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RESEARCH PAPER

The Öhningen Fossil-Lagerstätte: multi-proxy insights into the preservation of a unique window of Miocene biodiversity

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Abstract

The middle Miocene (c. 14–13 Ma) Öhningen Fossil-Lagerstätte is one of the most famous fossil deposits in Germany and one of the most important Cenozoic deposits worldwide. The Öhningen Fossil-Lagerstätte has been known since the Middle Ages, and the two quarries were already exploited around the year 1500 for building stone and lime. In addition to its abundant plants and vertebrate fauna, the soft-bodied biota preserved in Öhningen is diverse, including various insects, aquatic arthropods, and arachnids. While the Öhningen Fossil-Lagerstätte is often regarded as a single deposit in the literature, it is imperative to recognize that there are notable differences between the two separate outcrops. Not only are there variations in sedimentology, modes of preservation of the soft-bodied fossils, and fossil diversity at the outcrop scale, but these elements can also vary within even a few centimetres of the same exposure. Part of this variation can be attributed to changing depositional environments and seasonality, but modern weathering and historical collections bias may also play significant roles. However, understanding the correlative nature of these proxies is in its infancy. Here we present new data from sedimentological, petrographic, paleontological, and electron microscopy with elemental mapping investigations to showcase the importance of a multi-proxy approach to the understanding of this convoluted deposit. The aim is to provide improved clarity into the paleoecological and taphonomic questions that have plagued Lake Öhningen for decades.

Keywords Cenozoic · Germany · Taphonomy · Depositional environment · Paleoecology · Exceptional preservation

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Introduction

The Miocene has yielded a remarkable number of Konservat-Lagerstätten (*sensu* Seilacher, 1970; Kimmig & Schiffbauer, 2024), with deposits preserving weakly skeletonized (or soft-bodied) fossil taxa (e.g., Allison & Briggs, 1993). These Konservat-Lagerstätten include: Pucking Biota (Austria), Bes-Konak Basin (Turkey), Foulden Maar (New Zealand), Radoboj (Croatia), Shanwang Biota (China), Savage Canyon Formation (USA), Buffalo Canyon Formation (USA), Chojaburu Formation (Japan), Botchi Formation (Russia), Stavropol (Russia), Barstow Formation (USA), Clarkia Lake Deposits (USA), Koyasawa River Locality (Japan), Kamiwada (Japan), Kabutoiwa Formation (Japan), Chita (Japan), Libros (Spain), Randecker Maar (Germany), Ribesalbes (Spain), Hindon Maar (New Zealand), Mfwanganu and Ruzinga Islands (Kenya), Tunjice (Slovenia), Tungen Hills (Kenya), Hrutagil (Iceland), Lava Camp Mine (USA), Grubstake Formation (USA), Alba Evaporite (Italy), Monte Castellaro (Italy), Langenau (Germany), Engelswies (Germany), the Steinheim Basin (Germany), Höwenegg (Germany), and Öhningen (Germany) (Bottjer et al., 2016; Muscente et al., 2017 and references therein, Rasser et al., accepted; Uhl et al. 2024). Among these deposits is the Öhningen ("Oeningen" in older literature) Fossil-Lagerstätte (will be henceforth referred to as Öhningen), a middle Miocene (c. 13.7 Ma; Rasser et al., 2026) lacustrine Konservat-Lagerstätte located at the western margin of Lake Constance in southwestern Germany (Fig. 1).

Öhningen preserves diverse fossils of soft-bodied and skeletonized taxa, dominated by plant and insect fossils (Heer, 1865; review in Rasser et al., accepted), and is famous for the iconic giant salamander *Andrias scheuchzeri* (Westphal, 1958). The exceptional preservation of soft-bodied taxa at Öhningen has attracted repeated attention, but the underlying taphonomic processes have not been systematically investigated with modern analytical techniques. At the same time, historical collecting practices, selective quarrying of distinct horizons, and numerous fossil forgeries have introduced significant anthropogenic biases into the available collections (Stauber, 1939; Jörg, 1966).

Despite more than two centuries of collecting and taxonomic studies, fundamental aspects of the Öhningen Fossil-Lagerstätte remain poorly constrained. The original outcrops are no longer accessible, as the upper outcrop is filled in, and the exact location of the lower outcrop is unknown, but should be across the street of the former Ziegelhof at GPS coordinates 47.670408, 8.926807 (Smith & Georgalis, in press). The precise position of most historically collected specimens within the succession remains also unknown (Rutte, 1956; Jörg, 1966; Rasser et al., 2023).

In this study, we combine sedimentological and petrographic observations with scanning electron microscopy and energy-dispersive X-ray spectroscopy (SEM–EDS) of selected plants, invertebrate, and vertebrate fossils from Öhningen. Our aims are to characterize the main depositional processes in the accessible part of the succession, document the dominant modes of fossil preservation and associated mineral phases, and evaluate how environmental conditions, diagenesis, and collection history together shaped the exceptional fossil record at Öhningen. This multi-proxy approach provides a refined framework for interpreting the Öhningen Fossil-Lagerstätte and contributes to a broader understanding of Miocene Konservat-Lagerstätten in Central Europe.

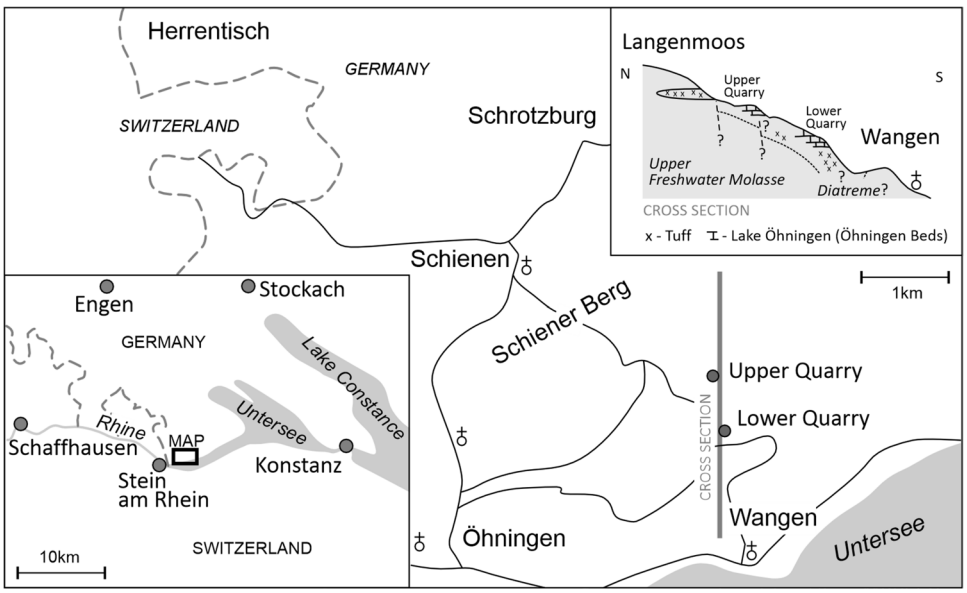


Fig. 1 Localities of the Öhningen beds in the so-called Upper and Lower Quarry (coordinates: see main text; modified from Rasser et al., 2023). Cross section after Schreiner (1984); note that the existence of a diatreme and the maar-nature of Lake Öhningen is currently under discussion

Table 1 Details of the Öhningen specimens analyzed in this study

Specimen #	Taxonomic designation on label	Description	Locality on label	Matrix	Preservation	Figures
SMNK-Pal 29883	*Formica lignitum*	Ant	Öhningen	Ca-carbonate and clays	Kerogenization	Fig. 7A, Supplement 1-3
SMNK-Pal 29868	*Capnodis* sp.	Beetle	Öhningen	Ca-carbonate	Kerogenization	Fig. 8A, Supplement 1-3
SMNK-Pal 29870	*Libellula doris*	Dragonfly larva	Öhningen	Ca-carbonate	Kerogenization	Fig. 8B, Supplement 1-3
SMNK-Pal 8527	*Xylocopa senilis*	Bee	Öhningen	Ca-carbonate	Kerogenization	Fig. 7B, Supplement 1-3
SMNK-Pal 29881	Cicadellinae indet.	Cicada	Öhningen	Ca-carbonate and clays	Kerogenization	Supplement 1 & 2
SMNK-Pal 76075	*Homelys minor*	Shrimp	Öhningen	Ca-carbonate and clays	Ca-phosphate	Fig. 9, Supplement 1-3
SMNK-Pal 76068	*Homelys minor*	Shrimp	Öhningen	Ca-carbonate	Ca-phosphate	Supplement 1 & 2
SMNK-Pal 30818	*Tinca furcata*	Fish	Öhningen	Ca-carbonate	Ca-phosphate	Fig. 10A, Supplement 1-3
SMNK-Pal 30848	*Gobio analis*	Fish	Öhningen	Ca-carbonate and clays	Ca-phosphate	Fig. 10B, Supplement 1-3
SMNK-Pal 29806	Anura indet.	Frog	Öhningen	Ca-Mg carbonate	Calcium fluorophosphate	Fig. 11, Supplement 1-3
SMNK-Pal 64259	indet.	Likely decayed leaf with gall at petiole	Öhningen	Ca-Mg carbonate	Iron oxides (likely pyrite weathering)	Fig. 12A, Supplement 1-3
SMNK-Pal 64285	cf. *Podocarpium*	Leaf	Öhningen	Ca-Mg carbonate	Carbon (Kerogenization) and sulfur	Fig. 12B, Supplement 1-3

Materials and methods

All examined specimens (Table 1) are housed at the Staatliches Museum für Naturkunde Karlsruhe (SMNK), Karlsruhe, Germany. Names of taxa are quoted according to the historical collection labels, since new identifications are unavailable. The exact stratigraphic level within the Öhningen beds succession is unknown for the complete collection material. The specimens were selected as they show a relatively complete preservation of the morphology, cover an array of groups, and originate from diverse excavations of the Öhningen Fossil-Lagerstätte. The specimens were photographed with a Keyence VHX 7000 digital microscope under white light. The colour, contrast, and brightness of the images were adjusted using Adobe Photoshop. Specimen measurements were made from photographs in ImageJ (Schneider et al., 2012).

