

DISAPPEARED ALMOST WITHOUT A TRACE: TAPHONOMIC PATHWAYS AND THE RECOGNITION OF HIDDEN BIOTURBATION EVENTS IN EOCENE STORM DEPOSITS (PAUJÍ FORMATION, LAKE MARACAIBO, VENEZUELA)

Luis A. BUATOIS¹, Manuel DELGADO² & M. Gabriela MÁNGANO¹

¹ Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK S7N 5E2, Canada; e-mails: luis.buatois@usask.ca, gabriela.mangano@usask.ca

² División Oriente, Gerencia de Exploración, PDVSA, Edificio PDVSA, Nivel Plaza, Modulo A, Puerto La Cruz, 6023, Venezuela; e-mail: delgadomc@pdvsa.com

Buatois, L. A., Delgado, M. & Mángano, M. G., 2015. Disappeared almost without a trace: Taphonomic pathways and the recognition of hidden bioturbation events in Eocene storm deposits (Paují Formation, Lake Maracaibo, Venezuela). *Annales Societatis Geologorum Poloniae*, 85: 473–479.

Abstract: Shallow-marine deposits, included in the “Basal Sands” of the Eocene Paují Formation of the Maracaibo Basin in western Venezuela, record deposition in foreshore to lower offshore settings. These deposits are stacked in coarsening-upward parasequences that reflect variable intensities and frequencies of storms. Of particular interest are sharp-based, amalgamated, hummocky cross-stratified and rippled, very fine-grained sandstone beds, observed in the core MOT-X from the Motatán Field. These beds record storm deposition, under purely oscillatory to combined flows in an offshore-transition setting. The amalgamated nature of the sandstone interval indicates repeated erosion, due to multiple storm events. The ichnofabrics in these tempestites result from a distinctive taphonomic pathway, reflecting the interplay between bioturbation events and storm erosion and deposition. The storm-related trace-fossil suite is represented by *Diplocraterion parallelum* and local occurrences of *Palaeophycus tubularis*, *Bergaueria* isp. and *Thalassinoides* isp., which is consistent with the relatively high energy of formation of these deposits. Fair-weather deposits are absent from the sandstone interval. However, high densities of *Chondrites* isp. are present in the infills of *Diplocraterion parallelum* and, more rarely, *Thalassinoides* isp. providing the sole evidence of the establishment of a resident fauna during inter-storm intervals. Deposits containing the fair-weather suites were erosionally removed during the subsequent storm. The deep-tier emplacement of *Chondrites* and the ability of its producer to rework other biogenic structures favour preservation, allowing recognition of a “hidden” bioturbation event that otherwise might have remained undetected.

Key words: Trace fossils, ichnofabric, taphonomic pathways, tempestites, shallow marine, Eocene.

Manuscript received 13 December 2014, accepted 1 July 2015

INTRODUCTION

The ichnofabric approach provides a comprehensive way of analysing bioturbated deposits (Bromley and Ekdale, 1986; Bromley, 1990, 1996). A number of related concepts are central to this research programme, including tiering structure, ichnoguilds, and degree of bioturbation (Bromley, 1990, 1996; Ekdale *et al.*, 2012). We demonstrate how the evaluation of taphonomic pathways can be a substantial component in ichnofabric analysis, as well. This conceptual tool, originally proposed for body-fossil taphonomy (Meldahl and Flessa, 1990), was subsequently imported to and expanded for ichnology in an attempt to decipher successions of events, reflecting the interplay between depositional/erosional events, bioturbation and preservational processes in specific sedimentary environments (Buatois

and Mángano, 2004, 2011). In body-fossil taphonomy, the concept of taphonomic pathways refers to the sequence of inheritance of taphonomic features by skeletal remains. Meldahl and Flessa (1990) noted that shells in different environments typically acquire particular taphonomic features in a characteristic order, as a result of the relative influence of various taphonomic processes among different depositional environments. Similarly, ichnofabrics are the product of different preservational trajectories (i.e., taphonomic pathways), shaped by the interplay of biological, physical and chemical processes that characterise a diverse range of depositional settings (Buatois and Mángano, 2011). The nature of taphonomic pathways in ichnology has been explored in lacustrine (Zhang *et al.*, 1998; Buatois and Mángano,



Fig. 1. Location map of the Motatán Field in the Maracaibo Basin.

2004, 2007), fluvial (Buatois and Mángano, 2004, 2007; Buatois *et al.*, 2007) and tidal (Desjardins *et al.*, 2010; Pearson *et al.*, 2013) settings.

The aim of this paper is to illustrate the use of the taphonomic pathways concept to reveal subtly preserved bioturbation events in the stratigraphic record that can be easily missed and to show how they can help unravel storm dynamics in the middle Eocene shallow-marine deposits of the Paují Formation of the Lake Maracaibo area, in western Venezuela (Fig. 1).

