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RESEARCH PAPER

Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodela, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate

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Abstract The Early to Middle Miocene fossil locality Sandelzhausen has yielded 48 species of ectothermic vertebrates and thus represents one of the most diverse ectotherm faunas of Miocene age. Thirty-five taxa of fishes, amphibians and reptiles, including three new species: *Pelobates fahlbuschi* nov. sp. (Pelobatidae, the most abundant vertebrate), *Tropidophorus bavaricus* nov. sp. (Lygosominae) and *Bavaricordylus molassicus* nov. sp. (Cordylidae), are described. Three additional species are new, but are not named yet: Ranidae indet. nov. gen. et sp., Anguidae gen. indet. sp. nov. and *Palaeoblanus* sp. nov. (Amphisbaenidae). In order to reconstruct the palaeoenvironment and past hydrologic conditions, a new methodology (the tooth replacement method, TRM) is introduced, which allows for the detection of autochthonous components within freshwater fish taphocoenose. TRM is tested on 45 localities from the Upper Freshwater Molasse and gives reasonable results in agreement with other analytical approaches. It is therefore viewed as a reliable method to distinguish perennial from seasonal water conditions at the Sandelzhausen locality. Using the TRM it was demonstrated that the palaeohydrology of Sandelzhausen is characterized by a change from temporary water to permanent water conditions. During the period of temporary water conditions (units B to D1, lower part) the ecosystem was driven by seasonal inundations, and the remaining riparian pools have yielded no autochthonous fish population, but acted as spawning places for amphibians (amphibian pool). A mostly open habitat in the close vicinity, with sandy and non-groundwater-affected soils during the dry season, is suggested based on the absolute dominance of the spadefoot *Pelobates fahlbuschi* nov. sp. This ecosystem changed up-section (late part of unit D1 and during D2 and E) due to the establishment of permanent water conditions of riparian pond type, preserving an autochthonous *Palaeocarassius*/*Channa* fish population (fish pond). The reconstructed precipitation values suggest that the observed change in hydrologic conditions was probably driven by climate. The lower part of the section gives semi-arid/subhumid values, with 571 mm mean annual precipitation (MAP), whereas the upper part yields sub-humid/humid values of 847 mm MAP. The increase in precipitation by about 280 mm was perhaps caused by a less seasonal precipitation regime with concomitant higher regional groundwater tables during units D2 and E. Based on the occurrence of several thermophilous reptile species, and in agreement with palaeobotanical and oxygen isotope data, the climate of Sandelzhausen is interpreted as subtropical with mean annual temperatures from 18°C to 20.8°C, mean cold month temperatures from 12.6°C to 13.3°C and mean warm month temperatures from 25.1°C to 28.1°C.

Keywords Fishes · Amphibians · Reptiles · Taphonomy · Palaeoclimate · Palaeoenvironment

Kurzfassung Die unter- bis mittelmiozäne Fundstelle Sandelzhausen lieferte 48 Arten ektothermer Wirbeltiere und ist damit eine der reichhaltigsten kontinentalen Fisch- und Herpetofaunen des Miozäns. In der vorliegenden Arbeit werden 35 Arten von Fischen, Amphibien und Reptilen beschrieben, wovon drei neu sind: *Pelobates fahlbuschi* nov. sp. (das häufigste Wirbeltier der Fundstelle, Pelobatidae), *Tropidophorus bavaricus* nov. sp. (Lygosominae), *Bavaricordylus molassicus* nov. sp. (Cordylidae).

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Drei weitere Arten sind neu, können aber noch nicht namentlich aufgestellt werden: Ranidae indet. gen. et sp. nov., Anguidae gen. indet. sp. nov. und *Palaeoblanus* sp. nov. (Amphisbaenidae). Zur Rekonstruktion der Paläo-Umwelt und -Hydrologie wird eine neue Methode vorgestellt, welche das Erkennen von autochthonen Komponenten in Süßwasserfisch-Taphozönosen ermöglicht. Diese Methode beruht auf der Zahnwechselaktivität von Karpfenfischen und dient der Unterscheidung von permanenten und temporären Gewässertypen. Sie wurde anhand von 45 Lokalitäten der Oberen Süßwassermolasse erfolgreich getestet. Ihre Anwendung auf Sandelzhausen lässt einen deutlichen Wechsel im hydrologischen Regime erkennen: von temporären Gewässerbedingungen im unteren Teil des Profils (Schichten B bis unterer Abschnitt von D1) zu permanten Bedingungen (oberer Teil von Schicht D1 bis Schicht E). Die Dynamik des Ökosystems im unteren Profilabschnitt war geprägt durch saisonale Überschwemmungen. Die dabei sich bildenden temporären Gewässer (Auen-Tümpel) waren Laich-Gewässer für eine Vielzahl von Amphibien und besaßen keine autochthone Fisch-Fauna. Die umgebende Umwelt kann, insbesondere aufgrund der Dominanz der Schaufelkröte *Pelobates fahlbuschi* nov. sp., als relativ offene Landschaft mit sandigen, während der Trockenzeit nicht grundwasserbeeinflussten Böden charakterisiert werden. Das Ökosystem veränderte sich im höheren Abschnitt des Profils durch das Entstehen eines Gewässers mit permanenter Wasserführung (Auen-Weiher) und autochthoner Fisch-Populationen (*Palaeocarassius*/*Channa*-Vergesellschaftung). Die rekonstruierten Paläo-Niederschläge lassen eine klimatische Steuerung vermuten. Die Werte für den unteren Profilabschnitt deuten mit 571 mm Jahresniederschlag auf semi-aride bis sub-humide Verhältnisse hin, wohingegen im höheren Profilabschnitt mit 847 mm sub-humide bis humide Bedingungen ermittelt werden konnten. Die Zunahme der Niederschläge um bis zu 280 mm resultierte wahrscheinlich aus einer geringeren Saisonalität des Niederschlags und höheren regionalen Grundwasserständen während D2 und E und führte im Ergebnis zur Herausbildung permanenter Fisch-Gewässer. Auf der Grundlage des Vorkommens mehrerer thermophiler Reptilien-Arten und in Übereinstimmung mit paläobotanischen und Sauerstoffisotopen Daten kann das Klima als subtropisch charakterisiert werden, mit einer Jahresmitteltemperatur von 18°C bis 20.8°C, einer Temperatur des kältesten Monats von 12.6°C bis 13.3°C, und einer Temperatur des wärmsten Monats von 25.1°C bis 28.1°C.

Schlüsselwörter Fische · Amphibien · Reptilien · Taphonomie · Paläoklima · Paläoumwelt

Introduction

The Sandelzhausen locality (Fig. 1) has yielded the most abundant fossil record of vertebrates in the North Alpine Foreland Basin (NAFB). Excavations between 1959 and 2003 revealed an enormous amount of ectothermic vertebrate fossils by screen-washing technique of about 150 tons of sediment (Fahlbusch et al. 1972; Fahlbusch 2003; Moser, Rössner et al. 2009). The present paper is based on the study of approximately 12,000 osteological remains, nearly 6,000 of which are determinable at least to genus level. The exceptionally high abundance of these fossils gives the locality a special position within the Upper Freshwater Molasse.

Several earlier papers have focussed on ectothermic vertebrates from Sandelzhausen. The crocodile remains have been described by Scherer (1973, 1981), and the turtles by Schleich (1981). In 1983 Schleich published the first record of a chameleonid, and Szyndlar and Böhme (1993) mentioned the first snakes from Sandelzhausen. Fishes, amphibians and lizards have been communicated by Böhme (1999a). This paper demonstrates that Sandelzhausen has preserved an exceptionally high biodiversity containing many new species, which group this locality within the most important fossil deposits of Central Europe. However, a detailed description of the fauna was lacking to date. Apart from the previously described

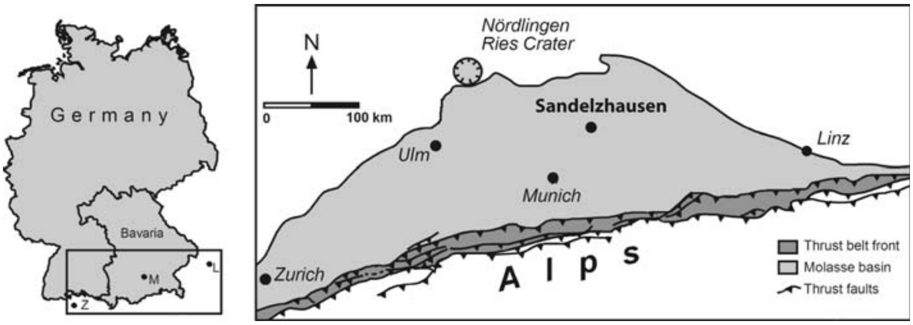


Fig. 1 Location of Sandelzhausen, and sketch map of the Molasse Basin

crocodiles and turtles, and the snakes which have been published by Szyndlar (2009), all other ectotherms are described herein.

The second goal of this paper is to point out the importance of ectothermic vertebrates in the reconstruction of the ancient environment and hydrology by establishing a taphonomy-based methodology to discriminate between permanent and temporary water bodies. Finally, progress in the estimation of palaeoclimatic parameters based on ectothermic vertebrates (Böhme 2003; Böhme et al. 2006) allows for the quantification of temperature and precipitation and thereby provides new data regarding the palaeoclimatic evolution in Central Europe close to the Early/Middle Miocene boundary.

Geological setting and stratigraphy

The Sandelzhausen locality (Fig. 1) is situated in the eastern part of the town of Mainburg, 70 km northeast of Munich and 27 km west of Landshut, in Lower Bavaria (coordinates: 48.6283 N, 11.796 E). The fossil-bearing section is about 2.5 m (rarely 3 m) thick and represents a fine-clastic intercalation near the top of the regionally widespread sands and gravels of the *Nördlicher Vollschotter*. This intercalation can be observed over several hundred meters between 443 and 449 m above sea level. The *Nördlicher Vollschotter* has been subdivided into a lower and upper part by Batsche (1957). In the Landshut–Mainburg area the upper part comprises several palaeosoil horizons, which can be traced over several tens of kilometers, of which the most important is the 7-m-thick *Zwischenmergel*. According to geologic mapping, the Sandelzhausen section is situated a few meters below the *Zwischenmergel* (Abdul-Aziz et al. 2008). Palaeomagnetic analysis of the Sandelzhausen profile reveal one inverse to normal magnetic reversal, which cannot unambiguously be correlated to the Global Polarity Timescale (Abdul-Aziz et al. 2008). The palaeomagnetic results of other sections in the Landshut–Mainburg area, together with biostratigraphic information, makes a correlation to the magnetic reversals C5Cn.2r/2n or C5Cn.1r/1n most reliable (Abdul-Aziz et al. 2008), placing Sandelzhausen at around 16.47 or 16.27 Ma, in the latest Early Miocene, near the Early/Middle Miocene boundary as it is currently defined (Lourens et al. 2004).

The Sandelzhausen section is subdivided based on lithological and sedimentological characters (Fig. 2). The litho-units can be characterized as follows [for more detailed information see Fahlbusch and Gall (1970); Fahlbusch et al. 1972; Schmid 2002; Fahlbusch 2003; Moser, Rössner et al. 2009].

Unit A

Fine to medium-sized gravels within a sandy to marly matrix. Pedogenic carbonate nodules and carbonatic cementations are very frequent. In contrast to units B to D, this unit contains only large mammal remains.

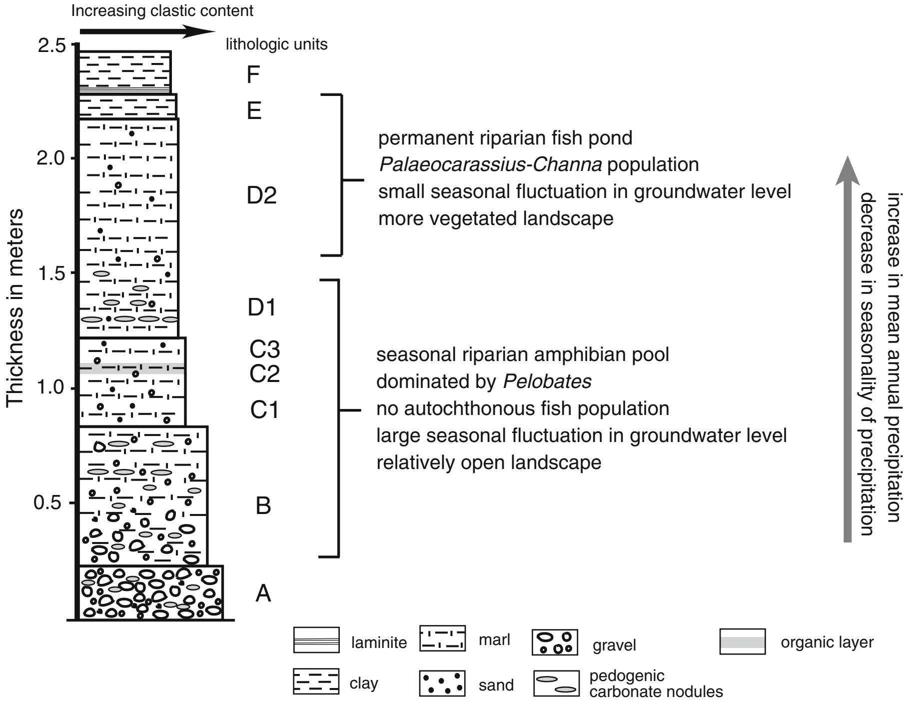


Fig. 2 Simplified profile of the Sandelzhausen section and a summary of palaeohydrologic, palaeoecologic, palaeoenvironmental results (see "Discussion")

Unit B

Sand- and gravel-rich marls with fining-upward grain-size distribution. Intercalated sand and palaeosoil horizons and pedogenic carbonate nodules are common, sometimes as distinct layers. Both large and small vertebrates are found.

Unit C

Marls with sparse sand and gravel content, lacking pedogenic carbonate nodules. This unit can be further subdivided into subunits C1 (grey–brown, gastropod-rich marl), C2 (dark brown to black marl, rich in organic matter, e.g. wood remains; ='coal layer') and C3 (grey–brown, gastropod-rich marl). The transition between unit C and D is gradual. Both large and small vertebrates are found.

Unit D

Silty and clayey marls with very low sand and gravel and high carbonate content. This unit is subdivided into subunit D1, with some pedogenic carbonate nodules, and D2, without pedogenic carbonate nodules. Both large and small vertebrates are found.

Unit E

Montmorillonite-rich silty clays. The fossils are mostly small-sized microvertebrates.

Unit F

This unit can be subdivided into subunits F1 (a fine laminated compact layer) and F2 (greenish fatty clay). Unit F has no fossil content.

Materials and methods

All Sandelzhausen fossils are deposited in the Bavarian State Collection for Palaeontology and Geology (BSPG) under the label 1959 II (omitted in the following text). For comparison with extant species the osteological collection (disarticulated skeletons) of the BSPG ("Brunner collection", label 1982 X) was used. Individual collection numbers are indicated in the systematic part.

Detailed taxonomic descriptions are given only for new species and taxa in open nomenclature. Descriptions for well-known species are referenced in the synonymy list.

The images of individual bones and teeth in plates 1 and 2 were made using raster electron microscope or digital microscope in the Section of Palaeontology at the Department for Earth and Environmental Science (LMU Munich).

The anatomical nomenclature in the systematic part follows Böhme (2002c) (fishes), Sanchiz (1998) (frogs), Roček (1984) (Scincomorpha), Klembara (1981) (Anguimorpha), Richter (1994) and Kosma (2004) (scincomorph tooth crown ornamentation).

Results

Systematic palaeontology

Class Actinopterygii Cope, 1887
Order Cypriniformes Bleeker, 1859
Family Cyprinidae Bonaparte, 1832
Subfamily Cyprininae Bonaparte, 1840
Genus *Palaeocarassius* Obrhelová, 1970
***Palaeocarassius* sp. A**
Figures 3d, 4a and 5A–D
1999a *Palaeocarassius* sp. Böhme: 489, Fig. 2.
2004 *Palaeocarassius* sp. Reichenbacher et al.: 87, Pl. 3 Fig. 5.

Material examined: 1,659 isolated pharyngeal teeth (7501–7509, 7535, 16244), 1 pharyngeal bone (7510), 13 serrated fin rays (7514, 7515, 16246), 85 first vertebrae (16245).

Comments: The genus *Palaeocarassius* comprises three species: *Palaeocarassius mydlovariensis* Obrhelová 1970, *P. priscus* (v. Meyer 1851), and *P. obesus* Gaudant 2000. Isolated pharyngeal teeth are unknown from *P. priscus*. The teeth of the other *Palaeocarassius* species are very similar to each other, except for the morphology of A1. According to Obrhelová (1990: Fig. 15 A–H) the A1 tooth of *P. mydlovariensis* is characterized by small protuberances below the hook (see also Reichenbacher et al. 2004: Pl. 3 Fig. 4). This feature is also present in *P. obesus* (Fig. 5E), which in addition has more robust and thicker teeth and a rather globular outline of the A1 tooth, compared with both *P. mydlovariensis* and *P.* sp. A. The Sandelzhausen *Palaeocarassius* teeth differ from *P. mydlovariensis* and *P. obesus* by a combination of characters: (1) relatively delicate and thin A2 to A5 teeth similar to *P. mydlovariensis* (Fig. 5A–B; best observable if viewed side by side under binoculars), (2) relatively slender A1 tooth (Fig. 5C) similar to *P. mydlovariensis* and (3) absence of small protuberances below the hook of the A1 tooth.

Another important and yet overlooked feature is the morphology of the spines on the posterior side of the serrated anterior dorsal and anal fin rays (Fig. 3). The type material of *P. priscus* from Unterkirchberg (collection Natural History Museum Stuttgart) shows several isolated, posteriorly serrated, anterior fin rays (Fig. 3a). On the medial side the spines display a distinct, not very sharp longitudinal ridge, resulting in a subtriangular cross-section of the spine. This is different from *P. obesus*, in which the ridge is absent and the spines are round in cross-section (Fig. 3c). Moreover, the spines of *P. obesus* are robust with a broad base, occupying nearly all the width of the fin ray. In the Sandelzhausen *Palaeocarassius* (Fig. 3d) the ridge is also present, but the

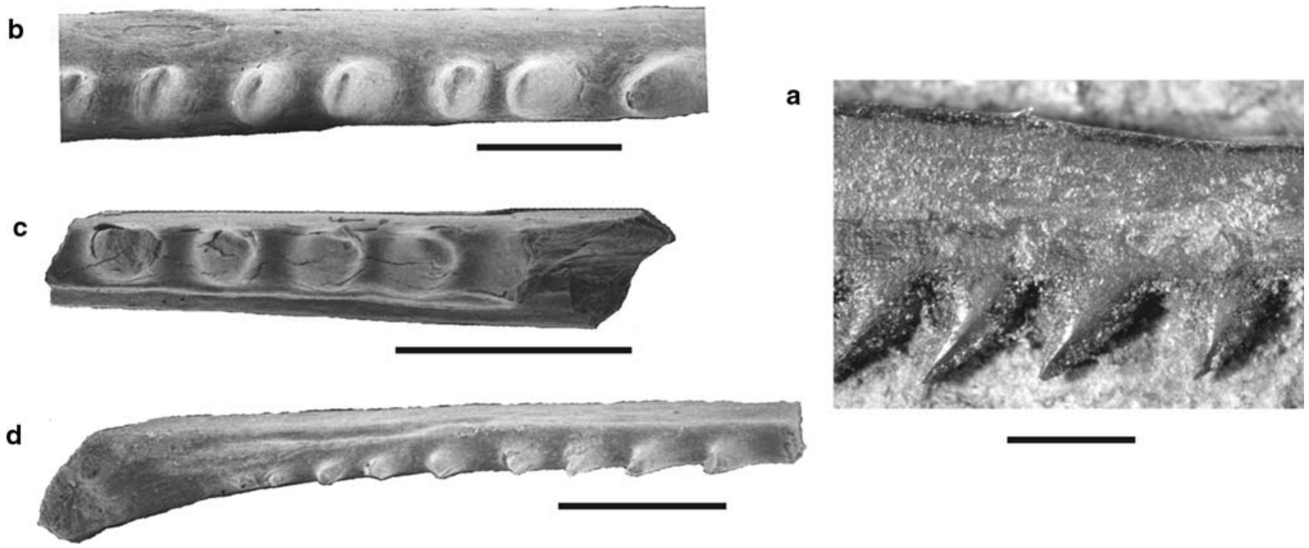


Fig. 3 Serrated fin spines of *Palaeocarassius*. **a** *Palaeocarassius priscus* from Unterkirchberg (SMNS 50961), **b** *Palaeocarassius* cf. *priscus* from Langenau 2 (BSPG 1976 XXI 60), **c** *Palaeocarassius obesus* from Sansan, violet layer (BSPG 1991 XV 31), **d** *Palaeocarassius* sp. A from Sandelzhausen (7514). *Scale bars* represent 1 mm

Fig. 4 The first vertebra in cyprinids is ophistocoelous with a round or oval condylus. This compact bone has good preservation potential and was used to estimate the minimum number of individuals. **a** *Palaeocarassius* sp. A (Sandelzhausen, 16247), **b** *Palaeoleuciscus* sp. A (Sandelzhausen, 16248). *Scale bars* represent 1 mm

base of the spines is narrow, occupying only half of the width of the fin ray. Unfortunately, the morphology of the spines in *P. mydlovariensis* is not known. A well-preserved but toothless pharyngeal bone from Sandelzhausen shows the bases of five pharyngeal teeth, which are aligned in one row. The tooth formula for the Sandelzhausen *Palaeocarassius* is therefore 5.0 (Fig. 5D; the tooth formula of the other species remains unknown). The first, ophistocoelous vertebra has an oval condylus (Fig. 4a).

