

The First Iguanodontid Dinosaur Tracks from the Swiss Alps (Schrattenkalk Formation, Aptian)

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Until now dinosaur tracks from Switzerland were only known from Triassic and Late Jurassic strata. We report here for the first time the occurrence of ornithopod tracks from the Schrattenkalk Formation (Late Aptian) from the Swiss Central Alps. The locality is situated in an abandoned quarry on the shore of Lake Lucerne close to the village of Beckenried.

The steeply inclined surface has more than 50 tracks (in three trackways) of ornithopod dinosaurs that are attributed to iguanodontids. Three trackways can be followed for distances of 25 to 35 m. The lengths the footprints (mean: 30 cm) point to animals ranging in size of from 4 to 6 m, with estimated hip heights between 1.8 and 2 m (hip height 6 FL) and 1.4 to 1.7 m (hip height 5 FL). One of the trackways shows two succesive manus impressions, indicating facultative quadrupedal gait.

The track bearing layer consists of shallow water micrites with traces of emersion, and it is overlain by bioclastic grainstones. Previously the Upper Schrattenkalk Member in the Helvetic realm was thought to have formed on a large shelf far away from any continents. The present discovery will shed new light on the paleogeographic position of the Helvetic nappes.

Keywords Dinosaur tracks, Iguanodontids, Late Aptian, Switzerland

INTRODUCTION

Although dinosaur tracks from the Late Triassic and Late Jurassic have been known for several years in Switzerland (Lockley and Meyer, 2000), the discovery of tracks in the central part of the Swiss Alps was quite a surprise, especially since they occur in carbonate sediments hitherto thought to have been deposited under fully marine conditions.

In the summer of 2000, a local geologist (Markus Weh) discovered unusual patterns on a limestone surface while swimming in the Lake of Lucerne (Fig. 1). Detailed photographs were presented in the same year to the authors, who visited the site in late fall of 2000. Subsequently fieldwork was organized

Address correspondence to Christian A. Meyer, Museum of Natural History Basel, Augustinergasse 2, P.O. Box, Basel CH-4001, Switzerland. E-mail: christian.meyer@bs.ch in order to map the site and make casts of the most important specimens.

The new locality lies in an abandoned quarry close to the shore of Lake Lucerne in the vicinity of the village Beckenried (Canton Nidwalden, Switzerland). The track bearing layer is at the east end, approximately 80 m above the quarry floor and covers 582 m^2 of surface.

GEOLOGICAL SETTING

The locality lies in the foremost front folds of the Drusberg nappe (Helvetic realm) and is situated in a now abandoned quarry at Risleten, about 3 km east of the village Beckenried (Canton Nidwalden, Fig. 1B). The strata dip 57° toward North Northwest. The track-bearing surface forms part of the Schrattenkalk Formation and can be attributed to the Upper Schrattenkalk Member. According to Fichter (1934) its age ranges from middle Lower Aptian to middle Upper Aptian (Fig. 2).

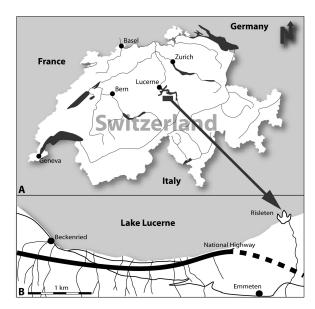


FIG. 1. Geographic setting of the new tracksite. (A) Map of Switzerland. (B) Close up of the locality.

Within the quarry about 45 m of limestone are exposed (Figs. 2, 3). The lower and upper parts of the section are made up of cross-bedded grain- to packstone that contain a large amount of miliolinid foraminfera, echinoderms, and rudist bivalves (*Requiena*). The grainstones often contain a large number of orbitolinid foraminifera (*Palorbitolina lenticularis*). The finer grained pack- to wackestones yield dasycladacean algae (Keller, 1983 and personal observations).

The trackbearing surface is a highly bioturbated packstone (biomicrite). Thin sections show that it is largely composed of miliolinid foraminifera (*Quinqueloculina*), recrystallized mollusc fragments, and sponge spiculae. Peloids, ostracods, oyster fragments, some echinoderms, and angular quartz grains are also present. The footprints are infilled by a wackestone with a high number of sponge spicules oriented parallel to the bedding plane and some miliolinid foraminifera. The texture reveals a cryptalgal fabric. The filling is finely laminated; toward the top, birds eye forming vugs can be observed.

