Sauropod trackway patterns expression of special behaviour related to substrate consistency? An example from the Late Jurassic of northwestern Switzerland

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Introduction

Since 2002, dinosaur tracks are excavated on the future course of the "Transjurane" highway (Canton Jura, Jura Mountains, northwestern Switzerland) (Marty et al., 2003). At the Combe Ronde tracksite (municipality of Chevenez) excavations have been concluded in 2005. Here, dinosaur tracks have been uncovered within a 65 cm thick sequence of inter- to supratidal calcareous laminites. These have been deposited during the Late Jurassic (approximately at the transition from the Early to the Late Kimmeridgian) on a carbonate platform, which was located at the Northern Tethys passive margin.

At the Combe Ronde tracksite 1167 dinosaur tracks have been documented on 8 successive surfaces. Most of the tracks are true tracks. However, some of the surfaces also exhibited undertracks (*sensu* Lockley, 1991) and overtracks, sometimes associated with each other and/or with true tracks on a single bedding plane. This indicates peculiar substrate and preservational conditions of the tracks. Thus, an identification of true tracks, undertracks and overtracks was only possible because all tracks were excavated and documented level-by-level. Together with the analysis of other sedimentological features such as desiccation cracks or ripple marks, this enabled to distinguish "true" palaeosurfaces (*sensu* Smith, 1993) from bedding planes. In addition to that, several tracks extracted in limestone blocks were cut into serial sections and facilitated the study of track formation and taphonomic history (Marty, 2005). This is a key point for consistent ichnotaxonomy and palaeoecological interpretations.

The main track level, situated at the base of the laminite sequence, was uncovered on a total surface of 570 m^2. It yielded the most diverse ichnocoenosis with two trackways of tiny sauropods (pes footprint length (FL)<25 cm), 12 trackways of medium-sized sauropods (25<FL<40 cm), one trackway of a minute theropod (FL<10 cm), 41 trackways of small theropods (10<FL<25 cm), and two trackways of medium-sized theropods (25<FL<30 cm). The main track level is considered a geotope (Marty et al., 2004) and will be protected for posterity. This will be realized by means of a bridge specifically built for this purpose.

Within the overlying laminites, only tracks of mostly medium-sized sauropods have been discovered. 12 trackways were identified, but most of the tracks are not arranged in trackways, as several surfaces were subjected to relatively intense dinoturbation (Lockley and Conrad, 1989).

Description of sauropod tracks and trackways

On all surfaces footprints are preserved as negative epichnia. Most of the sauropod tracks are 5-15 cm deep and well defined with large displacement rims. Generally, the track outline is clearly marked, but morphological details are missing. Pes prints are oval to sub-circular in shape. Their maximum width is generally located anterior to the centre. Manus prints are always wider than long and most are deeper in the anterior part. Their form varies between semicircular (D-shaped) and slightly horseshoed, depending on track depth and the degree of overprinting.

All trackways show a pronounced heteropody and are essentially narrow gauge, even if some show slight changes towards a wider gauge within the same trackway. Where present, manus prints are placed slightly farther away from the trackway midline than the pes prints. They show a negative manus rotation, which is generally higher than in the pes. However, trackway width, rotation of manus and pes, and the manus position with respect to the previous pes print and the trackway midline can vary between trackways and even in single trackways. This results in many different trackway configurations. Depending on the presence or absence of manus prints, the trackways can generally be described with four different trackway patterns:

— Quadrupedal trackways (manus and pes present)

— Manus-dominated trackways (quadrupedal trackways with deep manus prints and shallow, barely visible pes prints)
— Pes-dominated trackways (some manus prints absent and some deformed)
— Pes-only trackways

On the main track level, quadrupedal and pes-dominated (Fig. 1) trackways are common. On higher levels, pes-only, pes-dominated, and manus-dominated (Figs. 2 & 3) trackways, but no quadrupedal trackways have been observed.

