

A “turtle cemetery” from the Late Jurassic of Switzerland

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The Late Jurassic is a key period in turtle evolution, with the beginning of their secondary adaptation to life in the marine environment (Billon-Bruyat et al. 2005). In Western Europe, turtles are mainly known from coastal marine environments such as Canjuers, Cerin, Solnhofen and Solothurn (de Broin 1994). In Switzerland, the famous Solothurn Turtle Limestone (Late Kimmeridgian, Canton Solothurn) revealed a rich and diverse turtle assemblage (Bräm 1965).

Here we report a new turtle assemblage from the Swiss Jura mountains, discovered in the vicinity of the town of Porrentruy (Canton Jura). This discovery was made during systematic excavations in progress along the Transjurane highway (A16), nearby dinosaur tracksites (Marty et al. 2003). The depositional sequence belongs to the *Virgula* Member of the Reuchenette Formation (Late Kimmeridgian). The vertebrate remains comprise mainly turtles, including hitherto eleven carapaces (more or less complete and articulated), isolated bones and numerous carapace fragments, assigned to the Plesiochelyidae s.l. (Plesiochelyidae and 'Thalassemydidae'). Reptile remains also include some isolated teeth and bones of teleosaurid crocodylians (*Steneosaurus*, *Machimosaurus*) and rare pterosaur bones. The fauna also comprises chondrichthyes, osteichthyes, and invertebrates. Furthermore, plant macroremains are abundant.

Preliminary taphonomical observations show interesting features, such as the generally upside-down preservation of carapaces. Moreover, the new material sheds light on the evolution of turtle body size through the Mesozoic, by challenging the largest known pre-Cretaceous turtles.

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“Freshwater” sharks from the Swiss Upper Marine Molasse

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As part of recent research to try to constrain the palaeoceanographic and paleoclimatic conditions during the Miocene marine sedimentation in the circum-Alpine region, a number of geochemical approaches have been applied to well-preserved fossils as well as their embedding sediments (e.g., REE composition, $^{87}\text{Sr}/^{86}\text{Sr}$, $^{143}\text{Nd}/^{144}\text{Nd}$, $\delta^{18}\text{O}$ values).

While studying samples from the Swiss Upper Marine Molasse some “exotic” results have been obtained. Two shark teeth from the La Molière area have very low $\delta^{18}\text{O}$ values (11.3 ± 0.1 ‰) compared to teeth sampled from the same species in the same locality (20.7 to 21.8 ‰) as well as other localities in Switzerland, Germany, Austria, Hungary and Slovakia (range between 19.5 and 23.5 ‰; $n = 155$). Unlike the two exceptions, all other teeth can be interpreted as having formed under open-ocean conditions, with O-isotope compositions reflecting prevailing climatic conditions (Vennemann & Hegner, 1998; Vennemann et al., 2001; Janz & Vennemann, 2005; Kocsis & Vennemann, 2005).

Different compositions have also been measured for the $^{87}\text{Sr}/^{86}\text{Sr}$ of the two teeth from La Molière (0.707840 and 0.707812) and the other teeth of the Swiss Molasse (range between: 0.70842 to 0.70902). With regard to the Sr isotope measurements, most samples have $^{87}\text{Sr}/^{86}\text{Sr}$ compatible with Lower Miocene open ocean seawater. Some exceptions exist though having $^{87}\text{Sr}/^{86}\text{Sr}$ somewhat higher than expected for open ocean conditions that might reflect a local influence through erosion of high $^{87}\text{Sr}/^{86}\text{Sr}$ crystalline rocks, however their O-isotope compositions are still typical of those for teeth formed in an open marine environment.

In case of the two teeth of La Molière, the low values for $^{87}\text{Sr}/^{86}\text{Sr}$ correspond well to compositions

expected for freshwater whose isotopic composition is controlled by Mesozoic calcareous rocks of the Alps and the Jura mountains, known to have been exposed in the area surrounding the locality of La Molière during the Miocene (e.g., Schlunegger et al., 2001; Kuhlemann and Kempf, 2002).

