

# Preliminary Report on the Courtedoux Dinosaur Tracksite from the Kimmeridgian of Switzerland

**Daniel Marty, Wolfgang A. Hug, and Andreas Iberg**

*Section de paléontologie, Office de la culture, Hôtel des Halles, Porrentruy, Switzerland*

**Lionel Cavin**

*Department of Palaeontology, The Natural History Museum, London, United Kingdom*

**Christian A. Meyer**

*Naturhistorisches Museum Basel, Basel, Switzerland*

**Martin G. Lockley**

*University of Colorado at Denver, Department of Geology, Denver, Colorado, USA*

---

In 2002 a new dinosaur tracksite was discovered in calcareous laminites of early Late Kimmeridgian age along the future course of the “Transjurane” highway in Courtedoux, Canton Jura, Northern Switzerland. The site has an extraordinary scientific potential, as the laminites, which have been deposited in an intertidal to supratidal environment, contain at least 6 track-bearing levels in a total thickness of about 1 m. The laminites are being systematically excavated by the “Section de paléontologie” over an area of approximately 1500 m<sup>2</sup>. So far the main track level has been uncovered over an area of about 650 m<sup>2</sup>, which reveals 2 trackways of theropods and 17 trackways of sauropods. The sauropod tracks are the smallest known in the Kimmeridgian so far, and the trackways belong to the ichnogenus *Parabrontopodus*, which has been revealed for the first time in Switzerland. The tracksite belongs to the “Middle Kimmeridgian megatracksite” *sensu* Meyer (2000), and represents the most important dinosaur tracksite in Switzerland, perhaps with the potential for development into one of the world’s largest sauropod tracksites. It will be protected in situ underneath an especially constructed highway-bridge, thus offering opportunities for future research and the development of an interpretative center for education and tourism.

---

**Keywords** Sauropoda, Diplodocoidea, Theropoda, dinosaur track, *Parabrontopodus*, *Brontopodus*, megatracksite, Reuchenette Formation, Canton Jura, Switzerland.

---

Address correspondence to Daniel Marty, Section de paléontologie, Office de la culture, Hôtel des Halles, Case Postale 64, 2900 Porrentruy, Switzerland. E-mail: daniel.marty@palaeojura.ch

## INTRODUCTION

In the past few years there have been many discoveries involving dinosaur tracksites in Switzerland (Meyer, 1990, 1993; Mouchet, 1993; Meyer, 1994; Meyer and Hauser, 1994; Meyer and Lockley, 1996; Meyer, 1997; Ayer and Claude, 2001; Meyer and Thüring, 2003). As a result of the construction of the “Transjurane” highway, a new paleontological project, the “Section de paléontologie,” was established in February 2000 to save and examine the paleontological heritage of the future highway route in the Canton Jura, Northern Switzerland (Thüring and Hug, 2001; Marty et al., 2002b, submitted).

During archeological and paleontological prospecting along the future route, a new tracksite was discovered in Courtedoux in February 2002 (Marty et al., 2002a). The tracksite is situated in laminites with a thickness of about 1 m, in which 6 track-bearing levels and one level with body fossils (turtle bones) are known so far. The site is being further excavated on the future highway course over a total area of about 1500 m<sup>2</sup>. During the 2002 excavations, the main track level (level 1000), which forms the base of the laminite series (Fig. 9), has been uncovered on the whole width of the future highway course over an area of approximately 40 m long by 15 m wide and 650 m<sup>2</sup> in total area.

The surface of the main track level is smooth except in some areas where epikarsts have developed along normal faults and/or joints induced by the Rhine Graben rifting and the Jura folding (Fig. 1). The surface exhibits tracks of saurischian dinosaurs belonging to herbivorous sauropods and carnivorous theropods.



**FIG. 1.** Overview of the main track level of the Courtedoux tracksite. Water tank (on the middle left) for scale. Note the well-developed normal faults associated with the Rhine Graben rifting and the folding of the Jura mountain range.

Besides the track-excavations, the “Section de paléontologie” has also undertaken paleontological excavations in overlying marine marls (e.g., the “Marnes à *virgula*”) and limestones. Many invertebrates (aspidoceratid ammonites) and vertebrate remains (turtles, mesosuchian crocodiles, sharks, and bony fishes) have been recovered.

## GEOGRAPHICAL AND GEOLOGICAL SETTING

The Courtedoux tracksite is situated in Northern Switzerland, in the Ajoie district, Canton Jura, about 5 km west of the city of Porrentruy (Fig. 2).

The Ajoie district forms part of the tabular Jura mountain range (Schneider, 1960) and bedding at the site is sub-horizontal. The main structural features found associated with the track site are normal faults, induced by the Rhine Graben rifting and the folding of the Jura mountain range.

Chronostratigraphically the Ajoie district consists mainly of deposits of Oxfordian and Kimmeridgian age. The laminites of the tracksite are found between the Banné Member (Gygi, 2000) and the “Marnes à *virgula*” of the Reuchenette Formation and they are of early Late Kimmeridgian age (Fig. 3). The same laminites can be observed in outcrops at several other places around Courtedoux and in the Ajoie district. In fact, in 2002 sauropod tracks have already been reported from a temporary outcrop of the laminites about half a kilometer northwest of the Courtedoux tracksite. The occurrence of dinosaur tracks or even a distinct megatracksite with a considerable lateral extent may thus be suggested for much of the Ajoie district and may be confirmed by future excavations on the “Transjurane” highway.

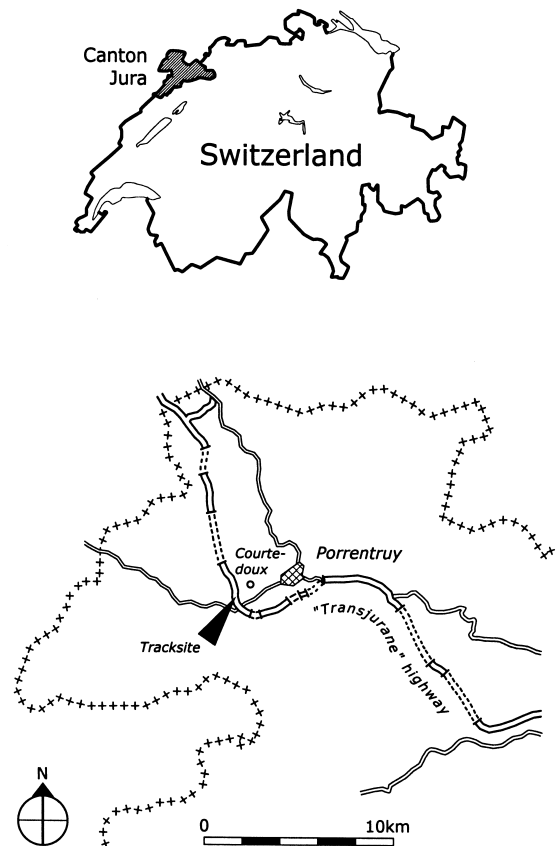
## METHODS

All tracks have been carefully excavated, and the main track level has been documented by means of a classical manual graphic technique, followed by digitization. Further, the new

Cyrax 2500 3D Laser Scanner (SmartScan Technology) has been applied for the first time in the field of paleontology (Leica Geosystems, 2003). The most important trackway segments have been casted with silicon rubber. All trackways have been serially numbered with the prefix S for sauropod and T for theropod (Fig. 7) and all trackway parameters (Leonardi, 1987; Thulborn, 1990; Lockley, 1991; Lockley and Hunt, 1995; Lockley and Meyer, 2000) have been measured in detail (Fig. 4), including footprint (pes and manus) size (length and width) and angle of rotation from trackway midline (pes and manus rotation), distance between midline and center of the manus, pace (step) and stride length of pes and manus, pace angulation of pes and manus, gleno-acetabular distance, internal and external trackway width, and trackway orientation. However, these data were not as yet subjected to statistical analyses, and this paper gives only a preliminary overview. A detailed analysis on the trackway—and other data that have been, and will be, compiled, and the impressive 3D results of the laser scanning will be published later.

