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Palaeoenvironmental significance of beds bioturbated by *Haentzschelinia ottoi* (Geinitz) in delta front facies, Lajas Formation (Middle Jurassic)

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ABSTRACT

The distribution of *Haentzschelinia ottoi* (Geinitz) is studied from the Lajas Formation (Middle Jurassic) of the Neuquén Basin in Arroyo Carreri. For this work were considered more than 200 specimens and their relation with the facies and other trace fossils, as well as the ichnofabric index (ii) and the bedding plane bioturbation index (bpbi) were determined. *H. ottoi* appears in fluvio-dominated delta front (FA2) and fluvio-dominated delta front to delta plain with tidal influence (FA3). In general, trace fossils correspond to deposit-feeders (*H. ottoi*, *Planolites*, ?*Taenidium*, ?*Parahaentzschelinia*), suggesting the development of an impoverished *Cruziana* ichnofacies. In particular, *H. ottoi* constitutes monoichnospecific associations with ii/bpbi = 2-3 (in FA2 and FA3) or more diverse associations with other trace fossils and ii/bpbi = 3-4 (only in FA3). The development of one association or another depends on the interplay between sediment discharge and salinity conditions. More diverse associations with ii/bpbi = 3-4 would be favoured by a rise in salinity under the influence of tides and enough time for substrate colonisation by other deposit-feeders. Lower salinity conditions or high frequency of sediment discharge would have given rise to monoichnospecific associations of *H. ottoi* with ii/bpbi = 2-3.

Keywords: *Dactyloidites*, trace fossils, salinity, sediment discharge, Jurassic.

RESUMEN

Se analizó la distribución de *Haentzschelinia ottoi* (Geinitz) en los afloramientos de la Formación Lajas (Jurásico Medio) de la localidad de arroyo Carreri en la Cuenca Neuquina. Se consideraron más de 200 ejemplares y su relación con las facies y con otras trazas fósiles, se determinaron los índices de icnofábrica (ii) y de bioturbación sobre el plano de estratificación (bpbi). *H. ottoi* aparece en facies de frente deltaico dominado por acción fluvial (FA2) y en facies de frente deltaico dominado por acción fluvial con influencia de mareas (FA3). En general, las trazas fósiles corresponden a depositívoros (*H. ottoi*, *Planolites*, ?*Taenidium*, ?*Parahaentzschelinia*), indicando el desarrollo de una icnofacies de *Cruziana* empobrecida. En particular *H. ottoi* aparece formando asociaciones monoicnoespecíficas con ii/bpbi = 2-3 (en FA2 y FA3) o asociaciones con otras trazas de depositívoros con ii/bpbi = 3-4 (solo en FA3). El desarrollo de una u otra se deberían a variaciones en la descarga de sedimento y a diferencias de salinidad. Las asociaciones con mayor diversidad y ii/bpbi = 3-4 estarían favorecidas por un aumento en la salinidad bajo la influencia de las mareas y tiempo suficiente para la colonización del sustrato por otros depositívoros. Baja salinidad o frecuentes descargas de sedimento habrían dado origen a asociaciones monoicnoespecíficas de *H. ottoi*.

Palabras clave: *Dactyloidites,* trazas fósiles, salinidad, descarga sedimentaria, Jurásico.

INTRODUCTION

The trace fossil *Haentzschelinia* (= *Dactyloidites*) *ottoi* is a multitiered rosette-like structure attributed to a deposit-feeder producer (fodinichnion) (Fürsich and Bromley 1985) which ranges from the Middle Jurassic to the Holocene, with Triassic appearances not illustrated or doubtful in age (Muñoz et al. 2019). There are numerous papers where *H. ottoi* is described and interpreted, standing out the works of Fürsich and Bromley (1985), Pickerill et al. (1993), and de Gibert et al. (1995) for their exhaustive understanding of the process of production of this trace fossil and the detailed morphological descriptions. Later, the type material has been re-described by Wilmsen and Niebuhr (2014), who also analysed new Cenomanian trace fossils and proposed an emended diagnosis.

H. ottoi usually occurs in fine to medium grained sandy marine or transitional settings. It has been frequently recorded in estuarine facies (de Gibert et al. 1995), shoreface deposits (Curran and Glumac 2021), and more frequently, in deltaic deposits (McIlroy 2005, Canale et al. 2016, 2020, Patel et al. 2023), for which a detailed analysis of this ichnospecies from an environmental point of view was presented by Agirrezabala and de Gibert (2004). Although uncommon, there are some records in carbonate deposits (Blissett and Pickerill 2004, Lazo et al. 2008; Srivastava et al. 2010, Mayoral et al. 2013, Curran and Glumac 2021). *H. ottoi* has been reported several times from the siliciclastic deposits of the Bathonian-Callovian Lajas Formation, either in tide dominated deposits (McIlroy et al. 2005) as well as in fluvial dominated delta front facies (Canale et al. 2015, 2016, 2020), and in shoreface deposits (Canale et al. 2020), among other mentions. Here we pay special attention to the assemblages developed in deltaic systems by focusing this work in the delta front facies of the Lajas Formation at Arroyo Carreri where *H. ottoi* varies in abundance and integrates distinctive associations, being particularly abundant in some horizons with tidal influence.

In general, trace fossil assemblages developed in deltaic deposits put in evidence environmental parameters which include high and discontinuous sedimentation rates, water turbidity, and salinity changes, among others. These processes are stress factors that give origin to assemblages with low diversity, low bioturbation intensity and dominance of deposit feeders (Agirrezabala and de Gibert 2004, MacEachern et al. 2005, Buatois and Mángano 2011). The trace fossils assemblages developed in the Lajas Formation do not evade these controls. The growing interest in deltaic systems and in the use of trace fossils as a tool to better understand depositional environments, turned the Lajas Formation into a case study that gave rise to numerous sedimentologic/ichnologic papers based on outcrop data (Poiré and del Valle, 1992, McIlroy et al. 2005, McIlroy 2007, Rossi and Steel 2016, Canale et al. 2015, 2016, 2020, Gugliotta et al. 2015, 2016a, b, Kurcinka et al. 2018) and core samples (Arregui 2019, Arregui and Rodríguez 2022), although none of those works were carried out in the Arroyo Carreri section studied here. In this locality, detailed facies analyses were carried out by Bermúdez (2018), López Cajaraville (2019), López Cajaraville and Kietzmann (2019), and Millán (2023), who recognised different subenvironments within an inertial river-dominated delta system: prodelta turbiditic lobes and thick prodelta muddy facies (Los Molles Formation), delta front and delta plain facies (Lajas Formation), and fluvial deposits (Challacó Formation). On the other hand, Kietzmann and Iglesia Llanos (2020) reported from this section the first record of crustacean coprolites for the Bajocian–Callovian of South America that occurs in association with terebellid agglutinated polychaetes within prodelta facies. Schencman et al. (2022) performed a preliminary provenance analysis of the sandstones, indicating the absence of compositional variations, which reflects stable conditions in the source area. Fernandez de la Rúa et al. (2023) presented a facies analysis for deltaic deposits of the Lajas Formation and slope facies of Los Molles Formation, which was complemented by a Magnetic Susceptibility Anisotropy (MSA) study, where the paleocurrents of the fine-grained facies can be established, as well as the progradation direction of the sedimentary system.

In this work we describe the occurrence of *H. ottoi* in the delta front fluvio-dominated deposits of the Lajas Formation at Arroyo Carreri section, and analyse its distribution in intervals with and without tidal influence with the purpose of characterising this trace fossil under both regimes.

NOMENCLATURE REVIEW OF *HAENTZSCHELINIA OTTOI*

This trace fossil is widely known under the name of *Dactyloidites ottoi*, but before this, it went through different denominations that can be consulted in greater detail in Fürsich and Bromley (1985), de Gibert et al. (1995), Wilmsen and Niebuhr (2014), Belaústegui et al. (2015), Boyd and

McIlroy (2016), and Patel et al. (2023). Among these, we can highlight that it was described for the first time by Geinitz (1849) as *Spongia ottoi* when it was interpreted as a sponge. The first one in understanding this structure as a trace fossil was Morin (1907) who compare it with fiddler crab feeding traces, but his contribution was ignored at that time, until Häntzschel (1930) recovered this idea from oblivion. Vyalov (1964) created the ichnogenus *Haentzschelinia* to accommodate this material and other two ichnospecies and Häntzschel (1975) set up its diagnosis, although information about branching of radial elements and obliqueness of central shaft was missing in it.

