The Middle Triassic vertebrate deposits of Kupferzell (Germany): palaeoenvironmental evolution of complex ecosystems

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Abstract

In 1977, within three months of excavation, a 500 m spanning road-cut near Kupferzell (southern Germany) produced a total of ~30,000 vertebrate remains from the Middle Triassic Lower Keuper. The bulk of the material stems from two temnospondyl amphibians, *Gerrothorax pulcherrimus* (~70%) and *Mastodonsaurus giganteus* (~30%), with the pseudosuchian archosaur *Batrachotomus kupferzellensis* ranging first among the other remains. Analyses of data collected during excavation, supplemented by new fieldwork, provide rich information on the sedimentary setting as well as the development of the fauna and their ecosystems. The sequence consists of: basal coaly mudstones (K1), massive siltstones (K2), green siliciclastic mudstones (K3), yellow to pale brown marlstones (K4), and yellow massive dolostones (K5). The deposits comprise a succession of similar water bodies that were emplaced on a lacustrine to floodplain setting in which carbonate muds dominated. Two main lake systems, with intermittent/periodical marine influence, as well as relatively stark periods of drought, harboured complex vertebrate ecosystems. These were dominated by a relatively high diversity of fishes and temnospondyl amphibians with a lesser, but notable, presence of archosaurs, forming the top predators of the trophic web. The sequence records alternating periods of flooding and desiccation, shaping a relatively complex environmental setting that was likely prone to the presence of life, eventually

becoming an exceptional fossil lagerstätte. Kupferzell, together with nearby contemporaneous localities, represent relatively diverse and complex ecosystems (including several top predators) that allow understanding the evolution and palaeoecology of Middle Triassic vertebrate communities, including the groups that diversified during the Mesozoic era.

Key words

Keuper, sedimentology, taphonomy, fossil lagerstätte, lacustrine, palaeoenvironmental evolution

1. Introduction

Middle Triassic vertebrate communities may form the key to our understanding of how modern biotic communities evolved. In recent years, our knowledge of the early stages of the Mesozoic has notably increased, especially because of a better understanding and sampling of localities of Early Triassic age (Romano et al., 2020). However, the terrestrial fossil record from the earliest part of the Triassic is still incomplete. An impoverishment of ecosystems has been hypothesised on the basis of harsh environmental conditions after the Permian–Triassic biotic crisis (Chen and Benton, 2012; Sun et al., 2012, Irmis and Whiteside, 2012). However, the magnitude of this mass extinction on land remains still unresolved and questioned (see Lucas, 2017, 2021 for discussion). The Middle Triassic fossil record is notably richer than that of the Early Triassic, showing that the so-called modern tetrapod groups already radiated were dominant in the ecosystems, with lepidosauromorphs, archosauriforms and pseudosuchians experiencing major diversifications, while temnospondyl amphibians were still abundant (e.g., Sues and Fraser, 2010; Schoch and Seegis, 2016). Nevertheless, even if the Middle Triassic ecosystems are better known than those of the Early Triassic, the temporal and geographic origin and/or diversification of some groups (which by the Late Triassic were globally distributed) remain still unclear. In order to overcome this lack of knowledge and potential biases in fossil preservation, integrative studies combining stratigraphical, sedimentological and palaeontological

analyses (i.e., leading to the identification of taphonomic pathways and palaeoecological features) are basic.

In this regard, the mixed terrestrial-shallow marine Lower Keuper facies from southwestern Germany are particularly informative for the understanding of Middle Triassic continental ecosystems and the identification of potential biases in the preservation of vertebrates. In this region, a range of fossil lagerstätten are known for their abundance of fossils and quality of preservation (Wild, 1980; Hagdorn et al., 2015; Schoch and Seegis, 2016; Schoch et al., 2018; Mujal and Schoch, 2020; Mujal et al., 2022). Among these, the Kupferzell locality was the first to be discovered and also yielded the largest quantity of vertebrate fossils collected in a single period. This locality was exploited in an emergency excavation during the construction of a highway in spring, 1977 and yielded a total of ~30,000 bones including numerous excellently preserved skulls and partial skeletons (Wild, 1978a, 1978b, 1979, 1980).

In this work, we describe and analyse in detail the stratigraphic and sedimentary framework of this locality that was first briefly characterised by Urlichs (1982). We focus on elucidating the palaeoenvironmental evolution of these rich and diverse vertebrate deposits. Despite a large number of publications dealing with the tetrapod fauna at Kupferzell (Gower, 1999; Schoch, 1999; Hellrung, 2003; Gower and Schoch, 2009; Schoch and Sues, 2014; Hagdorn et al., 2015; Schoch et al., 2018; Hinz et al., 2020; Mujal et al., 2022), no comprehensive sedimentological and detailed taphonomic analyses were hitherto available.

Here we intend to fill this gap by focusing on the rich data of this important fossil vertebrate lagerstätte. The objectives of the present work are to (1) describe the sedimentary and taphonomic features of the Kupferzell locality, (2) reconstruct the depositional history of the fossiliferous beds, and (3) compare the findings with those on the coeval and equally rich locality at Vellberg-Eschenau (Schoch and Seegis, 2016). The present work aims to contribute to a deeper understanding of the Middle Triassic terrestrial (lacustrine)-coastal ecosystems and their significance at the dawn of the Mesozoic.

2. Geological setting

The Kupferzell excavation site encompassed a 500 m long E–W strip along the federal highway (Autobahn) A6, located between Heilbronn and Nürnberg in southern Germany (Fig. 1). The fossiliferous horizons were exposed only during the road works, which lasted from March to the first days of June, 1977 (Wild, 1978a, 1978b). The Lower Keuper (Lettenkeuper, Erfurt Formation; Middle Triassic, late Ladinian, Longobardian) crops out over vast areas of the Hohenlohe plain in northern Württemberg (Fig. 1A). In the region of the Kupferzell (north) and Untermünkheim (south) municipalities, the upper part of the Erfurt Formation is regularly exposed in road cuts and during house building (Fig. 1B).

The succession was deposited in the Central European Basin (CEB; Etzold and Schweizer, 2005), which had intermittent connections to the Tethys Sea during the Triassic. In the study area, the 20–25 m spanning Lower Keuper (Erfurt Formation) overlies the 50–100 m thick Upper Muschelkalk (Warburg Formation; late Anisian–early Ladinian), a massive carbonate unit that formed in a shallow epicontinental sea (e.g., Franz et al., 2013, 2015; Hagdorn et al., 2021). The subsequent deposition of the Lower Keuper (late Ladinian) occurred within the framework of a restricted connection of the CEB with the Tethys (Pöppelreiter and Aigner, 2003, 2008). In N-NE direction, the succession is composed of more terrigenous deposits, whereas towards S-SW (including the study area) the unit consists of a mixed, alternating carbonate-siliciclastic succession (Fig. 1A) on an epicontinental platform (Brunner and Bruder, 1977; Brunner, 1980; Pöppelreiter and Aigner, 2003, 2008; Beutler et al., 1999; Franz et al., 2013; Nitsch, 2015). The Lower Keuper is overlain by the Middle Keuper (Grabfeld Formation; Carnian), which contains thick deposits of gypsum and fine-grained reddish siliciclastic deposits (e.g., Franz et al., 2014). Thus, from the Upper Muschelkalk to the Middle Keuper, transgressive-regressive sequences are recorded (Pöppelreiter and Aigner, 2003, 2008; Franz et al., 2013), and the Lower Keuper generally represents a transition from marine to terrestrial environments.

3. Methods

The first vertebrate fossils were found by the private collector Johann Wegele who informed Rupert Wild (Staatliches Museum für Naturkunde Stuttgart, SMNS),

who then set up a large-scale excavation in the course of the construction of the federal highway A6. The fossils were collected during the salvage campaign from March 14 to June 3, 1977 by a crew of the SMNS, supported by a number of volunteers, including engaged private collectors. All the recovered fossils stem from the Untere Graue Mergel (UGM, Lower Grey Marls) unit within the upper half of the Lower Keuper (Figs. 1A, 2). After removing the overlying, hard dolostone bed (the Anoplophora-Dolomite unit) with hydraulic shovels, the fossiliferous marlstones and mudstones were dug off by hand using picks and scrapers, and the vertebrate fossils were recovered using standard palaeontological procedures, including both mechanical and acid preparation (Wild, 1978a, 1978b, 1979). A total of 1000 m^2 were excavated. Preparation was carried out in the course of the following years at the SMNS lab facilities. Many of these fossils have now been prepared, but a large number of "common" specimens still awaits preparation, mostly single bones of *Gerrothorax* and *Mastodonsaurus*. Great quantities of fossiliferous marlstones and mudstones were screen-washed in the laboratory for microfossils, and the residues were hand-picked and sorted by a range of volunteers over 20 years. As many microvertebrate remains contain diagenetically generated cracks, screen washing usually produces more or less fragmented remains.

A second, smaller outcrop of the Lower Keuper was accessible for a short time in July 1983, about 1200 m east of the Kupferzell Autobahn (highway) site. Here, a trench for a gas pipeline was excavated, exposing yellow-brown marlstones rich in fish remains, probably correlating with the upper, yellow-brown unit K4 (see sections 4 and 6 below) at the Kupferzell site. This site is informally known as "Gasleitung Kupferzell" (Fig. 1B). Screen washing and subsequent picking of the residues from this site produced many well-preserved microvertebrate remains, mostly of fishes, but also including numerous tiny tetrapod bones and teeth.

At the excavation site, stratigraphic sections encompassing the whole outcropping portions of the Lower Keuper were measured by Urlichs (1982). Herein, these sections are reviewed and updated (Fig. 2). In the present work, we have extensively reviewed the available sedimentological samples, including large blocks embedding still unprepared fossils that allowed us to examine sedimentological features and reconstruct the stratigraphic succession of the most fossiliferous layers in

the main excavation sites (North- and South-side in Figs. 1B, 2). In order to provide a context of the Kupferzell lagerstätte within the Lower Keuper, we mainly follow the methods of Schoch and Seegis (2016). In the present work, each unit (a total of five) is identified by a number, running from base to top, and preceded with a "K" (referring to Kupferzell) (see also nomenclature of the layers for stratigraphically equivalent localities in Schoch and Seegis, 2016). This nomenclature has been correlated with the previous descriptions by Wild (1980) and Urlichs (1982), as well as with unpublished notes taken during the excavation.

In order to complement the facies descriptions, we have carried out a microfacies analysis by examining thin sections under a petrographic microscope Leica DM750P, with a camera Leica ICC50 W incorporated to photograph the samples (using the software LAS EZ v.3.4.0). Thin sections have been prepared at the SMNS lab facilities for the present study, following standard procedures for their production, with a thickness of ~25–30 μm. The thin sections include all the layers of the lagerstätte units (K3, K4) from different areas of the excavated site, as well as from the underlying unit (K2).

With the reconstruction of the stratigraphic profile in detail (layer by layer), including also lateral changes, the succession of facies and microfacies has been restored. Similarly, the distribution and relative abundance of lithological components, tetrapod remains and other fossils within the stratigraphic succession have been elucidated (Figs. 3, 4). In some cases, the layers in which bones were recovered were annotated during the excavations. In the cases where this was not done, we have examined the matrix remains around and within the bones, as well as the colour of the bones, and compared these features with those from which the layer was already known, allowing us to precisely (re-) locate the fossils within the stratigraphic succession.

The tetrapod bones from Kupferzell stored in the SMNS collections, as well as some from the Muschelkalkmuseum (MHI, Ingelfingen) were examined in detail in order to identify taphonomic features. We have primarily followed the methods and classification by Behrensmeyer (1978) and Haynes (1983) for the preservation stages and fractures of bones, respectively. Further references are included in the corresponding descriptions and interpretations.

Regarding the estimated proportions of the different taxa, the context in which the excavation took place, under much pressure due to the road construction, has to be considered. Approximately, remains of *Gerrothorax* represent around 70% of the finds, with those of *Mastodonsaurus* being somewhat less than 30%, while all other taxa are proportionally much less frequent (Wild, 1980). It is of course difficult to decide in retrospect how to count such amounts. Firstly, around only a quarter of all finds have been prepared and secondly, prior to the preparation, specific research was focused on skulls, mandibles and shoulder girdle bones, while smaller and postcranial elements had lower priority and are still awaiting preparation. Therefore, a recording of the prepared pieces may only reproduce a potentially biased image. In addition, it is also possible that smaller bones were not collected in the appropriate frequency during the excavation because the team was under enormous time pressure. It was inevitable that the careful recovery of the valuable skulls was in the foreground, and last but not least, surrounding bones may be sacrificed when large blocks protected by plaster jackets are prepared for extraction, which is inevitable even with the most modern excavation techniques. Overall, however, even after recounting the prepared and unprepared finds for *Gerrothorax* and *Mastodonsaurus*, a ratio of 2:1 is confirmed. It is surprising how rare other tetrapods and vertebrates are, because the ratio is different at all other well-known sites, as further discussed in the present work.

4. Stratigraphy, sedimentary facies and fossil content

The fossil-rich (mass accumulation) sequence is restricted to the upper part of the Untere Graue Mergel (UGM), immediately below the base of the Anoplophora-Dolomite (Figs. 1–4), forming the focus of the present work. This stratigraphic position has produced similar fossil lagerstätten in various localities within a range of 30 km, such as Kupferzell-Bauersbach, Vellberg-Eschenau, Ummenhofen, Ilshofen, Wolpertshausen and Crailsheim-Neidenfels (Urlichs, 1982; Hagdorn et al., 2015; Schoch and Seegis, 2016; Schoch et al., 2018).

The fossiliferous sequence from the upper portion of the UGM at Kupferzell was first described by Wild (1978a, 1978b, 1979, 1980) and Urlichs (1982). Here we provide a new and detailed description for all the units (each composed by either one

or multiple layers, see below) within the uppermost UGM succession together with new palaeoenvironmental interpretations. The features (e.g., thickness, lithology, colouration, sedimentary structures, and fossil contents) of each layer are mainly based on those from the main excavation sites (North- and South-sides in Figs. 1, 2), although they are further complemented with information from other sections nearby. Interestingly, some of these units present lateral facies changes (Urlichs, 1982), which are discussed in section 6 below.

The analysed sequence includes the following units, from base to top: (1) dark coaly mudstones with green mudstones in the top (K1: 70 cm); (2) brown to greenish-grey siltstones with red nodules (K2: 10–20 cm); (3) green mudstones with an erosive base and abundant mud cracks (K3: 10–25 cm); (4) yellow marlstones with erosive base (K4a: 5–10 cm) followed by light brown marlstones with calcitic crusts (K4b: 5–15 cm) and yellow marlstones with carbonate fossiliferous concretions (K4c: 20 cm); (5) massive yellow dolostone (K5: 20 cm). Units K1 to K4 correspond to the top of the UGM, whereas unit K5 forms the base of the Anoplophora-Dolomite (Figs. 2, 3). Units K3 and K4 constitute the main portion of the fossil lagerstätte (Figs. 3, 4).

4.1. Dark coal-bearing and green mudstones (K1: 70 cm)

The stratigraphic sequence of the Kupferzell fossil lagerstätte starts with a black-grey, coal-bearing clayey mudstones that contains small, broken bones, fish scales and teeth (Urlichs, 1982). The Lower Keuper coals have been identified as lignites (Nitsch, 2015). Coal seams embedded in mudstones and siltstones are known from many Lower Keuper localities of northern Württemberg (southern Germany) and are mostly found in the upper third of the UGM (Schoch and Seegis, 2016), but also in the Sandige Pflanzenschiefer, the unit of the underlying sequence (Quenstedt, 1880; Brunner, 1973, 1977; Urlichs, 1982; Weber, 1992; Pöppelreiter, 1999; Hagdorn et al., 2015; EM and RRS pers. obs.). In the vicinity of the Kupferzell excavation site, a thick coal-bearing mudstone unit was reported by Urlichs (1982) both west and east of the excavation area, being poorly exposed in the excavation site itself (Fig. 2). The lignite in the Lower Keuper originated either from autochthonous hygrophilic plants, as evidenced by horizons with abundant fossil roots (rhizocretions), or from plant

material that was washed in from the mainland and the shore region. In the latter case, the coal would thus be formed by the accumulation of allochthonous material. Conceivably, the short-term ingression of a shallow sea in the Kupferzell area might have prompted the presence of hygrophilic plants, while the hinterland was significantly drier (Nitsch, 2015). This is suggested by spores and pollen from such plant groups (Urlichs, 1982). Rivers and smaller streams probably transported plant remains into lagoons and restricted/protected areas at the sea shore. Elsewhere in these carbonaceous layers there are skulls and skeletal remains of mastodonsaurids, trematosaurids and plagiosaurids (e.g., in the Gaildorf locality, see Hagdorn et al., 2015), suggesting that these temnospondyl amphibians did not live far away from these settings. At Herdtlingshagen, 3 km east of the Kupferzell site (Figs. 1B, 2), Urlichs (1982) found a rich bivalve fauna (*Bakevellia*, *Myophoria*, *Unionites*) and brachiopods (*Coenothyris*) within the lateral equivalent of K1, accompanied by characeans, fish scales, and temnospondyl bones. The identified bivalves and brachiopods indicate a marine to brackish water settings (see Geyer et al., 2005), whereas characeans indicate more freshwater conditions (Urlichs, 1982). Therefore, as a whole, the unit K1 represents a mixture of environments, suggesting frequent transgression-regression episodes on the sea level.

4.2. Brown siltstones (K2: 10–20 cm)

The coal-bearing unit K1 is followed by 10–20 cm thick, hard, brown to greenish-grey siltstones. They contain dark red stains, reddish ironstone nodules, iron-impregnated root tubules, and horizontally orientated claystone flasers. This unit (K2) has been observed in a radius of at least 2.5 km. The siltstones are highly resistant to weathering and therefore much easier to find in fields than the unconsolidated mudstones and marlstones that embed them.