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The tectonic history of the Maracaibo Basin has been subdivided into four phases (Ghosh *et al.*, 1995): (1) Triassic–Jurassic graben, (2) Cretaceous back-arc to passive margin, (3) Paleocene–Eocene foreland, and (4) Oligocene–Pliocene compression and transpression. The strata considered here were deposited during the Eocene as part of the foreland phase.

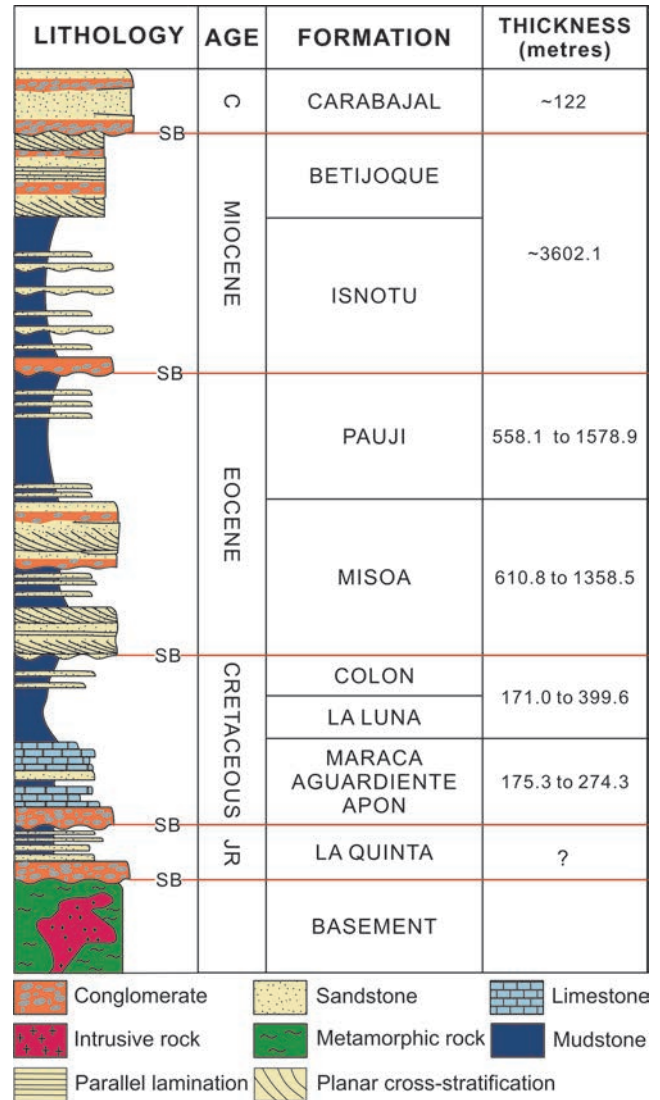


Fig. 2. Stratigraphy of the Maracaibo Basin (based on Benitez *et al.*, 1996) with position of 2nd-order sequence boundaries. Note stratigraphical position of the Paují Formation. Coarser-grained deposits near the base of the unit are referred to as the Basal Sands.

During the early to middle Eocene, a deltaic to tidal embayment formed, with clastic wedges advancing towards the northeast, as recorded by the Misoa Formation, one of the most prolific oil-producing units in Venezuela (Van Veen, 1972; González de Juana *et al.*, 1980; Maguregui and Tyler, 1991; Zambrano, 1995; Higgs, 1996). An increase in subsidence, coupled with a rise in sea level, took place by the middle Eocene, resulting in transgressive deposition of the Paují Formation (Fig. 2), which conformably overlies the Misoa Formation (Zambrano, 1995).

The Paují Formation, up to 1200 m thick, is dominated by mudstone and shale, with minor sandstones, encompassing a wide variety of depositional settings, ranging from foreshore to slope and in water depths perhaps reaching up to 500 m (González de Juana *et al.*, 1980). In contrast to the more restricted nature of the Misoa Formation, the Paují Formation is characterised by a more diverse and abundant body-fossil fauna, as well as a higher diversity of trace fos-

sils (Delgado *et al.*, 2001), indicating deposition under fully marine conditions. Overall, integration of sedimentological and palaeontological datasets indicates a deepening trend through the deposition of the Paují Formation (González de Juana *et al.*, 1980).

SEDIMENTOLOGY AND ICHNOLOGY OF THE STORM DEPOSITS

This study was conducted in the Motatán Field, where tempestites have been observed in four cores. Shallow-marine deposits in the Motatán Field represent the so-called “Basal Sands” of the Paují Formation, which record the onset of the transgression, signalling the transition from the marginal-marine Misoa Formation to the open-marine deposits, characteristic of the Paují Formation. The Basal Sands range from the foreshore to the lower offshore. The high-diversity ichnofauna present in the Basal Sands includes *Asterosoma*, *Chondrites*, *Diplocraterion*, *Helminthopsis*, *Ophiomorpha*, *Planolites*, *Palaeophycus*, *Rhizocorallium*, *Schaubcylindrichnus*, *Scolicia*, *Skolithos*, *Teichichnus*, “*Terebellina*” and *Thalassinoides*, among other ichnogenera (Delgado *et al.*, 2001). These deposits are stacked in coarsening-upward parasequences, showing variable intensities and frequencies of storms (MacEachern and Pemberton, 1992). In particular, this study deals with tempestites from core MOT-X.