Based on the combined characteristics of tooth and fin spine morphology, the material from Sandelzhausen cannot be assigned to one of the known species, and thus most probably represents a new species. However, I believe that the description of a new cyprinid species based on isolated teeth and spines is not appropriate. To distinguish the species from related forms it is formally referred to as *Palaeocarassius* sp. A.

In strong contrast to *Palaeoleuciscus* sp. A, all but one tooth (7508) are not attached to the pharyngeal bone and show structures of resorption around the base (Fig. 5A), indicating that virtually all teeth are accumulated in the sediment due to resorption (see section 'Taphonomy of fish remains: the tooth replacement method').

Spine morphology can be a powerful tool to distinguished species, since in recent cyprinins and barbins (those subfamilies with serrated fin rays) this feature shows significant differences between phylogenetically related species (Böhme, unpublished data).

Based on isolated otoliths, Schulz-Mirbach and Reichenbacher (2006) suggest a phylogenetic relationship between *Palaeocarassius* and *Abramis* resp. *Alburnus* (both Leuciscinae). However, the available *Palaeocarassius* skeletons clearly indicate several synapomorphies of the Cyprininae (e.g. strongly ossified and serrated spines in both dorsal and anal fins). Therefore, *Palaeocarassius* is phylogenetically closely related to *Carassius* (Obrhelová 1970; see also Jost et al. 2006), although the Western Eurasian species of *Palaeocarassius* (last occurrence in the late Middle Miocene) are probably not direct ancestors of *Carassius*, which first occurs in the Messinian, e.g. in Mongolia (Sytchevskaya 1989) and the Balkan Peninsula (Böhme, unpublished data).

Subfamily Leuciscinae Howes, 1991
Genus *Palaeoleuciscus* Obrhelová, 1969
***Palaeoleuciscus* sp. A**
Figures 4b and 5F
2003 *Palaeoleuciscus* sp. Sach et al.: 23, Pl. 1 Figs. 1–3.
2004 *Palaeoleuciscus* sp. A Reichenbacher et al.: 87, Pl. 3 Fig. 2.

Material examined: 9 isolated pharyngeal teeth (7536–7538, 16250–16254), 17 pharyngeal bone fragments with attached teeth (6515, 16255–16262), 1 operculum fragment (16249), 6 first vertebrae (16248).

Comments: According to Böhme (2002b: 18) the genus *Palaeoleuciscus* comprises two morphotypes, mainly distinguished by size, morphological robustness and facies distribution. *Palaeoleuciscus* sp. A is a small-sized form (up to 4 mm tooth length) with delicately built pharyngeal teeth. These teeth are common in slow-flowing waters and oxbow lakes (lithofacies types: clays, marls, sandy marls), whereas *Palaeoleuciscus* sp. B is characterized by large and robust teeth (up to 10 mm tooth length) and is found in faster-flowing rivers (lithofacies types: channel fill sands, sandy marls). The Sandelzhausen form clearly belongs to *Palaeoleuciscus* sp. A. Most of the specimens represent pharyngeal bone fragments (tooth formula 5.2), and only a few isolated teeth have been found. These teeth lack evidence for resorption around the base; instead they show mostly broken edges (Fig. 5F). This indicates that this species was not autochthonous in the Sandelzhausen water body (see section 'Taphonomy of fish remains: the tooth replacement method').

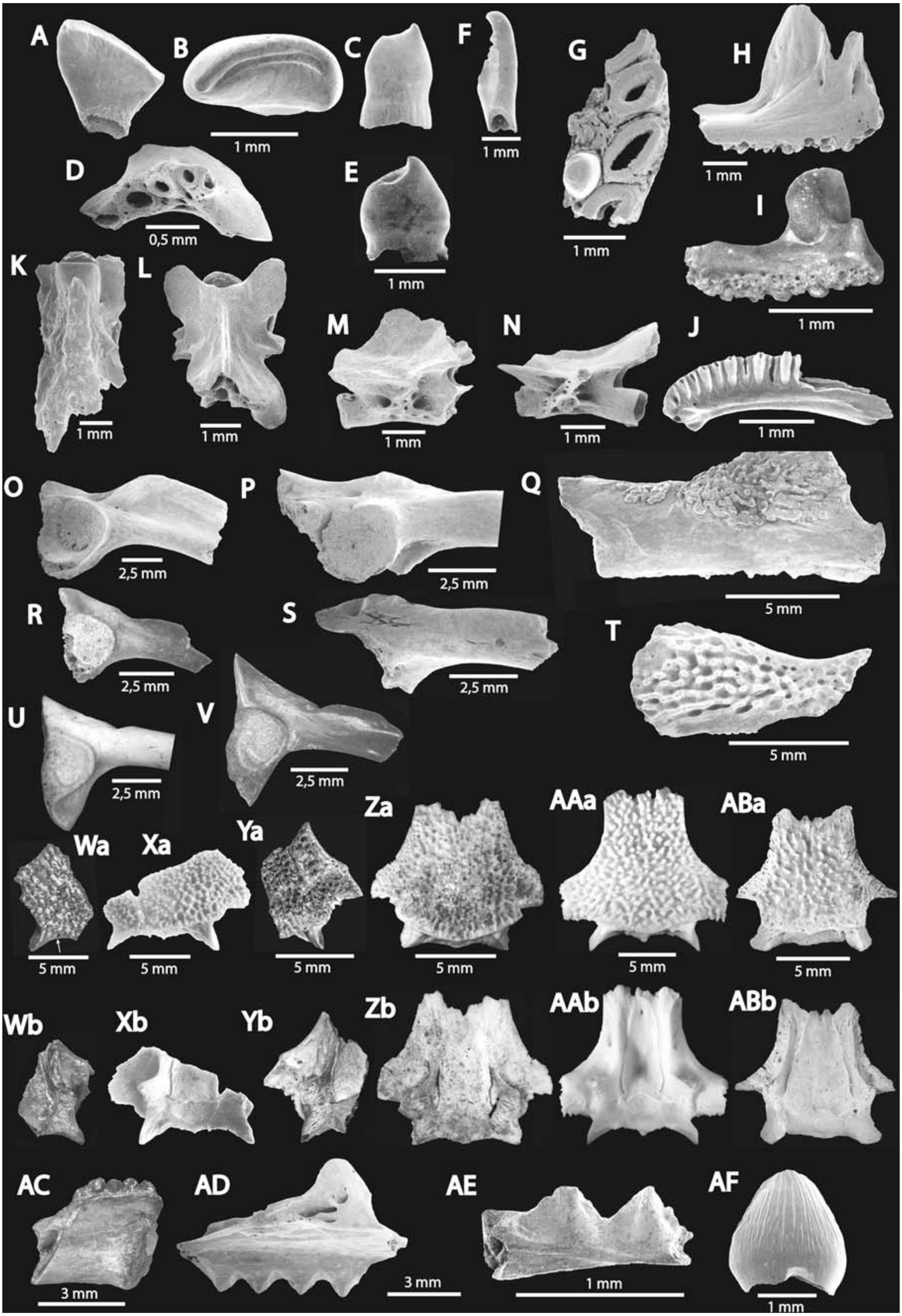
The first, ophistocoelous vertebra is characterized by a more or less round condylus (Fig. 4b). The single antero-dorsal operculum fragment is referred to this species, because it displays the large openings of the opercular canal, which is typical for leuciscins.

Order Channiformes Berg, 1940
Family Channidae Berg, 1940
Genus *Channa* Scopoli, 1770
***Channa elliptica* von Salis, 1967**
Figure 5G, H
1993 *Channa elliptica* von Salis. Reichenbacher: 363, Figs. 160, 162, 164–167, non Figs. 161, 163.
2003 *Channa elliptica* von Salis. Sach et al.: 13, Pl. 3 Figs. 5, 6.
2006 *Channa elliptica* von Salis. Jost et al.: 13, Fig. 16A–F.

Material examined: 68 vertebrae (6597–6599, 16268, 16269), 5 pharyngobranchial fragments (6596, 7524, 16263–16265), 1 premaxilla (6595), 1 dentary fragment (6594), over 70 isolated teeth (16266, 16267).

Comments: Apart from the cyprinid *Palaeocarassius*, channids (snakeheads) are the most characteristic fishes of the *Ältere* and *Mittlere Serie* of the Upper Freshwater Molasse. Snakehead fishes occur in every type of water and even in floodplain sediments and fissure fillings (Böhme 2002b), which is explained by their top carnivorous ecology, high potential for migration and partly amphibious lifestyle (Böhme 2004). Isolated cranial bones (primarily basioccipitals) indicate the presence of several species, or even genera (Böhme 2002b; Sach et al. 2003). However, the taxonomy of European fossil channids is based on otoliths (Reichenbacher 1993; Sach et al. 2003), and thus the specific allocation of a basioccipital type to an otolith type remains unresolved. No basioccipital of a channid has been reported from Sandelzhausen; however, a single otolith (now probably lost) indicates the presence of *Channa elliptica*, the most common species in the NAFB. The studied teeth and bones suggest a rather small maximum

Fig. 5 *A–D*: *Palaeocarassius* sp. A. *A*—posterior tooth, lateral view (7505); *B*—posterior tooth, dorsal view (7504); *C*—anterior (A1) tooth, lateral view (7501); *D*—pharyngeal bone (7510). *E*: *Palaeocarassius obesus* from Sansan (violet layer), anterior (A1) tooth, lateral view (BSPG 1991 XV 31). *F*: *Palaeoleuciscus* sp. A, pharyngeal tooth (7537). *G*, *H*: *Channa elliptica*, *G*—pharyngobranchial fragment (6596); *H*—premaxilla (6595). *I*: *Gobius* sp., premaxilla (16270). *J*: *Albanerpeton inexpectatum*, dentary (6518). *K*: *Chelotriton* sp., trunk vertebra, dorsal view (6516). *L*: *Salamandra sansaniensis*, trunk vertebra, dorsal view (6517). *M–N*: *Triturus* cf. *marmoratus*, *M*—posterior trunk vertebra, lateral view (6519); *N*—anterior trunk vertebra, lateral view (6520). *O*: *Pelophylax* sp., ilium (6521). *P*: *Bufo* cf. *viridis*, ilium (6508). *Q*: *Latonia gigantea*, maxilla (6513). *R*: *Eopelobates* sp., ilium (16330). *S*: *Bufo* sp., ilium (6509). *T*, *V*, *W*, *Y*: *Pelobates fahlbuschi* nov. sp.; *T*—maxilla (6514); *V*—ilium (16341); *W*—frontoparietal (16339; *Wa*—dorsal view, *Wb*—ventral view); *Y*—frontoparietal (holotype; 16338; *Ya*—dorsal view, *Yb*—ventral view). *U*: *Pelobates fuscus*, recent, ilium (BSPG 1982 X 5582). *X*: *Pelobates sanchizi*, frontoparietal (holotype), *Xa*—dorsal view, *Xb*—ventral view, from Venczel (2004: Pl. 1 Figs. *H–I*). *Z*: *Pelobates* nov. sp., frontoparietal, Petersbuch 38 B (MN 4), collection Naturmuseum Augsburg (coll. Rummel); *Za*—dorsal view, *Zb*—ventral view. *AA*: *Pelobates cultripes*, recent, frontoparietal (BSPG 1982 X 2399); *AAa*—dorsal view, *AAa*—ventral view. *AB*: *Pelobates syriacus*, recent, frontoparietal (BSPG 1982 X 2768); *ABa*—dorsal view, *ABa*—ventral view. *AC*, *AD*: *Chamaeleo* aff. *caroliquarti*, *AC*—left symphysis (16364); *AD*—maxilla (7529). *AE*: *Chamaeleo bavaricus*, maxilla fragment (7531). *AF*: *Diplocynodon styriacus*, hatchling tooth (6526) ▶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body size for the Sandelzhausen snakeheads, probably reaching no more than 20 cm in standard length.

Order Perciformes Bleeker, 1859
Family Gobiidae Bonaparte, 1832
Genus *Gobius* Linnaeus, 1758
***Gobius* sp.**
Figure 5I

Material examined: 1 premaxilla (16270), 1 left dentary fragment (16271), 1 jaw-bone fragment (16272).

Comments: It is difficult to determine isolated gobiid bones at the species level. However, a high diversity of gobiids in the Upper Freshwater Molasse (*Ältere Serie*) is documented based on otoliths with up to four sympatric species (Böhme and Reichenbacher 2003; Reichenbacher et al. 2004; Reichenbacher et al. 2008). Near the Early/Middle Miocene boundary gobiid diversity drops significantly in the NAFB, and only a single species is known from the *Mittlere Serie* (Sach et al. 2003).

Class Amphibia Linnaeus, 1758
Order Allocaudata Fox and Naylor, 1982
Family Albanerpetontidae Fox and Naylor, 1982
Genus *Albanerpeton* Estes and Hoffstetter, 1976
***Albanerpeton inexpectatum* Estes and Hoffstetter 1976**
Figure 5J

*1976 *Albanerpeton inexpectatum* Estes and Hoffstetter: 308, Pl. 5–9.

1999 *Albanerpeton inexpectatum* Estes and Hoffstetter. Böhme: 493.

2002 *Albanerpeton* sp.. Böhme: 340, Pl. 1 Figs. B–C.

2003 *Albanerpeton inexpectatum* Estes and Hoffstetter. Wiechmann: 84, Pls. 6–16.

2004 *Albanerpeton inexpectatum* Estes and Hoffstetter. Reichenbacher et al.: 87, Pl. 3 Fig. 7.

2008 *Albanerpeton inexpectatum* Estes and Hoffstetter. Gardner and Böhme: 195, Table 2.

2008 *Albanerpeton inexpectatum* Estes and Hoffstetter Böhme: 177, Pl. 1 Fig. 12.

Material examined: 2 dentaries (6518, 16273), 3 maxillae (16274–16276), 1 intermaxilla (16277), 2 vertebrae (16278).

Comments: The Late Oligocene to Early Miocene albanerpetontids of Central Europe belong to the species *Albanerpeton inexpectatum* (Wiechmann 2003; Gardner and Böhme 2008; Böhme 2008). They can be superabundant in some fissure fillings (e.g. Petersbuch 2, with about 2,000 bones), whereas normally they are rare in floodplain deposits. Gardner and Böhme (2008) interpret this pattern as a preferential adaptation of this fossorial species to karstified limestone plateaus. The record from Sandelzhausen is the youngest for this species in Germany. Albanerpetontids are so far restricted in the NAFB to the *Ältere Serie* (Early Miocene) of the Upper Freshwater Molasse.

Fig. 6 Atlas and trunk vertebrae of crocodile salamanders. **a**, **b**: *Chelotriton* sp. from Sandelzhausen (**a**—atlas, 7540; **b**—trunk vertebra, 7542), **c**, **d**: *Chelotriton* aff. *pliocenicus* from Petersbuch 2 (**c**—atlas, BSPG uncatalogued; **d**—trunk vertebra, BSPG uncatalogued), **e**, **f**: cf. *Tylototriton* sp. from Möhren 13 (**e**—atlas, BSPG uncatalogued; **f**—trunk vertebra, BSPG uncatalogued). *Scale bars* represent 2 mm ▶

Order Caudata Scopoli, 1777
Family Salamandridae Goldfuss, 1820
Genus *Salamandra* Laurenti, 1768
***Salamandra sansaniensis* Lartet, 1851**
Figure 5L

1976 *Salamandra sansaniensis* Estes and Hoffstetter: 300, Pls. 1, 2.

2000 *Salamandra sansaniensis* Rage and Hossini: 184.

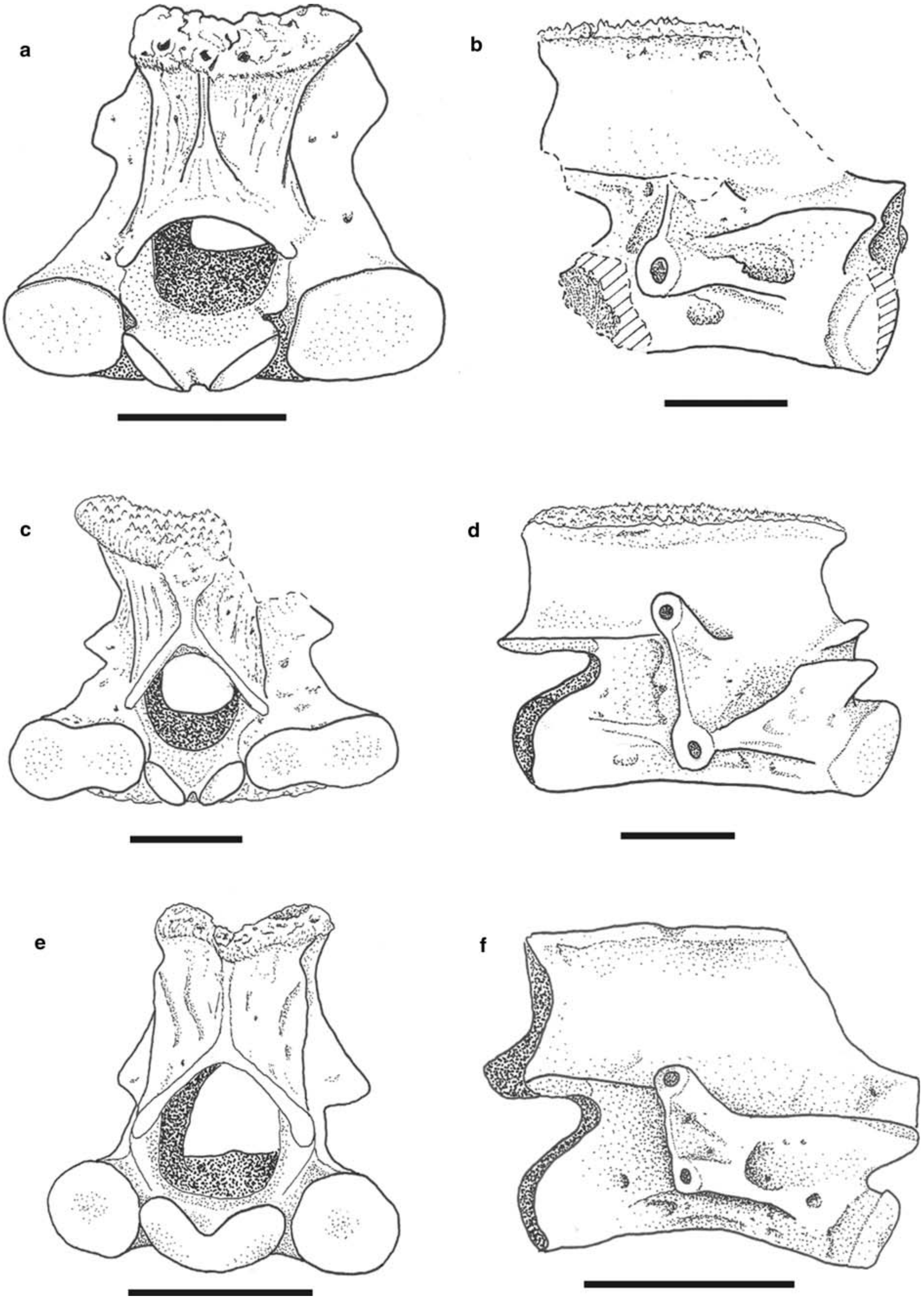
Material examined: 91 trunk and caudal vertebrae (6517, 16279, 16280), 1 atlas (16281), 3 occipital bones (16282–16284).

Comments: *Salamandra sansaniensis* vertebrae can easily be identified by their large size (up to 7 mm in Sandelzhausen). The vertebrae are broad, dorsoventrally flattened and have a low neural arch. The condylus bears a notochordal fossa. The species is usually rare in the Northalpine Foreland Basin, in contrast to the fissure fillings of the Franconian Alb. However, it is relatively common in Sandelzhausen (Table 2). It is the biggest non-cryptobranchid salamander in the Miocene, probably reaching more than 30 cm in total length—the largest size of the species in the MN4a of Petersbuch 2 (vertebrae length up to 10 mm).

Genus *Chelotriton* Pomel, 1853
***Chelotriton* sp.**
Figures 5K and 6a, b

Material examined: 1 atlas (7540), 25 trunk vertebrae (6516, 7542, 16289), 1 frontal fragment (16287), 1 squamosal (16285), 1 parasphenoid (16288), 3 maxillae (16290–16292), 6 dentaries (16293–16297), 5 cranial bone fragments (16298–16301), several ribs (16286, 16302).

Description and Comments: Cranial bones of *Chelotriton* are characterized by a dense pustular dermal ossification. The frontal from Sandelzhausen shows this type of sculpturing, like that from Coderet, the type locality for *C. paradoxus* (frontal type in Böhme 2008: Pl. 2 Fig. 2) and unlike that of aff. *Chelotriton* sp. from Oberleichtersbach (Böhme 2008: Pl. 2 Fig. 7). The same type of ossification is found on the top of the transversally broadened neural plates on vertebra (Figs. 5K and 6a, b). There are at least three types of *Chelotriton*-related species in the Oligocene and Miocene of southern Germany, which differ significantly in vertebra morphology (Fig. 6). Beside the


a
b
c
d
e
f

Sandelzhausen type, there are *Chelotriton* aff. *pliocenicus* from the MN4a of Petersbuch 2, and cf. *Tylototriton* sp. from the MP 22 of Möhren 13.