The thin section of this unit shows that the siltstones are mostly composed of small-sized sub-rounded to rounded quartz grains, all of them having similar size (Fig. 5A-C). The matrix is composed of claystones, mostly formed by tiny (often unidentifiable) minerals. Some phyllosilicate crystals of micaceous minerals (likely muscovite) with a size similar to that of the quartz grains are present. Quartz grains

(maximum size ~0.1 mm) represent around 40% of the components, whereas large mica crystals represent around 5%, or even less. The greenish colouration is given by subangular, equidimensional green clasts of chlorite that represent 5-10% of the components. No gradation or preferential orientation of any component is observed within the thin section. A distinctive feature is the presence of reddish opaque halos (Fig. 5A-C), generally oval-shaped and horizontally elongated, though sometimes they display irregular shapes and/or are arranged in multiple elongated bands parallel to each other. These reddish structures include quartz grains, which are notably less abundant than within the reddish halos. The oval-shaped halos may form concentric rings, with bands being less reddish in-between darker ones (Fig. 5A). The borders of the halos are either sharp or diffuse. The thickest rings display less quartz grains and are more opaque. Given the concentric, oval shape of most of these reddish structures, they most probably form pedogenetic nodules of ferric composition; i.e., representing the ironstone nodules mentioned by Urlichs (1982). During their growth they absorbed the quartz grains, explaining the reduction in abundance of this silicate.

The siltstones contain the bivalve *Myophoria transversa*, which tolerated normal saline waters (Geyer et al., 2005), suggesting that the unit K2 is of marine or lagoonal origin. In addition, its top contains sedimentary structures formed by rapid water flows (Wild, 1980). At the excavation site, the siltstones had an undulating upper surface (Wild, 1980; Urlichs, 1982; Fig. 2), suggesting erosional processes after its deposition, with elongated channels identified in some areas. Such gullies are evidence of channels or rapid water flows. Presumably, those were fluvial channels likely generated in the initial phases of a marine regression. As a whole, these siltstones represent the topmost part of a sequence with increasingly more shallow marine deposits that was eventually covered by sediments originated in freshwater conditions. In fact, the uneven relief on top of the siltstones is filled up by the green mudstones of the unit K3 (Urlichs, 1982; Fig. 2). On the other hand, non-marine influence during formation of K2 is indicated by the presence of the ostracod *Darwinula*, a genus that nowadays lives in freshwater or very weak brackish environments (Hagdorn et al., 2015). The siltstones of the unit K2 were present in outcrops to the west and southwest of the excavation, but absent towards the east (Fig. 2). At Wolpertshausen (12 km east of the Kupferzell site), a coquina with coaly flakes,

mass accumulations of bivalves (*Bakevellia*, *Myophoria* and *Pleuromya* at the base, *Unionites* in the top), has been reported by Urlichs (1982) and Hagdorn et al. (2015) in the stratigraphic level of unit K2.

In summary, this unit highlights the marine influence in the area, although it also testifies a regression trend, especially because of the increasing influence of the shore region and the settlement of freshwater settings as indicated by the overlying unit K3, as well as the presence of ferruginous nodules, further suggesting seasonally drained substrates (e.g., Tabor et al., 2008).

4.3. Green mudstones (K3: 10–25 cm)

The siltstones of the unit K2 are overlain by an unconsolidated, green mudstone sequence in which bones, teeth and fish scales are accumulated. This unit spans some 1.5 km E–W (Urlichs, 1982; RRS and DS pers. obs.). It forms the basal part of the Kupferzell fossil lagerstätte *sensu stricto*. In the periphery of the lagerstätte, it forms a rather undifferentiated olive-green mudstone sequence, whereas at the main excavation area two types of facies can be distinguished (Fig. 6).

In the excavated area, unit K3 contained large quantities of vertebrate fossils. Most finds consist of isolated bones that are well preserved and somewhat darker brown than those found in unit K4. Fishes are mostly represented by scales, sometimes accumulated in clusters, but never as articulated skeletons. The tetrapod finds include more than 10 complete skulls of *Mastodonsaurus giganteus* (Jaeger, 1828) that are excellently preserved but mostly somewhat flattened by compaction. They were all embedded with the dorsal side up, with one exception, which forms an unusually three-dimensionally preserved specimen (Schoch, 1999). In addition, at least one giant skeleton of *Mastodonsaurus* was found (SMNS 81310), covered by a calcareous crust, near the top of unit K3 (Wild, 1980), as well as hundreds of single bones from all parts of the skeleton, some of which containing bite traces (Mujal et al., 2022). The bulk of the material is formed by isolated elements of the plagiosaurid *Gerrothorax pulcherrimus* (Hellrung, 2003), which also includes a few disarticulated skeletons of that taxon. Notably, even skull elements of *Gerrothorax* were accumulated as single

bones in large quantities, indicating that there was sufficient time for the skulls to decay, despite their firm suturing.

Much rarer are single bones of the temnospondyls *Kupferzellia wildi* Schoch, 1997, *Plagiosuchus pustuliferus* (Fraas, 1896) and *Trematolestes hagdorni* Schoch, 2006, and the chroniosuchian *Bystrowiella schumanni* Witzmann et al., 2008, each of these represented by a few elements only (0.05% of the total hypodigm). Only few single bones of small amniotes were found among the microvertebrate remains, of which small vertebrae of a choristodere-like diapsid (Schoch, 2015) form the only identifiable taxon at present. Scores of tetrapod teeth were also found, mostly from *Mastodonsaurus* and smaller temnospondyls, accompanied by teeth of *Batrachotomus kupferzellensis* Gower, 1999 and a putatively fish-eating archosaur similar to, but not identical with *Jaxtasuchus salomoni* Schoch and Sues, 2014 (see tooth type R5 of Schoch et al., 2018). Notably, *Jaxtasuchus* itself and other reptiles common at Vellberg-Eschenau are absent.

Several disarticulated skeletons (4–5) of *Batrachotomus* were found on top of unit K3, with the upper surface of the bones reaching into the topping layer K4a (Wild, 1980). The yellow, marly sediment of layer K4a can still be seen inside tooth alveoli and unprepared parts of bones. These skeletons were apparently deposited after the formation of K3 and must have remained on the dry surface for a longer time.

The green mudstones are rich in fish remains, which include scales, bones and teeth from 14 fish taxa: the elasmobranchs *Acrodus* cf. *lateralis* Agassiz, 1839, *Hybodus* aff. *keuperianus* (Winkler, 1880), and *Lissodus subhercynicus* Dorka, 2001, the actinopterygians *Saurichthys* sp., a *Gyrolepis*-like palaeonisciform, an indeterminate actinopterygian with perleidid-like dentition, "*Thelodus*" *inflexus* Schmid, 1861, *Dipteronotus* sp., *Serrolepis suevicus* Dames, 1888, a redfieldiiform, a scanilepiform, an actinistian, a new medium-sized dipnoan (formerly identified as "*Ferganoceratodus concinnus*" [Plieninger, 1842]), and the large dipnoan *Ptychoceratodus serratus* (Agassiz, 1838) (see Schultze, 1981). Even though several of these taxa were evidently euryhaline, this whole association is typical for freshwater to oligohaline beds in the Lower Keuper (Böttcher, 2015; see also discussion in Pawlak et al., 2022).

Many tetrapod bones were accumulated in the channel-like depressions on top of unit K2 (Urlichs, 1982). Freshwater ostracods (*Darwinula liassica* [Brodie, 1843]) are much more abundant than euryhaline ostracods (*Pulviella teres* [Seebach, 1857],

383 *Speluncella elegans* Beutler and Gründel, 1963). The units K3 and K4 contain remains of
384 characean algae, whose reproductive organs (oogonia) were deposited in large
385 quantities.

386 Below we describe the two main types of deposits that form unit K3 (Fig. 6).
387 They show remarkable differences in composition (with a micritic or siliciclastic
388 matrix) as well as structure (massive or laminated). Of note, the facies type with non-
389 carbonate matrix and massive aspect (Figs. 5D, 6A-G; section 4.3.1 below) is more
390 common than the type with carbonate matrix and laminated/layered (Fig. 6H-J;
391 section 4.3.2 below). Because the excavation had to proceed under heavy time
392 pressure, detailed stratigraphic and sedimentological data could not be collected,
393 therefore, it is not possible to unravel with confidence the spatial distribution of these
394 two types of facies. The collected blocks encompassing the whole unit K3 show that
395 such unit is either the massive mudstones or the laminated mudstones, and no
396 combination or gradation from one facies to the other has been observed. Therefore, it
397 appears that the laminated mudstones (less abundant than the massive one) were
398 localised in specific areas. The two facies types also present similarities, the most
399 remarkable being the presence of green clasts (chlorite) that give the characteristic
400 green coloration to the unit K3 (Fig. 6).

401

402 *4.3.1. Massive non-carbonate green mudstones*

403 This facies is composed of relatively soft, pale green mudstones (Figs. 5D, E,
404 6A). Their grain size and microscopic composition (Fig. 6B-G) characterizes them as
405 fine, clayey siltstones, though the base is slightly coarser, being even very fine-grained
406 sandstones at some parts (Fig. 6F, G). These deposits were observed infilling the
407 depressions on top of the underlying massive siltstones (K2). This facies of unit K3 has
408 a massive aspect (Figs. 5D, E, 6A) and is pale olive green in fresh condition and light
409 green in the dry state. It splits into cm-thick units that have light brown or beige stains
410 on the (rough) bedding plane (Fig. 7A, B). Occasionally, there appear oval-shaped
411 fragments composed of claystones (i.e., finer-grained) that may correspond to clay
412 chips (Fig. 6A, B). A distinctive feature of this massive mudstone facies is the presence
413 of mud cracks (Fig. 7), described in detail in section 4.3.3 below.

These deposits contain numerous clay flakes of various colours, ranging from pale grey to intense green and light blue, as well as tiny muscovite flakes, the latter being well-visible in the thin sections (Fig. 6B-G). The clayey siltstones of K3 are poor in fossil remains. Fish scales and teeth (light brown) occur regularly only within the mud cracks, which belong the unit K4 (see section 4.3.3 below). When a piece of K3 is submerged in water, it decays into green, sterile clay clasts and the coarser fossiliferous matrix K4. A clear-cut lamination is absent in this facies of unit K3, but muscovite flakes and other clasts are loosely arranged in layers.

Thin sections of this facies of unit K3 (Fig. 6B-G) reveal a similar lithological composition to that of unit K2, but mineralogical proportions are notably different. Quartz grains in are sub-rounded to rounded as in unit K2, but they are generally much less abundant (around 10-15% of the components) and smaller than in unit K2; thus the claystone matrix predominates (Fig. 6B-E). Nevertheless, in localised small portions of the layer, and especially from the base of the unit K3 (Fig. 6F, G), quartz grains are slightly larger and more abundant (~20%), but in any case not as much as in the siltstones of the unit K2. Muscovite crystals (as revealed by their pale coloration and transparency from rock hand samples) are ~5% of the components, as in unit K2. The claystone matrix forms the bulk of the lithological components. Characteristic components of this layer are green, either equidimensional or horizontally elongated clasts of chlorite (Fig. 6B), present throughout the whole layer, giving the characteristic green colour of this unit. At the base of the unit (Fig. 6F, G), the green clasts usually are equidimensional, being mostly subangular to angular grains.

Some reddish, small and irregularly shaped elements similar to but smaller than the nodules from the unit K2 are present within the lower part of the layer (Fig. 6G). Sparse small clast-like fragments composed of relatively large calcite crystals are also present; sometimes these calcite crystals englobe small organic fragments (e.g., bones; Fig. 6B), which may act as nucleus for the formation of calcite (pedogenic) nodules, as observed in hand samples of unit K3. Bone fragments of fishes and tetrapods are relatively sparse and without any preferential orientation, even oblique with respect to the stratification. Ostracods are present, but scarce, being only abundant within the infilling sediment of the mud cracks within unit K3 described in section 4.3.3 below.

446 *4.3.2. Layered green mudstones with carbonate matrix*

447 The facies composed of laminated/layered mudstones with a carbonate matrix
448 of unit K3 (Fig. 6H-J) has a much higher microfossil content than the massive
449 mudstones described above. The layers (0.5–1 cm-thick) are usually defined by
450 changes in the grain size (as observed in the thin sections, see below), and sometimes
451 are relatively poorly defined, though still distinguishable with appropriate lighting.
452 The general thickness of the whole deposits with these features is 2 to 3 cm.
453 Microscopic composition and grain size characterise this unit as fine, marly siltstones.
454 These rocks decay rapidly when put in water, and fresh breaks are covered with
455 yellow, carbonaceous dust.

456 These carbonate mudstones contain thin-walled ostracods, dominated by the
457 freshwater taxon *Darwinula liassica*. The high concentration of vertebrate remains in
458 this matrix is either due to accumulation over long time, sorting of elements by water
459 flows, or both. The general scarcity of sedimentary structures produced by water flows
460 (only some clusters of quartz grains likely accumulated due to transport have been
461 observed) may favour the hypothesis of accumulation over a relatively long period of
462 time. Further components are charophyte oogonia, fish scales, bone fragments, clay
463 peloids, and minute pieces of coal. It was reported (Urlichs and Wild, pers. comm.
464 2020) that most large tetrapod bones and all skulls and skeletons were found in the
465 upper few centimetres of K3, which probably represents this facies of unit K3. Thus,
466 since layer K4a is erosive in some parts, the lower abundance of this facies with respect
467 to the massive mudstones described in section 4.3.1 above could be due to erosional
468 processes.

469 The thin sections of this laminated/layered facies (Fig. 6I, J) is characterised by
470 a micritic (carbonate mud) matrix. Quartz grains are sub-rounded and present a
471 heterogeneous distribution. In some parts they represent around 5% of the
472 components, whereas in some others they are accumulated, being ~50% (or even more)
473 of the components. In these accumulations, quartz grains define horizontal layers or
474 laminae (Fig. 6I, J). Of note, quartz grains are larger in the parts of the layer where they
475 are less abundant. Within the carbonate matrix, there seem to be sinuous,
476 interconnected lines defining the stratification (Fig. 6I). Bony remains are present, but
477 not very abundant; they are mostly elongated and parallel to the stratification (Fig. 6J).

Fish scales are numerous. Sparse, but very well identifiable, elongated fragments of intense green colour that are parallel to the stratification are also present.

4.3.3. Mud cracks in unit K3

The massive non-carbonate facies of unit K3 (see section 4.3.1 above) displays a network of mud cracks (Fig. 7) with two size classes: large cracks up to 2 cm wide (Fig. 7A), and innumerable small, closely-spaced, 1–5 mm wide cracks (Fig. 7B). These have remarkably smooth walls, possibly indicating repeated flooding events. They penetrate the whole unit, and are filled with the coarser marly sediment of the layer K4a that is rich in ostracod shells (Fig. 7C-E). Also, the top surface of the greenish unit K3 displays a relatively low relief, with shallow depressed areas, that can be of up to a few centimetres of height. This relief is filled up by deposits of layer K4a, with the contact boundary with the underlying greenish unit K3 being neatly defined (Fig. 5D, E).

The large cracks are up to 2 cm wide and make up polygons in T-junction (see Goehring et al., 2010) with a diameter of about 15–30 cm (Fig. 7A). Subordinated to these large cracks, the small ones build a dense network (Fig. 7B). Observation of mud cracks in present-day ponds (Fig. 8) allows inferring how those observed in unit K3 could have formed. Figure 8 shows Recent desiccation cracks that were flooded after their generation. In an early stage of their opening, large polygons with T-junction are formed, with subordinate, much smaller and narrower cracks covering large parts of the polygons and being either straight or sinuous (Fig. 8A). The initial stages of their infilling (Fig. 8B, C) show how the small, subordinate cracks are rapidly filled with sediment, while the larger ones remain well visible, though with (apparently) smoothed edges, thus actually also being filled with sediment. In later stages (Fig. 8D), the largest mud cracks are still visible, even when the surface is covered with coarser sediments and a new genesis of small cracks may be formed. In this sense, this shows how mud cracks can be preserved over time even if the substrate is flooded (i.e., rehydrated) again and another (eco-) system is developed on this new subaquatic setting (Fig. 8E-G). This would have been the case between the deposition of units K3 and K4, both formed in subaquatic settings and with a period of desiccation in between, as discussed in section 6 below. In addition, the T-junction indicates that mud

cracks did not undergo many processes or periods of hydration-desiccation (Goehring et al., 2010; Goehring, 2013), hence suggesting a prolonged drought period.

The thin-wall mud cracks are also visible in the thin sections (Fig. 7C-E). They are characterised by vertical to oblique thin lines of darker carbonate sediment (that of layer K4a), often with horizontal (lateral) ramifications. Towards the top of the layer, the small mud cracks become more abundant, being closer to each other. The carbonate infilling the cracks is micritic, and yields ostracods with the shells aligned to the walls of the cracks, which are conspicuously abundant. In fact, the sediment that infilled the cracks can be considered an ostracod packstone, also containing large quantities of minute fish scales and teeth.

As a whole, the network of the desiccation cracks resembles patterns known from palustrine deposits (Freytet and Plaziat, 1982; Freytet and Verrecchia, 2002; Alonso-Zarza and Wright, 2010), with numerous, closely-spaced cracks of different sizes and with curved walls (cf. Fig. 8). Although desiccation crack-like structures, such as syneresis cracks, can also develop under water preferably with increased salt content, these are much smaller and have a significantly different shape (Pratt, 1998), not consistent with the structures identified in Kupferzell. Instead, cracks of this size suggest that the water body completely dried out. In this sense, they could have been generated either during a prolonged desiccation period or by a rapid drying in a particularly hot climate (see further discussion in section 6 below).

Apart from the mud cracks, the infilling pattern of the unit K3 on the eroded, channelized siltstones of the unit K2 may also indicate (longer) periods of desiccation of the lake (Alonso-Zarza and Wright, 2010). Similarly, the preservation of *Gerrothorax* skeletons also suggests long periods of decay of the carcasses, in line with long-term subaerial exposure. Scavenging of the carcasses, even if direct evidence (e.g., bite traces) have not been reported on this taxon, cannot be discarded for the disarticulation and destruction of remains, especially considering the evidence of scavenging found from this locality (Mujal et al., 2022; see also section 5.4 below). Of note, the laminated, carbonate mudstones, which likely formed under a water flow, do not display desiccation cracks. Therefore, the sediments composing this facies possibly did not undergo long times of subaerial exposure, possibly indicating the existence of more

perennial pools or ponds within a generally desiccation period and pointing to a patchy landscape (see sections 5, 6 and 7 below).

4.4. Yellow and brown dolomitic marlstones (K4a–c)

The upper part of the fossiliferous sequence in the Kupferzell lagerstätte encompasses pale-coloured, yellow to brown marlstones (Figs. 5D, E, 9-11). Unlike the underlying green mudstones, they were only present in the 500 m strip of the excavation area, and their thickness and composition were subject to substantial lateral change. Whereas the thickness of K4 is greater in the western part (but its end is not exposed), it grades into a drift line towards the east, which contains fossil wood and heavily reworked tetrapod bones. Whereas unit K3 is a relatively monotonous stratigraphic succession (facies changes likely only occur laterally, see section 4.3 above), unit K4 can be stratigraphically divided into three well-differentiated sub-units, from base to top: K4a, K4b, K4c.

