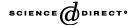


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Dinosaurs of Switzerland

Dinosaures de Suisse

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Abstract

Until 1960, the record of dinosaurs was rather poor in Switzerland. Between 1960 and 1980, several new localities with plateosaurid remains as well as prosauropod and theropod tracks were found in Late Triassic sabkha and floodplain environments. The discovery of large surfaces with sauropod tracks in the Late Jurassic of the Jura Mountains in 1987 triggered a stream of new data. More than 20 new localities with tracks from both sauropod and theropod dinosaurs in different stratigraphic levels have been found since then. The latest discoveries include trackways of iguanodontids from the Early Cretaceous of the central Swiss Alps and a large Late Jurassic surface with trackways of small sauropods in the northernmost part of the Jura Mountains. The best skeletal record comes from the Late Triassic, with scattered data from the Late Jurassic. The track and trackway record appears to be best in the Late Jurassic. To cite this article: C.A. Meyer, B. Thüring, C. R. Palevol 2 (2003) 103–117.

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Résumé

Avant 1960, les découvertes relatives aux dinosaures étaient très limitées en Suisse. Entre 1960 et 1980, plusieurs gisements contenant des restes de platéosauridés ainsi que des sites comportant des traces et des pistes de prosauropodes et de théropodes ont été découverts dans le Trias supérieur. En 1987, la découverte, dans le Jurassique supérieur du Jura suisse, de grandes surfaces portant des traces de sauropodes apportera un nouveau flux de données. Plus de vingt sites, dans différents niveaux stratigraphiques, contenant des traces de sauropodes et de théropodes, y ont été répertoriés depuis. Dans les toutes dernières découvertes sont incluses des traces et des pistes d'iguanodontidés du Crétacé inférieur des Alpes Centrales, ainsi que des pistes de petits sauropodes sur une grande dalle du Jurassique supérieur, dans le Nord du Jura. La plupart des restes d'ossements sont datés du Trias supérieur, tandis que les meilleures données ichnologiques proviennent du Jurassique supérieur. *Pour citer cet article : C.A. Meyer, B. Thüring, C. R. Palevol 2 (2003) 103–117*.

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Mots clés : Trias supérieur ; Jurassique supérieur ; Crétacé inférieur ; théropodes ; prosauropodes ; sauropodes ; Thyreophora ; traces

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1. Introduction

The first published record of Swiss dinosaurs goes back to 1856, when Rütimeyer announced bones of a giant reptile from the Late Triassic Knollenmergel near Niederschönthal. As early as 1825, Hugi mentioned that teeth of giant lizards had been found in the Late Jurassic Solothurn Turtle Limestone, but unfortunately no figures were published. In 1870, Greppin figured several bones of 'Megalosaurus' from the Late Jurassic of Moutier. Almost 100 years later in, 1961, geologists from the Federal Polytechnical Institute of Zurich briefly mentioned the discovery of dinosaur tracks from the Late Triassic in the Swiss National Park in southeastern Switzerland. In the same year, bones from a brick pit near Frick were tentatively assigned to Plateosaurus; they were found in the uppermost Triassic Knollenmergel (Norian).

The first account of dinosaur tracks from the Swiss Jura Mountains dates back to 1976, when a local chamois hunter remarked what he thought to be trackways of an unknown animal on a limestone slab near La Plagne (Biel); this discovery was announced in a local newspaper - citing a geology professor from Neuchâtel - as being the tracks of Iguanodon. In 1987, a large surface with sauropod tracks was discovered in a quarry near Lommiswil in shallow marine sediments. This site has proved something of a Rosetta stone for Swiss dinosaur ichnology. Several subsequent tracksite discoveries in the surrounding area revealed that they are associated with the same stratigraphic levels near the top of the Late Jurassic Reuchenette Formation. This means that the Lommiswil site forms part of a much larger megatracksite complex. Such megatracksites, also dubbed as 'dinosaur freeways' are best known from the western United States. The Swiss megatracksite was the first identified in Europe [16] and was attributed to the Brontopodus ichnofacies [19]. Since this initial discovery [18], stratigraphic target intervals have been recognized and additional sites have been found. Focused research in museum collections revealed that Switzerland is in fact not poor in dinosaur remains and yields a good potential for future research in this field. The present paper sets out to give a brief overview of the dinosaur fauna of Switzerland as it is known today (Figs. 1 and 2).

2. The Triassic

2.1. Bone record

The first dinosaurs in Switzerland were announced by Rütimeyer [24], in 1867, from the Late Triassic near Niederschönthal. The bones and a geological section were sent to him by Amanz Gressly in a letter dated 9 September 1856. The first sketch of the bones in which he attributed them to the phytosaur Belodon (in pencil) but overwrote it with the posauropod Gresslyosaurus (in ink) were found in the archives of the Basel Natural History Museum (Fig. 3). Subsequently, more bones were found and attributed to the plateosaurid Gresslyosaurus ingens. Galton [7] reviewed most of the skeletal remains and placed G. ingens in synonymy with Plateosaurus engelhardti. A large quantity of isolated bones were collected later from the area around Niederschönthal [26], but a taphonomic and sedimentological study of these assemblages is still needed.