The height/width ratio of the Sandelzhausen atlas is 0.78 (Fig. 6a), which is intermediate between *C.* aff. *pliocenicus* and cf. *Tylototriton* sp. The neural arch of the atlas is low; the anterodorsal margin is round and not thickened. The vertical cristae of the anterior neural arch roof do not connect with this margin. The lateral facets of the processus odontoideus are separated and relatively large. The condyli occipitalis are slightly oval. The sculpture of the dermal ossification of the neural crista is rugose to pustular. The morphology of the trunk vertebrae is very similar to *C. paradoxus* from Coderet; a zygosphene-zyganthrum articulation, like in the type of *C. pliocenicus* (Bailon 1989) and in *C.* aff. *pliocenicus*, is absent (Fig. 6d). The neural crista is very high. The posteriorly directed lamina of the praezygapophysis deflects slightly to the ventral (straight in cf. *Tylototriton* sp., Fig. 6f; strongly deflected in *C.* aff. *pliocenicus*, Fig. 6d) and ends between the diapophysis and the parapophysis, but closer to the latter (at the diapophysis in cf. *Tylototriton* sp.; at the parapophysis in *C.* aff. *pliocenicus*). Diapophysis and parapophysis are widely separated. The only preserved squamosal is relatively slender, like that seen in *Chelotriton*-like forms from Enspel (Roček, unpubl. data), and not longitudinally expanded like in *C. paradoxus* from Coderet ("frontal" type A in Böhme 2008: Pl. 2 Fig. 3). The rib of the third vertebra (16286) bears a single dorsal spine between the uncinate process and the proximal articulation. The remaining ribs lack the uncinate process and show maximally one dorsal spine (two to four in *C. paradoxus* from Coderet; Böhme 2008: Pl. 2 Fig. 6; up to ten in *C.* aff. *pliocenicus*; condition unknown in cf. *Tylototriton* sp.). Despite the similarities of the Sandelzhausen vertebrae to the type of *C. paradoxus* from Coderet, the differences in squamosal and rib morphology indicate that the Sandelzhausen specimens cannot be referred to this species until a revision of the genus resolves the taxonomic problems (see Böhme 2008).

Genus *Triturus* (Rafinesque, 1815?, 1820)

The genus *Triturus* was split in recent years into several genera based on molecular data. Because of serious nomenclatorial problems (Schmidtler 2004) there is as yet no consistency. For instance, the species *Triturus vulgaris* was placed in the genus *Lissotriton* (Bell 1839) by Garcia-Paris et al. (2004) and in *Lophinus* (Rafinesque 1815) by Litvinchuk et al. (2005). To circumvent these problems I use the traditional nomenclature of newts (cf. Thiesmeier and Grossenbacher 2004).

Triturus cf. *vulgaris* (Linnaeus, 1758)

Figure 7d–i

2004 *Triturus* cf. *vulgaris* Reichenbacher et al.: 87, Pl. 3 Fig. 9.

Material examined: 279 trunk vertebrae (6510, 6511, 16305, 16306), 6 atlas (16303, 16304), several cranial and postcranial remains (16314–16316).

Comments: The vertebrae are small (1.5–2 mm) and compact. The neural arch is anteriorly round to slightly broad oval and of normal height (1–1.3 times the height of the condyle) and only posteriorly vaulted and laterally compressed, showing the appearance of a reversed U in posterior view. The neural spine is of moderate height, indicating the subgenus *Palaeotriton* (sensu Bolkay 1928). In contrast to *T. boscai* and *T. montandoni* and the fossil species *T. roehrsi* the neural spine is thin, distally not broadened or covered with dermal bone. It is most similar to *T. helveticus* and *T. vulgaris*, although the spine in the fossils is somewhat lower compared with the recent forms. Both extant species are difficult to distinguish from each other based on vertebrae alone (it is much easier based on frontals, but it is difficult to decide which of the Sandelzhausen frontals belong to the described vertebrae). However, it is obvious that the posteriorly strongly vaulted neural arch is similar to the Mediterranean subspecies *T. vulgaris meridionalis* (BSPG 1982 X 4201). In the nominal form *T. v. vulgaris* (12 skeletons in the BSPG) and in *T. helveticus* (4 skeletons in the BSPG) the neural arch is broad-vaulted, more or less semi-oval. On the other side, in *T. v. meridionalis* the neural spine is significantly higher than in the nominal form and in *T. helveticus*. The fossils most probably represent a new species, but this is difficult to demonstrate at present. Therefore, it will be provisionally compared with *Triturus vulgaris*.

Triturus cf. *marmoratus* (Latreille 1800)

Figures 5M–N and 7a–c

1976 *Triturus* cf. *T. marmoratus* Estes and Hoffstetter: 303, Pls. 3, 4.

2000 *Triturus* cf. *T. marmoratus* Rage and Hossini: 190.

2005 *Triturus* cf. *T. marmoratus* Rage and Bailon: 417, Fig. 1C

Material examined: 15 atlas (16307), 183 trunk vertebrae (6512, 6519, 6520, 16308, 16309), 3 occipital bones (16310–16312), several cranial and postcranial remains (16313).

Comments: Larger vertebra (up to 3.5 mm) with vaulted neural arch, up to two times as high as the condyle in the anterior vertebra, and a high and thin dorsal spine up to 1.5 times as high as the centrum (the spine is partially broken in Fig. 5N). Similar vertebrae, referred to *Triturus* cf. *T. marmoratus* have frequently been found in late Early and Middle Miocene sediments and are described in detail by Estes and Hoffstetter (1976), Rage and Hossini (2000) and Rage and Bailon (2005). In the Sandelzhausen

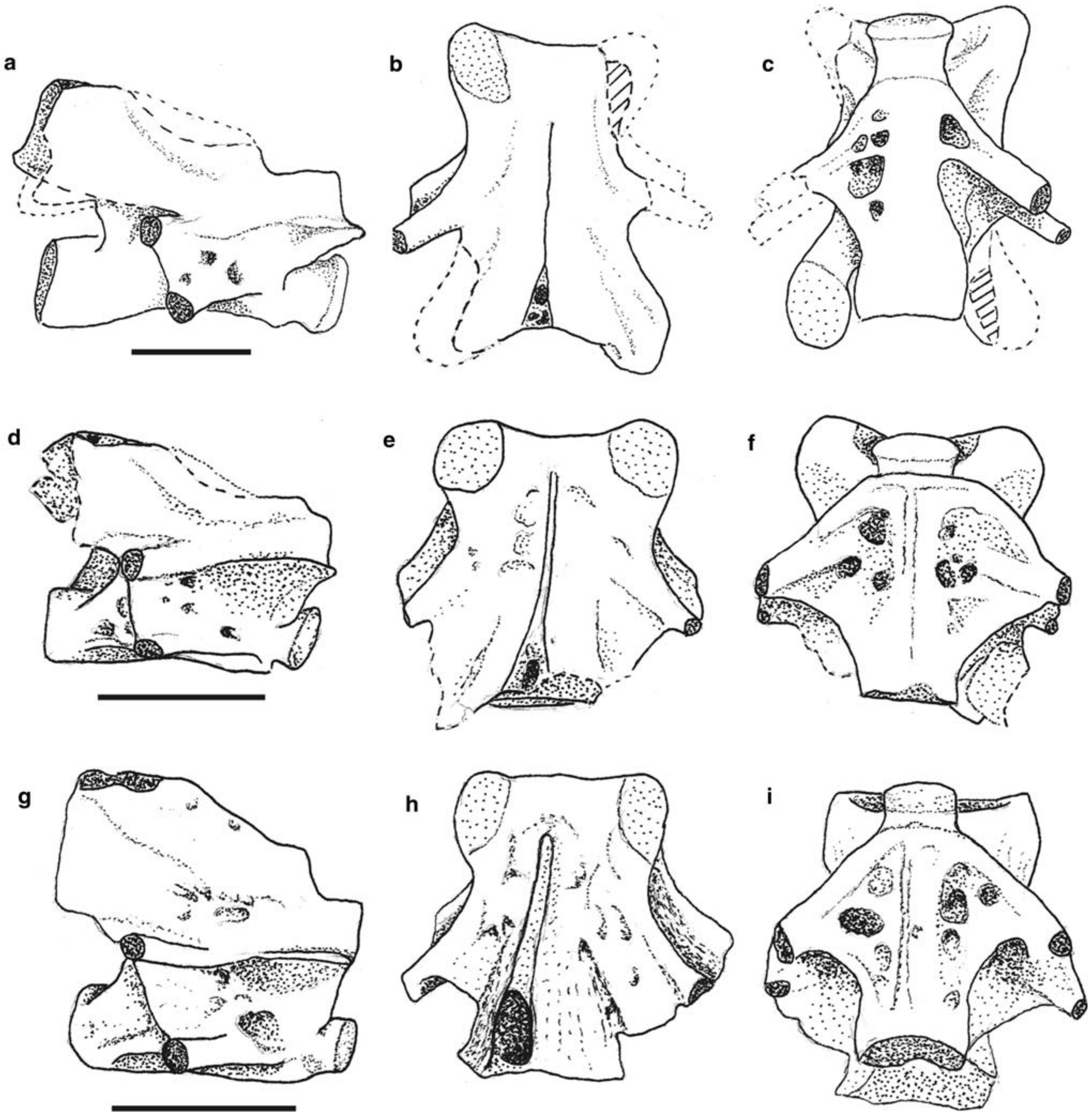


Fig. 7 Trunk vertebrae of newts from Sandelzhausen (*left lateral* view, *middle dorsal* view, *right ventral* view). **a**–**c**: *Triturus* cf. *marmoratus* (6512), **d**–**i**: *Triturus* cf. *vulgaris* (**d**–**f**, 6511; **g**–**i**, 6510). *Scale bars* represent 1 mm

specimens the neural arch seems to be higher than in the material from Béon 1 (Rage and Bailon 2005: Fig. 1c) and more similar to forms from La Grive (Estes and Hoffstetter 1976: Pl. 4) and the extant species (18 skeletons in the BSPG collection). However, a few details differ from the recent species. Some of the cranial elements (maxilla, frontal, prefrontal) are sculptured, unlike the living species, and the frontal has a longer and broader posterolateral process and elevated orbital margin.

Order Anura Rafinesque, 1815
Family Discoglossidae Günther, 1858
Genus *Latonia* v. Meyer, 1843
Latonia gigantea **(Lartet, 1851)**
Figure 5Q
1987 *Latonia feifari* Hodrová: 98, Figs. 1–7.
1994 *Latonia gigantea* Roček: 718, Figs. 1–17.
2000 *Latonia gigantea* Rage and Hossini: 194, Figs. 8–22.

2004 *Latonia gigantea* Reichenbacher et al.: 87, Pl. 3 Fig. 11.

2004 *Latonia gigantea* Venczel: 153, Fig. 1.

For older synonyms see Roček (1994) and Rage and Hossini (2000).

Material examined: 42 maxillae (6513, 6535—6541, 6543, 6544, 6555–6557, 16318–16320), 12 ilia (6503–6505, 6507, 6547–6549, 16321, 16322) and many other bones, including premaxilla, prearticular, vomer, frontoparietal, presacral vertebra, sacral vertebra, scapula, urostyl, radioulna, humerus, tibiofibula (6545, 6550–6553, 6558–6562, 6563–6568, 6593, 16323, 16324).

Comments: Discoglossids of the genus *Latonia* are the largest frogs in Sandelzhausen (and in Europe in general), reaching up to 20 cm snout–vent length (Roček 1994). Three species are known in this extinct genus (Roček 1994): *L. vertaizoni* Friant, 1944, *L. ragei* Hossini 1993 and *L. gigantea* (Lartet, 1851). *Latonia gigantea* can easily be identified by the presence of an irregular to vermicular sculpture on the labial side of the posterodorsal part of the maxilla (Fig. 5Q). During the late Early Miocene two species co-occur temporally but not spatially, which is indicated by the presence of *L. ragei* in late Karpatian sediments of the Korneuburg Basin (youngest record of this species; Böhme 2002) and *L. gigantea* in Ottnangian sediments of Dolnice (oldest record of this species; Hodrová 1987).

Family Pelobatidae Bonaparte 1850

Genus *Pelobates* Wagler 1830

Remarks: With over 180 individuals, the genus *Pelobates* represents the most common vertebrate in Sandelzhausen. The estimated minimum number of individuals is based on the maxilla, the most robust bone in pelobatids, in contrast to other anuran groups where ilia are usually best represented. This bone is underrepresented in Sandelzhausen compared with maxillae. This phenomenon has been described from Holocene deposits (Böhme 1983) and is probably related to the higher probability of breakage along the furrow on the ilia shaft proximal to the corpus ossis ilii.

***Pelobates fahlbuschi* nov. sp.**

Figure 5T, V, W, Y

1999 *Pelobates* nov. sp. Böhme: 490, Fig. 4.

Derivatio nominis: dedicated in memorian to Prof. Dr. Volker Fahlbusch († 30th October 2008)

Holotype: frontoparietal, 16338 (Fig. 5Y)

Type locality and horizon: Sandelzhausen, PQ 8-J, horizon C3/D1, 115–120 cm above base.

Referred material: 3 frontoparietals (16339, 16340, 16342), 148 frontoparietal and nasal fragments (16343–16345, 16352, 16355, 16356), 81 squamosals (16346, 16347), over 700 maxillae and maxilla fragments (5483, 6514, 16359), 93 intermaxillae (16357, 16358), 1 prearticular (16353), 1 parasphenoid (16354), 22 ilia (16348), 20 sacral vertebrae (16349), 1 urostyle (16361), 8 presacral vertebrae (16350), one atlas (16351).

Diagnosis: A species of the Oligo-Miocene *Pelobates* clade (sensu Venczel 2004, species with highly prominent pit-and-ridge sculpture on frontoparietal, squamosal and maxilla) that differs from *P. sanchizi* in the frontoparietal by broader tectum supraobitale, deep groove for arteria orbitonasalis on ventral side of the tectum supraorbitale, deeply concave posterior margin of the frontoparietal incrassation, and a foramen arteriae occipitalis lying medial to the paraoccipital process and visible from the dorsal side. It further differs from *P. sanchizi* in the squamosal by a broader lamella alaris, the development of a prominent posteroventral process, and a straight anterior border of the processus descendens of the ilium.

The squamosal of the new species differs from the fossil *P. decheni* by a more concave ventral border (ventral border of the zygomatic process and the lamellae alaris nearly perpendicular to each other), a delimited dorsal and posterodorsal process, a slender zygomatic process, and a somewhat narrower squamosal-frontoparietal suture being one-fifth to one-quarter of the inferred frontoparietal length (one-half in *P. decheni*). Ilium differs from recent and fossil *Pelobates* species by the presence of a shallow groove on the dorsolateral edge of the processus ascendens ilii, and a weak and oval, rough tuber superior between this groove and the spiral groove. Differs from recent pelobatids, but resembles *P. sanchizi* in the presence of a spinal nerve foramen in presacral vertebrae. In contrast to all recent species and *P. sanchizi*, a neural spine is missing in posterior presacral vertebrae.

Description of the holotype: The right side of the frontoparietal lacks the anterior part and the distal tip of the paraoccipital process. The dorsal surface is covered by a dense and prominent pit-and-ridge sculpture similar to *P. decheni*, *P. sanchizi* and an as-yet-undescribed species from the Miocene of Petersbuch 38. The bone is transversally convex, similar to all described *Pelobates* species, but unlike the new species from Petersbuch 38 where the dorsal surface is more or less flat.

The tectum supraorbitale is very broad and largely overlaps the posteromedial part of the endocranial orbit. The tectum is broader than in *P. cultripes* and *P. sanchizi* (Fig. 5Y) and probably of similar extent to in *P. decheni* (Böhme et al. 1982: Figs. 1–4).

On the medial rim of the tectum supraorbitale only one foramen is developed. It is a deep foramen situated on the anteromedial border of the processus lateralis inferior, representing the orifice of the distal part of the arteria occipitalis. The arteria occipitalis splits into the arteria orbitonasalis and arteria temporalis outside the pars contacta, e.g. below the tectum supraorbitale. In recent pelobatids the split of the arteria occipitalis is located more posterior, at the level of the processus lateralis inferior, within the pars contacta (Roček 1981: Fig. 28). In the recent species the proximal part of the arteria orbitonasalis is covered by bone (to a variable degree in *P. fuscus*), whereas it is free in the Sandelzhausen species. Therefore recent pelobatids show two foramina: the foramen arteriae temporalis at the anterolateral border of the processus lateralis inferior and more anteriorly the foramen arteriae orbitonasalis. The courses of both the arteria orbitonasalis and temporalis occur in the Sandelzhausen species as deep grooves, which are not developed in any recent species. In *P. sanchizi* the groove of the arteria orbitonasalis seems only weakly developed, whereas it is absent in *P.* nov. sp. from Petersbuch 38 (Fig. 5Z).

The pars contacta is elevated due to a well-developed processus posterior superior, similar to *P. fuscus*, *P. cultripes* and *P. sanchizi*, but unlike *P. syriacus* and the fossil species from Petersbuch 38, where the pars contacta is flat.

The posterior margin of the frontoparietal incrassation is deeply concave, indicating the partial development of the taenia tecti medialis (cf. Jarošová and Roček 1982). This is similar to *P.* nov. sp. from Petersbuch 38 (Fig. 5Z) and to some individuals of *P. cultripes* (Fig. 5AA). In recent species (and most *P. cultripes* individuals) the posterior margin of the frontoparietal incrassation is weakly concave to straight (Špinar 1976: Fig. 4; Jarošová and Roček 1982: Fig. 7; Roček 1984: Fig. 27). In the holotype of *P. sanchizi* the posterior margin is entirely straight (Fig. 5X; Venczel 2004: Fig. 6A). The lateral margins of the frontoparietal incrassation are straight in the Sandelzhausen species (Fig. 5Yb), and the new species from Petersbuch 38, *P. sanchizi*, and *P. syriacus* (Fig. 5Xb, Zb, ABb), whereas they are notched in their posterior part in *P. cultripes* (Fig. 5AAb) and *P. fuscus*.

The facies posterior is slightly convex between both paraoccipital processes. These processes are pointed and bear sharp dorsal edges, similar to *P. cultripes* and *P. sanchizi*. The proximal opening of the arteriae occipitalis is positioned medial to the paraoccipital process (in contrast to *P. fuscus*, where it lies dorsal) and is visible from the dorsal side (see arrow—Fig. 5Wa), in contrast to *P. cultripes*, *P. syriacus* and *P. sanchizi* (Figs. 5Xa, AAa, ABa), where it is visible only in posterior view.

Description of referred material: One left squamosal is nearly complete (16347); only the processus posterolateralis, the tip of the posterodorsal process and the most distal part of the squamosal-frontoparietal suture are broken off. The surface is similar to both fossil species *P. decheni* (Böhme et al. 1982) and *P. sanchizi* (Venczel 2004), covered by a dense and prominent pit-and-ridge sculpture. The lamella alaris is very broad and shows a distinct process on the posteroventral part. This posteroventral process is unknown from extant species, and occurs in a similar way in the fossil *P. decheni* and to a lesser extent in *P. sanchizi*. Due to the prominent posteroventral process the ventral side of the squamosal is strongly concave. The ventral border of the zygomatic process and the ventral border of the lamella alaris are nearly perpendicular to each other (obtuse angle in *P. decheni*). The zygomatic process is relatively robust, but slender compared with *P. decheni* and *P. sanchizi*. Midway, this process is somewhat constricted. The posterodorsal process is (as in *P. sanchizi*, *P. syriacus* and *P. veraldii*, and unlike *P. decheni* and *P. cultripes*) clearly delimited from the dorsal process. The dorsal process forms a broad suture to the frontoparietal. This suture is one-fifth to one-quarter of the length of the squamosal and frontoparietal, respectively (except in *P. fuscus* the squamosal and the frontoparietal are of about the same length in all *Pelobates* species). The postorbital bridge is therefore relatively broad.

As typical for the ilia of *Pelobates* species, the spiral groove between the iliac shaft and acetabulum is deep. In contrast to the shallow groove in *Eopelobates* it is well visible in lateral view (Fig. 5V). The processus descendens is short, similar to in *P. syriacus* and *P. sanchizi*, but unlike to *P. cultripes* and *P. fuscus* (Fig. 5U). The anterior border of the processus descendens is straight as in *P. syriacus*, whereas it is convex in *P. cultripes* and *P. fuscus* and slightly concave in *P. sanchizi*. The transition between the processus descendens and the acetabulum is sharply bent, whereas it is rounded in the recent species (uncertain in *P. sanchizi*). The striate symphysis on the medial surface of the acetabular region is moderately developed as in *P. fuscus* and *P. sanchizi*, but stronger than in *P. syriacus* and weaker than in *P. cultripes*. Unlike any fossil and recent *Pelobates* species a flat groove is developed on the dorsolateral edge of the processus ascendens, resulting in a weak, oval and rough tuber superior between this groove and the spiral groove. This feature can be observed in all ilia where this part of the bone is preserved. A similar tuber is developed in *Pelodytes caucasicus* (Böhme 1977: Fig. 8m).

