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Dynamic environmental conditions recorded by the trace fossil *Teichichnus* and event beds during deposition of the basal Vaca Muerta Formation in the central Neuquén Basin (Argentina)

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ABSTRACT

The mud-dominated part of the basal Vaca Muerta Formation in the central Neuquén Basin accumulated mainly under dysoxic conditions as indicated by the absence of both fine lamination and large burrows, typical of anoxic and oxic conditions, respectively. Event beds and large, strata-bound concretions preserving a nearly uncompacted sediment fabric document rather discontinuous deposition, in particular as concretions must reside within the zone of carbonate supersaturation for a prolonged period of time to form. The mudrock hosts numerous ash layers. Among them is a bed up to 40 cm-thick that was deposited by storm-induced currents and later became calcified. It contains abundant, winding Teichichnus up to 220 cm-long. The trace producers partly reworked their own spreite and probably applied a gardening and sequestrichnial nutritional strategy (that is collecting and stowing of nutritional material in the burrow for later utilization). The spreite fill documents depositional processes that delivered argillaceous sediment and provided oxygen. The ash originally constituting the Teichichnus bed originated from the volcanic arc west of the basin. In contrast, the erosive surface limiting the Teichichnus bed is covered by mud, implying sediment delivery from the east or south where rivers entered the basin while the climate was (at least seasonally) humid, whereas aridity increased towards the north. Consequently, an estuarine circulation likely developed and prevailed during the initial transgression of the lower Vaca Muerta Formation while cold Palaeo-Pacific water flowed into the subsiding and expanding basin. Later, during prevailing dry climate, an anti-estuarine circulation was probably established.

1. Introduction

Biogenic sedimentary structures are autochthonous indicators of environmental conditions and hence, are advantageous for sedimentological and palaeoecological analyses (e.g., Ekdale et al., 1984; Pemberton et al., 2001; Buatois and Mángano, 2011; Knaust and Bromley, 2012). Therefore, trace fossils and ichnofabrics provide valuable information on factors such as oxygenation and substrate properties. For muddy deposits, the mode in which organisms move through them or in which they construct their burrows reflects sediment consistency (e.g., Wetzel and Uchman, 1998; Goldring, 1999). Changes in the oxygen content of the bottom (respiration) water are reflected by various ichnologic parameters. Decreasing oxygenation, for example, causes a reduction in burrow size and penetration depth as well as disappearance of trace fossil groups of specific design, etc. (e.g., Bromley and Ekdale, 1984; Savrda and Bottjer, 1986; Martin, 2004). These trends have been substantiated by observations in the Recent (e.g., Sturdivant et al., 2012). In the case of rising oxygenation, the inverse trends occur;

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burrow penetration indeed. as depth increases. the shallowly-penetrating traces produced during lowered oxygen levels are overprinted by deeper ones formed later at higher oxygen levels. Dysoxic conditions are characterized by small 'crypto'-traces and indistinct, small biodeformational structures resulting in indistinctly bioturbated sediment. Under anoxic conditions, in contrast, sediments preserve fine lamination or physical sedimentary structures. Typically, Planolites, Thalassinoides, Zoophycos, and Chondrites belong to the trace fossil suite observed in relation to changes in oxygen level (e.g., Bromley and Ekdale, 1984; Savrda and Bottjer, 1986). However, in the studied case, except Thalassinoides, these traces are not present and the ichnofabric is dominated by Teichichnus.

Teichichnus represents a wall-like retrusive spreite burrow having the U-shaped causative tube on top, and thus resembles stacked gutters (Seilacher, 1955). Besides straight forms, winding to undulating ones have been observed (e.g., Buckman, 1996; for a review of the valid ichnotaxa see Knaust, 2018a). Teichichnus is produced in various environments ranging from marginal-marine to deep-sea (e.g., Knaust, 2017). It occurs mainly in fully marine settings but also in brackish environments (Goldring, 1971; Netto and Rossetti, 2003). Commonly, Teichichnus is present in muddy sand but occasionally in chalk, marl and deep-sea mud (e.g., Frey and Bromley, 1985; Bromley and Uchman, 2003; Mikuláš et al., 2009). The unknown, supposedly wormlike producers mainly follow a suspension- and/or deposit-feeding mode (Knaust, 2018a). They can respond to sedimentation and tolerate low oxygenation in both of which cases the U-shaped causative tube is of advantage. In aggrading sediments, the causative tube is displaced upward (e.g., Seilacher, 1955; Corner and Fjalstad, 1993). Some burrowers apply a Teichichnus behaviour when responding to sedimentation; for instance, crustaceans produce Sinusichnus in slowly accumulating sediment, but at enhanced deposition, tubes are shifted upward and a retrusive spreite system is formed (Belaústegui et al., 2014). In low-oxygen settings, U-tubes allow efficient ventilation (Wetzel, 1983; Savrda and Bottjer, 1989; Knaust, 2018a). However, Teichichnus does not belong to the trace fossil suite typical of de- or re-oxygenation (cf. Bromley and Ekdale, 1984; Savrda and Bottjer, 1986).

In the basal part of the Upper Jurassic to Lower Cretaceous Vaca Muerta Formation (Neuquén Basin, Argentina), remarkable *Teichichnus* occur in a volcanoclastic bed, intercalated into organic-rich mudrock, that later became calcified. In bedding-plane view, these burrows exhibit an unusual undulating to curved course and an extraordinary length, commonly exceeding 1.5 m. It is the purpose of the present study to describe these unusual *Teichichnus* specimens, to decipher their environmental meaning, and to relate them to the palaeoceanographic setting.

2. Geological setting

2.1. Geological background

The Neuquén Basin is located in west-central Argentina and covers an area of \sim 120,000 km². It formed in a back-arc position east of the evolving Andes and contains approximately 7000 m of Upper Triassic to Palaeogene strata (Leanza et al., 1977; Howell et al., 2005). The basin's northern part is relatively narrow, up to \sim 100 km-wide, whilst its southern Neuquén embayment is more than 500 km wide (Fig. 1). Historically, three major phases of basin development have been distinguished (Howell et al., 2005; Veiga et al., 2020; and references therein).

(1) Late Triassic to Early Jurassic synrift phase. The subduction of the Palaeo-Pacific plate underneath the South American margin of Gondwana caused intraplate back-arc extension that led to the formation of isolated rift basins, which were subsequently filled with terrestrial and volcanic deposits (Uliana and Legarreta, 1993; Vergani et al., 1995; Howell et al., 2005).

