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Triassic chirotheriid footprints from the Swiss Alps: ichnotaxonomy and depositional environment (Cantons Wallis & Glarus)

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Abstract Autochthonous Triassic sediments of the Vieux Emosson Formation near Lac d'Emosson, southwestern Switzerland, have yielded assemblages with abundant archosaur footprints that are assigned to chirotheriids based on pentadactyl pes and manus imprints with characteristic digit proportions. Tridactyl footprints formerly considered as those of dinosaurs are identified as incomplete extramorphological variants of chirotheriids. Recently discovered new sites, including a surface with about 1500 imprints, permit re-evaluation of ichnotaxonomy and modes of preservation. Most common are oval to circular impressions arranged in an "hourglass-like" shape, corresponding to pes-manus couples. Sediment displacement rims indicate the presence of true tracks rather than undertracks. A few well-preserved footprints with distinct digit traces allow closer assignments. Several chirotheriid ichnotaxa are present with *Chirotherium barthii*, ?*Chirotherium sickleri*, *Isochirotherium herculis*, Chirotheriidae cf. *Isochirotherium* isp. and indeterminate forms. This corresponds with characteristic assemblages from the Buntsandstein of the Germanic Basin. In the study area, the Vieux Emosson Formation is an up to 10 m thick fining-upward sequence with conglomerates, rippled sandstones, siltstones and mudstones and occasionally carbonate nodules. Sedimentological features such as high relief erosion, immature sediments, erosionally truncated metre-scale fining-upward sequences, palaeosols and unidirectional palaeocurrents clearly prove a fluvial depositional environment with sediment transport towards the northwest and the Germanic Basin. This contrasts with former assumptions of a coastal marine environment and a south-facing transport towards the Tethys. The footprints occur in the coarser lower portion of the sequence that is interpreted as a shallow braided river. From Obersand in the eastern Swiss Alps, a surface in dolomitic limestone (Röti Dolomite) is re-examined. The footprints are identified as *Chirotherium barthii* and were impressed in a carbonate tidal flat environment. Biostratigraphically, the occurrence of characteristic Buntsandstein assemblages with *Chirotherium barthii* supports an Anisian age of both locations.

Keywords Tetrapod footprint · Chirotheriids · Middle Triassic · Vieux Emosson VS · Obersand GL · Switzerland

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Introduction and history of research

Triassic tetrapod footprints are known from numerous localities in the Swiss Alps (Fig. 1). From the eastern part of the Swiss Alps, surfaces in Late Triassic carbonate deposits of the Piz dal Diavel (Engadin) region yielded more than 200 footprints of theropods and possible prosauropodomorph dinosaurs that were discovered in the early 1960s (Furrer 1993). Other Late Triassic dinosaur tracksites have been reported from the Parc Ela (Graubünden) (Meyer et al. 2013).

In the region of the Tödi mountain, near Obersand, Glarus, Feldmann and Furrer (2008) described surfaces with chirotheriid footprints in deposits known as the Röti Dolomite (Fig. 1; Table 1). Several trackways were illustrated by these authors and assigned to the ichnogenus *Isochirotherium*. The age of the strata was considered as Middle Triassic. According to Gisler et al. (2007), these sediments were part of a carbonate tidal flat and palynological data suggest an Anisian age.

From the western Swiss Alps, near Lac d'Emosson, the autochthonous Triassic contains surfaces with hundreds of tetrapod footprints that were described by Bronner and Demathieu (1977) and Demathieu and Weidmann (1982) from the Vieux Emosson locality (Fig. 2). The latter authors attributed several morphotypes to dinosaurian trackmakers, essentially based on the ichnotaxonomy of Ellenberger (1972) and footprints identified from the South African material. Furthermore, they introduced a number of new ichnotaxa. The presence of the chirotheriid ichnotaxa *Brachychirotherium* and *Isochirotherium* was also reported (Table 1). The age of the track-bearing strata was considered by these authors as Late Ladinian or Carnian, based largely on tetrapod tracks regarded as made by dinosaurs. The ichnotaxonomic assignment was questioned by Lockley and Meyer (2000) and Meyer and Thüring (2003), and they were tentatively assigned to chirotheriid trackmakers, also questioning the age of the deposits. Reinterpretation of the tracks at the Vieux Emosson site and analysis of nearby newly discovered trackways by Avanzini and Cavin (2009) and Cavin et al. (2012) suggested that the presence of the ichnotaxa *Isochirotherium soergeli* and *Chirotherium barthii* represented a "Chirothere assemblage" of archosaur trackways and indicated an older, Early to Middle Triassic (Late Olenekian to Early Ladinian) age, rather than a Late Triassic, age for the track-bearing strata (Table 1).

The autochthonous Triassic sediments of the Aiguilles Rouges Massif in southwestern Switzerland were extensively studied by Amberger (1960). On the basis of lithology, he concluded that the siliciclastic sequence unconformably overlying the Carboniferous/Permian

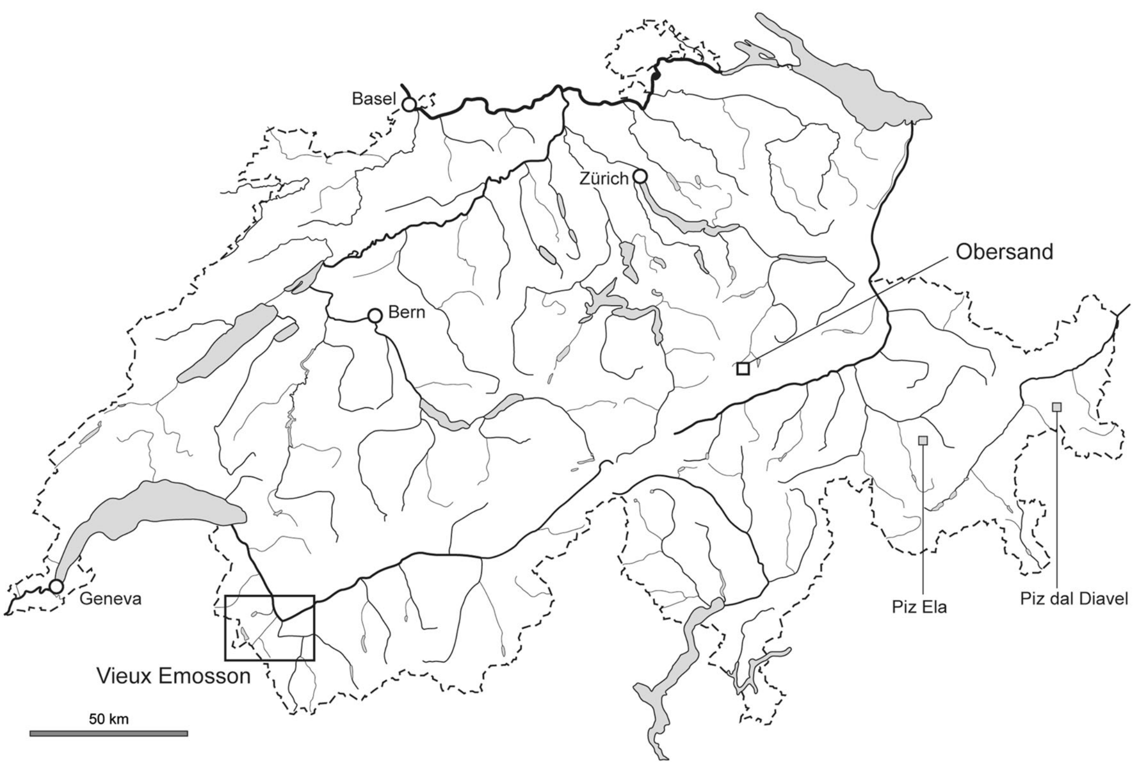

Fig. 1 Map showing position of Triassic archosaur (Vieux Emosson, Obersand) and dinosaur (Piz Ela, Piz dal Diavel) footprint localities in Switzerland

Table 1 History of ichnotaxonomical identification of Triassic tetrapod footprints from Switzerland

Ichnotaxonomy of Triassic tetrapod footprints from Switzerland								
Emosson region							Tödi (Glarus) region	
Bronner and Demathieu (1977)	Demathieu and Weidmann (1982)	Lockley and Meyer (2000)	Meyer and Thüring (2003)	Avanzini and Cavin (2009)	Cavin et al. (2012)	This paper	Feldmann and Furrer (2008)	This paper
Archosaur tracks	*Brachychirotherium* sp. *Isochirotherium* sp. *Paratrisauropus mirus**, *P. bronneri**, *P. latus** *Prototrisauropus* sp. *Deuterosauropodopus sedunensis** *Pachysaurichnium** *emossonense** *Bifidichnium** *ambiguum**	Enigmatic tracks	Chirotheriid tracks	*Isochirotherium* sp.	*Chirotherium* cf. *barthii*	*Isochirotherium herculis* cf. *I.* isp. *Chirotherium barthii* ? *C. sickleri* Chirotheriidae indet.	*Isochirotherium* cf. *I. archaeum*	*Chirotherium barthii*

Asterisk "*" means described new ichnogenera and ichnospecies, respectively

basement was part of the Alpine Buntsandstein, deposited in a shallow marine/sandy beach environment. Demathieu and Weidmann (1982) agreed with the marginal marine interpretation with an implication that the Triassic palaeoslope in the area was southward, towards the Tethyan Sea. Epard (1989) was the first to introduce a formal name for this sequence "Formation Vieux Emosson" and subdivided it into two members, a lower sandstone and an upper argillite member. The first consists of a series of coarse- to medium-grained sandstones followed by a sequence of clay and siltstones. He attributed the formation a Late Ladinian/Carnian age by citing Demathieu and Weidmann (1982).

The objective of our study was a systematic examination of all Triassic outcrops to provide an inventory of all tracksites, including previously undiscovered ones, and accurate stratigraphic correlations of these sites for testing the possibility of a megatracksite. Furthermore, detailed descriptions of the sedimentary units were obtained for an improved interpretation of depositional environments and for a refined palaeogeographic reconstruction of the region during the Triassic. Our field studies revealed the presence of 13 additional sites with vertebrate footprints (Fig. 2; Table 2). In 2012, three of us (CM, MW, BT) discovered several new surfaces with tetrapod footprints, including those at the La Veudale N locality in the Emosson region containing about 1500 footprints (Wizevich and Meyer 2012; Meyer et al. 2014; Klein et al. 2015) (Figs. 2, 3, 4). Obviously, these sites had been exposed by the recent retreat of larger snow cover. During the summer of 2013, an international group of researchers including the authors examined and documented these footprint surfaces in detail, together with those at the classic Vieux Emosson site and smaller findings at the nearby Scex Blanc locality (Figs. 2, 3; Table 2). Furthermore, in summer 2014, several other new localities with footprints were documented close to the French–Swiss border (Fig. 2; Table 2). During the same field season, some of the authors (HK, MW, CM) also re-examined the surface described by Feldmann and Furrer (2008) from the Obersand area (Glarus Alps).

The aim of this paper is to discuss the ichnotaxonomy of Triassic footprints from the Swiss Alps based on the results of our recent studies. Also, we re-evaluate their stratigraphic age based on the presence of biostratigraphically relevant morphotypes and ichnotaxa.