Of 20 sacral vertebrae from Sandelzhausen, 3 are fused to the urostyle. Of ten sacral vertebrae in *P. sanchizi*, one is fused (Venczel 2004). This condition varies from that seen in recent species, where the sacral vertebrae and the urostyle are generally fused, except in *P. cultripes* where 50% are fused (four of eight specimens in the BSPG osteological collection).

Similar to *P. sanchizi* and unlike recent species all posterior presacral vertebrae enclose a spinal nerve foramen. In contrast to all recent species and *P. sanchizi* the posterior presacral vertebrae lack a neural spine on the posterior margin of the neural lamina. In anterior presacral vertebrae the neural spine may be developed somewhat similarly to the posterior presacral vertebrae of *P. sanchizi* (Venczel 2004: Fig. 7J). The atlas bears a gracile neural spine which is only slightly longer than the posterior margin of the postzygapophysis (much longer in recent species).

Comments: Venczel (2004) suggested that two clades can be distinguished within *Pelobates* based on the sculpturing type of cranial bones: the recent species with isolated tubercles and crest-like structures, and the fossil species (*P. decheni*, *P. sanchizi*) with a prominent pit-and-ridge sculpture. *Pelobates fahlbuschi* nov. sp. clearly belongs to the latter group. According to Roček (1981: 148) the wide postorbital bridge is a plesiomorphic character state, best developed in the latest Oligocene *P. decheni* (Böhme et al. 1982). Following this interpretation, *P. fahlbuschi* nov. sp. is more advanced than *P. decheni*, but may be slightly more conservative than the Middle Miocene *P. sanchizi*. This interpretation is supported by the straight posterior margin of the frontoparietal incrassation in *P. sanchizi*. According to Špinar (1976) and Jarošová and Roček (1982) the morphology of the frontoparietal incrassation is taxonomically and phylogenetically significant. According to the latter authors straight margins represent the advanced evolutionary stages (reduction of the taenia tecti medialis et transversalis), supporting plesiomorphic conditions in *P. fahlbuschi* nov. sp. relative to *P. sanchizi*.

Genus *Eopelobates* Parker, 1929

***Eopelobates* sp.**

Figure 5R

2004 *Eopelobates* sp. Reichenbacher et al.: 87, Pl. 3 Fig. 12.

Material examined: 3 ilia (16330–16332), 5 maxillae (16333–1), 1 squamosal (16333–2), 1 frontoparietal fragment.

Description and comments: *Eopelobates* is a rare frog in Sandelzhausen. Only nine bones have been identified. Compared with the ilium of *Pelobates* (Fig. 5R, V), the pars ascendens is low and short and the dorsolateral furrow is poorly recognizable from the medial side. In recent and fossil *Pelobates* the furrow continues on the medial side. In this respect the ilium is similar to that described by Hodrová (1987: Fig. 9) as *Eopelobates* sp. from Dolnice. However, in this bone the pars ascendens is higher and longer, although shorter than in *Pelobates*. The eopelobatids from Sandelzhausen and Dolnice most probably belong to different species.

The *Eopelobates* maxilla shows a pit-and-ridge-type ornamentation, which is generally smoother than in the fossil *Pelobates* where isolated, prominent tubercles occur (Fig. 5T; Venczel 2004).

Family Bufonidae Gray, 1825

Genus *Bufo* Laurenti, 1768

***Bufo* cf. *viridis* Laurenti, 1768**

Figure 5P

2004 *Bufo* cf. *viridis* Venczel: 167, Fig. 8

Material examined: 6 ilia (6508, 6528, 6529, 6534, 16327, 16328, 16329–1), 3 sacral vertebrae (6531–6533), 1 urostyle (16360), 1 braincase (16329–2).

Comments: The ilia of bufonids are characterized by the absence of an iliac crest, and a well-developed dorsal protuberance, located above the anterior rim of the acetabulum. The contemporaneous European species of *Bufo* can easily be distinguished based on ilia (Böhme 1977; Bailon 1999). The Sandelzhausen specimens show a well-developed proximal constriction of the iliac shaft (preacetabular fossa), which is typical for *Bufo viridis* (green toad). Dorsal of the acetabulum, a shallow depression is found in three of the ilia (Fig. 5P), which may also be present in recent central European *B. viridis* individuals (one of three studied skeletons, BSPG 1982 X 4351). This depression is also found in some specimens of the large population from Petersbuch 2 (Böhme, unpublished results), the oldest Neogene toads from Europe. The recent Palaearctic green toads (*Bufo viridis* subgroup) represent several species (Stöck et al. 2006), which have not yet been studied with regard to osteology. Therefore, an open nomenclature is used for the Sandelzhausen species.

Remark: Petersbuch 2 is biostratigraphically older than the Spanish bufonid-bearing localities Buñol and Córcoles, because it is the oldest central European locality yielding modern cricetids (e.g. *Democricetodon*) and is therefore placed in MN4a, corresponding to Aragonian A (first occurrence of *Democricetodon*) or Aragonian B (first regular occurrence of *Democricetodon*) in the Spanish stratigraphic subdivision. Buñol and Córcoles are placed in the Aragonian C (Van der Made et al. 1998; Antoine et al. 2002) and consequently are younger.

***Bufo* sp.**

Figure 5S

Material examined: a single left ilium fragment (6509)

Description and comments: A second bufonid species is documented by a single ilium. The bone is characterized by a weak (nearly absent) preacetabular fossa, similar to in *B. bufo* or *B. calamita*. A lateroventral outgrowth on the ilial shaft ("calamita ridge") is also absent. The dorsal protuberance is sub-divided into two more or less transversal ridges, the distal one being somewhat higher. Most remarkably, a well-developed depression (supra-acetabular fossa) occurs proximally to the dorsal protuberance. This depression is significantly deeper than in *Bufo* cf. *viridis*. To my knowledge, a fossa of this kind is unknown in bufonids, at least in the European species.

The appearance of a second bufonid species has also been reported from Vieux-Collonges and La Grive (*Bufo* aff. *B. viridis* and *B.* sp. indet.; Bailon and Hossini 1990).

Family Ranidae Rafinesque-Schmaltz, 1818
Genus *Pelophylax* Fitzinger, 1843
***Pelophylax* sp.**
Figure 5O
1987 *Rana* sp. Hodrová: 109, Figs. 12–14.
2004 *Rana esculenta synklepton* Venczel: 169, Fig. 9.
2005 *Rana* sp. Rage and Bailon: 420, Fig. 3 A–C.

Material examined: 28 ilia (6521, 6569–6585, 16325) and many other bones, including presacral vertebra, sacral vertebra, scapula, humerus (6586–6592, 16326).

Comments: The green water frogs, formerly the *Rana ridibunda* group, are now placed in the genus *Pelophylax* Fitzinger, 1843 (Frost et al. 2006; Che et al. 2007). The living species of this genus are very difficult to distinguish from one another based on osteology. The most useful bone seems to be the fragile frontoparietal (Böhme 1977), which is virtually absent in pre-Pleistocene localities for taphonomic reasons. However, the characters at genus level are fairly robust (Böhme 1977; Sanchiz 1998; Bailon 1999). The genus is well represented in Sandelzhausen, by (besides other bones) 28 ilia, which all show characteristic features: a strong, oval and ventrally well-defined dorsal protuberance, which is very high; the iliac crest is also high, but the dorsal protuberance always overtops the crest; the presence of a well-developed supra-acetabular fossa.

Ranidae indet. nov. gen. et sp.
Figure 8

Material examined: 1 ilium (6542), 1 maxilla fragment (16317), 9 terminal phalanges (16462, 16463).

Description and comments: The left ilium is large and shows a round acetabular fossa, well-developed pars ascendens (partially broken), high iliac crest (partially broken) and a strong dorsal protuberance (Fig. 8a, b). The protuberance is round, knob-like and laterodorsally expanded, so that in dorsal view the protuberance is inclined relative to the bone axis (Fig. 8c). A preacetabular fossa is absent. In contrast to Discoglossidae, the pars ascendens is robust in caudal view (junctura ilioischiadica). The posterior fragment of a right maxilla has a broad and robust lamina horizontalis and lacks the pars facialis in its posterior part (Fig. 8d, e). In the anterior part of the bone fragment the pars facialis was present (although broken in the studied specimen). The posterior end of the lamina horizontalis is medially slightly broadened to a moderately developed pterygoid process (Fig. 8e). This process bears a sulcus in medial position, probably for articulation with the anterior ramus of pterygoid. The large dimensions of both bones indicate a body size of the frog comparable to that of *Latonia gigantea*.

The ilium and maxilla undoubtedly belong to a ranid frog, however both the size and morphologic details suggest a taxon other than *Pelophylax*. The absence of the preacetabular fossa and the round, knob-like and laterodorsally expanding dorsal protuberance are unknown in any species of *Pelophylax* and other extant or fossil European ranids. A maxillary pterygoid process is absent in *Pelophylax* (personal observation), but weakly developed, albeit without a sulcus, in *Rana* (*R. temporaria*, *R. arvalis*), the North American *Aquarana* (*A. catesbeiana*; both personal observations) and some African Raninae (Clarke 1981: 297). Well-preserved maxillae of early Neogene European Ranids have not been described to date, and thus it is possible that this maxilla belongs to forms described as *Pelophylax* sp. However, the large size of the studied bone suggests that this maxilla is taxonomical different from the smaller-sized *Pelophylax* sp.

Nine relatively large terminal phalanges show a highly unusual morphology (Fig. 8f–i). The phalanges are relatively short and robust with a broad proximal base (up to 2 mm). The distal ends are strongly laterally expanded and exhibit a warty crenated surface. Expanded distal ends in terminal phalanges are rare in ranids and of special taxonomic importance (Clarke 1981). The present morphology resembles state 5 of Clarke (1981, Fig. 10D), which occurs in *Lanzarana rageni*, a monospecific genus of dry savannah and semi-arid habitats endemic to Somalia (Lanza 1987). Phalanges of similar morphology occur also in the nearby locality Unterempfenbach 1d, which has the same stratigraphic age as Sandelzhausen (Abdul-Aziz et al. 2008).

The second ranid from Sandelzhausen obviously represents a new species and probably also a new genus. A detailed description will be provided in a separate paper.

Class Reptilia McCartney, 1802
Order Crocodyliformes Hay, 1930
Family Alligatoridae Gray, 1844
Genus *Diplocynodon* Pomel, 1847
***Diplocynodon styriacus* (Hofmann, 1885)**
Figure 5AF
1973 *Diplocynodon* cf. *gracilis* Scherer: 105, Pl. 4.
1973 *Diplocynodon* sp. Scherer: 111.
1978 *Diplocynodon* cf. *bueticonensis* Scherer: 68, Pl. 6.
1981 *Diplocynodon* cf. *bueticonensis* Scherer: 81.
1997 *Diplocynodon styriacus* Ginsburg and Bulot: 112, Figs. 1–9.
2002a *Diplocynodon styriacus* Böhme: 342, Pl. 2 Fig. E.

Material examined: 331 isolated teeth (6526, 7539, 16363)

Comments: The cranial and postcranial material of this small crocodile (~2 m) was described in detail by Scherer (1973, 1978, 1981) as *Diplocynodon* cf. *bueticonensis*, which, according to Ginsburg and Bulot (1997) is a

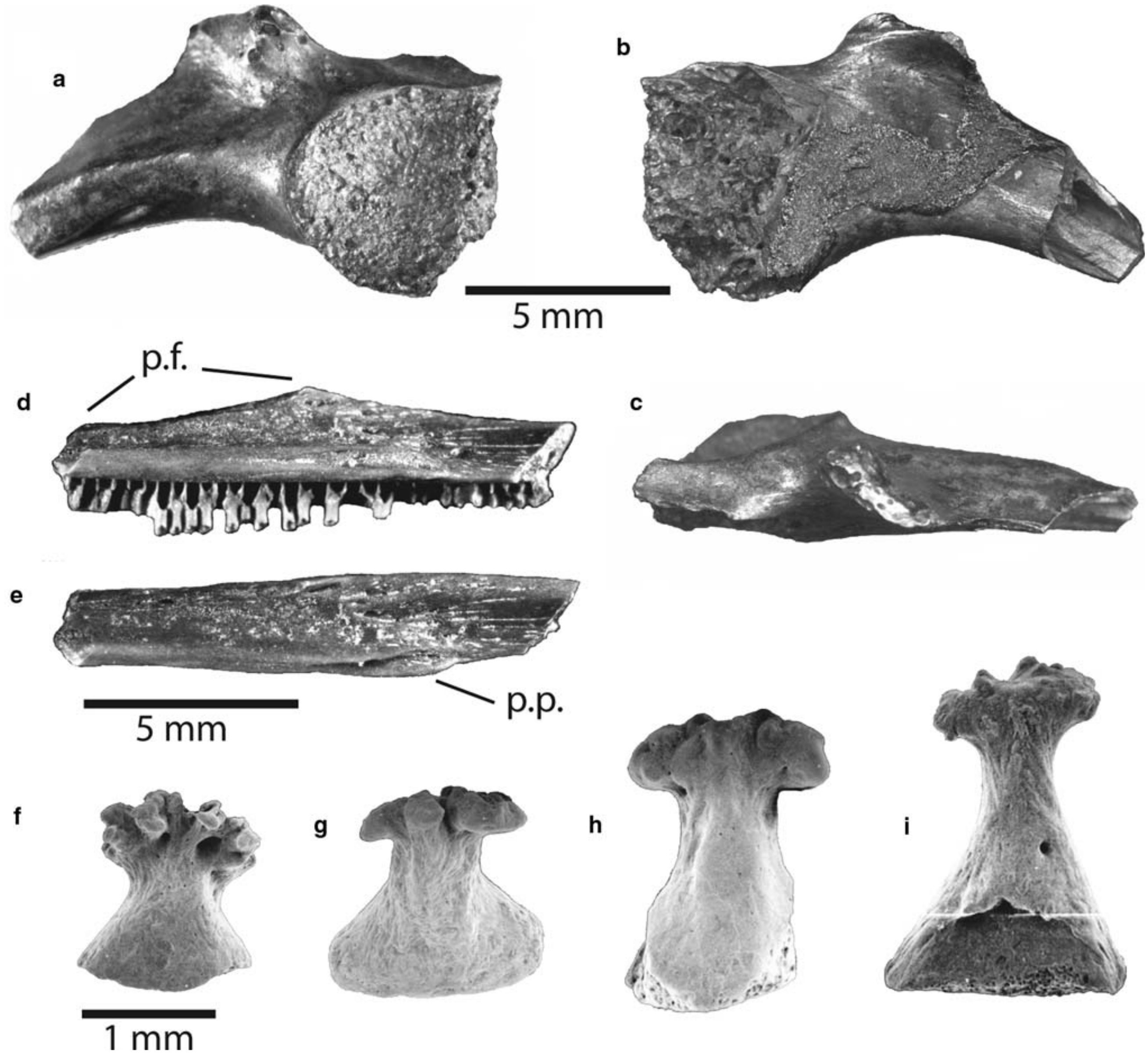


Fig. 8 Ranidae indet. gen. et sp. nov., left ilium (**a–c**; 6542), posterior fragment of a right maxilla (**d**, **e**; 16317), terminal phalanges (**f–i**; 16462). **a**: *lateral view*; **b**, **d**: *medial view*; **c**, **e**, **f–h**: *dorsal view*; **i**: ventral view. Abbreviations: p.f.: pars facialis, p.p.: pterygoid process

synonym of *Diplocynodon styriacus* (Hofmann 1885). Here I report a rich collection of isolated teeth (Table 2), most accumulated due to tooth replacement. A significant portion (about 20%) of the tooth crowns reach 1–3 mm height, and thus are very small (Fig. 5AF). These teeth are interpreted as belonging to hatchlings or very young juveniles (see Böhme 2002a: 342). Teeth over 10 mm long are comparatively rare (adult tooth size about 20 mm), indicating that the majority of the specimens represent juveniles.

Order Squamata Oppel, 1811
Suborder Iguania Cope, 1864
Family Chamaeleonidae Gray, 1827
Genus *Chamaeleo* Linneaus, 1759
***Chamaeleo* aff. *caroliquarti* Moody and Roček 1980**
Figure 5AC, AD

Material examined: 1 left maxilla (7529), 2 maxillary bone fragments (7530, 7541), 1 left symphysis (16364), 1 cranial bone fragment (16365)

Comments: *C. caroliquarti* was first described from Dolnice (MN4b) and Wintershof-West (MN3) by Moody and Roček (1980) and later from Merkur-Nord (MN3) by Schleich and Fejfar (1994). The maxilla fragments and mandibular symphysis from Sandelzhausen (Fig. 5AC, 5AD) agree well with this species, characterized by a large size and triangular and monocuspid acrodont teeth among other features. However, unpublished material from the contemporaneous site Gisseltshausen 1b indicates the existence of a second large chameleonid species, which will be described in a separate paper. The Sandelzhausen remains are not complete enough to determine to which of the species they belongs. Nevertheless, it shows affinities to *C. caroliquarti*.

This species represents the largest fossil chameleonid known so far, reaching a total size of probably over 50 cm, similar to the largest living chameleons *Calumma parsonii*, *Furcifer oustaleti* and *Chamaeleo melleri*. The Sandelzhausen specimens represent the stratigraphically youngest records of such large chameleonids in Europe, although my unpublished data indicate the survival of these animals in central Europe well into the Middle Miocene up to ~14.5 Ma (localities Laimering 2a and 3, Wannenwaldtobel 2).

***Chamaeleo bavaricus* Schleich, 1983**
Figure 5AE
*1983 *Chamaeleo bavaricus* Schleich: 78; Fig. 1

Holotype: left fragment of a dental (2066).

Material examined: beside the holotype, 3 maxilla fragments (5470, 6525, 7531).

Comments: The species was described by Schleich (1983). Since that time three new maxilla fragments have been discovered, however they do not provide additional information. Sandelzhausen is the first fossil locality yielding two chameleonid species. Although a detailed look at the stratigraphical distribution of both species within the Sandelzhausen profile (Table 2) supports the sympatry of both species only in the level C3/D1. Another locality where both species probably lived sympatrically is Laimering 2a (Böhme, unpublished).

Suborder Lacertilia Owen, 1842
Family Lacertidae Fitzinger, 1826
Genus *Lacerta* sensu latu Linnaeus, 1758

***Lacerta* s.l. sp. 1**
Figure 9A

Material examined: left dentary (16366).

Description: The left dentary of this medium-sized lacertid (maximum length of the dentary 6 mm) is nearly complete (the two most anterior tooth positions missing) and shows 18 tooth positions. The labial side bears four relatively large mental foramina. The corpus of the dentary is slender. The crista dentalis runs relatively straight. A sulcus dentalis is well developed. The lamina horizontalis is only weakly arched ventrally (all statements relative to *Lacerta* sp. 2, see below). Its height increases in the beginning, reaching the maximum thickness below the 9th and 10th tooth position (counted including the two missing anterior positions), and then becomes gradually thinner up to the last (20th) tooth position. On the ventral side of the lamina, the facet for the attachment of the splenial reaches to the 12th tooth position. The crista ventralis becomes constantly higher in posterior direction and is only slightly curved inward, so that the Meckel's groove is widely open ventromedially. The slender pleurodont teeth are unicuspid with only a slight tendency to a bicuspid condition. They overtop the crista dentalis by about one-third of their height.

Comments: See comments to *Lacerta* s.l. sp. 3 below.

***Lacerta* s.l. sp. 2**
Figure 9B

Material examined: left dentary (6522), 7 dentary fragments (5495, 16368–16373), left maxilla (16367), maxilla fragment (16374).

Description: The figured left dentary (Fig. 9B) is nearly complete (only a few of the posterior tooth positions are lacking) and shows the anterior 18 tooth positions. This is a relatively large species (dentary size more than 8 mm). The lamina horizontalis arches ventrally, especially in its anterior part. It has its maximum thickness already in the first third of the bone. Posteriorly it gradually becomes thinner, but still remains relatively high below the last preserved tooth position. The facet for the articulation of the splenial reaches to the 10th tooth position. Compared with *Lacerta* sp. 1, the crista ventralis does not significantly increase in height in posterior direction. This crista is curved inward, so that the Meckel's groove is slightly more closed than in the previous species. The teeth are relatively robust and clearly bicuspid. They overtop the crista dentalis by about one-half of their size. The tooth crowns bear strong culmines lateres and in between a few well-developed striae.

Comments: See comments to *Lacerta* s.l. sp. 3 below.

***Lacerta* s.l. sp. 3**

Material examined: 1 left dentary (16375), 1 left maxilla (16377), 14 dentary fragments (16376, 16381–16390), 3 maxilla fragments (16378–16380), 2 jaw fragments (16391, 16392).

Comments: This species is very similar to *Lacerta* sp. 2, but differs by its smaller size (dentaries 3–4 mm) and more weakly developed bicuspid teeth.

