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**5th International Symposium
on Lithographic Limestone
and Plattenkalk**

Abstracts and Field Guides

Edited by
Jean-Paul Billon-Bruyat, Daniel Marty, Loïc Costeur,
Christian A. Meyer & Basil Thüring

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Abstracts and Field Guides

Edited by
**Jean-Paul Billon-Bruyat, Daniel Marty, Loïc Costeur,
Christian A. Meyer & Basil Thüring**

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Preface

Dear participants,

Following the former editions (Lyon, 1991; Cuenca, 1995; Bergamo, 1999; Eichstätt/Solnhofen, 2005), we are pleased to welcome you to the 5th International Symposium on Lithographic Limestone and Plattenkalk at the Natural History Museum in Basel. This meeting is jointly organized by the Basel Natural History Museum (Christian A. Meyer, Basil Thüring, Loïc Costeur, Antoinette Hitz) and the scientific staff of the Palaeontology A16 in Porrentruy (Jean-Paul Billon-Bruyat, Daniel Marty); the *Naturmuseum Solothurn* (Silvan Thüring) and the *Staatliches Museum für Naturkunde Karlsruhe* (Dino Frey, Stefanie Monninger) are involved in the organization of the field-trips.

We are very happy that Dolf Seilacher accepted to be a keynote speaker, he who started the famous research initiative “Sonderforschungsbereich 53” on palaeoecology and Fossil Lagerstätten in Tübingen back in the 80ties. Furthermore, also his colleague from Yale Derek Briggs, who is an expert in modern molecular taphonomy, accepted to make a keynote contribution. Another “Yale” researcher (now in Tübingen), Walter Joyce, a junior scientist with a major interest in fossil turtles, is joining the keynote speakers. And, last but not least, Dino Frey, one of the leading experts of flying reptiles otherwise known as pterosaurs, will join us for the conference. All have one thing in common, they are all enthusiastic palaeontologists somehow related to Dolf’s hometown Tübingen, where the major revival of the Lithographic Limestone and Black Shale research took place.

The present volume contains abstracts of oral presentations and posters that span the entire focus of research. From geochemical evidence on sedimentation rates in lithographic limestones or new and exciting discoveries such as mantis shrimps or limulid and dinosaur trackways to palaeoenvironmental models of fish Lagerstätten.

We hope that you will enjoy the field-trips into the very heart of the Swiss Jura Mountains, where we will present you new and classic Late Jurassic fossil localities in the light of recent discoveries. Some of those – such as the Solothurn Turtle Limestone – are long known, others like the sites around Porrentruy (Canton Jura) were more recently discovered and are systematically excavated prior to the construction of the A16 highway. The pre-congress field-trip will lead us to the clay pit Unterfeld near

Frauenweiler (Rhine Graben, near Mannheim), famous for Oligocene fishes, birds, and mammals; this site is currently threatened by destruction.

We would like to thank the Canton Jura and the *Société jurassienne d'Emulation* for financing and publishing the Abstracts and Field Guides volume, and the Commission of the Swiss Palaeontological Memoirs for supporting the invitations of the keynote speakers and the supplementary issue (proceedings volume) in the Swiss Journal of Geosciences. We wish to express our gratitude to the International Association of Sedimentologists (IAS) for sponsoring student travel grants. Also, the support of the Swiss Palaeontological Society (SPS), the International Palaeontological Society (IPA), and the European Association of Vertebrate Palaeontologists (EAVP) is greatly acknowledged.

I myself remember well the 1991 meeting in Lyon, with a splendid field-trip to the Lithographic limestone quarry in Cerin under the hot sun, followed by a delicious and opulent lunch under white tents with tasty French wines. I hope that all of you will enjoy the scientific meeting as well as the field-trips and the exchange between old friends and new scientific contacts.

On behalf of the organizing committee

A handwritten signature in black ink, appearing to read 'Ch. Meyer', written in a cursive style.

Prof. Dr. Christian A. MEYER

Abstracts

The role of the Crato Formation (Aptian of the Araripe Basin, NE Brazil) fish fauna in palaeoenvironmental inferences

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The Crato Formation is known worldwide for the exceptional preservation of its fossils and for its diverse assemblage, representing one of the richest Gondwanan Konservat Lagerstätte. With about 200 nominal species described (including plants, invertebrates and vertebrates), the fossiliferous limestones of the Crato Formation (Nova Olinda Member) exhibit an abundant fish fauna dominated by the small gonorynchiform *Dastilbe crandalli*.

The Nova Olinda Member of the Crato Formation is considered as a lagoonal system with a stratified water body formed by a well-mixed and complex epilimnion with probably fluctuating salinity and a stagnant, anoxic, and hypersaline hypolimnion, suggested by the absence of bottom-dwelling organisms and by parameters such as the occurrence of biomarker molecules and salt pseudomorphs. Moreover, the influence of surrounding drainage contributing to this complex epilimnion seems to be evident when the fish fauna is considered. Certain taxa do appear to be marine such as the new vidalamiin amiiiform *Cratoamia longidorsalis* and the surface-living *Vinctifer* and *Cladocyclus*, both common in the nodules of the younger Santana Formation and known in other formations associated with typical marine taxa.

Additionally, the local and discontinuous occurrence of the outcrops of the Nova Olinda Member, mainly restricted to the eastern part of the basin, further suggests the existence of an interdigitated and restricted system of calm and vertically stratified waters, influenced by the income of freshwater drainage with tenuous, ephemeral, and local contact with the rising epicontinental marine waters.

Geochemical and mineralogical evidence for very high sedimentation rates in plattenkalks

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Two essential differences have been found between plattenkalks and (normal) bedded limestones. A geochemical contrast consists in different REE spectra of the two limestone facies. The spectra of plattenkalk resemble those of marine claystones (proven on the French locations Cerin and Montdardier, as well as on two Franconian sites, e.g. Solnhofen). The spectra of bedded limestones, however, are quite another type and are similar to seawater (Bausch et al. 2008). A mineralogical contrast is evident in the occurrence resp. absence of authigenic potassium feldspars. They can occur in relative pure bedded limestones; there they may form the bulk of the silt fraction in the insoluble residues (Möderl 2000). Plattenkalks very often exhibit comparable purity around 1% of insolubles), but they don't contain authigenic feldspars at all.

Both features might be explained by strongly different sedimentation rates. There are good reasons to estimate the sedimentation rates of the bedded limestones used in this study (Upper Oxfordian, Franconia) in the range of 1 cm/ky. On the other hand, the rates in Solnhofen plattenkalk are surely higher by the factor 10, maybe by the factor 20-30. In the case of (normal) bedded limestones there was time enough to equilibrate (more or less) the REE contents with seawater, and to form authigenic potassium feldspar (in a long term diagenetic process). If the plattenkalks sedimentation happened so rapidly that the REE spectrum of the detrital clay input was preserved, the authigenic feldspar formation could not be realized.

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Tetrapods from the Late Jurassic lithographic limestones and *Plattenkalke* of Western Europe: an updated comparative review

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Tetrapods from the Late Jurassic (Kimmeridgian–Tithonian) lithographic limestones and *Plattenkalke* of Western Europe have been deposited in protected costal marine environments of shallow carbonate platforms, on the Northern margin of the Tethys. These marine, costal marine and continental tetrapods have been in the focus of many detailed studies (e.g., the pterosaurs, the bird *Archaeopteryx*). Nonetheless, comparisons of the tetrapod assemblages at the regional (intracontinental) scale of Western Europe have attracted little attention, even though the excellent combination of a high-resolution stratigraphical frame and the abundance and exceptional preservation of the fossil material from this region offers a great potential in this regard. As noticed earlier by Broin et al. (1991) and Buffetaut (1994), the faunal resemblances (sometimes at the genus or species level) between sites of Franconia (Germany), Cerin and Canjuers (France) suggest that they belonged to a same biogeographical province. The widespread distribution of some small to medium-sized terrestrial tetrapods (e.g., the sphenodontid *Homoeosaurus*, atopusaurid crocodylians, the theropod dinosaur *Compsognathus*) indicates that land connections have existed throughout the region.

Buffetaut (1994) published a first descriptive study, mainly at the major group level, including the Late Jurassic assemblages of Franconia, Cerin, and Canjuers. He concluded to important resemblances and striking differences, the latter being explainable by different collecting histories, taphonomic biases, depositional environments, geological ages, and suggested that these tetrapod assemblages were unbalanced. Billon-Bruyat (2005) added three other Late Jurassic *Plattenkalk* localities to this comparison: Porrentruy (Switzerland), Solothurn (Switzerland) and Crayssac (France). He presented a qualitative comparison based on skeletal remains and ichnological (notably theropod and sauropod ichnites)

evidence, suggesting that the assemblages indicate balanced insular faunas. In addition, he attempted a quantitative study (cluster analysis, several similarity indices, UPGMA method) at the family level, showing that these communities are related but not as similar as previously thought.

Here, we report an update of this phenetic analysis, including the assemblage of the lithographic limestones of Nuspligen (Kimmeridgian, Germany), new specimens from Porrentruy (excavations in progress) and by testing the cluster analysis at the genus level. It comes out that the comparison is somewhat skewed by taxonomic problems. Even if the taxa chosen are assumed to be monophyletic, some groups need to be revised, at the genus and even at the family level (e.g., the turtles of the family “Plesiochelyidae”; see Joyce 2007). The resulting dendrograms confirm two major clusters, grouping the assemblages of “Franconia, Cerin, and Canjuers” and “Porrentruy and Solothurn” (a Swiss group). Nuspligen and Crayssac assemblages generally fall outside these two major clusters. At this time, the dendrograms seem to reflect more the different biases affecting the presence/absence of taxa than obvious fine-scale tetrapod palaeobiogeographic relationships.

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Molecular taphonomy

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Keynote

The preservation of organic tissues in fossils involves the molecular transformation of biomolecules to geomolecules by processes similar to those that generate sedimentary organic matter and ultimately result in the formation of kerogen. Such diagenesis can be investigated by analysing fossils and undertaking laboratory experiments involving decay and thermal maturation.

Recent results (Gaines et al. 2008) have shown that the preservation of carbonaceous material, albeit transformed from its original composition, is the primary explanation for the famous Burgess Shale type deposits of the Cambrian. Exceptional preservations are more abundant in the Cambrian than in younger rocks. The key to understanding the preservation of organic materials, however, lies in younger deposits. Previous investigations of molecular taphonomy focused on how long particular macromolecules survive in the rock record. Traces of chitin, for example, are present in beetle cuticles from Oligocene oil shales (Stankiewicz et al. 1997), but could not be detected in older strata.

While the length of time that biomolecules survive is an important question, more interesting is understanding how organic material is transformed diagenetically, what components are involved, and how soon this process starts. Chitin can be detected in Tertiary fossils but even these geologically young deposits show diagenetic change involving the formation of resistant long-chain aliphatic macromolecules. Experiments have been carried out on arthropods that occur as fossils (shrimp, scorpion and cockroach) to discover how the chitin-protein and associated lipids in the cuticle decay (Gupta et al. 2009a). The cockroach and scorpion cuticle decayed very slowly, but that of the shrimp decayed markedly within a month. Analysis of the shrimp cuticle at the end of the experiment revealed a newly formed component with a chain length up to C_{24} . The cuticle of the scorpion and cockroach were not transformed, reflecting their lesser degradation. It is clear from these results that lipids can become associated with macromolecules during the earliest stages of decay. In this way

components are incorporated that can give rise to the aliphatic-rich composition of organic fossils. The process starts within weeks.

How soon alteration begins is one question – another is which original components are necessary to form the long chain diagenetic product. Chemical analysis of leaves of modern *Metasequoia* (the dawn redwood), for example, showed that they consist of the cutin, lignin and polysaccharides but contain no resistant aliphatic constituent (Gupta et al. 2009b). Analysis of *Metasequoia* leaves that degraded naturally in ponds showed that internal tissues were lost while the cuticle tended to survive: lignin and cellulose decayed more rapidly than cutin. Thermal maturation experiments on cutin in the laboratory produced an aliphatic polymer of relatively short chain length. Fossil *Metasequoia* leaves from the Eocene of Washington State, on the other hand, showed a significant aliphatic component with chain length up to C₂₃. Maturation of living *Metasequoia* leaves likewise generated longer chain lengths, presumably due to the incorporation of leaf waxes. Maturation experiments on arthropods have shown that soluble lipids such as fatty acids are critical to the generation of the resistant aliphatic macromolecules that characterize fossils (Gupta et al. 2006).

The composition of different organic fossils within the same deposit reflects their original chemistry – fish scales, arthropods and plants from the Cretaceous Las Hoyas Formation of Spain are distinct (Gupta et al. 2008). All these fossils, however, are dominated by an aliphatic macromolecular component indicating a similar mode of diagenesis – the polymerization of labile molecules that were present in the original organism.

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Fossil Lagerstätten: skewed images or exceptional opportunities for understanding the fossil fish record?

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Fossil Lagerstätten represent extraordinary windows in the past for studying history of life. The fossil record of the ray-finned fishes (actinopterygians) from the Late Jurassic to the terminal Cretaceous shows bursts of diversity related to the occurrence of Lagerstätten, in particular the Late Jurassic lithographic limestone of Southern Germany and the early Late Cretaceous plattenkalk of Lebanon. These peaks of diversity, however, are difficult to interpret because diversity curves based on compilation of fossil occurrences do not directly mirror biological diversity. In fossil Lagerstätten the diversity is overestimated compared to other time intervals because the rate of fossilization of the organisms is proportionally high. This bias questions a direct biological interpretation of these peaks.

A way to distinguish sampling patterns from biologically driven patterns is to look at the phylogenetic relationships of the contemporaneous taxa composing the curves of diversity. Evolutionary distance between taxa composing an assemblage can be expressed as the average ghost lineage duration (AGD) of these taxa. Looking at the variation of the AGD through successive intervals of time allow distinguishing peaks caused by genuine biological radiations from peaks caused by sampling biases. When applied to the Late Jurassic and to the early Late Cretaceous peaks of diversity, AGD in both time intervals show different patterns. The AGD drops in the early Late Cretaceous and slightly increases in the Late Jurassic, which means that taxa known in the early Late Cretaceous are in average phylogenetically closer to each other (biological radiation) than in the Late Jurassic. The Late Jurassic peak appears to be a bias caused by the large amount of available fossils (a “lagerstätten effect”), while the early Late Cretaceous peak is caused by a genuine biological radiation

that occurred at that time (although a “lagerstätten effect” had probably enhanced the peak).

Qualitative studies of the taxonomic composition of fossiliferous assemblages is a promising tool to detect the signal of a genuine biological radiation in the fossil record, even if this signal is hidden by a biased curve of diversity caused by a “lagerstätten effect”.

Plattenkalks of the Middle Cambrian; Zhangxian Formation; W-China (lenticular, wavy textures caused by compaction)

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Remarkable bedding features occur in Middle Cambrian Plattenkalks from W-China. At the first glance parallel beds of up to 5 cm thickness might indicate horizontal bedding, alternation of marls and thin limestone beds. But a closer look reveals that the Plattenkalks have undergone a complex sedimentary and diagenetic compaction, pressure solution history. The Plattenkalks are characterized by wavy, stylolitic boundaries between single beds revealing different thickness of clay accumulation (Fig. 1). Most characteristic are the crosscutting relationships of stylolites, which only locally allow horizontal parallel surfaces of the beds. Most obvious is the lateral pinch out of beds with a maximum of 5 cm thickness within some centimetres.

The Middle and lower Upper Cambrian sequences consist of shallow water carbonates predominantly deposited in an outer to inner ramp environment. There occur mudrocks, storm deposits in the lower part and oolitic grainstones and tidal-flat lime mudstones in the upper part. The different facies types now are bordered by stylolites seams and show an intimate interfingering, commonly indenting fabric in which the primary sedimentary boundaries can be nevertheless well recognized.

A complex sedimentary, diagenetic and compactional model is discussed to reveal the development of these extraordinary Plattenkalks.



Figure 1: Characteristic appearance of the Middle Cambrian Plattenkalks with common pinch-out of beds (maximum thickness = 5 cm) within a lateral distance of some centimetres to decimetres. Parallel boundaries of single beds occur rarely. This results in the characteristic wavy texture of the Plattenkalks.

The Quarry of Ettliling, Bavaria – the new excavation site of the Jura-Museum Eichstätt

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Since summer 2007, the Jura-Museum Eichstätt is undertaking a scientific excavation in the Plattenkalk quarry of Ettliling (Markt Pförring), some 15 km south of Schamhaupten (Ebert & Kölbl-Ebert 2008b). So far, the excavation provided an immensely interesting spectrum of fossil fishes with many endemic species usually of exceptionally good preservation. These fishes are early teleosts as well as semionotids and other ganoid-scaled fish.

The Ettliling quarry is part of a larger Plattenkalk basin, the exact morphology of which is unknown. The time is Upper Jurassic, possibly Upper Kimmeridgian or Lower Tithonian. Ammonites, however, are very rare and badly preserved, and so exact dating has been impossible.

So far, the excavation documented 22 fish species, among them at least nine new species and a sparse accompanying fauna of some arthropods, brachiopods, molluscs, echinoderms, one juvenile turtle and possibly hydromedusae. Additionally, there are some plant fragments, isolated dragonfly wings and an ichnofauna. So far, there are no squid.

The food chains of Ettliling seem to have been dominated by fish. The exceptional preservation also of stomach content allows for a detailed investigation of this ecosystem (e.g., Ebert & Kölbl-Ebert 2008a).

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Flat flyers – pterosaurs in laminated limestone

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Keynote

Being invited to a keynote lecture on pterosaurs in laminated limestone as a zoologist, I asked an expert geologist for the definition of “laminated limestone”. Here are some useful suggestions: “Laminated limestones with pterosaurs... Hmmm”, “Solnhofen is not really a laminated limestone, but a plattenkalk”, or “Crato is a laminated limestone. It is couplets of calcite (sometimes dolomitised) with organic matter” (Expert, e-comm., 2009). With this profound information in hand, I decided to talk about pterosaurs from any fine grained deposit consisting of more or less undisturbed layers at millimetric scale. If the lamination is not of diagenetic origin, such sediments were mostly deposited under stagnant conditions in a variety of non-marine and marine environments and thus in general have an excellent fossilisation potential. From such laminated sediment the most spectacular fossils have been unearthed, amongst them pterosaurs, the flying reptiles of the Mesozoic.

Evolution and diversity

The time range of the pterosaur localities with laminated sediments spans from the Late Triassic (e.g. Calcari de Zorzino Formation near Bergamo, Italy) yielding the earliest known pterosaurs into the Late Cretaceous (e.g. Niobrara Chalk, North America), where some of the latest pterosaurs were discovered. A variety of pterosaur localities with laminated sediments throughout the Jurassic and Early Cretaceous provides direct evidence of pterosaurian evolution and temporal changes in pterosaurian diversity.

Palaeogeography

Laminated sediments are distributed all over the world. This helps to reconstruct at least aspects of the palaeogeography of pterosaurs and indicate dispersion corridors or barriers. For the reconstruction of the

pterosaurian palaeogeography also those localities are of importance, where pterosaurs are exceedingly rare, e.g., the Late Jurassic “sublithographic” Sannine Limestone (I like it!) from Lebanon or the huge Late Cretaceous laminated limestone of the Muzquiz area, Coahuila, Mexico.

Palaeobiology and biomechanics

The preservation quality in some laminated sediments, e.g., the Late Jurassic Solnhofen Plattenkalk in Bavaria, southern Germany, the Early Cretaceous Crato Formation, northeastern Brazil or the Jehol Formation, Early Cretaceous, Cina, is so brilliant that we now have information on the finest skeletal details and different soft tissue types of those flat fliers that the gate to their biology, physiology, locomotion and ontogeny is pushed open. Several deposits have yielded excellently preserved footprints confirming the pedal soft parts preserved in other localities. To date, pterosaurs are probably the best-known extinct vertebrates in the world and, due to their flight capabilities and the detailed knowledge of their flight apparatus, caught the interest of flight engineers and smart membrane manufacturers.

The oldest azhdarchoid pterosaur from the Late Jurassic Solnhofen Limestone (Blumenberg, Bavaria; Early Tithonian) of Southern Germany

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Based on an almost complete three-dimensionally preserved skeleton, a new genus and species of an azhdarchoid pterosaur from the Late Jurassic Solnhofen limestone (Early Tithonian) of the Eichstätt area (Bavaria, Germany) is described. The specimen is attributed to Azdarchoidea due to its glenoid fossa level with the sternum, the shovel-like shape of the sternal plate, the wide furca of the coracoid, the metacarpus being longer than radius and ulna, the femur being one third longer than the humerus, the femorotibial ratio, and the hammer-like shaped humerus among other diagnostic features. Under UV-light, soft tissue preservation around the imprint of the head is preserved. It consists of tiny flakes interpreted as remains of the skin. The outline of the head imprint suggests the presence of a cranial crest. The new pterosaurs species is the oldest record of the family Azhdarchidae and furthermore supports the Eurasian origin of the group that includes the largest flying animal ever.

News about the diversity of coleoid cephalopods from the Cenomanian Plattenkalks of Lebanon

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Thanks to the digging activities of the family Abi-Saad (Hâkel) and its scientific co-operation, the number of coleoid cephalopods that roamed the coastal waters of Lebanon during Cenomanian times is continuously increasing. In the past three years of research five new taxa have been recognised.

Glyphiteuthis abisaadiourum n. sp. Fuchs & Weis (in press) is a close relative of *Glyphiteuthis libanotica*, a familiar member of the coleoid fauna in Lebanon. The new form can be distinguished from *Gl. libanotica* by the presence of an obviously more slender gladius outline and by considerably longer arms. Another (very rare) form, which has been neglected in the course of previous taxonomic confusions (“*Palaeololigo* sp.”), needs to be urgently re-described. A possible specimen of this poorly known form has been found in the collections of the Museo Civico di Storia Naturale (Milan). It exhibits a gladius that shows similarities to teudopseid genera *Teudopsis*, *Palaeololigo* and *Glyphiteuthis*. The most spectacular discoveries, however, are the records of *Keuppia hyperbolaris*, *Keuppia levante* and *Stylet octopus annae*. The extraordinarily well-preserved specimens of these taxa represent the oldest known octopuses (Fuchs et al. 2009).

Each of the new taxa will be presented and described from tip to toe (i.e., from suckers to fins).

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Fuchs, D. and Weis, R. in press: A new vampyropod coleoid (Cephalopoda) from the Late Cretaceous (Cenomanian) Limestones of Hâdjoula (Lebanon). Fossil record.

The diet of the predator fish *Saurichthys* from two Middle Triassic Plattenkalk Lagerstätten in the Swiss Alps

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The actinopterygian *Saurichthys* is a cosmopolitan fish, known from freshwater and marine deposits of Early to Late Triassic age. *Saurichthys* was an important predator in the Triassic seas, which represented together with aquatic reptiles as ichthyosaurs or sauropterygians the top of the food web. The long snout with its rows of conical teeth suggests feeding on swimming prey, however only little is known from literature. Rieppel (1985: p. 53) described a specimen of *S. macrocephalus* from the Middle Triassic of Monte San Giorgio (Ticino), with a smaller specimen of *S. curionii* in the stomach area. Recently prepared material from the same locality in the Southern Alps and from the time equivalent Prosanto Formation in the Eastern Swiss Alps near Davos (Graubünden) include some exciting specimens of five different species of *Saurichthys*, yielding not fully digested prey in the mouth, throat or stomach.

Both localities in the Swiss Alps have an outstanding quality of preservation, resembling lithographic limestone or Plattenkalk Lagerstätten. At Monte San Giorgio, 50 specimens of *Saurichthys* have been excavated bed by bed by a team of Zürich University in 1970-1974 from the Early Ladinian Cassina beds of the Meride Formation (Furrer 2003). Recently a medium sized specimen of *S. curionii* with a smaller specimen of the same species stuck in its snout was prepared carefully.

Since 1993 another 50 well-preserved specimens of *Saurichthys* belonging to five different species were excavated bed by bed from a fossil-rich level in the upper part of the Prosanto Formation from the Eastern Swiss Alps near Davos. New U-Pb ages of a volcanic ash layer from the same horizon allowed a precise radiometric dating of this fauna (240.91 ± 0.26 mA, earliest Ladinian; Furrer et al. 2008). Two small specimens of *S. costasquamosus* and *S. paucitrichus* have nearly complete specimens of the small actinopterygian *Habroichthys minimus* in their stomach. Another small sauropterygian (*Neusticosaurus* sp.)

is stuck in the throat of the largest specimen with a length of 100 cm (*Saurichthys* spec. nov.), proving hunting of small reptiles by this big fish.

As suggested by Furrer (2004), these fossils document the relationship between prey and predator in the food web of the Middle Triassic shallow seas (Fig. 1).