Materials and methods

All footprints are preserved as concave epireliefs and were left in situ in the field. Footprint surfaces at La Veudale N locality were mapped using a 5-m square grid, demarcating position of each imprint by a dot. Ropes were used for

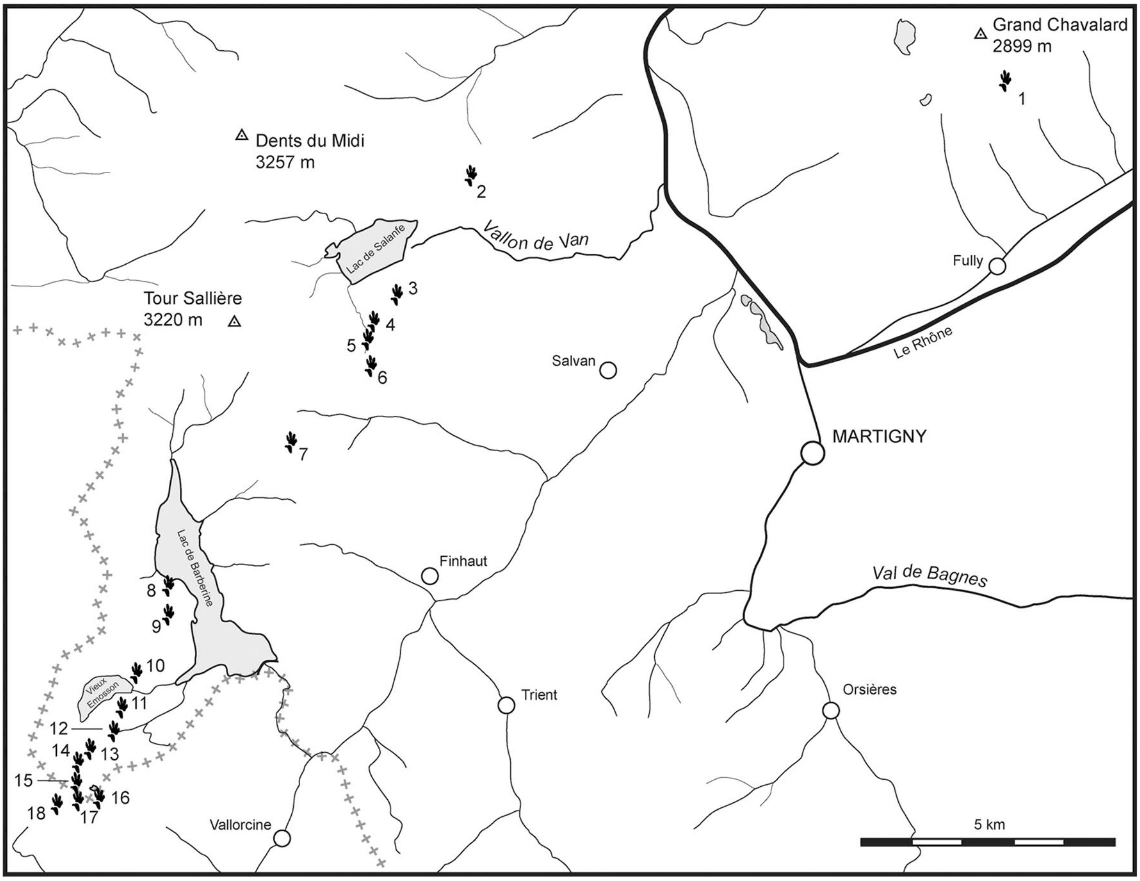

Fig. 2 Map showing position of Lower–Middle Triassic archosaur footprint localities around lake Vieux Emosson and in the western Swiss Alps and adjacent France (sites *16–18* are located in France). *Numbers* correspond to those in Table 2

mapping to access the steeply inclined surfaces. Best specimens were photographed under natural light conditions. Outlines were drawn on transparency film covering the original material and then digitized by a vector-based drawing software (Adobe Illustrator). Measurements were taken based on standard methods described by Haubold (1971b) and Leonardi (1987) (Table 3). Photogrammetry was used to document footprints at La Veudale N, Scex Blanc and Obersand localities using a 16mp Sony Nex-6 camera. The large-scale model of the La Veudale N site was generated using photographs taken from a nearby ridge using a 210-mm lens combined with close-range photographs taken using a 16–50 mm zoom lens. Digital models were produced in Agisoft Photoscan Professional Vers. 1.1.4, then scaled and cleaned in Meshlab and visualized using Autodesk Maya 2016. Multiple models were produced at cm, m, and whole-site scales, and subsequently merged. In total, 1317 photographs were used.

The Vieux Emosson Formation was characterized by 12 detailed sedimentological logs that were described at centimetre scale. Graphic representation of the logs from three tracksites (La Veudale N, Scex Blanc and Vieux Emosson) is shown in Fig. 3. Palaeocurrent measurements were obtained from planar foresets in tabular cross beds and from axes of trough cross beds exposed on bedding plane surfaces. Palaeocurrent directions from current ripples were measured on well-exposed ripple marks.

Geological setting

The Mesozoic autochthonous series covering the Aiguilles Rouges Massif were studied by Amberger (1960), Demathieu and Weidmann (1982) and Epard (1990) and were interpreted as shallow marine with alternating emersive episodes. Amberger (1960) proposed an Early Triassic age for the sandstones on the basis of lithological comparisons with the Helvetic Triassic of Glarus, Switzerland, and the Germanic Buntsandstein. On the basis of the interpretation of footprints from the Vieux-Emosson and, in particular, those regarded as produced by dinosaurs, Demathieu and Weidmann (1982) proposed a younger age for the trampled bed, i.e. Late Ladinian or Carnian (transition from the Middle to the Late Triassic). Lockley and Meyer (2000) and Meyer and Thüring (2003) questioned the dinosaur origin of the Vieux-Emosson footprints,

Table 2 Table of sections with archosaur track levels in the Vieux Emosson Formation (Late Olenekian to Early Anisian)

No.	Locality of tracks	Swiss C.	Lat long	Discovery	Altitude (m)	Level
1	Les Geules (Chavalard Dessus)	575.241 113.253	N46°10′13.0″ E7°07′05.0″	M. Burri (verified Meyer and Wizevich 2012)	2046	1
2	Col du Jorat	564.900 111.100	N46°09′03.6″ E6°59′09.4″	Meyer and Wizevich 2011	2173	1
3	Revers des Ottans	563.100 109.200		Bill Fitches 2000/verified Meyer 2002	2078	1
4	Lac des Otans			Meyer and Wizevich 2011		1
5	Ravin des Ottans	562.673 108.659	N46°07′42.2″ E6°57′20.6″	Meyer and Wizevich 2011	2080	1, 2, 3
6	Col d'Emaney	562.880 107.723	N46°07′11.9″ E6°57′30.5″	M. Burri (verified Meyer and Wizevich 2012)	2481	1
7	Cascade d'Emaney	561.310 106.448	N46°06′26.9″ E6°56′19.8″	Jean Boissonnas	2238	1
8	L'Arevassey	559.029 103.587	N46°04′51.1″ E6°54′24.2″	Meyer and Wizevich 2011	1986	1
9	Le Blettey	558.837 102698		Meyer and Wizevich 2011	2247	1
10	La Veudale N	557.798 100.909	N46°03′27.2″ E6°53′37.1″	Meyer, Wizevich and Thüring 2012	2304	1, 2
11	Tête de Gouilles	558.219 101.726		Meyer and Wizevich 2011	2519	1
12	Scex Blanc	557.755 100.562	N46°03′19.0″ E6°53′34.4″	Meyer andWizevich 2011	2418	1
13	Vieux Emosson	557.132 099.898	N46°02′57.5″ E6°53′07.0″	Bronner 1976	2384	1, 2
14	Vieux Emosson 2	557.104 099.802		Meyer and Wizevich 2011	2410	2
15	No name Lake (NW Lac Vert)	557.271 099.487		Meyer, Wizevich and Thüring 2012	2599	1
16	Pointe de la Terasse (Col des Corbeaux 1)	557.479 099.175	N46°02′35.7″ E6°53′22.4″	Meyer, Wizevich and Klein 2014	2656	1
17	Col des Corbeaux 2 (F)	557.087 099.229	N46°02′33.5″ E6°52′54.1″	Meyer, Wizevich and Klein 2014	2598	1, 2
18	Le Châtelet (F)	556.721 099.045	N46°02′30.5″ E6°52′46.5″	Meyer, Wizevich and Klein 2014	2497	1
	Crottes du Col (Lac de Barberine)	559.590 104.303	N46°05′20.5″ E6°54′58.3″		1896	

Same numbers as in Fig. 2

implicitly questioning the age of the site. In 2009, Avanzini and Cavin described a short trackway preserved on an isolated block near the Vieux Emosson site. They referred it to the ichnogenus *Isochirotherium*, close to *I. soergeli* and *I. lomasi*, which would indicate a probable Early or Middle Triassic age (Avanzini and Cavin 2009).

Sedimentology and depositional environment

Description The Vieux Emosson Formation lies unconformably on the Variscan polymetamorphosed basement of the Aguilles Rouge external massif. In the study area, the basement consists largely of mica schist and gneiss units intruded by granite (Raumer and Bussy 2004). In some areas, unweathered basement is sharply overlain by the Vieux Emosson Formation with up to 1 m of relief (nearly 10 m over the study area) along the contact. Locally, extensive weathering and dolomitic nodules indicate palaeosol development on the top of the basement, possibly during the Permian, but most probably during Early Triassic times (Demathieu and Weidmann 1982).

In the study area, the Vieux Emosson Formation consists of five lithofacies in a generally fining-upward sequence: conglomerate, trough cross-bedded sandstone, thin-bedded rippled sandstone, mudstone, and dolomite. The formation

