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Timing of infaunalization in shallow-marine early Paleozoic communities in Gondwanan settings: discriminating evolutionary and paleogeographic controls

M. Gabriela Mángano and Luis A. Buatois

ABSTRACT

Ichnofabric analysis of upper-offshore facies in a series of lower Paleozoic siliciclastic shallow-marine units of northwest Argentina revealed ichnofaunal changes that may record faunal turnovers at the macroevolutionary level. Comparative study reveals a pronounced difference between Furongian to lower Tremadocian and upper Tremadocian to Caradocian upper-offshore deposits, particularly in the fairweather suite of trace fossils. Furongian to lower Tremadocian upper-offshore deposits are dominated by shallow-tier structures, mostly cruzianids produced by trilobites. The bioturbation index of these deposits is typically 0 to 1, with trace fossils commonly emplaced parallel to bedding with little disturbance of the primary fabric. In contrast, upper Tremadocian to Caradocian upper-offshore deposits display more intense bioturbation (bioturbation index commonly between 2 and 4, but locally 5). The most significant innovation is the appearance of a mid-tier component represented by the ichnospecies *Trichophycus venosus*, which cross-cuts cruzianids and vermiform trace fossils emplaced at shallow depths. The early to late Tremadocian transition is regarded as a turning point for exploitation of the infaunal ecospace in high- to intermediate-latitude siliciclastic basins of Gondwana. Interestingly, the *Trichophycus* ichnofabric seems to have been present since the Early Cambrian in other paleocontinents, such as Baltica and Laurentia. Our study underscores the importance of comparing ecologic trends among different continents to further understand controls and timing of evolutionary innovations during major faunal radiations.

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INTRODUCTION

The early evolutionary history of endobenthic tiering and infaunalization is still poorly understood. An increase in burrowing depth and intensity through the Phanerozoic has been suggested (e.g., Thayer 1979, 1983). Earlier studies, focused on onshore-offshore trends in infaunalization, were

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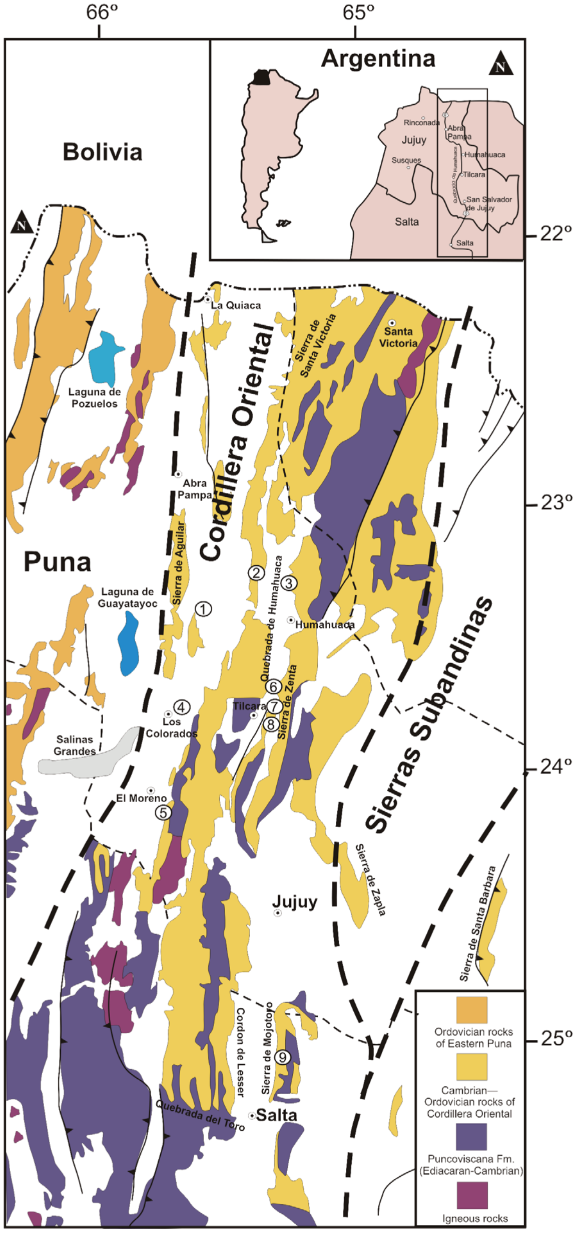

FIGURE 1. Distribution of the studied outcrops and location of measured sections in Cordillera Oriental, northwest Argentina (modified from Astini 2003). 1 = Quebrada Azul (Sierra de Cajas), 2 = Azul Pampa (including Cerro Crestón and Old Road), 3 = Arroyo Sapagua (including Sapagua East and West), 4 = Los Colorados, 5 = Angosto del Moreno, 6 = Quebrada de Moya and Chucalezna, 7 = Quebradas del Arenal and Humacha, 8 = Quebradas de Casa Colorada and Rupasca, 9 = Quebrada del Gallinato.

based on analysis of carbonate ichnofabrics in the Great Basin of the western United States (Droser and Bottjer 1988, 1989). In these carbonate systems, intense bioturbation developed first in nearshore environments and in offshore settings later (Droser and Bottjer 1989). Inner-shelf carbonates of the Great Basin reveal two major increases in the extent and depth of bioturbation during the early Paleozoic: the first between pre-trilobite and trilobite-bearing Cambrian rocks, and the second between the Middle and Late Ordovician (Droser and Bottjer 1989). Comparatively little is known about the timing and paleoenvironmental extent of infaunalization in siliciclastic settings, although a gradual increase throughout the Early Cambrian has been suggested (McIlroy and Logan 1999). More recently, a number of studies have proposed that sediments were firm near the surface during the Cambrian and Early Ordovician, allowing preservation of shallow-tier trace fossils with well-preserved scratch marks (Droser et al. 2002a, 2002b, 2004; Jensen et al. 2005). Also, an increase in ethologic variability and depth of bioturbation in offshore siliciclastics by the Middle Ordovician was noted by Mángano and Droser (2004). However, detailed integrated ichnofabric and facies analysis of this critical interval remains to be performed.

The lower Paleozoic Basin of Northwest Argentina (Figure 1) contains extensive outcrops of shallow-marine deposits that display stacked offshore-to-nearshore shallowing-upward cycles spanning the Late Cambrian to Caradocian interval (Buatois and Mángano 2003; Astini 2003; Astini et al. 2004; Buatois et al. 2006). This recurrent stratal pattern allows the ichnofabric of the same shallow-marine subenvironments to be compared through time, therefore permitting evolutionary controls to be identified. In addition, characterization of these Cambrian-Ordovician ichnofaunas provides information on intermediate to high-latitude shallow-marine infaunal communities, allowing comparisons with those from other paleogeographic regions. In this paper, we suggest that (1) a significant increase in the exploitation of infaunal ecospace occurred in upper-offshore environments between the early and late Tremadocian in Gondwana, and (2) infaunalization in high- to intermediate-latitude Gondwanic settings was delayed with respect to other paleocontinents, such as Baltica and Laurentia.

GEOLOGIC AND DEPOSITIONAL SETTING

The lower Paleozoic Northwest Argentina Basin is a retroarc foreland basin developed along

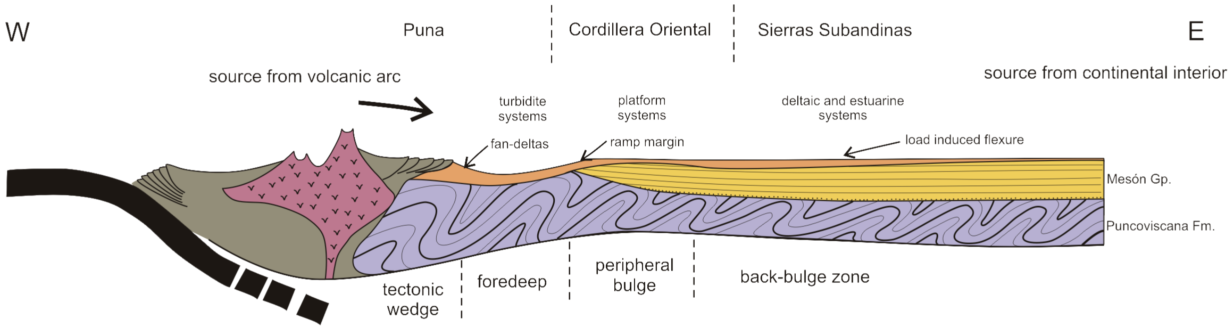

FIGURE 2. Tectonic setting of the lower Paleozoic Northwest Argentina Basin (modified from Astini 2003).

the margin of western Gondwanaland (Ramos 1999; Astini 2003) (Figure 2). The volcanic arc is known as the Faja Eruptiva de la Puna Occidental (Coira et al. 1982; Moya et al. 1993; Ramos 1999). Eastward prograding fan deltas fed turbidite systems that developed in the foredeep region (Astini 2003). The peripheral bulge and the back-bulge were dominated by a wave-dominated shallow-marine ramp punctuated by tide-dominated valley incisions and deltaic progradation (Astini 2003; Buatois and Mángano 2003; Buatois et al. 2006). This wave-dominated ramp is exposed along Cordillera Oriental and includes deposits ranging from the Furongian to the Ashgillian (see biostratigraphic information in Brussa et al. 2003; Waisfeld and Vaccari 2003). Wave-dominated shallow-marine successions comprise regionally extensive parasequences. Deposits commonly encompass shelf, lower- to upper-offshore, offshore-transition, and lower- to upper-shoreface settings (Buatois and Mángano 2003; Buatois et al. 2003a, 2006; Astini et al. 2004).

