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A Middle Triassic palaeontological gold mine: The vertebrate deposits of Vellberg (Germany)

Rainer R. Schoch *, Dieter Seegis

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, Germany

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ABSTRACT

The lacustrine deposits of Vellberg, southern Germany, rank among the richest vertebrate *fossil-lagerstätten* of the Triassic worldwide. Continued excavation over one decade produced two chondrichthyans, 14 taxa of bony fishes, seven temnospondyls, one chroniosuchian, the stem-turtle *Pappochelys*, two procolophonians, four lepidosauromorphs, a choristodere, four archosauriforms, three pseudosuchian archosaurs, and around ten further reptile taxa only known by teeth. Sedimentary facies, fossil assemblage composition, and taphonomy suggest this deposit comprises a succession of rather different water bodies, situated on a floodplain dominated by dolomitic muds: (1) a coal swamp with occasional reptiles and temnospondyls, (2) a large but shallow, brackish lagoon inhabited by *Bakevellia*, *Acrodus*, *Nothosaurus*, and the temnospondyl *Plagiosternum*, (3) a small and shallow, well-protected, oligohaline freshwater lake dominated by various temnospondyls, and (4) a larger (6 km) and deeper freshwater lake, again with a rich fauna of fishes, temnospondyls, and small aquatic reptiles that was eventually filled by dolomitic coastal muds. Reworking and desiccation cracks indicate repeated phases of regression and drought, during which bonebeds formed and skeletons of terrestrial tetrapods were deposited.

1. Introduction

The Middle Triassic epoch was a crucial time interval for the evolution of many vertebrate groups (Sues and Fraser, 2010). Rocks of this age are much richer in tetrapod remains than older strata, indicating a higher taxonomic diversity as compared with Early Triassic and late Palaeozoic faunas – or alternatively, a more favourable situation for the formation of *fossil-lagerstätten* from Middle Triassic time on. This relatively rapid increase in taxonomic diversity is at least partly due to the recovery of biotopes and their inhabitants after the catastrophic events resulting in the end-Permian mass extinction, which were responsible for the loss of more than 90% of species diversity (Chen & Benton, 2012). At any rate, reptiles underwent major diversification, with increasing numbers of archosauromorphs. Other clades, such as the lepidosaurs, choristoderes, and turtles, also must have evolved or flourished during that time, but their fossil record so far remained poor before the Late Triassic. Marine reptiles were abundant, such as sauropterygians (pachypleurosaurs, nothosaurs, placodonts) and thalattosaurs (Fraser and Sues, 2011). At the same time, a full range of taxa that dominated the late Paleozoic were still around, albeit with reduced diversity, including the parareptiles, dicynodonts, therocephalians, and non-mammalian cynodonts. Finally, various enigmatic forms and relict taxa, such as the anthracosaur-like chroniosuchians, are present in Middle Triassic rocks (Witzmann et al., 2008; Schoch et al., 2010).

Our ignorance of these Triassic forms and the roles they played in palaeo-ecosystems largely results from the paucity of good *fossil-lagerstätten*. Especially for deposits containing terrestrial tetrapods, few fossiliferous regions are known across Pangaea: the rich and diverse assemblages of the Chañares Formation (La Rioja, NW Argentina), Santa Maria Formation (SE Brazil), Bukobayskaya Svita in the southern Urals (Russia), Manda Formation of SW Tanzania, Upper Moenkopi Formation of Arizona and New Mexico, and finally the rich marine facies of Monte San Giorgio (Switzerland), Luoping and Panxian (both Yunnan, South China).

Historically, the first reported Middle Triassic deposits were the Muschelkalk and lower Keuper sequence of southern Germany and eastern France, which have been known for almost 200 years (Jaeger, 1828; Meyer, 1832, 1855), and are one part of the three-fold division of rocks in the Germanic Basin lending the Triassic Period its name. The lower Keuper (Lettenkeuper) produces famous vertebrate fossils, such as the giant temnospondyl *Mastodonsaurus giganteus*, a 5 m long amphibian (Meyer and Plieninger, 1844; Schoch, 1999). It is from these deposits that diverse tetrapod assemblages have been discovered in recent time, starting with an excavation during road construction near Kupferzell (Wild, 1980), which yielded thousands of bones, including excellent skulls and skeletons of the temnospondyls *Mastodonsaurus*, *Kupferzellia*, and *Gerrothorax*, and the pseudosuchian archosaur *Batrachotomus*

* Corresponding author.
E-mail address: rainer.schoch@smns-bw.de (R.R. Schoch).

