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Ichnology of the Alfarcito Member (Santa Rosita Formation) of northwestern Argentina: animal-substrate interactions in a lower Paleozoic wave-dominated shallow sea

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Abstract. The lower fine-grained interval of the Alfarcito Member of the Upper Cambrian-Tremadocian Santa Rosita Formation in northwestern Argentina represents an overall transgressive-regressive cycle, recording the establishment of an open-marine, shallow, low-gradient platform. Four main sedimentary facies have been recognized, environmentally ranging from the lower offshore to the lower/middle shoreface. Alternating and contrasting energy conditions due to repeated storm events superimposed on fairweather sediments were among the key controlling factors for trace fossil distribution and preservation. Fairweather and storm-related trace fossil assemblages are recognized. The first is the most diverse and includes the more varied behavioral strategies, such as locomotion (*Archaeonassa fossulata, Cruziana semiplicata, C. problematica, Cruziana* isp. and *Diplichnites* isp.); resting (*Rusophycus moyensis*, *R. carbonarius*, *Rusophycus* issp. and *Bergaueria* aff. *B. hemispherica*); pascichnia (*Dimorphichnus* aff. *D. quadrifidus*); feeding (*Arthrophycus minimus*, ?*Gyrolithes* isp., *Gyrophyllites* isp., ?*Phycodes* isp. and *Planolites reinecki*); and dwelling (*Palaeophycus tubularis, P. striatus*). This assemblage represents the *Cruziana* ichnofacies. The storm-related assemblage is monospecific and includes vertical dwelling traces (*Skolithos linearis*), and is attributed to the *Skolithos* ichnofacies. Integration of ichnologic and sedimentologic data allows proximal-distal trends in shallow-marine trace fossil assemblages along a nearshore-offshore transect to be reconstructed. High-energy conditions prevailed in lower and middle shoreface environments and bioturbation is restricted to vertical burrows (*Skolithos linearis*), recording colonization after storm events. Environmental conditions in the offshore transition and the upper offshore are more variable and reflect the alternation of high-energy storm events and low-energy fairweather mudstone deposition. The storm-related *Skolithos* ichnofacies is present, but alternates with the faiweather assemblage (*Cruziana* ichnofacies) that reaches a diversity maximum in the upper offshore. Trace fossils are scarce in lower offshore deposits, being restricted to a few non-descript burrows, mostly *Palaeophycus tubularis*. Shoreface deposits from the Alfarcito Member compare favorably with the strongly storm-dominated type. All these deposits are stacked to form regional coarsening-upward parasequences that record short-term progradational episodes separated by drowning surfaces. Vertical distribution of trace fossils parallels changes in stratal stacking patterns. Several ichnotaxa (especially *Cruziana semiplicata*, *Rusophycus moyensis* and *Arthrophycus minimus*) have biostratigraphic implications.

Resumen. ICNOLOGÍA DEL MIEMBRO ALFARCITO (FORMACIÓN SANTA ROSITA) DEL NOROESTE DE ARGENTINA: INTERACCIONES SUSTRATO-ANIMAL EN UN MAR SOMERO DEL PALEOZOICO INFERIOR DOMINADO POR OLEAJE. El intervalo inferior de grano fino del Miembro Alfarcito de la Formación Santa Rosita (Cámbrico Superior-Tremadociano) representa un ciclo general transgresivo-regresivo, registrando el establecimiento de una plataforma marina somera de bajo gradiente. Se reconocieron cuatro facies sedimentarias principales, cuyos ambientes varían entre costa-afuera bajo y *shoreface* bajo a medio. Entre los factores claves que controlaron la distribución de los icnofósiles y su preservación se encuentran las condiciones de energía alternantes y contrastantes debidas a eventos de tormenta repetidos superpuestos sobre sedimentos de buen tiempo. Se reconocieron asociaciones de trazas fósiles de buen tiempo y de tormenta. La primera es la más diversa e incluye la mayor variación de estrategias de comportamiento, tales como locomoción (*Archaeonassa fossulata, Cruziana semiplicata, C. problematica, Cruziana* isp. y *Diplichnites* isp.); reposo (*Rusophycus moyensis*, *R. carbonarius*, *Rusophycus* issp. y *Bergaueria* aff. *B. hemispherica*); pascichnia (*Dimorphichnus* aff. *D. quadrifidus*); alimentación (*Arthrophycus minimus*, ?*Gyrolithes* isp., *Gyrophyllites* isp., ?*Phycodes* isp. y *Planolites reinecki*); y habitación en dos ocasiones (*Palaeophycus tubularis, P. striatus*). Esta asociación representa la icnofacies de *Cruziana*. La asociación relacionada con tormentas es monoespecífica e incluye trazas de alojamiento vertical (*Skolithos linearis*), y se atribuye a la icnofacies de *Skolithos*. La integración de los datos icnológicos y sedimentológicos permite reconstruir las tendencias proximal-distales en las asociaciones de trazas fósiles marinas a lo largo de una transecta *nearshore-offshore*. En los ambientes de *shoreface* inferior y medio prevalecieron condiciones de alta energía y la bioturbación se halla restringida a excavaciones verticales (*Skolithos linearis*), registrando la colonización luego de los eventos de tormenta. Las condiciones ambientales en la transición a costa afuera y en costa afuera superior son más variables y reflejan la alternancia de eventos de tormenta de alta energía y depositación de fangolitas de buen tiempo y baja energía. Se halla presente la icnofacies de *Skolithos* relacionada con tormentas, la que alterna con la asociación de buen tiempo (icnofacies de *Cruziana*) que alcanza su máxima diversidad en el costa-afuera superior. Los icnofósiles son escasos en el *offshore* bajo, estando restringidos a unas pocas excavaciones, mayormente *Palaeophycus tubularis*. Los depósitos de *shoreface* del Miembro Alfarcito se pueden comparar con los tipos fuertemente dominados por tormentas. Todos estos depósitos forman parasecuencias granocrecientes que registran los cortos episodios progradacionales separados por superficies de inundación. La distribución vertical de las trazas fósiles acompaña los cambios en los patrones de depositación. Varios icnotaxones (especialmente *Cruziana semiplicata*, *Rusophycus moyensis* y *Arthrophycus minimus*) poseen interés bioestratigráfico.