In 1961 the children of a quality controller of a brickwork company found scraps of bones in the Knollenmergel at Gruhalde near Frick that were tentatively identified as remains of plateosaurids. Subsequently several excavations were made from 1976 until 1988 [25] (Fig. 4). The last excavation yielded one of the most complete skeletons ever found; it is attributed to Plateosaurus engelhardti. The fauna of the bone bed at Frick includes teeth of the theropod Liliensternus, shark and fish remains (Hybodus, Ceratodus, Lepidotus), and remains of aetosaurs, sphenodontids and cynodonts. In an extensive study of the Norian bone beds of Central Europe, Sander [25] came to the conclusion that the uniformly upright position of the carcasses argues for in-situ preservation. Depressions in the floodplain deposits of the Knollenmergel (Norian) must have formed efficient traps where the animals became mired and scavenged by theropods.

Scattered records of plateosaurid bones from Hallau, Beggingen and the Hauenstein railway tunnel demonstrate that this genus was widespread throughout northern Switzerland. In 1984, Late Triassic sediments near Corbeyrier yielded some isolated teeth that have been tentatively attributed to prosauropods [2].

2.2. Track record

One of Europe's most spectacularly located high altitude tracksites, at Piz dal Diavel (meaning "devil's

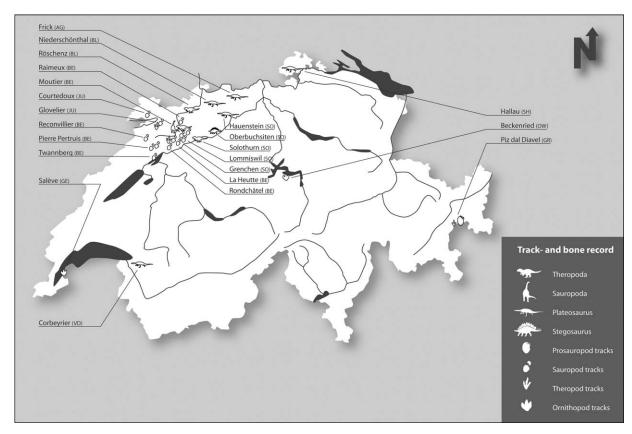


Fig. 1. Overview of dinosaur localities in Switzerland.

Fig. 1. Répartition géographique des localités à dinosaures en Suisse.

peak") in the Swiss Alps was discovered by geologists from the Federal Polytechnic Institute in the 1960's, but it took two decades until serious attempts were made to take a close look at this remote alpine site situated 2450 meters above sea level. In 1981, a team from the University of Zurich mapped the surface which covers approximately 2000 m², and made casts and molds of some of the tracks [6]. The tracks include a single trackway of the Tetrasauropus type, consisting of 25 footprints about 60 cm long. The step is short, about 1 m, the corresponding stride is about 2 m, and the trackmaker has been interpreted as a prosauropod probably a plateosaurid. This is a rare example of a large Tetrasauropus trackway from Europe. However, plateosaurid remains are abundant at Frick (Switzerland), and at Trossingen and Halberstadt in Germany. There are thirteen trackways attributed to theropod dinosaurs with footprints that range from 25-30 cm in size. Such tracks are large in comparison with theropod

tracks from other known Late Triassic localities. They are about the same size as tracks known from Wales that belong to the ichnogenus *Anchisauripus* [13]. Studies of the track-bearing surface reveal that it consists of a mudcracked dolomitic limestone that contains fish remains, ostracods and plant debris. The footprints occur in the Diavel formation (Hauptdolomit Group) within a regressive sequence that is interpreted as an infilling of a restricted lagoon in the dolomitic back-reef facies [5].

One of the most enigmatic tracksites from the Triassic is the Vieux Emosson locality in the southwest-ernmost part of Switzerland. This surface, originally-discovered by Georges Bronner in 1976, lies within a transgressive sequence of sandstone, shales and dolomites that overlies the altered basement of the Aiguilles Rouges Massif. Its age is thought to be Ladinian or Carnian. This site was described by Georges

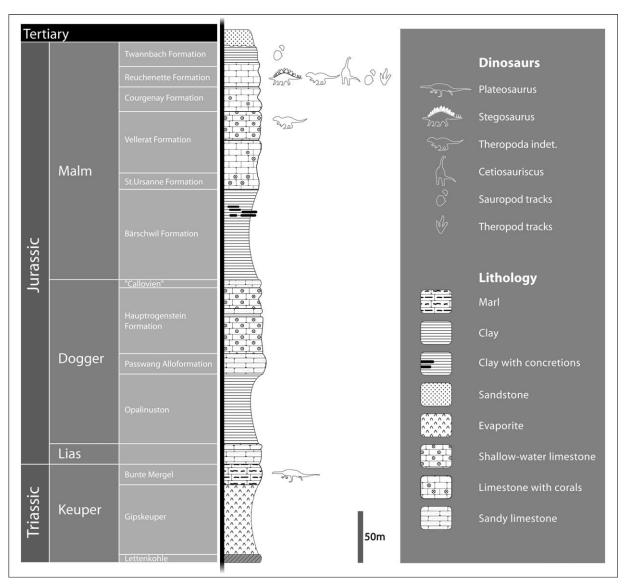


Fig. 2. General stratigraphy of Northern Switzerland with location of dinosaur sites.