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(Schoch, 1999; Gower, 1999; Hellrung, 2003). Shortly after, further material was found in nearby localities at Michelbach an der Bilz (Hagdorn, 1980) and Vellberg (Schoch, 2002), which led to the discovery of the temnospondyls *Trematolestes* and *Callistomordax* (Schoch, 2006, 2008). Since the 1990s, intensified collecting in a single pit, the Schumann Quarry at Vellberg, has produced a plethora of new finds, including numerous new tetrapod taxa (Witzmann et al., 2008 Sues and Schoch, 2013). Although the bulk of the material comprises an autochthonous lacustrine assemblage, consisting of fishes (selachians, actinistians, dipnoans, actinopterygians), temnospondyls, and diapsid reptiles, the most fascinating finds include various terrestrial reptiles, all of which represent new taxa (Schoch, 2015a, 2015b).

The scope of the present study includes the deposition and environmental setting of the deposits at Vellberg, which is the most diverse tetrapod assemblage of the European Middle Triassic, having yielded seven temnospondyls, one chroniosuchian, the ancient stem turtle *Pappochelys* (Schoch and Sues, 2015, 2016), and ~25 reptile taxa in a 30 cm thick sequence of mudstones, siltstones, and dolomites (Schoch, 2011a, 2011b). This sedimentary sequence, and especially its fossil content, is locally restricted and probably formed in shallow lagoonal and lake environments. The aims of this paper are to (1) describe the sedimentary features of this section, (2) analyze the taphonomic situation in each of the successive fossil-bearing layers, and (3) reconstruct the depositional history of the fossiliferous beds at Vellberg.

2. Geological setting

2.1. Location and excavation

The Vellberg locality is an active limestone pit east of Eschenau, a village in the municipality of Vellberg, northern Baden-Württemberg, Germany. Here, we refer to it as “Eschenau Quarry”, because a second pit at Vellberg, the Ummenhofen Quarry, should not be confused with it. In the Eschenau Quarry, the upper Muschelkalk is quarried down to a depth of 60 m. The limestone is used for pavement of roads and buildings, whereas the overlying lower Keuper sediments are removed with large excavators and dumped in old parts of the quarry. The pit has been quarried for 63 years (as of 2016), and was first described in the lower Keuper monograph of Brunner (1973) who described a stratigraphic section from this site. Spanning a range of 700 m (N—S) and 250 m (E–W) through the quarry (see local stratigraphy), further sections were measured by private collectors and the authors over a period of 20 years.

Since 1980, private collectors have been active in the lower Keuper sequence of the Eschenau Quarry, with increasing efforts since the 1990s. In cooperation with collectors, the Staatliches Museum für Naturkunde Stuttgart (SMNS) secured material from several horizons in the lower Keuper during the 1980s and 1990s, and in 2000, started focused scientific excavations. Continued quarrying by the owner, the Schumann family, removes an area of 40 × 25 m on average annually. Since 2000, continued excavation by SMNS was made possible in designated areas by the owner, usually in the range of 50 × 10 m per year.

