



Application of digital image treatment to the characterization and differentiation of deep-sea ichnofacies

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ABSTRACT

The ichnofacies model proposed by Seilacher in the 1960's stands as one of the main tools used in the ichnological research. Based on the integration of numerous ichnological and sedimentological observations, it entails a precise characterization of the trace fossil assemblage. Differentiation of trace fossils may be relatively easy in outcrops, but cores are a different matter, particularly modern marine cores. Difficulties are even more accentuated in deep-sea pelagic and hemipelagic, non-turbiditic, fine-grained deposits. The application of digital image treatment can facilitate trace fossil identification and improve deep-sea ichnofacies characterization on modern cores. The method proposed here was applied to cores from the IODP Expedition 339 (Site U1385). Eight ichnotaxa —*Chondrites*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Taenidium*, *Thalassinoides*, *Thalassinoides*-like structures and *Zoophycos*— as well as some horizontal grouped circular structures interpreted as trails (?*Nereites*) were recognized. The archetypical *Zoophycos* ichnofacies is identified, but characteristic elements belonging to the *Nereites* ichnofacies and to the distal expression of *Cruziana* ichnofacies are locally recognized. Thus, the applied methodology allows differentiating between different

RESUMEN

El modelo de icnofacies, propuesto por Seilacher en la década de los 60, es una de las principales herramientas aplicadas en icnología. Basado en la integración de numerosas observaciones icnológicas y sedimentológicas, una precisa caracterización de la asociación de icnotaxones es esencial en el análisis de icnofacies. La diferenciación de icnotaxones puede ser relativamente fácil en afloramiento, pero es comparativamente difícil en sondeos, especialmente si corresponden a materiales marinos modernos. La dificultad se acentúa cuando se trata de sedimentos pelágicos, hemipelágicos, no turbidíticos, de grano fino. Se propone la aplicación del tratamiento de imágenes para facilitar la identificación de icnotaxones y mejorar la caracterización de icnofacies marinas profundas en sondeos modernos. El método ha sido aplicado a sondeos de la Expedición 339 del IODP (Site U1385). Ocho icnotaxones, *Chondrites*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Taenidium*, *Thalassinoides*, estructuras similares a *Thalassinoides* y *Zoophycos*, y algunas formas circulares, densamente agrupadas, interpretadas como rastros horizontales (?*Nereites*), han sido reconocidas. Se ha identificado claramente la icnofacies de *Zoophycos*, aunque se reconocen elementos propios de las icnofacies de

expressions of the *Zoophycos* ichnofacies and to approach subtle changes in the involved environmental parameters affecting tracemakers.

Keywords: Trace fossils, ichnofacies, deep-sea, IODP Expedition 339, Site U1385, digital image treatment.

Nereites y de la expresión distal de icnofacies de *Cruziana*. La metodología aplicada facilita el reconocimiento de distintas expresiones de la icnofacies de *Zoophycos* y permite interpretar sutiles cambios en los parámetros ambientales que afectan a los bioturbadores.

Palabras clave: Icnofósiles, icnofacies, medios marinos profundos, Expedición 339 IODP, Site U1385, tratamiento digital de imágenes.

1. INTRODUCTION

The ichnofacies model, proposed by Seilacher during the 1960's (Seilacher, 1964, 1967), led to unprecedented development of ichnological analysis. This model is based on the identification of certain features shared by ichnotaxa during a longtime span that can be related to particular environmental conditions (Buatois & Mángano, 2011). Initially just six ichnofacies were proposed, but over the past five decades the model has been modified and expanded to embrace many more recurrent, archetypal (Seilacherian) ichnofacies that play an important role in basin analysis (see recent reviews in Buatois & Mángano, 2011; MacEachern *et al.*, 2010, 2012). To date, 15 archetypal marine and continental ichnofacies have been defined based on invertebrate trace fossil assemblages (Buatois & Mángano, 2011). Earlier papers focused on application of ichnofacies as palaeobathymeters (e.g., Seilacher, 1967; Frey & Pemberton, 1985; Bottjer *et al.*, 1987). However, palaeobathymetry is not the only controlling factor —ichnofacies depend on the interplay of many parameters, such as substrate, energy, food supply, oxygenation level and taphonomic features that control the distribution of tracemakers and determine the preservation of biogenic structures (e.g., Bromley, 1990, 1996; Wetzel, 1991; Buatois & Mángano, 1995; MacEachern *et al.*, 2007). Accordingly, detailed ichnofacies characterization has come to be an essential tool for palaeoenvironmental research, the interpretation of depositional settings, and basin analysis.