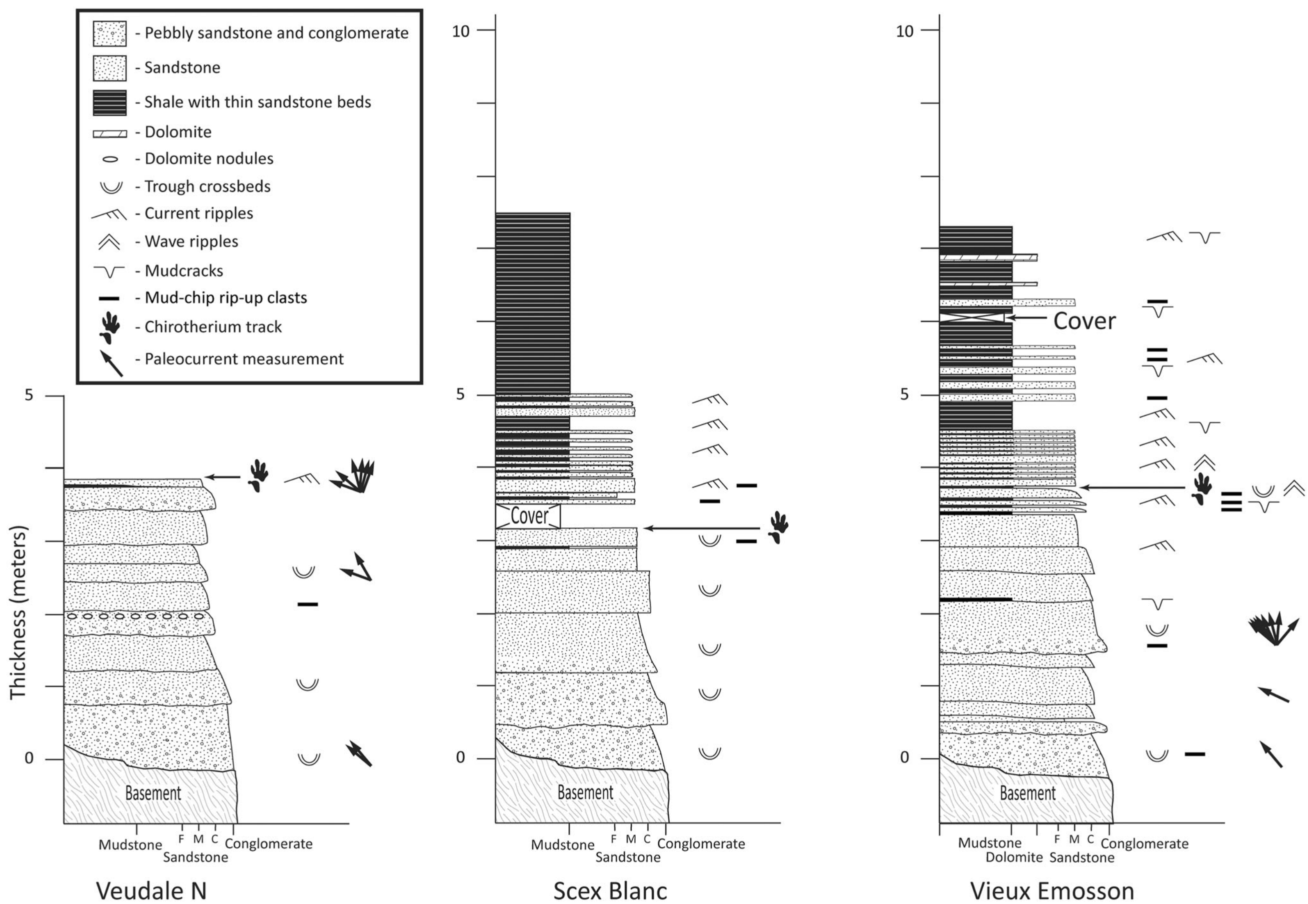

Fig. 3 Stratigraphic sections of the Vieux Emosson Formation at footprint localities of La Veudale N, Scex Blanc and Vieux Emosson (Fig. 2; Table 2) with position of track levels. Palaeocurrent azimuths (*arrows*) are displayed relative to north (up is to the north)

consists of a basal unit of sandstone and conglomerate overlain by a fine-grained unit of thin-bedded sandstone and shale, with minor dolomite near the top (Fig. 3). The lower unit corresponds to the sandstone member and the fine-grained unit is the argillite member of Epard (1989). However, Epard (1989) identified the top of the formation at the base of the first stratigraphic occurrence of dolomite beds, although he recognized that the transition was often gradual. The Vieux Emosson Formation in the study area is up to 10 m thick (Fig. 3), but the true thickness is not discernable because it is overlain by cataclastic breccias of the tectonically emplaced Helvetic nappe, and also because the upper fine-grained unit is typically poorly exposed.

The basal unit consists of up to 5 m of erosionally based, m-scale sequences that fine upwards, rarely capped by shale (<40 cm thick). Channel-form bases are rare. Conglomerate beds are sandy matrix-supported, with angular to subangular clasts up to 6 cm in size. Most clasts are quartz, but locally there are abundant metamorphic lithic fragments. Beds are 50 cm to a metre thick and generally overlie the basement, and are massive with rare cross beds.

Sandstone beds in the basal unit are very poorly sorted, commonly conglomeratic, and very coarse- to medium-grained. Beds are typically a few to several tens of cm thick, fining upward with scoured bottoms. Internally the beds are typically massive, often with poorly-defined horizontal laminations and outsized clasts (several cm diameter), but dm-scale (1–2 m wide) trough cross beds are common. Sandstones in the basal unit are feldspathic lithic arenites but mature compositionally to sublithic arenites towards the top of the unit. Rare red mottled beds contain cm-scale carbonate nodules or large desiccation cracks. Palaeocurrent data from trough cross beds and ripple marks have a unimodal pattern with a northwest transport direction (Fig. 3).

The fine-grained unit is a generally fining- and thinning-upward sequence of interbedded thin, rippled sandstone and mudstone beds, up to 7 m thick. Rippled sandstones are thin-bedded (cm- to dm-scale), coarse to fine-grained, and contain abundant current and wave ripple marks, small-scale cross stratification, mudcracks, mudstone rip-up clasts, and rare load casts. Trackways are found on the top of rippled beds at the transition between the basal and fine-grained units (Fig. 3).

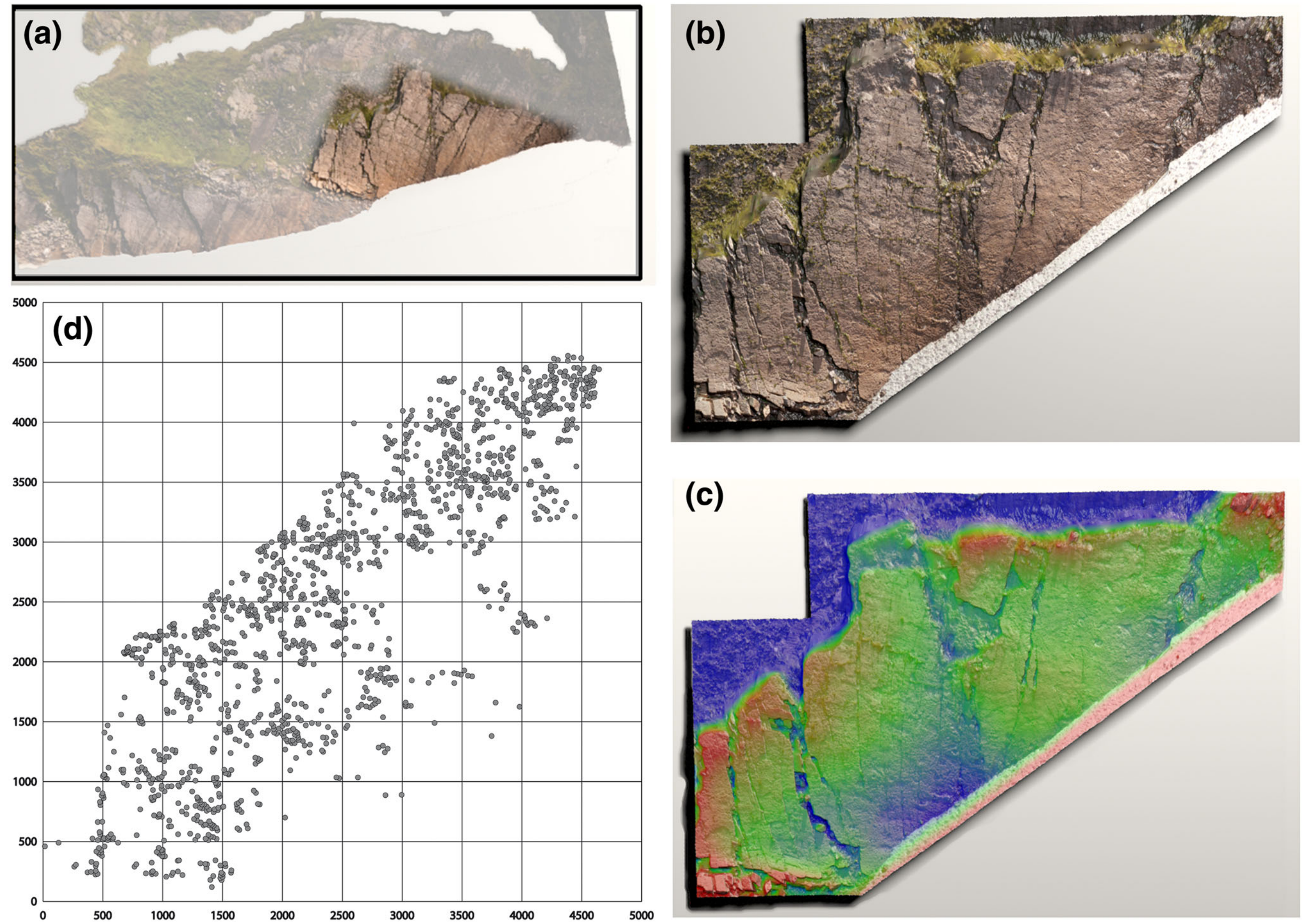

Fig. 4 **a–c** Photogrammetric models and overview of La Veudale N (Emosson region) tracksite, with **c** as coloured depth model. **d** Map of La Veudale N footprint surface with distribution of archosaur footprints corresponding to area in the photogrammetric model; *scale* in centimetres. Photogrammetric models by Peter Falkingham

The mudstones consist of red and green laminated mudstone with very thin (<cm) fine- to medium-grained sandstone layers. Where well exposed, the mudstone and very thin sandstone beds comprise 20–50 cm thick fining- and thinning-upward sequences nested within the fine-grained unit. Microscopic examination of the mudstones that appear to be devoid of sandstone reveals mm-scale, erosionally based, fining-upward (very fine sand to clay) lamina. Mudcracks and starved ripples are common. Palaeosols defined by texturally mottled and crinkly laminations (bioturbation?) and dolomitic nodules are rare.

Dolomite beds, up to 5 cm thick, are very fine-grained, weakly laminated, and are interbedded with the mudstones at the top of the fine-grained unit. In some areas, the dolomite beds contain extensive desiccation fractures.

Depositional environment Several features are incompatible with a coastal marine environment, and instead support a fluvial interpretation for the Vieux Emosson Formation:

- high-relief erosional surfaces, likely by channel incision;
- erosionally truncated metre-scale fining-upward sequences;
- immature sediments, especially poorly-sorted basal conglomerates and large angular clasts, indicate minimal abrasion and transport;
- decimeter-thick massive beds with many floating outsized clasts;
- strongly unidirectional palaeocurrents;
- near absence of bioturbation in fine-grained facies;
- palaeosols with carbonate nodules in both the basal and upper units.

Erosion of the Variscan mountain ranges to peneplains occurred in the Permian and early Triassic. A blanket of highly weathered Variscan metamorphic rock likely developed over the region. Downcutting of the basement by fluvial channels, possibly caused by rift-related uplift or a sea-level lowstand, led to the erosion of several metres of relief on the basement

Table 3 Measurements of chirotheriid footprints from the Triassic of Switzerland and France

Locality	La Veudale N					Scex Blanc		Vieux Emosson	C. d. Corbeaux 1 (F)				C. d'Emaney			Tödi (Glarus)			
Ichnotaxon	*Isochirotherium herculis*		*? C. sickleri*	Chirotheriidae Indet.		*C. barthii*		cf. *Isochirotherium* isp.	*? Chirotherium, ? Isochirotherium*				*C. barthii*			*Chirotherium barthii*			
Specimen													Bar 1	Bar 2	Bar 3	MP1	P2	P3	P4
pl	26.4	22.0	13.3	28.4	19.0	16.0	20.7	24.1	39.0	22.6	28.5	25.7	13.9	16.6	23.5	25.0	25.0	25.0	15.2
pw	16.8	20.2	9.0	24.8	12.8		11.0	19.2	34.0	20.2	23.8	16.8	7.3	6.8	12.7	25.0	17.0	16.0	9.7
pl/pw	1.5	1.1	1.4	1.1	1.4		1.8	1.2	1.1	1.1	1.1	1.5	1.9	2.4	1.8	1.0	1.4	1.5	1.5
ml	–	–	10.3	14.2	8.2	–	11.0	–	18.5	17.2	–	11.5	6.5	5.3	9.2	12.0	–	–	–
mw	–	–	9.3	16.7	8.2	–	8.2	–	24.0	17.3	–	15.2	4.5	4.2	6.2	6.0	–	–	–
ml/mw	–	–	1.1	0.8	1.0	–	1.3	–	0.7	0.9	–	0.7	1.4	1.2	1.4	2.0	–	–	–
δ	–	–	–	–	–	16°	0°	>20°*	–	–	–	–			6°*	–	–	–	–
γ	–	–	–	–	–	–	20°	–	–	–	–	–			6°*	–	–	–	–
PL	–	–	–	–	–	45–60	53.7	64	–	–	–	–	32.6	44.4	54.2	–	–	–	–
SL	–	–	–	–	–	100	–	–	–	–	–	–	61.3	88.4	–	–	–	–	–
TW	–	–	–	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–	–
PA	–	–	–	–	–	150°	170°	–	–	–	–	–	142°	160°	–	–	–	–	–

All localities in Switzerland except (F) in France. Measurements in centimetres and degrees; * estimated values

Pl pes length, *pw* pes width, *ml* manus length, *mw* manus width, *δ* rotation of pes relative to midline, *γ* rotation of manus relative to midline, *PL* pace length, *SL* stride length, *TW* trackway width, *PA* pace angulation

Grey columns Scex Blanc from Avanzini and Cavin (2009); C. d'Emaney from Cavin et al. (2012)

surface. The locally derived basement detritus was ultimately deposited by the fluvial system on gneiss of the Aiguilles Rouges massif as the Vieux Emosson Formation. Angular clasts and lithic-feldspathic compositions, supported by detrital zircon analyses (Wizevich et al. 2015), indicate short transport and derivation largely from local basement sources.