- (2) Early Jurassic to Early Cretaceous postrift phase. When the Palaeo-Pacific oceanic crust began to be subducted at a high angle beneath the western margin of Gondwana, the Neuquén Basin experienced thermal subsidence and a thick sediment succession accumulated above the synrift deposits (Vergani et al., 1995; Howell et al., 2005). The basin evolved into a shallow epeiric sea with ramp-type margins in the east and south (Legarreta and Uliana, 1991; Zeller et al., 2015). It was separated from the Palaeo-Pacific by a volcanic arc forming an island chain (e.g., Howell et al., 2005), but alternatively a continuous peninsula has been suggested (Vicente, 2005). Water exchange between Palaeo-Pacific and Neuquén Basin was thus more or less restricted but Sr/Ca ratios of marine carbonates nonetheless imply a rather permanent connection between both water bodies since the Sr/Ca values are in the same range (e.g., Alberti et al., 2020).
- (3) Late Cretaceous to Cenozoic foreland phase. As the dip of the subducted Palaeo-Pacific slab decreased, the basin became dominated by compression and finally inverted (Howell et al., 2005).

Of particular interest among the postrift sediments are thick successions of hydrocarbon source rocks, in particular the Late Jurassic to Early Cretaceous Vaca Muerta Formation (e.g., Stinco and Barredo, 2014). The Vaca Muerta-Quintuco-Picún Leufú succession (Fig. 2) represents a prograding system with gently inclined clinoforms; topsets are carbonates, silicates or a mixture thereof (Picún Leufú and Quintuco formations), whereas foresets and bottomsets are composed of the organic-rich siliciclastic mudrock of the Vaca Muerta Formation (e.g., Zeller et al., 2015; Rodriguez Blanco et al., 2022). Sediment was supplied from different sources; volcaniclastic material from the arc to the west, siliciclastics from the North Patagonian Massif to the south and the Sierra Pintada System to the east (e.g., Zeller et al., 2015, Fig. 1), and carbonates from shallow-marine domains in the northern part of the basin (e.g., Kietzmann et al., 2016). The carbonate system temporarily expanded southward in response to climate and sea-level changes (Zeller et al., 2015; Domínguez et al., 2020). The Vaca Muerta Formation formed under low-oxic to anoxic conditions as evidenced by rare to absent benthic body fossils, their small size where present, depauperate to absent bioturbation structures, sediment fabric and geochemical proxies (e.g., Doyle et al., 2005; Kietzmann et al., 2016; Krim et al., 2017, 2019). Later, during diagenesis, temperatures of at least 100° are recorded by 'beef' calcite veins that contain fluid hydrocarbons (Rodrigues et al., 2009; Weger et al., 2019; Larmier et al., 2021).

2.2. Environmental conditions during Vaca Muerta times

During the Late Jurassic to Early Cretaceous, prior to the break-up of Gondwana, South America stretched from 10° N to 55° S, and hence occupied a position similar to today's (e.g., Iglesias Llanos et al., 2006). The Neuquén Basin extended from $\sim 32^{\circ}$ S to $\sim 40^{\circ}$ S (e.g., Howell et al., 2005). Therefore, the basin was located within the transition from an arid climate in the north to warm, humid conditions south of $40^\circ~S$ (Volkheimer et al., 2008). The large continental area of Gondwana prior to its fragmentation fostered a monsoonal climate characterized by pronounced seasonality as suggested by general circulation model simulations (Moore et al., 1992; Sellwood and Valdes, 2006). During the Southern Hemisphere's summer (December-February), temperatures were hot (~35 °C) but moderated to ~15-20 °C during the winter (June-August); precipitation mainly occurred in the south whereas dryness increased towards the NE (Sellwood and Valdes, 2006), where evaporation probably exceeded precipitation. At the latitude of the Neuquén Basin, during the Southern winter, weakly northwesterly winds blew south of $\sim 36^{\circ}$ S and northeasterly further north, whereas strong monsoonal winds blew from S-SSW during the summer (Scherer and Goldberg, 2007). These winds could induce the upwelling of cold



Fig. 1. Location of the study area marked by red asterisk; inset showing Neuquén Basin (yellow) in South America.



Fig. 2. Stratigraphic scheme of the Vaca Muerta Formation in the area Yesera del Tromen near Chos Malal City (after Kietzmann et al., 2016; Veiga et al., 2020); white bar marks studied section.

water along the west coast of South America (Parrish and Curtis, 1982). Due to upwelling, poorly oxygenated bottom water might have formed at least seasonally along the Palaeo-Pacific margin facing the northern part of the Neuquén Basin (Parrish et al., 1982).

General circulation model results match climate indicators in the rock record. During the Upper Jurassic, desert sandstones formed in the Paraná Basin northeast of the Neuquén Basin (e.g., Scherer and Lavina, 2006). They record dry conditions and a prevailing wind direction from the SW (Scherer and Goldberg, 2007). Northward sediment transport along the shelf of the volcanic arc (Zeller et al., 2015) fits this scenario. To the south, an Upper Jurassic freshwater fish fauna records humid conditions in Patagonia (e.g., Sferco et al., 2015). Freshwater discharge to the Neuquén Basin from the North Patagonian Massif in the south is documented by siliciclastic shoreline deposits formed during the initial transgression of the Vaca Muerta Formation (e.g., Paz et al., 2021; Rodriguez Blanco et al., 2022).

3. Material and methods

The *Teichichnus* specimens were investigated at Yesera del Tromen near the city of Chos Malal (Neuquén Province, Argentina; Fig. 1). The volcaniclastic bed that was later calcified contains abundant, elongate *Teichichnus* and so is called T-bed below. It was studied in detail within a subtle valley (Outcrop-1) extending from $37^{\circ}17'58.2"S$, $69^{\circ}53'09.9"W$ to $37^{\circ}18'00.5"S$, $69^{\circ}53'16.2"W$. An additional outcrop exposing the same stratigraphic interval was studied about 2 km towards the northeast (Outcrop-2; coordinates $37^{\circ}17'15.06"S$, $69^{\circ}51'40.55"W$). The volcaniclastic T-bed that became later calcified is sandwiched between beds of organic-rich mudrock of the basal Vaca Muerta Formation a few meters above the transgressive surface to the Tordillo Formation (Ponce et al., 2015). Numerous strata-bound concretions of various sizes occur below, above and attached to the T-bed.

This study is based mainly on observations in the field. In the interval including the T-bed, a small sample was taken from each bed to prepare standard thin sections for microscopic and geochemical analysis.

