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Environmental factors affecting the development of the *Zoophycos* ichnofacies in the Lower Cretaceous Río Mayer Formation (Austral Basin, Patagonia)

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ABSTRACT

The Río Mayer Formation (Berriasian–Albian) is part of the basal infill of the Austral Basin, southwestern Gondwana. In the Los Glaciares National Park (Santa Cruz Province) seven sections were sedimentologically studied in detail. The investigated interval is mainly composed of black mudstones and shales interbedded with marls and fine-grained sandstones. The vertical distribution of these lithologies provided the basis to distinguish three major units (lower, middle and upper). In general, within the Río Mayer Formation, two different developments of the *Zoophycos* ichnofacies were recognized. First, in the middle unit (Valanginian–Hauterivian), this ichnofacies shows a high degree of bioturbation having a bioturbation index (BI) between 3 and 4; *Zoophycos* specimens are of large size, the spreiten are nearly 1 cm in height and more than 1 m in width. This ichnogenus is associated with *Chondrites* and *Bergaueria perata*. Environmentally this ichnofacies formed during a transgression, the sedimentation rates were very low and promoted the accumulation of benthic food in the outer shelf. Second, the *Zoophycos* ichnofacies in the upper unit (Albian) exhibits a less intense degree of bioturbation (BI between 0 and 1) and; *Zoophycos* is of relatively small size, the spreiten are 0.3 cm high and short. Typically are associated *Ophiomorpha*, *Chondrites*, *Palaeophycus* and *Teredolites*. When this ichnofacies formed, the prodelta margin prograded across the outer shelf and led to enhanced sedimentation rates further offshore resulting in the dilution of the nutrients.

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1. Introduction

The *Zoophycos* ichnofacies is frequently debated and discussed in the ichnological literature (cf. MacEachern et al., 2007a,b). In general, this ichnofacies shows low ichnodiversity or even a monospecific arrangement, it is dominated by trace fossils belonging to the ethological class fodinichnia, consisting of both simple and complex burrows, and of trace fossils having spreiten (Buatois et al., 2002; MacEachern et al., 2007a,b; Buatois and Mángano, 2011). The *Zoophycos* ichnofacies is stated to reflect calm conditions, from the outer shelf to bathyal zones or protected areas composed of muddy sediments that have oxygen-deficient pore water and are rich in organic matter (Seilacher, 1967; Frey and Pemberton, 1984, 1985). In the same way as the *Zoophycos* ichnogenus, this ichnofacies records a shift from shallow bathymetric zones in the Palaeozoic to deeper zones in the Mesozoic and Cenozoic (Wetzel and Werner, 1981; Bottjer et al., 1988; Buatois et al., 2002).

The main ichnological components of this ichnofacies are the ichnogenera *Zoophycos* and *Chondrites*, whose producers burrow deep into substrates having oxygen-deficient interstitial waters, but this does not necessarily mean poor oxygenation at the water-sediment interface (Wetzel, 1991; Bromley, 1996). It is important to note that the ichnogenus *Zoophycos* has been studied and debated intensely in the last decades, and it is considered as a palaeoenvironmental marker (especially for oxygen conditions) and a useful indicator of sedimentary breaks (among others, Wetzel and Werner, 1981; Ekdale and Lewis, 1991; Bromley, 1991; Uchman, 1995; Olivero and Gaillard, 1996; Löwemark and Schäfer, 2003; Olivero, 2007; Olivero and Gaillard, 2007; Gong et al., 2010; Rodríguez-Tovar et al., 2011; Wetzel et al., 2011).

The aim of this study is to analyse the occurrence of the *Zoophycos* ichnofacies in the Lower Cretaceous Río Mayer Formation (southwestern Gondwana) and to discuss the controlling factors for the contrasting appearance of this ichnofacies.

2. Geological background

2.1. The Austral Basin

The Austral Basin is located in the southernmost part of Patagonia (Fig. 1 A,B) and was filled mainly by siliciclastics between Jurassic and

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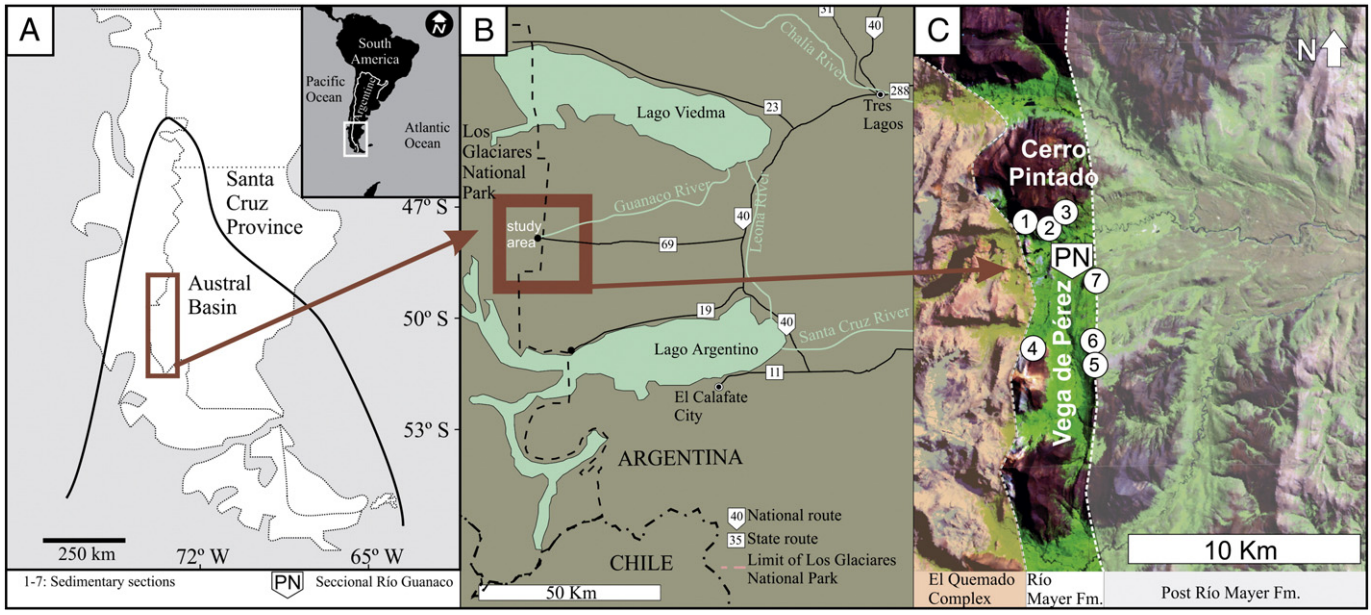

Fig. 1. Location map of the study area. A— Position of the Austral Basin in South America. B— Position of the study area in Argentina. C— Distribution of the deposits of the Río Mayer Formation at the Seccional Río Guanaco locality and location of the seven sedimentary sections logged at the field.