Deposition of basal unit took place in a shallow braided river system. Rare channel forms and the massive nature of many of the coarse-grained beds suggest high-sediment concentrations in poorly confined channels, possibly in flash floods (Pierson 2005). Carbonate nodules and extensive desiccation fractures in the basal unit indicate palaeosol development in an arid climate. The amalgamated nature of the coarse units suggests deposition in an area with low accommodation space.

Fine-grained facies are interpreted as floodplain, terminal splay and playa lake deposits. Periodic high-flow events generate unconfined, sheetwash flows that decelerate and deposit the sand-shale beds of the lower part of the unit in the proximal terminal splay (Hampton and Horton 2007; Sáez et al. 2007; Fisher et al. 2008). As flow continued more distally, the silts and clays were deposited via particle settling in the distal splay area. Nested cycles evident in outcrop are interpreted to represent lobe switching of the splay. Caliche soils formed in flood plain and at the fringe of the playa where subaerial exposure was greatest. Dolomite beds were deposits of the saline playa waters.

Palaeogeography Palaeocurrent data indicate sediment transport towards the northwest, from the Vindelician High towards the Germanic Basin, and not the Tethyan realm as postulated by others (e.g. Gisler et al. 2007). Our palaeogeographic reconstruction for the Emosson area is consistent with those previously developed for the nearby southwestern part of the Germanic Basin during the late Early-to early Middle Triassic (*cf.* Péron et al. 2005; Bourquin et al. 2006, 2009).

Footprint preservation

Generally, the footprints are poorly preserved and lack morphological details. They occur as negative epichnia (concave epirelief) on a sandstone bedding surface that shows some ripple marks as well as possible microbial mats. Only a few specimens show diagnostic features that allow a closer ichnotaxonomic assignment. In the Emosson material, the majority of footprints consists of oval to circular impressions in sandstone–siltstone, representing those of the pes and manus. Pes-manus couples often form an "hourglass-like" morphology, where the smaller circular manus is positioned anterior to the larger and elongated pes, sometimes being slightly overprinted by the latter at the posterior end (Figs. 5, 6). Partly, imprints show concentric structures and an outer sediment rim, superficially resembling the footprints of sauropodomorphs. Digit traces are sometimes visible at the anterior margin and in a posterolateral position, the latter obviously being the impression of digit V. Despite their indistinct shape, the marginal sediment displacement rim in an unlaminated sediment suggests the presence of true tracks, not

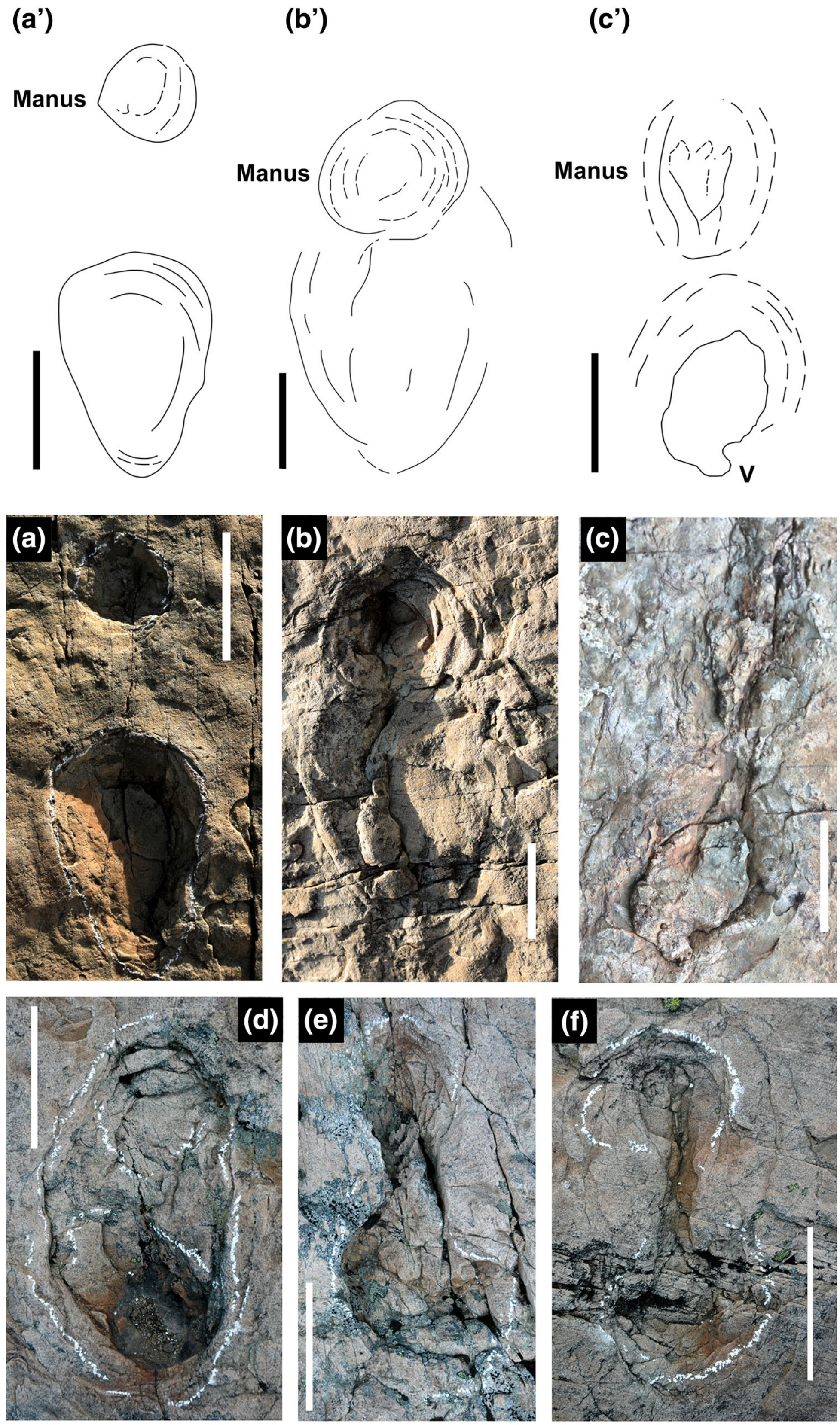

Fig. 5 Chirotheriid archosaur footprints from La Veudale N locality in typical preservation with "hourglass-like" shape, representing traces of the pes and the partly overprinted manus. **a**–**f** Photographs. **a'**–**c'** Outline drawings of the tracks in photographs **a**–**c**. **c**–**c'** is a possible pes-manus couple of *Chirotherium sickleri.* Note concentric deformation structures, marginal sediment displacement rim and remains of the infilling. *Scale bar* 10 cm

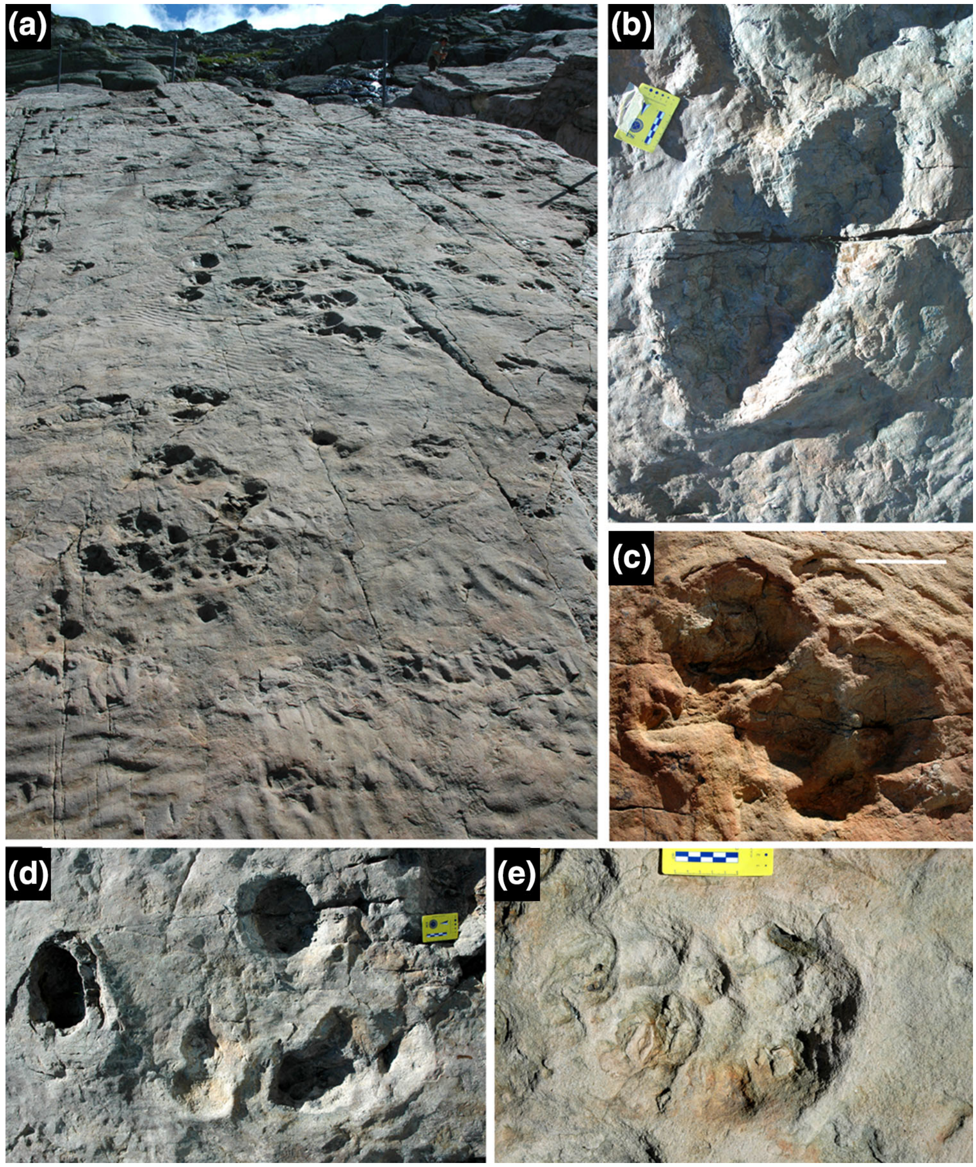

Fig. 6 **a–e** Photographs of chirotheriid archosaur footprints from classical Vieux Emosson locality (locality of Demathieu and Weidmann 1982) in typical preservation. Note "hourglass-like" (**b–d**) and "nodular" shape (**e**). *Scale bar* in **c**: 10 cm

undertracks. The natural mold (concave epirelief) footprints on the surfaces of the Emosson localities still show remnants of the infilling sediment.