4.4.1. Pale yellow marlstones (K4a: 5–10 cm)

The lower layer within the unit K4 consists of micritic, soft marlstones to dolostones. They contain peloids/rounded clasts that are composed of siltstones, fine-grained sandstones, and green claystones (Fig. 9).

This layer is composed of micritic calcite and is extremely rich in ostracods with the long axis of the shells aligned in parallel to the stratification (Fig. 9B). Charophytes are also relatively abundant, though not as much as the ostracods. Possibly, dissolved and fragmented parts of these elements build part of the fine, muddy carbonate matrix of this layer. Sub-rounded to rounded quartz grains represent the 2-5% of the components of layer K4a, being markedly less abundant than in unit K3. Bone fragments are more abundant than in unit K3, sometimes with sparry calcite covering them at least partially (Fig. 9C). Round clasts or peloids composed of siltstones, very fine-grained sandstones and claystones are present within the whole layer (Fig. 9D), but they are more abundant and larger in the lowermost 2 cm of the layer (Fig. 9A). These clasts correspond to eroded fragments from the underlying unit K3. The layer also shows a heterogeneous distribution of components and relative abundance: in

some parts relatively irregular seams of dark carbonate (micritic) matrix are present within a lighter carbonate matrix with more clasts and quartz grains (Fig. 9E). These seams are roughly parallel to the bedding plain, and may reflect the channelized structures observed in hand sample (Fig. 5D, E). In the upper part of the layer, coprolites are also identified. Notably, below a relatively large coprolite there appears to be a "precipitation shadow", with the sedimentary matrix being coarser, i.e., the calcite crystals/fragments are larger than in the rest of the layer (Fig. 9F). In fact, in this localised area below the coprolite, the matrix is more similar to that of the lowermost part of the layer, with a coarser aspect. All in all, this whole layer was formed under a water flow, as suggested by the disarticulated and oriented ostracod shells, the presence of rounded clasts eroded from the unit K3, and the sinuous, channel-like structures observed in the preserved sample including the whole K3-K4 sequence (Fig. 5D, E). Nonetheless, the deposition of layer K4a also underwent periods of carbonate precipitation, likely during stagnation of waters and the development (growth) of characeans, which may had built meadows (see section 6.2 below).

This unit yielded abundant and well-preserved ostracods (as observed in the thin sections; Fig. 9), oogonia of charophytes, isolated fish remains (mostly scales), small bone fragments, and larger tetrapod bones, including skulls and teeth. Some of the best-preserved skulls of *Mastodonsaurus* and a few skeletons of *Gerrothorax* were found in this horizon. Pseudosuchians and other terrestrial reptiles are mostly represented by their teeth, and there are very few isolated bones from the temnospondyls *Trematolestes* and *Plagiosuchus*. Even if less abundant, the tetrapods from the unit K4 are still somewhat better preserved than those of unit K3, and most *Gerrothorax* skeletons are articulated. This suggests lower water energy (which may be in agreement with the lower abundance of quartz with respect to unit K3) and limited or no exposure to reworking and weathering. Several skeletons of the plagiosaurid *Gerrothorax* are preserved with osteoderms in natural articulation.

4.4.2. Light brown marlstones (K4b: 5–15 cm)

Layer K4b consists of pale brown carbonate mudstones with a generally massive aspect (though a rough lamination or layering is observed in the examined

605 rock samples) and with darker round stains (Fig. 10A). Quartz represents <1% of the
606 components, only a few well-rounded grains are observed. Ostracods are present, but
607 they are much less abundant than in layer K4a. Their calcitic shells are irregularly
608 distributed. In some parts of the thin sections, ostracod shells are concentrated in
609 clusters, infilling oblique and sinuous to vertical irregular forms together with a
610 coarser carbonate matrix (Fig. 10B-F). These structures are also richer in quartz, being
611 slightly more abundant (2-5%) within this coarser matrix. The structures differ in
612 shape from the mud cracks observed within unit K3, being less penetrative and
613 relatively wider, with no lateral branching. Their walls have a relatively smooth shape
614 with no signs of cracking (Fig. 10B, C) as observed in mud cracks of K3, and they are
615 generally more oblique with respect to stratification. Ostracod shells within these
616 structures are oriented following the shape of the structure (Fig. 10C), indicating that
617 they were precipitated in them likely due to a water flow. As described in section 4.4.3
618 below, the sediment infilling these structures is more similar to that of layer K4c. All
619 in all, such structures most likely correspond to burrows, although some of them
620 outline more complex sinuous forms (Fig. 10B) that may not fit with this (tentative)
621 interpretation. If these structures were burrows, they could indicate periods of no
622 sedimentation and/or subaerial exposure, which may be in line with the erosive
623 nature of the subsequent layer K4c (see below). Charophytes and bone fragments are
624 sparse (Fig. 10D, E). A bivalve shell preserving its microstructure has also been
625 observed, suggesting favourable preservation conditions; therefore, the scarcity of
626 fossil of this layer could point to a reduced presence of biota.
627 Generally, layer K4b resembles the unit E7 from Vellberg-Eschenau (i.e., the
628 Anoplophora-Dolomite unit; see Schoch and Seegis, 2016). The top of this layer is a
629 sharp, erosive surface, with the overlying deposit being much coarser and richer in
630 quartz and bone fragments characteristic of layer K4c (Fig. 10F).
631
632 *4.4.3. Yellow marlstones with dolomitic concretions (K4c: 20 cm)*
633
634 In fresh state, this horizon of marlstones was reportedly yellow at its base and
635 brownish at the top (Wild, pers. comm. 2020). Layer K4c (Fig. 11) is somewhat similar
636 to layer K4a, but here ostracods are much less abundant, though still present (Fig. 11A).

Generally, the layer displays somewhat sinuous lamination, defined by slightly darker lines or seams of micritic sediment (Fig. 11A, B). This denotes that this layer was probably deposited under a water flow that partially eroded the previous layer (K4b; which is in sharp contact, Fig. 10F), possibly after a period of no sedimentation or desiccation (see section 6 below).

In the thin sections, quartz grains represent the ~10-15%, they are sub-rounded to rounded. Small oval-shaped clasts of siliciclastic composition are present (Fig. 11B-E). They are reminiscent to those observed in layer K4a, but much smaller and less abundant. Charophytes seem slightly more abundant than in layer K4a. Bone fragments preserved in 3D but also partially eroded are present (Fig. 11D, E). These elements, together with the fragmented and abraded (due to erosion) ostracod shells and charophytes (mostly oogonia) (Fig. 11F) as well as the seams and quartz grains indicate water flow and transportation.

Large calcareous concretions, some of them containing vertebrate fossils, were common in this layer (Urlichs, 1982). Teeth and skull bones of the large lungfish *Ptychoceratodus* were found in this layer. The deposition of the brownish layer indicates increased water cover, i.e., a renewed rise in groundwater. The tetrapod fossils from this horizon have an orange-brown colour and are more heavily crushed than those of layer K4a, except for those embedded in hard carbonate concretions. A partially disarticulated skeleton of *Gerrothorax* stems from this horizon (SMNS 84786), with an intact skull and hemimandibles located at a distance of 50 cm from the gently dissolved postcranium. Disarticulated skulls of *Mastodonsaurus* probably form the most common large finds in this layer, but there is not a single complete skull. Instead, several excellent, fully articulated skulls of *Kupferzellia*, including the type specimen, were embedded in this layer. Finally, a partial skeleton of the sauropterygian *Nothosaurus* (SMNS 80266), in which most of the bones preserve bite traces, was found in a concretion. In summary, this layer contains the best preserved specimens from the Kupferzell lagerstätte.

4.5. Anoplophora-Dolomite (K5)

The unit K5 consists of pale yellow, micritic, massive dolostones. It is lithologically very similar to horizon E7a at Vellberg-Eschenau (Schoch and Seegis, 2016). Yet unlike the latter deposit, where this unit produced abundant remains of *Batrachotomus* (see Schoch and Seegis, 2016), it appears to have been less fossiliferous at Kupferzell. Admittedly, the focus of attention during excavation was laid on the fossil-rich units K3 and K4. Based on observations of Rupert Wild and Max Urlichs, Schoch (1999) reported sparse remains from *Nothosaurus*, *Neusticosaurus* and *Tanystropheus* from this layer. All these taxa represent purportedly marine fauna, and thus may suggest an environmental change with more marine influence for the layer K5 with respect from the underlying layers. Noteworthy, as aforementioned, *Nothosaurus* remains have been found in the yellow-brown layer K4c, likely suggestive of a progressive trend towards increasing marine influence.

5. Vertebrate taphonomy

Similar to the situation in Vellberg-Eschenau (Schoch and Seegis, 2016), bones were often found accumulated in clusters (Wild, 1978a). They rarely formed relics of single individuals (Schoch, 1999; Hellrung, 2003; Gower and Schoch, 2009) but rather agglomerates of different specimens or even taxa. Articulated skeletons were almost absent, except for the heavily armoured temnospondyl *Gerrothorax pulcherrimus*.

This somewhat irregular distribution of fossils indicates a patchy environment (possibly a sabkha setting; see section 6 below) or a landscape composed of discrete water bodies, most likely small lakes spread on a vast epicontinental platform with intermittent connections to the sea. The patchiness of the original environment is also suggested by the lateral changes of facies observed by Urlichs (1982) throughout the region that houses the Kupferzell lagerstätte. Such environmental interpretation is further supported by the sedimentological differences, mainly within the most fossiliferous layers, between Kupferzell and Vellberg-Eschenau (see further discussion in section 7 below). Another important agent on bone modification and distribution is the presence of predators and scavengers roaming the area (e.g., Hungerbühler, 1998; Augustin et al., 2020; Drumheller et al., 2020), which was the case in the Lower Keuper,

where bite traces are relatively frequent on the bones of large tetrapods (Mujal et al., 2022).

Herein, we describe and interpret the main taphonomic features on the Lower Keuper bone assemblage (Fig. 12), with a special focus on the units K3 and K4, the most fossiliferous ones (Fig. 4). Generally, these features are not exclusive from a specific unit or layer of those studied (K1 to K5), but if they are, it is specified. The taphonomic features identified allow better defining the palaeoenvironmental settings of Kupferzell, thus they are also discussed here where appropriate.

5.1. Preservation and articulation

The vertebrate bones and teeth from Kupferzell are exceptionally well preserved (Fig. 12). This is for the most part due to their diagenetic impregnation with sparitic calcite, giving the bones stability and facilitating their preparation from the surrounding marly or clayey matrix (Fig. 12A). Yet, sometimes flakes of hard mineral crusts are attached to the bone surface that are difficult to remove mechanically or chemically. This is especially the case from the bones in layer K4c, many of them being at least partially embedded in a calcite crust (Fig. 12B). In this sense, most of the bones did not undergo a strong weathering process. Regarding the degree of weathering (see definitions in Behrensmeyer, 1978; Fiorillo, 1988; Ryan et al., 2001), most of the bones from Kupferzell are in the stage 1, with the bone surface showing incipient cracking that does not penetrate the bone and/or initial flaking, and with most portions of the surface being pristine (Fig. 12C-G). According to Wild (1980), weathering is mostly observed on bones of *Bystrowiella* (erroneously identified as a therapsid by Wild, 1980).

Some dentigerous bones of *Batrachotomus* show more extensive flaking and missing parts at their edges (Fig. 12E), which appears to indicate weathering stage 2. Teeth of *Batrachotomus* sometimes show partial loss of enamel or are longitudinally split, also pointing to weathering (Behrensmeyer, 1978). A similar network of cracking, with a "mosaic"-like pattern (see Behrensmeyer, 1978: fig. 3), has also been observed in some *Mastodonsaurus* bones (Fig. 12F). Such cracking also suggests more extensive weathering, and could be linked to a long time of exposure under during drought

periods; in fact, the bone in Fig. 12F preserves matrix of both units K3 and K4, between which an extensive network of desiccation cracks occurs.

Most of the bones are almost completely free from matrix, although some still preserve part of it due to their fragility or because they correspond to associated and/or articulated bones of a single specimen (Fig. 12A, B). Also, it is particularly notable that most of the bones, even though isolated or disarticulated, are complete. When parts of the bones are missing, it is usually because they were bitten/eaten (Mujal et al., 2022) or parts of them were not recovered (or lost) during the salvage excavation campaign. Only a few specimens seem to have been broken due to transport, which is suggested by their weathered aspect that occurred prior to fossilization.

Teeth of the pseudosuchian archosaur *Batrachotomus kupferzellensis* are very abundant (Gower, 1999; Schoch et al., 2018; Mujal et al., 2022), particularly from the unit K4, as evidenced by the yellow-brown colour of the sedimentary matrix remains (Fig. 12H-K). The overwhelming majority of them consists of tooth crowns with hollow bases, a feature that is due to resorption of the root during life (tooth replacement; Njau and Blumenshine, 2006), which demonstrates that these teeth were shed by living animals (Gower, 1999; Hungerbühler, 1998; Frey and Monninger, 2010). Only a few teeth with intact roots were found together with jaw bones (Gower, 1999; Mujal et al., 2022), suggesting that they had fallen out before the skeletal remains were covered with sediment. Thus, the carcasses of *Batrachotomus* underwent some degrees of decaying processes before their final burying (e.g., Fig. 12E). Similarly, skull bones of *Batrachotomus* were found disarticulated but adjacent to each other (slightly scattered), clearly corresponding to the same individuals (Gower, 1999; Gower and Schoch, 2009). According to Voorhies (1969), skulls are not easily transported by currents, in contrast to other elements such as ribs. This indicates that adjacent elements correspond to the same individual, further denoting decaying processes, as suggested for *Gerrothorax* specimens (see section 4.3 above). Considering the relatively good preservation of the majority of *Batrachotomus* bones, showing none or few cracking and/or flaking of the surfaces (Fig. 12E, L, M; see section 5.2 below), together with the fact that they are disarticulated (indicating that they were buried after the disappearance of most, if not

all, the soft tissues), their preservation is considered between stages 2 and 3 in the classification of Behrensmeyer (1978).

Bones of *Mastodonsaurus* likely underwent similar processes to those of *Batrachotomus*. Some elements are also found in clusters (Schoch, 1999) but they are completely disarticulated, indicating that the corpses underwent a certain period of exposition before the final burial. In addition, the relatively high frequency of bite traces (Mujal et al., 2022) indicates bone modification by scavengers or predators, which can be important agents in the resulting bone assemblages (e.g., Hungerbühler, 1998; Njau and Blumenschine, 2006; Haynes et al., 2020). Most of the finds consist of single, sometimes primarily incomplete bones. The few bone clusters identified (Schoch, 1999) consist of groups of vertebrae or sets of shoulder girdle bones belonging to single individuals of *Mastodonsaurus*. A giant skeleton of *Mastodonsaurus* (SMNS 81310), with a skull of some 120 cm length and a 145 cm long mandible was recovered from the green unit K3 (Schoch, 1999). This find includes a complete sequence of trunk vertebrae and ribs, some of which are covered with bite traces (Mujal et al., 2022).

Most temnospondyl skulls were found disarticulated from the mandibles, but are often preserved in close proximity. The only exception is a *Mastodonsaurus* specimen (SMNS 54677) where the jaws are still firmly articulated with the skull (Schoch, 1999: fig. 8); this was found in the top of unit K4a. Isolated skull bones of temnospondyls were abundant, and at least one totally dissociated skull of *Mastodonsaurus* (SMNS 80878) was recovered. As in the case of *Batrachotomus*, this is in agreement with a decay process of corpses, indicative of an exposure period of time (Behrensmeyer, 1978). Similarly, a totally disarticulated, yet almost complete skull roof of the large dipnoan *Ptychoceratodus serratus* was recovered from the yellow-brown unit K4c. The single bones were found far from another (Schultze, 1981), suggesting some kind of transport.

Only the yellow-brown layer K4c, forming the top of the Untere Graue Mergel (UGM) just below the Anoplophora-Dolomite (unit K5), produced a few articulated or semi-articulated skeletons of the plagiosaur *Gerrothorax* (e.g., Hellrung, 2003; Fig. 12B). Probably, the dermal armour plates of this temnospondyl prevented a higher degree of disarticulation as occurred in the other taxa. Also, the fact that partial and disarticulated skeletons of *Gerrothorax* have been found in other layers (e.g., Fig. 12A),

suggesting transport (see section 5.3 below), possibly shows that layer K4c formed under energy conditions lower than other layers, even though water currents are inferred for layer K4c (see section 4.4.3 above).

Another particular specimen is a disarticulated, fragmentary skeleton of the aquatic sauropterygian reptile *Nothosaurus* (SMNS 80266), usually found in marine deposits. It was found in the layer K4c, with most of the bones embedded in hard calcite concretions, sometimes with some fish scales as well. The skeleton preserves only bones of the posterior part of the trunk: vertebrae, pelvic girdle, and ribs (dorsal, sacral, and one fragmentary caudal). The presence of bite traces on several bones (mostly on ribs) of this partial skeleton indicate that scavengers were a further taphonomic agent of this specimen, which was possibly wash out from a marine/coastal setting (see section 6 below).

Except for rare patches of a few ganoid scales in mud crack fillings of the green unit K3, no associated fish remains were found. Obviously, no articulated skeletons of fishes are preserved at the Kupferzell site, because at least some accumulations of ganoid scales would have been recognised during the excavation, if present.