Key words. Ichnology. Trace fossils. Wave-dominated. Tempestites. Lower Paleozoic. Argentina.

Palabras clave. Icnología. Trazas fósiles. Dominado por oleaje. Tempestitas. Paleozoico inferior. Argentina.

Introduction

Invertebrate ichnofossils are abundant in lower Paleozoic deposits of northwestern Argentina. In particular, Cambrian-Ordovician ichnofaunas have been the focus of a series of studies during the 1970s and early 1980s (*e.g.* Aceñolaza, 1978; Aceñolaza and Durand, 1978; Aceñolaza and Fernández, 1978, 1984; Aceñolaza and Manca, 1982; Fernández and Lisiak, 1984). These essentially dealt with ichnofossil identification and ichnofacies recognition. However, in recent years there have been several attempts to refine previous ichnotaxonomic assess-

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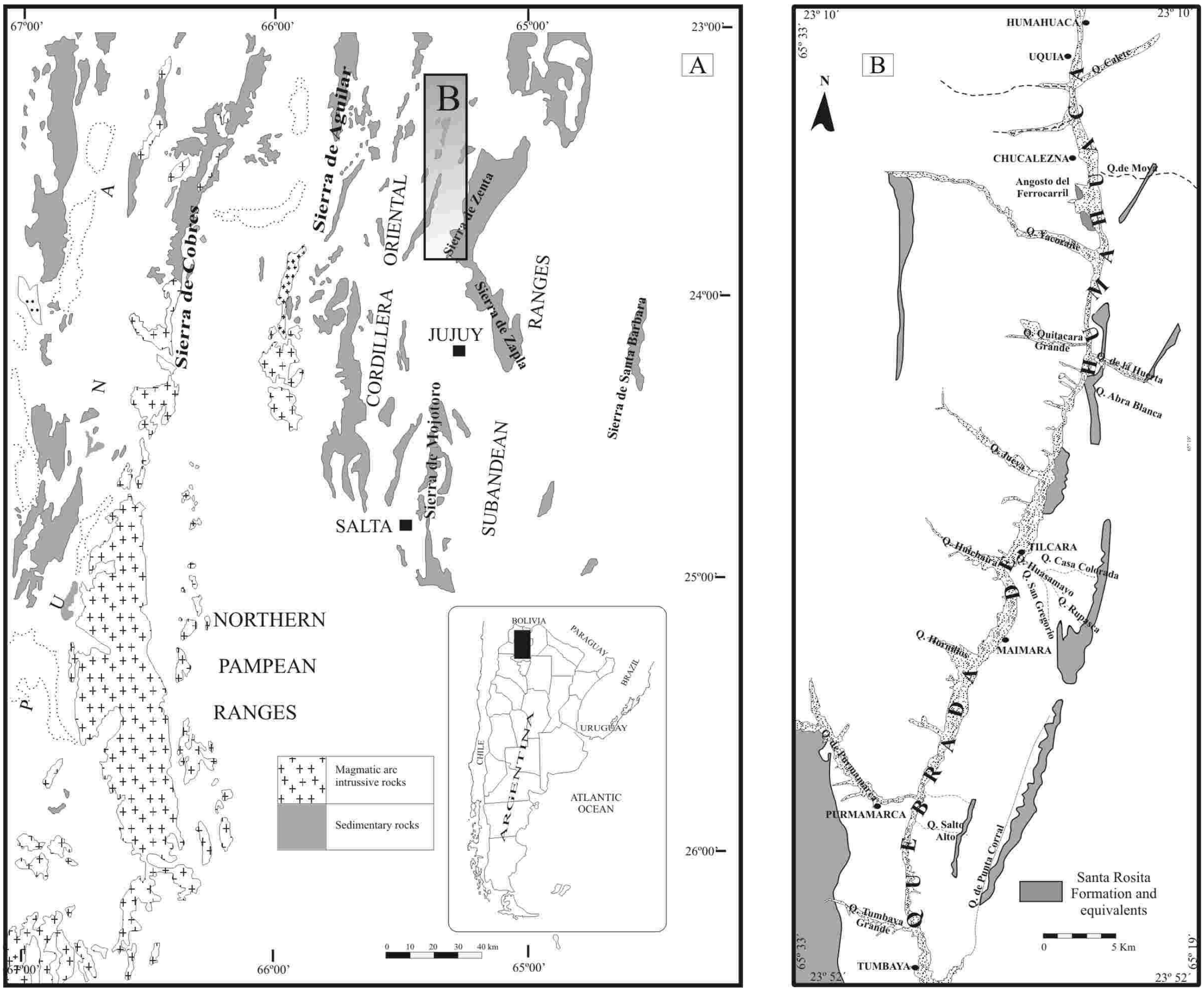

