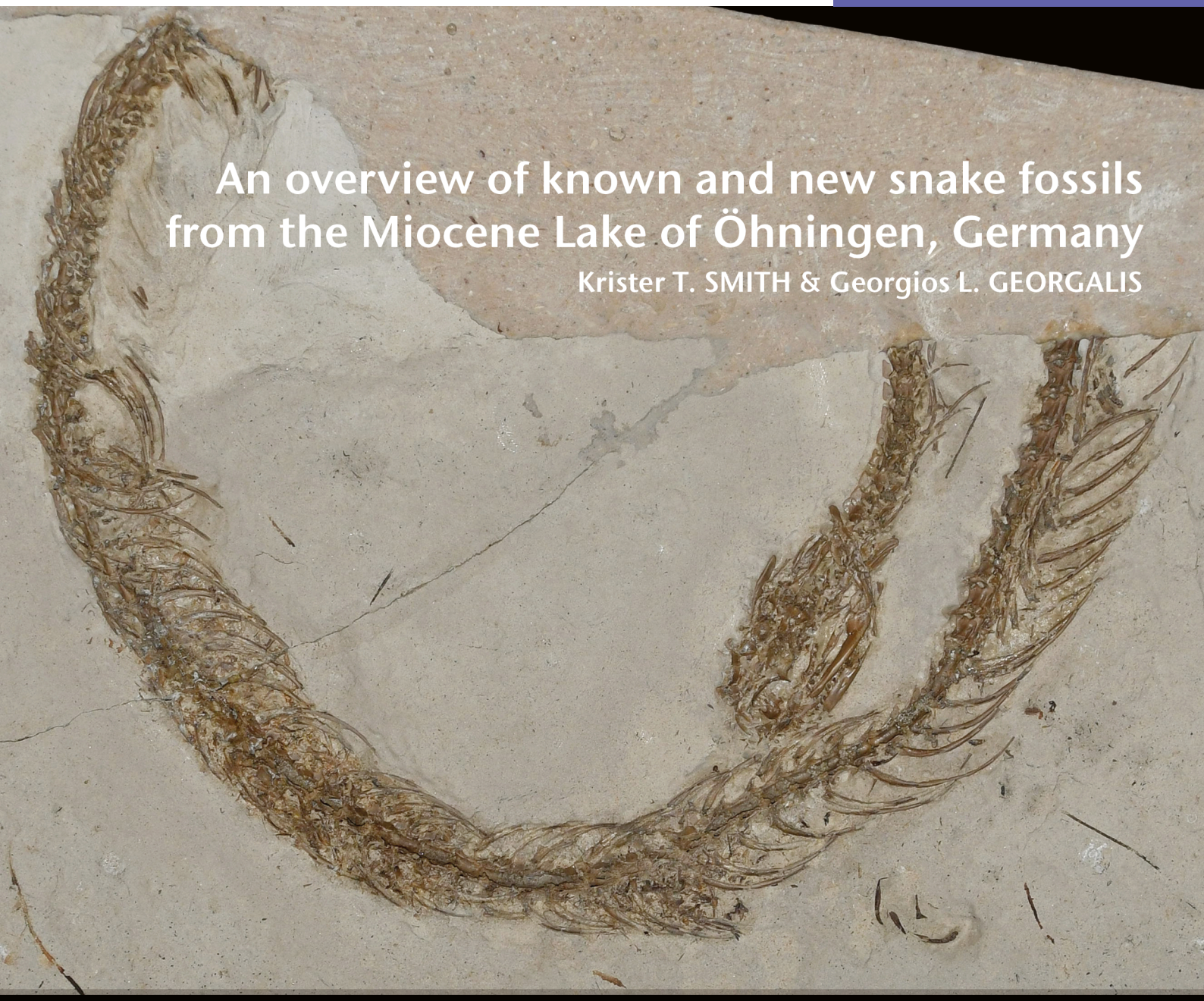
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2026 • 25 • 25

An overview of known and new snake fossils from the Miocene Lake of Öhningen, Germany

Krister T. SMITH & Georgios L. GEORGALIS



SNAKES FROM THE CENOZOIC OF EUROPE
– TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

Edited by Georgios L. GEORGALIS, Hussam ZAHER & Michel LAURIN

art. 25 (25) — Published on 4 November 2026
www.cr-palevol.fr

PUBLICATIONS SCIENTIFIQUES

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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / *print*) : 1631-0683/ ISSN (électronique / *electronic*) : 1777-571X

An overview of known and new snake fossils from the Miocene Lake of Öhningen, Germany

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Submitted on 1 April 2026 | Accepted on 20 May 2026 | Published on 4 November 2026

urn:lsid:zoobank.org:pub:4E0A7340-C05F-444E-A034-BFBA7DDB67A3

Smith K. T. & Georgalis G. L. 2026. — An overview of known and new snake fossils from the Miocene Lake of Öhningen, Germany, *in* Georgalis G. L., Zaher H. & Laurin M. (eds), Snakes from the Cenozoic of Europe – towards a macroevolutionary and palaeobiogeographic synthesis. *Comptes Rendus Palevol* 25 (25): 445-461. https://doi.org/10.5852/cr-palevol2026v25a25

ABSTRACT
We give an account of all known snake fossils from the Miocene lake of Öhningen (Oehningen, Oeningen, Œningen), Germany, which include the first fossil snake ever described. Öhningen is widely recognised as a maar lake, but strong physical evidence for this interpretation has not yet been presented. Eleven specimens, of which five are newly reported in this paper, and three taxonomic species (*Coluber owenii* Meyer, 1844b, *Coluber arcuatus* Meyer, 1845, and *Coluber kargii* Meyer, 1845) are attributed to Serpentes from this locality. They could derive from either of the two main quarries at Öhningen, the Upper and Lower Quarries, the latter of which we re-located and document photographically for the first time. At least three more possible snake specimens have been mentioned in the literature whose current whereabouts are unknown. We clarify the proper authorship of *C. owenii* and report the rediscovery of the lost holotypes of *C. owenii* and *C. arcuatus*. Two of the new specimens preserve the skull. All three taxonomic species have been considered *nomina dubia*, but the development of new analytical techniques, especially micro-computed tomography (μCT), calls for a re-evaluation of those taxonomic opinions on the basis of new data. Because Öhningen has such a long history of excavation and changing ownership, fossil collections from that locality are widely scattered. It is our hope that this account will draw attention to additional snake, or other, specimens currently unknown to science.

KEY WORDS
Miocene,
Serpentes,
Europe,
Lagerstätte.

