



A Several-Kilometer-Long Archosaur Route in the Triassic of the Swiss Alps

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The Mesozoic sedimentary cover of the Aiguilles Rouges Massif straddling the Swiss-French border has yielded several archosaur footprint sites dated to the Early or Middle Triassic and composed of mostly poorly preserved footprints lacking any orderly arrangement and resting on a megatracksite level. Here we describe two short archosaur trackways attributed to *Isochirotherium herculis* and located at ca. 2400 m asl in two distinct small valleys separated from each other by a linear distance of 6.4 km. Projection of both trackways onto the same plane showed that they were aligned with a deviation angle of only 3°. These aligned trackways are interpreted as remnants of a straight and narrow walking route taken by a single trackmaker species. It is possible that both trackway segments were made by the same individual. In the present landscape, the Triassic outcrops are small and scattered along a roughly straight NE-SW line. The orientation of the trackways agrees with the general orientation of the outcrops, which is very unlikely to be caused by chance only. We explain this apparent coincidence as resulting from the structural inheritance of a general NE-SW Paleozoic shear zone that controlled the orientation of the Vindelician High on which the archosaurs walked, then that defined the axis of the much later Massif uplift, and eventually affected the general orientation of the erosion that uncovered the trackways.

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INTRODUCTION

The last phase of the Alpine orogeny in the Western Alps was marked by the uplift of several massifs made of pre-Mesozoic crystalline basement, together with their Early Mesozoic sedimentary covers. The Aiguilles Rouges Massif was uplifted during the late Miocene (e.g., Valla et al., 2012). Its autochthonous Triassic cover, which crops out in several spots above the basement and under the thrust sheet “Nappe de Morcles,” is called the Vieux Emosson Formation. It consists of a basal unit composed of conglomerates and sandstones, and an upper unit composed of sandstones and mudstones, with thin dolomite beds near the top. Facies analyses indicate deposition in a continental fluvial lacustrine system, with the lower unit interpreted as having been deposited in braided streams and the upper unit as mainly representing deposition in a terminal splay – playa environment (Wizevich et al., 2019a). The sandstones have yielded assemblages of archosaur footprints scattered along a 28 km long and circa 100 m wide irregular band of sediments oriented NE-SW (Demathieu and Weidmann, 1982; Avanzini and Cavin, 2009; Cavin et al., 2012;

Klein et al., 2016; Wizevich et al., 2019a,b; **Figure 1**). Most of these sites consist of trampled surfaces forming a single large megatracksite (Meyer and Thüring, 2003; Klein et al., 2016).

Footprints are abundant but generally poorly preserved and lacking morphological details. Their original impression in wet and soft sediment, and the effects of recent erosion, make it difficult to identify the footprints taxonomically and to recognize trackways [scored 1 and 2 on the preservation scale of Marchetti et al. (2019)]. Only a few footprints show diagnostic features that allow ichnotaxonomic assignment (see Avanzini and Cavin, 2009; Cavin et al., 2012; Klein et al., 2016). In most places, the majority of footprints consist of oval to circular concave epirelief features on a sandstone bedding surface often showing ripple marks. The presence of outer rims in some cases suggests that footprints represent true tracks rather than undertracks.

Nine ichnotaxa including several dinosaurs were initially recognized in the ichnoassemblage (Demathieu and Weidmann, 1982), but recent reinterpretations (Klein et al., 2016) restricted the assemblage to chirotheriids (*Chirotherium barthii*, *Chirotherium sickleri*, *Isochirotherium herculis*, *Isochirotherium* sp.). The assemblage is characteristic of the Early Middle Triassic (Olenekian-Anisian) (Avanzini and Cavin, 2009; Klein et al., 2016). Because of the warm summers of recent decades, formerly

long-lasting snow fields have melted and two short trackways have been discovered near two previously studied sites separated by 6.4 km in a straight line. Both trackways are preserved at a level situated slightly below the main megatracksite (**Figures 1, 2**).