Fürsich and Bromley (1985) described the three-dimensional structure of this trace fossil for the first time and proposed a detailed interpretation of its mode of formation. They also proposed the synonymy of *Dactyloidites* Hall 1886, *Brooksella* Walcott 1896, and *Haentzschelinia* Vyalov 1964 considering that the three ichnogenera reflect the same basic behaviour pattern, being *Dactyloidites* the senior synonym.

The synonymy proposed by Fürsich and Bromley (1985) has been questioned by Vyalov (1989) and Schweigert (1998) who continued considering *Haentzschelinia* as a valid name different from *Dactyloidites* based on the morphological differences. Additionally, *Brooksella* has been reinterpreted as a pseudofossil by Runnegar and Fedonkin (1992) and recently by Nolan et al. (2023). Despite this, the denomination *Dactyloidites ottoi* has been, and still is, widely used in literature. In recent years, Wilmsen and Niebuhr (2014) supported the reassignment of *Haentzschelinia* to *Dactyloidites*, after a re-description of the type material of *Spongia otto*i and new Cretaceous material from Germany since, for them, the arguments against this synonymization are unfounded from an ichnotaxonomic viewpoint. Later, Belaústegui et al. (2015) listed in more detail the arguments against the synonymy, whose criteria we will adopt in this work. Some author, like Seilacher (2007), Buatois et al. (2016), and Muñoz et al. (2019), also followed the restitution of the ichnogenus *Haentzschelinia*. Based on this change, *Dactyloidites* is a name reserved for more simple radial structures common in early Paleozoic deposits (Jensen et al. 2013, Belaústegui et al. 2015).

Previous works carried out in different deposits of the Lajas Formation mentioned this trace fossil as *Dactyloidites* isp. (McIlroy et al. 2005, Canale et al. 2015) or as *Dactyloidites ottoi* (Gugliotta et al. 2015). However, it is important to highlight that the name *Haentzschelinia* had already been used by Canale et al. (2016, 2020) and Arregui and Rodríguez (2022) during their studies of trace fossils in outcrop and subsurface. In this work, the material from the Lajas Formation is here treated as *Haentzschelinia*. Furthermore, all the post-Paleozoic mentions to *Dactyloidites ottoi* will be considered as *Hantzchelinia ottoi*.

MATERIALS AND METHODS

Field work was carried out at Arroyo Carreri section (38°52’54”S, 70°26’36”W) of the Lajas Formation, outcropping 30 km west of the city of Zapala (Fig. 1). It involved the description of the complete sedimentary section taking into account geometry, lithology, and sedimentary structures for facies analysis. Lithofacies code follows Miall (1985). Trace fossils were recorded, and special attention was paid in their distribution and relative abundance, including more than 200 specimens of *H. ottoi*. Rock and trace fossil samples were collected for petrographic description and a more detail recognition of the internal structure. Descriptive criteria proposed by Fürsich and Bromley (1985) for *D. ottoi* are followed here.

The degree of bioturbation is expressed in term of ichnofabric index (ii) following Droser and Bottjer (1986, 1989), that varies from 1 (no bioturbation recorded) to 6 (bedding homogenized). This scheme is used to evaluate the ichnofabric as represented on the vertical surfaces. For the beds with *H. ottoi* studied at Arroyo Carreri the following ii have been recorded: ii2) discrete, isolated trace fossils with up to 10% of original bedding disturbed; ii3) approximately 10 to 40% of original bedding disturbed with burrows generally isolated, but locally overlap; 4) last vestiges of bedding discernible with approximately 40 to 60% disturbed, burrows overlap and are not always well defined. Additionally, the bedding plane bioturbation index (bpbi) proposed by Miller and Smail (1997) has been used to determine the degree of bioturbation on bedding plane. This index has the same categories as the ii of Droser and Bottjer (1986) and for *H. ottoi* at the studied locality it can be: 1) no bioturbation; 2) 0-10% disruption, that can be represented by zones of generalized disruption or by discrete trace fossils, where most of the structures are isolated; 3) 10 to 40% disruption with discrete traces, zones of disruption, or both; 4) 40 to 60% disruption with discrete traces and/or zones of generalized disruption, interpenetration of discrete structures is more common than in 3. For monoichnospecific horizons of *H. ottoi* it has been used applying the scheme for same size and shape and even distribution, and for horizons where other trace fossils are present, applying the scheme of different size, and shape and even distribution.

GEOLOGICAL SETTING

The Neuquén Basin was a retro-arc basin developed in Mesozoic times along the Pacific margin of South America (western Argentina) (Fig. 1a). The tectonic history of the basin is polyphasic due to the occurrence of several compressional and extensional phases that led to different major orogenies (Ramos 1999). The first corresponds to the Gondwana Orogeny, an extensional back-arc regime that took place during the Carboniferous-Middle Permian, followed by the compressive San Rafael Orogeny in the Middle Permian (Ramos 1988, Mpodozis and Ramos 1989). At this time to the south of the basin, the collision of the Patagonia terrain with Gondwana, would have prompted a regional penetrative deformation of the basement in the area of the Huincul Arch to the south of the study area (Mosquera et al. 2011). By the Late Permian – Early Triassic, a generalized extensional tectonic regime prompted the onset of acidic volcanism and tectonic subsidence (Llambías et al. 2003, 2007, Llambías and Leanza 2005, Schiuma and Llambías 2008).

This extensional regime continued throughout the Late Triassic–Early Jurassic, creating a series of narrow, isolated depocenters which thrived though large transcurrent fault systems that were initially filled with continental deposits of the Precuyo Cycle (Gulisano 1981, Vergani et al.

1995, D'Elia et al. 2012, 2015, Buchanan et al. 2017). The Early Jurassic–Late Cretaceous was characterised by a thermal subsidence regime with localized tectonic events. Depocenters continued to be filled with continental and marine siliciclastic, carbonate and evaporite deposits (Cuyo, Lotena, and Mendoza Groups; Gulisano et al. 1984, Legarreta and Gulisano 1989, Legarreta and Uliana 1991, 1996). During the later Early and Late Cretaceous, the third Andean Orogeny occurred, in which major compression caused by the subduction of the Pacific plate prompted the formation of the Agrio fold and thrust belt in the Paleogene (Zapata and Folguera 2005). Finally, by the middle Miocene the Quechua Orogeny in the Chilean-Argentinian Andes took place and reactivated the Agrio fold and thrust belt (Zapata and Folguera 2005, Folguera et al. 2004, 2007).

The Middle Jurassic in southern and central Neuquén is characterised by siliciclastic and minor carbonate facies of the Cuyo Group (Fig. 1b). This group originated as the result of an extensive marine transgression in the early Pliensbachian, with marine deposits of the shallow-water limestones of the Chachil Formation (Leanza 1992) in structural heights and deep marine Los Molles Formation (Weaver 1931) in depocentral areas, which overlie continental facies of the Precuyo Cycle (Gulisano et al. 1984, Leanza 1992). These units are interdigitated and followed by deltaic and shallow-marine deposits of the Lajas Formation (early Bajocian to early Callovian), and then by fluvial deposits of the Challacó Formation (Bathonian to early Callovian) (Gulisano 1981, Gulisano et al. 1984, Spalletti 1995, Zavala and González 2001). The Cuyo Group ended with the evaporitic and carbonate facies of the Tábanos Formation that resulted from the first disconnection with the Pacific Ocean (Riccardi and Gulisano 1992, Legarreta 2002).