Figure 1. A, Regional distribution of Upper Cambrian-Ordovician exposures in northwestern Argentina (after Moya, 1988, 1998) and location of the studied areas. **B,** Outcrop distribution of the Upper Cambrian-Tremadocian Santa Rosita Formation in the Quebrada de Humahuaca area (after Buatois and Mángano, 2003) / ***A,*** *Distribución regional de los afloramientos del Cámbrico Superior-Ordovícico del noroeste argentino (tomado de Moya, 1988, 1998) y ubicación de las áreas de estudio.* ***B,*** *Distribución de afloramientos de la Formación Santa Rosita (Cámbrico superior-Termadociano) en la quebrada de Humahuaca (tomado de Buatois y Mángano, 2003).*

ments, record new forms and track the sedimentologic and stratigraphic distribution of trace fossils in order to explore paleoecological, paleoenvironmental, sequence stratigraphic, biostratigraphic and evolutionary aspects of these ichnofaunas (for review see Mángano and Buatois, 2003). The Alfarcito Member is, therefore, appropriate for the multidimensional approach to ichnology advocated by the authors in previous studies (*e.g.* Mángano *et al.*, 2002a).

Extensive outcrops of the Upper Cambrian-Tremadocian Santa Rosita Formation are exposed in the Cordillera Oriental of northwestern Argentina (figure 1). This unit records a complex depositional history, encompassing a wide range of sedimentary environments, such as fluvial, tide-dominated estuarine, and wave-dominated shallow marine (Mángano and Buatois, 2002; Buatois and Mángano, 2003). In particular, the lower interval of the Alfarcito Member, which is the focus of this study, represents an overall transgressive-regressive cycle, recording the establishment of an open-marine, shallow, low-gradient platform, affected by fairweather and storm waves. Trace fossils are common in outcrops in the Quebrada de Humahuaca area (figure 1). The integration of ichnologic data within a sedimentologic and sequence stratigraphic framework allows us to evaluate in detail the significance of the Alfarcito ichnofauna. Additionally, we provide systematic descriptions and critically re-evaluate the taxonomic status of each of the ichnotaxa previously described.

Stratigraphic framework

The Upper Cambrian-Tremadocian Santa Rosita Formation overlies the upper Lower to Middle Cambrian Mesón Group and conformably underlies the Arenigian Acoite Formation. Both the Santa Rosita and Acoite formations are included in the Santa Victoria Group (Turner, 1960). Following the original interpretation by Moya (1998), the contact between the Mesón Group and the Santa Rosita Formation is regarded as an unconformity produced by a relative sea level fall (for discussion see Mángano and Buatois, 2004; Buatois and Mángano, 2005).

The stratigraphic nomenclature of Upper Cambrian to Tremadocian deposits in northwestern Argentina is confused. In most areas of Quebrada de Humahuaca, these strata have been included historically in the Santa Rosita Formation. A series of lithostratigraphic units were further defined by Harrington (1957) in the Cordón de Alfarcito area, including the Casa Colorada Shale, Alfarcito Limestone and Rupasca Shale. These units have been recently considered as members of the Santa Rosita Formation (Buatois and Mángano, 2003). Moya (1988) also proposed additional units, the Tilcara and Humacha formations, which were also regarded as members by Buatois and Mángano (2003). The Santa Rosita Formation has therefore been divided, from base to top, into five members: Tilcara, Casa Colorada, Alfarcito, Rupasca and Humacha members (Buatois and Mángano, 2003). This nomenclatural scheme preserves the traditional and widely used Santa Rosita Formation but at the same time recognizes its internal lithologic variability. However, ongoing research demonstrates a more complex stratigraphy and the current stratigraphic scheme is being revised at present.