Elemental composition was examined using a Scanning Electron Microscope (SEM) coupled with Energy Dispersive X-Ray Spectroscopy (EDS). The SEM-EDS imaging for all the other samples in the present study was conducted using a Hitachi FlexSEM 1000 housed in the Laboratory for Environmental and Raw Materials Analysis (LERA), Institute of Applied Geosciences, Karlsruhe Institute of Technology. Elemental map images were created using an Xplore 30 mm^2 EDS detector, processed and exported on AZtec software (version 6.2/Oxford). Specimens were analyzed uncoated. Analyses conducted on this instrument used the following operating conditions, with minor variation: beam accelerating voltage of 15 keV and current of 40 nA, a working distance of 10 mm ± 2 mm, and a chamber vacuum of 30 ± 5 Pa.

History

The research and collecting history of Öhningen extends back to the late Middle Ages when the two quarries were already exploited (c. 1500) for building stone and lime. In the 16th century, the Augustinian monks of the nearby monastery began to collect and sell fossils as curiosities: "Nature's Whims" (Stauber, 1939; Jörg, 1966). This marks the beginning of an organized fossil trade and the earliest phase of scientific interest, which intensified during the 18th century with the work of such scholars as Johann Jakob Scheuchzer. He described the most famous fossil from Öhningen, the giant salamander *Andrias scheuchzeri*. The skeleton was discovered in 1725 and described and figured as "*Homo diluvii testis*", freely translated to "Witness of the flood", the skeletal remains of a human drowned in the biblical deluge (Scheuchzer, 1726). It was Georges Cuvier who conclusively demonstrated in 1811 that it instead represents a giant salamander (Westphal, 1958). The later discoveries

of extant giant salamanders living in East Asia in the early 19th century established *Andrias scheuchzeri* not only as a fossil representative of this lineage, but also as a landmark specimen in the transition from biblical to modern Earth History.

In the 19th century, quarrying for building stone was accompanied by a flourishing commercial fossil market: Dealers and quarry owners extracted fossils specifically for sale and supplied museums and private collections all over the world (Stauber, 1939; Jörg, 1966). The strong demand encouraged extensive modifications and fossil forgeries (Fig. 2). Incomplete skeletons were completed, unrelated fragments were assembled into new "specimens", and even recent bones were occasionally embedded into slabs to increase their commercial value. This practice discredited fossils from Öhningen in the mid-19th century and still complicates taxonomic and taphonomic work today (Rietschel et al., 1985).

Scientific investigation of the deposits accompanied these commercial activities. A first stratigraphic profile of the upper quarry was recorded as early as 1805 by Karg, whose lithological terms and bed names later formed the basis for subsequent work (Karg, 1805; Rutte, 1956; Rasser et al., 2023). In parallel, the 19th century saw extensive descriptive work on the Öhningen fauna and flora by Oswald Heer in Zurich. In a series of monographs (Heer 1847, 1849, 1853, 1855, 1856, 1859, 1862), he described roughly 470 plant and about 830 insect species from the locality, comparing them with living relatives to infer a warm-temperate, humid climate (summary in Heer, 1865; Rutte, 1956). The first comprehensive geological treatment of the Öhningen beds was only provided much later by Rutte (1956), who conducted excavations and correlated the historical stonemasons' horizons with measured sections, and related them to the regional Molasse stratigraphy. This work yielded the first modern stratigraphic framework and remains a key reference for correlating historical bed names with lithological units (Rasser et al., 2023). After a long hiatus, new excavations were undertaken in 2021 by the natural history museums of Stuttgart (SMNS) and the SMNK, which re-opened part of the historical upper quarry and documented an approximately 8-m-thick succession of lacustrine sediments (Rasser et al., 2023).

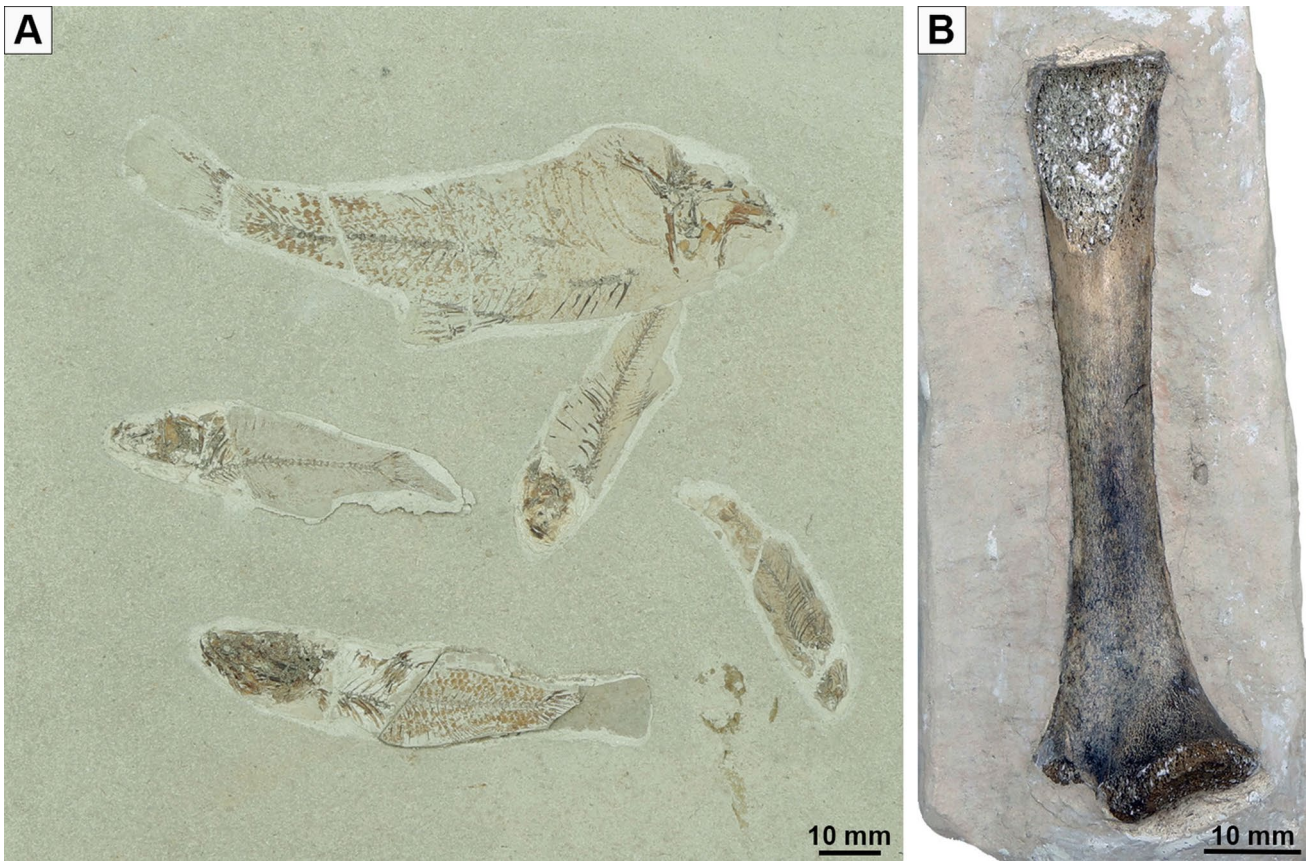


Fig. 2 Selected Öhningen fossil forgeries in the collections of the SMNK collection. **A** A sandstone with fish fossils attached with glue (SMNK-PAL 77078). **B** A sheep bone set in a limestone (SMNK-PAL 77079)

Locality, geological setting and depositional environment

The Öhningen Fossil-Lagerstätte is located on the southern flank of the Schienerberg, close to Wangen-Öhningen along the northern shore of Lake Constance (Fig. 1). This region is part of the Hegau volcanic complex, an area with active volcanism from c. 15 to 7 Ma (e.g., Keller 1985, Rahn & Selbekk, 2007; Zaugg et al., 2008). Sediments of the Miocene Upper Freshwater Molasse, such as the Glimmersand (fluvial channel deposits), are found in nearby outcrops of the northern Schienerberg area and were partly deposited simultaneously to the Öhningen lake strata (e.g., Hantke, 1954; Rutte, 1956; Giersch, 2004; Doppler et al., 2005; Uhl et al., 2006).

In this study, we conduct a classical facies analysis using the sediment composition, texture, sedimentary structures, and fossil data. The studied deposits document a lake depositional setting. However, as the depositional environment remains the same, the low-energy lacustrine depositional processes get frequently interrupted by higher-energetic processes, such as thunderstorms or heavy rainfall events, that affect the surroundings and the lake itself. During these events, the style of sedimentation and the fossil content change as material and organisms from nearby settings are transported into the lake, leaving event units with autochthonous and allochthonous elements.

Lake Öhningen was initially interpreted as a maar lake (e.g., Rutte, 1956; Doppler et al., 2005). However, there is no lithological or geophysical evidence for a maar origin (Lutz et al., 2000; Rasser et al., 2026; accepted). Moreover, it is still unclear whether the two quarry sites represent different stratigraphic levels of the lake, displaced by several meters along a major fault, or two separate small lakes. The size estimate of 500 x 960 m (Rutte, 1956) refers more likely to the outcrop, but not to the actual dimension of the lake.