Fig. 2. Stratigraphie générale du Nord de la Suisse, avec la situation des localités à dinosaures.

Demathieu and Marc Weidman [3]. Their study is somewhat anomalous, because nine ichnospecies are named on the basis of material that is in some cases rather dubious. Some genus names such as *Brachychirotherium* and *Isochirotherium* are known elsewhere, but some are new and are based on names coined by Ellenberger in his study of tracks from the Late Triassic and Early Jurassic of Southern Africa [4]. Since the publication in 1982, these ichnogenera have not been reported from other sites, suggesting that the names

have not been accepted as representative of distinctive morphotypes recognizable elsewhere. For example, *Bifidichnium ambiguum* looks like the track of an artiodactyl and may be some sort of artefact of preservation. As many of the details of the tracks are no longer visible, it is difficult to ascertain their taxonomic status. Up to now, there is no Early or Middle Triassic tracksite where nine ichnospecies are found, and certainly none with these ichnospecies. We therefore regard the interpretation of this site with some



Fig. 3. The first sketch of dinosaur bones from the Late Triassic of Niederschönthal. Original drawing by Rütimeyer and attributed to *Gresslyosaurus*.

Fig. 3. Première illustration des ossements de dinosaures du Trias supérieur provenant de Niederschönthal. Illustration originale par Rütimeyer, attribuée à *Gresslyosaurus*.

scepticism. A revision of these ichnotaxa is needed, but what we can say today is that none of those was left by dinosaurs.

It is interesting to note that several other sites have been encountered, also in parts of adjacent France, that seem to be all in the same stratigraphic unit. A new site in coeval strata some kilometres further north (courtesy of Bill Fitches) in the Lake Salanfe area shows faint imprints that can be attributed to chirotherids. This indicates that the Late Triassic footprint assemblage from the Aiguilles Rouges massif is most probably a megatracksite covering at least 45 km² that yields potential for further study and comparison. A megatracksite, as it is currently defined, is a regionally extensive single surface, or a very thin package of beds, that is track bearing or rich in tracks over a large



Fig. 4. The Late Triassic locality Frick with a view of an exposed partial skeleton of *Plateosaurus engelhardti* (Excavation 1985, courtesy B. Imhof).

Fig. 4. La localité Frick (Trias supérieur) vue de l'excavation avec un squelette partiel de *Plateosaurus engelhardti* (Excavation 1985, courtoisie B. Imhof).

area of the orders of hundreds to thousand square kilometres [13].

In 2000, a local alpinist, Joseph Oehler, observed unusual marks on a limestone surface in the Ladinian Rötidolomite in the Tödi-area (Canton of Glarus). This observation was brought to the attention of Markus Feldmann, a geologist, who issued a first note in a local journal in 2002. The surface is approximately 450 m² and shows at least three individual trackways. The tracks are currently under study. Despite their less than optimal preservation, it seems that they can be attributed to the non-dinosaurian ichnogenus *Brachychirotherium*.

3. The Late Jurassic

3.1. The bone record

3.1.1. Oxfordian

A single large dinosaur tooth - housed in the Museum of Natural History in Bern (A 6693) and discovered by speleologists – comes from the Silberloch cave near Röschenz, which was found in loose gravel at the cave bottom. We assume that the specimen was leached out from the surrounding limestone substrate of Oxfordian age. The tooth is serrated on the anterior and posterior edges and shows many similarities with the genus Ceratosaurus. In fact, teeth of allosaurid theropods are much more elongated and slender, with a round to oval cross-section, whereas those of Ceratosaurus are more triangular and show an elliptic crosssection. This genus is well known from the Late Jurassic of North America, but has recently also been reported from the same interval of the Guimarota mine in Portugal [23].

3.1.2. Early Kimmeridgian

In 1870 Greppin figured bones of a reptile under the name of *Megalosaurus meriani*, which came from the vicinity of Moutier [8]; included was a large tooth of an allosaurid theropod, but the specimen has been lost since then. It was first described by Huene [9], who attributed it to *Ornithopsis greppini*; Weishampel [15] erroneously reported that the skeletal remains were derived from the Virgula beds (Tithonian), but they come from the lower part of the Reuchenette Formation (Late Lower Kimmeridgian *sensu gallico*). According to the first report by Greppin, the bones came