Methods

A first inspection of the site was undertaken in 2000 by the authors and Markus Weh. Prior to mapping in early June, aerial photographs were taken in order to get an overall view. Subsequently a field campaign was organized in July 2002. Within two weeks, the whole surface was equipped with ropes, and the extent of surface as well as all tracks were individually mapped. Each individual footprint was measured, as shown in Fig. 4. The surface was overlain by a grid with 5 m squares that were used as reference points for the detailed mapping of the trackways. A lithological section of the whole sedimentary sequence was logged, and samples for thin sections were taken. The best trackway segment was cast in silicone rubber. As the handling

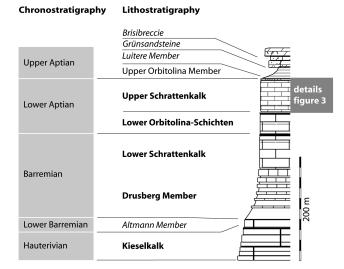
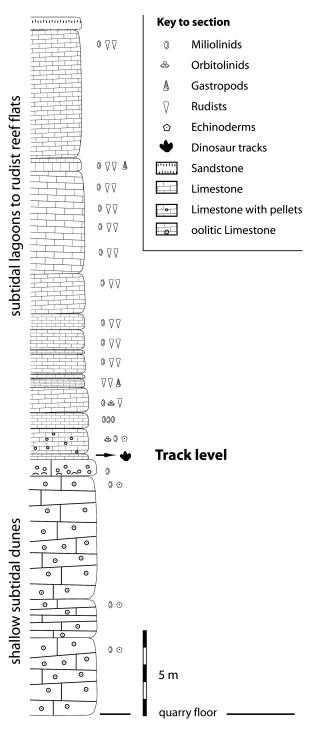
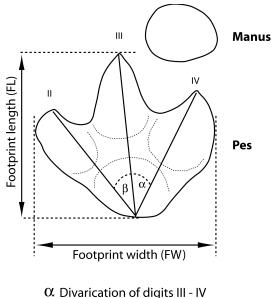


FIG. 2. Chronostratigraphic and lithostratigraphic framework of the Schrattenkalk Formation.







 β Divarication of digits II - III

A

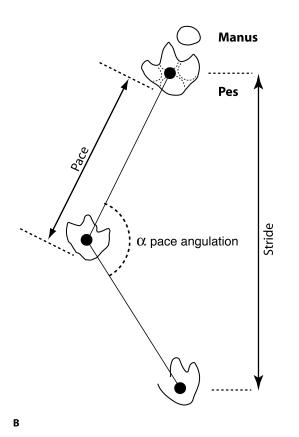


FIG. 4. Footprint measurements. (A) Individual measurements for single footprints. (B) Trackway parameters.

of large support moulds seemed impossible on the steep wall, some 150 m above the quarry floor, the mould was reinforced with two layers of nylon grid fabric. After the campaign, casts were produced at the Natural History Museum in Basel.

RESULTS

It is usually a difficult task to identify tridactyl trackmakers, as it is widely known that they could have been produced by either theropods or ornithopods. Up to now, there are no theropods known that have been even facultatively quadrupedal. However, some ornithopods could have placed their manus digits on the ground and seem to be the most likely track producers in this case. When compared with all known European Lower Cretaceous footprints attributed to iguanodontids, the Swiss material clearly differs in almost all characters.

Description

The trackbearing surface dips 57° towards 335 (NW) and comprises 582 m². Three trackways can be followed for distances of 25 m to 35 m (Figs. 5, 8, 9, and Table 1).

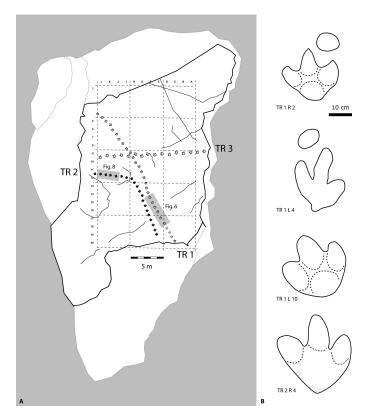


FIG. 5. Overview of the tracksite. (A) Map of trackways. (B) Outline drawings of best preserved single footprints.