RÉSUMÉ
Aperçu des fossiles de serpents connus et récents provenant du lac d'Öhningen, datant du Miocène, en Allemagne.
Nous présentons un inventaire de tous les fossiles de serpents connus provenant du lac miocène d'Öhningen (Oehningen, Oeningen, Œningen), en Allemagne, parmi lesquels figure le tout premier serpent fossile jamais décrit. Öhningen est largement reconnu comme un lac de maar, mais aucune preuve matérielle solide n'a encore été apportée à l'appui de cette interprétation. Onze spécimens, dont cinq sont signalés pour la première fois dans cet article, et trois espèces taxonomiques (*Coluber owenii* Meyer, 1844b, *Coluber arcuatus* Meyer, 1845, et *Coluber kargii* Meyer, 1845) sont attribués à l'ordre des Serpentes pour ce site. Ils pourraient provenir de l'une ou l'autre des deux carrières principales d'Öhningen, la carrière supérieure et la carrière inférieure, cette dernière ayant été relocalisée par nos soins et documentée par des photographies pour la première fois. Au moins trois autres spécimens de serpents potentiels ont été mentionnés dans la littérature, mais leur localisation actuelle est inconnue. Nous clarifions l'attribution correcte de *C. owenii* et signalons la redécouverte des holotypes perdus de *C. owenii* et de *C. arcuatus*. Deux des nouveaux spécimens conservent leur crâne. Ces trois espèces taxonomiques ont été considérées comme des *nomina dubia*, mais le développement de nouvelles techniques d'analyse, en particulier la microtomographie par ordinateur (µCT), appelle une réévaluation de ces avis taxonomiques sur la base de nouvelles données. Öhningen ayant connu une longue histoire de fouilles et de changements de propriétaires, les collections de fossiles provenant de ce site sont largement dispersées. Nous espérons que cet article attirera l'attention sur d'autres spécimens de serpents, ou d'autres espèces, actuellement inconnus de la science.

MOTS CLÉS
Miocene,
Serpentes,
Europe,
Lagerstätte.

INTRODUCTION

Maar lakes form by phreatomagmatic eruptions whereby near-surface magma encounters groundwater, leading to explosive vaporisation of the water and the creation of a crater (Lorenz 2003). Typically, the crater fills to form a lake. It is an under-appreciated fact that maar vulcanism, while not as spectacular as stratovolcanoes like Mts. Shasta, Fuji or Vesuvius, or shield volcanoes like Kilauea, is the second most common type of intraplate vulcanism, after cinder cones (Wohletz & Heiken 1992, *fide* Lorenz 2003). Numerous maar lakes, being relatively deep and still (Pirrung *et al.* 2004), are the site of *Konservat-Fossillagerstätten* (many are reviewed in Uhl *et al.* 2024), of which the Messel Pit of Germany is one of the most famous (e.g., Smith *et al.* 2018). Yet maar lake sediments are under-explored paleontologically, especially outside Europe (Uhl *et al.* 2024).

Probably the first purported maar deposits from which fossils were recovered are those of Öhningen (also written Oehningen, or in older literature Oeningen or Œningen), situated on the northern shore of Lower Lake Constance along the Swiss-German border (Fig. 1A), the headwater of the Rhine River. The history of study of Öhningen is rich and entertaining (Karg 1805; Pfannenstiel 1958; Jörg 1966), with some of the first fossils discovered and sold by Augustinian monks already in the 16th century, and later widespread forgeries. Öhningen is the type locality of *Andrias scheuchzeri*, originally described 300 years ago – in 1726 – as a human victim of the Deluge narrated in the biblical book of *Genesis*, subsequently reinterpreted in 1758 by Öhningen's town physician Johann Gessner (on this name, see below) as a catfish, amongst other misconceptions (Westphal 1958; Jörg 1966), and finally (and correctly) as a giant salamander of the family now known as Cryptobranchidae by Cuvier (1809). Prominent monographs describing or mentioning 1397 plant and insect species were published by the Swiss naturalist Oswald Heer (see Heer 1865; Cockerell 1915; Selmeier 1990), though both plants and insects are in need of revision (Cockerell 1915; Uhl *et al.* 2024). Curiously, because Heer included Öhningen in his monographs on Swiss fossils, many people, including scientists, erroneously deduced that Öhningen was located in Switzerland, whereas it is in fact in Germany (Cockerell 1915). Similar to Messel (reviewed in Smith *et al.* 2024), the long history of excavation at Öhningen by many generations, the changing ownership, and the commercial dealings with fossils has led to a scattering of the fossil remains across collections and museums around Europe and the world (Karg 1805; Jörg 1966; Uhl 2005).

It is the aim of the present paper to give an overview of the snake fossils from Öhningen, including those previously described, as well as new specimens that have come to light through interactions with various collection managers and organisations. It is thought (Szyndlar & Rage 2002) that the first fossil snake ever described is from Öhningen (Karg 1805). Hermann von Meyer gave two short reports (Meyer 1844a, b) and wrote a monograph (Meyer 1845) on the tetrapods of Öhningen. He described therein *Coluber owenii* Meyer, 1844b, *Coluber arcuatus* Meyer, 1845, and