Carbonate and organic carbon contents were measured using LECO RC612 equipment (Leco Corporation, St. Joseph, MI, USA). Samples were stepwise heated to (1) 110 °C, (2) 450 °C, and (3) 1100 °C, while the corresponding loss in weight and the amount of liberated CO_2 were recorded. During step (1) water evaporates, during step (2) organic matter is burnt, and during step (3) carbonate decays.

Samples for stable isotope measurements of oxygen and carbon were taken from macroscopically defined domains using a dental drill. About 0.2 mg of material were weighed out into 12 ml exetainers (Labco Limited, Lampeter, UK). These were purged with helium. Then phosphoric acid (100%) was added to react with the samples at 70 °C for 90 min. Isotopic analyses were performed by a Gasbench II coupled to a Delta V Plus mass spectrometer (Thermo Fisher Scientific, Bremen, Germany). The carbon and oxygen isotopic compositions were calibrated against international carbonate isotope reference materials (NBS19, NBS18, LSVEC), and expressed as δ^{13} C and δ^{18} O in % relative to Vienna Pee Dee Belemnite (VPDB). Based on routine analyses of the carbonate isotope standards analytical precision was $\leq \pm 0.1\%$ for δ^{13} C, and $\leq \pm 0.2\%$ for δ^{18} O.

4. Results

4.1. Macroscopic observations

In the following, the observations refer to Outcrop-1; additional observations from Outcrop-2 are outlined at the end of this section. The studied *Teichichnus* traces occur about 11 m above the base of the Vaca Muerta Formation within a \sim 30–40 cm-thick volcaniclastic bed that became later calcified (Figs. 3 and 4). The bed appears bipartite, as there is a sharp, rather flat surface separating an upper, *Teichichnus*-bearing, 27–32 cm-thick part from a mainly fine-grained, up to 5–10 cm-thick,

Yesera del Tromen area



Fig. 3. Schematic lithologic logs of the sections studied at Yesera del Tromen; left, Outcrop-1 (redrawn from Ponce et al., 2015, supplemented by new observations); right, Outcrop-2 located about 2 km to the NE.

lower part, which will be called 'underbed', that contains fossils preserved in three dimensions. The 'underbed' can be absent locally. The upper surface of the *Teichichnus*-bearing bed (T-bed) is mainly flat and erosive and exposes *Teichichnus* spreite structures but locally ripple-like undulations having 15-cm wavelength and 2-cm amplitude are present (Fig. 5B). The bed is sandwiched between organic-rich mudrock that shows undulating, irregularly thick lamination but no distinct, fine lamination. Ammonites left flattened imprints. No macroscopic burrows were observed in the mudrock. Commonly, large, strata-bound, ellipsoidal concretions several tens of centimetres in size occur (Fig. 4). Sharp-based, centimetric to decimetric limestone layers are present throughout the studied section.

Above and below the T-bed, convex 'halves' of ellipsoidal concretions are locally attached but the positions of concretions above and below do not match. They are up to 50–60 cm long, 30–50 cm wide and 10–20 cm thick. They preserve fossils in three dimensions (Fig. 4). The concretion 'halves' beneath the T-bed are connected with the 'underbed' both not considered as part of the T-bed.

The T-bed displays a poikilotopic fabric made up of densely packed dark angular calcite crystals, 2–8 mm in size (Fig. 5E; see below). The fill of *Teichichnus* is also poikilotopic but its densely packed crystals are only 0.2–1 mm in size. Because of bioturbation and recrystallization, no primary sedimentary structures are seen in the T-bed. Aside from *Teichichnus*, only a few *Thalassinoides* having 2 cm diameter were recognized in the T-bed and in the concretion 'halves' above (Fig. 5A).

The encountered Teichichnus specimens constitute ~10-30 area% of the fabric and commonly penetrate about 80-90% of the bed thickness. In vertical transverse section, the spreite is vertical to steeply inclined and of width ranging from 0.8 to 2.2 cm. Within a single specimen, the spreite width may vary by \pm 50% but does not increase from base to top (Fig. 5). In vertical longitudinal section, inclined tube segments representing the connection to the seafloor and the causative tube were rarely observed because of the erosive nature of the upper bed surface. Locally, the trace plunges into the bed and the top can be covered by up to 5 cm of sediment (Fig. 5E) in which case the lined causative tube was encountered in one specimen. It is 0.6 cm in diameter whereas the spreite below is 3 cm wide (Fig. 5E). On split surfaces along the spreite, vertical undulations are present without the expected systematically inclined, imbricate pattern (Figs. 5 and 6). These vertical undulations occur recurrently in the Teichichnus traces and are arranged in packages of retrusive spreite lamellae descending and ascending for 5-10 cm for a



Fig. 4. *Teichichnus*-bearing bed at Yesera del Tromen. (A) Outcrop-1, general arrangement of the *Teichichnus*-bearing bed sandwiched between mudrock; at the base are flat-topped concretion 'halves' and a diagenetic 'underbed', the top is truncated by an erosive surface, covered by a thin mud veneer, locally overlain by flat-based concretion 'halves'. (B) Outcrop-2, showing the position of the *Teichichnus*-bearing bed ~2.6 m above the marine transgressive surface (marked by yellow line) to the greenish Tordillo Formation; concretion 'halves' and 'underbed' were not developed; below the *Teichichnus*-bearing bed are somewhat more resistant, slightly concretionary carbonate-enriched beds (see Fig. 3).

distance of >10-20 cm. Notably, they overprint previously produced spreite domains. The lateral margins of *Teichichnus* show a considerable relief of several mm, protrusions and restrictions following individual lamellae (Fig. 5 D–G; 6 A).

The upper erosive surface of the T-bed exposes abundant Teichichnus traces; about 10–20 specimens per m² have been counted on average and locally 20-30 specimens per m². They appear to be dispersed and not clustered. An individual Teichichnus does not cross its own course but may intersect or overlap others for some distance (Fig. 6). The Teichichnus traces are extraordinarily long, usually between 120 and 150 cm, but one specimen was traced for 220 cm (Figs. 6 and 7). The burrows are composed of straight, curved and even U-shaped segments that are each up to a few tens of centimeters long. The curved to U-shaped segments show a similar radius of curvature of ~ 10 cm and deviate from the previous course by 60° –180° but commonly by 60° to either side (Figs. 6 and 7). Considering the traces' curved course, it is not surprising that no preferred orientation of burrows was recognized. The extreme length, curved course, and vertical undulations of lamellae packages characterize these traces (Fig. 8). They are assigned to Teichichnus isp. aff. T. zigzag (see below).

