



Research Article

The Middle Triassic vertebrate deposits of Michelbach an der Bilz (Baden-Württemberg, Germany): Environmental and climatic controls of ecosystems

Eudald Mujal^{a,b,*}, Orla G. Bath Enright^{a,c}, Hans Hagdorn^d, Rainer R. Schoch^{a,e}

^a Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany

^b Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ de les columnes, s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Catalonia, Spain

^c School of the Environment, Geography, and Geosciences, University of Portsmouth, Burnaby Road, Portsmouth, Hampshire PO1 3QL, UK

^d Muschelkalkmuseum, Schloss-Straße 11, 74653 Ingelfingen, Germany

^e Fachgebiet Paläontologie, Institut für Biologie, Universität Hohenheim, 70599 Stuttgart, Germany



ARTICLE INFO

Editor: Sun Jimin

Keywords:

Keuper
Taphonomy
Fossil lagerstätte
Palaeosols
Lacustrine
Central European Basin

ABSTRACT

The Middle Triassic was a critical epoch for vertebrate ecosystems, with the radiation of the so-called modern tetrapod lineages. Adding to more profound understanding of these ecosystems, we describe the palaeoenvironment of the Michelbach lagerstätte from the Lower Keuper Erfurt Formation (upper Ladinian, Germany) by investigating its sedimentology, taphonomy and fossil content. The deposits correspond to a ~ 1.8-m-thick succession of grey siliciclastic mudstones (Sandige Pflanzenschiefer unit, layers M1–M6) and yellowish carbonates (Anthrakontbank unit, layers M7–M8). Within six distinct lacustrine mudstone layers (M1–M6), the three basal ones bear a fair number of fish and tetrapod taxa. Molluscs (mostly bivalves) and plant remains (including small coal seams) are less abundant. Lake M1 was probably deep and not very favourable, inhabited by an impoverished fish fauna, and the temnospondyls *Plagiosuchus* and *Mastodonsaurus*. Lake M2 was the most diverse, with eight fish species, including dipnoans, and the temnospondyls *Plagiosuchus* and *Mastodonsaurus* as the dominant taxa, plus *Tatrasuchus*, *Callistomordax*, and *Gerrothorax* (at the latest phase), as complementary fauna. Lake M3 was shallower and harboured the temnospondyls *Trematolestes* and *Gerrothorax*. The successive shallow lacustrine to palustrine deposits of M4 to M6 are significantly less fossiliferous, with abundant carbonate nodules becoming larger upwards. The succession corresponds to a relatively low energy, intermittently water-logged setting, likely marginal lacustrine, where carcasses accumulated during dry periods. The abundant finds of isolated bones and teeth, often fragmented but preserving delicate details, suggest reworking and high-energy events (e.g., mud flows). Three successive cycles of palaeosols, from Vertisols to Calcisols, document an aridification trend and seasonality. The lacustrine system ended with a marine transgression (bonebed in M7, plus dolostones with gypsum nodules in M8) under a relatively arid climate. Overall, taphonomic features correlate with palaeoenvironmental evolution and climatic trends, showing how changing habitats shaped faunal assemblages.

1. Introduction

The Lower Keuper (late Ladinian, Middle Triassic) vertebrate fossil lagerstätten of southwestern Germany have recently yielded a wealth of data on the evolution and palaeoecology of vertebrate ecosystems during the Triassic (Hagdorn et al., 2015; Schoch and Seegis, 2016; Schoch et al., 2018, 2022, 2024; Mujal et al., 2022, 2025), especially

considering the paucity of vertebrate fossils in this time interval (Sues and Fraser, 2010). Reports from the more recently uncovered lagerstätte of Miedary, southern Poland (early Ladinian) add evidence on the diversity of vertebrate faunas in Lower Keuper facies, showing differential patterns of palaeoenvironmental distribution and relative proportions of vertebrate assemblages with respect to those in Germany (Pawlak et al., 2022; Czepiński et al., 2023). Generally, all Lower Keuper

* Corresponding author at: Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany.

E-mail address: eudald.mujalgrane@smns-bw.de (E. Mujal).

<https://doi.org/10.1016/j.gloplacha.2026.105723>

Received 10 May 2026; Received in revised form 11 September 2026; Accepted 13 September 2026

Available online 16 September 2026

0921-8181/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Open access funding enabled and organized by Projekt DEAL.

lagerstätten of the Central European Basin (CEB) contain similar or even the same faunas, though in different proportions (Mujal et al., 2025). This shows how similar, almost coeval, sedimentary units preserve generally consistent faunas, yet with noteworthy differences, especially regarding the habitats inferred for the taxa present, with the German lagerstätten preserving more terrestrial and less marine specimens than the Polish one. In this regard, the Lower Keuper in the CEB is an ideal case study to analyse how environmental and climatic conditions influenced the composition of Triassic ecosystems (Mujal et al., 2025), and ultimately the preservation of vertebrate remains (e.g., Behrensmeyer and Hook, 1992). The Middle Triassic epoch was also a key time in tetrapod evolution because several lineages flourished and became highly diversified (Ezcurra, 2010; Sues and Fraser, 2010). This diversification has been linked to the delayed recovery in the aftermath of the end-Permian mass extinction, the magnitude of which is still a matter of debate (Bond and Grasby, 2017; Lucas, 2017, 2021; Vajda et al., 2020; Dal Corso et al., 2022). In this regard, a better understanding of ecosystem dynamics during the Triassic can be achieved by analysing the palaeoenvironmental distribution of tetrapods throughout this period (e.g., Mujal et al., 2025).

Reconstruction of environmental settings based on stratigraphic and sedimentological data along with taphonomic analyses allow for the reconstruction of past ecosystems and palaeoecology (Behrensmeyer and Hook, 1992). In this context, lagerstätten from the Lower Keuper in the CEB (Hagdorn et al., 2015; Mujal et al., 2025) are especially relevant because exceptional preservation provides a more complete picture of organisms that were present and eventually of the whole ecosystem (Seilacher et al., 1985).

Here, we aim to address two related major research questions: (1) how did environmental settings and changing climatic conditions influence the distribution and preservation of tetrapods; (2) how did tetrapod assemblages respond to such environmental changes during the Middle Triassic? To do so, we analyse the Michelbach lagerstätte from southwestern Germany (Fig. 1A). Differing from previously analysed lagerstätten from this facies succession and region (Schoch and Seegis, 2016; Schoch et al., 2022), Michelbach is found in a stratigraphic unit older than those others (e.g., Hagdorn et al., 2015; Schoch and Mujal, 2022). This lagerstätte is different because of its faunal assemblage yielding the highest density of tetrapods, and the highest percentage of articulated skeletons (Hagdorn et al., 2015). Besides exemplifying the diversity of Middle Triassic ecosystems, Michelbach also widens the palaeoenvironmental settings in which different faunal assemblages are found. We describe in detail the stratigraphic succession to reconstruct the depositional history and how the palaeontological content, mainly focusing on tetrapod faunas, changes throughout. Here, we provide a detailed comparative framework, allowing for high-resolution insights of these Middle Triassic ecosystems in their climatic context, and an understanding of how faunal assemblages changed in relatively short periods of time.

2. Geological setting

The Michelbach lagerstätte is found in what was the southern part of the CEB, which during the Middle Triassic was located in the northern tropical region of Pangaea (Durand and Hagdorn, 2020; Hauschke et al., 2021; Mujal et al., 2025). The CEB formed a vast area that during

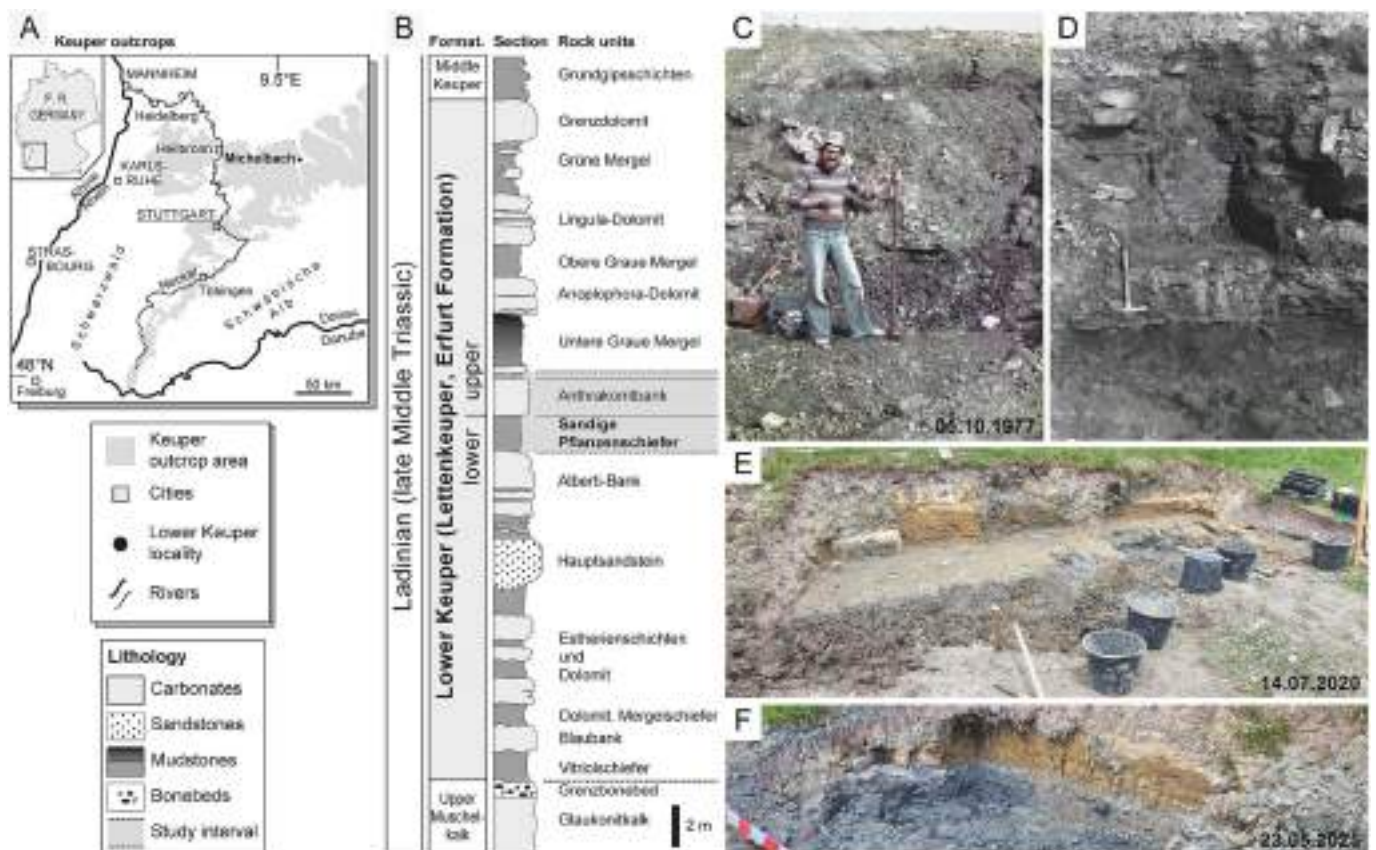


Fig. 1. Geographical and geological setting. A, Geographical map with the Keuper extension highlighted. B, General stratigraphic profile of the Lower Keuper with the study interval indicated. C, The Michelbach excavation site soon after its discovery. D, Profile of the studied succession in the last stages of excavation in 1980; hammer head at the level of layer M5, and bottom of the handle at the base of layer M8 (dolostone). E, The site in the early excavation stages in 2020. F, The site in the last day of excavation in 2025. In E and F, note the well-differentiation between the Sandige Pflanzenschiefer (grey layers; bottom) and the Anthrakonitbank (yellowish-ochre dolostone; top). A and B are modified from Schoch and Seegis (2016).

periods of high sea level acted as an epicontinental platform, or epeiric shelf, influenced by the Tethys Sea from the south and by the Scandinavian highs/mountains from the north, with the Rhenish and Bohemian massifs delimiting the western and eastern borders, respectively (Pöppelreiter, 1998; Pöppelreiter and Aigner, 2008; Nitsch, 2015; Hauschke et al., 2021; Mujal et al., 2025).

In the particularly fossiliferous northern Württemberg region of southern Germany, the Lower Keuper (Erfurt Formation, late Ladinian) forms a 25 m thick sequence of alternating siliciclastic mudstones, sandstones and carbonates (Brunner, 1973, 1977, 1980; Fig. 1B). Overall, this succession represents a regressive trend, from the marine carbonates of the Muschelkalk to the mixed Lower Keuper succession (Aigner and Bachmann, 1992; Beutler et al., 1999; Pöppelreiter and Aigner, 2008; Franz et al., 2013). The alternation of siliciclastic and carbonate units within the Lower Keuper represents a cyclical succession of marine- and terrestrial/coastal-dominated facies. Across the CEB, these facies are diachronous, showing the progression of the sea invading this vast area (Franz et al., 2013, 2018).

The Michelbach lagerstätte, which is the focus of this study, contains the Sandige Pflanzenschiefer (~ sandy plant shales), which is composed of several distinct siliciclastic and fossiliferous layers and corresponds to the top unit of the lower part of the Lower Keuper (Brunner, 1973, 1977, 1980; Urlachs, 1982; Fig. 1B). It is overlain by the Anthrakonitbank unit (the first one of the upper Lower Keuper), altogether building a cycle from terrestrial to marine settings. On top of the Anthrakonitbank lies the Untere Graue Mergel unit, which has been the focus of several studies on the rich vertebrate assemblages in the region (e.g., Hagdorn et al., 2015; Schoch and Seegis, 2016; Mujal et al., 2022; Schoch et al., 2022).

3. Material and methods

The Michelbach lagerstätte was discovered by one of us (H.H.) in 1977, with a subsequent set of excavations resulting in the recovery of multiple specimens, including articulated skeletons (Hagdorn, 1980; Hagdorn et al., 2015; Fig. 1C, D). It is located within a slope behind an old bus stop at Michelbach an der Bilz, south of Schwäbisch Hall in northern Baden-Württemberg, southwestern Germany. The site, unusually rich in tetrapod remains (Schoch, 2006, 2015a; Hagdorn et al., 2015), yields the currently only known fossil of a cynodont synapsid from the Lower Keuper, the tooth of *Nanogomphodon wildi* (Hopson and Sues, 2006; Ziegler and Schoch, 2015; Schoch et al., 2018). Besides, Michelbach is also the type locality of *Trematolestes hagdorni*, a trematosaur temnospondyl known from several skeletons plus more fragmentary remains that build a fairly complete ontogenetic series (Schoch, 2006; Schoch and Mujal, 2022).

In June 2020, our team from the Staatliches Museum für Naturkunde Stuttgart (SMNS) re-opened the site (Fig. 1E). From June to November 2020, systematic palaeontological excavations were carried out within a newly uncovered outcrop in the area excavated 40 years before (Hagdorn et al., 2015: fig. 14.11). A new area, adjacent to that already opened, was excavated in May 2025 (Fig. 1F). As a whole, an area of ~24 m² has been excavated. Microfossils were collected from each layer by screenwashing sediment samples, using four sieve sizes (0.850, 0.500, 0.180, and 0.125 mm) and picked with tweezers, aided with a dissecting microscope. More than 300 fossil bones (either isolated or in small clusters) and teeth, as well as more than 10 skeletons (including roughly complete and partial) were recovered. All material that has been prepared, examined, or is currently under preparation is in the lab and collection facilities of the SMNS.

During excavations, sedimentological data along with detailed stratigraphic sections were logged by using a tape metre measure. Potential lateral variations of each layer were also considered; nevertheless, layers are persistently found and distinguished from each other throughout the whole extension of the excavated area, with only some layers showing slight changes in thickness. Our study primarily focuses

on the Sandige Pflanzenschiefer, but we also superficially examined the overlying Anthrakonitbank unit.

Each layer that was identified was numbered, in increasing order from base to top, preceded by 'M' (for Michelbach). This follows the nomenclature used in Schoch and Mujal (2022) and in slightly younger lagerstätten from the Lower Keuper of Germany (Schoch and Seegis, 2016; Schoch et al., 2022).

In order to determine the palaeoenvironmental succession at Michelbach, we reviewed previous literature describing the Sandige Pflanzenschiefer in nearby regions (Brunner, 1973; Urlachs, 1982). Also, we examined first-hand this unit and the overlying Anthrakonitbank in the area of Vellberg-Eschenau (see also Mujal and Schoch, 2020).

Sedimentological samples were collected during all excavations. Polished slabs and thin sections of the fossiliferous layers and of carbonate nodules from distinct horizons (see Section 4 below) were prepared where it was feasible in the collected material using standard procedures. These samples were analysed by using a Leica DM750P petrographic microscope. Sedimentary facies and pedogenic features are described both from field observations and by analysing collected samples. Description and identification of palaeosols follows classifications by Gile et al. (1966), Machette (1985), Mack et al. (1993), Orr and Roberts (2024), plus other references cited for specific features mentioned throughout the text. The USDA Soil Taxonomy system (Soil Survey Staff, 2014) was used to define (palaeo-) soil horizons. Palaeosol identification was further compared and confirmed with data from Nitsch (2005), overall finding the same pedotypes. Colours (hue and chroma) of each layer were assessed from dry samples by using the Munsell Color System (Munsell Rock Color Book, 2009 Year Revised, 2023 Production; Geological Society of America).

The relationship between fossil remains and strata was assessed by documenting the orientation of fossils (when relevant) with respect to the stratification, the relative abundance of fossil taxa in each layer, their colouration and their state of preservation (accounting their completeness, articulation in the case of skeletal remains, and potential chemical and physical abrasion; for reference study, see Behrensmeyer, 1978). Previously collected specimens during the excavations of the 1980s were also examined.

4. Stratigraphy and taphonomy

A total of 9 layers (M1 to M9) were identified in the studied succession (Fig. 2). Our analyses focus especially on the Sandige Pflanzenschiefer, but we also provide more brief descriptions, plus interpretations (also following previous studies), from the Anthrakonitbank. The layers identified confirmed preliminary stratigraphic analyses by Hagdorn (1980) (see also Hagdorn et al., 2015; Schoch and Mujal, 2022). Layers M1 to M6 correspond to the Sandige Pflanzenschiefer, with a thickness of 87 cm; layers M7 and M8 correspond to the Anthrakonitbank, with a thickness of 97 cm; layer M9, here only briefly described, corresponds to the base of the Untere Graue Mergel (lower grey marls).

4.1. Layer M1 – Grey mudstones with deep desiccation cracks on top (37 cm thick)

Description. The first layer of the stratigraphic sequence is 37 cm thick and overlies the dolostones of the Albertibank unit (Hagdorn et al., 2015), which are flat at their top (Figs. 1B, 2). Deposits of layer M1 (Fig. 3) correspond to roughly laminated or layered mudstones, generally arranged in beds ~0.5–1 cm thick, with some distinct horizons. Laterally, layer M1 may become more massive with less differentiated levels. The predominant colour is grey (Fig. 3A–C), with some variations throughout the layer as described below (from base to top).