The fine-grained lower interval of the Alfarcito Member overlies estuarine deposits. These estuarine deposits are laterally restricted, recording the infill of fluvio-estuarine valleys incised into the underlying open-marine deposits of the Casa Colorada Member. Valley fill commenced with deposition in braided fluvial systems restricted to the valley axis, but the bulk of sedimentation is represented by estuarine deposits that onlapped the valley margins and accumulated during a subsequent transgression. This transgression eventually led to the establishment of open-marine conditions due to basin-wide flooding that blanketed estuarine deposits within the valley, as well as interfluve areas. Estuarine deposits are therefore replaced upward by marine facies (transgressive systems tract) of the Alfarcito Member. This member consists of greenish grey mudstone and thinly interbedded rippled and hummocky cross-stratified sandstone. The maximum flooding surface of this depositional sequence lies within lower offshore deposits that occur in the lowermost interval of the Alfarcito Member. These strata are overlain by lower offshore to offshore transition deposits forming a progradational parasequence set, which represents a highstand systems tract that makes up a significant part of the lower interval of the Alfarcito Member. High-resolution sequence stratigraphic analysis also reveals the presence of a sequence boundary within the lower fine-grained interval of the Alfarcito Member. This sequence boundary is detected by a change in the stacking pattern of parasequences, from progradational to retrogradational parasequence sets. No lowstand deposits are preserved in the study area and the sequence boundary is, therefore, a co-planar surface or flooding surface/sequence boundary. The transgressive systems tract of this second depositional sequence consists of upper to lower offshore deposits stacked forming a retrogradational sequence set. The maximum flooding surface commonly occurs in lower offshore deposits, but it may lie within upper offshore deposits in more proximal locations. Highstand deposits occur above the maximum flooding surface and consist of a progradational parasequence set, which includes deposits that range from the lower offshore into the lower/middle shoreface. This interval is abruptly overlain by forced-regressive shoreface sandstone.

The age of the Alfarcito Member has been controversial due to its sparse fauna and the absence of detailed measured sections that would have allowed accurate placement of paleontologic data in an appropriate stratigraphic framework. A series of studies were recently undertaken in the Alfarcito area, providing valuable biostratigraphic information (Zeballo *et al.*, 2005a,b; Zeballo and Tortello, 2005). In particular conodont and graptolite faunas suggest that the bulk of the Alfarcito Member is of early Tremadocian age. In previous studies, fine-grained facies overlying estuarine deposits in the Quebrada de Moya and adyacent areas were included in the Casa Colorada Member (Aceñolaza, 1996, 2003; Mángano *et al.*, 2002; Rubinstein *et al.*, 2003; Buatois and Mángano, 2003; Mángano and Buatois, 2003). Ongoing research will result in a revised stratigraphic scheme for the area and indicates that these strata should be included in the Alfarcito Member.

Systematic ichnology

Ichnotaxa are listed alphabetically. Most of the specimens described are housed at the collections of