## PRELIMINARY ANALYSIS OF THE DINOSAUR TRACKS

On the main track level (level 1000), more than 650 dinosaur footprints have been uncovered to date and about 400



**FIG. 2.** Location of the Courtedoux tracksite and the “Transjurane” highway in Northwestern Switzerland.

STAGE	FORMATION	TETHYAN REALM Hardenbol et al. (1998), <i>sensu gallico</i>			BOREAL REALM Hardenbol et al. (1998), <i>sensu anglico</i>				NEW RESULTS  Litho- and biostratigraphic key elements of the Ajoie	
		Ammonite zones	Sequences	Ages (Ma)	Time span according to Hardenbol et al. (1998)	Sequences	Ammonites			
							zones	sub-zones		horizons
Late Kimmeridgian	Reuchenette	EUDOXUS	MF	152.01	690 ka	Kim 6 MF	EUDOXUS	Contejeani	Yo Contejeani	③
			Kim 4			Kim 5 MF		Caletanum	Quercynum Caletanum	
Early K.	Reuchenette	ACANTHICUM	MF	152.70	400 ka	Kim 4 MF	MUTABILIS	Lallierianum	Schilleri Lallierianum	① ②
			Kim 3			Kim 3		Mutabilis	Mutabilis Attenuatus Desmonotus Linealis	
Early K.	Reuchenette	DIVISUM	MF	152.70	400 ka	MF	CYMODOCE	Chatelailonensis	Discoidus Chatelailonensis	Banné member
			MF			MF		Askeptus Manicata Aulinisa		

**FIG. 3.** Chrono-, bio- and lithostratigraphic context of the Courtedoux trackway site and the Kimmeridgian of the Ajoie district, showing the stratigraphic position of the Banné Member (Gygi, 2000), the track-bearing laminites and the fossiliferous “Marnes à virgula”. 1: *Orthaspidoceras schilleri* OPPEL, layer 3500, Courtedoux tracksite. 2: *Aspidoceras longispinum* SOWERBY, “Marnes à virgula”, Courtedoux tracksite. 3: *Aspidoceras caletanum* OPPEL, Courtedoux tracksite.

can be resolved into trackways of 17 sauropod and two theropod dinosaurs. The trackways are between 2.5 and 20 m long (Fig. 7).

**Sauropod Tracks and Trackways**

The tracks are in general well preserved as imprints (epichnia or negative epirelief), and exhibit most well defined sediment displacement rims. The sauropod trackways of the main track level are characterized by a large oval pes (foot) print, and a much smaller semicircular convex forward manus (hand) print. There is no evidence of claw impressions (Figs. 5 and 6). The size range for the pes prints is between 34.4 and 46.8 cm length and between 27.0 and 35.7 cm width. The corresponding range for the manus is of 8.5 to 12.8 cm and 17.5 to 25.5 cm, respectively. The pes is longer than wide and the manus wider than long.

Most of the sauropod trackways show preservation of both manus and pes tracks. Only trackway S9 is partially manus dominated. In most trackways preservation and imprint depth varies along the trackway and some can be followed for a few meters only (trackways S15 and S17). Nonetheless, it is possible to distinguish between generally deeper and shallower trackways, independent of the size of the footprints. All sauropod trackways are characterized by a narrow gauge with little or no space between the inside of the pes prints, or pes prints even intersecting the trackway midline. All are of the “small manus” type, showing a pronounced heteropody (foot size difference), the manus-pes size (footprint area) ratio being about 1:4. The mean manus rotation is negative (outward) and clearly more pronounced than is the mean negative pes rotation (Figs. 5 and 6). The centers of the manus prints are placed farther away from the trackway midline than are the centers of pes prints. Trackway S4 (Fig. 6) is the trackway with the most pronounced negative manus rotation. Such a high negative outward rotation might suggest that something unusual was going on in regards to the shifting of weight and walking mechanics.

**Tridactyl Tracks and Trackways**

The few tridactyl tracks of the main level are poorly preserved and possibly represent undertracks (Milàn and Bromley, 2003). The size range for the pes prints is between 24 and 29 cm length and between 27 and 34 cm width. They are generally slightly wider than long and don’t show any clear evidence for claw impressions. Two trackway segments are recognized (Fig. 7, T18 and T19). Both trackways are very narrow, have a high pace angulation (about 160 degrees), and a mean stride of 2.7 m. Most of the track and trackway features, except the length/width-ratio, are typical for theropods (Lockley, 2001), and both trackways are thus attributed to theropod dinosaurs.

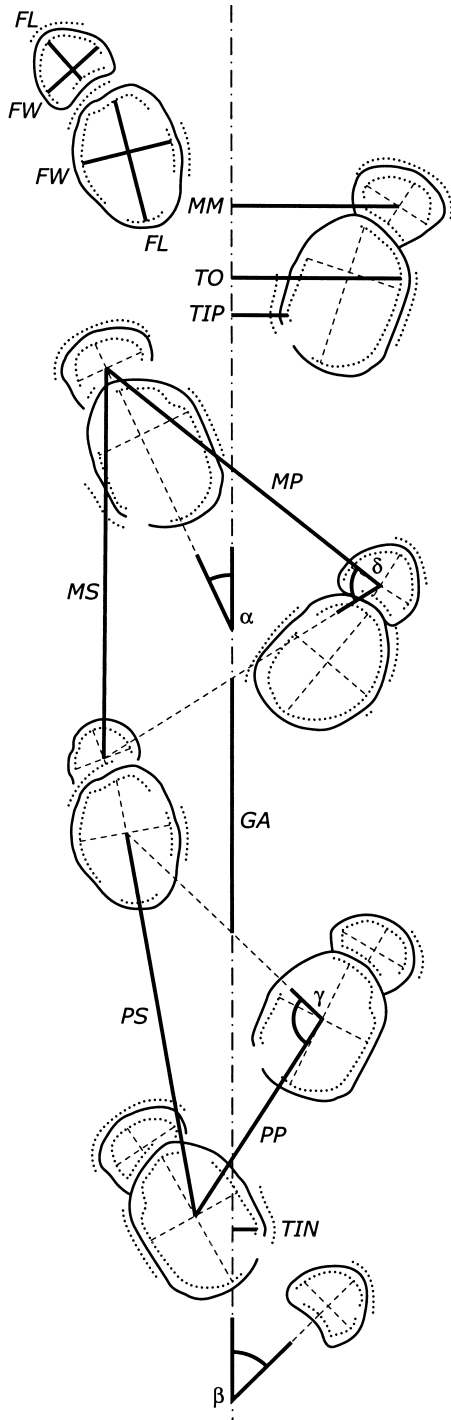
**Trackway Orientations**

The orientation of the trackways (Fig. 7) is a striking feature of the main track level. A bimodal pattern of sauropod trackways, each with approximate parallel trackway orientations can be observed. Ten trackways (S1, S2, S4, S5, S6, S7, S8, S12, S16, and S17) are oriented between north and north-northeast, intertrackway spacing being in the range of 2 to 4 m. Six trackways (S9, S10, S11, S13, S14, and S15) are oriented more or less in the opposite direction, south to southwest. Intertrackway spacing varies a lot and some trackways are found to cross each other (S9 and S10, S10, and S14).