At Outcrop-2 about 2 km away, *Teichichnus* does not differ from those at Outcrop-1 with respect to host sediment, geometry, size or fill. However, the T-bed occurs at only 2.6 m above the base of the Vaca Muerta Formation and is only up to 20 cm thick; neither convex concretions nor an 'underbed' are attached (Figs. 3 and 4). Imprints of flattened ammonite shells are common in the adjacent mudrock.

4.2. Microscopic observations

The host sediment was investigated in an uncompacted state in concretions sampled below and above the T-bed as well as in compacted mudrock adjacent to the concretions. In thin sections, no differences in sediment composition were recognized between the sampled concretions above and below the T-bed (Fig. 9). Preserved in early diagenetic concretions, the mudrock looks massive to crudely laminated while fine lamination has not been observed (Fig. 9B and C).

The early-cemented sediment exhibits a wacke- to packstone texture; the major components are pellets (0–20%), echinoderm and bivalve debris (10–20%), clay minerals (\sim 10–30%) and calcified radiolarian tests (10–20%) that exhibit a rather porous structure in thin sections



(caption on next page)

Fig. 5. (A) Concretion formed above the surface truncating the *Teichichnus* bed; the concretion preserves uncompacted *Thalassinoides* in its lower part (marked by black arrows); note the flat base of the concretion; position of this concretion is shown on Fig. 4A. (B) Locally occurring long-wavelength, low-amplitude, ripple-like structures forming the top of the *Teichichnus*-bearing bed; *Teichichnus* occurring about 5 cm below. (C) Upper erosive surface truncating the top of the *Teichichnus* bed exposing a curved *Teichichnus*; the preserved tube records reworking of the spreite. (D) A longitudinal, nearly vertical split surface exposing three *Teichichnus* specimens intersecting one another; note that the *Teichichnus* penetrate the bed almost completely but not the concretion 'half below. (E) Split surface exposing a *Teichichnus* in oblique longitudinal section exhibits overlapping packages of spreite lamellae (separated by white lines; displacement of lamellae indicated by white arrows); upper and lower boundary of *Teichichnus* marked by white stippled line. A previously produced *Teichichnus* is cut transversally; the spreite (marked by yellow line) is six-times wider than the causative tube (marked by red line); note poikilotopic host rock. (F) Vertical transverse split surface of the *Teichichnus*-bearing bed a concretion 'half attached below that contains an ammonite shell preserved in three dimensions (marked by black arrow); bulbous margin of the spreite marked by yellow line, spreite widening indicated by yellow arrows.

(Fig. 9B). In addition, variable, but little pyrite and recrystallized calcite spar (~20%) are present. The pellets are ellipsoidal being 200–400 μ m in diameter and 400–600 μ m in length. They are mainly composed of mud containing only few radiolarian tests. Between the different samples, the amount of components may vary $\pm 10\%$. In the compacted mudrock, the biogenic components are barely recognizable due to fragmentation and dissolution (Fig. 9A).

The material constituting the T-bed consists of recrystallized calcite (about 70%) exhibiting a poikilotopic fabric composed of crystals up to 8 mm in size (Fig. 9C and D). Occasionally, less than 5% fossil remains are present, mostly calcified radiolarians. The rest of the material consists chiefly of clay minerals and subordinately of feldspars within calcite crystals.

The fill of the *Teichichnus* clearly differs from the host sediment by the enrichment of argillaceous material in the spreite laminae. The spreite also exhibits a poikilotopic fabric but the calcite crystals are significantly smaller than in the host sediment, ranging from 0.5 to 2 mm in size (Fig. 9E and F). The amount of other components is rather low.

4.2.1. Geochemical data

The background mudrock contains 5–10% CaCO₃ and ~1% C_{org} (Fig. 10). Carbonate and organic matter contents of the sediment hosting *Teichichnus* are ~60–72% and ~0.8–1.1%, respectively. The fill of *Teichichnus* contains 62–68% CaCO₃ and ~1.2% C_{org}. Concretions, concretion 'halves' and 'underbed' contain 68–75% CaCO₃ and 0.8–1.0% C_{org} (Fig. 10). Stable isotope values of the T-bed range between –4 and –3‰ for δ^{13} C and –8 to –7‰ for δ^{18} O; for the 'underbed' and attached concretions in the mudrock below and above show δ^{13} C values of –11 to –12‰ and δ^{18} O values of –7 to –6‰ (the fill of the ammonite being somewhat heavier; Fig. 10). The stable isotope values of the T-bed plot between those of Tithonian pristine marine carbonate and andesitic volcanics (Fig. 11).

5. Interpretation

The massive appearance, crude lamination and absence of fine lamination in the organic-rich mudrock hosting the T-bed imply cryptobioturbation or shallow indistinct burrowing and thus, are suggestive of a dysoxic setting (e.g., Wetzel and Uchman, 2012; Löhr and Kennedy, 2015; Campetella et al., 2020; Paz et al., 2023). The absence of shelly benthic fauna supports this interpretation (e.g., Byers, 1977). The flattened imprints of ammonites are in line with this scenario; they record the consumption of some free oxygen by oxidation of organic matter, generating CO₂ that in turn led to dissolution of the shells (e.g., Aller, 1982; Aller and Cochran, 2019). Some ammonite shells in contact with concretions became pyritized in the upper part of the sulfate reduction zone (cf. Canfield and Raiswell, 1991). The shape, size and composition of faecal pellets justifies their assignment to Coprulus oblongus (e.g., Knaust, 2020). In low-oxygen settings, faecal pellets of both pelagic and benthic origin are typical (e.g., Brodie and Kemp, 1995; Löhr and Kennedy, 2015). The remains of bivalves and echinoderms are too small to be ascribed to a specific habitat. At the time of deposition, the study area

was not too far from the coast and floating benthic habitats such as drift wood or ammonites are likely to occur there (e.g., Seilacher, 1982). Radiolarian tests are typical of enhanced productivity (e.g., De Wever et al., 2014). Nutrients were likely provided by rivers or reworking of coastal plain deposits during transgression (e.g., Wetzel, 1991).