Ichnofacies characterization is not a mere listing of ichnotaxa. Rather, it is based on the integration of a complete data set that integrates ichnologic, sedimentologic, stratigraphic and taphonomic information. Still, precise ichnotaxonomic differentiation is fundamental for ichnofacies analysis, providing important palaeoecologic information (Wetzel, 1991). Such differentiation is relatively easy in outcrops, but complicated when working on core materials, owing to narrow views of, limited size and almost exclusive two-dimensional expression of trace fossils (e.g., Bromley, 1996; Wetzel, 2010; Dorador *et al.*, 2014a). The difficulty is even greater when working with modern marine cores, especially those of deep-sea,

pelagic-hemipelagic sediments in which trace fossils have diffuse boundaries and their infilling materials are visually very similar to the host sediment.

Several techniques have been developed to improve ichnotaxonomic differentiation in modern marine cores. Some of them, for instance X-ray scanning (e.g., Howard, 1968; Löwemark & Werner, 2001) and computed tomography (Joschko *et al.*, 1991; Rosenberg *et al.*, 2007, among others), require specialized methodology and instrumentation, making them comparatively complex, expensive and infrequently employed. Magwood & Ekdale (1994) used image treatment for ichnotaxa differentiation and ichnofabric visualization by means of matrix operations. However, the complexity of its application is an impediment for the widespread use of this method. Recently, an inexpensive high-resolution image treatment method that is easy to use was developed for the ichnological study of modern deep-sea marine cores. The advantages of this novel technique are: 1) differentiation between biodeformational structures and trace fossils (Dorador *et al.*, 2014a), 2) quantification of the percentage of bioturbation in an objective and semi-automatic way (Dorador *et al.*, 2014b), 3) knowledge of overlapping between trace fossils, tiering structure and penetration depth of some ichnotaxa (Dorador & Rodríguez-Tovar, 2014), and 4) enhancement of ichnofabric characterization (Rodríguez-Tovar & Dorador, 2014, 2015). This paper describes the usefulness of this high-resolution image technique for the ichnotaxonomic characterization of trace fossil assemblages pertaining to deep-sea ichnofacies in cores of modern marine deposits.

1.1. Deep-marine ichnofacies

Deep-marine sediments are mainly characterized by the *Zoophycos* and *Nereites* ichnofacies (Uchman & Wetzel, 2011; Wetzel & Uchman, 2012; Fig. 1).

The *Zoophycos* ichnofacies traditionally has been located between the *Cruziana* and *Nereites* ichnofacies, below storm-wave base in outer shelf to slope deposits (Seilacher, 1967; Uchman & Wetzel, 2011). Hence, it is considered as intermediate between ichnofacies typical

of inner shelf or offshore deposits (i.e., the *Cruziana* ichnofacies) and those of abyssal deposits (i.e., the *Nereites* ichnofacies) (Hubbard *et al.*, 2012). The *Zoophycos* ichnofacies is usually associated with fine-grained, pelagic and hemipelagic, non-turbiditic sediments, and with very low sedimentation rates. It is commonly linked to low-energy subtidal settings, periods of dysaerobic or anoxic conditions, and sediments with abundant organic matter. In this context, diversity is usually low and abundance is high, and the trace fossil assemblage is characterized by a prevalence of relatively simple to complex feeding structures with spreite, subordinate grazing traces, and the dominance of deep-tier forms of deposit feeders and farmers. One typical ichnogenus is *Zoophycos*, but *Chondrites* and *Phycosiphon* are also characteristic. *Cosmorhapha*, *Helminthopsis*, *Planolites*, *Scolicia*, *Spirophyton* and *Thalassinoides* are also present, as well as certain ichnospecies of *Nereites* (Buatois & Mángano, 2011; MacEachern *et al.*, 2012; Uchman & Wetzel, 2012; Table 1).