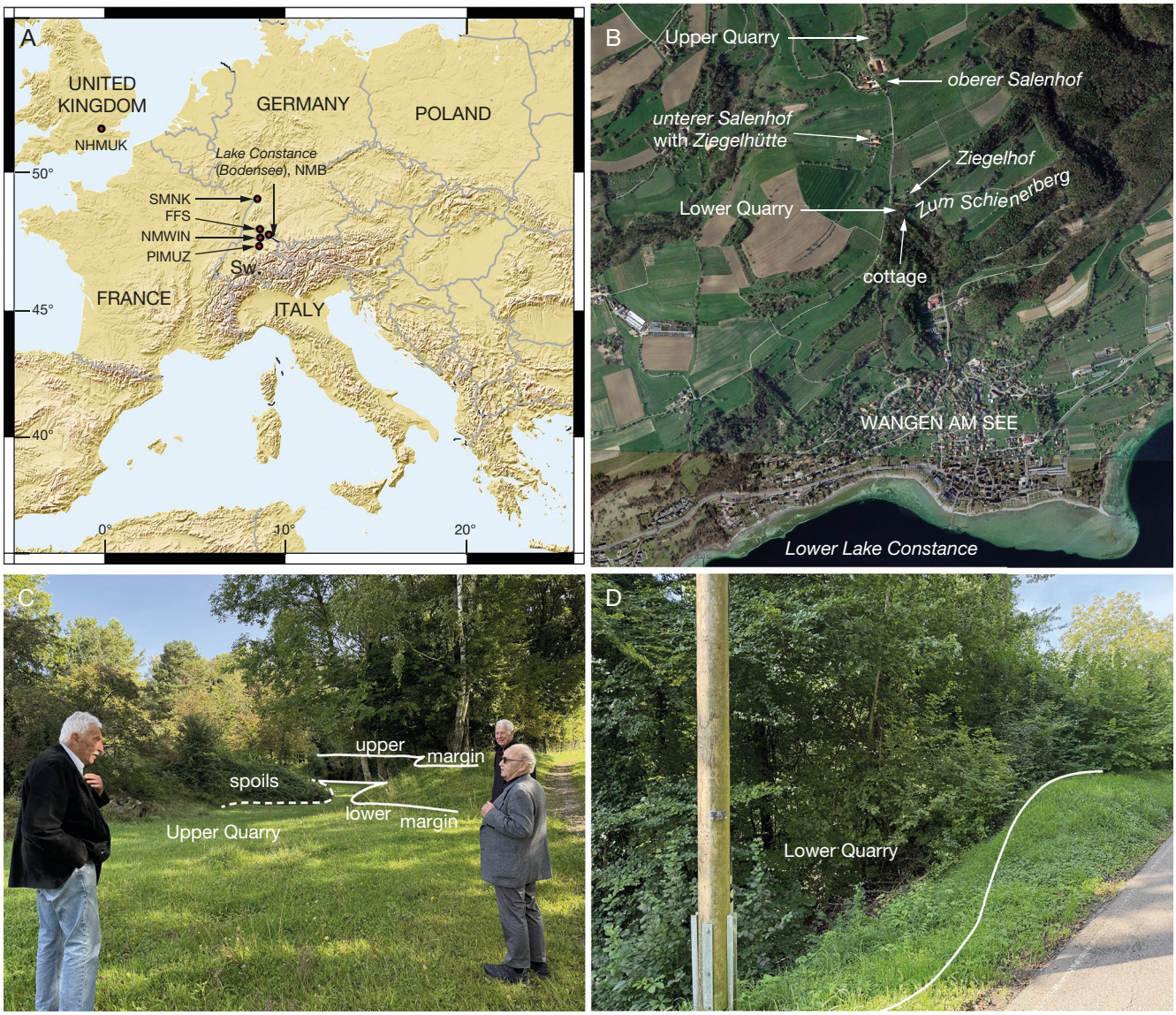


FIG. 1. — **A**, Shaded-relief map of Central Europe showing location of Lake Constance (*Bodensee*) at the German-Swiss (Sw.) border; **B**, satellite image of area around Wangen am See on the shore of Lower Lake Constance, showing the location of the Upper and Lower Quarries and other locations referred to in the main text; **C**, photograph of the *oberer Salenhof* (Upper) Quarry at Wangen (Öhningen). Upper and lower margin of former quarry indicated with **solid lines**; the location of 2021 trench is approximately in the kink in the lines and already hardly recognizable. Base of spoils pile (Selmeier 1990) indicated with a **dashed line**. Guides clockwise from upper right: Gerhard Ludes, Prof. Dr. Michael Bartels, and Werner Pflüger; **D**, looking down on wooded terrace from the road *Zum Schienerberg* at the approximate location of the *Ziegelhof*, the location of the Lower Quarry at Wangen (Öhningen). Upper margin of slope, which may mark the margin of the former quarry, indicated with a **solid line**. Abbreviations: **FFS**, collections of the Sovereign Princes of Fürstenberg (*fürstlich fürstenbergische Sammlungen*), Departments of Natural History (Paleontology), Donaueschingen; **NMWIN**, Naturmuseum Winterthur, Winterthur; **PIMUZ**, Paläontologisches Institut und Museum, Universität Zürich, Zurich; **SMNK**, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe. Photos: K. T. Smith.

Coluber kargii Meyer, 1845. Other specimens have landed in various collections over the years, and some have never been described or even mentioned. We fully expect that our catalog is incomplete. Unknown specimens are likely lurking in drawers or on display in other collections. Our primary goal is to stimulate further work on these exceptional specimens and perhaps to call the attention of collections managers and museum scientists to additional, unknown snake (and other) specimens from Öhningen. We also visited the site of the Öhningen localities in order to narrow down the location of, especially, the Lower Quarry.

ABBREVIATIONS

FFS Pz	collections of the Sovereign Princes of Fürstenberg (*fürstlich fürstenbergische Sammlungen*), Departments of Natural History (Paleontology), Donaueschingen;
NHMUK	Natural History Museum, London;
NMB	Naturmuseum Bodensee, Constance;
NMWIN	Naturmuseum Winterthur, Winterthur;
PIMUZ	Paläontologisches Institut und Museum, Universität Zürich, Zurich;
SMF-PH	Paleoherpetology collection, Senckenberg Research Institute, Frankfurt am Main;
SMNK	Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe (Fig. 1A).

A BRIEF SUMMARY OF ÖHNINGEN

The Middle Miocene (probably MN 7: Tobien 1986: 27; see also Heizmann 1992: 57) lake of Öhningen is part of the Hegau volcanic field (Heizmann 1992). Recent geochronologic work on the top of the sequence yielded a fission-track age of 13.7 ± 0.5 Ma, establishing a minimum age of the fossiliferous layers (Kimmig *et al.* in press). The host rock in which the Öhningen Beds (*Öhninger Schichten*, as they are known in German) are located is the Upper Freshwater Molasse (*obere Süßwassermolasse*). It should be stated that – to our knowledge – no physical evidence equivalent to that presented from Messel or other sites on the Sprendlinger Horst, such as a drill core with a typical maar lithic sequence (Felder & Harms 2004), has been adduced in support of a phreatomagmatic origin of the Öhningen basin. Moreover, it is even uncertain whether the outcrops of the Öhningen Beds represent only one basin or more than one. If there was only one basin, the original lake was at least 500 × 960 m (Rutte 1956), somewhat smaller than the minimum for Messel. The Öhningen Beds are highly variegated and have therefore been exploited for various commodities like paving stones, but also fossils, for centuries (e.g., Karg 1805; Jörg 1966). Although fossil deposits are typically named after the nearest municipality, in this case "Öhningen" became the reference, rather than "Wangen am See" (the name of the municipality in which it is actually located, and which now forms part of the town of Öhningen) because for many years the quarries were owned by authorities in Öhningen (Jörg 1966).

Historically there were two main quarries – the Upper and Lower Quarries (Fig. 1B) – separated by some 800 m in plan view and about 50 m in elevation (Rasser *et al.* 2023). Selmeier (1990) shows their approximate location on a map. The first rock quarrying at Öhningen, documented over 500 years ago, *c.* 1500 (Jörg 1966), took place at the Upper Quarry. It is located near the *oberer Salenhof* and was investigated sedimentologically by Karg (1805), Rutte (1956) and Rasser *et al.* (2023). [In German, *ober* means "upper" and *Hof* here means something like "farmstead"; *oberer Salenhof*, sometimes rendered *Obersalenhof* or even *Obersalen* (e.g., Selmeier 1990), is the proper name of a particular farmstead.] The original quarry wall collapsed (Uhl *et al.* 2024; G. Ludes & W. Pflüger, pers. comm. 2025) and is overgrown (Fig. 1C), and the area of the test excavation in 2021 (Rasser *et al.* 2023) is already hardly recognisable in September 2025. Fossils in the Upper Quarry are reported to be rare (Rutte 1956; Rasser *et al.* 2023). The exact location of the Lower Quarry, situated near the *Ziegelhof* (*Ziegel* means "brick"), is not precisely known (Rasser *et al.* 2023). However, it was certainly situated in the terraced, now wooded landscape (Fig. 1D) across the current paved road (*Zum Schienerberg*) from the *Ziegelhof* (G. Ludes & W. Pflüger, pers. comm. 2025). Probably this is the same disused quarry visited by Prof. Cockerell and his party (Cockerell 1915). Next to the disused quarry was a cottage that was visited in the summer by one Dr. Ernst Bacmeister and family (Cockerell 1915), which is the very one that still stands across the street from the *Ziegelhof* (G. Ludes, pers. comm. 2026).