As both O and Sr are known to be incorporated into the phosphate structure during growth of the teeth and are commonly robust to post-mortem alteration, we interpret these isotopic compositions as typical for the paleoenvironment in which the sharks lived, that is a freshwater origin of the two teeth from La Molière. All other teeth from this locality as well as the other localities recorded normal marine seawater. Thus according to our interpretation some Miocene sharks often visited rivers just as some living species do today (e.g. *Carcharhinus leucas*), and stayed long enough to form teeth recording the geochemical composition of the river water. This interpretation is supported by rare earth element patterns of the “freshwater” teeth, as they are similar to those of the other teeth from La Molière, all of which reflect diagenesis in a typical marine environment.

Accepting that the teeth have formed while the sharks were in a freshwater environment and given the same approximate temperature conditions as for their marine counterparts, the extremely low $\delta^{18}\text{O}$ values of the teeth suggest meteoric waters with minimum $\delta^{18}\text{O}$ values of about -10 ‰. As the O isotope composition of meteoric water is directly related to mean ambient temperature and this in turn to the mean altitude in mountainous areas (e.g., Schürch et al., 2003), these low values support a significant altitude of the Alps during the Lower Miocene (roughly similar to that of today). Collectively, the analyses to date indicate a Lower Miocene palaeogeographic

situation with a high mountain belt adjacent to a marginal sea, which generally has had good connections to the open oceans for most of the time.

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Mind the “Middle Jurassic” gap –

Bone versus track record in dinosaurs

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Up to now studies on vicariance biogeography or cladistic biogeography of dinosaurs have been performed with body fossils only. In the Triassic and Early Jurassic these methods have produced rather coherent patterns, probably due to the existence of Pangaea. They show a large cosmopolitan community of herrerasaurids, coelophysoids, prosauropods and basal ornithischians (Holtz et al. 2004).

The fossil record of body and trace fossils of dinosaurs in the Middle Jurassic consists of rather limited information. Today more than hundred locations are known to contain either trace or body fossils. Although scattered, they occur on all continents except on Antarctica. The best record including all stages comes from Europe where all groups of dinosaurs are present, whereas all other continents show only very few localities. A limited record is known from Africa and Australia. The break up of Pangaea is also recorded in the dinosaur communities resulting in only six taxa that are globally distributed. However, the global record indicates the presence of ceratosaurs, basal spinosaurs and carnosaurs among theropods, stegosaurs and various sauropods among herbivore dinosaurs.

If the bone and track record are combined a different pattern emerges. In the Aalenian the only skeletal and track record comes from Europe, in the Bajocian again Europe and Australia indicate skeletal remains of theropods and sauropods, whereas footprints indicate the presence of sauropods in all continents except Asia; theropod tracks are present in North America, Asia and Australia. The Bathonian indicates a skeletal record of theropods in Europe, Africa and Asia, sauropods in Europe and Asia and ornithischians in Europe only. The track record indicates theropods in North America and confirms the presence of theropods, sauropods and ornithischians in Europe and theropods and sauropods in Africa. In the Callovian sauropod remains are present

on all continents except Australia, theropods occur in South America, Europe, Africa and Asia, whereas ornithischians are found in Europe and Asia only. The track record adds sauropods to North and South America. Combining the record of both body and trace fossils gives a somewhat different picture, although we are far away to link particular trackways to specific vertebrate taxa. In this paper we would like to focus on similarities and differences in the global track record.

The Middle Jurassic dinosaur fossil record is poor and incomplete record during this time interval, when many dinosaur groups radiated. Recent discoveries of coeval dinosaur tracksites from Portugal, the United States and England have greatly enhanced our understanding.

We report here on an important skeletal and trace fossil record from Morocco that greatly enhances our understanding of global distribution of ichnotaxa. Lapparent (1955) described two partial postcranial skeletons, the sauropod *Cetiosaurus mogrebensis* and the theropod *Megalosaurus mersensis* from the El Mers area. These localities could be relocated and can be placed in the uppermost part of the El Mers Formation. Furthermore, Charroud & Feddan (1992) noted the presence of large sauropod bones from the Bathonian Gypsum marls of Boulhafa some 15 km west of El Mers. We report herein the first dinosaur tracks from the Middle Atlas Mountains in two different stratigraphic units with a total of thirteen different levels.