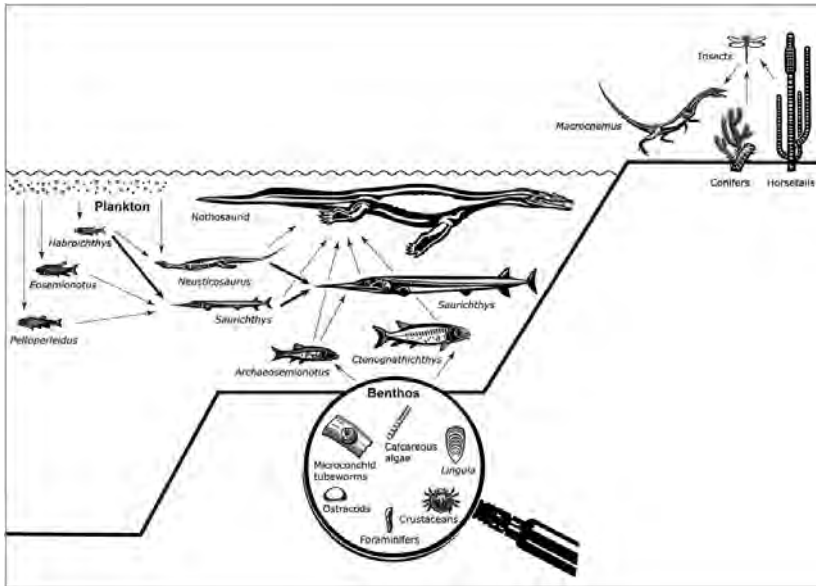


Figure 1: A simplified food web of the Middle Triassic seas. The proved relationships between prey and the actinopterygian *Saurichthys* are marked by bold arrows (modified from Furrer 2004).

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A giant limulid trackway from the lithographic limestones of Cerin (Upper Kimmeridgian, France)

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A well-preserved large limulid trackway, three metres long, is described in the Upper Kimmeridgian lithographic limestones of Cerin (Ain, France). It exhibits ten successive sets of imprints characterized by a pair of well-preserved four digitate main imprints (legs VI named pushers) and a variable number (mostly three pairs) of straight thin intermediate imprints (legs III to V).

The trackway is related to *Kouphichnium lithographicum* (Oppel, 1862). It is unusually wide and was probably made by a very large adult (approximately 38 cm wide and 80 cm long by reference to the proportions of the modern *Limulus polyphemus*). The straightness of the trackway, the great repeat distance (stride), the length of series of leg imprints, their slight angle to mid-line, the well-marked pusher (= leg VI) imprints and the absence of groove made by the telson all indicate a fast walking of a vigorous animal on the sea floor.

This walking trackway may be easily differentiated from other limulid traces illustrating crawling, ploughing and dying (mortichnia) trackways usually found in lithographic limestones or other deposits of the geological record. Main characteristics of these different limulid trackways may be evidenced.

The occurrence of a living adult in the Cerin restricted lagoon is probably related to a brief period with an efficient communication with the open sea. This occurrence also could indicate either a passive introduction of the animal into the lagoon either a spawning behaviour.

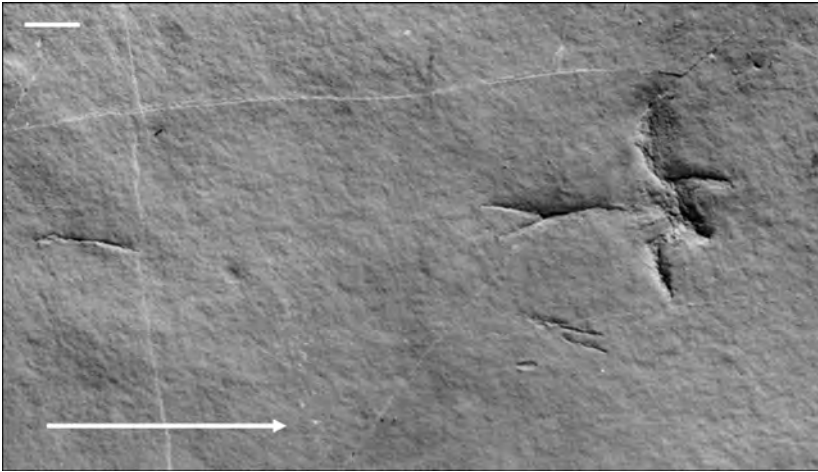


Figure 1: A pusher's imprint (VI) and two leg imprints (leg III bifid and leg IV simple) of the preceding set. The direction of locomotion is indicated by the arrow. Scale bar = 1 cm.

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Late Cretaceous open marine *Plattenkalk* localities in northeastern Mexico – Characteristics of the fossil fish assemblages

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An increasing demand for building stones in the north east of Mexico is presently producing a number of new quarries, particularly within the states of Coahuila and Nuevo León. As a result of this activity at least ten *Plattenkalk* localities have been mapped over the last ten years and among a diverse invertebrate fauna, fish are the most abundant vertebrates found within these fossil assemblages (Blanco et al. 2001; Stinnesbeck et al. 2005). A wide range of preservation types can be observed from specimens where mineralization has destroyed the original anatomical details to exceptionally preserved specimens showing soft parts and even colour patterns within the squamation.

The abundance of fossils varies widely within the *Plattenkalk* deposits depending on both locality and stratum. The richest locality in terms of fossil abundance within the region is located in the early Turonian deposits at Vallecillo where in the past ten years several hundreds of fish specimens were collected during quarrying and scientific excavations (Blanco-Piñon 2003; Ifrim et al. 2005; Ifrim 2006). The high number of specimens represents an assemblage of low taxonomic diversity. The analysis of size variation within a taxon and the investigation on stomach content clarifies several aspects of the palaeoecology of the fauna.

Taxonomical studies of the different fish assemblages discovered in the region show a palaeobiogeographical relationship with those of the

Western Interior Seaway of the North American continent as well as with the Western and Central Tethys and South Atlantic (Giersch et al. 2008). The current dataset already provides new insights into the Mid Cretaceous fish radiation in this region. The wide regional occurrence of the Mexican *Plattenkalk* deposits and their geological age range within the early Late Cretaceous allows for a more detailed study into the development of the fish assemblages in the Mesozoic Gulf of Mexico.

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New discoveries of mantis shrimps (Stomatopoda, Crustacea) in lithographic limestones from Solnhofen and Lebanon

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The (sub)lithographic limestones of Solnhofen and Lebanon are rich in crustacean fossils. The mantis shrimps (Stomatopoda), the sister group to all remaining Eumalacostraca, are well-represented. While stomatopod specimens from the Solnhofen lithographic limestones are long known to fluoresce when exposed to UV light, fossils from Lebanon and even from some areas close to Solnhofen, e.g., from Zandt, do not in general fluoresce under the same wavelengths. We found, however, that these fossils exhibit good fluorescence when exposed to green light. This highlights even tiny structures invisible under normal light. As most of the specimens we studied were just a few millimetres long, we used a fluorescence microscope with 50 or 100 times magnification to document the specimens in high detail. Several images in different focal planes in z-axis need to be taken, as not all areas are in focus on a single image. These image stacks are then fused (= image fusion). Moreover, it is necessary to take several of these image stacks in x- and y-axis not to miss any structure and to combine the fused images (= image stitching). This results in a high-resolution compound image, which forms the base for further investigations. Besides many finds of fossil adult stomatopods, also fossil larvae have been reported, but all specimens presumed as such turned out to be Thylacocephala, an arthropod group of yet unknown systematic affinity.

We report here (Fig. 1; Haug et al. 2008) the first definite find of a fossil stomatopod larva from Schernfeld near Eichstätt (Lower Tithonian, Eichstätt Formation, Solnhofen lithographic limestones). This specimen can be assigned to Stomatopoda because of its tri-flagellate antennulae and raptorial appendages. Other characters like the rostrum and the uropods indicate a larval state, confirmed by comparison to larval stages of recent species. Even more larval specimens discovered thereafter

are currently under investigation. Up to now, only the most posterior appendages of fossil mantis shrimps, i.e., uropods and pleopods, were known well enough to be useful morphological features in phylogenetic studies. Although Kunth (1870) mentioned one specimen with at least partly preserved raptorial appendages, he did not document these appendages by any drawing, and no details on this issue were published up to date. During our studies we found several specimens of apparently different species of stomatopods with well-preserved raptorial appendages. These data shed new light on the phylogeny within Stomatopoda and enabled us to create a reasonable evolutionary scenario of this taxon.

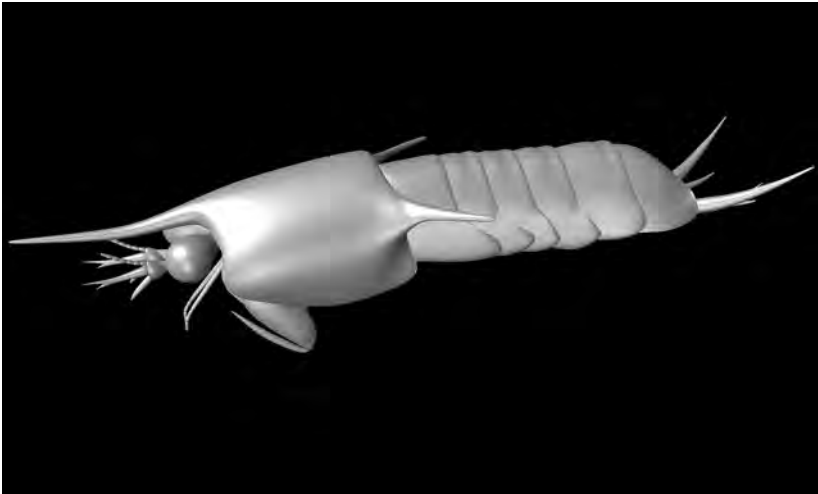


Figure 1: 3D model of the first true fossil stomatopod larva (*Scalda* sp.).

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Reconstructing ontogenetic sequences of fossil Crustacea from the Solnhofen lithographic limestones

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Developmental palaeobiology, i.e., the reconstruction of the ontogeny of fossil species, is a well-established field of research for example in Mollusca. For arthropods this field is mainly limited to the stiffened dorsal parts of trilobites and ostracodes. However, the reconstruction of the morphogenesis of structures comparable to that in recent species is possible for fossil arthropods. Yet, it requires a special mode of fossil preservation, in which not only details of the ventral surface, mainly the appendages, are preserved. Also different developmental stages have to be available. Two Palaeozoic lagerstätten, which yielded 3D preservation of the bodies and ontogenetic data are the Cambrian “Orsten”-type sites (Maas et al. 2006) and the Devonian Rhynie chert. These lagerstätten lack until now any evidence on Malacostraca. The Upper Jurassic lithographic limestones of Solnhofen, on the other hand, are one of the best sites for malacostracan fossils, showing detailed preservation of adult and larval specimens though flattened (e.g., Polz 1972). Yet, research on fossil Malacostraca from Solnhofen focused mainly on large specimens. To study also small specimens, we have adopted methods from other fields, such as composite fluorescence imaging (Haug et al. 2008). We also acquired the general composite imaging method for investigating smallest specimens with just a few millimetres in length. With these methods it was possible for us to identify a number of larval stomatopods. One of these could be affiliated with a juvenile stage to a new species. Developmental patterns could also be identified. One example is the morphogenetic change of the tail fan, i.e., uropods and pleotelson, of Stomatopoda from the juvenile to the adult state (Fig. 1). Such findings are important for recognising morphological differences not as interspecific but between ontogenetic stages. Based on these results the approach of developmental palaeobiology should be used to search for juvenile specimens misidentified as new species. Also evolutionary scenarios benefit from applying developmental palaeobiology. We documented, for

example, a drastic functional change of the antenna in the malacostracan taxon Achelata. This helped to identify heterochronic events, i.e., evolutionary changes in ontogeny, in the evolutionary lineage of Scyllaridae.

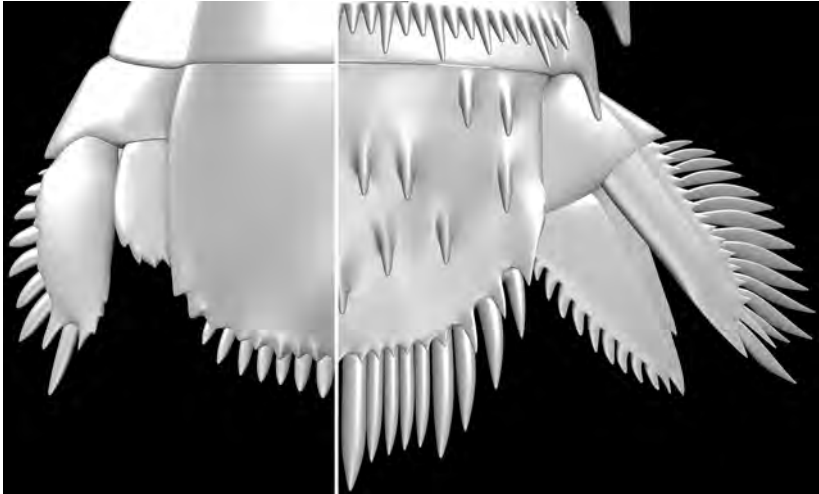


Figure 1: 3D model of *Sculda* sp.; left: juvenile tail fan, right: adult tail fan.

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Life and Death of *Saccocoma* – Functional morphology, feeding and taphonomy of the most common Plattenkalk fossil

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The morphology of the stalkless *Saccocoma tenella* is unique among crinoids. It is characterized by an extremely light skeleton with dish-like lateral wings on the proximal brachials and peculiar paired vertical processes or baffles on the more distal brachials. The arms are heavily branched. While the lateral dishes obviously are involved in the sinking process the role of the vertical processes has remained unanswered. Most authors assumed *Saccocoma* to have been planktonic or pelagic but Milsom (1994) and Manni et al. (1997) advocated a benthic lifestyle. This is rejected for morphological, environmental and taphonomic reasons. *Saccocoma* fed in the oxygenated layer of the water column, most probably on coccolithophorids. How exactly *Saccocoma* fed has so far not been explained in a satisfactory way. Pelagic crinoids have to move relative to the water to catch food. Seilacher & Hauff (2004) proposed a “snap swimming” model for *Saccocoma tenella*. They considered the commonly observed coiling of the arms not as a taphonomic artifact but as a frozen snapshot of swimming activity. In this model the vertical processes were connected by muscles that, upon contraction, loaded the elastic aboral ligament spring. Upon release of the energy thus stored the arm snapped back in an active stroke. However, there is no evidence that the processes were connected by muscles and proper coiling would have been impeded by the side branches. It also seems highly unlikely that large numbers of *Saccocoma tenella* were frozen in a swimming mode on the bedding planes. A taphonomic explanation for the coiled arms, as already proposed by Jaekel (1892), is, therefore, preferred. For swimming and food collection a “pulsating funnel” model is advocated. Contraction of the adoral muscles in the proximal region flexed the arms inward so that a funnel was formed. As a result, the animal was sinking but this was slowed by increased drag from the wings. The middle region and especially the distal, branched region with weakly developed muscles presumably

were more horizontal, forming a filtration fan. Upward movement of the fan allowed the animal to scoop plankton between the oral processes where the food grooves are situated. Relaxation of the muscles caused elastic recoil of the antagonistic aboral ligaments in the power stroke. During this phase the downward-concave wings of the widened funnel acted as paddles, pushing the cup upward. In contrast, extant stalked crinoids and comatulids form a filtration fan directed upstream; food particles impinge on adhesive tube feet extended between the pinnules. A prerequisite for the proposed model is that the animals floated with the cup directed downward. This is supported by the taphonomy.

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A palaeoenvironmental model for the formation of Mexican Cenomanian-Turonian (Late Cretaceous) open marine Plattenkalk

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The Vallecillo Plattenkalk is famous for its excellently preserved vertebrates, among them abundant fishes, but also mosasauroids and turtles (Buchy et al. 2005; Ifrim et al. 2005; Ifrim 2006; Ifrim et al. 2008). The continuous fossil record allows for detailed biostratigraphic subdivision by ammonites, inoceramid bivalves and planktonic foraminifers, with the most complete early Turonian record (Ifrim & Stinnesbeck 2007, 2008).

The Vallecillo Platy Limestone Member is now known from four localities, which are up to 300 km apart. During the sea-level highstand of the early Turonian, the submarine topography was smooth, and barriers that could inhibit the oceanic circulation, were absent. The “restricted-basin-model”, which can be applied to most Plattenkalk deposits hitherto known, is thus insufficient to explain the formation of Plattenkalk on the open shelf of the Gulf of Mexico. The compilation of results from micro- and nannofacies analyses, and of geochemical, sedimentological, statistical and palaeoceanographic data allows for a reconstruction of the palaeoenvironmental conditions under which the Vallecillo Plattenkalk formed during the latest Cenomanian to early Turonian on the outer shelf of the ancient Gulf of Mexico, transitional to the southern Western Interior Seaway of the North American continent.

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Inoceramids: environmental recorders of conditions of *Plattenkalk* formation

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Many *Plattenkalk* deposits are famous for their well-preserved fossils. However, circumstances of fossilisation and of *Plattenkalk* formation have been the subject of much discussion. This is mainly because benthic fossils which could provide insight into conditions of *Plattenkalk* formation are generally absent.

Plattenkalk deposits recently discovered in north-eastern Mexico were deposited on the open marine shelf during different times of the Late Cretaceous, e.g. the Cenomanian-Turonian boundary at Vallecillo, N.L. (Ifrim & Stinnesbeck 2008), or the Turonian-Coniacian boundary at Rosario, Coahuila (Stinnesbeck et al. 2005; Ifrim et al. 2007). Similar to other *Plattenkalks*, they yield well-preserved vertebrate fossil (Buchy et al. 2005; Ifrim et al. 2008), but in addition to these also contain inoceramid bivalves (Ifrim & Stinnesbeck 2008). These inoceramids comprise the only benthic organisms present in the localities (including ichno- and microfossils) and apparently existed under low oxygen conditions (Ifrim 2006). A forthcoming research project is aimed to study the palaeobiology of inoceramids and their potential as palaeoenvironmental proxy, including geochemical analyses of the inoceramid shells. These data are hoped to provide insight into the palaeoenvironmental parameters necessary for the formation of *Plattenkalk*.

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Experimental simulation of initial stages of fossilization by bacterial sealing – Implications for the formation of Las Hoyas Konservat-Lagerstätte (Lower Cretaceous, Iberian Ranges, Spain)

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Konservat deposits are distinguished by the quality of preservation of soft-bodied organisms. The particular preservation of Konservat-Lagerstätten has been explained in the framework of three boundaries of fossilisation: obrution, stagnation and bacterial sealing (Seilacher et al. 1985).

Las Hoyas is a Konservat Lagerstätte belonging to the La Huérguina Limestones Formation (Upper Barremian, Iberian Ranges, Spain) where freshwater, terrestrial and aerial organisms occur within the same sedimentary beds. Fossils do not show traces of transport, elements are not broken or abraded, 75% of the fossils are completely articulated, and many of them preserve a broad range of organic compounds: mineralised muscle, tissue imprints, chitin, cellulose, shelly and apatite skeletons. The importance of microbial mats at Las Hoyas to explain preservation has already been highlighted (Delclòs et al. 2003; Gupta et al. 2008), and their presence have been inferred from sedimentological and taphonomical data. The fossils of Las Hoyas are preserved in lithographic limestones that formed in a shallow lake located in a freshwater subtropical wetland. The lake experienced cyclical oscillations of water level. Microbial mats grew massively during dry periods, and are preserved as whitish-grey crypto-crystalline mosaics of calcium carbonate, arranged in undulated millimetric laminae. The taphonomical role of microbial mats has been

observed in the preservation of tissues imprints in tetrapods and frequent overlapping areas in the body of insects, among other examples.

Although bacterial sealing is often addressed as a capital factor involved in exceptional preservation, the real processes occurring when an organism remain is entrained in a microbial mat have never been directly observed or described.

An experimental simulation of the initial stages of fossilization by bacterial sealing was designed aiming to compare the results to the taphonomic features observed in the fossils of Las Hoyas. The experiment consisted on three tanks with microbial mats grown under controlled conditions in laboratory, lit up with halogen lamps (Osram Decostar). Control tank was not illuminate, and it lacked of microbial mat. The monitoring of this grown process showed that the composition of our microbial mat was similar to the natural one. *Microcoleus* was the predominant cyanobacteria, but it was also made up of *Lyngbya* and *Chroococcus*, and purple sulfur bacteria in the deeper layer. After growing the mats, 52 *Paracheirodon inessi* fishes were put down by asphyxia with N₂, and laid on the microbial mats or on the sediment in the tank control. In order to follow the decay process, variations in the morphometric parameters, observations with the Scanning Electron Microscope (SEM) and composition of possible precipitates by Energy Dispersive X-ray Analysis (EDX) were conducted.

Bodies were covered by mat in only 15 days, and an important delay in decay rate was observed. After three months, fishes covered by mat still conserved all fins, eyes were in good condition and tridimensional structure was conserved. In control bodies, eyes were decomposed, fins dismantled and the bodies collapsed. The observation with SEM showed also important differences within precipitates appeared. EDX Analysis showed that fishes covered by mat presented calcium carbonate, whereas fishes laid on sediment only showed NaCl precipitates.

These preliminary outcomes would indicate that the presence of microbial mats covering bodies has influence on the preservation, delaying in decay rate, and that it is involved in the surface mineralization.

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Fossil turtles from the Late Jurassic of Europe

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Keynote

Turtles are among the most enigmatic group of living vertebrates. The origin of their shell, the alleged placement of the shoulder girdle inside their ribcage, and their phylogenetic position among Tetrapoda have mystified scientists for over two centuries (e.g., Romer 1956; Carroll 1988; Lee 1996). It is in this regard that the oldest known fossil turtles have always played an important role, as they could be expected to help address some of these scientific puzzles.

For much of the 19th century, fossil turtles from the Late Jurassic of Europe were the oldest known representatives of the group and even fragmentary finds were given a disproportionate amount of attention. This led to a dizzying number of named species and often confusing phylogenetic assessments (e.g., Kuhn 1964; Mlynarski 1976). Classic localities include the lithographic limestone quarries of Germany and France, Solothurn in Switzerland, and the Purbeck limestone of southern England (e.g., Owen 1853; Meyer 1860; Bräm 1965; Gaffney 1976, Milner 2004). However, as soon as taxonomically older and phylogenetically more primitive turtles were found in the Late Triassic of Europe (Fraas 1913; Jaekel 1918), attention shifted immediately away from Late Jurassic turtles.

In recent years, European Late Jurassic turtles have been the focus of attention once again. Application of the morphometric methods of Joyce and Gauthier (2004) reveal that all turtles from the Late Jurassic of Europe are aquatic, whereas isotopic analyses hint at both marine and freshwater habitat preferences (Billon-Bruyat et al. 2005). More importantly, modern phylogenetic analyses clearly reveal that all primary turtle clades that existed in the Late Jurassic are found in Europe, in particular the stem lineages of Cryptodira, Pleurodira, and Paracryptodira (Joyce 2007). This is notable as these three clades are otherwise restricted throughout the Mesozoic to Asia, Gondwana, and North America, respectively (Joyce &

Lyson 2008). This indicates that Europe served as a faunal melting pot in the Late Jurassic, but that it did not serve as a biogeographic bridge.

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Synechodontiformes, a largely disregarded group of early modern sharks in the Jurassic

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All modern sharks, skates and rays, and those extinct taxa nested phylogenetically within modern clades are collectively called Neoselachii. They constitute a well-defined monophyletic clade, which is well supported by morphological and molecular data. The most important period in the evolution of modern sharks and batoids was the Mesozoic, especially the Jurassic, because their origin and first major radiation events occurred during this time span. Nevertheless, our understanding of early neoselachian diversities, taxonomies, and systematics are still very inadequate despite many recent achievements, which is mainly related to the nature of preservation, because neoselachian skeletons are mostly cartilaginous and consequently become scarcely and only under exceptional taphonomic conditions fossilized (e.g., lithographic limestones of South Germany). Isolated material, such as teeth, placoid scales or fin spines, conversely, is quite resistant and very abundant as fossils. Neoselachian teeth are generally considered to be useful for taxonomic purposes, although similar trophic adaptations might result in similar tooth morphologies in not closely related groups. The precise study of tooth morphologies in combination with fossilized skeletal elements is mostly the only way to establish systematically useful tooth characters for inferring interrelationships and diversity patterns through time. However, fossil localities with skeletal remains of neoselachians are very scarce. These skeletal remains are of utmost importance because they provide new insights into morphological traits, the early evolution and origins of neoselachians. Among the wide array of fossil neoselachian taxa reported from the Early and Late Jurassic is one group of sharks, the Synechodontiformes, which includes abundant taxa mostly based on isolated teeth. Although ranging from the Late Permian to the Paleocene and reported from the northern as well as the southern Hemisphere, they are a largely disregarded group of early modern sharks, whose importance for the evolution of modern sharks and rays was unrecognized.