Table 1. Common trace fossils registered in the distal expression of *Cruziana* ichnofacies, *Zoophycos* ichnofacies and *Nereites* ichnofacies. Note: Grey tone for more (dark) or less (light) abundant ichnotaxa.

Ichnotaxa	Distal expression of <i>Cruziana</i> ichnofacies	<i>Zoophycos</i> ichnofacies	<i>Nereites</i> ichnofacies
<i>Asterosoma</i>	—	—	—
<i>Chondrites</i>	—	—	—
<i>Cosmorhapha</i>	—	—	—
<i>Cylindrichnus</i>	—	—	—
<i>Graphoglyptids</i>	—	—	—
<i>Helminthopsis</i>	—	—	—
<i>Nereites</i>	—	—	—
<i>Ophiomorpha</i>	—	—	—
<i>Phycosiphon</i>	—	—	—
<i>Planolites</i>	—	—	—
<i>Rosselia</i>	—	—	—
<i>Scolicia</i>	—	—	—
<i>Spirophyton</i>	—	—	—
<i>Thalassinoides</i>	—	—	—
<i>Zoophycos</i>	—	—	—

The *Nereites* ichnofacies is common in basin-floor depositional environments characterized by very slow pelagic and hemipelagic background sedimentation interrupted by periodic turbidite deposition. Ichnodiversity is very high and abundance is high. Trace fossil assemblages are characterized by dominance of complex graphoglyptids

reflecting farming or trapping (in response to the slow accumulation of food), and the presence of grazing trails and feeding traces of detritus and deposit feeders; shallow-tier trace fossils are generally dominant (Buatois & Mángano, 2011; MacEachern *et al.*, 2012; Uchman & Wetzel, 2012). Taphonomy plays an important role in this ichnofacies, particularly in the preservation of delicate graphoglyptid structures (Uchman & Wetzel, 2012). This ichnofacies can be divided into three ichnosubfacies (Seilacher, 1974; Uchman, 2009) to distinguish the assemblages related to different parts of a turbidite (channel, lobes, etc.): 1) The *Ophiomorpha rudis* ichnosubfacies is related to thick-bedded sandstones in turbidite successions in channels or proximal lobes, and mainly consists of *Ophiomorpha*, *Scolicia*, and occasionally *Nereites* and *Chondrites* (Uchman, 2009; Buatois & Mángano, 2011); 2) the *Paleodictyon* ichnosubfacies is characterized by sandier, medium- to thin- bedded flysch deposits, featuring the presence of graphoglyptids; and 3) the *Nereites* ichnosubfacies represents the most distal part of turbidites (muddy distal flysch sediments) and is characterized by the presence of backfilled trace fossils such as *Nereites*, *Phycosiphon* or *Zoophycos* (Seilacher, 1974; Heard & Pickering, 2008; Knaust, 2009; Uchman, 2009; Buatois & Mángano, 2011; Uchman & Wetzel, 2012; Table 1). The succession of these three ichnosubfacies can be related to bathymetric trends from shallow to deeper parts, and with non-bathymetric trends from channel axis, levee to overbank or inter-channel areas (Uchman & Wetzel, 2012).

Additionally, the distal expression of the *Cruziana* ichnofacies can be identified together with the *Zoophycos* and *Nereites* ichnofacies in deep-sea settings. The archetypal *Cruziana* ichnofacies occurs from just slightly above fair-weather base to the storm-wave base, from the lower shoreface to the lower offshore, under moderate- to low-energy conditions. The wide range of zones, implying variations in palaeoenvironmental conditions and, hence, ichnological assemblages, allows for subdivisions of this archetypal *Cruziana* ichnofacies (MacEachern *et al.*, 1999, 2007). The distal expression of the *Cruziana* ichnofacies is transitional between the archetypal *Cruziana* ichnofacies and the archetypal *Zoophycos* ichnofacies in a basinward direction, usually from lower offshore toward inner shelf, and is associated with muddy siltstones and silty mudstones (MacEachern *et al.*, 1999, 2007; Buatois & Mángano, 2011). This distal expression of the *Cruziana* ichnofacies is dominated by feeding and grazing structures of deposit feeders, with suspension-feeding structures generally absent. There is an overall decrease in *Rosselia*, *Cylindrichnus*, *Asterosoma* and *Ophiomorpha*, with an increase in *Helminthopsis*, *Phycosiphon*, *Planolites*, *Thalassinoides* and *Zoophycos*, compared to the archetypal expression of the *Cruziana* ichnofacies (MacEachern *et al.*, 1999, 2007; Buatois & Mángano, 2011; Table 1).