For this study, integrated sedimentologic and ichnologic analyses were undertaken in the following units: (1) the Furongian Lampazar Formation; (2) the Furongian Casa Colorada Member of the Santa Rosita Formation; (3) the Furongian-lower Tremadocian Alfarcito Member of the Santa Rosita Formation; (4) the upper Tremadocian Rupasca Member of the Santa Rosita Formation; (5) the upper Tremadocian Humacha Member of the Santa Rosita Formation; (6) the lower to middle Arenigian Acoite Formation, and (7) the upper Llanvirnian to lower Caradocian Santa Gertrudis Formation.

MATERIALS AND METHODS

Our analysis is based on the study of approximately 4,560 m of Upper Cambrian-Ordovician strata. The Lampazar Formation is exposed in the western region of Cordillera Oriental (Figure 3.1), while the Santa Rosita is exposed in the eastern region (Figure 3.2) and the Santa Gertrudis Formation in the southern margin of Cordillera Oriental (Figure 3.3). The Acoite Formation is exposed in both the western and eastern regions of Cordillera Oriental (Figure 3.1-3.2). Sections were measured in various localities of Cordillera Oriental (Table 1).

Fieldwork activities are part of a long-term project dealing with the integration of sedimentologic, ichnologic, and sequence-stratigraphic data in order to characterize the early Paleozoic depositional evolution and macroevolutionary events in the Northwest Argentina Basin. Activities include basic mapping and standard sedimentary facies analysis based on bed-by-bed measuring of stratigraphic sections. Facies analysis was based on careful characterization of lithology, physical sedimentary structures, bed boundaries, and geometry. Ichnologic analysis involves trace-fossil sampling; recognition and identification of the ichnofossils present; measurement of abundance and distribution of individual ichnotaxa; measurement of degree of bioturbation; estimation of ichnodiversity; identification of trophic types and ethologic groups; reconstruction of tiering structure, and relationships among trace fossils, physical sedimentary structures, and bedding types. Photographs were taken to document the most significant sedimentologic attributes and those trace-fossil specimens that were not collected. Laboratory work was aimed to refine ichnologic observations performed in the field (e.g., study of polished slabs). In addition, we have compared our results with trace-fossil information from other areas in Gondwana, Baltica, and Laurentia based on a literature survey and a review of specimens housed at the Geological Institute of the University of Tübingen. Additional

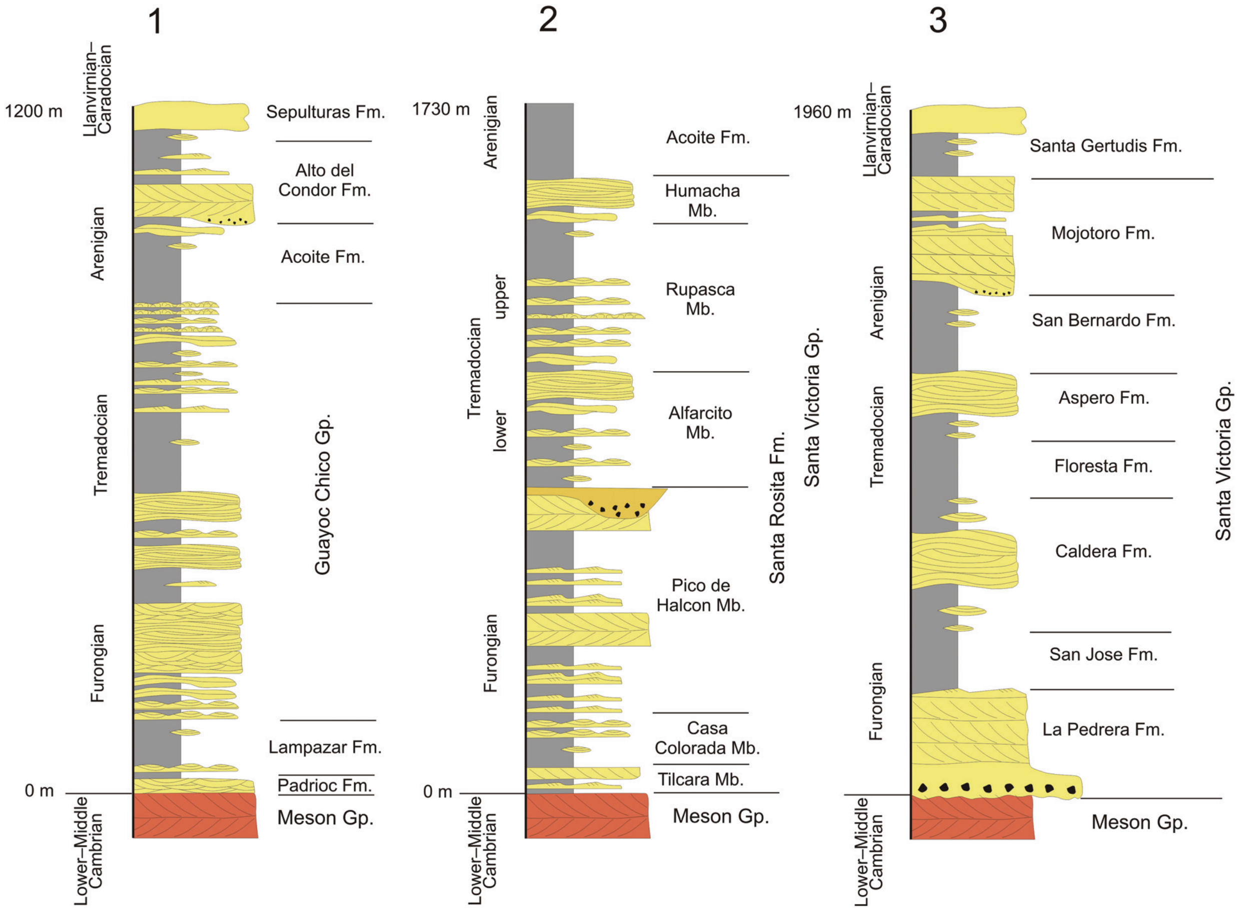

FIGURE 3. Lower Paleozoic stratigraphy of Cordillera Oriental (based on Turner 1960; Moya 1988, 1998; Astini 2003; Mángano and Buatois 2003, 2004; Buatois et al. 2003a, 2006; Astini et al. 2004, and Vaccari et al. 2008). 1. Schematic integrated section for the western region of Cordillera Oriental. 2. Schematic integrated section for the eastern region of Cordillera Oriental. 3. Schematic integrated section for the southern margin of Cordillera Oriental.

observations were made in the field in the Ordovician of the High Atlas of Morocco.

For this specific study, we have focused our analysis on deposits that, on sedimentologic criteria (see below), are identified as formed in the upper offshore. By restricting our study to a single bathymetric zone, we avoid comparing ichnofaunas formed under different environmental conditions and can, therefore, detect evolutionary controls. We follow the environmental zonation of MacEachern et al. (1999), and consider fairweather wave base as the base of the shoreface, and storm wave base as the base of the lower offshore. Within this scheme, the region between the fairweather wave base and the storm wave base is subdivided into offshore transition, upper offshore, and lower offshore, based on sedimentologic attributes (e.g., sandstone/mudstone ratio, tempestite architecture).

To evaluate the degree of infaunalization in lower Paleozoic upper-offshore deposits, we have framed our observations within the ichnofabric approach *sensu* Bromley and Ekdale (1986). An ichnofabric refers to any aspect of the texture and internal structure of a substrate resulting from bioturbation and bioerosion at any scale (Bromley and Ekdale 1986). As biogenic structures are almost always *in situ* records of behavior, ichnofabric analysis may provide important information on the ecology of endobenthic communities (e.g., Wetzel 2008). As part of analysis of the ichnofabric, the degree of bioturbation has been estimated, using the scheme of Taylor and Goldring (1993). This scheme comprises seven grades of bioturbation, ranging from 0 for unbioturbated sediments to 6 for those that have suffered complete bioturbation.

Table 1. Stratigraphic sections studied.

