

**Ectothermic vertebrates (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata) from the Upper Oligocene of Oberleichtersbach (Northern Bavaria, Germany)**

With 4 figs, 4 pls, 1 tabs

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**A b s t r a c t**

An overview about the ectothermic vertebrates from Oberleichtersbach (Northern Bavaria) is presented, which allows a unique insight into terminal Oligocene (MP30) continental biota. The fossil assemblage contains 43 taxa belonging to a great variety of groups (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata) and represents the worldwide most diverse ectothermic vertebrate fauna of Oligocene age. Several taxa show their first appearance in the fossil record (Cobitidae, *Albanerpeton inexpectatum*, *Andrias scheuchzeri*, *Triturus roehrsi*, *Discoglossus*, *Miolacerta*, *Merkurosaurus*, probably Viperidae) others show their youngest fossil record (aff. *Pseudeumeces*). Two species are described as new: *Cobitis primigenus* nov. sp. (Cobitidae), *Texasophis hecki* nov. sp. (Colubridae). The enigmatic choristodere *Lazarussuchus* is reported for the third time and probably also represents a new species. Palaeoecological analysis indicates the presence of a large, not very deep, well-oxygenated perennial doline lake with an intensely structured lake-margin and probably with a fluvial inflow. As indicated by diverse top-predators, the aquatic ecosystem was partitioned in various food chains belonging to different food webs. A relatively sparse arboreal vegetation cover on mostly badly drained soils probably surrounded the lake. The climate was subtropical (mean annual temperature > 14 °C) and humid (mean annual precipitation 1131 ± 261 mm).

**Key words:** Oligocene, freshwater fishes, amphibians, reptiles, *Lazarussuchus*, *Albanerpeton*

**K u r z f a s s u n g**

Die ektotherme Wirbeltierfauna von Oberleichtersbach erlaubt einen einmaligen Einblick in die terrestrische Lebewelt zum Ende des Oligozäns (MP30). Zur Fossilvergesellschaftung gehören 43 Taxa, die einer Vielzahl von Großgruppen angehören (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata). Die Fundstelle zeigt damit die weltweit höchste Diversität für eine ektotherme Wirbeltierfauna aus dem Oligozän. Für eine Vielzahl von Taxa konnte der stratigraphisch älteste Nachweis erbracht werden (Cobitidae, *Albanerpeton inexpectatum*, *Andrias scheuchzeri*, *Triturus roehrsi*, *Discoglossus*, *Miolacerta*, *Merkurosaurus*, wahrscheinlich Viperidae), für ein Taxon der stratigraphisch jüngste (aff. *Pseudeumeces*). Zwei Arten werden neu beschrieben: *Cobitis primigenus* nov. sp. (Cobitidae), *Texasophis hecki* nov. sp. (Colubridae). Der rätselhafte Choristodere *Lazarussuchus* wird hier zum dritten Mal nachgewiesen und repräsentiert wahrscheinlich eine neue Art. Die paläoökologische Analyse der Fauna legt die Existenz eines großen, nicht sehr tiefen, sauerstoffreichen und permanenten Dolinen Sees, mit intensiv strukturiertem Ufer und einen fluvialen Zufluss nahe. Der Nachweis mehrerer Top-Predatoren zeigt, dass ein komplexes aquatisches Ökosystem mit verschiedenen Nahrungsnetzen vorlag. Das nähere Seeumfeld trug wahrscheinlich keine sehr dichte Baum-Vegetation auf schlecht drainierten Böden. Die klimatischen Bedingungen waren subtropisch (Jahresmitteltemperatur > 14 °C) und humid (Jahresniederschlag 1131 ± 261 mm).

**Schlüsselworte:** Oligozän, Süßwasserfische, Amphibien, Reptilien, *Lazarussuchus*, *Albanerpeton*

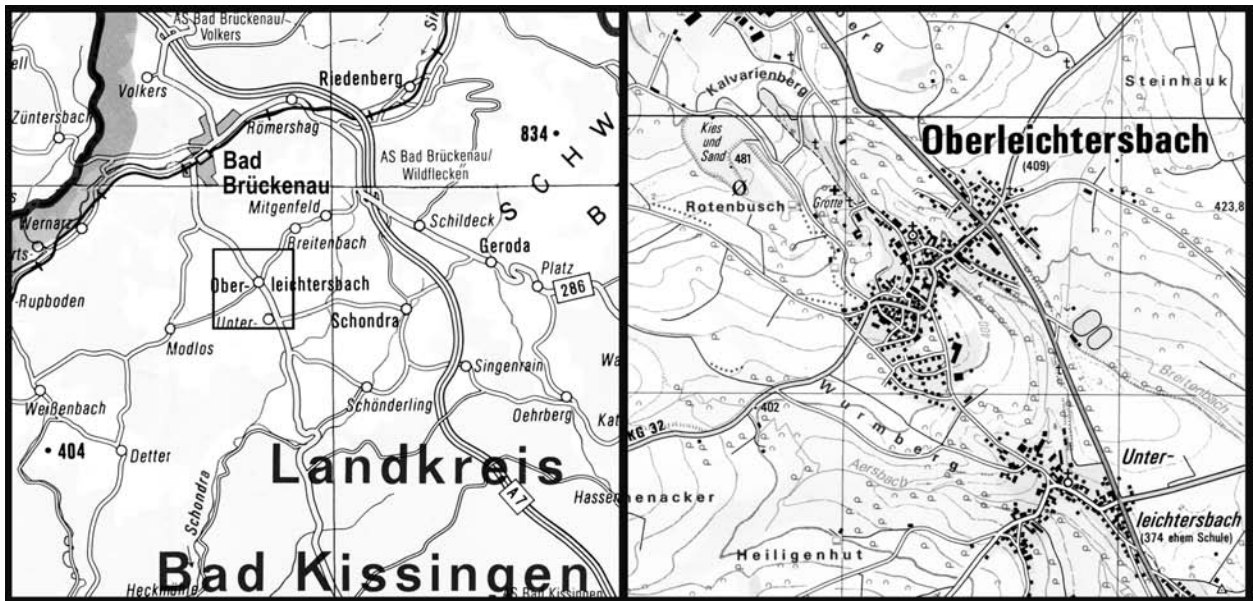


Fig. 1: Left: Position of Oberleichtersbach near Bad Brückenau in northern Lower Franconia (Bavaria). 1: 200.000. Right: Position of the doline (⊗) Oberleichtersbach on topographic chart 5724 Zeitlofs. 1: 25.000. (© Topographische Karte 1: 25.000, Bayerisches Landesvermessungsamt, Nr. 2705/05)

### Introduction

The end of the Oligocene was a time of intense climatic changes, leading to a global cooling with an intensification of East-Antarctic ice shield build-up near the Oligo-Miocene boundary (ZACHOS et al. 2001) accompanied by aridisation of the mid-latitudes (DUNAI et al. 2005). The study of ectothermic vertebrates, representing good environmental and climatic indicators, is important for describing the impact of climate change on continental ecosystems (BÖHME 2002 c). From the terminal Oligocene of Europe only few localities are well known (e. g. Coderet in France; Rott in Germany, MÖRS 1995), both belonging to ecosystems with special taphonomic circumstances (fissure filling and lake) and so probably reflect the ancient biodiversity only incomplete. Here I present the first results from the study of ectothermic vertebrates coming from Oberleichtersbach (fig. 1) – a new terminal Oligocene (MP30) locality in Northern Bavaria (Rhön Mountains). The geology of the locality indicates that the sediments belong to a doline filling, developed due to karstification of the Middle Triassic anhydrites of the middle Muschelkalk (MARTINI 2000). The Oberleichtersbach locality is of exceptional importance, because it has with 43 taxa (tab. 1) the worldwide most diverse ectothermic assemblage of comparable age, and it is shown that many of the taxa enlarge our stratigraphic knowledge considerably by new first and last occurrence

es. The investigation of the fauna from Oberleichtersbach provides therefore a unique insight into terminal Oligocene continental biota.

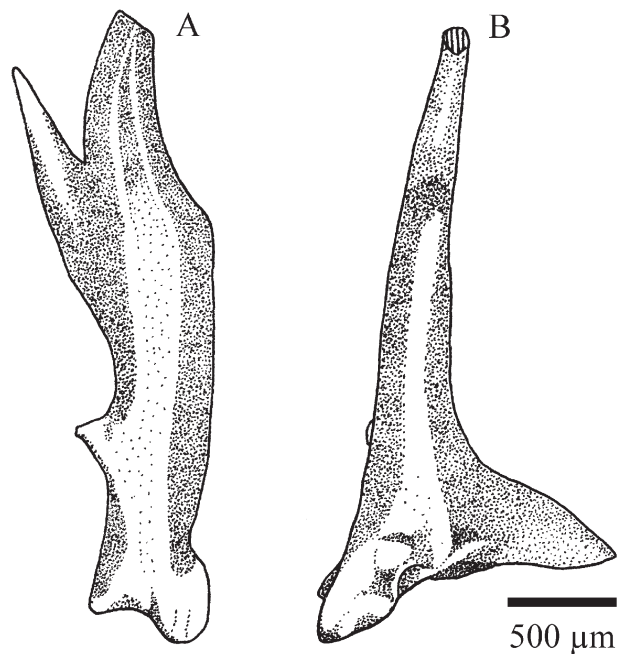


Fig. 2: *Cobitis primigenus* nov. sp., Oberleichtersbach, holotype, SMF P 9735, left lateroethmoid; A – ventral, B – medial.