FL (Digit III)	Digit IV	Digit II	FW	Pace	Stride	Angulation	α	β	Rel. stride	Footprint ratio
28.6	25.6	23.2	26.2	62.4	118.3	165	31.3	33.5	0.7	0.92
•	includes 14	measurable	footprint	s and was	made a by	slightly larger a	animal.			
Trackway 2 FL (Digit III)	includes 14 Digit IV	measurable Digit II	footprint: FW	s and was	made a by Stride	slightly larger a	animal. α	β	Rel. stride	Footprint ratio

FL						Angulation				
(Digit III)	Digit IV	Digit II	FW	Pace	Stride	(one value only)	α	β	Rel. stride	Footprint ratio
29.8	—	_	28	65.9	129.1	151.4	35	30	0.75	1.06

SYSTEMATIC ICHNOLOGY

Iguanodontipus Sarjeant, Delair & Lockley 1998 Iguanodontipus billsarjeanti n.ichnosp. (Fig. 6)

Derivatio nominis: Named in honor of Bill Sarjeant, who dedicated a great part of his life to the study of iguanodontid footprints.

Type material: A cast of trackway segment T1 (NMB K.S. 374) is kept in the Natural History Museum Basel (Figs. 8, 9).

Type horizon and locality: Risleten Quarry, Swiss Coord. 682 649/ 202 413, 428 m.a.sl. (quarry base). Upper Schrattenkalk Formation, age: Middle Lower Aptian to Middle Upper Aptian.

Description: Tridactyl pes wider than long, resulting in a footprint ratio between 0.92 and 1.06. Individual digits elongate, slightly rounded with interdigital angles that range between 30° and 35°. Digit III directed forward ending in a slightly rounded equilateral triangle, but slightly rounded. Interdigital angles (α , β) in all trackways consistently between 30° and 35°. Pace angulation between 150° and 175°. In trackway I (RP 2; Fig. 6), pad impressions can be observed. Pes length varies from 28 to 35 cm. The heel is triangular to smoothly rounded, claws are not defined. The manus is oval to almost round and lies close to the anterior of the apices of digits III and IV. All the trackways show slight inward rotation of the axes of pes of the third pedal digits. Pace measures between 62.4 and 71.7 cm.

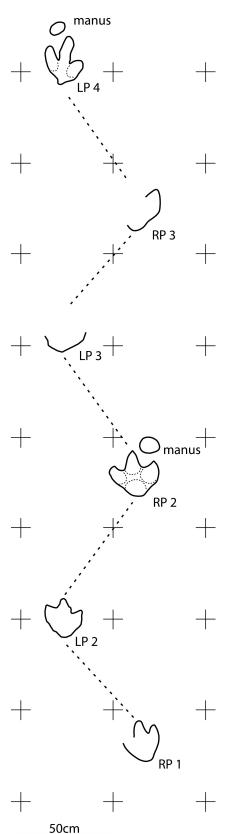
Discussion: Ichnites attributed to quadrupedal iguanodontids from Regumiel de la Sierra and Cabezon de Cameros are considerably larger (FL: 45 to 58.4 cm; Moratalla 1993, Figs. 7, 11) than those from Risleten. The manus of the Spanish material is anterior to the apex of digit IV, and differs in its more elongate overall shape. Both localities are geologically younger than Risleten and are placed into the Neocomian and Hautervian respectively. The oldest Spanish trackways come from the las Cerradicas locality, which has been assigned to the Lower to Middle Berriasian (Pérez-Lorente et al., 1997). The footprints are relatively small (FW: 23 cm). The manus is oval and is positioned close to the anterior margin of digit III. *Caririchnium magnificum* from the Lower Cretaceous Antenor Navarro Formation (Paraiba state, Brazil; Leonardi 1984) is much larger (FL: 50 cm) and has a quadripartite pes outline with the imprints of the digits clearly separated. The manus is positioned anterior to the apex of digit III.