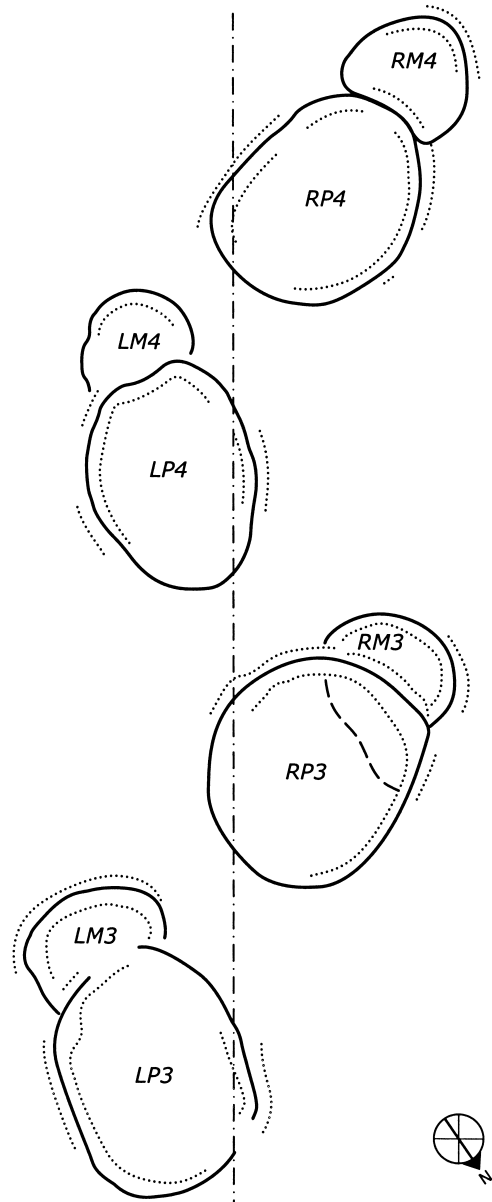
Only the sauropod trackway S3 (oriented toward the north-northwest) is at variance with this bimodal trend, as are the theropod trackways T18 and T19 (oriented towards the south and north, respectively).

**Sedimentology**

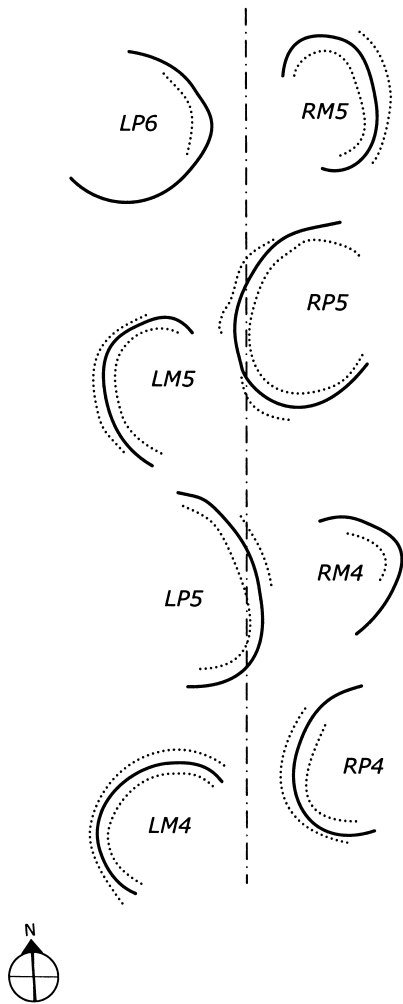
The sedimentological analysis is based on macro- and microscopic observations in the field and laboratory. Small-scale microfacies analysis was carried out in thin-sections and described using standard microfacies classification systems (Wilson, 1975; Flügel, 1982), and then assigned to specific facies



**FIG. 4.** Schematic diagram of a sauropod trackway, showing the essential features measured: footprint length (FL), footprint width (FW), pes rotation ( $\alpha$ ), manus rotation ( $\beta$ ), distance between midline and manus (MM), pes pace length (PP), manus pace length (MP), pes stride length (PS), manus stride length (MS), pes pace angulation ( $\gamma$ ), manus pace angulation ( $\delta$ ), gleno-acetabular distance (GA), trackway width inside-positive (TIP), trackway width inside-negative (TIN), and trackway width outside (TO).



**FIG. 5.** Section of sauropod trackway S10, characterized by a narrow gauge, large oval pes footprints and by much smaller semicircular manus footprints. This is the trackway with the least negative rotated manus position.



**FIG. 6.** Section of sauropod trackway S4, characterized by a narrow gauge, large oval pes footprints and by much smaller semicircular manus footprints. This is a trackway with a very pronounced negative manus rotation.

and facies zones (Hillgärtner, 1999; Hug, 2003). Macroscopic analyses in the field identified macro-sedimentary structures and fossils (Fig. 9).

Layer 950 (Fig. 8) is stratigraphically below the main track level, and can be described as a pack- to grainstone (Dunham, 1962). This layer is lithologically diverse, ranging from a biopelmicrite to a biopelsparite, and from an oomicrite to oosparite with rare intraclasts (Folk, 1962). Identified microfaunal elements are skeletal grains (benthic miliolid and cyclamminid foraminifers, algae and bivalves), non-skeletal grains (peloids, ooids, and intraclasts), quartz (less than 1%), early-diagenetic dolomite (up to 10%), and little organic matter. Macroscopic observations show a poor sorting of microfaunal elements and skeletal grains and no lamination or bioturbation. Centimeter-sized symmetrical parallel wave ripples can be observed on about two-thirds of the main track level (top of layer 950). The ripple crests have a prevailing orientation of southwest to northeast.

Based on the present facies analysis, the depositional environment can be interpreted as a mixed bioclastic-oolitic bar or

lower-beach deposit in a shallow-subtidal (layer 950) to intertidal (level 1000), semi-open lagoon with intermittent, low to moderate energy. Sedimentological analyses of the overlying track-bearing laminites are under study.

## DISCUSSION

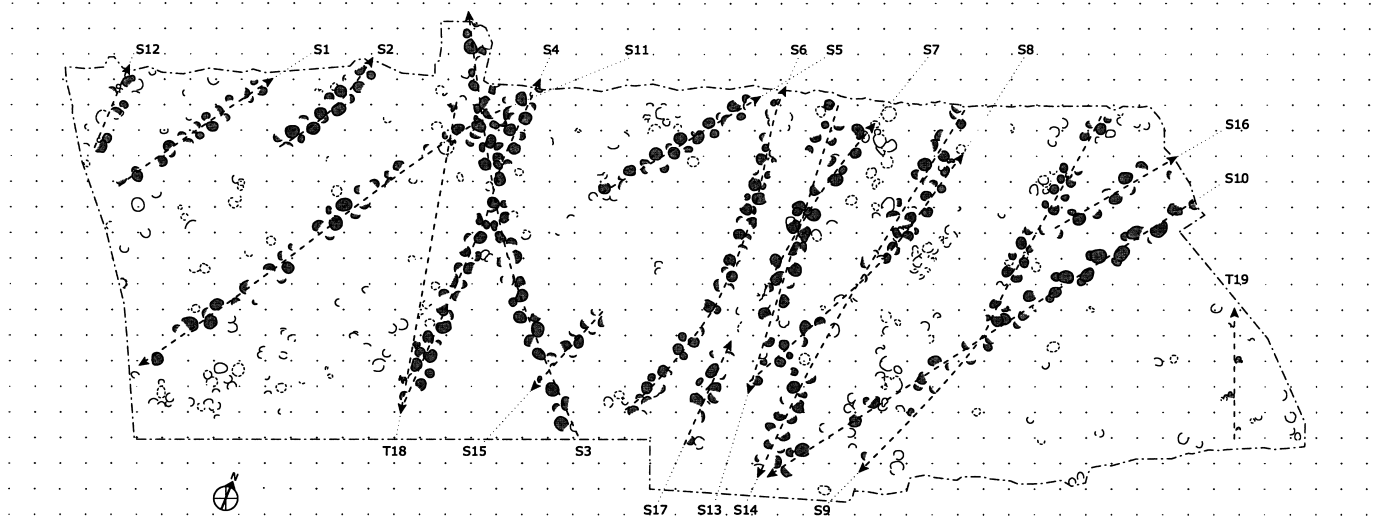
### Sauropod Trackway Analysis

#### *Systematic Affinities*

All sauropod trackways from the main track level represent relatively small animals in comparison with other sites, and in comparison with the maximum known size of sauropod tracks, which does not exceed a pes length of about 1 m in well-authenticated reports, where the footprint dimension is measured inside the track rim (Lockley et al., 2002a; Fig. 4). According to the formulas of Thulborn (1990, p. 252), the tracks and trackways indicate sauropods with a hip height of about 2–2.8 m (hip height = 5.9 × pes length), a total length of about 6–8.5 m (total length = 18 × pes length), and a gleno-acetabular distance between 0.7 m and 1.5 m. In fact, the Courtedoux tracksite reveals the smallest Kimmeridgian sauropod tracks known. Smaller sauropod tracks are so far only described from the Cretaceous Jindong Formation of South Korea (Lim et al., 1994), the Late Oxfordian of Poland (Gierlinski and Niedzwiedzki, 2002), and the Early Liassic Zagaje Formation of Poland (Gierlinski and Pienkowski, 1999). However, the existence of pes imprints up to a diameter of about 0.8 m on a higher level of the track-bearing laminites may suggest that the trackways of the main track level represent juvenile or subadult sauropods rather than a generally small species.