MATERIALS AND METHODS

Material

Cascade d'Emaney: The new trackway [Bar 4 (“Bar” corresponds to “Barberine,” the name of the mountain pass nearby)] was found in 2012 near the Cascade d'Emaney ichnosite of Cavin et al. (2012) (coordinates: N46°06'26.900''; E6°56'19.800'') (**Figure 1**). It is located about 8 m to the east of a couple of subparallel tracks assigned to an indeterminate chirotheriid, and consists of four preserved pes imprints that belong to a trackway that probably originally contained seven steps judging from the interpreted stride length (**Figure 2A**). Bar 4 is 10 m in total length and is precisely aligned with a pair of footprints (Bar 7) located 18 m toward the NE. The good alignment between Bar 4 and Bar 7, and the similarity in the length/width parameters of the pes imprints in both cases (**Table 1**), suggests that all six preserved pes imprints are remnants of a single, substantially longer trackway.

Bas Veudale: A new trackway named Bas Veudale was found in September 2015 by LC circa 20 m to the NNW (coordinates: N46°03'36''; E6°53'34'') (**Figure 1**) of a site previously studied by Klein et al. (2016) and called here Haut Veudale. The trackway (**Figure 2B**) is 4.6 m long and contains four pes and a single faint and uncertain manus imprint. The pace angulation characteristics are summed up in **Table 1**.

Methods

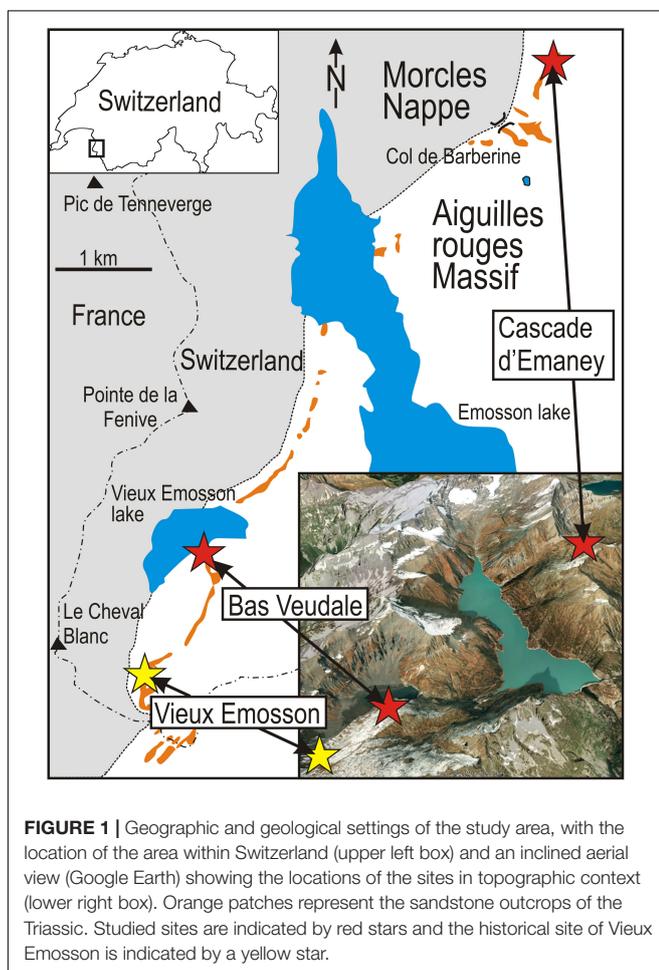
The trackway direction on the bedding plane was measured by plotting a horizontal line through the footprints (**Figure 3A**). The geometry of the study area is illustrated in **Figure 3B**. For both trackway-bearing surfaces, the dip magnitude, dip direction and trackway direction were all measured. The uniformity of dip throughout the study area (e.g., Amberger, 1960) allows the orientations of both trackways to be compared in the present plane of dip.

The new trackways were mapped by tracing the outlines of the footprints on acetate sheets, and a 3D photogrammetric reconstruction of the Bas Veudale trackway was produced. Because of the poor preservation of the footprints, we were not able to apply the standard protocol recently proposed for fossil ichnological studies (Falkingham et al., 2018). Comparisons between important parameters for the new trackways from both sites were done using Mann–Whitney tests for each parameter known from more than four measurements.