Between the *oberer Salenhof* and the *Ziegelhof* is the *unterer Salenhof* (*unter* here means "lower"). Here the so-called *Ziegelhütte* was located (*hütte* means "hut"). It is at this location that bricks were baked, and *Ziegelhütte*, a more widely used term, should not be confused with the *Ziegelhof*, where the Lower Quarry was located. It is said that the blue clay or *blauer Letten* was particularly useful in brick-making (O. Grundler, previous owner of the *oberer Salenhof*, pers. comm. to G. Ludes 2015). A *blauer Letten* is found both in the Upper and Lower Quarries and is the only bed that has been correlated between the two (O. Heer, *fide* Jörg 1966: 33), although it differs in thickness between them.

ANNOTATED CATALOG OF ÖHNINGEN SNAKES

Natural History Museum, London

Two specimens are present at NHMUK. Both were purchased in 1871 from the collection of the late Dutchman Prof. Jacob G. van Breda (Lydekker 1888). They are given in the catalog as coming from the quarries of *Ziegelhof* or *Obersalen* – the latter contraction refers to the same place as *oberer Salenhof* or *Obersalenhof* (see above).

NHMUK PV OR 42733 (Fig. 2A)

The specimen is a nearly complete skeleton. Lydekker (1888) considered that it could represent *Coluber kargii*. Szyndlar (1997), in contrast, noted the high number of vertebrae (*c.* 300 total count) and considered it a possible "boid" *sensu lato*, which today would include both boas and pythons, i.e., approximately Constrictores Oppel, 1811 (*sensu* Georgalis & Smith 2020). We tend to disagree with the latter opinion, especially when taking into consideration the relatively elongated centra of the trunk vertebrae, which instead point towards colubriform affinities (see Zaher *et al.* 2019). The specimen should be investigated with µCT, which could elucidate its anatomy and phylogenetic affinities.

NHMUK PV OR 42734 (Fig. 2B)

The specimen is a section only of 21 vertebrae – eight with osseous material, 13 as impressions, plus some scattered ribs (Szyndlar 1997) – and was not originally more complete. Lydekker (1888) referred this specimen to *Coluber owenii*. Szyndlar (1997: 215), in contrast, considered the specimen an indeterminate "non-natricine colubrid". We follow him in attributing the specimen to Colubroides indet.

Paläontologisches Institut Zürich, Universität Zürich

PIMUZ A/III 163 (Fig. 3A) and 164

This, the holotype (by sole designation) of *Coluber kargii* Meyer, 1845, is preserved as part and counterpart (Szyndlar 1992). It is widely considered the first fossil snake ever described (Szyndlar & Rage 2002) and the first snake reported from Öhningen, being described briefly and illustrated in the geological and



Fig. 2. — **A**, NHMUK PV OR 42733, skeleton of an indeterminate snake previously attributed to *Coluber kargii* Meyer, 1845; **B**, NHMUK PV OR 42734, articulated string of anterior trunk vertebrae of an indeterminate member of Colubroides, previously referred to *Coluber owenii* Meyer, 1844b. Scale bars: 1 cm. Photos: G. Georgalis.

paleontological report of Karg (1805: 30, pl. 2.2). In fact, Karg (1805: 30) wrote: "Ich stehe nicht an, dieses Fossil als das Überbleibsel der gemeinen Otter (*Coluber berus* L.) zu erklären." That is to say, he does not hesitate to identify the fossil as the remains of what is today called *Vipera berus* (Linnaeus, 1758), the common European Adder. It was described more fully by Hermann von Meyer (1845: pl. 6.2), who gave it its scientific name. Rochebrune (1880) referred it to the genus *Echidna* Merrem, 1820 (corresponding to the extant genus *Bitis* Gray, 1842, which has a similar content today) of the family Viperidae. Kuhn (1971) referred the species to *Vipera* Laurenti, 1768, with Rage (1984) following this genus placement and providing some short emended diagnosis for the species. Szyndlar (1992) redescribed the holotype, concurred with its viper affinities, and further considered the taxon likely to pertain to the "Oriental viper" group. However, he stated (p. 699) that "this conclusion is based on the geographic rather than morphological" grounds. He then recognised *C. kargii* as a *nomen dubium*. [For decades now the generic epithet has been surrounded by quotation marks, viz. "*Coluber*" *kargii*, to emphasise the fact that the attribution is in need of revision. However, that applies as well to the other species treated here,



Fig. 3. — **A**, Lithograph of PIMUZ A/III 163, holotype of *Coluber kargii* Meyer, 1845, from Meyer (1845: pl. 6.2). This specimen (the counterpart being PIMUZ A/III 164) was the first fossil snake ever described (Szyndlar & Rage 2002) and was first attributed by Karg (1805) to the species currently known as *Vipera berus* (Linnaeus, 1758). We follow Szyndlar (1992) in considering it Viperidae indet.; **B**, PIMUZ A/III 164, a referred specimen of *Coluber owenii* Meyer, 1844b, a section of vertebral column. We consider it Colubroides indet. Scale bar: B, 1 cm. Photo: G. Georgalis.

and the universal application of quotation marks (as in Kuhn 1971, for Öhningen snakes) would distract rather than illuminate in this case. We think it is sufficient to point out that *Coluber* was applied far more broadly in the past – consider Karg's (1805) attribution to *Coluber berus* – and that revision of all three taxonomic species is in order.]

PIMUZ A/III 688 (Fig. 3B)

The specimen was discovered before SMNK-PAL 76120 (see below) and given over to Hermann von Meyer in 1844 by Arnold Escher von der Linth in Zurich. Meyer described it, in 1845, as an indubitable specimen of *Coluber owenii*; as argued below, we consider it a referred specimen of that species. It is rather large, consisting of part of a vertebral column, whereby the vertebrae and ribs are only represented by fragments and impressions. Meyer (1845: 11) considered it to be a composite comprising a main string of *c.* 75 vertebrae to which additional pieces were artificially joined, some of which derive from the counterpart (on this point, see also SMNK-PAL 76683 below). Specifically, these "augmentations" comprise a second string of *c.* 50 vertebrae with a stronger curvature (probably, he supposed this to be from the counterpart) and the head of a different animal from Öhningen. Indeed, in this specimen the vertebral string on the right side (*c.* 50 vertebrae) has the cotyle-condyle articulation surface concave cranially, whereas the vertebral string on the left side (*c.* 75 vertebrae) has it concave caudally, so it is clear that these two strings were artificially joined, as Meyer (1845) indicated. We also point out that, whether or not the head comes from a different animal, it represents a snake. We illustrate the specimen here for the first time. Szyndlar (1997) considered the specimen cannot be identified below "family" level (today, roughly Colubroides Zaher *et al.* 2019).



Fig. 4. — **A**, Lithograph of SMNK-PAL 76120, holotype of *Coluber owenii* Meyer, 1844b, from Meyer (1845: pl. 7.1); **B**, SMNK-PAL 76120, rediscovered holotype of *Coluber owenii*. The specimen comprises a long string of vertebrae. Given the state of preservation, it seems likely that the specimen was originally complete with head, but large parts of the skeleton, including the head, are shown as missing in Meyer's (1845) illustration. Missing parts were fabricated at an unknown time after 1845. Scale bar: B, 1 cm. Photo: T. Schüßler.