The footprints on the surfaces of the Tödi locality in the eastern Swiss Alps occur in a dolomitic limestone and, therefore, are different in preservation compared with the Emosson tracks. Again they occur as negative epichnia. Numerous, very shallow imprints show distinct digit traces and their proportions. However, the whole surface is overprinted with glacial striations.

Some very few well-preserved footprints and trackways have been discovered in recent years on all these surfaces and allow a more distinct ichnotaxonomical assignment. The analysis is essentially based on these "elite tracks" and by comparison with the overall shape of other footprints on the trampled surface.

Systematic palaeontology

Ichnofamily Chirotheriidae Abel, 1935
Ichnogenus *Chirotherium* Kaup, 1835a
Type ichnospecies: *Chirotherium barthii* Kaup, 1835a
Chirotherium barthii Kaup, 1835a

2009 *Isochirotherium* sp.: Avanzini and Cavin, figs. 3, 4
2008 *Isochirotherium*, "Thecodont track": Feldmann and Furrer, fig. 9
2012 *Chirotherium* cf. *barthii*: Cavin et al., figs. 2c–d, 4, 5f

Diagnosis (emended after Peabody 1948; Haubold 1971a, b) Medium-sized to large chirotheriids, showing low trackway width, an average pace angulation of 170°, and relatively low stride length values. Manus more strongly turned outward than the pes (average

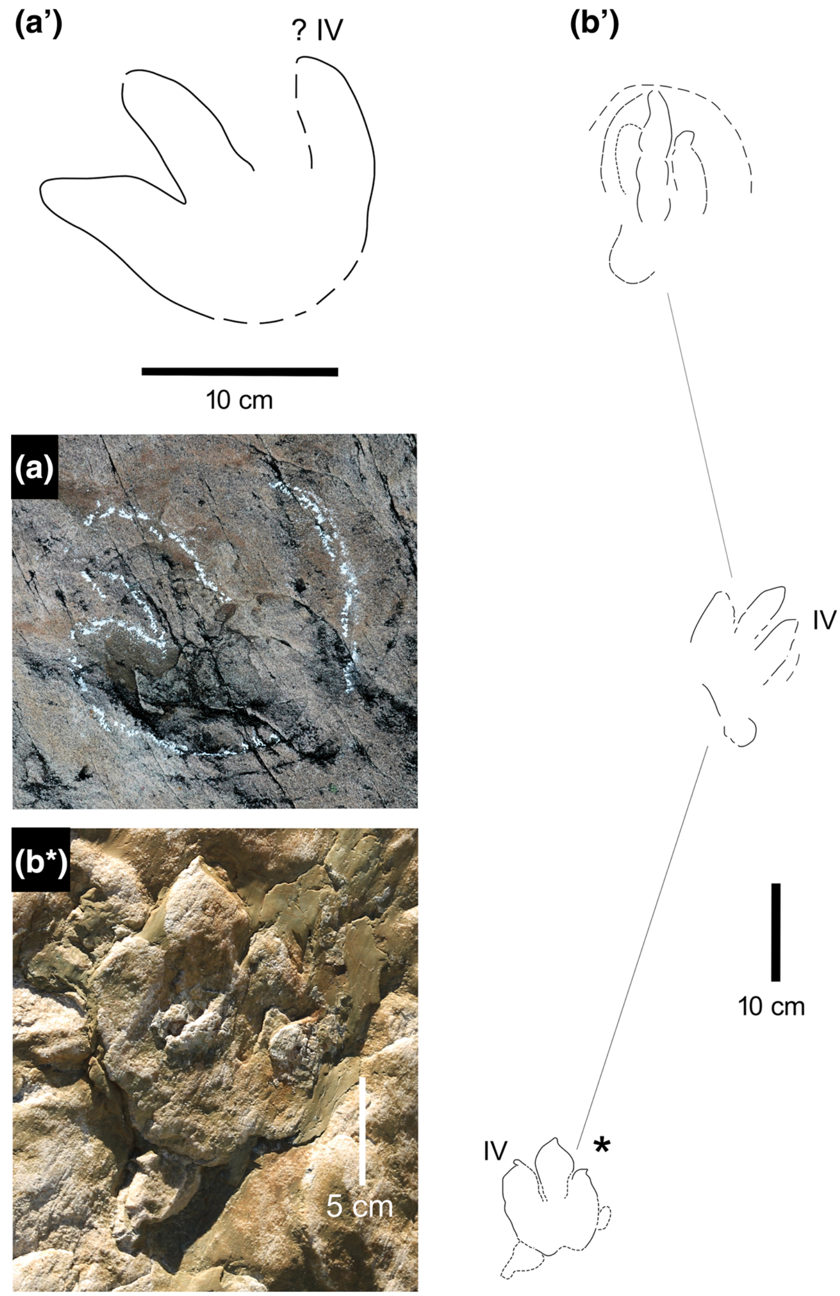

Fig. 7 Photographs (**a–b**) and outline drawings (**a'–b'**) of tridactyl-pentadactyl extramorphological variations of *Chirotherium barthii*. **a–a'** From La Veudale N locality, **b–b'** from Scex Blanc locality. *Asterisk* demarcates position of **b** in the trackway

25° and 9°, respectively). Pedal digit group I–IV relatively long and slender, with II–IV forming a symmetrical unit of which digit III is the longest. Digit I reduced, thinner than other digits and slightly posteriorly shifted. Proximal pads of digits I–IV form a posteriorly concave margin. Digit V with large circular basal pad positioned in line with digit IV, and with distinct, thin phalangeal portion that is strongly recurved. Manus with digit III longest, II and IV shorter and subequal to each other. Digits I and V short and occasionally absent. Digits IV and V laterally spread.

Material Isolated imprint from La Veudale N locality (Fig. 7a); trackway consisting of 3 consecutive pes imprints from Scex Blanc locality (Fig. 7b); trackway with 3 consecutive pes-manus sets and 1 pes from Vieux Emosson locality (Fig. 8a; Avanzini and Cavin 2009, fig. 3); partial trackway with 2 consecutive pes-manus sets from Cascade d'Emaney locality (Fig. 8b; Cavin et al. 2012, figs. 2d, 4, 5f); numerous isolated imprints from Obersand (Tödi, Glarus) locality (Figs. 9, 10). All specimens are left in the field.

Locality and horizon Vieux Emosson, Sex Blanc, La Veudale N and Cascade d'Emaney, Vieux Emossson

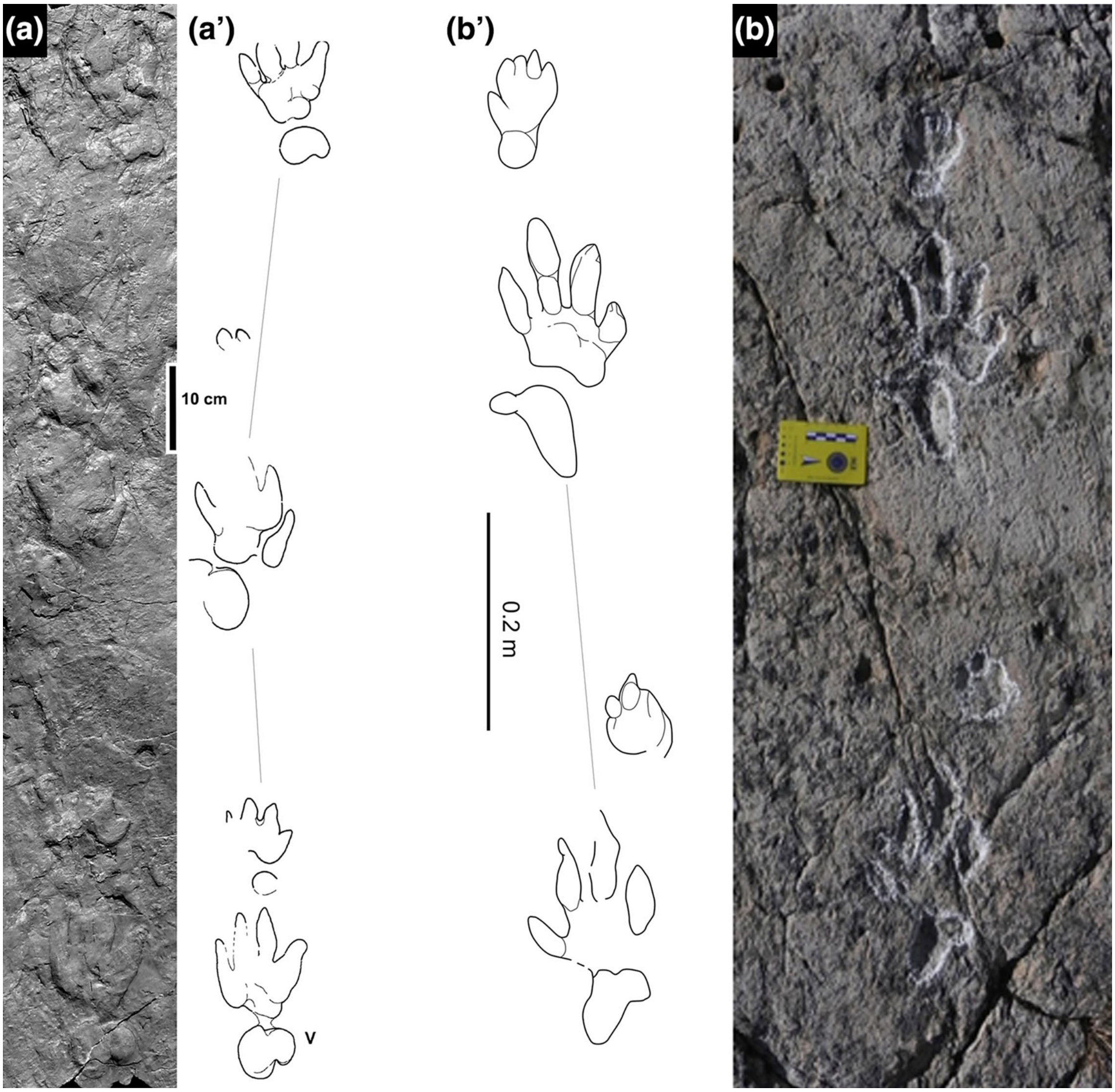

Fig. 8 Photographs (**a–b**) and corresponding outline drawings (**a'–b'**) of well-preserved *Chirotherium barthii* trackways. **a** from Vieux Emosson locality ("*Isochirotherium*" isp. after Avanzini and Cavin 2009). **b** from Cascade d'Emaney locality (*Chirotherium* cf. *C. barthii* after Cavin et al. 2012). Photographs and outline drawings from Avanzini and Cavin (2009) and Cavin et al. (2012)

Formation (Lower-Middle Triassic, Olenekian-Anisian); Obersand, Tödi (Glarus), Röti Dolomit (Middle Triassic, Anisian-Ladinian).