RESULTS

Stratigraphy

Klein et al. (2016) pointed out that most of the sites located along a 28 km transect in the Triassic cover of the Aiguilles Rouges Massif correspond to a single terrestrial megatracksite composed



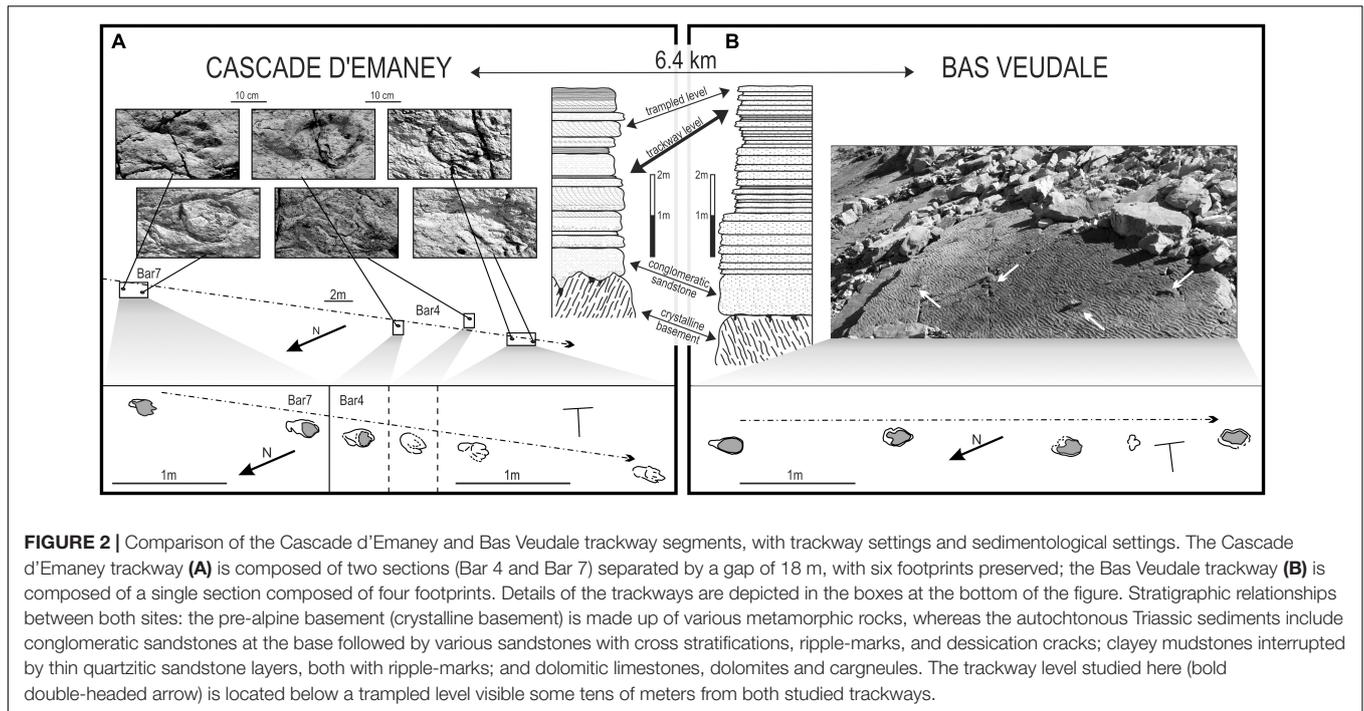


FIGURE 2 | Comparison of the Cascade d'Emaney and Bas Veudale trackway segments, with trackway settings and sedimentological settings. The Cascade d'Emaney trackway (**A**) is composed of two sections (Bar 4 and Bar 7) separated by a gap of 18 m, with six footprints preserved; the Bas Veudale trackway (**B**) is composed of a single section composed of four footprints. Details of the trackways are depicted in the boxes at the bottom of the figure. Stratigraphic relationships between both sites: the pre-alpine basement (crystalline basement) is made up of various metamorphic rocks, whereas the autochthonous Triassic sediments include conglomeratic sandstones at the base followed by various sandstones with cross stratifications, ripple-marks, and dessication cracks; clayey mudstones interrupted by thin quartzitic sandstone layers, both with ripple-marks; and dolomitic limestones, dolomites and cargneules. The trackway level studied here (bold double-headed arrow) is located below a trampled level visible some tens of meters from both studied trackways.