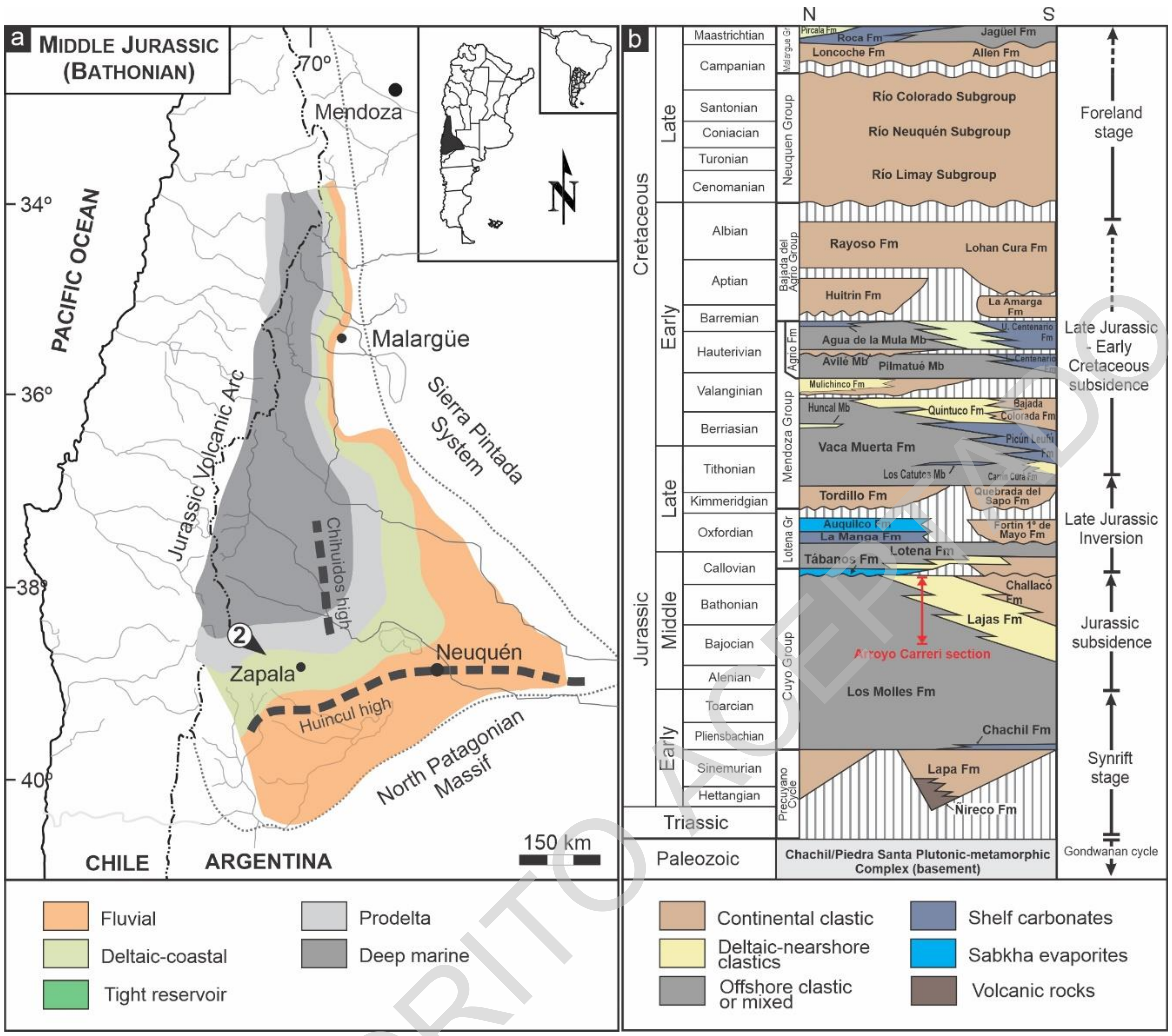


Figure 1. a) Location map of the Neuquén Basin and a paleogeographic map for the Bathonian and studied sections (modified after Legarreta and Uliana 1991). **b)** Chronostratigraphic chart of the Neuquén Basin for the southern and central Neuquén (modified after Leanza et al. 2020).

LAJAS FORMATION AT ARROYO CARRERI

Age of the section

The studied section consists in 600 m of marginal-marine and shallow-marine sandstones (Fig. 2), overlying the marine mudstones of the Los Molles Formation (late Bajocian-early Bathonian) and overlain by the continental deposits of the Challacó Formation (early Callovian). In the upper part of Los Molles Formation at Arroyo Carreri, Kietzmann and Iglesia Llanos (2020) reported ammonites belonging to the late Bajocian ROTUNDUM Standard Zone, the early Bathonian

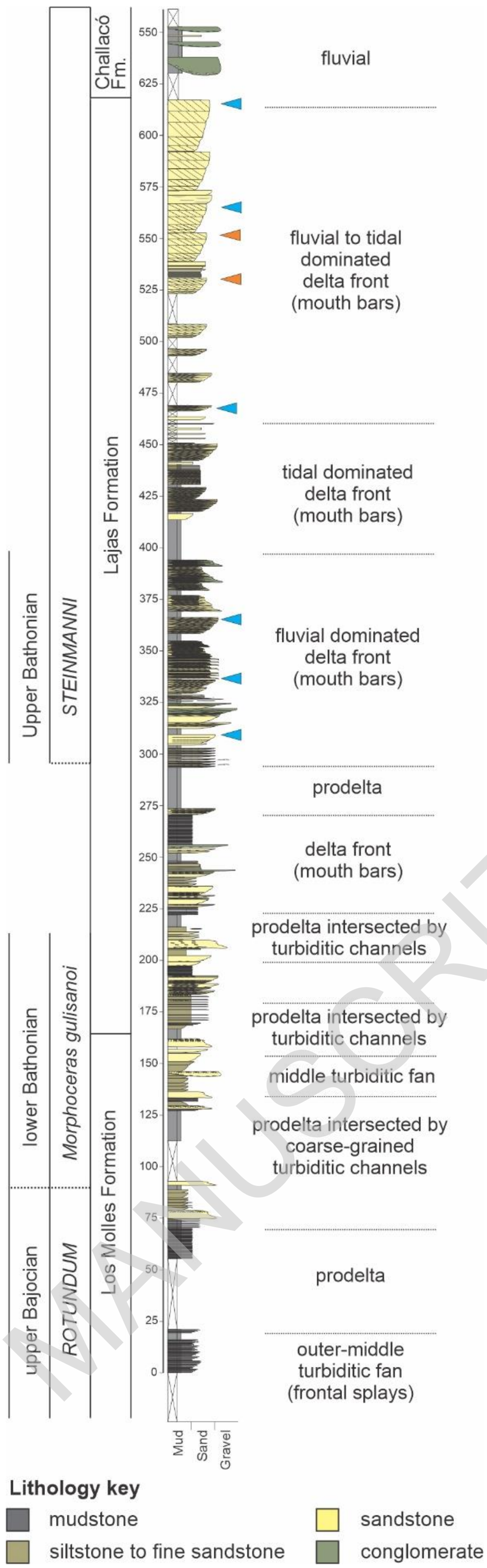
Lobosphinctes and *Morphoceras gulisanoi* Andean Zones, and for the Lajas Formation reported also ex-situ ammonite from the late Bathonian age STEINMANNI Standard Zone.

Facies analysis

A detailed sedimentologic study for this locality is beyond the scope of this paper, hence here only a short description of the facies will be done and a more complete facies analysis will be introduced in a paper now in process. Four facies associations have been recognised in this locality: prodelta, fluvio-dominated delta front, fluvio-dominated delta front with tidal influence, and subaqueous delta plain (Fig. 2). The abundance and distribution of the different facies associations allow interpreting this section as a fluvio-dominated delta with tidal influence in some intervals.

Facies association 1 (FA1) - delta plain: Facies association 1 is dominated by laminated to massive mudstones (Fl, Fm) with abundant plant debris, and occasionally heterolithic deposits. This facies appears for first time in the middle of the studied section and continue appearing for the rest of the succession through intervals of 2–4 m in thickness. It contains two types of interspersed sand-gravel lenticular bodies (Fig. 3a). First type is composed of 10-30 cm thick horizontal- and/or ripple-laminated sandstones (Sh, Sr), showing coarsening-upward trend, erosive bases and planar-convex lensoidal geometry. Second type consists of 50-80 cm thick thinning-upward sandy-conglomerate bodies, with massive conglomerates (SGm), and planar cross stratified and horizontal laminated sandstones (Sp, Sh). Bases are erosive and show lenticular to lentiform shape. Within these facies no fossil traces were recognized.