from a quarry at the 'Basse Montagne', where building stones for the high school were extracted at the time. There are 134 bones; most of them are laterally compressed and pertain to a small sauropod dinosaur (all the syntypes are housed in the collections of the Basel Natural History Museum, Figs. 5-7). The minimum number of individuals is two, based on the presence of two left femora (MH 349, MH 372; Fig. 5). McIntosh previously suggested the presence of at least four partial skeletons [15]. There is no skull material and most bones represent caudal vertebrae, limb bones, girdle elements and ribs. Dorsal vertebrae are poorly represented. MH 352 [21 (pl. 17, figs 24a-b)], is a centrum and partial neural arch that was identified as a dorsal centrum of a sauropod, but it actually pertains to the mesosuchian crocodile Machimosaurus hugii [11 (fig. 4)]. The Moutier sauropod and the genotype Cetiosauriscus stewarti share a number of common elements. The vertebrae of the two specimens is similar: each one has anteroposteriorly short anterior caudal vertebrae and more elongate distal vertebrae (Fig. 7). Significant differences are seen in the proportions of limb elements, most dramatically in the humerus. C. stewarti (BHMN R.3078) has a proportionally much more robust humerus. Furthermore, in anterior view, the shaft is proportionally more waisted and possesses a more prominently developed deltopectoral crest. Morphological differences suggest that the Swiss specimen and the English one represent different species of the same genus; therefore, we attribute the Moutier specimen to Cetiosauriscus greppini. Because the circumstances of the original discovery remain unclear a taphonomical interpretation cannot be given. However a broken femur shows several circular bite marks (Fig. 6b) that match the teeth of the mesosuchian crocodile Machimosaurus hugii. Some of the bones still show some matrix, which includes fragments of charcoal. The greenish marl suggests that the animals were buried in freshwater sediments. Catalogue reports from the Basel Museum show that some of the material was donated by Prof. Pagnard (Porrentruy) in 1866, some material was bought in the same year (high school of Delémont) and additional material was sold to the museum by Greppin in 1870.

A broken left femur is the first record of a stegosaur from southern Central Europe [20]. The specimen is housed in the Museum of Nature at Solothurn (NMS 20'171) and was found around 1950 by a private col-



Fig. 5. *Cetiosauriscus greppini* (Huene) from the Reuchenette Formation, 'Basses Montagnes', Moutier: (a) left ischium (HM 387); (b) right humerus (HM 260).

Fig. 5. Cetiosauriscus greppini (Huene) de la formation de Reuchenette, Basses Montagnes, Moutier: (a) ischion gauche (HM 387); (b) humérus droit (HM 260).

lector in a now abandoned quarry close to the village of Oberbuchsiten (Canton of Solothurn). It comes from the Wettingen member of the Villigen Formation (acanthicum zone, Lower Kimmeridgian). The bone is strikingly similar in its overall shape to the femur of Kentrosaurus aethiopicus from the Upper Jurassic of Tanzania. Given the range of the femoral variation in this taxon, a conclusive assignment cannot be made, but the material pertains to a stegosaur [20].

The Solothurn Turtle limestone (Upper Reuchenette Formation) has yielded a number of isolated theropod teeth, first figured by Huene [10]. Two of those are still in the collection of the Museum of Nature at Solothurn. Both teeth are serrated on the anterior and posterior edges and can be attributed to small theropods of un-

certain affinity (Fig. 8); they belong to two different genera. The smaller tooth might be attributed to a dromaeosaurid and is strikingly similar to teeth from the Late Jurassic of Portugal. Two bones were interpreted by Huene as pertaining to coelurosaurs and ornithopods are not of dinosaur origin. One is a possible praepubis of a mesosuchian crocodile and the other pertains to a large pterodactyl pterosaur [21].

3.2. Track record

3.2.1. Early Kimmeridgian

One of the Swiss national pastimes is rock climbing, and through this activity a number of dinosaur track-



Fig 6. Cetiosauriscus greppini (Huene) from the Reuchenette Formation, 'Basses Montagnes', Moutier: (a) left femur (HM 349), (b) partial left femur with bite marks (arrows; HM 372).

Fig. 6. Cetiosauriscus greppini (Huene) de la formation de Reuchenette, 'Basses Montagnes', Moutier: (a) fémur gauche (HM 349); (b) fémur gauche, avec traces de morsures (flèches; HM 372).

sites have been found. In fact, most of the dinosaur tracksites discovered in Switzerland were found by the senior author as a result of combining professional geology with rock climbing. The second largest dinosaur tracksite in Switzerland, in terms of surface area and number of footprints, was found in Moutier Canyon in the Jura Mountains. This site was discovered by the senior author and Martin Lockley in 1996 by prospecting a large surface (Moutier II); the previous year on a small surface nearby, sauropod tracks had been detected (Moutier I). The site is a well-known area for rock climbers, and has been seen by many people, but evidently by none that was looking for dinosaur tracks. It can be best described as a stomping ground where there is evidence of various degrees of trampling or dinoturbation. The result of a two-week survey in 1997

was the recognition of about 2000 footprints distributed more or less randomly across a steeply inclined surface of about 6000 m² (Figs. 9 and 10). Only a few tracks are sufficiently clear and only a few allowed us to distinguish large pes tracks and manus tracks. It is difficult to say much about the number of sauropod trackmakers that were in the area, the type (wide- or narrow-gauge), size (though some were as large as 1 m; Fig. 10), or direction of travel of these sauropods. Work is still in progress, in an attempt to explain why some tracks are very deep (40 cm) and others so shallow as to be barely perceptible [13]. The main tracksite occurs on a dense mudstone that shows birdeyes and is overlain by algal laminites. Further upsection two more levels with sauropod footprints can be seen, but the outcrop area is too small to provide additional