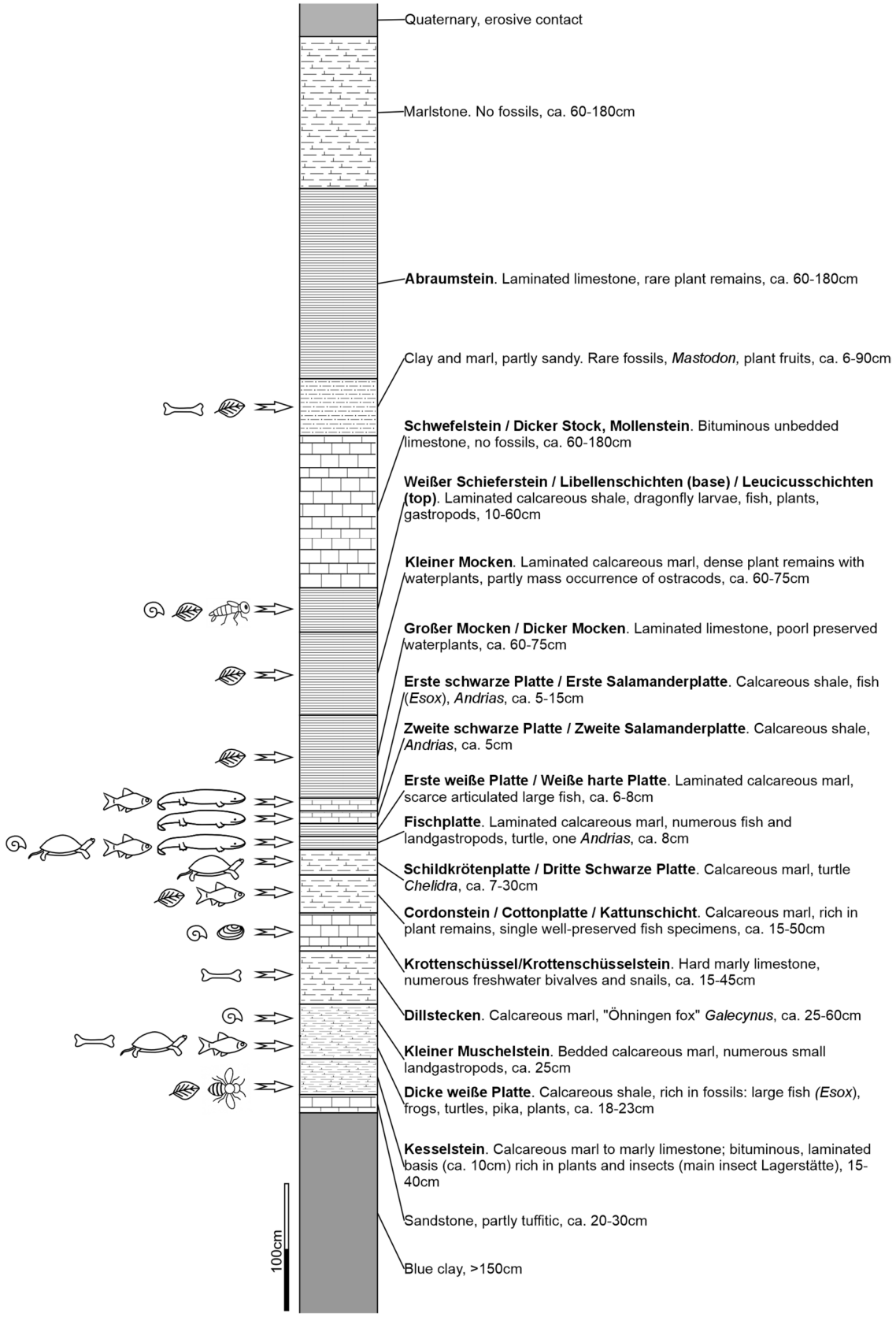
The Öhningen material was collected in two quarries: (1) the Upper Quarry next to Oberer Salenhof (coordinates: 47.67090, 8.92730) and (2) the Lower Quarry next to Ziegelhof (exact location of quarry unknown, coordinates of Ziegelhof: 47.67090, 8.92730), located only a few hundred meters away from each other (Fig. 1). In addition, fossils were picked up from freshly ploughed fields. Unfortunately, objects in collections mainly refer to the "Schiener Berg" as locality, but rarely name different quarries or the exact collection site. The Upper Quarry was abandoned, filled in several decades ago, and is no longer accessible. The only documentation of this site was published by Karg (1805), Murchison (1832), and Heer (1855, 1865), and summaries were provided by Rutte (1956). The comparison of historical sedimentary logs in Rutte (1956) revealed severe lateral changing facies on the former quarry area of ~ 250x100 m, reflecting a highly dynamic sedimentary basin: Fig. 3 comprises a tentative compilation of these logs. Hermann von Meyer (1845) already suggested that the different profiles described by Karg, Murchison and Heer may represent lateral variation as they represent different views into the deposits due to ongoing quarrying at the time. A recent excavation in 2021 (Rasser et al., 2023) was able to replicate lithofacies types described in Rutte (1956), but also documented features that had not been previously described, such as sediment deformation structures and ripples. Unfortunately, only ~ 8 m of the sedimentary sequence were accessible in 2021.

A complete sequence of Lake Öhningen has never been excavated or described. The base, and potential contact to the volcanic maar crater, was never reached, and the top of the deposits was eroded by glacial processes together with ~ 200 m of Molasse sediments (Schreiner, 1974). Thus, a full sequence from the initiation of the lake until its siltation does not exist and the total thickness remains unknown. Hence, the exact time frame of the Fossil-Lagerstätte in relation to the lake's evolution remains speculative. Fortunately, however, the age of the deposits has recently been fixed. Tobien (1986) and Heizmann (1992) relate the deposits to Mammal Neogene Zone MN7 (Middle Miocene), and recently (Rasser et al., 2026) applied apatite fission-track (AFT) dating to a tuffite (brownish, mica-rich fine silt- and sandstones) layer about 17 cm underneath the top of the succession, yielding an age of 13.7 ± 0.5 Ma (Lower Serravallian), which is in accordance with MN7.

Three lithofacies best characterize the depositional setting with internal and external processes, as well as the related habitat (Figs. 4, 5): (1) calcareous laminites and brown clays, (2) (graded) units with very high concentrations of plant fragments and/or shell hash, and (3) tuffites, seismites, and ripples.

Stagnant, potentially hostile phases are represented by calcareous laminites (mud to silt) and greenish to brown clays (Figs. 4A, 5B). Bioturbation and remains of lake fauna are absent. Layers rich in insects seem to represent low pressure systems, or thunderstorms, that caused sudden mass mortality with carcasses settling from suspension through the stagnant water column (Rasser et al., accepted). Laminated deposits of such stagnant phases occur throughout the sedimentary sequence, but dominate in the lower part (Fig. 3). Neuffer and Lutz (2000) interpreted Lake Öhningen as a meromictic, i.e., a standing, stratified water body lacking complete vertical water circulation, at least during reoccurring intervals (compare Rasser et al., accepted).

Episodes with both increased precipitation and river discharge are documented by coarser grained, silty to sandy units, which occasionally depict normal grading. Oftentimes, these units contain innumerable plant fragments (Fig. 4C; Fig. 5B–D). The high content of organic material


Quaternary, erosive contact
Marlstone. No fossils, ca. 60-180cm
Abraumstein. Laminated limestone, rare plant remains, ca. 60-180cm
Clay and marl, partly sandy. Rare fossils, *Mastodon*, plant fruits, ca. 6-90cm
Schwefelstein / Dicker Stock, Mollenstein. Bituminous unbedded limestone, no fossils, ca. 60-180cm
Weißer Schieferstein / Libellenschichten (base) / Leucicusschichten (top). Laminated calcareous shale, dragonfly larvae, fish, plants, gastropods, 10-60cm
Kleiner Mocken. Laminated calcareous marl, dense plant remains with waterplants, partly mass occurrence of ostracods, ca. 60-75cm
Großer Mocken / Dicker Mocken. Laminated limestone, poorl preserved waterplants, ca. 60-75cm
Erste schwarze Platte / Erste Salamanderplatte. Calcareous shale, fish (*Esox*), *Andrias*, ca. 5-15cm
Zweite schwarze Platte / Zweite Salamanderplatte. Calcareous shale, *Andrias*, ca. 5cm
Erste weiße Platte / Weiße harte Platte. Laminated calcareous marl, scarce articulated large fish, ca. 6-8cm
Fischplatte. Laminated calcareous marl, numerous fish and landgastropods, turtle, one *Andrias*, ca. 8cm
Schildkrötenplatte / Dritte Schwarze Platte. Calcareous marl, turtle *Chelidra*, ca. 7-30cm
Cordonstein / Cottonplatte / Kattunschicht. Calcareous marl, rich in plant remains, single well-preserved fish specimens, ca. 15-50cm
Krottenschüssel/Krottenschüsselstein. Hard marly limestone, numerous freshwater bivalves and snails, ca. 15-45cm
Dillstecken. Calcareous marl, "Öhningen fox" *Galecynus*, ca. 25-60cm
Kleiner Muschelstein. Bedded calcareous marl, numerous small landgastropods, ca. 25cm
Dicke weiße Platte. Calcareous shale, rich in fossils: large fish *(Esox)*, frogs, turtles, pika, plants, ca. 18-23cm
Kesselstein. Calcareous marl to marly limestone; bituminous, laminated basis (ca. 10cm) rich in plants and insects (main insect Lagerstätte), 15-40cm
Sandstone, partly tuffitic, ca. 20-30cm
Blue clay, >150cm
100cm

◂**Fig. 3** Sedimentary log of the Öhningen beds of the upper quarry with historical geological and stonemasons' terminology, summarized after Karg (1805; updated by Bruckmann in 1850) and Heer (1858, updated by Anonymous in 1897); details in Rutte (1956) and Rasser et al. (2023); only a few beds of the historical logs can be correlated with the latter two studies. Note that the historical geological terms cannot always be translated into current terminology; therefore, the lithologies must be considered tentative

washed into the lake can be recognized by a slightly bituminous smell of some of these units.

Compared to the low-energy background deposition, lamination, grainsize, and fossil content of the sediments depict that during phases of heavy rainfall, increased runoff and eventually high sediment influx from hillslopes in the surrounding catchment occurred. Consequently, plant remains and parautochthonous faunal elements, such as carcasses of the giant salamander, were washed into the lake.

External processes in the surroundings temporarily influenced the deposition and potentially also the living environment (Fig. 6). Synsedimentary volcanic activity of nearby volcanoes is evident by tuffites (Fig. 4A). The pyroclastic components may have settled from ash clouds and been washed into the lake during successive heavy rainfalls. The tuffite layers are a few millimeters to several centimeters thick, either massive or slightly normally graded. Soft-sediment deformation structures, like load structures and mud volcanoes, were caused by seismic shaking during volcanogenic earthquakes (Fig. 4B). The structures are attributed to dewatering and vertical motion of sediment with different densities during earthquakes (e.g., Lee et al., 2010). In addition, few stratigraphic horizons depict ripples. These silt- to sandstones were most likely deposited during phases of shallow lake level when wind shear agitated the water column (Fig. 4C, D). The source of the silt and sand are most likely reworked sediments from the surrounding Upper Freshwater Molasse deposits. Unfortunately, the 19th century sedimentological studies and logs (compiled in Fig. 3) do not mention features such as tuffites, sedimentary ripples, rapid lateral pinching-out of beds, and synsedimentary sliding and folding (Rutte, 1956; Rasser et al., 2023). This complicates the stratigraphic correlation of former studies crucial for palaeoenvironmental interpretations.