Discussion

Recently, Wright (2005) recommended that sauropod trackways should be classified on the basis of manus and pes morphology only, and that trackway configuration should not be used for ichnotaxonomical descriptions. A similar approach has been presented by Dalla Vecchia and Tarlao (2000), who grouped sauropod ichnotaxa on the basis of manual print morphology. However, the configuration of quadrupedal trackways, in particular trackway width (gauge), but also heteropody and the position of manus and pes, have been used as diagnostic features in the description of sauropod ichnotaxa (e.g. *Brontopodus sensu* Farlow et al., 1989; *Parabrontopodus* in Lockley et al., 1994a) and their attribution to possible trackmakers (Wilson and Carrano, 1999).

At the Combe Ronde tracksite, the most regular quadrupedal trackways exhibit a narrow gauge with pronounced heteropody, similar to other Late Jurassic sauropod trackways, which are commonly attributed to the ichnotaxon *Parabrontopodus*.

However, the present tracksite is a good example for the variability of sauropod trackways, as different trackway patterns have been observed on different surfaces, and as quadrupedal trackways are rare or even absent on several surfaces. Moreover, on the main track level different trackway configurations exist between multiple parallel trackways, which are suggested to have been left by groups of sauropods moving together.

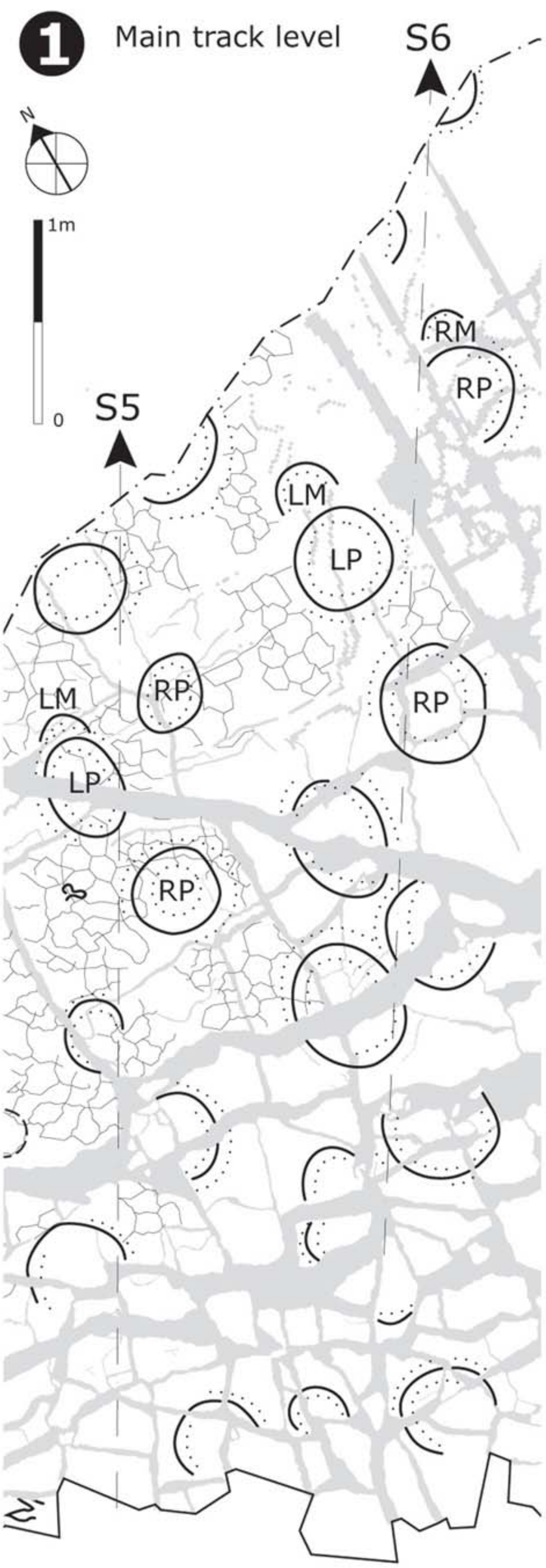
Pes-only trackways have frequently been regarded as trackways of relatively fast moving sauropods, where the pes overprints the manus (e.g. Meyer, 1990). The same may be true for pes-dominated trackways. This might be confirmed for the Combe Ronde tracksite by further statistical analyses.