Of particular significance is a storm sandstone unit encased in a fair-weather mudstone, locally displaying sandstone lenses. These fair-weather deposits are characterised by an indistinct bioturbation mottling. The intercalation of storm sandstone and fair-weather mudstone is characteristic of the offshore transition, which is located immediately below the fair-weather wave base and well above the storm wave base (Buatois and Mángano, 2011). This unit consists of five sharp-based, very fine-grained sandstone beds showing hummocky cross-stratification and ripples, forming a 26-cm-thick bedset that records storm deposition under purely oscillatory to combined flows (Fig. 3A–C). The amalgamated nature of the sandstone interval indicates repeated erosional events, due to several storms. The storm-related trace-fossil suite is mostly represented by *Diplocraterion parallelum* Torell, which occurs in two of the sandstone layers, although small specimens are apparent in the uppermost storm layer, as well. In addition, the sandstone unit contains a few specimens of *Palaeophycus tubularis* Hall and one specimen of *Bergaueria* isp. and *Thalassinoides* isp., the latter cross-cutting *Diplocraterion parallelum*. The spreite of *Diplocraterion parallelum* are made of light sand laminae, alternating with dark mudstone laminae. The presence of this ichnotaxon is consistent with the relatively high energy of formation of these deposits. In addition, the truncated tops of these burrows further support strong erosion, due to repeated storm events. In a strict sense, fair-weather deposits are not intercalated within the sandstone unit. However, high densities of *Chondrites* isp. are preserved in the infills of *Diplocraterion parallelum*, as well as in the only observed specimen of *Thalassinoides* isp., giving rise to patchy, composite ichnofabrics, the sig-

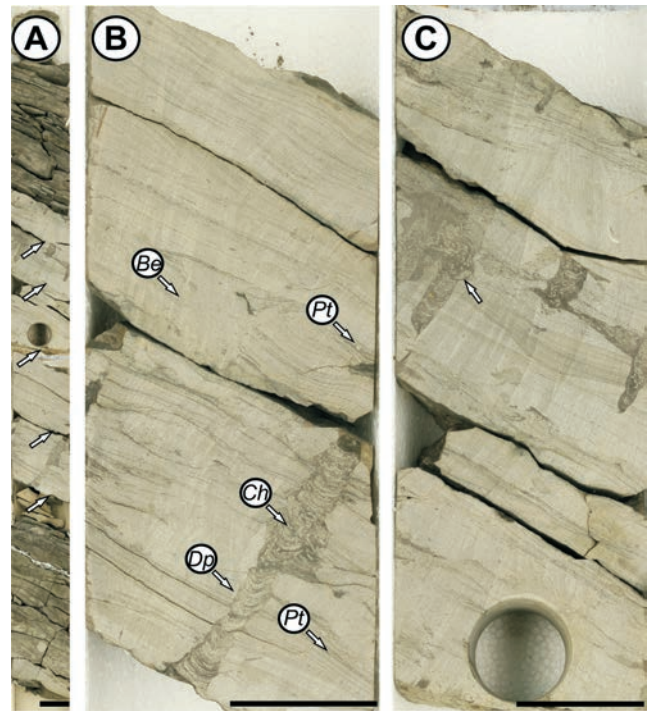
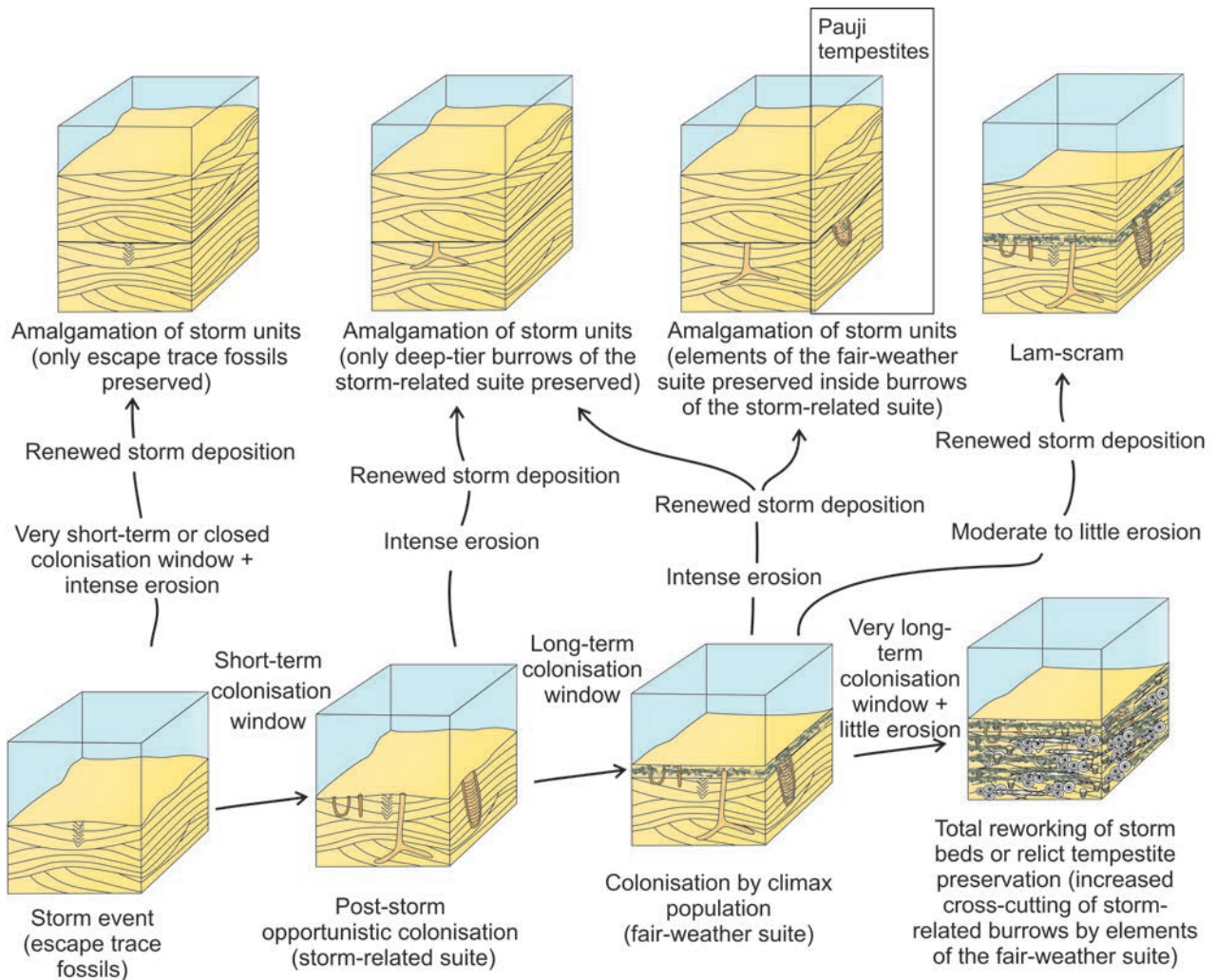