Fig. 5. — **A**, Lithograph of a part of SMNK-PAL 76683, holotype of *Coluber arcuatus* Meyer, 1845, from Meyer (1845: pl. 2.5); **B**, SMNK-PAL 76683, rediscovered holotype of *Coluber arcuatus*. The specimen was originally illustrated as a string of approximately 54 vertebrae. The part and counterpart slabs have been joined, and a fish tail and possible fish head added to it, between 1845 and 1958 (when a photograph was published by Pfannenstiel). Present evidence does not allow the specimen to be identified more precisely than Colubroides indet., but we hesitate to pronounce it a *nomen dubium* until it has been studied by µCT. Scale bar: B, 1 cm. Photo: J. Weidke.

Staatliches Museum für Naturkunde Karlsruhe
SMNK-PAL 76120 (formerly SMNK te-mi 126, TE 58) (Fig. 4)
The specimen consists of a long, looping vertebral string, missing a section of the posterior middle and the anterior portion with the head. It was discovered in 1843, briefly reported under the name *Coluber owenii* by Hermann von Meyer in 1844 (see below), and fully described and illustrated by the same author in 1845 (pl. 7.1; Fig. 4A). Szyndlar & Böhme (1993: 389) reported that it had been lent to an unknown person in 1982 and is considered lost. In the course of this study, the specimen was rediscovered and returned to SMNK, after which it was assigned the new specimen number given above. Missing parts of the holotype were fabricated (Fig. 4B), perhaps before 1958, because fabrication of a different sort occurred by 1958 in the holotype of *Coluber arcuatus* (see below).

The status of this specimen requires comment. The ICZN requires a description of taxonomic characters to establish a species. In his first report of January, 1844, Meyer (1844a: 330-331) wrote that the vertebral column, if it were complete, would measure no less than three feet ("fast wichtiger aber ist ein grosser Theil von der Wirbelsäule einer Schlange, welche vollständig nicht weniger als 3 Fuss Länge besessen haben kann"). Otherwise, he only states that it is built like those of the "Nattern" (something like Colubroidea today), without

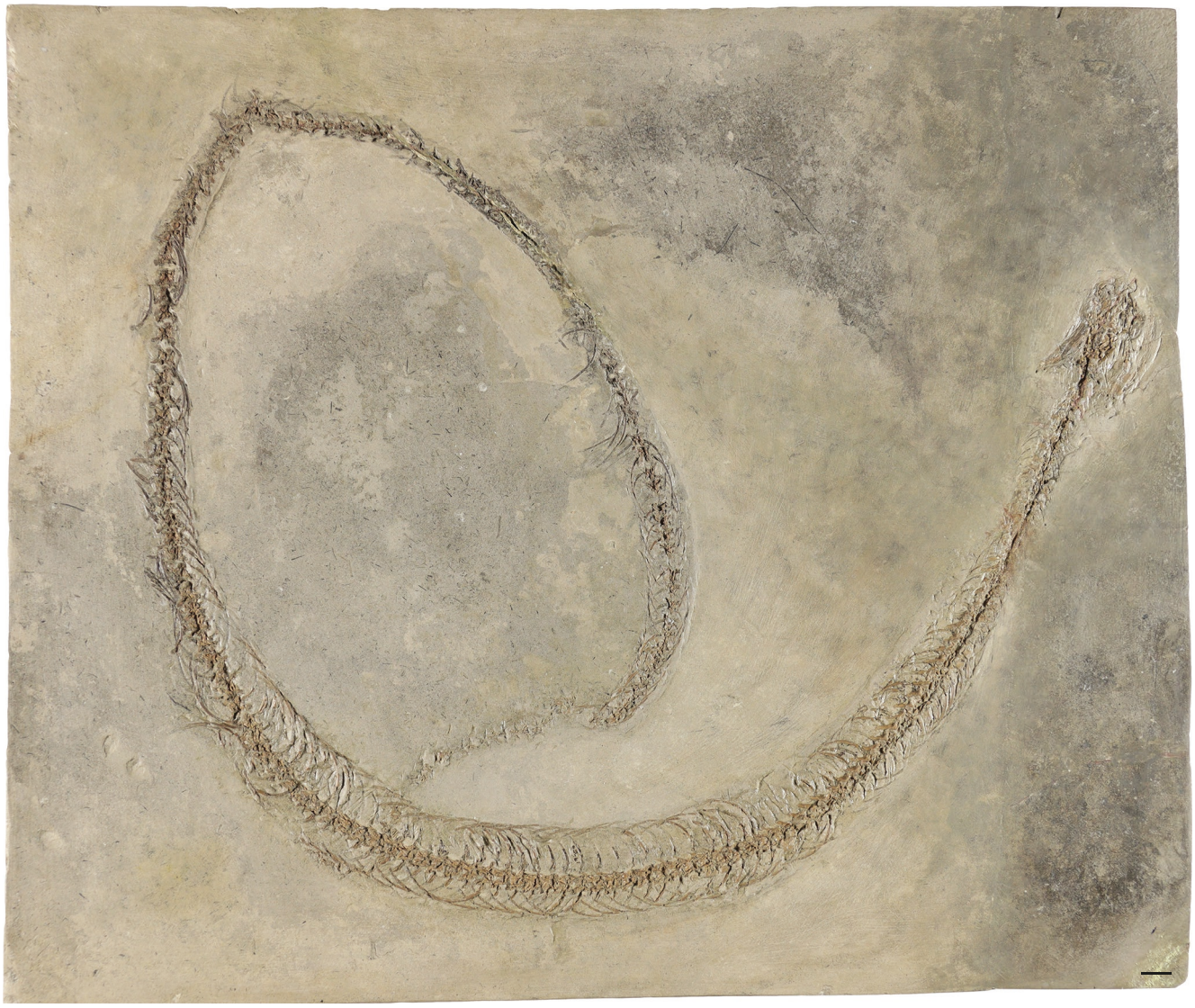


Fig. 6. — SMNK-PAL 76701, a newly reported complete skeleton of Colubroides indet. Substantial parts of most bones are missing and either were present on the counterpart (whose fate is unknown) or lost to damage. The vertebral count is low and the body rather thick in the middle. Scale bar: 1 cm. Photo: A. Vogel.