Overview of the Öhningen biota and palaeoecology

As much as Öhningen material has been collected since the Middle Ages, and the fossils of the locality have been intensively studied, very little is known about the palaeoecology. Additionally, many of the over 1500 described species from Öhningen are in urgent need of revision, likely resulting in a significantly fewer total number of taxa (e.g., Hantke, 1965; Fikáček & Schmied, 2013). It is also very important to understand that these fossils do not represent a single ecosystem: Insect fossils, lake invertebrate fossils, and vertebrate fossils rarely co-occur (Fig. 3). Additionally, the lack of stratigraphic information with many of the museum specimens will not allow a systematic ecosystem reconstruction through the lifecycle of the deposit.

Hantke (1965) concluded, based on the flora, that the Öhningen Schrotzburg deposit located near the Öhningen Fossil-Lagerstätte was likely deposited in a warm (~ 15°C) and humid (1300–1400 mm average annual precipitation) environment with little seasonality. Similar temperature and precipitation data were later confirmed by Uhl et al. (2003, 2006). Hantke, however, mentioned the Öhningen Fossil-Lagerstätte was likely deposited under a slightly warmer and drier climate. This interpretation is based on the dominating presence of *Cinnamomum* and *Populus* leaves, accompanied by oak and maple leaves. However, Uhl et al. (2006) pointed out that the identified *Cinnamomum polymorphum* leafs are actually *Daphnogene polymorpha* and have no known extant relatives, and as such should be excluded from palaeoclimate reconstruction. Oswald Heer (1855, 1856, 1859, 1865, 1879) described 475 plant species from Öhningen, but Hantke (1965) already suggested that the plant diversity is likely closer to 150 species. Unfortunately, the urgent review of the Heer's Öhningen plant fossils in the collections of the ETH Zürich, as suggested by Hantke and subsequently many other authors, never happened. In addition to these specimens, it would also be important to restudy the specimens at the Naturmuseum Winterthur, the Naturhistoriska Riksmuseet in Stockholm, and the SMNK, as well as other collections, where several more of Heer's types and other specimens are reposited (e.g., Heer 1855, 1856, 1859, 1865, 1879; Uhl et al., 2024).

While there is likely a significant collection bias towards plant and insect fossils (Salvador et al., 2022), it is still plausible to assume that the terrestrial fauna was dominated by insects, based on the sheer species richness and abundance of Öhningen insect fossils in museum collections. This is also supported by the number of published animal taxa. For example, Selmeier (1990) counted the following described animal species:

- 826 insect species
- 29 spider species
- 7 crab species (shrimp not noted)
- 4 bivalve species
- 32 fish species
- 12 reptilian and amphibian species
- 6 bird species
- 6 mammal species

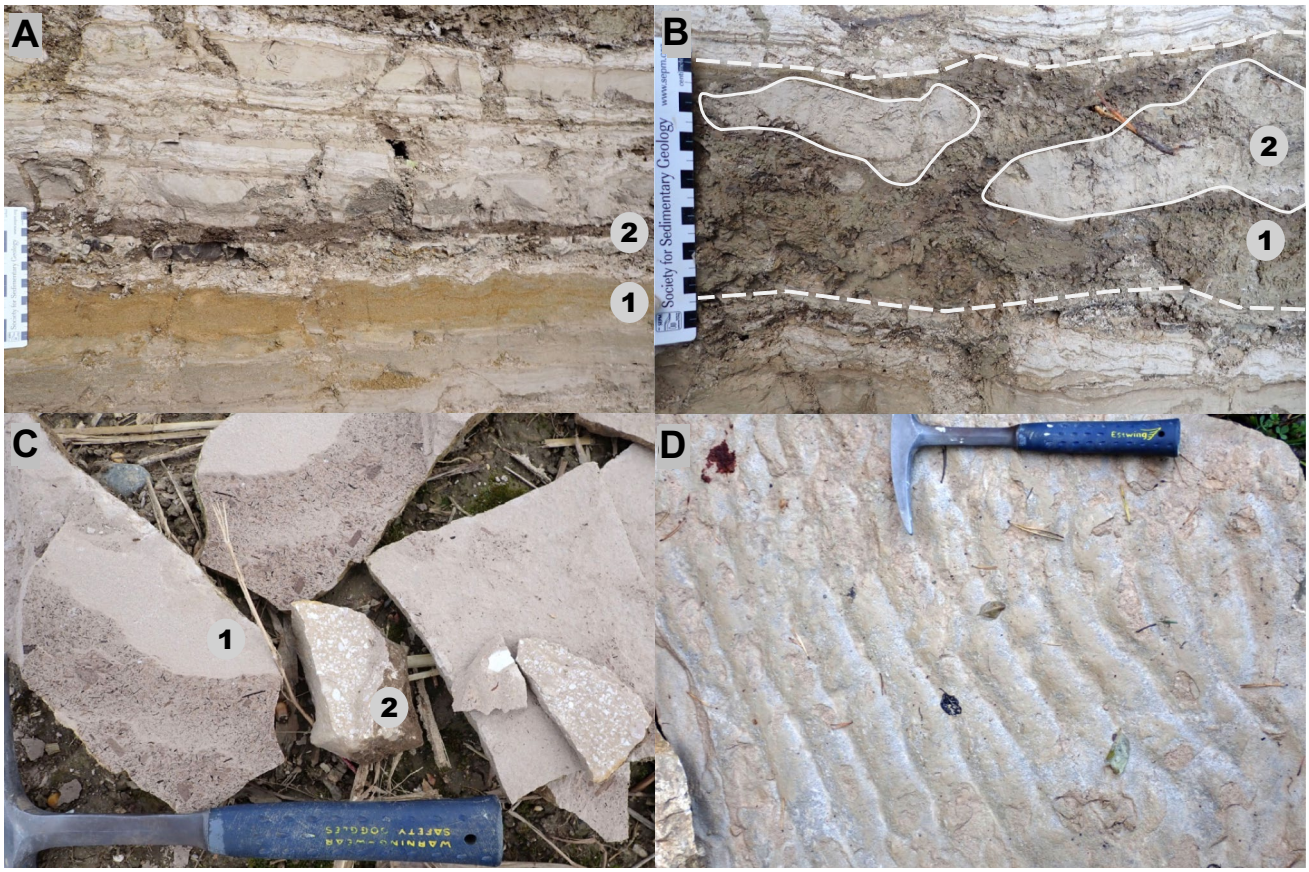


Fig. 4 Lithofacies in the Upper Quarry. **A** Greyish laminates intercalated with a sandy to silty tuffite (1) and brown clay (2). **B** 15 cm thick clay (1) unit with deformed intraclasts of sand (2), interpreted as related to regional seismic activity. **C** Calcareous silt with accumulations of plant fragments (1) and shell fragments (2). **D** Symmetrical oscillation ripples

While these numbers are unlikely to represent the true species richness, for example, Salvador et al. (2022) identified five bivalve and five gastropod species, and there are multiple reviews of insect groups (Michael Engel, personal communication) and reptile species (Krister Smith, personal communication) in progress, they do provide a glimpse of the fauna that lived in and around Lake Öhningen during its short-lived existence.

The lake itself had a relatively diverse fauna (Fig. 6). The most common vertebrate fossils in Öhningen are fish, and the most common genus is *Leuciscus* (Rietschel et al., 1985; Salvador et al., 2022). Additionally, at least ten mollusc species and several crustaceans called the lake home. This species richness suggests that if Öhningen was a meromictic lake (i.e., a stratified lake with layers of water that do not intermix), as has been suggested in the past (Neuffer & Lutz 2000; Rasser et al., accepted), then there must have been areas where benthic organisms could live, likely near the edge of the lake. This has been documented from other meromictic lakes like the Eocene Fossil Lake, USA (e.g., Grande 1984, 2013) or the Pliocene Willershausen Lake, Germany (e.g., Briggs et al., 1998). Whether the frogs and salamanders lived directly in the lake is unclear, they might have also lived in a tributary or on the lakeshore and had been moved into the lake postmortem or during reproduction. However, the often-complete preservation suggests little and if so, non-turbulent transport of the specimens.

Fossil preservation

The specimens from the Öhningen Fossil-Lagerstätte show a variety of preservation modes but the animal fossils are predominantly preserved as kerogenized/carbonaceous compressions and calcium phosphates. A full summary of the elemental preservation is provided in Table 1: All EDS elemental maps are included in Figs. 7, 8, 9 and 10. Soft-tissue preservation occurs in all animal specimens, apart from the frog (SMNK-Pal 29806).