The muddy nature of these deposits suggests a low energy setting controlled by fallout of suspended fine material. Lamination in mudstones derives from episodic sedimentation. Sandy coarsening-upward beds with erosive base and planar-convex lenticular geometry are interpreted as crevasse splays, whereas that thinning-upward sandy-conglomerate bodies are interpreted as secondary distributary channels within an interdistributary bay successions (Coleman and Prior 1982; Bhattacharya and Walker 1992, Bhattacharya 2010).



upper Bajocian
lower Bathonian
Upper Bathonian
ROTUNDUM
Morphoceras gulisanoi
STEINMANNI
Los Molles Formation
Lajas Formation
Challacó Fm.
fluvial
fluvial to tidal dominated delta front (mouth bars)
tidal dominated delta front (mouth bars)
fluvial dominated delta front (mouth bars)
prodelta
delta front (mouth bars)
prodelta intersected by turbiditic channels
prodelta intersected by turbiditic channels
middle turbiditic fan
prodelta intersected by coarse-grained turbiditic channels
prodelta
outer-middle turbiditic fan (frontal splays)
Mud
Sand
Gravel
Lithology key
mudstone
siltstone to fine sandstone
sandstone
conglomerate

Figure 2. Lithology log of the Arroyo Carreri section, with age information, according to ammonite biostratigraphy (Riccardi pers. comm. in Kietzmann and Iglesia Llanos 2020), and lithostratigraphic units. The beds with the highest abundance of *H. ottoi* are indicated by arrows: blue arrows for monoichnospecific beds of *H. ottoi* and orange arrows for diverse associations of trace fossils dominated by *H. ottoi*.

Facies association 2 (FA2) - Fluvio-dominated delta front: Facies association 2 consists of coarsening upward cycles up to 1 m in thickness with laminated mudstones (Fl), horizontal laminated sandstones (Sh), ripple laminated sandstones (Sr), bioturbated massive sandstones (Sm), and/or sandstones with convolute lamination or fluid-escape structures, that pass to planar or trough cross-stratified sandstones (Sp, St), and planar stratified coarse-grained sandstones to fine-grained conglomerates (SGp, Gp) (Fig. 3b). The stacking of mouth bars constitutes coarsening-upward successions (up to 3.5 m in thickness). Current ripples and microbial induced sedimentary structures can appear at the top of these cycles. Trace fossils are dominated by *Haentzschelinia ottoi*, while *Paleophycus* isp. has been recorded, as well. Other beds have *Ophiomorpha* with a discontinuous and scarce record. This facies is well represented throughout all the succession.

Facies association 2 is construed as a delta front dominated by fluvial action. The coarsening-upward cycles represented by large-scale cross-stratified sandstones are interpreted as constructive mouth bars (Van Heerden and Roberts 1988, Plink-Björklund and Steel 2005, Bhattacharya 2006) and their stacking led to the development of deltaic lobes. Microbially induced sedimentary structures, suggest low-energy stages and would have developed during the gradual abandonment of the active lobe. The trace fossils association indicates fluctuations in fluvial discharges and variations in the water energy, sedimentation rate, and salinity (Pemberton et al. 1992, MacEachern et al. 2005, Canale et al. 2016).

Facies association 3 (FA3) - Fluvio-dominated delta front to delta plain with tidal influence: Facies association 3 consists of lightly coarsening and thickening-upward cycles (10–20 m). These cycles are internally divided in 1-3 m thick sets starting with bidirectional cross-stratified sandstones (Sp_b) or cross-stratified sandstones with mud drapes (Sp_C) (Fig. 3c-e), with an erosive surface that cannibalizes previous deposits. This is followed by inclined heterolithic stratification (IHS). Trace fossils are represented by *Ophiomorpha* isp. (Fig. 3d), *Haentzschelinia ottoi*, *Planolites* isp. and *Gyrochorte* isp. It is worth highlighting that the first two can constitute moderately to highly bioturbed beds (ii = 3-4) but do not appear together. This facies dominates over 60 m in the middle section of the succession.

Bidirectional cross-stratified sandstones (Sp_b) and cross-stratified sandstones with mud drapes (Sp_C) are typical evidence for tide-influenced settings (Dalrymple et al. 2003). However, coarsening and thickening-upward trends, suggest the progradation of lobed forms like mouth bars (Bhattacharya 2006). Inclined heterolithic stratification indicate lateral migration of sinuous channels, and development of point bars (Smith 1987, 1988, Thomas et al. 1987, Eberth 1996, Dalrymple et al. 2003, Dalrymple and Choi 2007), and here would be related with small intertidal channels in areas with high suspended-sediment concentrations (Bridges and Leeder 1976, de Mowbray 1983). FA 3 is interpreted as a tidal-influenced delta front to delta plain.

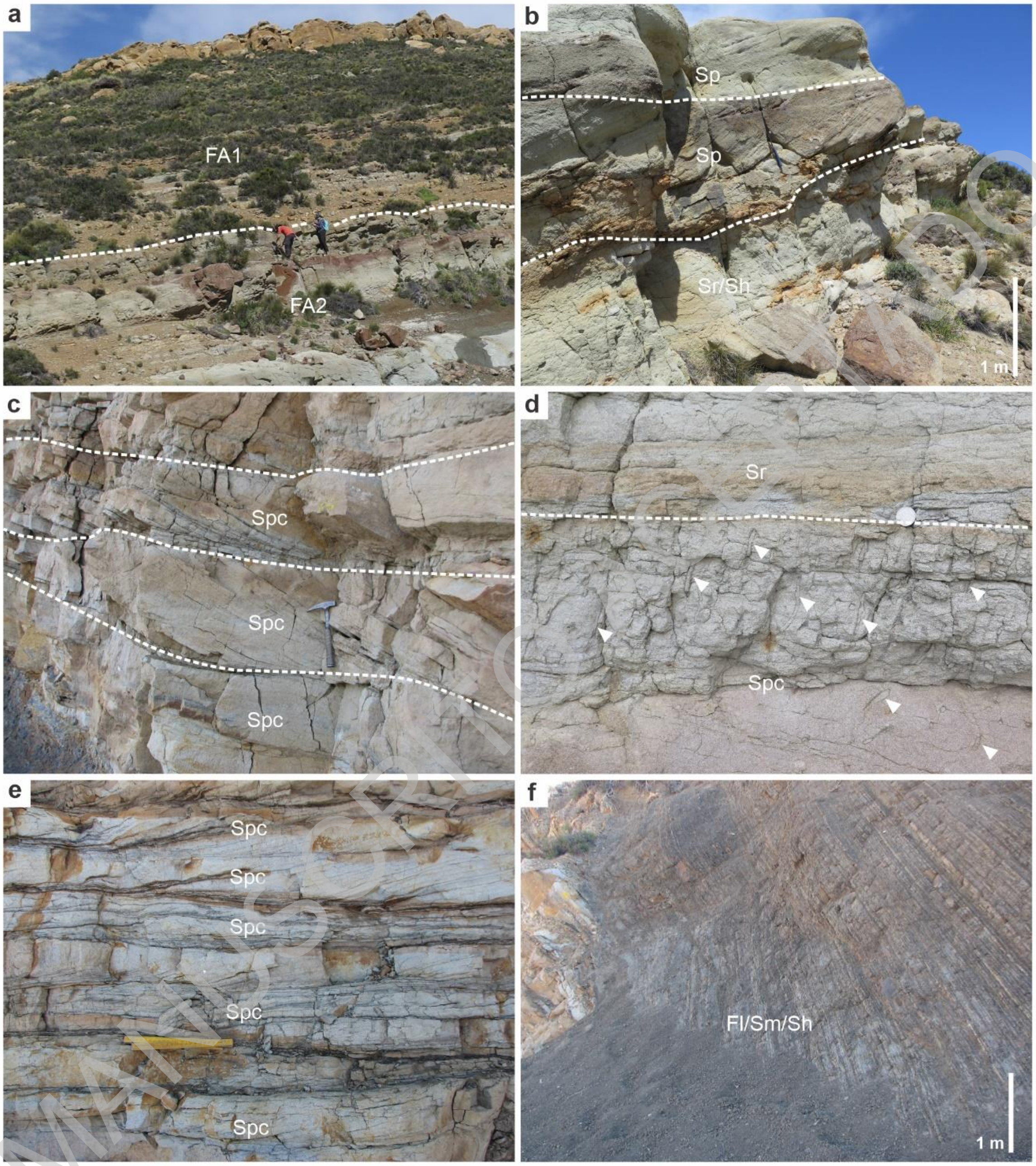


Figure 3. Facies associations recognised in Arroyo Carreri section of the Lajas Formation: a) General view of facies association 1 (delta plain) and facies association 2 (fluvio-dominated delta front), showing initially small coarsening-upward cycles, above a succession formed by sandy channels, with muddy overbanks, and in the upper part, sandy-gravelly channels of higher hierarchy; b) River-dominated mouth bar deposits of facies association 2, showing typical coarsening-upward trend; c-e) Tidal-influenced mouth bar deposits of facies association 3, characterized by their bipolarity, presence of mud drapes and bioturbated surfaces with *Ophiomorpha* (white arrows); f) Muddy

deposits of facies association 3 (prodelta) with intercalations of thin beds of sandstones. Scales: hammer (in c) = 33 cm, coin (in d) = 2 cm, meter (in e) = 20 cm. References: Sp) planar cross-stratified sandstones, Spc) cross-stratified sandstones with mud drapes, Fl) laminated mudstones, Sm) massive sandstones, Sh) horizontal laminated sandstones.