The narrow-gauge trackways, strong heteropody (small manus), and outwardly rotated manus are characteristic of the ichnogenus *Parabrontopodus* (Farlow, 1992; Lockley and Santos 1993; Lockley et al., 1994a; Lockley and Meyer, 2000), which can easily be distinguished from the ichnogenus *Brontopodus*, which exhibits wide-gauge trackways (manus and pes prints well away from the trackway midline) with relatively large manus prints (reduced heteropody), usually directed forward and closer to the trackway midline (Farlow et al., 1989; Lockley et al., 1994a).

The ichnogenus *Parabrontopodus* is attributed to basal sauropods, basal macronarians, or the diplodocoidea *sensu* Wilson and Sereno (1998) (Day et al., 2002), which are all narrow-hipped sauropods with a compressed body construction and/or feet planted near the sagittal plane (Wilson and Sereno, 1998). Farlow (1992) argued that *Brontopodus* trackmakers might also have angled their legs inward with respect to the sagittal plane. However, the disappearance of narrow-gauge trackways in the Cretaceous (Lockley et al., 1994c), leaving only wide-gauge forms in association with brachiosaurid-titanosaurid-dominated faunas, argues against this possibility. Wilson and Carrano (1999) also suggested that wide-gauge trackways were the products of wide-gauge sauropods, rather than narrow-gauge sauropods of different sizes or engaged in different behaviors. Thus, *Brontopodus* trackways are commonly attributed to the



**FIG. 7.** Site map of the so far uncovered main track level (level 1000), which is situated at the base of the laminite series. The total area is about 650 m<sup>2</sup>. About 400 of 650 observed tracks are resolved into 17 sauropod and 2 theropod trackways. S stands for sauropod and T for theropod respectively. Tracks that can be attributed to trackways are shown in grey. Note the bimodal sauropod trackway pattern.

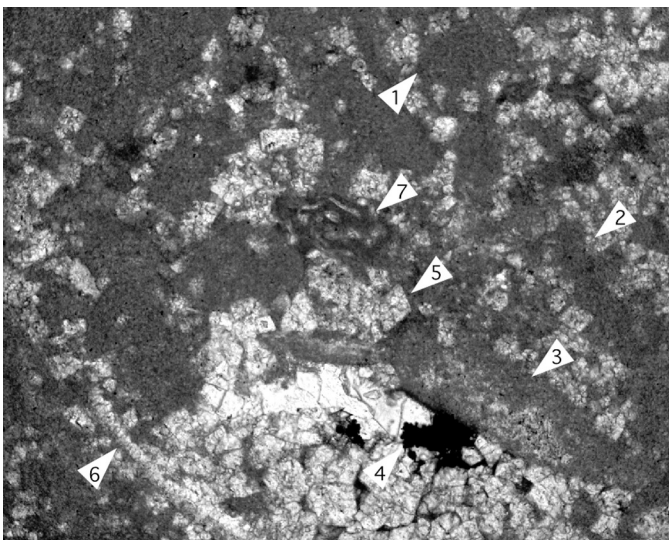
more derived and robust brachiosaurids or titanosaurs (Lockley et al., 1994a, 1994c; Wilson and Carrano, 1999; Henderson, 2002; Lockley et al., 2002a, 2002b). Generally speaking, the ichnogenus *Parabrontopodus* indicates sauropods with large hind limbs, longer tails, and smaller neck and heads, whereas the ichnogenus *Brontopodus* indicates sauropods with larger front limbs, shorter tails, and larger heads and necks.

The Courtedoux tracksite is the first site to reveal clear evidence for *Parabrontopodus* trackways in Switzerland. Other Late Jurassic tracksites with distinct *Parabrontopodus* trackways are so far only documented from the Upper Jurassic of

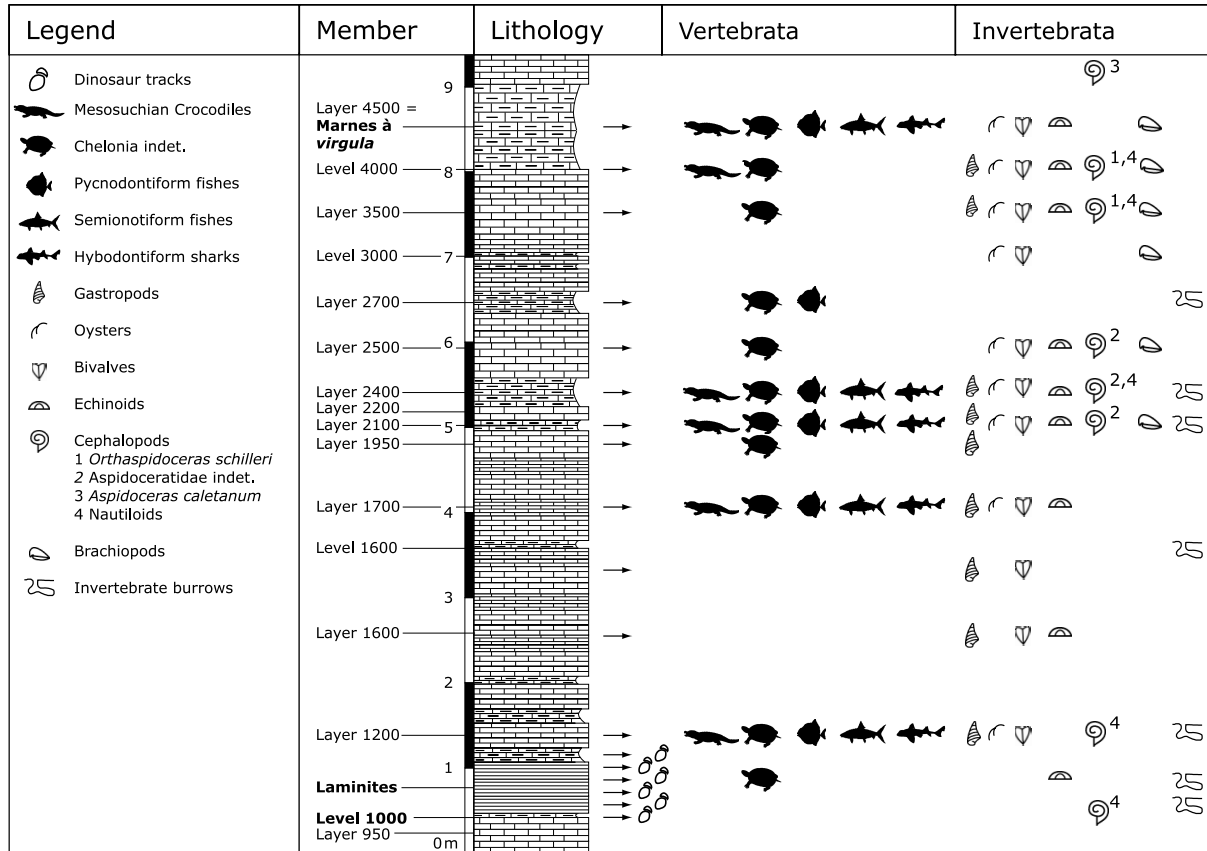
Portugal and the U.S. (Lockley et al., 1994c; Meyer et al., 1994; Lockley and Meyer, 2000). In the Kimmeridgian of Barkhausen, Germany (Kaefer and Lapparent, 1974), the ichnogenus *Parabrontopodus* may be represented (Lockley and Meyer, 2000; p. 161), though the preservation of these trackways is less than optimal (Lockley, unpublished data). Recently, *Parabrontopodus* trackways have been reported from the Tithonian of Chile (Moreno and Pino, 2002) and from possibly Upper Tithonian sediments of the Adriatic carbonate platform of Croatia (Mezga et al., 2003). Thus, the Courtedoux site is one of the youngest sites exhibiting *Parabrontopodus* trackways. Given that slightly younger tracks such as those found in the Late Kimmeridgian of Lommiswil, Switzerland (Meyer, 1990, 1993) are of the wide-gauge *Brontopodus* type, the Courtedoux site is important for giving evidence of the presence of a different, more primitive group of sauropods somewhat earlier in the Late Kimmeridgian of Northern Switzerland. Lockley and Meyer (2000, p. 169) suggest that the change to predominantly wide-gauge trackways occurred between the Kimmeridgian and Tithonian (Portlandian). However, this can only be very speculative until a larger database is amassed, and if the ichnogenus *Parabrontopodus* is not found in any younger ichnocoenoses (e.g., Lockley et al., 2000b; Moreno and Pino, 2002; Mezga et al., 2003).