mentioning any particular point of resemblance. Because Meyer (1844a) only suggested a potential size estimation for the animal when alive, we think that this does not fulfil the requirements of the ICZN to establish a new species name, and this usage of *Coluber owenii* is a *nomen nudum*. In May of the same year, Meyer (1844b) provided the first real mention of a character of the species. More precisely, Meyer (1844b: 565) wrote that the vertebrae of *C. owenii* differ from the holotype of *Coluber podolicus* Meyer, 1844b, another new species that he was describing from Ukraine ("Podolien"), in having a larger and more posteriorly directed postzygapophysis. We consider this usage to establish the name *Coluber owenii* and the authorship to be Meyer (1844b), contrary to the prevailing opinion that has credited authorship to Meyer (1844a) (e.g., Rage 1984; Szyndlar 1997; Wallach *et al.* 2014) or Meyer (1845) (e.g., Kuhn 1939, 1963). However, while Meyer (1844b) clearly gives characters of the vertebrae, it is not clear which specimens he was referring to. In the following year he described an additional specimen of *C. owenii* (PIMUZ A/III 688; see above), which he received in 1844 (Meyer 1845: 11), as well as *C. arcuatus* (see below). It seems most probable that in Meyer (1844b), written some time before May of that year, he still had available only the one specimen, now given as SMNK-PAL 76120; accordingly, that specimen should be considered the holotype. However, if it can be determined (for instance) that Mr. Escher sent Meyer specimen PIMUZ A/III 688 at the beginning of 1844, then it might be considered that SMNK-PAL 76120 and PIMUZ A/III 688 (fully described in 1845) comprise the syntypes. In that case, it should be pointed out that, in referring to SMNK-PAL 76120 as the "holotype", Rage (1984) would have established it as the lectotype of *C. owenii*, following the ICZN (1999: Articles 74.5 and 74.6) for the designation of lectotypes prior to 2000; that would make PIMUZ A/III 688 the paralectotype.

Coluber owenii was originally conceived as having probable affinities to the group currently known as Natricidae, hence its original classification as *Coluber* (*Tropidonotus*?) *owenii* by Meyer (1844a), *Tropidonotus* Boie, 1826 being a current synonym of *Natrix* Laurenti, 1768. The species was later transferred to *Elaphis* Bonaparte, 1834 in Bonaparte 1832-1841 (i.e., a synonym of *Elaphe* Fitzinger *in* Wagler, 1833) by Rochebrune (1880), a genus-level opinion that was followed by subsequent authors (e.g., Boettger 1884; Lydekker 1888; Kuhn 1939, 1963). Szyndlar & Böhme (1993) considered *C. owenii* a *nomen dubium*. It is currently impossible to decipher whether the holotype and referred specimens of *C. owenii* are truly conspecific, and we anticipate that future µCT studies of these two important specimens may shed some light on this taxonomic issue.

SMNK-PAL 76683 (formerly SMNK Oe 337, TE 57) (Fig. 5)
This specimen is the holotype (by sole designation) of *Coluber arcuatus* Meyer, 1845. Its current appearance is unlike the illustration that accompanied the first description (Meyer (1845: pl. 5.2; Fig. 5A). Pfannenstiel (1958: fig. 10) illustrated it with a photograph in its current state (Fig. 5B), labelling it in the caption as a *gefälschtes Aalskelett* ("eel skeleton forgery"). Apparently it was examined in this condition by Szyndlar (1997), who also considered it to be an eel and the specimen figured by Meyer (1845) to be lost. Rochebrune (1880) and Szyndlar (1997) did not believe that the illustration of the holotype by Meyer (1845) could be distinguished with certainty from an eel. In the course of this study it was discovered that the "lost" holotype was never lost but was in fact present in the place it always was.

SMNK-PAL 76683 in its current form is a composite formed of the part and the counterpart of the holotype (see also PIMUZ A/III 688 above) as well as additions including a head and a fish tail. The slab shown by Meyer (1845: pl. 5.2) appears to be the part of the specimen currently attached to the fish tail. [Lithographs from the 19th century usually mirror specimens – e.g., Georgalis 2017; Georgalis *et al.* 2021 – but in the present case, the lithograph of what is now the holotype of *Coluber owenii* is not mirrored (Meyer 1845: pl. 7.1; see above), so we can reasonably assume this is also true of the lithograph of the holotype of *C. arcuatus*.] The counterpart, not illustrated by Meyer (1845), was physically attached to the part, and the point of attachment is clearly shown by a kink in the vertebral column where the orientation of the ribs also reverses. The head of SMNK-PAL 76683 also appears to be a fabrication, possibly a badly preserved actinopterygian fish head. Thus, we can report that the holotype of *C. arcuatus* has been rediscovered in the place it always was, though not in the condition illustrated in 1845. The part and counterpart slabs are certainly from a snake. Szyndlar & Böhme (1993) considered *C. arcuatus* a *nomen dubium*. Wallach *et al.* (2014) treated *C. arcuatus* as a valid species and placed it in the extant genus *Hierophis* Fitzinger, 1834 *in* Bonaparte, 1832-1841, but they provided no justification for that act.

SMNK-PAL 76701 (newly reported here) (Fig. 6)
This specimen is referred on its label to *Coluber owenii*. It was borrowed from the SMNK collection in the year 1982 for a special display in the Museum für Naturkunde (now Museum Natur und Mensch) in Freiburg, was packed up during renovations, and rediscovered while opening boxes in 2024 (N. Widemann, pers. comm. 2025). Substantial parts of the osseous matter of the specimen are missing. Some bone remains in the impressions. Most importantly, the skull is preserved (even if the bones here, like the vertebrae, are severely damaged). Although the low vertebral count is a noteworthy similarity to *C. kargii*, a robust identification, even a preliminary one, based on this specimen in the absence of a µCT scan is not possible. We currently regard it as Colubroides indet.

Naturmuseum Bodensee, Constance
NMB.Fos 8863 (newly reported here) (Fig. 7)
This specimen was displayed on a wall in the museum for some considerable time, but there is no documentation concerning its provenance or ownership history (M. Kroth, pers. comm. 2024). The specimen is preserved on a thin (*c.* 5 mm thick) slab of matrix that is laminated in cross-section. The slab, in turn, is embedded in an artificial resin plate, similar but not identical in color to the matrix, that supports it from below and fills out the edges where the vertebral column terminates. The snake probably came to lie on its back, and the right jaw fell down over the left jaw during the process of decay.

Preserved on NMB.Fos 8863 is the head with the first *c.* 13 anterior trunk vertebrae in articulation and a separate string of *c.* 61 articulated mid-trunk vertebrae. While it cannot be demonstrated conclusively, the similar size and preservation as well as the close spatial proximity strongly suggest that both strings pertain to the same individual. The ribs are mostly in articulation with the vertebrae. The first string of vertebrae terminates and the second string begins and terminates at the same broken edge. The vertebrae are lightly built, with a prominent haemal keel that is deeply undercut by the subcentral grooves. About halfway along its length, the haemal keel grows suddenly more prominent and displays a distinct ventral flattening, but at its posterior end it is flush with the ventral margin of the condyle; this condition is similar to that seen in some "rat-snakes" (the name we apply to clade 10 of Colubridae in Zaher *et al.* 2019), such as *Orthriophis taeniurus* (Cope, 1861) SMF-PH 143 and *Euprepiophis mandarinus* (Cantor, 1842) SMF-PH 142 and, at least in posterior trunk vertebrae, in *Zamenis situla* (Linnaeus, 1758) SMF-PH 825. Parapophyseal processes are absent.