## Systematic Palaeontology

Table 1: Faunal list of ectothermic vertebrates from Oberleichtersbach

	Cobitidae	<i>Cobitis primigenus</i> nov. sp.
Teleostei	Cyprinidae	<i>Palaeorutilus</i> sp. 1
		<i>Palaeorutilus</i> sp. 2
		Gobioninae sp. A
		Gobioninae sp. B
		Gobioninae sp. C (cf. <i>Varhostichthys eurystomus</i> (TROSCHEL 1861)) <i>Tarsichthys macrurus</i> (AGASSIZ 1834)
Allocaudata	Albanerpetontidae	<i>Albanerpeton inexpectatum</i> ESTES & HOFFSTETTER 1976
Urodela	Cryptobranchidae	<i>Andrias scheuchzeri</i> (HOLL 1831)
	Salamandridae	<i>Chioglossa</i> cf. <i>meini</i> ESTES & HOFFSTETTER 1976 aff. <i>Chelotriton</i> sp.
		<i>Triturus roersi</i> HERRE 1955 <i>Triturus</i> sp.
		Salamandridae indet. (? aff. <i>Brachycormus noachicus</i> GOLDFUSS 1831)
Anura	Discoglossidae	<i>Discoglossus</i> sp. (cf. <i>D. troscheli</i> (MEYER 1852))
	Palaeobatrachidae	<i>Palaeobatrachus</i> sp. 1 (aff. <i>P. robustus</i> HOSSINI & RAGE 1999)
		<i>Palaeobatrachus</i> sp. 2 (aff. <i>Albionbatrachus wightensis</i> MESZOELY et al. 1984)
	Palaeobatrachidae	<i>Palaeobatrachus</i> sp. 3 (aff. <i>P. laubei</i> BIEBER 1881 vel <i>P. diluvianus</i> (GOLDFUSS 1831))
		Pelobatidae
	Ranidae	<i>Rana (ridibunda)</i> sp. (cf. <i>R. meriani</i> MEYER 1853)
Testudines	Testudinidae	<i>Testudo</i> sp. aff. <i>Geochelone</i>
	Trionychidae	<i>Trionyx</i> sp.
	Chelydridae	<i>Chelydropsis</i> cf. <i>decheni</i> (MEYER 1854)
	Emydidae	<i>Palaeochelys mlynarskii</i> HERVET & LAPPARENT DE BROIN 2000 Emydidae indet.
Choristodera		<i>Lazarussuchus</i> nov. sp.
Crocodylia	Alligatoridae	<i>Diplocynodon</i> sp.
	Amphisbaenidae	Amphisbaenidae indet. aff. <i>Pseudeumeces</i> <i>Miolacerta</i> sp.
Squamata	Lacertidae	<i>Lacerta</i> sp. 1
		<i>Lacerta</i> sp. 2
		<i>Lacerta</i> sp. 3
		<i>Lacerta</i> sp. 4
	Anguidae	<i>Ophisaurus</i> sp. cf. <i>Anguis</i> sp.
	Shinisauridae	<i>Merkurosaurus</i> sp.
	Aniliidae	<i>Eoanilius oligocenicus</i> SZYNDLAR 1994
	Colubridae	<i>Texasophis hecki</i> nov. sp.
		Colubrinae indet.
	Viperidae	? Viperidae indet.

### Fishes (Teleostei)

Cypriniformes, Cobitidae: *Cobitis primigenus* nov. sp.; Cyprinidae, Phoxininae: *Palaeorutilus* sp. 1, *Palaeorutilus* sp. 2; Gobioninae: Gobioninae sp. A, Gobioninae sp. B, Gobioninae sp. C (cf. *Varhostichthys eurystomus*); Tincinae: *Tarsichthys macrurus*). (pl. 1, figs 1–11)

Fishes are represented by two families of the Cypriniformes: the Cobitidae (loaches) and the Cyprinidae (minnows). The oldest loaches up to now be described by

OBRHELOVA (1990) from the Lower Miocene (MN3) of Brestany (Preschen, North Bohemian Basin) based on articulated skeletons (*Cobitis ioannis* OBRHELOVA 1990, *Nemachilus tener* OBRHELOVA 1967). The remains from Oberleichtersbach represent therefore the most ancient representatives of this Old World family. The most characteristic bone in disarticulated material is the lateroethmoid (BÖHME 2002 a, SYTCHEVSKAYA 1989). Six lateroethmoids are found in the studied material, belonging to at least four individuals. These bones show the

typical morphology of *Cobitis* (spiny loach), but differ from all known fossil taxa and described therefore as a new species.

*Cobitis* LINNAEUS 1758  
*Cobitis primigenus* nov. sp.  
(pl. 1, fig. 1 a–c; fig. 2)

**H o l o t y p e** : left lateroethmoid (Collection of Senckenbergische Naturforschende Gesellschaft, SMF P 9735)

**T y p e l o c a l i t y** : Oberleichtersbach, Rhön Mountains, Germany

**S t r a t i g r a p h i c a l a g e** : uppermost Oligocene, MP30

**D e r i v a t i o n o m i n i s** : from latin primus (first) and genus (ancestor).

**P a r a t y p e s** : five lateroethmoids, SMF P 9748–9752

**D i a g n o s i s** (terminology after SYTCHEVSKAYA 1989 and BÖHME 2002 a): A small species of *Cobitis* (size range of lateroethmoid 2.1 to 2.5 mm), the lateroethmoid of which differs from *C. martinii* by its slender shape, slender posteromedial spine, longer posterolateral spine, weaker medial projection and a small, spiny lateral projection.

**R e m a r k s** : It is impossible to compare the new species to taxa based on complete skeletons (e.g. *C. iohannis*, *C. centrochir* AGASSIZ 1835), because in the latter the lateroethmoids are not preserved (BÖHME 2002 a). Therefore, the comparison is only feasible with species described on isolated lateroethmoids. The only European species which is erected on isolated lateroethmoids is *C. martinii* BÖHME 2002 from the Upper Miocene (MN9) of Götzendorf (BÖHME 2002 a) which differs clearly (see diagnosis). SYTCHEVSKAYA (1989) described six species belonging to the genera *Cobitis* and *Sabanajewia* from the Middle and Upper Miocene of Central Asia. The lateroethmoid of *Cobitis primigenus* nov. sp. differs from all these species by its smaller size (Asian lateroethmoids are between 3 and 7 mm in length) and resembles most closely the morphology of *C. ichberchae* SYTCHEVSKAYA 1989 and *C. centralasiae* SYTCHEVSKAYA 1989. It differs from the first species by a longer posterolateral spine and a more proximal position of the lateral projection, and from the latter species by a more slender shape and stronger rostromedial process.

Minnnows (Cyprinidae) are documented by six species coming from three subfamilies: Gobioninae, Tincinae, and Phoxininae. The Gobioninae with three species are most divers. Typical gobionin teeth are hooked, show a smooth medial crest, and the lateral tooth flank remains flat, without a crest; in contrast to tincins, phoxinins and leuciscins there is no defined masticatory area (pl. 1, fig. 3, 4). Those teeth are typical in Oligocene sediments of Europe (e.g. North Alpine Lower Freshwater Molasse, Rott – drillings; personal observations), but isolated, small sized teeth are difficult to be determined more precisely. In Oberleichtersbach, several pharyngeal bones

with attached teeth are preserved, which allow a better determination of this material. Two small sized gobionines not differing significantly in tooth shape could be distinguished based on pharyngeal arch morphology (nomenclature after COBURN & CAVENDER 1992). Gobioninae sp. A (pl. 1, fig. 7) shows a very slender anterior process, the anterior angle is not developed; the tooth formula is 4–5.3 (four or five teeth in the external row, three in the internal row). In contrast, Gobioninae sp. B shows a somewhat stronger anterior process with a recess on the external side behind the A5 tooth and a weak developed anterior angle; the tooth formula is 5.3 (pl. 1, fig. 6). The teeth of both species are slender with a relatively large A5 tooth, and are similar to the morphology of the extant *Gobio albipinnatus* (LUKASCH 1933) and *G. gobio* (LINNAEUS 1758). They represent probably two new species, but new sampling in Oberleichtersbach will probably reveal better material for a detailed description. The third gobionin (Gobioninae sp. C) is a large sized fish with strong and robust teeth of general gobionin morphology. The medial crest on the teeth is not sharp like in the small sized Gobioninae sp. A and B, and the lateral side is somewhat bellied proximal to the hook (pl. 1, fig. 4). The pharyngeal arch shows a robust anterior process and a slightly developed anterior angle. The A5 tooth is significantly smaller than the previous ones (in contrast to Gobioninae sp. A and B), and the tooth formula is 5.2 (pl. 1, fig. 11). These pharyngeal bones with attached teeth resemble closely a toothed pharyngeal arch from Rott (collection University Bonn, UB-Ro 4132) figured by GAUDANT (1988, 2002) and isolated teeth from Rott drillings figured by MÖRS (1995) as *Tarsichthys macrurus*. These materials neither belong to *Tarsichthys*, neither to the species *macrurus* (except the tooth in fig. 12 in MÖRS 1995). The genus *Tarsichthys* was erected by TROSCHEL (1854) on *T. tarsiger* (UB-Ro 4100), a male individual of *Leuciscus macrura* AGASSIZ 1834. *Tarsichthys* TROSCHEL 1854 is a senior synonym to *Palaeotınca* OBRHELOVA 1970. Individuals of *Tarsichthys macrurus* reached in the Rott locality never more than 150 mm in standard length. In addition to the pharyngeal arch UB-Ro 4132, assigned in GAUDANT (1988, 2002) to *Tarsichthys macrurus*, there are several cranial bones on the same plate, belonging to the same individual of large size, about 250 mm in standard length. Some bones, especially the operculum and the cleithrum show substantial difference to bones from *T. macrurus*, but are identical to the bones of large fishes from Rott like “*Leuciscus*” *eurystomus* (UB-Ro 4099), “*L.*” *remotus* (UB-Ro 4104), “*L.*” *pleisiopterus* (UB-Ro 4106), and “*L.*” *gloriosus*. These names are given by TROSCHEL (1861) but the specimens are never described adequately. BÖHME (in MARTIN 1996) placed them in the genus *Varhostichthys* Obrhelova 1969. Later GAUDANT (2002) referred to this view, but placed them in the genus *Protothymallus* LAUBE 1901. He suggests that *Varhostichthys* is a junior synonym to *Protothymallus*. However, the type specimens of both taxa, *V. brevis* and *P. elongatus*, differ significantly and



thus they should treat as different genera (even if both are gobionins, BÖHME 2007). The large Rott specimens (225 to 300 mm in standard length) resemble more closely *Varhostichthys* (among others because of scale morphology). The large gobionine from Oberleichtersbach will be referred with caution to this taxon and will be named here as Gobioninae sp. C (cf. *Varhostichthys eurystomus*).

The aforementioned *Tarsichthys macrurus* (Tincinae) is also present in Oberleichtersbach by isolated teeth and tooth bearing pharyngeal bones (pl. 1, fig. 5, 10). The material indicates a tooth formula for this species of 4 or 5.1.