The first, lowermost 7 cm of layer M1 are dark greenish grey (5G 4/1) and arranged in relatively well differentiated 0.5–1 cm thick layers (Fig. 3A). They are followed by a 6 cm thick interval of more finely

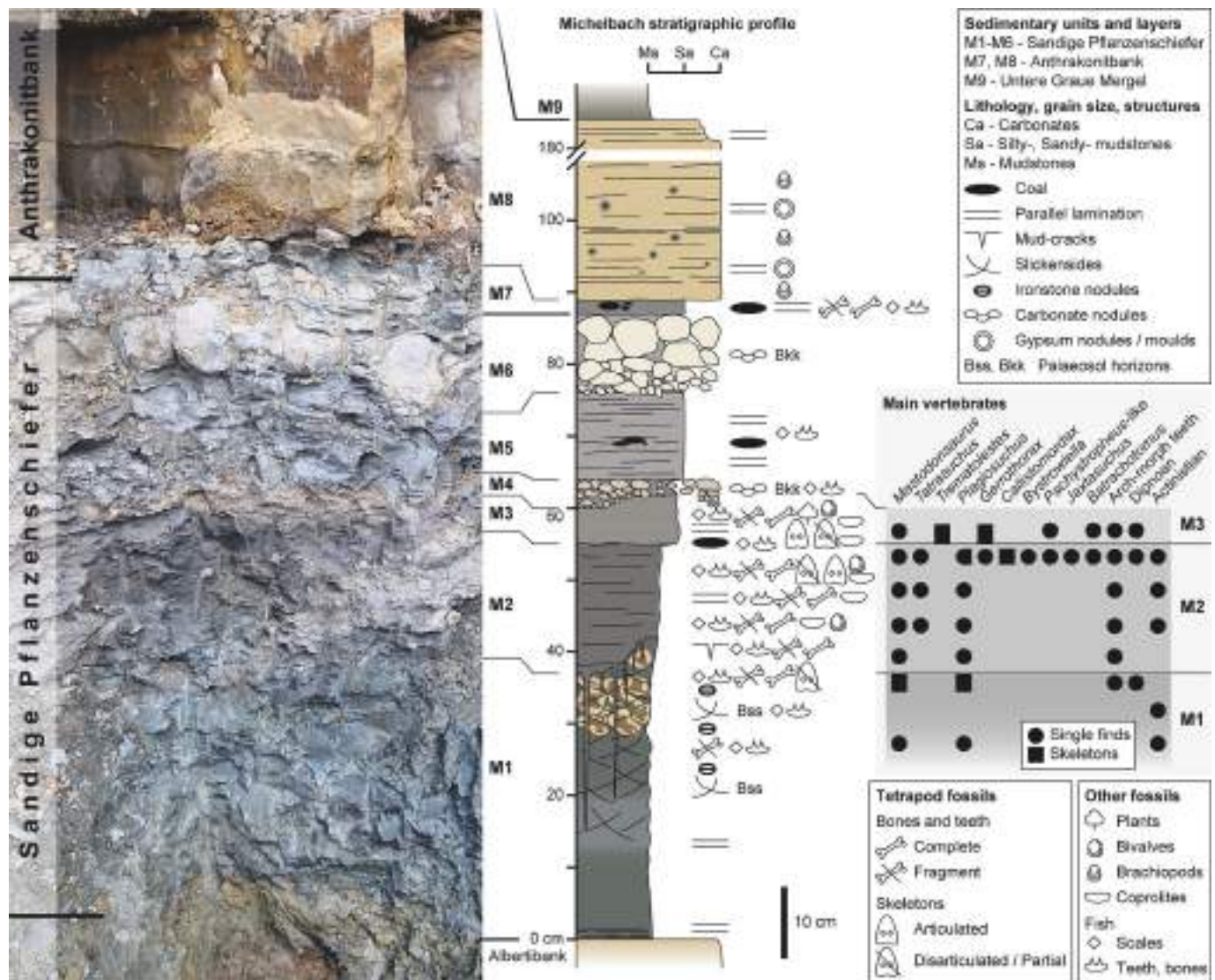


Fig. 2. Detailed stratigraphic profile of the studied succession. On the left, photograph from 23rd May 2025 showing the entire Sandige Pflanzenschiefer (note the top surface of the Albertbank at the bottom, in ochre-greenish colours) and the lower part of the Anthrakonitbank. In the middle, stratigraphic log with main sedimentary features and fossils; note correlation of the identified layers between the photograph and the log.

laminated mudstones, yet the same layering as the basal portion is present (Fig. 3B). Such finer lamination makes this interval softer in texture, especially in wet samples, and orange stains from oxidation may be more abundant. The overlying 6 cm, also layered, have a slightly different colour (medium bluish grey, 5B 5/1), and display abundant slightly concave surfaces that are somewhat shiny and contain striations in the sloping direction. These surfaces, which correspond to slickensides (Fig. 3D–H), are often conjugated, forming relatively large oval-shaped patches or lenses. The hardness of these deposits is subject to abrupt lateral change, linked to the polished and striated surfaces. In this 6 cm thick, medium bluish grey portion of the layer mud-cracks are present. These structures start at the top of layer M1 and are infilled with a matrix rich in fish scales, corresponding to the lithology of layer M2 (Fig. 3I–L; see further in Section 4.2 below). The overlying 8 cm are again dark greenish grey (5G 4/1). They have a slightly more massive aspect than the lower parts, but layering is still present (Fig. 3C). The uppermost 10 cm display the same colour and massive aspect, yet layered, but show an increase in fish scales.

In most parts of the excavated area, the mid-upper portion of layer M1 (from the lowermost level with slickensides and mud-cracks, i.e., the top 25 cm of this layer) contains patches and seams combining light

green-yellow, purple, ochre, and brownish-orange colours (Fig. 3N–O). When wet, samples with lighter colours are softer than the ochre and brownish ones. The darker portions are sometimes arranged in small, oval-shaped seams that may result in relatively compact pieces, which likely correspond to wedge-shaped peds (sensu Orr and Roberts, 2024; see interpretations below). In some portions of the excavated area this 25 cm thick interval has a somewhat nodular aspect because of the amalgamation of slickensides (Fig. 3H). In the microsample fraction, small (1–2 mm wide) red to dark red clasts, some including brassy-yellow tones, are present (Fig. 3M).

Mud-cracks (Fig. 3I–L), always infilled with sediment rich in fish scales (characteristic of layer M2, see Section 4.2 below), are more abundant in the top 11 cm of layer M1 (i.e., only the larger mud-cracks reach lower portions of the layer), and their thickness (up to 1 cm wide) and depth vary. Mud-cracks are more abundant in, but not exclusively from, the areas with less oxidation colours.

Fossil content. Macro-vertebrate remains are mainly found in the upper portion of the unit, especially at the interface with layer M2. Tetrapod bones are usually dark brown, but some isolated elements (usually fragmented and worn) are much lighter (beige); these latter correspond to reworked bones. Disarticulated skeletons of the

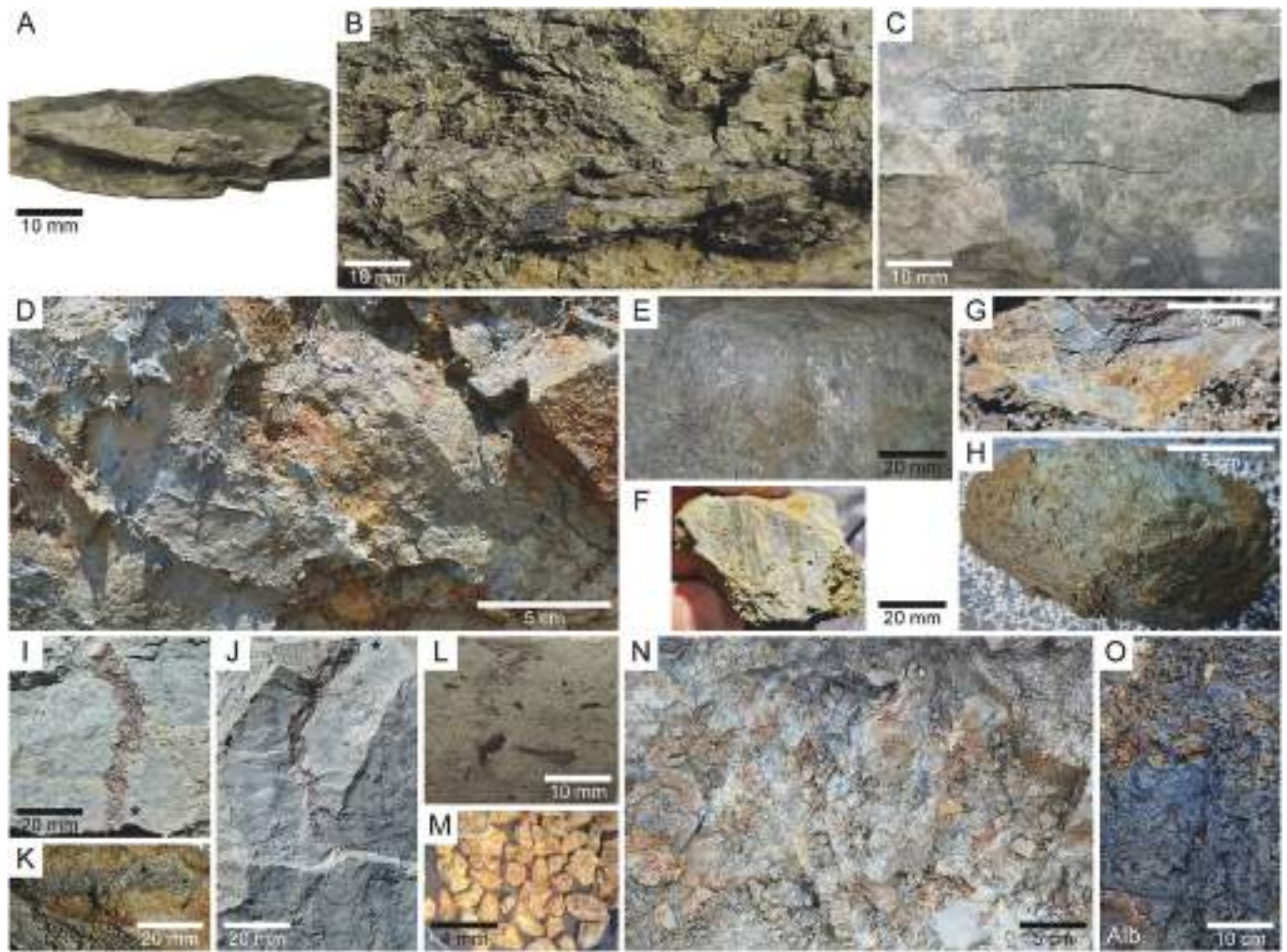


Fig. 3. Sedimentary features from layer M1. A, Lowermost portion. B, Lower to mid portion (starting at 7 cm from the base). C, Top portion. D–H, Slickensides, including: extensive polished surface (viewed from below, D); shiny, slightly striated surface (E); markedly striated and highly inclined surface (F); conjugated, oblique planes (viewed in cross section, G); oval-shaped hardened patch or lens (H). I–L, Mud-cracks, including: relatively thick crack infilled with darker sediment and fish scales viewed in cross section (I) and from the underside (J) (the asterisks mark the orientation point between photographs); thick crack infilled with abundant fish scales cross-cutting an ochre-coloured patch (K); polished section of a mud-crack infilled with darker sediment and fish scales (L). M, Small red clasts (ironstone nodules). N–O, Ochre-dominated colouration (hydromorphism) from the upper portion of the layer; in (O), the whole extension of the layer is exposed, with the white dashed line marking the boundary with the underlying Albertibank (Alb.). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

plagiosaurid *Plagiosuchus pustuliferus* form the most common finds. In 1978, remains of five or more skeletons without skulls and additional bones of *Plagiosuchus* were collected (Hagdorn et al., 2015). In 2020, we also found a partial skull of this taxon (Fig. 4A). Bones within these clusters are disarticulated, lack any preferential orientation, and some of them are oblique with respect to stratification (i.e., generally chaotically distributed). Juveniles of the capitosaur *Mastodonsaurus* (generally centra and shoulder girdle elements, but also a partial skull) occur less frequently in the top level (Fig. 4B). Generally, bones are well-preserved but very often fragmented with straight break margins, suggesting they were broken in the postmortem period (e.g., Green and Schultz, 2017). Reworked bone fragments are sometimes associated, even within mud-cracks (see also Section 4.2 below). Notably, complete clavicle and interclavicle bones of *Plagiosuchus* were embedded as multiple fragments with markedly straight edges.

Fish scales (*Gyrolepis* sp., *Serrolepis* sp.) are heterogeneously distributed throughout the whole lateral extension of the excavated area, being very abundant in some portions and completely absent in others. The general pattern throughout the layer, in any case, is that (small) fish scales become more abundant towards the top of the layer. A

single, worn lungfish tooth plate has been recovered from layer M1.

Interpretation. This layer represents a period of deposition under fluctuating groundwater conditions, presumably caused by alternated seasons of flooding and desiccation. In this sense, the diverse colouration, especially in the upper 25 cm, indicates intermittent hydromorphism, suggesting an early pedogenic stage and relatively marked seasonality (Mack et al., 1993). The polished and striated surfaces oblique to stratification that characterise slickensides indicate fluctuating waters after deposition, with shrinking and swelling of clays resulting in preferential orientations of minerals; this soil formation-process also generated peds (Mack et al., 1993; Tabor et al., 2008; Orr and Roberts, 2024). Such features are pedogenic, indicative of soil development under seasonal conditions. Altogether, these features are characteristic of Bss horizons (Soil Survey Staff, 2014) and thus correspond to a Vertisol (Mack et al., 1993; Marriott and Wright, 1993; Orr and Roberts, 2024). An additional pedogenic feature is the presence of reddish clasts, which correspond to ironstone nodules. Some probably include also pyrite (as the brassy patina suggests); such structures have been found elsewhere in the Sandige Pflanzenschiefer and other units of the Lower Keuper (Ulrichs, 1982; Schoch et al., 2022; see also Section

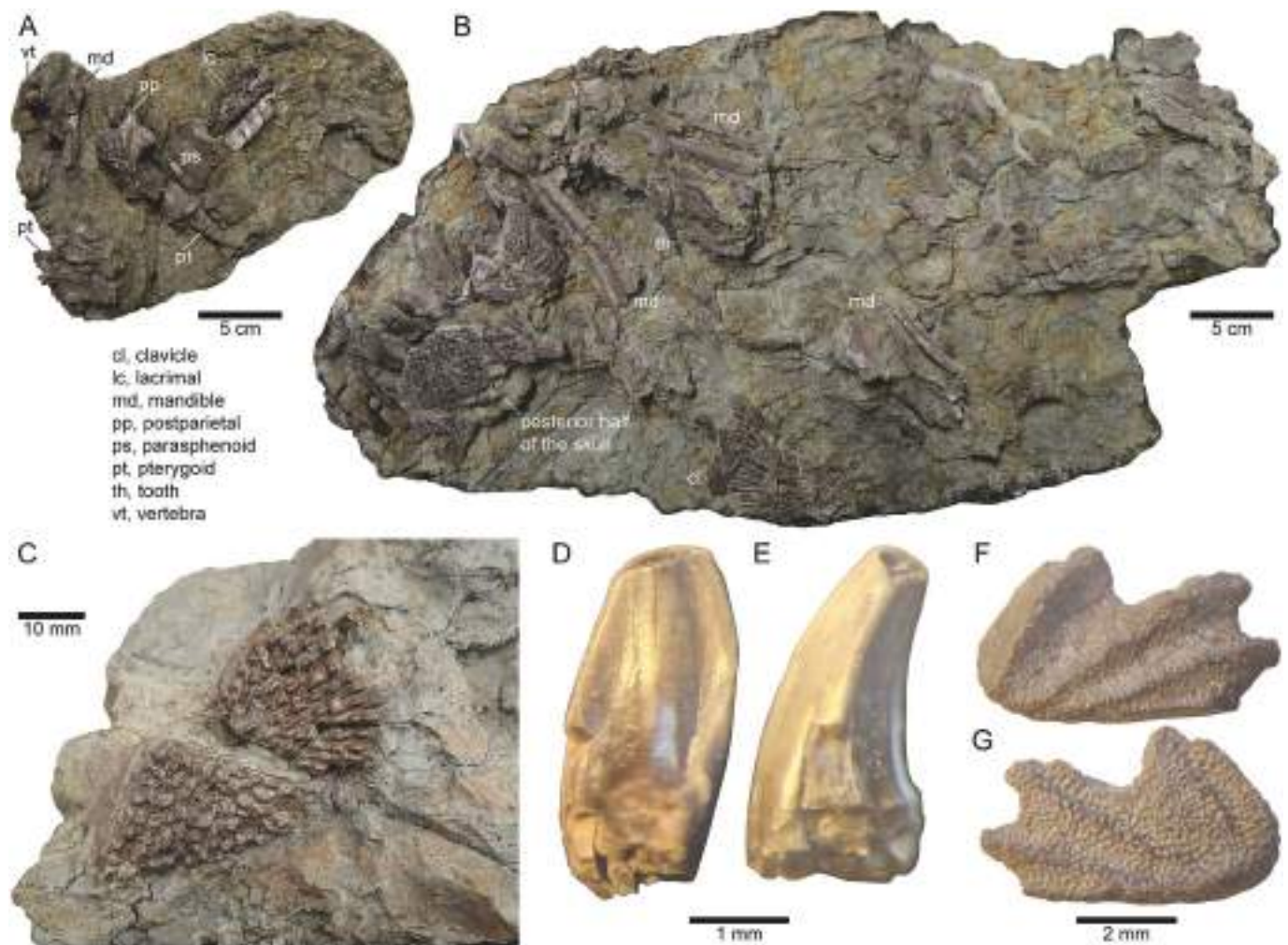


Fig. 4. Selected fossils and taphonomic features from layer M1. A–B, Bone clusters with elements chaotically organised corresponding to partial skeletons, including skull remains, of *Plagiosuchus* (A) and a juvenile *Mastodonsaurus* (B). C, Fractured platy bone fragment with pustular ornamentation of *Plagiosuchus*; note in situ displacement of fragments within the matrix. Note that fossils in (A–C) are preserved in a clayey matrix with hydromorphic colours from the upper part of the layer. D–E, Shovel-shaped tooth without serrations of an unknown archosauromorph taxon in lingual (D) and lateral (E) views. F–G, Lungfish tooth plate showing evidence of weathering (enameloid not present) in occlusal (F) and ventral (G) views.

4.10 below). The whole set of features, including slickensides, mud-cracks, hydromorphic-colouration of sedimentary patches, and iron-stone nodules, allow classifying the whole pedogenic horizon of layer M1 as a gleyed Vertisol, a palaeosol indicative of subhumid climatic conditions (e.g., Tabor et al., 2008). During pedogenesis, bones likely underwent breakage, with the shrink-swell cycles of the clayey substrate; this may explain some fractured bones with slight displacement of the fragments (Fig. 4C).

The lack of preferential orientation, and generally chaotic distribution of bones, together with the high frequency of fragmented elements, yet preserving delicate details, can be interpreted as mass transport in short-lived cohesive mud flows (or more broadly as gravity-flow processes). Bones could have remained within a relatively cohesive muddy matrix, where they would have been fragmented due to cataclasis (i.e., impacting with other bones and/or other clasts within the sediment; see Scherzer and Varricchio, 2010), but still remained protected from erosion and weathering. Once the flow slowed and stopped, the clasts and bones would have been ‘frozen’ within the cohesive matrix, and thus bones would not have been (re-) oriented according to the stratification (e.g., Britt et al., 2009; Fondevilla et al., 2017). Besides, some bones already buried were eroded and re-incorporated within those mud flows, becoming reworked elements. Interestingly, bone surfaces are generally well preserved, with little weathering, corresponding to stages 0 to 1 of

Behrensmeier (1978).

Partial skeletons and bone clusters (from the same individual) suggest that carcasses remained subaerially exposed during a certain period. This could also explain, together with short-lived cohesive mud flows, the amount of bone breakage and fragmentation. Similarly, the large mud-cracks on the topmost part of the layer indicate a likely prolonged desiccation period that lasted until the end of this depositional cycle, subsequently overlain by deposits of the next cycle composing layer M2. This indicates that the water body of M1 dried up entirely before the new water body of M2 formed (see Section 5.1 below). Therefore, a period of sedimentary interruption took place between deposition of layers M1 and M2. During exposure of M1, with periodic desiccation and wetting of the substrate (i.e., during the formation of a vertic soil), an uneven relief was generated, which probably included phases of erosion and re-sedimentation. Nevertheless, the abundant mud-cracks indicate potential preservation of an A horizon in Vertisols (Marriott and Wright, 1993), suggesting minimal erosion of the substrate, although erosion and re-sedimentation of deposits seem also likely (especially considering the presence of light coloured and notably worn bones, indicated reworking), resulting in truncated profiles (e.g., Kraus, 1999). Such relief was subsequently evenly infilled with sediments that formed layer M2 (see Sections 4.2 and 5.1 below).