Description Tridactyl-pentadactyl pes and manus imprints. The pes shows a symmetrical digit group II–IV with digit III being longest. Digit I is shorter than digits II and IV and posteriorly shifted relative to digits II–IV. Digit V has a distinct circular to oval basal pad and a laterally spread or backward curved phalangeal portion that is separated from the former by a distinct constriction. If preserved, the manus is pentadactyl, rounded and relatively large; digit III is the longest; digit IV is relatively short. Trackways are narrow with a pace angulation reaching 142°–170° (Avanzini and Cavin 2009; Cavin et al. 2012). Pes with slight outward rotation (0°–16°), manus with stronger outward rotation (20°) relative to the midline than the pes. Two groups of pes size can be observed. The larger is about 20–25 cm, the smaller 14–17 cm in length (Table 3). Details such as impressions of phalangeal and metatarsophalangeal pads and claws are mostly indistinct due to the poor preservation.

A short trackway with three successive tridactyl to pentadactyl pes imprints (16 cm in length) from the Sex Blanc locality (Fig. 7b) lacks associated manus imprints due to the poor preservation, or alternatively, to complete overprinting by the pes. The pes imprints are symmetrical along digit III which is longest. Digit I is preserved with a short segment only in the first imprint of the trackway.

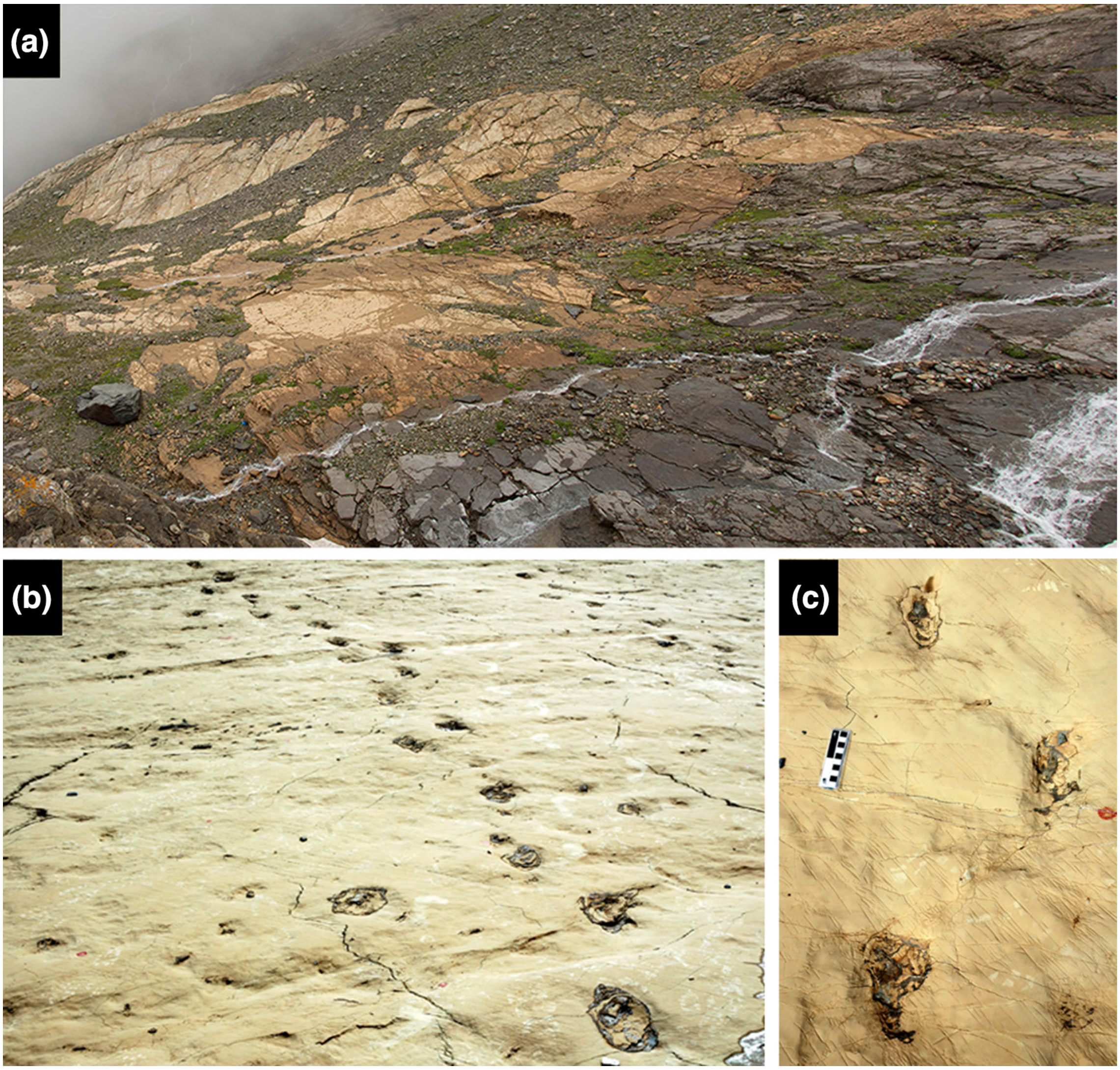

Fig. 9 Chirotheriid archosaur footprints at Obersand (Tödi, Glarus) locality in the eastern Swiss Alps preserved in dolomitic limestone. **a** Overview of tracksite. **b–c** Surface with pes and manus imprints. Ostensible "trackway" pattern is an effect of different overlapping and partly eroded trackways

Digit V is represented by a circular to oval pad posteromedially to the digit group II–IV. Digits vary in shape from elongate slender to short and broad rounded. Small triangular claw traces are visible in the first imprint of the trackway. Pes imprints are rotated outwards relative to the midline by 16° on average.

Pentadactyl chirotheriid pes imprints from the Obersand (Tödi, Glarus) locality (Figs. 9, 10) are about 15 and 25 cm in length and occasionally have an indistinctly preserved associated manus imprint. The pes imprints are slender, elongate and plantigrade to semiplantigrade. The preservation on a surface in dolomitic rock is poor, the digits being represented by elongated thin traces with accuminate distal ends and lacking distinct phalangeal pad impressions. Digit III appears to be the longest, digits II and IV are shorter and subequal in length, and digit I is shortest. Digit V consists of an oval basal pad that is occasionally elongated into a "heel" and a thinner, distal phalangeal portion that is largely everted or backward curved. A striking preservational feature is the presence of extensive v- or u-shaped interdigital hypeces.

Discussion Only a few tracks and trackways from the surfaces of the Vieux Emosson Formation and Röti Dolomite allow an ichnotaxonomic assignment more precise than "Chirotheriidae indet". Cavin et al. (2012, figs. 2c–d, 4; Fig. 8b) described a trackway segment from the Cascade d'Emaney locality that they tentatively assigned to *Chirotherium* cf. *barthii*. The overall shape of the pes imprints with the symmetrical digit group II–IV, the relatively short digit I and the backward curved digit V match the

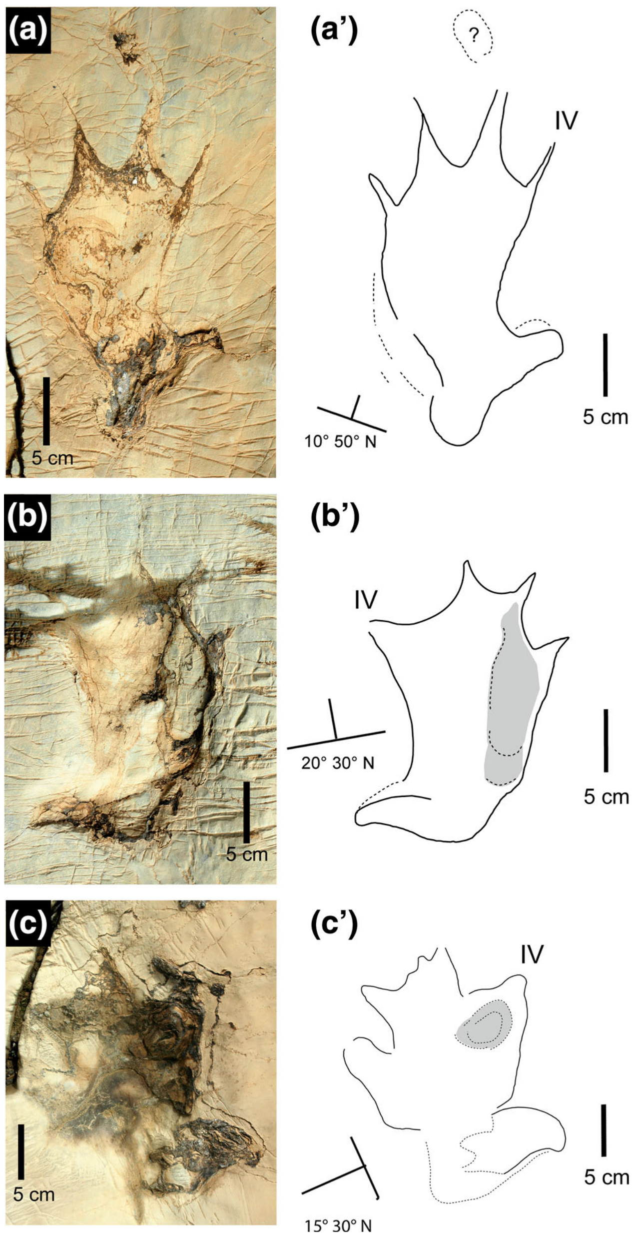

Fig. 10 Photographs (**a–c**) and outline drawings (**a'–c'**) of *Chirotherium barthii* pes and ?manus imprints from the Obersand (Tödi, Glarus) locality of the eastern Swiss Alps. Outline drawings with demarcated orientation in the field. Note that the track preservation on a surface in dolomitic rock is poor, the digits being represented by elongated thin traces with accuminate distal ends and lacking distinct phalangeal pad impressions

morphology of typical *Chirotherium barthii* as described from the type locality in the Solling Formation (Middle Buntsandstein) of Hildburghausen, Germany (Soergel 1925; Haubold 1971a, b, 2006; Fig. 12a). A chirotheriid ichnotaxon similar to *C. barthii* in morphology is *Isochirotherium soergeli* (Haubold 1971a, fig. 20; Fig. 12j). However, the latter shows a smaller manus imprint relative to the pes imprint (1:6.5 vs. 1:3 in *C. barthii*; Haubold 1971a). In the specimen from Cascade d'Emaney, this ratio is 1:3 as in typical *C. barthii*. Also, in *I. soergeli* digit IV is subequal with digit I whereas in the Cascade d'Emaney specimen digit I is distinctly shorter than digit IV. Because of the strong morphological congruence with *C. barthii*, the latter is assigned here to *Chirotherium barthii*.

Avanzini and Cavin (2009, figs. 3, 4; Fig. 8a) describe a trackway from a loose block near the Vieux Emosson locality that they assign to *Isochirotherium* sp. This material is re-assigned here to *Chirotherium barthii* and differentiated from *Isochirotherium* based on the following features: (1) narrow trackway with orientation of pes imprints nearly parallel to the trackway midline, whereas in *Isochirotherium*, the pes imprints are strongly outward rotated, about 22° on average in *Isochirotherium soergeli* (Haubold 1971a); (2) relative large manus showing a manus: pes ratio of 1:3, whereas in *I. soergeli* this ratio is 1:6.5 (Haubold, 1971a). The "*Isochirotherium*-like" relatively short digit IV in the interpretive drawing of Avanzini and Cavin (2009) may reflect poor preservation.

The short trackway consisting of three successive pes imprints from the Scex Blanc locality (Fig. 7b) is assigned here to *Chirotherium barthii* based on the symmetrical digit group II–IV with digit III being longest, which is different from the proportions seen in *C. sickleri* (see below) where digit IV is distinctly longer than digit II.