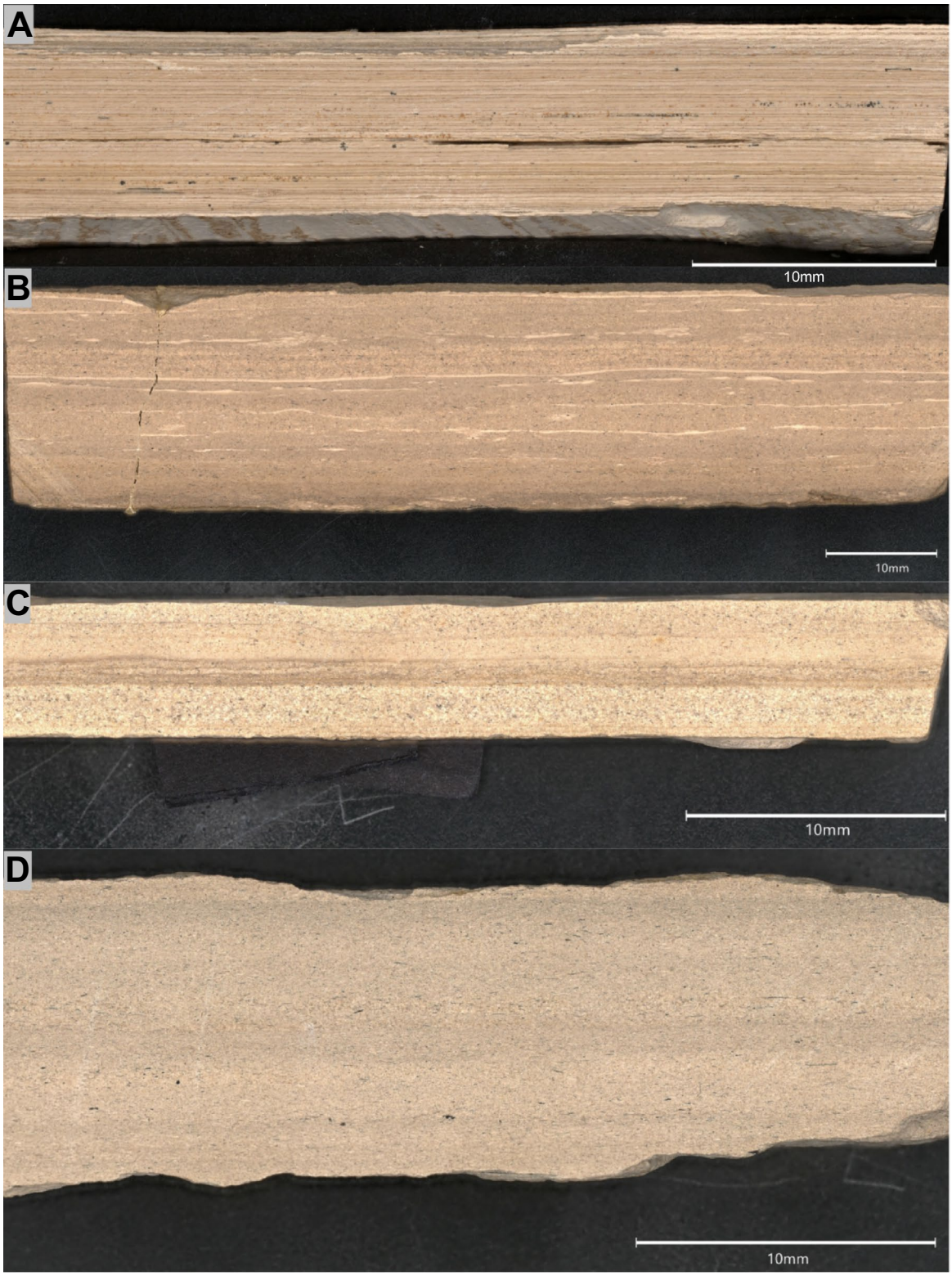


Fig. 5 Lithofacies in cut samples (all bars 1 cm). **A** Uniform very fine laminites deposited under stagnant conditions. **B** Succession of light calcareous laminites and silty brownish-grey layers that contain numerous plant fragments (dark spots). **C** Alternating coarse and fine layers, faintly graded. All layers contain numerous plant fragments (dark spots). **D** Layered siltstone with plant fragments (dark spots)

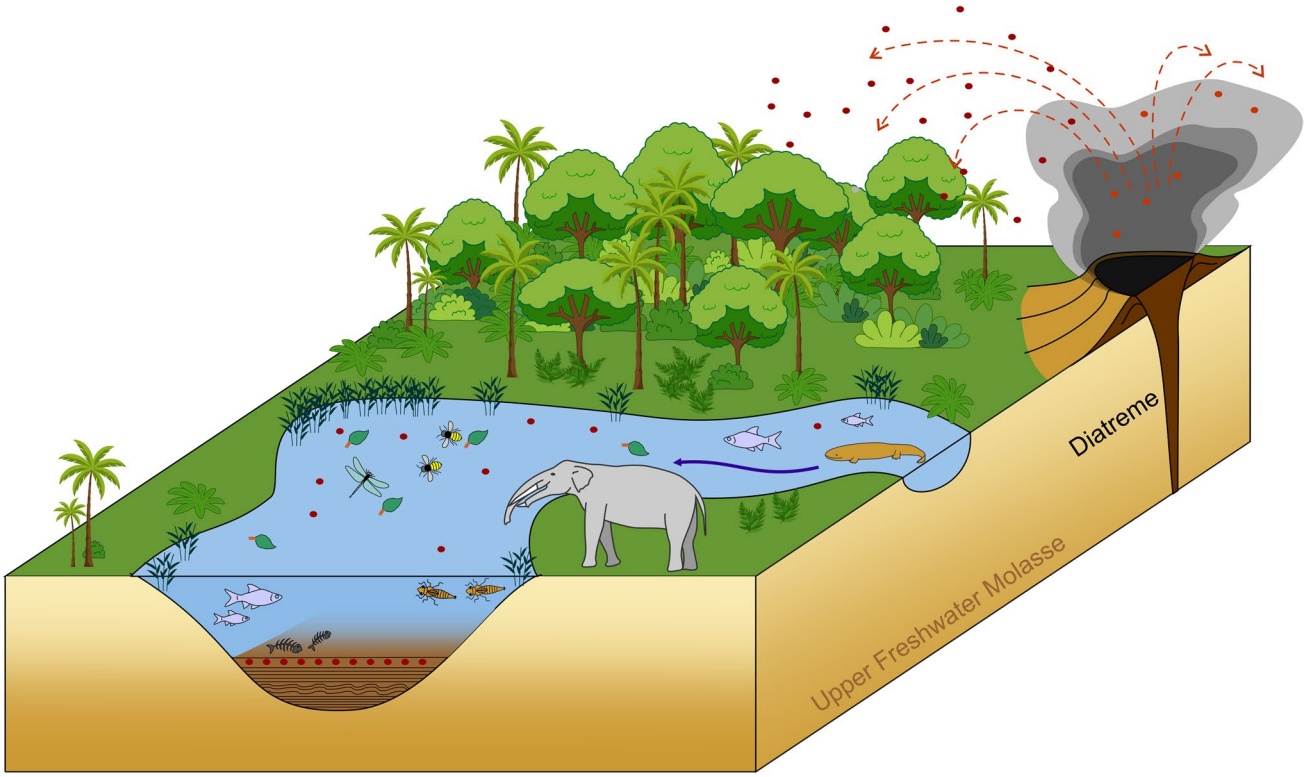


Fig. 6 Generalized scheme of the depositional environment and habitat of Lake Öhningen. Low-energy phases with laminites and clays were interrupted by episodic volcanic eruptions, earthquakes, and reoccurring phases of increased precipitation that washed external material (sediment, flora and fauna) into the lake. Sporadic thunderstorms may be responsible for insect event beds

Preservation dominated by kerogenization or carbonaceous compression is present in fossils with sclerotized cuticle, e.g., nonbiomineralized insect carapaces and appendages (Figs. 7, 8, Supplement 1, 2). The animal fossils preserved in this manner can illustrate fine morphological details, like the wing venation (Supplement 1) and thicker cuticles are usually preserved as darker patches (Supplement 1). When carbon is present in the analyzed specimens, it tends to be clearly delimited from the surrounding matrix (Figs. 7A–B, 8A–B). In addition to sclerotized cuticles, the soft-tissues in fish are also preserved by kerogenization or carbonaceous compression (Fig. 10A, B) (Supplement 2, 3). Finally, the analyzed leaf fossil is also partially preserved by kerogenization (Fig. 12B), but as Öhningen plants can be preserved in several different preservational states (Dieter Uhl, personal communication 2026), this data should be taken as preliminary.

Many arthropod cuticles are non-biomineralized or weakly biomineralized tissues (e.g., in insects, some xiphosurans, krill, amphipods) that are decay resistant (e.g., McNamara et al., 2010) and are often preserved as organic remains in Fossil-Lagerstätten. The arthropod cuticles from Öhningen are well preserved, and some of the insects appear to preserve internal structures, like the gut (Supplement 1), suggesting that the specimens underwent partial decomposition but stopped before only degradation-resistant body parts remained. As no other elements are incorporated into the organic remains, it can be assumed that there was little to no diagenetic influence. The only specimen showing early diagenetic signals is the bee (SMNK-PAL 8527), which preserves a calcium phosphatic halo (Fig. 7B), but neither the fossil itself, nor the matrix surrounding the halo, show any presence of phosphorus. The halo might be a product of bacterial activity during decomposition that changed the chemical microenvironment around the bee (e.g., Briggs et al., 1993; Briggs & Kear, 1994; Briggs & Wilby 1996; Wilby & Briggs, 1997; Clements et al., 2022).

The preservation of the fish soft-tissues as kerogenization or carbonaceous remains also indicate little to no diagenetic influence. However, the plant preservation in Öhningen is rather poor (Dieter Uhl, personal communication 2026).

The presence of calcium and phosphorus is found in crustacean cuticles (Fig. 9), as well as in vertebrate bones (Figs. 10A, B, 11). The frog bones are also enriched in fluorine (Fig. 11).