Section	Stratigraphic Unit	Age
Quebrada del Gallinato (Sierra de Mojotoro)	Santa Gertrudis Formation	late Llanvirnian-early Caradocian
Los Colorados Azul Pampa	Acoite Formation	early-middle Arenigian
Quebrada de Humacha	Humacha Member (Santa Rosita Formation)	late Tremadocian
Quebrada de Rupasca Quebrada de Casa Colorada Quebrada del Arenal Angosto del Ferrocarril de Chucalezna	Rupasca Member (Santa Rosita Formation)	late Tremadocian
Quebrada de Rupasca Quebrada de Casa Colorada Quebrada de Abra Blanca Quebrada de Moya Angosto del Morro de Chucalezna Arroyo Sapagua West Arroyo Sapagua East (Pintayoc) Cerro Crestón (Azul Pampa) Old Road (Azul Pampa)	Alfarcito Member (Santa Rosita Formation)	Furongian-early Tremadocian
Quebrada de Rupasca Quebrada de Casa Colorada Quebrada de Abra Blanca	Casa Colorada Member (Santa Rosita Formation)	Furongian
Quebrada Azul (Sierra de Cajas) Angosto del Moreno	Lampazar Formation	Furongian

CHARACTERISTICS AND INTERPRETATION OF UPPER-OFFSHORE DEPOSITS

Upper-offshore deposits consist of laterally persistent, yellowish green and gray parallel-laminated mudstone with thin, tabular, typically erosively-based, light grey, very fine-grained, silty sandstone beds (Figure 4.1-4.2). Parallel lamination, combined-flow ripple cross-lamination, and symmetrical to near-symmetrical ripples with rounded tops are common. Microhummocky and hummocky cross-stratification, current-rippled cross-lamination, gutter casts, small load casts, and tool marks occur locally. Fragments of brachiopods (including lingulids), trilobites and crinoids, as well as conodonts, are present in shell lags. Articulated and semi-articulated trilobites are locally common within the mudstone units (Waisfeld and Vaccari 2003).

Upper-offshore deposits represent alternating background suspension fallout in a low-energy setting punctuated by distal storm deposition. The presence of micro-hummocky cross-stratification, combined-flow ripple cross-lamination, symmetrical to near-symmetrical ripples and gutter casts indicates periodic disruption by storm flows in an otherwise low-energy environment dominated by slow accumulation of silt-sized particles during fair-weather conditions (Buatois and Mángano 2003).

UPPER-OFFSHORE ICHNOFABRICS IN THE LOWER PALEOZOIC NORTHWEST ARGENTINA BASIN

As is the case of most storm-influenced offshore deposits (e.g., Pemberton and Frey 1984; Pemberton and MacEachern 1997), two trace-fossil suites (fairweather and storm-related) characterize these upper-offshore deposits. The fairweather suite reflects the activity of the benthic community developed under stable and rather predictable conditions. This suite records the activity of populations displaying K-selected or climax strategies. The storm-related suite indicates colonization after the storm event. This second trace-fossil suite is produced by an opportunistic community displaying r-selected population strategies in an unstable environment characterized by stressful conditions. The storm-related suite in the upper-offshore deposits studied consists of vertical structures, such as *Skolithos*, *Arenicolites,* and rarely *Diplocraterion*, produced by suspension feeders and preserved as endichnial structures in sandstone tempestites. Escape structures are dominant in

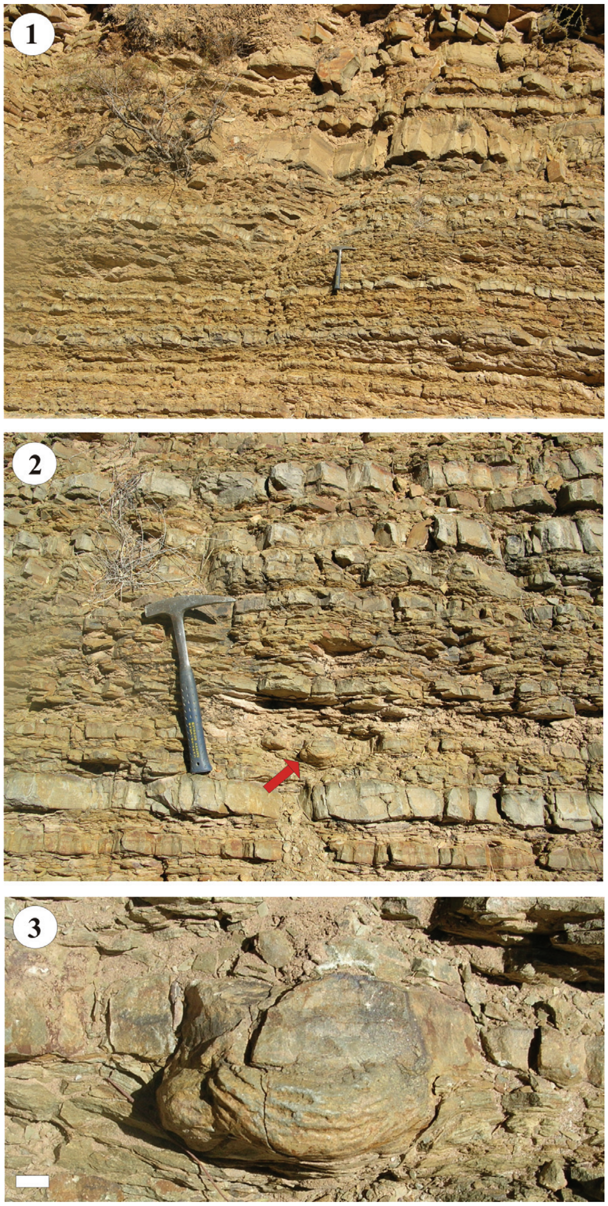

FIGURE 4. Shallow-marine siliciclastic deposits, Furongian-lower Tremadocian Alfarcito Member, Santa Rosita Formation, Quebrada del Abra Blanca, Jujuy Province. 1. Parasequence showing upper-offshore deposits passing upwards into offshore-transition deposits having more regular intercalations of storm-generated hummocky cross-stratified sandstone and fairweather siltstone. 2. Close-up of upper-offshore deposits shown in 1. Note excellent preservation of interbedded sandstone tempestites in the absence of intense burrowing. The ichnofauna typically present in these deposits is dominated by shallow-tier trilobite trace fossils, such as *Cruziana* and *Rusophycus* (arrow), with well-preserved scratch marks. 3. Close-up of the *Rusophycus* specimen illustrated in 2. Scale bar equals 1 cm.

some thin silty fine-grained sandstone tempestites. The storm-related suite does not display significant changes in ichnotaxonomic composition, density of burrows and penetration depth through the Cambrian-Ordovician, and seems to be less sensitive to evolutionary events (Mángano and Buatois 2003). Accordingly, we focus our discussion on the ichnofabric produced by the fairweather fauna.

Furongian to Lower Tremadocian Ichnofabrics

These ichnofabrics are present in the Lampazar Formation; the Casa Colorada Member of the Santa Rosita Formation, and the Alfarcito Member of the Santa Rosita Formation (Figure 5, Figure 6). Furongian to lower Tremadocian upper-offshore ichnofabrics resulting from the activities of the resident fauna are dominated by epifaunal to shallow-tier structures. Therefore, bioturbation index of the fairweather deposits is typically 0-1, with trace fossils commonly emplaced and observed parallel to bedding-plane. Accordingly, little disturbance of the primary fabric is present (Figure 4.1-4.3).

The ichnology of these deposits have been documented in previous contributions (e.g., Mángano et al. 2005a). The fairweather suite consists of trilobite-produced trace fossils (*C. problematica*, *Cruziana semiplicata*, *Cruziana* isp., *Dimorphichnus* aff. *D. quadrifidus*, *Diplichnites* isp., *Monomorphichnus multilineatus,* *R. carbonarius*, *Rusophycus moyensis*, *Rusophycus* isp.), vermiform burrows (*Archaeonassa fossulata*, *Arthrophycus minimus*, ?*Gyrolithes* isp., *Palaeophycus tubularis*, *P. striatus*, *Phycodes* isp.) and rare plug-shaped burrows (*Bergaueria* aff. *B. hemispherica*). The storm-related suite is commonly monospecific and consists of *Skolithos linearis*. Overall, the fairweather suite displays a bias toward shallow-tier infaunal communities, defining an essentially two-dimensional ichnofabric.

Upper Tremadocian-Caradocian Ichnofabrics

These ichnofabrics have been studied in the the Rupasca Member of the Santa Rosita Formation (Figure 7, Figure 8); the Humacha Member of the Santa Rosita Formation; the Acoite Formation, and the Santa Gertrudis Formation. Compared to older deposits in the area, upper Tremadocian-Caradocian upper-offshore fairweather deposits display a remarkable increase in the degree of bioturbation, with a bioturbation index commonly ranging between 2 and 4, but locally reaching 5. As in the Furongian-lower Tremadocian ichnofabrics, shallow-tiers are represented by trilobite-produced trace fossils. During the late Tremadocian, the ich-