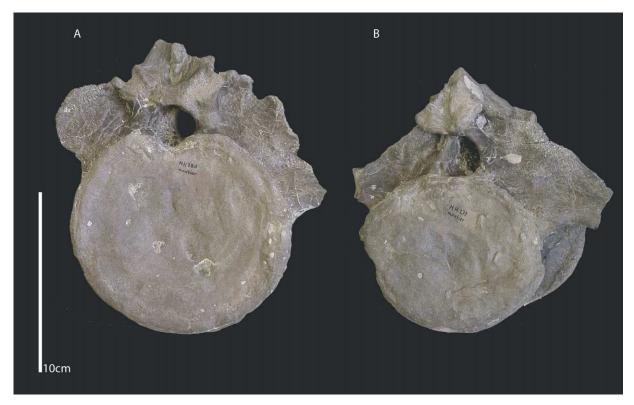


Fig. 7. Cetiosauriscus greppini (Huene) from the Reuchenette Formation, 'Basses Montagnes', Moutier: (a) proximal dorsal vertebrae, anterior view (HM 277); (b) proximal dorsal vertebrae, anterior view (HM 280).

Fig. 7. Cetiosauriscus greppini (Huene) de la formation de Reuchenette, 'Basses Montagnes', Moutier: (a) vertèbre dorsale proximale, vue antérieure (HM 277); (b) vertèbre dorsale proximale, vue antérieure (HM 280).

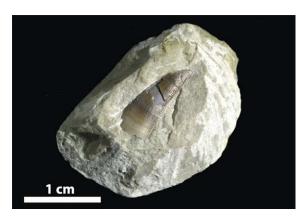


Fig. 8. Tooth of a small theropod dinosaur from the Solothurn Turtle Limestone (Upper Reuchenette Formation, Late Kimmeridgian) found near Solothurn.

Fig. 8. Dent d'un petit théropode des Calcaires à tortues de Soleure (formation de Reuchenette supérieur, Kimméridgien supérieur) trouvée près de Soleure.

information. Stratigraphically, the site has to be placed in the lower part of the Reuchenette Formation. It was formed in an inter- to supratidal environment. About 300 m southwest of the tracksite, coeval strata have yielded the skeletal remains of the above-mentioned *Cetiosauriscus*.

Close by in the southern part of the Moutier anticline, two small sites with sauropod footprints occur on the same level (Moutier III, IV). Further east, close to the village of Corcelles, two additional surfaces with moderately preserved footprints of sauropods were discovered by Philippe Saunier in 1996. In 1998 Bernhard Hostettler, a local amateur, discovered a surface with sauropod footprints along a new roadcut in the vicinity of Glovelier. Later on, Georges-Alain Beuchat, a teacher from Glovelier, discovered a surface with a theropod trackway in the vicinity (Fig. 11). One of our Masters students, Pascal Tschudin, found another surface with several parallel trackways of sau-



Fig. 9. Aerial view of the Moutier (Moutier II) dinosaur tracksite (Reuchenette Formation, Late Early Kimmeridgian).
Fig. 9. Vue aérienne du site à traces de dinosaures de Moutier

(Moutier II, formation de Reuchenette, Kimméridgien inférieur).

ropods in the same locality. All of those occur within the lower part of the Reuchenette Formation and are currently under study. In January 2000, a surface with one moderately preserved trackway of a sauropod was discovered by a local amateur and subsequently reported [1] near Frinvilier. The tracklevel is most probably situated within the lower part of the Reuchenette Formation and forms part of a megatracksite.

The most recent discovery was made in early April 2002 by archaeologists prospecting along the future highway A 16 through the Jura Mountains, near Courtedoux. The site was cleared and mapped by the 'Section de paléontologie' and comprises about 500 m², with more than 500 footprints. A preliminary study by the authors shows that the tracks can be attributed to small-sized narrow gauge sauropods that belong to the ichnogenus *Parabrontopodus*, commonly attributed to

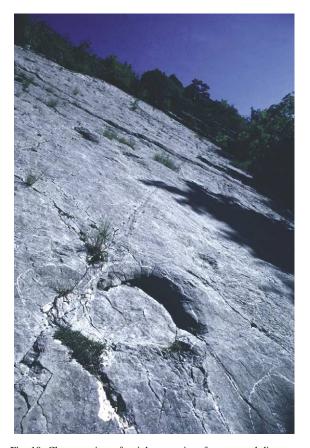


Fig. 10. Close-up view of a right pes print of a sauropod dinosaur (footprint length: 1 m) from the Moutier-II tracksite.
Fig. 10. Empreinte du pied droit d'un dinosaure sauropode (longueur de l'empreinte : 1 m) du site Moutier II.



Fig. 11. Trackway of a medium sized theropod from Glovelier (Lower Reuchenette Formation, Late Early Kimmeridgian). Fig. 11. Piste d'un théropode de taille moyenne de Glovelier (formation de Reuchenette, Kimméridgien inférieur).

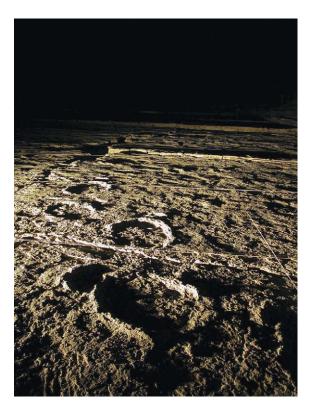


Fig. 12. Trackway of a narrow gauge sauropod form the Combe Ronde site near Courtedoux (Lower Reuchenette Formation, Late Early Kimmeridgian).