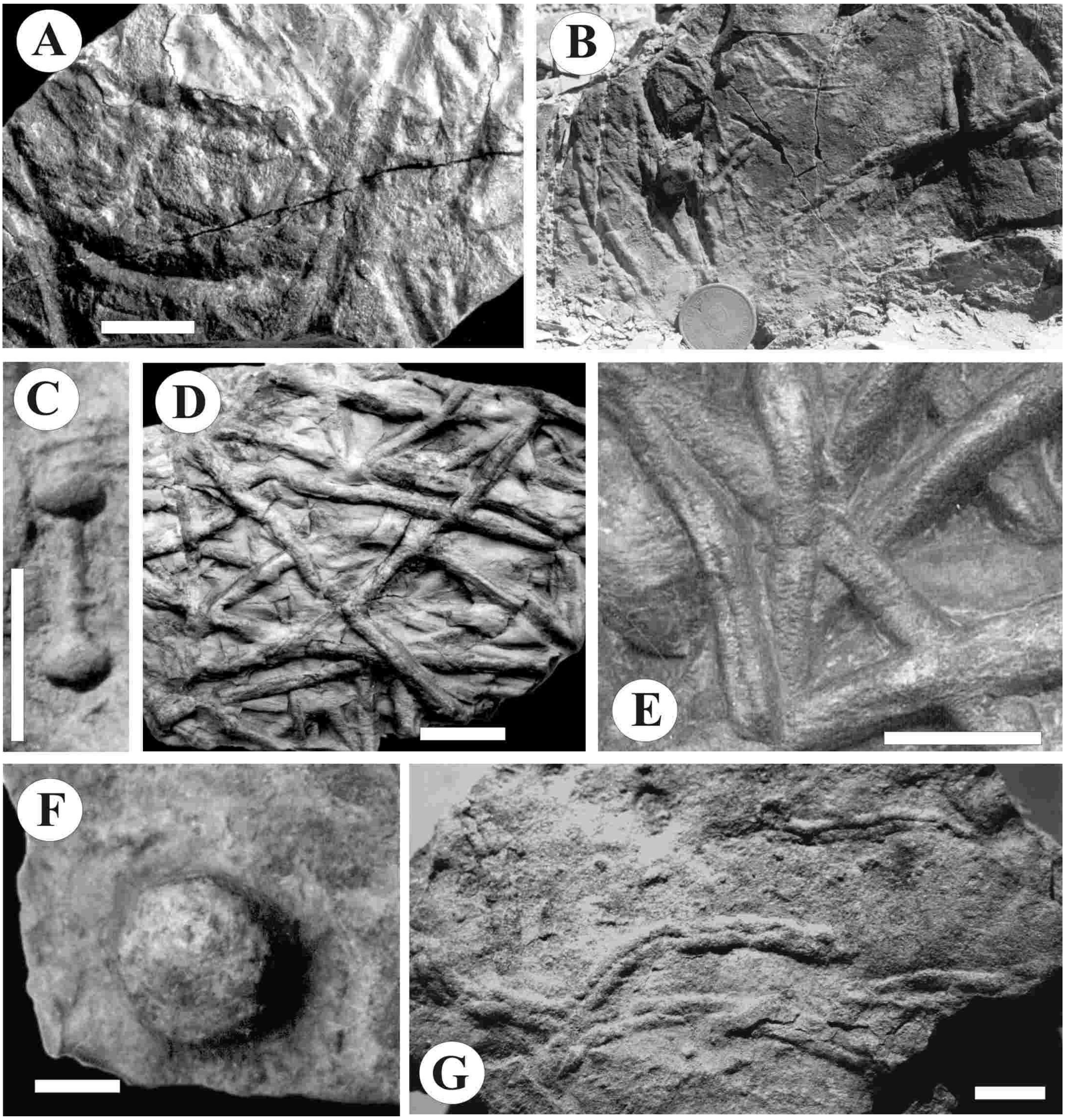

Figure 2. Trace fossils of the Alfarcito Member / *Trazas fósiles del miembro Alfarcito.* **A,** ***Archaeonassa fossulata***. PIL 14951. Angosto del Morro de Chucalezna. **B,** ***Archaeonassa fossulata***. Field photograph. Angosto del Morro de Chucalezna. **C,** ***Arthraria antiquata***. PIL 12529. Quebrada de Abra Blanca. **D,** ***Arthrophycus minimus.*** PIL 14947. Angosto del Morro de Chucalezna. **E,** ***Arthrophycus minimus.*** PIL 14950. Close-up showing annulae and ventral median groove. Angosto del Morro de Chucalezna. **F,** ***Bergaueria*** aff. ***B. hemispherica.*** PIL 14980. Angosto del Morro de Chucalezna. **G,** ***Cruziana problematica***. PIL 14175. Quebrada de Rupasca. Scale bar / *Escala*: 1 cm. Coin / *Moneda*: 1.8 cm.

Invertebrate Paleontology of the Instituto Miguel Lillo (Universidad Nacional de Tucumán) (PIL). Other slabs are housed at the Invertebrate Paleontology Collection of the Paleontological Museum Egidio Feruglio (MPEF-IC). Additional specimens, particularly those that were difficult to collect without damage, were studied directly in the field. We also re-describe specimens published previously and provide a reconsideration of their taxonomic status. Recently, Mángano and Buatois (2003) reviewed lower Paleozoic ichnofaunas from Argentina and provided re-assessments of previous identifications in various papers. Ichnotaxonomic comments are based on the material illustrated by Aceñolaza and Aceñolaza (2003).

Ichnogenus ***Archaeonassa*** Fenton and Fenton, 1937
Archaeonassa fossulata Fenton and Fenton, 1937
Figures 2.A-B

Material. Two slabs (PIL 14174 and 14951) containing 10 specimens, and approximately 20 additional specimens studied in the field.

Description. Straight to sinuous traces having a median groove flanked by rounded ridges. The flanking ridges are very well developed, and locally display an undulating morphology. In cross-sectional view the median groove commonly displays a V-shaped morphology. Trace width is 6.2-11.6 mm. Maximum length observed is 91.2 mm. Preserved as positive epirelief in fine- to very fine-grained sandstone.

Remarks. The ichnotaxonomic status of *Archaeonassa* is still uncertain (see discussion in Buckman, 1994; Yochelson and Fedonkin, 1997). A single ichnospecies, *Archaeonassa fossulata*, is known. It is interpreted as a grazing trace (pascichnion) produced by a wide variety of invertebrates, including arthropods and mollusks (Buckman, 1994; Yochelson and Fedonkin, 1997).

Occurrence. This ichnotaxon occurs sporadically, typically forming monospecific assemblages in the Quebrada de Moya, Angosto del Morro de Chucalezna and Quebrada de Rupasca sections.