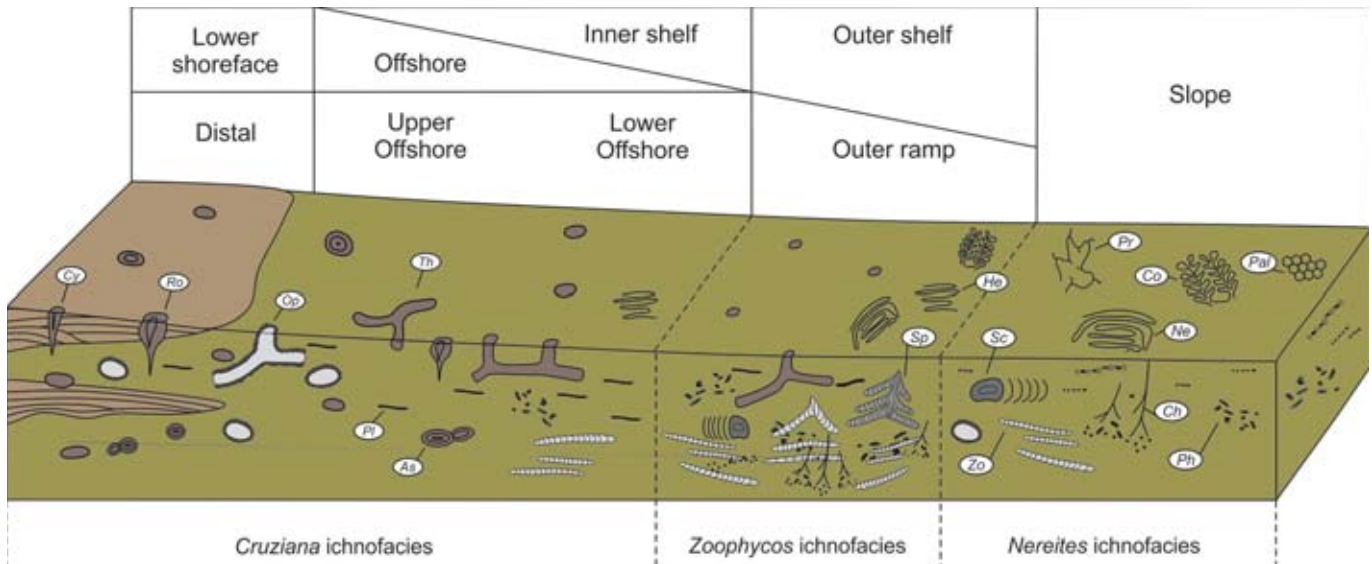


Figure 1. Schematic ichnofacies diagram showing the distribution of the most common ichnogenera along a proximal-distal trend, from sublittoral to abyssal zone. Modified from Buatois & Mángano (2011) and Pemberton *et al.* (2012). *As*, *Asterosoma*; *Ch*, *Chondrites*; *Co*, *Cosmorhaphis*; *Cy*, *Cylindrichnus*; *He*, *Helminthopsis*; *Ne*, *Nereites*; *Op*, *Ophiomorpha*; *Pal*, *Paleodictyon*; *Ph*, *Phycosiphon*; *Pl*, *Planolites*; *Pr*, *Protopaleodictyon*; *Ro*, *Rosselia*; *Sc*, *Scolicia*; *Sp*, *Spirophyton*; *Th*, *Thalassinoides*; *Zo*, *Zoophycos*.