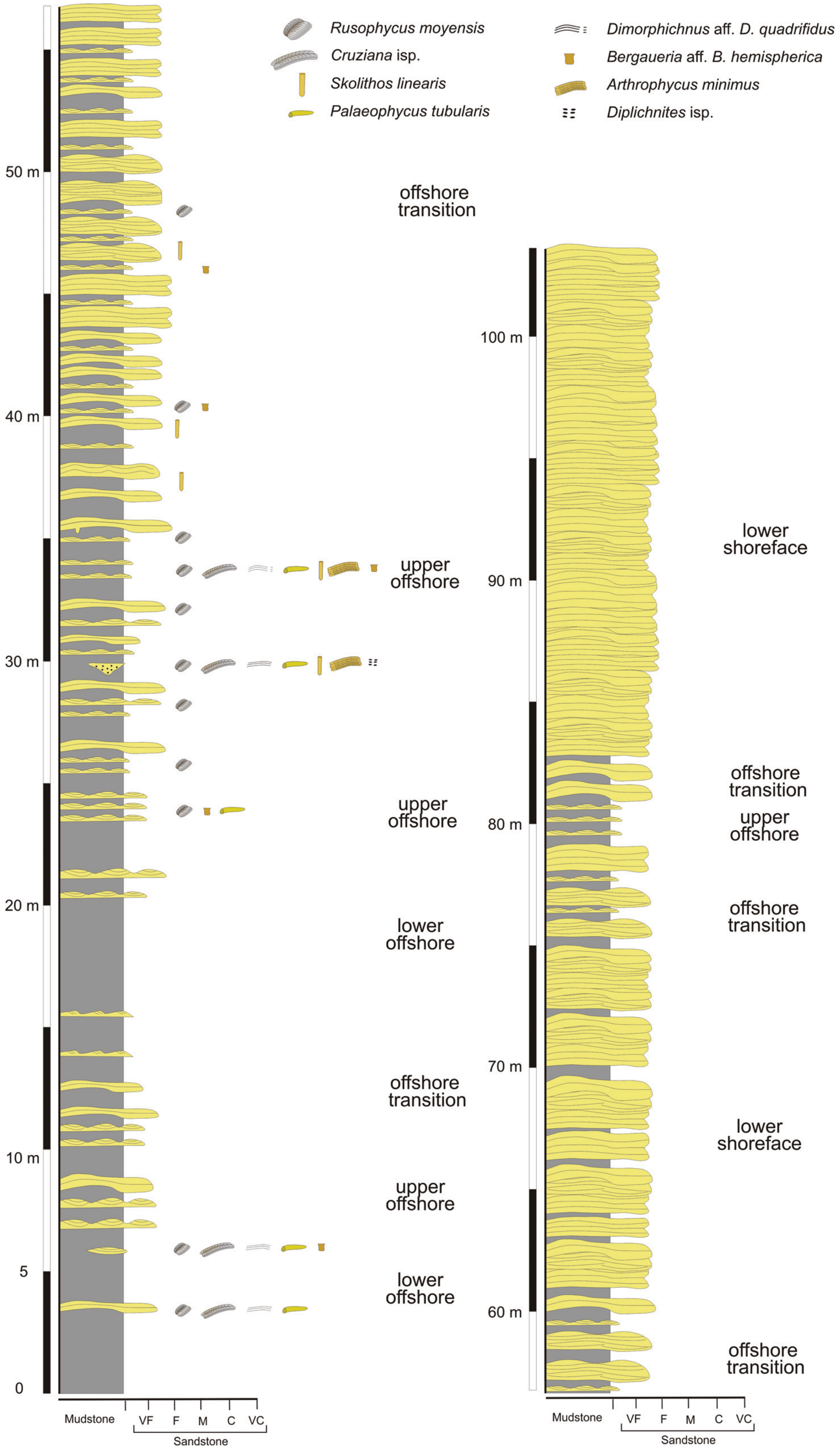

FIGURE 5. Sedimentologic and ichnologic log of the Furongian-lower Tremadocian Alfarcito Member at Angosto del Morro de Chucalezna.

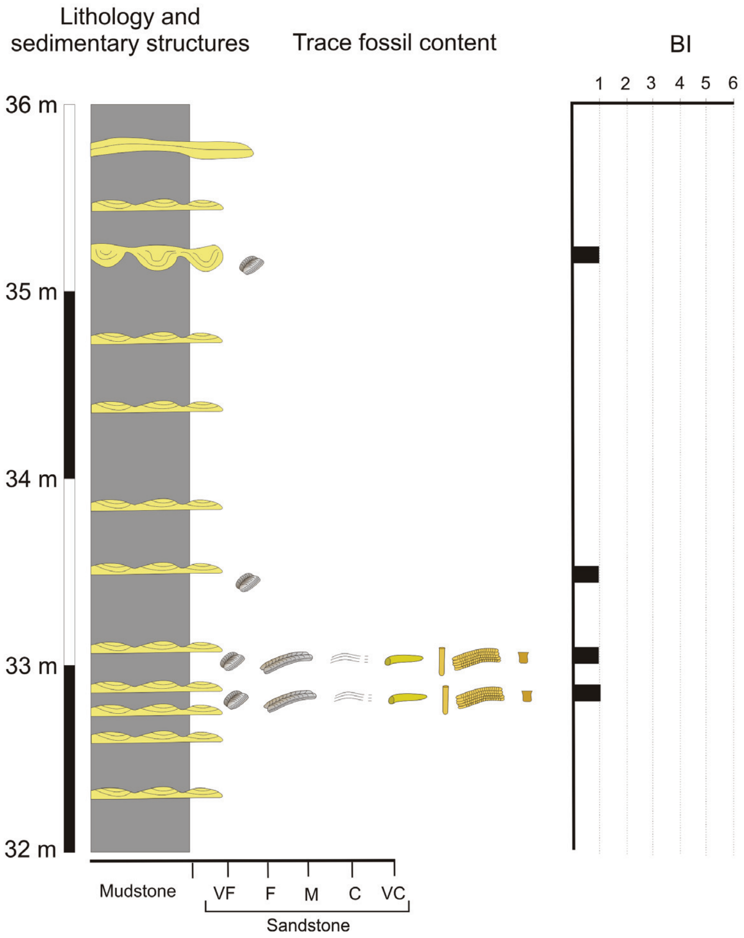

FIGURE 6. Detailed sedimentologic and ichnologic log of a selected interval of the Furongian-lower Tremadocian Alfarcito Member at Angosto del Morro de Chucalezna. Note persistent low intensities of bioturbation.

nospecies *Cruziana rugosa* is added, most likely reflecting the initial phase of trilobite faunal turnover recorded in the basin (Waisfeld et al. 1999). Some of the members of this group were able to increase significantly the depth of bioturbation compared to the shallow ribbon-like structures of the *Cruziana semiplicata* group. In strata of the marginal-marine Mojotoro Formation (Arenigian), *C. rugosa* can reach up to 30 cm deep in abandoned estuarine-channel sandstone (Mángano et al. 2001).

However, and in contrast to older deposits, the most significant innovation in terms of effects on the sedimentary fabric is the appearance of a mid-tier component represented by the ichnospecies *Trichophycus venosus*, which cross-cuts the more shallowly emplaced trilobite-produced trace fossils and many vermiform structures (Figure 9.1). Although this ichnospecies is particularly abundant in upper-offshore deposits, it is locally present also in offshore-transition deposits, albeit in lower densities.

Trichophycus venosus consists of endichnial, relatively large, straight to slightly curved, shallow U-shaped structures (Figure 9.2) with oval (i.e., flattened) to subcylindrical cross-section and a complex set of scratch marks on the ventral and lateral surfaces of the burrow. Burrows are 0.5-3.6 cm wide (but typically 1.5-2.5 cm), and individual branches are up to 50 cm long on well-exposed bedding planes. Maximum penetration depth as recorded in compacted mudstone is 12 cm. As originally noted by Osgood (1970), *Trichophycus* is typically abundant and gregarious, tending to occur as dense assemblages producing significant disturbance of the primary fabric (Figure 9.4-6, Figure 10.6-10.7).

On some bedding-plane views, the network of structures resembles *Thalassinoides* mazes. On close inspection, however, the apparent mazes result mostly from overcrossing or false bifurca-