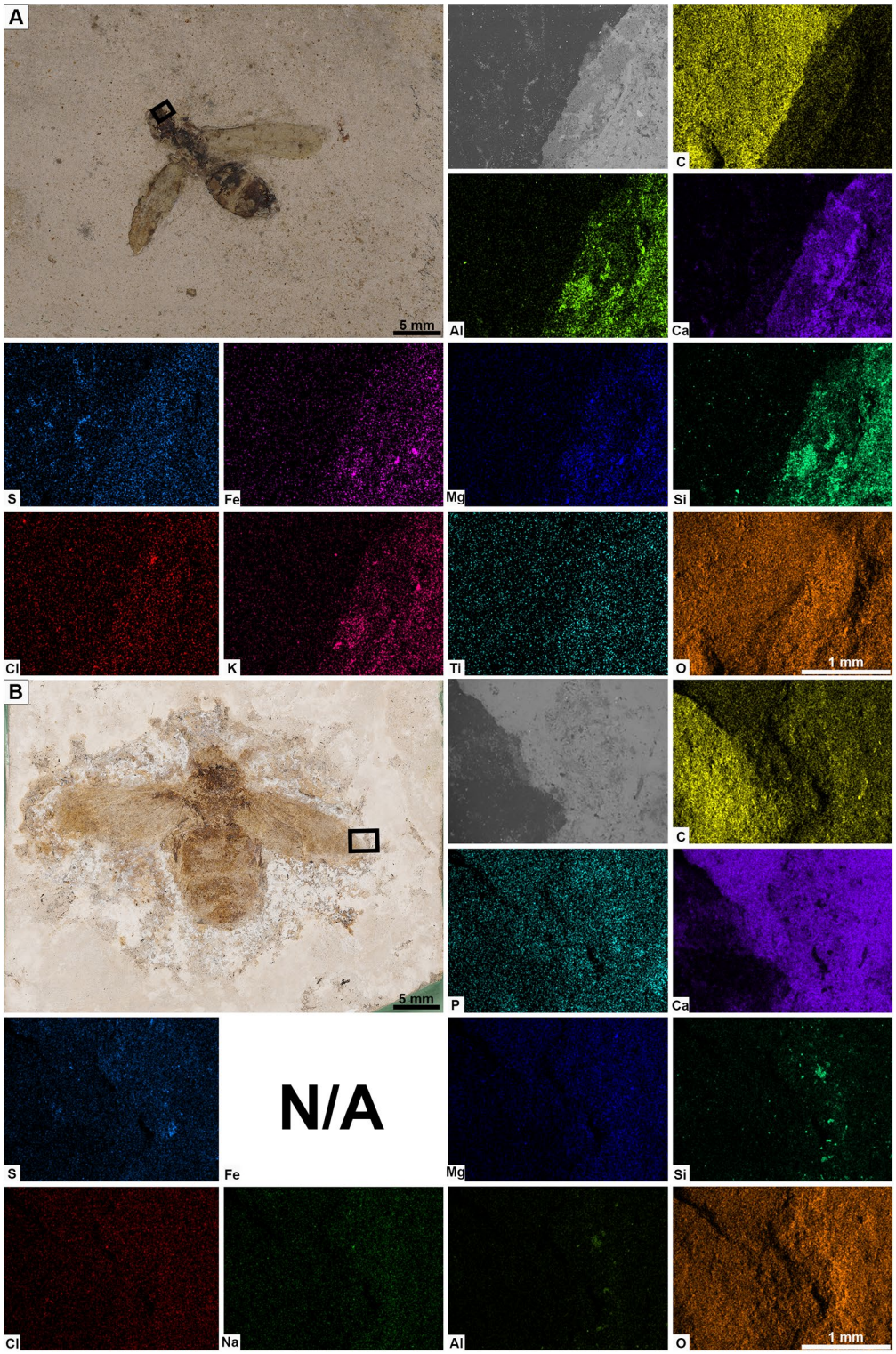


Fig. 7 Photographs and associated SEM–EDS elemental maps of the area highlighted by boxes in the pictures of selected insect fossils of diverse preservation from the Öhningen Fossil-Lagerstätte. Elements mapped are noted in the lower left corner, initial grey image is a backscattered electron image of the mapped area. **A** SMNK-PAL 29883, the ant *Formica lignitum*. **B** SMNK-PAL 8527, the holotype of the bee *Xylocopa senilis*

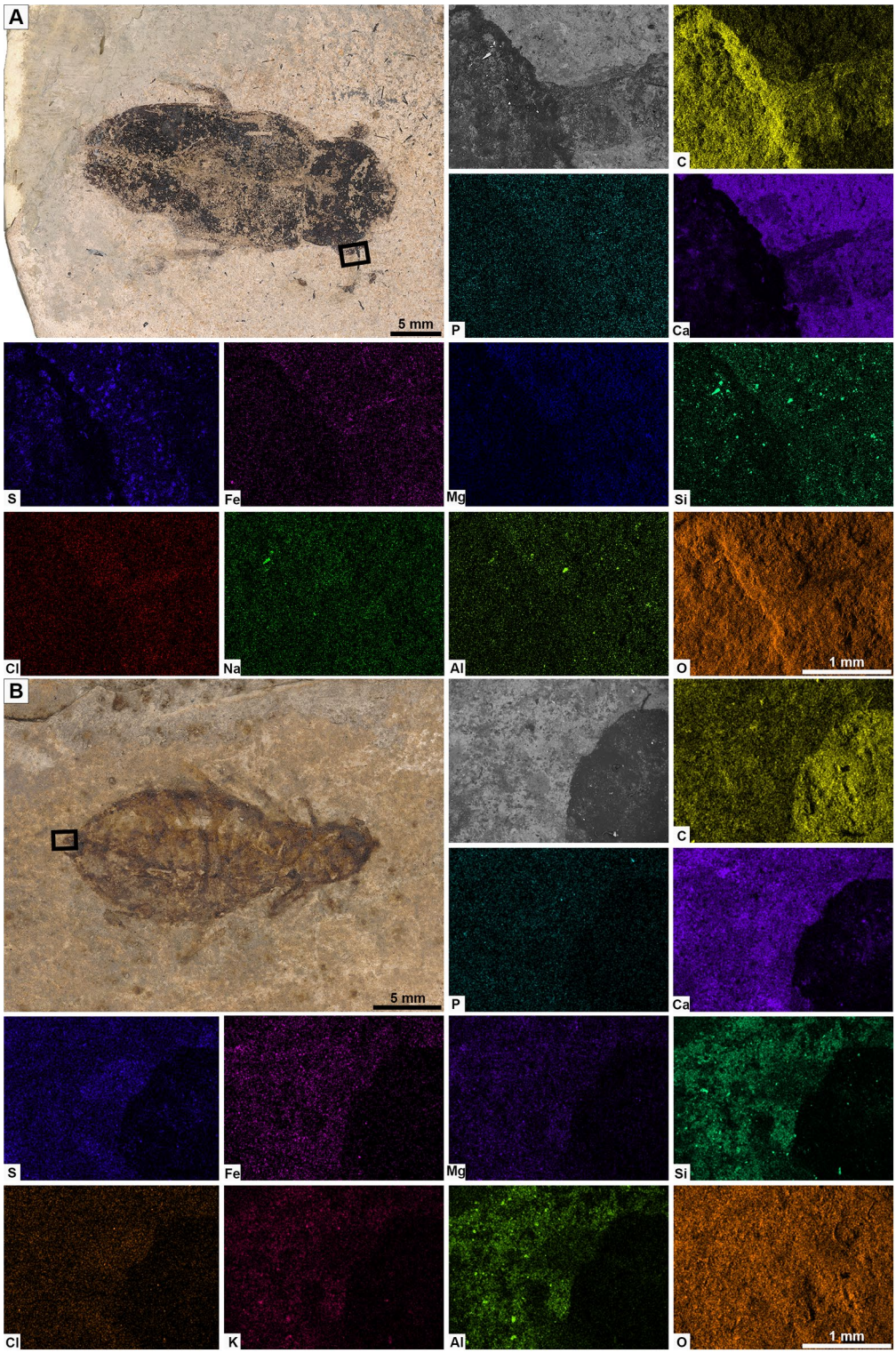


Fig. 8 Photographs and associated SEM–EDS elemental maps of the area highlighted by boxes in the pictures of selected insect fossils of diverse preservation from the Öhningen Fossil-Lagerstätte. Elements mapped are noted in the lower left corner, initial grey image is a backscattered electron image of the mapped area. **A** SMNK-PAL 29868, the beetle *Capnodis* sp. **B** SMNK-PAL 29870, the dragonfly larva *Libellula doris*

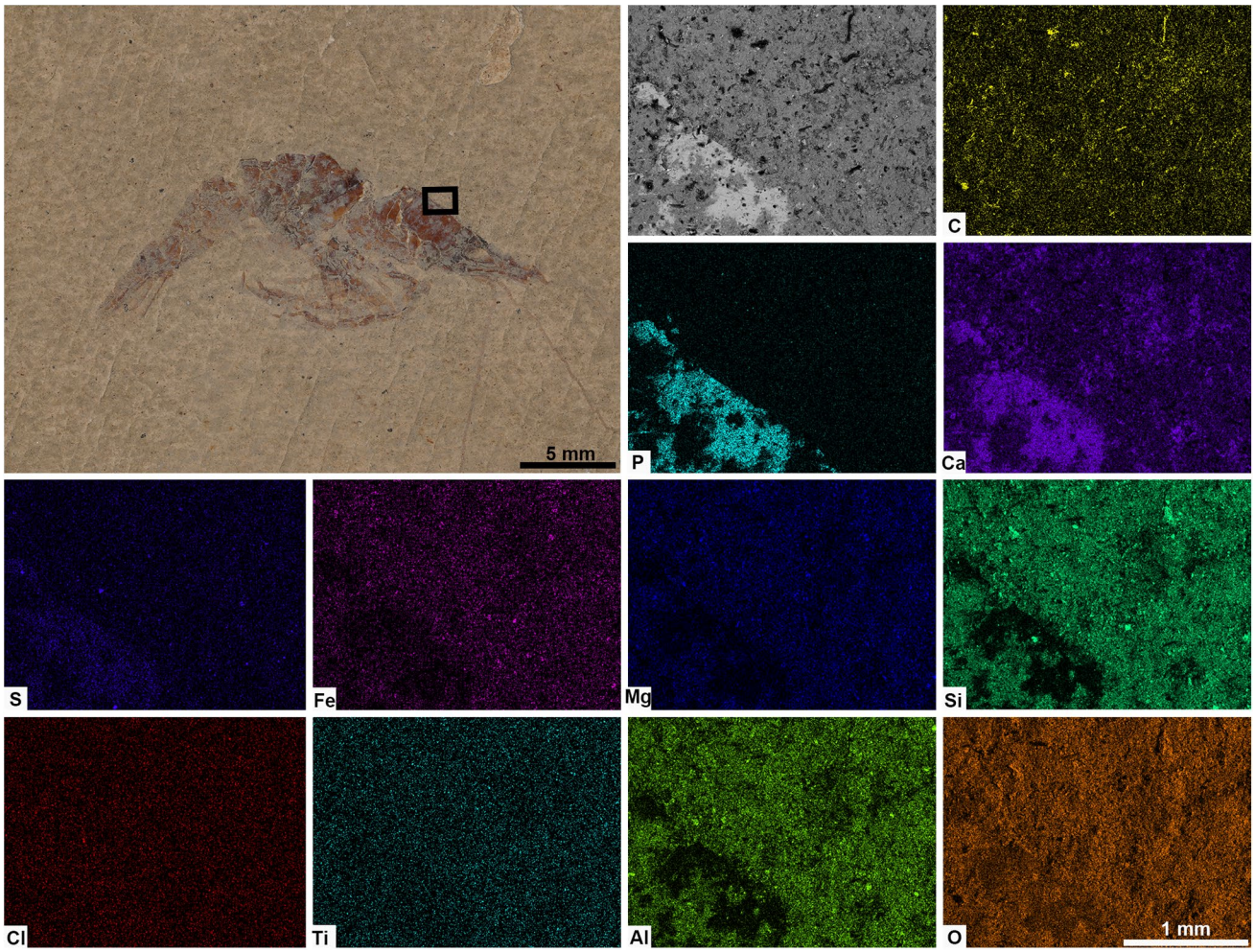


Fig. 9 Photograph and associated SEM–EDS elemental maps of the area highlighted by boxes in the picture of the shrimp fossil *Homelys minor* (SMNK-PAL 76075) from the Öhningen Fossil-Lagerstätte. Elements mapped are noted in the lower left corner, initial grey image is a backscattered electron image of the mapped area