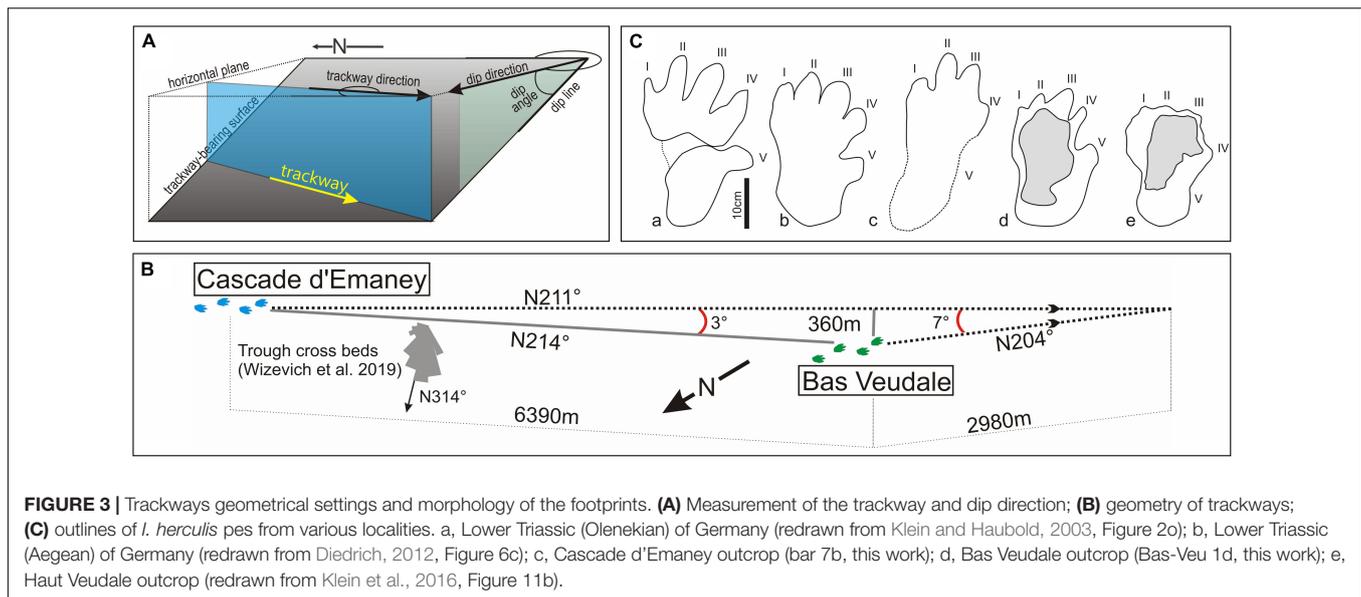
TABLE 1 | Measurements (in centimeters) of *Isochirotherium herculis* footprints from three Triassic localities in SW Switzerland.

Locality	Trackways	Dip	Orientation	Footprints	PL	PW	ML	MW	OP	PA			
Cascade d'Emaney, 2242 masl	Bar 4	52° N290°	N211°	Bar 4a	28	11.5	–	–	150	–			
				Bar 4b	26.5	15	–	–	–	–			
				Bar 4c	23	15	–	–	–	–			
				Bar 4d	28	16	–	–	–	–			
	Bar 7			Bar 7a	28	14.5	–	–	–	137	–		
				Bar 7b	23.5	14	–	–	–	–	–		
				Bar 4 + 7			Bar 4 mean	26.38	14.38	–	–	–	–
							Bar 7 mean	25.75	14.25	–	–	–	–
				Bar 4 + 7 mean	26.17	14.33	–	–	143.5	–			
Bas Veudale, 2250 masl	Bas-Veu 1	48° N286°	N204°	Bas-Veu 1a	29	14.5	–	–	147	–			
				Bas-Veu 1b	25	16	–	–	145	174°			
				Bas-Veu 1c	26	17	10	13	143	174°			
				Bas-Veu 1d	28	16.5	–	–	–	–			
	Bas-Veu 1 mean			27	16	–	–	145	174°				
Haut Veudale, 2304 masl	Haut-Veu 1			Haut-Veu 1	26.4	16.8	–	–	–	–			
				Haut-Veu 1	22	20.2	–	–	–	–			