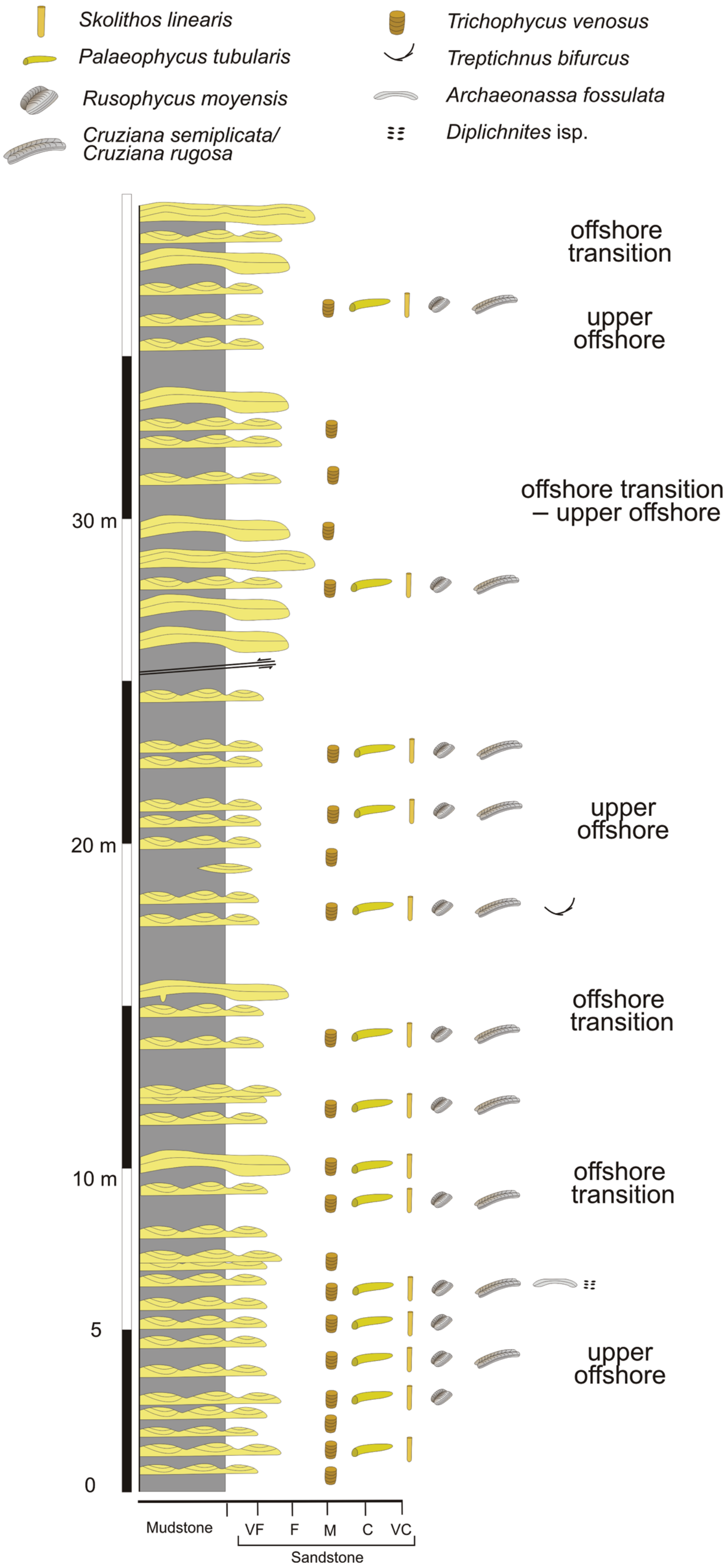

FIGURE 7. Sedimentologic and ichnologic log of the upper Tremadocian Rupasca Member at Angosto del Ferrocarril.

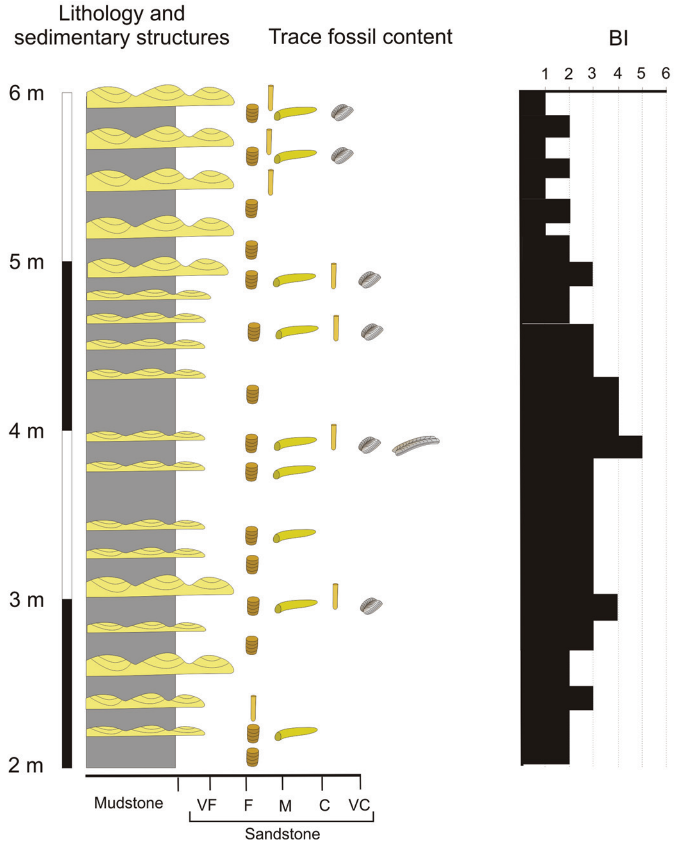

FIGURE 8. Detailed sedimentologic and ichnologic log of a selected interval of the upper Tremadocian Rupasca Member at Angosto del Ferrocarril. Note moderate to high intensities of bioturbation and the dominance of *Trichophycus venosus*.

tions. True vertical bifurcations are present locally, defining inclined shafts (Figure 9.1, 9.3), most likely connected to the sediment-water interface. In cross-section view, the structures display a retrusive spreite consisting of gutter-shaped laminae that typically pass upwards into either almost flat laminae (Figure 9.4-6, Figure 10.3-10.5, 10.7) or occasionally, slightly convex upward laminae; the latter are most common in the uppermost part of the spreite (Figure 10.7). Spreite is typically quite sandy in nature (Figure 10.5, 10.7). However, some specimens may be dominantly silt-fill, displaying a very subtle lamination (Figure 10.4). Most specimens show thin mudstone (stylolitized) laminae alternating with laminae of fine-grained sandstone (Figure 10.3).

The most distinctive feature of *Trichophycus,* the presence of scratch marks, is however, dependent on the nature of the substrate. Other architectural characteristics, such as very wide U-shaped burrows with vertical bifurcations or the fact that in intensely bioturbated fabrics structures tend to run parallel to previous burrows (Figure 10.6), seem to be features distinctive of *Trichophycus* (in comparison to similar forms such as *Teichichnus*). Although scratch marks vary in the degree of preservation largely reflecting different sediments, multiple, longitudinal, subparallel scratch marks are present, at least locally. Longitudinal scratch marks (0.6-1.8 mm wide, 1-1.5 mm apart) are always best preserved and typically dominate at the base of the structure (Figure 10.2). Shaggy, closely spaced, oblique, scratch marks (< 1 mm wide) on the lateral boundaries of the burrow cross-cut the coarser, longitudinal scratches (Figure 10.1). Typically, these thinner scratch marks tend to be asymptotic toward the basal part of the structure. Button-like endings displaying radial scratch marks, such as those described by Osgood (1970) and Jensen (1990) have not been observed.

During the Arenigian, *Thalassinoides* isp. is also locally present (Figure 11), resulting in increased disturbance of fine-grained deposits (Mángano and Buatois 2003). A further increase in the extent of bioturbation is suggested by the Caradocian upper-offshore deposits studied, in which