The predominant calcium phosphate signal in the analyzed shrimps is consistent with other records of crustacean fossils (e.g., Briggs et al., 1993; Briggs & Kear, 1994; Briggs & Wilby, 1996; Wilby & Briggs, 1997; Page et al., 2009; Oliveira et al., 2015; Maguire et al., 2018; Vrazo et al., 2018; Barros et al., 2019; Bicknell et al., 2024; 2025; Liu et al., 2024; Martí Mus & López-Rojas, 2024). However, the few studies on modern crustaceans show that calcium phosphate is typically low in concentration and spatially restricted (e.g., Kunkel et al., 2012; Bentov et al., 2016; Bentov et al., 2021). Bicknell et al. (2026) discuss this issue in detail and suggest three potential hypotheses: (1) extinct crustaceans incorporated calcium phosphate into their exoskeletons more frequently than their modern descendants; (2) crustacean cuticle might be predisposed to diagenetic replacement by calcium phosphate; or (3) that acid preparation methods of modern crustacean cuticles might lead to a falsification of the actual chemical composition. At this point in time, the primary or secondary origin of the calcium phosphate in the shrimp fossils will not be resolved, but additional studies on fossil and modern crustaceans should be able to shed light on the issue. As the preservation of the other fossils shows little to no diagenetic overprint, and the soft tissues in the Öhningen fish are preserved as kerogenized/carbonaceous compressions, it is suggested that if the calcium phosphate is secondary in the shrimp, then it was likely an early diagenetic replacement.

The bones of vertebrates are composed of calcium phosphate minerals such as bioapatite (e.g., Szpak, 2011) and are comparatively easy to be preserved because of their high

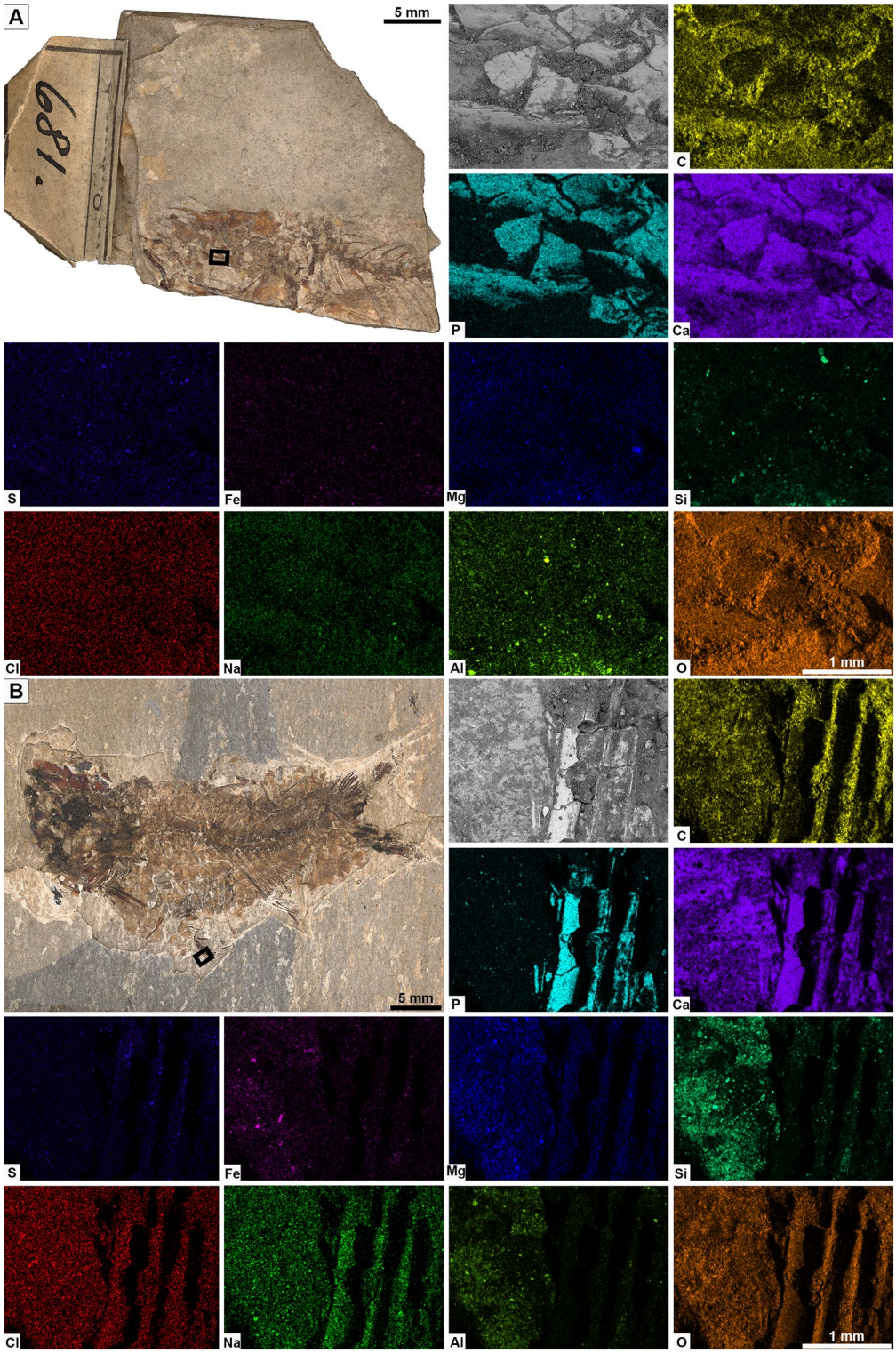


Fig. 10 Photographs and associated SEM–EDS elemental maps of the area highlighted by boxes in the pictures of selected vertebrate fossils of diverse preservation from the Öhningen Fossil-Lagerstätte. Elements mapped are noted in the lower left corner, initial grey image is a backscattered electron image of the mapped area. **A** SMNK-PAL 30818, the fish *Tinca furcata*. **B** SMNK-PAL 30848, the fish *Gobio analis*

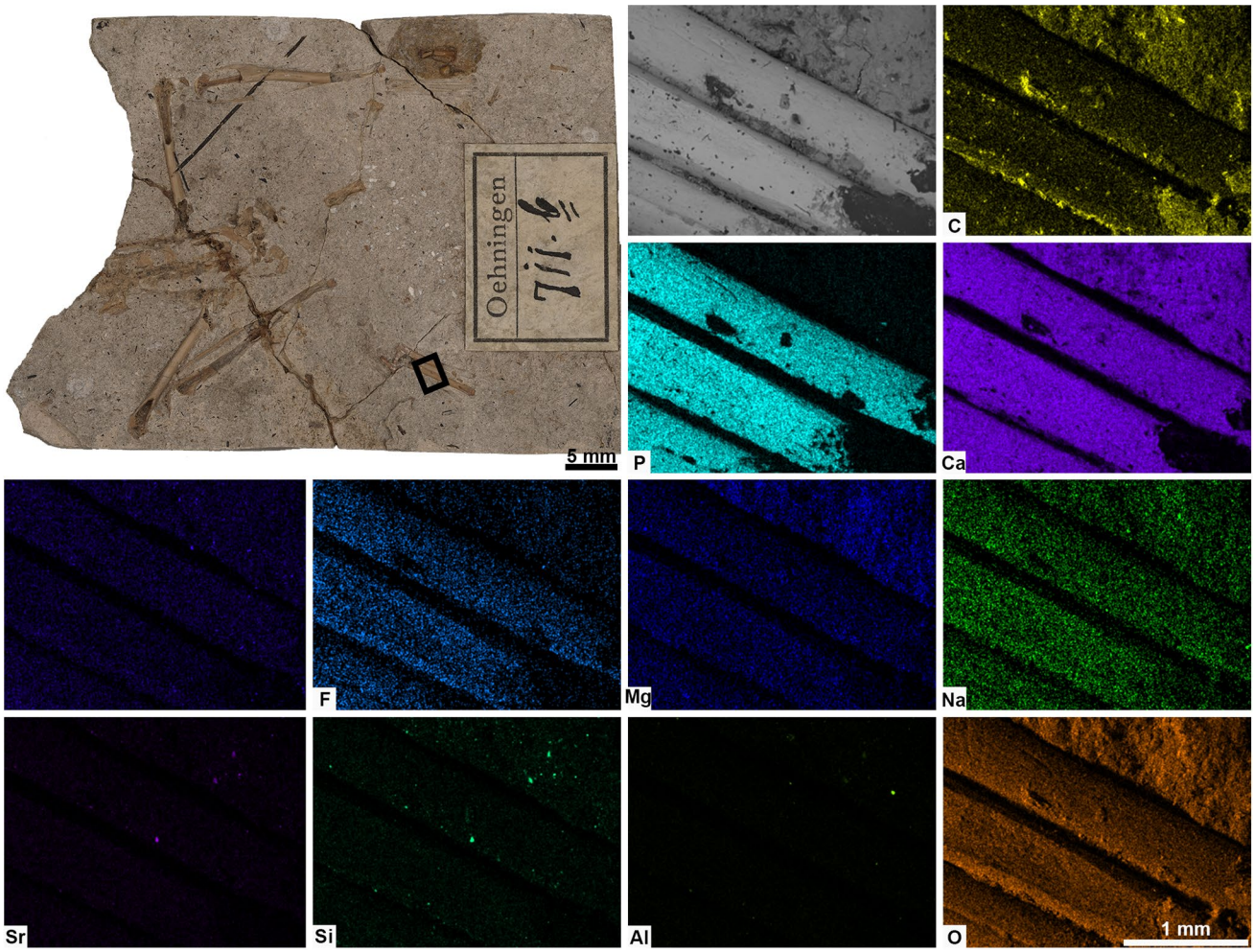


Fig. 11 Photograph and associated SEM–EDS elemental maps of the area highlighted by boxes in the pictures of an anuran specimen (SMNK-PAL 29806) from the Öhningen Fossil-Lagerstätte. Elements mapped are noted in the lower left corner, initial grey image is a backscattered electron image of the mapped area. SEM-EDS maps rotated 100 degrees from the specimen

decomposition resistance (e.g., Sansom et al., 2010; Clements et al., 2022). It has also been observed very early that fluorine can be incorporated into the calcium phosphate minerals (e.g., Wilson, 1895). Therefore, as the soft-tissues of the fossil fish are preserved as kerogenized/carbonaceous residues (Fig. 10A, B), it suggests little to no diagenetic replacement.