Fig. 3. Tempestites in core MOT-X, Motatán Field, Middle Eocene, Paují Formation, Maracaibo Basin. Core width is 6 cm. **A.** General view of storm sandstone interval encased in fair-weather mudstone-dominated intervals. Arrows show boundaries of discrete storm layers. **B.** Fair-weather *Chondrites* isp. (*Ch*) preserved within the infill of storm-related *Diplocraterion parallelum* (*Dp*) in one of the tempestites. Note associated *Bergaueria* isp. (*Be*) and *Palaeophycus tubularis* (*Pt*). **C.** Close-up of another tempestitute showing the same association of *Chondrites* isp. and *Diplocraterion parallelum*. One of the specimens of *Diplocraterion parallelum* is cross-cut by *Thalassinoides* isp., which in turn shows reworking by the *Chondrites* producer (arrow). Note the presence of tiny specimens of *Diplocraterion parallelum* in the uppermost bed.

nificance of which is addressed below. *Chondrites* isp. is filled with sand. From a preservational standpoint, this occurrence of *Chondrites* represents an example of concealed bed-junction preservation (*sensu* Simpson, 1957), because the burrows appear to be isolated within an interval of different lithology.

DISCUSSION

Alternating and contrasting hydrodynamic energy levels, due to repeated storm events, are arguably the most important limiting factor for trace-fossil distribution in wave-dominated, shallow-marine settings (e.g., Pemberton and Frey, 1984; Vossler and Pemberton, 1989; Frey, 1990; Frey and Goldring, 1992; Pemberton *et al.*, 1992; MacEachern and Pemberton, 1992; Pemberton and MacEachern, 1997; Buatois *et al.*, 2002, 2003; Mángano *et al.*, 2005; Carmona *et al.*, 2008; Savrda *et al.*, 2010; Buatois and Mángano, 2011; Angulo and Buatois, 2012). Storm events typically result in erosion followed by rapid deposition, which in turn



Decreased intensity and frequency of storms

TRACE FOSSILS

- Arenicolites* *Asterosoma* *Chondrites* *Diplocraterion* Escape trace fossils
- Ophiomorpha* *Phycosiphon* *Planolites* *Rosselia* *Skolithos*
- Teichichnus* *Zoophycos*

Fig. 4. Taphonomic pathways of storm-affected shallow-marine settings (based on Buatois and Mángano, 2011). Note location of Paují ichnofabrics within this framework. Diagenetic overprints are not illustrated for the sake of simplicity.

is followed by a waning phase and the re-establishment of fair-weather sedimentation under a lower-energy regime. The combination of strong erosion and rapid deposition imposes significant stress on shallow-water benthic communities.