Facies association 4 (FA1) – Prodelta: It consists in coarsening and thickening upward, massive to horizontal laminated mudstone deposits (Fm, Fl), 20-40 cm thick. Some horizontal laminated and current ripple laminated sandstones (Sh, Sr) are interspersed among mudstone facies, showing thickness of 2–10 cm (Fig. 3f). These deposits contain abundant plant debris, and trace fossils of the *Cruziana* ichnofacies, such as *Thalassinoides* and *Planolites*.

Laminated and massive mudstones (Fl, Fm) are interpreted as fallout of suspended fine material, probably as hypopycnal plumes, and accumulated below the storm wave base. Sandy deposits are probably associated with turbidity currents generated by gravitational collapse of mouth bars (Bhattacharya 2010, Shanmugam 2018) or by hyperpycnal flows during exceptional river discharges (Mulder et al. 2003, Steel et al. 2016, Zavala and Arcuri 2016). The thick development of these deposits and the described features enable us to interpret FA1 as a prodelta setting (Bates 1953, Bhattacharya and Walker 1992, Bhattacharya 2006, 2010, Gomis-Cartesio et al. 2017).

HAENTZSCHELINIA OTTOI **IN ARROYO CARRERI SECTION**

Ichnogenus *Haentzschelinia* Vyalov 1964

Ichnospecies *Haentzschelinia ottoi* (Geinitz 1849)

Diagnosis (emended by Wilmsen and Niebuhr 2014): Fan-shaped, rarely palmate *spreiten* structure originating from a central, vertical to oblique shaft leading downwards into the sediment. The radial elements are subhorizontal protrusive vertical *spreiten* (probes), mostly forming incomplete circular rosettes of 200º-270º. Number of radial elements up to 20 due to branching (bi- and trifurcation) of 6-9 primary probes. Diameter of rosettes between 30 and 75 mm, width of radial elements between 4 and 6 mm.

Ethology and producer: This trace fossil is produced by a deposit feeder reworking the sediment (Fürsich and Bromley 1985; de Gibert et al. 1995). This behaviour is described in detail by Fürsich and Bromley (1985) who considered that the producer would have been a worm-like organism possibly with a proboscis that it would have used to rework the sediment. This interpretation is supported by Wilmsen and Niebuhr (2014) who connected it with the feeding behaviour of modern lugworm *Arenicola marina* studied by Rijken (1979).

Material: Over 200 specimens were described in outcrop and fragments from 3 specimens were collected for petrographic description.

Taphonomy: H. ottoi is preserved as full-relief structures. When weathering exposed the rosettes in the upper surface of bedding plane, these are preserved as convex epireliefs. Less frequently is preserved in the lower surface of bedding plane as convex hiporelief. The occurrence of some incomplete specimens is also attributed to weathering.

Description: Rosette-like structures with a diameter that varies between 4 and 5 cm. Each rosette has radial elements arranged in fans covering slightly more than half a circle (Fig. 4a). These radial elements diverge from a vertical to subvertical central shaft in a number up to 6, but probably this number is higher taking into account the poor preservation of some specimens. Usually, the central shaft is not preserved, instead, it is replaced by bioturbated sediment with a diameter of 7-15 mm, which is at least twice the diameter of the radial elements. Radial elements are elongated, 2-5 mm width relatively constant for each rosette, and can branch further once or twice (fig. 4a). Radial elements have an ellipsoidal cross-section with its hight slightly larger than its width, with a convex upper part and a convex or a gently concave lower base (Fig. 4b-c). These elements are arranged in up to four tiers, although more frequently two or three, with a constant orientation within a single rosette (Fig. 4b-d), appearing parallel to stratification or slightly inclined downwards. Rosettes with four tiers can reach 4.5 cm in hight.

The host rock is made of fine- to medium-grained lithic feldsarenites and litharenites, composed by monocrystalline quartz, plagioclase, potassium feldspars, and volcanic lithic fragments. Minor proportions of plutonic, metamorphic and sedimentary fragments, micas and heavy minerals are also present. The host rock and the radial elements have the same petrographic composition and textures.

The internal structure of the radial elements consists of menisci and *spreite*-lamination. Vertical *spreite*-lamination is recognised in cross-section of each radial elements as thin u-shaped laminae of 200 µm in thickness, which collectively reach up to 5 mm (Fig. 4e-f). When observed throughout a longitudinal section of the rays, it is possible to appreciate a poorly defined lamination (Fig. 4g-h). Menisci described by Fürsich and Bromley (1985) are not observed in the thin sections studied here.