A basinward differentiation of the archetypical *Cruziana* ichnofacies – *Zoophycos* ichnofacies – *Nereites* ichnofacies must be manifest in the associated ichnological and sedimentological features. Yet the characterization of particular ichnofacies is hardly discernible in their transitions. The distal expression of the *Cruziana* ichnofacies can be interdigitated with the *Zoophycos* ichnofacies, and differentiation between the *Zoophycos* ichnofacies and the *Nereites* ichnofacies can be difficult in the case of fine-grained, distal turbidites, when sedimentation is more or less constant and low.

2. MATERIALS AND METHODS

The full section of Site U1385 from the IODP Expedition 339 (Expedition 339 Scientists, 2013a; Hernández-Molina *et al.*, 2013) was studied. This Site is located on the West Iberian margin (37°34.285'N, 10°7.562'W, Fig.2), on a spur, near the Core MD95-2042 (the “Shackleton Site”), a location with special relevance when studying millennial-scale climate variability over the last glacial cycles (Shackleton *et al.*, 2000, 2004) or interpreting global environmental conditions based on correlations with worldwide records (Expedition 339 Scientists, 2013b; Hodell *et al.*, 2013, 2015). The record of this site mainly comprises four cores from around 150 m penetration depth each (U1385A, U1385B, U1385D, and U1385E; total recovery of core U1385C is around 10 m),

representing continuous deposition from ~1.45 Ma ago to the Holocene (Expedition 339 Scientists, 2013b; Hodell *et al.*, 2013, 2015). Sediments are mainly composed by bioturbated calcareous muds and calcareous clays; primary sedimentary structures were not observed (Expedition 339 Scientists, 2013a, b).

High-resolution digital image treatment (Dorador & Rodríguez-Tovar, 2014, 2015; Dorador *et al.*, 2014a, b; Rodríguez-Tovar *et al.*, 2015a, b; Takashimizu *et al.*, 2015) was applied to original images, scanned with 500 dpi image resolution, of cores from Site U1385 (Expedition 339 Scientists, 2013c). These images were treated following the modifications proposed by Dorador *et al.* (2014a) to improve the visibility of trace fossils and ichnotaxonomic determination. This modification entails three image adjustments: 1) *levels*, 2) *brightness* and 3) *vibrance* (Dorador *et al.*, 2014a). The *Levels* adjustment involves stretching of the histogram according to colour extremes, modifying three parameters (black, grey and white). Black and white are established to represent the extreme values of the histogram, while the grey value is modified to make the image darker or lighter. The *Brightness* adjustment of reflected light can be used to modify two parameters, brightness and contrast. High values in both parameters mean a greater amount of reflected light and greater contrast of the image. Finally, the *vibrance* adjustment corrects the yellowish tone that is produced during execution of the two previous adjustments, using as values vibrance and saturation. After several modifications, the most positive results for the

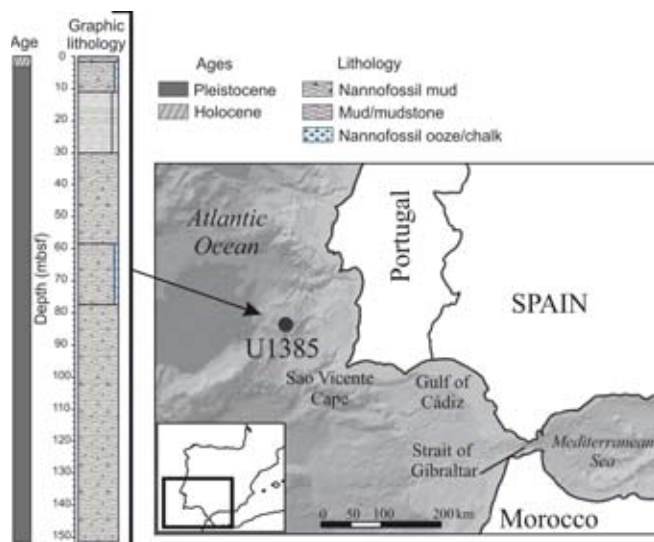


Figure 2. Location of Site U1385, IODP Expedition 339, and lithologic log for the site.

selected adjustments were obtained for *levels* from 25 to 32 black, 0.43 to 0.75 grey and 92 to 100 white; *brightness* from -32 to -12 and contrast from 43 to 65; and *vibrance* from -7 to -11 for the vibrance parameter and from -12 to -18 for saturation values.