Cenozoic times. The initiation of this basin was linked to an extensional phase during the Late Jurassic when a thick syn-rift sequence, the so-called the El Quemado Complex, formed (Féraud et al., 1999; Pankhurst et al., 2000). This volcano-sedimentary complex is highly variable in thickness, reaching up to 150 m at the San Martín Lake (120 km northwards from Río Guanaco locality), while toward the south it is more than 1000 m thick (Riccardi, 1971; Ramos et al., 1982; Kraemer and Riccardi, 1997). On top of this complex, shallow-marine deposits of the Springhill Formation accumulated between the Tithonian and the Berriasian in response to an initial transgressive phase (Kraemer and Riccardi, 1997; Richiano, 2012). In the study area this unit varies in thickness between 15 and 70 m and fills half-grabens over the El Quemado Complex (Kraemer and Riccardi, 1997; Richiano, 2012). The acceleration of the transgression during the Berriasian led to the accumulation of black shales of the Río Mayer Formation, marking the first episode of offshore sedimentation in the basin and the onset of post-rift conditions (Arbe, 2002; Richiano, 2012).

2.2. The Río Mayer Formation in the study area

Previous studies of the Río Mayer Formation showed its deposition between Berriasian and Albian times (Arbe and Hechem, 1984; Kraemer and Riccardi, 1997; Richiano, 2012; Richiano et al., 2012). The diverse fossil content was analysed by many researchers, especially the ammonoid fauna (i.e. Leanza, 1970; Riccardi, 1971, 1988; Kraemer and Riccardi, 1997; Aguirre Urreta, 2002); recently the trace fossils were studied in detail (Richiano and Poiré, 2010; Richiano et al., 2012, 2013).

The study area is located between the Argentino and Viedma lakes in Santa Cruz Province at the Seccional Río Guanaco (S 49° 57′ 11″; W 72° 04′ 56″) of Los Glaciares National Park (Fig. 1B,C). The studied interval is 250-m thick and it can be subdivided lithologically into three units (Fig. 2; Richiano, 2012; Richiano et al., 2012). These units are grouped into two major environments having different facies developments (Fig. 3).

The lower unit, covered by sections 1 and (partly) 2, is mainly composed of laminated black shales interbedded with marl levels. Trace fossils have not been observed in this unit, but ammonites and belemnites are abundant. This unit is interpreted as having accumulated in an outer shelf setting. Two fossiliferous levels (2 and 3, Fig. 2) assigned to this unit were reported by Kraemer and Riccardi (1997) and correspond to early Berriasian and early Valanginian ages. The middle unit, partly covered by sections 2 and 4, is 40 m thick, is composed of intensely bioturbated dark marls and shales. This unit is characterized by a well-preserved and highly evolved *Zoophycos* ichnofacies (Richiano and Poiré, 2010; Richiano et al., 2013). Body fossils are common, especially belemnites. These fossils represent a *Belemnopsis* fauna that corresponds to a Valanginian–Hauterivian age (Aguirre Urreta, 2002; Richiano, 2012). The upper unit, partly covered by sections 2 to 7, is marked by massive black shales with intercalations of very-fine- to fine-grained sandstones and, less frequently, conglomerates. In this unit, both debris flows and distal low-density turbidity current deposits were identified (Richiano, 2012; Richiano et al., 2012). *Zoophycos* isp., *Chondrites* isp., *Palaeophycus* isp. and *Ophiomorpha* isp. occur associated with moulds of petrified wood containing *Teredolites* isp. (Richiano and Poiré, 2010; Richiano et al., 2013). The frequent intercalation of sandstones in the uppermost part of the unit is related to the distal influence of deltas comprising the Piedra Clavada Formation (Richiano, 2012; Richiano et al., 2012). Two fossiliferous levels were recorded toward the top of this unit, containing *Birostrina* cf. *concentrica* and *Mortoniceras* cf *arietiforme* pointing to an Albian–Cenomanian age (Arbe and Hechem, 1984; Kraemer and Riccardi, 1997) (Fig. 2).

Considering the estimated ages using the fossil content and the thickness of each unit, we are able to infer the sedimentation rates for the Río Mayer Formation at the study area. In this sense, the values obtained are only useful for comparisons between the intervals with *Zoophycos* ichnofacies, and hardly match the real sedimentation rates. Accurate estimations of sedimentation rates should include more precise ages and the differential compaction of each lithology considered. Taking into account these caveats, the middle unit of the Río Mayer Formation is 40 m thick and occupied ca. 10.4 Ma (Valanginian–Hauterivian; Cohen et al., 2014). The sedimentation rate for the middle unit is approximately 3.85 mm/ka (3.85 m/Ma). The uppermost part of the upper unit is 100 m thick and was deposited in 12.5 Ma (during the Albian; Cohen et al., 2014), which represents a sedimentation rate of 8 mm/ka (8 m/Ma).

The organic matter content in the Río Mayer Formation shows differences between the three units considered (Richiano, 2014): the lower