Ichnogenus ***Arthraria*** Billings, 1872
Arthraria antiquata Billings, 1872
Figure 2.C

Material. Two slabs (PIL 12529 and 12531) containing five specimens. PIL 12530 mentioned by Aceñolaza and Manca (1982) could not be located.

Description. Horizontal trace having a dumb-bell shape with a shallower stem connecting two deeply impressed hemispherical to oval terminations. Trace length is 5.0-7.7 mm. Termination width is 2.6-3.5 mm. Although none of the collected material has been sectioned, none crosses 1-2 cm thick sandstone layers. Preserved as positive hyporeliefs at the base of very fine-grained sandstone.

Remarks. This ichnotaxon was originally assigned to *Bifungites* isp. by Aceñolaza and Manca (1982), but subsequently it was changed to *Arthraria antiquata* (Aceñolaza and Aceñolaza, 2003, fig. 2N). This is in agreement with Mángano and Buatois (2003), who also placed these specimens in *Arthraria antiquata*. This ichnotaxon has been reviewed and redefined by Fillion and Pickerill (1984) who separated it from *Bifungites* and *Diplocraterion*. The ichnotaxon *Bifungites* is problematic. Desio´s type specimens of *Bifungites* were lost during World War II (Gutschick and Lamborn, 1975) and no topotype material can be collected because Desio (1940) did not indicate the type location (Fillion and Pickerill, 1984). Additionally, Desio (1940) did not provide a description of the structure in 3D. Thus, it could well be a junior synonym of *Arthraria*. This ichnogenus probably represents either dwelling (domichnia) or feeding (fodinichia) structures. Its producer is uncertain, most likely a worm-like organism (Fillion and Pickerill, 1984).

Occurrence. This ichnotaxon is very rare in the Quebrada de Abra Blanca section.

Ichnogenus ***Arthrophycus*** Hall, 1852
Arthrophycus minimus Mángano, Buatois and Muñiz Guinea, 2005
Figures 2.D-E

Material. Fifteen slabs [PIL 13212, 13213 (a and b), 13214, 13215, 14946 (three slabs), 14947 (two slabs), 14948, 14949, 14950, 14602 and 14603], containing approximately 30 specimens. A possible epichnial specimen is preserved in PIL 15187.

Description. Small, long, relatively shallow structures. Specimens are unbranched or have a few side branches, typically running straight or smoothly curving along bedding planes for long distances. Diameter is 1.8-4.5 mm. Maximum observed length is 20 cm. Structures display a distinctive ventral median groove, subcircular to square cross-section and delicate, 0.10-0.35 mm wide, regular annulation. Structures occur as dense monospecific assemblages, where overcrossing is a common feature. True branching is locally present, but does not tend to form palmate structures. Spreite is typically retrusive. Preserved as positive hyporelief in very fine-grained sandstone.

Remarks. *Arthrophycus minimus* has been recently proposed by Mángano *et al.* (2005). This ichnospecies displays all the diagnostic features of *Arthrophycus*, including regular transverse, distinct annulation, a shallow median depression, square cross-section and predominantly horizontal components with a secondary teichichnoid spreite (Seilacher, 2000). In terms of general morphology and searching strategy, this ichnospecies resemble *Arthrophycus brongniartii protrusiva* (Seilacher, 2000). However, annulae are less pronounced in *A. minimus* than in *A. brongniartti* (Harlan, 1832). Additionally, *A. minimus* is of markedly smaller size (commonly an order of magnitude) than the other *Arthrophycus* ichnospecies. *Arthrophycus* is distinguished from the related ichnogenus *Phycodes* Richter 1850 by its branching pattern, which commonly consists of a master tunnel that tends to form distal palmate bundles (*A. alleghaniensis* Hall, 1852) or explore the sediment in a dominantly horizontal, individual, straight fashion (as in *A. brongniartii* and *A. minimus*). The ichnogenus *Torrowangea* Webby, 1970 is characterized by transverse constrictions rather than regular annulae and lacks the typical branching pattern, teichichnoid spreite, square cross-section and ventral median groove of *Arthrophycus* (Mángano *et al.*, 2005). Specimens illustrated by Mángano and Buatois (2003, pl. 1, figs. 4, 5) as *Arthrophycus* isp. were included in *A. minimus* by Mángano *et al.* (2005). Unpublished specimens labeled as *Didymaulichnus* sp. at the Instituto Miguel Lillo collection (PIL 13212, 13213 and 13214) are also included in *A. minimus* (Mángano *et al.*, 2005). Another example of *A. minimus* was also illustrated as "*Arthrophycus* cf. *alleganensis*" (*lapsus calami*) by Aceñolaza and Aceñolaza (2003, fig. 20). *Arthrophycus minimus* is a feeding trace (fodinichnion) most likely produced by worm-like organisms. Evidence for a trilobite producer is lacking because specimens of *A. minimus* do not show segments arranged angularly which would indicate a short body (*cf.* Rindsberg and Martin, 2003), but have a turning ratio suggesting a relatively long animal.