In summary, there are some major differences between units K3 and K4. In K3, vertebrate fossils are more abundant, but usually disarticulated and isolated, though including also some bone clusters suggesting the presence of water flows that accumulated different elements (Fig. 12A). In K4, fossils are less abundant, but their preservation is better in terms of bone weathering and articulation (Fig. 12B). This indicates a decrease of water energy from K3 to K4, with a clear interruption in the development of the settings between the two units, marked by a likely prolonged period of desiccation; the chronology of events is discussed in section 6 below. Besides this, bones from these two units change in colour, with those of K3 (Fig. 12A, C) being darker than those of K4 (Fig. 12B, D). A remarkable feature of the bones (and more generally clasts, including also coprolites) from unit K4 is that they have a precipitation rim of sparry calcite. This rim may not surround the entire bone or clast, but it is at least present in the stratigraphically lower surface of each element (e.g., Fig. 9F). This indicates a precipitation phase during diagenesis, with a washing of the carbonate of the matrix that (re-) precipitated around the clasts and in the likely diagenetic cracks

824 generated within the layer. This crust would have also prompted a better preservation
825 of the elements in unit K4 (Fig. 12B, G).
826
827 *5.2. Fracturing*
828
829 All the fracture types defined by Haynes (1983) (see also Ryan et al., 2001;
830 Haynes et al., 2021) have been identified in the Kupferzell bones. These include:
831 longitudinal, spiral (green) and transverse/compression fractures (Fig. 12C, D, G, L,
832 M). These fractures are generally considered green, i.e., they occurred (relatively) soon
833 after the death of the individuals. The peculiar mosaic-like pattern of fracturing of
834 uncertain origin identified by Behrensmeyer (1978) is also present in some Kupferzell
835 bones (Fig. 12F). Some other fractures from indeterminate causes, as well as fractures
836 due to collecting and specimen manipulation, have also been identified.
837 A particular type of fracture morphology and arrangement is that observed on
838 the ends of limb bones and on rib heads, i.e., in elongated bones. These fractures are
839 semi-circular, with the concave side facing towards the outer part of the bone; they
840 often occur in multiple sets, being aligned and thus giving a stepped aspect to the
841 fractured portion (Fig. 12C, D, L). Such fractures were probably generated by a
842 differential compactness of the bone, being higher in the midshaft (i.e., more dense)
843 than in the ends (see Hugi and Scheyer, 2012). This is indeed the case for the
844 *Batrachotomus* teeth still preserving at least part of their roots, which are hollow and
845 thus collapse easily.
846 Spiral and oblique fractures, also showing right angle offsets, all interpreted as
847 green fractures (Haynes, 1983; Haynes et al., 2021; see also Britt et al., 2009) (Fig. 12G,
848 M), are commonly found on ribs of *Mastodonsaurus*, as well as on *Nothosaurus*, and in
849 some bones of *Batrachotomus*. Other fractures may have also occurred due to
850 trampling, with bones broken in different parts, but with fractured surfaces clearly not
851 being recent (i.e., surfaces are slightly smoothed, and sedimentary matrix and/or
852 calcite crystals are usually covering them). Other fractures that probably occurred due
853 to trampling are sets of radial fractures that widen towards the central point (Fig. 12F),
854 suggesting that pressure was applied on the widest point or area of the fracture. These

radiating structures are especially well seen in some platy bones, i.e., those with relatively large surfaces.

Other relatively common fractures, well observed in some plagiosaur (e.g., *Gerrothorax*) skeletons, seem to have been produced due to desiccation. This is in agreement with the palaeoenvironmental setting indicated by the presence of relatively abundant desiccation cracks on the layers, especially penetrating on the unit K3 and generated before the deposition of the unit K4. Similarly, this also supports the long period of decay of carcasses interpreted for *Gerrothorax* (see section 4.3 above).

Some of the thin interclaviculae of *Gerrothorax* were embedded in an incomplete state, often with their anterior part missing, the breakage planes being almost planar and straight to slightly curved. In *Plagiosuchus*, some fragments of platy shoulder girdle bones were found widely separated from each other but could be fitted together again. The fragments differ partly in colour, suggesting that the bones were broken prior to their burial in the sediment, and then being again reworked and hydraulically concentrated together with fresh bones in the lagerstätte.

Teeth of *Batrachotomus* are sometimes transversely dissected by calcite-filled cracks, up to eight parallel, sometimes bifurcating cracks having been observed (Fig. 12H, I). Interestingly, fractures are generally neat: even if the broken parts of the teeth are separated some millimetres by the infilling sediment, they fit well together. In most cases, fractures are transverse and/or oblique to the tooth long axis (Fig. 12H, I), but some teeth are longitudinally split with the two halves slightly displaced; in all cases they were infilled with sediment and diagenetically cemented with calcite. They could have been generated due to desiccation, though this cannot be confirmed. Some cracked teeth have the broken fragments displaced (slightly scattered or spread, like if they had "exploded") from their original position (Fig. 12J, K), most likely because they were trampled after being shed. In summary, teeth could have been broken due to desiccation, due to trampling or both. In tusks of *Mastodonsaurus*, this phenomenon is much rarer, and there are never more than 2-3 calcite-filled cracks.

5.3. Orientation and sorting

Except for one specimen (SMNS 54675, the most 3D-preserved), all other skulls of *Mastodonsaurus* were found facing with their dorsal side up. Their longitudinal axis was SE-NW-oriented, and the heavy occiput pointed towards the southeast (Urlichs, pers. comm. 2015). As long bones often exhibited also a SE-NW-orientation (Wild, 1978a), these observations point to alignment of the bones following southeast-bound currents. Together with skulls, other plate-like bones of temnospondyls, such as interclavicles, are especially abundant, also pointing to their enhanced transportability with respect to bones with non-platy morphologies. Some platy bones were found in a more or less vertical position (Wild, 1978) (cf. Fig. 12F), sometimes being broken likely due to compaction. They were possibly washed into mud cracks, as suggested by some vertically orientated small bones that were lying in such cracks during the preparation of fossiliferous sediment blocks.

Evidence of transport is also suggested by the accumulation of some bones of different individuals and taxa in clusters, especially in the unit K3 (Wild, 1980). Some bones, including partial skeletons in this unit (e.g., Fig. 12A) are chaotically oriented, being oblique with respect to stratification. Especially in the case of partial skeletons, represented by clusters of bones of disarticulated skeletons, the orientation of the elements (which are often fragmented but preserving delicate details; i.e., fractures) indicates transport of the skeletons or decaying carcasses in a mud flow (e.g., Britt et al., 2009). The muddy matrix would have protected bones from erosion or abrasion, yet they could have been broken due to impacts with other bones or other hard clasts. Due to transport, some elements would have been lost, and when the mass transport stopped, the bones would have remained in their position, with no preferential orientation (Fig. 12A), in a rather cohesive muddy matrix. Outside of unit K3, the cranial bones of the giant lungfish *Ptychoceratodus* were found scattered in a relatively large area of the yellow and brown layers K4b and K4c (Schultze, 1981).

5.4. Predation/scavenging and bioerosion as taphonomic agents

5.4.1. Predation and scavenging: bite traces

Many bones from the Kupferzell site are covered by bite traces (Mujal et al., 2022). This feature was already mentioned by Wild (1978a, 1978b, 1979, 1980). Schoch

and Seegis (2016) reported bones with bite traces from the equivalent layers of the Vellberg-Eschenau site, and more recently, Mujal et al. (2022) described the whole bite trace assemblage for the UGM, with around 95% of the bitten bones coming from Kupferzell.

At Kupferzell, bite traces have been regularly identified on bones of four tetrapod taxa: *Mastodonsaurus*, *Plagiosuchus*, *Batrachotomus*, and *Nothosaurus* (Mujal et al., 2022). In addition, there is a single evidence of a bite trace on a rib of the chroniosuchid *Bystrowiella*. Although *Gerrothorax* is by far the most abundant tetrapod genus, only a single bone fragment of this temnospondyl contains potential bite traces.

According to Mujal et al. (2022), six main types of bite traces can be distinguished, which include the following ichnotaxa (see Mikuláš et al., 2006; Jacobsen and Bromley, 2009; for taphonomic terminology see Binford, 1981 and D'Amore and Blumenschine, 2009, 2012 for taphonomic terminology; for additional classifications and terms, e.g., dentalites, see Hunt and Lucas, 2021): *Knethichnus parallelum* Jacobsen and Bromley, 2009, corresponding to parallel grooves generated by denticles of ziphodont teeth; *Nihilichnus nihilicus* Mikuláš et al., 2006, round to oval, sometimes bisected, punctures; *Linichnus serratus* Jacobsen and Bromley, 2009, grooves with serrated margin, with a range of linear morphologies, from straight to strongly curved (hook-shaped); *Brutalichnus*, recorded by two clearly differentiated morphotypes, both with roughly serrated margins and reaching cancellous bone (large round- to oval-shaped hole, and V-/triangle-shaped trace at the bone margin); *Machichnus*-like, corresponding to small hacks (punctures plus short grooves) found in dense clusters.

Most of the bite traces are found on bones of *Mastodonsaurus*. The second taxon ranked by the quantity of bitten bones is *Batrachotomus*, while on other taxa bite traces are not frequent. In the case of the partial skeleton of *Nothosaurus* (SMNS 80266, corresponding to a single individual), most of the bones contain bite traces, suggesting a complete exploitation of the carcass, as it is the case of *Mastodonsaurus* (see discussion in Mujal et al., 2022). The overwhelming majority of bite traces can be attributed to *Batrachotomus*, on account of the serrated imprints of ziphodont tooth carinae on the bones (i.e., *Knethichnus parallelum*, and *Linichnus serratus* as well; Mujal et al., 2022). Biting traces on heads of limbs suggest that *Batrachotomus* preyed even on large

Mastodonsaurus specimens (Mujal et al., 2022). In summary, both scavenging and predatory behaviours (as well as cannibalism) can be inferred for *Batrachotomus*.

In addition to scavenging and hunting large temnospondyls, there is also evidence for cannibalistic habits of *Batrachotomus*. This is indicated by the relatively large number of ribs and pelvic girdle bones with *Knethichnus parallelum* and *Linichnus serratus* biting ichnotaxa. Considering the similar biting patterns to those found on bones of *Mastodonsaurus* and the concentration of the traces to the trunk and pelvic regions, the bite traces on bones of *Batrachotomus* indicate scavenging rather than predation (Mujal et al., 2022). The frequency and associations of bite traces referred to *Batrachotomus* are most similar to those produced by extinct and extant crocodyliforms (Njau and Gilbert, 2016), indicating a conserved feeding ecology in the pseudosuchian lineage (Mujal et al., 2022).

Several bones with bite traces come from in-between the green (K3) and yellow (K4a) layers, indicating that bones remained exposed for a relatively long time after the formation of the green layer (unit K3) and the sedimentation of the yellow one (unit K4), probably during relatively long drought period(s), as the large mud cracks suggest (see section 4 above). This preservation of bones between two layers is also suggestive of trampling, as occurs in Recent bone assemblages (Haynes et al., 2020).

Trampling is not only suggested by some fractured bones (see section 5.2 above), but also by those embedded between layers K3 and K4a (Fig. 12F, N, O). In this case, bones (and some teeth) were partly buried within layer K3, with orientations that would not have occurred under normal sedimentary processes. Their odd positions suggest trampling by tetrapods as most plausible explanation. This hypothesis is based on similar orientations of trampled bones of Recent elephants, some of which being subsequently scavenged by carnivores (Haynes et al., 2020). Some of the Kupferzell bones show similar features and orientations, such as the *Mastodonsaurus* humerus SMNS 81171 (Fig. 12O) and femur SMNS 81169, both containing relatively abundant bite traces produced by *Batrachotomus* (Mujal et al., 2022) and also embedded between units K3 and K4. Additional elements of *Mastodonsaurus* preserve matrix that indicates their embedding between two layers, such as a scapulacoracoid (Fig. 12F) and a fang (Fig. 11N). The fang preserves round holes likely due to chemical weathering whereas the scapulocoracoid contains cracks suggesting bone flaking probably caused by

desiccation (Behrensmeyer, 1978). These bones embedded between two layers indicate long times of exposure. This would explain also the large mud cracks and the change in colour of the sediments, suggesting some sort of chemical change in the local lake environment.

5.4.2. Inferred corrosion by gastric acids

The two most fossiliferous units at Kupferzell (K3 and K4) produced a number of comparatively large vertebrate remains that are heavily worn. Firstly, some lungfish tooth plates (*Ptychoceratodus*) still attached to their (incomplete) jaw bones have lost all of the enamel (Fig. 12P). Compared to complete specimens with their enamel layer intact, the shape of these lungfish tooth plates appears to be altered strangely. Secondly, in a number of temnospondyl vertebrae (including some smaller *Mastodonsaurus* vertebrae, e.g., SMNS 81230, 84160, and uncatalogued specimens) the cortical bone layer is partly or totally missing (Fig. 12Q, R), or the vertebrae are just consisting of rounded chips of the cancellous bone. These features suggest that these lungfish teeth and temnospondyl bones were digested, so that gastric acids would have caused strong chemical corrosion of the phosphatic substance of these elements. It is unclear if the corroded elements were excreted through the digestive tract, encased in coprolites), or if they were orally expelled as regurgitalites (in general, bromalites; see Gordon et al., 2020). At least the dipnoan tooth plates and jaw bones are completely devoid of any traces of coprolite substance, so the latter explanation seems more plausible for them. Similar pellets of fairly complete skeletons have also been recovered from Vellberg-Eschenau (Schoch and Seegis, 2016; Sues et al. 2020). It still remains unclear whether the producers of such bromalites (mostly regurgitalites) were relatively large *Mastodonsaurus*, *Batrachotomus* or both. Since this behaviour has already been described in pseudosuchians (Gordon et al., 2020), being a further evidence of shared habits with crocodylians, at least some of the regurgitalites could have been produced by *Batrachotomus* (see also discussion in Mujal et al., 2022).

Coprolites of all sizes (up to 7 cm large, mostly 0.5–2 cm) were abundant and may contain fish (actinopterygian) scales and even jaws. Most of them are oval-shaped, some have an even more elongated shape; in cross section, they are circular to oval. The largest ones were probably produced by *Mastodonsaurus*. The presence of

coprolites indicates that their producers inhabited (or at least frequently roamed) the area (see also Schoch and Seegis, 2016). Considering the fragmentary nature of the so far few bone and tooth remains found within coprolites, the previously mentioned bones and teeth with signs of corrosion (much larger than the average size of the coprolites) (e.g., Fig. 12O-R) were probably regurgitated.

6. Depositional history

The sedimentological features of the most fossiliferous units of Kupferzell (K3 and K4), together with their palaeontological contents, allow a reconstruction of the depositional history (Fig. 13). We have identified two main phases within the fossiliferous units. It should be noted that these layers are subject to lateral variation over hundreds of metres (Urlichs, 1982). Despite this variation, a general stratigraphic stacking pattern is still recognisable within the Untere Graue Mergel (UGM), and thus correlations are possible (Fig. 2). Therefore, such deposits might reflect basin-scale processes, as it has been identified at the level of the major units composing the Lower Keuper (Erfurt Fm.), at the scale of the Central European Basin (CEB) (e.g., Pöppelreiter and Aigner, 2003, 2008; Franz et al., 2013; Nitsch, 2015).

The Kupferzell units were deposited in a distal floodplain that underwent different episodes of drought and flooding by the sea from the southwest, similar to the depositional history at Vellberg-Eschenau (Schoch and Seegis, 2016). In Kupferzell, two main phases of lacustrine (or lacustrine-like) deposition building up the fossil lagerstätte (units K3 and K4) are identified (Fig. 13). They are preceded by an interval of highly changing environments (from marine to peat lake or swamp) in a generally more open setting (units K1 and K2). After the sedimentation of the fossil-rich units K3 and K4, a more open (marine) setting rich in carbonate (unit K5) was established.

6.1. Rock sequence at the base of the lagerstätte

The base of the studied sequence is consistent with the widespread, typical facies of the Lower Keuper in northern Württemberg, traditionally known as "Lettenkohle" (see also Brunner, 1973; Schoch and Seegis, 2016). The dark coaly

mudstones (K1) were probably deposited in a vast swampy area, covered by a rich hygrophilic vegetation and with intermittent marine or fluvial influence (Nitsch, 2015). The latter prompted inputs of water flows with transportation of plant debris that contributed in the eventual formation of coal. These deposits generally represent a lagoonal-estuarine-lacustrine water system in which tetrapod faunas existed, though not as taxonomically diverse as in units K3 and K4. In most of these deposits, tetrapod remains were not accumulated and are therefore much less abundant than in the lagerstätten localities. Nonetheless, as suggested for freshwater peat swamps associated with salt-marsh estuaries (Behrensmeyer and Hook, 1992), taphonomic biases in the preservation of tetrapods possibly exist for unit K1. Generally, deposits of unit K1 might have formed during a period of increasing accommodation, prompting the accumulation of plant debris (e.g., Pöppelreiter and Aigner, 2003 and references therein). At any rate, they represent a setting with extensive plant growth.

The swampy, densely vegetated environment was succeeded by settings with a stronger marine influence. A relatively abrupt change in the basin, possibly prompted by a rapid marine transgression, is indicated by bivalves that tolerated saline waters (*Myophoria transversa*). At Kupferzell, these are embedded in hard siltstones (K2), which probably correlate with coquinas with the same bivalve faunas in closely located sections (Urlichs, 1982; Hagdorn et al., 2015).

This marine incursion probably did not last long, as the presence of oxidised (reddish) ironstone nodules and freshwater ostracods (*Darwinula*) within unit K2 indicates. In addition, the presence of root traces denotes stabilization of the substrate. Eventually, probably responding to the regression of the sea, the silty deposits of unit K2 were overrun by water flows originating in terrestrial environments that partially eroded them and left the distinctive, N-S oriented channels reported by Wild (1980) and Urlichs (1982).

6.2. Lake Kupferzell K3

The first lake deposit is documented by the basal sequence of green mudstones (K3). The relatively silty facies at Kupferzell-Bauersbach is present in a 2×2 km area, with a 0.5×0.1 km large belt of high bone accumulation in its centre. This is embedded

in a larger occurrence of green mudstones covering some 6×4 km size. To the north and east, the green mudstones grade into grey claystones, indicating a somewhat deeper and calmer depositional environment. The whole setting suggests a water body that was shallower to the west and deeper to the north and east; its further extension remains unclear. A rich fish fauna was found in microfossil samples northeast of the Kupferzell excavation ("Gasleitung" site, Fig. 1B), confirming the same lake fauna for the grey mudstones.

We interpret the green mudstones as littoral facies of a lacustrine system (Fig. 13). The silt, a relic of the sediments that formed unit K2, was probably transported by rivers into the basin, as well as some of the vertebrate bones (e.g., *Bystrowiella*). It contains characeans and ostracods (see Urlichs, 1982) that indicate well-aerated and clear water, probably housing characean meadows, and providing excellent living conditions for diverse fishes and lake bottom-dwelling predators (*Gerrothorax*). The abundance of characeans indicates a water depth of less than 10 m (Cohen and Thouin, 1987). The association of characeans and *Darwinula* suggests oligo- to mesotrophic conditions, probably influenced by the intense plankton-feeding activity of the ostracods.