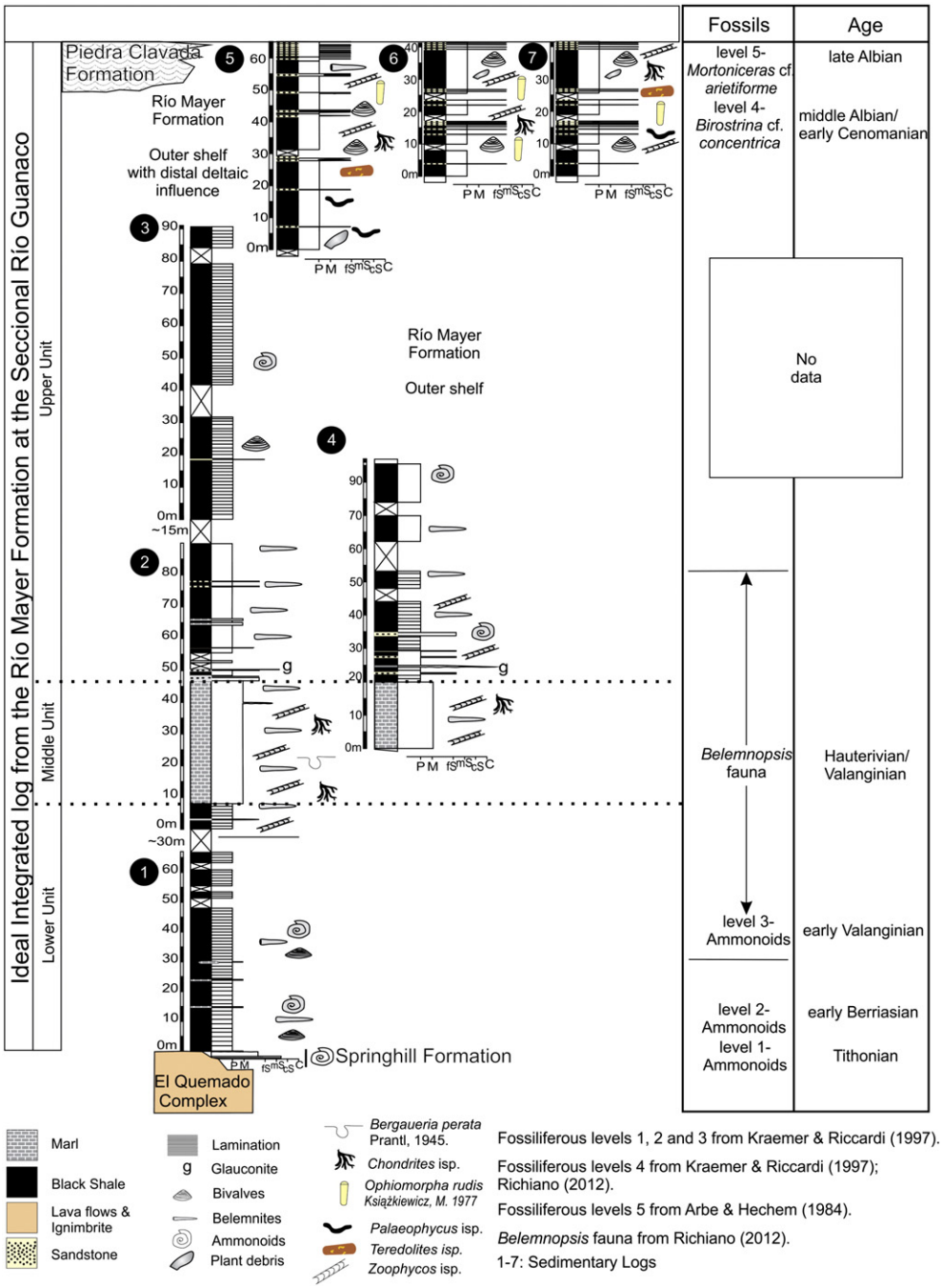

Fig. 2. Sedimentary sections of the Lower Cretaceous Río Mayer Formation recovered at the Seccional Río Guanaco locality. The formation was divided into three units, each one with particular fossil content and ages (see text for details). P: Pelite; M: marl; fS: fine-grained sandstones; mS: medium-grained sandstone; cS: coarse-grained sandstone; C: conglomerate. Modified from Richiano et al. (2012) and Richiano (2014).

unit has the highest TOC content (between 0.07 and 2.81%, average 1.25%), in the middle unit the organic-matter content is very low (between 0 and 0.58%; average 0.18%) and finally the upper unit shows moderate TOC values at the base (0.5–2%, average 1.12%) and extremely low values toward the top.

3. *Zoophycos* ichnofacies in the Río Mayer Formation

Ichnogenera representative of the *Zoophycos* ichnofacies have been observed in sections 2 and 4 to 7 in the Seccional Río Guanaco locality (Figs. 1, 2). To estimate the intensity of bioturbation the Bioturbation Index (BI) was used, following the criteria of Taylor and Goldring (1993). Large parts of the Río Mayer Formation show a BI = 0 except for the middle unit and the uppermost 50 m. The size of the traces (e.g. spreiten thickness) was directly measured in the field or later in the laboratory by using field photographs. The *Zoophycos* ichnofacies observed within the middle unit of the Río Mayer Formation (sections 2 and 4) mainly comprises *Zoophycos* and *Chondrites* associated with some *Bergaueria* specimens (Fig. 4A). The middle unit developed between the Valanginian and Hauterivian in this region. This bioturbated

Units	Facies	Sedimentological Processes		Fossil Content	Palaeoenvironments
Lower & Middle	Massive mudstones (Fm)-Laminated mudstones (Fl)- Mudstones with nodules(Fn)-Massive marls (Mm)- Bioturbated marls (Mb)	Hemipelagic deposition		Marine (ammonites; belemnites; bivalves)	MARINE Outer Shelf
	Glauconitic sandstones (Sg)	Autigenic deposition			
	Massive sandstones (Sm)-Laminated sandstones (Sl)-Sandstones with parallel stratification (Sp)	Turbiditic flows	Episodic Sedimentation		
	Massive conglomerates with intraclasts (Cmi)	Debris flows			
Upper	Massive mudstones (Fm)	Hemipelagic deposition		Marine & continental (ammonites; bivalves; tree fragments)	MARINE Outer Shelf influenced by deltaic activity
	Massive sandstones (Sm)- Laminated sandstones (Sl)	Turbiditic flows	Episodic Sedimentation		

Fig. 3. Summary of sedimentary facies, sedimentological processes, fossil content and interpreted palaeoenvironments for the three units of the Río Mayer Formation at Seccional Río Guanaco locality (modified from Richiano, 2014).

interval is c. 40 m thick, composed of marl beds up to 0.5 m thick (Fig. 4B). The mean BI of the middle unit is between 3 and 4. The *Zoophycos* specimens in this interval are characterized by large planar forms, usually laterally extended from 80 cm to more than 1 m. These planar forms are characterized by a planar to sub-planar lamina developing parallel to the bedding plane. In cross-section the spreiten are 1 cm thick on average, ranging from 0.7 to 1.2 cm (Fig. 4C–H). Sinistral forms and cross-cutting relationships between different *Zoophycos* isp. specimens have been recognized in this interval (Fig. 4E–G). It is possible to recognize that the trace starts almost vertically, but then it usually becomes horizontal roughly parallel to bedding (Fig. 4H). This finding indicates that the causative tube reaches the sediment-water interface only at the upper apex, as suggested by Olivero and Gaillard (1996).