The first set of track localities lies in the middle of the Ich Timellaline and J'bel Bou Akrabène Formation (Bathonian). Outcrops in the canyon of the Oued Tamghilt east of El Mers, have yielded three localities that contain an important set of dinosaur trackways. So far tridactyl footprints and trackways attributed to theropods have been found. Smaller

footprints (Footprint Length: 15 – 30 cm) show slender toes, larger footprints (FL: 40 cm) have blunt toes and can be attributed to the ichnogenus *Megalosauripus*. Furthermore, we have mapped a series of very large sauropod trackways (pes length up to 130 cm) that are narrow gauged (sensu Lockley et al. 1994). Size, trackway width as well as missing toe or pollex impressions suggest the ichnogenus *Breviparopus*. The second set of trackbearing surfaces has been located at the base of the El Mers Formation (Late Bathonian to Callovian). Here mainly small theropod footprints (FL: 20 cm) have been observed; isolated footprints of large sauropods (FL: 100 cm) have also been recorded. Sedimentary structures as well as abundant remains of wood indicate a deposition in a shallow siliciclastic tidal flat.

The vertebrate ichnofacies of the El Mers area is in many ways similar to the one encountered in the Iouaridène and Taguelft basin in the High Atlas (400 km to the west). All the localities show the presence of the narrow-gauged ichnotaxon *Breviparopus* indicating the presence of very large but slender eusauropod. *Megalosauripus* attributed to a large theropod is equally present in all these deposits in Morocco. In comparison with other Middle Jurassic localities (England, USA, Portugal) the Moroccan sites display the highest diversity of track morphotypes. However, there are striking similarities and differences. Whereas the ichnotaxon *Megalosauripus* has been found in England and Morocco, but is missing in Western North America, a small but very peculiar ichnotaxon *Carmelopodus* can be found in England, Morocco as well as in the USA. Furthermore, a medium sized theropod morphotype (FL 20 cm) occurs in all the areas as well. These theropods were apparently widespread on all three continents. The narrow gauge sauropod ichnotaxon *Breviparopus* is so far restricted to North Africa. In Europe (Portugal, England) only the narrow gauge sauropod ichnotaxon *Parabrontopodus* can be found. Furthermore trackways of wide-gauge sauropods in England demonstrate the presence of titanosauridform sauropods, not present elsewhere. These observations clearly demonstrate, that in the Middle Jurassic of Europe and North Africa different sauropod taxa occurred, despite the lack of detailed information on skeletal taxa. On the other hand theropod of different sizes were apparently widespread in North Africa, Europe and the USA.

Combining the bone and track record in specific time slices can greatly improve our knowledge and fill the gap of apparently missing data. Nevertheless, in the past many authors have argued that those gaps in the vertebrate record reflect a taphonomic megabias related to sea level fluctuations. Many researchers speculated that for instance Mid Cretaceous eustatic highstands did reduce the number of low land areas suitable to the preservation of terrestrial faunas (Smith 2001). This is in clear contrast, f.e. to the eustatic high in the Campanian/ Maastichtian that shows an increasing number of localities when compared to the Mid Cretaceous eustatic low stands with only few known occurrences. Fara (2002) compared estimates of sea-level variations, land surfaces and the proportions of Lazarus tetrapod taxa in the Late Jurassic to Eocene interval and found a negative correlation. Taking into account the record of dinosaur trace and body fossils from the so called “Middle Jurassic” gap, we see that almost all stages show the presence of the group and the Callovian with a sea level high stand has the best track and body fossil record. We think that the apparent missing record during the Middle Jurassic is mainly due to sample bias.

