The vertebrate fauna of the Lower Keuper Albertibank (Erfurt Formation, Middle Triassic) in the vicinity of Schwäbisch Hall (Baden-Württemberg, Germany)

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Abstract

In the vicinity of Schwäbisch Hall, the Lower Keuper (Ladinian) Albertibank is characterized by a small-scale lateral facies change and a distinctive fauna composed of ostracods, fishes, and lower tetrapods, comprising the remarkably abundant polzbergiid actinopterygian *Serrolepis suevicus*, small unidentified species of ?Redfieldiiformes and Saurichthyidae, the small brackish water shark *Lonchidion*, two dipnoans, a large coelacanthiform, the temnospondyl amphibians *Mastodonsaurus* and *Gerrothorax*, a small nothosaur, and the "rauisuchian" *Batrachotomus*. Facies and fauna give evidence of an occasionally dry falling lacustrine environment. The dentition of *Serrolepis* is indicative of a specialized durophagous diet, presumably on ostracods.

Keywords: Lower Keuper, Albertibank, Ladinian, Southwest Germany, vertebrate fauna, durophagous diet.

Zusammenfassung

Die Albertibank des Unterkeupers (Ladinium) im Raum Schwäbisch Hall ist durch kleinräumlichen lateralen Fazieswechsel und eine Fauna von Ostrakoden, Fischen und niederen Tetrapoden gekennzeichnet. Besonders häufig ist der polzbergiide Actinopterygier *Serrolepis suevicus*, seltener sind unbestimmte kleine Arten der ?Redfieldiiformes und der Saurichthyidae, der Brackwasserhai *Lonchidion*, zwei Dipnoer-Arten, ein großer Coelacanthiforme, die temnospondylen Amphibien *Mastodonsaurus* und *Gerrothorax*, ein kleiner Nothosaurier und der „Rauisuchier" *Batrachotomus*. Fazies und Fauna lassen auf ein gelegentlich trockenfallendes lakustrines Habitat schließen. Die Bezahnung von *Serrolepis* legt eine spezialisierte durophage Ernährung, vermutlich von Ostrakoden nahe.

Contents

1. Introduction

In the Germanic Triassic, the Lower Keuper or Lettenkeuper ('Lettenkohle' of the older literature) occupies a transitional position between the marine limestones of the Upper Muschelkalk and the predominantly terrestrial sediments of the Middle Keuper. The Lettenkeuper is characterized by a small scale cyclical change of (1) sandstones and claystones with limnic-fluviolacustrine and deltaic-palustrine floras and faunas; (2) carbonates and claystones with brackish or marine faunas. In Southwest Germany these carbonate beds may contain gypsum nodules or even relics of halite crystals, indicating evaporitic-pedogene processes after their deposition (NITSCH 2005). The sandstones, containing heavy minerals of Cadomian age (PAUL et al. 2008), prograded from Scandinavia's Caledonian Mountains over the entire Central European Basin as far southward as the German-Swiss border area along the upper reaches of River Rhine. Their channel systems may incise into older deposits as deep as the top of the Upper Muschelkalk. While the 40–60 m thick fluvio-lacustrine facies dominates the northern and central parts of the Germanic Basin, the Lower Keuper becomes increasingly carbonate-dominated and thins out to less than 20 m towards Southwest Germany and Switzerland (NITSCH 2005, ETZOLD & SCHWEIZER 2005).

Based on nine minor cycles that can be interpreted as orbital 100 ka and 400 ka cycles, a duration of approximately 1.2 Ma has been estimated for the Lower Keuper by Menning et al. (2005) and Nitsch (2005). Assuming eight cycles, Kozur & Bachmann (2008) estimate a duration of 0.8 Ma. The Lower Keuper is of early late Ladinian (Longobardian) age. It was deposited under a dry, subtropical climate, with monsoonal winds bringing periodic precipitation from the Western Tethys (Parrish 1999).

The Lower Keuper of the Hohenlohe and Schwäbisch Hall Counties (Northeast Baden-Württemberg) is famous for its vertebrate Lagerstätten that yielded diverse reptile, amphibian, and fish faunas, among them *Mastodonsaurus*, the largest amphibian ever found, or *Batrachotomus*, the best known rauisuchian reptile (Schoch 2006). However, it was the small polzbergiid fish *Serrolepis suevicus* Dames, 1888 that gave reason for the present investigation. Recently, the genus *Serrolepis* has regained attention upon the location of the type material in the collection of the Humboldt Museum für Naturkunde in Berlin by Lombardo & Tintori (2004). Additional new finds of articulated material are described in detail elsewhere (Mutter & Hagdorn, in prep.). The present paper intends to give an overview of facies and fauna of the Albertibank around Schwäbisch Hall, to compare it to nearby outcrops, and to reconstruct the palaeoecological position of *Serrolepis* in this depositional environment.

As a common and abundant faunal element, *Serrolepis* must have played an important role in the food chain of certain Lower Keuper water bodies. Its characteristic deep scales with strongly serrated posterior edges were collected for the first time by Quenstedt during field work

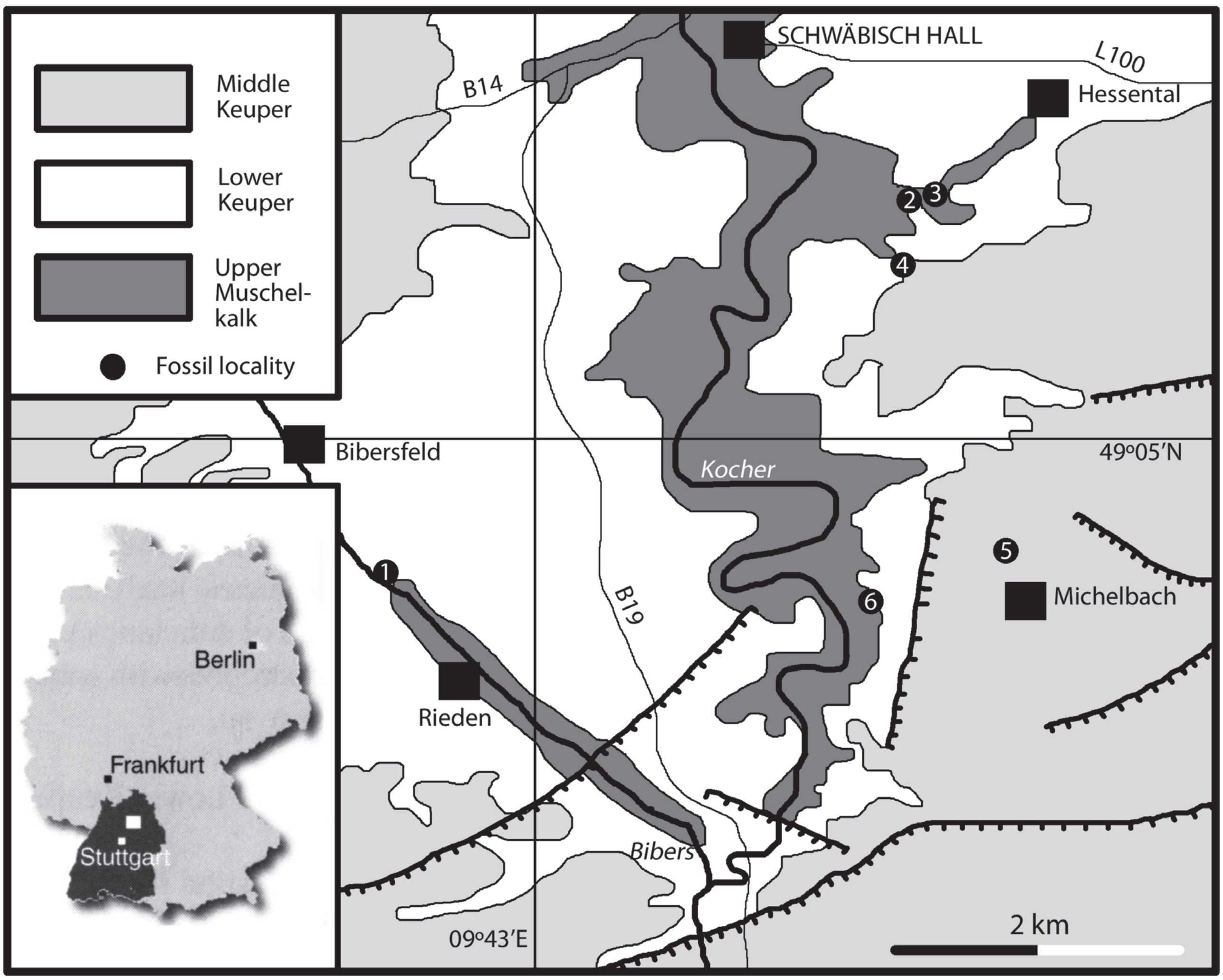

Fig. 1. Geological sketch map of the vicinity of Schwäbisch Hall (northeast Baden-Württemberg) with position of Albertibank outcrops. Kastenhof (1), Scheuermann Quarry (2), Hirsch Quarry (3), Taubenhof Quarry (4), Michelbach-Leitenäcker (5), Wilhelmsglück Quarry (6). For locality data see appendix 1.