Chondrites isp. is preserved as small burrow systems branching at a nearly constant acute angle. Two morphologies were distinguished. One group is constituted by dendritic tunnels 0.5 to 1.5 mm wide; the first-order tunnels reach a length of 2 cm, while the second-order ones are seldom longer than 1 cm. The other morphological group is dominated by generally short (less than 2 cm) and straight or gently curved in plan view second-order tunnels, 0.1 to 0.4 cm in diameter (Fig. 4I–J). Occasionally, some *Bergaueria perata* Prantl, 1945, specimens occur in this interval (Fig. 4K). This ichnospecies shows smooth external surfaces, a hemispherical shape (about 2 cm in diameter) and has a small depression in the central region of the trace.

In contrast, trace fossils also assigned to the *Zoophycos* ichnofacies of the upper unit of the Río Mayer Formation at the Seccional Río Guanaco locality (Sections 5, 6 and 7), generally show a short lateral extent of the spreiten of *Zoophycos* and isolated *Chondrites*. Moreover, the average BI of the unit is between 0 and 1. Associated are ichnogenera *Ophiomorpha* and *Palaeophycus* (Fig. 5H–K). Another component also present in this association is the ichnogenus *Teredolites* (Fig. 5L), which occurs in (now petrified) wood. All of these features distinguish this *Zoophycos* ichnofacies from that described above (Fig. 5A–G).

The *Zoophycos* specimens in this interval are characterized by planar forms, similar to the ones present in the middle unit, but shorter in lateral extent (less than 0.5 m). In some cases *Zoophycos* appears in a "Christmas tree" pattern (Fig. 5C), showing two clearly opposing directions of shift of the causative tube that occur on either side of the nearly vertical axial part that, however, never showed the central tube (Fig. 5D). In general, the thickness of the spreiten is between 0.3 and 0.5 cm (Fig. 5C–E) and hence, considerably smaller than that of the *Zoophycos* found in the middle unit. *Chondrites* isp. occurs sporadically in this interval, showing similar features as the one described above (Fig. 5C, F–G). *Ophiomorpha rudis* (Książkiewicz, 1977) is composed of straight tubes in shaley strata filled by sandstone. The diameter of the galleries and pellets together varies between 1.5 and 2.5 cm, whereas their length can reach 0.5 m (Fig. 5H). The filling is usually massive and the outer surface shows pellets, but sometimes it has small, unreinforced sectors (Fig. 5I). The red external colouration indicates later oxidation by weathering, which is in accordance with the oxygen conditions inferred using TOC in the upper unit (Richiano, 2014). The tunnel system communicated to the upper sandy levels through vertical shafts (Fig. 5J). The tunnel joints are generally in "Y"-shaped junctions, and to a lesser extent "T"-shaped junctions. A maze distribution is sometimes present as abundant sub-horizontal galleries superimposed on the same bedding plane. *Palaeophycus* is also present, but less abundant than the other trace fossils in this interval (Fig. 5K). It is characterized by smooth excavations between 0.5 and 1 cm wide, commonly with straight to slightly curved courses and lengths that can reach 10 cm. Finally, *Teredolites* isp. occurs within this interval in moulds of (now petrified) wood imported by distal turbidity currents. This trace fossil usually has a 1-cm long "flattened tear" shape (Fig. 5L).

4. Environmental factors

The Río Mayer Formation formed in a fully marine outer shelf setting broadly recognized in the Austral Basin (Arbe, 2002; Richiano et al., 2012). Among the environmental and extrinsic factors that could influence the formation of burrows, sedimentation rate, benthic food content, and the oxygen content are the most important for the development of the *Zoophycos* ichnofacies in the Río Mayer Formation.

4.1. Sedimentation rates and benthic food supply (Fig. 6)

In modern outer shelf areas, the sedimentation rate is very low, ranging between 10 mm/ka and 200 mm/ka (Stow et al., 2001). Fluctuating sediment input can be approximated to some degree by evaluating the abundance of turbidites, which in the Río Mayer Formation are closely related to relative sea-level changes (Richiano et al., 2012, 2013). Thus, sedimentation rate will be described together with the sequence stratigraphy. The two intervals where the *Zoophycos* ichnofacies was recognized belong to quite different sequence stratigraphic divisions (Arbe, 2002; Richiano, 2012, 2014) (Fig. 6). The middle unit of the Río Mayer Formation was deposited during a regional transgression that led to the migration of the littoral areas to the external zones of the basin (TST [transgressive systems tract]; Fig. 6). The TST is characterized in the study area by a sharp, flat transgressive surface that divides the littoral deposits of the Springhill Formation from the offshore sediments of the Río Mayer Formation. Littoral sedimentation is interpreted to have moved more than 100 km northwards (to the Lago San Martín locality) at this time. This situation lead to lowered sedimentation rates in offshore areas, resulting in pronounced environmental stability (free of turbidites) for the *Zoophycos* trace makers. According to Olivero and Gaillard (1996), the presence of *Zoophycos* often implies an incipient induration of the sea floor deposits while sediment deposition is very low to zero. Moreover, *Zoophycos*