Fig. 12. Piste d'un sauropode de type narrow gauge du site Combe Ronde, près de Courtedoux (formation de Reuchenette, Kimméridgien inférieur).

diplodocid sauropods. This is the first site in Switzerland yielding the ichnotaxon; all other Late Jurassic tracksites from northern Switzerland indicate the presence of the wide-gauge-type ichnotaxon Brontopodus. Trackway parameters suggest animals of approximately 2 m hip height and a gleno-acetabular distance of 1.2 m [14]. The estimated length of the hind limb of the diplodocid Cetiosauriscus (around 1.95 m) mentioned above, and the fact that it was found in coeval strata, strongly support the hypothesis that Cetiosauriscus could have left the tracks at the Combe Ronde site, near Courtedoux (Fig. 12). On the whole, six parallel sauropod trackways can be seen. Two theropod trackway segments confirm that this assemblage forms part of the *Brontopodus* ichnofacies coined by Lockley et al. [12]. The tracksite can be dated by aspidoceratid ammonites to the basal Late Kimmeridgian. All of the sites occur within the same stratigraphic interval and

are therefore another good example of a megatracksite covering more than 250 km² (Fig. 13).

3.2.2. Late Kimmeridgian

Switzerland is famous for limestones, especially those from the Jura Mountains that give their name to the Jurassic time period. They are traditionally regarded as marine, so no one would expect them to contain much evidence of terrestrial animals such as dinosaurs. One such deposit, rich in marine vertebrate fossils, such as turtles, crocodiles and fishes, is the Solothurn Turtle limestone exposed in various quarries and natural outcrops in the vicinity of the town of Solothurn. In a quarry near the small village of Lommiswil, Meyer [16] identified what turned out to be the first Late Jurassic dinosaur tracks reported from Switzerland. Given the attention that many geologists have focused on quarries such as the one at Lommiswil, it is surprising that tracks are 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 m, 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 toe impressions. On the whole 450 individual footprints can be seen, and more were exposed in recent years with ongoing quarry operations. The general trackway configuration, however, reveals that the trackmaker was of the wide-gauge variety (Fig. 14). Within the same megatracksite level, several small sites have been found (Fig. 15), including a small surface near Grenchen, another close to Bürenberg, and several around La Heutte [17]. One surface at the La Heutte site yielded a single, shallow imprint of a theropod [17]. This confirmed that the megatracksite represents an example of the Brontopodus ichnofacies [12]. The above-mentioned tracks of 'Iguanodon' near La Plagne within the same megatracksite turned out to be imprints of small sauropods.

3.2.3. Tithonian

In the Pierre Pertuis area three different levels with sauropod footprints have been found in 1995. The best-preserved surface is stratigraphically situated in the lower part of the Twannbach Formation. The small, steeply inclined surface (50°) shows two trackways of wide-gauged sauropods. Close to the village of Twann

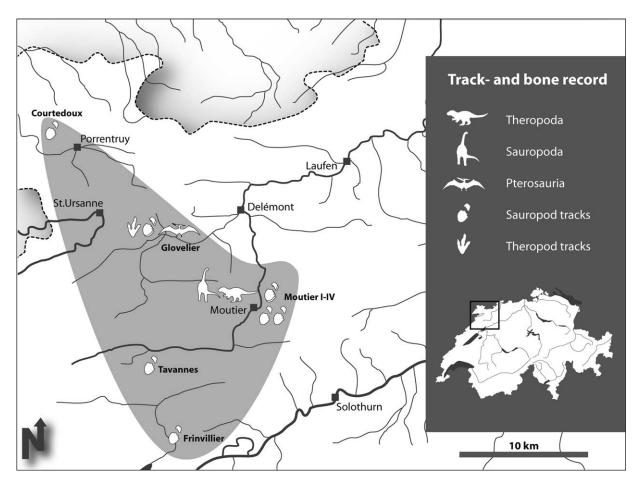


Fig. 13. Geographic extent of the megatracksite in the Lower Reuchenette Formation with principal track and bone localities.

Fig. 13. Extension géographique du « megatracksite » dans la formation de Reuchenette inférieure, avec les gisements principaux.

at Burgflueh, Michel Monbaron (Fribourg) observed an approximately 20 m² surface with dinosaur tracks. On close inspection, nine very shallow imprints can be seen, forming a trackway of a medium-sized sauropod; this level is in the Lower Twannbach Formation [19].

4. Cretaceous

Track record

In 2001, a local newspaper announced the discovery of a single footprint in a Berriasian limestone cliff in the Mont Salève area near Geneva; it was attributed to a theropod, but to date this material is unpublished.

In the summer of 2000, the geologist Markus Weh discovered an unusual pattern on a limestone surface



Fig. 14. View of the Lommiswil dinosaur tracksite (Upper Reuchenette Formation, Late Kimmeridgian) with casting staff for scale. Fig. 14. Vue du site de Lommisiwil (formation de Reuchenette supérieure, Kimméridgien supérieur) avec équipe de moulage donnant l'échelle.