The T-bed is interpreted as an event deposit consisting of reworked ash that later became calcified; such beds, characterized by a poikilotopic fabric, are common in the Vaca Muerta Formation (e.g., Kietzmann et al., 2016, 2020; Rutman et al., 2021). Aside from the locally preserved long-wavelength ripples typical of a tempestite, primary sedimentary structures are absent due to bioturbation and recrystallization. Nonetheless, a tempestitic origin of the T-bed is suggested because of several reasons. (1) The sharp bounding surfaces characterize an event bed. (2) The T-bed is rather thick and consists of material contrasting with the muddy background sediment in terms of grain size and composition since the relict fabric implies originally silt- to sand-sized, rather angular volcanic ash (cf. Kietzmann et al., 2016, 2020). (3) The T-bed contains \sim 1% C_{org} but airborne volcanic ash contains very little organic matter as, for instance, the Pinatubo-1991 ash in the South China Sea (<0.1%; Wetzel, 2008, 2009). Thus, the T-bed represents reworked and redeposited volcaniclastic material rather than a pristine ashfall deposit. (4) The ash was probably delivered from the volcanic arc area to the west because wind cannot transport coarse ash in large quantities far from its source (e.g., Wiesner et al., 2004). (5) A rather shallow depositional water depth around storm-wave base is likely because the T-bed occurs 11 m at Outcrop-1, and even less (2.6 m) at Outcrop-2, above a marine transgressive surface that had nearly flat relief (Domínguez et al., 2020; Paz et al., 2021). The T-bed is assigned to the middle to outer ramp facies associations FA2/FA3 of Kietzmann et al. (2016).

Given that the T-bed represents an isochronous marker bed and the coastal plain of the Tordillo Formation underneath had a very low relief (see above), the considerable variations in thickness and the stratal arrangement in the lower part of the Vaca Muerta Formation between Outcrops 1 and 2 (Fig. 3) imply differential subsidence. This is not unusual for the Vaca Muerta Formation (Domínguez et al., 2020).

The sharp lower boundary separating the *Teichichnus*-bearing interval from the 'underbed' is interpreted to have formed by the erosive phase of storm-induced currents (cf. Aigner, 1982, 1985, Fig. 12). Concretion 'halves' and 'underbed' are of diagenetic origin. The consistent form of concretion 'halves' implies their formation after deposition of the T-bed for three reasons.

- (1) The thickness of the T-bed varies due to varying flow conditions during storms; hence, erosion likely reworked down to varying sediment depths. Thus, more or less than half of an ellipsoidal concretion should also occur, but it does not.
- (2) The concretion 'halves' on top of the T-bed definitely postdate event-bed deposition.
- (3) Formation of concretions prior to T-bed deposition and their later truncation is rather unlikely because the host mud had low permeability, such that seawater could only slowly percolate and provide ions in amounts sufficient for concretion growth, in particular Ca²⁺ as well as sulfate reacting with organic matter (simplified as CH₂O; Burdige, 2007) to form bicarbonate



Fig. 6. Details of the *Teichichnus*-bearing bed. (A) Longitudinal vertical split surface showing overlapping packages of undulating spreite lamellae (separated by white lines) indicating reworking of previously produced burrow parts. (B) 90° turn of the spreite exposed on a vertical, turning split surface; white line c indicating burrow course, arrows marking truncated lamellae package. (C) Upper erosive surface truncating the *Teichichnus*-bearing bed exposing two traces that follow the same course for about 20 cm (implying a sequorichnial behaviour). (D) Upper erosive surface truncating the *Teichichnus*-bearing bed exposing the winding course of three traces for more than 1 m.



Fig. 7. Schematic course of three *Teichichnus* exposed on the upper erosive bed surface. Commonly, the curvature of the *Teichichnus* courses exhibits a rather uniform radius of \sim 10 cm.



Fig. 8. Scheme showing main characteristics of winding, elongate *Teichichnus*; note truncated lamellae packages. The tip of the trace was not observed and is tentatively shown only on one side.

(subsumed by the equation $2CH_2O + SO_4^{2-} = 2HCO_3^- + H_2S$ or $2Ca^{2+} + 2CH_2O + SO_4^{2-} = 2CaCO_3 + H_2S + 2H^+$; e.g., Burdige, 2007; Rodriguez Blanco et al., 2022).

The 'underbed' and the concretion 'halves' formed within the sulfate reduction zone as evidenced by the presence of pyrite, in particular that replacing ammonite shells, and δ^{13} C values (e.g., Canfield and Raiswell, 1991; Coleman, 1993; Raiswell and Fisher, 2004). They became cemented, very likely pervasively, at a shallow depth in sediment as indicated by fossils preserved in three dimensions and a minus-cement porosity of 65–70% that is usually encountered near the surface of muddy sediments (e.g., Wetzel, 1990).

The currents depositing the T-bed originated in shallow water and carried not only oxygenated water and ash but also organisms, and when traversing organic-rich mud some of it was entrained. After deposition, oxygenated bottom and pore water was available at least for a short while as observed in other cases (e.g., Grimm and Föllmi, 1994; Wetzel and Uchman, 2001). 'Imported' organisms could settle and start to produce *Teichichnus* and *Thalassinoides* (Fig. 12). Taking the spreite

thickness as a proxy for body size, the similar size of the studied specimens implies that the *Teichichnus* producers settled during a rather distinct time window, probably all at once. After deposition of the T-bed, the redox boundary migrated upward as is common in organic-rich sediments (e.g., Wetzel and Uchman, 2001; Katsev et al., 2006). In modern sediments, anoxic conditions can be established below and in a centimetric event layer in less than three years (e.g., Haeckel et al., 2001). Thus, the U-burrow of *Teichichnus* becomes advantageous for respiration in the anoxic host sediment. The originally high permeability of the T-bed facilitated circulation of water rich in bicarbonate drained from compacting mud below and produced within the sulfate reduction zone, both contributing to the calcification of ash. This process was enhanced by cations liberated from silicates when anoxic, acidic conditions developed in the T-bed (e.g., Wallmann et al., 2008; Bojanowski, 2014; Torres et al., 2020).

The retrusive *Teichichnus* spreite documents that currents deposited sediment and provided sufficient oxygen, since the size (= spreite width) of the studied *Teichichnus* traces is similar to that formed under well oxygenated conditions (1–2.5 cm; e. g, Frey and Bromley, 1985; Carmona et al., 2008). Because the production of the long *Teichichnus* takes time oxygenated conditions prevailed on the seafloor for some years or even longer. Therefore, the T-bed habitat was not restricted too much by oxygen or benthic food.