Data for the Haut Veudale footprints is from Klein et al. (2016). PL, pes length; PW, pes width; ML, manus length; MW, manus width; OP, oblique pace; PA, pace angulation.

mainly of trampled areas of poorly preserved chirotheriid footprints. They noticed that most of the 18 outcrops they examined contained a single footprint level at the top of the basal sandstone conglomerate unit, although five of them contained two or three distinct track levels located 1 m or less above the top of the basal sandstone (Klein et al., 2016; Wizevich et al., 2019a). The new Bas Veudale track is probably situated some tens of centimeters below the Haut Veudale trampled level, although faults, and falling rocks make it impossible to observe the precise stratigraphic relationship between these two

surfaces (Figure 2). We consider this lower level to correspond to the track-bearing level at the Cascade d'Emaney site for the following reasons: (1) The trampled level is situated a few decimeters above the newly identified track-bearing level in both cases; (2) readily identifiable tracks occur at both sites, but are absent on the trampled level and elsewhere in the section; and (3) *C. herculis* tracks from both sites are characterized by similar parameters. The new trackways thus indicate the presence of a track-bearing layer located under the previously recognized megatracksite, and extending over several square



kilometers. This new level is still poorly documented because it is located within the sandstone series, making it less prone to exposure by erosion.

Trackways

Morphometric parameters for the new trackways and for each footprint are given in **Table 1**, and a photogrammetric rendering of the Bas Veudal trackway is presented in **Supplementary Information (Supplementary Video S1)**. The distance between the two trackways is 6.4 km and a straight line between the two outcrops is oriented at 214° from the north (**Figure 3B**). Trigonometric calculations indicate that a deviation of 3° of the direction of the Emaney trackway would cause this trackway, if it continued for a distance of 6.4 km, to intersect the trackway at Bas Veudale. Three degrees is considered to be within the error range of the measurement of the trackways directions.

At the Cascade d'Emaney site, Bar 4 and Bar 7 cannot be compared statistically to each other because Bar 7 contains only two footprints. However, the similar mean pes lengths (25.75 cm and 26.38 cm) and the mean pes widths (14.25 cm and 14.38 cm) of footprints from both trackway segments, together with their good spatial alignment, suggest that these trackway segments could have been made by the same animal despite being separated by a gap of 8 m. Comparison between the Cascade d'Emaney trackway (Bars 4 and 7) and the Bas Veudale trackway shows no significant difference in pes length or pes width (Mann–Whitney test, $p > 0.05$). Only two oblique paces (OP) can be measured in the Cascade d'Emaney trackway, and consequently they cannot be statistically compared to the three OP in the Bas Veudale trackway. It is worth noting, however, that the average OP length values for both trackways are very close (143.5 cm, $N = 2$ for Cascade d'Emaney, and 145 cm, $N = 3$ for Bas Veudale).

Both trackways are referred with caution to the ichnospecies *Isochirotherium herculus*. Two footprints from the trampled megatracksite surface located nearby Bas Veudale and studied by

Klein et al. (2016) were previously referred to this taxon (Klein et al., 2016). These two footprints are morphometrically similar to those from both trackways described here (**Table 1**). Although the pes outlines is poorly preserved in most footprints forming both trackways, the relative digits lengths, when they can be assessed, are similar to those seen in the two previously described isolated footprints: the digits II and III are longest and subequal in length, or digit III is slightly longer (**Figure 3C**). The pace angulation is only measurable for two strides from the Bas Veudale site, but lies within the range of pace angulations measured by Diedrich (2015) for trackways of *Isochirotherium herculus* from the Middle Triassic of the Germanic Basin, respectively, 174° in the Swiss site and 169° – 178° in the German site. However, referral of the footprints to *Isochirotherium herculus* is uncertain because of their poor quality. However, the main concern of the present study is the comparing the two trackway segments rather establishing their ichnosystematic identification.