These efforts, supported by private collectors, produce over a thousand finds each year, including skeletons of temnospondyls, chroniosuchians, and various terrestrial reptiles (e.g., Schoch, 2006, 2008; Witzmann et al., 2008). In 2008 and 2010, particularly rich pockets with articulated reptile skeletons were discovered, which yielded several new reptile taxa (Schoch, 2011a, 2011b; Schoch and Sues, 2014, 2015). The richest bed, a grey claystone sequence of only 5–12 cm thickness, produced a total of two chondrichthyans, 14 bony fishes (*Serrolepis*, *Dipteronotus,* redfieldiids, a large scanilepiform, actinistians, and dipnoans, among others; Fig. 9), six temnospondyls (*Mastodonsaurus*, *Kupferzellia*, *Callistomordax*, *Trematolestes*, *Gerrothorax*, and *Plagiosuchus*), one chroniosuchian (*Bystrowiella*), the enigmatic amniote *Colognathus* (Sues and Schoch, 2013), the stem-turtle *Pappochelys* (Schoch and Sues, 2015), a diapsid with choristoderan features, a rhynchocephalian (Jones et al., 2013), the doswelliid archosauriform *Jaxtasuchus* (1.2 m; Schoch and Sues, 2014), a herbivorous archosauriform similar to *Azendohsaurus* (40 cm), a small archosauriform with numerous rows of armour plates resembling those of *Vancleavea* (25 cm), a *Euparkeria*-like taxon (80–120 cm), a medium-sized pseudosuchian (2 m, Schoch, 2011b), and the large suchian *Batrachotomus* (4–5 m; Gower and Schoch, 2009). An assessment of dental morphotypes suggests minimum of 25 amniote taxa present in the grey mudstone beds alone (Schoch, 2015b).

Due to the wealth of recovered specimens, the (often time-consuming) preparation has focused on the more interesting finds. That is why a detailed statistical analysis of different skeletal elements or preservation types cannot be given for the moment, and only semi-quantitative statements are possible.

2.2. Regional stratigraphy

The lower Keuper (Erfurt Formation) is a mixed siliciclastic-carbonate sequence overlying the marine Muschelkalk series (Fig. 1). It ranges across the Central European (Germanic) Basin, from Switzerland to the Baltic Sea (Pöppelreiter, 1998; Beutler et al., 1999). In northern Baden-Württemberg (south-central Germany), the lower Keuper ranges between 20 and 25 m in thickness (Brunner, 1980; Brunner and Bruder, 1977). In contrast to the fully marine Muschelkalk, the lower Keuper was dominated by two alternating regimes, fluvial and marine, which produced three different complexes of sedimentary facies: (1) river channels (from the NE) with estuaries, (2) a wide range of lakes, and (3) marine transgressions (from the SW Burgundy gate of the Tethys). The lower Keuper floodplains, lakes and lagoons covered most of southern and central Germany.

In contrast to channel-rich central and northern Germany, only three fluvial progradations reached the northern Württemberg region, which was instead dominated by numerous marine transgressions and lagoonal sequences (Etzold and Schweizer, 2005). The six most geographically extensive marine transgressions are the carbonatic Blaubank, Albertibank, Anthrakonitbank, Anoplophora Dolomite, Lingula Dolomite, and Grenzdolomit (Fig. 1). These horizons are usually dolomitic and contain bivalves and marine reptiles.

The most fossiliferous vertebrate deposits are located within the mudstone sequences, especially the Sandige Pflanzenschiefer and Untere Graue Mergel. These beds form a 1–2.5 m thick sequence of dark mudstones and carbonatic siltstones rich in coal and bonebeds (Zeller, 1908; Brunner, 1973; Pöppelreiter, 1998). The fossil-bearing deposits of Kupferzell are part of the the Untere Graue Mergel sequence, as do similar localities near Wolpertshausen, Ilshofen, Ummenhofen, and Eschenau (Urlichs, 1982; Schoch, 2002).

2.3. Local stratigraphy

At the Eschenau Quarry, detailed stratigraphic sections have been measured over a period of 25 years (Figs. 2–4). The sequence studied here encompasses the upper part of the Untere Graue Mergel (Lower Grey Marls) and the base of the Anoplophora Dolomite (Anoplophora Schichten). This fossiliferous sequence was described by Schoch (2002) and includes (from bottom to top, ‘E’ referring to Eschenau Quarry): (1) dark coaly mudstones (E1: 5–10 cm), (2) light green mudstones (E2: 2–5 cm), (3) a coquina that is only locally developed (E3: 0–4 cm), (4) green to grey siltstones rich in the bivalve *Bakevellia* (E4: 15–40 cm), (5) brown carbonate-rich siltstones (E5: 5–15 cm), (6) green to grey mudstones (E6: 5–20 cm), rich in organic material, with a basal bonebed, and (7) a light brown dolomitic marlstone to dolomite (E7: 30–50 cm), forming the basalmost of three dolomitic units (Anoplophora Dolomite).