Most synechodontiform taxa, especially the stratigraphic oldest forms, are only reported from isolated material such as teeth. The scarcity of

skeletal remains (only a few at the beginning of this revision three years ago), morphological similarities of isolated teeth and the lack of comparable extant representatives caused major controversies. These debates are related to the questions if *Synechodontiformes* is a monophyletic group and the confusing taxonomy of the most diverse family within *Synechodontiformes* – the *Palaeospinacidae*. Additionally, the systematic position of *Synechodontiformes* within *Neoselachii* is still discussed and most taxa have been very controversial in recent decades. Many authors consider *synechodontiform* sharks to be a monophyletic group with affinities to certain members of *galeomorphs*, while others place them into closer relationship with *Squalidae*, or stated they are paraphyletic within different *galeomorph* groups. The major problem is that there is no phylogenetic analysis employing cladistic principles available so far including all taxa assigned to this group.

A revision of holomorphic specimens of fossil sharks and rays housed in several collections of Europe and the USA in addition to recently recovered specimens from the lithographic limestones of Nusplingen and the Solnhofen area (South Germany), enabled the discovery of several hitherto *synechodontiform* taxa including abundant skeletal remains especially from Upper Jurassic of Germany. *Synechodontiformes* is a very abundant and amongst the most diverse *neoselachian* groups during the Mesozoic, especially the Jurassic period. According to the results of the revision of skeletal material of *neoselachians* and phylogenetic analyses, taxa previously assigned to *Synechodontiformes* constitute a monophyletic group, which is sister to all living sharks and correspondingly represent stem-group *neoselachians*. In the Upper Jurassic lithographic limestones of South Germany, *synechodontiform* sharks are more diverse and abundant than previously assumed and generally misidentified. For instance, several small shark specimens were randomly assigned to different *carcharhiniforms* (e.g., *Macrourogaleus*, “*Palaeoscyllium*”). *Macrourogaleus* is shown to be sister to *Paraorthacodus* here. Both are characterized, inter alia, by a single dorsal fin. Most other small specimens identified as “*Palaeoscyllium*” either belong to *Synechodus* or *Paraorthacodus*.

A revision of Cow Sharks (Chondrichthyes, Hexanchiformes) from the Jurassic of Europe

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Cow Sharks (the Hexanchiformes) form a monophyletic group of squalomorph sharks and are represented by three living genera with four valid species. They are conspicuously characterized by an “extra” pair of gill arches (one in *Hexanchus*, two in *Heptranchias* and *Notorhynchus*), a single dorsal fin and very characteristic dentitions comprising labiolingually flattened saw-like teeth (Fig. 1A). Their fossil record is dominated by isolated teeth and extends back into the Jurassic. The earliest occurrences are from the Lower Jurassic of Switzerland (*Notidanus arzoensis*), SW Germany (*Notidanus amalthei*) and NW Germany (*Hexanchus? widenrothi*). A single species, *Notidanus contrarius*, was reported from the Middle Jurassic (Bajocian) of Bavaria. Late Jurassic records are more numerous. *Notidanus muensteri* is known from the Oxfordian of Switzerland, Kimmeridgian of Baden-Württemberg and Tithonian of Bavaria, *Notidanus eximius* and *N. intermedius* from the Tithonian of Bavaria. The latter species is based only on a pathological lower tooth that belongs to *Notidanus serratus*. Two species, *Notidanus huegeliae* and *Notidanus serratus* were reported from the Kimmeridgian of Baden-Württemberg. Most of the taxa are based on isolated teeth (except *Notidanus muensteri*). Different taxonomic and systematic concepts of extinct and extant hexanchiforms were presented in the last decades. For instance, *N. muensteri*, which was assigned to *Eonotidanus*, was transferred to the genus *Notidanooides* based on a slightly disarticulated skeleton (without preserved body-outline) from the upper Kimmeridgian of Nusplingen. Additional fossils from the Tithonian of Bavaria subsequently were assigned to this species based on the presence of a single dorsal fin as it occurs in extant forms (Fig. 1B). A comprehensive revision of Jurassic sharks and rays, however, provided sound evidence that the Bavarian specimens belong to a different group of modern sharks, the Synchondontiformes. Consequently, the number and arrangement of paired and unpaired fins in Jurassic hexanchiforms remains ambiguous.

The Late Jurassic taxa *N. arzoensis*, *N. eximius*, *N. huegeliae* and *N. daviesi* are considered to be junior synonyms of *N. muensteri*.

A second genus, *Paranotidanus*, was introduced for Jurassic hexanchiforms with teeth displaying serrations at the base of the mesial cutting edge of the principle cusp (e.g., *N. serratus*). This name, however, represents a *nomen nudum* and the genus name “*Eonotidanus*” is currently used for those forms.

According to the present knowledge, two hexanchiforms occur in the Upper Jurassic of S Germany contrary to the view of most scientists: *Notidanoides muensteri* from the Oxfordian of Switzerland, Kimmeridgian of Nusplingen, and lower Tithonian of Bavaria, and “*Eonotidanus*” *serratus* from the Kimmeridgian of Nusplingen and Tithonian of Solnhofen. “*Eonotidanus*” *serratus* also occurs in the Oxfordian of England.



Figure 1: *Notidanoides muensteri* from Solnhofen. **A:** Isolated tooth. **B:** Holomorphic specimen based erroneously on the presence of a single dorsal fin.

The Oxfordian/Kimmeridgian boundary in the eastern and southern parts of the Paris Basin: comparison of two mudstone formations: *Calcaire à astartes* and *Calcaires lités supérieurs*

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To place the Oxfordian/Kimmeridgian (O/K) boundary (Upper Jurassic) is a real headache for the scientific community. The International Subcommission on Jurassic Stratigraphy proposes a potential stratotype (GSSP) in the north of the Isle of Skye (Scotland). But this choice is controversial because of the global provincialism of ammonite during the Late Jurassic which complicates any attempts to correlate boreal realm with others realms. The question is to place the O/K boundary between the Planula zone and the Platynota zone in the submediterranean province or between the Rozenkrantzi and the Bauhini zone in the boreal province.

Furthermore, regions of carbonate platforms where no ammonite was observed add to the complexity of the situation. It is the case of the eastern edge of the Paris Basin where the limit should be placed within a succession of barrier and lagoonal limestones that includes the *Calcaire à astartes*, a formation dominated by a mudstone facies. The lack of ammonites encourages investigate the biostratigraphic power of other fossil taxa like brachiopods, foraminifers, palynomorphs and to get sedimentary and paleoenvironmental changes through macrofossils, organic matter geochemistry and isotopic data. Such an integrated stratigraphy will enable us to better understand the drowning of the Oxfordian carbonate platform during the Early Kimmeridgian.

The different wells made by the French National Radioactive Waste Management Agency (ANDRA) and a detailed study of the Gudmont-Villiers (Haute-Marne, France) outcrop gives us some results that can be compared with others sections in western Europe. In order to understand

the similarities and the evolution of environments of carbonate platform within the Paris Basin, we decided to compare successions between the Haute-Marne/Lorraine platform (Eastern Paris Basin) and the Berry region (Southern Paris Basin).

Similar successions of marine mudstones providing evidence of environments of carbonate platform were observed in the *Calcaire à astartes* Formation (eastern part of the Paris Basin) and in the *Calcaires lités supérieurs* Formation (southern part of the Paris Basin), where many ammonites were found. Mainly based on microfauna and palynomorphs, detailed correlations between the two successions will be presented: these correlations enable the East of the Paris basin section to be more accurately placed than previously within its regional chronostratigraphical context.

Formation and preservation of Late Jurassic dinosaur track-bearing tidal-flat laminites (Canton Jura, NW Switzerland) through microbial mats

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Recently, an increasing number of investigations comparing fossil and modern microorganisms highlighted the role of microbial mats in the formation of minerals and diagenetic processes leading to the development of sedimentary rocks including lithographic limestones and trace fossils. More specifically, on recent tidal flats, the sporadic growth of microbial mats alternating with carbonate precipitation may lead to the formation of biolaminated sediments, where vertebrate tracks (true tracks, undertracks, overtracks) are easily preserved (Marty et al. 2009). However, because microbial mats are mainly composed of extracellular polymeric substances (EPS) containing over 70% of water, the former presence of microbial mats in the fossil record can only with electron microscopy be proven unambiguously (Pacton et al. 2007).

This study is based on Late Jurassic (Kimmeridgian) dinosaur track-bearing laminites from NW Switzerland near Porrentruy, which formed on tidal flats of the Jura carbonate platform (Marty 2008). Macrosedimentary structures (i.e., dinosaur tracks, desiccation cracks, ripple & wrinkle marks) of superimposed palaeosurfaces were documented and analysed and a high-resolution microfacies analysis was carried out. Of selected samples the total organic carbon content was determined by Rock-Eval pyrolysis, and mineralogical (including clay minerals) analyses were performed by standard X-ray diffraction. The organic matter (OM) was then isolated from the mineral fraction using a standard palynological preparation technique in order to analyse it on thin sections with optical microscopy using natural light and blue-light fluorescence, and on ultrathin sections with transmission electron microscopy (TEM).

The former presence of microbial mats is suggested by the stromatolitic appearance of the laminites in the field; crypt microbial lamination

and fenestrae in thin sections (i.e., a laminated alternation of OM and minerals); polygonal desiccation cracks, pustular nodules, and wrinkle marks on palaeosurfaces; and by associated track features such as (internal) overtracks.

TEM observations show heterogeneous OM mainly composed of a more or less fluffy alveolar network corresponding to exopolymeric substances (EPS), sometimes of “curly” and ovoid bodies with thick membranes corresponding to bacterial and algal cell walls, and accessorially of complex fibrous structures with a strong contrast and characteristic lamellae indicating terrestrial fragments (plants). Further, ultralaminae displaying diffuse outlines and a relatively small thickness (80 nm) have also been observed. According to the classification of Pacton et al. (2008) they can be attributed to bacterial cell walls indicating a low degradation level in the OM cycle. This evidence suggests that the laminites were mainly formed by the sporadic growth of photosynthetic microbial mats occasionally incorporating terrestrial plants.

We conclude that the studied laminite intervals formed in a tidal flat environment subjected to desiccation and rehydration (due to a regularly or episodically covering with shallow water) allowing the growth of microbial mats and hence the formation and preservation of dinosaur tracks. Today, such conditions are typically observed on higher intertidal to supratidal flats. Consequently, the palaeoenvironment of the laminites from NW Switzerland was clearly more terrestrial (i.e., characterized by a higher exposure index) when compared with the Kimmeridgian to Tithonian (sub)lithographic limestones from Cerin (shallow lagoon to intertidal; Gaillard et al. 1994), Orbagnoux (shallow lagoon; Tribouvillard et al. 1999), and Solnhofen (deeper lagoon; Seilacher 2008).

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Palaeobiology of *Iberomeryx minor* (Mammalia, Artiodactyla) from the lithographic limestone of Soulce (Early Oligocene, Jura, Switzerland)

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Iberomeryx is a small ruminant from the Early Oligocene of Eurasia. This genus, essentially known by few dental remains, is still poorly documented. Its phylogeny stays rather enigmatic, and its palaeobiology very approximate. Three species have been described: the type species *I. parvus* from the Benara locality in Georgia (Gabounia 1966), *I. savagei* discovered in the Kargil Formation from India (Nanda & Sahni 1990) and the west European species *I. minor* from Itardies, Mounayne, Raynal and Roqueprune 2 in Quercy (Remy et al. 1987), Montalban in Spain (Golpe-Posse 1974), and Lovagny, Soulce and La Beuchille in the Swiss Molasse Basin (Becker et al. 2004). The European localities are dated to the Rupelian and correspond mainly to MP23 (European mammal biozone). Based on the short tooth-crown height and the bunoselenodont pattern of the molars, Sudre (1984) and Becker et al. (2004) proposed a folivore/ frugivore diet for *Iberomeryx*.

Iberomeryx from Soulce (Rupelian, NW Switzerland) was first announced by Stehlin (in Fleury 1910) and first described by Gaudant (1979) as *Cryptomeryx gaudryi*. It is preserved in a lacustrine lithographic conservation bed 95 cm thick, rich in plants (Fleury 1910). It represents the most complete mandible with a partially persevered ramus. Moreover, the imprint of unpreserved hard parts due to particular taphonomic processes permits to complete the outline of the mandible. Based on a new description of the specimen and relative warp analysis (24 landmarks) of 75 extant and fossil ruminant mandibles from 23 genera, this study proposes a preliminary discussion on the phylogeny and the diet of the genus *Iberomeryx*.

Relative warp analysis permits to differentiate Pecora and Tragulina on the first axis thanks to the length of the diastema and the mandible ankle. As suggested by Sudre (1984), *Iberomeryx* is close to the extant Tragulina by the shape of its mandible. But the latter is clearly different of those of the Tragulidae, the only extant family in Tragulina. The difference is essentially due to a stockier mandible (condylar process, mandible ramus and *corpus mandibulae*) and a deeper mandibular incisure. Additionally, we observe no diastema and well bunodont teeth. *Iberomeryx* may be considered as a Tragulina based on the general shape of its mandible and its jaw teeth, but probably in a new family. Moreover, its diet could not be strictly folivore/frugivore, but it could possibly also exceptionally eat some meat matter.

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The fish fauna of Frauenweiler clay pit (Oligocene, Rupelian; Baden-Württemberg, S Germany): an updated review in special consideration of new records

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About 32 million years ago, during the Rupelian stage of the Oligocene, a waterway connected the North Sea with the prealpine marginal sea. At the bottom of this sea, sands and clay stones were deposited which formerly were exploited in numerous sand- and clay pits along the Upper Rhine Rift Valley. One of them is Grube Unterfeld. It is located in the vicinity of the small village of Frauenweiler, about 13 km south of Heidelberg (Baden-Württemberg, S Germany). Therefore, it is also known as Frauenweiler clay pit. Unfortunately, the quarrying activities became uneconomical and were stopped some years ago. Since that time, the pit was used as a commercial landfill. Presently, it is already extensively backfilled with building rubble and ground excavation materials. Only a very restricted area is accessible for excavations today.

During the last few decades, Grube Unterfeld became well-known for palaeontologists and neontologists as it still was in operation and many new specimens were being found. Furthermore, many fossils are completely articulated because they were deposited in a stratified water body. Anoxic conditions towards the sea ground prevented the decay of organic matter. Due to the transfer preparation technique, the skeletons provide excellent information concerning even highly delicate and fragile morphological structures.

Synopses of the fish fauna and descriptions of particular taxa display a broad scope of more than 70 nominal genera and species (Micklich & Parin 1996; Parin & Micklich 1996a, b; Micklich 1998; Hovestadt & Hovestadt-Euler 1999, 2002; Sakamoto et al. 2003, 2004; Micklich 2005; Parin & Astakhov 2007). However, many of the present identifications of genera and higher taxa are preliminary. Detailed studies of their systematics and morphology will not only result in the recognition of additional

forms but will also shed new light on the evolution, life history and palaeodiversity of numerous elasmobranch and bony fishes groups. Only recently, a partially articulated skeleton of a sand tiger (*Carcharias gus-trowensis*) was described, with several embryos in situ. And within the bony fishes the first fossil specimens of the tholichthys larval stage of a butterfly fish (Chaetodontidae) were found. New records of benthic fishes (e.g., Triglidae, Lophiidae) show that the anoxic conditions probably existed in the uppermost bottom layers and not in the water column.

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The fish fauna of the Solothurn Turtle Limestone

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Since the beginning of the 19th century the surroundings of Solothurn (NW Switzerland) have been famous for their fossil marine turtles (Bräm 1965). Also notable are fossils of other reptiles (fish, crocodiles) and invertebrates (e.g., Meyer 1988, 1989, 1994a, b), as well as trackways of large sauropods (Meyer 1990). Historically, the Solothurn Turtle Limestone was quarried for building-stone, which exposed the fossil-bearing layers. With the closure of the region's last quarries no further fossil material was unearthed until 1986 when the re-opening of an old quarry offered a unique opportunity for a modern palaeontological excavation (Meyer 1994b). The excavations allowed a review of Solothurn's fossil fish fauna that has not been dealt with since Agassiz (1833-44). The focus of this study is a revision of the historic fossils of the Natural Museum of Solothurn and examination and classification of the newly excavated specimens that are mainly isolated teeth and jaw fragments. The resulting inventory confirmed the historic specimens, and revealed the presence of species previously not known from the Solothurn area. The Solothurn Turtle Limestone contains a diverse fish fauna composed of both basal cartilaginous (Chimaeras, Hybodontids) and bony fishes (Semionotids, Pycnodontids), and more modern fish types (Heterodontids; Caturids and Oligopleurids, Aspidorhynchids).

Chimaeras: *?Ischyodus*

Hybodontids: *Asteracanthus*, *Hybodus*, *?Polyacrodus*

Heterodontids: *Heterodontus*

Semionotids: *Lepidotes*

Pycnodontids: *?Eomesodon*, *Gyrodus*, *?Macromesodon*, *Proscinetes*

Caturids and Oligopleurids: *Callopterus*, *Caturus*, *Ionoscopus*

Aspidorhynchids: *Belonostomus*

Specimens that could not clearly be identified include parts of a hybodont snout, a heterodontid vertebra, scales and the cleithrum of a halecomorph fish and a left lower jaw possibly of a lobefin.

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Relationships between the Pesciara di Bolca and the Monte Postale *Fossil-Lagerstätten* (Lessini Mts., northern Italy)

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Very close (about 300 m) to the world-famous Pesciara di Bolca *Fossil-Lagerstätte*, the Monte Postale is the only locality where it is possible to follow a more or less complete sedimentary succession. Despite their closeness, the geological and stratigraphical relationships between the Pesciara and the Monte Postale are still poorly known. This is mainly due to the widespread volcanic and volcanoclastic deposits that, together with tectonic movements of different ages, extensively dismembered and displaced the sedimentary rocks. Therefore, there is no continuity between the limestone of the Pesciara succession and the similar rocks of the Monte Postale, on the opposite side of the valley.

At present, the stratigraphy of the Monte Postale succession is still founded on the sketch and description of Fabiani (1914). More recently, Massari & Sorbini (1975) described only a part, about 30 m thick, of the Monte Postale succession. We recently re-examined the whole succession, measuring a composite stratigraphic section made up by two sections (lower and upper) separated by a fault (the Monte Postale fault). The preliminary results of the study of the samples collected revealed that the upper section, bearing quite rich *Alveolina* assemblages could be dated to the SBZ 11 biozone, i.e., Middle Cuisian (Ypresian). The upper section contains laminated micritic limestone with fish and plants, which are therefore contemporary to the similar limestone of the Pesciara section.

The characters of the Monte Postale laminated limestone (MPLL) are in some way different from that of the Pesciara (PLL), because the MPLL bear often bad-preserved fishes (Massimo Cerato, pers. comm.) as compared with the ones coming from the PLL. Moreover, the Monte Postale succession includes a significant thickness of “normal” limestone, very rich in benthonic fossils (especially *Alveolina*), witnessing the prolonged conditions of normally oxygenated sea bottom, with some intervals of

oxygen depletion marked by the MPLL. In the Pesciara section, all the larger foraminifers and other benthic fossils were transported and redeposited in an anoxic environment with terrigenous inputs mainly due to aeolian transport (Schwark et al. 2009).

According to these data, we can provisionally conclude that the Monte Postale succession represents a palaeoenvironment more open to marine circulation and consequently better oxygenated than the Pesciara “basin”. More detailed analyses are required to better precise the palaeoenvironmental evolution in the Monte Postale succession.

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Methodology of systematic excavation and documentation of dinosaur tracksites along the Transjurane highway (Canton Jura, NW Switzerland)

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Since 2002, the Palaeontology A16 has excavated dinosaur tracksites near Porrentruy along the future course of the Transjurane highway A16. This resulted in the development of a complex excavation-, documentation-, and protection-methodology of dinosaur tracksites.

First, tracksites are located by geological surveying followed by palaeontological prospecting with shovel excavators. Large-scale excavations are then planned and scheduled in agreement with the civil engineering office prior to the construction of the highway. The tracks are found on multiple superimposed palaeosurfaces within horizontally bedded laminites of Late Kimmeridgian age, which accordingly have to be excavated level-by-level. At the beginning of an excavation, as much overburden as possible is removed with the aid of shovel excavators. Within the laminites, the track-bearing levels are then excavated and cleaned with hand tools, a time-consuming and difficult affair.

Tracks are then searched for, identified, and whenever possible attributed to trackways. This includes analyses at night with oblique lighting, indispensable to find and study small tracks and track details. Simultaneously, all tracks are outlined with black chalk and labelled on the surface itself using specified acronyms. Subsequently, tracks and trackways are analyzed and described, and their parameters measured in a consistent fashion and gathered in a database. They are also photographed including stereoscopic photographs of selected tracks. Further,

macrosedimentary features (e.g., desiccation cracks, ripple marks) are analyzed and the encasing sediment is logged and sampled.

Afterwards, a geo-referenced 2x2 metre grid is installed on the surface and tracks and normal faults are drawn at a scale of 1:10 or 1:20. These drawings are vectorized in the office and assembled in a map. As outline drawings represent one person's simplified interpretation of a complex three-dimensional object, the most important palaeosurfaces are likewise documented with 3D imaging techniques using high-resolution laser scanning and extreme close-range (2-10 m from camera to object) photogrammetry. These are merged in a virtual 3D model, on the basis of which tracks and trackways can easily be vectorized and their parameters measured in CAD software, if previously they were labelled and outlined with chalk. Similarly assembled data can later also be integrated into a GIS database.

If a surface is going to be destroyed or exposed to weathering after excavation the 3D documentation is the most accurate way to document its original state, especially if applied together with complementary, classical illustrative and descriptive techniques as well as replicas. Consequently, future generations of researchers will have access to virtually the same database. Nonetheless, judging by our own experience, the 3D methods cannot fully replace careful observations and descriptions of the actual tracks in the field because the interpretation of small tracks or track details (e.g., digital pads, claws, skin impressions), poorly-preserved tracks, and/or crossing trackways (track interferences) is a difficult and subjective task done at best on the original specimens. Also, 3D methods are expensive and cannot always be applied. Another drawback is that adequate safeguarding of the imaging data for posterity may be difficult to guarantee. After their documentation, the most important tracks and trackways are either recovered as slabs or replicated, and then the underlying level is excavated. Such level-by-level excavation and documentation offer important insight into the formation, taphonomy, and preservation of tracks, notably the identification of undertracks, true tracks, and overtracks.

At the end of an excavation recovered slabs, samples, and replicas are archived, and the documentation (e.g., photographs, track parameters, etc.) is assembled in a database (collection and documentation management). The main track level of the Transjurane tracksites is commonly located at the top of massive limestone and at the base of laminites. Consequently, it cannot be removed and will be either covered or (partially) destroyed by the construction of the highway. The importance of a tracksite has to be evaluated "in context" based on abundance, quality, and uniqueness of the tracks. Whenever possible it has to be preserved as a geotope *in situ*. Actually, a tracksite is already preserved for posterity by the construction of an additional highway bridge.

The history and future of the Upper Jurassic lithographic limestone quarry of Canjuers, France and its fossils

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Canjuers-Les Bessons is one of the most important fossil sites of the Upper Jurassic in France and produced over several years a rich collection of fossil plants, invertebrates, and vertebrates. Located in the department of Var in the southeast of France, close to Aiguine the fossil bearing limestones are situated at the border of the Petit Plan de Canjuers plateau (860 m above sea level) and stretch over an area of 15 ha. The lithographic limestone quarry of Canjuers was first known to the public for its production of calcareous plates, or 'dalles de Provence'. Soon after the first appearance of fossils, palaeontological excavations led by the Muséum National d'Histoire Naturelle in Paris unearthed a splendid collection of marine and terrestrial Upper Jurassic fossils. The Jurassic sediments in Canjuers provide evidence that the fossilized fauna and flora were that of a lagoonal environment situated behind a chain of coral reefs but in close proximity to the Tethys Sea (Atrops 1994). The palaeogeographic association of several genera of ammonites recovered from the lithographic limestones of Canjuers has been well compared to the ammonite fauna in Franconia that is characteristic of the Lower Tithonian suggesting a similar age (Lower Tithonian, *Mucronatum* zone) for the corresponding palaeofauna in Canjuers (Atrops 1994). Compared to other lithographic limestone quarries in Western Europe, the Canjuers sediments are older than the Montsec limestones in Spain (Soriano & Delclòs 2006) but younger than the Cerin outcrops of the French Jura (Enay et al. 1994), the Solnhofen limestones in Germany (Schweigert 1993), and slightly younger than the Crayssac limestones in France (Hantzpergue & Lafaurie 1983; Hantzpergue 1989).