#### *Gregarious Behavior*

On the main track level, a bimodal sauropod trackway pattern with more or less the same orientation as the small-scale ripple crests can be observed. Only sauropod trackway S3 and the theropod trackways T18 and T19 are at variance with this bimodal trend. The trackways that contribute to each component of the bimodal sauropod trackway pattern are more or less parallel, but intertrackway spacing is irregular, imprint depth clearly varies and several trackways even cross each other.



**FIG. 8.** Thin-section CTD-SCR-950.3 (uppermost part of layer 950), pack-to grainstone (Dunham, 1962) bio-, pel-, oo-micrite to -sparite (Folk, 1962), showing small ooids (1), peloids (2), intraclasts (3), organic matter (4), dolomite (5), bivalve shell fragment (6) and benthic miliolid foraminifer (7). Image width is 6 mm.



**FIG. 9.** Simplified cross section of the Courtedoux site. The main track level (level 1000) forms the base of the track-bearing laminite series. Paleontological excavations are also carried out in overlying fossiliferous marine marls and limestones (Marty et al., 2003). Layer refers to a whole unit (bed) and level only to a distinct surface (e.g. track-level or a hardground), respectively.

Parallel alignment of sauropod trackways is a common phenomenon at many sauropod tracksites and is regarded as evidence for gregarious behavior (Lockley et al., 1994b; Lockley, 1995; Lockley and Hunt, 1995; Lockley, 1997). Nonetheless, to suggest local shoreline-controlled travel and/or gregarious behavior of several groups of sauropods for the main track level, more data are needed.

*Chronology of Track Making*

The relative timing of the sequence of tracks made by the sauropods and theropods can be estimated from the imprint depth of tracks and from the trackway interaction at “crossroads.”

On the main track level, several of the sauropod trackways are crossing each other. Of special interest is the sauropod crossroads involving the three trackways S3, S4, and S11 (Figs. 10 and 7). Trackway interaction shows clearly that sauropod S11 passed first, followed by S4 and finally S3. Amongst these three trackways, S11 is the weakest impressed and most poorly preserved. Trackways S4 and S3, respectively, are each better preserved and more deeply impressed.

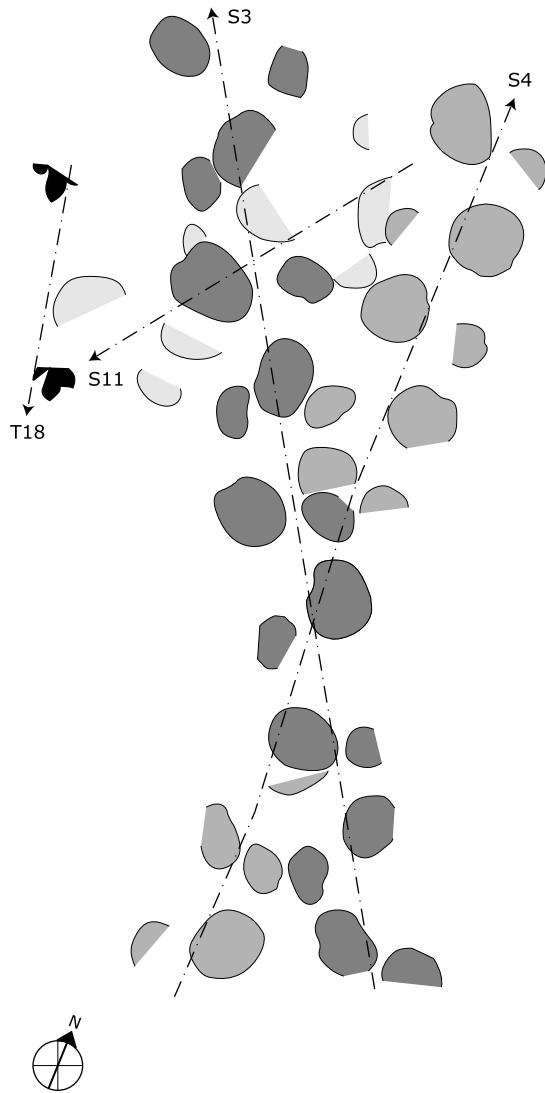
Generally speaking, differential depth of tracks may indicate different water content of the sediment at the time of passage (Meyer and Hauser, 1994). Waterlogged substrates thus exhibit

more deeply impressed footprints than firmer sediment. Normally, while sediment is gradually draining free of water and becoming firmer, the earliest formed footprints tend to be more deeply impressed than the later ones. However, the reverse process may take place: e.g., the substrate may get wetter with time. Evidence of trackway interaction from crossroads may resolve this dilemma and, in this case, shows clearly that on the main track level the latter situation prevailed. The most deeply impressed trackway (S3) clearly overprints more shallow trackways (S4 and S11), suggesting that the sediment, after a period of drying, got at least partially waterlogged again. This could be explained by a brief tidal flooding.

**Paleoecology and Paleogeography**

*Ichnofacies*

The repeated association of sauropod and large (robust) theropod tracks in carbonate substrates is currently defined as the *Brontopodus* ichnofacies (Lockley et al., 1994d). This label is generalized and can be used to accommodate any repeated association of sauropod tracks (including *Parabrontopodus* and related types) with large theropod tracks (Meyer and Pittman, 1994; Lockley and Meyer, 2000). The Courtedoux tracksite thus falls into this general category.



**FIG. 10.** Sauropod “crossroads” of trackways S3, S4 and S11. Tracks are displayed schematically. S11 passed first, followed by S4 and finally S3.

However, to be consistent in ichnofacies definitions it is necessary to keep track of occurrences in the distribution of the ichnogenus *Brontopodus* and *Parabrontopodus* and their relationship to facies. The ichnogenus *Brontopodus* extends in time from at least the Middle Jurassic to the Late Cretaceous, and is represented in North and South America, Europe, and Asia (Lockley et al., 1994c; Santos et al., 1994; Schulp and Brox, 1999; Day et al., 2000; Lockley et al., 2002a). The ichnogenus *Parabrontopodus* is described from carbonate substrates of the Middle and Late Jurassic of Europe, South and North America (Lockley and Santos, 1993; Lockley et al., 1994a, 1994c; Lockley and Meyer, 2000; Day et al., 2002; Moreno and Pino, 2002; Mezga et al., 2003). Further, it is reported from the Early Jurassic of Europe (Dalla Vecchia, 1994; Avanzini et al., 1997; Gierlinski, 1997; Gierlinski and Sawicki, 1998; Gierlinski and Pienkowski, 1999; Avanzini et al., 2001), but not always associated with carbonate substrates.