Occasionally, when ichnotaxonomical determination is particularly complicated due to similar geometries in different ichnotaxa, the high-resolution digital image method was supplemented by the quantification and comparison of pixel values in the infilling material of these ichnotaxa (Dorador & Rodríguez-Tovar, 2014).

3. RESULTS

3.1. Ichnotaxa and ichnofacies characterization

The proposed methodology allowed for differentiation of eight ichnotaxa in the studied cores from Site U1385. Trace fossil assemblages, similar to the one differentiated by Rodríguez-Tovar & Dorador (2014), consist of abundant *Planolites*, common *Palaeophycus* and *Thalassinoides*, together with less abundant *Taenidium* and *Thalassinoides*-like structures, localized *Zoophycos* and *Chondrites*, and rare *Phycosiphon* and horizontal trails (?*Nereites*) (Fig. 3). *Chondrites* is observed as clusters of very small circular to elliptical spots and short tubes. *Palaeophycus* consists of circular to subcircular, unbranched lined cylindrical structures infilled by material having the same lithology as the host rock. *Phycosiphon* was registered as randomly oriented patches of horizontal, curved small lobes,

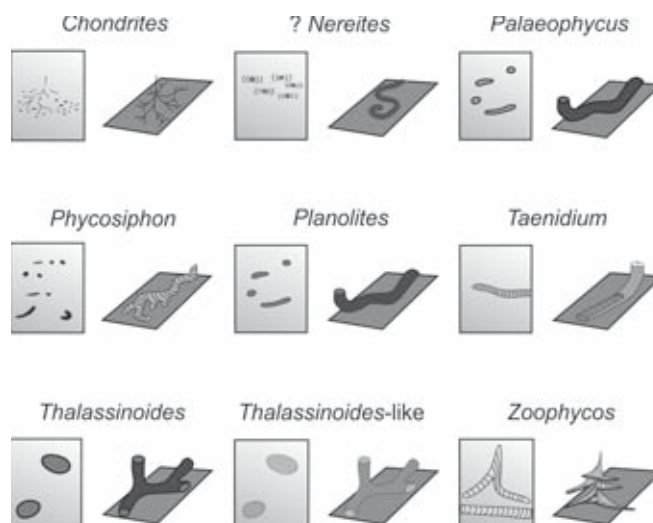


Figure 3. Schematic drawings, in 2D and 3D, of trace fossils identified in the study cores (following Wetzel & Uchman, 2012).

showing dark, fine-grained cylindrical to circular cores. *Planolites* appears as circular to subcircular unbranched cylindrical unlined tubular forms, filled with sediment of different material than that of the host sediment. *Taenidium* was found as horizontal to oblique, simple, straight to sinuous, unlined tubular meniscate structures. *Thalassinoides* are larger circular to subcircular oval spots and straight or slightly winding horizontal to oblique cylinders. *Thalassinoides*-like structures are similar to *Thalassinoides*, but show a variably developed irregular wall and diffuse shape. *Zoophycos* consists of repeated, horizontal to subhorizontal, spreite structures. Densely packed large black circular forms, enveloped by light sediments probably associated with horizontal trails, are tentatively assigned to ?*Nereites*.

Trace fossil assemblages, together with sedimentological features of the studied deposits, allowed us to identify the *Zoophycos* ichnofacies, especially well-represented in those intervals where *Zoophycos* is dominant. *Zoophycos*, locally accompanied by *Chondrites*, was seen to locally crosscut *Planolites* and *Thalassinoides*. Even though the *Zoophycos* ichnofacies could be clearly differentiated, observed trace fossil assemblages in some intervals of the studied cores could be related to the distal expression of the *Cruziana* ichnofacies and to the *Nereites* ichnofacies (Fig. 4). Intervals characterized by abundant *Planolites*, *Thalassinoides* and *Thalassinoides*-like structures, the subordinate presence of *Palaeophycus* and *Taenidium*, and rare *Chondrites* and *Zoophycos*, can be assigned to the distal expression of *Cruziana* ichnofacies, while, the local record of densely-packed, large, black circular forms enveloped by light sediments (?*Nereites*), may reveal the presence of grazing trails typical of the *Nereites* ichnofacies.