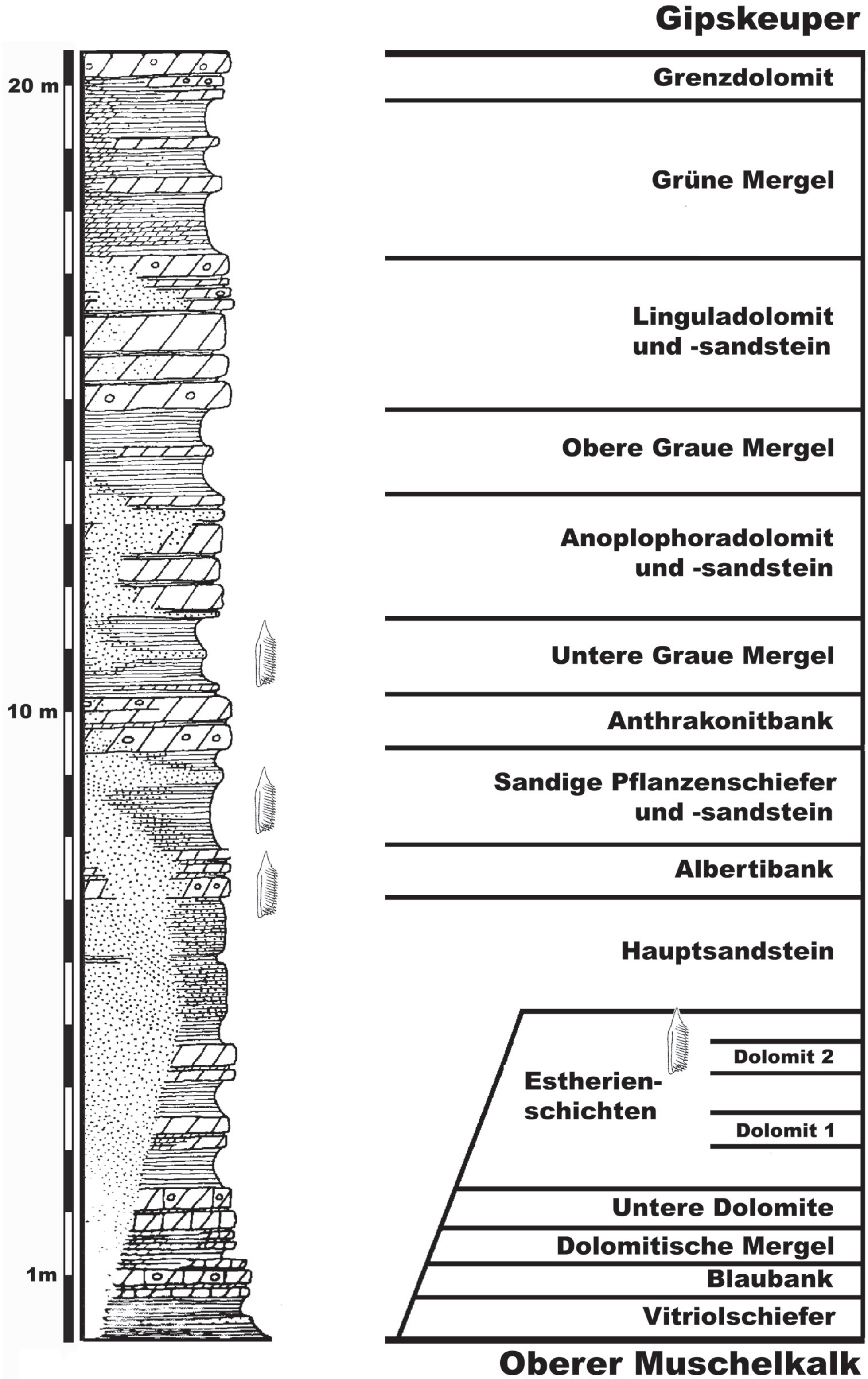

Fig. 2. Lithostratigraphic units of the Lower Keuper in northern Baden-Württemberg with major *Serrolepis* occurences. Modified after BRUNNER & BRUDER (1981).

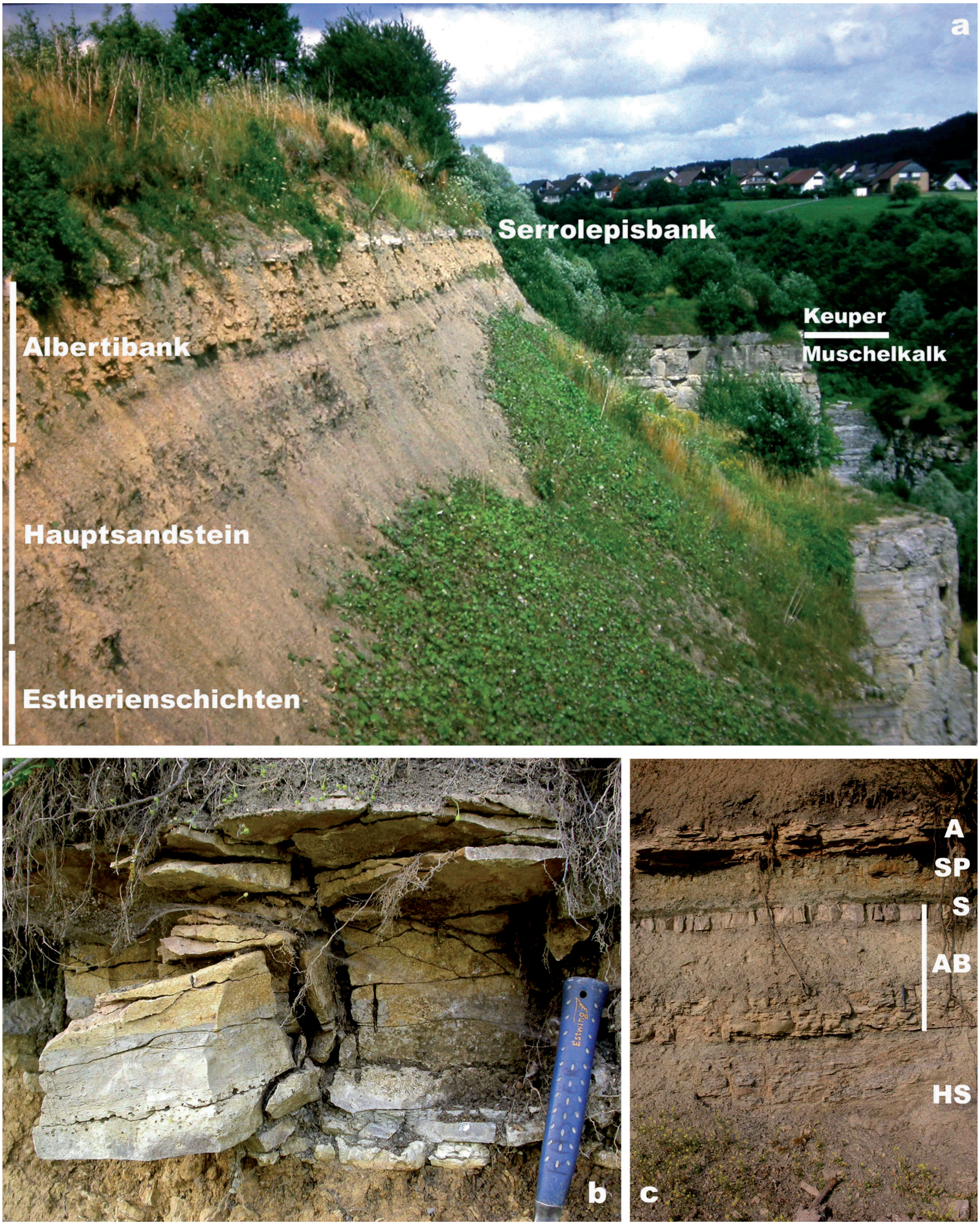

Fig. 3. Lower Keuper outcrops in the vicinity of Schwäbisch Hall. – **a**. Abandoned Scheuermann Quarry with Lower Keuper overlying Upper Muschelkalk limestones. The Hauptsandstein in inter-channel facies. **b**. Serrolepisbank in the Scheuermann Quarry with halite voids indicating pedogene processes. **c**. Lower Keuper at Wilhelmsglück with Hauptsandstein (HS), Albertibank (AB, approx. thickness 1 m) with two carbonate beds, the upper one being the Serrolepisbank (S), Sandige Pflanzenschiefer (SP) with coaly marls at base, and Anthrakonitbank (A) with marine bivalves *(Hoernesia socialis).*

for the 'Geognostische Spezialkarte von Württemberg' (geological map of Württemberg) in 1874 and 1879 in several quarries around Schwäbisch Hall (QUENSTEDT 1880; Fig. 1). In this area, the finely grained, greenish Lower Keuper Sandstone was quarried in many pits. During the 19th century the quarrying activities increased, especially along the valley of River Bibers (HAGDORN 1990). There, claystone and some carbonate beds overlying the working stone were removed and put aside on dumps that became famous for their abundant vertebrate fossils, especially for large dipnoan (ceratodont) tooth plates. The most fossiliferous locality, which yielded also temnospondyl bones and rauisuchian teeth, was the Kastenhof Quarry at the Lämmerberg near the village of Rieden (Fig. 1), often referred to as 'Bibersfeld', a nearby village. It was this Kastenhof Quarry from where QUENSTEDT mentioned the eye catching, serrated *Serrolepis* scales that occurred abundantly in almost black, coaly claystones covering a bituminous limestone bed ('Stinkstein') and, more rarely, also inside the limestone that he called 'Serrolepisbank' (*Serrolepis* bed; QUENSTEDT 1880: 21). In terms of the modern Lower Keuper lithostratigraphic nomenclature (BRUNNER 1973, PÖPPELREITER 1999, ETZOLD & SCHWEIZER 2005, NITSCH 2005), the 'Serrolepisbank' is equivalent to the upper limestone bed of the Albertibank, one of the major marker horizons of the Lower Keuper (Fig. 2). However, for the vicinity of Schwäbisch Hall we still use the term 'Serrolepisbank' when dealing with this upper limestone bed of the Albertibank.

Later, QUENSTEDT (1885: 323, pl. 25, fig. 18) also diagnosed and figured *Serrolepis* scales, but it was DAMES (1888) who established the nominal species *Serrolepis suevicus* based on QUENSTEDT's material. The abandoned Kastenhof Quarry has to be considered the type locality of this taxon. Today, *Serrolepis* is known from at least four levels within the Lower Keuper (Fig. 2). Downsection of the Albertibank, the most important level lies in the Estherienschichten 3 (in particular at locality Illingen in central Württemberg). Upsection of the Albertibank, *Serrolepis* levels were located in the Sandige Pflanzenschiefer (in particular at Michelbach an der Bilz near Schwäbisch Hall, and at Zwingelhausen near Backnang), and the Untere Graue Mergel (e. g. at Kupferzell and Eschenau, both localities near Schwäbisch Hall). For locality data see Appendix 1 and 2.

Today, most of the historical quarries in the Bibers valley have disappeared under filling material and vegetation. The only existing quarry, next to the village of Rieden, still exposes the sandstone but the overlying strata are overgrown. However, a section of the Kastenhof Quarry measured by QUENSTEDT (1880) allows bed-by-bed correlation with the nearby quarries on the right side of River Kocher (Fig. 1). Only in two of these the Serrolepisbank is still exposed but hardly accessible. These are the former Scheuermann and Hirsch quarries in Schwäbisch Hall-Steinbach that make up one large outcrop today (Fig. 3). For a combined section see ZELLER (1907) and BRUNNER (1973: fig. 21). The majority of the new material under description has been collected from fallen blocks in these quarries, which are nowadays protected as a natural reserve area.

Institutional abbreviations

MHI Muschelkalkmuseum Hagdorn Ingelfingen
SMNS Staatliches Museum für Naturkunde Stuttgart

Acknowledgements

We thank RONALD BÖTTCHER (Stuttgart) for assistance with specimens in his care at SMNS, discussion and important information. HUBERT DONÀ (Markgröningen), made available his well-preserved finds from other Lower Keuper localities and stratigraphical horizons for study and comparison with the Serrolepisbank specimens. WERNER KUGLER (Crailsheim), donated articulated fish material from the Estherienschichten of Vellberg-Eschenau to the Alberti Foundation. KLAUS-PETER KELBER (Würzburg), EDGAR NITSCH (Freiburg im Breisgau), and STIG WALSH (Edinburgh) read earlier drafts of the manuscript. The research of RJM was supported by a Marie Curie Intra-European Fellowship within the 6th European Community Framework Programme (MEIF-CT-2006-023691), the Foundation Dr. Robert und Lina Thyll-Dürr (Arlesheim, Switzerland), and in the final stage his research was supported by a Postdoctoral Research Fellowship at the University of the Witwatersrand, Johannesburg, South Africa. We gratefully acknowledge helpful comments and corrections by RONALD BÖTTCHER and DIETER SEEGIS (Stuttgart) who reviewed the manuscript most carefully and shared their knowledge of Keuper faunas with us.