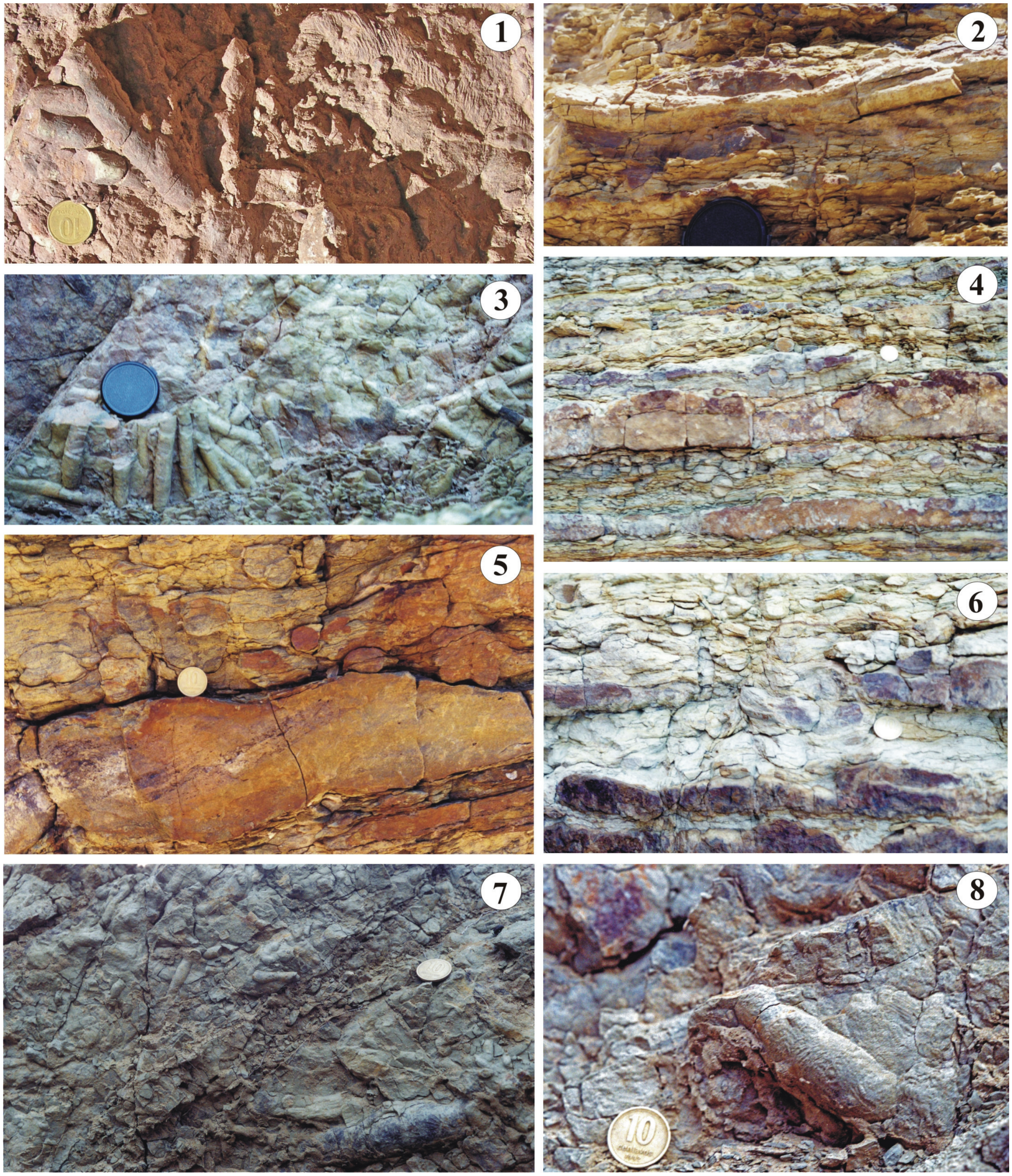

FIGURE 9. The *Trichophycus* ichnofabric. 1. *Trichophycus venosus* cross-cutting *Cruziana rugosa* at the base of a storm sandstone. Note scratch marks in both ichnotaxa. 2. U-shaped morphology of *T. venosus*. 3. High density of *T. venosus* at the base of a sandstone tempestite. 4 and 5. Intense bioturbation by *T. venosus* confined to fairweather mudstone without penetrating into the underlying sandstone tempestite. 6. *Trichophycus venosus* in both fairweather mudstone and storm sandstone, leading to major disturbance of the primary sedimentary fabric. 7. General view of a sandstone tempestite layer displaying several specimens of *T. venosus*. 8. Close-up of a specimen of *T. venosus* showing well-developed scratch marks. 1 and 3 are from the Humacha Member at Quebrada de Humacha. 2, 4, 5, and 6 are from the Rupasca Member at Angosto de Chucalezna. 7 and 8 are from the Acoite Formation at Quebrada de Los Colorados. Coin is 1.8 cm wide. Lens cover is 5.5 cm wide.

FIGURE 10. Close-ups of *Trichophycus venosus*. 1. Specimen with coarse longitudinal scratch marks clearly visible in the lower part of the structure, and finer, oblique scratch marks on the sides of the structure. 2. Same specimen as in 1, showing coarse longitudinal scratch marks and transversal constriction-like ridges locally develop (right). 3. Detail of spreite structure. Sand laminae are separated by thin stylolytes. 4. Tempestite displaying microhumocky cross-stratification. Note the presence of escape structures (center left). The cluster structure on the upper left is *Phycodes* isp. (note the spreite laminae are mud-dominated rather than sand-dominated). *Trichophycus* specimen on the left also displays mud-rich spreite laminae. 5. *Trichophycus* displaying a distinctive flat spreite (center). The other two specimens, to the right and to the left, are camouflaged with the host rock (i.e., similar lithology). 6. Base showing high density of *Trichophycus* surrounded by fine-grained siltstone. 7. Cross-sectional view showing a thoroughly bioturbated silty sandstone. Note that almost a 100% of the polished surface corresponds to *Trichophycus* spreite. Scale bars equal 1 cm.

tempestite preservation is more limited. However, our data are restricted to only one section of the Santa Gertrudis Formation. These deposits may have been more weakly influenced by storm action, therefore allowing thorough bioturbation to occur (Mángano and Buatois 2003). In these deposits the intense bioturbation has reduced the preservation potential of shallow-tier trace fossils, including trilobite-produced trace fossils, which are only represented by a few *Cruziana* specimens.

INFAUNALIZATION IN OFFSHORE ENVIRONMENTS: THE IMPORTANCE OF THE *TRICHOPHYCUS* ICHNOFABRIC

Comparison of the Furongian to lower Tremadocian and upper Tremadocian to Caradocian upper-offshore deposits (Figure 12) reveals differences between the two in both the taxonomic composition of the trace-fossil assemblages and especially, the nature of the ichnofabric. While Furongian-lower Tremadocian upper-offshore deposits are characterized by two-dimensional ichnofabrics in fairweather suites, the upper Tremado-

FIGURE 11. *Thalassinoides* isp., early to middle Arenigian Acoite Formation, Azul Pampa, Jujuy Province. Specimen housed at Instituto Miguel Lillo, University of Tucuman, PIL 12578. Coin is 1.8 cm wide.

cian-Caradocian deposits display three-dimensional *Trichophycus* ichnofabrics, resulting in significant disruption of the primary sedimentary fabric. This ichnofabric reflects more extensive infaunal ecospace utilization by the late Tremadocian.

Trichophycus is currently interpreted as a feeding trace (fodinichnion) or dwelling trace (domichnion) (Seilacher and Meischner 1965; Osgood 1970; Seilacher 1983, 2007; Fillion and Pickerill 1990; Jensen 1997). The retrusive sand-dominated spreite is most likely produced by sediment that passively infilled the structure, being packed against the floor by the producer (Osgood 1970). The striated ornamentation, the sharp outline, and the passive fill suggest an open burrow (Osgood 1970; Fillion and Pickerill 1990; Jensen 1997; Droser et al. 2004). The well-developed striations imply excavation in a relatively firm substrate, consistent with a mid-tier emplacement below the sediment-water interface. The striated ornamentation of *Trichophycus* indicates the presence of some sort of scraping tool in the producer. Traditionally arthropods and annelids have been invoked as potential tracemakers (Seilacher and Meischner 1965; Osgood 1970; Jensen 1997). Seilacher and Meischner (1965) suggested trilobites, although the type material of *Trichophycus* is unilobed, and scratch marks do not display a typical trilobite-like arrangement (see Osgood 1970). Accordingly, a form referred to as *Teichichnus duplex* by Schlirf and Bromley (2007), which is bilobed and ornamented with transverse to oblique scratch marks, is more reminiscent of *Cruziana* rather than *Teichichnus* or *Trichophycus*. Jensen (1997) related the presence of radiating sets of striae to a symmetric radial digging apparatus akin to the spiny proboscis of priapulid worms. Although button-like terminations are not present in our material, their abasence is most likely considered a preservational bias.

It has been proposed that the depth and extent of the mixed layer has increased through the Paleozoic (Droser et al. 2004). As a result of a very shallow mixed layer during the early Paleozoic, firmground conditions occur near the sediment surface. This fact may have favoured preservation of shallow-tier trilobite trails and resting traces with well-developed scratch marks. An overall decrease in the abundance and diversity of *Cruziana* and *Rusophycus* occurs through the Paleozoic (Seilacher 1970, 1992; Mángano and Droser 2004; Droser et al. 2004); trilobite-produced trace fossils are most characteristic of Cambrian to Lower Ordovician strata (Mangano and Droser 2004). Notably, while Lower Ordovician offshore deposits

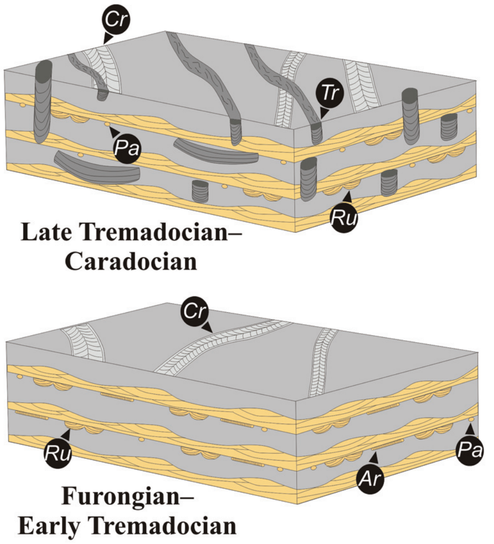

FIGURE 12. Changes in ecospace utilization in upper-offshore deposits through the early Paleozoic in northwest Argentina in connection with the establishment of the *Trichophycus* ichnofabrics. Furongian to early Tremadocian ichnofaunas are dominated by shallow-tier trace fossils, such as various ichnospecies of *Cruziana* (*Cr*), *Rusophycus* (*Ru*) and *Palaeophycus* (*Pa*), and the ichnospecies *Arthrophycus minimus* (*Ar*). Late Tremadocian to Caradocian ichnofaunas are characterized by the appearance of the mid-tier *Trichophycus* (*Tr*).

contain abundant, diverse, trilobite-produced biogenic structures (e.g., *Cruziana*, *Rusophycus*, *Dimorphichnus*), these are rarely the dominant component in Upper Ordovician fully marine deposits (Mángano and Droser 2004). In contrast, *Trichophycus* ichnofabrics are well represented through the rest of the Ordovician. The addition of *Thalassinoides* isp. during the Arenigian resulted in increased reworking of fine-grained deposits.

Endobenthic organisms partition the energy sources available by inhabiting different tiers. In the absence of episodic sedimentation, tiered communities move upwards to maintain the same relative position as sedimentation gradually accretes (Bromley 1996). Pronounced, rapid changes in environmental conditions, as from storm processes, affect infaunal communities and thus their tiering profiles strongly. In the deposits studied, distal storm events have frequently interrupted fair-weather bioturbation. In most cases, *Trichophycus* burrows penetrate into the thin sandstone tempestites, resulting in thorough bioturbation of storm deposits (Figure 10.7). However, relatively thick sandstone beds may have acted as a physical barrier to the producer, as specimens of *Trichophycus* can be observed penetrating into the mudstone and reaching the top of the underlying sandstone bed without crossing it.