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Exceptional preservation of embryos in the Middle Triassic actinopterygian *Saurichthys* from Monte San Giorgio, Switzerland

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New excavations in the famous Monte San Giorgio area, close to the historical sites where the Cassina beds crop out (Lower Meride Limestone, Ladinian), have been started in 2006 by the Museo Cantonale di Storia Naturale, Lugano (Stockar this volume).

The new outcrop consists of an almost 3 m thick interval of mainly interbedded finely laminated, organic-rich shales and limestones with intercalated thicker bituminous micritic and marly limestones deposited in oxygen-depleted bottom water. Along with sauropterygian fragmentary remains, the new excavations yielded many complete and well-preserved specimens of the large (up to 0.5 m standard length) predatory actinopterygian fish *Saurichthys* (mainly *S. curionii*, but *S. macrocephalus* is also present), along with other smaller fishes like *Archaeosemionotus*, *Eosemionotus* (not previously reported from these beds), and *Peltopleurus*. Among the prepared specimens, four specimens of *Saurichthys* contain embryos, and in one specimen (MCSN 8016, Fig. 1A) sixteen very small embryos (skull mean length 6 mm) are present. These latter show a peculiarity not reported so far for other *Saurichthys* embryos: each skull is associated with a tiny, narrow and elongate structure which, at higher magnifications (Fig. 1B), appears as a short and narrow cylinder, either curled or comma shaped. The nearly one-to-one association between the embryonic skulls and the narrow cylinders suggests that they represent some postcranial structure of the embryos. Chemical investigation (Renesto & Stockar in press) revealed the phosphatic nature of these structures. Phosphatization may occur for soft parts if the microenvironmental conditions around the carcass are modified by bacterial activity. The size and length of these structures with respect to the associated skulls are compatible with the axial musculature and recall the morphology of embryos of extant fishes, so that the curled narrow cylinders may

represent the fossilized musculature of the embryos, and each segment may correspond to a somite. A SEM (Scanning Electron Microscope) observation confirmed the metameric structure of the cylinder. This discovery is of particular relevance because fossil embryos with preserved soft parts are extremely rare. In addition, although viviparity had previously been described for *Saurichthys*, the new specimens are rather better evidence and add further support to this reproductive mode.

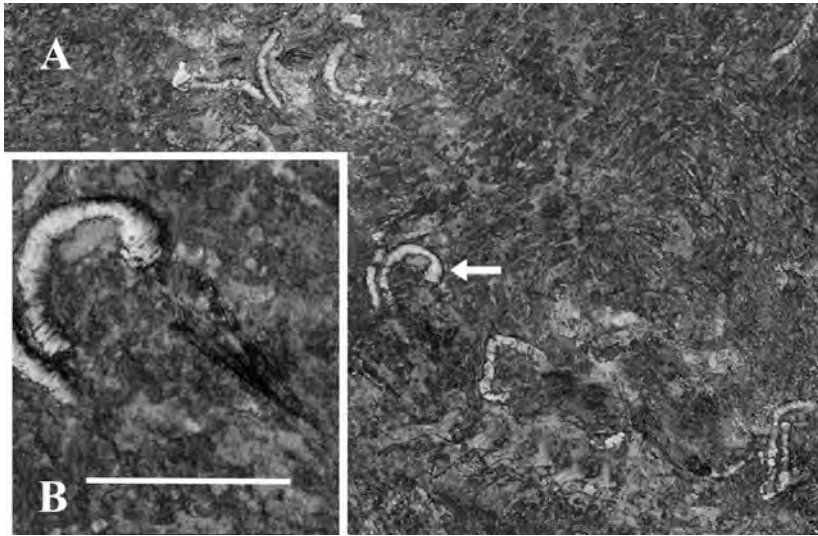


Figure 1: *Saurichthys curionii*. **A:** Body cavity of MCSN 8016 with preserved embryos. **B:** High magnification detail of the embryo indicated by arrow. Scale bar = 0.5 cm.

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The basins of the lithographic limestone of Southern Germany and the rise of new life: fish groups

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Some of the recent continental lakes in the world are good examples of rapid speciation of one particular taxon (e.g., many species of Cichlidae in some African lakes) or of one taxon in process of speciation as revealed by the high level of morphological variation (e.g., *Orestias agassizi* in Titicaca Lake, South America). While one group is undergoing an evident process of speciation, others inhabiting the same lake are not, so that the operating evolutionary mechanisms, in the same lake and at the same time, have different response by different biological groups. Among fossils lakes, the Eocene lake of Mahenge in Tanzania is another example with cichlids as the dominant group (in number of species as well as number of individuals), in contrast to any other taxon found in the lake (e.g., Kaiser et al. 2006).

The Plattenkalk basins in the southern Franconian Alb during the Late Jurassic times can be interpreted as part of a big lake with connection to the Tethys Sea a somewhat different situation in comparison to strict continental lakes. In addition, another difference is that not all the basins in the Plattenkalk are identical in age, but this is an important element in the understanding of the diversification of taxa and of their fate from older to younger basins. We will analyze here whether the Solnhofen Plattenkalk basins show some common aspects with the speciation process shown in certain particular continental lakes or not.

We have studied the faunal composition, as far it is known, from selected basins (e.g., Brunn, Ettling, Daiting, Schamhaupten, Solnhofen) of the Plattenkalks and discovered three common points to all of them: (1) the best represented group in number of species as well as in individuals, is that of the teleostomorphs (*sensu* Arratia 2001), especially of the “true” teleosts (*sensu* Arratia 1999, 2004); (2) the taxonomy of many fishes is incompletely known so that many taxa are determined, with doubt, at the generic level and left as unknown species, nevertheless the few good identifiable taxa demonstrate variation through time and from basin to basin; and (3) that the knowledge of all localities is still

incomplete as demonstrated, intermittently, by the discovery of new taxa. The identification problem is more evident in more recently discovered basins such as Ettlting (unknown precise age; see table 1 in Ebber & Kölbl-Ebber 2008) and Schamhaupten (Kimmeridgian; see Viohl & Zapp 2007), but it is not a rule because fishes from older known basins like Zandt and Daiting are also incompletely known.

One of the best known fish groups of the Plattenkalk basins are the teleosts. The large clade Teleostei is represented here by lineages that are extinct today as for instance basal teleosts such as *Tharsis*, *Ascalabos*, and ichthyodectiforms, but also by basal members of the crown-group Teleostei such as the elopiforms (e.g., *Anaethalion*, *Elopsomolos*, and *Daitingichthys*), ostariophysans (e.g., *Tischlingerichthys*), and euteleosts (e.g., *Leptolepides* and *Orthogonikleithrus*) (e.g., Arratia 1997, 2004). In addition to the “true” teleosts, there are also numerous species assigned to the genus *Pholidophorus*, order “Pholidophoriformes”. However, the genus “*Pholidophorus*” as well as the “pholidophoriforms” are a non-monophyletic groups (e.g., Arratia 2000a). Consequently, the “pholidophoriforms” from the Plattenkalk are currently under revision by G. Arratia.

Our studies reveal that among the known teleostean taxa, apparently, a few species such as *Tharsis dubius* and *Leptolepides sprattiformes* are recovered from the Kimmeridgian to the late Late Jurassic. However, when these species are closely examined along the temporal dimension, they show intermediate morphological changes that make it difficult to interpret their evolving characters as part of a species in process of speciation or as new species. Among the intraspecific variation detected in *Tharsis* for example, the progressive development of the sensory tubules of the sensory canals and the variation in number and structure of the vertebrae, and of their associated elements can be mentioned. In contrast, there are other species, e.g., *Orthogonikleithrus leichi* and *O. hoelli*, that show a very local distribution, lived for a very restricted period of time, but they stand at the base of the most successful line of teleosts, the Euteleostei. Others like the elopiforms (e.g., *Anaethalion*, *Elopsomolos*) had their most important radiation in the Late Jurassic, in the Plattenkalk basins (Arratia 2000b), and in contrast to the euteleosts, the group survives today with few species.

Thus, studying the individuals of a potential taxon locally, and then comparing them with similar individuals throughout time will permit us to understand the variation involved and consequently the proper systematics of the taxon under study. The Plattenkalk basins offer this unique opportunity of local and temporal study of the taxa and their process of speciation. The age of the localities is critical (Schweigert 2007) for such studies, one million years makes a difference.

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Ammonites from the Nusplingen Lithographic Limestone (Upper Kimmeridgian, SW Germany): what they tell us about their palaeobiology

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The lithographic limestone of Nusplingen is the most important Fossilagerstätte in the Upper Jurassic of SW Germany (Dietl & Schweigert 2004). Scientific and commercial attempts to exploit this locality and ongoing excavations by the Stuttgart Natural History Museum brought to light more than 350 taxa of fossil animals and plants. Among these, ammonites and their aptychi are the most common macrofossils. In the Jurassic, ammonites show the most rapid evolution rate of all invertebrates and are therefore successfully used as guide fossils. They allow a precise dating of this fossil site into the Late Kimmeridgian (*Beckeri* Zone, *Ulmense* Subzone; Schweigert 1998). The ammonites are mostly compressed, with the aragonitic parts of the shells completely dissolved and the phosphatic siphuncles preserved. Many specimens are incomplete and exhibit a lethal damage. The damage is mostly located in the first third of the body-chamber, just in front of the phragmocone. The attack must have happened in the water column because otherwise we would expect the broken fragments lying besides the shell. It is also clear from these observations that the predator attacked the ammonite from above and not from the frontal side. Therefore we can exclude benthic animals such as crustaceans to be the predators. In contrast, the phragmocones are only rarely damaged. From stomach contents of possible nektonic predators we found examples that ammonites were fed by themselves (cannibalism), coleoids, and marine crocodiles. Most likely ammonites were also hunted by fishes, but there is no evidence yet from stomach contents. Bitten isolated aptychi or regurgitates with bitten aptychi occur frequently.

Many ammonite shells exhibit an overgrowth with small oysters. This overgrowth often occurred during the lifetime of the ammonites. Post-

mortem settling, however, is also recorded. Besides oysters only very few other settlers occur, e.g., thecideid brachiopods and cirripeds.

Many ammonites are preserved with their beaks, especially with the lower jaw, the aptychus (Schweigert & Dietl 1999, 2001). The aptychus allows a systematic placement of the ammonites in addition to shell morphology, and it was possible to prove dimorphism in distinct taxa such as *Sutneria* and *Physodoceras*. In contrast to the Solnhofen Lithographic Limestones (Keupp 2007) the corresponding upper beaks are much more frequent in Nusplingen, especially within bituminous beds. Some of the upper beaks were also found *in situ*. Originally they were not calcified but consisted of organic protein matter, which is now coalified or dissolved. Surprisingly, no remains of radulae were recorded. Both upper jaw and corresponding aptychus have equal dimensions in some genera (aspidoceratids), or the upper jaws are smaller than the aptychi (oppleiids). The aptychi are covered on their concave side with an organic layer in carbonaceous preservation. This layer occurs either still *in situ*, or it was separately buried. The different jaw apparatuses of genera correspond to different prey which is known from stomach or crop contents that consist of e.g. planktic crinoids, aptychi, sponge spicules, or phosphatic material (Schweigert & Dietl 1999). In few cases remains of the ammonites' soft parts are preserved. They are represented by a coalified matter within the body-chamber, but it is impossible to reconstruct details of its anatomy. Soft parts outside the body-chamber are unknown.

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Biomats and preservation in lithographic limestones

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Keynote

Lithographic limestones are rightly celebrated as a particular kind of Lagerstätten, in which the exceptional preservation of fossils provides us with unusual palaeobiological information. In the prototype, Solnhofen, the vertebrate *Archaeopteryx* and the echinoderm *Saccocoma* stand for this approach. Taphonomy, in contrast, focuses on the origin of such Bonanzas and their distinction from another group of conservation lagerstaetten, bituminous shales.

Both groups formed below wave base in silled basins, where quiet and toxic bottom waters excluded benthic animals. Therefore carcasses escaped disarticulation by scavengers, and depositional structures did not get disturb by burrowers. Yet, bottoms were not lifeless. Anaerobic bacteria covered the sediment surface with an organic coating that enhanced bedding planes – almost like in Proterozoic oceans (biolaminites). Also, the diagnostic degradation of ammonite shells (empty phragmocones; dissolution of the aragonitic shell, but not of the calcitic aptychi and the organic periostracum; compactional flattening) is almost identical in the two facies. What makes the difference?

Probably the size and setting of the basins, as well as climate, played a major role. While bituminous shales formed during moist and relatively cool periods and commonly in large basins, lithographic limestones are restricted to smaller depressions in warm seas with high carbonate production. This implies steeper slopes so that slow background sedimentation was commonly interrupted by turbidity currents that imported carbonate muds from shallow areas in a matter of hours. In contrast to sandy turbidites, most of these events did not disrupt the local microbial films; but their load led to the development of large-scale elephant skin structures.

Turbidity currents also introduced *live* benthic animals, such as juvenile limulids. Their death marches are recorded as undertrack *Mortichnia*

on the pre-event biomat, while the trace maker itself became buried a few millimeters higher within the turbiditic mud.

Other events included slumps of already compacted muds, with enclosed fossils being deformed according to their preservational state. Even rarer was in-place shock deformation by earthquakes. Spectacular *seismites* in the Cretaceous lithographic limestones of Tlayua (Mexico) depict compactional gradients within the top sediment.

Water chemistry in the oxygenated surface layer can be inferred from the marine versus non-marine plankton or nekton, while hypersalinity in the bottom water is indicated by osmotic dehydration. It led to characteristic bends in the articulated skeletons of vertebrates, echinoderms and arthropods. At the same time, such post-mortem deformations may be used as indicators for the consistency and stickiness of the biomat below.

Eventually, *diagenesis* developed the biological and sedimentary record like an exposed film. Here, the selective fate and redistribution of different carbonate species played the major role. It reduced the aragonitic ammonite shells to flexible periostracal membranes, while the template of the original bedding became enhanced by concentration of carbonate cement in the loosely packed event layers, separated from adjacent background sediment by microbial films. This process (a special kind of “diagenetic bedding”) produced the differentiation of “Fleins” and “Fäulen” beds, which allow slabs to be quarried without splitting.

The ultimate and most difficult question is the fate of the *organic* compounds. As in bituminous shales, organic particles must have settled from the oxygenated part of the water column and been imported by turbidity currents. They would originally have escaped recycling on the non-benthic bottoms. Where did this dispersed organic carbon go? In many cases, lithographic limestones never reached the zone of the oil kitchen. Did the organic carbon leak by another process or was it consumed in-place by lithic bacteria?

Remaining problems, like this one, can best be solved by comparison of many examples or by meetings like the present one, in which scientists of different specialisations and experiences focus on the same subject, lithographic limestones.

The Middle Triassic Cassina beds – First results from a new excavation in the Monte San Giorgio UNESCO WHL site (Switzerland)

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Cassina beds (Lower Meride Limestone, Ladinian) belong to the world-known vertebrate levels of Monte San Giorgio Lagerstätte (Canton Ticino, Switzerland). A new research project started in 2006 by the Museo Cantonale di Storia Naturale, Lugano, includes for the first time micro-palaeontology, microfacies analysis, taphonomy and palaeoecology of the whole sequence, the upper third of which has so far been excavated on a surface of around 40 m². These data complete those derived from new vertebrate finds (mainly fishes represented by the genera *Saurichthys*, *Archaeosemionotus*, *Eosemionotus* and *Peltopleurus*) and allow a better characterization of the basin.

The studied sequence records a continuous background sedimentation mirroring fluctuating but generally oxygen-depleted conditions on the bottom of a basin below the wave base and adjacent to a shallow-water carbonate platform. The background sedimentation on a dysoxic to episodically anoxic seafloor resulted in a finely laminated sequence of black shales and limestones, bearing a monotypic meiofauna of a quasianaerobic biofacies.

Turbidites and volcanic layers account for short-lived events related to the instability of basin margins and to volcanic eruptions respectively. Terrestrial macroflora remains document the presence of land areas nearby. Widespread occurrence of carbonate nodules suggests a pulsating input from the adjoining Salvatore platform from which shallow-water taxa were swept into the basin during major storms. Platform-derived biota includes dasycladaleans and a characteristic foraminiferal assemblage (*Endotriadella*, *Endotriada*, *Hoyenella*, “*Trochammina*”, *Cornuspira*). This occurrence suggests a depositional setting close to the basin margin.

A mosaic of biostratinomic processes affects the vertebrate skeletons and in turn reflects relatively dynamic bottom-water conditions rather

than permanently anoxic ones. Disarticulation is most intense in the front part of the body (head and abdominal cavity; Fig. 1), but the detailed pathways of the process clearly vary between representatives of different species. Disintegration patterns are similar to those resulting from decay processes caused by bacteria; only in a few cases, a limited influence of scavengers or bottom currents cannot be excluded. However, the common excellent preservation of fish skeletons indicates an early cessation of decay after death. Sealing by microbial mats, protecting carcasses against disintegration, may account for the excellent preservation of the vertebrates. Moreover, limiting the diffusion of chemical elements, biofilms created particular geochemical microenvironments favourable to mineralization of soft parts (Renesto & Stockar this volume, in press).

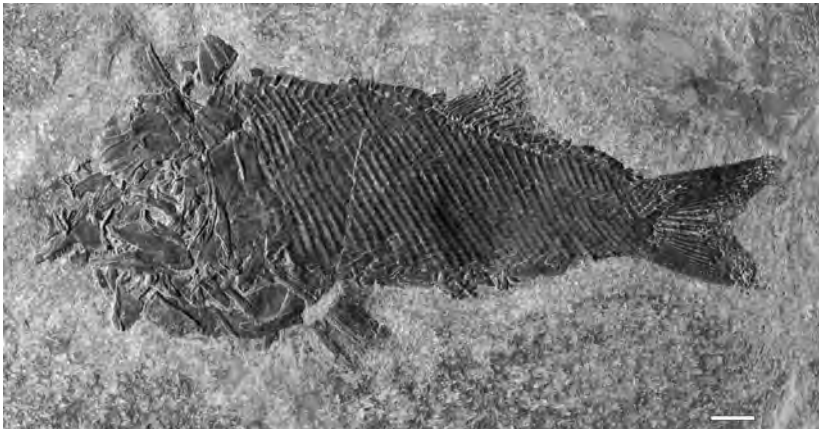


Figure 1: Typical preservation pattern in *Archaeosemionotus*. Scale bar = 1 cm.

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Field Guides

The Kraichgau Caribbean – Field guide to the clay pit Unterfeld near Frauenweiler and Rauenberg, Rupelian, Early Oligocene

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Introduction

Since Roman times the clay pits along the Langenbrücker Senke between the cities of Karlsruhe and Heidelberg yielded valuable psephitic dark clays for terracotta production, the Gold of Rauenberg (Fig. 1). First excavations took place in the 1950ies. Since then mainly private collectors excavated thousands of fossils in the shadow of wheel loaders and excavators, mostly in weekend emergency campaigns. Most of these fossils ended up in private collections, many others found their way into public museums, partially donated by honest and cooperative private collectors. Until the year 2005, the last regional clay pit, named “Unterfeld” was operated by the roof tile and terracotta company Trost GmbH. The discovery of the oldest known hummingbird, *Eurotrochilus inexpectatus* (Mayr 2004a; Fig. 4) triggered first scientific excavations in the north-eastern corner of the pit, this time in the shadow of rapidly growing infill heaps in the context with legal re-cultivation duties. Finally, the security situation became so dodgy (e.g., Fig. 6) that excavations were terminated, but the company promised to leave the last outcrop untouched until all options to rescue the locality into summer 2009 or longer were evaluated. With a meeting on the 18th of May 2009 with the responsible persons from state, region, the City of Rauenberg and science first steps were coined to rescue this unique site for long lasting scientific excavation campaigns and resulted in the permit for the 5th International Symposium on Lithographic Limestone and Plattenkalk to visit the site.

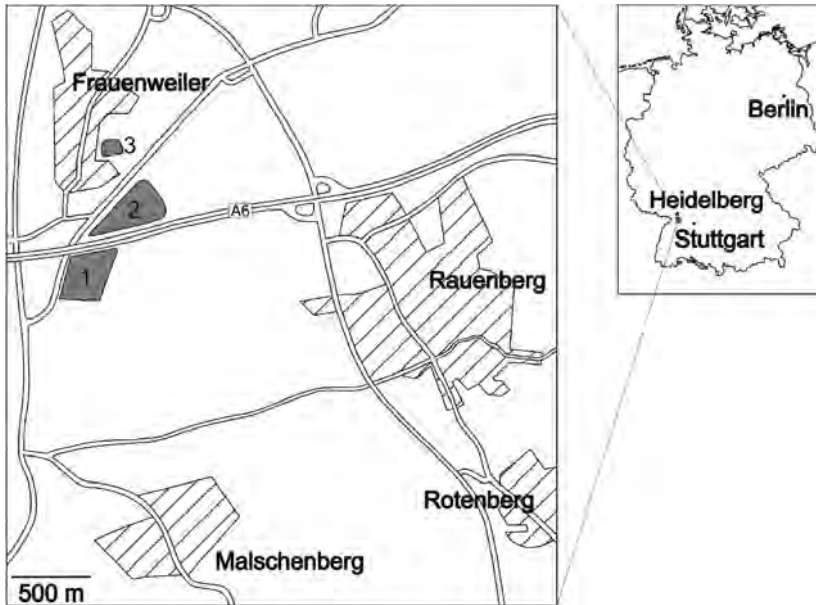


Figure 1: Positions of the clay pits Unterfeld (1), Frauenweiler-Wiesen (2) and Rohrlach (3).

Geology and palaeoenvironment

The Rupelian clays were deposited along the eastern coastline of a strait that connected the Boreal Sea with the southern Paratethys south of the City of Basel (Fig. 2). Benthic foraminifers like *Spiroplectamina carinata*, *Cibicides dutemplei* and *Cyclammina placenta* indicate a deposition depth of about 150 to 200 metres at the foot of the cliff (Grimm et al. 2002). However, other biota, such as the superabundant snipe fish *Aeoliscus heinrichi* and other teleosts, but also oysters and pelycopod gastropods indicate shallow water environments. Littoral thallophytic algae, plant remains, land birds and insects are not only prove evidence that this coastal seam must have been very narrow, but also hint to the mouth of a slow flowing river in the vicinity, which passed through a back land swamp or gallery forest full of life. The dense pattern of different terrestrial, limnic, littoral, shallow and deep marine environments combined with intercalations of dysoxic and poikiloxic seafloor conditions and short transportation distances makes the clay pit Unterfeld to an extraordinary window into Rupelian life, despite the low sedimentation rate (Grimm et al. 2002).



Figure 2: Distribution of land and sea during the Middle Oligocene (redrawn after Probst 1986); blue: sea, grey: land.

According to the predominant fossil contents, the fine grained black clays are sub-divided into three distinct beds. The *Meletta* Beds which are named after the abundant clupeid teleost *Sardinella sardinites*, formerly *Meletta sardinites* formed the top of the section along the southern margin of the pit, which is now covered by infill. The *Meletta* Beds were full of three dimensionally preserved gastropods, echinoderms and bivalves and occasionally yielded crustaceans, plant materials and, rarely fossils from the nearby land. The “Fischschiefer” or “Fish Shale” (Fig. 3) are marked by mass occurrence of the snipe fish *Aeoliscus heinrichi*. The name “Fish Shales” is indicative for millimetrically laminated sections of

Zeiteinheit		Randzone		Grabeninneres		
Quartär		Löß, Lehm, Schotter, Flugsande		Sand, Schotter, im Westen Löß		
Pliozän		Sande, lokal Ton, Lignit, am Gebirgsrand Schotter		Sande (Klebsande) lokal Ton mit Torflager		
Miozän		?		?		
Oligozän	24,6 Mio.J.	Chatthium	Hydrobien-Schichten Corbicula-Schichten Cerithien-Schichten		Mergel mit Kohlenschnüren sandige Kalke	
			Süßwasserkalke, Kalksande		Bunte Niederrödenener Schichten	
	Rupelium	Meeresand	Cyrenen-Mergel		Graue Mergel	Cyrenen-Mergel
			Meletta-Schichten			Meletta-Schichten
			Fischschiefer			Fischschiefer
			Foraminiferen-Mergel			Foraminiferen-Mergel
	38 Mio.J.	Latdorfium	Konglomerate	Sandige Mergel, Gips	Obere Pechelbronner Schichten	
			Fossilreiche Zone		Mittlere Pechelbronner Schichten	
			Konglomerate	Sande	Rote Zone	Untere Pechelbronner Schichten
	Eozän		Süßwasserkalke		Lymnäen-Mergel	
		Basiston		Basiston		

Figure 3: The Rheingraben section (in German). Zeiteinheit = time unit, Randzone = marginal zone, Grabeninneres = centre of rift. Please refer to the Rupelium unit, which is subdivided into the Meletta Beds, the Fish Shale and the Foraminifera Marls. Only the Fish Shales are visible in the outcrop (modified after Trunkó 1984).

dark grey platy marls, which are intercalating with up to 500 mm thick banks of massive mudstone. While at the bottom of the Fish Shale oxygen rich waters frequently reached the seafloor, the condition become more and more dysoxic towards the top of the section with an increasing quality of preservation. The bottom of the section is formed by the

Foraminiferenmergel or Foraminifera Marls, which are consisting of barely layered marly clays with varying sand contents. Layers with benthic foraminifera indicate the periodical presence of oxygen at the sea floor. Today, the Fish Shale is the only accessible part of the section.