Plagiosuchus was a gill-breathing obligate water-dweller and bound

to die during phases of drought like the closely related plagiosaur *Gerrothorax* (Damiani et al., 2009; Witzmann and Schoch, 2013, 2026). In this sense, some of the sharp breaks (with straight edges) and fractures observed in some specimens, which occurred in the postmortem phase (e.g., Green and Schultz, 2017), could correspond to in situ breaking due to desiccation, a feature also known from the Untere Graue Mergel, in layer E5 from Vellberg-Eschenau (Schoch and Seegis, 2016) and layer K3 from Kupferzell (Schoch et al., 2022).

4.2. Layer M2 – Layered grey mudstones with bonebeds (13–18 cm thick)

Description. This layer, ranging from 13 to 18 cm in thickness, is composed of medium dark grey (N4) mudstones with a notable silty component (in parts of the excavated area, the layer laterally grades into very fine-grained sandstones), and contains abundant fish scales. The base of layer M2 consists of a well differentiated, tabular 1 cm thick bed (Fig. 5A–B). Generally, a rough horizontal stratification (0.5–1 cm thick layers) with internal lamination is present, both from the same sediment and, especially, from the abundant fish scales of this layer. In some parts, fish scales are densely packed, forming elongate seams that are 1 to 2 cm thick, corresponding to bonebeds (Fig. 5C).

Generally, layer M2 has a tabular geometry, with plane parallel lower and upper boundaries (Fig. 5D). However, in some parts of the excavated area, its thickness can change laterally, but no clear erosional structures are observed (Fig. 5E).

The top of the layer M2 contains one or several 1–3 mm-thick bonebeds arranged in patches rather than in continuous layers (Fig. 5F). These bonebeds contain tiny fish scales and bone fragments and are light brown in colour, which is given by the accumulation of vertebrate remains, apparently differing from the dark grey mudstones. In places, the same material (mainly fish scales and bone fragments) that make up these bonebeds fill short vertical or oblique fractures in the sediment, likely corresponding or related to former desiccation cracks. In fact, in one sample (Fig. 5G) we identified lighter grey sediment without scales (similar to layer M3, see Section 4.3 below) cross-cutting the fish scale-

rich matrix of layer M2. These structures are most probably mud-cracks. Where the bonebeds at the top of layer M2 are not present, the boundary with layer M3 is still well recognisable by both a change in colour of the rock and a sharp drop in the amount of fish scales present (Fig. 5H).

Fossil content. Layer M2 contains the most diverse fauna (Fig. 6). At least eight different fish taxa were identified on the basis of isolated scales, teeth and bones in the screen washed samples (see also Böttcher, 2015): the lungfish (Fig. 6N–O) *Ptychoceratodus serratus* (including both adult and juvenile specimens; Hagdorn et al., 2015) and *Ceratodus* cf. *concinus*, an indeterminate actinistian, the polzbergiid *Serrolepis suevicus*, the semionotid *Aphelolepis delphi*, the ray-finned *Saurichthys apicalis*, the palaeonisciform *Gyrolepis quenstedtii*, and the hybondontiform elasmobranch *Lissodus nodosus*.

The largest taxa were the temnospondyls. Two genera are present throughout, *Plagiosuchus* (Figs. 5A–B, 6A–C) and *Mastodonsaurus* (Fig. 6D–E, H). At the upper part of M2, *Plagiosuchus* is mainly represented by isolated bones, but sometimes it is found in clusters that probably belong to the same individual. Similarly, other bone clusters of *Plagiosuchus* include more fragmentary elements, together with high concentration of fish scales, and coprolites also present, in a finely laminated, silty matrix. An ascending process of a large clavicle of *Mastodonsaurus* displays small, sinuous and smoothed grooves (Fig. 6H) representing traces made by insects or roots, structures also observed on bones and teeth from Vellberg-Eschenau (Schoch and Seegis, 2016; E.M. pers. obs.). *Tatrasuchus wildi* is present only as sporadic single skull bones and vertebrae. *Callistomordax* is represented by two specimens, a single exoccipital from the upper portion of the layer, and an almost completely articulated skeleton with limited crushing, preserving its 3D morphology (Fig. 6F–G). This skeleton also comes from the top of layer M2, and the sedimentary matrix immediately in contact is that of layer M3, suggesting burrowing behaviour. In fact, next to the skeleton there are other remains that suggest transport and reworking, indicating a different burial history for the *Callistomordax* skeleton. These remains include a fragmented interclavicle and a?humerus of *Gerrothorax*, a taxon otherwise unknown from layer M2 (except from a small, likely

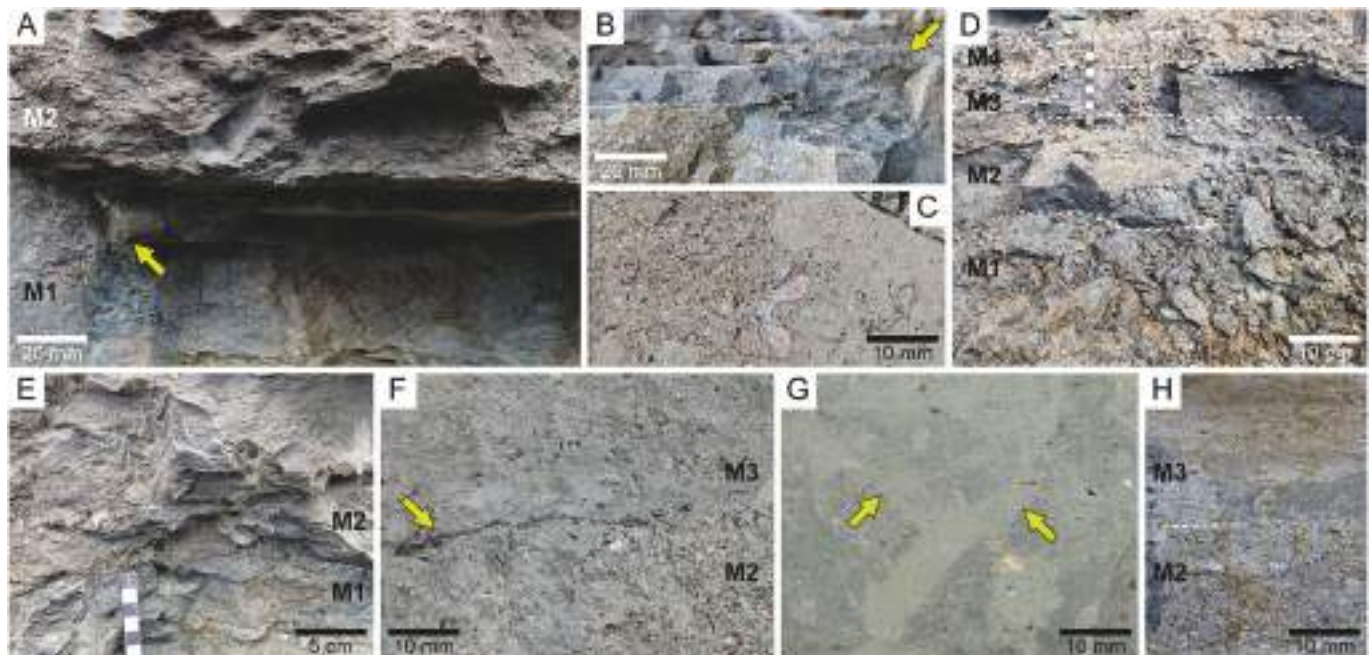


Fig. 5. Sedimentary features from layer M2. A–B, Base of the layer, with a distinct tabular, 1 cm thick interval; arrow points to a *Plagiosuchus* vertebra (A) and its natural mould (B). C, Dense accumulation of fish scales with a *Bystrowiella* osteoderm partially covered. D, Tabular aspect of the layer, with plane parallel lower and upper boundaries. E, Wavy relief between layers M1 and M2 (partially marked with white dashed lines). F, Dark-coloured bonebed and thin coal seam (arrowed) on top of the layer (sample cut obliquely to stratification). G, Potential mud-cracks (structures infilled with sediment like that of layer M3), viewed from below. H, Sharp, but non-erosive, boundary from layers M2 (rich in fish scales) to M3.

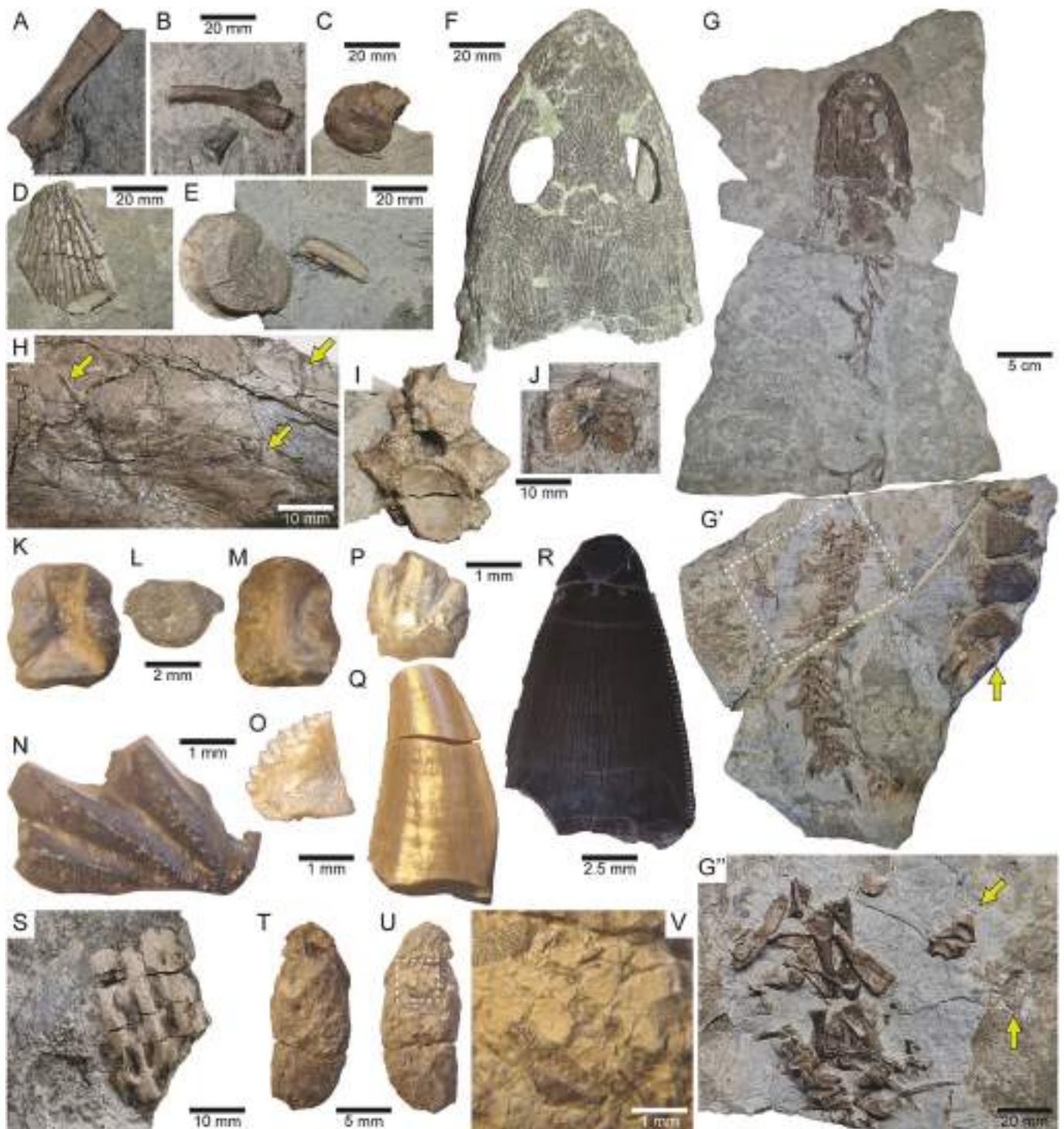


Fig. 6. Selected fossils and taphonomic features from layer M2. A–C, *Plagiosuchus*, including an ilium (A), a rib with the distal end missing (B), and a vertebral centrum (C). D–E, *Mastodonsaurus*, including an ornamented bone fragment (D), and a centrum with an unidentified light-coloured bone fragment (E). F–G, *Calistomordax kugleri*, including skull in dorsal view (F), the main two blocks preserving the specimen (G–G'), and a close up of the pelvic-hindlimb region of one of the counter blocks (G'') (squared in white dashed line in G''); note that the postcranial skeleton was prepared from the underside (i.e., the carcass was lying with the dorsal side up), the arrow in (G') points to fragmented and chaotically organised *Gerrothorax* bones (interclavicle and humerus) at the same horizon, the arrow in (G'') points to foreign bone fragments. H, Potential insect traces (some arrowed) on a *Mastodonsaurus* clavicle fragment. I–J, *Bystrowiella*, including a centrum in anterior view (I) and a small-sized osteoderm (same as in Fig. 5C; J). K–M, Sauropterygian centrum in dorsal (K), anterior (L) and ventral (M) views. N–O, Dipnoan tooth plates including an almost complete slightly worn specimen in occlusal view (N), and a well-preserved crest fragment in lateral view (from the transition with layer M3) (O). P, Tanystropheid (likely *Tanystropheus*) tricuspid tooth. Q–R, Serrated (ziphodont) teeth from *Polymorphodon adolfi* (Q) and *Batrachotomus kupferzellensis* (R). S, Light-coloured, worn bone fragment. T–V, Coprolite (likely from a temnospondyl) with fish fragments and desiccation cracks on top, including views from the stratigraphically lower (T) and upper (U) sides, and close-up of cracks and fish scales (V) (squared in U).

digested vertebral centrum), with fragments chaotically oriented, as well as two worn centra of either *Mastodonsaurus* or *Tatrasuchus*.

In the upper part of M2, vertebrae of the chroniosuchid *Bystrowiella* (including also a small-sized osteoderm of a juvenile; Fig. 6I–J), an undescribed *Pachystropheus*-like taxon known from Vellberg-Eschenau and Kupferzell (see Schoch, 2015b; Mujal et al., 2025), the doswellioid archosauriform *Jaxtasuchus*, and the pseudosuchian archosaur *Batrachotomus* are present (Fig. 6R), all represented only with isolated elements (Hagdorn et al., 2015).

Disarticulated elements, such as fragments of planar bones (e.g., skull and pectoral girdle bones of temnospondyls) and cylindrical elements (mostly vertebrae), form the bulk of the material. As in layer M1, most of the bones are dark brown, but several fragmented and worn elements are beige (Fig. 6S), indicating reworking. These latter are more often chaotically organised within the layer. Fish scales are very abundant. The sediment is very similar to that of the bonebed of the layer M7, but the fauna is different (lacustrine in layer M2, fully marine in M7).

Vertebrate (likely tetrapod) coprolites are relatively frequent, indicating that their producers inhabited, or at least roamed, this area. Coprolites at the top of layer M2, at the interface with layer M3, show a cracked upper surface (Fig. 6T–V), indicating exposure and desiccation. Generally, bones are abundant with variable colourations, ranging from dark brown (dominating) to light brown-pinkish (rare); this indicates different phases of bone deposition and preservation, with some being reworked (Schoch and Seegis, 2016; Fig. 6S). They are usually fragmented but preserve delicate details. Bones are often oblique with respect to stratification (Fig. 6A–E, G', S), especially those with light colouration. These features also indicate transportation processes, as in layer M1.

The most common invertebrates are bivalves (*Unionites brevis*), which are preserved as both imprints without periostracum in the laminated part and coquinas with preserved shells in the bonebed patches (Hagdorn, 2015). Furthermore, small tubular, helical carbonate structures with transverse ridges are present in layer M2, which have been identified as *Microconchus aberrans* (Warth, 1982; Hagdorn, 2015). In some area, the top of layer M2 preserves clusters of bivalves, which may correspond to accumulations like the bonebeds described above.

The microfossil fraction of layer M2 delivered several identifiable tetrapod remains: diverse tooth morphotypes mainly equivalent to those described by Schoch et al. (2018) from the Lower Keuper, which correspond to temnospondyls (usually conical and with longitudinal ridges, and in some cases slightly curved) and archosauromorphs (usually blade-like shaped crowns, either with smooth or serrated carinae); and a small sauropterygian vertebral centrum (Fig. 6K–M). A single tricuspid tooth attributable to a tanystropheid archosauromorph (likely *Tanystropheus*) has also been identified (Fig. 6P). Among archosauromorph ziphodont teeth, some display denticles pointing upward, likely corresponding to the archosauriform *Polymorphodon adolfi* (Sues et al., 2020; Fig. 6Q).

In the screen-washed material of layer M2 filling the desiccation cracks on top of layer M1, the type specimen (a single tooth) of the synapsid *Nanogomophodon wildi* was found (Hopson and Sues, 2006). These mud-cracks also yield other fragmentary remains, as well as some serrated archosauromorph teeth (at least one likely corresponding to *Polymorphodon adolfi*), generally fitting with the other microfossil finds of layer M2.

Interpretation. Considering the mode of bone preservation, layer M2 probably formed in mud flows similar to those inferred for layer M1. They occurred during episodes of relatively high energy, possibly linked to storms. Nevertheless, the presence of coprolites, which appeared frequently during the excavations, also points out to periods of quiescence, when tetrapods inhabited the lake.

The entire sequence is full of isolated and often broken bones, yet bone surfaces generally show low to no cracking, indicating little weathering (stages 0 to 1 of Behrensmeyer, 1978; only a few bones show slightly more weathering, likely a late stage 1). Fractures are relatively

sharp, not aligned with bone tissue or structures (e.g., with bone fibres), indicating that bones were broken in the postmortem phase but prior to fossilization (Haynes, 1983; Green and Schultz, 2017). This probably documents an early depositional phase of the sequence encompassing layer M2 that was eroded and reincorporated into mud flows, which is consistent with observations in similar deposits from the Untere Graue Mergel unit at Vellberg-Eschenau (Schoch and Seegis, 2016) and Kupferzell (Schoch et al., 2022).

The lateral thickness variations of layer M2 probably result from the infilling of the relief left after deposition of layer M1. The uneven relief at the top of layer M1 does not appear to be erosional because of the deposition of M2, but rather because of the pedogenesis that layer M1 underwent, resulting in a Vertisol (shrinking/swelling of clays, generating slickensides typical of Bss horizons, and abundant mud-cracks, typical of A horizons; see Section 4.1 above; Mack et al., 1993; Marriott and Wright, 1993). Therefore, the lateral continuity defining the boundary between horizons (from layer M1 to M2) can be considered wavy (sensu Orr and Roberts, 2024).

Overall, this set of features suggests that layer M2 records multiple events and phases. These are clearly differentiated from those that formed layer M1, which is in line with the differences in both lithology and fossil content and distribution. Also similar to layer M1, although less marked, the top of layer M2 shows evidence of desiccation.

4.3. Layer M3 – Laminated sandy-silty mudstones (5 cm thick)

Description. The layer (Fig. 7) is apparently dark grey in moist condition, but it is much lighter when dry (medium grey, N5). The thickness of layer M3 is constant at 5 cm (Figs. 5D, 7A), except in areas where the overlying layer has a very low number of nodules (see also Section 4.4 below), reaching an apparent thickness of 9 cm. It is divided into ~0.5 cm silty-mudstone laminae, and fine mudstone laminae that are planar laminated (Fig. 7B), being more marked than those of layer M2. In thin section (Fig. 7C) lamination is less evident, mainly recognised from coarser fossil fragments. Layer M3 generally contains much fewer fish scales than M2, and they are not confined to single bonebed layers or patches. Therefore, the boundary between these two layers is well defined because of the sharp drop of fish scales (Fig. 5F, H), as well as the change of colour (from dark to medium grey), and also for the occasional presence of small bonebeds and small coal seams (Fig. 5F). Otherwise, no sedimentary discontinuities (e.g., erosive base) are observed between layers M2 and M3. Some portions of layer M3 are coarser (Fig. 7A), becoming sandy, and in these portions layers are usually relatively well-defined. Some layers are composed of very fine- to fine-grained sandstones with light to dark tones and ochre seams. The lower part may contain more fish scales than the rest of the layer (Fig. 7C–D), but never building bonebeds or seams as in layer M2. The middle part is harder, with still fewer fish scales than the rest of layer M3, and poorly laminated, displaying a more massive aspect (Fig. 7E). Small clusters of tiny pyrite crystals (identified in the microsamples) are sometimes present; these could potentially be related to poorly oxygenated waters (see Section 5.1.1 below). The uppermost part of layer M3 is generally well laminated (Fig. 7F), sometimes defining clear planes (Fig. 7G), and only a few millimetres from layer M4, the colour of the rock may slightly change, likely influenced by the nodules of the overlying layer, becoming greenish grey (SGY 6/1).