Pre-Pleistocene lacertids are very difficult to determine at species level based on isolated bones, because this diverse group (*Lacerta* sensu latu) is anatomically generalized and only shows a few characteristic features at species and even genus level. Nevertheless, the three Sandelzhausen species can easily be distinguished from each other, but a comparison with other described lacertids of comparable age, e.g. from Dolnice (Czech Republic, MN4b; Roček 1984), Sansan (France, MN6; Augé and Rage 2000), Korneuburg Basin (Austria, MN5; Böhme 2002), Béon 1 (France, MN4b; Rage and Bailon 2005) remains impossible until a detailed revision of the group has been conducted.

Genus *Edlartetia* Augé and Rage, 2000
***Edlartetia sansaniensis* Augé and Rage, 2000**
Figure 9E

Material examined: dentary fragment (16393).

Comments: The left dentary fragment bears seven tooth positions. The facet on the lamina ventralis for the articulation of the splenial reaches up to the fourth preserved tooth position. Despite its fragmentary preservation, determination of this bone is possible because of the unique tooth morphology known only from *Edlartetia sansaniensis* (Augé and Rage 2000: Figs. 4–6). The tooth shafts are strongly constricted immediately above the level of the crista dentalis. The tooth crowns are slightly pointed, more or less triangular or drop shaped. Except for a crista distalis (posterior cutting edge) in one tooth the crown ornamentation consists of a few rough bulges. This type of tooth crown ornamentation is unknown from recent lacertids (Augé and Rage 2000) and so unique that I refer the Sandelzhausen fragment to the Sansan species.

Genus *Miolacerta* Roček, 1984
cf. *Miolacerta tenuis* Roček, 1984
Figure 9C

Material examined: 2 dentary fragments (6523, 16394).

Comments: The fragmentarily preserved dentaries show the characteristic tricuspid tooth morphology of *Miolacerta tenuis* (Roček 1984: Pl. 6 Figs. 5–7) from Dolnice (also present in Lacertidae gen. et sp. indet. from Béon, Rage and Bailon 2005: Fig. 3E, *M. tenuis* from Kohfidisch, Austria, MN11, Tempfer 2005: Pl. 5a, and *Lacerta* s.l. sp. 2 from the Korneuburg Basin, Böhme 2002a: Pl. 2 Fig. B). Since similar tooth morphologies may occur in several extant lacertid lineages (cf. Kosma 2004), relation of the studied material to the Czech species must remain tentative.

Family Scincidae Gray, 182
Subfamily Lygosominae Mittleman, 1952
Genus *Tropidophorus* Dumeril and Bibron, 1839
***Tropidophorus bavaricus* nov. sp.**
Figure 9F

Holotype: left dentary with 12 tooth positions (16395).

Type locality: Sandelzhausen, Late Karpatian, late OSM C+D (for description of the section and stratigraphy see Abdul-Aziz et al. 2008).

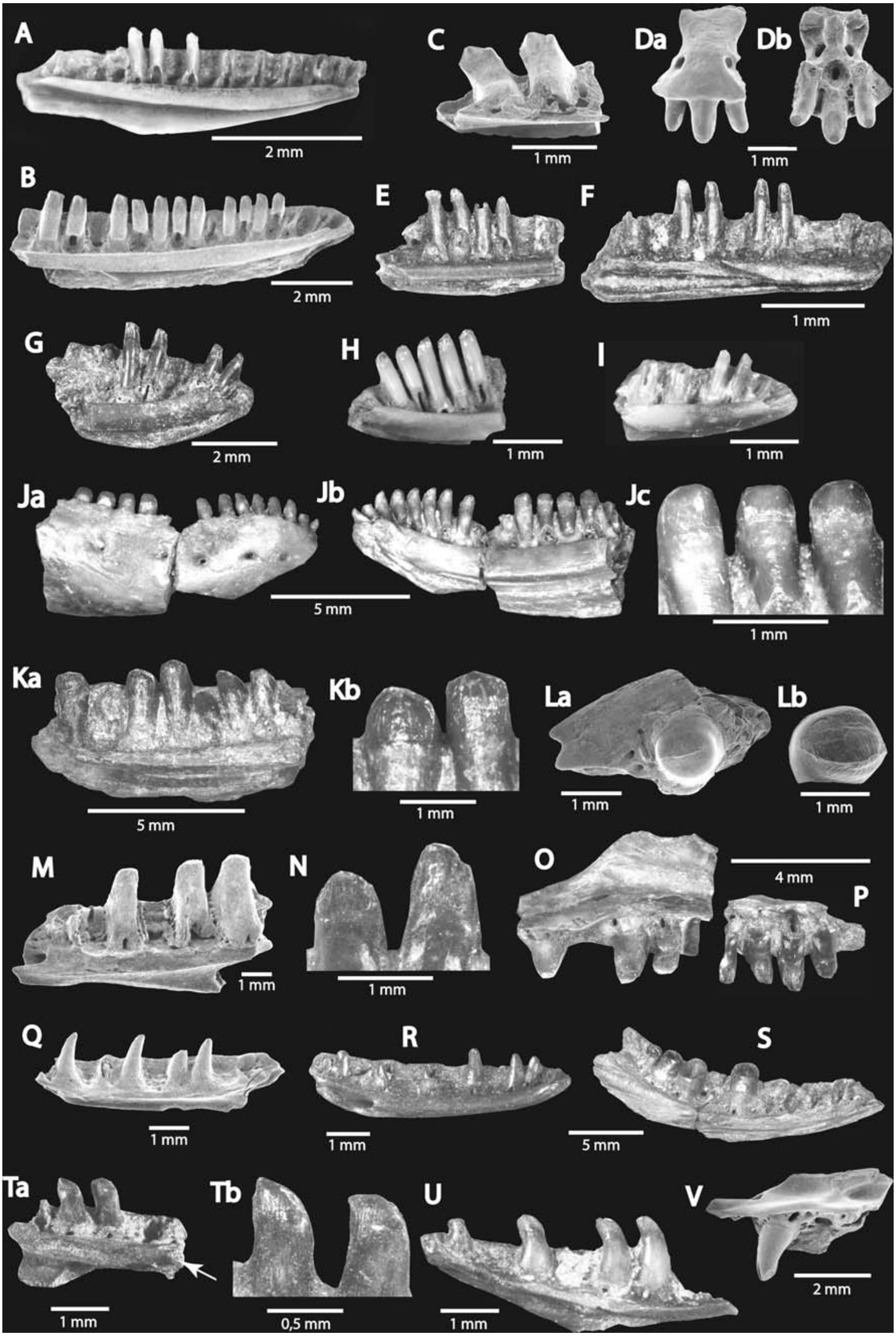
Etymology: referring to Bavaria, southeast Germany.

Referred material: fragmentary left dentary with five tooth positions (16396), fragmentary right dentary with nine tooth positions (16397).

Diagnosis: A small lygosomine skink, closely resembling representatives of the extant genus *Tropidophorus* based on the anterior restriction of the Meckel's groove to a narrow split, the high and slender teeth, and the tooth crown ornamentation, characterized by a longer crista medialis than crista distalis, development of a cuspis lingualis, inward recurved short and prominent culmines lateres, and presence of indistinct striae. The antrum intercristatum is lacking. The ratio of the tooth length to the diameter of the tooth neck is 4.5:1.0. The teeth overtop the crista dentalis by more than one-third of their height.

Description of the holotype: The small and slender dentary (3 mm length) lacks the anterior and most posterior parts. Twelve teeth positions and four intact teeth are preserved. The smooth labial side bears three large labial foramina. The crista dentalis is bumpy. The straight lamina horizontalis is anteriorly broad and ventrally vaulted. Behind the sixth preserved tooth position the lamina gradually becomes thinner and ends below the ninth tooth position. In this part the ventral side of the lamina shows a facet for the attachment of the splenial, which reaches up to the seventh or eighth preserved tooth position. The ventrally straight crista ventralis runs largely parallel to the lamina horizontalis and is curved in medial direction; thus the Meckel's groove is opened medioventrally by a narrow split below the anterior sixth tooth position. The dentary shelf is anteriorly wide and deep and forms a well-developed sulcus dentalis. The teeth are pleurodont, narrow (the tooth base is not significantly broadened) and relatively high, overtopping the crista dentalis by more than one-third of their height. The ratio of tooth length to diameter of tooth neck is 4.5:1.0. The tooth crowns are unicuspid. The lingual side of the tooth crown is concave, the labial side convex. Both anterior and posterior crown flanks bear cutting edges (crista mesialis and distalis sensu Richter 1994) joining in an obtuse-angeled and posterolingually orientated tip (cuspis labialis sensu Richter 1994). A cuspis

Fig. 9 *A*: *Lacerta* s.l. sp. 1, dentary (16366). *B*: *Lacerta* s.l. sp. 2, dentary (6522). *C*: cf. *Miolacerta tenuis*, dentary fragment (6523). *D*: *Palaeoblanus* nov. sp., intermaxilla (*Da*: external view, *Db*: internal view, 5478). *E*: *Edlartetia sansaniensis*, left dentary fragment (16393). *F*: *Tropidophorus bavaricus* nov. sp., dentary (holotype, 16395). *G*: Scincidae sp. 1, dentary fragment (16398). *H, I*: Scincidae sp. 2, dentary fragments (16400 (*H*), 16401 (*I*)). *J*: *Bavaricordylus molassicus*, dentary (holotype), Puttenhausen B (BSPG 2008 XXIV 1); *Ja*: labial view, *Jb*: lingual view, *Jc*: tooth crowns. *K, L, N–P*: *Bavaricordylus* cf. *molassicus*, *Ka*: dentary, labial view (16402); *Kb*: dentary tooth crowns (16402); *La*: posteriormost dentary teeth (7510); *Lb*: isolate posterior teeth (7525); *N*: maxilla tooth crowns (16403); *O*: anterior maxilla fragment (16403); *P*: posterior maxilla fragment (16404). *M*: *Ophisaurus* sp. *I* (sensu Roček 1984), dentary fragment (6524). *Q, R*: *Ophisaurus* sp., dentaries (6527 (*Q*), 16426 (*R*)). *S*: *Pseudopus laurillardi*, dentary (16413). *T, U*: Anguidae gen. indet. sp. nov., *Ta*: dentary fragment (16459), arrow marks the position of the spina splenialis; *Tb*: tooth crowns (16459); *U*: maxilla fragment (16460). *V*: cf. *Ophisaurus* cf. *spinari* (sensu Roček 1984), maxilla (7527)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lingualis seems to be developed in two of the four teeth. The antrum intercristatum (sensu Kosma 2004) is lacking. The tip is situated behind the midpoint, so that the cusp is asymmetric. Both cristae mesialis and distalis transform into short but prominent culmines lateres (sensu Richter 1994), which slightly recurve inward. On the lingual side of the crown, between the culmines lateres a few indistinct striae are developed.

Comparison: The general crown ornamentation and the morphology of the teeth and dentary, especially the anteriorly restricted opening of the Meckel's groove, indicate a representative of the family Scincidae, especially the Lygosominae. It differs from *Bavariascincus mabuyaformes* Kosma 2004, the only formally described Miocene skink of Europe, in its smaller size and more gracile mandible, a more restricted Meckel's groove, a thinner posterior lamina horizontalis, teeth more strongly overtopping the crista dentalis, pointed (not blunt) teeth, not restricted tooth necks, and by shorter culmines lateres. The small-sized European copper skink (*Ablepharus kitaibellii*, BSPG 1982 X 4761), the only extant lygosomine skink of Europe, differs from the new species by a fully closed Meckel's groove up the most posterior teeth and a much smaller ratio of tooth length to tooth neck. The dentary and tooth morphology seems most similar to the semi-aquatic lygosomine water skinks of the genus *Tropidophorus*. Compared with the osteologically known Southeast-Asian members of this genus the fossil dentary is most similar to *T. berdmorei* and *T. robinsoni* based on the crown ornamentation and ratio of tooth length to tooth neck (see Kosma 2004: 96–98, Pl. IX Figs. 4–8). However, it differs from all members of the genus in the absence of an antrum intercristatum. The two most closely related recent species live in southern China (Yunnan; up to about 24°N, just south of Kunming), Vietnam, Laos, Thailand and Myanmar in semi-aquatic and humid habitats. *T. berdmorei* favours small, rocky, forested streams and lives along the banks and under rocks in the stream bed (Cox et al. 1998). Based on molecular data, Honda et al. (2006) concluded that the basal diversification within the genus *Tropidophorus* occurs at the beginning of the Miocene (23 Ma). The new species represents the first fossil record of the genus *Tropidophorus* and lygosomine skinks in Europe in general. Because of the close morphological similarities to recent water skinks of the genus *Tropidophorus*, a semi-aquatic lifestyle can be assumed for *T. bavaricus* nov. sp. too.

Subfamily indet.

Scincidae indet. 1

Figure 9G

Material examined: left dentary fragment (16398), left dentary symphysis (16399).

Description and comparison: The anterior dentary fragment shows the first nine tooth positions. On the labial side of the robust bone four labial foramina are located. A sulcus dentalis is well developed. The lamina horizontalis is high. On the ventral side of the lamina, below the seventh tooth position, the anterior end of the facet for the articulation of the splenial is visible. The Meckel's groove is relatively deep (compared with Scincidae indet. 2) due to the well-developed lamina ventralis. The teeth are pleurodont and narrow. The tooth crowns are unicuspid and have well-expressed cutting edges (cristae mesialis and distalis sensu Richter 1994). The crista mesialis is longer than the crista distalis. Between the short culmines lateres are up to ten well-developed striae. The species differs from *Bavariascincus mabuyaformis* in the more anterior articulation of the splenial. A more detailed comparison with this species is not possible, because the only two dentaries of *B. mabuyaformis* (from Petersbuch 2 and Rembach, both MN4) lack the anterior part.

Scincidae indet. 2

Figures 9H, I

Material examined: 1 right (16400) and 1 left dentary fragment (16401).

Description and comparison: Two anterior dentary fragments are preserved. They differ from Scincidae sp. 1 in the smaller dimensions, more posteriorly articulated splenial (not below the anteriormost 11th tooth position), shorter lamina ventralis in the symphyseal region and therefore shallower Meckel's groove. The tooth morphology and crown ornamentation are similar in the two Sandelzhausen scincid species. A comparison with *B. mabuyaformis* is not possible (see above).

Family Cordylidae Mertens, 1937

In the Sandelzhausen material several large-sized scincomorph remains occur that most probably belong to the Cordylidae, a family which is described here for the first time from the NAFB. Previously, Neogene cordylids from Europe were only known from the Early Miocene of Dolnice (*Palaeocordylus bohemicus* Roček 1984), Obergänserndorf (Cordylidae indet., Austria, MN5, Böhme 2002a), Petersbuch 2 (*Bavaricordylus ornatus*, Germany, MN4a, Kosma 2004) and Puttenhausen (Cordylidae indet., Germany, MN5, Abdul-Aziz et al. 2008). The Sandelzhausen specimens differ from *Palaeocordylus bohemicus* and represent a new species of *Bavaricordylus*. However, the material is not complete enough to formally erect a new species. The following description is therefore based on a more complete specimen from the slightly older, nearby located Puttenhausen section. The nomenclature of the tooth crown ornamentation follows Richter (1994) and Kosma (2004).

Genus *Bavaricordylus* Kosma 2004

***Bavaricordylus molassicus* nov. sp.**

Figure 9J

Holotype: anterior part of right dentary with 15 tooth positions (BSPG 2008 XXIV 1).

Referred material: posterior fragment of a right dentary bearing the last seven tooth positions (BSPG 2008 XXIV 2).

Type locality: Puttenhausen B, Late Karpatian, late OSM C+D (for description of the section and stratigraphy see Abdul-Aziz et al. 2008).

Etymology: referring to the first description of a cordylid from the North Alpine Molasse Basin.

Diagnosis: A robust and large-sized cordylid with a dentary characterized by a wide ventromedially opened Meckelian groove, very robust and uniformly high lamina horizontalis at least up to the 15th tooth position, and an anteriorly attached splenial (at the 7th tooth position). A narrow sulcus dentalis is developed up to the last tooth position. The dentition is heterodont; the anterior teeth are narrower with pointed and slightly posteriorly bent crowns. The posterior teeth are robust and blunt. Their distal part (above the crista dentalis) is slightly narrower than the basal part. The ornamentation of the lingual crown in posterior teeth is characterized by the absence of anguli mesiales and distales, up to 12 less-prominent striae, and by short and delicate culmines lateres which do not join each other on the lingual side of the tooth. Striae occur also on the labial side of the tooth crown. The most posterior teeth are still subpleurodont, very low and bear a longitudinal crista on the top of their crowns.

Description of the holotype: The robust dentary bears the 15 anteriormost tooth positions. The labial side of the dentary is rough and shows five mental foramina. The sulcus dentalis is well developed and narrow. The lamina horizontalis is very robust; it broadens behind the symphyseal area and remains at about the same thickness at least up to the last preserved tooth position. The crista ventralis is straight and ventrally directed, so that the Meckel's groove is widely open ventromedially. The anterior part of the Meckel's groove runs slightly dorsomedially below the sixth tooth position and enters deep into the symphyseal area. The articulation surface for the splenial reaches up to the beginning of the symphyseal area below the seventh tooth position. All teeth are unicuspid and blunt, however the anterior eight teeth are slightly bent in posterior direction at their crowns and are narrower than the posterior ones, which are upright and show transversally expanded tooth bases and flattened flanks. The basal part of the posterior teeth is slightly narrower than the part above the crista dentalis. These teeth are not swollen lingually at the level of the crista dentalis. From the labial side the tooth crowns overtop the crista dentalis by one-third of the height of the dentary at the 7th tooth position and by one-eighth at the 14th tooth position.

The lingual aspect of the tooth crowns shows a characteristic ornamentation. The culmines lateres are rather indistinct and short. They do not join each other on the lingual tooth side. The anguli mesiales and distales are not developed. Up to 12 short and mostly indistinct striae are developed between the culmines lateres. The labial side of the tooth crown may also be slightly striated.

Description of the referred material: The posterior fragment of a right dentary bears the last seven, still subpleurodont tooth positions. The lamina horizontalis is broken off. The teeth are robust and very low, only slightly overtopping the crista dentalis. They are clearly striated on both the lingual and labial side and bear a longitudinal crista on the top of the crowns. A narrow sulcus dentalis is developed up to the last tooth position.

Comparison: The new species differs from *Palaeocordylus bohemicus* Roček 1984 by a straight crista ventralis, therefore wider open Meckel's groove, constantly high lamina horizontalis at least up to the 15th tooth position, more anteriorly attached splenial (7th tooth position instead of 9th), more pronounced heterodonty due to anterior tooth crowns that are slightly bent in posterior direction, relatively narrow basal part of the posterior teeth and broader distal part, absence of anguli mesiales and distales, and shorter and more delicate culmines lateres which do not join each other on the lingual side.

Especially the general posterior tooth morphology of the new species corresponds to that seen in *Bavaricordylus ornatus*. It differs from this species and from Cordylidae indet. of the Korneuburg Basin (Böhme 2002a: Pl. 2 Figs. G–P) by a broader dentary shelf, a generally finer tooth crown ornamentation, the absence of anguli mesiales et distales, and by shorter, less prominent and fewer striae (12 versus up to 20 in *B. ornatus*).

***Bavaricordylus* cf. *molassicus* nov. sp.**

Figure 9K–L, N–P

Material examined: 2 right maxillary fragments (16403, 16404), 1 left dentary fragment (16402), posterior dentary fragment (7510), 2 isolated posterior dentary teeth (7525, 7532).

Description: The dentary fragment from the second half of the bone bears eight tooth positions (Fig. 9Ka). The most posterior teeth are lacking. The dentary shelf is narrow, but well developed. The lamina horizontalis narrows constantly in posterior direction. The teeth are blunt, transversally expanded at their bases and flattened along the flanks below the crista dentalis. They are slightly narrower in their basal part than above the crista dentalis. The newly replaced and unworn sixth tooth from behind is slightly pointed. The tooth crown ornamentation shows indistinct and short culmines lateres, which do not join each other on the lingual tooth side (Fig. 9Kb). Anguli mesiales and distales are developed. The area between both culmines shows about ten short and indistinct striae. Striae are also developed on the labial side of the tooth crown.

The posterior dentary fragment bears one very low tooth crown with a prominent longitudinal ridge on the top, but no striations (Fig. 9La). Of similar morphology is an isolated crown, however it shows both lingual and labial striae (Fig. 9Lb).

Both anterior and posterior maxilla fragments are tentatively referred to this species, based on their large size, similar heterodonty and tooth crown ornamentation, the transversally expanded tooth bases, and the presence of striae on the labial crown sides (Fig. 9N–P). The external surface of the maxilla is smooth and pierced by a row of mental foramina running parallel to the crista dentalis. The alveolar foramen probably occurs at the third (second preserved) tooth position from behind. The heterodonty is similar to that in the type mandible of *Bavaricordylus molassicus* nov. sp. The anterior teeth are more slender; their crowns are slightly posterior bent, pointed and somewhat bicuspid. Their ornamentation resembles that of the anterior tooth crowns of the mandible (Fig. 9N). The posterior maxillary teeth are very robust, blunt and strongly transversally expanded. Ornamentation was present, but details are obscured by the state of preservation.