2. Geological background

2.1 Stratigraphy and depositional environment

Albertibank and the overlying Sandige Pflanzenschiefer make up the Albertischichten Member of the Erfurt Formation (ETZOLD & SCHWEIZER 2005). The Albertibank is a single or bipartite carbonate bed (the upper bed being the Serrolepisbank) that can be traced over hundreds of kilometres in Southwest Germany (BRUNNER 1973) and is tentatively correlated with Dolomite Horizon D in Thuringia and in Northwest Germany (BRUCKSCHEN & SCHRÖDER 1994, DOCKTER [& LANGBEIN] 1995, NITSCH 2005). In terms of cyclostratigraphy, the Albertibank represents the top of the Kästner-cycle E5 (NITSCH 2005) that commences with the Hauptsandstein and ends with coaly claystones at the base of the Sandige Pflanzenschiefer. This type of transgressive small-scale cycles is typical for the Lower Keuper. The Albertibank was deposited directly above the normal flood plain facies of the Hauptsandstein. However, locally the carbonate bed may grade into a sandstone or a claystone complex replacing the entire Albertischichten Member and immediately overlying the Hauptsandstein (Fig. 2).

2.2. Lithofacies and fossil distribution of the Serrolepisbank

In the vicinity of Schwäbisch Hall the Albertibank is a 140 cm thick carbonate-dominated section ending with the up to 30 cm thick Serrolepisbank (Fig. 3). Facies and fossil content of the Serrolepisbank are laterally changing in a small scale pattern that can be observed in the Scheuermann/Hirsch quarries across an overall lateral extension of 200 m.

In the Scheuermann Quarry (Fig. 3 a, b), it is a light gray, slightly dolomitic, anthracolitic ostracod-biomicrite. Up to 5 mm thick vertical mud cracks partitioning the bed may be filled with light brownish dolomitic marl. In addition, in its lower part it has many cubic voids measuring up to 10 mm (Fig. 3b), some of which are filled with the same brownish marl and ostracod shells. Ostracods are preserved as isolated valves as well as double-valved carapaces with a micritic or coarse-crystalline calcite infilling. The cubic voids probably originate from halite cubes that formed in the soft sediment and were dissolved after consolidation of the carbonate mud. This interpretation is further corroborated by ostracod shells and small vertebrate remains projecting into the voids that were probably occupied by halite crystals (Brunner 1973, Brunner & Hagdorn 1985). Towards the top, irregular patches with a slightly higher clay or coal content, lighter or darker than the matrix, indicate sediment reworking. The uppermost 5 cm are ochre coloured and split irregularly parallel to the bedding.

Some 150 m farther to the East, in the adjacent Hirsch Quarry, the Serrolepisbank is slightly thicker and does not show any halite voids or mud-cracks. However, towards its top, the bed turns darker gray and is more anthracolitic and slightly bituminous. Its uppermost 3 cm are laminated and split into paper-thin sheets. Articulated and associated small fish skeletons in different stages of disarticulation are restricted to this laminated uppermost level. In this layer, isolated scales and bones are usually most abundant and are oriented parallel to the bedding plane. Generally, in the lower part of the Serrolepisbank, vertebrate remains are less abundant, completely isolated, and irregularly embedded (often perpendicular to the bedding plane).

Concordant with the changing facies, the vertebrate content of the Serrolepisbank changes within the 200 m lateral extension of the Scheuermann/Hirsch quarries. Ceratodont tooth-plates have been found only within a radius of approximately 10–15 m in the Scheuermann Quarry, and the articulated small fish remains are restricted to a comparably small area in the Hirsch Quarry.

The Serrolepisbank has not yielded any vertebrate remains in the Wilhelmsglück Quarry 3.5 km farther to the South (Fig. 3c). In the Eschenau and Ummenhofen quarries 10 km farther Southeast, the Serrolepisbank is dolomitic with up to 15 cm thick gypsum nodules or voids from dissolved gypsum. These outcrops yielded a vertebra of *Batrachotomus* and a few poorly preserved indetermined vertebrate remains.

3. The Serrolepisbank Fauna

3.1. Material and methods

The vertebrate material under study has been collected by the first author during the last 40 years in the Scheuermann and Hirsch quarries near Schwäbisch Hall-Steinbach. Since the closure of these quarries in the late 1960s, the Serrolepisbank, which crops out high up in the ledge, is hardly accessible. All specimens were collected from fallen blocks and prepared by acid solution. After splitting the sheets of the thinly bedded top layer, the small fish skeletons were covered with 2–3 mm thick layers of polyester resin (Akemi®) and etched with diluted acetic acid. Using this transfer method, usually both sides of one specimen could be prepared in detail. Thicker bones were glued with acryl acetate. After the etching process, such bones are fixed by a thin, translucent acryl acetate sheet. During the etching process, dark brown coaly residual mud from the anthracolitic material has to be removed under running water with a soft paint brush. For photography some of the fragile material was coated with ammonium chloride.

The material was donated to the Friedrich von Alberti-Stiftung der Hohenloher Schotterwerke in 2007 and is deposited in the Muschelkalkmuseum Ingelfingen. Additional material is housed in the Staatliches Museum für Naturkunde Stuttgart.

3.2. Invertebrates

The Serrolepisbank did not yield any marine or restricted marine bivalves or any conchostracans, which elsewhere have been found in the Albertibank and in other Lower Keuper carbonate beds (Prosi 1928: 47 ff.). The only invertebrate fossils are the above mentioned ostracods. Due to the solid limestone, it is difficult to isolate and determine them. Polished sections give evidence for their attribution to the family Darwinulidae; furthermore, members of the genus *Speluncella*, a widespread taxon in brackish to freshwater Lower Keuper deposits (Urlichs 1982), are abundant.

3.3. Vertebrates

In the Serrolepisbank outcrops around Schwäbisch Hall, the following vertebrates have been found:

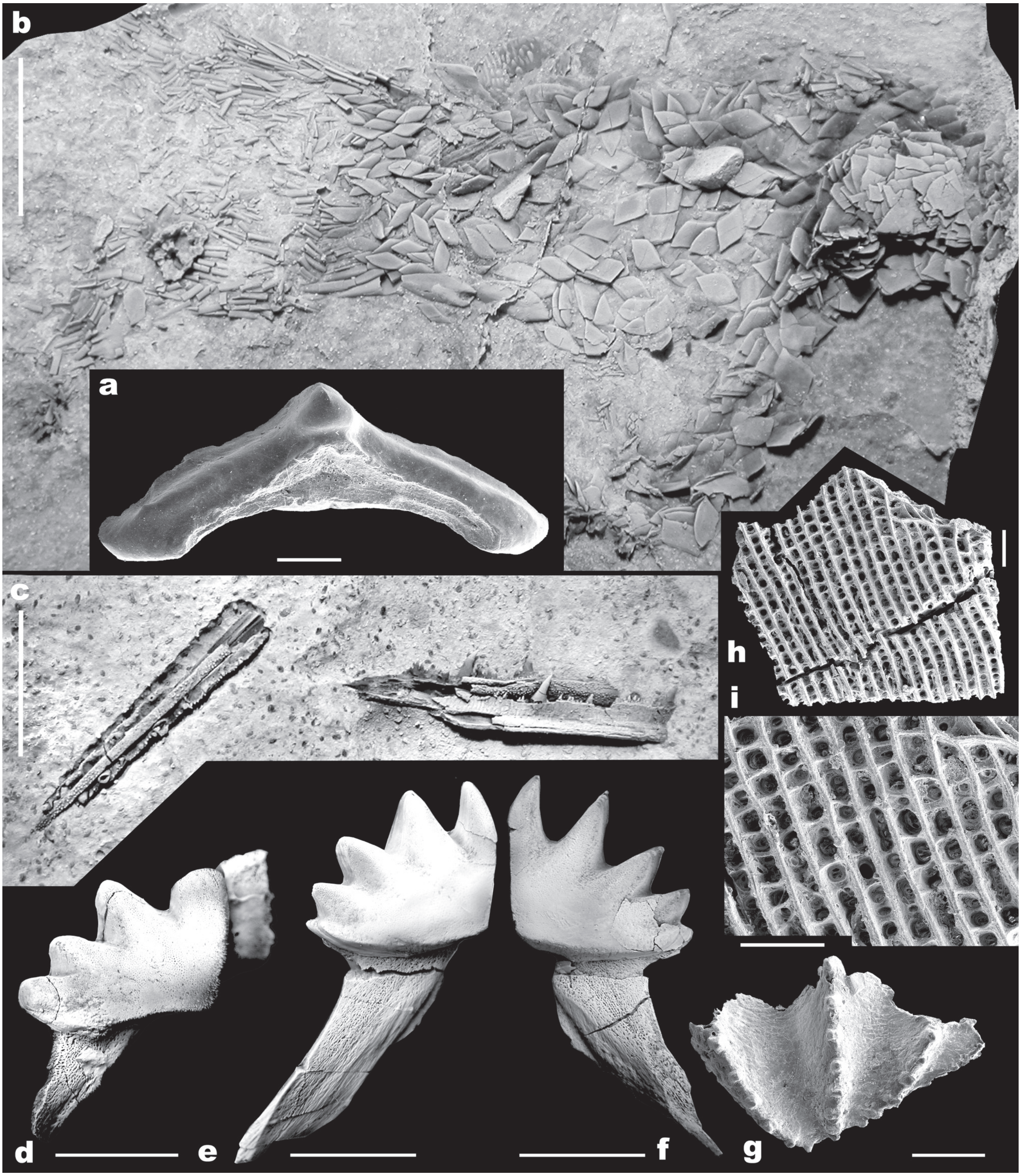

Fig. 4. Serrolepisbank Fauna. – **a**. *Lonchidion* sp., lateral tooth crown, in oblique labio-basal view; MHI 1748/49; scale 0.2 mm. **b**. ?Redfieldiiformes gen. et sp. indet.; MHI 1748/11a; scale 10 mm. **c**. *Saurichthys* sp., rostrum; MHI 1748/27; scale 10 mm. **d**–**i**. *"Ceratodus" concinnus* Plieninger, 1844. **d**. Left prearticular bone with tooth plate; MHI 647/1; scale 10 mm. **e**. Right pterygoid with tooth plate; MHI 647/2; scale 10 mm. **f**. Left pterygoid with tooth plate; MHI 647/3; scale 10 mm. **g**. Tooth plate of larva with tuberculated crest; MHI 1748/50; scale 0.5 mm. **h**–**i**. Fragment of scale; MHI 1748/51; scales 0.2 mm. – c–f whitened with ammonium chloride.

Elasmobranchii Bonaparte, 1838
Euselachii Hay, 1902
Hybodontoidea Owen, 1846
Lonchidiidae Hermann, 1977
Lonchidion Estes, 1964

Lonchidion sp.
Fig. 4a

Elasmobranch teeth no longer than 3 mm are rarely found in remnants from acid preparation. Anterior and mesial teeth have a strong occlusal crest and a labial peg and lack striation. Lateral teeth are long and narrow and have a longitudinal crest that is mesially crossed by a second crest. The Serrolepisbank material is attributed to *Lonchidion*, a genus that has been synonymized with *Lissodus* by Duffin (1985, 2001). However, according to Rees & Underwood (2002), the gracile appearance clearly separates this genus from *Lissodus*. Moreover, the much larger posterior lateral teeth with labial nodes that are typical for *Lissodus nodosus* have not been found in the Serrolepisbank. *Lonchidion* being most common in the Cretaceous appears as early as the Muschelkalk/Keuper boundary bonebed (Patterson 1966). Yet Fischer (2008), in an extensive overview of almost all described species of *Lissodus* or *Lonchidion*, prefers to treat *Lissodus* as a fossil form genus, questioning the validity of *Lonchidion* again. According to Rees & Underwood (2002), *Lonchidion* was more diverse in non-marine environments and was apparently tolerant towards salinity.