Thin sections of layer M3 (Fig. 7C) show dispersed tiny (sub millimetre), rounded quartz grains (representing <5% of the matrix). Oval-shaped mud-chips parallel to stratification and somewhat imbricated are present, being more abundant towards the base.

Fossil content. In layer M3, tetrapod bones are usually aligned parallel (or subparallel) to the stratification and less abundant than in layer M2. However, finds are more complete in M3, including articulated skeletons of temnospondyls. Generally, the colours of the bones range from pale brown to dark brown, with larger bones usually being darker. Two taxa occur in articulated to semi-articulated skeletons: (1) the temnospondyl

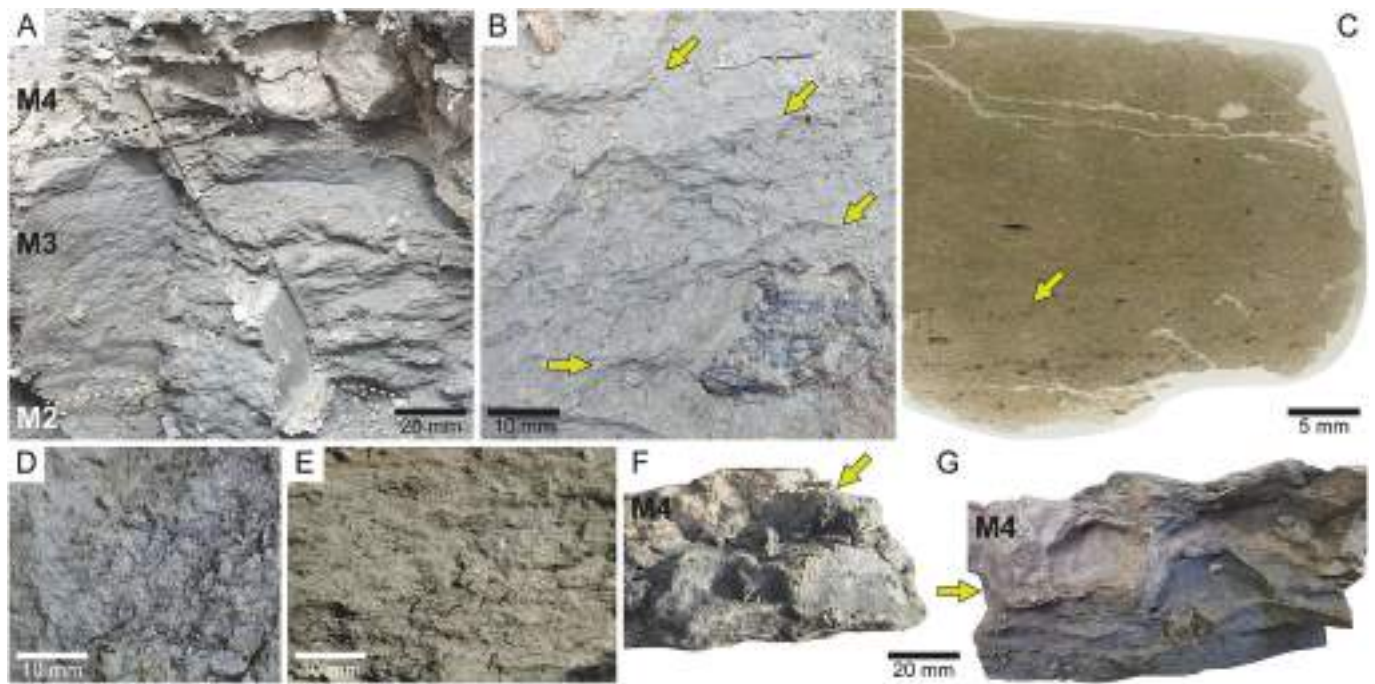


Fig. 7. Sedimentary features from layer M3. A, Relatively massive and silty portion with only rough layering visible on the right side of the photograph. B, Oblique exposure with more evident layering (marked with arrows); the dark coloured portion on the bottom right part corresponds to the snout of *Trematolestes hagdorni* in Fig. 8B. C, Photomicrograph of a thin section of the lower portion of the layer; the arrow points to an oval-shaped mud-chip; note the presence of darker elements (fish scales and other organic fragments) especially concentrated at the base of the layer. D, Base of the layer from the underside; the dark portions correspond to a bonebed. E, Massive aspect in cross section. F–G, Top of the layer, with the overlying nodules from M4 (arrows mark the boundary), being either massive (F) or layered (G).

Trematolestes hagdorni, which is present with specimens of different sizes that give an excellent ontogenetic series (Schoch and Mujal, 2022; Fig. 8), and (2) the plagiosaurid *Gerrothorax pulcherrimus* (Fig. 9A–D) whose specimens are usually not as well articulated as *Trematolestes* and are much less common. Layer M3 is the type horizon of *Trematolestes hagdorni*, of which five largely articulated juvenile skeletons were found in 1979 (Hagdorn, 1980; Schoch, 2006) and two skeletons and isolated bones in 2020 (Schoch and Mujal, 2022). These were found at the base of unit M3. The large, subadult specimen (16 cm skull length) found in 2020 has a postcranium that is characteristically curved and disarticulated in the tail region, much like the type specimen excavated in 1979 (Schoch, 2006); in fact, most of the *Trematolestes* skeletons show this curled position (Fig. 8A–F). This horizon also yielded a partial skeleton of *Gerrothorax* (Fig. 9A–D) that had a WSW–ENE orientation, like the holotype skeleton of *Trematolestes* (Hagdorn et al., 2015). Instead, the *Trematolestes* skeleton found in 2020 was NNW–SSE oriented. Besides different degrees of articulation of these skeletons, other common taphonomic features are relatively sharp fractures formed in the postmortem phase. Many of the fractured bones show a slight displacement of fragments (Fig. 8B).

In addition to *Trematolestes* and *Gerrothorax*, intercentra of small *Mastodonsaurus* specimens, as well as tusks (Fig. 9E), are relatively abundant; other fragmentary temnospondyl elements (Fig. 9F) are also present. A small-sized (~7 mm long) vertebra of a *Pachystropeus*-like taxon (which is particularly abundant in the Untere Graue Mergel of Kupferzell and Vellberg: Schoch and Seegis, 2016; Schoch et al., 2022; Mujal et al., 2025) was found 2 cm above the base of layer M3 (Fig. 9G). 1 cm above this vertebra, a *Batrachotomus* tooth (likely from the premaxilla) with high wear (abrasion according to Mujal et al., 2022) on the mesial carina and low wear on the distal carina, and a likely resorbed root was found (Fig. 9H); an additional tooth of this pseudosuchian (Fig. 9I) was also found next to a *Gerrothorax* skeleton (Fig. 9A–D). A tooth of the sauropterygian *Nothosaurus*, together with a plant fragment, was recovered at the same level of the *Pachystropeus*-like taxon. Other

archosauromorph teeth appeared in the microsamples.

Fish scales (*Gyrolepis*, *Aphelolepis*, *Serrolepis*) are common in some parts of layer M3. Lungfish remains (tooth plates; Fig. 9J) are rare, with only 3 specimens found so far. Bivalves are also observed with shells usually deformed and with some fractures; however, their structure and fine details of the ornamentation are well-preserved (Fig. 9K). Coprolites, though present, are rare elements in the layer. *Microconchus* may also be present, although occurring less frequently than in layer M2.

Plant remains were reported by Hagdorn et al. (2015), and more recent excavations confirmed their abundance. These include weak imprints and coaly sheets, which in some cases are found in close association with *Trematolestes* specimens (Fig. 8A), as well as relatively large, elongated fragments preserved as carbonaceous impressions that probably correspond to *Neocalamites* (Fig. 9L).

Interpretation. The deposits of layer M3 probably formed in a more proximal area of the lake. The lack of sedimentary discontinuity, but with a rather sharp transition between layers M2 and M3 indicates a sudden change in the system dynamics, from relatively deep to shallow/nearshore lacustrine settings. The bonebeds at the top of layer M2 suggest desiccation event(s) and/or diminishing of the energy of the system, in line with the transition towards proximal areas of the lake during the deposition of M3. Desiccation is also indicated by cracked top surfaces of coprolites at the interface M2–M3 (Fig. 6T–V). In addition, the faunas are different, with *Trematolestes* not only making its first appearance but also forming the dominant large predator.

The articulated skulls and skeletons within layer M3 indicate an energy decrease of the system: a gentle transport of light bones occurred, but the system did not have enough energy to disarticulate whole skeletons. If tetrapod carcasses were transported, articulated specimens indicate that this happened during early stages of decay, because otherwise skeletons would have been disarticulated. Particularly, different skeletons of *Trematolestes* show various (early) stages of decay, characteristically with somewhat curved trunk and the tail flipped over (Fig. 8). These latter features could indicate desiccation, with carcasses

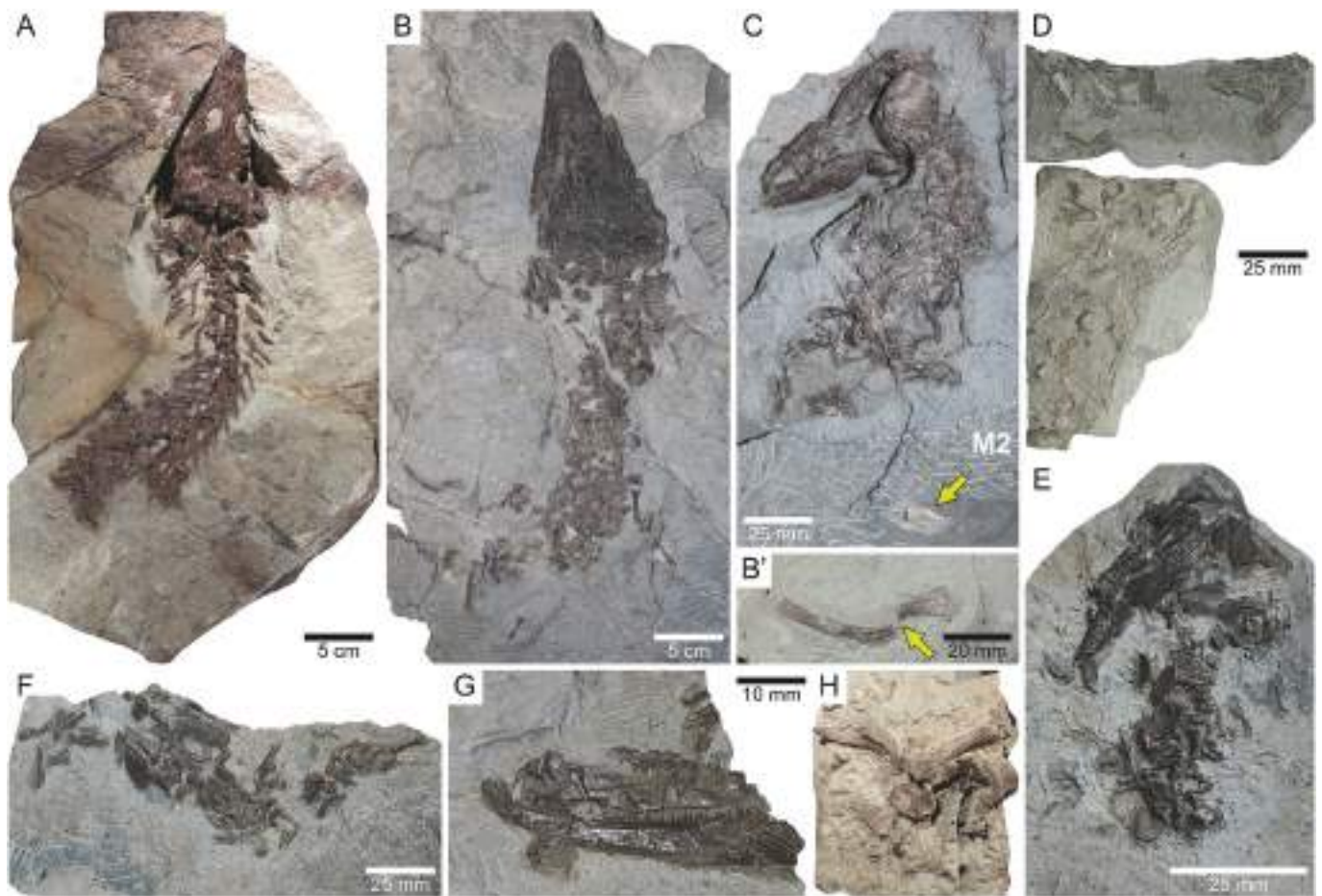


Fig. 8. Carcass decay of selected *Trematolestes hagdorni* specimens from layer M3. A, Holotype specimen (SMNS 81790), articulated skeleton with most of the tail missing; note the presence of carbonaceous plant impressions at the top portion, on both sides of the skull. B, Disarticulated skeleton but with several bones still in anatomical association; B' includes a fractured rib (squared in white dashed line in B) with in situ displacement (arrow). C, Small-sized skeleton slightly disarticulated; the arrow points to a reworked bone fragment. D, Small-sized skeleton with the postcranium slightly disarticulated (bottom block) and skull highly disarticulated (upper block). E, Small-sized skeleton highly disarticulated with bones slightly mixed up. F, Small-sized disarticulated skeleton but with bones still somewhat anatomically associated. G, Disarticulated lower jaws. H, Small-sized partial postcranial skeleton, only preserving a few vertebrae and ribs. Note the curled arrangement of the most complete carcasses (A–F). Note that overall skeletons are preserved with the dorsal side up (e.g., those in A and B are prepared from the topside, whereas that in C is prepared from the underside).

drying up on the lake shore. Such interpretation is supported by the presence of *Gerrothorax* skeletons showing some parts well articulated, and others (slightly) scattered and fragmented. The presence of a *Batrachotomus* tooth next to a *Gerrothorax* skeleton plus the randomly disarticulated parts such skeleton (unlikely to be caused by any particular flow mechanisms) may indicate scavenging by the pseudosuchian, but this is speculative. Despite the increased evidence of desiccation (i. e., subaerial exposure) with respect to layers M1 and M2, in general, bones within layer M3 still show little weathering, mainly stage 1 of Behrensmeyer (1978).

Generally, fossil remains from layer M3 are parallel to stratification (i.e., horizontal), in agreement with minor flow regime in the system. Density flows were less common than in layers M1 and, especially, M2, most likely related to a closer position to the shore of layer M3. The presence of plants and terrestrial taxa (e.g., *Batrachotomus*) also suggests that this setting was closer to the shore. At the same time, presence of purportedly marine taxa (e.g., *Nothosaurus*, represented by a single tooth that might have been washed in) indicates potential connections to (marginal) marine settings (for similar interpretations in similar settings, see Schoch et al., 2022). Hypothetically, occasional incursion of sea water occurred during storms, although there is no current evidence of storm deposits. Most plant remains were probably transported, though the small coal seams at the base of the layer and the coaly sheets

could indicate incipient soil formation. However, this remains speculative because no root traces nor any other evidence of in situ elements have been observed.

4.4. Layer M4 – Light-coloured small nodules in grey mudstones (2–4 cm thick)

Description. Carbonate nodules form the bulk of layer M4 (Figs. 7F–G, 10), ranging from 2 to 4 cm thick. They are embedded in a sedimentary matrix consisting of grey mudstone. Nodules are oval-shaped, though some are relatively round, with the maximum axis commonly of 1–3 cm, and rarely attaining a maximum diameter of 9 cm in the top of the unit. The nodules have a light brown to yellow colour and are composed of micritic mudstone (i.e., carbonate). They are markedly flattened by compaction and are tightly packed both in different levels and laterally. Their size generally increases from the base to the top of layer M4.

The sedimentary matrix part of this unit agrees with that of layer M3 (generally medium grey, N5; but with some areas that are greenish grey, 5GY 6/1) and differs from that of layer M5 in its darker colour in moist condition and the rather grey than blue-grey colour in dry condition. The nodules and their relative abundance are not homogeneously distributed along the total extension of the excavated outcrop: they are generally contacting one another, but in some regions nodules are

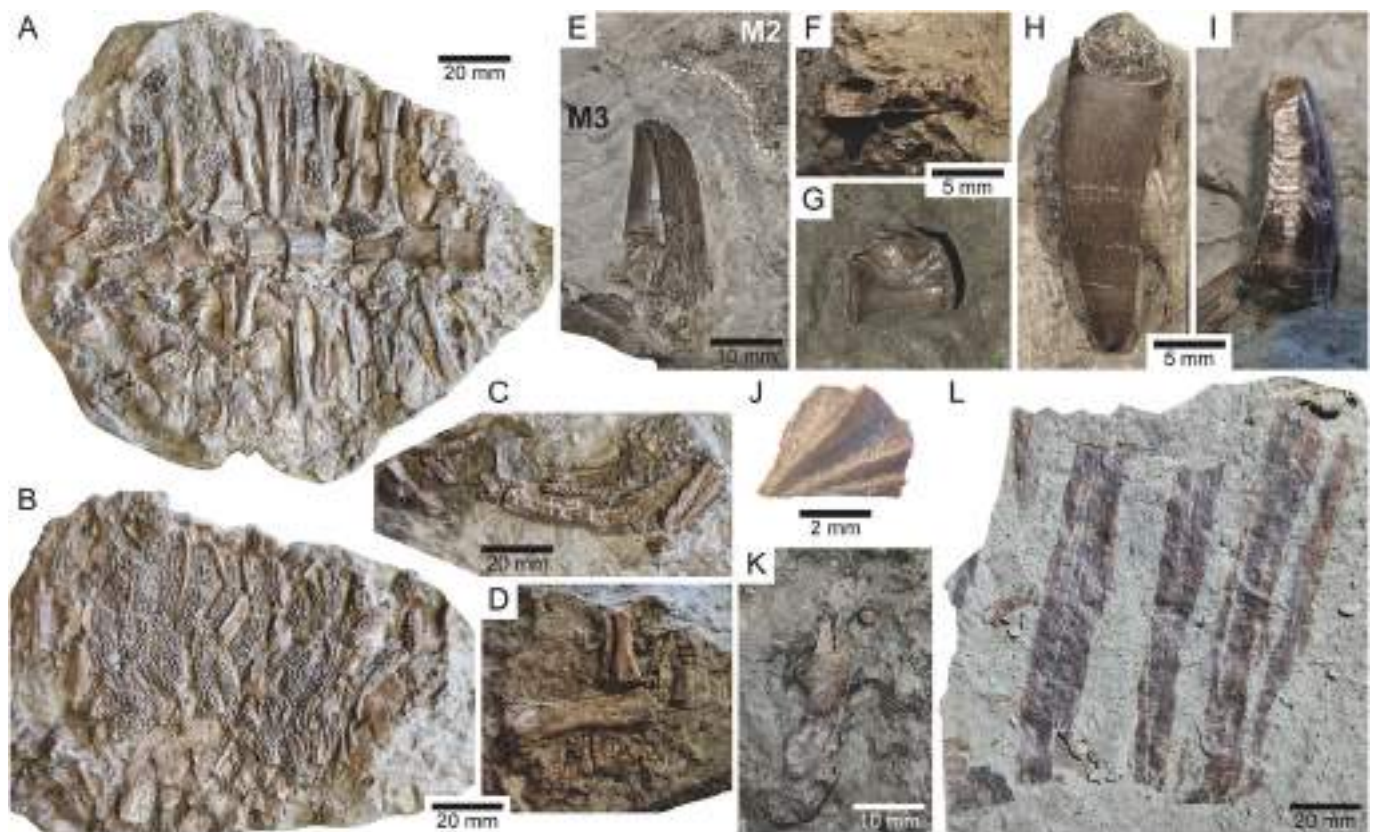


Fig. 9. Selected fossils and taphonomic features from layer M3. A–D, Semiarticulated, almost complete *Gerrothorax* skeleton, including the trunk region with dorsal osteoderms disarticulated (A), partially articulated dermal armour from the ventral side (B), disarticulated and fragmented portion of the left mandible (C), partially disarticulated hindlimb (D). E, *Mastodonsaurus* tooth with extensive wear (spalling and abrasion) from the base of the layer. F, Fragment of a temnospondyl jaw. G, Vertebral centrum of a *Pachystropheus*-like taxon. H–I, *Batrachotomus* shed teeth, including a premaxillary one (H) and a dentary element found associated with the *Gerrothorax* skeleton in (A–D). J, Partial dipnoan tooth plate in occlusal view. K, Crushed bivalve preserving the shell. L, Carbonaceous impressions of plants (*Neocalamites*).

smaller and less abundant, event being completely surrounded by matrix; in some other parts nodules are larger than the average (1–3 cm) and laterally elongated, likely resulting from the coalescence of two or more nodules, forming a single one. This coalescence of different nodules is observed in the thin sections, where a nodule appears to be absorbed within another, larger, one. In the extreme case nodules form a roughly tabular massive layer (Fig. 10). In some areas of this stratigraphic horizon nodules are almost absent, mainly a few floating on a muddy matrix; because of that, as mentioned in Section 4.3 above, in these areas the underlying layer M3 is apparently thicker than the usual (i.e., almost 9 cm instead of 5 cm thick).