Ichnofabrics in wave-dominated, shallow-marine settings are the result of a number of taphonomic pathways, reflecting the complex interplay between bioturbation events, storm erosion and deposition (Fig. 4). The frequency and intensity of storms dictate the length of the colonisation window, control styles of bioturbation, and thus impact on the

nature of the resulting ichnofabrics. In addition to escape trace fossils, which may be produced as an immediate response to avoid burial during high rates of sediment deposition, two contrasting trace-fossil suites are present in storm-dominated settings: the storm-related suite and the fair-weather suite (Pemberton and Frey, 1984; Pemberton and MacEachern, 1997). The storm-related trace-fossil suite records colonisation immediately after the storm event, and is produced by an opportunistic community displaying r-selected population strategies. Infaunal organisms burrow down

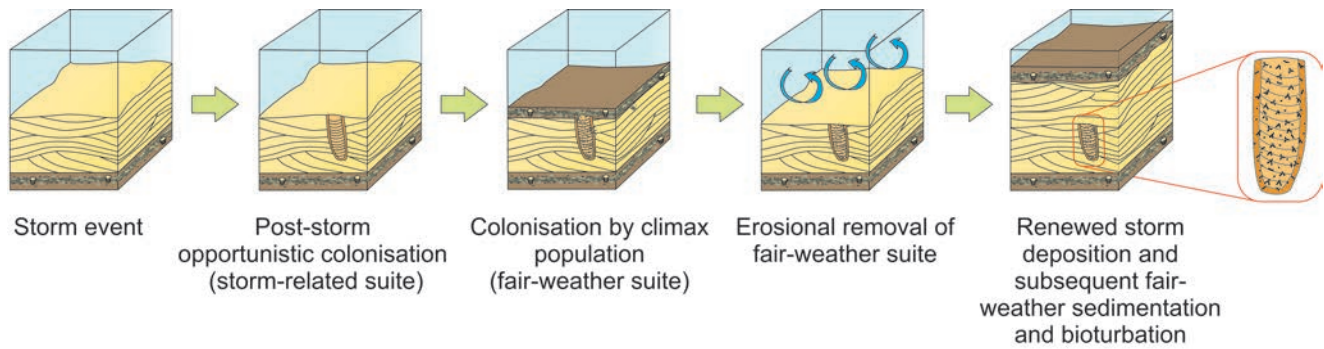


Fig. 5. Schematic diagram illustrating the succession of depositional, erosional and bioturbation events for the Paují tempestites. To simplify the diagram, only one event of erosion and subsequent deposition are shown. See Figure 4 for legend.

from a colonisation surface, located at the top of the event bed. The fair-weather suite, recording the activity of the resident benthic community, develops under more stable and rather predictable conditions, reflecting K-selected population strategies.

Strong intensity and frequency of storms typically result in very short-term, poorly developed ichnofauna (commonly subject to subsequent erosion) to negligible colonisation windows. Therefore, the fair-weather suite is inhibited and instead amalgamated storm deposits occur; these tempestites contain only the storm-related suite or, under the most extreme storm regime, they are unburrowed (MacEachern and Pemberton, 1992; Mángano *et al.*, 2005). In contrast, under moderate intensity and frequency of storms, deposits show an intercalation of laminated storm beds (sparsely bioturbated or typically unbioturbated), and strongly bioturbated fair-weather deposits, resulting in the so-called “lam-scrum” pattern (Howard, 1978; MacEachern and Pemberton, 1992). Deposits formed under moderate intensity and frequency of storms are typically characterised by reflecting longer colonisation windows under limited erosion, resulting in the alternation of the storm-related suite, if present, and the fair-weather suite. Finally, deposits formed under low frequency and intensity of storms are characterised by relatively minor amounts of tempestites. These deposits tend to be dominated by elements of the fair-weather suite, typically displaying high ichnodiversity. Storm beds, if present at all, are commonly intensely obliterated by biogenic reworking (e.g., Carmona *et al.*, 2008; Angulo and Buatois, 2012).

In the MOT-X tempestites studied, the storm-related suite is represented by the U-shaped burrow *Diplocraterion parallelum* (Fig. 5) and, to a lesser extent, by *Palaeophycus tubularis*, *Bergaueria* *isp.* and *Thalassinoides* *isp.* No fair-weather deposits are present within the sandstone interval studied in the MOT-X core, which may be taken as indicative of the strong intensity and high frequency of storms. However, the presence of a patchy, composite ichnofabric of *Chondrites* *isp.* within *Diplocraterion parallelum* and locally *Thalassinoides* *isp.* burrow fills in the sandstone interval is here regarded as evidence of an otherwise unrepresented resident fauna. Fair-weather deposits that contained the bulk of the fair-weather suite were erosionally removed during the subsequent storm (Fig. 5). In a sense, this is analo-

gous to the case of tubular tempestites, in which the only record of a storm event is preserved within burrow fills (Tedesco and Wanless, 1991).