The dichotomy of facies of unit K3 (massive and non-carbonate *vs.* laminated and carbonate) may be explained by its transition from unit K2: the laminated facies contain much more carbonate than the massive ones, and the quartz grains are also usually larger and more angular in the laminated facies, being accumulated in horizontal bands that define such lamination. This type of facies (which is less abundant than the massive one) may represent episodes of more energetic conditions, reminiscent of those during the deposition of unit K2, within the generally low water flow that characterised the sedimentation of unit K3. The decrease of quartz grain size from base to top in sequences of the massive facies type of unit K3 is also relevant, because this further documents the energy decrease from unit K2 to unit K3. The low content of carbonate in the massive facies would indicate less-aerated waters and thus explaining the lower number of characeans observed in the thin sections. The reddish nodules at the base of the massive facies of unit K3, which are reminiscent to those of unit K2, also denote the transitional nature between the two units.

Freshwater conditions are suggested for K3 by the environmental affinities of the preserved taxa (e.g., dominance of *Darwinula liassica*) and the absence of euhaline bivalves (e.g., *Myophoria*, *Bakevellia*). However, the occurrence of euryhaline ostracods (*Speluncella teres* and others), albeit rarer than the freshwater taxon, suggests that salinity may have fluctuated. It is possible that *Speluncella* was restricted to certain layers, but because of the absence of laminae and the generally low thickness of unit K3, resolution is not fine-scaled enough to test this hypothesis. Environmental fluctuations are further suggested by the microanatomical analysis of bone growth in *Gerrothorax*, and have been interpreted as caused by periodic changes in salinity (Sanchez and Schoch, 2013).

Urlichs (1982) reported that the sediments of unit K3 infilled the channels and gullies on top of the siltstones of the unit K2; we refer to the water flow that produced the gullies as *Event 1* (see Fig. 13 for an overview of events). These must have been caused by water currents flowing in N-S orientation, an observation roughly consistent with the NW-SE orientation of elongated elements reported by Wild (1980). The deposition of unit K3 occurred after substantial erosion of different sediments in the vicinity, because it contains clasts of various composition; these are predominantly composed of claystones, although the presence of quartz grains and reddish nodules (the latter only at the base of the unit) like those from the unit K2 is remarkable, further denoting a transition from units K2 to K3, though with a relatively sharp drop of quartz grains (Fig. 3). Considering the similar composition (but with different proportions of quartz content) between units K2 and K3, the initial deposition of unit K3 was part of *Event 1*, representing its latest phase. Considering the rather sterile sediment in the lower part of K3, the water flow is unlikely to have transported carcasses or single bones of vertebrates in larger quantities – the numerous fossils from the green mudstones stem from the uppermost horizon of K3. The water currents might have been produced by inflowing freshwater from rivers into the local Kupferzell basin, where a freshwater lake (K3) with characeans and ostracods was established (*Event 2*).

The poor carbonate content of the dominant facies of unit K3 suggests that this lake was constantly fed by freshwater influx by a river large enough to produce currents that were able to align long bones and skulls in the putative NW-SE flow

direction. In this regard, deposits of unit K3 most likely correspond to the infilling and eventual plugging of the gullies generated on top of unit K2, thus showing a sequence of energy decrease from K2 to K3. This may also explain why the upper part of K3 is much richer in fossils than the lower part, with a decrease of the water energy throughout the sedimentation of K3, conditions would have been more favourable towards the top of the unit.

Fluctuations of salinity, as suggested by the mixed ostracod fauna and the histological variation of *Gerrothorax* (Sanchez and Schoch, 2013) could stem from eroded brackish sediments in the vicinity or from salt aerosols (Nitsch, 2003). Alternatively, it could simply reflect occasional input from a nearby brackish water body. The latter alternative is supported by the sections to the SW of Kupferzell (Schwäbisch Hall-Hessental, Michelbach an der Bilz, Gaildorf-Schleifrain) in which lagoonal deposits dominate the top of the Untere Graue Mergel sequence. In addition, the region northeast of the Kupferzell area also harboured a lagoon, as preserved in the quarry at Kirchberg an der Jagst.

In a subsequent *Event 3*, a diverse fish fauna was established in Lake K3. This fauna formed a complex trophic web similar to the one known from Vellberg-Eschenau (Schoch and Seegis, 2016). At Kupferzell, it includes three sharks, eight actinopterygians, one actinistian and two lungfishes. The preserved littoral zone was inhabited by two main temnospondyl predators, *Gerrothorax* and *Mastodonsaurus*. The dominance of *Gerrothorax* is noteworthy, as this taxon was widespread and geologically long-lived but usually not preserved with large samples (Schoch and Witzmann, 2011). Its abundance in the K3 fauna indicates excellent living conditions and little competition by other large predators. This heavily armoured bottom dweller was evidently not an able swimmer and therefore bound to habitats with a constant supply of prey, most likely fishes in the size range of polzbergiids (*Serrolepis*, *Dipteronotus*) and redfieldiids. In the recently studied lake deposits at Vellberg (units E5 and E6; Schoch and Seegis, 2016), *Gerrothorax* was rare, either because the preserved environments were less favourable for that taxon or because of competition by a more diverse temnospondyl fauna (*Callistomordax*, *Plagiosuchus*, *Kupferzellia*, *Trematolestes*). *Gerrothorax* and the ostracod *Darwinula*, which was unable to produce aestivating eggs, required a constant water body for their life cycle and thus suggest a perennial lake.

The abundance of high-bodied polzbergiid fishes (*Serrolepis*, *Dipteronotus*) suggests a habitat that was differentiated at a small scale, possibly influenced by characean meadows and a locally structured lake floor.

The abundance of single bones was probably caused by a combination of factors: (1) disarticulation by predators (particularly *Mastodonsaurus* and possibly *Batrachotomus*), (2) water currents (sorting with preference of platy elements) and (3) accumulation over longer time, suggesting low rates of sedimentation.

Lake K3 eventually dried up in the Kupferzell area (*Event 4*), resulting in deep-reaching cracks and a hardened surface, on which numerous skulls and at least one partial, giant skeleton of *Mastodonsaurus* were found, as well as partial skeletons of *Batrachotomus*. Many of these finds still have green mudstones on their lower and yellow marlstones on their upper sides. The richness of skeletal material on this surface probably represents a mass mortality event, which attracted terrestrial predators such as *Batrachotomus* (Wild, 1980). These large predators probably caused the disarticulation of the temnospondyl skeletons as well as the trampling phenomena reported in sections 5.2 and 5.4 above. The deep cracks filled with yellow-brown sediment and abundant ostracods of layer K4a were generated in the depositional phase after the formation of unit K3 (*Event 5*), as also suggested by the compositional change between units K3 and K4, indicating an interruption of sedimentation and the settlement of different environmental or climatic conditions. Subsequent inundations of the mud plain successively covered the bones with a calcareous mud layer and prevented them from getting weathered. Such phases of inundation and drying are indicated by *Batrachotomus* teeth that show many parallel, calcite-cemented cracks (Fig. 11H-K). Conceivably, there were a few cycles of inundation-desiccation, this can be explained by the shape of the mud cracks, which have a T-junction geometry rather than Y-junction (see discussion in: Goehring et al., 2010; Goehring, 2013; compare Figs. 7A, B and 8).

6.3. Lake Kupferzell K4

The K4 sequence formed in a shallow, carbonate-rich lake environment that housed a rich benthos. The ostracod *Darwinula* was abundant, accompanied by the 14

aforementioned fish taxa, essentially the same as in K3. The yellow carbonate mud that filled the desiccation cracks on the topmost surface of K3 is consistent with the subsequently deposited marlstones (Figs. 5D, E, 7). A major difference between units K3 and K4, with the mud cracks separating them and a sharp change in composition (especially regarding the content of carbonate and ostracods, which is much higher in K4) is observed. This marks an environmental change between the two units. We conclude that the depositional regime changed after *Event 4* (a prolonged desiccation period), when a mud richer in carbonate, ostracods and microvertebrates, but equally rich in characeans, was deposited.

The base of the K4a sequence includes stacked, 5–20 cm wide channel-fills that indicate migrating gullies in the early phase of deposition. Such channels might have been caused by water stemming from an inflowing river or small delta (*Event 5*). The sediment contains peloids of green mudstones and siltstones, equivalent to that from unit K3 (Fig. 9A), thus being probably reworked from unit K3 after that lake had dried up. Despite sedimentological differences, the palaeoecology of the lake was apparently very similar to that of K3, with the notable exception that remains of *Gerrothorax* are much rarer, albeit confined to articulated skeletons. This horizon also produced excellent skulls of *Mastodonsaurus*, which often include attached mandibles. Disarticulation of skulls does occur on a much smaller scale compared with that of unit K3. This indicates lower energy conditions in the lake K4 compared to K3, also allowing a much higher concentration of carbonate mud. This is consistent with the lower terrigenous (detritical) input in K4a compared to K3, exemplified by the drop in the abundance of quartz grains from K3 to K4.

The tetrapods were mostly found at the top of the K4a unit, similar to the situation in K3 and the skull-bearing surface of E6c at Vellberg-Eschenau (Schoch and Seegis, 2016). In sum, these observations testify that very local and short-term droughts occurred, producing minor desiccation cracks, and probably locally restricted annihilation of the aquatic fauna. Predation dismembered the skeletons (Mujal et al., 2022) but there was not enough time to disarticulate skulls; these were concealed by the subsequent, fast sedimentation. Environmentally, and considering the similar ecosystems ecology, the K4a setting was probably not much different from the littoral

zone preserved by K3, but with a different supply of sediment, both regarding the source and the rate of supply.

The subsequently deposited layer K4b is slightly lighter, the generally more massive aspect and poor lamination suggests quieter conditions in the deposition. It must have formed under a calmer sedimentation regime than K4a, with equal amount of carbonate but less silt, and likely represents a slightly deeper lake facies. Like K4a, the pale brown mudstones of layer K4b are absent west of the Kupferzell excavation area, but they extend further N–NE, where they grade into darker grey mudstones that are also rich in fish scales.

Finally, the sequence K4c appears to represent the return of a more coastal setting. The increasing frequency of *Darwinula* (Urlichs, pers. comm. 2021) suggests the dominance of freshwater conditions, which agrees with the tetrapod fauna, consisting of *Mastodonsaurus*, *Gerrothorax* and the 3 m long capitosaur *Kupferzellia*. The lack of juvenile *Mastodonsaurus* in layer K4c, which are very common in other lake deposits (Vellberg-Eschenau, Wolpertshausen, Michelbach an der Bilz), is remarkable. Whereas the presence of two large capitosaur predators indicates better living conditions (more abundant or diverse larger prey) than in the preceding lake phases, the occurrence of mostly large adult specimens of *Mastodonsaurus* forms a pattern consistent with ecological character displacement (Schluter and McPhail, 1992), with *Mastodonsaurus* and *Kupferzellia* separating more clearly in size to focus on different prey size. The frequency of *Batrachotomus* teeth and the occurrence of a *Nothosaurus* skeleton with bite traces of *Batrachotomus* (Mujal et al., 2022) are evidence of repeated drying and flooding, probably with water from different sources. The nothosaurid was probably washed in, or immigrated during a short-term connection with a lagoonal water body, possibly the large lagoon preserved in the Schwäbisch Hall-Gaildorf region.

The marlstones of the layers K4a–c are locally more restricted than the unit K3. There is a clear topographic difference between these three layers: whereas layer K4a ended at the eastern margin of the excavation area and graded into a drift line (Urlichs, pers. comm. 2021), its western extension ends somewhere east of the highway bridge south of Bauersbach (where it is definitely absent), giving a range of 600–800 m only. To the north and northeast, layer K4a ends abruptly, but its southern extension

remains unknown. This forms the smallest area among the K4 layers, and possibly represents a locally restricted carbonate mud somewhat remote from the littoral zone. To the west, it is replaced by green mudstones similar to the K3 sequence, which suggests that the littoral lake environment had persisted there for a longer time; following this line of evidence, the littoral zone of Lake K3–4 was probably aligned in the area between Übrigshausen, Westernach and Bauersbach.

The resemblance of the yellow marlstones to the Anoplophora-Dolomite at Vellberg-Eschenau (Schoch and Seegis, 2016) is remarkable. Conceivably, layer K4a formed on a carbonate mudflat that fell dry episodically but was mostly covered by shallow freshwater. Characeans and ostracods were even more abundant than in unit K3, consistent with the higher carbonate content. As the fish and tetrapod faunas from units K3 and K4a are essentially identical, it is highly probable that the two facies formed in neighbouring environments of the same lake basin; the longer persistence of the green mudstone facies west of the Kupferzell lagerstätte agrees with this interpretation. Therefore, even if a stark drought period took place in the excavation area at the end of the deposition of unit K3, some relic water bodies probably persisted.

Finally, temnospondyl bones with marks of low weathering (mostly stage 1) and abundant bite traces produced by ziphodont teeth also suggest that there were repeated phases when parts of the lake floor fell dry, enabling the archosaur *Batrachotomus* to scavenge on amphibian carcasses (Mujal et al., 2022). This scenario is supported by the presence of abundant detached *Batrachotomus* teeth whose pulpa is still filled with yellow-brown marlstones (in several cases also including fish scales). In other fossil assemblages with archosaurs and theropod dinosaurs, similar occurrences of teeth and partially preserved skeletons indicate relatively low-energy environments roamed by scavengers (Hungerbühler, 1998; Augustin et al., 2020).

The abundance of polzbergiid fish (*Dipteronotus*, *Serrolepis*) remains suggests a structured habitat (e.g., charophyte meadows; see also discussion in Zhao et al., 2020 and Liu et al., 2021), because these disk-shaped fishes were adapted to maneuver on a narrow range. In this sense, the setting provided sufficient food supply, possibly consisting of small arthropods. The relatively abundant fragments of very small actinistian bones and the low frequency of bigger ones suggest that the K4-Kupferzell setting was used as a nursery ground by these fishes. Similarly, the abundance of

Gerrothorax remains (up to 80 individuals) indicates a stable population of this plagiosaur (Hellrung, 2003), further denoting a well-established ecosystem in a subaquatic setting.

Nothosaurus, a sauropterygian reptile that inhabited near-coastal settings or even open marine environments (Klein et al., 2016), was present in the layer K4c (Wild, 1980; Hinz et al., 2020). As mentioned by Hinz et al. (2020), this suggests a greater marine influence on the environments at Kupferzell than previously thought. We suggest that during time of deposition of the top sequence of the UGM unit, the Kupferzell area might have been located on the most proximal (inland) zone of a tidal flat, i.e., the supratidal region. In a sabkha setting there are usually long periods of desiccation, and these environments are only flooded by the sea during spring tides (Lasemi et al., 2012). Thus, the environment is similar or equivalent to a lacustrine system as herein discussed for the UGM in Kupferzell. Also, the yellow dolostones composing the Anoplophora-Dolomite (unit K5) display large moulds of gypsum nodules (also found in the Anthrakonitbank, the previous carbonate unit, see Hagdorn et al., 2015; Mujal and Schoch, 2020), and such structures in these facies are characteristic from sabkha settings (Lasemi et al., 2012). This points to a certain degree of salinity in the waters. In this sense, Bachmann (2002) related the precipitation of gypsum within carbonates to a high salinity at the top of the *Lingula*-Dolomit (an upper unit within the Lower Keuper: Fig. 1A). This further indicates a restricted marine environment, which in the case of the topmost part of the UGM and the base of the Anoplophora-Dolomite, would be a sabkha or sabkha-like setting.

The unit K5 marks the end of the depositional history of the Kupferzell lake K4. Due to the presence of marine reptiles (see Schoch, 1999), these carbonates suggest marine conditions, representing a new transgression phase. Nevertheless, the presence of *Unionites brevis* (see Urlichs, 1982), a freshwater to brackish bivalve, indicates that in any case this was a mixed environment, still with terrestrial influence/input. This suggests a slightly different palaeoenvironmental setting than at Vellberg-Eschenau, where the base of these carbonates contains *Mastodonsaurus* and *Batrachotomus*, i.e., a more terrestrialised/continental setting. We interpret the base of the Anoplophora Dolomite in the northern Württemberg region as a very shallow-water, coastal setting, probably not unlike the tidal flats of K4, and possibly in continuity with them. In this

model, some areas were under stronger influence of marine systems (Kupferzell) whereas others remained more protected from the open sea (Vellberg-Eschenau), possibly by some geographical barriers. In fact, the succession at Vellberg-Eschenau shows a transition to more terrestrial conditions from layers E4 to E6 at the top of the UGM (Schoch and Seegis, 2016), denoting fluctuations in the degree of salinity (likely correlated to marine influence) of the environments. Similarly, within and on top of layer E7a (base of the Anoplophora-Dolomite) in Vellberg-Eschenau *Batrachotomus* remains are particularly abundant (Schoch and Seegis, 2016).

7. Palaeoecology and ecosystem evolution

7.1. General features

The profound similarities between the contemporaneous vertebrate faunas of Kupferzell (Fig. 4) and Vellberg-Eschenau (Schoch and Seegis, 2016) and the lithological differences between the main fossiliferous layers prompt a more detailed comparison. Both deposits are interpreted as lacustrine, based on the presence of numerous non-marine taxa. On the other hand, there is some evidence of marine influence in both settings for certain periods (or seasons), as sporadic remains of sauropterygian carcasses (*Nothosaurus*) have been reported from both localities (Schoch and Seegis, 2016; Hinz et al., 2020). We have concluded above that these lakes developed in a sabkha-like setting, located on the most proximal part of a tidal flat that experienced frequent, and probably prolonged, periods of desiccation.

The most fossiliferous layer at Vellberg-Eschenau (E6) is a deposit of dark grey, bedded claystones, very different from the silty and marly, light coloured deposits of Kupferzell (units K3 and K4). Despite these differences, both localities have a very similar faunal range (for comparison, see Schoch and Seegis, 2016). Thus, even though there are lateral changes in facies (see also Urlichs, 1982), the biotic components of the ecosystems were the same. Therefore, despite the existence of different, small-sized depocentres that built up independent lakes (especially in terms of sediment supply), there were no major physical barriers for the biota. In summary, this points to a well-stabilized, structured and diverse ecosystem yielding both aquatic dependant and

terrestrial faunas. Both lagerstätten are characterised by the preponderance of bony fishes and temnospondyls, and the presence of a more terrestrial top predator, represented by the pseudosuchian *Batrachotomus* (see discussion in Mujal et al., 2022), is noteworthy.