The British specimens attributed to *Iguanodontipus burreyi* and *Iguanodontipus* sp. respectively come from the Purbeck Limestone group (Early Berriasian; Sarjeant et al., 1998; Lockley and Wright, 2001). The pes outline is poorly preserved but indicates a higher interdigital angle than the Swiss specimens. The manus is consistently positioned well outside digit IV. Much of the this is also true for the specimens from the Wealden Group (Mid-Late Berriasian) of the famous Münchehagen locality near Hannover (Fischer, 1998; Lockley and Meyer, 2000). Although footprint length is in the range of the measured means of the Swiss specimens, their overall shapes are quadripartite. In contrast, both the British and German specimens show triangular outlines of the manus prints which involve digits II–IV.

The Croatian material from Veli Briun (Brioni Island; Late Albian, Tislar et al., 1998) is so far the geologically youngest occurrence of ornithopod tracks in Europe (Dalla Vecchia et al., 2002). Their outlines are not very well preserved, and most of the footprints are still filled with limestone and each has a high interdigital angle, as can be seen in the British specimens. However, no manus impressions are preserved (pers. obs., 2002), and it is quite possible that these tracks were left by hadrosaurs or other ornithopods. A recently discovered locality on Gallia, the private island of the Croatian president, shows iguanodontid footprints with clear quadripartite, distinctive outlines, and more

TABLE 1

Trackway 1 consists of 14 measurable footprints. It is the only trackway that also has manus imprints. Standard measurements were



rounded digit impressions (pers. obs., 2002) but lack associated manus prints.

CONCLUSIONS

The overall outlines as well as the sizes and the shapes of pes and manus of the Swiss specimens are clearly different from all other known European Cretaceous iguanodontid footprints.

The position of the manus indicates that one individual placed its hand close to the midline of the trackway, with the dorsal surface of the manus facing forward. Regarding the shape of the manus, our sample shows a rounded to slightly oval outline, suggesting that the animal placed its webbed feet on the ground, resulting in a narrower trackway than demonstrated by Wright (1999) for the British specimens. The animals were moving at relatively high speeds when they made the tracks. Using Alexander's formula (Alexander, 1976), we calculate the animals were walking at 20 km/h to 22 km/h; calculating speed with a different formula (Thulborn, 1990) results in estimated speeds of 43 km/h to 49 km/h, which seem to be too high. We estimate the sizes of the animals range between 4 to 6 m in length.

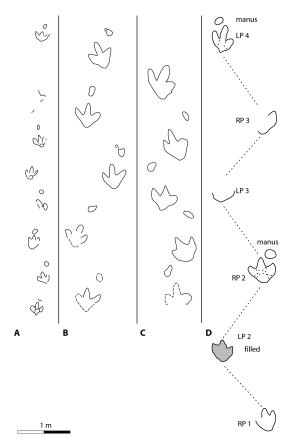


FIG. 6. Outline drawing of the trackway type (NMB K.S. 374, location see Fig .5A) of *Iguanodontipus* n.sp. from the Late Albian Schrattenkalk Formation (Risleten, Beckenried).

FIG. 7. Four trackways of quadrupedal ornithopods from Spain and Switzerland (drawn to scale). (A) Las Cerradicas. (B) Regumel de la Sierra. (C) Cabezon de Cameros (after Lockley and Meyer, 2001). (D) Risleten quarry (this paper).

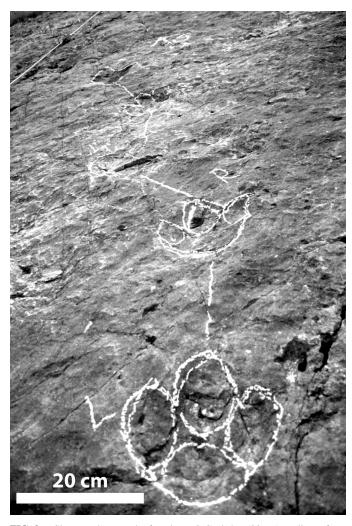


FIG. 8. Close up photograph of trackway 2. Scale bar (20 cm) applies to foreground.