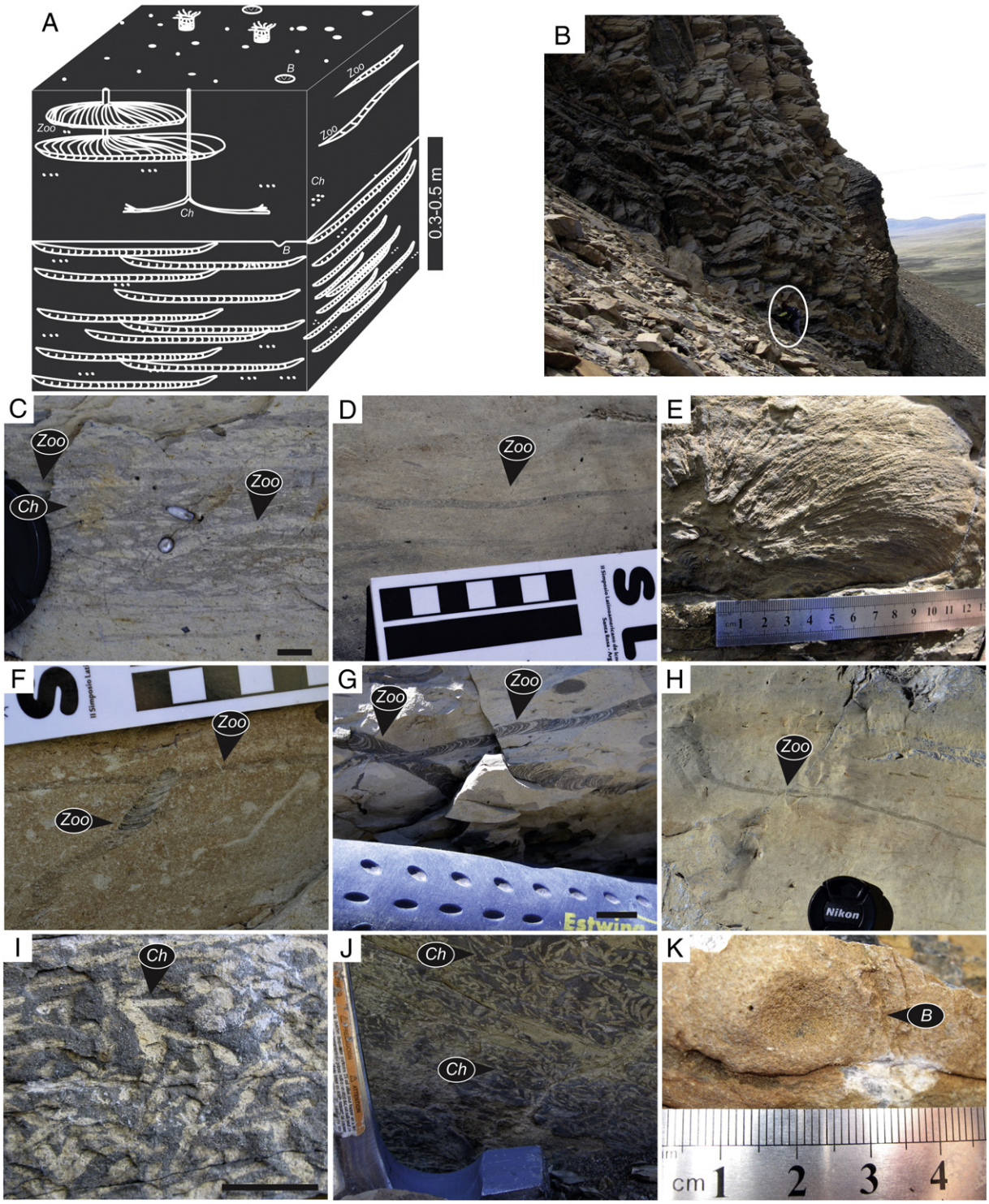

Fig. 4. Trace fossils and field view of the middle unit of the Río Mayer Formation at Seccional Río Guanaco locality. A— Block diagram showing the distribution of the main trace fossils in this unit. B— General view of the middle unit deposits of the Río Mayer Formation from sedimentary section 2 (person for scale). C— Detail of one marl level intensely bioturbated by *Zoophycos* and *Chondrites* ichnogenera. D— Planar lamina of *Zoophycos*. E— Plan view of sinistral-coiling *Zoophycos*. F and G— Cross-cutting relationships between *Zoophycos* specimens. H— Picture showing that the tube of *Zoophycos* starts almost vertical, and then turns to the horizontal plane, parallel to bedding (view perpendicular to bedding). I and J— Dominant morphology of the *Chondrites* isp. recovered from this unit. K— *Bergaueria perata* Prantl, 1945 substratal view. Scale bar: 1 cm; camera lens: 5.2 cm. B = *Bergaueria*; Ch = *Chondrites*; Zoo = *Zoophycos*.

may indicate breaks in sedimentation. This situation alternates with periods of greater sediment supply, presumably of proximal (inner shelf) origin and usually rich in benthic food (Olivero and Gaillard, 1996). The low sedimentation rates estimated for this unit could have promoted the accumulation of huge quantities of benthic food in the outer shelf environment. The predominance of large *Zoophycos* specimens suggests a rather stable environment, in which the trace-producing organisms explored large volumes of high-nutrient sediment.