The other two cyprinids belong to the Phoxininae (pl. 1, fig. 8, 9). This subfamily can be distinguished from the Leuciscinae on isolated teeth and pharyngeal arch material based on the following characters (see BÖHME 2001, COBURN & CAVENDER 1992, CAVENDER & COBURN 1992): leuciscins have usually well developed anterior and posterior angles on the pharyngeal arch, a serrated medial crest on teeth and up to three teeth in the inner row, whereas phoxinins have a rounded pharyngeal arch (no posterior angle), a slightly developed anterior angle, smooth medial crest and usually none or one teeth in the inner row. The only Oligocene phoxinin genera from Europe are *Palaeorutilus* (BÖHME 1996, 2001) and aff. *Phoxinus* (SCHULZ-MIRBACH & REICHENBACHER 2006). The taxon aff. *Phoxinus* is based on otoliths and cannot be compared. *Palaeorutilus* is known from the MP 30 of Rott by the species *P. papyraceus* (BRONN 1828), preserved as articulated skeletons without pharyngeal bones. Disarticulated *Palaeorutilus* pharyngeal arches from the Rott boreholes (MÖRS 1995) reveal diverse tooth formula (4.1 – most common, 4.2, 4.3 and 5.2; BÖHME 1996) previously integrated into *P. papyraceus*.

The Oberleichtersbach phoxinins show a pharyngeal arch type with slightly developed anterior and no posterior angle, the teeth with smooth or wrinkled medial crests (pl. 1, fig. 2) and tooth formula 5.1 (pl. 1, fig. 8) and 5.3 (pl. 1, fig. 9). Both specimens could be assigned to different species: *Palaeorutilus* sp. 1 (pl. 1, fig. 8) with a broader anterior angle, a stronger bent posterior process and one tooth at the inner row, is somewhat larger and more robust than *Palaeorutilus* sp. 2 (pl. 1, fig. 9) with a small pointed anterior angle, a comparatively straight posterior process and three teeth at the inner row. This indicates that probably also the Rott-borehole phoxinins belong to different species, and that *Palaeorutilus* differs from extant phoxinins by the presence of more than one tooth in the inner row, at least in some species.

A comparison with both Upper Oligocene *Palaeorutilus* species *P. enspelensis* (BÖHME 1996) (MP28 from Enspel, BÖHME 2001) and *P. papyraceus* (MP30 from Rott, BÖHME 1996) is not possible at the moment, because of the articulated preservation of the type material (the teeth referred to *P. papyraceus* by MÖRS 1995 doesn't belong to phoxinins but instead to gobionins).

Gobionins, phoxinins and tincins belong to the typical (and only) European cyprinid subfamilies of the

Oligocene (BÖHME 2001, 2007), known since the Lower Oligocene (phoxinins since MP21, gobionins since MP21/22, tincins since MP24).

### Tailed amphibians (Allocaudata, Urodela)

Albanerpetontidae: *Albanerpeton inexpectatum*; Cryptobranchidae: *Andrias scheuchzeri*; Salamandridae: *Chioglossa* cf. *meini*, *Triturus roehrsi*, *Triturus* sp., aff. *Chelotriton* sp. and Salamandridae indet. (? aff. *Brachycormus noachicus*) (pl. 1, figs 12–14, pl. 2, figs 1–9, pl. 3, fig. 1).

The tailed amphibians are represented by the orders Allocaudata (albanerpetontids) and Urodela. The albanerpetontid material comprises three dentals and two vertebrae. The dentals (pl. 1, fig. 12) are morphologically identical with *Albanerpeton inexpectatum* ESTES & HOFFSTETTER 1976 from the type locality La Grive (ESTES & HOFFSTETTER 1976) and the Central European Lower and Middle Miocene localities Petersbuch 2, Randecker Maar, Obergänsersdorf, Teiritzberg, Adelschlag, and Sandelzhausen (BÖHME 1999, 2002 b, WIECHMANN 2003, REICHENBACHER et al. 2004) and are referred to this species. *Albanerpeton inexpectatum* and *A. pannonicus* are the last representatives of the Allocaudata – a diversified group from the Mesozoic and early Paleogene. Until now both species are known from the late Early Miocene (MN4 of Petersbuch 2, GARDNER & BÖHME 2008) to the latest Pliocene (MN17 of Rivoli Veronese, DELFINO & SALA 2007). The Oberleichtersbach fossil represents the world's first record of an albanerpetontid from the Oligocene and the oldest record of *A. inexpectatum* (however author's unpublished data indicate the presence of *Albanerpeton* in southern Germany already since the beginning of the Oligocene, MP21 of Möhren 12).

The Urodela are represented in Oberleichtersbach by two families: the Cryptobranchidae (hellbenders) and the Salamandridae (true salamanders and newts). The cryptobranchid *Andrias scheuchzeri* (HOLL 1831) is documented by a left maxilla (pl. 1, fig. 13 a), a right mandible (not figured) and 43 isolated teeth (pl. 1, fig. 13 b, c). This maxilla indicates a large specimen, reaching probably 120 cm in length, whereas the dental originated from a small, probably immature specimen (25 to 30 cm). The very typical teeth of *Andrias scheuchzeri* were first described from the Lower Miocene by BOETTCHER (1987). Besides the long known *Andrias scheuchzeri* from Rott the Oberleichtersbach Giant Salamander is the oldest known cryptobranchid from Europe.

The family Salamandridae is represented by five species: *Chioglossa* cf. *meini* ESTES & HOFFSTETTER 1976, *Triturus roehrsi* HERRE 1955, *Triturus* sp., aff. *Chelotriton* sp. and Salamandridae indet. (? aff. *Brachycormus noachicus* GOLDFUSS 1831).

*Chioglossa cf. meini*, represented by eight vertebrae (pl. 1, fig. 14), differs from the nominal species by a few characters (smaller size, dorsal lateral cristae between praezygapophyses and rib-bearers absent or very indistinct) and could represent a new species.

*Triturus roehrsi* is represented by 40 trunk vertebrae (nine of them belonging to one individual) and additional cranial and postcranial elements. It closely resemble the type material (ESTES 1983) and the material from Oberdorf (SANCHIZ 1998 a) in the height of the neural arch and neural spine, the development of the ventral lamina of the transverse process, the broadened and posterior forked lamina of the neural spine (pl. 2, fig. 8), the very indistinct or absent frontosquamosal arch, the extensive sculptured frontals and other cranial features (not figured). *Triturus roehrsi* was previously known from the Miocene (MN4 to MN6; the so called species from the MN9 of Götzendorf, MIKLAS 2002, probably does not belong not to *T. roehrsi*) of the Central Paratethys area, so that this record is the westernmost and oldest of this species.

A single vertebra only (pl. 3, fig. 1) documents an additional newt (*Triturus* sp.). It differs significantly from *T. roehrsi* and all extant *Triturus* species available for comparison (*T. alpestris* (LAURENTI 1768), *T. bolcai* (LATASTE 1879), *T. cristatus* (LAURENTI 1768), *T. helveticus* (RAZOUKOWSKY 1789), *T. marmoratus* (LATREILLE 1800), *T. vittatus* (JENYNS 1835), *T. vulgaris* (LINNAEUS 1758)), so that its taxonomic relationships remains obscure.

The taxonomy within the salamandrid group II sensu ESTES (1983), including the genera *Chelotriton*, *Echinotriton*, *Tylototriton* and *Brachyormus* is highly confusing, mainly due to the difficulty to compare complete preserved skeletons with isolated bones. A key question is the nature of the species *Chelotriton paradoxus* POMEL 1853, described on isolated bones from Langy (Lower Miocene) and Chafours (Upper Oligocene, POMEL 1853), which both are lost. Later ESTES (1983) designated an isolated vertebra from Coderet (Cod. 12, Museum National D'Histoire Naturelle, Paris) as the neotype. But studies on cranial elements by the author, especially frontals from Coderet show that two species of the salamandrid group II occur in this locality which probably do not or not significantly differ in vertebrate morphology. Both crocodile salamander types from Coderet (Collection University Claude Bernard Lyon Nr. 345001 to 345007) are named *Chelotriton* sp. A and sp. B here and show the following characters:

*Chelotriton* sp. A from Coderet (pl. 2, fig. 3): Frontal broader as long, or nearly as broad as long; anterior border straight (margo praefrontalis et praemaxillaris), no lateral recess for the praefrontal; frontosquamosal process very broad (broad-ellipsoid in cross section), bend off with an angle of 45 degree from the axis of the bone; posterior part of the medial margin laterally inclined, open a triangular space between both frontals which was probably not occupied by the parietals (no bony sutures on these frontal margins) and therefore left the endocranium

uncovered; table of the frontal slightly convex, the orbital margin is not elevated; the dermal sculpture is pustular, very regular and dense. The most characteristic features of the ventral side are the enormously enlarged and ossified lateral and posterior margins (taenia tecti transversalis et marginalis) of the frontal fenestra (pl. 2, fig. 3 e) and the absence of an anterior margin (pl. 2, fig. 3 a, b). This heavily ossified chondrocranial roof of the braincase is unknown from any fossil or recent salamander. [After the submission of this manuscript I received personal information from Martin Ivanov (Brno) that, according to unpublished Slovak material, the Coderet frontals type A could be interpreted as squamosals. This will change the conclusions about the taxonomy of the Coderet material, but not about the Oberleichtersbach crocodile salamander, which remains clearly separated from *Chelotriton paradoxus*.]

*Chelotriton* sp. B from Coderet (pl. 2, fig. 2): Frontals longer than broad; showing well separated margo praefrontalis et praemaxillaris by an anterior-lateral recess for the praefrontal (praefrontal contribute to the antero-medial orbital margin); frontosquamosal process narrower than in type A (ovoid in cross section), bend off with an angle of 30 to 35 degree from the axis of the bone; medial margin straight, no lateral inclination on the posterior part and therefore fully covering of the endocranium; table of the frontal flat, the orbital margin and the frontosquamosal process are slightly elevated; the dermal sculpture is pustular, but pustules are arranged in ridges. The sculpture is not so regular like in type A and especially medial to the frontoparietal process and in the anteromedial part more even. The ventral side shows an oval frontal fenestrum with normal developed lateral, posterior and anterior margins which are not enlarged (pl. 2, fig. 2 a, b, e).