Although there is no direct evidence of the fair-weather community, it may be possible to further speculate regarding its nature. Extremely dense concentrations of *Chondrites* at the top of tempestites have been suggested as indicative of the burial of high quantities of organic matter during storms (Vossler and Pemberton, 1988). Although this may indicate rapid colonisation after the storm, the complex morphology of *Chondrites* favors K-selected strategies and an affinity with climax populations (Bromley, 1996). In the case of the MOT-X deposits, the patchy distribution of *Chondrites* indicates exploitation of the organic-rich content within previously produced deep-tier *Diplocraterion parallelum* and, to a lesser extent, *Thalassinoides* *isp.* In fact, there is general agreement that *Chondrites* is a deep-tier ichnotaxon that typically characterises mature communities (Bromley, 1996). Its deep-tier emplacement and the ability of the *Chondrites*-maker to re-burrow the fills of other biogenic structures favour preservation and allow recognition of a “hidden” bioturbation event, which otherwise might have remained undetected. Also, its common presence in mature infaunal communities favours the hypothesis of relatively long colonisation windows between events, indicating that, although the intensity of storms was high, the frequency of them may have been relatively moderate. This interpretation is also supported by the presence of a diverse fair-weather trace-fossil suite in other intervals of the “Basal Sands” of the Paují Formation in the same oil field (Delgado *et al.*, 2001), as well as by the intense mottling in the associated fair-weather fine-grained deposits.

According to Savrda (2007), two commonly independent factors are involved in trace-fossil taphonomy: completeness of the preserved record of biogenic activity (ichnological fidelity) and degree of ichnofossil visibility. Whereas some ichnofabrics may have high fidelity, some or all trace fossils may be difficult to discern, therefore showing limited trace-fossil visibility. In contrast, some ichnofabrics may have low fidelity (i.e., reflecting only the work of a small part of the original tracemaker community), but some discrete ichnotaxa may be well expressed. More recently, Savrda (2014) added temporal resolution (i.e. the degree to which an ichnofabric is a time-averaged record of

biogenic activity) and temporal completeness (i.e. the percentage of the total time recorded in an ichnofabric that is actually represented by the preserved ichnofauna) as relevant parameters. He noted that temporal resolution typically covariates with ichnological fidelity. Because of strong erosion, storm-dominated shallow-marine settings are particularly complex with regard to these parameters. Savrda *et al.* (2010) documented an example of weakly bioturbated tempestites within otherwise unbioturbated fair-weather deposits that accumulated in the offshore transition. Fair-weather conditions were inhospitable for bioturbation, but a community of allochthonous tracemakers was established immediately after and perhaps during storm deposition. Savrda (2014) argued that this situation led to an ichnofabric of high fidelity and high temporal resolution.

Under normal marine conditions favouring bioturbation, ichnofabrics in weakly storm-affected settings typically reflect long colonisation windows and somewhat resemble those from pelagic settings. In pelagic settings, there is a selective preservation of deep tiers (resulting in low ichnological fidelity and increased visibility of the deep tier), and an extended residence time of sediment in the zone of active bioturbation (resulting in low temporal resolution; Savrda, 2014). Although these conditions are not as marked in weakly storm-affected settings, still ichnological fidelity and temporal resolution may be regarded as relatively low, owing to the fact that long colonisation windows and slow sedimentation rates result in the extended residence time of sediment in the zone of active bioturbation. In moderately storm-affected settings, temporal resolution may even increase due to short-term colonisation windows, but ichnological fidelity is hampered by a bias towards deeper structures that survived the erosional events. Finally, these parameters are hard to evaluate in strongly storm-dominated settings, because there is little ichnological evidence. In the case of very high-energy settings, this may simply reveal the lack of colonisation windows, but in less extreme cases the possibility of complete removal of biogenic structures by erosion cannot be disregarded, indicating zero fidelity and temporal resolution. In the case of the Paují tempestites, the identification of *Chondrites* reworking *Diplocraterion* and, to a lesser extent, *Thalassinoides*, may help to evaluate these parameters, although temporal resolution and ichnological fidelity still may be regarded as low.

Acknowledgments

We would like to thank Richard Bromley and Ulla Asgaard for constant inspiration and support. This manuscript has been improved, thanks to the detailed and useful reviews by Francisco Tognoli and an anonymous referee. We thank Petróleos de Venezuela (PDVSA) for allowing the publication of this study.