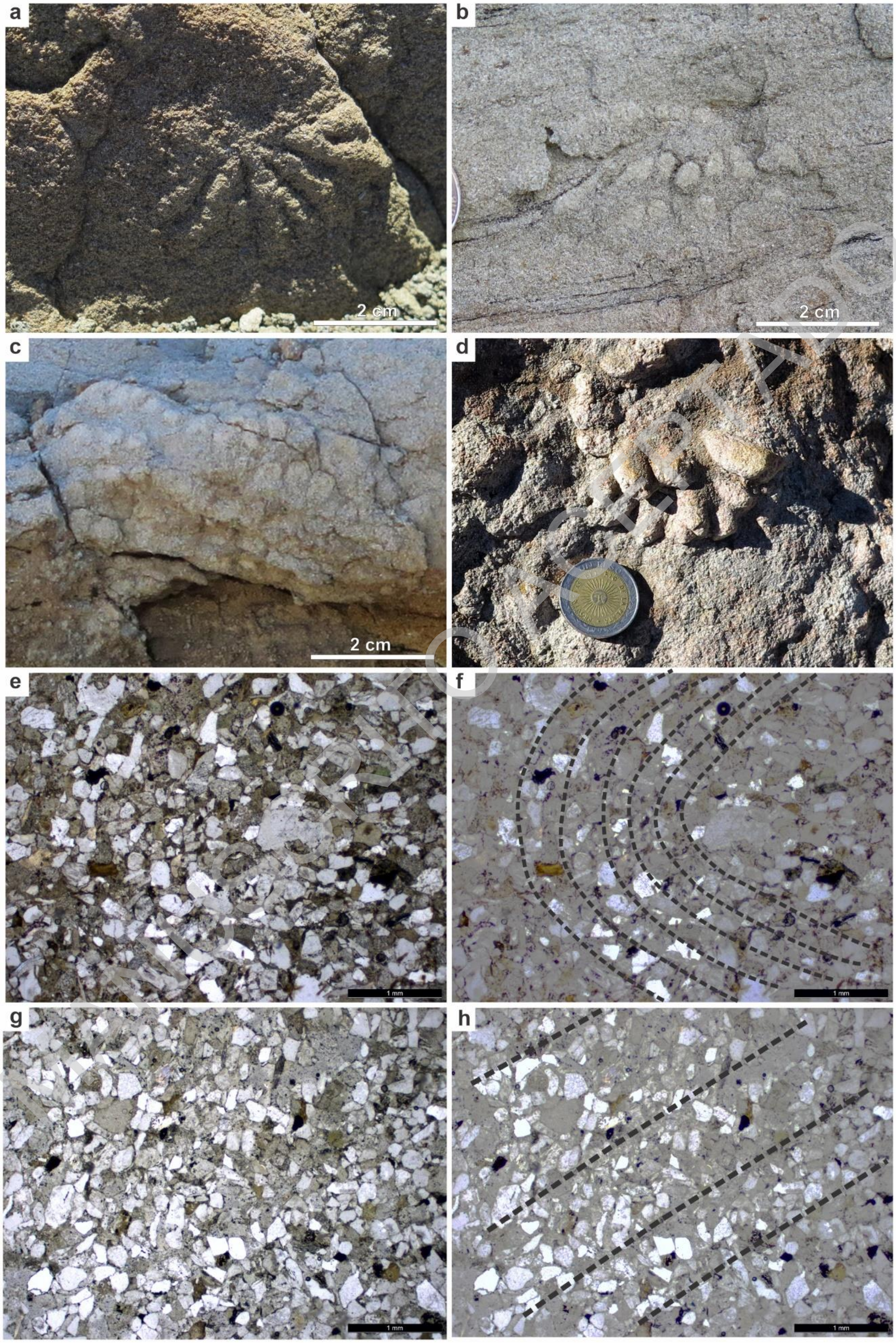

a
b
c
d
e
f
g
h
2 cm
2 cm
2 cm
1 mm
1 mm
1 mm
1 mm

Figure 4. a-d) *H. ottoi* in outcrop a) Weathered upper surface of bedding plane showing the uppermost preserved tier of one specimen of *H. ottoi* where it is possible to appreciate the bifurcation of the radial elements; b) Cross-section of *H. ottoi* showing at least three tiers where it is possible to appreciate the outline of the radial elements with a convex upper part and a convex or a gently concave lower base; c) Similar to b but here with 4 tiers, probably from two adjacent specimens based on its wide distribution (detailed view from figure 5b); d) Weathered *H. ottoi* with three tiers. e-h) Thin sections of *Haentzschelinia ottoi* showing the internal structure of vertical *spreiten*: e-f) View of a radial element in cross-section showing the vertical *spreiten* as thin u-shaped laminae, each image is arranged to show the curvature of the *spreiten*, with the upper side of the radial element to the left and the lower side to the right of the photo; g-h) View of radial elements in longitudinal section.

Remarks: The studied specimens can be assigned to *H. ottoi* on the basis of their constructional pattern. The features observed in these specimens are mostly similar to those observed by Fürsich and Bromley (1985) for Cretaceous specimens of Greenland and by de Gibert et al. (1995) for Miocene specimens of Catalonia.

There are some features not appreciated here due to the poor preservation including the dip of the radial elements and the pattern of ramification of the rays. Regarding the latter, it is not possible to differentiate between primary and secondary branching points and the distribution of primary elements as seen in other occasions for this ichnogenus (Fürsich and Bromley 1985, Pickerill et al. 1993). The number of radial elements is usually underestimated as consequence of weathering on the upper surface (Fig. 4a). Also, the internal structure of the radial elements is poorly defined as consequence of the homogeneous lithology which prevents a clear definition of the internal lamination seen by Fürsich and Bromley (1985) in the specimens they studied. The absence of the central shaft is common for this ichnogenus due to taphonomic loss since this requires a passive infill to be preserved or it would collapse (de Gibert et al. 1995).

Additionally, a bias is introduced by the type of exposure of the specimens, that is, the specimens have been observed in plan-view or in cross-section, not both, preventing their complete reconstruction. In this way, it was not possible to record the number of tiers of specimens from highly bioturbated surfaces given that these were appreciated in plan view.

Occurrence: The distribution of *H. ottoi* varies according with the facies (Fig. 2). In deposits of facies association 2 (fluvial dominated delta front), *H. ottoi* appears in mouth bar deposits up to 1 m in thickness and its abundance increases towards the top of the deltaic lobes (Fig. 5a). This trace fossil constitutes usually monoichnospecific horizons appearing as isolated specimens (ii and bpbi = 2) or in small groups (ii and bpbi = 2-3) (Fig. 5b). Even though other trace fossils have been recognised in these deposits (e.g., *Ophiomorpha*) they were not recorded at the same beds as *H. ottoi*. Occasionally, *Planolites* has been observed as isolated specimens. An underestimation of other ichnogenera is possible taking into account that most of the views correspond to cross-section exposures, thus making it difficult the recognition of trace fossils preserved on horizontal surfaces.

In facies association 3 (fluvial dominated delta front with tidal influence), *H. ottoi* constitutes monoichnospecific horizons with ii and bpbi of 2 (Fig. 5c-d) or is a component of more diverse assemblages with an ii and bpbi of 3-4 (Fig. 5e-f). These assemblages include *Planolites*, ?*Taenidium*, and ?*Parahaentzschelinia*, although *H. ottoi* is always the dominant ichnotaxon. These bioturbed horizons occur at the top of sandy beds interpreted as mouth bars, while trace fossils are lacking or are represented by isolated specimens in the underlying mouth bars that build each deltaic lobe with a ii and bpbi or 1-2 (Fig. 5e). An underestimation of trace fossils is possible in these mouth bars due to the scarcity of horizontal surfaces exposed (Fig. 5e).

In general, either in FA2 or in FA3, the specimens of *H. ottoi* display a regular size and, when grouped, they are arranged close to each other, but never overlapping each other. By contrast, horizontal trace fossils of deposit feeders cross-cut *H. ottoi,* evidencing an order of colonisation. Although *Ophiomorpha* was recorded in this outcrop, mostly in FA3, it never appears in the same horizons as *H. ottoi*.