Fossil content. Only very rare fossil remains come from this layer. These include a few fish scales and teeth, and *Microconchus* sp.

Interpretation. Layer M4 represents the topmost part of a palaeosol with calcic features, as shown by the presence of the carbonate nodules (Mack et al., 1993). This layer corresponds to a Bkk horizon (Soil Survey Staff, 2014) in the stage III of calcic soil development, according to the classifications of Gile et al. (1966) and Machette (1985) (see also Alonso-Zarza, 2003). The mudstone matrix embedding the nodules is essentially the same as that of layer M3. Thus, the whole pedogenic process, culminating with the development of the carbonate nodules of layer M4, involves also layers M2 and M3, in combination building up a depositional sequence (see Section 5.1 below). Size differences of nodules within layer M4, as well as the observed absorptions of some nodules within others, indicate that there were several generations of nodule formation under semiarid conditions (e.g., Gile et al., 1966; Alonso-Zarza, 2003).

4.5. Layer M5 – Light blueish-grey stratified sandy mudstones (12 cm thick)

Description. Widely stratified sandy mudstones building a 12 cm thick layer (Figs. 2, 10), with a colour between medium light grey (N6), medium dark grey (N4) and medium blueish grey (5B 5/1). Stratification is in the 0.3–0.5 cm range, and in some portions reaching 1 cm in thickness (Fig. 10). In the field, fresh surfaces show that layers are distinguished by slight changes in colour (from lighter to darker grey; Fig. 10), and in dry samples layers may split physically, becoming more distinguishable. Several successive horizons within layer M5 contain 2–5 mm long clasts of different colour (blue, yellow, darker grey), along with coaly chunks/seams. In places, larger (2–5 cm) chunks of coal were found in close proximity to each other. Some layers have a more ochre-greenish colouration, they are irregularly distributed, not being completely continuous within a single layer and forming a patchy network. As a whole, layer M5 roughly shows a colouration lightening, with a somewhat dark grey part and a lighter grey upper part. Some portions of the layer are very fine-grained; in these portions micaceous grains (likely muscovite) are recognisable.

Fossil content. Layer M5 is generally poor in fossils. Occasional finds are single fish scales (*Serrolepis*) and teeth (*Saurichthys*), as well as *Microconchus* sp. Hagdorn et al. (2015) reported fossil plants, but we interpret these as recent rootlets, of which we found abundant evidence during the 2020 excavations.

Interpretation. These mudstones formed under more differentiated conditions with respect to the previous layers. Low energy phases alternated with relatively high energy periods, with density flows that

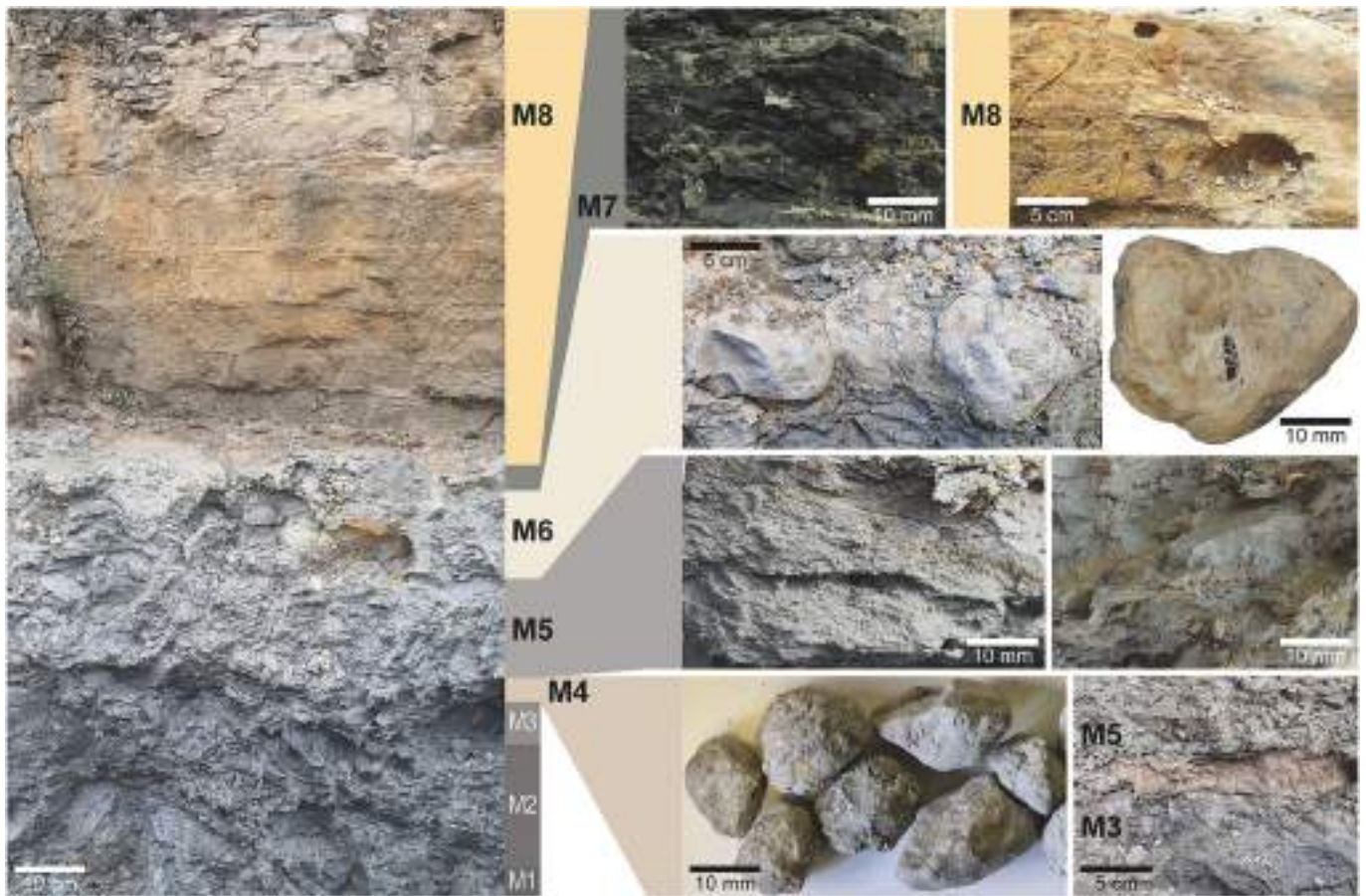


Fig. 10. Sedimentary features from layers M4, M5, M6, M7, and M8. The photograph on the left shows the whole succession; note the change in colour within the Sandige Pflanzenschiefer, with layers M1–M3 markedly darker than layers M4–M6; note also the tabular layering of the dolostone (layer M8). Layer M4: rounded, small-sized nodules (centre), and massive layer (coalesced nodules; right). Layer M5: Silty and layered aspect, with also oxidation colours following stratification. Layer M6: Extremely large, coalescing nodules (centre), and nodule with a dark element (right). Layer M7 (top centre photograph): Coal fragment within the marine bonebed. Layer M8 (top right photograph): Moulds of gypsum nodules within the tabular dolostone.

produced the clast-rich (sandier) beds. The bright colouration of some portions is bound to surfaces of slickensides and indicates hydromorphic conditions, derived from periods of water saturation (e.g., Mack et al., 1993; Orr and Roberts, 2024). Nonetheless, the patchiness in colouration of the deposits indicates that the water table fluctuated, pointing to alternating seasons of desiccation and flooding. In summary, these features suggest early pedogenic stages, with incipient formation of slickensides, under a seasonal climate regime (Mack et al., 1993), though less marked than those inferred for layers M1 and M2.

4.6. Layer M6 – Light-coloured large nodules in blueish-grey mudstones (11 cm thick)

Description. This 11 cm thick layer is mainly built up by very large carbonate nodules (up to 15 cm in diameter) of yellow to ochre colour and with silty to marly aspect, displaying the same composition and structures than those of layer M4 (Figs. 2, 10). Smaller nodules, on the size range of those from layer M4, are also present. As in layer M4, nodules are organised by size within the layer, with the larger ones on top and reducing in size deeper into the layer. The matrix is composed of greasy mudstones, it is generally blueish to light grey, and ochre patches are also present. Blackish/brownish fragments that resemble fish scales are preserved within some nodules (Fig. 10). In the area excavated in 2025, nodules are extremely large, in some cases coalescing and forming a continuous horizon.

Fossil contents. Besides the aforementioned dark coloured elements present in some nodules (Fig. 10), no other fossil remains have been

found in this layer.

Interpretation. This horizon is similar to that of layer M4, the main difference being the size of the nodules, much larger in layer M6. The nodules indicate typical calcic pedogenic processes (e.g., Machette, 1985; Mack et al., 1993), with larger ones on top, becoming successively smaller towards the bottom of the layer. As layer M4, this layer also represents a Bkk horizon (Soil Survey Staff, 2014) in the stage III of calcic soils development, according to the classifications of Gile et al. (1966) and Machette (1985). The larger size of the nodules respect to those of layer M4 indicates more arid conditions in layer M6, and/or a more prolonged exposition and thus a longer period of pedogenesis, in a more advanced phase of the stage III of calcic soil development (Machette, 1985). In this sense the areas with larger nodules, almost forming a continuous horizon, may correspond to stage IV (as defined by Machette, 1985).

4.7. Layer M7 – Basal bonebed of the Anthrakonitbank (2 cm thick)

Description. Silty 2 cm thick layer, with relatively abundant fish scales and other bone fragments. Some portions display cross lamination (Fig. 2) corresponding to wave ripples. The colour of the deposits is dark grey. This layer hardly detaches from the overlying dolostone composing layer M8. Coal seams are present in some areas (Fig. 10). In the area excavated in 2025, layer M7 appears thicker (up to 7 cm), coinciding with extremely large nodules of layer M6.

Fossil content. The bonebed mainly preserves remains of *Gyrolepis*, *Neusticosaurus* and *Nothosaurus*.

Interpretation. Differing from the lower bonebeds of the Sandige Pflanzenschiefer, this one only yields marine fauna. Thus, it was most probably formed in a setting with more marine influence than the underlying units, especially of layers M1 and M2. The inferred marine conditions are in accordance with the overlying dolostone (e.g., Hagdorn et al., 2015). In fact, layer M7 corresponds to the base of the Anthrakonitbank, which usually is also a bonebed containing marine remains, as well as abundant fish scales (Hagdorn et al., 2015; Mujal and Schoch, 2020).

4.8. Layer M8 – Anthrakonitbank dolostone (95 cm thick)

Description. Layer M8 forms a 95 cm thick succession of light brown-grey, silty, dolostone (Figs. 2, 10). The dolostone is well layered, giving the unit a marked tabular aspect. Thicknesses of the layers range between 4 and 10 cm, usually around 5 cm per layer. Round to oval-shaped holes of 1 to 10 cm of diameter in their long axis (mostly parallel to stratification) are present throughout the succession (Fig. 10). Some of them display surfaces covered with sparry calcite.

Fossil content. The most characteristic fossil of this unit is the brachiopod *Lingularia* (Hagdorn, 2015). Hagdorn et al. (2015) also reported the presence of clam shrimps and the marine mollusc *Hoernesia socialis*.

Interpretation. The presence of a dolostone overlying a marine bonebed and covering the mudstone deposits is suggestive of a marine transgression, as interpreted elsewhere in the Lower Keuper, that prompted the precipitation of carbonate muds (Brunner, 1977; Bachmann, 2002; Pöppelreiter and Aigner, 2003, 2008; Hagdorn et al., 2015). Thus, this is in agreement with a trend towards marine conditions, with the original sediments composing the dolostone deposited in marine settings. The holes found throughout these carbonate deposits, also those partially infilled with calcite, correspond to moulds of gypsum nodules (e.g., Brunner, 1973; Bachmann, 2002; Hagdorn et al., 2015) as those found in supratidal facies of relatively arid and semiarid environments (Lasemi et al., 2012). This is in accordance with the interpretation of the climate evolution for the whole succession (see Section 5.2 below). Mujal and Schoch (2020) reported temnospondyl tracks (most probably capitosaurids) from the basalmost carbonate layer of the Anthrakonitbank at Vellberg-Eschenau, interpreting it as microbial mats from a marginal, restricted marine setting.

4.9. Layer M9 – Untere Graue Mergel (up to 1 m exposed)

Description. This unit is built up by light grey mudstones. In Michelbach, only a short portion of the basalmost part of the unit, usually highly weathered, is presently exposed. In the 1977 excavation up to 1 m of this unit was observed, but in slope available in the 2020 and 2025 excavations only ~0.5 m was uncovered.

Interpretation. Generally, the Untere Graue Mergel unit is interpreted as successive depositional sequences within lacustrine systems with certain marine influence. Since the analysis of this unit is out of the scope of the present work, we refer the reader to Schoch and Seegis (2016) and Schoch et al. (2022), who studied the UGM and its fossil content in detail, especially its uppermost part, in neighbouring localities.

4.10. The Sandige Pflanzenschiefer in neighbouring areas

To obtain a broader perspective of the Sandige Pflanzenschiefer, we compiled available stratigraphic and sedimentological data from this unit, based both on previous literature and our own observations. Brunner (1973) provided a general description of the unit, summarising all the features observed in multiple localities from northern Baden-Württemberg. Urlichs (1982) described the Sandige Pflanzenschiefer in the Kupferzell area, being consistent with the findings of Brunner (1973) (see also Schoch et al., 2022: fig. 2). More recently, we examined in

detail this unit in Vellberg-Eschenau, and the sedimentary succession mostly resembles those reported by the previous authors, showing slight differences with the stratigraphic profile of Michelbach (Fig. 11). In the localities studied by Brunner (1973), the thickness of the Sandige Pflanzenschiefer ranges between 40 and 360 cm, with an average of ~125 cm. This is slightly more than the thickness in Michelbach (87 cm), but still within the same range.

According to Brunner (1973), the Sandige Pflanzenschiefer consists of sandy claystones to marlstones (~mudstones) with predominance of mica, mostly of olive-grey to grey-green or olive colours and of light grey to olive-grey colours in a lesser degree. Whitish deposits have also been observed and, generally, the unit is layered. In the region NE to E from Michelbach, Brunner (1973) also documented the presence of sandstones overlying the Albertibank, the carbonate unit immediately below the Sandige Pflanzenschiefer (Fig. 1). Such sandstones would correspond to sandy inputs of freshwater flows not strictly related to the Hauptsandstein (main sandstone), which is the unit stratigraphically below the Albertibank (Fig. 1) that in some regions extends to stratigraphically higher levels (Brunner, 1973, 1977, 1980; Nitsch, 2015). Indeed, in some other regions the Sandige Pflanzenschiefer unit is absent, being replaced by the Hauptsandstein (Brunner, 1973, 1977, 1980). This author identified coal layers within the upper third of the Sandige Pflanzenschiefer (consistent with our findings in layers M3 and M5 in Michelbach), and also on top of the unit (consistent with layer M7 in Michelbach). More occasionally, coal is documented in the middle part of the unit.

Fossil content within this unit is documented by Brunner (1973), and includes plant debris, accumulations of the bivalve *Anoplophora*, and clam shrimps (spinicaudatans of 'conchostrachans'). Burrows and short-extended bonebeds are reported as rare occurrences. The brachiopods *Gervilleia subcostata* and *Lingularia tenuissima*, and also *Microconchus germanicus* are also present (see Hagdorn, 2015, and references therein).

In the area of Kupferzell (~12.2 km north of Michelbach), according to Urlichs (1982), the Sandige Pflanzenschiefer is composed of grey-blue to grey marlstones to claystones (mudstones), which display a dark grey to black clayey horizon with plant remains in the lower third (see also Schoch et al., 2022: fig. 2). Characteristic structures or elements are red ironstone nodules within grey to black coaly claystones to coals in that lower part of the unit, found in the localities from Herdtlingshausen, Brachbach and Wolpertshausen (East from Kupferzell; Urlichs, 1982). Considering the stratigraphic position, these red ironstone nodules may be equivalent to those in layer M1 in Michelbach, yet there these are particularly small (Fig. 3M).

Fossil content reported by Urlichs (1982) includes the bivalves *Myophoria transversa* and particularly large (up to 6 cm long) specimens of *Unionites letticus*. Furthermore, in the middle part of the unit in Kupferzell-Bauersbach to Hergershof, a 15–20 cm thick sandstone with calcareous cement was also identified by Urlichs (1982). This author reported the following bivalves from the sandstone: *Myophoria transversa*, *Pleuromya* cf. *elongata* and *Bakevella goldfussi*, being particularly common in Bauersbach; and *Unionites letticus* and *U. brevis* dominating near Brachbach and Herdtlingshausen. These faunas yield some palaeoenvironmental information: *M. transversa* is indicative of a normal to restricted marine setting, while *Unionites* spp. suggest hyposaline environments (see also Geyer et al., 2005), fitting with the overall picture of the unit (see also Section 5 below). In the sections measured by Urlichs (1982), the Sandige Pflanzenschiefer ranges between 160 and 280 cm thick, with a thickness average of ~210 cm, notably thicker than in Michelbach (87 cm thick).