REFERENCES

- Angulo, S. & Buatois, L. A., 2012. Ichnology of an Upper Devonian – Lower Mississippian low-energy seaway: the Bakken Formation of subsurface Saskatchewan, Canada: Assessing paleoenvironmental controls and biotic responses. *Palaogeography, Palaeoclimatology, Palaeoecology*, 315–316: 46–60.
- Benitez, R., Kabbabe, T. & Orribo, J. M., 1996. *Estudio Integrado de los yacimientos presentes en las formaciones Paují y Missoa en el Domo Norte del Campo Motatán, Estado Zulia*. Trabajo Especial de Grado, Universidad Central de Venezuela, Unpublished.
- Bromley, R. G., 1990. *Trace Fossils. Biology and Taphonomy*. Unwin Hyman, London, 280 pp.
- Bromley, R. G. 1996. *Trace Fossils. Biology, Taphonomy and Applications*. Chapman & Hall, London, 361 pp.
- Bromley, R. G. & Ekdale, A. A., 1986. Composite ichnofabrics and tiering of burrows. *Geological Magazine*, 123: 59–65.
- Buatois, L. A., Bromley, R. G., Mángano, M. G., Belloso, E. & Carmona, N. B., 2003. Ichnology of shallow marine deposits in the Miocene Chenque Formation of Patagonia: Complex ecologic structure and niche partitioning in Neogene ecosystems. In: Buatois, L. A. & Mángano, M. G. (eds), *Icnología: Hacia una convergencia entre geología y biología. Publicación Especial de la Asociación Paleontológica Argentina*, 9: 85–95.
- Buatois, L. A. & Mángano, M. G., 2004. Animal-substrate interactions in freshwater environments: applications of ichnology in facies and sequence stratigraphic analysis of fluvio-lacustrine successions. In: McIlroy, D. (ed.), *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Geological Society Special Publication*, 228: 311–333.
- Buatois, L. A. & Mángano, M. G., 2007. Invertebrate ichnology of continental freshwater environments. In: Miller, W., III (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 285–323.
- Buatois, L. A. & Mángano, M. G., 2011. *Ichnology: Organism-Substrate Interactions in Space and Time*. Cambridge University Press, Cambridge, 358 pp.
- Buatois, L. A., Mángano, M. G., Alissa, A. & Carr, T. R., 2002. Sequence stratigraphic and sedimentologic significance of biogenic structures from a late Paleozoic marginal to open-marine reservoir, Morrow Sandstone, subsurface of southwest Kansas, USA. *Sedimentary Geology*, 152: 99–132.
- Buatois, L. A., Uba, C. E., Mángano, M. G. & Hulka, C., 2007. Deep bioturbation in continental environments: Evidence from Miocene fluvial deposits of Bolivia. In: Bromley, R. G., Buatois, L. A., Mángano, M. G., Genise, J. F. & Melchor, R. N. (eds), *Sediment-Organism Interactions: A Multifaceted Ichnology. Society for Sedimentary Geology, Special Publication*, 88: 123–136.
- Carmona, N. B., Buatois, L. A., Mángano, M. G. & Bromley, R. G., 2008. Ichnology of the Lower Miocene Chenque Formation, Patagonia, Argentina: Animal – substrate interactions and the Modern Evolutionary Fauna. *Ameghiniana*, 45: 93–122.
- Delgado, M., Kabbabe, T., Sampson, E. & Chacartegui, F., 2001. Ichnofossils as a tool for environmental interpretation, Paují and Missoa formations, Barúa and Motatán fields, Zulia and Trujillo states, Venezuela. *VI International Ichnofabric Workshop Abstracts, Isla Margarita & Puerto La Cruz*, p. 27.
- Desjardins, P. R., Mángano, M. G., Buatois, L. A. & Pratt, B. R., 2010. *Skolithos* pipe rock and associated ichnofabrics in the Fort Mountain Formation, Gog Group: Colonization trends and environmental controls in an Early Cambrian subtidal sandbar complex. *Lethaia*, 43: 507–528.
- Ekdale, A., Bromley, R. G. & Knaust, D., 2012. The ichnofabric concept: In: Knaust, D. & Bromley, R. G. (eds), *Trace Fossils as Indicators of Sedimentary Environments. Developments in Sedimentology*, 64: 139–155. Elsevier, Amsterdam.
- Frey, R. W., 1990. Trace fossils and hummocky cross-stratification, Upper Cretaceous of Utah. *Palaaios*, 5: 203–218.