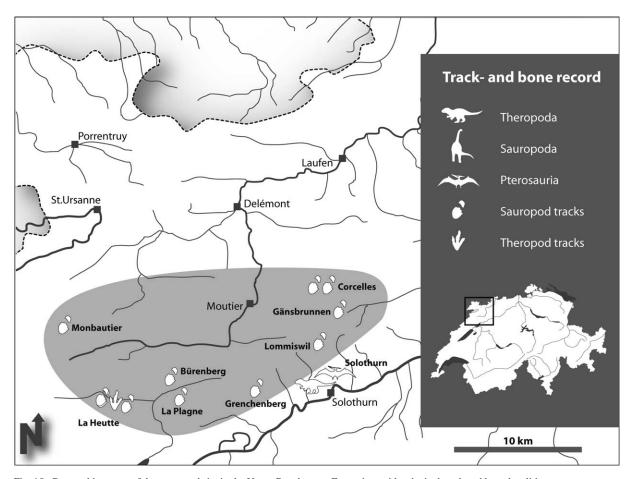


Fig. 15. Geographic extent of the megatracksite in the Upper Reuchenette Formation, with principal track and bone localities. Fig. 15. Extension géographique du *megatracksite* dans la formation de Reuchenette supérieure, avec les gisements principaux.

while swimming in Lake Lucerne [22]. Photographs of a close-up investigation were subsequently presented to the author in the same year. The new site lies in an abandoned quarry close to the shore of Lake Lucerne in the vicinity of the village of Beckenried (Canton of Nidwalden). Prior to mapping in alpinisitic style, the surface was photographed by helicopter. The best footprints and one trackway have been cast.

The steeply inclined surface yields more than 200 tracks of adult ornithopods (Fig. 16). The rounded digits with no claw impressions and their rounded heel as well as the presence of manus imprints clearly attributes these footprints to iguanodontids. Three trackways can be followed for a distance of 25, 27 and 35 m, respectively. The length of the footprints (mean: 30 cm) points to animals with a size of about 5 to 6 m,

indicating hip heights between 1.8 and 2 m. The animals moved at relatively slow speed (2 to 3.8 km h^{-1}). One trackway shows also the typically rounded manus impressions, indicating quadrupedal gait.

The substrate consists of shallow-water micrites, with traces of emersion, and is overlain by high-energy rudist grainstones. The Upper Schrattenkalk is the youngest member of the Schrattenkalk Formation. Its age ranges from middle Lower Aptian to middle Upper Aptian. Up until now, the deposition of the Upper Schrattenkalk Member in the Helvetic realm was thought to have formed on a large shelf far from any continents. This recent discovery will shed new light on the palaeogeographic position of the Helvetic nappes [19].

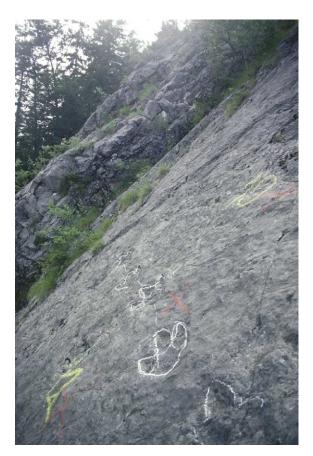


Fig. 16. A trackway of an iguanodontid dinosaur from the Schrattenkalk Formation (Aptian) in the Risleten quarry, near Beckenried. Fig. 16. Piste d'un iguanodontidé de la formation de Schrattenkalk (Aptien) dans la carrière Risleten, près de Beckenried.

5. Summary and prospectus

The dinosaur bone record of Switzerland includes one prosauropod (*Plateosaurus*), a theropod (*Liliensternus*), a carnosaur (*Ceratosaurus*), a diplodocid sauropod (*Cetiosauriscus*), an allosaurid theropod, two other theropod species (one of them being a possible dromaeosaurid) and a stegosaur. The track record reveals two different sauropods (one a diplodocid, the other a brachiosaurid-like sauropod), at least two different theropods as well as iguanodontids.

Since the discovery of the first large tracksite in the Jura Mountains in the 1987, many additional sites have been found in stratigraphic levels from the Late Jurassic to the Early Cretaceous. We predict that in the near future more tracksites will be found. Both the Schrattenkalk Formation in the Central Swiss Alps and the

Late Jurassic Reuchenette Formation have an especially great potential for future discoveries. Some sandy shore deposits within the Late Oxfordian in the area around Biel have yielded remains of pterosaurs and terrestrial plants; we would therefore not be surprised if skeletal remains and tracks of dinosaurs were discovered in the future.