However, the T-bed's low ichnodiversity comprising only Teichichnus and Thalassinoides implies demanding conditions. Presumably, the sharp, angular volcaniclastic particles constituting the host sediment might have been hostile to other burrowing organisms. The Teichichnus producers lined their causative tubes with mud and mucus (1) to stabilize them in a loose and grainy substrate and (2) to minimize the impact of sharp, angular grains, since such Teichichnus are interpreted to have wormlike producers (Lima and Netto, 2012) whereas other potential Teichichnus producers like arthropods and holothurians (e.g., Schlirf and Bromley, 2007; Knaust, 2018a) were probably less affected. The producers of Thalassinoides, probably crustaceans (e.g., Bromley, 1996), are less sensitive to this type of host sediment and may even prefer rather loose, fine sediment (cf. John et al., 2012). The mud enriched within the spreite documents delivery of terrigenous fine-grained material rich in organic matter because the Corg content of the Teichichnus traces is higher and the poikilotopic calcite is much finer than in the host sediment. The origin of this sediment remains speculative because of later erosion and recrystallization; probably it was a mixture of ash and mud since the sediment causing the upward shift of the causative tube was very likely also emplaced in the spreite. The mud in the spreite might have hindered recrystallization of ash to calcite (cf. Bathurst, 1975).

How the very long spreite was produced can only be conjectured because it is not fully exposed due to its extreme long, winding course. The vertical undulations of lamellae packages record stepwise burrow production and explain the varying width of the spreite because previously produced spreite domains were reworked even at the burrow base.

The horizontally and vertically curved tube segments influence whether the flow in the tube becomes laminar and swirling, the latter promoting in-plane fluid mixing (e.g., Taylor, 1929; Cookson et al., 2009; Tang et al., 2016). Tube segments of differing curvature in a series configuration increase these effects (e.g., Cookson et al., 2019). In this way, the flux of ions and dissolved agents across the tube wall may become enhanced (e.g., Coppola and Caro, 2008). Furthermore, in-plane mixing moves particles away from the wall to the core of flow and reduces deposition of particles in the tube (e.g., Ha et al., 2017).

The extreme length of the burrow, the winding course, its presence in organic-rich sediment, and the partial reworking of its own spreite facilitate different nutritional strategies. Among them, suspension- and deposit-feeding are well established (e.g., Knaust, 2018a) and not addressed here. In addition, *Teichichnus* producers could have applied a gardening and sequestrichnial behaviour (i.e. collecting and stowing nutritive material in a burrow for later utilization and/or fermentation).



Fig. 9. Photomicrographs of mudrock, host rock and *Teichichnus*. (A) Compacted mudrock. (B) Uncompacted mudrock preserved in early diagenetic concretion; arrows marking radiolarian tests. (C) Fine-grained host sediment preserved uncompacted in a concretion in plane light containing pellets (p) and radiolarian tests (r). (D) Poikilotopic rock hosting *Teichichnus* in polarized light. (E) *Teichichnus* spreite (sp) in poikilotopic host rock (h) in plane light. (F) Same as (E) but in polarized light.

Oxygenated water in a tube within organic-rich, anoxic sediment causes a steep geochemical gradient that fosters microbial activity (e.g., Meysman et al., 2010). Utilization of these microbes by ingesting them or using their metabolic products represents a gardening behaviour (e. g., Vallon et al., 2016). However, microbes may grow slowly (e.g., Konhauser, 2007). Therefore, a long tube is of advantage because it allows more time between phases of microbial harvesting along the tube wall. Reworking of one's own spreite recorded by the vertically undulating packages of spreite lamellae indicate 'auto-coprophagy' as described by Jumars et al. (1990) from modern sediment; these authors figured a sipunculid producing a *Teichichnus*-like spreite. The reworking of previously stored organic-rich material is typical of a sequestrichnial behaviour (e.g., Uchman and Wetzel, 2016, 2017). Furthermore, reworking of the own spreite records thigmotactic capabilities, which are also evidenced when a Teichichnus producer followed another for some distance, documenting a sequorichnial behaviour (e.g., Nara and Ikari, 2011; Wetzel et al., 2020).

A severe erosional event shaped the top of the T-bed and removed nearly all causative tubes of *Teichichnus* traces including their inhabitants (Fig. 12). Only organisms in deeply penetrating *Thalassinoides* shafts survived as these burrows are present in concretion 'halves' atop the T-bed (Fig. 5A). After the event, mud accumulated, the geochemical zones were reestablished, and concretion formation started at some nuclei. Their growth towards the T-bed, however, was prevented by the still high permeability of the ash in the T-bed, which depleted its alkalinity while becoming calcified in a pre-compactional stage (Kietzmann et al., 2020). The concretion 'halves' above the T-bed also record times of lowered or interrupted sedimentation; to grow they must have resided for at least some hundreds of years in the zone of carbonate supersaturation (e.g., Raiswell and Fisher, 2004; Lash, 2018; Blouet et al., 2021). Consequently, the concretions document discontinuous sedimentation characteristic of a sedimentary hiatus (e.g., Wetzel and Allia, 2000; Zatoń et al., 2011; Wetzel and Bojanowski, 2022).

The assignment of the studied *Teichichnus* to an ichnospecies is problematic since no specimen could be studied completely due to its extreme length, curved course and occurrence in solid rock. Even if that were possible, the upper part is usually truncated. Furthermore, different ichnotaxobases have been applied to *Teichichnus*, such as overall burrow shape, course, laterally diverging spreite, etc. (Knaust, 2018a). Considering the characteristics of the studied *Teichichnus*, it is assigned to *Teichichnus* isp. aff. *T. zigzag* because of some similarities despite some differences with Frey and Bromley's (1985) original diagnosis and Knaust's (2018a, b) emended diagnosis of *T. zigzag*. The original diagnosis includes specimens "in which cross-sectional views of the spreite exhibit a marked zigzag pattern; the overall width of the zigzagged spreite considerably exceeds the diameter of component



Fig. 10. Stable isotope, carbonate and organic carbon (C_{org}) data of samples taken from various parts of the *Teichichnus*-bearing bed and adjacent sediment in a schematic section; black diamonds refer to samples for which no stable isotope values have been determined.

burrow fill forming the spreite" (Frey and Bromley, 1985, p. 813). In Knaust's (2018a, p. 393) emended diagnosis, *T. zigzag* represents "arcuate to V-shaped burrows arranged in a subvertical plane with a tripartite burrow architecture consisting of a convex-down laminated



Fig. 11. Cross-plot of oxygen and carbon stable isotope data; data located between pristine Tithonian marine carbonates (blue field after del Rosario Lanz et al., 2021; black star after Veizer et al., 1999) and andesitic material (grey field after Rutman et al., 2021).

lower part, a terminal causative tube with passive fill, and a convex-up laminated, vertically laminated or homogeneous upper part. In cross-section, the spreite exhibits a marked zigzag pattern".