The differences between the frontal types are distinct enough to separate both at the species and even at generic levels. In some features, the *Chelotriton* type A frontals resemble the conditions in the recent *Echinotriton andersoni* (BOULENGER 1892), whereas type B match more the morphology of the recent species *Tylototriton verrucosus* ANDERSON 1871 (see NUSSBAUM & BRODIE 1982). The question, whether type A and B belong to *Chelotriton paradoxus* is difficult to answer, because the numerous associated vertebrae in the Coderet collection's (large samples of the collection in Lyon, Basel and Munich were investigated) show one type of trunk vertebra. Only the atlas could probably be of taxonomic value. Besides the normal atlas morphology (atlas type A, pl. 2, fig. 1 a) with lateral elongated anterior cotyles and a well developed processus odontoideus (= tuberculum interglenoideum), which is known from 33 specimens (Lyon collection) from all Coderet levels (except D1 and G1), one atlas (atlas type B, pl. 2, fig. 1 b) from Coderet sample E1 differs clearly in possessing large round anterior cotyles and lacking the processus odontoideus. If this is not a pathological configuration it reflects clearly a dis-

tinct taxon. In addition: frontals of *Chelotriton* type A are the most common. In the collection from Lyon, 12 right and 7 left "type A" frontals are present, coming from all levels of the fissure filling except levels F1, F2 and G1. Type B is known only by one right and one left frontal from the E1 level (not belonging to the same individual). Assuming that atlas type B and frontal type B (coming both from level E1) are belonging to the same taxon, whereas atlas and frontal types A do belong to another, the latter one is the most common (33 individuals in all levels), whereas the first taxon is rare (probably two individuals from level E1). This could give an argument to decide that frontal and atlas type A belongs to *Chelotriton paradoxus* POMEL 1853, whereas frontal and atlas type B belong to a new species or even genus. In addition: a lot of isolated ribs (120 in total) occur in Coderet in all levels. Two third of them have only one dorsal spine and probably belonging to posterior vertebrae. One third, belonging to anterior or mid-trunk vertebrae, shows two (rarely up to four) dorsal spines (pl. 2, fig. 6), indicating further analogues for *Chelotriton paradoxus* (sensu frontal and atlas type A) to the genus *Echinotriton* (NUSSBAUM & BRODIE 1982).

These descriptions indicate that vertebral morphology alone is insufficient for taxonomic allocation within the salamandrid group II (sensu ESTES 1983) and that remains previously subsumed under the name *Chelotriton paradoxus* may reflect different species and even genera.

The Oberleichtersbach "*Chelotriton*" material belongs to at least four individuals. Frontals differ clearly from both types described from Coderet. The sculpture is arranged in a vermicular to pit-and ridge (and not a pustular) type and the fronto-squamosal process is comparatively smooth (pl. 2, fig. 7). The fronto-squamosal process bends off with an angle of 30 degree from the axis of the frontal. An antero-lateral recess for the praefrontal is present, although shorter than in Coderet type B. The medial margin is broken-off. From the ventral side an oval frontal fenestrum is developed in which the margins are not enlarged. These features show some similarities to the Coderet frontal type B, but differ clearly in the type of sculpture. The maxilla, the parietal, the squamosal and the quadratojugal fragments show a pustular sculpture like in the Coderet material. This type of sculpture, especially on the squamosal, seems to be typical in all *Chelotriton*-like forms, regardless their specific assignments. Vertebrae (pl. 2, fig. 4) are similar to that from Coderet, the only two differences are a better development of anterior and posterior crests between the centrum and the ventral rib-bearers on mid-trunk vertebrae, and smaller, poorer ossified dermal plates on the neural spines (in most cases they are broken away from the centra). The atlas shows a normal development, with oval anterior cotyles and a processus odontoideus. The ribs have only one dorsal spine (pl. 2, fig. 5).

In conclusion: the Oberleichtersbach crocodile salamander differs in frontal, vertebra and rib morphology

from the Coderet material, therefore the name *Chelotriton paradoxus* cannot be referred to these remains. If the Coderet frontal type A really belongs to the nominal species, then *Chelotriton paradoxus* does not occur in the Upper Oligocene lacustrine localities of Germany (Rott, Orsberg, Enspel). In the future, it would be necessary to study the Coderet material in more detail and probably to re-designate the neotype of *Chelotriton paradoxus*. Provisionally, the Oberleichtersbach crocodile salamander is classified as aff. *Chelotriton* sp.

Two vertebrae (one mid- and one posterior trunk vertebra) of a peculiar morphology, unknown from extant species (pl. 2, fig. 9), represent the last salamandrid taxon. The vertebrae are small (length 1.8 mm), compact, and ophistocoelous. The condylus is small, rounded, without a notochordal fossa, and separated from the centrum only by a small constriction. The neural arch is low. The neural spine is relatively low, divided posteriorly and covered with a dermal plate sculptured by pits. Prae- and postzygapophysals are small. Between the praezygapophysal and the distal rib-bearer a horizontal lamina is developed. The anterior and especially the posterior crests between the centrum and the ventral rib-bearers are very prominent and bear small subcentral foramina. In some respect (size, compactness, neural arch morphology, crests between centrum and ventral rib-bearers) they resemble *Salamandrina*, but this genus differs significantly by the presence of a zygosphene, by a larger condylus well separated from the centrum and by a broader constriction and by showing a notochordal fossa. It is difficult to compare these vertebrae with *Brachycormus noachicus* GOLDFUSS 1831, an articulated species of comparative size known from Orsberg. ESTES (1983) described vertebrae with a pustular sculpture on dermal plates of this species, whereas ROCEK (1996) who restudied the material did not mention that feature. The material referred to *Brachycormus noachicus* probably includes different species (as ROCEK already suggested), and one of them (specimen from the British Museum of Natural History No. 30268, figured in ESTES (1983) and ROCEK (1996)) can probably be related to the two vertebrae described herein. On the other hand, ROCEK (1996) concluded that *Brachycormus* is a neotenus relative of *Triturus*. This raises the question of the relationship of *Brachycormus noachicus* (excluding the London specimen) to *Triturus roehrsi* described herein.

### Frogs (Anura)

Discoglossidae: *Discoglossus* sp. (cf. *D. troscheli*); Palaeobatrachidae: *Palaeobatrachus* sp. 1 (aff. *P. robustus*, *Palaeobatrachus* sp. 2 (aff. *Albionbatrachus wightensis*), *Palaeobatrachus* sp. 3 (aff. *P. laubei* vel *diluvianus*); Ranidae: *Rana (ridibunda)* sp.; Pelobatidae: *Pelobates* sp., *Eopelobates* sp. (pl. 3, figs 2–4, 6–8).



Frog remains belonging to nearly 80 individuals are the most abundant ectothermic vertebrate group in Oberleichtersbach. Among them is most dominant with 49 individuals a small to medium sized discoglossid which can be referred to *Discoglossus*, because of the presence of only one coronoid process on the prearticular (pl. 3, fig. 2 b), the typical morphology of the ilium (pl. 3, fig. 2 a) and a smooth outer surface of both maxilla and frontoparietals (not figured). These remains are the oldest unquestioned remains of the genus *Discoglossus* so far. They could belong to *D. troscheli* (MEYER 1852) described from Rott, a species based on an articulated specimen (WUTTKE 1996) not reviewed in modern times (SANCHIZ 1998 b).

Palaeobatrachids are present by several cranial and postcranial bones from at least 15 individuals. They represented three species differing clearly in the morphology of their frontoparietals. Two taxa have a well-delimited frontoparietal table and probably represent new species. In the first species (pl. 3, fig. 7; *Palaeobatrachus* sp. 1 aff. *P. robustus*) the frontoparietal table is smooth, relatively broad, medially slightly constricted and ends posterior into three short points (one sagittal, two lateral). In the general morphology it closely resembles *Palaeobatrachus robustus* HOSSINI & RAGE 1999 from the earliest Miocene of France (HOSSINI & RAGE 1999). It differs from this species by its smaller size and less robust ossification and the fact that the posterior end of the frontoparietal table is straight between the sagittal and lateral points, whereas it is concave in *P. robustus*.

The second species (pl. 3, fig. 8; *Palaeobatrachus* sp. 2 aff. *Albionbatrachus wightensis*), which is the most common palaeobatrachid, has a narrow frontoparietal table which is not markedly constricted medially. Small pits and slight furrows ornament his surface. On the posterior end of the table the sagittal point is short, whereas both lateral points extending into the paroccipital processes by long and prominent crests. In this respect, it shows affinities to the frontoparietal of *Albionbatrachus wightensis* MESZOELY et al. 1984 from the Late Eocene of the Isle of Wight (MESZOELY et al. 1984). It differs from this species by its weaker ornamentation and the narrower and posterior bended paroccipital crests.

The third species (*Palaeobatrachus* sp. 3 aff. *P. laubei* vel *diluvianus*; not figured here because it belongs to new material of the Walter Heck collection, Oberleichtersbach, provide to the author just after the manuscript submission) is the largest palaeobatrachid and is characterized by a flat, not well-delimited frontoparietal table, which is posterior very broad and medially distinctly constricted. The posterior border of the table is straight, i.e. the sagittal point is absent and both lateral points are small. This species seems most closely related to *Palaeobatrachus laubei* BIEBER 1881 and *P. diluvianus* (GOLDFUSS 1831) (see ŠPINAR 1972). The differences in preservation between the disarticulated bones of this study and the articulated skeletons on which both species are based preclude a more detailed comparison.

Ranids are the largest frogs in size of this locality and documented by remains of 10 individuals of the *Rana ridibunda* group (green water frogs; pl. 3, fig. 3). The two ranids from Rott (*Rana noeggerathi* MEYER 1852, *R. meriani* MEYER 1853) belong according SANCHIZ (1998 b) to the same group, but a comparison with both species is impossible because of their articulated preservation and lacking revision.

Rare elements in the Oberleichtersbach frog fauna are pelobatids, which are documented by one individual from *Pelobates* sp. (pl. 3, fig. 6) and *Eopelobates* sp. (pl. 3, fig. 4) respectively, distinguishable by the morphology and the sculpture of the maxilla. A comparison with *P. decheni* TROSCHEL 1861 (BÖHME et al. 1982) and *E. anthracinus* PARKER 1929 (ŠPINAR & ROCEK 1984) is not possible, because of the articulated preservation of both materials.

### Turtels (Testudines)

Chelydridae: *Chelydropsis* cf. *decheni*; Emydidae: *Palaeochelys mlynarskii*, Emydidae indet.; Testudinidae: *Testudo* sp., aff. *Geochelone* sp.; Trionychidae: *Trionyx* sp. (pl. 4, fig. 7).