Material: MHI 647/18, 1748/49 and uncatalogued teeth from remnants of acid preparation.

Osteichthyes Huxley, 1880
Actinopterygii Cope, 1891
Saurichthyformes Aldinger, 1937
Saurichthyidae Stensiö, 1925
Saurichthys Agassiz, 1835

Saurichthys sp.
Fig. 4c

Saurichthys is represented by a 32 mm long fragment of the rostrum (praemaxillaries). The sides are delicately striated perpendicular to the long axis. The dentition comprises teeth of two size classes: Large, backward curved teeth in some distance from one another, with a delicately striated socket and a smooth tip, and several much smaller teeth in the gaps between them. The vomeres are densely packed with small tubercular teeth. Due to the fragmentary preservation of the *Saurichthys* material from the Germanic Triassic, which needs revision, it is presently not possible to assign the fragment to a species. Fragments of *Saurichthys* rostra with striated lateral sides from the Middle Keuper Lehrberg Beds (Steigerwald Formation) were described as *S. irregularis* by Oertle (1928). However, the teeth of this species have delicately striated cusps and should therefore be kept apart from *Saurichthys* (Seegis 1997: 140). The teeth of the Serrolepisbank *Saurichthys* have smooth cusps.

Material: 1 fragmentary rostrum, MHI 1748/27.

Perleidiformes Berg, 1937
Polzbergiidae Griffith, 1977
Serrolepis Quenstedt, 1885

Serrolepis suevicus Dames, 1888
Figs. 5a–i, 6a–f

The investigated material of *Serrolepis suevicus* appears to fall into two morphotypes and several size classes. This small species is a primitive polzbergiid actinopterygian with parasemionotid and perleidid affinities alike. A deep-bodied and a slender-fusiform morphotype can be distinguished but only the latter morphotype has so far been positively identified from the Schwäbisch Hall Serrolepisbank. The species has a deep skull with laterally broadened extrascapulars, the postrostral is either absent or fused with the rostral. Characteristically, there is a well-rounded posterior plate in the maxilla, a serrated lower posterior border in preopercle, and a fairly well-developed yet quite variable dentition. The lateral scales of the anterior squamation are deepened and reveal a rich ganoin ornament, and there are ridge scales with fairly large and spiny 'processes' and slender-oblong fringing fulcra in front of all fins except the pectoral fins. The caudal fin shows at least five epaxial rays.

The available new material is described in more detail elsewhere (Mutter & Hagdorn, in prep.). The genus *Serrolepis* is now understood as a highly specialized, small stem-neopterygian with a short head and powerful jaws with variable body shape and dentition.

Due to post-mortem effects and the nature of preservation of the material, we are unable to reconstruct the slender-fusiform morphotype from the Serrolepisbank precisely. Yet the shape of the lateral flank scales and the number of horizontal scale rows clearly indicate differences if compared with the deep-bodied morphotype. The slender-fusiform morphotype from the Serrolepisbank (locus typicus and stratum typicum) has to be regarded *Serrolepis suevicus*. For the deep-bodied morphotype no name is presently available.

Material: 16 fragmentary skeletons: MHI 647/10, 647/11, 647/12a + b, 647/13a + b, 647/14a + b, 1748/1a + b, 1748/2a + b, 1748/7a + b, 1748/8, 1748/9, 1748/12a + b, 1748/3a + b, 1748/13, 1748/20, 1748/22a + b, 1748/23; 8 maxillaries, MHI 1748/14a + b, 1748/16, 2033/1–2033/4; 3 dentaries, MHI 716/1–716/3; 2 pterygoids with tooth clusters, MHI 2033/5–2033/6; fragments of

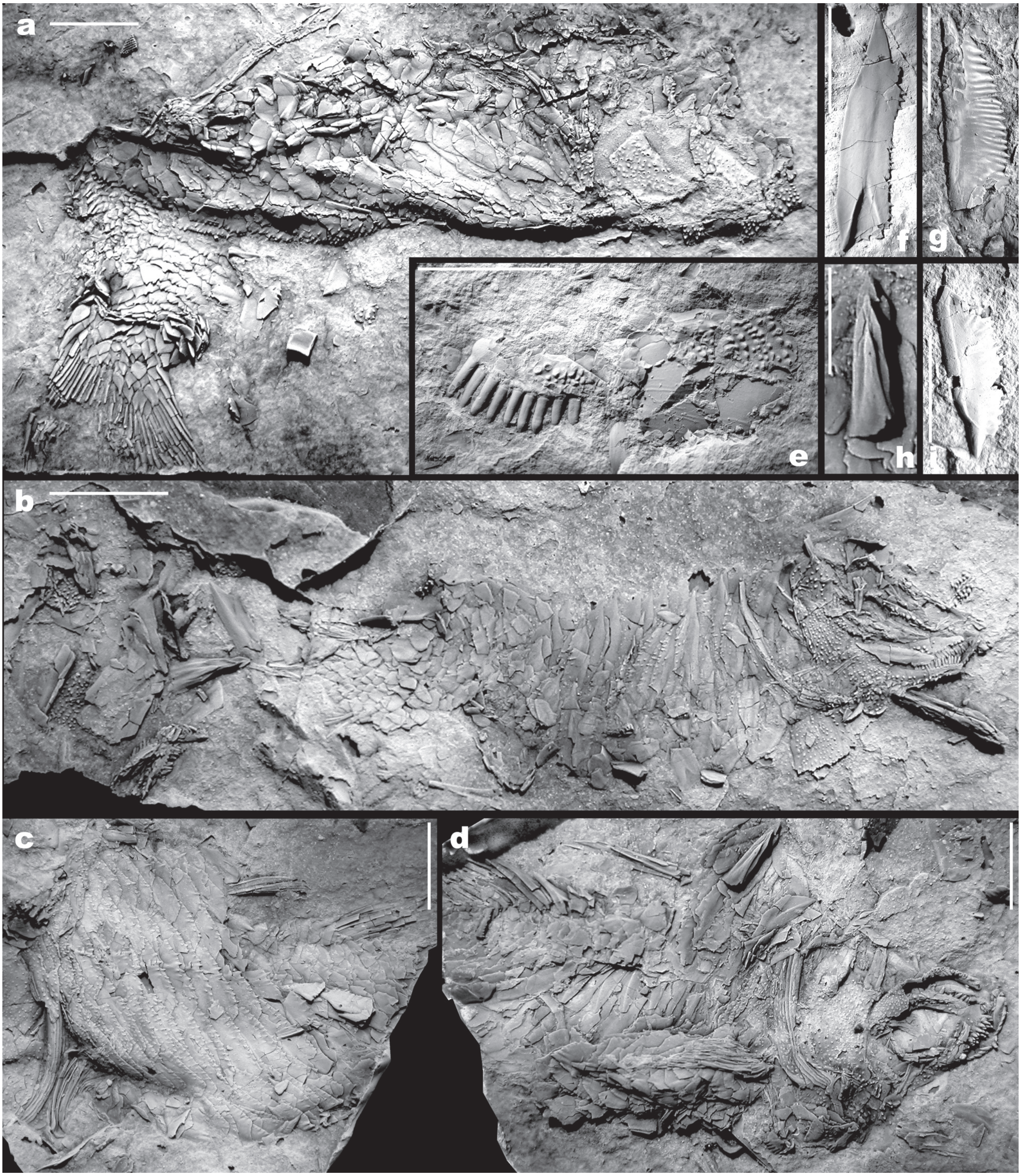

Fig. 5. Serrolepisbank Fauna. *Serrolepis suevicus* Dames, 1888. – **a**. Fragmentary skeleton with well preserved tail fin; MHI 1748/9; scale 5 mm. **b**. Fragmentary skeleton with well preserved skull (skull enlarged in Fig. 6a); MHI 1748/3; scale 5 mm. **c**–**d**. Fragmentary skeleton with well preserved skull (skull enlarged in Fig. 6b, dorsal scale enlarged Fig. 5h); MHI 1748/10a, b; scales 5 mm. **e**. Left maxillary, MHI 1748/13; scale 5 mm. **f**. Scale of large individual, interior view; MHI 1748/17; scale 5 mm. **g**, **i**. Scales of large individuals, exterior view; MHI 647/7; scales 5 mm. **h**. Dorsal scales of small individual; MHI 1748/10a; scale 3 mm. – All specimens whitened with ammonium chloride.