The footprints from the surface at the Obersand (Tödi, Glarus) locality were described as "Thecodont" or "*Chirotherium*" tracks and compared with *Isochirotherium* by Feldmann and Furrer (2008). However, the symmetrical digit group II–IV, and the short, posteriorly shifted digit I suggest an assignment to *Chirotherium barthii*. Trackway interpretations by Feldmann and Furrer (2008) could not be confirmed when we re-investigated the tracksite in summer 2014. Obviously, interpretative trackway drawings of these authors are based on different parallel and overlapping trackways that were partly eroded, thus obscuring their true pattern. Some step length values given by Feldmann and Furrer (2008) are twice as large as those known from the global record of chirotheriids. This suggests that in their trackway map, some imprints are missing.

?*Chirotherium sickleri* Kaup 1835b

Diagnosis (emended after Haubold 1971a, b), Trackway narrow with long strides, pace angulation 160°, pes with stronger outward rotation than the manus (average 21° and 10°, respectively). Digit IV in the pes slightly shorter than III but much longer than II. Digit I thin and short but with minor posterior shift compared with *C. barthii*. Digit V with slender recurved phalangeal portion and slightly enlarged basal pad. Manus with digit IV being proportionately longer than in *C. barthii*.

Material A pes manus couple from La Veudale N locality (Fig. 5c).

Locality and horizon Emosson, La Veudale N locality, Vieux Emosson Formation (Olenekian-Anisian).

Description Relatively slender pentadactyl pes imprint that has a length of 13.3 cm and a width of 9 cm (measured along the preserved trackfilling as a proxy of the true shape). Digit III appears to be longest, and digit V is strongly everted. A second imprint that is associated with, is more rounded in shape and has a length of 10.3 cm and a width of 9.3 cm (Table 3). The pes outward rotation is higher than the manus outward rotation relative to the (imaginary) trackway midline, the difference being about 25°.

Discussion The overall shape of the pes resembles that of the ichnogenus *Chirotherium* (compare Fig. 12a–g). If the specimen really is a related pes-manus couple, then the relative position of the pes and the stronger outward rotation compared with the manus suggests an assignment to the ichnospecies *C. sickleri* that is common, for example in the Buntsandstein of the Germanic Basin, co-occurring with *C. barthii* on the same surfaces.

Compared with *C. sickleri*, *C. barthii* shows a stronger outward rotation of the manus relative to the pes (average 25° and 9°, respectively), whereas in the former, the pes is more strongly outward rotated (average 10° and 21°, respectively) (Haubold 1971a). Even if absolute size of footprints is not relevant for their ichnotaxonomic assignment, the co-occurence of small-sized *Chirotherium* with large ones on the same surface points to a typical Buntsandstein assemblage with *C. barthii* and *C. sickleri*. Both ichnospecies could also be reflected in the different-sized *Chirotherium* footprints on the surfaces of the Obersand (Tödi, Glarus) locality (see above). However, this is mere speculation, and the poor preservation does not allow a concrete determination. Therefore, we consider this assignment questionable.

Ichnogenus *Isochirotherium* Haubold 1971
Isochirotherium herculis (Egerton 1838)

1982 *Isochirotherium* sp.: Demathieu and Weidmann, figs. 3b, 7b
2009 "possible *Isochirotherium* sp.": Avanzini and Cavin, fig. 7a
2009 *Isochirotherium* sp.: Avanzini and Cavin, fig. 7b

Diagnosis (after Haubold 1971a) Largest known chirotheriids, pes length >30 cm; pace angulation 140°–160°; ratio stride : pes length = 4.5 : 1; larger outward rotation of manus traces relative to pes traces (average 41° and 30°, respectively); digit II ín the pes mostly as long as digit III, occasionally longer than digit III; digit divarication I–IV more than 50°; cross axis angle 80°; digit group I–IV wider than long and coalesced with digit V; manus mostly preserved with digits I–IV only.

Material Large pes imprint from La Veudale N locality (Fig. 11b). A large second specimen of similar overall shape, possibly of same assignment (Fig. 11a).

Locality and horizon Emosson, La Veudale N locality, Vieux Emosson Formation (Lower-Middle Triassic, Olenekian-Anisian).

Description Broad plantigrade pes imprints with wide short digits. Imprints show pes lengths of 26.4 and 22.0 cm and pes widths of 16.8 and 20.2 cm, respectively (Table 3). Digit V is posterolaterally positioned and represented by a massive oval basal pad. Digit proportions with digits II and III being longest and subequal in length or digit III being slightly longer. Digits I and IV are shorter and subequal in length. Digits II–V show broad rounded distal ends, whereas digit I shows a blunt claw trace.

Discussion Digit proportions of the Emosson tracks with the dominance of digits II and III and the shorter digits I and IV match the diagnostic features of *Isochirotherium.* From other chirotheriids, it is different by (1) the relatively longer digit I (*Chirotherium*, *Brachychirotherium*) and (2) the shorter digit IV (*Protochirotherium*, *Synaptichnium*). The broad sole surface and robust digits are similar to *Isochirotherium herculis* Egerton 1838. It is well known from the Middle Triassic of Great Britain and from the Germanic Basin. In particular, the Solling Formation (Middle Buntsandstein, Early Anisian) from Thuringia (Germany) has yielded well-preserved material (Haubold 1971a, b; Puff and Klein 2011; Fig. 12h). Therefore, we assign these footprints from the Vieux Emosson Formation to *Isochirotherium herculis*.

Chirotheriidae cf. *Isochirotherium* isp.

Material Partial trackway with two successive pes imprints (Fig. 11c).

Locality and horizon Vieux Emosson locality, Vieux Emosson Formation (Early-Middle Triassic, Olenekian-Anisian).

Description A single step with strongly outward rotated (estimated >20°) pes imprints showing a length of 24.1 cm and a width of 19.2 cm. The pace length is 64 cm (Table 3). The imprints show a compact anterior digit group with indistinctly preserved short digits of subequal lengths. Digit V is posterolaterally positioned and preserved with an oval basal pad that is strongly everted.

Discussion The poor preservation does not allow a concrete ichnotaxonomic assignment. Especially the digit proportions are indistinct. However, the strong outward rotation of the pes imprints is characteristic for *Isochirotherium.* The pes in

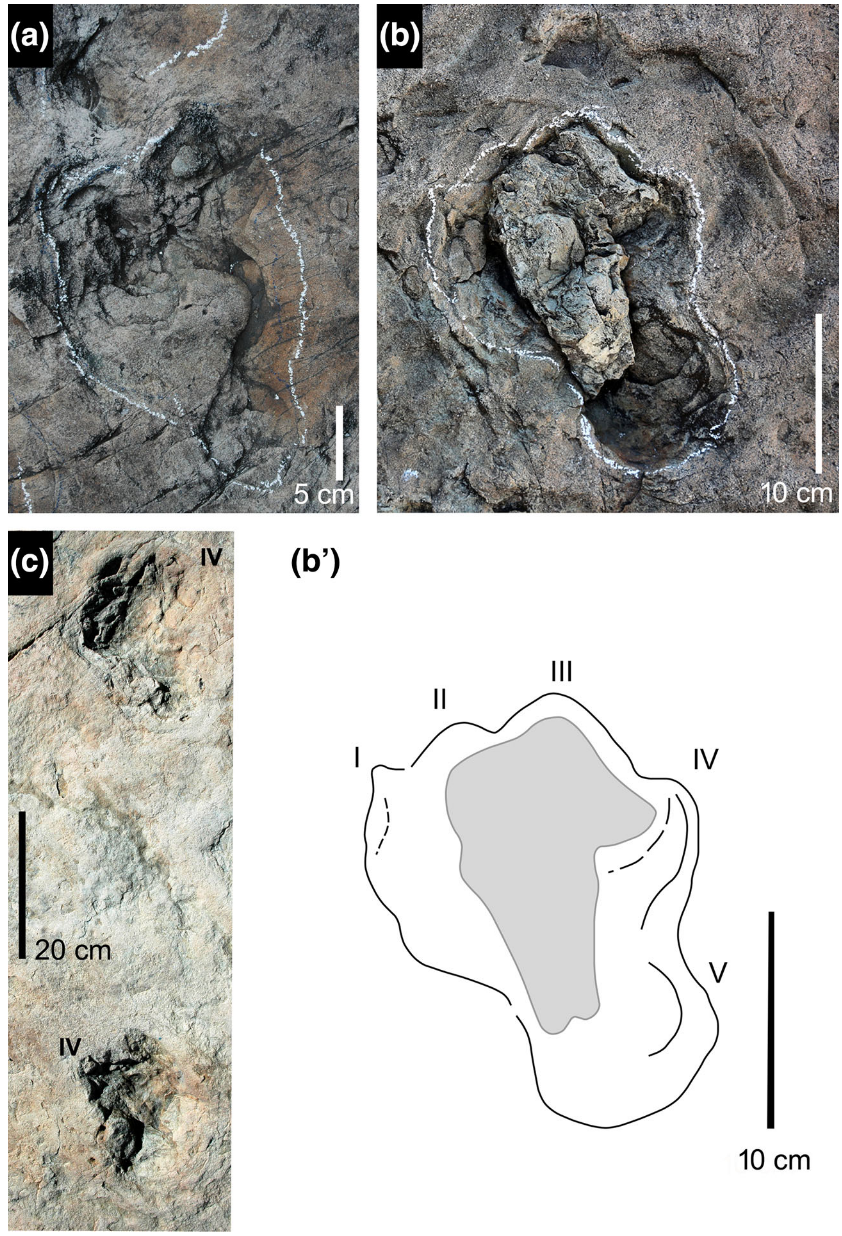

Fig. 11 *Isochirotherium* footprints from surfaces of the Emosson region. **a** Possible *I. herculis* pes imprint. **b** *I. herculis* pes imprint with posterolaterally positioned impression of digit V, as photograph (**b**) and outline drawing (**b'**). **c** cf. *Isochirotherium* isp. partial trackway with two successive pes imprints. Note pronounced pes outward rotation in **c**

the type ichnospecies *Isochirotherium soergeli* has an average outward rotation of 22° (Haubold 1971a). Strong outward rotation of pes imprints is also seen in *Synaptichnium*; however, even in poor preservation, the latter would exhibit a distinct ectaxonic shape, and the tracks from Vieux Emosson lack this feature. Therefore, we tentatively assign these footprints to cf. *Isochirotherium* isp.