Occurrence. This ichnotaxon is abundant and tends to form monospecific assemblages in the Quebrada de Moya and Angosto del Morro de Chucalezna sections. Occasionally it is associated with *Rusophycus moyensis*.

Ichnogenus **Bergaueria** Prantl, 1946
Bergaueria* aff. *Bergaueria hemispherica Crimes, Legg, Marcos and Arboleya, 1977
Figure 2.F

Material. Two slabs (PIL 14176 and 14980) containing two specimens and 5 additional specimens studied in the field.

Description. Unornamented, simple plug-shaped structures oriented perpendicular to bedding. A central depression is absent. Diameter is 6.7-8.2 mm. Preserved as positive hyporeliefs in fine- to very fine-grained sandstone.

Remarks. Plug-shaped burrows, such as *Bergaueria* and *Conostichus* Lesquereux 1876, have been reviewed by Pemberton *et al.* (1988). The Casa Colorada specimens display the diagnostic morphology of *B. hemispherica* (Crimes *et al.*, 1977; Pemberton *et al.*, 1988). However, *B. hemispherica* is a relatively large form (43-60 mm wide), whereas the size range of the Casa Colorada specimens is considerably smaller. Mángano and Buatois (2003) noted that although *Bergaueria* has been commonly mentioned in the local literature (*e.g.* Aceñolaza, 1978; Aceñolaza and Fernández, 1978; Fernández and Lisiak, 1984; di Cunzolo *et al.*, 2003; Aceñolaza and Nieva, 2003), few specimens have been collected and adequately illustrated. Most of these Cambrian-Ordovician specimens assigned to *Bergaueria* or other plug-shaped burrows should be removed from this group (Mángano and Buatois, 2003). Study in the field of the structures recorded as *Bergaueria* isp. by Aceñolaza and Nieva (2003, fig. 6.G) clearly revealed an inorganic origin, most likely sand grains aggregations. *Bergaueria* is commonly interpreted as the resting (cubichnia) or dwelling (domichnia) structures of cerianthid or actinarian anemones (Pemberton *et al.*, 1988). Vertical repetition may indicate equilibrium (retrusive slow adjustments in relation to sedimentation) or escape structures (retrusive fugichnial reaction related to episodic sedimentation, typically as storm deposition).

Occurrence. This ichnotaxon is relatively rare and has been recorded in the Quebrada de Moya and Angosto del Morro de Chucalezna sections.

Ichnogenus ***Cruziana*** d'Orbigny, 1842
Cruziana problematica (Schindewolf, 1921)
Figure 2.G

Material. One slab (PIL 14175) containing 6 specimens.

Description. Relatively small bilobed structures displaying mostly smooth lobes separated by a relatively shallow, but well-defined median furrow. Faint, thin, transverse to high V-angle retroverse scratch marks can be observed in some specimens. Trace width is 3.1-4.2 mm. Maximum length observed is 53.5 mm. Traces are straight to curved. Preserved as positive hyporelief in fine- to very fine-grained sandstone.

Remarks. The presence of scratch marks distinguishes *Cruziana problematica* from the smooth bilobate trace *Didymaulichnus* Rouault 1850. Poorly preserved, small specimens of *C. semiplicata* resemble *C. problematica*. However, small specimens of *C. semiplicata* show, at least locally, a four-lobe morphology and marginal marks. Re-study of the type specimens of *Fraena tenella* Linnarsson 1871 by Jensen (1997) revealed that this ichnospecies belongs to *Cruziana* and appears identical to *C. problematica*. Therefore, he regarded *C. problematica* as a junior synonym of *C. tenella*. However, *C. tenella* is a poorly known ichnospecies and the more widely recorded *C. problematica* (*e.g.* Bromley and Asgaard, 1979; Fillion and Pickerill, 1990) is retained to promote nomenclatural stability (Mángano *et al.*, 2002a). *Cruziana problematica* resulted from locomotion (repichnion) or combined activity of search for food and locomotion (pascichnion) of trilobites, or other arthropods (Seilacher, 1953; Bromley and Asgaard, 1979; Pollard, 1985; Jensen, 1997).

Occurrence. This ichnospecies is relatively rare and occurs in the Quebrada de Rupasca.

Cruziana semiplicata Salter, 1853

Material. Approximately 20 specimens studied in the field.

Description. Straight to slightly curved, bilobate traces, occasionally forming part of large circles. Internal lobes commonly are well developed and composed of irregular, moderately coarse, endopodal scratch marks, forming a V-angle 80-105°, but commonly 80°-90°. Scratch marks are locally bifid, but degree of preservation complicates identification of the claw formula. External lobes are commonly incipient or directly absent. Marginal marks are occasionally present. On the left lobe, the marginal mark is separated from the endopodal lobe. Endopodal scratch marks are almost perpendicular in the anterior region, but the angle decreases towards the posterior region. A marginal crest is observed in the median to posterior region. Trace width is 22.2-37.3 mm. Maximum length observed is 108.5 mm. Preserved as positive hyporelief in fine- to very fine-grained sandstone.