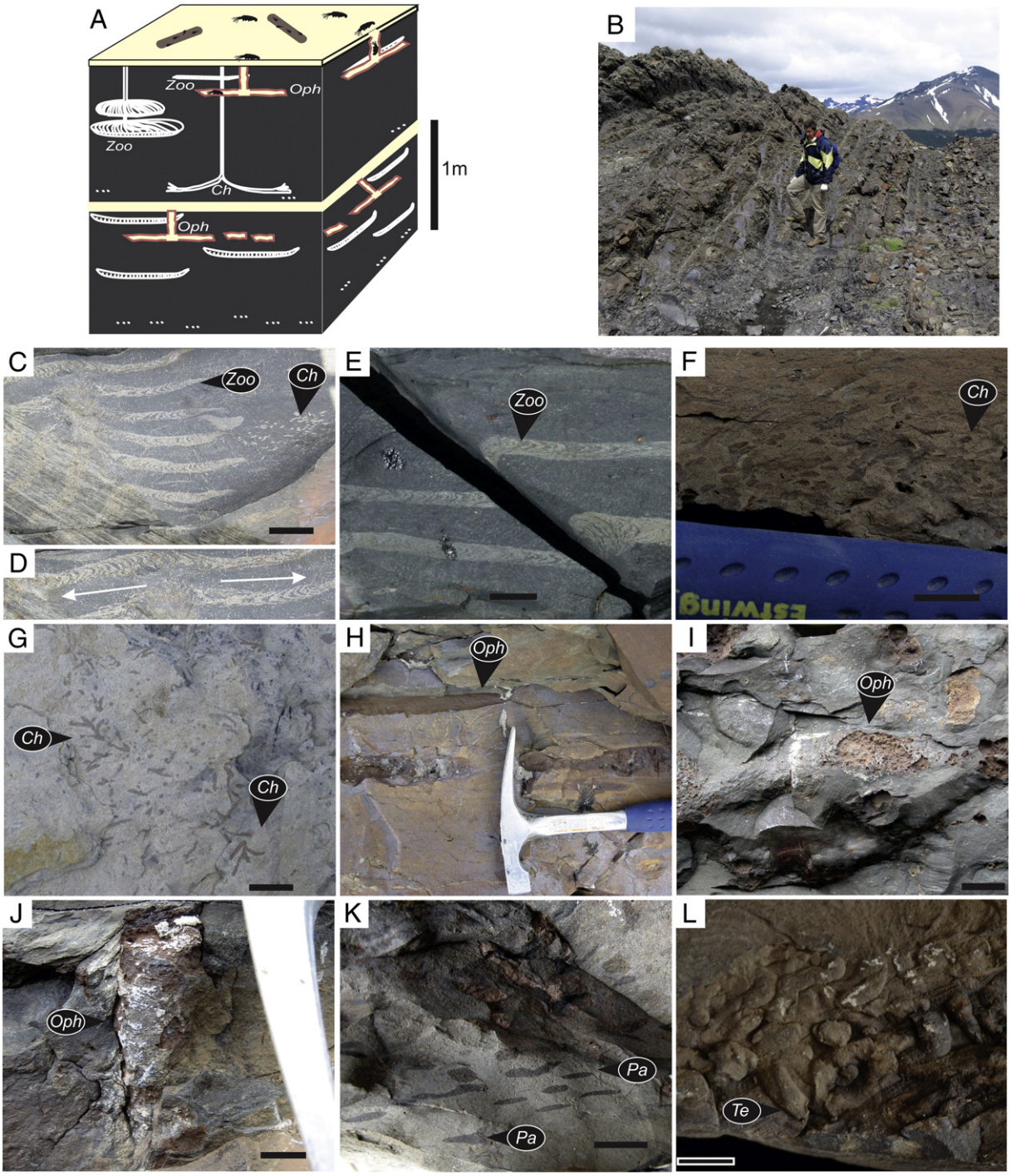

Fig. 5. Trace fossils and field view of the upper unit of the Río Mayer Formation at Seccional Río Guanaco locality. A— Block diagram showing the idealized distribution of the main trace fossils in this unit developed between sandy deposits of low-density turbidity currents (yellow). B— General view of the upper unit deposits of the Río Mayer Formation from sedimentary section 5 (person for scale). C— *Zoophycos* appearing with a "Christmas tree" pattern. D— Detail of C, showing the two contrary directions (white arrows) of migration of the marginal tube. E— Planar lamina of *Zoophycos* in cross sectional view. F and G— *Chondrites* isp. from the upper section showing less dense distribution than in the middle section. H— Horizontal galleries of *Ophiomorpha rudis*. I— Pelleted and oxidized external wall of *Ophiomorpha rudis*. J— Vertical shaft of *Ophiomorpha rudis* showing sparse distribution of pellets. K— *Palaeophycus* isp., the host rock and the infill of the trace is massive pelite and the different colouration was previously attributed to diagenesis (see Richiano et al., 2013). L— Moulds of *Teredolites* isp. associated with replaced wood fragments. Scale bar: 1 cm. Ch = *Chondrites*; Oph = *Ophiomorpha*; Zoo = *Zoophycos*; Te = *Teredolites*.

The upper unit of the formation accumulated within a different sequence stratigraphic context (Arbe, 2002; Richiano, 2012, 2014), with sedimentation rates being higher than the previous ones. In this regard, the second interval that now bears the *Zoophycos* ichnofacies developed in the final stage of a highstand systems tract (HST; Fig. 6). This HST is evidenced by the principal stage of the delta progradation of the Piedra Clavada Formation. This unit occupied a large portion (outcrops with more than 50 km of continuity) of the Austral Basin during the Albian

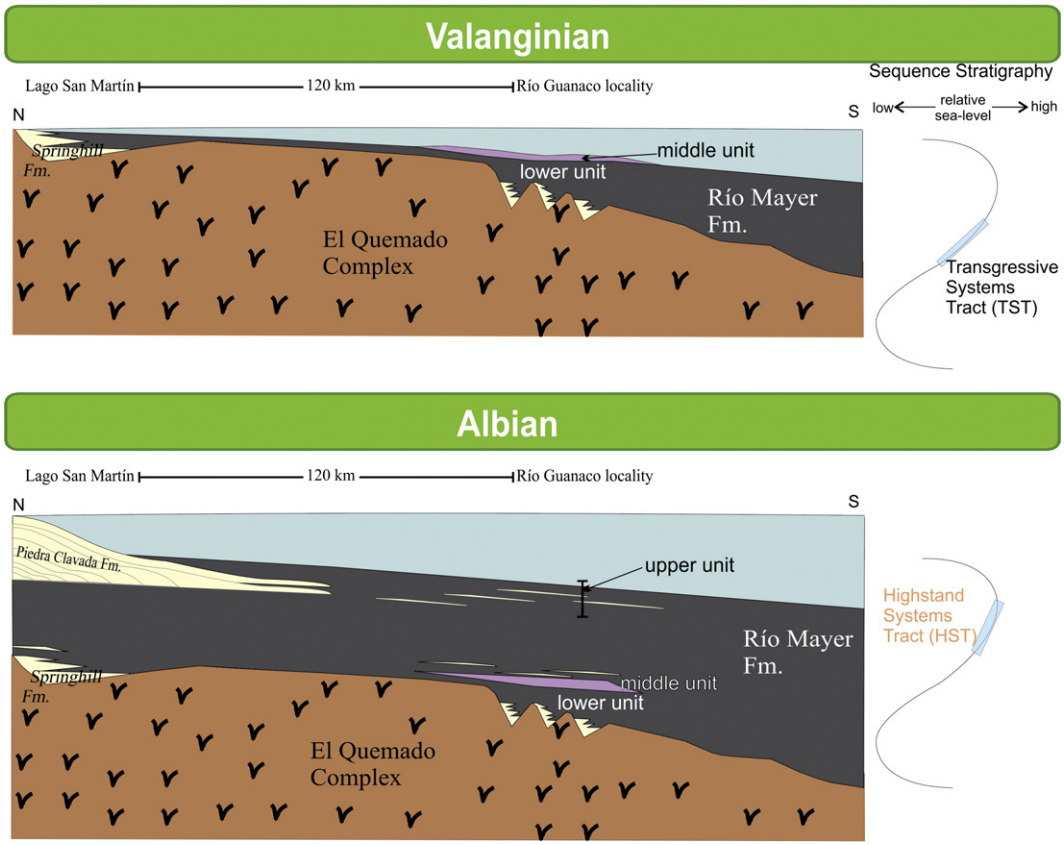

Fig. 6. General scheme of the Río Mayer Formation sedimentation and sequence stratigraphy during Valanginian and Albian time in the study area. During the Valanginian a general transgression took place that generated the deposition of the littoral Springhill Formation at Lago San Martín (120 km northward Seccional Río Guanaco locality). In this context, the marly middle unit of the Río Mayer Formation suggests very low sediment supply. During the Albian, the progradation of a deltaic system from the north occurred, generating higher sedimentation rates in the study area. Sequence stratigraphic context modified from Arbe (2002) and Richiano (2012).