The skull is colubroidean, with a long, triangular, posteriorly directed quadrate, an extended supratemporal, an ectopterygoid that expands strongly and bifurcates anteriorly, a prefrontal foramen, delicately built jaws, and a dentary with a closed-and-fused Meckelian groove. As in many Eurasian rat-snakes, such as *Orthriophis taeniurus* SMF-PH 143, *Hierophis viridiflavus* (Lacépède, 1789) SMF-PH 819 and *Zamenis situla* SMF-PH 825, there is a prominent prearticular ala, and the postfrontal (*sensu* Zaher & Smith 2020) fails to



Fig. 7. — NMB.Fos 8863, newly reported partial skeleton including skull provisionally referred to Colubridae. Scale bar: 1 cm. Photo: M. Kroth.



Fig. 8. — NMWIN 14251, an articulated string of anterior trunk vertebrae together with ribs, newly reported here. The specimen is attributed to Colubroides indet. Scale bar: 1 cm. Photo: S. Scherrer.

Table 1. — Summary of snake specimens (Serpentes) currently documented from the Miocene locality of Öhningen, Germany. There is currently no information concerning which of the two main quarries the specimens derive from. Three specimens mentioned by Karg (1805) are currently unaccounted for. For institutional abbreviations, see main text.

Specimen	Past taxonomy	Current taxonomy	First mention
NHMUK PV OR 42733	*Coluber kargii*	Colubroides indet.	Lydekker 1888
NHMUK PV OR 42734	*Coluber owenii*	Serpentes indet.	Lydekker 1888
PIMUZ A/III 163 and 164	*Coluber kargii* (holotype)	Viperidae indet.	Karg 1805
PIMUZ A/III 688	*Coluber owenii*	Colubroides indet.	Meyer 1845
SMNK-PAL 76120	*Coluber owenii* (holotype)	Colubroides indet.	Meyer 1844a
SMNK-PAL 76683	*Coluber arcuatus* (holotype)	Colubroides indet.	Meyer 1845
SMNK-PAL 76701	–	Colubroides indet.	This study
NMB.Fos 8863	–	Colubridae indet.	This study
NMWIN 14251	–	Colubroides indet.	This study
FFS Pz 4922	–	Serpentes indet.	This study
FFS Pz 4776	–	Serpentes(?) indet.	This study

contact the frontal. In its more V-shaped rather than pentagonal parietal table it most resembles species of *Hierophis* [*Hierophis viridiflavus* SMF-PH 73, *Hierophis gemonensis* (Laurenti, 1768) SMF-PH 76]. The genera *Hierophis* and *Zamenis* Wagler, 1830 have both been reported from the Middle Miocene (Ivanov 2022).

An affinity with Eurasian rat-snakes is probable but must be more carefully explored with additional comparisons and μCT, which we plan to do in a future study. Additionally, the specimen preserves gut contents, which will furnish the first direct evidence on diet in a Miocene snake.

Naturmuseum Winterthur

NMWIN 14251 (formerly Nr. 22; newly reported here) (Fig. 8)

The natural history museum in Winterthur, Switzerland, located about 21 km southwest of Öhningen, has one snake specimen from Öhningen. It bears the specimen number 22 and is identified as "*Elaphis owenii*", which today would be rendered as *Coluber owenii*. Direct evidence concerning the provenance of this specimen is currently lacking, but the orthography of the specimen label and number are similar to those of a collection of fishes from Öhningen that were bought at a time when the museum was part of the Winterthur City Library (S. Scherrer, pers. comm. 2025).

The specimen consists of the remains of at least 29 vertebrae in a more or less articulated string. They are lightly built and seen in ventral to left ventrolateral aspect on the sediment block. A prominent, narrow haemal keel is present, and the subcentral grooves are relatively deep and extend to the anterior end of the centrum, suggesting this may pertain to a more posterior segment of the vertebral column. Parapophyseal processes are absent. A short, posteriorly projecting hypapophysis is also present, as is found in some rat-snakes (e.g., *Euprepiophis mandarinus* SMF-PH 142, *Orthriophis taeniurus* SMF-PH 143), but the hypapophysis is not as prominent as in Natricidae [e.g., *Natrix natrix* (Linnaeus, 1758) SMF-PH 83]. Some ribs, partly articulated and partly out of their anatomical position, are also present. We tentatively consider the specimen as Colubroides indet., but a μCT scan is needed to better understand vertebral morphology.



Fig. 9. — **A**, FFS Pz 4922, a long string of articulated trunk vertebrae, newly reported here. Most of the bony substance has been lost, and the plate itself is friable. The specimen is cataloged as *Coluber owenii* Meyer, 1844b. It like that it is a snake, but given the state of preservation we consider it Serpentes indet.; **B**, FFS Pz 4776, an articulated section of vertebrae and ribs with a possibly original head, newly reported here. The specimen is cataloged as *Coluber owenii*, but further study is needed to determine whether it is genuine and truly a snake. Scale bars: 1 cm. Photos: K. T. Smith.

Fürstlich Fürstenbergische Sammlungen, Donaueschingen

FFS Pz 4922 (newly reported here) (Fig. 9A)
This specimen is listed in the catalog as "*Coluber owenii*". To our knowledge it has not yet been reported or studied closely by a specialist. The specimen is preserved on a very delicate and friable slab. It consists mostly of impressions of at least 100 vertebrae, the osseous material having been never part of this slab or having subsequently been damaged. The impressions appear to be of the neural spines, and their long, narrow character suggests that the specimen could indeed pertain to Colubroides (see Zaher *et al.* 2019).

FFS Pz 4776 (newly reported here) (Fig. 9B)
This specimen is listed in the catalog as "*Coluber owenii*", and a fossil leaf is preserved on the same slab. To our knowledge it has not yet been studied closely by a specialist. A skull and anterior vertebral column are present, but they are poorly preserved, and further study is needed to determine whether the specimen is genuine and indeed pertains to a snake.

Unknown collections

Karg (1805: 30) noted three further possible snake specimens: one in the collection of the Rheinau Monastery, Switzerland, another with *Chorherr* [canon] *Gessner*, and a third in the "Fürstlich-Meersburgische Sammlung" (Collection of the Sovereign Princes of Meersburg). The first two were repeated by Meyer (1845), although he was not convinced by Karg's identifications. Concerning the second specimen, it will also be noted that, according to Jörg (1966), the *Chorherrenstift Öhningen* (canonry of Öhningen) once owned the quarries, but this was long before Karg's time (prior to 1534). The whereabouts of this specimen are currently unknown. Concerning the third specimen, a *fürstlich meersburgische Sammlung* does not currently exist, but it is unlikely that the specimen in question is one of the FFS or SMNK specimens, because Karg specifically notes that it is about 1 foot long and nearly straight ("fast gerade ausgestrekt").