Turtle remains are numerous, but preserved only as isolated plates or limb bones. Six species are present belonging to the families Chelydridae, Emydidae, Testudinidae and Trionychidae (tab. 1). The full aquatic snapping turtle *Chelydropsis* cf. *decheni* (MEYER 1854) is most abundant. Several plastron and carapax remains belong to an undetermined species of *Testudo*, and to the water turtle *Palaeochelys mlynarskii* HERVET & LAPPARENT DE BROIN 2000 characterized by longitudinal medial and lateral keels on the dorsal shell (pl. 4, fig. 7; HERVET & LAPPARENT DE BROIN 2000). A second water turtle could be present, but the relationships are still unclear (Emydidae indet.). The rarest turtles in Oberleichtersbach are the soft-shell or river turtle *Trionyx* sp., documented by one characteristically sculptured pleural fragment (not figured), and a second land turtle known only by one plastron fragment (not figured). It differs from *Testudo* in having rising (= geochelonid according to SCHLEICH 1988) scutal furrows, typical for large land turtles of the genus *Geochelone* sensu lato (SCHLEICH 1988).

### Choristoders (Choristodera)

Choristodera inc. sed.: *Lazarussuchus* nov. sp.  
(pl. 3, fig. 10)

The Choristodera are aquatic, gavial-like diapsids known mainly from the Mesozoic and Paleogene (Late Triassic to Early Eocene, GAO & FOX 1998). The discovery of the Late Oligocene to Early Miocene genus *Lazarussuchus* (HECHT 1992, EVANS & KLEMBARA 2005) enlarged their



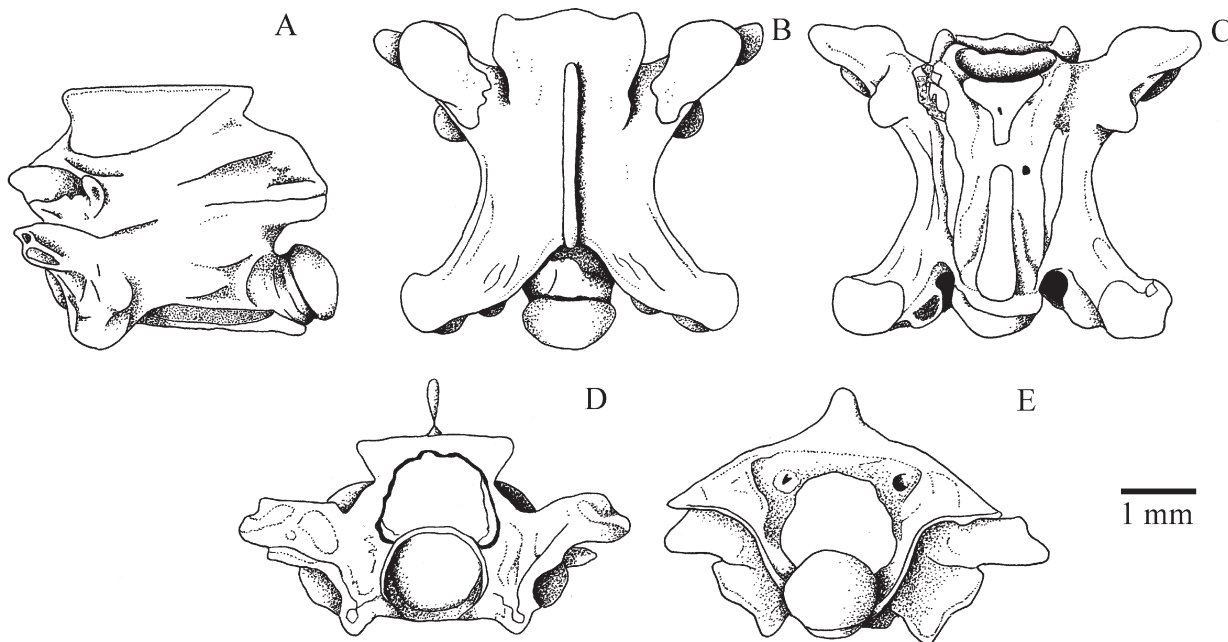


Fig. 3: *Texasophis hecki* nov. sp., Oberleichtersbach, holotype, trunk vertebra (SMF P 5014); A – lateral, B – dorsal, C – ventral, D – anterior, E – posterior

stratigraphical occurrence significantly. Up to now two species are known, each from a single locality: *L. inexpectatus* HECHT 1992, based on an articulated skeleton from the Late Oligocene of Armissan (France) and *L. dvoraki* EVANS & KLEMBARA 2005, based on disarticulated bones from the Early Miocene, (MN3) of Merkur (Czech Republic). The Oberleichtersbach *Lazarussuchon* material (pl. 3, fig. 10), which comprises about 25 bones, differs from *L. inexpectatus* by a shorter premaxilla (not figured). This bone is unknown from *L. dvoraki*, but other cranial elements suggest that the Oberleichtersbach form is probably a new species, which will be described in a separate paper.

### Crocodyles (Crocodylia)

Alligatoroidea: *Diplocynodon* sp.  
(pl. 3, fig. 5)

Crocodyles are documented by 28 isolated teeth, coming from both juvenile and adult individuals. The morphology is typical for the widespread genus *Diplocynodon* (pl. 3, fig. 5). The bases of all teeth show resorption structures which indicate tooth replacement. The smallest teeth are 1.5 mm in length and probably originated from early post-hatchling stages. These indicate that the Oberleichtersbach ecosystem was a habitat for a permanent *Diplocynodon* population. One tooth from Rott, figured in MÖRS (1995) as *Esox* sp., belongs also to *Diplocynodon*.

### Lizards and snakes (Squamata)

Amphisbaenidae: Amphisbaenidae indet.; Lacertidae: aff. *Pseudeumeces*, *Miolacerta* sp., *Lacerta* sp. 1, *Lacerta* sp. 2, *Lacerta* sp. 3, *Lacerta* sp. 4; Anguidae: *Ophisaurus* sp., cf. *Anguis* sp.; Shinisauridae: *Merkurosaurus* sp.; Aniliidae: *Eoanilius oligocenicus*; Colubridae: *Texasophis hecki* nov. sp., Colubrinae indet.; Viperidae: ? Viperidae indet. (pl. 3, fig. 9, 11–12, pl. 4, fig. 1–6, 8–10).

Scincomorph reptiles are represented by six species. One single molariform tooth (pl. 4, fig. 4) resembles several amblyodont lizards known from the French Oligocene (RAGE 1987). Because of his subrectangular outline it will be provisionally referred here to the genus *Pseudeumeces* HOFFSTETTER 1944 known from MP25 to MP28 (AUGE & RAGE 1995, AUGE 2005).

A very tiny lacertid (length of the dentary 3 to 4 mm) is characterized by tricuspid teeth (pl. 3, fig. 11 a), and thus resembles in size and morphology the genus *Miolacerta* ROCEK 1984, known hitherto only from the Miocene.

Additional four lacertid taxa (*Lacerta* sp. 1, 2, 3, 4) with bicuspid teeth in the posterior part of the dentary, distinguishable by size and tooth morphology, complete the relative diverse lizard fauna (pl. 3, fig. 11 b, 12 and pl. 4, fig. 2, 3).

Glass lizards (Anguidae) are represented by cranial and postcranial elements as well as osteoderms of *Ophisaurus* (pl. 4, fig. 6). The second anguid (cf. *Anguis* sp.),

known only by vertebrae (pl. 4, fig. 5) and osteoderms, belongs to a small sized animal that closely resembles the vertebra morphology of the extant genus *Anguis*.

Few angiomorph dental remains and some osteoderms show shinisaurid characteristics. In dentary teeth the tooth base is lingually expanded (pl. 4, fig. 1 a). The osteoderms are small (up to 3 mm), oval and non-imbricate (pl. 4, fig. 1 b). They are characterized by a very strong and high keel and show, both at the inner and the outer surface, a sculpture with high ridges and deep pits, sometimes perforate the osteoderm. This material is very similar to the first described European shinisaurid *Merkurosaurus ornatus* from the Early Miocene of the Czech Republic (KLEMBARA 2008) and is referred here to this genus. For a detailed comparison with the Miocene species the present material lacks sufficient preserved cranial bones, but it seems that the base of the dentary teeth in *Merkurosaurus* sp. is more bulbous than in *M. ornatus* (KLEMBARA 2008). Members of the family Shinisauridae are known from the Cretaceous of Asia and the Early Eocene of North America (for references see KLEMBARA 2008). The only extant representative of this family is *Shinisaurus crocodilurus* which lives in Vietnam and Southern China. This second discovery of *Merkurosaurus* represent the first record of a shinisaurid from the Oligocene and confirms that this family is a rare but temporal and spatial widespread member of the northern hemispheric ecosystems.

Worm lizards (Amphisbaenidae) are documented by a single vertebra (pl. 3, fig. 9) which show typical amphisbaenian characters due to the absence of a neural spine and the parallel lateral borders of the centrum.

Snakes are generally rare in the studied material. Only 19 trunk vertebrae are available. Ten vertebrae belong to a new species of the colubrid genus *Texasophis* (see below, *T. hecki* nov. sp.), known from the Oligocene to the Middle Miocene of Europe and North America (HOLMAN 2000, SZYNDLAR 1991). Besides an undetermined small-sized colubrine (Colubrinae indet.), two badly preserved vertebrae of a possible viper (?Viperidae indet.) are present (pl. 4, fig. 9). After affirmation, this record would be the worldwide oldest of the family. A single vertebra belongs to a fossorial snake of the family Aniliidae (*Eoanilius oligocenicus* SZYNDLAR 1994, pl. 4, fig. 8).

Colubrinae OPPEL 1811

*Texasophis* HOLMAN 1977

*Texasophis hecki* nov. sp.

(pl. 4, fig. 10; fig. 3)

**Holotype:** One trunk vertebra, SMF R 5014.

**Type locality:** Oberleichtersbach, Rhön Mountains, Germany.

**Stratigraphical age:** uppermost Oligocene, MP30.

**Derivatio nominis:** Dedicated to Walter HECK from Oberleichtersbach who collected most of the fossils described in this paper.

**Paratypes:** eight vertebrae, SMF R 5015-5022

**Diagnosis:** Differs from all members of the genus (except *T. wilsoni* HOLMAN 1984) by larger and well developed praezygapophysal processes. Differs from *T. bohemiacus* SZYNDLAR 1987 by a three lobed zygosphenal roof, subcircular prae- and postzygapophysal facets, horizontal orientated praezygapophysal process, and a divided synapophyses. Differs from the second European species *T. meini* RAGE & HOLMAN 1984 by having a much narrower haemal keel. It differs from the North American species by: larger size and distinctly concave border of the neural arch, narrower haemal keel and small paracotylar foramina (*T. fossilis* HOLMAN 1977), from *T. galbreathi* HOLMAN 1984 by the anterior narrower haemal keel and more massive vertebrae. It most resembles *T. wilsoni*, especially by an elongated and posteriorly undercut neural spine, well developed praezygapophysal processes, subcircular (ovoid) praezygapophysal facets, and divided synapophyses. The new species differs from *T. wilsoni* by a three lobed zygosphenal roof, a missing anterior tubercle and the less distinct anterior overhang of the neural spine, the anteriorly narrower haemal keel, and its smaller vertebral size.