Elevated iron in the form of oxide- and/or oxyhydroxide-weathering products are only present in the plant fossils (Fig. 12A, B). They might be a weathering product of pyrite, but no crystals or crystal morphs are observed. The petiole (Fig. 12A) also preserves some titanium, an element that has been shown to appear naturally in some plants (Dumon & Ernst, 1988), or to sometimes accumulate in early diagenetic stages in organic matter of plants (Strullu-Derrien et al., 2019). However, the presence of Ti can be an instrumental artifact, owing to the overlap of the barium Lα and titanium Kα x-ray energies and the direct spatial overlap in their elemental maps. However, this is unlikely in this case, as no barium has been detected in the sample, and you would expect both elements to be detected with a similar pattern (e.g., Whitaker et al., 2022).

The sampled fossils show clade and tissue specific variation in preservation, which is consistent with the original biologic material: Arthropod cuticle, bone, soft-tissues, and plant (Fig. 12). Each clade displays a different mode of preservation, as is expected between insects, crustaceans, anurans, fish, and plants. However, none of the clades show signs of complete authigenic mineral replacement, and most fossils show no signs of authigenic mineral replacement.

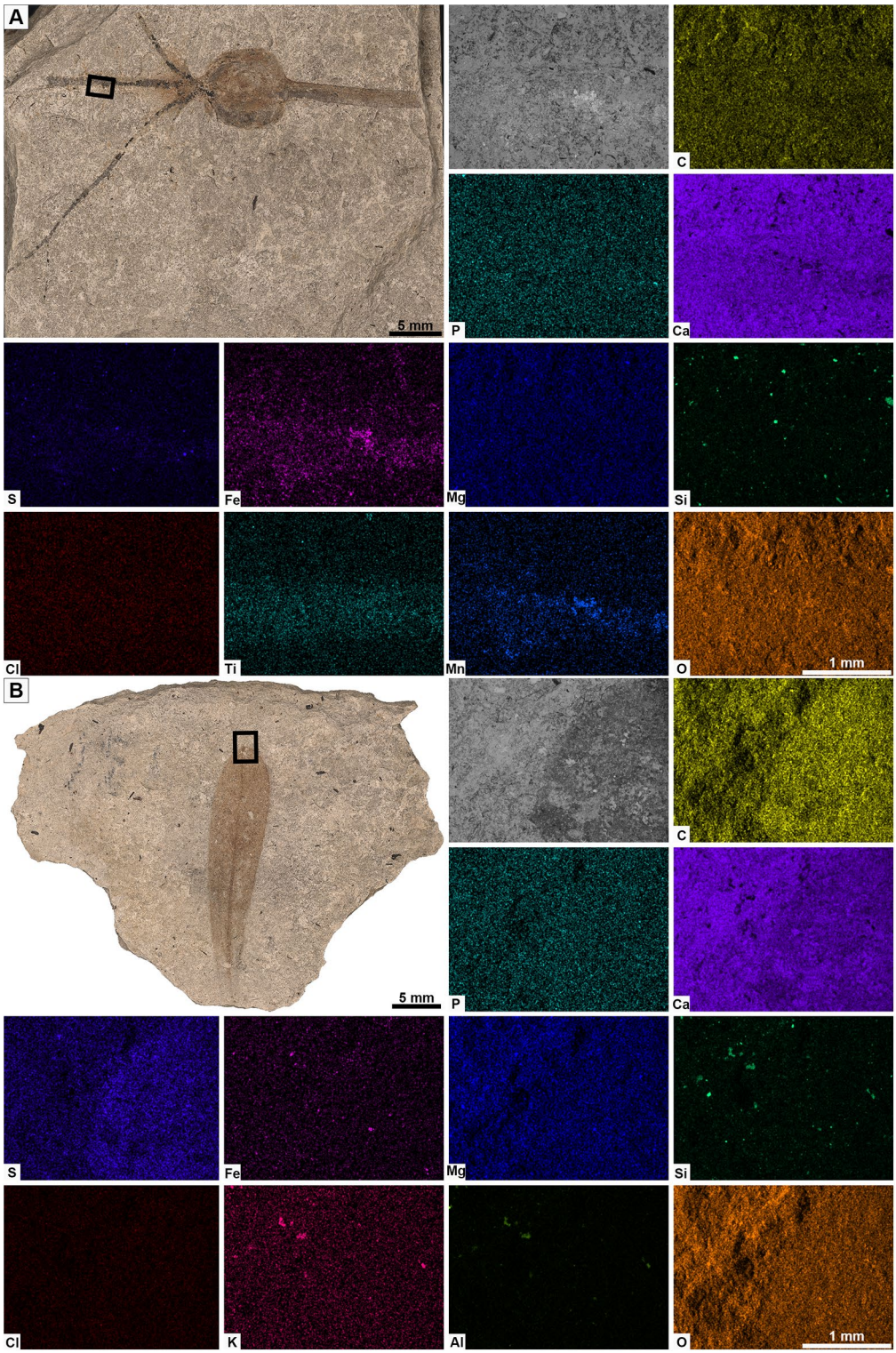


Fig. 12 Photograph and associated SEM–EDS elemental maps of the area highlighted by boxes in the pictures of selected plant fossils of diverse preservation from the Öhningen Fossil-Lagerstätte. Elements mapped are noted in the lower left corner, initial grey image is a backscattered electron image of the mapped area. **A** SMNK-PAL 64259, a gall. **B** SMNK-PAL 64285, a leaf of cf. *Podocarpium*

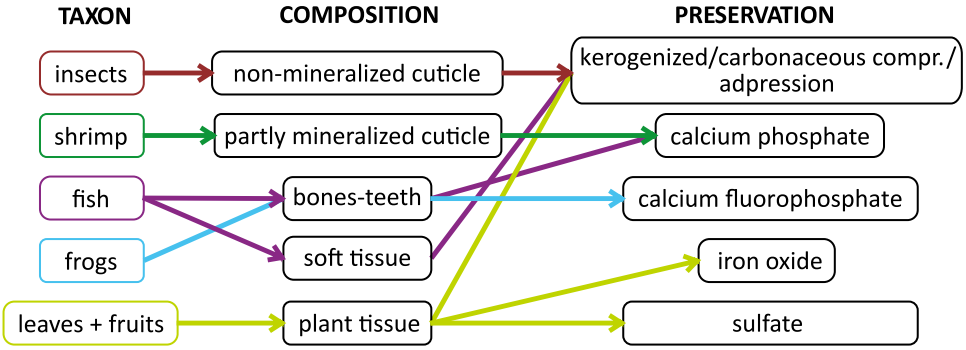


Fig. 13 Preservation pathways of selected clades of the Öhningen Fossil-Lagerstätte: Links between taxonomic group, original composition of hard and soft parts, and dominant preservation mode in Öhningen

The matrix of the analyzed specimens provides some evidence that Heer's fossils might have been collected from a different layer as later specimens, as they all preserve in nearly pure carbonates. The other specimens come from carbonates with some clay content, or calcium-magnesium carbonates. The calcium-magnesium carbonates do not appear to preserve soft-tissues, but only contain plant remains and bones in this study. Heer (1855, 1856, 1859) did, however, provide information in his monographs on the layers from which the plant fossils had been collected. Following this, if specimens in museum collections are identifiable as Heer plant fossils, then these may be able to be correlated through sedimentological and geochemical analyses of the sediment to later specimens. However, the lack of precise sampling or stratigraphic data, the unknown exact location of the lower quarry that Heer sampled, and the multiple horizons preserving fossils do not allow for any conclusions at this point in time. Additionally, there appears to be a clear collection bias towards complete specimens in the collections of the SMNK, and many other Öhningen collections, which suggests that other anthropogenic biases (e.g., Whitaker & Kimmig, 2020), for example selective collection of certain layers, likely took place. This has also been noticed by Salvador et al. (2022), who observed a bias towards plants and insects in the Öhningen collections they studied, which can be seconded for the SMNK collections (see Fig. 13).

Summary

The Öhningen Fossil-Lagerstätte of southern Germany preserves a diverse, well-skeletonized and soft-bodied fauna, and plant biota of middle Miocene age (c. 13.7 Ma). It provides insight into the freshwater life in central Europe around the time of the last climatic warm period, and together with other Fossil-Lagerstätten from the Miocene of southern Germany (Langenau, Engelswies, Randeck Maar, the Steinheim Basin, and Höwenegg) (Rasser et al., accepted), provides a unique window into the biodiversity changes in this important period of climatic change.

Although historically interpreted as a maar lake (a relatively deep crater lake in which stratification can develop), both the sedimentology and taphonomy presented in this and recent studies do not support this interpretation, but rather address Lake Öhningen as a river-related lake, such as a floodplain or oxbow lake.

Additionally, what is nowadays referred to as the Öhningen Fossil-Lagerstätte is not the biota of a single layer or unit within one outcrop, but the biota of several stratigraphically separated levels, many of which preserving exceptionally preserved fossils: There are at least two outcrops. The stratigraphic levels likely represent different lake water levels and might even represent different palaeoenvironments, as the faunal assemblages and sedimentology change (Fig. 3). The presented SEM-EDS data provide the first information on the preservation of the fossils from Öhningen and show that independent of the stratigraphic layer, as far as can be assumed from the historical collections, the animal fossils show little to no diagenetic overprint.

Finally, recent progress has been made in understanding the stratigraphic and sedimentological context of Öhningen; however, the missing stratigraphic data for much of the historical museum collections make it nearly impossible to assign them to certain intervals, with the exception of most of the insects, which are restricted to the lowermost fossiliferous deposits and the salamanders, which are found further up (Fig. 3) (Rasser et al., 2023). New excavations will be able to provide more clarity of the stratigraphic distribution of fossils within the deposit and only then will it be possible to work out the various taphonomic pathways that allowed soft-bodied preservation in this key window of Miocene life.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12542-026-00800-0.

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Data availability All data are included in the paper and the supplement.

Declarations

Conflict of interest All the authors declare no conflict of interest.

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