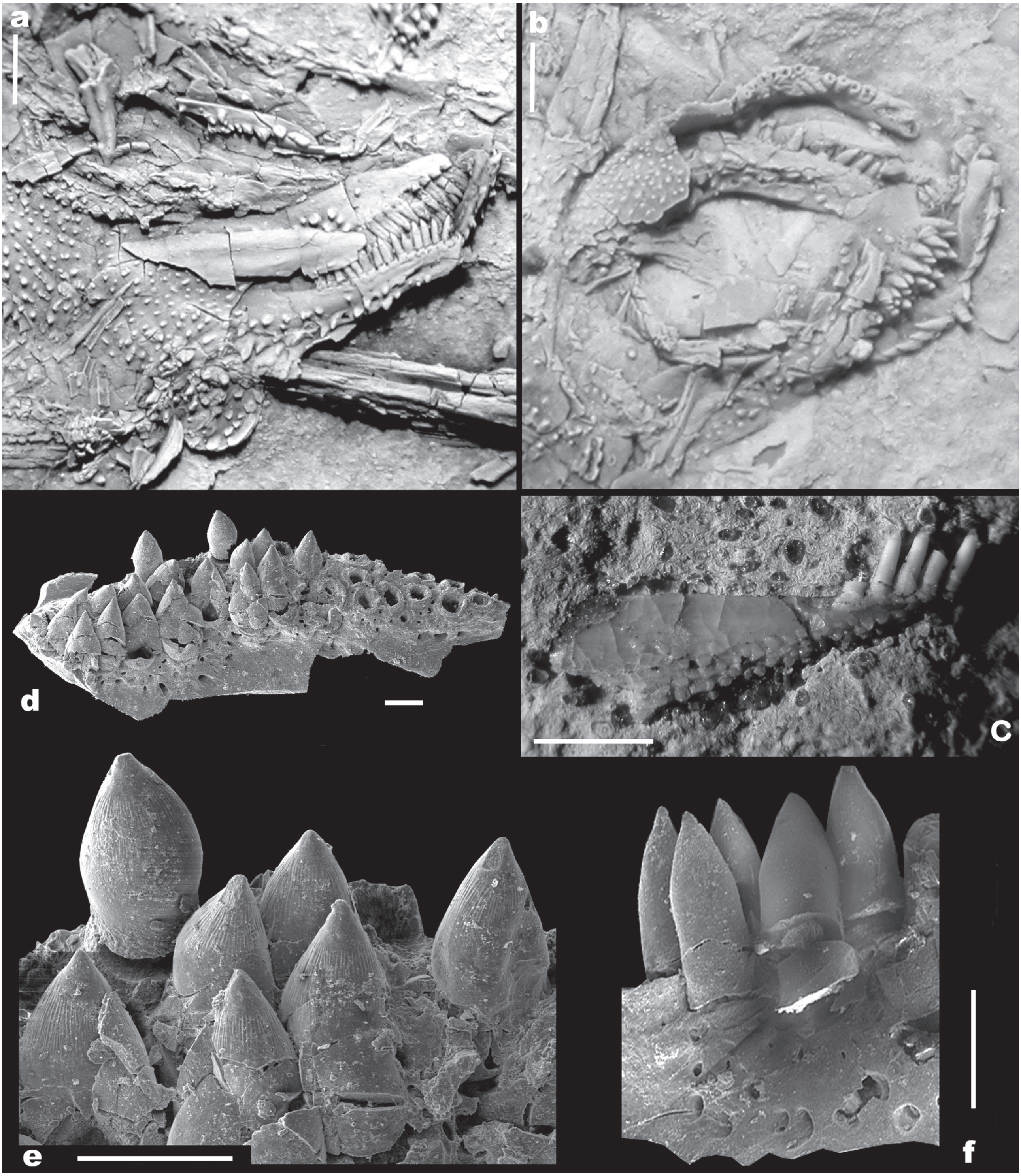

Fig. 6. Serrolepisbank Fauna. *Serrolepis suevicus* Dames, 1888. – **a**. Skull of small individual; MHI 1748/3; scale 1 mm. **b**. Skull of small individual; MHI 1748/10a; scale 1 mm. **c**. Dentary; MHI 716/3; scale 2 mm. **d**, **e**. Pterygoid fragment with anterior tooth cluster; MHI 2033/5; Scales 0.2 mm. **f**. Pterygoid fragment with tooth cluster; MHI 2033/6; scale 0.2 mm. – a–b whitened with ammonium chloride.

tooth bearing bones from remants of etching process, MHI 647/15; isolated scales, MHI 43/1–43/6, 647/16–647/17, 1748/4–1748/9, 1748/15a + b, 1748/17, 1748/26; uncatalogued scales and bones from remnants of acid preparation.

?Redfieldiiformes BERG, 1940

?Redfieldiiformes fam., gen. et sp. indet.
Fig. 4b

The two fragmentary and dissociated skeletons are of approx. 6 cm overall length. The scales are smooth throughout the squamation and all scales have a pitted surface and a straight posterior margin. Occasionally, an additional acute tip is intercalated at about half way down the margin. In the middle of the flank, the scales are about twice as deep as wide. The pore-bearing scales look very much like those from the Lehrberg Beds described by SEEGIS (1997: pl. 22, figs. 15–16) and attributed to the Redfieldiidae.

Material: 2 fragmentary skeletons: MHI 1748/5, 1748/11a + b; uncatalogued scales from remnants of acid preparation.

Sarcopterygii ROMER, 1955
Actinistia COPE, 1871
Coelacanthiformes BERG, 1940
?Coelacanthidae AGASSIZ, 1843

?Coelacanthidae gen. et sp. indet.
Fig. 7a–n

The bulk of the larger bones in the Serrolepisbank can be attributed to an unidentified coelacanthiform. Isolated bones of the skull give evidence for a medium-sized to large fish. Although coelacanthiform fishes were reported from each of the Germanic Triassic groups, their diversity is not sufficiently known, due to a very provisional state of morphological description of the available material. Articulated but poorly preserved skeletons of small coelacanthiforms from the Upper Buntsandstein Grès à Voltzia (early Anisian) of Eastern France and from the Middle Keuper Coburg Sandstone (late Carnian/early Norian) of Franconia were figured by GALL (1971: 62) and by DEHM (1956, 1957) but not attributed to a genus. From the Upper Muschelkalk (late Anisian), articulated skeletons of *Hainbergia granulata* and *Garnbergia ommata* were described by SCHWEIZER (1966) and MARTIN & WENZ (1984), the latter being assigned to families Mawsoniidae by FOREY (1998), to Whiteidae by SCHULTZE (2004), or to an undetermined family by CLEMENT (2005). An isolated basisphenoid was reported from the Lower Muschelkalk by ALDINGER (1930), a pterygoid from the Middle Muschelkalk by SCHULTZE & MÖLLER (1986). Several articulated coelacanthiform skeletons have been masterly prepared from Upper Muschelkalk limestone nodules by private collectors and await description. SEEGIS (1997) attributed isolated bones from the Middle Keuper Lehrberg Beds (late Carnian) to *Chinlea* and to aff. *Hainbergia*. Moreover, the existence of large coelacanthiforms in the Lower Keuper water bodies has been proven by the swimming trace *Parundichna schoelli* preserved at the base of a large Lower Keuper Hauptsandstein slab from Rot am See near Crailsheim. The analysis of this trace yielded evidence for a coelacanthiform that grew as large as 1.5 m (SIMON et al. 2003).

The Serrolepisbank coelacanthiform material represents different growth stages of a single species with gulars ranging from 22–115 mm and pterygoids from 31–71 mm length. Taken the gular length one twelfth of the total length as measured in *Ticinepomis* from the Middle Triassic Besano Formation of Switzerland (RIEPPEL 1980), the largest individuals of the Serrolepisbank coelacanthiform reached approx. 1.3 m. Yet identification at present is not possible.

Material: isolated bones from a disarticulated skull and shoulder girdle, MHI 647/5; 3 basisphenoids, MHI 1748/34, 1748/35, 2038/1; 3 parasphenoids, MHI 1748/29, 2038/4, 2038/50; 10 pterygoids, MHI 647/7, 1748/33, 2038/6–2038/13; 1 quadratum, MHI 2038/28; 3 urohyals 2038/2–2038/3, 2038/5; 3 ceratohyals, MHI 2038/51–2038/53; 10 opercula, MHI 610, 647/4, 2038/14–2038/21; 2 fronto-dermosphenotica, MHI 1748/24, 1748/25; 3 parieto-intertemporals, MHI 2038/26–2038/27, 2038/49; 1 praeopercular, MHI 2038/22; unidentified dermal bones of skull roof, MHI 647/9, 2038/23–2038/25, 2038/29–2038/32, 2038/48, 2038/50, 2038/58; 3 angulars, MHI 2038/33–2038/34, 2038/47; 1 splenial, MHI 2038/35; 1 dental, MHI 2038/36; 13 gularia, MHI 647/6, 1702, 1748/32, 2038/37–2038/46; 3 cleithra, MHI 2038/55–2038/57; 1 clavicula, MHI 1748/31; 1 pelvis, MHI 2038/65; 1 basal plate of the posterior dorsal or anal fin, MHI 2038/66; 1 anterior dorsal fin with the basal plate, MHI 1703; 2 lepidotrichia, MHI 2038/67–2038/68; 2 scales, MHI 2038/69; uncatalogued isolated lepidotrichia and bone fragments from remnants of acid preparation.

Dipnoiformes CLOUTHIER & AHLBERG, 1995
Dipnoi MÜLLER, 1845
Ceratodontoidei NIKOLSKI, 1954
Ptychoceratodontidae MARTIN, 1982
Ptychoceratodus JAEKEL, 1926

Ptychoceratodus serratus (AGASSIZ, 1838)

This large ceratodontoid has strongly serrated tooth plates with an irregularly wrinkled surface that differs from the evenly and finely pitted surface of *Ceratodus* as indicated by the etymology of its junior synonym, *P. runcinatus* (PLIENINGER, 1844). In the Serrolepisbank, it is much rarer than *"C." concinnus*. One of the two available juvenile tooth plates (length 11 mm) has irregular

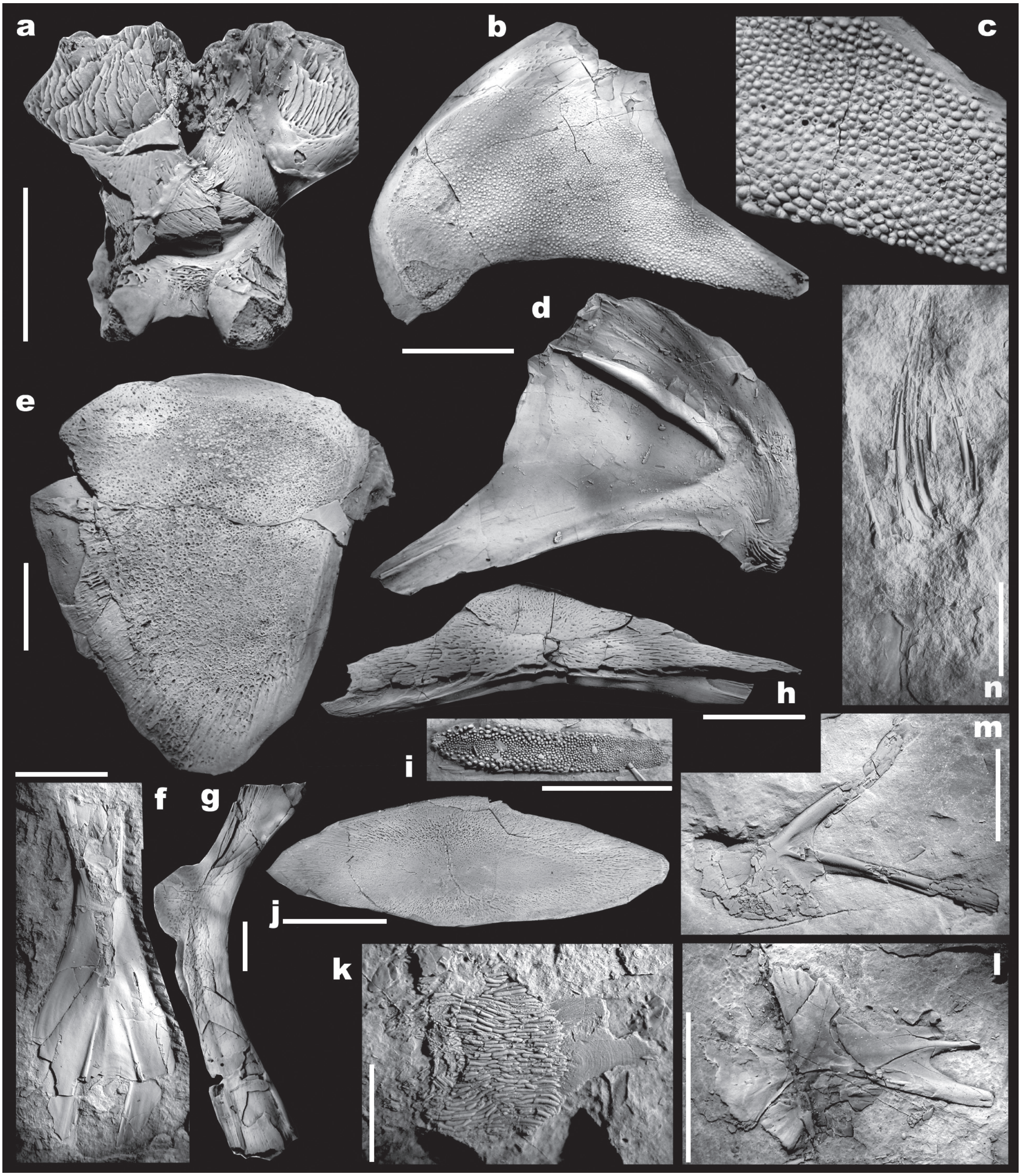

Fig. 7. Serrolepisbank Fauna. ?Coelacanthidae gen. et sp. indet. – **a**. Basisphenoid in posterior view; MHI 1748/35; scale 10 mm. **b–d**. Left pterygoid in lateral view and enlarged to show dentition; MHI 647/7; scale 10 mm. **e**. Operculum in lateral view; MHI 2038/14; scale 10 mm. **f**. Urohyal; MHI 2038/2; scale 10 mm. **g**. Ceratohyal; MHI 2038/51; scale 10 mm. **h**. Angular; MHI 2038/4; scale 10 mm. **i**. Anterior part of parashenoid; MHI 2038/50; scale 5 mm. **j**. Gular; MHI 2038/38; scale 10 mm. **k**. Scale; MHI 2038/69; scale 5 mm. **l**. Pelvis; MHI 2038/65; scale 10 mm. **m**. Basal plate of posterior or anal fin; MHI 2038/66; scale 10 mm. **n**. Anterior dorsal fin with basal plate; MHI 1703; scale 10 mm. – All specimens whitened with ammonium chloride.

tubercles on the crests of the ridges. *P. serratus* was the only ceratodontoid found in the Sandige Pflanzenschiefer at Michelbach an der Bilz.