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Paleogene ostracofauna and reworked Foraminifera of the Southern Upper Rhine Graben (S-URG): paleoecological and paleogeographical implications

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We present here the paleoecological and paleogeographical results obtained from two boreholes Allschwil-2 and DP-202 (south of Mulhouse) drilled in the S-URG. Detailed Paleoecology (especially salinity) deduced from the ostracod fauna will be presented in Pirkenseer & Berger (this volume). Moreover, this ostracod fauna allows also a first paleogeographic interpretation concerning the marine relationships during the Late Rupelian. Fig. 1 compares the common species between the Southern Rhine graben (18 species) and the ostracofauna published from other areas, namely

Figure 1. Paleogeographic relationships during the Late Rupelian, based on ostracods:

1. Mainz Basin (North Sea origin) : 9 spec.
2. Paris Basin : 8 spec.
3. Middle Upper Rhine Graben (Strasbourg area): 10 spec
4. Jura Molasse (Laufen Basin) : 18 spec.
5. Subalpine Molasse East (Grisiger Mergel) : 8 spec.
6. Subalp. Molasse West ("Marnes de Vaulruz): 2 spec.
7. Aquitaine Basin : 6 spec.

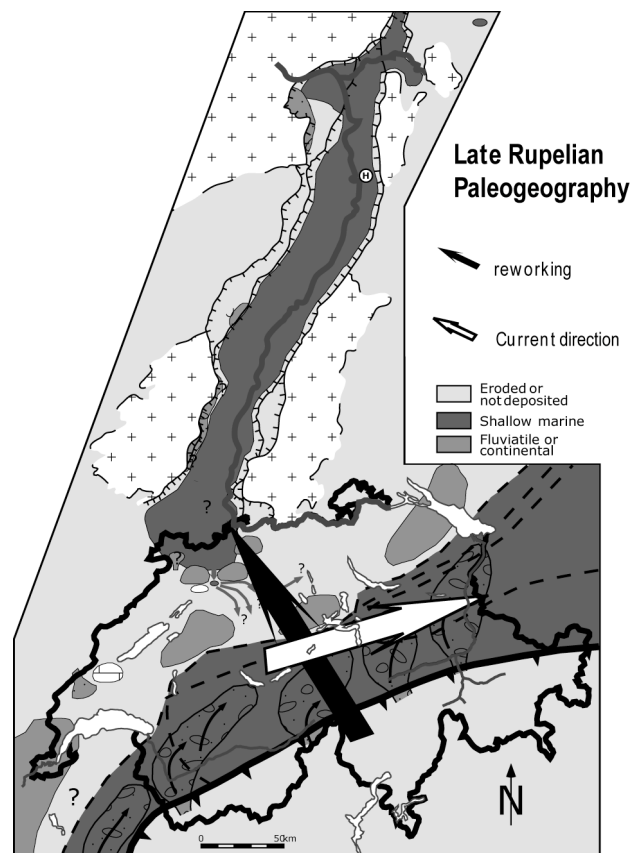
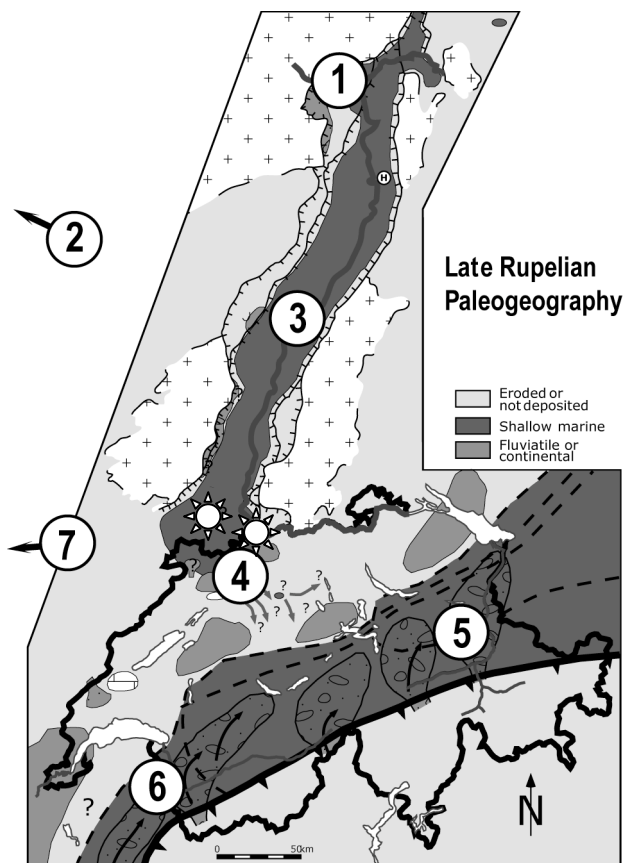


Figure 2. Paleogeography and reworking material : contradiction ?