Thus, most sites with *Brontopodus* trackways, but not all sites with *Parabrontopodus* trackways, fall into the broadly defined *Brontopodus* ichnofacies.

#### Megatracksite

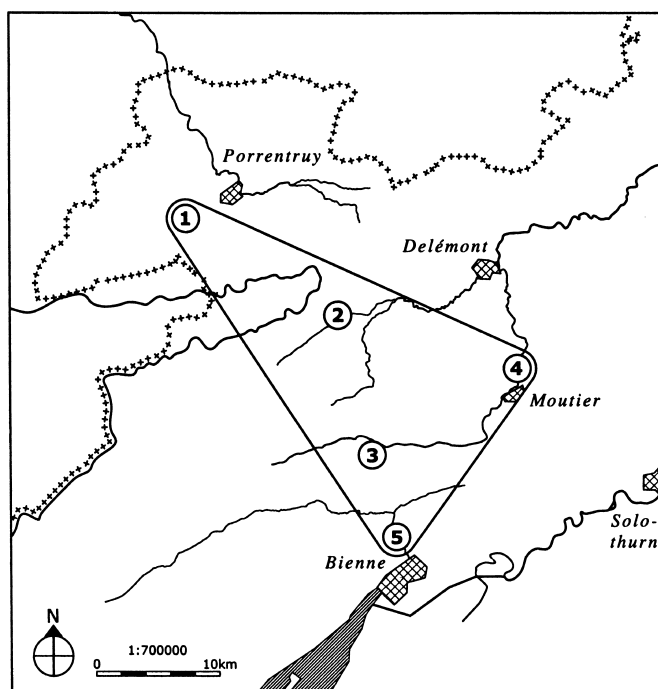
A megatracksite or “dinosaur freeway,” as currently defined, is a regionally extensive single surface or very thin package of beds, that is, track-bearing or track-rich over a large area on the order of hundreds to thousands of square kilometers, owing to the dynamics of sea-level fluctuation (Lockley, 1991, 1997; Lockley and Meyer, 2000). Megatracksites are becoming more and more important for paleogeographical reconstructions, and this is also true for the Late Jurassic of northwestern Switzerland. However, the large ichnological and stratigraphic megatracksites have been referred to with general terminology. Thus, pending further study, we advocate caution in using such terminology to imply precise meanings. For example, while a megatracksite may at first appear as a distinct marker horizon, it may be diachronous, as are most facies (Lockley, 1997). Similarly, megatracksites with several tracksites in relatively close stratigraphic proximity, as in Switzerland or the Cretaceous of Texas (Lockley and Hunt, 1995) and Spain (Moratalla and Sanz, 1997; Lockley and Meyer, 2000), may have more complex genetic (and spatio-temporal) relationships than are obvious at first glance. Even so, most megatracksites have been defined on the basis of a substantial number of discrete sites distributed on a regional scale. This is also the case in Switzerland.

At present, more than 20 Late Jurassic dinosaur tracksites are known from several places in northern Switzerland. Meyer and Thüning (2003) divide them fairly equally between a “megatracksite in the Lower Reuchenette Formation” and a “megatracksite in the Upper Reuchenette Formation,” which have previously been labeled “Middle Kimmeridgian megatracksite” and “Late Kimmeridgian megatracksite,” respectively (Meyer, 2000). However, as the Kimmeridgian is only formally divided into the Early (Lower) and Late (Upper) Kimmeridgian, the term Middle Kimmeridgian megatracksite is questionable. The same is true for “Lower” and “Upper Reuchenette Formation,” as the Reuchenette Formation is formally not divided (Thalman, 1966; Gygi, 2000). Such terminology will probably resolve itself in time as more tracksites are discovered and their chrono-, bio-, litho- and sequence stratigraphic contexts are studied more closely. For the time being, we use the terms *sensu* Meyer (2000).

The track-bearing laminites of the Courtedoux site can be dated by means of aspidoceratid ammonites to the early Late Kimmeridgian (*Mutabilis* zone) (Fig. 3), and the site can be attributed to the Middle Kimmeridgian megatracksite (*sensu* Meyer, 2000) and the “megatracksite in the Lower Reuchenette Formation” (*sensu* Meyer and Thüning, 2003), respectively. On the map, Courtedoux forms the northwestern apex of a geographical triangle of about 15 km height and 30 km width with a total area of about 230 km<sup>2</sup> (Fig. 11).

Nonetheless, one should remember that all other tracksites (Moutier I–IV, Glovelier I–II, Reconvilier, Frinvilier) that are





**FIG. 11.** Geographic extent of the “Middle Kimmeridgian megatracksite” (*sensu* Meyer, 2000) of Northwestern Switzerland. Courtedoux (1), Glovelier I–II (2), Reconvilier (3), Moutier I–IV (4) and Frinvilier (5).

currently attributed to the Middle Kimmeridgian megatracksite (Meyer, 2000; Ayer and Claude, 2001; Meyer and Thüring, 2003) have not been precisely dated. Ayer and Claude (2001) for example attribute the Frinvilier site to the Middle Kimmeridgian megatracksite, even if they assign it to the “basal” Kimmeridgian. Thus, it is possible that the Courtedoux site is younger than other sites of the Middle Kimmeridgian megatracksite.

#### *Paleoenvironment*

During the early Late Kimmeridgian, today’s northwestern Swiss Jura Mountains developed as a shallow carbonate-dominated platform at the threshold between boreal depositional areas to the northwest (Paris Basin) and the Tethys Ocean to the south. The climate was subtropical (Bertling and Insalaco, 1998), paleolatitude being about 35°N (Frakes et al., 1992).

Small-scale sea-level drops created vast emergent areas in a carbonate lagoon and tidal flat environment, which allowed terrestrial animals, such as saurischian dinosaurs, to traverse exposed flats and to access the platform from the coastal zone of the “Süddeutsche Schwelle” in the northeast (Meyer and Schmidt-Kaler, 1989), which was located at the southeastern border of the London-Brabant Massif. Meyer and Lockley (1996) also suggested a connection between the northwestern Jura platform and the Massif Central. On the platform, a patchwork of large islands and/or smaller landmasses can be postulated. Large saurischian dinosaur populations suggest the presence of large vegetated areas as a food supply (Meyer and

Lockley, 1996). The islands and/or smaller landmasses have been surrounded by open to closed lagoons with variable degree of restriction. Large tidal flats, where sea-level fluctuations created sub-, inter- and supratidal depositional environments, which allowed the preservation of terrestrial ichnocoenoses in sediments such as calcareous laminites.

#### CONCLUSIONS

The Courtedoux tracksite has only just begun to be excavated and analyzed. For the following reasons, it is clearly one of the most important sauropod tracksites worldwide:

1. The laminites of the Courtedoux site represent an enormous track-data resource with a great potential for new discoveries, as at least 6 track-bearing levels are found in about 1 m of laminites. This is one of the highest densities of track-bearing layers ever recorded in such a small depositional unit (see also Lim et al., 1994; McCrea and Currie, 1998). Moreover, the 17 sauropod trackways on the main track level already make the Courtedoux site the second largest concentration of sauropod trackways on a single surface in terms of raw numbers in the Jurassic (Marty et al., submitted). As the same laminites can also be observed in outcrops at several places in the Ajoie district, and as a sauropod track has already been reported half a kilometer from the main Courtedoux tracksite, the occurrence of dinosaur tracks or even a distinct megatracksite with a considerable lateral extent may be suggested for much of the Ajoie district and may be substantiated by future excavations on the “Transjurane” highway.
2. For the first time a paleontological survey (“Section de paléontologie”) is able to systematically excavate and document a track-bearing site on such a large surface. Newly exposed tracks will thus be very well preserved, as they have never been exposed to direct weathering.
3. The tracksite can be unequivocally assigned to the early Late Kimmeridgian based on aspidoceratid ammonites (Figs. 3 and 9) and will be placed in a broad paleoecological context, as further studies are carried out on the excavations of the overlying fossiliferous strata.
4. The Courtedoux tracksite reveals the smallest known sauropod tracks in the Kimmeridgian and the first evidence for the ichnogenus *Parabrontopodus* in Switzerland. Given that, the ichnogenus *Brontopodus* is found in the slightly younger Late Kimmeridgian deposits of Lommiswil, Switzerland (Meyer, 1990, 1993), the Courtedoux site is important for giving evidence of the presence of a different, more primitive group of sauropods in northern Switzerland.
5. The Courtedoux tracksite will be protected underneath an especially constructed highway-bridge, thus offering opportunities for future research. This protection may also allow for the development of an interpretative center for education and tourism (Marty et al., submitted).