Material: 1 mould of a juvenile left praearticular tooth plate, MHI 410; 1 fragment of a juvenile tooth plate, MHI 1748/42.

? Ptychoceratodontidae MARTIN, 1982

"Ceratodus" concinnus PLIENINGER, 1844
Fig. 4d–i

Most of the Serrolepisbank ceratodontoid tooth plates correspond in shape with *"Ceratodus" concinnus* from the late Carnian Middle Keuper Lehrbergbänke. According to SEEGIS (1997), the skull roof of *"C." concinnus* differs from all other ceratodontoids. Therefore, he suggests to establish a new genus of family Ptychoceratodontidae for *"C." concinnus*. CAVIN et al. (2007) discuss an inclusion of *"C." concinnus* into the genus *Ferganoceratodus*.

The upper jaw (pterygoid) tooth plates have five ridges and the lower jaw (praearticular) tooth plates have four ridges that are less prominent and sharp than those of *Ptychoceratodus serratus* but more prominent and sharper than in *Ceratodus kaupi*. The sharp tooth plate ridges had rather a cutting than a crushing function. In these characters and in their much smaller size they differ from both of these common Lower Keuper lungfish tooth plates, which reach a maximum length of more than 100 mm *(C. kaupi)* and 80 mm *(P. serratus)*. The Serrolepisbank material comprises isolated tooth plates of juveniles (larvae) less than 2 mm with tuberculated crests, and adult individuals of up to 20 mm with smooth crests, most of them still attached to the pterygoid or the praearticular bones respectively. The juvenile tooth plates and the fragmentary scales were selected from acid preparation remnants. Although the fossil record and preservation of the Serrolepisbank fish remains are very good, no bones of the ceratodontoid skull plating have been found.

Material: 1 left praearticular with tooth plate of a juvenile individual, MHI 709; 2 left praearticulars with tooth plate, MHI 647/1, 1748/36; right praearticular with tooth plate, MHI 1748/38; right pterygoid with tooth plate, MHI 647/2; right pterygoid without tooth plate, MHI 2034; fragment of right pterygoid with tooth plate 1748/37; left pterygoid with tooth plate, MHI 647/3. Scale fragment, MHI 1748/51. Uncataloged fragments of ceratodontoid scales from remnants of acid solution.

Amphibia LINNÉ, 1758
Temnospondyli ZITTEL, 1890
Capitosauroidea SAEVE-SÖDERBERG, 1935
Mastodonsauridae WATSON, 1919
Mastodonsaurus JAEGER, 1828

Mastodonsaurus giganteus (JAEGER, 1828)
Fig. 8c

Mastodonsaurus is the most common Lower Keuper temnospondyl. It has been recorded from the Upper Muschelkalk *nodosus* biozone (early Ladinian) to the Obere Graue Mergel of the Lower Keuper (SCHOCH 1999, 2002). However, the Serrolepisbank has yielded only one fragment of a tusk of a small individual that corresponds in every respects with other *Mastodonsaurus* teeth.

Material: 1 tusk of a small individual (MHI 22).

Plagiosauridae ABEL, 1919
Gerrothorax NILSSON, 1937

Gerrothorax pulcherrimus (E. FRAAS, 1913)
Fig. 8a, b

In several Lower Keuper fossil lagerstaetten, *Gerrothorax* is the most common temnospondyl (SCHOCH 2002). Two skull fragments and some osteoderms give evidence for the presence of this small plagiosaur. The well preserved praemaxillary teeth have two smooth cutting edges. The present material corresponds with *Gerrothorax pustuloglomeratus* from the Untere Graue Mergel of Kupferzell-Bauersbach (HELLRUNG 2003), a taxon that was treated as a junior synonym of *G. pulcherrimus* by JENKINS et al. (2008).

Material: 1 right half of a skull, MHI 1348/1; 1 parietal with fragments of the right skull half, MHI 1348/2; 1 tooth, MHI 1348/6; 1 left tabular, MHI 1748/39; 3 osteoderms, MHI 1348/3–1348/5.

Reptilia LINNÉ, 1758
Diapsida OSBORN, 1903
Sauropterygia OWEN, 1860
Eosauropterygia RIEPPEL, 1994
Eusauropterygia TSCHANZ, 1989 (in BÜRGIN et al. 1989)
Nothosauridae BAUR, 1889
Nothosaurus MÜNSTER, 1834

Nothosaurus sp.
Fig. 8f

The Serrolepisbank has yielded only three fragmentary bones that can be assigned to *Nothosaurus*. However, none of them is diagnostic at the species level. In other Lower Keuper vertebrate fossil lagerstaetten, e. g., the basal bonebed of the Anthrakonitbank of Kirchberg an der Jagst, three species have been found, which represent three size classes, among them *Nothosaurus edingerae*. In its small size the Serrolepisbank material fits *N. edingerae*. However, the postcranium of this otherwise

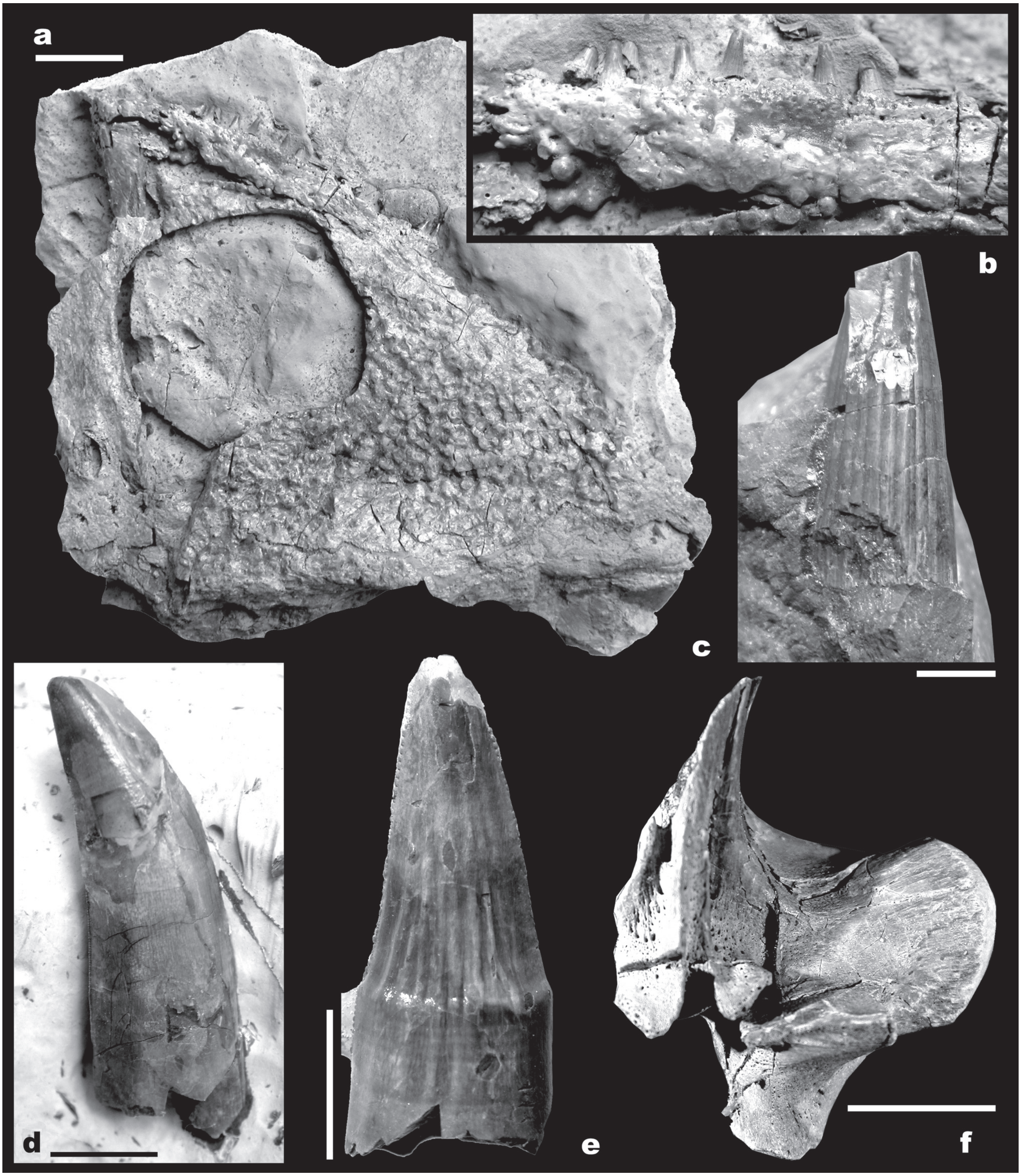

Fig. 8. Serrolepisbank Fauna. – **a**–**b**. *Gerrothorax pulcherrimus* (E. FRAAS, 1913), skull fragment in dorsal view, praemaxilla with teeth enlarged; MHI 1348/1; scale 10 mm. **c**. *Mastodonsaurus giganteus* (JAEGER, 1828), tusk; MHI 22; scale 5 mm. **d**. *Batrachotomus kupferzellensis* GOWER, 1999, tooth; MHI 1400; scale 10 mm. **e**. ?Suchia indet., tooth; MHI 1748/46; scale 5 mm. **f**. *Nothosaurus* sp., neural arch of dorsal vertebra; MHI 1748/43; scale 10 mm.

well diagnosed taxon is still unknown. Moreover, the processus spinosus of MHI 1748/43 is so fragmentarily preserved that it remains uncertain whether it was high as in *N. mirabilis*, or low as in the *N. jagisteus* lineage. From a stratigraphic viewpoint, assignment to *N. edingerae*, the latest representative of genus *Nothosaurus* ranging from upper Lettenkeuper to upper Gipskeuper (Grabfeld Formation, Anatinabank, earliest Carnian; HAGDORN & RIEPPEL 2000) seems to be most probable.