Comparison: The smooth external maxilla surface contrasts with *Palaeocordylus bohemicus* (Roček 1984: 17) and Cordylidae indet. (Böhme 2002a: Pl. 2 Figs. I, K), where the area between the fenestra exonaria and the orbit is sculptured. The general morphology and ornamentation of the dentary teeth differ also from *Palaeocordylus bohemicus*, but correspond to *Bavaricordylus molassicus* nov. sp., except for the presence of anguli mesiales and distales, which are developed in the type of *B. ornatus*. However, *B. ornatus* differs by more strongly accentuated crown ornamentation with more numerous striae and a narrower sulcus dentalis. Therefore the Sandelzhausen cordylids are referred with some reservation to the new species.

Cordylidae indet.

Material examined: posterior left dentary fragment (16405), jaw fragment (16406).

Description: There is probably a second cordylid species present in Sandelzhausen. The posterior fragment of a left dentary preserves the last seven tooth positions. The lamina horizontalis is very thin and terminates behind the level of the most posterior tooth by running labially up to the crista dentalis, thereby leaving a space of about one tooth width behind the last tooth. This is different from *Bavaricordylus molassicus* nov. sp., where the lamina horizontalis ends at the posterior border of the last tooth. The dentary shelf and sulcus dentalis are well developed. The subpleurodont teeth are robust, transversally widened and positioned close to each other. Moreover, they are blunt and high, still significantly overtopping the crista dentalis by nearly one-half of their length. The crown ornamentation of the posteriormost teeth is similar to the teeth from the middle part of the dentary of *Bavaricordylus molassicus* nov. sp. The teeth therefore differ significantly from the new species and from *Palaeocordylus bohemicus*, where the most posterior dentary teeth are very low with a longitudinal crista at the top of the crown.

A small jaw fragment (16406) could either belong to the dentary or the maxilla. It bears the same tooth morphology and crown ornamentation on both labial and lingual sides as both other cordylids described here, but it is impossible to verify a closer relationship.

Scincomorpha indet.

Material examined: 2 intermaxillae (16409, 16410), 2 dentary fragments (16407, 16408), 2 jaw fragments (16411, 16412).

Comments: Several intermaxillae and jaw fragments cannot be assigned to a specific group within the Scincomorpha.

Suborder Anguimorpha Fürbinger, 1900
Family Anguidae Gray, 1825
Genus *Pseudopus* Merrem, 1820
***Pseudopus laurillardi* (Lartet, 1851)**
Figure 9S

2000 *Pseudopus laurillardi* (Lartet, 1851) Augé and Rage: 276, Figs. 9–13.

2005 *Pseudopus laurillardi* (Lartet, 1851) Rage and Bailon: 422, Fig. 4.

Material examined: 2 dentaries (16413, 16414), 2 dentary fragments (7518, 16469), 3 maxilla (16417, 16453, 16467), 1 isolate tooth (16468), 1 palatine (16418), 1 pterygoids (16419, 16420), 6 trunk vertebra (16415, 16464–16466, 16470), 1 caudal vertebra (16416), several osteoderms (16425).

Comments: The Early and Middle Miocene *Pseudopus* species, the largest genus of the subfamily Anguinae. The osteology of the large anguid bones from Sandelzhausen corresponds well with the emended diagnosis of *P. laurillardi* (Augé and Rage 2000), e.g. the dentary shelf strongly extending medially producing a wide and deep sulcus dentalis, and the opening of the alveolar canal lies in level between the third and fourth tooth from behind. Based on these characteristics the material is referred to this species.

Genus *Ophisaurus* Daudin, 1803
***Ophisaurus* sp.**
Figure 9Q, R

Material examined: 2 right dentaries (6527, 16426), 7 right dentary fragments (7526, 16430, 16431, 16435, 16436, 16443, 16452), 1 left dentary (16432), 8 maxilla fragments (16427, 16433, 16434, 16437, 16440, 16442, 16447, 16449), 2 jaw fragments (16450, 16451), 1 intermaxilla (16441), 2 parietals (16429, 16446), 1 pterygoid (16438), 1 palatine (16439), 4 vertebra (16428, 16444, 16445, 16448), several osteoderms (16425).

Description: The dentaries are slender and small (up to 7–8 mm in length) and possess a well-developed, flat dentary shelf without a sulcus dentalis. Its external surface bears four mental foramina. The Meckel's groove is open lateroventrally. A posterior symphyseal outgrow, as described for *O.* cf. *spinari* (Roček 1984), is not developed. The spina splenialis is situated between the third and fourth tooth position from behind, whereas the alveolar foramen is located very posteriorly, below the last but one tooth position. The total number of tooth positions is 13. The teeth are subpleurodont and relatively high in 6527 (Fig. 9Q), in lingual view nearly half of their height is exposed above the crista dentalis. In 16426 (Fig. 9R) tooth height is lower, but it remains unclear whether this is due to preservation (?digestion) or a natural difference. The tooth cusps do not show signs of striation.

Both preserved parietals are very fragmentary. On the ornamented dorsal surface the occipital sulcus is round and borders a small, oval occipital shield, resembling *O. fejfari* (Klembara 1981: Fig. 2). However, the preservation of the two specimens does not suffice to be useful for further comparison. They are only provisionally combined with both dentary remains.

Comparison: Based on the general morphology of the dentaries, the tooth height and number, as well as the smooth tooth cusps, the material most closely resembles *Ophisaurus* sp. 1 described from Sansan (Augé and Rage 2000: Fig. 14). The specimens clearly differ from the three mandibles (*O.* cf. *spinari*, *O.* sp. I, *O.* sp. II) described by Roček (1984) from Dolnice, the type locality of *Ophisaurus fejfari*, *O. spinari* and *O.* (?) *robustus* (Klembara 1979). These species are based on parietals.

Ophisaurus **sp. I sensu Roček, 1984**

Figure 9M

Material examined: right and left dentary fragments (6524, 7519, 16454, 16455), 6 maxilla fragments (5477, 5494, 7516, 16456–16458).

Description and comments: The dentary and maxillary teeth are subpleurodont, blunt or rounded, and transversally expanded at their base. The tooth crowns do not show signs of striation. The dentary shelf is comparatively narrow and flat, a sulcus dentalis is absent. On the left posterior dentary fragment a well-developed facet for the attachment of the coronoid is preserved. Based on the absence of a sulcus dentalis and the tooth morphology, the fragmentary Sandelzhausen specimens resemble *Ophisaurus* sp. I described by Roček (1984: 40, Pl. 10 Fig. 3) from Dolnice.

cf. ***Ophisaurus*** **cf.** ***spinari*** **sensu Roček, 1984**

Figure 9V

Material examined: 3 maxilla fragments (7517, 7525, 7527)

Description and comments: A third representative of *Ophisaurus* is indicated by two maxilla fragments. This species is distinctly larger than *Ophisaurus* sp. and has rather pointed teeth unlike *Ophisaurus* sp. I (sensu Roček 1984). The tips of the teeth show a well-pronounced cutting edge on the anterior side, which is also developed on the posterior side to a lesser degree. This tooth morphology resembles *Ophisaurus* cf. *spinari* described by Roček (1984) from Dolnice.

Anguidae gen. indet. nov. sp.

Figure 9T, U

Material examined: 1 left (16459) and 1 right (7528) dentary fragment, 1 right maxilla fragment (16460).

Description: The tooth morphology of this species is unique among the studied material. In both the dentary and the maxilla the teeth are subpleurodont, close to each other, relatively robust and their base is not much widened. The most striking feature is the strong posterior inflexion of the teeth in fang-like fashion. The crowns are labiolingually flattened and bent in posteromedial direction. The crowns are anteriorly and posteriorly defined by cutting edges which join in the obtuse tip, leading to a more or less triangular outline of the cusp. The tip is situated slightly behind the midpoint, so that the cusp is asymmetrically. On the medial cusp side a conspicuous striation of about 20 parallel striae is particularly well developed on the maxillary teeth (Fig. 9 U). The labial side of the cusp is smooth.

The dentary (Fig. 9 T) shows the last five tooth positions. The labial wall of the bone is broken. A medial, well-developed facet for the articulation of the coronoid reaches to between the third and fourth tooth position from behind. The small spina splenialis is situated below the fifth tooth position from behind (the position of the spina is marked by an arrow in Fig. 9Ta). Thus the anterior inferior alveolar foramen is small, located below the fourth tooth position from behind, and is dorsally and anteriorly bordered by the lamina horizontalis. The dentary shelf is narrow; a sulcus dentalis is absent. The maxilla fragment (Fig. 9 U) bears the posterior seven tooth positions, where the infraorbital foramen is situated above the fifth tooth position from behind. Posterior to the infraorbital foramen runs a relatively deep and broad groove for the articulation with the jugal.

Comparison: The posterior position of the anterior inferior alveolar foramen bordered dorsally and anteriorly by the dentary and the peculiar tooth morphology is indicative of a member of the Anguidae (Estes 1983: 134). The cusp morphology and ornamentation differ from the three *Ophisaurus* species (*O.* cf. *spinari*, *O.* sp. I, *O.* sp. II) described by Roček (1984) from the Early Miocene of Dolnice, as well as from both species (*O.* sp. 1, *O.* sp. 2) described by Augé and Rage (2000) from Sansan. However, the *Ophisaurus* sp. 2 from Sansan has a similar, nearly triangular outline of the cusp, but lacks cutting edges and striations. The material clearly represents a new species, but is too fragmentary to be formally described yet. It remains unclear at present whether the species represents a member of *Ophisaurus* or an independent lineage.

With regard to ecology, fang-like teeth occur in burrowing scincomorphs (e.g. *Sphenomorphus muelleri*, Kosma 2004: Fig. 90) and anguimorphs (e.g. *Anguis fragilis*) adapted to feeding on soil animals such as ants and earthworms (Kosma 2004: 89).

Suborder Amphisbaenia Gray, 1844
Family Amphisbaenidae Gray, 1825
Genus *Palaeoblanus* Schleich, 1988
***Palaeoblanus* nov. sp.**
Figure 9D

Material examined: 1 intermaxilla (5478), 1 posterior dentary fragment (16461).

Description: The fragmentary intermaxilla lacks the distal parts of the processus nasalis and maxillaris and the lamina horizontalis. The processus nasalis is slightly restricted proximally. At the level of this restriction two large foramina are developed, opened from the visceral and dorsal side. Three teeth are preserved, all of which are robust with rounded crowns. The central tooth is the largest. The neighbouring lateral teeth slightly deviate from the central one. Although reduced in size, the lateral teeth are strong. Their diameter is about 70% of the central tooth.

Comments: The intermaxilla of the genus *Palaeoblanus* (Schleich 1988: Figs. 2G, 3–1), and the only species *P. tobieni*, differs from both extant European *Blanus* species (*B. cinereus*, BSPG 1982 X 4364; *B. strauchi*, BSPG 1982 X 2737) and the fossil *B. antiquus* (Schleich 1985) by much larger foramina basal to the nasal process, stronger teeth, and less reduced lateral teeth (diameter of the lateral teeth about 65% of the central tooth in *P. tobieni*; 55% in the fossil *B. antiquus*, Schleich 1985: Fig. 1; 56% in *B. strauchi*). These features clearly indicate that the Sandelzhausen specimen belongs to the genus *Palaeoblanus* (see also Böhme 1999b). It differs from *P. tobieni* in the divergent lateral teeth, which are parallel to the central tooth in the nominal species. This is distinct enough to be separated at species level. However, most fossil amphisbaenid species are described on the basis of dentaries, which is usually the most common bone. Therefore, the formal description of a new species is postponed until well-preserved dentaries are available. The dentary is too fragmentary to give any further information.

The maximal width of the described fragment is 2 mm, so the Sandelzhausen specimen is about twice as large as the bone in *P. tobieni* and the recent European *Blanus* species, in which the width of a complete intermaxilla is about 1.5 mm.

Remark: The intermaxilla of the extant *B. cinereus* from the Spanish province of Almería figured in Schleich (1985: Fig. 2) clearly differs from the intermaxilla of *B. cinereus* in the Munich osteological collection (labelled as coming from “Spain”). The differences are significant: very slender nasal process and central tooth not significantly enlarged relative to the lateral teeth, both absent in the Schleich specimen. Interestingly, a recent molecular study (Albert et al. 2007) indicates two highly supported Iberian clades of *Blanus* (a southwestern clade and a central clade) with deep divergence in time (5.2 Ma), which may represent independent taxonomic units. The Almería province geographically belongs to the central clade. I speculate that the significant osteological differences of the specimen described in Schleich (1983) from the Munich specimen may reflect this taxonomical split.

Taphonomy of fish remains: the tooth replacement method

The record of fossil fishes does not necessarily indicate that the fossil-bearing sediment was deposited in a permanent water body or within water at all. Fishes are an important component of the diet of various terrestrial predators (Martini and Reichenbacher 1993) and thus may also be deposited outside their habitat (e.g. in karstic fissures). Some freshwater fishes show a semi-terrestrial lifestyle (e.g. snakeheads), and thus can also be found in various non-aquatic environments (Böhme 2004). An alluvial plain may be flooded for several weeks or even months, and fish carcasses may be buried in floodplain sediments. Furthermore, many shallow water bodies in semiarid, seasonal climates occur temporarily and are inhabited by transient fish populations (Unmack 2001). The existence of such habitats depends on the regional groundwater level, flood dynamics, geomorphology or precipitation/evaporation ratio. The reconstruction of these palaeohydrologic systems is not only crucial for palaeoenvironmental and palaeoecologic studies, but also gives further important information concerning palaeoclimate.

For this purpose a new methodology is applied which allows detecting autochthonous components within a fish taphocoenosis. The new method is based on tooth replacement quotients of cyprinid fishes, which allows to distinguish teeth deposited in sediments from perennial water bodies with an autochthonous and permanent fish community (lacustrine and fluvial sediments) from teeth in sediments of temporary water bodies (seasonal rivulets, lake, pond and floodplain sediments) with a non-permanent fish community or parautochthonous/allochthonous fish remains.

Cyprinid fishes are characterized by continuous lifetime pharyngeal tooth replacement which is independent from environmental factors (Peyer 1980). Isolated teeth in sediments can be identified as replaced in vivo if they bear traces of resorption around the base (Fig. 5A). Conversely, basally fractured teeth without traces of resorption or teeth detached from the pharyngeal bone derive from skeletons due to post mortem breakage (Fig. 5F). Resorptive teeth in sediments are therefore indicative of life processes of fishes in the water column, whereas broken teeth (and cranial and postcranial bones) indicate the accumulation of dead fish bodies. The latter does not necessarily occur within the habitat of the fishes (e.g. carcasses on floodplains). Similarly, if ponds in an alluvial plain contain water only after a flooding event or during the rainy season, their sediments may contain fish remains which do not indicate permanent lacustrine conditions.

The accumulation rate of in vivo-replaced pharyngeal teeth in the sediment depends on population density, population residence time within the water body and persistence of the water body.

It is assumed that in temporary water bodies (with short residence time and high mortality rate of fishes) the number of replaced teeth is lower than in permanent water bodies with higher residence time and normal fish mortality.

This previous assumption results in the following equations:

$$A \times Z \times k \gg \frac{R}{I} \tag{1}$$

for temporary water bodies, and

$$A \times Z \times k \cong \frac{R}{I} \tag{2}$$

for perennial water bodies, where A denotes the mean individual age in years (species constant), Z the individual number of pharyngeal teeth (species constant), and k the frequency of tooth replacement per year (according to Peyer 1980 each tooth is replaced once a year in cyprinids). The number of replaced teeth (R) and the minimal number of individuals (I) are obtained from the fossil record. The latter can easily be estimated by the characteristic first ophistocoelous vertebra (Fig. 4), which is a compact bone with good preservation potential. The condylus of this vertebra is round in all studied extant leuciscins and it is assumed to be round in the fossil leuciscin *Palaeoleuciscus* (Fig. 4b) as well. The condylus is strongly oval in many extant cyprinins and barbins. This condition is assigned to the fossil cyprinin *Palaeocarassius* (Fig. 4a).

For example, *Palaeocarassius* sp. A, the most common cyprinid genus of the Upper Freshwater Molasse (Böhme 2002b; see systematic part), possesses ten pharyngeal teeth ($Z = 10$), five on each pharyngeal bone (teeth formula 5.0; Fig. 5D). Based on their small maximum body size of 5–10 cm the mean individual age for this *Palaeocarassius* species can be estimated to be 2 years ($A = 2$). If $k = 1$ (see above), the expected number of replaced teeth per individual and life-cycle for *Palaeocarassius* is 20. If the habitat coincides with the place of death (as is the case in small and shallow limno-fluvial waters), a R/I quotient of about 20 can be expected for perennial waters. Conversely, temporary waters are expected to show a much lower quotient (<10). In large and deep lakes, the cyprinid habitat and place of death is not necessarily the same (e.g. pelagial habitat and burial of skeletons in littoral sediments). In such cases, pelagial sediments will show a much higher R/I quotient than the expected number of replaced teeth per individual and life-cycle.

For two other frequent Upper Freshwater Molasse cyprinid genera, *Palaeoleuciscus* and *Barbus* s.l., the term $A \times Z \times k$ is 24 ($Z = 14$, $A = 2$ for *Palaeoleuciscus*) and 48 ($Z = 16$, $A = 3$ for *Barbus* s.l.).

Assuming that less than 50% of the expected number of replaced teeth per individual and life-cycle is indicative of temporary water bodies, the following equations result from Eqs. 1 and 2:

$$\frac{R/I}{A \times Z \times k} < 0.5 \tag{3}$$

for temporary water bodies (including floodplain sediments and predatory accumulations) and

$$\frac{R/I}{A \times Z \times k} > 0.5 \tag{4}$$

for perennial waters. The quotient in Eqs. 3 and 4 is here referred to as the tooth replacement quotient (TRQ).

To test the tooth replacement method, I investigated 45 cyprinid-bearing localities from the Early and Middle Miocene Upper Freshwater Molasse (Table 1). The fossil material belongs to the genera *Palaeocarassius*, *Palaeoleuciscus* and *Barbus* s.l. and is comprised of more than 8,400 replaced pharyngeal teeth from more than 400 individuals.

In 20 localities the TRQ is greater than 0.5 for at least one species (Fig. 10). According to Eq. 4 these sediments are thought to be derived from perennial waters. Considering the sedimentology and accompanying fossil remains, many of these samples belong to lacustrine or fluvial sediments rich in aquatic gastropods, unionid shells and/or charophytes (see Table 1 for details and references):

Table 1 Numbers of resorptive pharyngeal teeth (*R*), minimal numbers of cyprinid individuals (*I*), the tooth replacement quotient (TRQ) and facial interpretation, and the sedimentological characteristics of 45 localities from the Upper Freshwater Molasse of southern Germany

	Palaeocarassius ssp.				*Palaeoleuciscus* ssp.				*Barbus* s.l. ssp.				TRQ		References
Localities	*R*	*I*	*R*/*I*	TRQ	*R*	*I*	*R*/*I*	TRQ	*R*	*I*	*R*/*I*	TRQ	Interpretation	Sedimentology	
(1) Adelschlag	2,379	41	58.0	2.90	79	2	39.5	1.65					Perennial	Dark, organic-rich layer	Fahlbusch (1964)
(2) Untereichen-Altenstadt 565 m	307	9	34.1	1.71	296	8	37.0	1.54	54	1	54.0	1.125	Perennial	Sandy braided river deposit	Prieto et al. (2009)
(3) Arth 1b	2	1	2.0	0.10	2	2	1.0	0.04					Temporary	Gravelly marl	This paper
(4) Attenfeld	223	8	27.9	1.39	16	1	16.0	0.67					Perennial	Lake sediment	Reichenbacher et al. (2004)
(5) Burtenbach 1b	130	7	18.6	0.93	31	2	15.5	0.65	16	1	16.0	0.333	Perennial	Lake sediment	This paper
(6) Denkendorf-Nord W, violette Lage	4	1	4.0	0.20	3	1	3.0	0.13					Temporary	Purple marly palaeosoil, B horizon	This paper
(7) Denkendorf-Nord S, violette Lage	9	2	4.5	0.23	1	1	1.0	0.04					Temporary	Purple marly palaeosoil, B horizon	This paper
(8) Denkendorf-Süd, Schneckenlage	53	1	53.0	2.65	25	1	25.0	1.04					Perennial	Lake sediment	This paper
(9) Derching 1a	3	5	0.6	0.03	3	4	0.8	0.03					Temporary	Bluish marl	This paper
(10) Derching 1b					95	4	23.8	0.99					Perennial	Yellowish sandy marl, extremely rich in charophytes	This paper
(11) Dieshof, unterer Mergel	139	15	9.3	0.46	6	1	6.0	0.25					Temporary	? Floodplain sediment	This paper
(12) Edelbeuren-Mauerkopf	14	1	14.0	0.70	18	1	18.0	0.75					Perennial	Reworked marls in fine sands	Sach (1999), Sach et al. (2003)
(13) Eitensheim	3	2	1.5	0.08	1	1	1.0	0.04					Temporary	"Browncoal" or dark duff	Fahlbusch (1964)
(14) Gallenbach 2a	29	2	14.5	0.73	139	6	23.2	0.97					Perennial	Limnic marl within *Gallenbach Schotter*	Fiest (1989)
(15) Gallenbach 2b	1	1	1.0	0.05	1	1	1,0	0.04					Temporary	Floodplain sediment (top *Gallenbacher Doppelmergel*)	Fiest (1989)
(16) Gisseltshausen 1b									1	1	1.0	0.021	Temporary	Reworked marl with pedogenic carbonate concretions	Heissig (1989)
(17) Goldberg/Ries, coll. Karnekamp					186	59	3.2	0.13	8	1	8.0	0.167	Temporary	Bone accumulation by birds of prey at the Ries crater wall	This paper
(18) Goldern	43	2	21.5	1.08	106	2	53.0	2.21					Perennial	Sands and bluish-greenish marls, rich in *Unio* shells	Mayr et al. (1988)
(19) Gottschlag 1b					168	3	56.0	2.33	168	3	56.0	1.167	Perennial	Fluvial sands with *Margaritifera*	Heissig (1989)