The studied *Teichichnus* traces partially match these diagnoses, specifically by (1) a spreite that is clearly wider than the causative tube (Fig. 5E) suggesting its lateral shift, (2) a rough lateral margin displaying a well-developed relief resembling *T. zigzag* but less pronounced, (3) the vertical undulation of lamellae packages documenting also a downward displacement of the causative tube although no protrusive spreite was observed, and (4) the considerable length of *T. zigzag* exceeding 95 cm at the type locality (Frey and Bromley, 1985, p. 813).

6. Discussion

The studied *Teichichnus* are in some aspects similar to *T. zigzag* but also differ from it in others. (1) The causative tube was definitely shifted laterally but less than in *T. zigzag*. (2) The lateral protrusions of *T. zigzag* figured by Frey and Bromley (1985, Fig. 7B, C), are acute and display a radius of curvature smaller than that of the causative tube; hence, they suggest that lateral relief of *T. zigzag* in the type material was enhanced by differential compaction. However, to evaluate this, trace and host sediment need to be studied in more detail. (3) The producer of the studied *Teichichnus* also worked downward but a protrusive spreite was not observed in contrast to *T. zigzag*. (4) The studied *Teichichnus* traces exhibit a curved to bent course. For *T. zigzag* such a burrow course cannot be excluded because it was not studied on bedding planes. Consequently, because of all these similarities, differences and uncertainties it seems appropriate to assign the studied burrows to *Teichichnus* isp. aff. *T. zigzag*.

Teichichnus preferably occurs in rapidly aggrading sediments making an upward shift of the causative tube advantageous. This may explain why *Teichichnus* is not a member of the standard de- and reoxygenation trace fossil successions because these were established for organic-rich



Repeated deposition of mud (and fine ash) by weak currents while bioturbation is going on



Long-lasting hyperpycnal flow





Slow sedimentation Weak currents Mud deposition **Bioturbation** Thalassinoides production Teichichnus truncation erosion 5 3 R 1 \bigcirc (\mathbf{D})

Diagenetic underbed and concretion formation

Fig. 12. Schematic development of the Teichichnus-bearing interval. (A) Continuous and episodic mud deposition forms a mud-dominated interval. (B) Presumably a storm erodes some of the mud. (C) A tempestite composed of volcaniclastic material covered by mud accumulates. (D) Organisms settle on the event bed and produce Teichichnus. (E)-(H) Thin sediment veneers form recurrently while Teichichnus is still produced. (I) Supposedly, a long-lasting hyperpychal flow reworks the seafloor down to the tempestite, truncates it and (J) covers it with mud. (K) Locally, concretions start to form in the newly deposited mud having a planar surface towards the truncated event bed. (L) Thalassinoides producers penetrate the incipient concretions while further mud accumulates.

black shales that accumulated at low rates in shelf, epicontinental or deep-marine settings (cf. Bromley and Ekdale, 1984; Savrda and Bottjer, 1986; Martin, 2004).

In fact, Teichichnus producers appear to be well adapted to rapidly aggrading settings, such as delta-front deposits experiencing pulsed, high sedimentation and (very likely) salinity fluctuations (Buckman, 1996); up to several centimetres to a few decimetres of sediment may accumulate per year (Corner and Fjalstad, 1993). These Teichichnus traces are 5–20 mm wide and up to 50 cm long and show an undulating winding course that is probably advantageous because the swirling flow induced in the causative tube can reduce sediment deposition therein (see above). Teichichnus producers must also tolerate grain-size changes; their traces are a common element of the shelf ichnofauna in heterolithic millimetric to centimetric sand and mud beds (e.g., Bland and Goldring, 1995). Teichichnus is a typical constituent of the Cruziana ichnofacies that is usually affected by tempestites (e.g., Buatois and Mángano, 2011). In such settings, Teichichnus producers may not only respond to

deposition but also to erosion by forming a protrusive spreite (e.g., Knaust, 2018a, b).

Teichichnus is commonly a few tens of centimetres long (e.g., Knaust, 2017). Nonetheless, T. rectus >148 cm and T. zigzag >95 cm in length have been described from Cretaceous chalk though they were interpreted then as fodinichnia (Frey and Bromley, 1985). In contrast, although enriched in relatively purified carbonate (coccoliths, etc.), these burrows could likely represent long 'microbial reactors' (see above) because they were constructed in anoxic host sediment covered by well oxygenated bottom water as indicated by a diverse, 'normal'-sized ichnofauna (cf. Frey and Bromley, 1985). Gardening behaviour matches this scenario and could have been applied for additional nutrition. Such a behaviour is also suggested for Cambrian Teichichnus enriched in fossil debris; first, it was interpreted as a feeding-faecal structure (Mikuláš et al., 1996) and later as a gardening burrow (Mikuláš, 2001). This trace was originally named Rejkovicichnus but was later synonymized with Teichichnus (see Knaust, 2018a). Accordingly,

Teichichnus producers probably applied gardening behaviour already in the early Phanerozoic, and the vertical undulations of purely retrusive lamellae packages, which have not previously been reported, provide further evidence not only for such a nutritional mode, but also for sequestrichnial behaviour.

The absence of traces typical of re-oxygenation, such as Chondrites, below the T-bed implies either an abrupt onset of oxygenation related to the depositional event or that the transitional deposits were eroded. The Teichichnus size militates well oxygenated conditions, presumably for several years (see above). Subsequently, Teichichnus disappeared probably due to erosion of the causative tubes and their inhabitants and only some deep-living Thalassinoides producers survived. Thereafter, Thalassinoides also disappeared, but traces indicating a gradual deoxygenation are lacking; evidently the oxygen supply decreased rapidly. The disappearance of Teichichnus coincides with the disappearance of ash and thus, indicates also a change in the sediment routing systems. Therefore, the spreite material stores information about the currents delivering sediment and providing oxygen. The material incorporated into the spreite consisted only subordinately of hemipelagic material because of the low amount of radiolarian tests but mainly of mud and ash that was delivered by currents probably originating in the area of the volcanic arc to the west. These currents were presumably less erosive and they preferentially entrained fine-grained organic-rich surface sediments. Because Teichichnus was produced during the still ongoing transgression of the Vaca Muerta Formation, this scenario is not unlikely because marine water definitely spilled over the arc to fill the subsiding and expanding basin. Storms reworking shallowwater areas could have transferred some coarse material basinward (e. g., Zeller et al., 2015; Kietzmann et al., 2016; Paz et al., 2022a).