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References

- J. Ayer, B. Claude, Découverte d'une piste de dinosaure sauropode dans le Kimméridgien de la région de Bienne (Jura central, canton de Berne, Suisse), Bull. Soc. Neuchâtel. Sci. Nat. 24 (2001) 149–159.
- [2] W. Brinkmann, Paläontologisches Museum der Universität Zürich - Führer durch die Ausstellung, Verlag des Paläontologischen Instituts und der Universität, Zurich, Switzerland, 1994.
- [3] G. Demathieu, M. Weidmann, Les empreintes de pas de reptiles dans le Trias du vieux Emosson (Finhaut, Valais, Suisse), Eclog. Geol. Helv. 75 (3) (1982) 721–757.
- [4] P. Ellenberger, Contribution à la classification des pistes de vertébrés du Trias; les types du Stormberg d'Afrique du Sud (2), Palaeovertebrata, Laboratoire de paléontologie des Vertébrés, Montpellier, 1974 (mémoire extraordinaire).
- [5] H. Furrer, Dinosaurs on the mud flats of a Late Triassic carbonate platform in the Swiss Alps, Abstr, 1st Int. Congr. Paleoecology, Int. Palaeontol. Assoc., Lyon, 1983.
- [6] H. Furrer, Entdeckung und Untersuchung der Dinosaurierfährten im Nationalpark Zernez, Schweiz, Cratschla Ediziun Specials 1, 1993.
- [7] P.M. Galton, Prosauropod dinosaur *Plateosaurus* (= Gresslyosaurus) (Saurischia; Sauropodomorpha) from the Upper Triassic of Switzerland, Paleontol, Geol 20 (1986) 167–183.
- [8] J.G. Greppin, Description géologique du Jura bernois et de quelques districts adjacents, Matériaux pour la carte géologique de la Suisse 8 (1870) 1–357.
- [9] F. von Huene, Über einen Sauropoden aus dem oberen Malm des Berner Jura, Eclog. Geol. Helv. 17 (1) (1922) 80–94.

- [10] F. von Huene, Die Saurierfauna des Portlandkalkes von Solothurn, Eclog. Geol. Helv. 19 (1926) 584–603.
- [11] B. Krebs, Der Jura-Krokodilier Machimosaurus H. von Meyer, Palaeontol. Z. 41 (1967) 46–59.
- [12] M. Lockley, A. Hunt, C.A. Meyer, Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy, in: S. Donovan (Ed.), The Palaeobiology of Trace Fossils, Belhaven Press, London, 1994, pp. 241–268.
- [13] M.G. Lockley, C.A. Meyer, The Dinosaur tracks and other fossil footprints of Europe, Columbia University Press, New York, 2001.
- [14] D. Marty, W. Hug, C.A. Meyer, L. Cavin, M.G. Lockley, Preliminary report of a dinosaur tracksite from Late Jurassic of northwestern Switzerland, Abstracts European Paleontological Association Workshop on Freshwater & Brackish (Paleo)Ecosystems, Fribourg, Switzerland, 2002.
- [15] J.S. McIntosh, Sauropoda, in: D.B. Weishampel, P. Dodson, H. Osmolska (Eds.), The Dinosauria, University of California Press, Berkeley, CA, 1990, pp. 345–401.
- [16] C.A. Meyer, A sauropod megatracksite from the Late Jurassic of northern Switzerland, Ichnos 2 (1993) 1–10.
- [17] C.A. Meyer, M. Hauser, Additional theropod and sauropod prints from the Upper Jurassic megatracksite of northern Switzerland, in: M.G. Lockley, V.F. dos Santos, C.A. Meyer, A.P. Hunt (Eds.), Aspects of Sauropod Paleobiology, 10, Gaia, Lisboa, 1994, pp. 49–56.
- [18] C.A. Meyer, J.G. Pittman, A comparison between the Brontopodus ichnofacies of Portugal, Switzerland and Texas, in: M.G. Lockley, V.F. dos Santos, C.A. Meyer, A.P. Hunt (Eds.), Aspects of sauropod paleobiology, 10, Gaia, Lisboa, 1994, pp. 125–134.

- [19] C.A. Meyer, M.G. Lockley, The Late Jurassic continental record of northern Switzerland: evidence and implications, in: M. Morales (Ed.), The continental Jurassic, Museum of Northern Arizona, Flagstaff, 1996, pp. 421–426.
- [20] C.A. Meyer, A.P. Hunt, The first stegosaurian dinosaur (Ornitischia: Thyreophora) form the Late Jurassic of Switzerland, Neues Jahrb. Geol. Palaeontol. Monatshefte (1998) 141–145.
- [21] C.A. Meyer, A.P. Hunt, The first pterosaurs from the Late Jurassic of Switzerland: evidence for the largest Jurassic flying animal, Oryctos 2 (1999) 111–116.
- [22] C.A. Meyer, M. Weh, K. Graf, S. Bucher, B. Thüring, S. Boll, The first Cretaceous dinosaur tracks from the Swiss Helvetic Realm, Abstr, 6th Eur. Vertebrate Palaeontology Workshop, Florence, Italy, 2001.
- [23] O. Rauhut, The dinosaur fauna from the Guimarota mine, in: T. Martin, B. Krebs (Eds.), Guimarota: a Jurassic Ecosystem, Pfeil, München, Germany, 2000, pp. 75–82.
- [24] L. Rütimeyer, Reptilienknochen aus dem Keuper, Verh. Schweiz. Ges. Naturwiss. XLI (1856) 62–64.
- [25] P.M. Sander, The Norian Plateosaurs Bonebeds of Central Europe and their taphonomy, Palaeogeogr. Palaeoclimatol. Palaeoecol. 93 (1992) 255–299.
- [26] K.M. Tanner, Die Keuper-Lias-Fundstelle von Niederschönthal, Kanton Baselland, Bull. Verein. Schweiz. Petrol.-Geologen und Ingenieure 44 (/106) (1978) 13–23.