Manus-dominated and manus-only trackways on the other hand are the cause of an intense debate. They have been interpreted as undertracks (Lockley and Rice, 199; Lockley et al., 1994b, Vila et al., 2005), trackways of partially submerged sauropods (Wilson and Fisher, 2003), and trackways of swimming sauropods (e.g., Lee and Huh, 2002). Henderson (2004) recently suggested that sauropods — even if they probably have not been able to swim — could successfully walk in water that was as deep as their chest height and in particular *Brachiosaurus* and *Camarasaurus* doing this could leave manus-only trackways. In this context, a narrow gauge, regular, manus-dominated trackway of the Combe Ronde tracksite is of particular interest (Figs. 2 & 3). It consists of true tracks and has been excavated on a mud-cracked and consequently emersive palaeosurface. The manus prints are well defined, relatively deep, and anteriorly inclined and bounded by a large displacement rim. Pes prints are very faint and barely visible. Subjected to weathering, this trackway would quickly alter into a manus-only trackway, which could be interpreted as an “undertrack trackway”.

It is suggested that the different observed trackway patterns and the variations in trackway configuration reflect special behaviour (e.g. walking speed, acceleration and slow-down phases, gait) rather than distinct ichnotaxa. Behaviour is at least to some extent related to the palaeoenvironment, namely the substrate consistency, as an animal does not behave the same way when moving over a stable or unstable surface. Substrate consistency and yield strength (cohesion), on the other hand, are a function of moisture content. These are the most important factors controlling track formation (morphology) and preservation (Allen, 1997; Manning, 2004). Consequently substrate consistency controls track morphology and might have an impact on trackway configuration and patterns (cf. Farlow, 1992). Thus, the absence of quadrupedal sauropod trackways and small tridactyl tracks within the laminites is probably related to a slight change in palaeoenvironment and substrate consistency. It is possible that either special substrate and/or preservational conditions prevented the preservation of small tridactyl tracks or that their producers avoided this environment.

Conclusions

The Combe Ronde tracksite exhibits diverse sauropod trackway configurations and patterns. For the moment it cannot be excluded that some of these variations are related to complex behaviour, different size classes, or even different trackmakers. Nevertheless, it is suggested that most of these variations



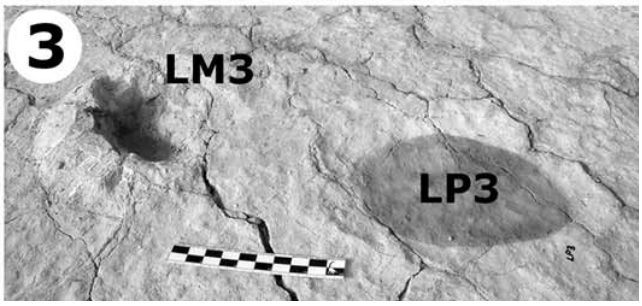


Fig. 1 — Pes-dominated parallel trackways S5 and S6 of the main track level, which form part of a group of 11 parallel trackways. The desiccation crack system and cracks related to karstification along small normal faults are shown in grey. **Fig. 2 — Regular, manus-dominated trackway S1 of palaeosurface 540, located approximately 40 cm above the main track level. Fig. 3 — Detail of the same trackway, showing the left manus LM3 and pes LP3, respectively.** The manus print is well defined, anteriorly inclined and bounded by a displacement rim, whilst the pes print is a faint depression without displacement rim. Scale bars are 20 cm. Tracks have been painted with water-soluble colour. Illumination from top left.

are related to behaviour, and that behaviour is at least partially related to substrate consistency and the palaeoenvironment.

Interpretations of complex behaviour without a description of the sedimentology and taphonomic history of the tracks and the tracksite should be avoided. For instance, it has first to be shown that during track impression a surface was situated below the water surface, in order to infer swimming sauropods from manus-only trackways. Finally, descriptions of sauropod ichnotaxa should be based on true manus and pes tracks exhibiting morphological details and regular quadrupedal trackways without overprinting.

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