In the vicinity of Michelbach an der Bilz, ~1 km SW from the excavation site, the quarry of Wilhelmshöf exposes the whole Lower Keuper succession (Aigner et al., 1990; Aigner and Bachmann, 1992). There, the Sandige Pflanzenschiefer unit appears somewhat different from the one studied in detail. The stratigraphic profile in Aigner et al. (1990) and Aigner and Bachmann (1992) shows a relatively deeply erosive sandstone channel deposit from the top of the unit. This may be

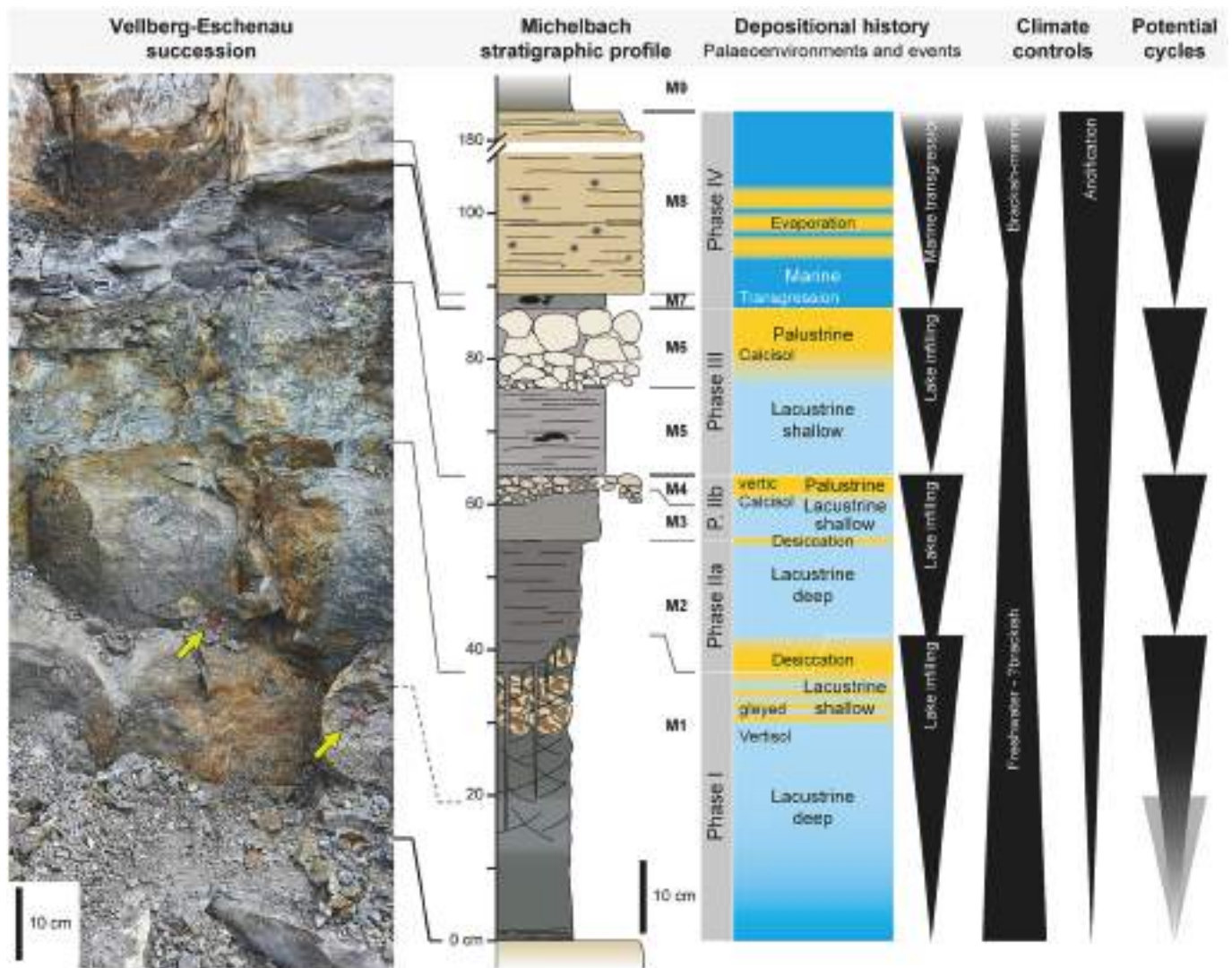


Fig. 11. Stratigraphic correlation between Michelbach and Vellberg-Eschenau successions, and palaeoenvironmental evolution, climate trend, and potential cycles throughout the Sandige Pflanzenschiefer and Anthrakonitbank units. Arrows in the Vellberg-Eschenau succession point to large red nodules. Grey triangle in the potential cycles indicate an alternative interpretation to divide layer M1 in two cycles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

equivalent to the sandstone deposits reported by Brunner (1973), and this shows how the succession can change locally. In fact, in a recent visit to the quarry by one of us (H.H.), in the present available exposure of the succession, this sandstone channel deposit is not observed. Generally, such local changes are likely indicative of a rather proximal lacustrine succession, which is in line with the presence of pedogenic horizons (see also Section 5.1 below).

At the Schumann quarry, Vellberg-Eschenau (10 km east of Michelbach), we examined the Sandige Pflanzenschiefer (thickness of 82.5 cm) and the Anthrakonitbank (thickness of ~90 cm) units (Fig. 11; see also Mujal and Schoch, 2020), identifying the following layers, from base to top:

- The base of the Sandige Pflanzenschiefer, immediately overlaying the Albertbank carbonates (which have a flat top as in Michelbach), is composed of a ~2 cm thick dark grey, finely laminated layer of very fine-grained sandstone to siltstone. This layer is overlain by a ~46 cm thick interval of fine- to very fine-grained sandstones with carbonised plant fragments. In the mid-lower part of these deposits there are reddish nodules, some with small-sized pyrite crystals and patches inside. These nodules, again, indicate that this part is likely

stratigraphically equivalent to layer M1 in Michelbach, and also to the coaly horizons with ironstone nodules reported by Urlichs (1982) in the lower portion of this unit. Just below the reddish nodules, there is a rough stratification plane, with fine-grained sandstones immediately below.

- The interval above the sandy deposits is composed of grey-olive green siltstones with very light (yellowish) hydromorphic colours. There are also some ochre-orange-brown stains. Overall they may represent redoximorphic conditions. This interval is 20 cm thick and can be divided in three: (1) the lower part is a 6 cm thick layer of soft, light grey-greenish mudstones; (2) the middle part is 6 cm thick and consists of siltstone without hydromorphic colours and contains rhizocretions; (3) the upper part is 8 cm thick and with the same composition and colouration as the lower part. This whole interval is possibly equivalent to layers M2 to M4 in Michelbach. Hydromorphic colours indicate intermittent exposure and periodical well-drained substrates. Rhizocretions suggest stabilisation of the soil with plants, possibly in subaerial conditions, which would be equivalent to the carbonate nodule horizon in layer M4 at Michelbach.

- The top of the Sandige Pflanzenschiefer is composed of a 14.5 cm thick unit of finely laminated very fine-grained sandstones of grey colour with plant remains that are partly carbonised. This interval displays coarser seams of sandstone with irregular shapes and distribution. Such a detrital input in the succession possibly correlates with the sequence M5–M6 in Michelbach, which also suggest more subaerial conditions, building the generally terrestrialisation trend of this unit.
- The base of the Anthrakonitbank is a bonebed, sedimentologically equivalent to layer M7 in Michelbach. Mujal and Schoch (2020) reported abundant fish scales, as well as a *Nothosaurus* tooth; generally, there are ample, indeterminate bone fragments. The overlying dolostone (~90 cm thick) is also layered and contains gypsum moulds mostly found within the lower half of the unit, as well as potentially gas-escape structures (Mujal and Schoch, 2020). Of note, these authors described temnospondyl tracks on top of the first layer of the Anthrakonitbank, on the uneven surfaces corresponding to microbial mats.

Lithologically, the Sandige Pflanzenschiefer in Michelbach is somewhat different from the unit in the aforementioned localities. Nevertheless, the depositional setting is fairly equivalent, corresponding to a lacustrine succession with a terrestrialisation trend and an increase of aridity, including desiccation features and marine influence. The most striking difference is in the fossil content, especially regarding vertebrates, with Michelbach being particularly rich (though only in the lower-mid portion: the upper portion of layer M1, and layers M2 and M3), and the other Sandige Pflanzenschiefer successions yielding almost no vertebrate remains, with the exception of sparse remains in Brachbach and Herdtlingshagen, at the vicinity of Kupferzell (Urlichs, 1982; see also Schoch et al., 2022: fig. 2). Similarly, sandy facies and plant remains, which are rather characteristic of this Lower Keuper unit (e.g., Brunner, 1973), are localised in Michelbach, only present in layers M3 and M5.

5. Discussion

5.1. Depositional history of the Michelbach lagerstätte

The regular thickness, with only slight variations of the studied layers in the Sandige Pflanzenschiefer and Anthrakonitbank in Michelbach (Figs. 2, 10), and their entire extension and homogeneity along the whole outcrop (Fig. 1E), permit analysis of the depositional history of this succession. Three main depositional sequences, consistent with progressive environmental and climate changes, can be identified throughout the Sandige Pflanzenschiefer (phases I to III), ending with the onset of the Anthrakonitbank carbonate deposits (phase IV).

As shown in Section 4.10 above, the Sandige Pflanzenschiefer deposits in regions out from Michelbach exhibit slightly different sedimentological features, but the stratigraphic stacking pattern is most likely traceable at kilometric scale (Brunner, 1973; Urlichs, 1982; Aigner et al., 1990; Pöppelreiter and Aigner, 2008; E.M., H.H., R.R.S. pers. obs.). Interestingly, ironstone nodules (as those in layer M1) are associated with redoximorphic conditions, and thus present in gleyed Vertisols (Tabor et al., 2008; Orr and Roberts, 2024). Therefore, these horizons may be stratigraphically equivalent to, and appear, as a suitable horizon to pinpoint these successions. All in all, the depositional history outlined below may be extrapolated to other, coeval successions.

A shared feature in all Sandige Pflanzenschiefer localities is the presence of coal, especially in the upper third of the unit. Even with the existing lithological differences, in both Michelbach and Vellberg-Eschenau localities three main depositional phases/sequences can be identified (Fig. 11). In Brunner (1973) and Urlichs (1982), descriptions of the unit do not include a detailed depositional history. Still, the overall stratigraphic and sedimentary succession fits with that of Michelbach, showing a progressive terrestrialisation. Michelbach

therefore represents a unique spot for fossils from the Sandige Pflanzenschiefer, yielding the appropriate lithological conditions for the preservation of vertebrate remains. This allows for the reconstruction of depositional history of the unit together with its biota (Fig. 12). At the same time, the identification of equivalent depositional phases, especially between Michelbach and Vellberg-Eschenau as first-hand observations, allows drawing broader interpretations for the evolution of these vertebrate ecosystems along with climate, not only at the scale of the CEB, but also for the Triassic.

5.1.1. Phase I: Deep lake (layer M1)

The grey mudstones with small ironstone nodules, slickensides in the upper portion and large-scale desiccation cracks on top probably formed in a deep lake basin that dried up completely at the end of the depositional history of this first unit. The first phase, Lake M1, was inhabited by the freshwater temnospondyl *Plagiosuchus* and its putative prey, such as the actinopterygian fish *Serrolepis*. The apex predator was *Mastodonsaurus giganteus*, present with juveniles only. The latter feature might indicate that the lake was not as large as the ones excavated at Kupferzell and Vellberg-Eschenau (Schoch and Seegis, 2016; Schoch et al., 2022, 2024). In addition, the rather short faunal list indicates a water body with less favourable conditions, possibly being stratified. However, the presence of the bottom-dwelling *Plagiosuchus*, a perennibranchiate temnospondyl (Damiani et al., 2009), suggests that the lake offered a permanent food supply and formed a relatively stable water body.

This phase ended with the desiccation of the lacustrine system, likely due to prolonged arid conditions. The notably deep mud-cracks originating on top of layer M1 were infilled with sediment very rich in fish scales, characteristic of layer M2. This further marks a non-deposition interval during this aridity period, in which terrestrial conditions prevailed. Such conditions are also suggested by the presence of archosauriform teeth, likely from terrestrial taxa (e.g., Schoch et al., 2018), in these mud-cracks, but not within layer M1 itself. In addition, slickensides denote pedogenesis by repeated shrink-swell periods of the clayey substrate, resulting in a Bss horizon, which formed underneath the potential A horizon, dominated by the presence of mud-cracks (e.g., Marriott and Wright, 1993). This also implies periodical subaerial exposure, as well as the formation of an uneven relief, which may explain the thickness variation of the overlying layer M2.

Such uneven or wavy relief (sensu Orr and Roberts, 2024) is also in line with the uneven distribution of hydromorphic colours at the upper portion of layer M1. In the latest stages of Lake M1, flooding of the substrate was restricted to the deeper zones, leaving shallower areas to subaerial exposure followed by oxidation. Altogether, ironstone nodules, slickensides and hydromorphic colours, plus mud-cracks within a dominantly grey siliciclastic mudstone are features typical of gleyed Vertisols. These palaeosols usually form in climates with marked seasonality in overall subhumid conditions (Mack et al., 1993; Tabor et al., 2008; Orr and Roberts, 2024).

Considering the dominance of greyish and greenish colours with subordinate yellow, ochre, and brown-orange patches, periods with the presence of water (entirely flooding the lake) predominated. Thus, oxidation took place after the water table completely evaporated, during pedogenesis, at the end of the depositional history of these sediments.

Potential sediment loading, causing instabilities in the deposits could have generated sediment-gravity flows of the relatively cohesive mud, imbedding and transporting of decomposing carcasses of the temnospondyl amphibians and reworking of exhumed bones. Reworking of exhumed bones together with more recently deceased carcasses suggest that deposits were re-sedimented, which might hint to a relatively low sedimentation rate (e.g., Kraus, 1999) and thus a low input of sediment in the system. This points to a relatively low energetic lake with periods of rapid sedimentation from gravity flows, overall corresponding to an episodic system. At the top of layer M1, bone clusters of single individuals of plagiosaurids, which were obligatory subaquatic temnospondyls (Damiani et al., 2009), suggest that these animals died during

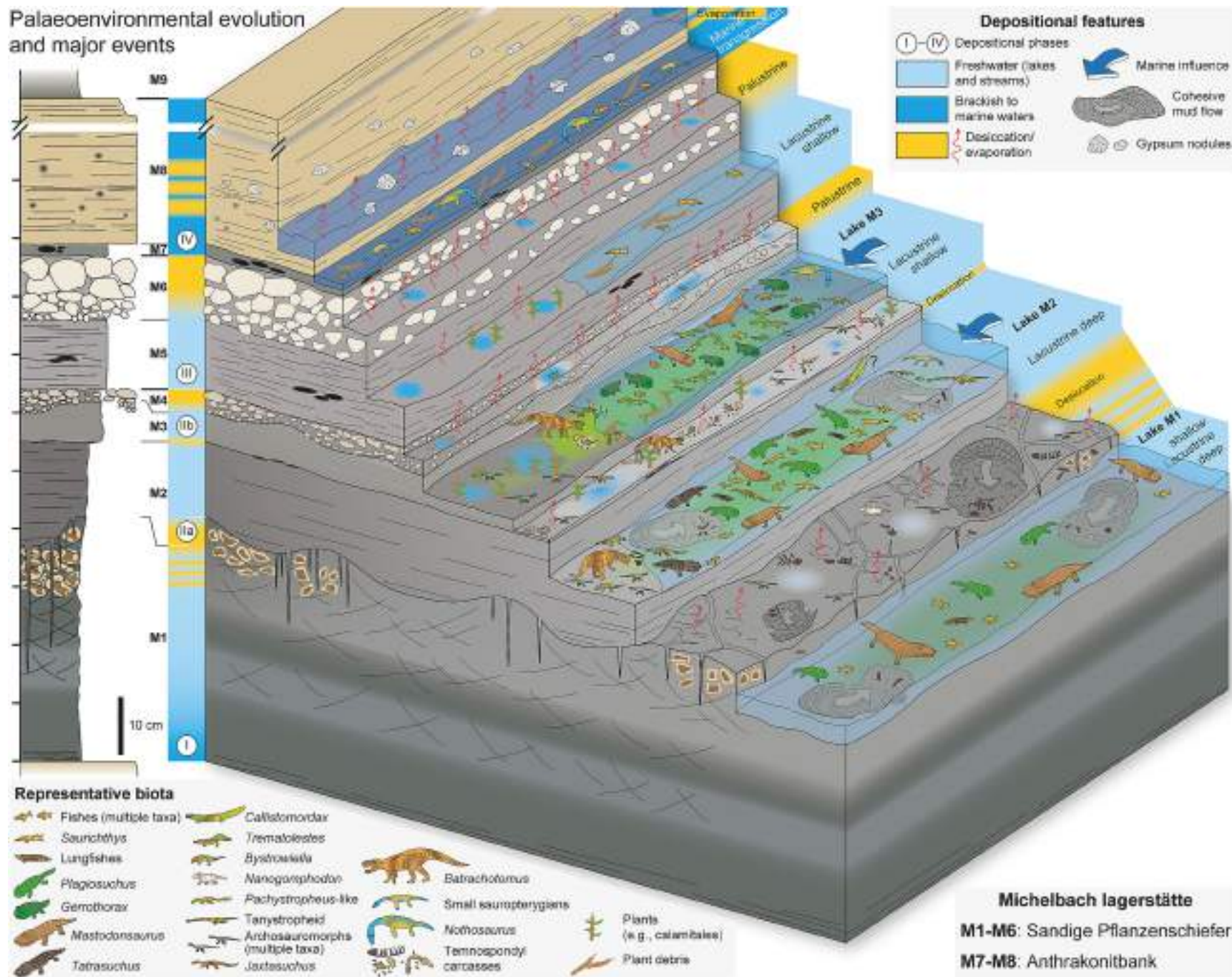


Fig. 12. Reconstruction of the palaeoenvironmental evolution, based on the depositional history, in Michelbach. Most representative biota and sedimentary structures depicted. Biota and palaeoenvironments are not to scale.

droughts, when lake water was completely evaporated, likely when mud-cracks formed.

The relatively high frequency of fragmented bones may be explained by two main factors or processes, namely pedogenesis and short-lived cohesive/hyperconcentrated sediment-gravity flows. No evidence of scavenging or predation have been observed, thus carcasses were likely buried soon after the animals died. In any case, the presence of partial skeletons of both *Plagiosuchus* and *Mastodonsaurus* and the inferred minor transportation of carcasses suggest that deposits of layer M1 constituted their actual habitat. Therefore, most of the bone breakage observed is probably due to pedogenesis, with shrink-swell cycles of the substrate because of water fluctuation (with arid periods resulting in desiccation), and the absence of evidence of carcass consumption is possibly a consequence of the clayey, soft substrate that might have hindered the presence of larger predators or scavengers. Alternatively, the pyrite identified in the microsamples could potentially be indicative of low oxygenation and possibly stratification of the lake, which are factors that would also result in a reduced presence of predators or scavengers.

Within layer M1, bones are more abundant in the upper portion. This is the opposite pattern of gravity flow-generated bonebeds, in which bones tend to be less abundant and smaller upwards (e.g., [Fondevilla et al., 2017](#)). Therefore, the observed pattern in layer M1 fits better with a multistorey formation, with episodic sediment-gravity flow influxes into the system, and bone distribution mainly driven by pedogenic processes. The lack of fossils in the lower portion would be indicative of less favourable conditions for faunas during the earliest phase of Lake M1 due to the transition from a marine phase, represented by the underlying Albertbank.

5.1.2. Phase IIa: Rich freshwater lake (layer M2)

The sedimentary sequence of layer M2 likely formed in a freshwater lake (as *Unionites brevis* and the vertebrate fauna suggest; [Geyer et al., 2005](#); [Schoch and Seegis, 2016](#)) that was subject to periodical catastrophic events (e.g., gravity flows from the slope and/or storms resulting in short-lived mud flows), which induced reworking of deposits; this corresponds generally to an episodic system. These did not only disarticulate skeletons and accumulated bonebeds but also transported bones of terrestrial or shore-dwelling animals (*Bystrowiella*, *Jaxtasuchus*, *Batrachotomus*) into the lake basin. Of note, the lack of erosional structures between layers M1 and M2, and the potential preservation of a pedogenic A horizon at the top of layer M1 point to minimal to no erosion between the two depositional phases. At the same time, this set of features point to a non-sedimentation period, allowing for the development of a soil horizon.

The dark grey colour and uniform appearance of sedimentary components suggest that rocks of layer M2, and the following layer M3, formed under stagnating conditions in a somewhat deeper lake than the one preserved in the subsequent M5 sequence (see [Section 5.1.4](#) below), but possibly shallower than that of layer M1. Lake M2 was rich in fish and temnospondyl taxa, with evidence of three larger predators (*Plagiosuchus*: 1 m, *Tatrasuchus*: 2.5 m, juvenile *Mastodonsaurus*: 3 m). *Plagiosuchus* was a suction-feeding, poorly mobile bottom-dweller ([Damiani et al., 2009](#)). The larger, heavier capitosaur *Tatrasuchus* is known from Kupferzell to have preferred the shore areas where it acted as an ambush predator ([Schoch et al., 2022](#)); the few remains found in layer M2 are all single elements that may have been washed in from some distance. *Tatrasuchus* therefore may not have been autochthonous in the Lake M2 basin. In contrast, *Mastodonsaurus*, the apex predator, evidently fed on its temnospondyl relatives. Bite marks likely stemming from *Mastodonsaurus* and regurgitated skeletons of *Callistomordax* and *Trematolestes* are known from the UGM at Vellberg-Eschenau (e.g., [Schoch and Seegis, 2016](#); [Mujal et al., 2022](#); [Schoch et al., 2024](#)), and thus the same behaviour can be extrapolated at the Michelbach system.