(Arbe, 2002). In this context, times of high sedimentation rates and low benthic food content promoted by dilution, the *Zoophycos* producer constructed lobes of only little lateral extent, mainly forming short, coiled *Zoophycos* with a small diameter. The frequent arrival of distal turbidity currents along the Albian outer shelf at the Seccional Río Guanaco locality might have recurrently interrupted bioturbation by the *Zoophycos* trace makers.

Consequently, development of the *Zoophycos* ichnofacies in the Río Mayer Formation appears to be related to the availability of food, which in turn is controlled by the dilution caused by the sedimentation rate. Similar relationships between sedimentation rate and benthic food supply vs intensity of bioturbation by *Zoophycos* were described by Rodríguez-Tovar et al. (2011), however the origin of the different amounts of sediment and benthic food supply was interpreted by these authors to be related to monsoonal fluctuations.

Seasonal variability in the activity of *Zoophycos* producer was discussed by many researchers, among others Löwemark et al. (2006), Wetzel (2010), Wetzel et al. (2011) and Rodríguez-Tovar et al. (2011). This relationship is very difficult to elucidate for the Río Mayer Formation as the *Zoophycos* ichnofacies in this stratigraphic unit developed in very contrasting conditions, which could not have been connected to seasonal changes. During the deposition of the middle unit, the sedimentary input from the continent was minimal, and the potential catchment areas of the rivers draining to the basin are unknown. For the upper unit, the sedimentation rate was quite high, but it is very difficult to estimate the delivery of organic matter to the seafloor from the data obtained in the field. Furthermore, the variability in sedimentation rate can only be deciphered for low-frequency changes on a sequence stratigraphic scale and not for high-frequency seasonal variability. Taking into account this scenario, we hypothesize that, probably during the Valanginian, dryer conditions prevailed than during the Albian. In this context, during the deposition of the upper unit of the Río Mayer Formation, large amount of sediments were provided by the large rivers that formed the delta of Piedra Clavada Formation. Thus, nutrients were diluted by high sediment input, which resulted in low quantities of benthic food in the seafloor.

To sum up, the occurrence of the *Zoophycos* ichnofacies can be related to the availability of benthic food, which is controlled by the dilution effect produced by variable sedimentation rates. Sedimentation rates were very low during the mixed-composition (marls) TST and high in the siliciclastic HST (Fig. 6).

4.2. Oxygenation (Fig. 7)

The Río Mayer Formation has three well-differentiated sectors from a palaeo-oxygenation point of view, which, however, only partially match its lithological subdivision (Richiano, 2012, 2014; Richiano et al., 2012). In two of these intervals, the *Zoophycos* ichnofacies is developed with different expression. Firstly, anoxic conditions prevailed in the lower unit of the Río Mayer Formation as a response to the main transgression that took place in the Berriasian. These anoxic conditions during the Berriasian–early Valanginian prevented bioturbation and led to the formation of well-laminated black shales with high TOC (Fig. 7) and low Ce anomaly and MnO content (Richiano, 2014).

After that, as the main transgression continued, the middle unit formed during the ca. Valanginian–Hauterivian. The terrigenous

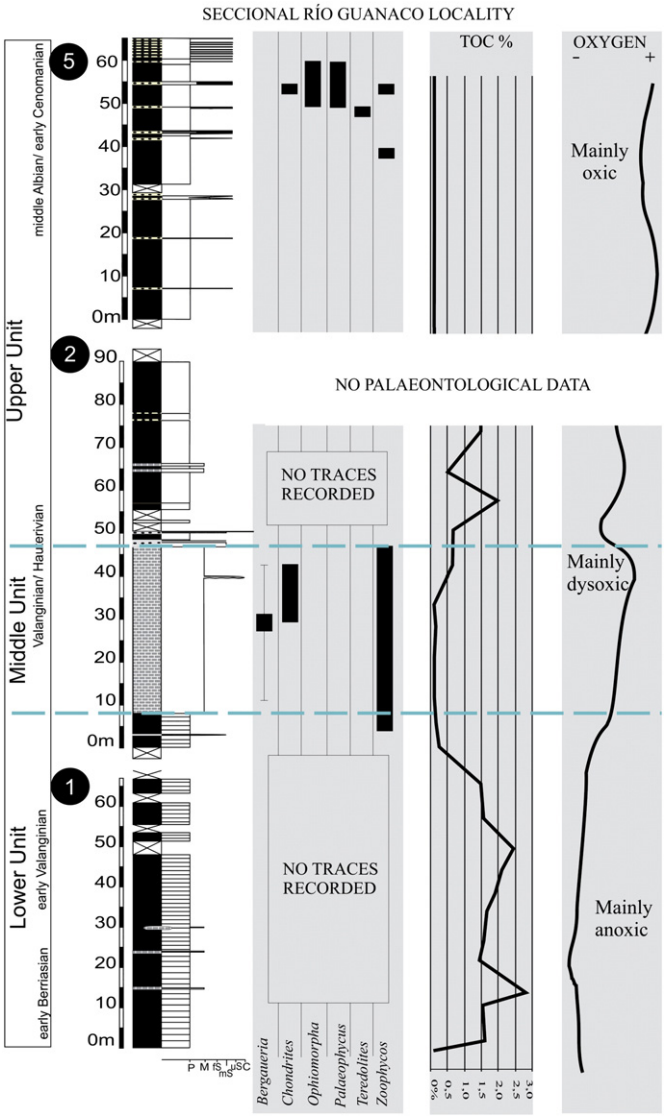

Fig. 7. Relative palaeo-oxygenation curve proposed for the Austral Basin in southwestern Gondwana during the Early Cretaceous based on sedimentology, total organic carbon (TOC) content and trace fossil content. Captions as for Fig. 2. Modified from Richiano (2014).

sediment input to the basin was very low and the marls accumulated. During this time, the deposits were intensely bioturbated (BI = 4) and the produced trace fossils can be ascribed to the *Zoophycos* ichnofacies. The low diversity assemblage of indistinct burrows (often biodeformational structures) and their shallow penetration imply dysoxic conditions. These conditions were favourable for the *Zoophycos* trace-makers, which took the opportunity to explore large volumes of sea floor sediments rich in benthic food without competition from other endobenthic organisms.