These results lead to the following preliminary conclusions :

- a) The Jura Molasse (4) and the South Rhine Graben ostracod faunas are clearly similar.
- b) There was probably no marine connection between the Western Alpine Sea and the Rhine Graben during this time.
- c) An origin from the North Sea is very probable.

Concerning the reworked foraminifera, the detailed analyse is presented in Pirkenseer & al. (this volume). A first preliminary conclusion would be to find an origin in the Alpine domain (Helvetic?). But two very important questions remain unsolved :

1. The Helvetic domain was only in erosion since the Middle Miocene. How can we have reworked forams already during the Rupelian?
2. How can we imagine reworked forams transported from South to North whereas the general marine current is from West to East? See fig.2

To be discussed ...

This paper is a part of the PhD of C. Pirkenseer, actually in progress. Thanks go to the SNF Projects No 2000-66935 and 200020-109457 for financial support.

New frontiers in reconstructing sauropod dinosaurs

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With more than 30 m length and presumably more than 26 tons of body mass, sauropods are the largest terrestrial vertebrates (Upchurch et al. 2004). Reconstructions of their life-style have changed over the last century from depicting sluggish, snorkeling shallow-water dwellers to gregarious terrestrial giants. Most remarkably, sauropods show a variety of different neck types, ranging from moderately long to extremely long necks. Soft-tissue reconstructions, biomechanical investigations, calculations of neck flexibility by studying mobility of articulations and the cervical ribs, and reconstructions of the shoulder girdle were used here for a new model for sauropod neck support and overall body posture.

The soft-part reconstructions are based on comparisons with extant birds and crocodylians. Osteological correlates in the sauropod neck vertebrae indicate a segmented dorsal and lateral, a laterocostal and a ventral axial muscle mass, as well as strong dorsal supraspinal and interspinal elastic ligaments (Fig. 1). Sauropod neck vertebrae were surrounded and penetrated by pneumatic structures and therefore air-filled, like the vertebrae of birds. Osteological traces of these pneumatic diverticula indicate that the room between the rami of bifurcate neural spines was filled by pneumatic diverticula (Fig. 1) and there was an overall system of two ventral and one dorsal hose-like pneumatic canals. The pneumatic diverticula of the neck were connected with a paired air sac in the shoulder region, which itself was connected to the lung. It is plausible that the degree of stiffness of the pneumatic system in sauropods could be regulated, similar to recent birds. Therefore, pneumatic diverticula in the sauropod neck most probably contributed to neck support, forming pneumatically stabilizing structures. Pneumatic diverticula and their hollowing out of the neck vertebrae of sauropods also served as a weight-saving device. They lighten for example the 11 m

long neck of *Brachiosaurus* up to 25%, as compared to a non-pneumatized neck.

Biomechanically, the sauropod neck can be described as a segmented beam, anchored at the trunk and loaded by gravity. In this neck, the dorsal ligament system elastically suspended the neck and together with the ventral rib ligaments launched the elastic recoil after lateral and ventral movements. Because of the additional pneumatic support, few muscle forces were needed to stabilise the neck, so that sauropod necks represent a true lightweight-construction.