**Description:** The material shows the typical features of the genus *Texasophis* (HOLMAN 2000, SZYNDLAR 1987, 1991, RAGE & HOLMAN 1984): elongated vertebrae with a moderately vaulted neural arch and a low and long neural spine reaching anteriorly the zygosphenal. The neural spine extends slightly beyond the posterior border of the neural arch. In lateral view, it distinctly overhangs the neural arch posterior but only slightly anterior. An anterior tubercle on the neural spine (HOLMAN 2000) is missing. In dorsal view, the zygosphenal roof is three lobed. The centrum shows a very robust distinct haemal keel, which posteriorly (behind the subcentral foramina) is slightly broader and flattened. Laterally the haemal keel is delimited by very deep subcentral grooves and distinct subcentral ridges. Behind the subcentral foramina, the subcentral grooves are slightly enlarged (only seen on the holotype). The prae- and postzygapophysal facets are subcircular; the praezygapophysal process is well developed and horizontally orientated in anterior view. The synapophyses are divided into distinct diapophyseal and parapophyseal portions. The lateral, subcentral and paracotylar foramina are distinct and small.

#### **Palaeoecology, environmental reconstruction and climate**

The Oberleichtersbach fossil assemblage contains a highly diverse (43 taxa) and abundant (> 170 individuals) ectothermic vertebrate fauna, which shows ecologically adaptations to various environments. The species can be

grouped according to BÖHME et al. (2006) with respect to their dependence on light and water and their physiological adaptations into six ecolophysiological groups (number of taxa, approximate number of individuals, and included taxa in brackets).

**Aquatic group** (17 taxa, ca. 70 individuals; *Cobitis primigenus* nov. sp., *Palaeorutilus* sp. 1 and 2, Gobioninae sp. A to C, *Tarsichthys macrurus*, *Andrias scheuchzeri*, *Palaeobatrachus* sp. 1 to 3, *Diplocynodon* sp., *Lazarussuchus* sp., *Chelydropsis* cf. *decheni*, *Trionyx* sp., *Palaeochelys mlynarskii*, Emydidae indet.). The group includes the fishes, and among the tetrapod taxa those which spend their whole life-cycle very near or in the water. The large sized tetrapods of the aquatic group need permanent water bodies as a buffering medium against temperature extremes. If the water dried out, it is difficult for them to find shadow environment for aestivation.

**Heliophob group** (2 taxa, 3 individuals; *Chioglossa* cf. *meini*, *Merkurosaurus* sp.): Taxa without cutaneous control of evaporative water loss (thermoregulation by evaporative cooling). They exploit shadowed and moist environments covered by dense vegetation, preferentially along streams. Because of high accounts of cutaneous respiration, they prefer habitats with small diurnal amplitude in both atmospheric water vapour content (high in average) and air temperature (low in average). The shinisaurid *Merkurosaurus* is grouped here because of his close relationships to the extant *Shinisaurus crocodilurus* (KLEMBARA 2008), a species which, because of its life-style and distribution, may belong to this group (BÖHME et al. 2006).

**Semi-aquatic group** (3 taxa, ca. 13 individuals; Salamandridae indet. (? aff. *Brachycormus noachicus*), aff. *Chelotriton* sp., *Rana (ridibunda)* sp.): Tetrapods of smaller body size which spend a significant part of their life cycle in the water and are able to survive on land if the water body dried out. This taxa are small enough (in contrast to some aquatic members) to aestivate during the dry season under stones or in small fissures.

**Peri-aquatic group** (4 taxa, ca. 60 individuals: *Triturus roersi*, *Triturus* sp., *Discoglossus* sp., *Eopelobates* sp.): Taxa live only during reproduction in the water and spend the remaining of their life cycle near (perennial or periodic) water-bodies.

**Woodland group** (1 taxon, 1 individual: aff. *Geochelone* sensu lato): This group contains woodland taxa, e.g. heliophile taxa (see below) with large body size. They need vegetation cover for cooling their body temperature (large and giant turtles).

**Heliophil group** (11 taxa, ca. 25 individuals: aff. *Pseudeumeces*, *Miolacerta* sp., *Lacerta* sp. 1 to 4, *Ophisaurus* sp., *Texasophis* nov. sp., Colubrinae indet., ?Viperidae indet., *Testudo* sp.): Taxa relying on behavioural mechanisms to thermoregulation (e. g. basking) and cutaneous control of evaporative water loss (e. g. osteoscutes). They exploit more open and dryer environment where sunlight

may reach the ground. The prevailing respiration surface is the lung. They prefer habitats with large diurnal amplitude in both atmospheric water vapour content (low in average) and air temperature (high in average). Their body size is small to medium, enabling these taxa to use shadow places below stones or in fissures for cooling down. They are largely independent from the existence of water-bodies.

**Subterranean group** (5 taxa, 7 individuals: *Albanerpeton inexpectatum*, *Pelobates* sp., cf. *Anguis* sp., Amphisbaenidae indet., *Eoanilius oligocenicus*): Fossorial taxa that spend most of their life cycle in the soil or in organic matter. They prefer soft, well-oxygenated and well-drained soils. *Eoanilius oligocenicus* is placed in this group, because the only recent representative of the Aniliidae, the South American *Anilius scytale*, spends the daylight hours beneath forest-floor litter and forage on the surface at night (ZUG et al. 2001).

Both divers fish (7 taxa) and full-aquatic tetrapod (10 taxa) faunas and the fact that a significant part (46 %) of all individuals belong to the aquatic and semi-aquatic groups, indicate the presence of a large and perennial lake with an intensely structured lake-margin. The coexistence of six aquatic top predators (*Andrias*, *Diplocynodon*, *Lazarussuchus*, *Merkurosaurus*, *Chelydropsis*, *Trionyx*) suggests a partitioning in various food chains belonging to different ecosystems (pelagic, littoral, lake-bottom, lake-margin).

The most dominant taxon (ca. 27 % of all recorded individuals) is the frog *Discoglossus*. His extant relatives live in habitats with dense vegetation very near the water body.

Some taxa can be associated with floating water. These are the loach (*Cobitis*), the gudgeons (Gobioninae sp. A, B, C), the gold-striped salamander (*Chioglossa*), and to a lesser extent the soft-shell turtle (*Trionyx*) and probably the shinisaurid (*Merkurosaurus*). All species of the genus *Cobitis* live benthic in clear, oxygen rich waters, with sandy, sometimes rocky bottom. The best-known species, *C. taenia* LINNAEUS 1758, prefers small, sandy and oligotrophic rivers or brooks with medium stream velocity (STERBA 1962). Most West-Eurasian gudgeons (genus *Gobio*) are benthic fishes, which inhabit fast flowing rivers with sand or gravel bottom in the upper reaches, and few may occur in the lower reaches of rivers or even in still waters (LADIGES & VOGT 1979). The only extant representative of the gold-striped salamander (*C. lusitanica* BOCAGE 1864) usually lives along the borders of streams with overhanging vegetation and moss-covered rocks. Larvae are rheophilous and appear in permanent rapidly flowing streams with highly oxygenated water (GASC 1997). Soft-shell turtles lives in rivers and lakes (ZUG et al. 2001), but the ecology of the nearest living relative to the European soft-shells *T. triunguis* (BÖHME 1995) and the fossil record suggest that they primarily lived in rivers or lakes with fluvial inflow. The



species	index
<i>Albanerpeton inexpectatum</i>	0,0917
<i>Andrias scheuchzeri</i>	1
<i>Chioglossa</i> cf. <i>meini</i>	0,9768
<i>Salamandridae</i> indet. (aff. <i>Brachycormus noachicus</i> )	0,513
aff. <i>Chelotriton</i> sp.	0,513
<i>Triturus roersi</i>	0,3918
<i>Triturus</i> sp.	0,3918
<i>Discoglossus</i> sp. (cf. <i>D. troscheli</i> )	0,3918
<i>Eopelobates</i> sp.	0,3918
<i>Pelobates</i> sp.	0,0917
<i>Palaeobatrachus</i> sp. 1	1
<i>Palaeobatrachus</i> sp. 2	1
<i>Palaeobatrachus</i> sp. 3	1
<i>Rana (ridibunda)</i> sp. (cf. <i>R. meriani</i> )	0,513
<i>Lazarussuchus</i> sp.	1
<i>Trionyx</i> sp.	1
<i>Chelydropsis</i> cf. <i>decheni</i>	1
<i>Palaeochelys mlynarskii</i>	1
<i>Emydidae</i> indet.	1
aff. <i>Ergilemys</i> sp.	0,513
<i>Testudo</i> sp.	0
<i>Amphisbaenidae</i> indet.	0,0917
<i>Diplocynodon</i> sp.	1
aff. <i>Pseudeumeces</i> sp.	0
<i>Lacerta</i> sp. 1	0
<i>Lacerta</i> sp. 2	0
<i>Lacerta</i> sp. 3	0
<i>Lacerta</i> sp. 4	0
<i>Miolacerta</i> sp.	0
cf. <i>Anguis</i> sp.	0,0917
<i>Ophisaurus</i> sp.	0
<i>Merkurosaurus</i> sp.	0,9768
<i>Eoanilius oligocenicus</i>	0,0917
<b>ecophysiological index</b>	0,4858
<b>mean annual precipitation (in mm)</b>	1131
<b>95% prediction interval (in mm)</b>	261

Fig. 4: Ectothermic vertebrate species from Oberleichtersbach used for estimation of palaeoprecipitation (BÖHME et al. 2006). Indices in the left row according to the respective ecophysiological groups (heliophil – 0, subterranean – 0.0917, peri-aquatic – 0.3918, semi-aquatic and woodland – 0.513, heliophil – 0.9768, aquatic – 1; see BÖHME et al. 2006 for details)

nearest living relative of *Merkurosaurus*, the East Asian *Shinisaurus*, lives mostly along mountain streams (ZUG et al. 2001). Altogether, this indicates that the Oberleichtersbach lake was probably well oxygenated down to the bottom (? no chemocline), not very deep, and probably had a fluvial inflow.