The Fish Shale is extraordinarily rich in fossils. More than 70 species of fishes have been described from there (e.g., Micklich & Parin 1996; Micklich 1998). Most species comprise shallow water dwellers and/or are juvenile. However, pelagic and abyssal forms occur as well in abundance like gill rakers of *Cetorhinus parvus*, different species of Scomridae (Micklich & Hildebrand 2005) and *Lepidopus clarisianus*. Less recognised is the assemblage of secondarily aquatic and terrestrial biota

The avian theropods comprise trogons (Trogonidae), petrels (Procellariidae), the oldest known passerines (Passeriformes) and woodpeckers (Piciformes); Mayr et al. 2002; Mayr 2004a, b, 2005; Mayr & Manegold 2004). The biggest surprise was the discovery of the oldest known humming bird (*Eurotrochilus inexpectatus*, Trochilidae; Mayr 2004a; Fig. 4), which not only pushed back the origin of this enigmatic group of birds by some 25 mio years, but also shifted it into Old Europe. The avian assemblage is dominated by terrestrial birds, whereas the sea birds with two described species are underrepresented. Bats

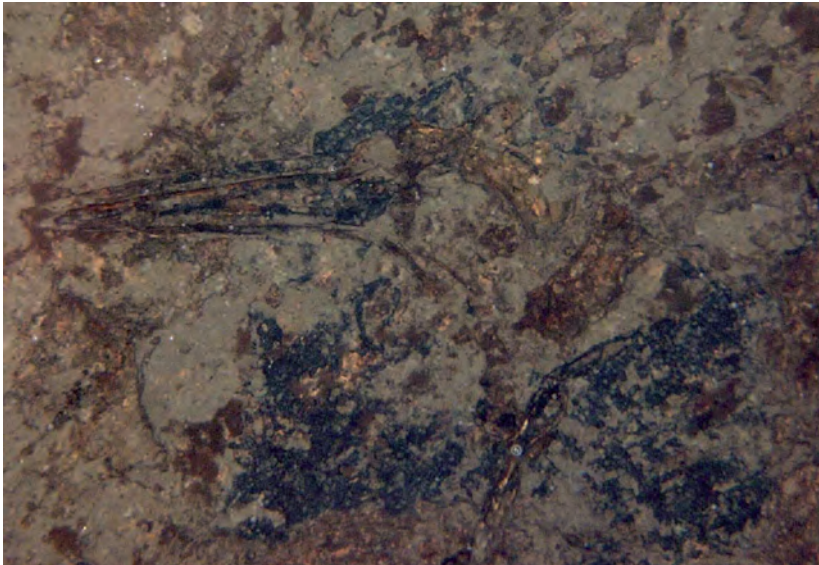


Figure 4: *Eurotrochilus inexpectatus* (Trochilidae). This specimen was poked out with a spade by a student in the year 2005 during an excursion. The beak is 30 mm long.

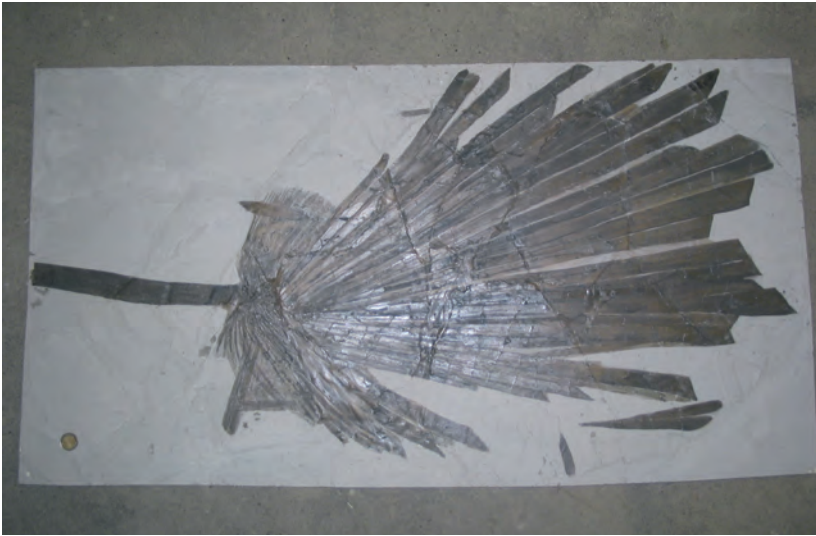


Figure 5: A palm leaf. The scale is a two-euro coin (bottom left).

(Microchiroptera), sea turtles (Chelonidae), sea cows (Sirenia) and the fragmentary mandible of the creodont *Apterodon* are exceedingly rare.

The insect assemblage is very rich for a coastal marine environment. Due to taphonomical bias the assemblage mostly comprises beetles (Coleoptera) and bugs (Heteroptera), but there are also records of an apocrite hymenopteran, a butterfly or trichopteran (Amphiesmenoptera) and a possible mantid (Mantodea), all with little fossilisation potential (Monninger 2009).

The presence of abundant lauraceans, areaceans (Fig. 5) and conifers in the back lands is evidenced by nicely preserved leaves. While leaves show cuticula preservation, wood is compressed and coaly, lacking any structure. Ferns and thallophytic algae are very rare.

Benthic life occurs in distinct layers, which decrease in abundance towards the top of the Fish Shale. There are single layers with extensive bioturbation. The burrows occasionally protrude into the dysoxic beds below. The diameter of the tunnels reaches from half a millimetre to more than 10 mm. Benthic foraminifera are occasionally abundant and easily visible without a hand lens.



Figure 6: One of the landslides that terminated the excavation in autumn 2008. The grey material represents the Fish Shale.

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The field-trip (Monday 17th August): information and instructions

The trip: On the way from Basel to Karlsruhe we will travel north-bound through the Oberrheingraben, the silent rift that traces the strait that connected the Boreal Sea with the Paratethys during the Oligocene. On the right you will see the mountains of the Black Forest (Coo-coo Clock Mountains), on the left, in the far distance, the Vosges and, when reaching the Karlsruhe area, the Pfalz Forrest. Level with Karlsruhe, the Black Forrest terminates and the Kraichgau begins, the Toscana of Germany. On the way from Basel to the north, the geology changes from granite and gneiss basement to the Triassic Buntsandstein level with Freiburg and finally to Triassic Muschelkalk in the Kraichgau. Northwest of Freiburg you might see the Kaiserstuhl which is a volcanic structure of Tertiary age. Due to rifting the land between the Black Forest and the River Rhine form a rift shoulder with an exceedingly complicated geology, which is dominated by Mesozoic sediments covered by thick Löss beds. Depending on the soils and the geological underground you will observe a variety of orchards, crops, hop field for making beer, cannabis (mostly for fibre production) and tobacco fields. The vineyards yield some of the finest wines of the county and finally, in the sandy areas of the Quarternary rift infill of the Rhine there are asparagus, potato and corn fields, especially in the northern part of the trip. The Kraichgau, especially the area around the City of Rauenberg is recognised for its excellent wines, sausages and great hospitality. If you want to buy wine in Rauenberg – let us know.

The clay pit: If you want to enter the pit you will be asked to fill and sign a form that excludes the owner of the pit from any responsibility. The coach will park outside the terrain and you will have to walk for about 800 metres along a dirt road into the pit. When entering the digging area we will provide an introduction to the site and its specialities and – if there are not too many people – you might experience some decent digging, wheelbarrow pushing shovelling etc. A hand lens and decent footwear is appreciated. In case of rain, the clay pit converts into a slippery mud puddle with no more friction for any kind of footwear – with the exception of glacier spikes probably. In this case, we do not dig but go for an alternative.

Further programme: This will remain a secret!

Field-trip to the excavations in the Late Jurassic along the future Transjurane highway near Porrentruy (Canton Jura, NW Switzerland): dinosaur tracks, marine vertebrates and invertebrates

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1. Introduction

This one-day field-trip (21.08.2009) to the Late Jurassic palaeontological excavations sites along the future course of the federal highway A16 "Transjurane" near Porrentruy (Canton Jura, NW Switzerland) accompanies the 5th International Symposium on Lithographic Limestone and Plattenkalk.

First, we will visit the excavations in the Late Kimmeridgian Marnes à *virgula*. These claystones are extremely rich in small oysters ("*Exogyra virgula*", *Nanogyra* sp.) and they frequently bear marine vertebrates, notably fishes, turtles and crocodylians. Besides remains of marine vertebrates, the under- and overlying (marly) limestones yield a diverse and rich invertebrate fauna, which was first described by Thurmann & Etallon (1861-1864). It is thus possible to collect typical Jura fossils such as *Ceratomya* sp., *Homomya* sp., *Pholadomya* sp., *Sellithyris* sp., and others on the excavation sites.

Afterwards, we will move to two dinosaur tracksites, which are situated in immediate geographic and stratigraphic proximity to the Marnes à *virgula* excavations. The tracksites are located in two different laminite intervals of slightly different age at the transition from the Early to the Late Kimmeridgian. Tracks of sauropod and theropod dinosaurs will be observed during daylight and after dinner at night. Therefore, we will install a special nocturnal illumination; so don't forget to bring your camera!

Because the visited sites are located close to active highway construction sites we will have to provide you with safety vests, and we recommend you to wear good (closed) shoes.

1.1 History of the Palaeontology A16

Even though in Switzerland archaeological survey projects exist for federal highways since 1960, the importance of safeguarding the palaeontological heritage was only recently recognized. As a result of the construction of the Transjurane highway a new project, further named Palaeontology A16, was established in February 2000 in the Canton Jura. Initially named *Section de paléontologie*, this project is now integrated in the *Section d'archéologie et paléontologie* of the *Office de la culture* of the Canton Jura. The Palaeontology A16 is financed by the Swiss Federal Roads Authority (95%) and the Canton Jura (5%). Its purpose is to excavate and document the palaeontological heritage along the future highway course in the Canton Jura, and to make it accessible for scientific research (e.g., Marty & Hug, 2003; Hug et al. 2004; Marty et al., 2004; Ayer et al., 2005, 2006).

1.2 Methodology of the Palaeontology A16

Palaeontological and sedimentological prospection combined with geological mapping determines the approximate position of the most promising beds on the highway course (Fig. 1A). Afterwards, prospective excavations are performed using a shovel excavator (Fig. 1B). If significant findings are made, an excavation can be planned. Large-scale excavations may last up to several years and are carried out well before the construction of the highway, scheduled in agreement with the civil engineering office (Fig. 1C, D). Important discoveries are sometimes made during the construction of the highway. In this case, a suitable solution for an emergency excavation has to be worked out with the highway engineers in charge.

The excavation of macrofossils happens in the field applying classical palaeontological techniques (Fig. 1D) but also include the use of heavy machines to extract large blocs (Fig. 1E). Microfossils are isolated in the laboratory by screen-washing. Modern documentation techniques such as laser scanning (Leica Geosystems 2003) and photogrammetry (Fig. 2) are also applied (see also Paratte et al. this volume). This completes the classical documentation techniques such as graphic documentations (Fig. 1F) and casts, and enables a virtual reconstruction of the tracksites (e.g., Hurum et al. 2006; Bates et al. 2008a, b). This is particularly important,



Figure 1: Methodology of the palaeontology A16. **A:** The study of reference quarries is important to locate fossiliferous beds on the highway course. The “La Combe” quarry near Chevenez is a reference section (Jank et al. 2006a, b) for the upper Reuchenette Formation (Early to Late Kimmeridgian). The section that can be observed during the excursion is located between the intermediate levels and the Coral Limestones. **B:** Palaeontological prospecting (near Porrentruy) allows identifying the most important beds and determines the approximate position of a future excavation area. **C:** Excavation of the main track level at the Chevenez–Combe Ronde tracksite. Overburden was removed with heavy shovel excavators. This site is meanwhile protected by the extension of the highway bridge, which is visible in the upper left of the picture. **D:** Excavation of the Marnes à *virgula* with a shovel excavator. In the foreground a branch of a wood is uncovered with fine handtools (photograph by Patrick Dumas / Look at Sciences). **E:** Extraction of a track-bearing surface, cut into several blocs, at the Courtedoux–Bois de Sylleux tracksite, level 1040. **F:** Graphic documentation of a turtle carapace in the Marnes à *virgula* (Courtedoux–Tchâfouè).

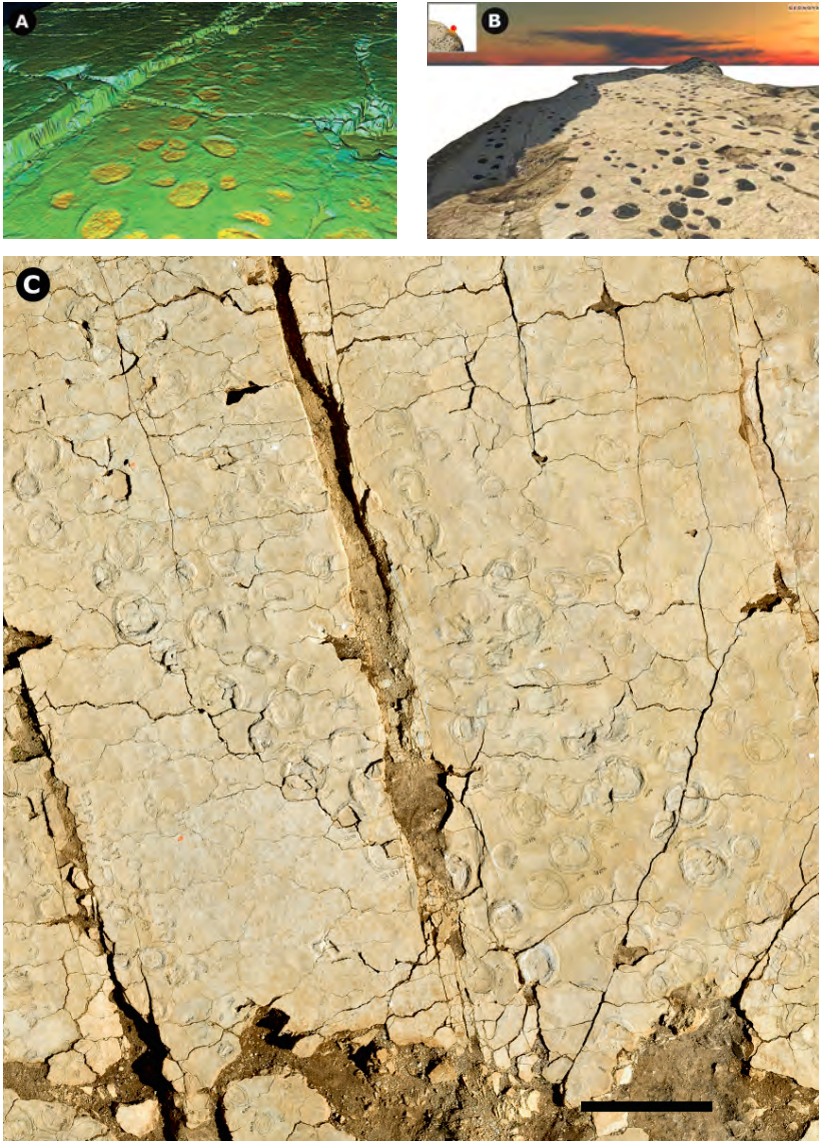


Figure 2: High-resolution (in the order of 1-2 mm) laserscanning and close-range (2-10 m from camera to object) photogrammetry of dinosaur track-bearing surfaces. **A:** Laserscan of a cross-roads of three sauropod trackways (Courtedoux–Sur Combe Ronde tracksite, main track level). **B:** Virtual 3D model of a track-bearing surface based on photogrammetric and laserscanning data (Courtedoux–Tehâfouè, main track level). **C:** Photogrammetry of a surface with several parallel sauropod trackways. Courtedoux–Bois de Sylleux tracksite, level 1040, scale bar is 1 m.

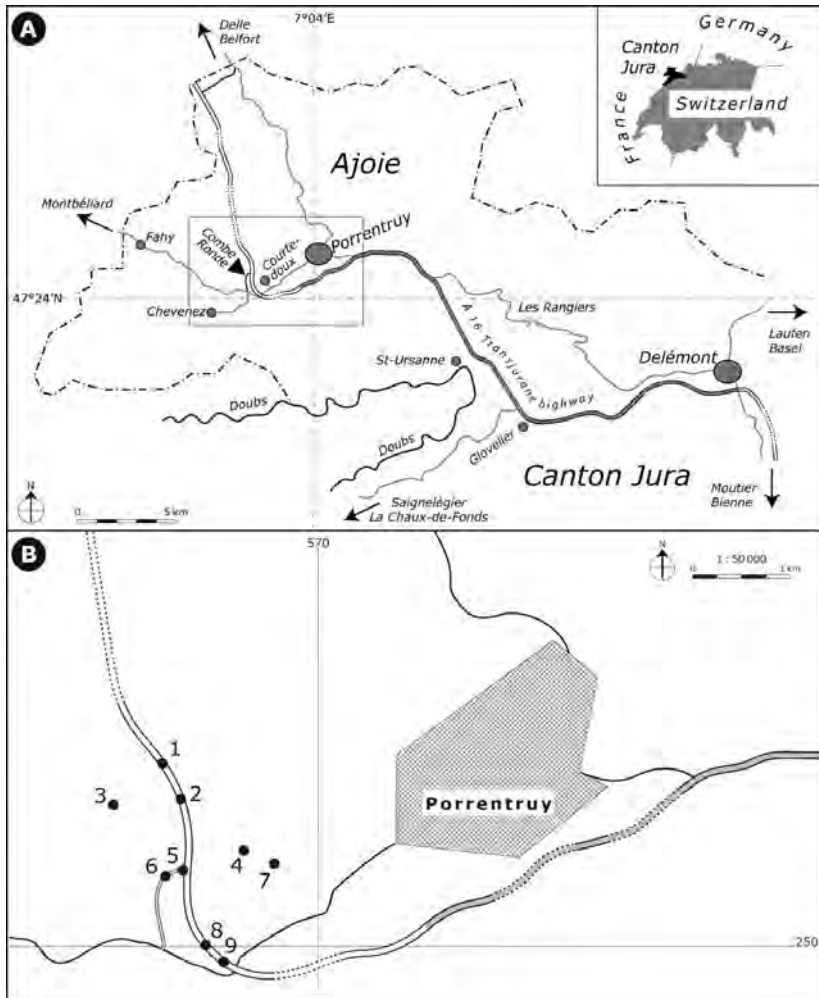


Figure 3: A: Geographical setting of the Ajoie district (NW Switzerland) and the Late Jurassic excavations and tracksites along the Transjurane highway; inset shows location within Switzerland. The box encompasses the map shown in B. B: Close-up of the area around Courtedoux and Chevezey with the tracksites of the Transjurane highway and the trackways outside the highway indicated. From north to south: (1) Courtedoux–Béchat Bovais, (2) Courtedoux–Bois de Sylleux, (3) Courtedoux–Pommerats, (4) Courtedoux–Oratoire, (5) Courtedoux–Tchâfouè, (6) Chevezey–Combe Ronde, (7) Courtedoux–Dessus Latchire, (8) Courtedoux–Sur Combe Ronde and (9) Chevezey–Crat. The field trip will lead us to the “Bois de Sylleux” and “Béchat Bovais” sites. The Marnes à *virgula* are currently excavated at the Courtedoux–Bois de Sylleux. Other sites where the Marnes à *virgula* were or will be excavated are Courtedoux–Tchâfouè and Courtedoux–Sur Combe Ronde.

if a track-bearing surface is later displaced, covered up, or destroyed (e.g., Lockley & Matthews 2007).

At the end of an excavation recovered fossils and slabs, samples, casts and replicas are archived, and the documentation (e.g., illustrations, photographs, track parameters, etc.) is assembled in a database (collection and documentation management).

All sites excavated by the Palaeontology A16 are named in a binominal way: first the community is indicated, followed by the name of the site. Accordingly, the Courtedoux–Béchat Bovais tracksite is the “Béchat Bovais” tracksite on the parish area of Courtedoux. For each site an acronym is defined, which is composed of two times three capital letters, separated by a hyphen, e.g., CTD-BSY for the Courtedoux–Bois de Sylleux site.

2. Geographical and geological setting

The Late Jurassic excavation sites and tracksites of the Palaeontology A16 are all located in the Ajoie district of the Canton Jura (NW Switzerland) on a plateau between Courtedoux and Chevenez about 6 km to the west of Porrentruy (Fig. 3). The Ajoie district borders in the south the Delémont and Franches-Montagnes districts and most parts are relatively flat with a mean elevation around 500 metres. The dominant morphological features are dry valleys, which have been generated by karstic dissolution (main process) and fluvial erosion (accessory process) along faults (Braillard 2006a, b).

The Ajoie is located at the eastern end of the Rhine-Bresse transfer zone between the Folded Jura Mountains to the south and east and the Upper Rhine Graben and Vosges Mountains to the north (Fig. 4). It belongs almost entirely to the Tabular Jura, which consists of slabs of sub-horizontally layered Mesozoic strata (Trümpy 1980). In the south of the Ajoie, near the front of the Folded Jura (Mont Terri anticline), detached folds of the Folded Jura are overthrust onto the Tabular Jura (Tschopp 1960). From the Eocene to the Pleistocene, five tectonic phases created a complex set of fractures in the bedrock, as well as small, low amplitude anticlines (Giamboni et al. 2004; Ustaszewski et al. 2005; Braillard 2006b).

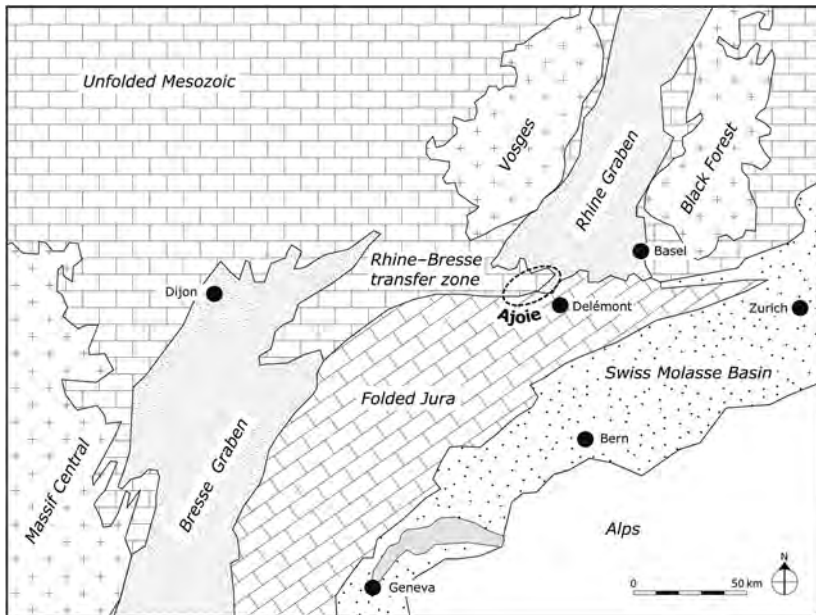


Figure 4: General geological setting showing the position of the Jura arc and the Ajoie. Redrawn after Brailard (2006a, b) and modified from Marty et al. (2007).