Three types of neck support can be distinguished. Sauropod necks can be mainly supported from dorsally by ligaments and pneumatic diverticula. This type of bracing is realised in taxa like *Apatosaurus* or *Dicraeosaurus*, displaying a ventrally oriented neck posture (Stevens & Parrish 1999), a long, triangular skull with peg-like teeth, and were most probably bottom-related browser. The other extreme is a mainly ventrally supported neck as present in taxa like *Mamenchisaurus* or *Euhelopus*. Here, the cervical ribs form long overlapping bundles acting as a kind of multiple-leaf-spring. Necks of this type are moderately horizontal-ventrally oriented. They have a short and high skull and spoon-like teeth, browsing most probably at a low level. However, most sauropods have a combined dorsoventral bracing system of the neck, supported both by dorsal ligaments, ventral cervical ribs and pneumatic systems. This is the case in *Diplodocus*, *Camarasaurus*, or *Brachiosaurus*, with variably ventrally or horizontally held necks (Stevens & Parrish 1999) and skull types. A combined dorsoventral neck support therefore allows a wide variety of sauropod feeding types.

The orientation of the scapulocoracoid in sauropod dinosaurs was reconstructed based on comparative anatomical investigations of pectoral girdles

of extant amniotes. In the reconstruction proposed here, the scapula of sauropods stands at an angle of more than 50° to the horizontal plane in mechanical coherence with the sternal apparatus including the coracoids. The shoulder articular surface is directed mediolaterally, so that the humerus can swing in a sagittal plane and the forelimb has a vertical, or columnar, posture.

There are certain differences in the angulation of the scapulocoracoid in different sauropods, which have important effects for the overall body posture, neck posture and indicate different construction types (Fig. 2). In a body posture with the shoulder girdle lying relatively higher than the sacrum, the centre of gravity must have been positioned much closer to the pelvis than previously reconstructed (Henderson 2004). Therefore, in *Camarasaurus* or *Brachiosaurus*, relatively more body mass would be transmitted to the hindlimbs and relatively fewer mass to the forelimbs during the support phase of walking, whereas in *Diplodocus*, the body mass might be much more evenly distributed between fore and hind limbs (Fig. 2). These reconstructions are confirmed by the presences of narrow gauge and wide gauge trackways in the fossil record (e.g., Lockley et al. 1994) and give a reasonable osteological explanation for the often observed differences in manus and pes imprint depths. The position of the shoulder girdle and vertebral column in the trunk determines also the direction of the neck from the shoulder girdle (Fig. 2). Interestingly, the body posture, neck support system and the morphology of neck vertebrae indicate that no sauropod had an upright, vertically held neck and head.

Combining osteological, soft-part and biomechanical features yields biomechanically consistent models for overall postures in sauropods. The holistic reconstructions of the sauropod body therefore add to our knowledge of fossil ecosystems and open a new view of sauropod ecology, especially in terms of their feeding mechanisms, diet and interspecific relations in Mesozoic terrestrial ecosystems.

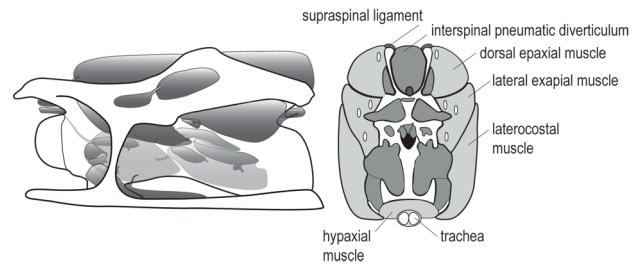


Figure 1. Reconstructions of soft-parts in a neck vertebra of *Diplodocus*, left side: lateral view with pneumatic diverticula; right side: transverse cross section.

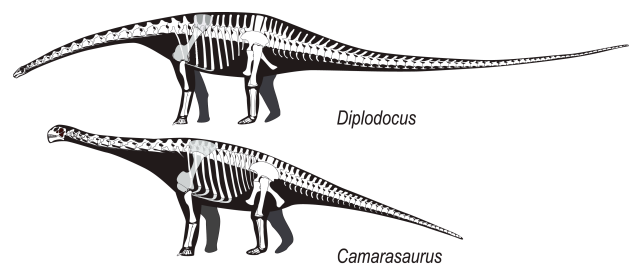


Figure 2. Reconstruction of overall body posture of the sauropods *Diplodocus* and *Camarasaurus*.

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