In contrast to younger Paleozoic and post-Paleozoic marine deposits (e.g., Mángano et al. 2002; Buatois et al. 2003b; Carmona et al. 2008), deep infaunal ecospace is not colonized, and the tiering structure remains relatively simple. In fact, in the studied offshore deposits *Trichophycus* is commonly the only mid-tier component, in contrast to younger marine deposits that typically display a large variety of mid-tier trace fossils dominated by those produced by crustacean (Carmona et al. 2004, 2008).

DISCUSSION: PALEOGEOGRAPHIC DIACHRONEITY OF INFAUNALIZATION

The Ordovician was characterized by the most extensive global radiation (at species to order level) in the history of the biosphere (Miller 2004). Our knowledge of this radiation has increased by looking at the diversity trajectories of different taxa (see papers in Webby et al. 2004). Very few studies, however, have explored the potential of trace fossils to yield insights into the Ordovician radiation (e.g., Mángano and Droser 2004). Our data from upper-offshore facies in northwest Argentina indicate that the early to late Tremadocian interval represents a critical time, during which exploitation of infaunal ecospace increased, resulting in the establishment of a mid-tier benthos represented by *Trichophycus venosus* (Figure 12). As a result, the preservation potential of shallow tiers was significantly reduced, and shallowly emplaced trilobite-produced trace fossils (often showing conspicuous scratch marks) became less common in fully marine settings by the end of the period. The pristine preservation of thin tempestites in Cambrian to Lower Ordovician shallow-marine deposits most likely reflects the restriction of the benthic fauna to the uppermost zones of the sediment and the absence of true sediment bulldozers (Mángano et al. 2005a).

The *Trichophycus* ichnofabric has been recorded in other Ordovician units from Gondwana, including Iraq (e.g., Seilacher and Meischner 1965) and Morocco (unpublished data). While the Middle East and South America represent intermediate latitudes, North Africa occupied high latitudes during the Ordovician (Fortey and Cocks 2003). The *Trichophycus* ichnofabric is conspicuous in upper-offshore deposits of the Lower Arenigian Upper

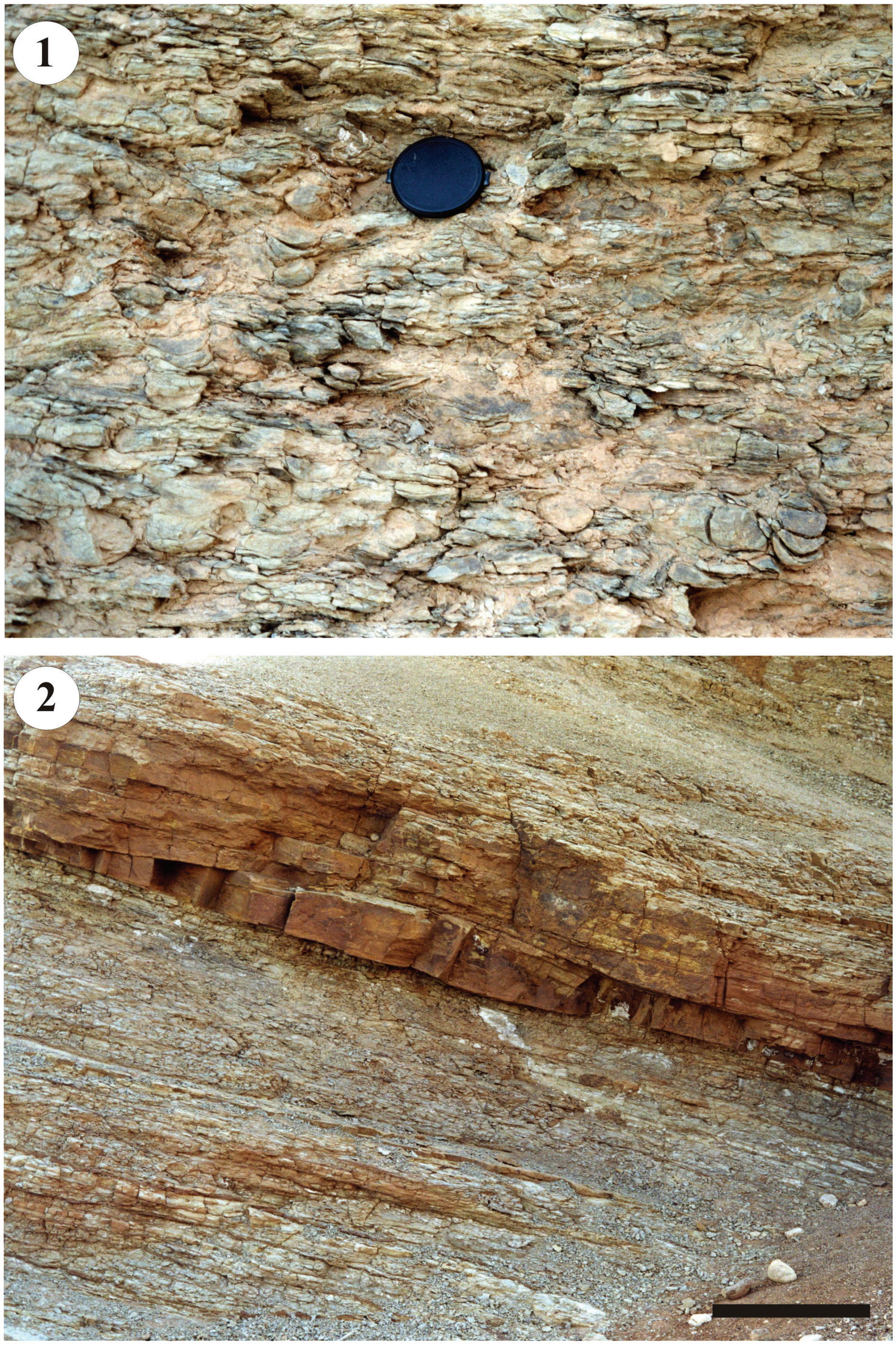

FIGURE 13. The lower Arenigian Upper Fezouta Formation, Imini succession, Central High Atlas.1. Close-up view of the *Trichophycus* ichnofabric. Lens cover is 5.5 cm. 2. Discrete hummocky cross-stratified sandstone layer within a mudstone-dominated unit. Scale bar equals 1 m.

Fezouta Formation of the Central High Atlas and Anti Atlas (Figure 13.1). These deposits accumulated under the influence of periodic storms as indicated by discrete layers of hummocky cross-stratified very fine-grained sandstone within mudstone-dominated intervals (Figure 13.2). However, paucity of estenohaline body fossils and local decrease in bioturbation intensity and trace-fossil diversity suggest stressed conditions suggestive of

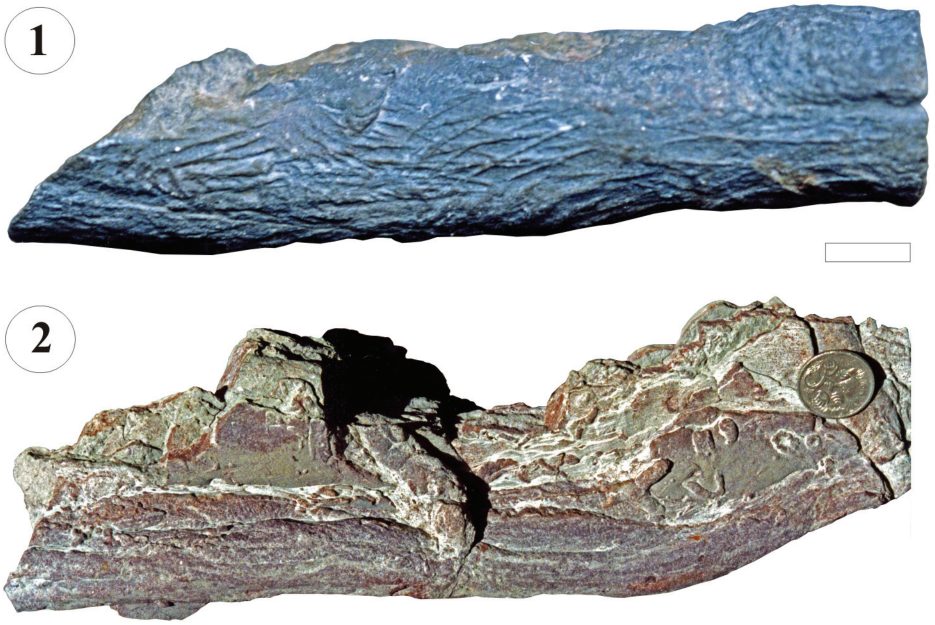

FIGURE 14. *Trichophycus venosus* from Baltica and Avalonia. 1. Arenigian, Wabana Group, Bell Island, Newfoundland, Canada. Scale bar equals 1 cm. 2. Lower Cambrian, Mickwitzia Sandstone, Västergötland, Sweden. Coin is 1.9 cm. Specimens housed at the Geological Institute of the University of Tübingen.

periodic freshwater discharge due to deltaic influence (see also Hamoumi 2001).