## ACKNOWLEDGEMENTS

The “Section de paléontologie” is financed by the Swiss Federal Roads Authority (FEDRO) and by the Canton Jura (at 95% and 5% levels respectively).

For their excellent collaboration and their great interest in the Courtedoux site, we are grateful to the following technical and political instances: Federal Roads Authority (FEDRO), ministers of the Canton Jura government, deputies of the Canton Jura parliament, road construction office of the Canton Jura (Ponts et Chaussée), environmental protection office of the Canton Jura (OEPN), municipal councilors of Courtedoux, and the head engineer of the Transjurane highway of the Canton Jura (R. Bläuer).

We thank Pierre-Alain Borgeaud and his team (“équipe de sondages de la Section d’archéologie du Canton du Jura”), who originally found the tracksite, for the excellent collaboration, and all technical staff who participated in the excavation of the Courtedoux site.

We finally thank Paul Barrett for useful information on sauropod evolution and phylogeny and the reviewers R.A. Gansglouff and G. Gierlinski who helped to improve the manuscript by their helpful and useful comments.

## REFERENCES

- Ayer, J. and Claude, B. 2001. Découverte d’une piste de dinosaure sauropode dans le Kimméridgien de la Région de Bienne (Jura Central, Canton de Berne, Suisse). *Bulletin de la Société Neuchâteloise des Sciences Naturelles*, 124:149–159.
- Avanzini, M., Frisia, S., Van Den Driesche, K., and Keppens, E. 1997. A dinosaur tracksite in an Early Liassic tidal flat in Northern Italy: paleoenvironmental reconstruction from sedimentology and geochemistry. *Palaios*, 12:538–551.
- Avanzini, M., Leonardi, G., and Tomasi, R. 2001. Enigmatic Dinosaur Trackways from the Lower Jurassic (Pliensbachian) of the Sarca Valley, Northeast Italy. *Ichnos*, 8:235–242.
- Berling, M. and Insalaco, E. 1998. Late Jurassic coral/microbial reefs from the northern Paris Basin—Facies, Palaeoecology and Palaeobiogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 139:139–175.
- Dalla Vecchia, F. M. 1994. Jurassic and Cretaceous sauropod evidence in the Mesozoic carbonate platforms of the Southern Alps and Dinarids. *Gaia*, 10:65–73.
- Day, J. J., Upchurch, P., Norman, D. B., Gale, A. S., and Powell, H. P. 2002. Sauropod Trackways, Evolution, and Behavior. *Science*, 296:1659.
- Dunham, R. J. 1962. Classification of carbonate rocks according to depositional texture. In Ham, W. E. (ed.), *Classification of carbonate rocks. American Association of Petroleum Geologists, Memoir*, 1:108–121.
- Farlow, J. O., Pittman, J. G., and Hawthorne, J. M. 1989. Brontopodus birdi, Lower Cretaceous Sauropod Footprints from the U.S. Gulf Coastal Plain. In Gillette, D. G. and Lockley, M. G. (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, New York: 367–394.
- Farlow, J. O. 1992. Sauropod tracks and trackmakers: Integrating the ichnological and skeletal record. *Zubia*, 10:89–138.
- Flügel, E. 1982. *Microfacies analysis of limestones*. Springer-Verlag, Berlin: 633 pp.
- Folk, R. L. 1962. Spectral subdivision of limestone types. In Ham, W. E. (ed.), *Classification of carbonate rocks. American Association of Petroleum Geologists, Memoir*, 1:62–84.
- Frakes, L. A., Francis, J. E., and Sykes, R. M. 1992. *Climate modes of the Phanerozoic*. Cambridge University Press, Cambridge: 274 pp.
- Gierlinski, G. 1997. Sauropod tracks in the Early Jurassic of Poland. *Acta Palaeontologica Polonica*, 42:533–538.
- Gierlinski, G. and Niedzwiedzki, G. 2002. Dinosaur footprints from the Upper Jurassic of Blaziny, Poland. *Geological Quarterly*, 46:463–465.
- Gierlinski, G. and Pienkowski, G. 1999. Dinosaur track assemblages from the Hettangian of Poland. *Geological Quarterly*, 43:329–346.
- Gierlinski, G. and Sawicki, G. 1998. New sauropod tracks from the Lower Jurassic of Poland. *Geological Quarterly*, 42:477–480.
- Gygi, R. A. 2000. Annotated index of lithostratigraphic units currently used in the Upper Jurassic of Northern Switzerland. *Eclogae geologicae Helvetiae*, 93:125–146.
- Hardenbol, J., Thierry, J., Farelly, M. B., Jacquin, T., De Graciansky, P.-C., and Vail, P. R. 1998. Jurassic chrono-stratigraphy. In De Graciansky, P.-C., Hardenbol, J., Jacquin, T., Vail, P. R., and Farley, M. B. (eds.), *Sequence Stratigraphy of European Basins. Special Publication of the Society for Sedimentary Geology*, 60: chart.
- Henderson, D. 2002. Wide and narrow gauge sauropod trackways as a consequence of body mass distribution and the requirement for stability. *Journal of Vertebrate Paleontology*, 22:64A.
- Hillgärtner, H. 1999. The evolution of the French Jura platform during the Late Berriasian to Early Valanginian: controlling factors and timing. *GeoFocus* 1, Fribourg: 203 pp.
- Hug, W. A. 2003. Sequenzielle Faziesentwicklung der Karbonatplattform des Schweizer Jura im Späten Oxford und frühesten Kimmeridge. *GeoFocus* 7, Fribourg: 154 pp.
- Kaever, M. and Lapparent, F. de 1974. Les traces de pas de Dinosaures du Jurassique de Barkhausen (Basse Saxe, Allemagne). *Bulletin de la Société Géologique France*, (7)XVI, 5:516–525.
- Leica Geosystems. 2003. Sensationelle Dinosaurier-Fussspuren mit 3D-Laser-mass. *Vermessung Photogrammetrie Kulturtechnik*, 1/2003: 36–38.
- Leonardi, G. 1987. *Glossary and Manual of Tetrapod Footprint Palaeoichnology*. Departamento Nacional da Produção Mineral, Brasília, Brasil, 75 pp.
- Lim, S.-K., Lockley, M. G., Yang, S.-Y., Fleming, R. F., and Houck, K. 1994. A preliminary report on sauropod tracksites from the Cretaceous of Korea. *Gaia*, 10:109–117.
- Lockley, M. G. 1991. *Tracking dinosaurs: A New Look at an Ancient World*. Cambridge University Press, New York: 238 pp.
- Lockley, M. G. 1995. Track Records. *Natural History*, 104:46–51.
- Lockley, M. G. 1997. The paleoecological and paleoenvironmental importance of dinosaur footprints. In Farlow, J. O. and Brett-Surnam, M. K. (eds.), *The complete dinosaur*. Indiana University Press, Bloomington and Indianapolis: 554–578.
- Lockley, M. G. 2001. Trackways—dinosaur locomotion. In Briggs, D. E. G. and Crowther, P. (eds.), *Palaeobiology II*. Blackwell, Oxford: 412–416.
- Lockley, M. G., Farlow, J. O., and Meyer, C. A. 1994a. Brontopodus and Parabrontopodus ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia*, 10:135–146.
- Lockley, M. G. and Hunt, A. P. 1995. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. Columbia University Press, New York: 338 pp.
- Lockley, M. G., Hunt, A. P., and Meyer, C. A. 1994d. Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy. In Donovan, S. K. (ed.), *The Paleoecology of trace fossils*. The John Hopkins University Press, Baltimore: 241–268.
- Lockley, M. G., Meyer, C. A., Hunt, A. P., and Lucas, S. G. 1994c. The distribution of sauropod tracks and trackmakers. *Gaia*, 10:233–248.
- Lockley, M. G. and Meyer, C. A. 2000. *Dinosaur Tracks and other fossil footprints of Europe*. Columbia University Press, New York: 323 pp.
- Lockley, M. G., Meyer, C. A., and Santos, V. F. 1994b. Trackway evidence for a herd of juvenile sauropods from the Late Jurassic of Portugal. *Gaia*, 10:27–36.
- Lockley, M. G. and Santos, V. F. 1993. A preliminary report on sauropod trackways from the Avelino Site, Sesimbra Region, Upper Jurassic, Portugal. *Gaia*, 6:38–42.
- Lockley, M. G., Schulp, A., Meyer, C. A., Leonardi, G., and Kerumba-Mamani, D. 2002a. Titanosaurid trackways from the Late Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research*, 23:383–400.