Table 1 continued

	Palaeocarassius ssp.				*Palaeoleuciscus* ssp.				*Barbus* s.l. ssp.				TRQ		References
Localities	*R*	*I*	*R*/*I*	TRQ	*R*	*I*	*R*/*I*	TRQ	*R*	*I*	*R*/*I*	TRQ	Interpretation	Sedimentology	
(20) Griesbeckerzell 1a					189	6	31.5	1.31	189	6	31.5	0.656	Perennial	Channel-fill sediment, brockhorizon	This paper
(21) Günzburg 1/2	13	1	13.0	0.65									Perennial	Limnic marl, rich in aquatic gastropods and unionid shells	This paper
(22) Hahnenberg/Ries					450	1	450.0	18.75	44	1	44.0	0.917	Perennial	Pelagial sediments of the Ries crater lake	This paper
(23) Hessellohe	3	1	3.0	0.15									Temporary	Sandy “browncoal” or dark duff	Dehm (1951), Fahlbusch (1964)
(24) Hitzhofen 1	583	29	20.1	1.01	18	1	18.0	0.75					Perennial	Brownish and bluish marls rich in aquatic gastropods	This paper
(25) Hitzhofen 1+2	150	6	25.0	1.25	38	2	19.0	0.79					Perennial	Undifferentiated, see localities 24 and 26	
(26) Hitzhofen 2	806	23	35.0	1.75	74	3	24.7	1.03					Perennial	Brown marly organic silt, rich in aquatic gastropods	This paper
(27) Kleineisenbach					1	1	1.0	0,04					Temporary	Sandy marls, rich in terrestrial gastropods	Fahlbusch (1975)
(28) Laimering 1a					12	1	12.0	0.50					Temporary	Pedogenic overprinted alluvial sediments	Fiest (1989), Schmid (2002)
(29) Laimering 3									1	1	1.0	0.021	Temporary	Floodplain sediment with pedogenic carbonate concretions	Fiest (1989), Heissig (2006)
(30) Laimering 5					11	3	3.7	0.15	6	1	6.0	0.125	Temporary	Reworked clays and marls	Heissig (2006)
(31) Langenmoosen	134	9	14.9	0.74	61	3	20.3	0.85	9	1	9.0	0.188	Perennial	Reworked marly sediments within fine sands	Dehm (1952), Fahlbusch (1964)
(32) Maßendorf	1	1	1.0	0.05									Temporary	Grey-green clayey marl with pedogenic carbonate concretions	Schötz (1983)
(33) Oberbernbach 1	1	1	1.0	0.05	2	1	2.0	0.08	1	1	1.0	0.021	Temporary	Dark palaeosoil, A horizon	This paper
(34) Rembach	4	1	4.0	0,20									Temporary	Blue-green marls	Ziegler and Fahlbusch (1986)
(35) Schafhof	15	2	7.5	0.38									Temporary	Dark marls, rich in terrestrial and aquatic gastropods	Gall (1969)
(36) Schönenberg (bei Jettingen)	56	2	28.0	1.40	8	1	8.0	0.33	67	1	67.0	1.396	Perennial	Marly fine sands	Fahlbusch (1964)
(37) Undorf, Kohleton	26	2	13.0	0.65	13	1	13.0	0.54					Perennial	Limnic clay	This paper
(38) Undorf, Bahnstrecke	74	2	37.0	1.85	59	2	29.5	1.23					Perennial	Unknown	Fahlbusch (1964)
(39) Unterhausen	98	9	10.9	0.54	11	1	11.0	0.46					? Temporary	Dark marls	This paper

Table 1 continued

Localities	*Palaeocarassius* ssp.				*Palaeoleuciscus* ssp.				*Barbus* s.l. ssp.				TRQ	Sedimentology	References
	R	*I*	*R*/*I*	TRQ	*R*	*I*	*R*/*I*	TRQ	*R*	*I*	*R*/*I*	TRQ	Interpretation		
(40) Unterneul 1a	1	1	1.0	0.05	1	1	1.0	0.04					Temporary	Alluvial marl with pedogenic carbonate concretions	Fiest (1989)
(41) Walda 1	176	22	8.0	0.40	4	2	2.0	0.08					Temporary	Dark marls	This paper
(42) Wannenwaldtobel 2	36	8	4.5	0.23	220	29	7.6	0.32					Temporary	Carbonate-rich marl with terrestrial and aquatic gastropods	Sach (1999), Sach et al. (2003)
(43) Ziemetshausen 1c					1	1	1.0	0.04					Temporary	Reworked sediments within a sandy braided river deposit	Heissig (1989), Maurer (2006)
(44) Ziemetshausen 1d	5	1	5.0	0.25	2	1	2.0	0.08					Temporary	Reworked sediments within a sandy braided river deposit	Heissig (1989), Maurer (2006)
(45) Ziemetshausen 1e	1	1	1.0	0.05	2	1	2.0	0.08	2	0			Temporary	Reworked sediments within a sandy braided river deposit	Heissig (1989), Maurer (2006)

a few derive from layers of reworked marls within fluvial sediments. Some samples such as Denkendorf-Süd, Adelschlag, Undorf-Bahnstrecke and Hitzhofen 2 (entries 1, 8, 24 and 38 in Table 1; Fig. 10) show a TRQ well above 1.5. These localities are situated on the northern border of the NAFB, where especially during the Karpatian, a large lake system existed (Reichenbacher et al. 2004, 2008). I interpret the increased TRQ as an indication of pelagial or central lake sediments. In larger lakes there is an increasing partitioning between pelagial and littoral habitats. Due to the influence of wind-induced waves, dead fishes will accumulate comparatively more in the littoral zone (lake margin or strandline; Weigelt 1999), thus increasing the TRQ in central lake sediments.

A similar explanation is given for the extremely high TRQ (18.75) of the Hahnenberg/Ries locality (entry 22 in Table 1; Fig. 10). The sediments come from the large and deep Ries crater lake and represent pelagial facies. The high number of resorbed pharyngeal teeth contrasts with the very low number of recorded individuals. It can be speculated that most fish carcasses are buried near the shallow water at the crater margin or became victims of avian predation. The latter interpretation is supported by the results from the Goldberg locality (entry 17 in Table 1; Fig. 10), situated in karstic caves on the islands of the inner Ries crater wall. The mass accumulation of bones is certainly due to piscivorous waterbirds, similar to the nearby Steinberg locality (Heizmann and Fahlbusch 1983). Consequently, the TRQ of Goldberg is very low (entry 17 in Table 1): 0.13 for *Palaeoleuciscus* and 0.17 for *Barbus* s.l. Apart from Goldberg, 24 other localities can be classified as temporary water bodies, floodplain sediments and/or predatory accumulations. Many of these localities come from palaeosoils in floodplain catenas, some from reworked sediments (probably palaeosoils). These soils may generally be interpreted as alluvial soils covered by water only during floods (Schmid 2002). Other samples (e.g. Arth 1b, Kleineisenbach, Schafhof, Wannenwaldtobel 2; entries 3, 27, 35 and 42 in Table 1 and Fig. 10) represent marls rich in both terrestrial and aquatic gastropods, which may indicate the presence of seasonally dry, temporary water bodies.

In conclusion, the tooth replacement method gives reasonable results which are consistent with other analytical approaches. It is therefore suggested to represent a reliable method of distinguishing perennial from temporary water conditions in the Sandelzhausen locality.

Discussion

Faunal composition

The fishes, amphibians and reptiles described in this paper belong to 35 taxa (Table 2). Together with five turtle

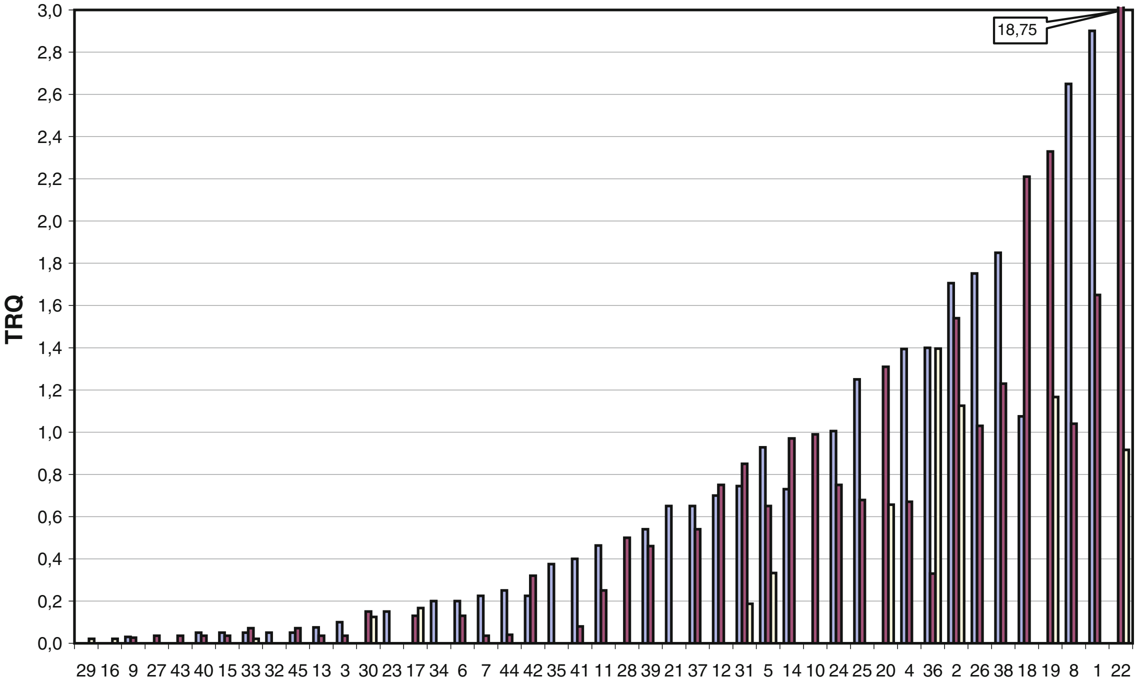

Fig. 10 Tooth replacement quotient (TRQ) for the genera *Palaeocarassius* (*blue bars*), *Palaeoleuciscus* (*red bars*) and *Barbus* s.l. (*yellow bars*) for the 45 Upper Freshwater Molasse localities in order of increasing highest TRQ per locality. The locality numbers (*x*-axis) refer to the numbers in Table 1

(Table 2; Schleich 1981) and eight snake species (Szyndlar 2009) the ectothermic vertebrate fauna of Sandelzhausen comprises 48 taxa and hence represents one of the most diverse Miocene ectotherm faunas worldwide.

Fishes from four taxa are documented. *Palaeocarassius* sp. A and *Channa elliptica* are most abundant. This association is very characteristic for the Upper Freshwater Molasse (Böhme 1999a) and restricted to shallow water, slightly eutrophic riparian ponds with detritus-based foodwebs (Böhme 2002b). The aquatic or semi-aquatic vertebrate fauna is further characterized by two species of newts (*Triturus* cf. *vulgaris*, *T.* cf. *marmoratus*), green frog (*Pelophylax* sp.), water frog (Ranidae gen. indet. sp. nov.), crocodile (*Diplocynodon styriacus*) and, for the first time described as fossil, a water skink (*Tropidophorus bavaricus* nov. sp.). Crocodile remains are frequent, but basically documented by hatchling teeth. Newts are especially abundant in the lower part of the section, as is the case for the two other semi-aquatic salamanders *Salamandra sansaniensis* and *Chelotriton* sp. The high frequency of *S. sansaniensis* is of special interest, since it is a rare animal in Molasse deposits (Böhme, unpublished data). *Latonia gigantea*, *Eopelobates* sp. and probably also *Bufo* sp. are peri-aquatic (sensu Böhme et al. 2006) frogs, which are found with low to medium abundance.

The terrestrial elements are clearly dominated by a new species of the spadefoot *Pelobates fahlbuschi* nov. sp. This animal is documented with nearly 200 individuals (certainly more because not all screen-washed material was considered) and probably represents the most frequent vertebrate in Sandelzhausen. Relatively rare are records of the second terrestrial frog *Bufo* cf. *viridis*, recorded only for the lower part of the section. The scincomorph families are very diverse: the Lacertidae (lizards) occur with four species, the Scincidae (skinks) with three species and Cordylidae (girdled lizards) with two species, one of which is new to science (*Bavaricordylus molassicus*). The rare fossils of these taxa are scattered through the section. For the first time two chameleonid species have been described syntopically. Besides the already known dwarf chameleon *Chamaeleo bavaricus* (Schleich 1983), a giant chameleon was found (*C.* aff. *caroliquarti*). Anguids (glass lizards), which are often found in the form of osteoderms, are also diverse and documented by five species, including a probably new one (Anguidae gen. indet. sp. nov.). This rare new species shows a typical dentary morphology that is characteristic for fossorial scincomorphs and anguimorphs. The relatively common *Ophisaurus* sp. can probably also be interpreted as fossorial, because it is a very small-sized species compared with the recent *Anguis fragilis*. Two other fossorial taxa are *Albanerpeton inexpectatum* (albanerpetontid) and *Palaeoblanus* nov. sp. (worm lizard), both preserved in low abundance.

The turtles are dominated by the peri-aquatic *Clemmydopsis turnauenis* (Schleich 1981). All turtles are recorded throughout the profile, except the giant terrestrial

Table 2 List of fish, amphibian and reptile taxa by lithological unit from Sandelzhausen (including the rare decapod remains; turtles according to Schleich 1981; excluding snakes, see Szyndlar (2009) and their supposed ecophysiological groups (according to Böhme et al. 2006)

Taxon	B	C1	C2	C3/D1	D2	E	Ecophysiologic group
Palaeocarassius sp. A	5	13	6	184	317	1135	–
Palaeoleuciscus sp. A	1	1	1	9	7	10	–
Gobius sp.	–	–	–	2	–	1	–
Channa elliptica	7	8	8	76	14	28	–
Albanerpeton inexpectatum	–	1	1	6	–	–	Fossorial
Salamandra sansaniensis	73	5	3	15	–	–	Peri-aquatic
Chelotriton sp.	15	2	3	13	1	11	Peri-aquatic
Triturus cf. *vulgaris*	140	11	18	107	1	8	Peri-aquatic
Triturus cf. *marmoratus*	30	12	5	142	2	12	Semi-aquatic
Latonia gigantea	2	8	7	23	2	4	Peri-aquatic
Pelobates fahlbuschi nov. sp.	42	96	37	776	5	15	Fossorial
Eopelobates sp.	–	–	–	8	2	–	Peri-aquatic
Bufo cf. *viridis*	3	1	–	7	–	–	Heliophile
Bufo sp.	–	–	–	1	–	–	Peri-aquatic
Pelophylax sp.	6	3	2	20	2	2	Semi-aquatic
Ranidae indet. nov. gen. et sp.	–	5	4	2	–	–	Semi-aquatic
Diplocynodon styriacus	19	32	30	205	51	41	Aquatic
Chamaeleo aff. *caroliquarti*	4	–	–	1	–	–	Arborial
Chamaeleo bavaricus	–	–	–	3	–	–	Arborial
Lacerta sp. 1	–	1	–	–	–	–	Heliophile
Lacerta sp. 2	4	1	–	5	–	–	Heliophile
Lacerta sp. 3	2	4	1	9	1	2	Heliophile
Edlartetia sansaniensis	–	–	–	1	–	–	? Heliophile
Cf. *Miolacerta tenuis*	–	–	1	1	–	–	Heliophile
Tropidophorus bavaricus nov. sp.	–	–	–	1	–	–	Peri-aquatic
Scincodae indet. 1	–	–	1	–	1	–	Heliophile
Scincidae indet. 2	–	–	1	–	1	–	Heliophile
Bavaricordylus cf. *molassicus* nov. sp.	–	1	1	3	–	–	Heliophile
Cordylidae indet.	–	–	–	2	–	–	Heliophile
Scincomorpha indet.	–	1	–	3	2	–	–
Anguidae (Osteoderms)	91	879	110	1197	15	141	–
Pseudopus laurillardi	5	3	–	14	1	1	Heliophile
Ophisaurus sp.	3	3	4	11	1	2	Fossorial
Ophisaurus sp. I (sensu Roček 1984)	1	3	2	5	–	–	Heliophile
Cf. *Ophisaurus* cf. *spinari* (sensu Roček 1984)	–	1	2	–	–	–	Heliophile
Anguidae gen. indet. nov. sp.	–	3	–	–	–	–	Fossorial
Palaeoblanus nov. sp.	–	–	1	–	–	–	Fossorial
Testudo rectogularis	×	×	×	×	×	×	Heliophile
Geochelone cf. *perpinniana*	1	–	–	–	–	–	Woodland
Mauremys sophiae	×	×	×	×	×	×	Aquatic
Clemmydopsis turnauensis	×	–	–	×	×	×	Peri-aquatic
Trionyx sp.	?	–	–	–	×	×	Aquatic

Numbers refer to the counts of identifiable specimens (for *Palaeocarassius* sp. A, only teeth). The test sample data from PQ 40-S are not included. Crosses indicate the presence of the taxon without counts. Note that the proportions of screen-washed sediments are variable between units and cannot be reconstructed with confidence tortoise *Geochelone perpiniana* found only in unit B and the full-aquatic *Trionyx* sp. found only in the upper part of the section.

Despite the large amount of recovered fossil specimens and high diversity, several taxa that are common in Upper Freshwater Molasse sediments elsewhere are lacking. These include especially the water dogs (*Mioproteus caucasicus*), barbels (*Barbus* s.l.) and loaches (*Cobitis*). The absence of these taxa is probably due to unfavourable stillwater conditions (see also Prieto et al. 2009). Most of the extant barbels and loaches are rheophilic, and rheophily can also been suggested for *Mioproteus*. According to the frequent occurrence in fluvial sediments this fossil proteid was probably ecologically more related to the North American genus *Necturus* (stream habitats) than to the European *Proteus* (cave environments). All three mentioned taxa occur in the nearby located Maßendorf locality (Böhme, unpublished data), which has the same biostratigraphic age as Sandelzhausen (Abdul-Aziz et al. 2008).

The absence of other taxa can be explained by stratigraphical (the giant salamander *Andrias* is found only at the base of the Upper Freshwater Molasse and in the *Jüngere Serie*; the monitor lizard *Varanus* is found in the Upper Freshwater Molasse only in the *Mittlere* and *Jüngere Serie*; both personal observations) and taphonomical reasons (gracile cyprinodontids), or they are generally rare in Molasse sediments (*Palaeobatrachus*, *Pelodytes*, gekkonids, agamids).

Palaeohydrology, palaeoecosystem and palaeoenvironment of Sandelzhausen

Fahlbusch et al. (1972: 342) characterized the habitat of Sandelzhausen as a moist and swampy, repeatedly flooded fluvial plain, with several water bodies and more or less closed forest coverage. To investigate the habitat characteristics in greater detail and especially within a temporal scale (lithologic units B to E, see Fig. 2), ectothermic vertebrates are a good proxy indicator, because many show territorial behaviour (low migration ability) and are closely bound to certain environmental and ecological conditions (stenotopic, stenoecic).

The palaeoenvironmental conditions during the sedimentation of litho-units A and F cannot be defined in detail, because unit A only yields large mammals and screen-washing was not possible due to the heavy carbonatic cementation, and unit F does not contain fossils.

Fortunately, all studied fossils have been excavated with their exact position within the section, yielding information on the lithologic unit, centimetres above the base or above the 'coal layer' (=unit C2), and the grid square (PQ). All specimens can therefore be allocated to a specific unit, except for units C3 and D1. They were combined into a single sample (C3/D1) for screen-washing, mostly due to difficulties in discriminating both sedimentary units in the field.