The sedimentary deposits of Lake M2 resemble those of Lake E6 in Vellberg-Eschenau in their dark grey colour (likely indicating poor

drainage, with a perennial, or almost perennial water table), the absence of charophytes, and the dominance of clayey matrix (bonebeds, absence of clear stratification; see [Schoch and Seegis, 2016](#)). However, the fauna is more consistent with Lake K3 at Kupferzell-Bauersbach ([Schoch et al., 2022](#)), especially in the dominance of a plagiosaurid (*Gerrothorax* in Lake K3; *Plagiosuchus* in Lake M2) and *Mastodonsaurus*. The fish fauna of layer M2 includes eight species, as contrasted with 12–13 at Kupferzell (K3, K4) and Vellberg (E5, E6); this is also consistent with the small size of *Mastodonsaurus* (see also discussion in [Schoch et al., 2024](#)). This indicates a somewhat less rich ecosystem in Lake M2, possibly restricted by lake size, diversity of nutrients or some unknown lake properties. This is also in line with the apparently restricted distribution of tetrapod fossils in the Sandige Pflanzenschiefer (see [Section 4.10](#) above).

As inferred for layer M1, during drought periods in Phase IIa, potential instabilities and/or high energy episodes (e.g., storms) could have generated cohesive mud flows that transported sediments together with abundant biotic remains (acting as clasts) into the lake basin. These eventually formed the bonebed lenses identified within layer M2. These rather occasional, catastrophic events also resulted in the erosion and reworking of already buried elements (e.g., light coloured and worn bones), which were reincorporated in the system and eventually re-sedimented. The presence of coprolites, however, indicates a predominance of calm periods. Layer M2 is the most fossiliferous in Michelbach, suggesting that during this phase of the whole depositional history the lake had the highest input of nutrients. Hypothetically, water influx from surrounding, mainly terrestrial, areas to the lake system was continuous, which could be explained by the high number of elements from terrestrial reptiles in layer M2, the largest in the Michelbach succession.

5.1.3. Phase IIb: Shallow open lake (layers M3–M4)

Layer M3 formed in the same depositional sequence of layer M2, within the same lake basin, as the lack of sedimentary discontinuity between the two layers indicate. At the same time, the sharp changes in lithology and fossil content, mainly characterised by the drop of fish scales, are suggestive of a sudden change in the environmental conditions. Layer M3 formed in an area closer to the lake shore than layer M2, with increased detrital input resulting in an impoverished fauna.

The faunas of layer M3, dominated by *Trematolestes*, correspond to an autochthonous assemblage (e.g., [Schoch and Mujal, 2022](#)) preserved under more favourable conditions with continuous low-energy laminar flows. This is indicated by the drop of bonebed seams from layers M2 to M3 as well as by the relatively common articulated specimens in layer M3 ([Hagdorn, 1980](#); see [Section 4](#) above). The presence of shed teeth of *Batrachotomus* suggests that this taxon roamed this area, indicating periods of subaerial conditions or much shallower waters, also in line with the presence of plant debris. In any case, fairly articulated *Gerrothorax* skeletons, without evidence of transport, indicate that the taxon inhabited this lake, implying relatively prolonged periods of subaquatic conditions. Notably, in Lake M3 this plagiosaurid replaced *Plagiosuchus*. This change could hypothetically stem from a combination of environmental and ecological factors: these two taxa probably occupied similar ecological niches, thus being competitors that likely did not usually coexist (e.g., [Schoch et al., 2025](#): fig. 9); at the same time, *Plagiosuchus* had better swimming abilities than *Gerrothorax* ([Witzmann and Schoch, 2026](#)), thus the former could dwell in less aerated/oxygenated waters than the latter, which would fit with the change from Lakes M1 and M2 to Lake M3, the latter lacustrine system being more oxygenated and shallower than the two former ones.

Despite Lake M3 being predominantly freshwater, the presence of a *Nothosaurus* tooth suggests sporadic influence of marine settings. This tooth was found close to plant debris (fragmentary *Neocalamites*), which is indicative of mixing of sediment and elements from different environments. Therefore, a certain degree of transportation for some elements existed. The sandy layers and seams interbedded within the mudstone deposits, the lighter colour of the sediment with less organic

content with respect to layer M2, and the reduced abundance of fish scales also point to a major terrestrial influence for layer M3, yet in an overall very low energy regime.

Inferred from its skeleton, *Trematolestes* was an agile aquatic predator with good swimming abilities (Schoch, 2006; Schoch and Mujal, 2022). In the Untere Graue Mergel, it is known from very few fragments in Kupferzell (Schoch et al., 2022) and occurs rarely in the units E5 and E6 from Vellberg-Eschenau (Schoch and Seegis, 2016). However, in layer M3, it is a surprisingly common temnospondyl (Schoch and Mujal, 2022), suggesting that these deposits of the Sandige Pflanzenschiefer in Michelbach preserve an autochthonous habitat of that taxon.

The shallow water table during the Lake M3 phase, likely shallower than in other fossil lagerstätten with similar faunas (e.g., Vellberg-Eschenau, see Schoch and Seegis, 2016) would have precluded the establishment of populations of larger predatory amphibians (e.g., *Tatrasuchus* and *Mastodonsaurus*), and obligate subaquatic taxa such as *Gerrothorax* could only be present in higher sustained lake levels. Potential transportation of carcasses is suggested by the WSW-ENE alignment of some skeletons from *Gerrothorax* and *Trematolestes* (Hagdorn et al., 2015). If such transport occurred, it was not long-lived or highly energetic, because the skeletons are still articulated, and no sedimentary structures of high flow regime have been observed. On the other hand, the curled position of most of the *Trematolestes* skeletons (Fig. 8) indicates that carcasses underwent desiccation during droughts. At the same time, these skeletons show variable degrees of decay (disarticulation), suggesting multiple flooding-desiccation periods or cycles (i.e., similar to the seasonality inferred for layers M1 and M2).

The depositional phase of this lacustrine system, with a progressive shallowing of the water table, ended with the complete desiccation of the lake and the development of a Calcisol. This is inferred from the presence of carbonate nodules building up layer M4, with a mudstone matrix equivalent to layer M3. Carbonate nodules are characteristic of pedogenic development in semiarid and arid climates with low precipitation regimes, as well as in palustrine environments (Machette, 1985; Mack et al., 1993; Alonso-Zarza, 2003; Alonso-Zarza and Wright, 2010). In this sense, layers M2, M3 and M4 constitute a single depositional sequence (here Phase II), with the system evolving from a relatively deep freshwater lake, to a shallower, yet open one, finally ending in a palustrine setting (cf. Alonso-Zarza, 2003). The pedogenic features of the whole succession point to the development of a vertic Calcisol, characterised by seasonality, with desiccation periods, and semiarid climatic conditions (e.g., Machette, 1985; Tabor et al., 2008).

5.1.4. Phase III: Shallow impoverished lake (layers M5–M6)

The sequence including layers M5 and M6 records a terrestrialisation of the depositional system, with a higher clastic input with respect to the preceding deposits. The almost complete absence of fossils (with only a few micro-remains) is suggestive of less favourable conditions for the establishment of faunal communities and/or a much lower preservation potential. In the same line, the large carbonate nodules indicate prolonged periods of desiccation and subaerial exposure under semiarid conditions (Machette, 1985; Mack et al., 1993; Alonso-Zarza, 2003; Tabor et al., 2008; Alonso-Zarza and Wright, 2010).

Coaly pieces within layer M5 suggest that the lake basin was shallower and/or the shore was closer than in the preceding units. In addition, the pedogenic nodules from layer M6 are much larger than those of layer M4, indicating a longer time of subaerial exposure that permitted nodules to grow larger, in some parts already forming a more continuous layer (Fig. 10), although both layers are still within stage III of calcic soil development (Machette, 1985). The larger size of the nodules could rather point to increased aridity, also explaining the low number of fossil remains, overall showing harsher environmental conditions than in the previous phase.

Overall, the stratigraphic sequence of layers M5–M6 mirrors that of layers M3–M4, mainly differing on the fossil content (M3 notably rich vs. M5 impoverished) and nodule size (small in M4 vs. large in M6).

Therefore, layers M5 and M6 represent a much shallower lake than that of layers M3 and M4, also ending in a palustrine system.

5.1.5. Phase IV: Marine transgression (layers M7–M8)

The end of the lacustrine depositional history in Michelbach is marked by the onset of the Anthrakonitbank, with a basal bonebed (layer M7) followed by tabular dolostones with gypsum moulds (layer M8). The bonebed was deposited during a marine transgression that led to the precipitation of carbonate muds (resulting in dolostones) and represents the first phase of the marine flooding (Aigner et al., 1990). During this phase, debris transported by relatively rapid flows was deposited (Hagdorn et al., 2015). Carbonate mud deposition would have been seasonal/cyclical, as the clearly differentiated layers indicate. The presence of gypsum (or gypsum moulds) is indicative of relatively arid conditions and high salinity (e.g., Bachmann, 2002; Lasemi et al., 2012; Orr and Roberts, 2024). This is in agreement with the interpreted restricted marginal marine setting for this unit (Bachmann, 2002; Mujal and Schoch, 2020), as well as with an overall sabkha-like setting (e.g., Schreiber et al., 1986) also suggested for the overlying Untere Graue Mergel unit (Schoch et al., 2022). Similarly, fitting with this picture of the Lower Keuper, Nitsch (2015) suggested that the environments outside the lakes and rivers were gypsum deserts.

5.2. The Michelbach lagerstätte in the Triassic climatic context

Pedogenic features in the Michelbach succession provide hints at climate changes throughout the depositional history of the Sandige Pflanzenschiefer (layers M1 to M6) and Anthrakonitbank (layers M7 and M8), and how these may have also influenced faunas therein. The bulk of fossil material comes from the interval ranging from the upper portion of layer M1 to layer M3 (Fig. 2). This coincides with the interval showing the least arid conditions of the whole succession, as well as the deeper lacustrine settings (Fig. 11). Therefore, both climate and environments were suitable for stable and complex ecosystems in this interval (Fig. 12). Nevertheless, arid periods resulting in desiccation, with subaerial exposure, are also recorded, indicating a marked seasonality, which may correspond to annual changes. Regardless, faunas were present, again, indicating stability of ecosystems.

Overall, an aridification trend is observed from the Sandige Pflanzenschiefer to the Anthrakonitbank, which evolved cyclically, as the stepped sedimentary-pedogenic succession shows (Fig. 11), from base to top: (1) Vertisol in layer M1, (2) vertic Calcisol in layers M2–M4, (3) Calcisol in layers M5–M6, gypsum nodules of arid origin in layer M8. Along with this marked aridification, a trend towards more quiet conditions (and shallower lacustrine settings) is recorded in the fossiliferous succession: remains are overall chaotically oriented in layers M1 and M2, whereas in layer M3 they are parallel to stratification, and several skeletons appear articulated. Also, the presence of both terrestrial and marine fossils (e.g., plants, nothosaurs, terrestrial archosaurs) in layer M3 suggests that the lacustrine system became more open than that represented by layers M1 and M2. Interestingly, the bivalve *Unionites brevis* in layer M2 indicates freshwater conditions (e.g., Urlichs, 1982; Geyer et al., 2005), whereas scarce remains of *Nothosaurus* (mainly teeth) in layer M3 suggest a marine influence. The absence of rhizocretions suggests that plants were mainly washed in, and coal seams could represent accumulations of plant debris from the potentially nearby shore, as is the case in the slightly younger Kupferzell lagerstätte (Schoch et al., 2022; see also discussion in Schoch and Seegis, 2016). At the same time, the number of fossils markedly decreases throughout the Sandige Pflanzenschiefer succession, eventually with layer M5 only preserving a few microfossils. The other conspicuous change is the onset of the Anthrakonitbank, starting with a rich marine bonebed (layer M7), succeeded by dolostones with gypsum nodules (layer M8) indicating arid conditions. This responds to the apparently contradictory picture between layers M2 and M3: despite Lake M2 being deeper than Lake M3, the latter had more marine influence than the former because of the

progressive sea level rise. This builds a complex picture of environmental and climate changes, with an aridification and terrestrialisation trend, in which the lacustrine system became progressively shallower (Sandige Pflanzenschiefer) and culminated with a marine transgression under arid conditions (Anthrakonitbank). Noteworthy, this trend is the same observed in these units at Vellberg-Eschenau (see Section 4.10 above; Fig. 11). The whole cycle from siliciclastic-dominated to carbonate-dominated deposits that these two units represent is generally repeated throughout the whole Lower Keuper succession, which records a major progradational-retrogradational cycle (Franz et al., 2013), and can be traced at basin scale (Brunner, 1973, 1977, 1980; Aigner et al., 1990; Pöppelreiter and Aigner, 2003, 2008; Franz et al., 2013, 2015). This records a pulse or the onset of the Tethys Sea during the transition from the marine Muschelkalk to the overall terrestrial Middle Keuper (Franz et al., 2013). In fact, the patterns described above, are also found at a larger scale: a more pronounced marine transgression occurred at the end of the Lower Keuper sedimentation with the Grenzdolomit (Aigner and Bachmann, 1992; Franz et al., 2013, 2015); this topmost unit includes diverse bivalve faunas, occasional cephalopods and sauroptrygians. This transgression extended far into the CEB (Franz et al., 2015), and even to the overlying Grabfeld Formation (which corresponds to the lower part of the Middle Keuper). Of note, the formation yields evidence of aridity, with the presence of gypsum, as well as of marine influence, with the presence of hypersaline bivalves (*Costatoria goldfussia*) and marine reptiles (*Simosaurus* and *Nothosaurus*). In this regard, this trend at basin scale appears similar to that of the Michelbach succession. Therefore, the studied lagerstätte preserves a cyclical pattern that reflects the broader trend of the basin (e.g., Franz et al., 2013, 2015), being a good proxy to understanding events at larger scale.

In the context of climate change, the succession from the Sandige Pflanzenschiefer to the Anthrakonitbank shows an interesting transition, with an aridification due to warming (greenhouse or hothouse) that likely induced or prompted a sea level rise. At the same time, we observe smaller scale cycles within the succession (corresponding to the phases of the depositional history), which generally reflect the marked cyclicity (alternating siliciclastic-carbonate succession) inferred for the Lower Keuper as a whole (Pöppelreiter and Aigner, 2003, 2008; Nitsch, 2005, 2015; Paul, 2021). Paul (2021) suggested an overall subhumid climate for the Erfurt Formation; however, this only partly applies to our findings for the Sandige Pflanzenschiefer and Anthrakonitbank: subhumid conditions are inferred for layer M1, with the identification of a gleyed Vertisol; in the overlaying deposits semiarid to arid conditions are interpreted, with the presence of vertic Calcisol (layers M2 to M4), Calcisol (layers M5 and M6), and gypsum nodules (layer M8). This, again, reflects marked cyclicity (likely related to climate conditions) and thus a complex scenario that can be reconstructed when examined in detail (i.e., at outcrop level).

In this broader context, as mentioned above this succession shows signs of ecosystem complexity and stability only a few million years after the beginning of the Triassic Period. On one side, in a very short interval (from layers M1 to M3), presumably representing a short period of time (~a few thousands of years; Franz et al., 2018), different faunal communities are observed. This shows that these diverse faunas could quickly adapt, expand and colonise different environments according to their more favourable conditions. This is reminiscent of the slightly younger Vellberg-Eschenau and Kupferzell lagerstätten, with multiple trophic levels including also several top predators (Schoch and Seegis, 2016; Mujal et al., 2022; Schoch et al., 2022, 2024). Interestingly, the slightly older Miedary site also preserves a rich and likely complex ecosystem (Pawlak et al., 2022; Czepeński et al., 2023), complementing the picture of the whole Lower Keuper in the CEB (e.g., Mujal et al., 2025). Remarkably all these localities preserve equivalent and/or very similar taxa, with the main differences being on relative proportions of each assemblage, showing that these faunas were well established. On the other side, Zhao et al. (2020) and Liu et al. (2021) suggested that the presence of coal (indicative of humid periods) in Middle Triassic

lacustrine successions is an indicator of ecosystems recovery in the aftermath of the end-Permian mass extinction. This is relevant in the case of Michelbach, because coal is present despite the aridification trend, showing that these environments could still produce it. In other words, there was enough organic matter (basically plants) to accumulate and form coal seams. Furthermore, these ecosystems were rapidly established after the regression of the sea likely suggesting that vertebrate communities existed elsewhere and could effectively colonise newly available habitats.

6. Conclusions

The Michelbach locality forms one of the most important examples of vertebrate lagerstätten in the German Middle Triassic. It yielded two new taxa, the temnospondyl *Trematolestes hagdorni* and the cynodont *Nanogomphodon wildi*, along with numerous other vertebrates known from other deposits. More importantly, it encompasses successive lake deposits that show substantial differences in lithology and fauna (Figs. 11, 12). Pedogenic features further indicate that the excavated rock sequence documents an increasing aridification and warming, culminating with a sea level rise.

These data provide a unique opportunity to study the impact of climate change on Triassic lake ecosystems. Some 12 Myr after the end-Permian mass extinction, the lakes of the Lower Keuper (Erfurt Formation) were populated by highly diverse fish faunas and trophic webs with aquatic tetrapods that included one to five metre long temnospondyls, as well as relatively large pseudosuchian predators (Hagdorn et al., 2015; Schoch and Seegis, 2016; Mujal et al., 2022; Schoch et al., 2022, 2024). In addition to the large aquatic stem-amphibians, a range of amphibious or aquatic diapsid reptiles have recently been identified in the same lake deposits (Schoch, 2015b), and the disparity of piscivorous teeth suggest that this is only the tip of the iceberg (Schoch et al., 2018). Hence, the trophic webs within the Lower Keuper lakes were complex (e.g., Schoch et al., 2022), indicating excellent conditions and high productivity.

The Michelbach lagerstätte preserves a local succession of increasingly shallower lakes that were subject to increasingly arid conditions (Fig. 11). The lakes were smaller than those of the Untere Graue Mergel section known from Kupferzell, Vellberg-Eschenau, Ummenhofen and Wolpertshausen, but they resembled some of them in lithology and faunal content.

As Michelbach exemplifies a succession of smaller, more local water bodies compared with those documented in Kupferzell and Vellberg-Eschenau, it adds to our understanding of diversity between Middle Triassic lake habitats and ecosystems (e.g., Mujal et al., 2025). The most peculiar feature is the high abundance of *Trematolestes* in layer M3, with the bulk of the material stemming from juveniles and the total absence of adult *Mastodonsaurus* throughout the deposits. In addition, Michelbach is only the second locality after Vellberg-Eschenau in which *Calistomordax* has been found. Along with *Plagiosuchus* and *Gerrothorax*, it shows that the lake floor was habitable.

At Michelbach, the shallowing-upward trend correlates with marked biotic responses: (1) an increase in taxic diversity from Lakes M1 to M2, followed by a continuous decrease from M2 to M3 and into M4, (2) a change in the dominant temnospondyl faunas from *Plagiosuchus* to *Gerrothorax* from Lakes M2 to M3, (3) the immigration of *Trematolestes* into the shallower Lake M3, and (4) the disappearance of aquatic tetrapods in M4 and M5, correlating with strongly reduced fish diversity. In sum, the studied succession illustrates the evolution of increasingly shallower environments with decreasing habitability, possibly linked to increasing aridity. This distribution of fossils, concentrated on the lower part of the unit, appears to correlate with the inferred climate change. The potential cyclicity, primarily suggested by the palaeosol succession, controlled the lake system, with water bodies becoming shallower after each cycle due to the general aridification trend, changing from sub-humid to semiarid conditions. This was likely in response to climate warming that ended with a marine transgression under arid conditions.