The high abundance of plagiosaurid remains in Kupferzell is remarkable, accounting for at least half of the tetrapod specimens. The dorsoventrally flattened *Gerrothorax* lived as a bottom-dweller in subaquatic environments, and its abundance indicates perennial water bodies. In any case, such lakes eventually underwent desiccation, which led to mass mortality events of the plagiosaurids and all the fishes in these ecosystems. The abundance of the large capitosaur *Mastodonsaurus*, which is considered by its sheer size the top predator in these lacustrine ecosystems, is a much more widespread feature shared with the deposits at Vellberg-Eschenau and many other localities in the region (Schoch and Seegis, 2016) as well as in Thuringia (Hagdorn et al., 2015).

These lacustrine faunas sometimes contain taxa from terrestrial environments, such as parareptiles, small diapsids, archosauriforms and pseudosuchian archosaurs (Schoch, 2015). In addition, mud cracks and bone flaking indicate repeated subaerial exposure. Altogether, these features evidence a mixture of material from different environments, similar to the Grenzbonebed which contains faunas from both lacustrine and shallow marine habitats (Hagdorn et al., 2015). It is plausible that a substantial portion of the isolated bones that contribute to the bone clusters and accumulations in unit K3 was transported from the proper habitats of the preserved taxa. Prefossilisation, as indicated by the frequent amount and mode of bone fragmentation, confirms the allochthonous or parautochtonous state of some taxa, adding to the interpretation of a small-scale, patchy setting. However, at Kupferzell, most of the prefossilised bones stem from the same temnospondyl taxa as the skeletons, which suggests that the fragmentary bones were reworked from nearby deposits of the same or a very similar water body.

7.2. Scenario of environmental and ecological evolution

The reported observations can be compiled to create a detailed scenario for the fossiliferous sequence at Kupferzell (Fig. 13). After a long period in which coal-producing swamps had existed on a vast plain in the northern Württemberg region (K1), a minor sea level rise led to a short-term incursion of shallow marine water in the Kupferzell area (K2). Subsequent partial erosion produced m-wide channels on top of the K2 unit, followed by the deposition of silty claystones (K3) of lacustrine origin. The initial phase of this deposition was not particularly favourable for the settlement of ecosystems, as the low number of fossil remains in the first half of unit K3 suggests.

Once fully established, this water body (Lake Kupferzell K3) harboured diverse freshwater fishes and the temnospondyls *Gerrothorax*, *Mastodonsaurus* and *Kupferzellia*. These formed the main predators in the lake, whereas the temnospondyls *Trematolestes* and *Plagiosuchus* probably lived in separate, but nearby water bodies, because their fragmentary bones were occasionally washed into the basin at the Kupferzell site, probably in periods of raised water levels. Remarkably, in Triassic fossil sites elsewhere (e.g., Sulej, 2002; Shishkin and Sulej, 2009; Lucas et al., 2010; Fortuny et al., 2011; Schoch, 2018), bone assemblages (including bone beds) of multiple individuals of a single taxon (with one or two additional taxa) are present. They differ from the condition observed in Kupferzell and other Lower Keuper localities, where multiple temnospondyl taxa coexisted; yet, only two taxa were dominant in Kupferzell (*Gerrothorax* and *Mastodonsaurus*). In this sense, the Lower Keuper lagerstätten (e.g., Hagdorn et al., 2015; Schoch and Seegis, 2016; Schoch et al., 2018) may show that, in localities with lower faunal diversity, potential biases exist. These may be environmental and/or preservational in nature. In fact, this is also the case in the Triassic tetrapod footprint record (De Jaime-Soguero et al., 2021; Klein and Lucas, 2021), with a conspicuous low number of temnospondyl footprints despite those were common components of the Triassic ecosystems as shown by the skeletal record. This is most probably due to an environmental bias against the preservation of temnospondyl ichnites (Mujal and Schoch, 2020).

The chroniosuchian *Bystrowiella* probably dwelled more remote regions of rivers that occasionally washed its heavily worn skeletal remains into the locality. The lake shore was roamed by large archosaurs (*Batrachotomus*) looking for prey and carcasses (Mujal et al., 2022). An ostracod-rich, marly sediment enriched with

vertebrate skeletal elements accumulated at the lake bottom. Periodically, enhanced levels of precipitation led to the increase of rivers, eroding parts of the lake shores and taking large amounts of unconsolidated lake sediments, incorporating vertebrate remains and carcasses in the sedimentary matrix (cf. Fig. 12A). This was the source for the large amount of reworked, prefossilised bones in the unit K3 of the lagerstätte. In one or more such events, water flowed as flash floods to the west where it oozed away on the mudplain, filling up the mud cracks with fossiliferous marl and repeatedly leaving a marly blanket with vertebrate bones and occasional carcasses behind. As shown by the large mud cracks on top of K3 (Fig. 7A), the plain lay dry for a long period marking the end of the depositional cycle of the lake. Individuals of *Batrachotomus* roamed on the remaining dry plain, feeding on carcasses of *Mastodonsaurus* and even conspecifics (Mujal et al., 2022) that had died by catastrophic inundations or by droughts. Of note, as in other Triassic localities (Hungerbühler, 1998; França et al., 2011; Nesbitt et al., 2020), different individuals of pseudosuchians have been found together, suggesting a hypothetical gregarious behaviour in the group (Nesbitt et al., 2020). In fact, considering the direct evidence of interaction in *Batrachotomus* such social behaviour is plausible (Mujal et al., 2022).

The plain was subsequently covered by a perennial freshwater body, here referred to as Lake Kupferzell K4. The conditions apparently became favourable sooner than during the evolution of Lake Kupferzell K3, permitting a faster settlement of freshwater dwellers and the build-up of a lake ecosystem. The lake floor consisted of calcareous marly sediments (layer K4a), and charophyte meadows and ostracods were more abundant than in Lake K3. The fish fauna was somewhat less diverse than that of Lake K3, and *Gerrothorax* was less frequent than *Mastodonsaurus*. Like in Lake K3, the caiman-like capitosaur *Kupferzellia* was also present, suggesting that this new water body was equally rich in nutrients than the former. Sedimentation was fast enough that *Gerrothorax* skeletons could be preserved in articulation or with skeletal elements scattered over a small area only (Hellrung, 2003; Fig. 12B). However, the lack of articulated fish skeletons and absence of sedimentary lamination point to an active organic life at the oxygenated lake bottom.

After the first phase of Lake K4, the basin fell dry and was subsequently filled with flow deposits and partially reworked sediments (horizon K4a). Then, a deeper

water table with calmer energy conditions was established, characterised by carbonate muds and less abundant ostracods and charophytes (horizon K4b). In the final phase of Lake K4, light-brown, finely laminated marlstones (horizon K4c) were deposited, indicating a shallower third and final phase of the lake. In K4c, quartz grains are much more abundant than in K4b, and the presence of lamination suggests increased water currents.

The concentration of skulls of *Mastodonsaurus* and *Kupferzellia* at the top of the K4 sequence suggests a further event of shallowing with an eventual desiccation of the lake with mass mortality among the fishes and temnospondyls. Widespread disarticulation of skeletons was probably caused by water currents. This horizon is similar to the top of E6d at Vellberg-Eschenau in sedimentary features as well as the accumulation of temnospondyl skulls (Schoch and Seegis, 2016). A similar taphonomic sequence has been inferred for other temnospondyl bone assemblages (Lucas et al., 2010).

At Kupferzell, the overlying Anoplophora-Dolomite (K5) were probably deposited on a carbonate mud plain. The facies at Kupferzell is consistent with the lithologically very similar and stratigraphically equivalent unit E7 at the Vellberg-Eschenau site (Schoch and Seegis, 2016). Except for sporadic bone remains (Kupferzell) or rare *Batrachotomus* and *Mastodonsaurus* skeletons (Vellberg-Eschenau), fossils are absent in these coastal dolostones; this environment was probably hostile to most invertebrates, with extremely shallow salty water that frequently dried out completely.

8. Conclusions

Our analysis of the Middle Triassic Kupferzell fossil lagerstätte revealed two successive lakes that harboured similar ecosystems. These were dominated by freshwater fishes and temnospondyl apex predators, with occasional incursions of terrestrial archosaurs in the littoral zone. The larger environment, a carbonate mudplain with coexisting large brackish lagoons (10–20 km) and small freshwater lakes (5–10 km), covered a vast area including the generally similar fossil lagerstätte of Vellberg-Eschenau and others in the vicinity. The lagoons appear to have been

relatively long-lived and stable, whereas the lakes fluctuated on a shorter time scale with repeated periods of partial droughts.

The studied lake systems built on top of more widespread and uniform marine-lagoonal sequences, and probably document a progressing shallowing and eventual closure of the basin. The formation of the small lakes allowed the establishment of rich ecosystems, including aquatic and riparian organisms, and encompassing taxa that tolerated saline waters. The Kupferzell fossil lagerstätte preserves the evolution of two clearly differentiated lakes, separated by an intense drought period. This fits well in a sabkha setting, a proximal supratidal flat with only occasional marine influence.

The exceptional Kupferzell fossil lagerstätte was not only taxonomically diverse, but also rich in taphonomic features, permitting the reconstruction of palaeoecological traits of some taxa (e.g., Mujal et al., 2022). By their richness and quality of preservation, the Kupferzell and Vellberg-Eschenau deposits rank among the best known Middle Triassic vertebrate deposits. The faunal richness in both abundance and diversity of the Lower Keuper suggests that potential environmental and/or preservational biases (rather than impoverished ecosystems) exist in other Triassic localities. Several trophic levels are identified, including different apex predators. They preserve a rich, complex and well-structured ecosystem, despite the frequent occurrence of droughts that often reshaped the environmental settings.

Future work on these Triassic lake deposits may study (1) the wider geographic distribution and topographical diversity of these depositional basins, (2) the ecological diversity and distinctness between lakes, and (3) the evolution of complex ecosystems and trophic webs during the Triassic, in the rise and dominance of the archosaur lineage. Considering its vast outcrop area, the excellent study conditions and the quantity of as yet unstudied fossil lagerstätten, the Central European Basin will continue to provide case studies for these topics.

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Figures

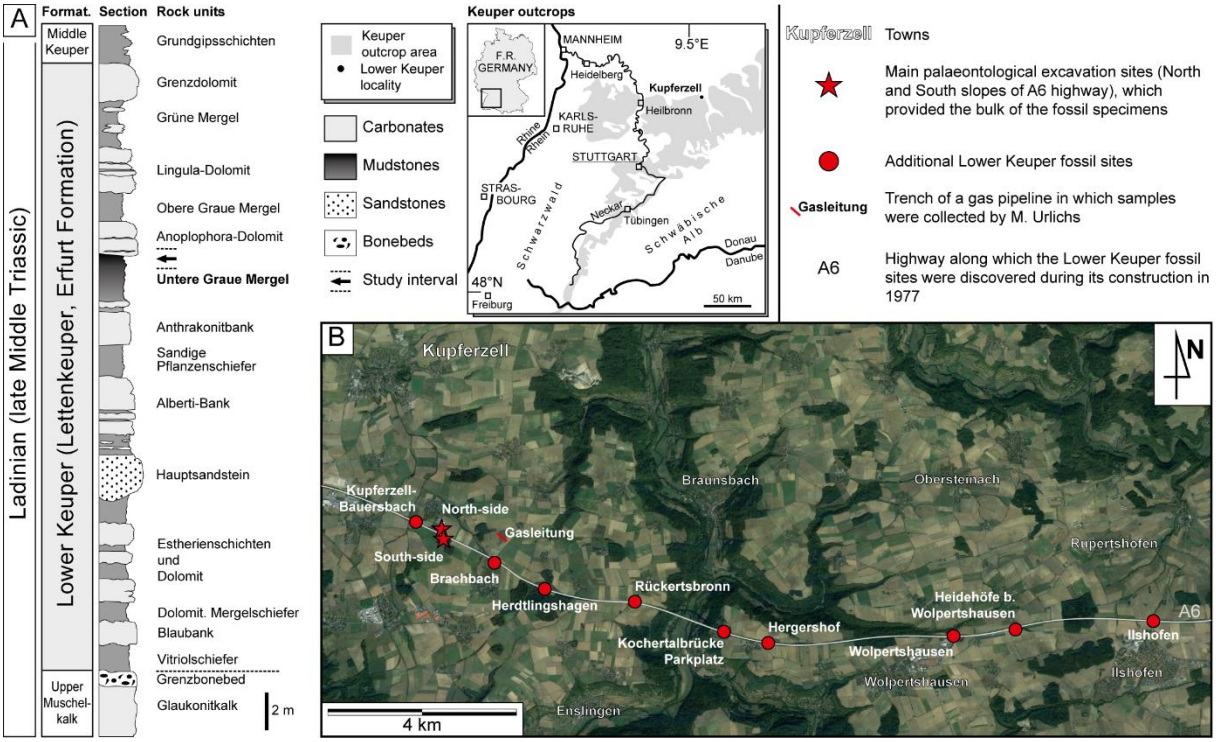

Figure 1. Geographical and geological setting. **A**, General stratigraphic section of the Lower Keuper and geographic map highlighting the Keuper extension in grey (modified from Schoch and Seegis, 2016). **B**, Satellite image (base image from Google Earth) showing the different fossil sites (including the two main excavation areas) where Lower Keuper sections (see Fig. 2) were logged.

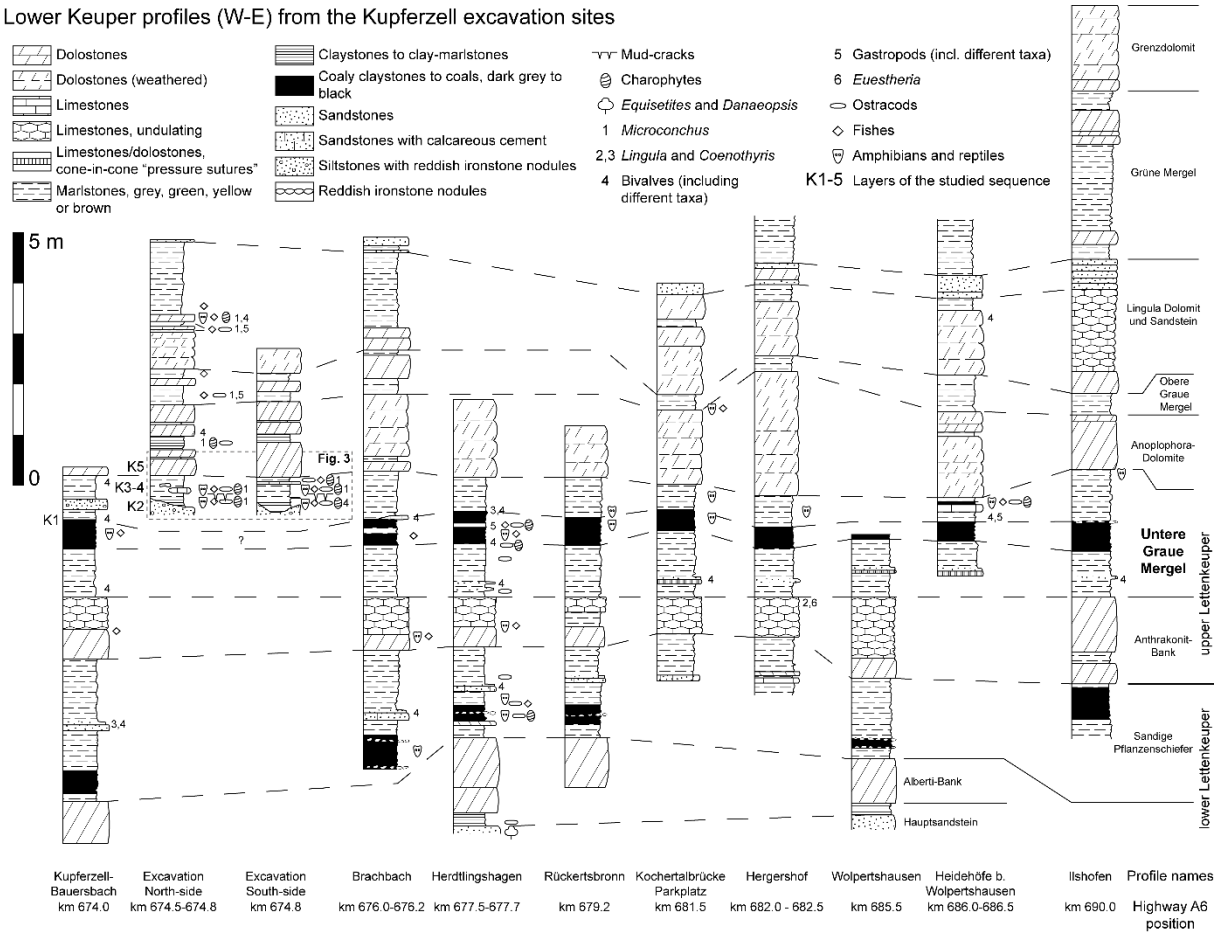

Figure 2. Detailed stratigraphic panel of the Lower Keuper at Kupferzell and nearby localities along the highway A6. Exact location of each section is shown in Fig. 1B. Modified and updated from Urlichs (1982).