The palaeohydrology of Sandelzhausen

Fishes are present in every sampled lithologic unit (Table 2), albeit with strongly variable abundance and taphonomy. They are rare in units B to C2 and frequent in units C3 to E. Regarding cyprinids, the teeth of *Palaeocarassius* sp. A are virtually all accumulated in vivo due to tooth replacement, whereas the remains of *Palaeoleuciscus* sp. A seem to be consistently allochthonous (see descriptions of the species). To evaluate whether the water bodies in the different units are temporary or permanent, the above-described tooth replacement method was applied to *Palaeocarassius* sp. A (Table 3). The TRQ is very low (<0.5) for units B, C1 and C2, clearly indicating that, during sedimentation of these layers, temporary water conditions existed. In units D2 and E the TRQ is between 1.0 and 2.0, which is characteristic of permanent water bodies and may indicate shallow lake conditions. In the combined sample of units C3 + D1 the TRQ is 0.53. This is, according to Eqs. 3 and 4, in a transitional position between conditions assumed for temporary and permanent water bodies. To evaluate in greater detail if the switch in the hydrologic system from seasonal to perennial water conditions occurs in the course of units C3 and D1, I analysed a test sample taken from PQ 40-S in which both units were well distinguishable lithologically. The size of the sample from unit C3 (0–10 cm above C2) was 60 kg. From the lower part of unit D1 (10–20 cm above C2) 15 kg of sediments was analysed. The results are given in Table 5. The tooth counts for *Palaeocarassius* sp. A (three teeth in C3, three teeth in D1) were used to calculate the TRQ of unit C3 and the lower part of D1 independently (Table 3). The results indicate that both samples clearly

Table 3 Raw data (*R*, number of resorptive teeth; *I*, minimal number of individuals) for calculating the tooth replacement quotient (TRQ) for *Palaeocarassius* sp. A from unit B to E

Unit	*R*	*I*	*R*/*I*	TRQ
B	5	1	5.00	0.25
C1	2	13	0.15	0.01
C2	2	6	0.33	0.02
C3	3	1	3.00	0.15
C3/D1	179	17	10.53	0.53
D1	3	1	3.00	0.15
D2	314	13	24.15	1.21
E	1,135	34	33.38	1.67

The data for lithologic units C3 and D1 are obtained from the test sample in PQ 40-S (see text for details)

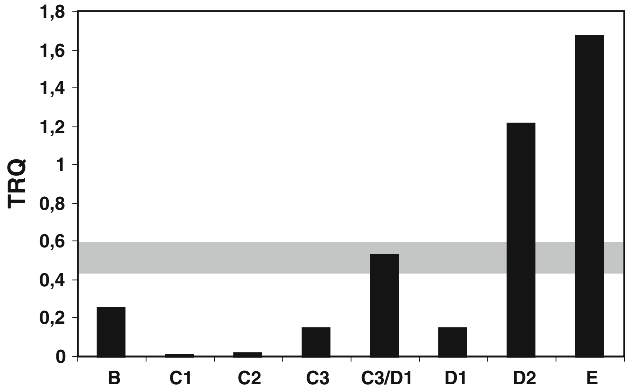

Fig. 11 Tooth replacement quotient (TRQ) for lithologic units B to E (for raw data see Table 3). The results for units C3 and D1 are obtained from the test sample in PQ 40-S (see text for details). The *grey-shaded bar* represents the assumed transition interval between seasonal and perennial water conditions

represent seasonal water conditions (Fig. 11). The relatively high TRQ value of the combined C3 + D1 data set is interpreted as affected by higher tooth abundance from the upper part of unit D1. This indicates that fully permanent lake conditions did not become established before the end of unit D1 (permanent in this context means the existence of a lake over several years without desiccation). Taking into account the resolution of the methodology and sampling, the palaeohydrologic conditions in Sandelzhausen probably changed relative abruptly from temporary waters in the lower part (unit B to early D1) to permanent waters in the upper part of the section (Fig. 11).

The palaeoecosystems of Sandelzhausen

It has been demonstrated that the palaeohydrology of units B to D1 (lower part) is characterized by temporary water conditions, having water only during the rainy season or after flood events. Floods are most probably also responsible for the coarse-grained components in this part of the section (Fahlbusch et al. 1972). This suggests that during this period the dynamics of the ecosystem was driven by seasonal inundations. Water bodies remained after the regression of high water, forming riparian pools. Based on the taphonomy of the fish remains, these seasonal pools had no autochthonous fish population. The desiccations of the pools (drying cracks and pedogenic carbonate nodules recorded from unit B and C; Schmid 2002) were unfavourable for the establishment of an autochthonous fish population. Conversely, the pools act as spawning grounds for crocodiles, salamanders (*Chelotriton* and the newts) and the seven recorded frog species (Table 4), and thus can be regarded as amphibian pools. According to the classification system of Molasse palaeoecosystems by Böhme (2000), units B to D1 (lower part) can be ranked as riparian pool type. These results correspond well with the palaeopedological studies of Schmid (2002), who interprets units B to C2 as sheet flood deposits and C3/D1 as a riparian gleysol under temporary water conditions.

Table 4 Minimal numbers of individuals of fishes (only autochthonous) and amphibians from units B to E

Taxon	B	C1	C2	C3/D1	D2	E
Palaeocarassius sp. A	×	×	×	×	13	34
Channa elliptica	×	×	×	×	1	1
Albanerpeton inexpectatum	–	–	1	2	–	–
Salamandra sansaniensis	5	1	1	1	–	–
Chelotriton sp.	1	1	–	1	–	2
Triturus cf. *vulgaris*	10	1	2	8	1	2
Triturus cf. *marmoratus*	6	1	1	9	1	2
Latonia gigantea	1	3	4	11	2	2
Pelobates fahlbuschi nov. sp.	9	15	10	161	2	5
Eopelobates sp.	–	–	–	3	2	–
Bufo cf. *viridis*	2	1	–	2	–	–
Bufo sp.			–	1	–	–
Pelophylax sp.	3	1	–	7	1	1
Ranidae nov. gen. et sp.	–	–	1	1	–	–

Crosses indicate that a taxon is present but allochthonous

The relatively frequent occurrence of *Salamandra sansaniensis* in unit B (Table 4; Fig. 12) further suggests the existence of running-water environments. The larvae of the recent fire salamander (*S. salamandra*) are rheophilous and require oligotrophic, fish-free brooks for their development (Günther 1996). Similar adaptation can be hypothesized for *S. sansaniensis*. The existence of brooks may be supported by the occurrence of small, sand-rich channels in unit B (unit B2b of Fahlbusch and Gall 1970). It is possible that these brooks formed under the influence of groundwater (perennial springs) during the rainy season (alluvial rheocrenes of Zollhöfer et al. 2000). By supplying water to the ponds, they may have also delayed desiccation of the ponds. My test sample from PQ 40-S revealed a high amount of charophytes in units C3 and lower part of D1, belonging to *Nitellopsis* (*Tectochara*) *meriani*, *Lychnothamnus* sp., and *Chara* sp., which can be regarded as an indicator of oligotrophic shallow water conditions inhabited by charophytes as pioneer vegetation (Feist et al. 2005).

The palaeohydrological change in the late unit D1 and D2 resulted in a new palaeoecosystem of riparian pond type (Böhme 2000). Here the waters were permanent and yielded an autochthonous fish population (Fig. 12) of the *Palaeocarassius*/*Channa* type, which characterizes the ecosystem as fish pond. Both fishes are able to survive the very low-oxygen conditions. The snakeheads (*Channa*) breathe atmospheric oxygen with a labyrinth-like

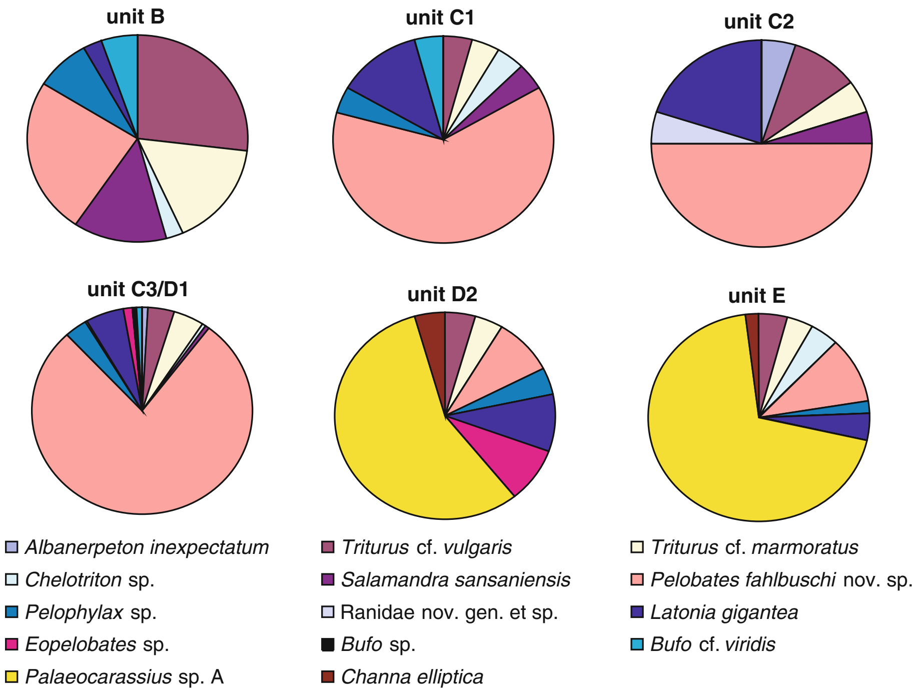

Fig. 12 Fish and amphibian faunal assemblages (minimal numbers of individuals, see Table 4) of units B to E. Note that only the autochthonous fishes are plotted

suprabranchial organ in the upper gill chamber (Munshi 1985; Böhme 2004), while the possible nearest living relatives of *Palaeocarassius*, *Carassius carassius* and *C. auratus*, are able to increase the respiratory surface of the gills significantly to survive hypoxia (Sollid et al. 2003). Within the amphibian fauna, aquatic species such as *Pelophylax* sp., which does not relocate from the spawning habitat during the entire lifetime except some meters, are relatively frequent (Fig. 12). This result corresponds to that of Schmid (2002: 154). Although this author did not analyze units D2 and E, he found that in the upper part of unit D1 the hydrodynamic regime changed and that the sedimentology is indicative of permanent water conditions with gyttja sedimentation (*Unterwasser-Rohboden*), which are typical for groundwater-fed ponds (limnocrenes of Zollhöfer et al. 2000).

The Sandelzhausen environment

It is important to note that the reconstruction of the environment (landscape) of Sandelzhausen based on ectothermic vertebrates is spatially constrained. Due to the reduced mobility of all taxa, statements are only valid for a limited area of probably a few 100 m surrounding the habitat. On the other hand, they provide more reliable information on this closest vicinity than do mammals, since these show broader migratory behaviour (large mammals) or are accumulated by birds of prey (Prieto 2007). An important fossil for landscape reconstruction is *Pelobates fahlbuschi* nov. sp., because it is by far the most frequent vertebrate in Sandelzhausen (Tables 2, 4; Fig. 12).

Under the assumption of similar ecological adaptation compared with extant representatives of the genus, the dominance of *Pelobates fahlbuschi* nov. sp. in unit C suggests an open habitat with sandy and non-groundwater-influenced soils. Recent representatives of the genus are well adapted to a terrestrial mode of life. They prefer open landscapes (including dunes) and show a nocturnal lifestyle (except during the spawning time), and live hidden in mostly self-dug burrows up to 2 m deep during daylight (Gasc et al. 2004; Böhme 2002b). A prehallux (spade), which enhances burrowing ability in extant pelobatids, is not recorded in skeletons of the Late Oligocene *Pelobates decheni* from Enspel (MP 28, Mertz et al. 2007; personal observations, M. Wuttke, Mainz, and Z. Rocék, Prag). Therefore, the presence of fossorial lifestyle for this population seems uncertain. However, the burrowing specialization is regarded as a plesiomorphic character in pelobatids, which was lost in *Eopelobates* (Henrici 1994, Henrici and Haynes 2006). Furthermore, the distribution of recent *Pelobates* species is strongly affected by the nature of the soil (Hildenhagen et al. 1981), and they prefer sandy gravelly soils with grain size of 0.5–3.0 mm (Meissner 1970). Such soils were certainly present in Sandelzhausen, since the fossiliferous marly sediments overlay gravely sand of the *Nördlicher Vollschotter* (see section "Geological setting and stratigraphy" and Moser, Rössner et al. 2009), a situation that might be interpreted as an abandoned channel. The interpretation of the landscape as a relatively open environment during the lower part of the section can further be corroborated by the presence of *Bufo* cf. *viridis*, the cordylids and various lacertids and anguids. The green toads (*Bufo viridis* subgroup), although adapted to various environments, avoid densely wooded areas and are frequently found in open habitats, even in deserts and semi-deserts (Kuzmin 1995; Gasc et al. 2004). Most species of cordylids live in open and rocky environments (Spawls et al. 2002). In such habitats, lizards and anguids show higher diversity in the Recent, as has been documented based on the five species from both families in Sandelzhausen. On the other hand, the presence of two *Chamaeleo* species indicates a vegetated area. The recent chamaeleons of East Africa and Madagascar show ecological differentiation with regard to size. The large species lives arboreally, inhabiting the branches of larger trees (and does not leave them). In contrast, small species usually live on small shrubs and periodically (when searching for shrubs) or permanently as ground-dwellers (Spawls et al. 2002). Also the large tortoise *Geochelone* cf. *perpinniana*, present in unit B, could be an indicator of some kind of vegetation cover since large terrestrial reptiles need shadowed places for cooling down their body temperature (Böhme et al. 2006).

In summary, the majority of information, especially on the abundance of the spadefoot *Pelobates fahlbuschi* nov. sp., points to a relatively open environmental conditions in the close vicinity, probably within an abandoned fluvial channel, during the lower part of the section, although forested (or vegetated) areas possibly existed as a minor component of the habitat. During the upper part of the profile a more densely forested environment may have existed (see also Moser, Niederhöfer and Falkner et al. 2009), but the ectotherm data are less conclusive due to the relatively few terrestrial elements in the lake deposits.

Palaeoclimate of Sandelzhausen

Ectothermic vertebrates represent a well-established proxy indicator in terrestrial palaeoclimatology (Markwick 1998; Böhme 2003; Böhme et al. 2006). They enable quantification of the climatic factors temperature and precipitation. Temperature reconstruction is based on an actualistic index-taxon approach using the nearest living relatives of the most thermophile element in a fossil fauna. This gives a lower limit for a certain parameter, e.g. mean annual temperature (MAT), mean temperature of the coldest month (CMT) or mean temperature of the warmest month (WMT).

In Sandelzhausen several thermophile taxa occur: *Diplocynodon styriacus*, *Tropidophorus bavaricus* nov. sp., *Bavaricordylus* cf. *molassicus*, Cordylidae indet., *Chamaeleon* aff. *caroliquarti*, *Chamaeleon bavaricus* and *Geochelone* cf. *perpinniana*. Their assumed nearest living relatives and minimum temperature requirements are given in Table 5. Several taxa required MATs of at least 17°C. The probably most thermophilous element seems to be the water skink *Tropidophorus*, which today lives in Southeast Asia at latitudes up to 24°N (Greer and Biswas 2004), where minimum MAT values of about 18°C are found. The combined data set for Sandelzhausen suggests MAT > 18°C, CMT > 12.6°C and WMT > 25.1°C. These values concur with palaeobotanical data, which have been reconstructed by the coexistence approach using xylofloras from the late part of the *Ältere Serie* (Böhme et al. 2007): MAT 15.7–20.8°C, CMT 4.8–13.3°C, WMT 24.7–28.1°C. A combination of these temperature estimates (xyloflora, ectothermic vertebrates) results in a MAT ranging from 18°C to 20.8°C, CMT from 12.6°C to 13.3°C and WMT from 25.1°C to 28.1°C.

The estimation of the mean annual palaeoprecipitation (MAP) follows the method of Böhme et al. (2006) using the relative abundance of ecophysiological groups (Table 2). This method groups amphibians and reptiles according to their ecophysiological strategies and adaptations in maintaining thermoregulation, water balance and oxygen uptake. The relative frequency of these groups in recent communities can be used to establish an ecophysiological index for communities, which shows a significant correlation with mean annual precipitation ($r^2 = 0.88$). Applying this relationship to fossil communities results in palaeoprecipitation estimates with average errors of

Table 5 The most thermophilic reptiles from Sandelzhausen, their assumed nearest living relatives (NLR) and minimum temperature requirements (in °C: MAT—mean annual temperature, CMT—mean cold month temperature, WMT—mean warm month temperature)

Thermophile species	NLR	MAT	CMT	WMT
Diplocynodon stviacus	*Crocodylia*	14.2	5.5	~16
Tropidophorus bavaricus nov. sp.	*Tropidophorus*	~18	~12	~23
Bavaricordylus cf. *molassicus*	Cordylidae	17.0	12.6	21.5
Cordylidae indet.	Cordylidae	17.0	12.6	21.5
Chamaeleon aff. *caroliquarti*	Chamaeleonidae	17.4	10.8	25.1
Chamaeleon bavaricus	Chamaeleonidae	17.4	10.8	25.1
Geochelone cf. *perpinniana*	*Geochelone*	17.0	12.6	21.5

Data according to Haller-Probst (1997) and Markwick (1998)

±250–275 mm (Böhme et al. 2006). This palaeoprecipitation tool is applicable in fossil assemblages with rich amphibian and reptile records that show relatively low taphonomical bias with respect to herpetofauna, such as alluvial sediments, palaeosoils, caves, fissure fillings, pond and swamp deposits, and channel-fill sediments. It is important to note that, in contrast to palaeobotanical methodologies, the method is less facies dependent and is applicable to both wet and dry end-members of the climate system.

Because Sandelzhausen reflects two ecosystems in superposition (see below), I calculated the precipitation for units B to D1 and D2 to E separately. The lower part of the section yields a MAP of 571 ± 252 mm, whereas the upper part results in MAP of 847 ± 254 mm. Compared with results based on the xyloflora proxy for the later part of the *Ältere Serie* (MAP 828–1.362 mm; Böhme et al. 2007), the palaeobotanical method indicates higher precipitation values, although within error. This probably reflects the fact that the fossil wood comes from fluvial gravel and sand deposits of the *Nördlicher Vollschotter*, which may represent the humid end-member condition. The results for Sandelzhausen suggest an increase in precipitation up-section, from semi-arid/sub-humid values in units B to D1 to sub-humid/humid values in units D2 and E. This is in accordance with the interpretation of the lower part of the section as sheet flood deposits by Schmid (2002: 151), who compared this type of sedimentation to that of wadis after intense rainfall. In addition, it is well known from recent species of *Pelobates* and other spadefoots that the start of the spawning migration is triggered by extrinsic factors by the beginning of the rainy season ("anuran xeric breeding pattern"), contrary to many other frogs in which intrinsic factors trigger spawning migration. Under inter-annual hydrological variability, spadefoots have more constant breeding success than other frogs (Jakob et al. 2003). The seasonal, semi-arid/sub-humid climate in units B to D1 therefore could be an explanation for the super-abundance of *Pelobates fahlbuschi* sp. nov. in Sandelzhausen.

Conclusions

The description of 35 species of fishes, amphibians and reptiles increases the number of ectothermic vertebrates from Sandelzhausen to 48 taxa (including five turtle species from Schleich 1981 and eight snake taxa from Szyndlar 2009). This locality thus represents one of the most diverse terrestrial ectotherm faunas of Miocene age. Three species are described as new: *Pelobates fahlbuschi* nov. sp. (spadefoot, Pelobatidae; the most abundant vertebrate of the locality), *Tropidophorus bavaricus* nov. sp. (waterskink, Lygosominae) and *Bavaricordylus molassicus* nov. sp. (girdled lizard, Cordylidae). Three additional species are new, but are not formally described yet because the material is incomplete: Ranidae gen. indet. sp. nov. (water frog), Anguidae gen. indet. sp. nov. (glass lizard) and *Palaeoblanus* sp. nov. (worm lizard).

Using the newly established tooth replacement method I demonstrated that the palaeohydrology of Sandelzhausen is characterized by a change from temporary water conditions in units B to D1 (lower part) to permanent lake conditions in the upper part of unit D1 to unit E (Fig. 2).

During units B to D1 (lower part) the ecosystem was influenced by seasonal inundations. The remaining riparian pools were temporary and did not yield autochthonous fish populations, but acted as spawning places for amphibians (amphibian pool) and crocodiles. The possible presence of alluvial rheocrenes (brooks fed by groundwater-induced perennial springs) during the rainy season is suggested. A mostly open habitat in the near vicinity with sandy and non-groundwater-affected soils during the dry season is suggested based on the dominance of *Pelobates fahlbuschi* nov. sp.

The ecosystem of the upper part of the section in the upper part of unit D1 and during D2 and E is characterized by permanent water conditions of riparian pond type and has yielded an autochthonous *Palaeocarassius*/*Channa* fish population (fish pond).

The reconstruction of the ecosystems and environment matches with the results of the mollusc-based study by Moser, Niederhöfer and Falkner et al. (2009). A generally humid and forested environment has been reconstructed by Tütken and Vennemann (2009) based on carbon and oxygen isotope composition of tooth enamel from large herbivorous mammals. However, the strontium isotope composition indicates that the carbon and oxygen isotope signal may reflect environments from the eastern part of the Molasse and not the vicinity of Sandelzhausen (Tütken and Vennemann 2009). Moreover, these authors did not differentiate their samples into the sedimentary units of the profile, so that within-section variations are not deducible.

The climate of Sandelzhausen was subtropical with a MAT from 18°C to 20.8°C, CMT from 12.6°C to 13.3°C and WMT from 25.1°C to 28.1°C. The MAT estimation corresponds to the calculation based on phosphate oxygen isotopes from herbivore mammal teeth (Tütken and Vennemann 2009), resulting in a MAT of 18.7 ± 1.7°C. The reconstructed precipitation values (bioclimatic analysis of amphibians and reptiles) suggest that the observed change in the hydrologic conditions was probably climatically driven. The lower part of the section gives semi-arid/sub-humid values with MAP of 571 mm, whereas the upper part shows sub-humid/humid values of 847 mm MAP. The increase in precipitation by about 280 mm may have resulted from a less seasonal precipitation regime with concomitantly less variation of the regional groundwater table during units D2 and E, leading to the establishment of a fish pond with permanent water conditions.

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