DISCUSSION

A Rectilinear Route

The orientations of the *I. herculus* trackway segments from Cascade d'Emaney and Bas Veudale differ by only 3° (**Figure 3B**). So far, these two track segments are the only ones recognized in this layer, or in any nearby one, and it is likely that their alignment indicates that they belong to a single rectilinear main route. Within the same stratigraphic level at the Cascade d'Emaney site, two subparallel trackways 7 and 5 m long (Bar 1 and Bar 2 in Cavin et al., 2012) were previously referred to indeterminate chirotheriids by Cavin et al. (2012) and to *C. barthii* by Klein et al. (2016). Both show a general SW orientation similar to that of the new trackway (with a slight westward shift, i.e., $N230^\circ$ for Bar 1 and Bar 2 contra $N211^\circ$ for the new trackway), thus supporting the interpretation that the trackmakers had a preferred direction.

The ripple marks visible in the Bas Veudale outcrop (Figure 2B, and Supplementary Video S1) are the result of wave-induced currents on fine sand in a shallow body of water located in a proximal terminal splay (or an abandoned channel). The current direction inferred from these wave ripples is parallel to some paleocurrent measurements of Wizevich et al. (2019a), who calculated paleocurrents from trough cross-beds (average N314°) and ripple marks (average N327°). The overall transport direction is northwest (Wizevich et al., 2019a), implying flow from the Vindelician High toward the Germanic basin (and not toward the Tethyan realm as previously thought). This current orientation is approximately perpendicular to the route followed by *I. herculis* (Figures 3B, 4A).

Chirotheriid tracks are generally surmised to have been made by carnivorous archosaurs. Today, most carnivorous mammals rarely move in a straight line or for long distances. Empirical observations indicate that the daily movement distance (the sum of straight-line distances between consecutive locations during continuous 24 h radio tracking) is always three to ten times

longer than the straight line distance (shortest distance between locations at the beginning and end of a 24 h tracking period) for the Iriomote cat (*Prionailurus bengalensis iriomotensis*) (Schmidt et al., 2003), the wolf (*Canis lupus*) (Jędrzejewski et al., 2001), and for the lynx (*Lynx lynx*) (Jędrzejewski et al., 2002). Such behaviors are inconsistent with the straight kilometers-long route inferred here. However, migrations along straight routes are well known in some large ungulates. The longest African migration, occurring in Namibia and Botswana, is that of the Burchell's zebra (*Equus quagga*), with some individuals traveling 50 km per day along highly linear and unidirectional routes (Naidoo et al., 2016). One particular population of North American pronghorn (*Antilocapra americana*) moves nearly 50 km per day along a corridor averaging only 2 km wide, and has apparently been using this route for at least 6000 years (Berger et al., 2006). The use by mammals of an invariant corridor that is topographically constrained, particularly by the need to pass through bottlenecks, might be a good analog for the straight movement of archosaurs along the probably relatively narrow