The specimen in the Rheinau Monastery (like that in the Meersburg collection), Karg admitted, could be that of a *Blindschleiche* (Slow Worm, *Anguis fragilis* Linnaeus, 1758). It will be noted that Čerňanský & Klembara (2017) reported the limbless anguine lizard *Ophisaurus holeci* Klembara, 2015, based on specimen SMNK-PAL 8541, from Öhningen. The Rheinau Monastery closed in 1862, and some specimens and objects in the collection were transferred to museums and libraries in Switzerland (B. Zureich, pers. comm. 2025). Specifically, some objects ended up in what is now the Schweizerisches Landesmuseum in Zurich (Swiss National Museum in Zurich) and in the Kunstverein Winterthur (Art Society of Winterthur), whereas others were sold off, discarded, or incinerated (S. Aregger, pers. comm. 2025). There is no indication that such a fossil snake from Öhningen ended up in PIMUZ. Furthermore, the Naturmuseum Winterthur, at the time, was part of the city library (*Stadtbibliothek*), not the Art Society (S. Scherrer, pers. comm. 2025). Although NMWIN 14251 probably derives from the 19th century, during which time NMWIN bought or otherwise acquired many specimens from Öhningen, there is no evidence that it comes from the Rheinau Monastery. Accordingly, the fate of the second specimen mentioned by Karg (1805) is also unknown.

DISCUSSION

We could locate ten snake specimens, together with one questionable occurrence, from Öhningen (Table 1). As far as we can tell, the provenance of all specimens is poorly documented. On the one hand, the great heterogeneity of the Öhningen Beds (Karg 1805; Rutte 1956; Rasser *et al.* 2023) could prove very helpful in pinpointing the origin of specimens, insofar as the sediment on the fossil-bearing slabs can be studied and compared with known beds. On the other hand, the discontinuance of the Lower Quarry (at the *Ziegelhof*), makes a direct comparison with these sediments more difficult. One could hope that some distinctive aspect of the slabs could tie some of these snake specimens to slabs on which insects or plants are preserved. If the Lower Quarry were to be re-opened, more direct comparisons could follow.

Three taxonomic species of snake are known from Öhningen thus far: *Coluber owenii*, *Coluber arcuatus* and *Coluber kargii*. The holotype of the first was rediscovered in the course of this study, and the holotype of the second was also accounted for, rediscovered as a composite. All three were considered *nomina dubia* (Szyndlar 1992: 699; Szyndlar & Böhme 1993: 389, 390), to which therefore further specimens cannot be referred. However, the discovery of additional specimens of snake fossils from Öhningen, especially those with cranial remains (NMB. Fos 8863, SMNK-PAL 76701), and the development of new analytical techniques (μCT), calls for a re-evaluation of this material (which could of course end with the same conclusion). The third species, *C. kargii*, has long been recognised as a member of Viperidae (Karg 1805; Rochebrune 1880; Kuhn 1963; Rage 1984; Szyndlar 1992; Szyndlar & Böhme 1993; Szyndlar & Rage 2002) and is currently under study (GG, pers. comm.).

The discovery of new specimens in the course of this study has been largely serendipitous. The first author's attention was drawn to NMB.Fos 8863 by the director of the Naturmuseum Bodensee, Martina Kroth, who had read some articles about snake studies at Messel. She arranged for a local newspaper article about the specimen, which was read by Ursula Eichem of Wangen am See, who pointed it out to Dr. Michael Bartels, chairman of the Museum Fischerhaus Wangen-Öhningen. Dr. Bartels not only pointed out another skeleton in their collection (which turned out to be the holotype of *Coluber owenii*, previously thought to be lost) but suggested a further natural history collection in Winterthur, Switzerland, that could have fossil snakes from Öhningen. Inquiry there yielded the specimen noted above. At the same time, inquiry by Dr. Norbert Widemann of the Museum Natur und Mensch in Freiburg am Breisgau concerning fossils borrowed by his predecessor from SMNK revealed that these included a previously unknown snake specimen from Öhningen, and he further pointed out that Öhningen snakes might be present in the Fürstenberg collections (FFS) and a variety of other collections.

The five new specimens treated in this paper might not be all. The catalog above indicates three further possible specimens whose whereabouts are unknown. We contacted another ten Swiss collections known to host fossils from Öhningen (Museum Allerheiligen in Schaffhausen, the Natural History Museums of Basel, Bern, Fribourg, and Geneva, Natureum Lausanne, Museum Luzern, Naturmuseum Olten, Naturmuseum Solothurn, and Naturmuseum St. Gallen), but none of them reported snake fossils. It is our hope that the present work will call further attention to Öhningen collections throughout Europe, not just on the part of taxonomic specialists but most especially on the part of curators, who can point out further unknown specimens and collections that would enhance our understanding of this fascinating and tumultuous interval (Ivanov 2022; Georgalis *et al.* 2025) of the Neogene snake record.

Acknowledgements

We thank Martina Kroth (Naturmuseum Bodensee; also photo), who ultimately initiated this project by contacting one of us (KTS) concerning their snake fossil. We thank the following for access to specimens: Dr. Jörg Martin and Ricarda Szalay (FFS), Drs. Norbert Widemann, Silke Stolle and Edgar Dürrenberger (Museum Natur und Mensch, Freiburg am Breisgau), Sandra Scherrer (NMWIN; also photo), Drs. Julien Kimmig (SMNK) and Jannik Weidke (SMNK, now Staatliches Naturhistorisches Museum, Braunschweig), Dr. Marc Jones (NHMUK), and Profs. Christian Klug, Torsten Scheyer and Marcelo Sánchez-Villagra (PIMUZ). Dr. Weidke first suggested that the holotype of *Coluber arcuatus* could be part of a composite.

We thank the following curators for information concerning their collections of Öhningen fossils: Dr. Urs Weibel (Museum Allerheiligen, Schaffhausen), Dr. Ursula Menkveld-Gfeller (Naturhistorisches Museum Bern), Dr. Christian Pünterer (Naturhistorisches Museum Fribourg), Mr. Robin Marchant (Natureum Lausanne), Dr. Benedikt Holz (Museum Luzern), Pia Geiger-Schütz (Naturmuseum Olten), and Dr. Madeleine Geiger (Naturmuseum St. Gallen). We thank Dr. Norbert Widemann (Museum Natur und Mensch) for suggesting that we contact the institutions listed in the foregoing sentence.

We thank the photographers of the Museum Fischerhaus Öhningen-Wangen (Tina Schüßler), Museum Natur und Mensch in Freiburg (Martin Steiner), and SMF (Anika Vogel) for documenting the specimens faithfully. We are indebted to Dr. Michael Bartels, Gerhard Ludes, and Werner Pflüger (Wangen am See, Öhningen) for reaching out concerning Öhningen specimens and most especially for their time and generosity in sharing information concerning historical excavations in the quarries. We are grateful to Stephan Aregger and Beatrix Zureich (Catholic Church of / Katholische Kirche Rheinau) for historical information concerning the fate of the specimen mentioned by Karg (1805) that was in the possession of the monastery there. We used the AI engine "perplexity.ai" to understand the old-fashioned German phrase "Ich stehe nicht an" in context.

GLG acknowledges funding from the research project no. 2024/55/D/ST10/01545, financed by the National Science Center of Poland (Naradowe Centrum Nauki).

We thank Hugues-Alexandre Blain and two anonymous reviewers for their constructive comments as well as the acting editor, Dr. Michel Laurin, Hussam Zaher, Adenise Lopez and Audrina Neveu, for their careful attention.

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Submitted on 1 April 2026;
accepted on 20 May 2026;
published on 4 November 2026.