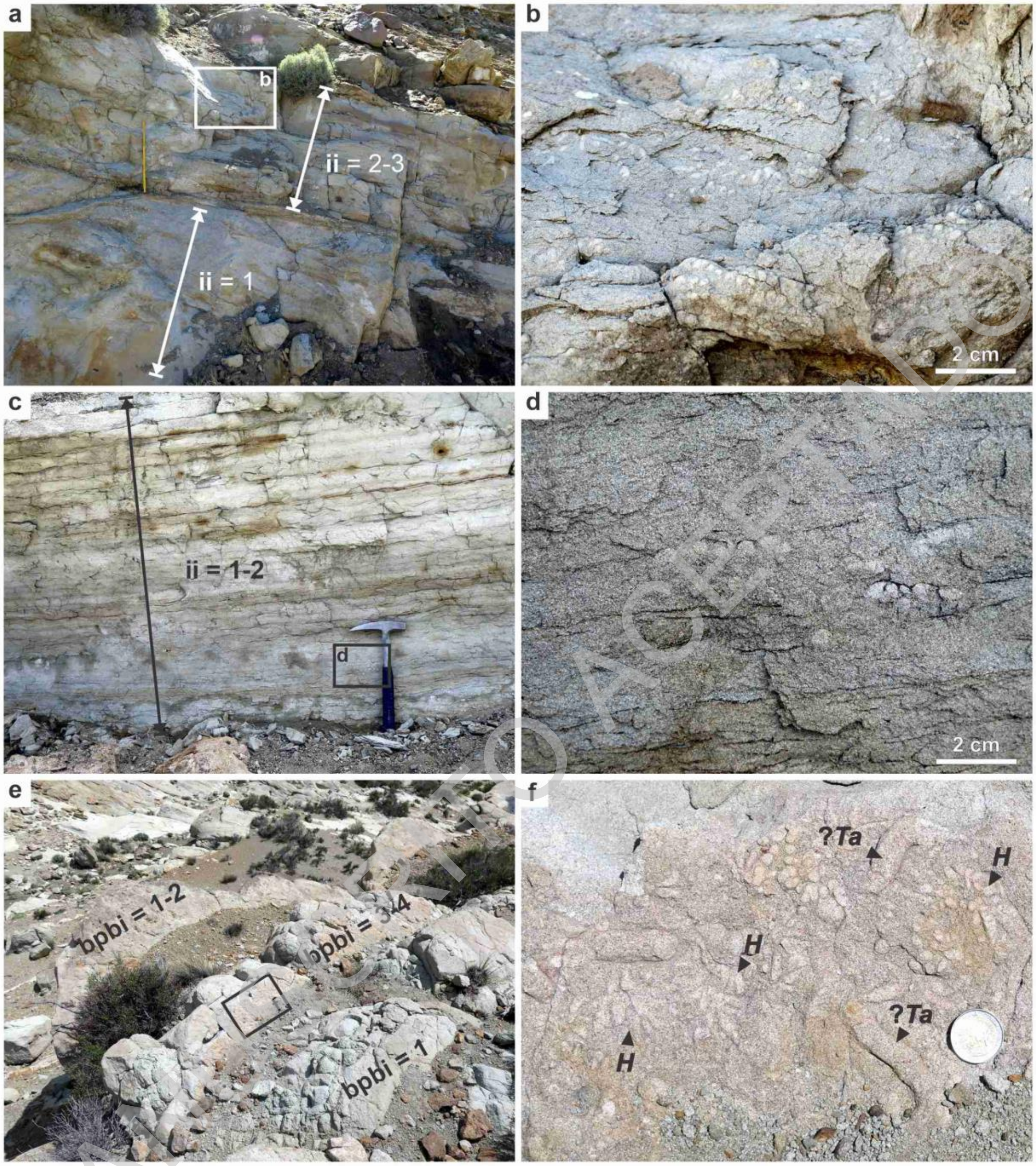


Figure 5. a-b) *H. ottoi* in fluvio-dominated delta front deposits (FA2); c-f) *H. ottoi* in fluvio-dominated delta front to delta plain with tidal influence deposits (FA3); c-d) Mouth bar deposits with isolated specimens (ii = 1-2); e-f) Upper surface of mouth bars with different intensities of bioturbation, including one surface moderate to highly bioturbed (bpbi = 3-4) showing *Haentzschelinia ottoi* (H) and ?*Taenidium* (?Ta). Scales: hammer = 33 cm, coin = 2 cm. References: ii) ichnofabric index, bpbi) bedding plane bioturbation index.

DISCUSSION

Environment at Arroyo Carreri and the settlement of *H. ottoi*

H. ottoi occurs more frequently in shallow-water, nearshore to deltaic, nutrient rich siliciclastic settings (Wilmsen and Niebuhr 2014). The information published for this trace fossil and its associated environments have been compiled by de Gibert et al. (1995), and later by Agirrezabala and de Gibert (2004). Data from the last 10 years are summarised here in Table 1, and these records and the trace fossils studied in this work are consistent with those already known with the exception of the poorly preserved specimens of Blisset and Pickerill (2004) recorded in deep sea waters, and the not illustrated *Haentzschelinia* horizon recorded in offshore settings by Beatty et al. (2008).

In Arroyo Carreri *H. ottoi* appears in delta front facies (FA2 and FA3) and its settlement and distribution is controlled by river-dominated deltaic sedimentary processes. Impoverish ichnofaunas are expected for these settings due to salinity fluctuations, high turbidity, and high and discontinuous rates of sedimentation, among other factors (MacEachern et al. 2005, Buatois and Mángano 2011). High suspended loads of fine-material prevent the colonisation by suspension-feeders while high amounts of organic detritus favour the colonisation by deposit-feeders. Thus, the *Skolithos* ichnofacies is suppressed or poorly developed and only a low diversity and disperse *Cruziana* ichnofacies dominated by deposit feeders occurs under such conditions (Gingras et al. 1998, Agirrezabala and de Gibert 2004, Buatois and Mángano 2011), as seen in the studied deposits with deposit-feeders dominating the scene.

The highest abundance of *H. ottoi* is recorded towards the top of abandoned deltaic lobes, hence, the interruption in the sedimentation would be determining for its settlement. Agirrezabala and de Gibert (2004) point out that the production of *H. ottoi* responds to rapid opportunistic colonisation following a sediment discharge and the frequency of these events of discharge controls the abundance of trace fossils in one horizon. This would be a decisive factor to understand the distribution of trace fossils in Arroyo Carreri, and specially they scarcity in active deltaic lobes where time between sedimentary discharges would have been short hence preventing any long-term colonisation. Thus, the greatest abundance of trace fossils is located at the top of abandoned deltaic lobes, evidencing the interruption in the sedimentation. Therefore, deposit-feeders dominate the substrate and the abundance of trace fossils is higher towards the top of deltaic lobes. However, sediment suspended loads and frequency of discharge are not enough to explain the differences in abundance and richness observed between FA2 and FA3, where only in the last one is recorded a diverse association of deposit-feeder trace fossils reaching a bpbi of 3-4 (Fig. 5f-g). Availability of oxygen also should be discarded as a constraining factor since it is expected to be similar in both facies.

Tides could have had a determining role in the settlement of trace fossils in Arroyo Carreri. In FA3 is expected a higher salinity than in FA2 as consequence of the influx of sea water induced by tides (Matsoukis et al. 2022), allowing the development of a more diverse ichnofauna, here represented by *H. ottoi*, ?*Parahaentzschelinia*, and horizontal trace fossils of other deposit feeders as *Planolites* and ?*Taenidium*. When comparing monoichnospecific *H. ottoi*-bearing surfaces in FA2 with the associations of deposit feeders recorded in some beds of FA3, differences in richness could be understood as the result of changes in salinity conditions.

However, even when salinity conditions would favour a more diverse ichnofauna, in some beds of FA3 only a few specimens of *H. ottoi* developed reaching a bpbi and ii = 2. The cross-cut of *H. ottoi* by horizontal trace fossils of deposit feeders observed in the surfaces with bpbi = 3-4 evidences a certain order of colonisation where *H. ottoi* producers were the first to arrive. Thus, surfaces with discrete trace fossils would have been colonized by the *H. ottoi* producers, but colonisation windows would have closed before the settlement of the producers of other trace fossils, probably due to sediment discharge.

It has to be taken into consideration that changes in organic matter content could have contributed to support a more abundant association of deposit feeders for the crowded surfaces in FA3. Although it is not possible to verify this with the current data, changes in the availability of organic matter as consequence of the rise in the tidal influence cannot be ruled out. Bustin (1988), for the Tertiary Niger delta, considered the possibility that changes in the relative significance of tides, waves and river energy may affect the size and geometry of the delta plain, frequency of flooding, and associated erosion of organic matter. Additionally, changes in climate and production of organic matter in time would contribute to modify the availability and type of organic matter. If these changes happened, differences in richness among different surfaces in FA3 still would be mainly related to sediment discharge.

Depth can be ruled out as a constraining factor for the development of the crowded surfaces in FA3. Agirrezabala and de Gibert (2004) found that for Gilbert-type deltas and mouth bar-type deltas, *H. ottoi* is restricted to less than 3 m in depth and *Haentzschelinia* producer would have a low tolerance to subaerial exposure. Based on this, surfaces with *H. ottoi* in Arroyo Carreri would have developed between 0 and 3 m in depth, which is not a constraining depth for the producer of *Planolites* or *Taenidium*, as well as for many other deposit feeders documented in very shallow marine or transitional settings (Buatois and Mángano 2011). So, the absence of these trace fossils would not be related to depth.

Used name	Reference	Age	Location	Host rock	palaeoenvironment
Dactyloidites ottoi	Agirrezabala and de Gibert 2004	Early Cretaceous	Western Pyrenees, Spain	Sandstones	Gilbert-type delta and mouth bar-type delta
Dactyloidites ottoi	Blissett and Pickerill 2004	Eocene-Miocene		Limestones	Deep sea waters
*Dactyloidites**	McIlroy et al. (2005)	Middle Jurassic	Data from a 48 km-long cliff line (N-S orientation) in southern Neuquén Basin, Argentina	Sandstones	Tidal flats, tidal channels, distributary channels