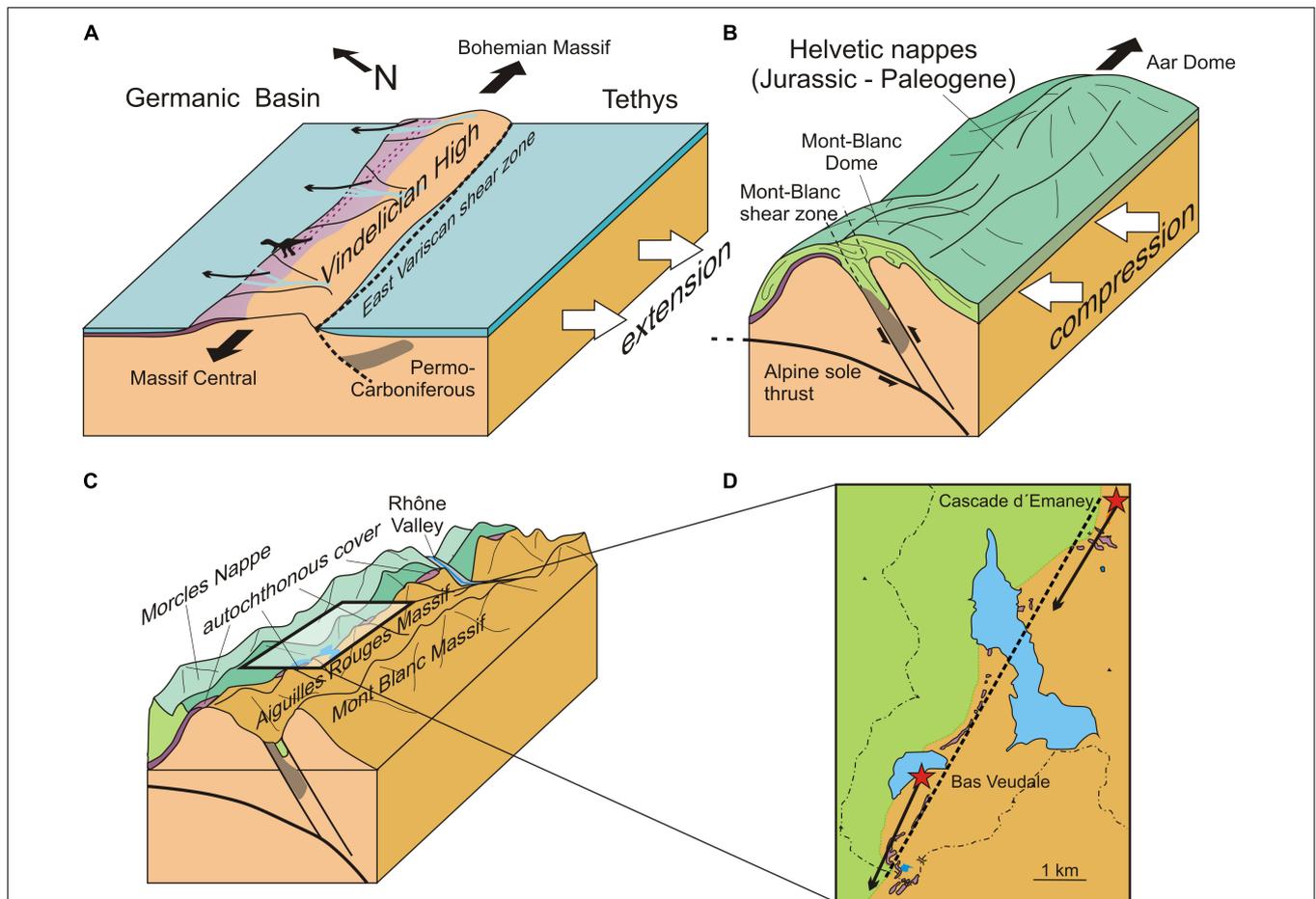


FIGURE 4 | Highly schematic representation of the paleogeographic and tectonic evolution of the study area, illustrating the basis of the correspondence between the alignment of the Triassic outcrops and the direction of both trackways (not to scale). **(A)** Triassic, the archosaurs move along the Vindelician High that separated the Tethys Ocean from the Germanic Basin during the beginning of the Tethyan rifting; **(B)** Miocene, the trackway bearing layers are uplifted and tilted during the Alpine orogeny; **(C)** Recent, erosion exposes the levels with the trackways; **(D)** Recent, simplified geological map. The dotted line indicates the alignment of the outcrops and the arrows indicate the orientation of the trackways. Adapted from Ballèvre et al. (2018) **(A)**; von Tscharnner et al. (2016) **(B)**; Leloup et al. (2005) **(B,C)**.