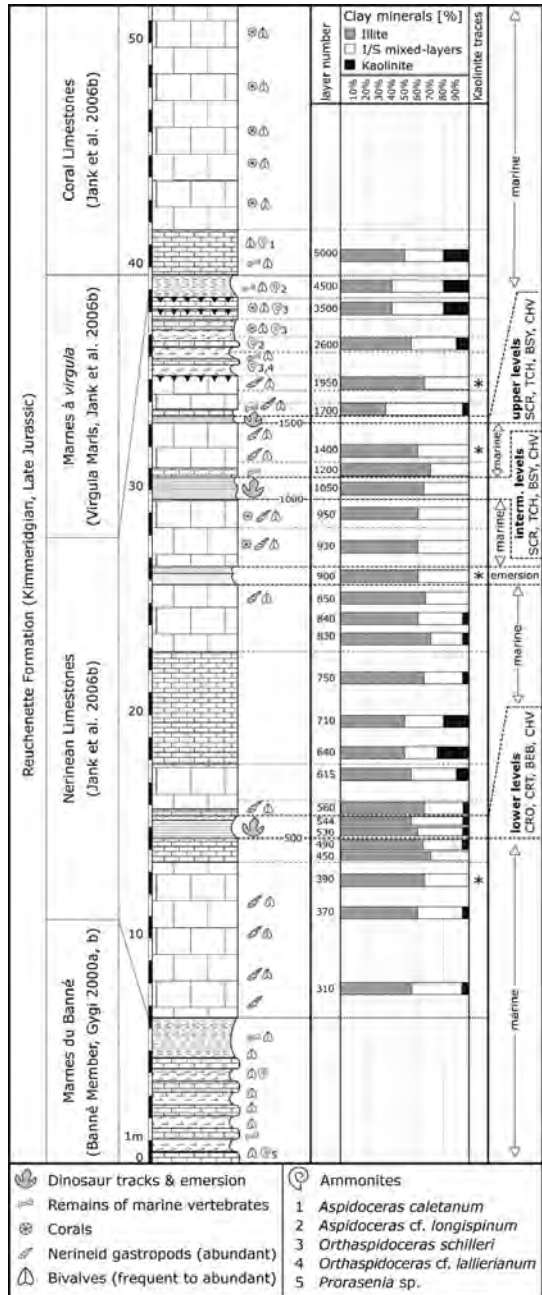
3. Stratigraphical setting

The Ajoie district is almost entirely composed of sedimentary rocks attributed to the St-Ursanne, Vellerat, Courgenay, and Reuchenette Formations and their respective members, which are Middle Oxfordian to Late Kimmeridgian (*sensu gallico*) in age (e.g., Gygi 1995, 2000a, b; Gygi et al. 1998).

The visited excavations are located in the Reuchenette Formation between the Marnes du Banné (Banné Member *sensu* Gygi, 2000a, b) and the Marnes à *virgula* (Virgula Member *sensu lato* of Gygi 2000a, b; northern Virgula Marls in Jank et al. 2006a; Virgula Marls in Jank et al. 2006b; lower Virgula Member in Colombié & Rameil, 2007). In between, i.e. within the Nerinean Limestones defined by Jank et al. (2006b), three emersive intervals, named lower (track) levels, intermediate (track) levels, and upper (track) levels reveal dinosaur tracks and testify prolonged periods of emersion of the Jura carbonate platform (Fig. 5).

The Reuchenette Formation was originally defined by Thalmann (1966). In the Ajoie region it has a maximum thickness of more than

Figure 5: Schematic figure of the lithological succession of the Reuchenette Formation between the Marnes du Banné and the Marnes à *virgula*. So far, three track-bearing intervals, named lower, intermediate, and upper levels and are indicated in the right column. The abbreviations indicate which levels crop out at which tracksite, from bottom to top: CRO = Chevezé-Combe Ronde; CRT = Chevezé-Crat; BEB = Courtedoux-Béchat Bovais; CHV = Chevezé-La Combe (quarry); SCR = Courtedoux-Sur Combe Ronde; TCH = Courtedoux-Tchâfoué; BSY = Courtedoux-Bois de Sylleux. The Marnes à *virgula* are located about 5 m above the upper track levels. Also indicated is the position of ammonites, and for selected layers the clay mineralogy, which was analyzed by J.-F. Deconinck (University of Dijon). From Marty (2008).



STAGE	FORMATION	TETHYAN REALM Hardenbol et al. (1998), <i>sensu gallico</i>			BOREAL REALM Hardenbol et al. (1998), <i>sensu anglico</i>			Approximate position of the three track-bearing laminites intervals	
		Ammonite zones		Time span according to Hardenbol et al. (1998)	Sequences	zones	Ammonites		
		Ammonite zones	Sequences	Ages (Ma)	Sequences	zones	sub-zones		horizons
Late Kimmeridgian	Reuchenette	EUDOXUS	MF		Kim 6 MF	EUDOXUS	Contejeani	Vo Contejeani Quercyrum Caletonium	Biostratigraphic & lithostratigraphic key elements of the Transjura trackites - <i>O. caletanum</i> "Coral Limestones" Marnes à <i>virgula</i> <i>O. schilleri</i>
		ACANTHICUM	MF	152.01	Kim 4 MF	MUTABILIS	Orthocera	Calvescens Hybridus Orthocera	
		DIVISUM	MF	152.70	Kim 3 MF	CYMODOCE	Chateilaillonensis	Schilleri Lallierianum Mutabilis Attenuatus Desmonotus Lineatus Discoidus Chateilaillonensis Askepius Ranicata Aulinea	

Figure 6: Chrono-, bio- and lithostratigraphical context of the Kimmeridgian Reuchenette Formation and the three track-bearing levels of the dinosaur track-sites in Ajoie, Canton Jura: Tethyan (*sensu gallico*) and boreal (*sensu anglico*) ammonite zonations, sequence boundaries Kim3 to Kim4, and maximum-flooding surface (MF) according to Hantzpergue et al. (1997) and Hardenbol et al. (1998).

140 m (Jank et al. 2006a). Mineralo-stratigraphic, sequence-stratigraphic, and cyclostratigraphic studies carried out by Mouchet (1998), Colombié (2002), Colombié & Strasser (2003, 2005), Jank et al. (2006a, b, c), and Keller et al. (2006) in the Kimmeridgian and by Rameil (2005) in the Late Kimmeridgian and Tithonian provide the lithostratigraphical frame and put forward a Tethyan-to-Boreal correlation for the Kimmeridgian (Jank et al. 2006a, c; Colombié & Rameil 2007). A cyclostratigraphical synthesis is given by Strasser (2007).

Since the excavations of the Palaeontology A16 started, many ammonites have been discovered establishing a well-defined biostratigraphical frame for the Reuchenette Formation of northwestern Switzerland (Figs. 5, 6; Jank et al. 2006a, b, c). The newly discovered ammonites place the interval between the Marnes du Banné and the Marnes à *virgula* between the late Early Kimmeridgian and the early Late Kimmeridgian (Figs. 5, 6).

During this fieldtrip we will visit the Courtedoux–Bois de Sylleux site, where the Marnes à *virgula* and the intermediate and upper track levels are excavated, and the Courtedoux–Béchat Bovais tracksite, where the lower track-bearing levels are excavated.

Generally, the track-bearing levels can be described as a marly, platy limestone or biolaminite, even though the upper levels are much thinner and marlier than the lower and intermediate levels. Within the intermediate levels, suggested to represent an elementary sequence of 20 kyr, dinosaur tracks have been found on at least 14 distinct surfaces suggesting the recurrent presence of dinosaurs in a supratidal flat to marsh environment (Marty et al. 2006). Besides dinosaur tracks, invertebrate burrows (e.g., *Thalassinoides*), desiccation cracks, and ripple and wrinkle marks are also commonly found, and can be observed during the fieldtrip.

The lower track levels are situated about 10 metres above the Marnes du Banné and approximately at the boundary from the Early and the Late Kimmeridgian (Figs. 5, 6) that is somewhere in between the Tethyan sequence boundaries Kim3 and Kim4 of Hardenbol et al. (1998). The sequence boundary Kim4 probably corresponds to the upper track levels, even though it was placed by Colombié & Rameil (2007: fig. 10) in the intermediate levels. Assuming that Kim4 corresponds to the upper levels, the intermediate levels could be correlated with the laminated beds of the small-scale sequence 22 of Colombié (2002: fig. 5.1) and of the small-scale sequence 52 of Strasser (2007: fig. 10).

The Marnes à *virgula* can be interpreted as transgressive or and/or maximum flooding deposits of small-scale sequence 24 of Colombié (2002) and small-scale sequence 54 of Strasser (2007). Accordingly, a small-scale depositional sequence, corresponding to the 100 kyr

Mylankovitch cycle (Strasser et al. 1999, 2006), can be postulated for the deposits between the upper track levels and the Marnes à *virgula*.

4. Palaeogeographical, palaeoenvironmental and palaeoclimatological setting

During the Late Jurassic, the original position of today's Jura Mountains was located at the northern margin of the oceanic Ligurian Tethys (e.g., Gygi 1990; Thierry et al. 2000; Stampfli & Borel 2002) as a large, structurally complex shallow carbonate platform (Fig. 7). This platform was at a palaeolatitude of around 30° N, at the threshold between the Paris Basin to the northwest and the Tethys Ocean to the south and thus, influenced by both the Tethyan and Boreal realms (Ziegler 1988; Dercourt et al. 1994; Smith et al. 1994; Dercourt et al. 2000; Thierry 2000a, b).

During the Late Jurassic, the western Tethys was already subjected to sinistral translative movements between Africa and Laurasia induced by northward propagation of the Atlantic spreading axis. As a consequence of these movements, compressional stresses developed in the eastern parts of the Tethys, whereas in the western parts sea-floor spreading diminished. Supported by accelerated rifting in the North Atlantic, this led to a general thermal doming and associated sea-level fall, which caused widespread emergence (Late Kimmerian unconformity) of the Hercynian-Armorican, London-Brabant, Central, Rhenish, and Bohemian Massifs (Meyer & Schmidt-Kaler 1989; Dercourt et al. 2000; Thierry 2000a, b).

The Jura carbonate platform was subdivided into open lagoons, internal lagoons, ooid shoals, reef barriers, tidal flats, supratidal flats and marshes, and land surfaces (e.g., Colombié 2002; Hug 2003; Colombié & Strasser 2005; Marty 2005; Jank et al. 2006a, c; Rameil 2005; Védrine 2007; Védrine et al. 2007). Lagoonal facies rich in carbonate-producing organisms, coral patch-reefs and ooid shoals testify to warm, subtropical waters. Water depths varied between a few tens of metres in the open lagoons to intertidal and supratidal along the coasts. Controlled by syn-sedimentary tectonics, epicontinental basins developed mainly to the south of the platform (Allenbach 2001; Allenbach & Wetzel 2006). Consequently, the Kimmeridgian of the Ajoie is essentially made up of shallow marine carbonates and marls, in function of terrestrial input related to eustatic sea-level changes and climatic conditions.

Small-scale sea-level drops repeatedly created vast emergent areas as is proven by the numerous dinosaur tracksites of the Jura arc. Hence, dinosaurs habitually entered this coastal marine environment (Fig. 8) from the *Süddeutsche Schwelle* (located at the south-eastern border of the London-

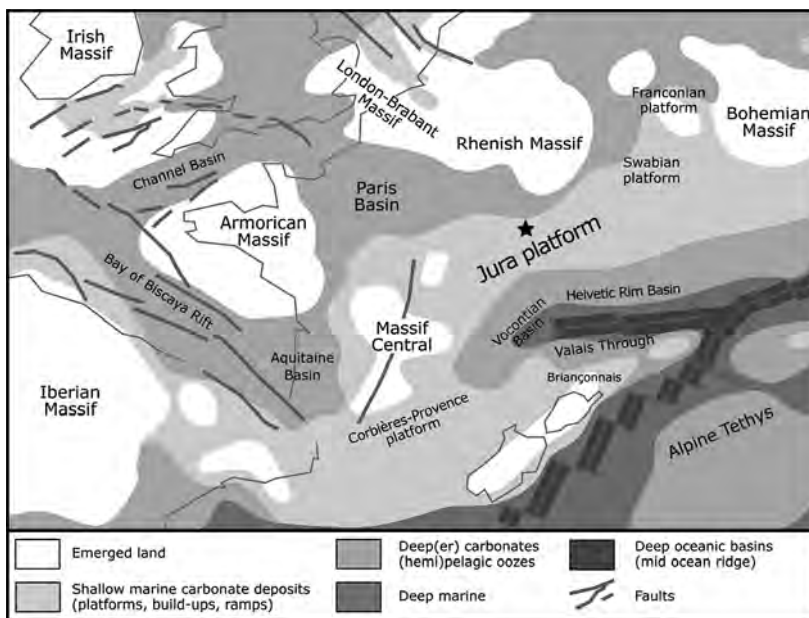


Figure 7: Palaeogeographic setting of the Jura carbonate platform during the Kimmeridgian (Late Jurassic, approximately 152 Ma). After Thierry et al. (2000a, b). The palaeogeographical position of Corsica and Sardinia is interpreted differently in other reconstructions (e.g., Stampfli et al. 2002). Asterisk marks the approximate position of the study area.

Brabant Massif) in the northeast, or from the Massif Central in the south-west (Meyer & Lockley 1996; Meyer et al. 2006).

During the Kimmeridgian, the climate of the Jura carbonate platform was subtropical, and is generally considered semi-arid to arid (e.g., Hallam 1984, 1985; Frakes et al. 1992; Moore et al. 1992; Ross et al. 1992; Moore & Ross 1994; Weissert & Mohr 1996; Bertling & Insalaco 1998; Billon-Bruyat et al. 2005). Periodically, especially during Oxfordian times, siliciclastics originating from the Bohemian and the Central massifs were shed onto the platform and into the basins (e.g., Gygi & Persoz 1986; Pittet 1996), which implies generally more humid conditions. In the Kimmeridgian, siliciclastics are less abundant and evaporites occur, suggesting an evolution towards a generally more arid climate (Colombié 2002; Hug 2003). This is also supported by the generally low content of kaolinite in the clay mineral fraction of the interval between the Marnes du Banné and the Marnes à *virgula* (Fig. 5).

On the Jura carbonate platform, clays are often associated with the shallowest and/or early transgressive phase. This is explained by an



Figure 8: Interpretation of the near-coastal palaeoenvironment (drawing by T. Yilmaz).

increased erosional potential in the hinterland following a rapid fall of relative sea level, possibly in combination with increased rainfall in the hinterland due to climatic changes depending on atmospheric circulation patterns (e.g., Mouchet 1998; Strasser & Hillgärtner 1998; Strasser et al. 1999; Hug 2003). If the clay minerals were formed and/or eroded in the hinterland (i.e., in the Rhenish Massif and the London-Brabant Massif to the N-NW, the Bohemian Massif to the NE, or the Massif Central to the SW) they were transported from the parent rocks in the continental source area to the Jura carbonate platform by water currents or by wind, as it has been suggested for the detrital quartz (e.g., Bolliger & Buri 1967, 1970; Gygi & Persoz 1986; Hug 2003). Since the increase in kaolinite is associated with the most normal marine conditions and the highest generation in accommodation space, it is suggested that the kaolinite was reworked in the hinterland and not on the Jura carbonate platform. However, Waite et al. (2009) recently postulated the existence of terra rossa-type soils on the platform as a possible source for kaolinite. Another possibility is that immature palaeosols on the platform were a source for the mixed layer clay minerals and could explain the low kaolinite/illite ratio.

5. Dinosaur track excavations

Dinosaur bones of *Cetiosauriscus greppini* von Huene, 1927 were discovered already in the 19th century in the Early Kimmeridgian of the Basse Montagne quarry, which is located near Moutier, Canton Berne

(Greppin 1870; von Huene 1922; Schwarz et al. 2007). However, the first dinosaur tracks were discovered only in 1989 in the Lommiswil quarry near Solothurn (Meyer 1990). This attested for the first time unequivocally the presence of larger and connected landmasses on the Jura carbonate platform during the Late Jurassic (Meyer 1993). Lockley & Meyer (2000) stated that “the classic Jura region is full of tracks that were previously not known to exist”. Indeed, since the initial track discovery in the Lommiswil quarry, more than 20 tracksites have been discovered in the Late Jurassic of the Swiss Jura Mountains (review in Meyer & Thüring 2003), culminating in the discoveries in the Ajoie (Canton Jura) along the Transjurane highway (Marty et al. 2007), and more recently also in the French part of the Jura Mountains near Coisia (Le Loeuff et al. 2006) and Loulle (Mazin & Hantzpergue 2006).

Consequently, dinosaur tracksites became useful not only regarding scientific research, but also regarding the high level of media and public interest and their great educational value. Today, the tracksites of the Jura Mountains are generally considered as geotopes, or as important parts of the natural heritage (Marty et al. 2004). Accordingly, the larger sites are now in the focus of a more popular and touristic interest. For these reasons, the Canton Jura has allocated in August 2008 3.5 million Swiss Francs to the “Paléojura” project in order to valorize the dinosaur tracksites and the palaeontological heritage in general in terms of science, education, and tourism (www.palaeojura.ch/projetcantonal/f/).

On the future course of the Transjurane highway, the Courtedoux–Sur Combe Ronde tracksite was the first dinosaur tracksite discovered and excavated in 2002. Marty et al. (2003) reported from the main track level 17 sauropod trackways, which they assigned to the ichnogenus *Parabrontopodus*, and two tridactyl, bipedal trackways, attributed to large theropods. The Chevenez–Combe Ronde site was the second tracksite discovered on the future course of a feeder road to the Transjurane highway and is in the focus of the PhD thesis of Marty (2008).

Meanwhile, on the Transjurane highway, dinosaur tracks were found and (partially) excavated on six extensive tracksites, in a nearby quarry in Chevenez (associated with the construction of the highway), and also on several sites beside the Transjurane highway due to cantonal prospecting (Fig. 3). These excavations resulted in several contiguous outcrops, and the so far excavated track-bearing surfaces sum up to more than 16'000 square metres.

The particularity of the Transjurane tracksites is that they reveal tracks within three stratigraphic intervals (Fig. 5), and each of these intervals yields tracks on several superimposed levels. Currently, tracks have been found on over thirty distinct levels. This resulted (by the end of 2008) in

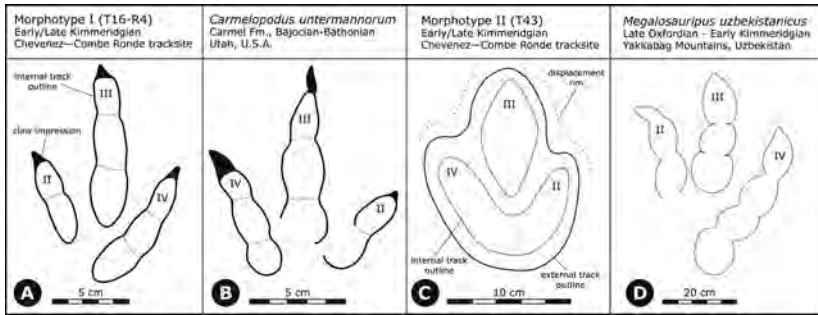


Figure 9: **A:** Typical track (T16-R4) of the Chevenez–Combe Ronde site attributed to morphotype I. **B:** Outline drawing of *Carmelopodus* after Lockley et al. (1998a: fig. 9, right track, p. 264). **C:** Schematic outline drawing of T43-R2 of the Combe Ronde tracksite highlighting the typical features of morphotype II, which shares typical features of *Therangospodus* and ornithopod ichnotaxa. **D:** Outline drawing of *Megalosauripus* after Lockley et al. (1998b: fig. 8, lower right, p. 325); identification of digits after trackway shown in their figure 12d. Modified from Marty (2008).

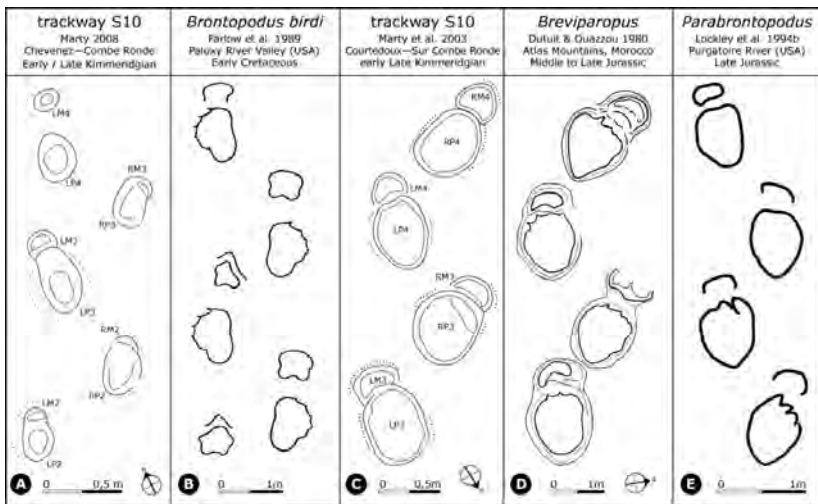


Figure 10: Comparison of trackway S10 from the main track level of the Chevenez–Combe Ronde site and trackway S10 from the main track level of the Courtedoux–Sur Combe Ronde site with other Middle to Late Jurassic and Early Cretaceous sauropod ichnogenera. **A:** Trackway S10 from main track level of the Chevenez–Combe Ronde site. **B:** Redrawn after Farlow et al. (1989: fig. 42.3, p. 374). **C:** Redrawn after Marty et al. (2003: fig. 5, p. 212). **D:** Redrawn after Ishigaki (1989: fig. 9.5, p. 85). **E:** Redrawn after Lockley et al. (1986: fig. 7b, p. 1170). From Marty (2008).

the systematic excavation and documentation of dozens of ichnoassemblages with a total of over 6400 dinosaur tracks including 177 trackways of sauropods and 234 trackways of bipedal dinosaurs. Because many tracks were located on superimposed levels and had to be destroyed by the ongoing excavations, dozens of casts were fabricated and considerable track-bearing surfaces were displaced and recovered, resulting in a large track collection actually stored in the repositories of the Palaeontology A16 in Porrentruy. Additionally, the most important surfaces were also documented by laserscanning and photogrammetry. All this results in an important ichnological database and track collection, which is currently in a phase of organization and assessment by the Palaeontology A16.

All these excavated ichnoassemblages are referred to as “Ajoie ichnoassemblages” (Marty, 2008), which is characterized by the dominance of minute and small tridactyl tracks (Fig. 9A), tracks of medium-sized to large bipedal dinosaurs (Fig. 9C), and by tracks of tiny to large sauropods (Fig. 10). Sauropod trackways are narrow-gauge (Fig. 10C) and (very) wide-gauge (Fig. 10A) possibly indicating the presence of the ichnogenera *Parabrontopodus* and *Brontopodus* (Marty 2008), which are commonly attributed to basal and derived sauropods, respectively (Wilson & Carrano 1999).

5.1 The Courtedoux–Bois de Sylleux tracksite

At “Bois de Sylleux”, track excavations started in the year 2004 and they will end in 2009. Afterwards, the site is covered and partially destroyed by the construction of the Transjurane highway and will not be accessible anymore.

During the excursion, dinosaur tracks of sauropods and theropods (Fig. 12), ripple marks (Fig. 11C), desiccation cracks (Fig. 11D), microbial “build-ups”, and invertebrate burrows (e.g., *Thalassinoides*) will be visible on different surfaces of the intermediate and upper track levels. The intermediate track levels are characterized by a pronounced biolaminated (stromatolithic) appearance and small, pustular microbial “build-ups” on the main track level (Fig. 11A).

So far, the excavations at “Bois de Sylleux” yielded remarkable discoveries, such as tracks of small to medium-sized tridactyl, bipedal dinosaurs (probably theropods), of huge sauropods (up to 1.1 m pes length, Figs. 12A, B), of very large theropods (ca. 0.8 m pes length, Fig. 12A, D), and notably of tiny “baby” sauropods (around 10 cm pes length). The most important tracks were casted and/or extracted and are not visible in the field anymore, but casts of these tracks will be shown during the fieldtrip.