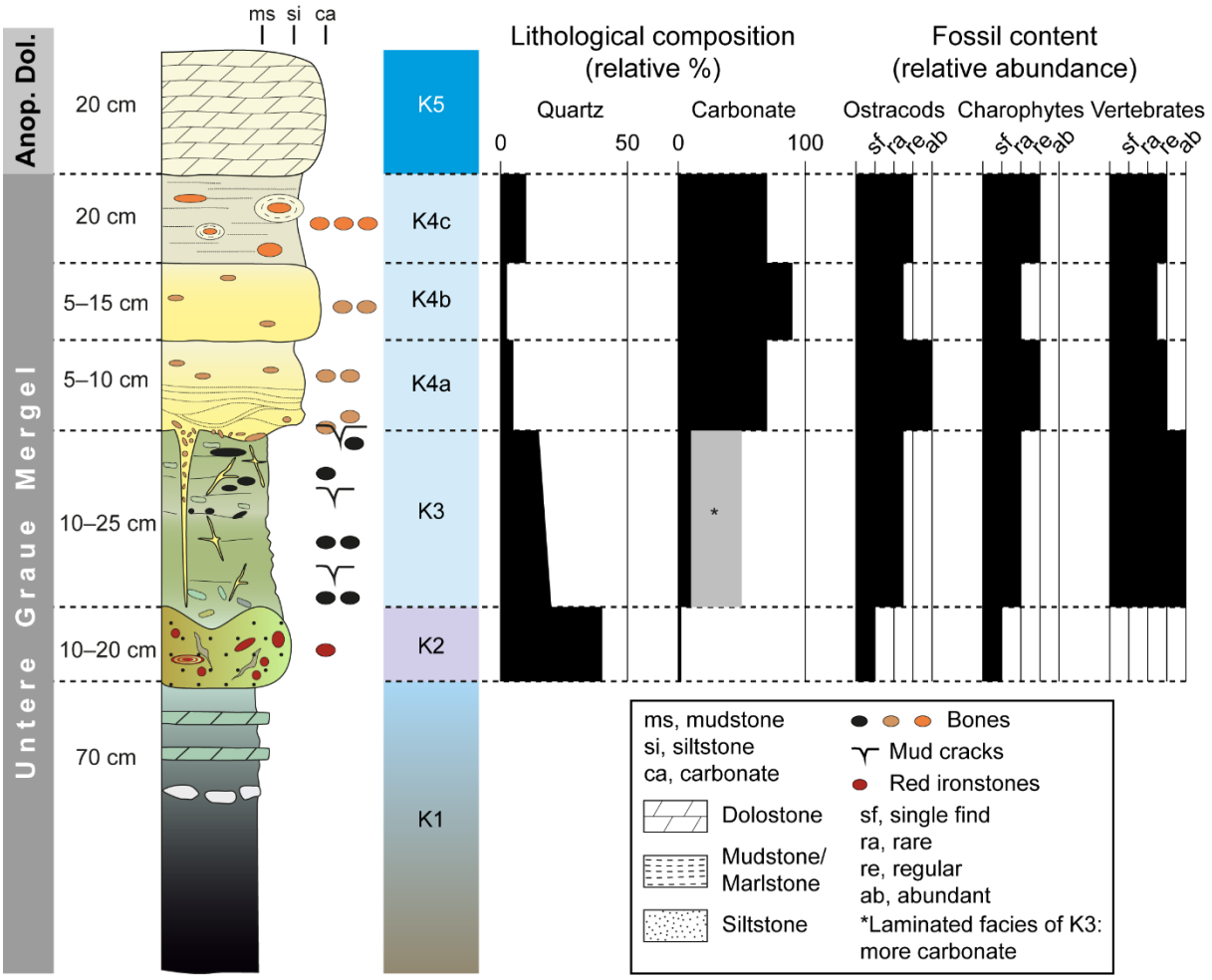

Figure 3. Detailed stratigraphic profile of Kupferzell at the main excavation site with lithological and sedimentological features, and relative abundance of fossil content. Percentages of quartz and carbonate of each unit are based on the petrographic thin sections.

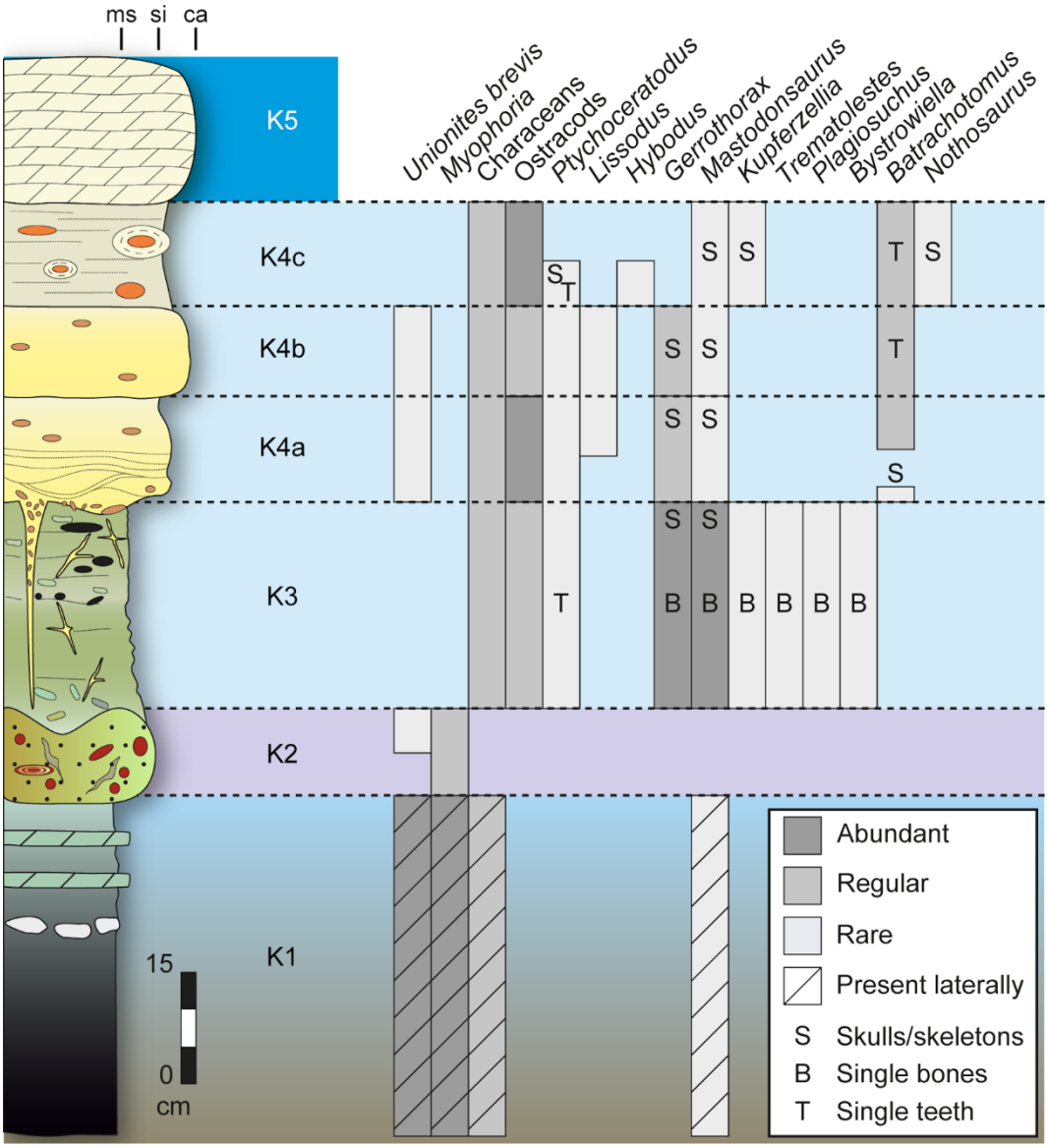

Figure 4. Distribution and relative abundance of fossils at the main excavation site in Kupferzell.

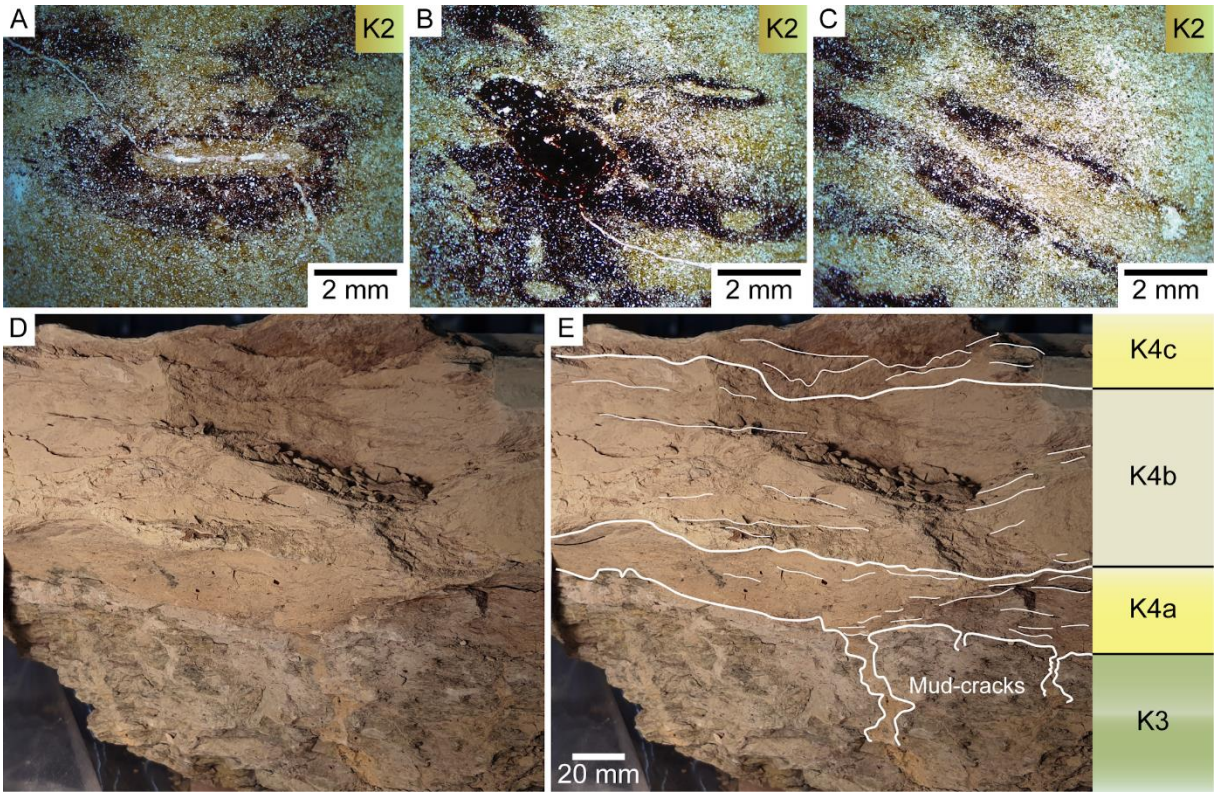

Figure 5. Stratigraphy and sedimentological features. **A–C**, Photomicrographs of unit K2, siltstones showing a relatively high abundance of quartz grains and the characteristic oval-shaped halos making bands (A), with irregular distribution and less quartz content (B), and also in oblique orientation with respect to stratification (C). **D–E**, Hand sample of units K3 (massive facies) and K4 showing the identified layers and the characteristic mud-cracks between them.

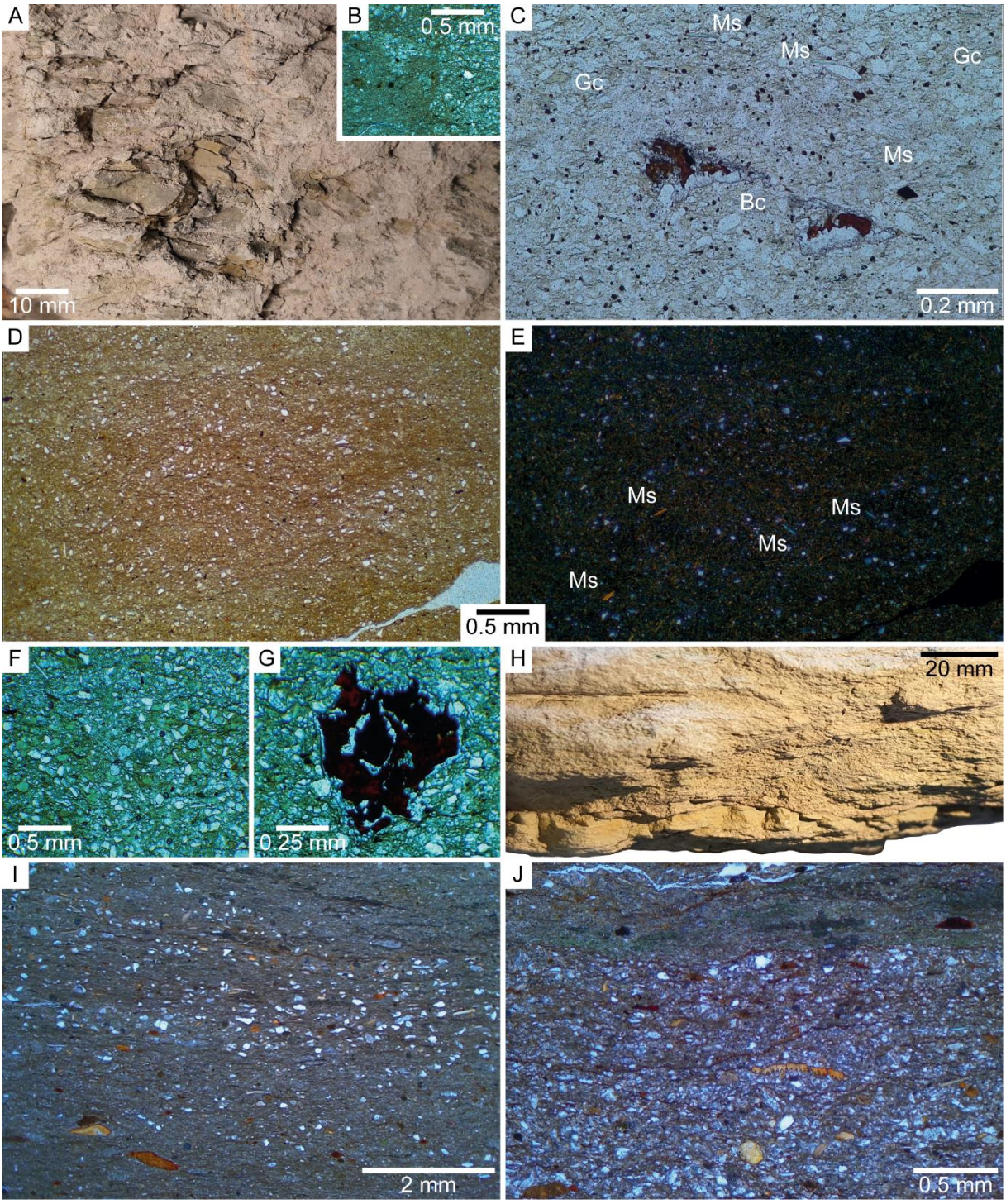

Figure 6. Unit K3. **A–G**, Massive non-carbonate facies (see also Fig. 7); **A**, hand sample of green mudstones with massive aspect and potential aggregations of clayey sediments; **B–G**, photomicrograph showing a relatively high content (~10–20%) of quartz and much less abundant micaceous minerals (~5%) within a clayey matrix with green clasts of chlorite and a few bone fragments; quartz grains are more abundant at the base of the sequence (F), also including red nodules (G) as in K2. **H–J**, Layered/laminated carbonate facies; **H**, hand sample; **I–J**, photomicrographs.

Abbreviations: Bc, bone embedded in calcite; Gc, green clasts (chlorite); Ms, micaceous minerals.

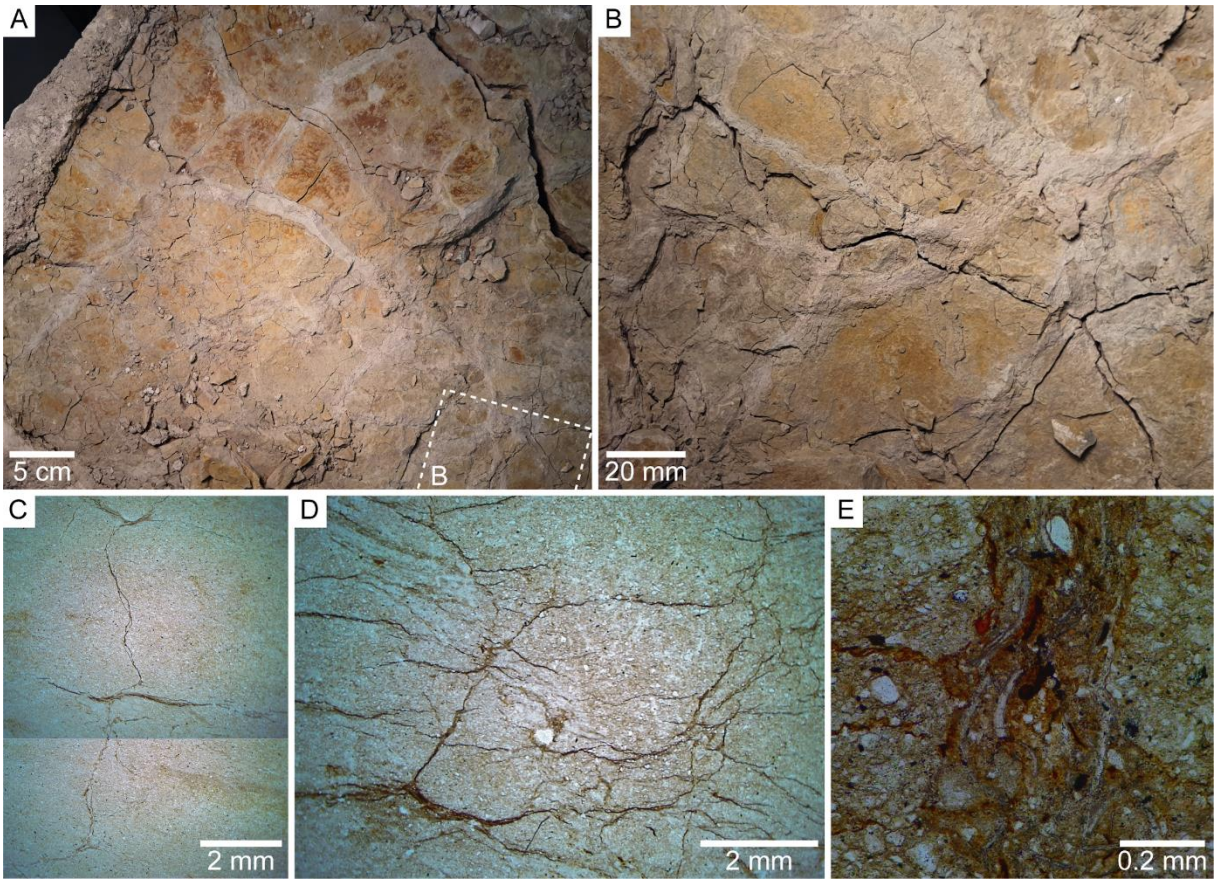

Figure 7. Mud cracks penetrating unit K3. **A–B**, Mud cracks in plain view (bottom surface of unit K3) showing large and thick mud-cracks in T-junction (A) and smaller subordinate cracks (B). **C–E**, Photomicrographs of mud cracks (thin dark-brown lines) from: **C**, the lower part of the unit, where cracks are sparse, mostly vertical lines with short lateral ramifications; **D**, the upper part showing a denser net of cracks from vertical to horizontal orientations; **E**, detail of a crack, infilled with ostracod shells and darker carbonate sediments of layer K4a.