Since no diagnostic features are preserved in the mud covering the Tbed, it cannot be decided which process caused the truncation of the Tbed, storm-induced or other currents such as severe hyperpycnal flows. However, if the mud covering the upper surface of the T-bed was related to the erosional event, then this surface was probably shaped by a longlasting hyperpycnal flow like those that were recognized in outcrops not too far away from the study area (Otharán et al., 2018, 2020). In any event, oxygen was still provided and the *Thalassinoides* producers continued to burrow.

Consequently, the long-term low-oxic to dysoxic conditions during deposition of the muddy parts of the basal Vaca Muerta Formation were repeatedly affected by currents of varying strength spilling over from the Palaeo-Pacific and hyperpycnal flows. This scenario is similar to that described for the basal Vaca Muerta Formation about 500 km to the south in the Zapala area; the lithofacies is typical of an offshore transition domain characterized by event beds and mass movements (Krim et al., 2017). Similarly, to the north, in the Mendoza area, long-term anoxic to dysoxic conditions were interrupted by oxygenation events characterized by Chondrites and Thalassinoides (Doyle et al., 2005). Therefore, the general setting along the eastern margin of the Neuquén Basin during the early transgression of the Vaca Muerta Formation appears to have been rather similar with respect to depositional processes; the tendency towards low-oxic to anoxic conditions was repeatedly interrupted by oxygenation phases caused by storms, hyperpycnal flows, and water flowing in from the Palaeo-Pacific that lead to bottom current activity of varying intensity (Paz et al., 2022a, b).

During the ongoing transgression, when water depth already exceeded the zone mixed by waves, the water body was prone to become stratified. At least seasonally, cold, dense marine water flowing in from the Palaeo-Pacific could constitute the bottom water body that was covered by buyoant freshwater discharged by rivers in the south and east (Fig. 13). During low discharge, the rivers delivered suspended material (hypopycnal flows and interflows), whereas during flood hyperpycnal flows could form (e.g., Otharán et al., 2020). Thus, an estuarine circulation very likely developed when freshwater discharge was high (cf. Paz et al., 2022a). Towards the north, increasing evaporation and decreasing precipitation might have favoured the formation



Fig. 13. Possible arrangement of water masses in the Neuquén Basin during the time of the Lower Vaca Muerta Formation (three dimensional view modified from Schwarz et al., 2006). During the initial transgression spill-over of marine water from the Palaeo-Pacific Ocean and freshwater discharge by rivers from the South led to development of an estuarine circulation. Subordinately, some dense saline water might have formed in the (semi-)arid area to the north.

of dense, saline, warm water that could sink to the basin floor, but its oxygen content would have been low because solubility of oxygen decreases with increasing temperature (e.g., Open University Course Team, 1995). Layers rich in biogenic carbonate intercalated with muddy basin-interior deposits document such transport (Kietzmann et al., 2016, 2020; Paz et al., 2022a). During dry periods, such an anti-estuarine circulation might have replaced the estuarine circulation established in humid periods (Paz et al., 2022a). In the transgression, the inflow of Palaeo-Pacific water probably prevailed to fill the still expanding and subsiding basin (Fig. 13). Regarding the oxygen content of this water, it can only be speculated because seasonal coastal upwelling in the Palaeo-Pacific affected this region of South America (e.g., Parrish and Curtis, 1982). However, the water spilling over from the Pacific probably became oxygenated by wave mixing when traversing the shallow-water area of the volcanic arc. Likely, it was funnelled into some inlets traversing the volcanic arc between islands. The bottom-water oxygen in the Neuquén Basin was consumed by organic matter settling to the seafloor, since high nutrient supply by both rivers and reworking of coastal plains during transgression fueled primary production. With increasing water depth, stratification of the water body became stabler.

The basal Vaca Muerta Formation represents a dynamic setting with respect to both sediment delivery namely siliciclastics from the continent, volcanic material from the arc in the west and carbonates from the (northern) basin margin/clinoform tops. In addition, water circulation during initial transgression was characterized by water inflow from the Palaeo-Pacific and freshwater from land. All the factors and processes are recorded by the T-bed consisting of current-reworked volcaniclastic material, whereas the *Teichichnus* traces are enriched in mud. Following a pronounced erosional phase during which the T-bed was truncated, the T-bed was covered with mud. Stratiform concretions, in addition, record discontinuous deposition.

7. Conclusions

The basal interval of the Vaca Muerta Formation represents a dynamic depositional setting. Sediment accumulation during the deposition of the lower part of the basinal Vaca Muerta Formation was rather discontinuous as evidenced by strata-bound concretions a few tens of centimetres in size, which must have resided within the same geochemical zone during a growth that may have taken several hundreds to thousands of years during which starved sedimentation prevailed.

Repeated hydraulic events such as storms, hyperpycnal or other density-driven flows like spillover of cold dense water from the Palaeo-Pacific interrupted the long-term (background) dysoxic conditions. The latter are documented by organic-rich mudrock exhibiting crude, irregular lamination while fine, parallel lamination typical of anoxic black shale settings is absent. Shallowly penetrating, small organisms very likely churned the sediment.

Storm-induced currents deposited a remarkable ash bed up to 30 cm thick, that later became calcified. It was colonized by producers of *Teichichnus* isp. aff. *T. zigzag* reaching a size similar to that typical of oxic conditions. Presumably, after initial deposition subsequent spill-over events of Palaeo-Pacific water provided oxygen and deposited ash and mud that led the *Teichichnus* producers to shift their causative tube upward. Since *Teichichnus* is not among the trace fossil suite typically of de- or re-oxygenation, its presence was presumably caused by considerable sediment aggradation.

The extreme length reaching >220 cm and the curved course including U-turns of *Teichichnus* indicate sufficient supply of oxygenated water and benthic food provided together with fine ash and mud by bottom currents generated by cold, dense Palaeo-Pacific water spilling over the volcanic arc in the west.

The causative tube of *Teichichnus* located in anoxic sediment was flushed with oxygenated water and a steep geochemical gradient developed across the tube wall that fostered microbial activity making the tube a long microbial reactor. Therefore, gardening behaviour is likely. Moreover, previously formed spreite domains were locally reworked as indicated by vertically undulating lamellae packages that overprint pre-existing lamellae and thus, document sequestrichnial behaviour, since organic-rich material was collected and stowed in the burrow for later utilization by the *Teichichnus* producer.

CRediT authorship contribution statement

Andreas Wetzel: Writing – original draft, Investigation, Conceptualization. Noelia B. Carmona: Writing – review & editing, Investigation, Conceptualization. Juan J. Ponce: Writing – review & editing, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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