The ichnogenus *Trichophycus* is also present in the peri-Gondwanic microcontinent Avalonia. It has been documented in Arenigian siliciclastic marine deposits of the Wabana Group in Newfoundland (Fillion and Pickerill 1990; Droser et al. 2004) (Figure 14.1). In contrast to the examples from northwest Argentina, specimens from the Lower Ordovician Grebes Nest Point Formation of Newfoundland seem to have occupied a shallow-tier position (Droser et al. 2004). Interestingly, *Trichophycus* is not known from the older Upper Cambrian-Tremadocian deposits of Newfoundland, which have been studied intensely (Fillion and Pickerill 1990). *Trichophycus* is also present in Caradocian marine deposits of Wales (Pickerill 1977). The information available from Newfoundland and Wales is consistent with the timing of the first appearance of *Trichophycus* in various regions of Gondwana.

However, comparisons with similar ichnofabrics in other paleocontinents, such as Laurentia and Baltica, suggest that infaunalization in offshore siliciclastic environments was most likely diachronic. In Laurentia, the ichnogenus *Trichophycus* has been extensively recorded, particularly in Upper Ordovician rocks of United States, including Ohio (e.g., Osgood 1970) and Georgia (Frey and Chowns 1972; Martin 1993), and in Ontario, Canada (Stanley and Pickerill 1998), being also present in the Lower Cambrian Gog Group of the Rocky Mountains (Magwood and Pemberton 1988; Desjardins et al. 2010). In Baltica, a mid-tier dominated by *Trichophycus* is present in shallow-marine siliciclastic deposits of Early Cambrian to Ordovician age (e.g., Seilacher and Meischner 1965; Jensen 1997; Knaust 2004) (Figure 14.2). In Laurentia and Baltica, this ichnogenus tends to occur in a wide variety of depositional environments, including not only storm-influenced offshore settings (Kerr and Eyles 1991), but also estuaries (Martin 1993). Further studies are needed to characterize the different occurrences of the *Trichophycus* ichnofabric in these settings. The evidence available suggests that infaunalization in offshore siliciclastics occurred in Laurentia and Baltica as part of the Cambrian radiation. The delayed appearance of *Trichophycus* in Gondwana may reflect a subsequent dispersal and migration, or behavioral convergence by different producers during the Ordovician diversification event.

Other trace fossils, such as arthrophycids and teichichnids, are somewhat similar to *Trichophycus* in terms of overall morphology and in some cases functional significance. Although evaluation of evolutionary trends displayed by these trace fossils in the various paleocontinents requires more extensive datasets, some patterns seem to be apparent. Three ichnogenera, *Daedalus*, *Arthrophycus* and *Phycodes*, are included in Arthrophycidae (Seilacher 2000). This ichnofamily is characterized by fine morphologic details, in particular unique transversal annulations (Seilacher 2000), and is essentially a product of the Ordovician radiation, although some of its most simple representatives are known since the Cambrian (Mángano et al. 2005b).

Daedalus occupies a deep-tier position, reaching depths of up to 90 cm (Seilacher 2000). It is restricted to relatively high-energy clean sandstones, and ranges in age from Arenigian to Early Silurian, displaying more precise biostratigraphic significance at ichnospecies level (Seilacher 2000). *Arthrophycus* is mostly a mid-tier form, particularly in the case of Lower Silurian ichnospecies, such as *A. alleghaniensis* and *A. lateralis.* The Lower Ordovician to Lower Silurian *A. brongniartii* (=*A. linearis*) occupies shallow tiers. The oldest representative, the Late Cambrian to Early Ordovician *A. minimus*, is a very shallow-tier form that occurs in upper-offshore deposits of the Alfarcito Member in northwest Argentina (Mángano et al. 2005b). The tiering position of *Phycodes* also varies at ichnospecies level. The earliest representative is *Phycodes palmatus*, which is known since the Early Cambrian (Crimes and Anderson 1985; Narbonne et al. 1987; Jensen 1997) and is typically a very shallow-tier ichnospecies. Tremadocian to Lower Arenigian ichnospecies, such as *P. ungulatus* and *P. wabanensis* (Fillion and Pickerill 1990), seem to have occupied a shallow tier. In contrast, some of the later forms (the uppermost Arenigian *P. fusiforme*, the upper Arenigian-lower Llanvirnian *P. parallelum*, and the Caradocian-Ashgillian *P. flabellum*) are mid-tier forms (Seilacher 2000). *Phycodes circinatus*, also a shallow-tier form, typically occurs in Lower Ordovician rocks in Gondwana, but may extend to those of Middle Ordovician age in Laurentia (Fillion and Pickerill 1990). Seilacher (2000) noted that the arthrophycid nature of *Phycodes* is less well founded. This doubt is especially true of the earliest representatives in which the diagnostic fingerprints of the family (i.e., arthrophycid corrugations) are not present. In general *Arthrophycus* and *Phycodes* show a tendency to occupy slightly deeper tiers through the Ordovician and, in the case of the former, into the Silurian.

Although the ichnogenera *Syringomorpha* and *Helichone* have been referred to as teichichnids by Seilacher (2007), *Teichichnus* itself is the most representative element of this group and that most similar to *Trichophycus*. However, the ichnotaxonomy of *Teichichnus* is in need of revision, and potential evolutionary trends remain unidentified. *Teichichnus rectus* is the most common ichnospecies. It is a facies-crossing form, typically occupying shallow to mid tiers, which is common not only in fully marine settings but also in brackish-water environments since the Cambrian (Buatois et al. 2005). Lower Paleozoic examples of *T. rectus* are commonly shallower tier than younger specimens (e.g. Buckman 1996). *Teichichnus stellatus* is a shallow-tier form that occurs in Arenigian offshore to shelf deposits of northern Spain (Baldwin 1977). However, its radial morphology suggests that this ichnospecies may be removed from *Teichichnus* and placed in some of the many ichnogenera available for rosette trace fossils. Notably, in its type locality *T. stellatus* occurs in the same interval than radial ichnofossils referred to as *Volkichnium* ?*volki* by Baldwin (1977), opening the possibility that *T. stellatus* is a preservational variant of the latter. Alternatively, re-examination of the lower Paleozoic outcrops of northern Spain suggests that the radial morphology may have resulted from the intersection of several specimens of *T. rectus* (García Ramos, personal commun., 2009). Other ichnospecies of *Teichichnus* (e.g., *T. spiralis*, *T zigzag*, *T. sigmoidalis*) are post-Paleozoic and may occupy mid to relatively deep tiers (Frey and Bromley 1985; Buatois et al. 2003b; Seilacher 2007; Carmona et al. 2008).

The need to identify ecologic differences among Ordovician faunas at local, regional, and inter-continental scales has been advocated by Miller (2004). Studies on different fossil groups have helped to reveal whether global diversity trajectories resemble those at local and regional scales. The emerging view is that both the timing of diversification and the accompanying ecologic changes were diachronous across the different environments and paleocontinents (Webby et al. 2004; Harper 2006). For example, diversification of some brachiopod groups (e.g., plectambonitoids) was delayed in Gondwana with respect to Baltica (Harper et al. 2004). The opposite trend, however, was proposed for bivalves, which seem to have radiated first in Gondwana and later migrated to lower latitudes (Cope and Babin 1999; Sánchez and Babin 2003; Cope 2004; Sánchez 2008). Studies of trilobite and brachiopod faunas from the Argentinean basins have noted a slight decoupling between diversification events in this region and those at global scale (Waisfeld et al. 1999, 2003). These studies emphasize the need to consider how geodynamic histories and paleogeography play a role in shaping diversity trajectories.

Some of these trajectories may be linked to latitudinal differences. Some of the areas of Gondwana discussed herein (Argentina and Morocco) occupied high to intermediate latitudes during the early Paleozoic, while Laurentia was located at low latitudes. However, although Cambrian paleomagnetic data for Baltica are controversial, a position at mid latitudes is the most likely (Smith 2001). This pattern indicates a more complex paleogeographic pattern of infaunalization and suggests that factors other than latitude may have played a role in the diachronic trajectories of ecologic innovation across the different paleocontinents. Our study underscores the importance of expanding the database of Cambrian-Ordovician ichnofaunas to account for ecologic differences among regions.

CONCLUSIONS

1. Ichnofabric analysis of upper-offshore deposits in northwest Argentina shows a sharp contrast between Furongian to lower Tremadocian and upper Tremadocian to Caradocian units.
2. Furongian to lower Tremadocian upper-offshore deposits are dominated by very shallow-tier structures produced by trilobites and shallow-tier worm structures (e.g., *Arthrophycus minimus*, *Palaeophycus tubularis*, *Phycodes* isp.), with little disturbance of the primary fabric (BI = 0-1).
3. Upper Tremadocian-Caradocian upper-offshore deposits show a remarkable increase in degree of bioturbation (BI = 2-4, locally 5), and are characterized by the mid-tier *Trichophycus venosus* cross-cutting the more shallowly emplaced trilobite and worm trace fossils.
4. The early to late Tremadocian transition seems to have been a turning point for exploitation of the infaunal ecospace in high- to intermediate-latitude siliciclastic basins of Gondwana.
5. Similar ichnofabrics, however, appear to have been present since the Early Cambrian in other paleocontinents, such as Baltica and Laurentia, suggesting that infaunalization and the development of a mid-tier benthos in these regions were a consequence of the Cambrian explosion. The delayed appearance of *Trichophycus* in Gondwana may reflect a subsequent dispersal and migration, or alternatively, behavioral convergence by different producers during the Ordovician diversification event.

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