Vindelician High. The ichnofossil record also shows evidence of long and roughly unidirectional movement, although much shorter than the route conjectured to exist in this study, especially among Jurassic theropods, and sauropods. The longest measured theropod trackway worldwide is a *Megalosauripus* trackway from the Late Jurassic of Turkmenistan that extends for 311 m and forms a slightly undulating straight line (Lockley et al., 1996; Fanti et al., 2013), while a Lower Cretaceous site in the Jiaguan Formation, SW China, yielded a straight trackway of cf. *Eubrontes* with a length of 69 m (Xing et al., 2015). The site of Plagne, France, has yielded a rather rectilinear sauropod trackway 155 m long (Mazin et al., 2017). In the Middle Jurassic of Oxfordshire, UK, the Ardley Quarry has yielded several theropod and sauropod straight trackways that reach 180 and 200 m in length, respectively (Day et al., 2004). The Cenozoic record is poorer, but mention can be made of a late Miocene trackway site in the United Arab Emirates showing the straight movement of a herd of proboscideans over approximately 200 m (Bibi et al., 2012).

Parallel Orientation of the Trackways and the Series of Outcrops

Beyond the alignment of two trackway segments separated by several kilometers, another striking feature of these sites is that the orientation of the inferred route matches the alignment in the present landscape of the Triassic outcrops along a 28 km long and 100 m wide band (Figure 4D). There is no *a priori* reason why the orientation of the straight route should mirror the alignment of outcrops shaped by orogenic and erosional processes entirely independent of the movements of the archosaurs. This situation, however, can be explained by examining the geological processes that shaped the Triassic topography and contributed to establishing the layout of the modern trackways-bearing outcrops.

In the Middle Triassic, the “Germanic Trias” to the north and the “Alpine Trias” to the south, were separated by the Vindelician High, an exposed low-elevation area oriented roughly ENE – WSW (Ballèvre et al., 2018) along which the tracemakers moved (Figure 4A). The WSW – ENE orientation of the Vindelician High was dictated by the orientation of the remnant of the Permian East-Variscan shear zone (Ballèvre et al., 2018). Structural inheritance plays a major role in the fact that the Helvetic zone and the East-Variscan shear zone roughly conform to the SW – NE orientation of alpine paleogeographic domain boundaries. Moreover, tectonic faults that occurred during the Late Carboniferous and the Permian were reactivated during Triassic-Jurassic rifting as well as during the Alpine shortening (Leloup et al., 2005; Ballèvre et al., 2018). During the Tethyan rifting, the southern part of the Germanic Basin was controlled by the reactivation of these Variscan faults transmitted from the Tethyan rift system to its northern periphery (Szulc, 1999, 2000; Stollhofen et al., 2008). The uplift and tilting of the Aiguilles Rouges and Mont-Blanc massifs occurred along an axis that followed the East-Variscan shear zone, and consequently also the axis of Vindelician High, and produced the Mont-Blanc and the Aar domes extending to the northeast (Figure 4B). Pleistocene

glacial erosion affected the boundary between the basement and the Morcles nappe along this SW – NE axis, and unearthed the Triassic cover along the original Vindelician High, whose orientation corresponds to that of the trackway (Figures 4C,D).

Although poorly preserved, both trackway segments are similar enough with respect to footprint parameters and track orientation to suggest that they form parts of a single route, at least 6.4 km long, left by trackmakers belonging to the same species, and possibly even made by the same individual. The alignment of the Triassic fossiliferous outcrops corresponds to the general direction of the trackways. This surprising concordance is explained by the Triassic topography, whose orientation corresponds to that of a major tectonic structure that was reactivated during Alpine uplift and influenced the orientation of later erosion. Hence, a 240-million-years-old fleeting animal behavior has been preserved on a large scale even through a major orogenic event.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/Supplementary Material.

AUTHOR CONTRIBUTIONS

LC and AP contributed equally to the analysis of the data and to the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/feart.2020.00004/full#supplementary-material>

VIDEO S1 | Photogrammetric rendering of the Bas Veudale trackway.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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