Material: 1 centrum of dorsal vertebra, MHI 1738/40; 1 neural arch of dorsal vertebra, MHI 1748/43; 1 thoracal rib, MHI 1748/30.

Archosauria COPE, 1869
Crurotarsi SERENO & ARCUCCI, 1990
Suchia KREBS, 1974
Batrachotomus GOWER, 1999

Batrachotomus kupferzellensis GOWER, 1999
Fig. 8d

A 9 cm long tooth of the "rauisuchian" archosaur *Batrachotomus* from Schwäbisch Hall was described by FRAAS (1900) as a new species of *Zanclodon*, a genus with an extremely difficult taxonomic history (GALTON 2001). FRAAS regarded these teeth with two serrated cutting edges from the Lower and Middle Keuper of Southwest Germany as early representatives of the dinosaurs. The stratigraphic position of his *"Zanclodon Schützii"* was erroneously said to be Trigonodusdolomit (Upper Muschelkalk), but there is no doubt that the specimen came from the Lower Keuper ("Dolomit der Lettenkohle", WAGNER 1937: 29). A less complete but equally sized specimen without its root preserved from the Serrolepisbank of Rieden was already described and figured by QUENSTEDT (1885: 178, pl. 12, figs. 19, 20) and attributed to *Cladyodon crenatus*; HAGDORN (1990) re-figured this specimen from the Tübingen collection. v. HUENE (1907–1908: 238, pl. 98, fig. 4) connected *"Zanclodon" schuetzii* with the large vertebrae of the protorosaur *Tanystropheus* from the Upper Muschelkalk of Crailsheim that he interpreted as caudal vertebrae of a dinosaur related to *Coelophysis* and attributed the specimen to *Tanystrophaeus* [sic!] *conspicuus* H. v. MEYER?.

The laterally compressed teeth are slightly recurved and serrated at both edges. Only in MHI 1400 parts of the root are preserved, whereas the original of *"Zanclodon" schuetzii* (SMNS 53538) has a 6 cm long root and is definitely a maxillary tooth. According to size and morphology, the Serrolepisbank material can confidently be attributed to *Batrachotomus kupferzellensis* and corresponds to the well documented material from the Untere Graue Mergel of Kupferzell-Bauersbach and Vellberg-Eschenau (GOWER 1999).

Material: 6 isolated teeth, MHI 1400, 1748/43–1748/47.

?Suchia indet.
Fig. 8e

An isolated tooth with serrated edges differs from *Batrachotomus*. The crown is 20 mm long and only fragments of the root are preserved; distally from an annulus 6 mm above the base, the tooth is constricted and laterally more compressed and the ornamentation of shallow grooves and ridges becomes more pronounced. Serrated edges at both sides of the basal 6 mm clearly indicate that this is part of the crown and not of the root. *Batrachotomus* teeth have no annulus and their sides are smooth throughout. At present, this tooth cannot be attributed to any known taxon.

Material: 1 tooth, MHI 2035.

Superorder indet.
Doswelliidae WEEMS, 1980

Doswelliidae gen. et sp. indet.
Fig. 9

A single osteoderm similar in shape and size to osteoderms from the Untere Graue Mergel of Vellberg-Eschenau that are assigned to the family Doswelliidae (pers. communication R. SCHOCH, Stuttgart).

Material: 1 osteoderm, MHI 2078.

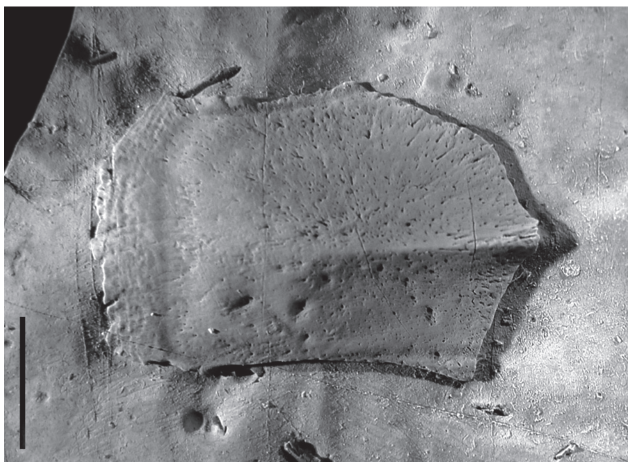

Fig. 9. Osteoderm of a doswelliid reptile (det. Dr. R. SCHOCH); MHI 2078. – Whitened with ammonium chloride. Scale 5 mm.

4. Palaeoecology

4.1. Palaeoecology of the Serrolepisbank

The rich vertebrate faunal assemblages collected from different horizons in the Southwest German Lower Keuper have stimulated reconstructions of early late Ladinian palaeoenvironments (Schoch 2002, 2006). The Lower Keuper is characterized by an extraordinarily small scale lateral and vertical facies change that hampers lithostratigraphical correlation even within short distances. However, bed-by-bed correlation of the 100 ka cycles in measured sections from nearby outcrops give evidence for patchy palaeoenvironments of brackish lakes or lagoons, lake shores, and sand-filled channels with horsetail swamps in between. Comparable to the better known Untere Graue Mergel, the change in the lateral facies of the Albertibank is indicative of a palaeoenvironmental change that provided different habitats. Although the Serrolepisbank contains densely packed vertebrate remains, it is not a bonebed sensu stricto because (1) the vertebrate remains are not abraded or fragmented as a result of prefossilisation, (2) its matrix is a lutitic limestone devoid of other clasts than vertebrate ossicles without any indication of condensation, and (3) it does not contain any unequivocal marine faunal elements that are typical for all other Keuper and Muschelkalk bonebeds (Reif 1971, Hagdorn & Reif 1988).

The lateral extension of the limestone facies of the Serrolepisbank with its diverse vertebrate fauna is restricted to an area of less than 130 km^2 in the vicinity of Schwäbisch Hall. In the Scheuermann and Hirsch quarries of Schwäbisch Hall-Steinbach, the Serrolepisbank with local mud-cracks and voids resulting from dissolved halite crystals is indicative of intermittent, short-term pedogenetic processes during deposition. The small area with laminated, bituminous, anthracolithic limestone at the top that yielded the articulated fish skeletons is interpreted as a rest pond of a larger water body in which an impoverished fauna of relatively small actinopterygians has accumulated before they died, possibly during periods of drought.

Brackish to freshwater lakes of the Lower Keuper, e. g. the *Serrolepis* lake, contain a more or less diverse suite of actinopterygians that are found in association with a guild of large predatory species. Among these, *Saurichthys* is generally regarded as a marine genus, however, it has also been reported from the lacustrine, oligohaline to freshwater Upper Lehrberg Bed of the Middle Keuper (late Carnian) (Seegis 1997). The same is true for the small lonchidiid shark genus *Lonchidion* which was more diverse in non-marine environments and tolerated a wide range of salinity (Rees & Underwood 2002). The lungfish, the coelacanth, and the temnospondyls were also freshwater or brackish water faunal elements and the archosaurs were terrestrial. Typical marine Lower Keuper faunal elements that occur abundantly in many bonebeds, such as the hybodontiform sharks *Hybodus*, *Acrodus*, *Polyacrodus*, *Palaeobates*, the basal actinopterygians *Colobodus*, *Gyrolepis*, *Birgeria*, and large *Saurichthys* are absent. No large marine nothosaurs or armoured cyamodontoid placodonts, which occur in several Lower Keuper horizons, have been found in the Serrolepisbank. For faunistic spectra of different Lower Keuper bonebeds see Hagdorn & Reif (1988).

The local abundance of *Serrolepis suevicus* in the Serrolepisbank is interpreted in association with the above-mentioned vertebrates. The spectacular dentition of *Serrolepis* yields evidence of an adaptation to a semi- or full-durophagous dietary specialization as has been stated for the polzbergiid *Felberia* from the Ladinian and Carnian of the Southern Alps (Lombardo & Tintori 2004). The long, protruding, chisel-shaped dentary and maxillary teeth with pointed tips probably served for seizing hard prey particles that were crushed by densely packed batteries of bloated teeth on palatal bones. As ostracods are the only but very abundant invertebrate fossils in the Serrolepisbank it is tempting to suggest a prey-predator interaction between them and *Serrolepis suevicus*. This interpretation is supported by bicuspid teeth from upsection *Serrolepis* bearing palaeocommunities (Mutter & Hagdorn in prep.). If their tentative attribution to *Serrolepis* is correct, they would indicate an adaptive trend towards dietary specialization within this genus.

One is tempted to assume a predatory behaviour, feeding style and diet comparable to *Felberia excelsa* due to the verticalized jaw suspensorium with pivotal articulation underneath the orbit. *Serrolepis* is considerably smaller than *Felberia* and only the deepest lateral flank scales may exceed a depth/width ratio of 3 : 1.

Presumably the small actinopterygians (*Serrolepis* and the small ?redfieldiiform) and juvenile ceratodonts were preyed upon by coelacanths, *Saurichthys*, and *Gerrothorax*, which in return belonged to the prey spectrum of *Mastodonsaurus*, the largest predator in Ladinian brackish and freshwater habitats. The large terrestrial suchian predators may have invaded the dry-falling '*Serrolepis* bays', scavenging on larger fish and amphibian carcasses. This would explain the lack of articulated larger fish skeletons in the Serrolepisbank.

In general, the fossil content and preservation yield evidence for a depositional environment in an estuarine, brackish or limnic, occasionally dry-falling part of the Albertibank lake. Towards the West (Unterohrn), abundant unionoid and bakevelliid bivalves, conchostracans, darwinulid ostracods, and dipnoans and temnospondyls still indicate limnic-brackish conditions, possibly with an intermittent marine influx at the top of the 1.5 m thick Albertibank (*Neusticosaurus* remains). Farther to the West (Badenia), the Albertibank was deposited under restricted marine conditions, as indicated by myophoriid bivalves. Towards the North (Franconia), environmental conditions were brackish-limnic and turned to be limnic and almost unfossiliferous in Thuringia. Some 10 km farther to the East (Vellberg), the Serrolepisbank has become dolomitic with pedogenic sulphate nodules.

4.2. Comparable habitats from the Germanic Triassic

Palaeocommunities with a similar vertebrate composition can be found in further stratigraphic horizons within the Lower Keuper and also in the Middle Keuper and the Upper Buntsandstein. Some of these have already been described and analyzed. For an overview of the Lower Keuper vertebrate Lagerstätten in Northern Baden-Württemberg and in Thuringia, see HAGDORN et al. (in prep.).