- Frey, R. W. & Goldring, R., 1992. Marine event beds and recolonization surfaces as revealed by trace fossil analysis. *Geological Magazine*, 129: 325–335.
- Ghosh, S., Pestman, P., Melendez, P., Bartok, P., Lorente, M., Duran, I., Pittelli, R., Rull, V., Mompert, L., White, C., Dominguez, C., Oropeza, C. & Travaglio, F. 1995. *Síntesis Geológica, Marco Secuencial y Perspectivas Exploratorias del Eoceno de la Cuenca de Maracaibo*. Maraven S. A., Caracas, EPC-13494.
- Gonzalez de Juana, C., Iturralde, J. M. & Picard, X., 1980. *Geología de Venezuela y de sus Cuencas Petrolíferas*, Tercera Edición. Ed. Foninves, Caracas, 1031 pp.
- Higgs, R., 1996. A new facies model for the Misoa Formation (Eocene), Venezuela's main oil reservoir. *Journal of Petroleum Geology*, 19: 249–269.
- Howard, J. D., 1978. Sedimentology and trace fossils. In: Basan, P. B. (ed.), *Trace Fossil Concepts. Society for Sedimentary Geology Short Course Notes*, 5: 11–42.
- MacEachern, J. A. & Pemberton, S. G., 1992. Ichnological aspects of Cretaceous shoreface successions and shoreface variability in the Western Interior Seaway of North America. In: Pemberton, S. G. (ed.), *Applications of Ichnology to Petroleum Exploration: A Core Workshop. Society for Sedimentary Geology Core Workshop*, 17: 57–84.
- Maguregui, J. & Tyler, N., 1991. Evolution of Middle Eocene tide-dominated deltaic sandstones, Lagunillas field, Maracaibo basin, western Venezuela. In: Miall, A. D. & Tyler, N. (eds), *The Three-Dimensional Facies Architecture of Terrigenous Clastic Sediments and its Implications for Hydrocarbon Discovery and Recovery. Society for Sedimentary Geology, Concepts in Sedimentology and Paleontology*, 3: 233–244.
- Mángano, M. G., Buatois, L. A. & Muniz Guinea, F., 2005. Ichnology of the Alfarcito Member (Santa Rosita Formation) of northwestern Argentina: animal-substrate interactions in a lower Paleozoic wave-dominated shallow sea. *Ameghiniana*, 42: 641–668.
- Meldahl, K. H. & Flessa, K. W., 1990. Taphonomic pathways and comparative biofacies and taphofacies in a Recent intertidal/shallow shelf environment. *Lethaia*, 23: 43–60.
- Pearson, N. J., Mángano, M. G., Buatois, L. A., Casadío, S. & Rodríguez Raising, M., 2013. Environmental variability of *Maccaronichnus* ichnofabrics in Eocene tidal-embayment deposits of southern Patagonia, Argentina. *Lethaia*, 46: 341–354.
- Pemberton, S. G. & Frey, R. W., 1984. Ichnology of storm-influenced shallow marine sequence: Cardium Formation (Upper Cretaceous) at Seebe, Alberta. In: Stott, D. F. & Glass, D. J. (eds), *The Mesozoic of Middle North America. Canadian Society of Petroleum Geologists Memoir*, 9: 281–304.
- Pemberton, S. G. & MacEachern J. A., 1997. The ichnological signature of storm deposits: The use of trace fossils in event stratigraphy. In: Brett, C. E. & Baird, G. C. (eds), *Paleontological Events. Stratigraphic, Ecological and Evolutionary Implications*. Columbia University Press, New York, pp. 73–109.
- Savrda, C. E., 2007. Taphonomy of trace fossils. In: Miller, W. III (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 92–109.
- Savrda, C. E., 2014. Limited ichnologic fidelity and temporal resolution in pelagic sediments: Paleoenvironmental and paleoecologic implications. *Palaios*, 29: 210–217.
- Savrda, C. E., Counts, J. W., Bigham, E. & Martin, S., 2010. Ichnology of siliceous facies in the Eocene Tallahatta Formation (eastern United States Gulf Coastal Plain): implications for depositional conditions, storm processes, and diagenesis. *Palaios*, 25: 642–655.
- Simpson, S., 1957. On the trace fossil *Chondrites*. *Quarterly Journal Geological Society of London*, 112: 475–479.
- Tedesco, L. P. & Wanless, H. R., 1991. Generation of sedimentary fabrics and facies by repetitive excavation and storm infilling of burrow networks, Holocene of South Florida and Caicos Platform, B.W.I. *Palaios*, 6: 326–343.
- Van Veen, F. R., 1972. Ambientes sedimentarios de las formaciones Mirador y Misoa del Eoceno inferior y medio en la Cuenca del Lago de Maracaibo. *Venezuela Ministerio de Minas e Hidrocarburos, IV Congreso Geológico Venezolano, Caracas, 1969, Memoria, Boletín de Geología, Publicación Especial*, 5: 1073–1104.
- Vossler, S. M. & Pemberton, S. G., 1988. Superabundant *Chondrites*: a response to storm buried organic material? *Lethaia*, 21: 94.
- Vossler, S. M. & Pemberton, S. G., 1989. Ichnology and plaeoecology of offshore deposits in the Cardium Formation (Turonian, Alberta, Canada). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 74: 217–239.
- Zambrano, E., 1995. *Síntesis geológica, marco secuencial y perspectivas exploratorias del Eoceno de la Cuenca de Maracaibo*. Maraven, Internal Report.
- Zhang, G., Buatois, L. A., Mángano, M. G. & Aceñolaza, F. G., 1998. Sedimentary facies and environmental ichnology of a Permian playa-lake complex in western Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 138: 221–243.