Dactyloidites ottoi	De Gibert et al. 2007	Eocene	Sant Llorenç del Munt, Ebro Basin, NE Spain	Sandstone	Deltaic front
Dactyloidites ottoi	Lazo et al. 2008	Late Jurassic	Mendoza, Argentina	Oolitic peloidal bioclastic intraclastic packstone-grainstone	Lower shoreface
Haentzschelinia horizon (not illustrated)	Beatty et al. 2008	Early Triassic	NE British Columbia, Canada	Sandstones (storm-generated sediment gravity flows)	Offshore
Dactiloidites ottoi	Srivastava et al. 2010	Middle Jurassic	Kachchh, India	Calcareous sandstones	Sublittoral
Dactyloidites ottoi	Mayoral et al. 2013	Miocene-Pliocene	Cape Verde Archipelago	Sandy bioclastic limestones	Fair-weather suit (shallow marine)
Dactyloidites ottoi	Wilmsen and Niebuhr 2014	Late Cretaceous	Saxony (including revision of type material) and Bavaria	Sandstones	Transition zone (between fair weather storm wave base)
*Dactyloidites ottoi**	Canale et al. (2015)	Middle Jurassic	Portada Covunco and Sierra de la Vaca Muerta, Neuquén Basin, Argentina	Sandstones	Delta front
*Haentzschelinia ottoi***	Belaústegui et al. (2015)	Middle Miocene		Sandstones	Shallow marine (estuarine facies?)
*Dactyloidites ottoi**	Gugliotta et al. (2016a,b)	Middle Jurassic	Bajada de Los Molles	Sandstones	Crevasse channels and crevasse mouth bars
*Datyloidites ottoi**	Rossi and Steel (2016)		Lohan Mahuida hill, Neuquén Basin, Argentina	Sandstones	Lower delta plain and tidally reworked bars and dunes
*Dactyloidites**	Kurcinka et al. (2018)	Middle Jurassic	Los Molles, Neuquén Basin	Sandstones	Fluvial and distributary channels, tidal inlets
Dactyloidites ottoi	Aguilar (2020)	Miocene	Costa Rica	Sandstones	Upper shoreface
*Haentzschelinia ottoi**	Canale et al. (2020)	Middle Jurassic	Bajada de Los Molles, Cuenca Neuquina	Sandstones	

*Dactyloidites peniculus****	Tournadour et al. (2020)	Miocene	New Caledonia	Sandstones	Delta front
Dactyloidites ottoi	Curran and Glumac (2021)	Pleistocene	Bahamas	Calcarenites	Very-shallow marine facies
*Haentzschelinia**	Arregui and Rodríguez (2022)	Middle Jurassic	Neuquén engulfment, Neuquén Basin (subsurface data)		Delta front
Dactyloidites ottoi	Patel et al. (2023)	Early Cretaceous	Kachch Mainland, India	Sandstones	Deltaic environment

Table 1: Records of *D. ottoi* and *H. ottoi* since 2004 to date, constituting an updating of the summary tables compiled by De Gibert et al. (1995) and Agirrezabala and de Gibert (2004). References to other ichnospecies (e.g., *Dactyloidites peniculus* by Uchman and Pervesler 2007 and Pervesler et al. 2011 or *Dactyloidites cabanasi* by Gámez Vintaned et al. 06) are not included in this table, neither the reference to *Dactyloidites* isp. (except for Lajas Formation) or the references to *Dactyloidites* for Cambrian material (Jensen et al. 2010) which is not comparable with *Haentzschelinia ottoi,* neither with *Dactyloidites* references from well-cores as the one of Celis et al. (2021).

* Works carried out in Lajas Formation.

** Corresponds to specimens with an angular dispersion of rays that covers the whole circle, which is unusual for *Dactyloidites ottoi*.

*** Defined as *Dactyloidites peniculus* in the figure, the description is not included in the paper and specimens illustrated in figure 10c look like *H. ottoi*, including the fact that *D. peniculus* is apparently unbranched whereas the material observed by Tournadour et al. (2020) shows bifurcations.

Ichnofossil assemblages

As mentioned before, surfaces with ii/bpbi = 3-4 carry *H. ottoi* with *Planolites*, ?*Taenidium*, ?*Parahaentzschelinia*, and possibly with other trace fossils not determined in this work. Some horizontal trace fossils were assigned to *Taenidium* on the basis of their lack of wall and the homogeneous, non-compartimentalised meniscate backfills (Keighley and Pickerill, 1994), although the last one is poorly defined, reason why the identification is dubious. Additionally, there are some specimens that probably correspond to ?*Parahaentzschelinia*, an ichnogenus already recognised in other sections of Lajas Formation (McIlroy et al. 2005, Arregui and Rodríguez 2022).

The presence of *Planolites* on the same surfaces with *H. ottoi* in the highly bioturbed surfaces of FA3 is an assemblage frequently observed in deltaic deposits of Lajas Formation in other localities (Canale et al. 2015, Gugliotta et al. 2015, 2016a,b, Kurcinka et al. 2018) and in other units (Agirrezabala and de Gibert 2004).

If there is an underestimation of *Parahaentzschelinia* or *Taenidium*, the interpretation proposed for the more crowded bioturbed surfaces in FA3 does not change, taking into account that all the mentioned trace fossils are produced by the activity of opportunistic deposit-feeders

(Pemberton et al. 2001), evidencing the high abundance of organic matter in substrate. This association found in Arroyo Carreri constitutes an impoverished expression of the *Cruziana* ichnofacies, common in deltaic facies (Buatois and Mángano 2011) and a mature community was never reached for the studied surfaces.

In addition to the trace fossils just mentioned, there is *Ophiomorpha*. Only one bed with moderate to abundant (ii = 3-4) *Ophiomorpha* Lundgren, 1891 (Fig. 3d) was recorded in FA3 and a few isolated specimens scattered throughout FA2 and FA3, constituting impoverish examples of the *Skolithos* ichnofacies. *Ophiomorpha* is a trace fossil usually produced by thalassinidean decapods which serves as semipermanent dwelling and feeding burrow, and it is produced in fine-grained to medium-grained sand deposited under relatively high-energy conditions (Frey et al. 1978, Buatois and Mángano 2011). Referring to the bed with abundant specimens of *Ophiomorpha* (Fig. 3d), this is the only ichnogenus recorded in these beds and constitutes a dense accumulation of vertical shafts and poorly preserved isolated horizontal galleries. The absence of other trace fossils in this bed could be a preservational bias since the top shows evidence of erosion and more superficial trace fossils would not have been preserved. This would imply a great digging depth for the crustaceans since the traces do not exceed 0.5 cm in diameter and are up to 15 cm in length preserved. Alternatively, the absence of other trace fossils can be explained on the basis of the instability of the substrate, suitable for the construction of *Ophiomorpha* (Pryor 1975, Frey et al. 1978, Buatois and Mángano 2011), but not for the colonisation by *Haentzschelinia ottoi* producers or the preservation of this trace fossil or any other of the aforementioned.

These hypotheses give an explanation for the absence of *H. ottoi* in the deposits where *Ophiomorpha* appears but do not explain why *Ophiomorpha* is not observed where *H. ottoi* is recorded. About this, conditions that favoured the colonisation by deposit-feeders possibly prevented the colonisation by thalassinidean crustaceans. In this way, thalassinidean can be suspension-feeders or deposit-feeders (Bromley 1996), if the builders of the *Ophiomorpha* galleries in Arroyo Carreri were obligatory suspension-feeders, high suspended loads of fine-material would have created a hostile medium for their settlement.

CONCLUSIONS

The study of the distribution and abundance of *Haentzschelinia ottoi* in Arroyo Carreri section of the Lajas Formation revealed that this ichnospecies appears as isolated specimens (ii and bpbi = 2) or as part of more diverse associations with moderate to high abundance of specimens (ii and bpbi = 3-4). The former occurs in fluvio-dominated delta front deposits with or without tidal influence (FA3 and FA2 respectively), while the second one only appears in FA3. These differences could be understood as the result of the interplay between sedimentary discharge and salinity conditions.

In both facies the ichnofauna is dominated by deposit feeders as consequence of the high abundance of organic matter in substrate Additionally, high suspended loads of fine-material prevented the colonisation by suspension-feeders, suppressing the *Skolithos* ichnofacies.

The diverse associations observed in FA3 would respond to the influence of tides, since the influx of sea water would produce a rise in salinity, thus creating the conditions for the settlement of a more varied ichnofauna with marine affinity. Sediment discharge would have controlled the abundance of trace fossils in both facies. *H. ottoi* shows its highest abundance towards the top of abandoned deltaic lobes evidencing a favourable response to an interruption in sediment discharge. Absence or scarcity of trace fossils on top surfaces of underlying mouth bars that build each deltaic lobe in FA3 would be consequence of the closure of the colonisation window by sediment discharge preventing the arrival and settlement of the producers of most trace fossils apart from the pioneer specimens of *H. ottoi*.

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