Sandige Pflanzenschiefer – In its type area around Schwäbisch Hall, the Serrolepisbank is overlain by dark and coaly claystones still rich in small vertebrate remains. This layer is the base of the Sandige Pflanzenschiefer, a lithostratigraphic unit forming the base of the upsection Cycle E6 (Fig. 2). However, the coaly base is interpreted as the top of the underlying cycle E5 (NITSCH 2005). In 1976, this horizon overlying mud-cracked claystones yielded a rich fauna of well preserved vertebrates in a road construction site at Michelbach an der Bilz, 2.9 km SSE of the Scheuermann Quarry (Fig. 1; for locality data see Appendix 1). However, in the nearby Wilhelmsglück Quarry situated 0.6 km to the West, this horizon yielded no vertebrate material at all. The mud cracks give evidence for an original water body drying up. The Michelbach faunal assemblage comprises abundant *Serrolepis* and other actinopterygian scales, rare *Ptychoceratodus* tooth plates and skull bones of the Serrolepisbank coelacanthiform, the temnospondyls *Trematolestes* (articulated skeleton of the type specimen), *Kupferzellia*, *Mastodonsaurus*, and the plagiosaurs *Gerrothorax* and *Plagiosuchus.* Fragments of an unidentified choristodere, the chroniosuchian *Bystrowiella*, a doswelliid archosauromorph, and other archosaurs including the “rauisuchian” *Batrachotomus* are less abundant (HAGDORN 1980, SCHOCH 2006). This vertebrate fauna is almost identical with the Serrolepisbank fauna, however, tetrapods are more diverse and less rare.

Albertibank – At Unterohrn 21.5 km farther to the Northwest (for locality data see Appendix 2), the Albertibank contains a more diverse invertebrate fauna and a distinct macroflora. Here, the up to 1.75 m thick dolomitic limestone bed wedges out within the outcrop in dark grey claystones and re-appears after a few metres. A separate bed that could be correlated to the Serrolepisbank is not present. Near the bed-top are mm-thin layers with densely packed conchostracans *(Euestheria minuta)* and sparsely distributed small vertebrate remains. Accumulations of the large brackish water bivalves *Unionites longus* and *Bakevellia substriata* are distributed in patches, as well as patchy areas with unidentified roots, which, however, are not in situ. The most remarkable and abundant floral elements are sporophylls of the lycopsid *Lepacyclotes* (former *Annalepis zeilleri*) and metre-sized rhizomes with radially arranged roots that are likely to belong to this lycopsid. Vertebrates are represented by scales of unidentified small actinopterygian fish, *Ceratodus* sp., *Plagiosternum granulosum*, *Mastodonsaurus giganteus*, *Neusticosaurus pusillus*, and a small nothosaur. *Serrolepis* has not been found in this outcrop. *Neusticosaurus* is an abundant faunal element of dolomite beds derived from marine incursions into the Southwest German Lettenkeuper estuaries. Among all Lower Keuper temnospondyls, *Plagiosternum* is the only one that is found in brackish to marine sediments. This data gives evidence for an intermittently stronger marine influence in the Unterohrn Albertibank compared to the Schwäbisch Hall Serrolepisbank. Presumably, the thick carbonate bed wedging out within a few metres delineates the shoreline of a channel or a river branch entering the brackish water body with the lycopsid rhizomes eroded and embedded in the carbonatic sediment.

Untere Graue Mergel – The upsection Cycle E7 commences with the Untere Graue Mergel that may be developed in clastic facies (Fig. 2; NITSCH 2005). The upper part of this horizon yielded most of the Lower Keuper vertebrate Lagerstätten in the Hohenlohe area. The fossil sites of Kupferzell (9.3 km NW of Schwäbisch Hall) and Vellberg-Eschenau (10 km E of Schwäbisch Hall) have been described in detail (SCHOCH & WILD 1999, SCHOCH 2002). For locality data see Appendix 2. Individual layers of these Lagerstätten contain abundant scales and bones of *Serrolepis* and small ?semionotid and ?redfieldiid fish, together with more or less diverse remains of temnospondyls and archosauriforms. Again, deep mud-cracks of the underlying marlstones at the Kupferzell site give evidence for accumulations of disarticulated carcasses and bones transported by currents into a brackish to freshwater lake that had fallen dry before. However, in both localities several subsequent fossil horizons with changing faunistic compositions within a few decimetres indicate changing depositional conditions.

Middle Keuper Lehrbergbänke – During the late Carnian, shallow lakes and playas expanded over large parts of the slowly subsiding foreland of the Vindelician-Bohemian Massif, which have been studied in a monograph by SEEGIS (1997). According to this author, several carbonate beds in this unit, the Lehrbergbänke, yielded invertebrate and vertebrate faunas. It is the Upper Lehrbergbank that contains a fauna partly resembling the Serrolepisbank fauna. However, these beds are devoid of *Serrolepis suevicus*. The invertebrates comprise abundant limnic-brackish molluscs, ostracods, and conchostracans, fully aquatic vertebrates are represented by a lonchidiid shark, a palaeoniscid, a redfieldiid, a saurichthyid and three semionotid fish, two coelacanthiforms and the dipnoans *“Ceratodus” concinnus* and *Ptychoceratodus philippsi*. Temnospondyls are represented by one or two metoposaur species and by a rare *Gerrothorax*, reptiles only known by teeth belonging to unidentifiable phytosaurs and cynodontians.

Upper Buntsandstein Grès à Voltzia – The habitat of the small deep bodied polzbergiid *Dipteronotus atavus* and its associated vertebrate fauna of the early Anisian Grès à Voltzia of the Vosges Mountains (Eastern France) and of Badenia close to the western border of the Central European Basin (Gall 1971, Jörg 1969a, b) likewise resembled the habitat reconstructed from the Serrolepisbank and neighbouring stratigraphic horizons near Schwäbisch Hall. The conditions for preservation even of delicate soft parts were much better in these fossiliferous claystone lenses that were deposited in deltaic water bodies of an alluvial plain and yielded a broad variety of insects and other arthropods (Gall et al. 2006). Actinopterygians are represented by a small saurichthyid, the semionotid *Pericentrophorus*, the polzbergiid *Dipteronotus*, sarcopterygians by an unidentified small coelacanthid, the temnospondyls by *Eocyclotosaurus*, and the reptiles by an unidentified skeleton fragment (Gall et al. 2006). Marine vertebrates are not present. On the family level, this vertebrate faunal assemblage resembles the Serrolepisbank fauna, although it is approx. 10 Ma older.

4.3. Palaeoecological signature of "*Serrolepis* lakes"

The Serrolepisbank fauna represents a limnic to brackish estuarine vertebrate palaeocommunity typical for late Middle Triassic lakes in the southwestern part of the Germanic Basin. The Serrolepisbank actinopterygian fauna is dominated by small polzbergiids and ?redfieldiiforms. Presumably, *Serrolepis* was specialized in feeding on ostracods, which were seized by long, pointed dentary and maxillary teeth and crushed by dense batteries of bloated teeth on palatal bones. *Serrolepis* was living in freshwater and/or brackish water and is not found in bonebeds derived from marine sediments. The small actinopterygians were preyed upon by saurichthyids, coelacanthids, and temnospondyls. In the mud-cracked Sandige Pflanzenschiefer claystones of the nearby Michelbach Fossillagerstätte, current-transported vertebrate carcasses were concentrated, possibly in river branches entering lakes that had dried up before. Among these, *Trematolestes* is a typical piscivore with an elongate snout, and the plagiosaur *Gerrothorax* was probably a specialized large-mouth predator ambushing its prey. The top position in the food chain was held by the capitosaurid *Mastodonsaurus giganteus*. This temnospondyl reached total lengths of more than five metres. During dry periods, terrestrial archosaurs such as *Batrachotomus* invaded the dried-up water bodies scavenging on larger fish and tetrapods from the rest ponds.

Similar habitats existed already in late Anisian times, close to the western margin of the southern Germanic Basin in an estuarine landscape of the Upper Buntsandstein Grès à Voltzia. However, polzbergiid fish are represented by *Dipteronotus*. Polzbergiids have not been found in the late Carnian Lehrberg lakes, which are otherwise characterized by a similar vertebrate palaeocommunity. The polzbergiid *Felberia excelsa* inhabited marine environments in the late Ladinian Kalkschieferzone of the Meride Limestone in Lombardy and Switzerland; the same is true for the larger *Felberia carnica* from the early Carnian Formazione di Gorno of Lombardy and Friuli (Lombardo & Tintori 2004). From these occurrences one may conclude that some of the polzbergiid perleidiform fish adapted to fully marine environments during late Middle Triassic times.

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Appendix 1. Serrolepisbank localities near Schwäbisch Hall.

1. Kastenhof near Rosengarten-Rieden; abandoned quarry on the Lämmerberg (QUENSTEDT's locality, Type locality of *Serrolepis*). TK 25: 6924 Gaildorf; R 35 51 090, H 54 74 400
2. Schwäbisch Hall-Steinbach; abandoned Scheuermann Quarry. TK 25: 6824 Schwäbisch Hall, R 35 55 500, H 54 40 590
3. Schwäbisch Hall-Steinbach; abandoned Hirsch Quarry. TK 25: 6824 Schwäbisch Hall, R 35 55 725, H 54 40 640
4. Schwäbisch Hall-Hessental; abandoned Taubenhof Quarry. TK 25: 6924 Gaildorf; R 35 55 470, H 54 40 015
5. Michelbach an der Bilz, Leitenäcker; road construction site 1976. TK 25: 6924 Gaildorf; R 35 55 755, H 54 37 525
6. Wilhelmsglück; Schneider Quarry. TK 25: 6924 Gaildorf; R 35 55 030, H 54 37 400

Appendix 2. Additional Lower Keuper *Serrolepis* localities in Northern Baden-Württemberg.

1. Illingen, Sämann Quarry, TK 25: 7019 Mühlacker, R: 34 95 800, H: 54 23 150 (Estherienschichten 3, 20–30 cm above Dolomite 2)
2. Zwingelhausen, Gläser Quarry, TK 25: 7022 Backnang, R: 35 27 800, H: 54 24 000 (Sandige Pflanzenschiefer)
3. Kupferzell, road cut of BAB6, TK 25: 6824 Schwäbisch Hall, R: 35 51 800, H: 54 51 050 (Untere Graue Mergel)
4. Vellberg-Eschenau, Schumann Quarry, TK 25: 6925 Obersontheim, R: 35 65 800, H: 54 38 250 (Untere Graue Mergel)
5. Obersontheim-Ummenhofen, Schneider Quarry, TK 25: Obersontheim, R: 35 64 700, H: 54 38 800 (Untere Graue Mergel)
6. Öhringen-Unterohrn, bmk Quarry, TK 25: 6722 Öhringen, R: 35 33 750, H: 54 53 000 (Albertibank)

Appendix 3. Section of the Albertischichten Member, Scheuermann Quarry.

(from top to base):

(1) <20 cm greenish claystones
(2) 27 cm gray limestone (ostracod-biomicrite), with vertical shrinkage cracks and with numerous voids from halite crystals that are filled with light brownish mud. Increasingly laminated and anthraconitic toward the top (Serrolepisbank).
(3) 100 cm ochre-coloured dolomitic marls interbedded with thinly bedded dolomicrites
(4) 10 cm greyish dolomicrite
(5) 15 cm greenish claystone
(6) 12 cm reddish-grey shaly claystone
(7) 30 cm grayish-green sandy and silty claystone with plant fragments
(8) 10 cm greenish-gray shaly sandstone
(9) 90 cm greenish-gray sandy claystones and shaly sandstones