The relatively high diversity and abundance of heliophil in comparison to heliophob and woodland taxa suggests a sparse arboreal vegetation cover near the lake. The low abundance of spade foots (*Pelobates*) and worm lizards (*Amphisbaenidae*) may reflect the retreat of well drained soils (other fossorial animals could live under forest-floor litter), perhaps due to higher groundwater levels. The sparse arboreal vegetation and the high

groundwater level probably reflect the special edaphic conditions developing over clay rich lithologies of the Middle Muschelkalk.

The dominance of tetrapods from the aquatic, semi-aquatic, periaquatic, woodland and heliophob groups (20 taxa) in comparison with tetrapods of the heliophil group (11 taxa) suggests rather wet and humid climate conditions. To get quantitative precipitation values the methodology of BÖHME et al. (2006) is applied, which is based on the frequency of the aforementioned ecophysiological groups within herpetological communities (excluding non-fossorial snakes). Figure 4 gives a summary of the taxa used for the precipitation estimation. The regression equation (equation #6 in BÖHME et al. 2006) results in an estimated mean annual precipitation for the Oberleichtersbach locality of  $1.131 \pm 261$  mm. This value fits very well with palaeobotanical estimates from the terminal Oligocene of Central Europe (Lower Rhine, Weissensteiner, Lausitz and North Alpine Foreland Basins), ranging around  $\sim 1.100 \pm 300$  mm mean annual precipitation (MOSBRUGGER et al. 2005). Furthermore, the presence of crocodiles indicates that the mean annual temperature was at least over  $14.2^\circ\text{C}$  and the cold month (winter) temperature over  $5^\circ\text{C}$  (MARKWICK 1998). This also fits well with palaeobotanical estimates especially from the atlantic influenced Lower Rhine Basin, whereas for the North Alpine Foreland Basin slightly lower winter temperatures ( $< 5^\circ\text{C}$ ) are recorded (MOSBRUGGER et al. 2005). In summary: ectothermic vertebrates indicate that the climate during the time represented by the Oberleichtersbach doline lake sediments was subtropical and humid, in this respect similar to Southern China today.

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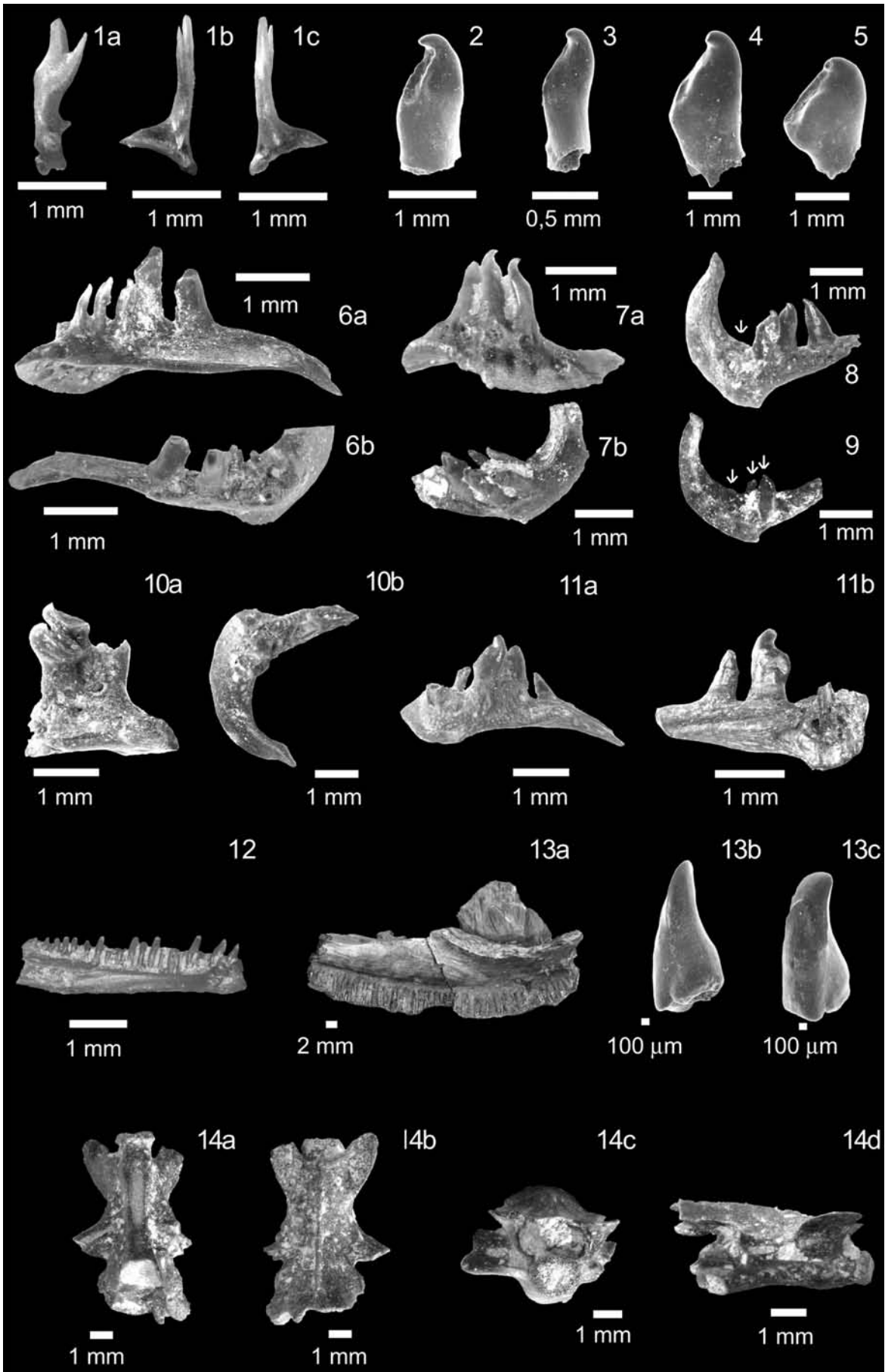
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Plates 1–4

**Plate 1**

- Fig. 1: *Cobitis primigenus* nov. sp., Oberlechtersbach, holotype, SMF P 9735, left lateroethmoid; a – dorsal, b – lateral, c – medial
- Fig. 2: *Palaeorutilus* sp. vel sp. 2, Oberlechtersbach, isolated pharyngeal tooth, SMF P 9736
- Fig. 3: Gobioninae sp. A vel sp. B, Oberlechtersbach, isolated pharyngeal tooth, SMF P 9737
- Figs 4, 11: Gobioninae sp. C (cf. *Varhostichthys eurystomus*), Oberlechtersbach. Fig 4: isolated pharyngeal tooth (SMF P 9738); fig. 11 a, b: pharyngeal bone fragments; a – lateral (SMF P 9739), b – medial (SMF P 9740)
- Figs 5, 10: *Tarsichthys macrurus*, Oberlechtersbach. Fig. 5: isolated pharyngeal tooth (SMF P 9741); Fig. 10 a, b: pharyngeal bone fragments; a – anterior (SMF P 9742), b – dorsal (SMF P 9743)
- Fig. 6: Gobioninae sp. B, Oberlechtersbach, pharyngeal bone fragment (SMF P 9744); a – medial, b – dorsal
- Fig. 7: Gobioninae sp. A, Oberlechtersbach, pharyngeal bone fragment (SMF P 9745); a – lateral, b – dorsal
- Fig. 8: *Palaeorutilus* sp. 1, Oberlechtersbach, pharyngeal bone fragment (SMF P 9746), dorsal view
- Fig. 9: *Palaeorutilus* sp. 2, Oberlechtersbach, pharyngeal bone fragment (SMF P 9747), dorsal view
- Fig. 12: *Albanerpeton inexpectatum*, Oberlechtersbach, left dental (SMF A 607), lingual view
- Fig. 13: *Andrias scheuchzeri*, Oberlechtersbach; Fig. 13 a – left maxilla (SMF A 608), lingual view, Fig. 13 b, c: isolate tooth (SMF A 609); b – lateral, c – latero-labial
- Fig. 14: *Chioglossa* cf. *meini*, Oberlechtersbach, mid-trunk vertebra (SMF A 610); a – ventral, b – dorsal, c – anterior, d – lateral