Toward the top of the formation, the deltaic Piedra Clavada Formation (Aptian–Albian) prograded from the northern edge of the basin. Oxygenation of the seafloor improved considerably in the upper part of the unit recorded by an increased ichnodiversity and low TOC values from the Aptian to the Cenomanian (Richiano, 2014). The lowering of the TOC values compared to the underlying deposits could result from the interplay between better oxygenation and dilution caused by enhanced sedimentation rate (Wetzel, 2008; Wetzel et al., 2011). Under these circumstances, the producers of *Zoophycos* competed with the *Ophiomorpha* and *Palaeophycus* trace makers in a seafloor having a lower concentration of benthic food than previously available and in an environment recurrently affected by fluctuating sediment input in a distal deltaic setting. A similar scenario to the presented one with respect to the amount of TOC vs. *Zoophycos* was described by Olivero (1996) for the Mesozoic of France.

5. Conclusions

Two considerably different developments of the *Zoophycos* ichnofacies were recognized in the Río Mayer Formation as a consequence of different palaeoenvironmental conditions. The combination of high benthic food contents, low sedimentation rates, relatively stable environments and dysaerobic conditions that developed during a TST in the middle unit of the studied interval made it possible for the *Zoophycos* trace-makers to use the substrate efficiently, resulting in the highest BI recognized for the Río Mayer Formation (Fig. 8). On the other hand, the upper unit of the studied interval shows low quantities of benthic food, high sedimentation rates and better oxygenation. This habitat in front of a delta was frequently affected during a late HST by distal turbidity currents, which repeatedly interrupted the activity of *Zoophycos* trace-makers resulting in low bioturbation intensity (Fig. 8).

The differences in size and height of the *Zoophycos* lobes/spreiten between the two intervals recovered in the Río Mayer Formation at the Seccional Río Guanaco locality could reflect the interaction between substrate and differing populations of the trace maker. Under quite stable environmental conditions, the *Zoophycos* producers and hence, the resulting *Zoophycos* traces had different sizes. In contrast to the situation previously described, the repeated arrival of low-density turbidity currents to the outer shelf resulted in recurrent disturbance of the *Zoophycos*-producer population. This factor might have stressed the benthic animals and only small-sized traces were produced. It is already known that under stress conditions there is a tendency toward smaller organisms (Wetzel, 1991), and this could be the most plausible explanation for the small diameter tunnels of the bioturbated interval of the upper unit.

The significantly different development and bioturbation intensity of the two intervals assigned to the *Zoophycos* ichnofacies in the Río Mayer Formation were strongly affected by the availability of food and the environmental stability; both factors were conditioned by the sedimentation rates. When the environment was rich in nutrients, and stable, with a low sedimentation rate, the deposits became highly bioturbated by the organisms producing burrows belonging to the *Zoophycos* ichnofacies. In less stable environments, related to distal turbidity flows, higher sedimentation rates and low benthic food quantities, bioturbation was less intense and the burrows were smaller.

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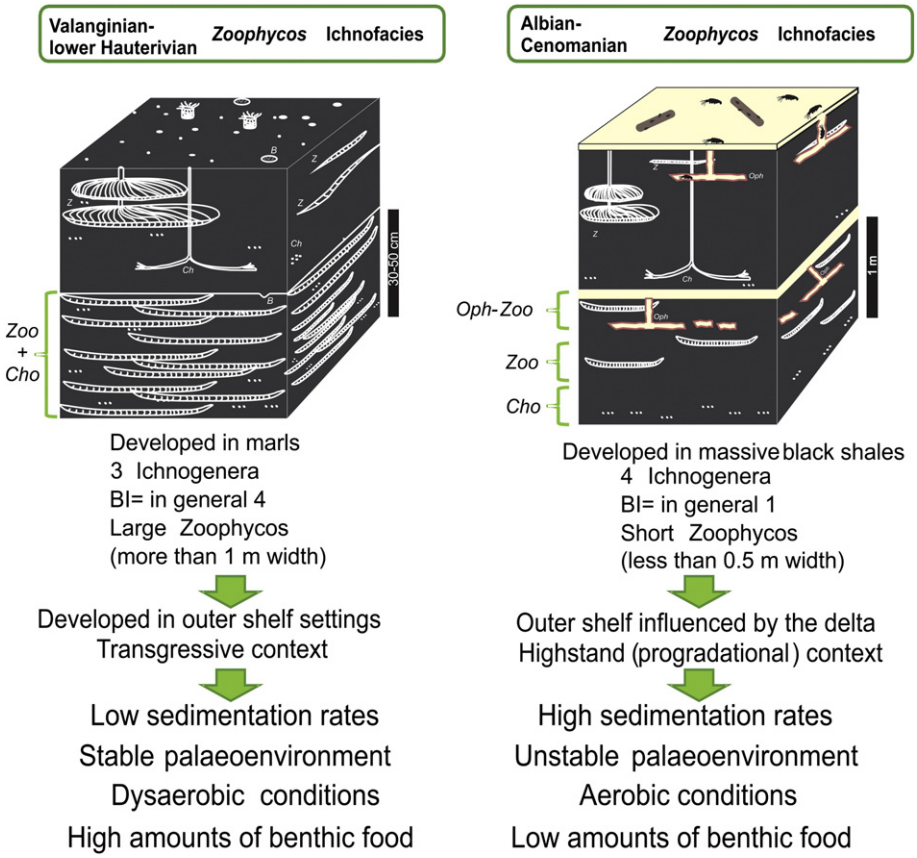

Fig. 8. Comparison of the main aspects of the Valanginian–Lower Hauterivian (middle unit) vs Albian–Cenomanian (upper unit) with regard to development of the *Zoophycos* ichnofacies in Río Mayer Formation at Seccional Río Guanaco locality.

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