Chirotheriidae indet.
1982 *Paratrisauropus latus* n. sp.: Demathieu and Weidmann, figs. 5, 8a, 9, 13A
1982 *Brachychirotherium* sp.: Demathieu and Weidmann, figs. 6a, 7a
1982 *Paratrisauropus mirus* n. sp.: Demathieu and Weidmann, figs. 6c, 7c
1982 *Paratrisauropus bronneri* n. sp.: Demathieu and Weidmann, fig. 7d, 8b
1982 *Prototrisauropus* sp.: Demathieu and Weidmann, fig. 11
1982 *Deuterosauropodopus sedunensis* n. sp.: Demathieu and Weidmann, figs. 13B, 14A
1982 *Pachysaurichnium emossonense* n. g. n. sp.: Demathieu and Weidmann, figs. 13C, 14B
1982 *Bifidichnium ambiguum* n. gen. n. sp.: Demathieu and Weidmann, figs. 13D, 14C
2009 *Paratrisauropus latus*: Avanzini and Cavin, fig. 5a
2009 *Paratrisauropus bronneri*: Avanzini and Cavin, fig. 5b
2009 *Paratrisauropus mirus*: Avanzini and Cavin, fig. 5c

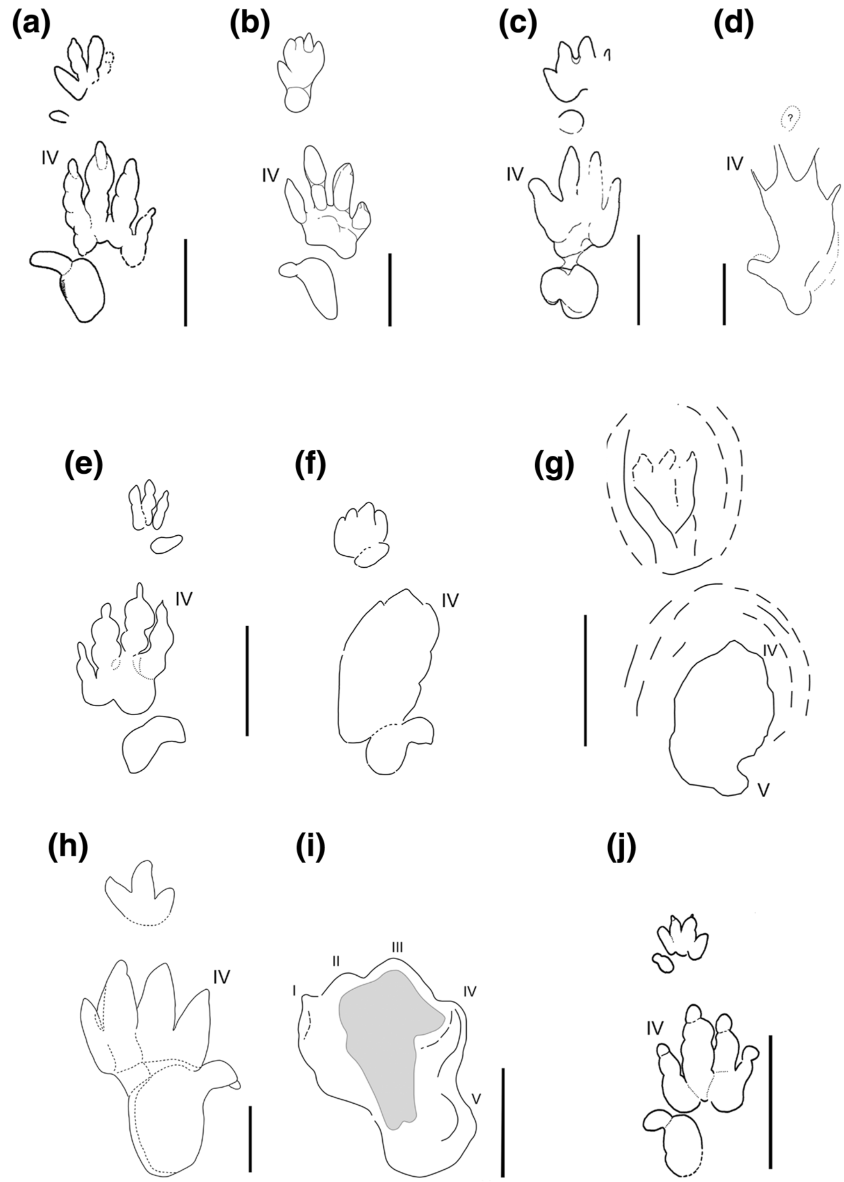

Fig. 12 Comparison of chirotheriid footprints from the Swiss Alps with similar morphotypes and ichnotaxa from the Solling Formation (Buntsandstein, Early Anisian) of the Germanic Basin. **a** *Chirotherium barthii* from type locality Hildburghausen, Germany. **b–c** *C. barthii* from Cascade d'Emaney (b) and Vieux Emosson (c) localities. **d** *C. barthii* pes and possible manus imprint from Obersand (Tödi, Glarus) locality. **e–f** *Chirotherium sickleri* from type locality Hildburghausen, Germany. **g** Possible *C. sickleri* pes-manus set from La Veudale N locality. **h** *Isochirotherium herculis* from Buntsandstein of Germany. **i.** *I. herculis* pes imprint from La Veudale N locality. **j** *I. soergeli* from Buntsandstein of Germany. **a**, **e**, **f**, **h**, **j** from Haubold (1971a); **b** from Cavin et al. (2012); **c** from Avanzini and Cavin (2009). *Scale bar* 10 cm

2009 *Deuterosauropus sedunensis* ("chirotheroid track"): Avanzini and Cavin, fig. 6
2012 "*Deuterosauropodopus*", "*Prototrisauropus*" "*Pachysaurichnium*", "*Paratrisauropus*" ("chirotheriid footprints"): Cavin et al., fig. 5a–e

Material More than 1500 pes and manus imprints of oval to circular shape (Figs. 5a–b, d–f, 6)
Locality and horizon La Veudale N, Vieux Emosson, Col de Corbeaux 1 and 2, Vieux Emosson Formation. Le Châtelet (Lower-Middle Triassic, Olenekian-Anisian).
Description Imprints (up to 39 cm in length) that mostly lack distinct digit impressions (Table 3). They show concentric sediment rims, slightly resembling the tracks of sauropodomorphs from the Jurassic-Cretaceous. Two morphotypes can be distinguished:

Morphotype A. Elongate-oval pes imprints and associated circular manus imprints in a distance of some centimetres anterior to the former (Fig. 5a).

Morphotype B. Hourglass-like shaped imprints (Fig. 5b, d–f).
Discussion Whereas Morphotype A clearly represents pes-manus couples, this seems to be not distinct for Morphotype B. Here, the smaller circular impression may represent the posteriorly overstepped manus or, alternatively in some cases, the impression of pedal digit V/"heel".

Ichnostratigraphy and age constraints

Generally, tetrapod footprints are useful for biostratigraphy, especially in units where body fossils are missing such as the track-bearing strata described here (Lucas 2007;

Klein and Haubold 2007; Klein and Lucas 2010a). An issue, however, is the poor preservation of the Triassic chirotheriid tracks of the Swiss Alps and related ichnotaxonomical problems. Not least because of their interpretation of ichnotaxa and the purported dinosaur origin of some of these, Demathieu and Weidmann (1982) considered the footprint-bearing strata of the Emosson region as Ladinian–Carnian in age. In recent years, however, new discoveries of footprints that have been assigned to the ichnogenera *Isochirotherium* and *Chirotherium* (Avanzini and Cavin 2009; Cavin et al. 2012) raised doubt about this age assignment.

As shown above, especially the Emosson tetrapod ichnofauna is similar to characteristic assemblages of the Buntsandstein from the Germanic Basin. *Chirotherium barthii* is a globally distributed ichnotaxon demarcating the *Chirotherium barthii* biochron of Klein and Lucas (2010a) that principally can be cross correlated with the Anisian, and the Perovkan landvertebrate Faunachron (LVF) of Lucas (1998, 2010). The first appearance datum of *C. barthii* (FAD) is the Olenekian-Anisian boundary. It is known from numerous localities in Germany (Haubold 1971a, b, 2006), France (Demathieu 1970), Great Britain (King et al. 2005), Spain (Gand et al. 2010; Fortuny et al. 2011; Díaz-Martínez et al. 2015; Díaz-Martínez and Pérez-García 2012) and Italy (Avanzini and Mietto 2008; Avanzini and Wachtler 2012). Furthermore, the ichnotaxon is known from North America (Peabody 1948; Klein and Lucas 2010b), South America (Melchor and De Valais 2006), North Africa (Morocco) (Klein et al. 2011) and China (Xing et al. 2013).

Isochirotherium is a characteristic Middle Triassic (Anisian-Ladinian) ichnotaxon and present in the Germanic Buntsandstein (Anisian). The ichnospecies *Isochirotherium herculis* is known from deposits of Great Britain (Olenekian-Anisian) (King et al. 2005; Clark and Corrance 2009), from Germany (Buntsandstein, Anisian) (Haubold 1971a, b; Diedrich 2009, 2015; Puff and Klein 2011) and possibly from North America (Moenkopi Group) (Klein and Lucas 2010b).

The possible occurrence of *C. sickleri* in the Emosson assemblage would match other "Buntsandstein ichnoassemblages" perfectly. However, the presence of this ichnotaxon cannot be proven without any doubts.

The assemblage from the Röti Dolomit (Obersand, Glarus) locality with *Chirotherium barthii* indicates a Middle Triassic (probably Anisian) age of the track-bearing strata, as has been suggested earlier by Feldmann and Furrer (2008).

Megatracksite and section correlation

The majority of trackways are located at the top of the basal conglomerate–sandstone facies association (and the others are located within a metre stratigraphically above this surface). Using the track level as a stratigraphic marker bed indicates that there are several metres of palaeorelief over the study area.

Most of the outcrops show one track level, five of them display two or three different track levels within the basal facies association. 18 outcrops have been examined and all reveal the presence of single footprints or trackways (Table 2). From the easternmost site at Les Geueles (VS, Fully) to the most southwestern site in adjacent France (Le Châtelet), the tracksites cover a distance of more than 28 km in the same stratigraphic position. This suggests that all sites form part of a megatracksite. The latter were defined as regionally extensive vertebrate track-bearing units associated with single surfaces, single beds, or thin stratigraphic complexes (Lockley 1989, 1991; Lockley and Pittmann 1989; Pittman 1989).

This is (possibly) one of the few examples of a "terrestrial megatracksite" not related with a "coastal plain system" (not influenced by the dynamics of sea-level change). Diedrich (2009, 2015) suggested a megatracksite with chirotheriid and small lacertoid tracks in marginal marine (tidal flat) Muschelkalk deposits of the Germanic Basin.

Continental and coastal plain environments can be characterized by different archetypal tetrapod ichnofacies (Hunt and Lucas 2007). The studied sections contain no invertebrate ichnofossils at all; therefore, we attribute the sites to the *Batrachichnus* ichnofacies sensu Hunt and Lucas (2007). The latter is characterized by the dominance of trackways of quadrupedal carnivores with a moderate ichnodiversity. More specifically, we attribute the studied tracksites to the *Chirotherium* ichnocoenosis, which is typical of distal alluvial fans and fluvial plains from the Devonian to the Triassic (Buatois and Mángano 2011).

Conclusions

Triassic tetrapod footprints known thus far from the Vieux Emosson Formation of southwestern Switzerland and from the Röti Dolomite of the eastern Swiss Alps are, without exception, members of the chirotheriid family and assigned to the ichnotaxa *Chirotherium barthii*, ?*C. sickleri*, *Isochirotherium herculis*, cf. *Isochirotherium* isp. and indeterminate forms. Purported tridactyl dinosaurian morphotypes are incomplete extramorphological variations.

Twelve additional tracksites were discovered, including one with more than 1500 footprints; a lithologic correlation of seven of the sites suggests that the trackways compose a terrestrial megatracksite.

In the Vieux Emosson Formation, deposition of conglomerate and sandstone facies took place in shallow bedload-dominated streams, not in marine environments as was proposed earlier. Fine-grained facies are interpreted as floodplain, terminal splay, and playa lake deposits. The northwestern palaeoslope supports drainage of the region into the Germanic Basin, and not the Tethyan realm as postulated by others. Further, the Vieux Emosson Formation in southwestern Switzerland is equivalent in age and facies to the Buntsandstein facies. This is supported by a footprint assemblage that represents a characteristic Buntsandstein ichnofauna that biostratigraphically can be assigned to the *Chirotherium barthii* biochron (Anisian). The occurrence of this ichnospecies suggests a similar age also for the assemblage from the Röti Dolomite at Obersand in eastern Switzerland.

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