Above the intermediate levels follows a 20-30 cm thick lag deposit with an accumulation of oysters at the base, and which is rich in marine

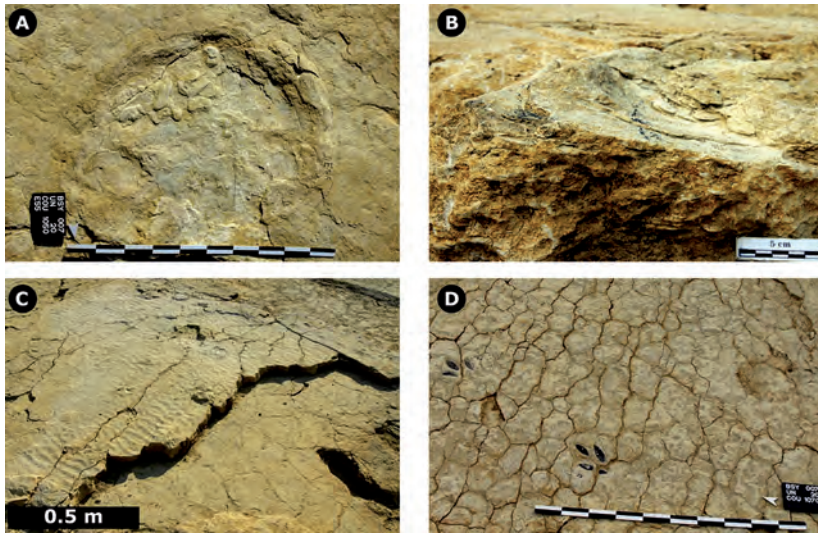


Figure 11: Courtedoux–Bois de Sylleux tracksite. **A:** Sauropod track (main track level) modified by the growth of pustular microbial mats. **B:** Displacement rim of a sauropod track in cross-sectional view. Internal overtracks to the right of the displacement rim can be explained by repeated growth of smooth microbial mats within the track. **C:** Level with bifurcated wave ripples on the left and a surface with desiccation cracks just one level below on the right. **D:** Level with prism cracks and tridactyl tracks (coloured). Scale bars in A and D are 1 m, and 5 cm in B.

vertebrate remains and nautiloids, bivalves and large gastropods, and black pebbles. Above the upper levels follows another lag deposit, which differs from the lower one because of the absence of nautiloids and black pebbles. However, intraclasts are in places abundant and may form breccias. Vertebrate remains and well-preserved bivalves and gastropods (including *Harpagodes oceani*) are also common. Both lag deposits are characterized by a high percentage of marine invertebrate and vertebrate macrofossils. This indicates some condensation and time-averaging (e.g., Fürsich 1978), which is typical after a rapid deepening following emersion, when carbonate production is still reduced because the carbonate factory has to start up again (e.g., Kendall & Schlager 1981; Wright & Burgess 2005).

Between the lower and upper levels massif Nerinean limestones with mass accumulations of nerineoidean gastropods can be observed. The macro and microfacies of the rocks with these nerineoidean assemblages suggest that their occurrence was related to water depth, physical energy within the habitat, sedimentation rate, substrate stability, and food supply. Typical nerineoidean shells are high-spined and exhibit unique spiral

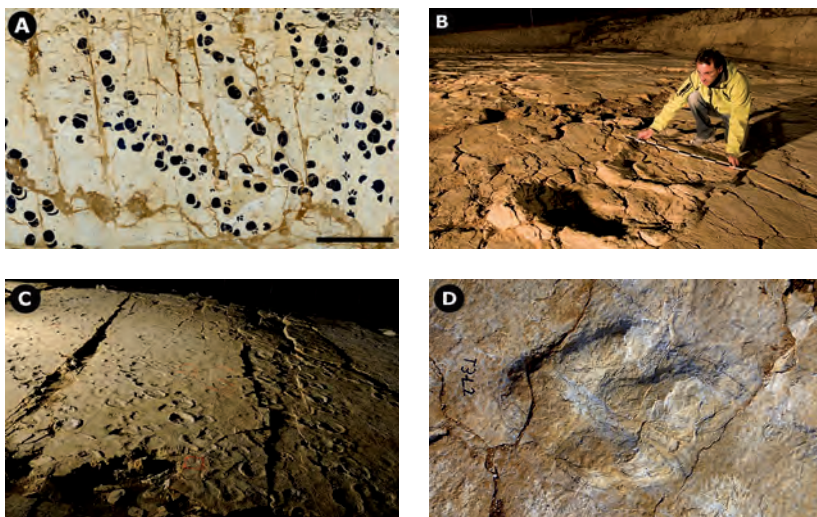


Figure 12: Dinosaur tracks of the Courtedoux–Bois de Sylleux tracksite. **A:** Photogrammetry (by Perrinjaquet) of level 1050, October 2007: some of the large theropod tracks were extracted and casts will be shown during the excursion. Note that tracks are coloured. Scale bar is approximately 5 m. **B:** Pes manus pair of a huge sauropod. Level 1050, scale bar is 1 m (photograph by Patrick Dumas / Look at Sciences). **C:** Multiple parallel trackways of small to medium-sized sauropods. Level 1040, diameter of tracks approximately 30 cm, picture taken at night. **D:** *Megalosauripus*-like left track of a large theropod. Track length is 35 cm, level 1035, trackway T3. Note wrinkle marks in the upper right, probably indicating the former presence of microbial mats.

laminae (folds) on the internal walls. Mass accumulations consisting of large, heavy individuals are believed to represent a semi-sessile, suspension-feeding community that utilized an external food source. During times of enhanced precipitation and run-off from the hinterland, terrestrial organic matter may have been supplied into the shallow sea, thus forming a source of food for the nerineoids. Alternatively, relative sea level change during transgression may have led to large-scale coastal erosion and flooding of the platform, also potentially leading to a mobilization of organic matter and clays. Size and morphology of the high-spined shells seem to indicate a trend towards maximal external volume. Development of folds within the shell is interpreted as a modification to maintain a small internal volume. The faunal and floral composition of the strata indicates a suspension-rich, high-energy environment with a low sedimentation rate and a stable substrate. This allowed mass colonization by epifaunal nerineoids, which, in turn, formed a framework-like structure. The heavy shells acted as a grid, trapping the sediment in between. In this way, a reinforced carbonate accumulation formed (Waite et al. 2008).

5.2 The Courtedoux–Béchat Bovais tracksite

With a total surface of more than 4000 m² this is the largest tracksite on the future highway course. Excavations started in 2004 in the area that is now covered with the highway construction runway. Several trackways of medium-sized to large sauropods were found in that area crossing each other (Fig. 13A).

The surface that will be visited during the fieldtrip was uncovered from 2006 to 2008 and dinosaur tracks are currently visible on level 515 and on the main track level (level 500). In between the level 510 with well-developed desiccation cracks (Fig. 13D) and shallow undertracks stemming from level 515 can be observed. In the southern part of the tracksite, tridactyl tracks of minute to small bipedal dinosaurs, and tracks of tiny sauropods can be observed on the main track level.

Over the largest surface of the site, however, level 515 is currently cropping out and will be documented in 2009 including laserscanning and photogrammetry. The particularity of level 515 is the presence of some very long (up to nearly 100 m) sauropod trackways running all over the site (Fig. 13B, C), and some of these show considerable changes in trackway configuration (e.g., gauge, change from pes-only to quadrupedal patterns, etc.) along their course, and also in track preservation due to lateral differences in sediment consistency.

For the fieldtrip, a platform and an illumination will be installed to observe the tracks at night.

5.3 Formation, taphonomy, and preservation of fossil vertebrate tracks in biolaminites

Vertebrate tracks are at the interface of sedimentological, palaeontological, and biomechanical research, because they result from the complex interaction of a foot with the substrate in a given environment (Padian & Olsen 1984; Unwin 1989). Their study is a complex matter, and they can only be fully understood if they are analyzed using an interdisciplinary approach. After the “renaissance” of vertebrate ichnology (e.g. Lockley 1987), considerable progress has been made during the last few years in experimental ichnology and neoichnology, and more attention has also been paid to the sedimentological analysis of fossil vertebrate tracks and track preservation (e.g., Allen 1997; Milàn 2006; Milàn & Bromley 2006; Scott et al. 2007).

Vertebrate tracks should first be seen as deformed and lithified sediment or as macrosedimentary structures, which offer a great potential for

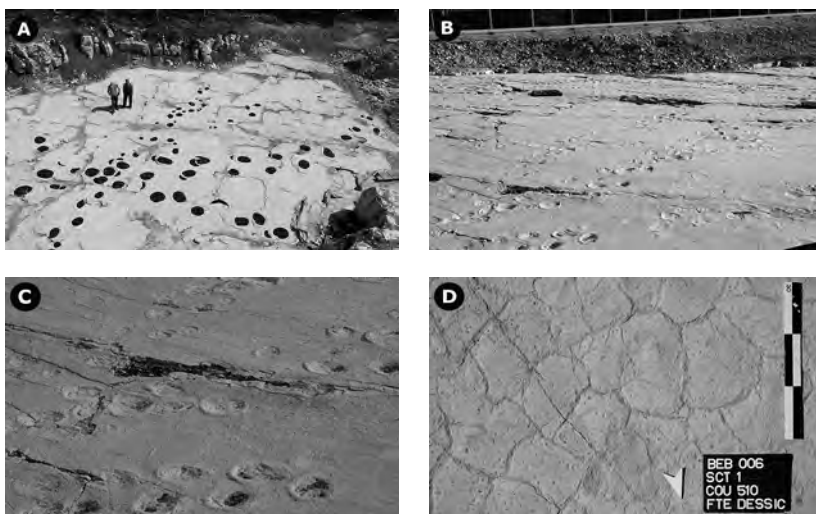


Figure 13: Courtedoux–Béchat Bovais tracksite. **A:** Crossroads of three sauropod trackways on level 515. **B:** Overview of level 515, which will be visible during the fieldtrip. Note the numerous trackways of medium-sized sauropod dinosaurs. The diameter of the pes tracks is around 40 cm. In the background, the highway construction runway. **C:** Close-up of the area in the lower left of B: note the well-developed displacement rims indicating that the sediment was moist to water-saturated at the time of track formation. **D:** Level 510 with well-developed desiccation cracks.

sedimentological and palaeoenvironmental interpretations, as they can be seen as a palaeo-engineering test of the substrate (e.g., Nadon 2001). Notably the tracks of large vertebrates exert a heavy impact on the substrate of a given environment and at a given time. This impact leads to the formation of specific structures on the sediment surface (true tracks, overall track) but also within the sediment underneath and around the track, for instance in the form of undertracks in laminated sediment or in the form of underprints and deep tracks in unlaminated, deep, and water-saturated sediment. The true track corresponds to the sediment surface that was in direct contact with the foot and the overall track encompasses the true track and all structures such as displacement rims, ejecta, or other extramorphological features associated with the true track (Fig. 14).

When a foot is put in a perfect way onto an ideal substrate, true tracks may exceptionally reveal the impression of the foot anatomy. Only such tracks can readily be identified as unmodified true tracks and should be used for ichnotaxonomy and the identification of the trackmaker. Unfortunately, such details are often not recorded because the trackmaker's feet aren't suitable to leave such traces, or because the animal is too

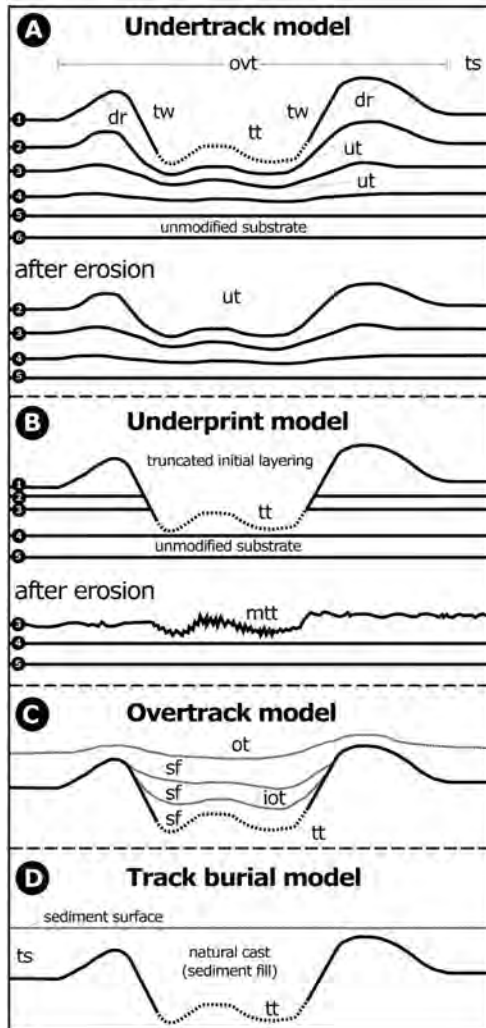


Figure 14: Schematical longitudinal sections through tracks explaining the terminology used: displacement rim (dr), overall track (ovt), sediment fill (sf), tracked surface (ts), track wall (tw), true track (tt), undertrack (ut). **A:** Undertrack model showing the formation of undertracks through the compression of laminated sediment by pressure of the foot. **B:** Underprint model: foot is breaking through the initial layering and the print is not left on the original sediment surface. When the sediment is split at a deeper level the overall track is less complete. With ongoing erosion the overall track is less complete and the true track modified, leading to the formation of a modified true track (mtt). **C:** Overtrack model and formation of internal overtracks (iot) and an overtrack layer (otl). **D:** In the track burial model the track is buried by rapid and important sedimentation, forming a natural cast without overtrack. From Marty (2008).

heavy or too light to leave recognizable prints. Moreover, ill-defined prints are created during running or jumping, because the soles are covered with mud, because the substrate is too dry or too soft, or simply because weathering or erosion destroys the footprints (e.g., Cohen et al. 1991; Nadon 2001). Moreover, this is further complicated in the fossil record where footprints undergo different stages of taphonomy and are at different stages within the diagenetic sequence of development. Consequently, only a very small proportion of the tracks in a given area are capable of yielding diagnostic taxonomic information about the animals that made them.

Taphonomic processes acting on a track after its formation depend on sedimentary processes affecting the depositional environment. Most exposed and consolidated vertebrate tracks are affected by taphonomic processes, which occur after their registration and lead to the formation of modified true tracks or weathered tracks. Destructive processes include vertebrate trampling, insect and other invertebrate bioturbation, root growth, weathering processes (heavy rainfall, wind deflation, desiccation with associated cracking and fracturing), deformation through displacive growth of evaporites, flooding and subsequent wave and seiche reworking or fluctuations of the groundwater table (e.g., Scott et al. 2007). These processes hinder footprint preservation or at least modify or obliterate the original true track, leaving behind a modified true track. Furthermore, accretion and erosion may occur on many time-scales and a track can repeatedly be partly filled by sediment, or partly or wholly emptied. Thus, the rapid consolidation of a footprint is crucial to prevent obliteration and deformation prior to and/or during subsequent burial. This is possible by early cementation, rapid covering by sediment in association with major storms, and overgrowth by microbial mats.

On recent carbonate and siliciclastic tidal flats, a wide range of footprint morphologies is produced by the same trackmaker due to differences in water content and nature of the substrate and the ubiquitous microbial mats. The growth parameters of the microbial mats are very facies specific and can be linked to the environment, which can be expressed by the exposure index. Microbial mats play an important role after footprint formation because they consolidate or lithify shortly after track formation and preserve a track, or because renewed and/or repeated growth of the microbial mat may modify a true track leading to the formation of modified true tracks, internal overtracks, and overtracks. During periods of drought, the mats consolidate rapidly, getting hard and rigid and making it almost impossible even for a heavy trackmaker to leave a footprint. Moreover, such consolidated microbial mats resist heavy rainfall and new footprints can only be made once a new microbial community is in place after renewed wetting. This narrows the time-frame during which foot-

prints are registered and diminishes the time-averaging of an ichnocoenosis (Marty et al. 2009).

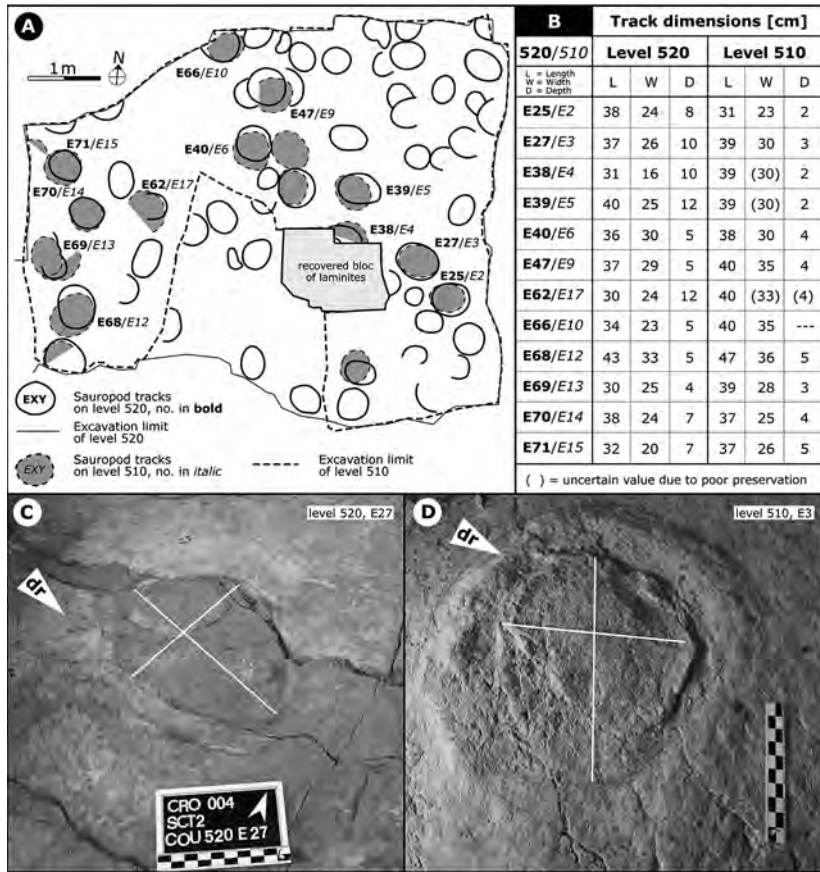


Figure 15: Chevenez–Combe Ronde tracksite, excavation area 2: Comparison of the excavated levels 510 and 520. **A:** Superimposition of the maps (modified maps of the Palaeontology A16). About half of the tracks of level 520 were not found on level 510. Almost all tracks of level 510 were also found on level 520, and the congruity is very good. Those tracks of level 510, which were not found on level 520 are probably undertracks from level 515, which was not excavated in this area because it was amalgamated with layer 520. **B:** Table showing the track dimensions of measured tracks, occurring on both levels. Note that almost all tracks of level 520 are clearly smaller and deeper than those of level 510, which are comparatively larger and shallower. **C:** Level 520, track E27: deep track with a large and broad displacement rim (dr). **D:** Level 510, track E3 (same track as in C): shallow undertrack with a small and narrow, weakly-developed displacement rim. Scale bars in C and D are 20 cm, long and short axes are indicated. From Marty (2008).

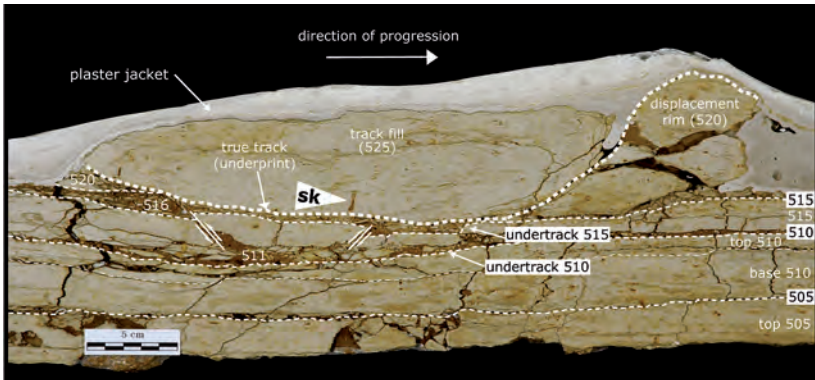


Figure 16: Chevenez–Combe Ronde tracksite, excavation area 3: Cross-section of sauropod pes track T16 of level 520. The track is clearly marked by the large, homogeneous displacement rim to the right, and the fractured and compacted zone underneath the homogeneous track fill in the centre of the picture. In the middle of the track fill, “sk” points to a *Skolithos*-type burrow. Faint undertracks without displacement rims are discernible on levels 515 and 510. Layer 505 is unaffected by the track formation, either due to earlier consolidation or due to insufficient track penetration depth. Track penetration depth amounts to about 6–9 cm. Layer 520 is compacted and completely thinned out in the middle of the print, in a way that an underprint is formed on top of layer 516. Note the uplifted block of layer 515 in the middle part of the track, between the two thrust faults. Layer 510 is less fractured but at the top significantly compacted, especially at the rear of the print. This may indicate that the sauropod put more weight on the posterior part of the foot than on the anterior part. Scale bar is 5 cm, from Marty (2008).

These processes observed on recent tidal flats can be inferred from fossil tracks. This is facilitated by systematic level-by-level excavations of track-bearing intervals as well as by the analysis of the overlying and underlying layer in the case of a single track-bearing level. The level-by-level documentation of superposed surfaces enables to identify true tracks and to distinguish them from undertracks and overtracks, which is often not possible from a purely morphological point of view (Fig. 15). Generally, undertracks are increasingly worse defined, i.e., shallower (decrease in vertical topography), larger (increase in horizontal dimensions), and have narrower and smaller (weakly-developed) displacement rims than their corresponding true tracks (Fig. 15). Overtracks are shallower but rather larger than their true counterparts. The internal outline is poorly defined and, if present, displacement rims are broader and flatter when compared with those of the true tracks (Marty 2008). True tracks with displacement rims and undertracks without can be observed on the Courtedoux–Béchat Bovais tracksite during the fieldtrip.

Poorly-defined tracks can be cut into serial sections to study the underlying sediment (Fig. 16). This provides insight into the substrate

properties at the time of track formation and into the kinematics of the trackmaker. A stack of undertracks indicates biolaminated sediment, whilst the absence of any undertracks may point to a thick and non-laminated sediment layer. The truncation of track structures by an undeformed layer can be explained by consolidation of that layer prior to the formation of the track, which is important for reconstructing the consolidation history of the sediment. Finally, track morphology and associated track structures that resulted from taphonomic processes can be linked to the exposure index, making tracks useful in reconstructing the tidal-flat palaeoenvironment.

6. Excavations in the Marnes à *virgula*

These marls are up to 1 m thick (Fig. 17B), beige to dark-grey, glauconitic, oyster-rich (*Nanogyra* sp.). They could also be described as a *Nanogyra* shellbed. The abundance of *Nanogyra* is poorly understood but encrusted bivalves (e.g., *Gervillia*) and vertebrate remains indicate that they grew at least partially *in situ* (Fürsich & Oschmann 1986a). This suggests that this shellbed is of biogenic origin, even though a sedimentologic origin (e.g., transport and accumulation by storms) cannot be excluded as well. A biogenic accumulation could have been favoured by an environment with restricted conditions such as high bottom salinity or reduced oxygen, and the growth of *Nanogyra* could be related to “blooms” during periods of less hostile conditions. The general depositional setting is considered a shallow subtidal, protected marine environment (Jank et al. 2006a, c).

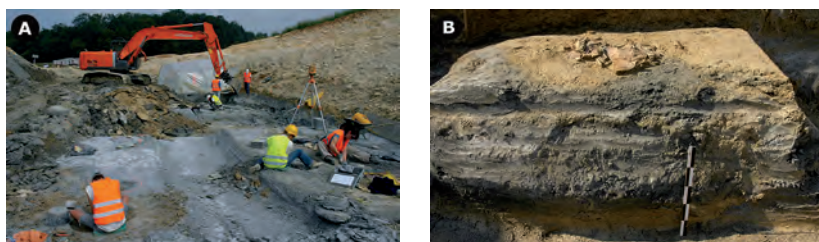


Figure 17: Excavations in the Marnes à *virgula*. **A:** Excavation activity at Courtedoux–Tchâfouè, where the marls are dark-grey. **B:** Section showing the thickness of the Marnes à *virgula*; a turtle carapace can be observed in the upper part of the marls. Scale bar is 50 cm in B.