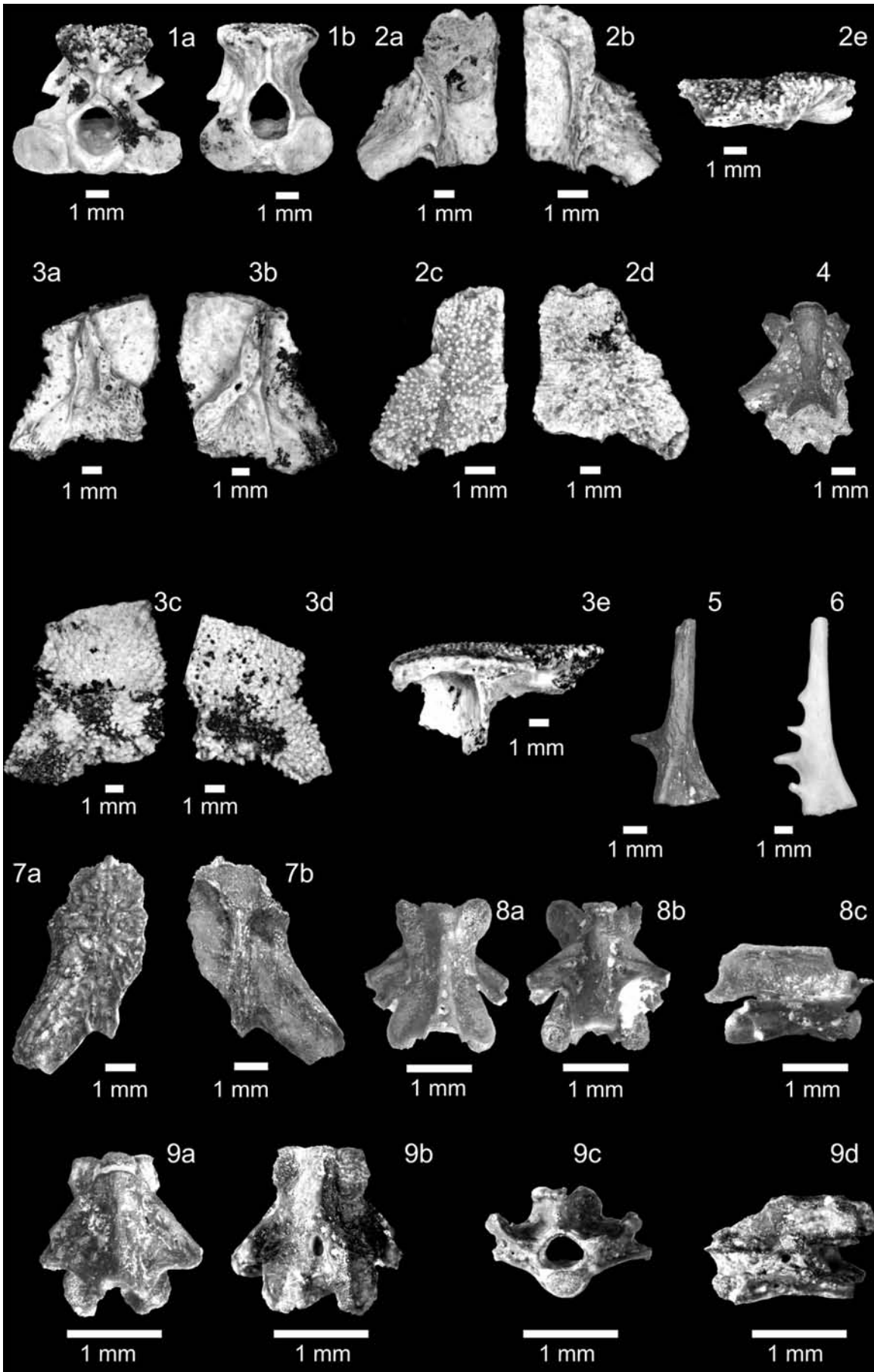
**Plate 2**

Figs 1–3, 6: *Chelotriton* ssp., Coderet (Allier Basin), material collection University Claude Bernard Lyon (Nr. 345001–345007); Fig. 1 a: atlas type A, Coderet sample E1; anterior view; Fig. 1 b: atlas type B, Coderet sample E1; anterior view; Fig. 2 a–e: frontal type A, Coderet sample E1; a, b – ventral, c, d – dorsal, e – anterior (view on the margo nasalis et praefrontalis). Figure 2 a–e belongs to the same specimen respectively; Fig. 3 a–e: frontal type B, Coderet sample E1; a, b – ventral, c, d – dorsal, e – anterior (view on the margo nasalis et praefrontalis). Figure 3 a–e belongs to the same specimen respectively; Fig. 6: rib from the mid-trunk area, Coderet sample E1; dorsal view

Figs 4, 5, 7: aff. *Chelotriton* sp., Oberleichtersbach; Fig. 4: vertebra fragment (SMF A 611); ventral view; Fig. 5: rib from the mid-trunk area (SMF A 612); ventral view; Fig. 7 a, b: left frontal (SMF A 613); a – dorsal, b – ventral

Fig. 8: *Triturus roehrsi*, Oberleichtersbach, mid-trunk vertebra (SMF A 614); a – dorsal, b – ventral, c - lateral

Fig. 9: Salamandridae indet (aff. *Brachycormus noachicus*), Oberleichtersbach, mid-trunk vertebra (SMF A 615); a – ventral, b – dorsal, c – anterior, d – lateral



**Plate 3**

Fig. 1: *Triturus* sp., Oberleichtersbach, mid-trunk vertebra (SMF A 616); a – dorsal, b – anterior, c – lateral

Fig. 2: *Discoglossus* sp. (cf. *D. troscheli*), Oberleichtersbach; a – left proximal ilium (SMF A 617), lateral view; b – left prearticular (SMF A 618), dorsal view

Fig. 3: *Rana (ridibunda)* sp. (cf. *R. meriani*), Oberleichtersbach, left proximal ilium (SMF A 619); lateral view

Fig. 4: *Eopelobates* sp., Oberleichtersbach, right maxilla (SMF A 620); a – lingual, b – labial

Fig. 5: *Diplocynodon* sp., Oberleichtersbach, isolated tooth (SMF R 4999); lateral view

Fig. 6: *Pelobates* sp., Oberleichtersbach, right maxilla (SMF A 621); a – lingual, b – labial

Fig. 7: *Palaeobatrachus* sp. 1 (aff. *Palaeobatrachus robustus*), Oberleichtersbach, posterior frontoparietal fragment (SMF A 622); dorsal view

Fig. 8: *Palaeobatrachus* sp. 2 (aff. *Albionbatrachus wightensis*), Oberleichtersbach, posterior frontoparietal fragment (SMF A 623); dorsal view

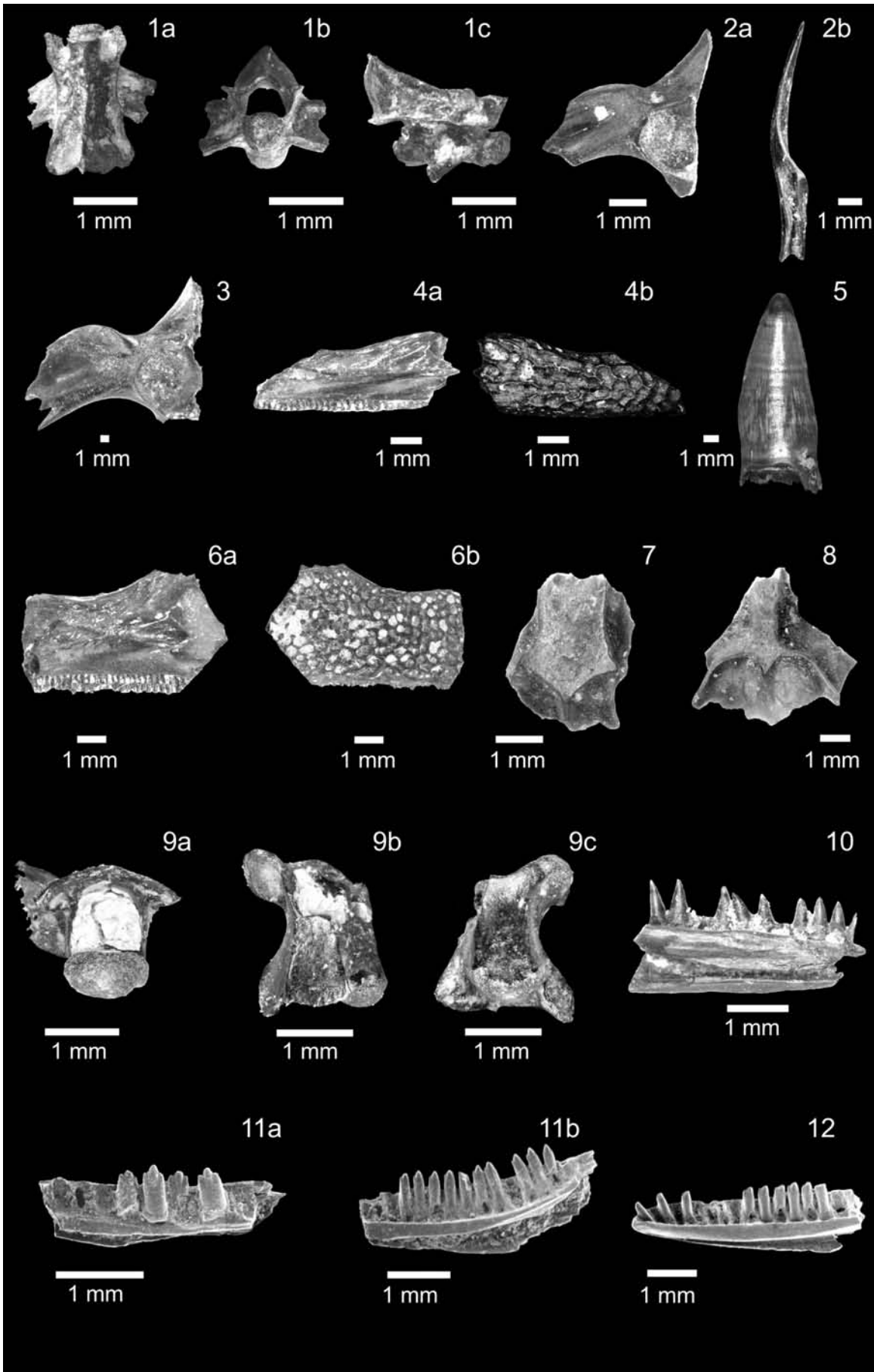
Fig. 9: Amphisbaenidae indet., Oberleichtersbach, trunk vertebra (SMF R 4998); a – posterior, b – orsal, c – ventral

Fig. 10: *Lazarussuchus* nov. sp., Oberleichtersbach, left dental fragment (SMF R 5000); medial view

Fig. 11 a: *Miolacerta* sp., Oberleichtersbach, right dental fragment (SMF R 5001); lingual view

Fig. 11 b: *Lacerta* sp. 1, Oberleichtersbach, right dental fragment (SMF R 5002); lingual view

Fig. 12: *Lacerta* sp. 2, Oberleichtersbach, right dental (SMF R 5003); lingual view





**Plate 4**

- Fig. 1: *Merkurosaurus* sp., Oberleichtersbach; a – left dental fragment (SMF R 5004); lingual view; b – osteoderm (SMF R 5005); dorsal view
- Fig. 2: *Lacerta* sp. 3, Oberleichtersbach, left dental fragment (SMF R 5006); lingual view
- Fig. 3: *Lacerta* sp. 4, Oberleichtersbach, right dental (SMF R 5007); lingual view
- Fig. 4: aff. *Pseudeumeces* sp., Oberleichtersbach, isolated tooth crown (SMF R 5008); occlusal view
- Fig. 5: *Anguis* sp., Oberleichtersbach, vertebra (SMF R 5009); a – ventral, b – dorsal, c – posterior
- Fig. 6: *Ophisaurus* sp., Oberleichtersbach, vertebra (SMF R 5010); a – ventral, b – dorsal, c – posterior
- Fig. 7: *Palaeochelys mlynarskii*, Oberleichtersbach, left pleural (SMF R 5011); a – dorsal, b – lateral
- Fig. 8: *Eoanilius oligocenicus*, Oberleichtersbach, vertebra (SMF R 5012); a – ventral, b – dorsal, c – posterior, d – anterior, e – lateral
- Fig. 9: ?Viperidae indet., Oberleichtersbach, trunk vertebra (SMF R 5013); a – dorsal, b – ventral, c – posterior, d – anterior, e – lateral
- Fig. 10: *Texasophis hecki* nov. sp., Oberleichtersbach, holotype, trunk vertebra (SMF R 5014); a – ventral, b – dorsal, c – anterior, d – posterior, e – lateral