Geological and sedimentological observations suggest that the tracks were formed during a sea-level-high stand. Prior to the formation of the tracks, massive cross-bedded limestone with shallow water fossils interpreted as shallow sudtidal dunes were formed. The filling of the tracks indicate inter- to supratidal conditions (algal laminites). The following sediments are made up of massive pack- to grainstones that contain abundant rudists and gastropods, and are most likely lagoonal sediments with a minor input of high energy deposits (cross bedded limestones).

The trackways clearly indicate prolonged exposure of the carbonate platform on the southernmost shore of the northern Tethys. It would not be surprising if this first record of trackways in the Helvetic realm triggers other discoveries in the near future.

The trackways are further examples of iguandontids in a carbonate platform environment, which is in contrast to the vertebrate ichnofacies concept developed by Lockley et al. (1994).



FIG. 9. Close up of right pes 2 of trackway 1 (see Fig. 5). Scale bar 10 cm.

Usually the *Caririchnium* ichnofacies is confined to Cretaceous siliciclastic, fluvial sediments, whereas our example and at least several others (Briuni, Dalla Vecchia, et al., 2002; Gallia, pers. obs., 2002; Purbeck, Lockley, and Wright, 2001) form an exception to the observed occurrences such as those known from Spain or Germany.

The question remains as to where the species of dinosaur migrated to the northern shore of the Tethys. Taking into account the paleogeographic situation in the Late Aptian, the only possibilities are an origin from either the Rhenish Massif or the London Brabant massif, i.e., from Northwestern Germany, Belgium, or southern England (Fig. 11). The Iberian and Massif Central Meseta were connected at that time but were separated

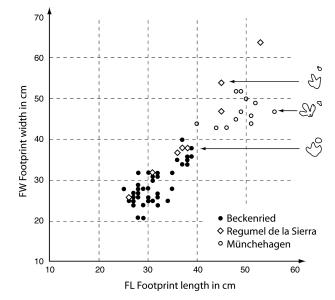


FIG. 10. Size comparison of German (Münchehagen), Spanish (Regumel de la Sierra) and Swiss specimens (data from Fischer, 1998 and Moratalla, 1993).

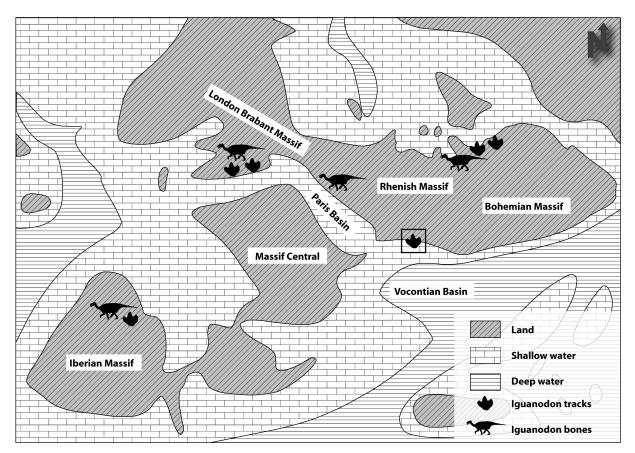


FIG. 11. Palaeogeography of the Late Albian in Central Europe showing track and bone localities of iguanodontid ornithopods.

from the northern Tethys realm by shallow water. The next closest known locality in the south with iguanodontid tracks is in Istria (Dalla Vecchia et al., 2002) and was paleogeographically separated from the Swiss site by deep water; the animals that made the tracks most likely immigrated from Africa (Bosellini, 2002).

ACKNOWLEDGEMENTS

We would like to thank the Stiftung Lebensraum und Gebirge for funding part of our field work in Beckenried. We express our gratitude to Oskas Wuest for his logistic and gastronomic support. Stefan Bucher, Silvan Thüring, Samuel Boll, and Markus Weh provided on-site assistance. The help of Antoine Heitz and Daniel Oppliger (Natural History Museum Basel) was greatly appreciated. Discussions with Beat Keller about the sedimentary environment were very helpful. Thanks to Zlatan Bajraktarevic and Alexander Mezga (Zagbreb), we could visit the Cretaceous track sites in southern Istria and had access to restricted areas on the islands Brioni and Gallia. We would like to thank the editors of this special volume for inviting us to contribute to the memory of the late Bill Sarjeant. Last but not least we wish to express our thanks to Phil Currie and an anonymous reviewer who helped to improve the manuscript.

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