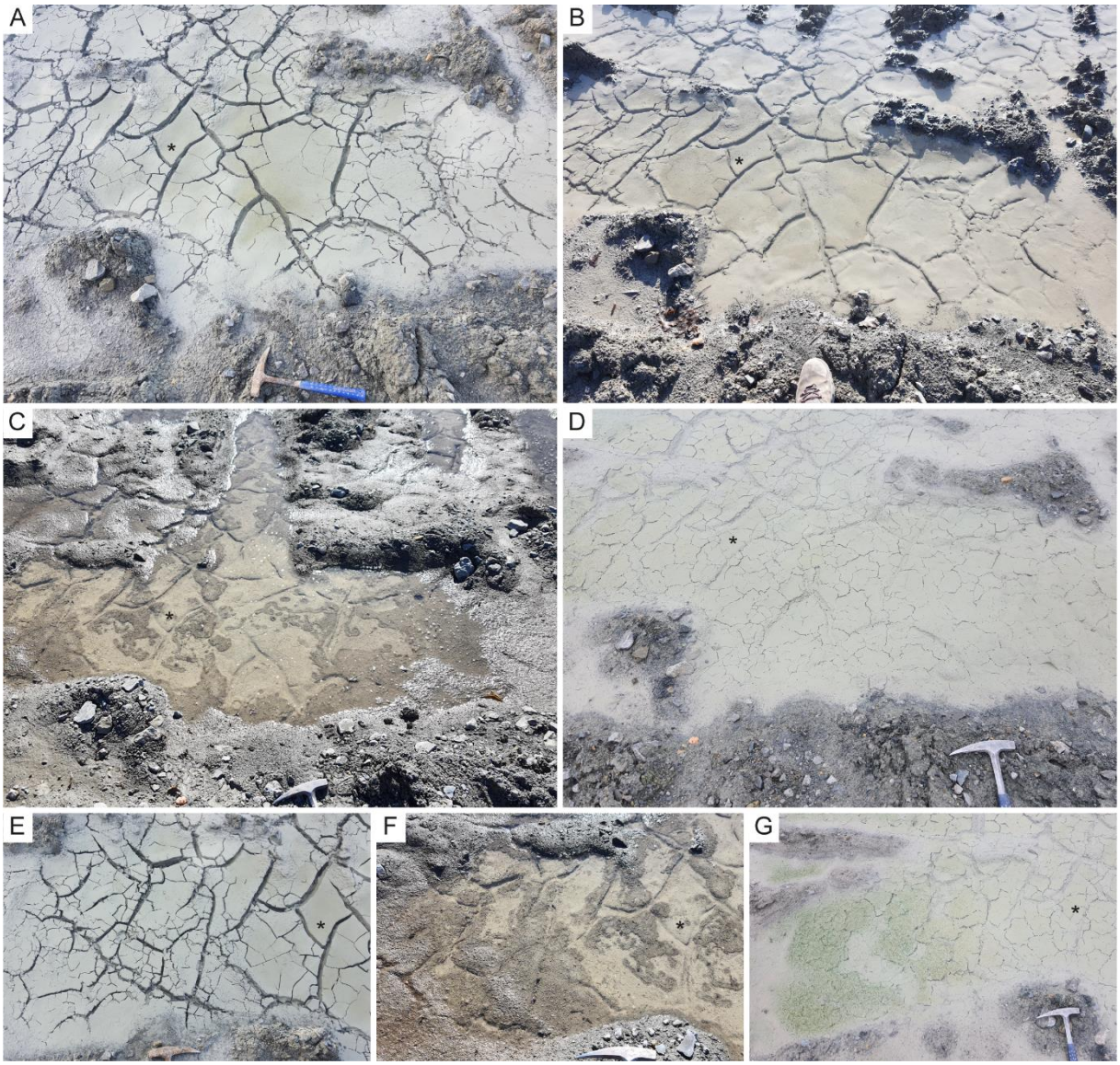

Figure 8. Present-day desiccation mud cracks in T-junction and with smaller subordinate cracks developed in a small pond (in both photographs covered by water) developed on mud deposits from the Eschenau quarry (sediment originates from the Lower Keuper facies mixed with pulverised carbonates from the Muschelkalk facies). **A**, Mud cracks recently generated (October 15th, 2021). **B–D**, Progressive covering of mud cracks with mud: November 11th, 2021 (B), March 8th, 2022 (C), April 27th, 2022 (D). **E–G**, Close up of the pond with the fresh cracks (October 15th, 2021; E), their infilling (March 8th, 2022; F), and the growing of green algae (April 27th, 2022; G), altogether mirroring the environmental evolution between units K3 and K4. Hammer in A is 30 cm long. Asterisks (*) indicate equivalent point in all photographs.

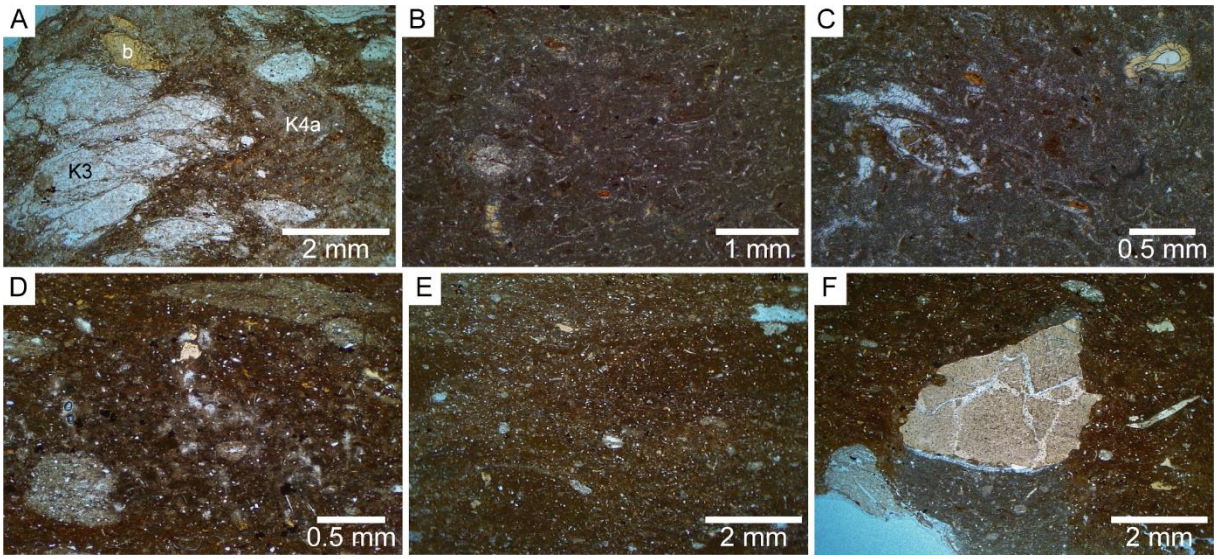

Figure 9. Photomicrographs of layer K4a. **A**, Peloids/clasts of layer K3 incorporated mostly within the base of the darker layer K4a; bone fragments (b) are also present. **B**, General aspect of K4a, being very rich in ostracod shells and less abundant characean fragments (e.g., centre-left of the image) within a brown micritic matrix with seldom quartz grains. **C**, Bone fragments embedded in sparry calcite. **D–E**, Heterogeneous, chaotically organised aspect of the layer, though a rough horizontal and undulated lamination is observed. **F**, Large fractured coprolite partially embedded in sparry calcite, more concentrated on the bottom surface; below it the layer displays a different aspect, possibly due to (re-) precipitation of carbonate diagenetic fluids.

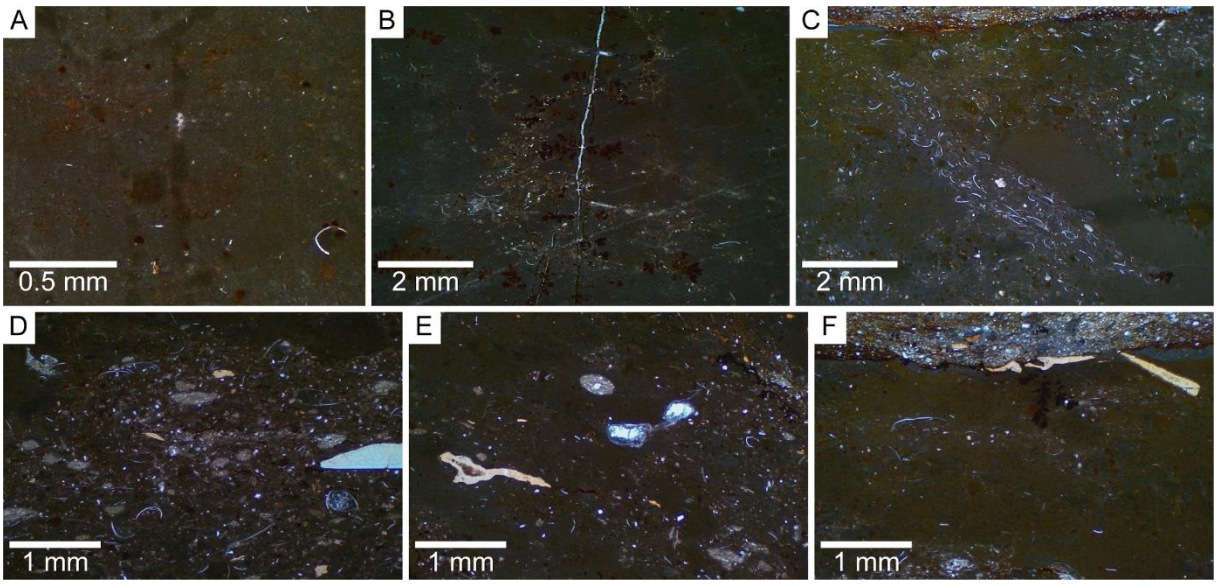

Figure 10. Photomicrographs of layer K4b. **A**, Typical aspect of the layer (wackestone), being a massive micritic brown carbonate with rounded darker stains, possibly diagenetic peloids, and with seldom ostracods shells, bioclasts and very sporadic

quartz grains. **B–C**, Potential burrows infilled with a coarser (lighter coloured) matrix with abundant ostracods and subordinate quartz grains. **D–E**, Chaotically organised portions containing more abundant bioclasts, mainly including ostracods, characeans and bones. **F**, Boundary with layer K4c (see also top part of C), which is sharp and undulated, indicating potential erosion.

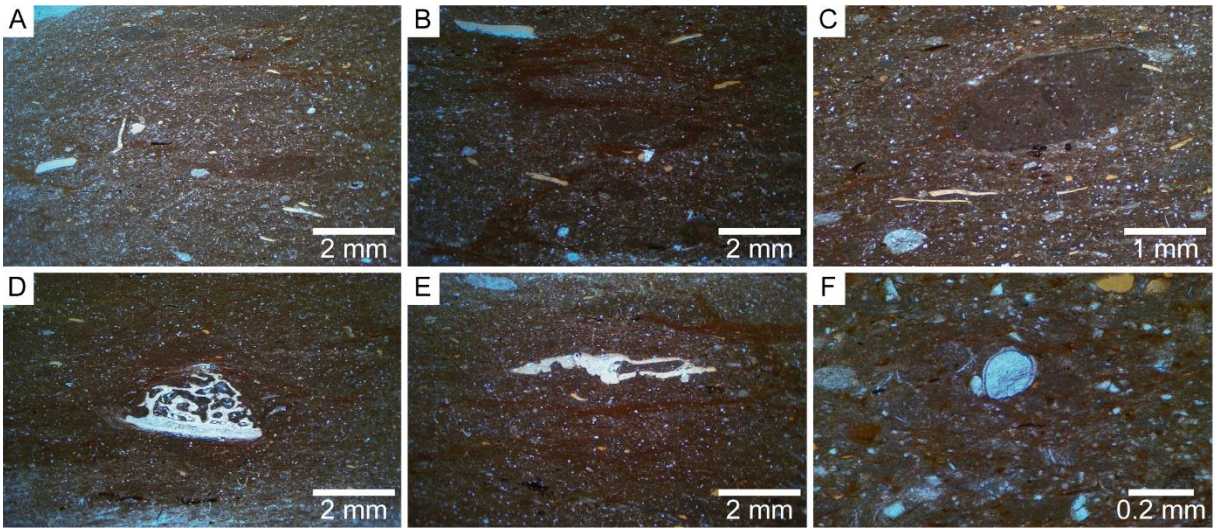

Figure 11. Photomicrographs of layer K4c. **A–B**, Typical aspect, with irregularly distributed horizontal seams, abundant ostracod shells and subordinate bone fragments (sometimes oblique to stratification) and quartz grains; note similarities with layer K4a. **C**, Relatively large oval-shaped peloid, possibly being a reworked clast of the same layer. **D–E**, Large well preserved bone fragments partially embedded in sparry calcited. **F**, Detail of the layer with a well preserved, but slightly eroded (abraded) characean oogonia.

Figure 12. Taphonomic features of tetrapod remains from Kupferzell. **A–B**, Skeletons of *Gerrothorax* showing different preservations linked to the sedimentary unit; **A**, partial, disarticulated skeleton with bones chaotically oriented on top of unit K3. **B**, Fairly complete, disarticulated (but with elements approximately in place) skeleton covered with a carbonate crust within layer K4c. **C–D**, Femora of *Gerrothorax* (SMNS 81450 (C), 81454 (D)) showing different coloration according to the unit (C is from K3 and D is from K4) as well as semi-circular (cf) and transverse (tf) fractures. **E**, Right hemimandible of *Batrachotomus* (SMNS 52970) showing a mosaic pattern of fractures

(mf). **F**, Mandible fragment of *Mastodonsaurus* with sedimentary matrix of both units K3 and K4, as well as radial fractures (rf) and a mosaic pattern of fractures (mf) types. **G**, Dorsal rib of *Nothosaurus* (SMNS 80266) with spiral to oblique fractures (of) including right angle offsets (fracture on the left). **H–K**, Teeth of *Batrachotomus* showing multiple parallel fractures infilled with calcitic sediment and completely dividing the teeth in neat breaks (H, I), as well as fractures infilled with sediment and teeth fragments displaced chaotically (J, K). **L**, Proximal end of a *Batrachotomus* right ulna (SMNS 80275) with longitudinal (lf) and semi-circular (cf) fractures. **M**, Distal end of a *Batrachotomus* right pubis (SMNS 52970) with a spiral fracture (sf). **N–O**, Tusk (SMNS 83276 (N)) and left humerus (SMNS 81171 (O)) of *Mastodonsaurus* with sedimentary matrix of both units K3 and K4; note also the round holes in the base of the tusk, possibly due to chemical dissolution. **P**, Dipnoan mandible tooth (SMNS 56866) with the enameloid abraded. **Q–R**, Small-sized vertebral centra of *Mastodonsaurus* (SMNS 84094 (Q), 84098 (R)) with chemically abraded surfaces.

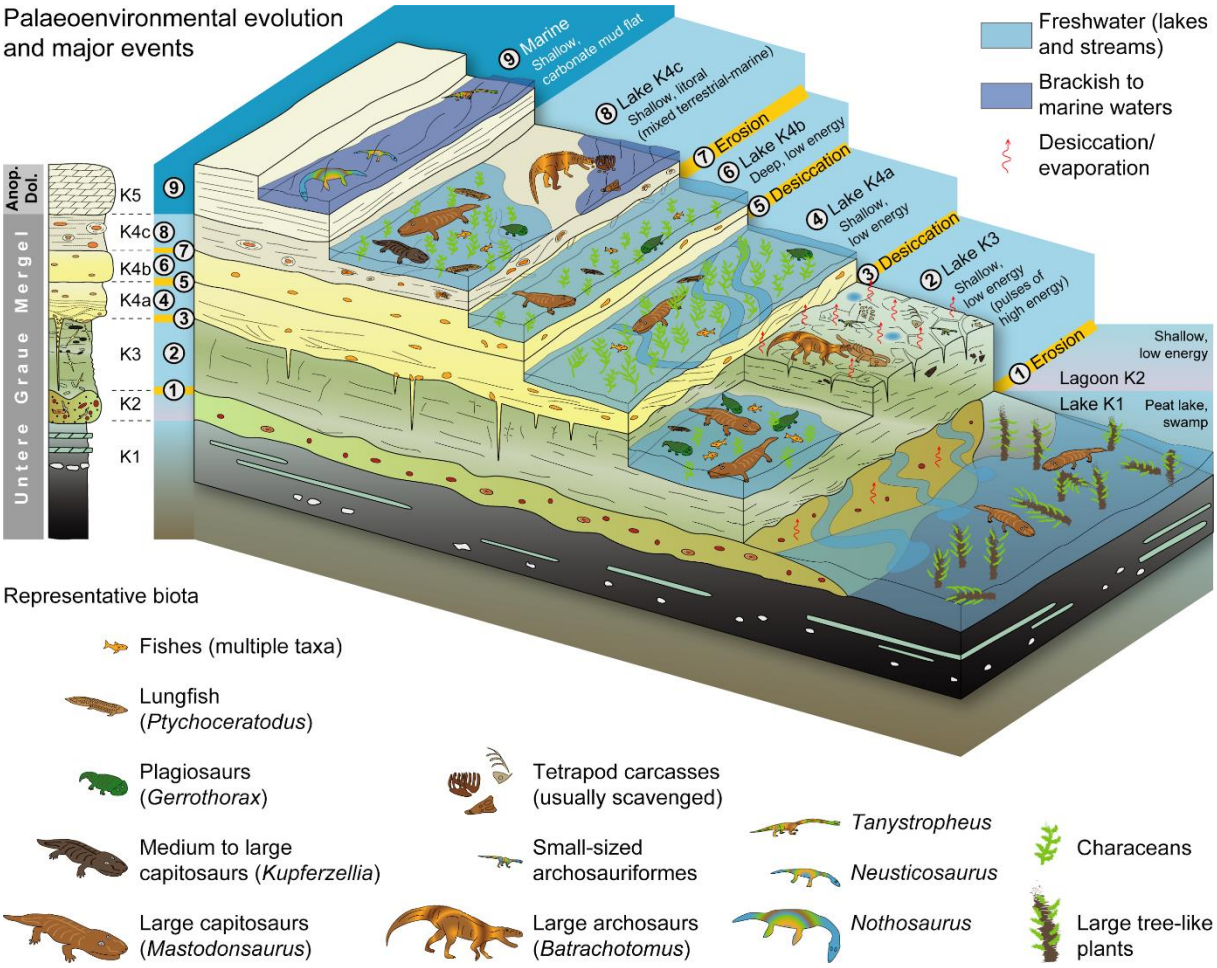

Figure 13. Reconstruction of the palaeoenvironmental evolution in Kupferzell. The main events are indicated and the most representative taxa and sedimentary structures are depicted.