- Lockley, M. G., Wright, J. L., White, D., Li, J., Lu, F. L., Hong, L., and Matsukawa, M. 2002b. The first sauropod trackways from China. *Cretaceous Research*, 23:363–381.
- Marty, D., Cavin, L., and Hug, W. A. 2002b. Preliminary report of the excavations at the Late Jurassic Courtedoux dinosaur tracksite carried out by the “Section de paléontologie” (Canton Jura, Northern Switzerland). Abstract, 3<sup>ème</sup> Symposium “Georges Cuvier”, 27–31 October 2002, Montbéliard, France.
- Marty, D., Cavin, L., Hug, W. A., Meyer, C. A., and Lockley, M. G. 2002a. Preliminary report of a dinosaur trackway site in the Late Jurassic of Courtedoux, Northern Switzerland. Abstract, Workshop on Freshwater & Brackish (Paleo) Ecosystems, European Palaeontological Association, 23–25 September 2002, Fribourg, Switzerland.
- Marty, D., Cavin, L., Hug, W. A., Jordan, P. A., Lockley, M. G., and Meyer, C. A. submitted. The protection, conservation and sustainable use of the Courtedoux dinosaur tracksite, Canton Jura, Switzerland. *Revue de Paléobiologie*, édition spéciale du “3<sup>e</sup> Symposium Georges Cuvier”.
- McCrea, R. T. and Currie, P. J. 1998. A preliminary report on dinosaur tracksites in the Lower Cretaceous (Albian) Gates Formation near Grande Cache, Alberta. In Lucas, S. G., Kirkland, J. I., and Estep, J. W. (eds.), Lower and Middle Cretaceous Terrestrial Ecosystems. *New Mexico Museum of Natural History and Science Bulletin*, 14:155–162.
- Meyer, C. A. 1990. Sauropod tracks from the Upper Jurassic Reuchenette Formation (Kimmeridgian, Lommiswil, Kt. Solothurn) of Northern Switzerland. *Eclogae Geologicae Helveticae*, 82:389–397.
- Meyer, C. A., 1993. A sauropod dinosaur megatracksite from the Late Jurassic of Northern Switzerland. *Ichnos*, 3:29–38.
- Meyer, C. A. 1994. A new sauropod print site from the Upper Jurassic of Northern Switzerland (Kimmeridgian, Montbautier, Kt. Bern) by Ph. Mouchet—A Reply. *Revue de Paléobiologie*, 13:427–428.
- Meyer, C. A. 1997. Die grosse Spurenplatte in der Schlucht von Moutier. *Schweizer Strahler*, 11:142–146.
- Meyer, C. A. 2000. Ein Jura-Querschnitt von Solothurn bis Basel (Exkursion C1 und C2 am 27–28, April 2000). *Jahresbericht Mitteilungen Oberrheinischer Geologischer Verein*, 82:41–54.
- Meyer, C. A. and Hauser, M. 1994. New sauropod and theropod tracksites from the Upper Jurassic megatracksite of Northern Switzerland. *Gaia*, 10:49–56.
- Meyer, C. A. and Pittman, J. G. 1994. A comparison between the *Brontopodus* Ichnofacies of Portugal, Switzerland, and Texas. *Gaia*, 10:125–133.
- Meyer, C. A. and Lockley, M. G. 1996. The Late Jurassic continental record of Northern Switzerland—evidence and implications. In Morales, M. (ed.), The continental Jurassic. Museum of Northern Arizona, Flagstaff: 421–426.
- Meyer, C. A., Lockley, M. G., Robinson, J. W., and Santos, V. F. dos 1994. A Comparison of well-preserved sauropod tracks from the Late Jurassic of Portugal and the Western United States: evidence and implications. *Gaia*, 10:57–64.
- Meyer, C. A. and Thüring, B. 2003. Dinosaurs of Switzerland. *Comptes Rendus Palevol*, 2:103–117.
- Meyer, R. F. K. and Schmidt-Kaler, H. 1989. Paläogeographischer Atlas des süddeutschen Oberjura (Malm). *Geologisches Jahrbuch*, 115:77.
- Mezga, A., Bajraktarevic, Z., Tetovic, B. C., and Gusic, I. 2003. First record of the dinosaurs in the Late Jurassic sediments of Istria, Croatia (preliminary report). 1<sup>st</sup> Meeting of the European Association of Vertebrate Palaeontology, Basel, 15–19 of July, Abstract Volume, p. 30.
- Milàn, J. and Bromley, R. G. 2003. How to distinguish a true track from an undertrack: experimental work with artificial substrates. 1<sup>st</sup> Meeting of the European Association of Vertebrate Palaeontology, Basel, 15–19 of July, Abstract Volume, p. 31.
- Moratalla, J. J. and Sanz, J. L. 1997. Cameros Basin megatracksite. In Currie, P. J. and Padian, K. (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego: 87–90.
- Moreno, K. and Pino, M. 2002. Huellas de dinosaurios en la Formacion Banos del Flaco (Titoniano-Jurasico Superior), VI Region, Chile: paleoetologia y paleoambiente. *Revista Geológica de Chile*, 29:151–165.
- Mouchet, P. 1993. A new sauropod print site from the Upper Jurassic of Northern Switzerland (“Kimmeridgian”, Montbautier, Kt. Bern). *Révue de Paléobiologie*, 12:345–349.
- Santos, V. F. dos, Lockley, M. G., Meyer, C. A., Carvalho, J., Galopim de Carvalho, A. M., and Moratalla, J. J. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia*, 10:5–14.
- Schneider, A. 1960. Geologie des Gebietes von Siegfriedblatt Porrentruy. Inauguraldissertation, University of Basel, 73 pp.
- Schulp, A. S. and Brokx, W. A. 1999. Maastrichtian sauropod footprints from the Fumanya site, Bergueda, Spain. *Ichnos*, 6:239–250.
- Thalmann, H.-K. 1966. Zur Stratigraphie des oberen Malm im südlichen Berner und Solothurner Jura. Inauguraldissertation, University of Bern, 125 pp.
- Thulborn, R. A. 1990. *Dinosaur Tracks*. Chapman & Hall, London, 410 pp.
- Thüring, B. and Hug, W. A. 2001. The first official palaeontological survey in Switzerland Section de paléontologie. Abstract, 9th Swiss Sed Meeting, Fribourg, Switzerland.
- Wilson, J. A. and Carrano, M. T. 1999. Titanosaurs and the origin of “wide-gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology*, 25:252–267.
- Wilson, J. A. and Sereno, P. C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir*, 5:1–68, supplement to *Journal of Vertebrate Paleontology* 18.
- Wilson, J. L. 1975. *Carbonate facies in geologic history*. Springer-Verlag, Berlin: 471 pp.