The Marnes à *virgula* are subjected to systematic excavations (Fig. 17) because they yield a rich and diverse coastal marine assemblage of invertebrates (bivalves, gastropods, cephalopods, crustaceans, echinoids) but

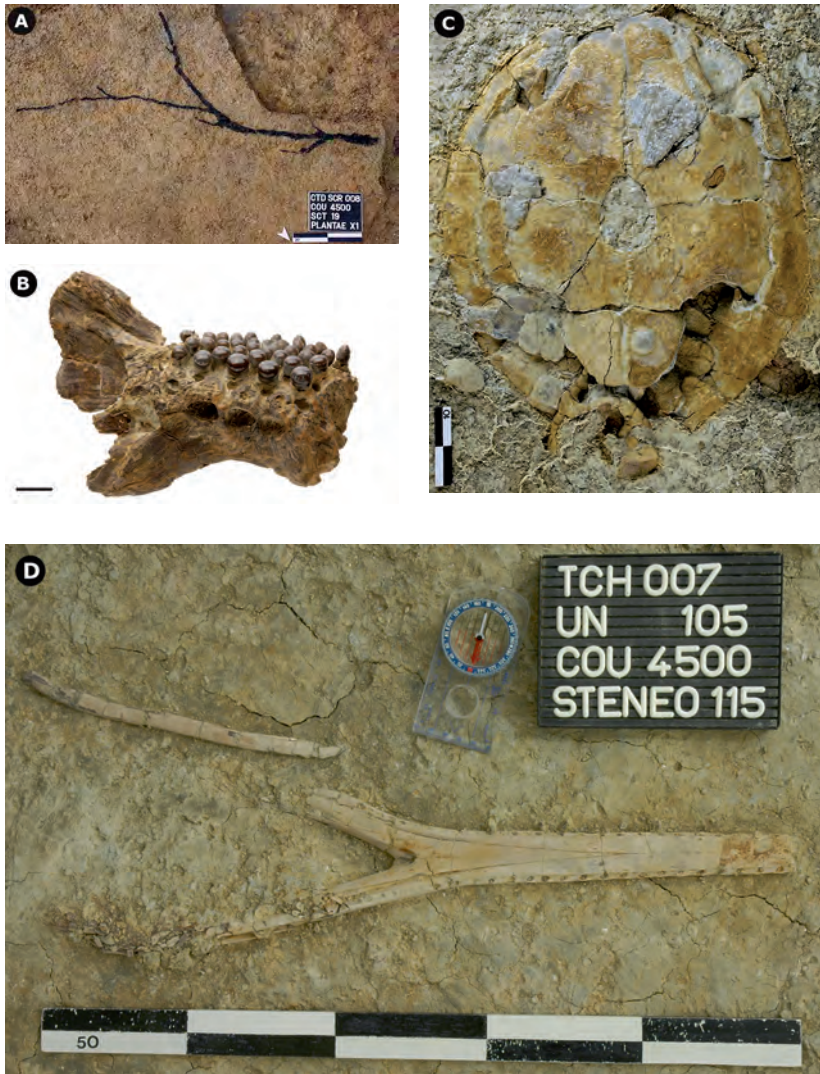


Figure 18: Selected wood and vertebrate fossils from the Marnes à virgula. **A:** SCR008-45, branch of the fossil wood *Protocupressinoxylon purbeckensis* (Conifera, Cheirolepidiaceae) from Courtedoux–Sur Combe Ronde. **B:** TCH005-353, lower jaw (left, lingual view) of *Lepidotes* sp. (Osteichthyes, Semionotidae) from Courtedoux–Tchâfouè. **C:** BSY006-307, articulated plastron and carapace (ventral view) of *Plesiochelys* sp. (Testudines, “Plesiochelyidae”) from Courtedoux–Bois de Sylleux; the pelvis is preserved at the bottom part of the specimen. **D:** TCH007-115, lower jaw of *Steneosaurus* sp. (Crocodylia, Teleosauridae) from Courtedoux–Tchâfouè. Scale bars are 20 cm in A, 1 cm in B, 10 cm in C, 50 cm in D.

mainly of vertebrates (chondrichthyes, osteichthyes, turtles, crocodylians, pterosaurs), notably hundreds of remains of turtles, including more than forty carapaces of plesiochelyids (Marty & Billon-Bruyat 2004; Billon-Bruyat, 2005a, b). In addition, these marls are very rich in fossil wood, with branched axes reaching up to 1.75 m in length. This wood has been identified as *Protocupressinoxylon purbeckensis* Francis, 1983 (Philippe et al. in press).

During the field-trip we will focus on excavation techniques (Fig. 17A) and show typical fossils of woods, fishes, turtles and crocodylians (Fig. 18).

7. Sedimentology below and above the Marnes à *virgula*

A cleaned part of the hardground (marking the base of the Marnes à *virgula*) can be seen during the field-trip.

This well-developed hardground is, strongly encrusted by oysters and serpulids and perforated by *Trypanites* and *Gastrochaenolites*. On this hardground ammonites (*Orthaspidoceras schilleri*) and large infaunal bivalves (*Ceratomya* sp., *Pholadomya* sp.) in life position crop out. Both are encrusted and perforated, suggesting that the sediment was consolidated up to the level with the infaunal bivalves and since these are infaunal bivalve, that the overlying sediment was eroded prior to the formation of the hardground. This goes in hand with the lack of pre-omission burrows. This hardground marks the base of the Marnes à *virgula*, which corresponds to the base of the *Eudoxus* zone since *Orthaspidoceras schilleri* is not found in the Marnes à *virgula* anymore (Fig. 5).

The hardground is situated at the top of a fossiliferous shellbed where it is possible to collect fossils, especially typical Late Jurassic invertebrates (bivalves, gastropods, brachiopods, etc.) on site. Within this invertebrate shellbed below the hardground several rather poorly-developed hardgrounds have further been identified and are probably related to taphonomic feedback because of the high percentage of endobenthic invertebrate shells of the soft ground assemblage below (e.g., Kidwell & Jablonski 1983; Kidwell & Aigner 1985; Kidwell 1991, 1993).

In 2008, a disarticulated skeleton of a marine crocodylian was discovered in this hardground at Courtedoux–Bois de Sylleux (Fig. 19). The skeleton is in preparation; at this time, it is composed of the major part of the skull and jaws, some isolated teeth, numerous vertebrae, some ribs and a femur. According to these elements, it is provisionally ascribed to the metriorhynchid genus *Metriorhynchus* Meyer, 1830. This discovery adds a new taxon to the thalattosuchians discovered on the Transjurane,



Figure 19: BSY008-465, a disarticulated skeleton of *Metriorhynchus* sp. (Crocodylia, Metriorhynchidae). Scale bar is 0.5 m.

along with the teleosaurids *Steneosaurus*, *Machimosaurus* and the metriorhynchid *Dakosaurus*.

On top of the Marnes à *virgula* carbonate sedimentation starts again and several marly limestone beds are dominated by the shells of small oysters (probably *Nanogyra*) and can be described as densely-packed, bioclast-supported shellbeds with bioclast/bioclast contacts (*sensu* Kidwell & Holland 1991). Similar shellbeds with *Nanogyra virgula* have been interpreted as storm shellbeds by Fürsich & Oschmann (1986b). In these layers the ammonite *Aspidoceras caletanum* was identified suggesting that the Marnes à *virgula* correspond to the Orthocera subzone of the *Eudoxus* zone, because in the hardground located at the base of the Marnes à *virgula*, the ammonite *Orthaspidoceras schilleri* is frequently found (Figs. 5, 6).

About 5-10 m above the Marnes à *virgula* clays are almost absent and carbonate deposition dominates again expressed by white, chalky limestones (Coral Limestones of Jank et al. 2006b) with abundant corals, interpreted as coral meadows, and invertebrates.

Along the section below and above the Marnes à *virgula*, different benthic macroinvertebrate associations (e.g., Fürsich 1976, 1977, 1981; Fürsich & Werner 1986; Werner 1986; Oschmann 1988) and biostratigraphic types (classifications in Aigner 1985; Kidwell 1986; Kidwell et al. 1986; Allison & Briggs 1991; Kidwell & Holland 1991; Fürsich 1995) can be observed.

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Late Jurassic marginal marine ecosystems of the Southern Jura Mountains

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Field Guide for the 5th International Symposium on Lithographic Limestone and Plattenkalk

Saturday 22nd August

Program

- 8.30 a.m. Departure from Basel (Münsterplatz) by bus
- Stop 1 Steingrueben quarry in Lommiswil
- Stop 2 Short stop for Amanz Gressly's grave
- Lunch in St. Niklaus
- Stop 3 Zetter quarry
- Stop 4 Naturmuseum Solothurn, collections and exhibits
- Followed by an official reception at the Museum
- Return to Basel, arrival around 6.30 p.m.

Basel – Solothurn – Lommiswil – St. Niklaus – Solothurn – Basel

Stop 1: Quarry Steingrueben, Lommiswil

(Topographical map 1: 25'000 sheet 1106 Moutier
Koord. 654 700/245 000)

A couple of years ago, the Steingrueben quarry has been reactivated to extract the famous “Solothurn marble” that stems from the uppermost part of the Reuchenette Formation (Late Kimmeridgian; *Autissiodorensis* zone; Meyer & Pittmann 1994). The three quarried beds are very fossiliferous and can be correlated with the famous Solothurn Turtle Limestone that crops out close to the city that has given its name to this member. Above those beds thin-plated, micritic limestones can be seen. They form part of the Twannbach Formation, ammonites found further to the east indicate a Tithonian age (*Gigas* zone). Carapax and plastron remains of marine turtles (*Plesiochelys etalloni*), as well as hybodontid sharks (*Asteracanthus*) and chelae of hermit crabs (*Goniochirus*) have been found. Very common are cross-sections of nerineid gastropods (*Ptygmatis*, *Cossmannea*, *Eunerinea*), the sclerosponge *Cladocoropsis mirabilis* and strong bioturbation by decapod crustaceans (*Thalassinoides*). In 1994 a large slab with a lower jaw and several postcranial elements of *Steneosaurus* has been found; it can be seen in the Museum of Nature in Solothurn.

In 1989 Meyer identified what turned out to be the first Late Jurassic dinosaur tracks reported from Switzerland (Meyer 1993). Given the attention that many geologists have focused on quarries such as the one at Lommiswil it is surprising that tracks were so easily overlooked. At Lommiswil individual tracks are up to a metre or more in diameter and one trackway can be traced for about 90 metres, making it one of the longest in Europe. Track morphology and trackway pattern clearly identify them as those of large sauropods. The tracks are not so well preserved that they reveal clear details such as digit impressions. On the whole more than 500 individual footprints can be seen, and more were exposed in recent years with ongoing quarry operations. The track level is overlain by a stromatolitic layer, covered by coarse calcarenites containing black pebbles with birds-eyes. Those pond and supratidal marsh deposits were formed during a low stand. The top of the stromatolitic layer is strongly eroded with penetrating *Thalassinoides* burrows and must be regarded as sequence boundary. On top of this layer three beds with nerineid gastropods can be seen (cf. last paragraph); they form part of the transgressive system tract and end with a maximum flooding surface. The latter coincides with the lithostratigraphic boundary of the overlying Twannbach Formation (Fig. 1).

Moreover, since the original discovery of the site, two stratigraphically deeper track levels have been detected that contain both true tracks and



Figure 1: Steingrueben Quarry in Lommiswil. The inclined surface on the left is the main dinosaur track level. The white dashed line indicates the lithostratigraphic boundary between the Reuchenette Formation (Kimmeridgian; Solothurn Turtle Limestone Member, below) and the Twannbach Formation (Tithonian; above). Scale: geologists below white dashed line.

underprints. The general trackway configuration reveals that the track-maker was of the wide-gauge variety.

Within the same megatracksite several small sites have been found: a small surface near Grenchen, another close to Bürenberg and several around La Heutte and Biel (Meyer & Lockley 1996). Just recently, the Grenchen site has been reexamined and revealed a short trackway segment of an intermediate sized theropod. For a review of most of the dinosaur sites in Switzerland see Meyer & Thüring (2003).

The uppermost part of the Solothurn Turtle Limestone contains mass accumulations of nerineid gastropods and this was one of the reasons why they have been exploited as building stones since Roman times. Most of the Swiss cities have at least one or several fountains from the 17th or 18th century that are made of those limestones.

The facies suggest that the occurrence of the gastropod accumulations is related, amongst other factors, to substrate stability and food supply. They mainly consist of large, heavy individuals that are believed to represent a semisessile, suspension feeding lifestyle. Isotope studies show that during times of enhanced precipitation and run-off from the hinterland, the terrestrial organic matter supplied an important source of food for the nerineoids (Waite 2005). The faunal composition of the

strata indicates a suspension-rich, high-energy environment with a low-sedimentation rate and a stable substrate. This allowed mass colonization by epifaunal nerineoids where the heavy shells formed a hedge-like structure, trapping the sediment in between. In this way, a reinforced carbonate accumulation formed (Waite et al. 2008).

Stop 2: Church of St. Niklaus

(Topographical map 1: 25'000 sheet 1107 Balsthal,
Koord. 230.080/ 608.100)

Here is the grave of one of the most important Swiss geologists, Amanz Gressly (1814–1865), who introduced the term “facies” into geology. In 1984, the overgrowing plants on his tomb have been completely removed that made the famous epitaph – composed by himself – visible again (Stampfli 1986).

GRESSLIUS INTERIIT LAPIDUM	<i>Gressly perished,</i>
CONSUMPTUS AMORE	<i>because of his never ending love for rocks</i>
UNDIQUE COLLECTIS	<i>he collected them everywhere;</i>
NON FUIT HAUSTA FAMES.	<i>with a never resulting studiousness</i>
PONIMUS HOC SAXUM.	<i>Let us put him a rock right here!</i>
MEHERCLE TOTUS OPERTUS	<i>Only when, oh Hercules</i>
GRESSLIUS HOC SAXO	<i>Gressly is completely covered by this rock</i>
NUNC SATIATUS ERIT.	<i>he will finally be satisfied.</i>

The blueprint of the tombstone was made by F.V. Lang (sketchbook p. 81; Archive Naturmuseum Solothurn); the basal limestone blocks imitate the inclined strata of the Jura Mountains. The lateral pillars loom around a stalactite-adorned cave that shows a butterfly in its centre. This animal had probably a special significance for Gressly, as in his field books a poem dedicated to butterflies can be found. From Lang’s blueprint we can deduce that the base originally carried several fossils. However, only mounting holes can be seen today and the originals must have been stolen.

Stop 3: Zetter quarry

(Topographical map 1: 25'000 sheet 1107 Balsthal,
Koord. 230.180/ 607.740).

The quarry was most probably closed in the early 1920 ties before it shortly reopened in 1986. During this time new material of marine turtles has been discovered. This led to several excavation campaigns and a research project from 1986 to 1989 (Meyer 1989, 1994). The Solothurn Turtle Limestone forms the uppermost member of Reuchenette Formation that has been dated by ammonites (*Autissiodorensis* zone; Meyer & Pittmann 1994). The type locality in the Biberstein quarry (Koord. 607.865/ 230.115) is now filled up. The base of the member (Halbwilde Bank in figure 2) as defined by Meyer & Jordan (2000) can be correlated with the stromatolithic layer that overlays the dinosaur track level in Lommiswil and elsewhere in the Weissenstein anticline. This layer has been identified as sequence boundary K3 in Gygi et al. (1998).

The Fauna of the Solothurn Turtle Limestone

The main marine turtle yielding layer, the so-called “Rätschenbank”, is slightly marly at its base and can be classified as an echinoderm biomicrite. Within this bed of 90 cm we can observe eight horizons with turtles in a different preservation stage. They occur in all possible decay stages, form single abraded bone fragments to almost completely articulated turtles including skulls.

Up to now more than five hundred carapace fragments of different sizes have been recovered, smaller fragments not included. Amongst those are several complete carapaces and plastra of *Plesiochelys etalloni* Etallon and *Eurysternum ignoratum* Bräm. Isolated fragments of carapaces of the same individual are often dispersed over several square metres. Some remains show post-mortem incrustations by oysters (*Nanogyra*) or Pascichnia of regular echinoids (*Gnathichnus pentax*; Meyer 1989). Some carapax remains show signs of crushing that can be interpreted as bite marks of mesosuchian crocodiles (*Machimosaurus*). Other marine reptiles include teeth, cranial and postcranial remains of *Steneosaurus* and isolated teeth that can be attributed to large plesiosaurs (*Liopleurodon*). Amongst the chondrichthyans, jaws of chimaeroids (*Ischyodus*) and teeth of sharks (*Hybodus*, *Asteracanthus*, *Heterodontus*, *Polyacrodus*) can be observed. The most frequent fishes are pycnodontid such as *Proscinetes*, *Gyrodus*, *Eomesodon*, *Macromesodon* and *Coelodus*. Semiotid fishes (*Lepidotes*), Caturids (*Caturus*, *Callopterus*) and Aspidorhynchids (*Belenostomus*) are also known (Müller 1994).

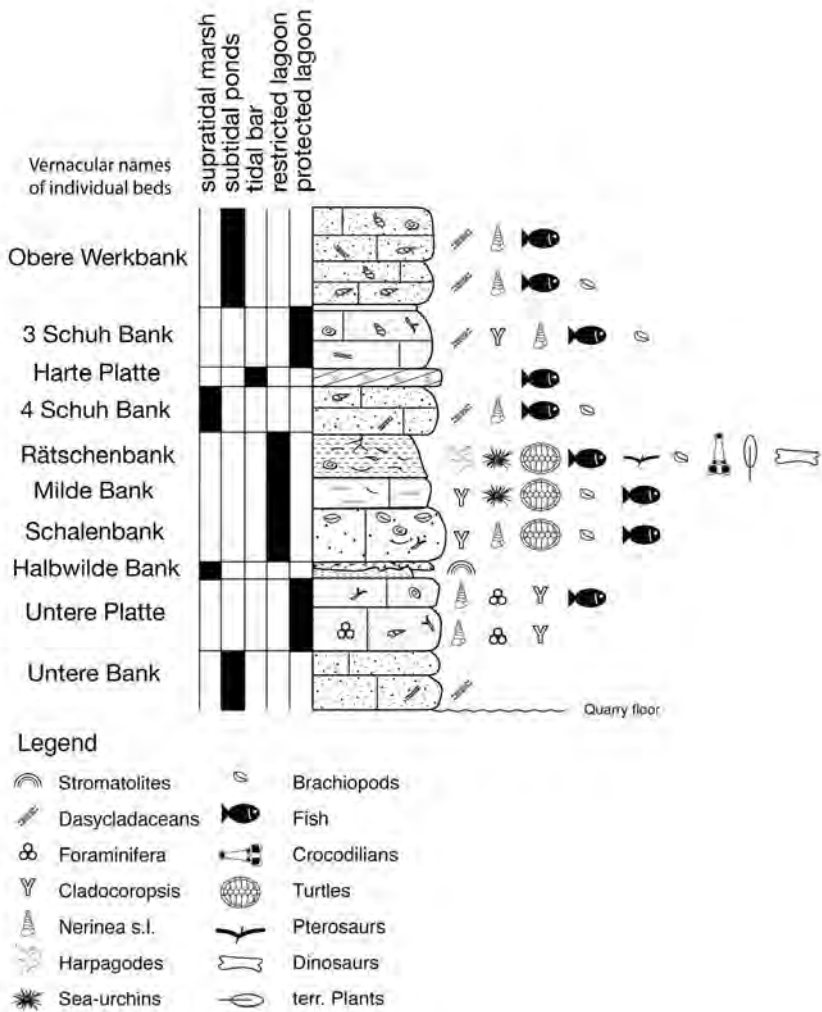


Figure 2: Zetter Quarry, in St. Niklaus. Geological section with main faunal composition, depositional environment and vernacular names of individual quarried beds.

Huene (1926) was the first to give an overview of the reptile fauna of the Solothurn Turtle Limestone. Amongst others, he noted the presence of a fibula of a coelurosaurian, of which he sent sketches to Baron F. Nopsca in Vienna for identification. After more than seventy years and a complete preparation of the specimen it turned out to be the wing phalanx II of a large pterodactyloid pterosaur with a wingspan between 3.5 and 5 m (Meyer & Hunt 1999). Three isolated teeth kept in the collections of the Naturmuseum Solothurn indicate the presence of at least two different theropods; one of them can be attributed to a small dromaesaurid.

The most frequent invertebrates are strombid gastropods (*Harpagodes oceani* Brongniart) and hemicidaroid sea urchins (*Hemicidaris mitra* Agassiz), the latter frequently with attached primary and secondary spines preserved. The whole bed is intensively bioturbated and only show faint signs of stratification. The lower and upper surfaces are covered with *Thalassinoides*; the internal part frequently contains *Rhizocorallium*. Apart from lobster-like decapods such as *Eryma* or *Glyphaea* and hermit crabs (*Goniochirus*, *Orhomalus*), remains of indeterminable penaeids have been found. Endobenthic bivalves occur frequently (*Protocardia*, *Myophorella*), epibenthic forms include the genera *Camptonectes*, *Brachydontes* and *Grammatodon*. Nerindeid gastropods (*Cryptoplocus*) and small echinoids (*Pseudodiadema*, *Hemipedina*) occur but to a lesser extent. Naticid gastropods (*Globularia*) are sometimes preserved with original colour bandings on the shell. Completely preserved astropectiniden starfishes are also known (*Pentasteria*; Meyer 1988).

Palaeoecological observations reveal a linear correlation between the amount of bioturbation and fossil density. The highest fossil density occurs at the base where bioturbation is minimal whereas higher in the horizon fossil density decreases and bioturbation gets more intense.

The “Rätschenbank” has the highest faunal diversity and at the same time the highest content of C_{org} when compared to the complete sequence of the STL member (Meyer 1994). Optimal conditions led to a continuous development of a stable ecosystem with an individual- and species rich benthic community that formed the base for a diverse nectic community of fishes and reptiles. This could be one of the reasons for the high density of marine turtles. Whether nesting grounds were close by as previously stated by Lang (1863) cannot be definitively proven but seems possible, as some badly preserved remains of turtle eggs have been found.

The accumulation of different types of marine turtles such as more necto-benthic forms (*Platycheilus*) and those well adapted for open waters (*Plesiocheilus*) must have had other reasons. Most of the turtles occur as disarticulated or dispersed individuals; complete specimens are rare. One

of the reasons for this mass accumulation may have been the primary food sources within the lagoon. On the other hand, the occurrence of lethal bite marks and also healed injuries indicate a “biological” accumulation of dead animals by marine crocodylians (Meyer 1991). Bite marks could also be observed on brachiopods (Sulser & Meyer 1998), those might have been made by durophagous pycnodontid fishes or selachians with crushing teeth (*Asteracanthus*, *Hybodus*).

Facies and palaeoecology indicate subtidal deposition in a shallow marine lagoon. The diverse fish- and reptile fauna and sedimentological observations suggest a small embayment that was protected by shallow bars towards SE, towards SW however a connection to the open sea existed. The occurrence of porostromate algae (*Marinella*) indicates very shallow and clear water. Thalmann (1966) suggested the presence of fresh water on the base of a single ostracod. However the occurrence of completely articulated sea-urchins speaks in favour of stenohaline conditions.

Stop 4: Naturmuseum Solothurn: Exhibits and collection of fossil turtles

Probably since Roman times the “Solothurn Marble” has been quarried in the Verena anticline north of Solothurn. At the turn of the 19th century the priest and teacher Franz Josef Hugi (1798–1855) discovered many fossils in the active quarries of the area (Fig. 3). During his prospecting time he found remains of large marine turtles and recognized early on the importance of these fossils. With his discoveries he caused quite a stir because he showed the locals that millions of years ago, these animals populated the Jurassic beaches around the town.



In 1825 the first Natural History Museum Solothurn was established, the base formed Hugi’s private collection. Hugi prompted the city council of Solothurn to issue a law that all quarry-owners who didn’t hand over the fossil turtles to the Museum would lose their permits. For each turtle the Museum would receive, they would get a finding fee. Despite this early law on the local fossil turtles, many can be found in

Figure 3: In 1825 Franz Josef Hugi (1791–1855) donated his fossil turtles from Solothurn to the Museum. Pencil drawing by L. Haug.

different collections, such as the Natural History Museum London. The financial incentive led some of the quarry owners to fabricate concrete turtles made out of real bones (Fig. 4).

The first publication of the fossil turtles and the invertebrates was a monograph in 1867 by Rütimeyer & Lang (Fig. 5). In the 20th century, most of the thirteen quarries of the area had to be closed due to economical reasons. Nevertheless, scientific work continued with specimens of the Museum collection (cf. Bräm 1965; Gaffney 1975, 1976; Fig. 6). In 1986 one of the quarries (Zetter quarry) had been reactivated for a short time and this gave the opportunity for a couple of systematic excavations (see Stop 3).



Figure 4: Fossil turtle made from single pieces of different individuals and put together with concrete to fake a complete specimen in order to get a financial reward from the city.



Figure 5: Ink drawing of a *Platycheilus oberndorferi* Wagner published in Rütimeyer & Lang (1867).

Eight new taxa of turtles have been described (*Plesiochelys santcaeverenae* Rütimeyer, *Craspedochelys picteti* Rütimeyer, *Thalassemys hugii* Rütimeyer, *Thalassemys moseri* Bräm, *Eurysternum ignoratum* Bräm, *Tropidemys langi* Rütimeyer, *Plesiochelys solodurensis* Rütimeyer, *Plesiochelys etalloni* Pictet & Humbert) and their validity and phylogenetic position are still under debate (cf. Rütimeyer 1873; Bräm 1965; Gaffney 1975; Lapparent de Broin et al. 1996; Joyce 2000; Lapparent de Broin 2001; Scheyer 2007).

The turtles of Solothurn belong to the earliest discoveries of marine turtles. Today, they are considered to be the worldwide most significant occurrence of Late Jurassic turtles and still form part of major research topics (see Scheyer 2009).



Figure 6: View of a part of the collection in the Natural History Museum Solothurn showing large slabs with fossils from the Solothurn Turtle Limestone.

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