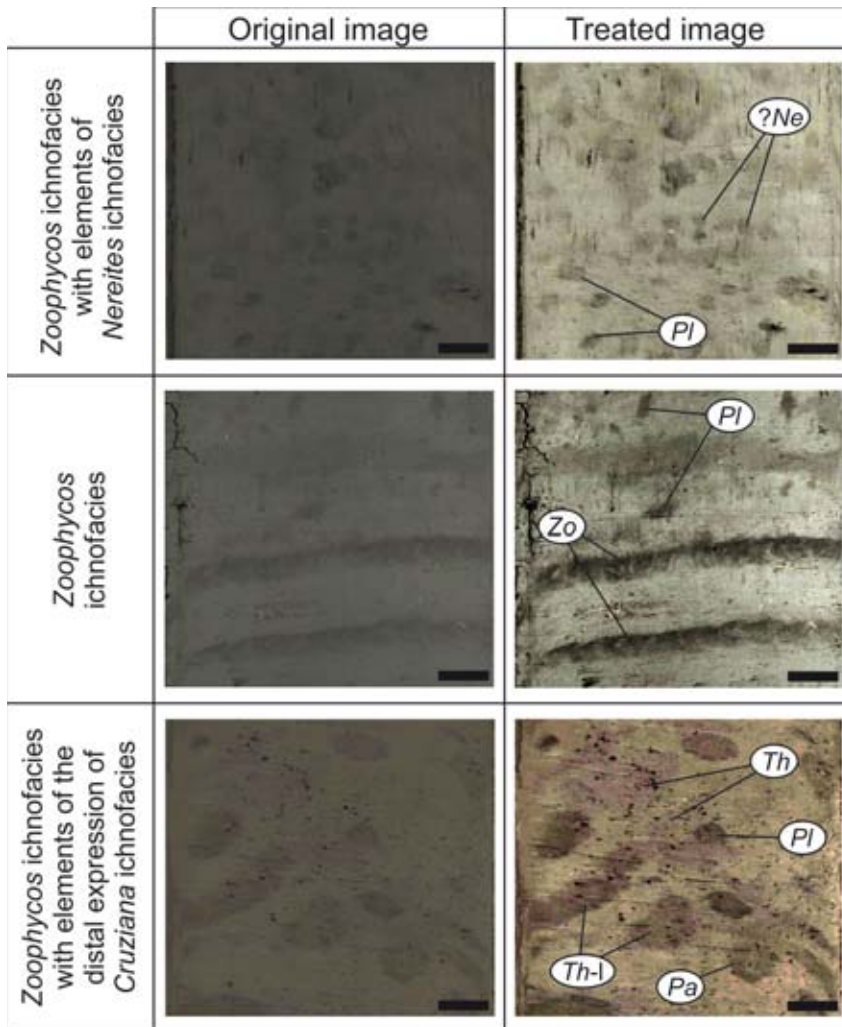


Figure 4. Examples of the three expressions of the *Zoophycos* ichnofacies identified in this study (archetypical *Zoophycos* ichnofacies, *Zoophycos* ichnofacies with elements of the distal *Cruziana* ichnofacies, and *Zoophycos* ichnofacies with elements of the *Nereites* ichnofacies). ?*Ne*, ?*Nereites*; *Pa*, *Palaeophycus*; *Pl*, *Planolites*; *Th*, *Thalassinoides*; *Th-l*, *Thalassinoides*-like structures; *Zo*, *Zoophycos*. Scale bar 1 cm.

4. DISCUSSION

Sedimentological and ichnological data from Site U1385 are compatible with deposition under low-energy conditions in a deep-sea hemipelagic setting. The sediments in the studied cores mainly consists of mudstone (Expedition 339 Scientists, 2013b), with a relatively constant grain size, deposited by suspension fall-out. Trace fossil assemblages generally support good bottom- and pore-water conditions and organic matter availability, with only exceptional variations in these parameters (Rodríguez-Tovar & Dorador, 2014). Precise ichnofacies characterization might therefore be very useful to refine palaeoenvironmental interpretations.