In summary, the Michelbach lagerstätte serves as an example of the evolution of ecosystems during the Middle Triassic, as well as a model of faunal adaptation under environmental and climate changes.

CRediT authorship contribution statement

Eudald Mujal: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Resources. **Orla G. Bath Enright:** Writing – review & editing, Investigation, Validation. **Hans Hagdorn:** Writing – review & editing, Investigation, Resources, Validation. **Rainer R. Schoch:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Data curation, Formal analysis, Investigation, Resources, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are indebted to Norbert Adorf and Isabell Rosin (SMNS) for the organisation of the excavation and preparation of specimens. Erin Maxwell, Gabriela Sobral, Andreas Radecker, and Michel Rabe (all SMNS) are thanked for field assistance. We acknowledge Christoph Wimmer-Pfeil (SMNS) for the skilful preparation of thin sections and other sedimentological samples, and Lucrezia Ferrari (SMNS) for sediment screenwashing and picking of microfossils. The mayors, technicians and inhabitants from Michelbach an der Bilz are warmly thanked for their hospitality and support during fieldwork. We gratefully acknowledge the reviews by P. John Hancox and an anonymous reviewer and the editor Prof. Jimin Sun, which helped to improve the original manuscript. This work received support from the Deutsche Forschungsgemeinschaft (DFG) with the project 508778113 (MU 5245/1-1) and is a contribution to the DFG Research Unit FOR 5581. Open Access funding enabled and organised by Projekt DEAL.

Data availability

All relevant data is included in this study. All fossils in this study are available for collection visits at the SMNS.

References

- Aigner, T., Bachmann, G.H., 1992. Sequence-stratigraphic framework of the German Triassic. *Sediment. Geol.* 80, 115–135.
- Aigner, T., Bachmann, G.H., Hagdorn, H., 1990. Zyklische Stratigraphie und Ablagerungsbedingungen von Hauptmuschelkalk, Lettenkeuper und Gipskeuper in Nordost-Württemberg. *Jb. Mitt. Oberrh. geol. Ver.* 72, 125–143.
- Alonso-Zarza, M., A., 2003. Palaeoenvironmental significance of palustrine carbonates and calcretes in the geological record. *Earth-Sci. Rev.* 60, 261–298.
- Alonso-Zarza, A.M., Wright, V.P., 2010. Palustrine carbonates. In: Alonso-Zarza, A.M., Tanner, L.H. (Eds.), *Carbonates in Continental Settings. Developments in Sedimentology*, 61, pp. 103–131.
- Bachmann, G.H., 2002. A Lamellibranch-Stromatolite Bioherm in the lower Keuper (Ladinian, Middle Triassic), South Germany. *Facies* 46, 83–88.
- Behrensmeyer, A.K., 1978. Taphonomic and ecological information from bone weathering. *Paleobiology* 4, 150–162.
- Behrensmeyer, A.K., Hook, R.W., 1992. Palaeoenvironmental contexts and taphonomic modes in the terrestrial fossil record. In: Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D., Wing, S.L. (Eds.), *Terrestrial Ecosystems through Time. University of Chicago Press*, pp. 15–136.
- Beutler, G., Hauschke, N., Nitsch, E., 1999. Faziesentwicklung des Keupers im Germanischen Becken. In: Hauschke, N., Wilde, V. (Eds.), *Trias. Eine Ganz Andere Welt. Dr. Friedrich Pfeil, München*, pp. 129–174.
- Bond, D.P.G., Grasby, S.E., 2017. On the causes of mass extinctions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 478, 3–29.
- Böttcher, R., 2015. Fische des Lettenkeupers. In: Hagdorn, H., Schoch, R.R., Schweigert, G. (Eds.), *Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern*, 2015. *Palaeodiversity Sonderband*, pp. 141–202.
- Britt, B.B., Eberth, D.A., Scheetz, R.D., Greenhalgh, B.W., Stadtman, K.L., 2009. Taphonomy of debris-flow hosted dinosaur bonebeds at Dalton Wells, Utah (Lower Cretaceous, Cedar Mountain Formation, USA). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 280, 1–22.
- Brunner, H., 1973. Stratigraphische und sedimentpetrographische Untersuchungen am Unteren Keuper (Lettenkeuper, Trias) im nördlichen Baden-Württemberg. *Arb. Inst. Geol. Paläontol. Univ. Stuttgart*, N.F. 70, 1–85.
- Brunner, H., 1977. Zur Stratigraphie und Sedimentpetrographie des Unteren Keupers (Lettenkeuper, Trias) im nördlichen Baden-Württemberg. *Jb. Mitt. Oberrh. geol. Ver.*, N.F. 59, 169–193.
- Brunner, H., 1980. Zur Stratigraphie des Unteren Keupers (Lettenkeuper, Trias) im nordwestlichen Baden-Württemberg. *Jb. Mitt. Oberrh. geol. Ver.*, N.F. 62, 207–216.
- Czepiński, L., Pawlak, W., Rytel, A., Talandá, M., Szczygielski, T., Sulej, T., 2023. A new Middle Triassic vertebrate assemblage from Miedary (southern Poland). *J. Vertebr. Paleontol.* 43, e2265445.
- Dal Corso, J., Song, H., Callegaro, S., Chu, D., Sun, Y., Hilton, J., Grasby, S.E., Joachimski, M.M., Wignall, P.B., 2022. Environmental crises at the Permian–Triassic mass extinction. *Nat. Rev. Earth. Environ.* 3, 197–214.
- Damiani, R.J., Schoch, R.R., Hellrung, H., Werneburg, R., Gastou, S., 2009. The plagiosaurid temnospondyl *Plagiosuchus pustuliferus* (Amphibia: Temnospondyli) from the Middle Triassic of Germany: anatomy and functional morphology of the skull. *Zool. J. Linnean Soc.* 155, 348–373.
- Durand, M., Hagdorn, H., 2020. Der Muschelkalk im nordöstlichen Frankreich. In: Deutsche Stratigraphische Kommission (Ed.), *Stratigraphie von Deutschland XIII. — Muschelkalk*, vol. 2. *Schrift. dtsh. Ges. Geowiss.*, pp. 1096–1121, 91.
- Ezcurra, M.D., 2010. Biogeography of Triassic tetrapods: evidence for provincialism and driven sympatric cladogenesis in the early evolution of modern tetrapod lineages. *Proc. R. Soc. B* 277, 2547–2552.
- Fondevilla, V., Vicente, A., Battista, F., Sellés, A.G., Dinarès-Turell, J., Martín-Closas, C., Anadón, P., Vila, B., Razzolini, N.L., Galobart, À., Oms, O., 2017. Geology and taphonomy of the L'Espinau dinosaur bonebed, a singular lagoonal site from the Maastrichtian of South-Central Pyrenees. *Sediment. Geol.* 355, 75–92.
- Franz, M., Henniger, M., Barnasch, J., 2013. The strong diachronous Muschelkalk/Keuper facies shift in the Central European Basin: implications from the type-section of the Erfurt Formation (Lower Keuper, Triassic) and basin-wide correlations. *Int. J. Earth Sci. (Geol. Rundsch.)* 102, 761–780.
- Franz, M., Kaiser, S.L., Fischer, J., Heunisch, C., Kustatscher, E., Luppold, F.W., Berner, U., Röhlh, H.-G., 2015. Eustatic and climatic control on the Upper Muschelkalk Sea (late Anisian/Ladinian) in the Central European Basin. *Glob. Planet. Chang.* 135, 1–27.
- Franz, M., Bachmann, G.H., Barnasch, J., Heunisch, C., Röhlh, H.-G., 2018. Der Keuper in der Stratigraphischen Tabelle von Deutschland 2016 – kontinuierliche Sedimentation in der norddeutschen Beckenfazies (Variante B) / The Keuper Group in the Stratigraphic Table of Germany 2016 – continuous sedimentation in the North German Basin (variant B). *Z. Dt. Ges. Geowiss.* 169, 203–224.
- Geyer, G., Hautmann, M., Hagdorn, H., Ockert, W., Streng, M., 2005. Well-preserved mollusks from the Lower Keuper (Ladinian) of Hohenlohe (Southwest Germany). *Paläontol. Z.* 79, 429–460.
- Gile, L.H., Peterson, F.F., Grossman, R.B., 1966. Morphological and genetic sequences of carbonate accumulation in desert soils. *Soil Sci.* 101 (5), 347–360.
- Green, A.E., Schultz, J.J., 2017. An examination of the transition of fracture characteristics in long bones from fresh to dry in central Florida: evaluating the timing of injury. *J. Forensic Sci.* 62, 282–291.
- Hagdorn, H., 1980. Saurierreste aus dem Lettenkeuper im Landkreis Schwäbisch Hall. *Der Haalquell* 32, 25–27.
- Hagdorn, H., 2015. Wirbellose des Lettenkeupers. In: Hagdorn, H., Schoch, R.R., Schweigert, G. (Eds.), *Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern*, 2015. *Palaeodiversity Sonderband*, pp. 107–140.
- Hagdorn, H., Schoch, R.R., Seegis, D., Werneburg, R., 2015. Wirbeltierlagerstätten im Lettenkeuper. In: Hagdorn, H., Schoch, R.R., Schweigert, G. (Eds.), *Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern*, 2015. *Palaeodiversity Sonderband*, pp. 325–358.
- Hauschke, N., Franz, M., Bachmann, G.H., 2021. *Trias – Aufbruch in das Erdmittelalter 1*. Verlag Dr. Friedrich Pfeil, 353 p.
- Haynes, G., 1983. Frequencies of spiral and green-bone fractures on ungulate limb bones in modern surface assemblages. *Am. Antiq.* 48, 102–114.
- Hopson, J., Sues, H.D., 2006. A traversodontid cynodont from the Middle Triassic (Ladinian) of Baden-Württemberg. *Paläontol. Z.* 80, 124–129.
- Kraus, M.J., 1999. Paleosols in clastic sedimentary rocks: their geologic applications. *Earth Sci. Rev.* 47 (1), 41–70.
- Lasemi, Y., Jahani, D., Amin-Rasouli, H., Lasemi, Z., 2012. Ancient carbonate tidalites. In: Davis, Jr., R.A., Dalrymple, R.W. (Eds.), *Principles of Tidal Sedimentology*. Springer, pp. 567–607.
- Liu, H., Qiu, Z., Zou, C., Fu, J., Zhang, W., Tao, H., Li, S., Zhou, S., Wang, L., Chen, Z.-Q., 2021. Environmental changes in the Middle Triassic lacustrine basin (Ordos, North China): implication for biotic recovery of freshwater ecosystem following the Permian–Triassic mass extinction. *Glob. Planet. Chang.* 204, 103559.
- Lucas, S.G., 2017. Permian tetrapod extinction events. *Earth Sci. Rev.* 170, 31–60.
- Lucas, S.G., 2021. Nonmarine mass extinctions. *Paleontol. Res.* 25, 329–344.
- Machette, M.N., 1985. Calcic soils of the southwestern United States. *Geol. Soc. Am. Spec. Pap.* 203, 1–22.
- Mack, G.H., James, W.C., Monger, H.C., 1993. Classification of paleosols. *Geol. Soc. Am. Bull.* 105 (2), 129–136.

- Marriott, S., Wright, V., 1993. Palaeosols as indicators of geomorphic stability in two Old Red Sandstone alluvial suites, South Wales. *J. Geol. Soc.* 150 (6), 1109–1120.
- Mujal, E., Schoch, R.R., 2020. Middle Triassic (Ladinian) amphibian tracks from the lower Keuper succession of southern Germany: implications for temnospondyl locomotion and track preservation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 543, 109625.
- Mujal, E., Foth, C., Maxwell, E.E., Seegis, D., Schoch, R.R., 2022. Feeding habits of the Middle Triassic pseudosuchian *Batrachotomus kupferzellensis* from Germany and palaeoecological implications for archosaurs. *Palaeontology* 65, e12597.
- Mujal, E., Sues, H.-D., Moreno, R., Schaeffer, J., Sobral, G., Chakravorti, S., Spiekman, S. N.F., Schoch, R.R., 2025. Triassic terrestrial tetrapod faunas of the central European Basin, their stratigraphical distribution, and their palaeoenvironments. *Earth Sci. Rev.* 264, 105085.
- Nitsch, E., 2005. Paläoböden im süddeutschen Keuper (Exkursion E am 31. März 2005). *Jber. Mitt. Oberrhein. Geol. Ver., N.F.* 87, 135–176.
- Nitsch, E., 2015. Fazies und Ablagerungsräume. In: Hagdorn, H., Schoch, R.R., Schweigert, G. (Eds.), *Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern*, 2015. *Palaeodiversity Sonderband*, pp. 285–324.
- Orr, T.J., Roberts, E.M., 2024. A review and field guide for the standardized description and sampling of paleosols. *Earth Sci. Rev.* 253, 104788.
- Paul, J., 2021. Klima der Trias im Germanischen Becken. In: Hauschke, N., Franz, M., Bachmann, G.H. (Eds.), *Trias – Aufbruch in das Erdmittelalter 1*. Verlag Dr. Friedrich Pfeil, pp. 152–157.
- Pawlak, W., Rozwalak, P., Sulej, T., 2022. Triassic fish faunas from Miedary (Upper Silesia, Poland) and their implications for understanding paleosalinity. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 590, 110860.
- Pöppelreiter, M., 1998. Controls on epeiric successions exemplified with the mixed siliciclastic–carbonate lower Keuper (Ladinian, German Basin). *Tübinger Geowiss. Arb. A* 51, 1–126.
- Pöppelreiter, M., Aigner, T., 2003. Unconventional pattern of reservoir facies distribution in epeiric successions: lessons from an outcrop analog (Lower Keuper, Germany). *AAPG Bull.* 87 (1), 39–70.
- Pöppelreiter, M., Aigner, T., 2008. High-resolution sequence stratigraphy, facies patterns and controls in a mixed epeiric shelf: implications for reservoir prediction (Lower Keuper, Triassic, German Basin). *Geol. Assoc. Can. Spec. Pap.* 48, 283–301.
- Scherzer, B.A., Varricchio, D.J., 2010. Taphonomy of a juvenile lambeosaurine bonebed from the Two Medicine Formation (Campanian) of Montana, United States. *Palaos* 25, 780–795.
- Schoch, R.R., 2006. A complete trematosaurid amphibian from the Middle Triassic of Germany. *J. Vertebr. Paleontol.* 26, 29–43.
- Schoch, R.R., 2015a. Amphibien und chroniosuchier. In: Hagdorn, H., Schoch, R.R., Schweigert, G. (Eds.), *Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern*, 2015. *Palaeodiversity Sonderband*, pp. 203–230.
- Schoch, R.R., 2015b. Reptilien des Lettenkeupers. In: Hagdorn, H., Schoch, R.R., Schweigert, G. (Eds.), *Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern*, 2015. *Palaeodiversity Sonderband*, pp. 231–264.
- Schoch, R.R., Mujal, E., 2022. Ontogeny and adult osteology of the Middle Triassic temnospondyl *Trematolestes hagdorni*. *N. Jb. Geol. Paläont. (Abh.)* 306, 265–286.
- Schoch, R.R., Seegis, D., 2016. A Middle Triassic palaeontological gold mine: the vertebrate deposits of Vellberg (Germany). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 459, 249–267.
- Schoch, R.R., Ullmann, F., Rozynek, B., Ziegler, R., Seegis, D., Sues, H.-D., 2018. Tetrapod diversity and palaeoecology in the German Middle Triassic (Lower Keuper) documented by tooth morphotypes. *Palaeobiodiver. Palaeoenviron.* 98, 615–638.
- Schoch, R.R., Seegis, D., Mujal, E., 2022. The Middle Triassic vertebrate deposits of Kupferzell (Germany): palaeoenvironmental evolution of complex ecosystems. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 603, 111181.
- Schoch, R.R., Witzmann, F., Moreno, R., Werneburg, R., Mujal, E., 2024. Growing giants: ontogeny and life history of the temnospondyl *Mastodonsaurus giganteus* from the Middle Triassic of Germany. *Fossil Rec.* 27, 401–422.
- Schoch, R.R., Gastou, S., Steyer, J.-S., Mujal, E., Moreno, R., Witzmann, F., 2025. Morphology and ontogeny of the plagiosaurid temnospondyl *Plagiosternum granulolum* from the Middle Triassic of Germany. *PalZ.* <https://doi.org/10.1007/s12542-025-00748-7>.
- Schreiber, B.C., Tucker, M.E., Till, R., 1986. Arid shorelines and evaporites. In: Reading, H.G. (Ed.), *Sedimentary Environments and Facies*. Blackwell Scientific Publications, pp. 189–228.
- Seilacher, A., Reif, W.-E., Westphal, F., 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philos. Trans. R. Soc. B* 311, 5–23.
- Soil Survey Staff, 2014. *Keys to Soil Taxonomy*. United States Department of Agriculture, Natural Resources Conservation Service, 372 pp.
- Sues, H.-D., Fraser, N.C., 2010. *Triassic Life on Land: The Great Transition*. Columbia Univ. Press, New York.
- Sues, H.-D., Schoch, R.R., Sobral, G., Irmis, R.B., 2020. A new archosauriform reptile with distinctive teeth from the Middle Triassic (Ladinian) of Germany. *J. Vertebr. Paleontol.* 40 (1), e1764968.
- Tabor, N.J., Montañez, I.P., Scotese, C.R., Poulsen, C.J., Mack, G.H., 2008. Paleosol archives of environmental and climatic history in paleotropical Western Euramerica during the latest Pennsylvanian through early Permian. In: Fielding, C.R., Frank, T. D., Isbell, J.L. (Eds.), *Resolving the Late Paleozoic Ice Age in Time and Space*, vol. 441. Geological Society of America Special Paper, pp. 291–304.
- Ullrichs, M., 1982. Zur Stratigraphie und Fossilführung des Lettenkeupers (Ob. Trias) bei Schwäbisch Hall (Baden-Württemberg). *Jber. Mitt. Oberrhein. Geol. Ver.* 64, 213–224.
- Vajda, V., McLoughlin, S., Mays, C., Frank, T.D., Fielding, C.R., Tevyaw, A., Lehsten, V., Bocking, M., Nicoll, R.S., 2020. End-Permian (252 Mya) deforestation, wildfires and flooding—an ancient biotic crisis with lessons for the present. *Earth Planet. Sci. Lett.* 529, 115875.
- Warth, M., 1982. Vorkommen von Spirorbis (Annelida, Polychaeta) im Lettenkeuper (Unterkeuper, Obere Trias) von Nordwürttemberg. *Jh. Ges. Naturkunde Württemberg* 137, 87–98.
- Witzmann, F., Schoch, R.R., 2013. Reconstruction of cranial and hyobranchial muscles in the Triassic temnospondyl *Gerrothorax* provides evidence for akinetic suction feeding. *J. Morphol.* 274, 525–542.
- Witzmann, F., Schoch, R.R., 2026. Postcranial morphology and ontogeny of the Middle Triassic plagiosaurid temnospondyl *Gerrothorax pulcherrimus* and the increased body-flattening of bottom-dwelling plagiosaurs. *Zool. J. Linnean Soc.* 206 (1), zlafl95.
- Zhao, X., Zheng, D., Xie, G., Jenkyns, H.C., Guan, C., Fang, Y., He, J., Yuan, X., Xue, N., Wang, H., Li, S., Jarzembowski, E.A., Zhang, H., Wang, B., 2020. Recovery of lacustrine ecosystems after the end-Permian mass extinction. *Geology* 48, 609–613.
- Ziegler, R., Schoch, R.R., 2015. Synapsiden (Säugerähnliche) im Lettenkeuper. In: Hagdorn, H., Schoch, R.R., Schweigert, G. (Eds.), *Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern*, 2015. *Palaeodiversity Sonderband*, pp. 265–266.