As indicated above, generalized archetypical *Zoophycos* ichnofacies could be differentiated, but particular ichnotaxa may correspond to the distal expression of *Cruziana* ichnofacies (i.e., frequent *Thalassinoides* and *Thalassinoides*-like) or to the *Nereites* ichnofacies (i.e., ?*Nereites*). Before making any conclusive ichnofacies assignments, it is necessary to consider that: 1) these particular ichnotaxa are also registered in the *Zoophycos*

ichnofacies, 2) other typical elements of both the distal expression of the *Cruziana* and the *Nereites* ichnofacies are absent, and 3) the *Zoophycos* ichnofacies shows intergradation landward with the distal *Cruziana* ichnofacies and basinward with the *Nereites* ichnofacies. On this basis the *Zoophycos* ichnofacies can be considered as the only one registered in the studied succession, but with variations, including its archetypical expression and those showing elements also registered in the distal expression of *Cruziana* ichnofacies or in the *Nereites* ichnofacies.

The proposed discrimination among three distinct expressions of the *Zoophycos* ichnofacies is relevant when interpreting the depositional environment of the studied succession. Environmental parameters influencing tracemakers —sedimentation rate, energy conditions, sea level, oxygenation, and food supply, among others— vary with distance from shore. Thus, the distinct ichnofacies expressions could help recognize changing depositional conditions. A clear example would be the core section seen in Figure 5, corresponding to core U1385A-15H-3-A from Site U1385 of IODP Expedition 339. Overall,



Figure 5. Differentiation between the *Zoophycos* ichnofacies with elements of the distal expression of *Cruziana* ichnofacies and the archetypal *Zoophycos* ichnofacies in core U1385A-15H-3-A. *Ch*, *Chondrites*; *Ph*, *Phycosiphon*; *Pl*, *Planolites*; *Th*, *Thalassinoides*; *Zo*, *Zoophycos*. Scale bar 1 cm.

it has a mottled background ichnofabric, on which some discrete trace fossils can be observed. The trace fossil assemblage consists of dominant *Zoophycos* and subordinate *Chondrites*, *Planolites* and *Thalassinoides*, indicating the *Zoophycos* ichnofacies. In this generalized context, however, stratigraphical variations are recognized. From the bottom to top of the core *Zoophycos* progressively decreases in abundance and eventually disappears (in the upper part), while the abundance of *Planolites* and *Thalassinoides* increase significantly. This could be interpreted as a continuous change from the archetypal *Zoophycos* ichnofacies to the *Zoophycos* ichnofacies with elements of the distal expression of the *Cruziana* ichnofacies. This subtle change might be related to minor changes in the palaeoenvironmental conditions (e.g., slight increase in oxygenation, food content and/or deposition rate associated with more proximal depositional settings).

5. CONCLUSIONS

A high-resolution image procedure was applied to cores from Site U1385 (IODP Expedition 339) to improve characterization of deep-sea ichnofacies. This method is mainly based on the modification of three image adjustments: *levels*, *brightness* and *vibrance*, together with pixel analysis.

Eight ichnotaxa were recognized (*Chondrites*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Taenidium*, *Thalassinoides*, *Thalassinoides*-like structures and *Zoophycos*) along with undefined horizontal trails (?*Nereites*). Variations in trace fossil diversity and abundance occur throughout the succession.

Sedimentological and ichnological data indicate the dominance (exclusiveness) of the *Zoophycos* ichnofacies, but reveal three different expressions: 1) archetypal *Zoophycos* ichnofacies, characterized by dominance of *Zoophycos*, with subordinate *Chondrites*, *Planolites*, *Thalassinoides* and *Thalassinoides*-like structures; 2) *Zoophycos* ichnofacies with elements of the distal expression of the *Cruziana* ichnofacies, consisting of common *Planolites*, *Thalassinoides* and *Thalassinoides*-like structures; and 3) *Zoophycos* ichnofacies with elements of the *Nereites* ichnofacies, characterized by the presence of horizontal, grouped circular structures interpreted as grazing trails (?*Nereites*).

Vertical variations in the three expressions of the *Zoophycos* ichnofacies point to subtle changes in the depositional conditions potentially related to temporal variations in distance from shore, sedimentation rate, oxygenation and/or food content.

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