Remarks. *Cruziana semiplicata* is the most well known representative of the *semiplicata* group (Seilacher, 1970). This ichnospecies is characterized by lateral exopodal brushings and typically trifid endopodal marks. Distinction between *Cruziana semiplicata* and the morphologically close *C. tortworthi* has been addressed by Mángano and Buatois (2003). The latter exhibits common marginal ridges, occasional exopodal marks, and endopodal scratch marks are clearly grouped in bundles (*cf.* Crimes, 1975; Pickerill and Fillion, 1983; Fillion and Pickerill, 1990). Additionally, this ichnospecies is commonly wider than *C. semiplicata*, even at the same stratigraphic levels (Crimes, 1975). *Cruziana tortworthi* may represent a link between the *semiplicata* and *rugosa* groups (Crimes, 1975). Specimens from lower Paleozoic strata of northwestern Argentina included in *Roualtia lyelli* (Roualt, 1850) by Ramos (1973) and *Cruziana* aff. *C. breadstoni* by Aceñolaza and Durand (1978), Aceñolaza (1978) and Aceñolaza and Fernández (1978) were reassigned to *C. semiplicata* by Mángano and Buatois (2003). Circling behavior in *Cruziana semiplicata* most likely records a search-for-food strategy (pascichnion). In contrast, other occurrences are commonly interpreted as locomotion traces (repichnia) probably produced by olenids (Crimes, 1970, 1975; Orlowski *et al*., 1970; Aceñolaza and Durand, 1978; Fortey and Seilacher, 1997; Zylinska, 1999; Mángano and Buatois, 2003). Fortey and Seilacher (1997) proposed *Maladioidella* as the possible tracemaker of *C. semiplicata* based on the recurrent association of both taxa in the Upper Cambrian of Oman as well as in other Gondwanan localities. However, *Maladioidella* is not present in many other localities where *C. semiplicata* is well documented, such as the Holy Cross Mountains in Poland (Zylinska, 1999) and the Upper Cambrian-Tremadocian strata of northwestern Argentina. As suggested by Zylinska (1999), other olenid trilobites with similar general morphology (presence of conspicuous genal spine, similar outline, etc.) may also be responsible for this widely distributed Gondwanan ichnospecies (see also Mángano and Waisfeld, 2004). Additionally, the stratigraphic change in size ranges suggests that *C. semiplicata* in Upper Cambrian and Tremadocian rocks is not the product of a single trilobite species (Mángano and Buatois, 2003).

Occurrence. This ichnospecies is relatively common in the Quebrada del Abra Blanca, Quebrada de Moya, Angosto del Morro de Chucalezna and Quebrada de Rupasca sections.

Ichnogenus ***Dimorphichnus*** Seilacher, 1955
Dimorphichnus aff. ***D. quadrifidus*** Seilacher, 1990
Figures 3.A-C

Material. Five slabs (PIL 14952, 14953, 14911, 15180 and 15181) containing six specimens and four additional specimens studied in the field.

Description. Asymmetrical trackways with two different types of impressions, long straight or, more rarely, sigmoidal (rakers) and short and comma-shaped (pushers). Both types are arranged in alternating series. In palimpsest surfaces superimposition of series may make difficult to identify individual trackways. The number of claw impressions varies from three to six in rakers (commonly three or four) and three to four in pushers. Raker impression width is 0.4-1.8 mm and length is 8.5-18.6 mm. Pusher impression width is 0.7-1.9 mm and length is 2.0-2.8 mm. Preserved as positive hyporelief in very fine-grained sandstone.

Remarks. Distinction between *Dimorphichnus* and *Monomorphichnus* Crimes 1970 is complicated. The latter includes series of straight to sigmoidal scratch marks, isolated or commonly grouped in sets and repeated laterally (Crimes, 1970). Seilacher (1985, 1990) suggested that the type specimen of *M. bilinearis* Crimes 1970 displays partially superimposed long raking marks and also subtle elongate pushing marks. Accordingly, he proposed that *Monomorphichnus* is a junior synonym of *Dimorphichnus*. This proposal was rejected by Fillion and Pickerill (1990), who stated that pushing marks are not visible in the type material of *M. bilinearis*. Mángano and Buatois (2003) noted that if the type specimen of *M. bilinearis* turns out to be *Dimorphichus*-like, there will be many structures presently included in *Monomorphichnus* (*e.g., M. multilineatus*) that are not easy to relocate in *Dimorphichnus* without expanding its ichnogeneric concept. Therefore, they temporarily retained *Monomorphichnus* until a comprehensive revision is undertaken. The identification of *Dimorphichnus* is complicated by the problem of undertrack fallout (*cf.* Goldring and Seilacher, 1971). This led Seilacher

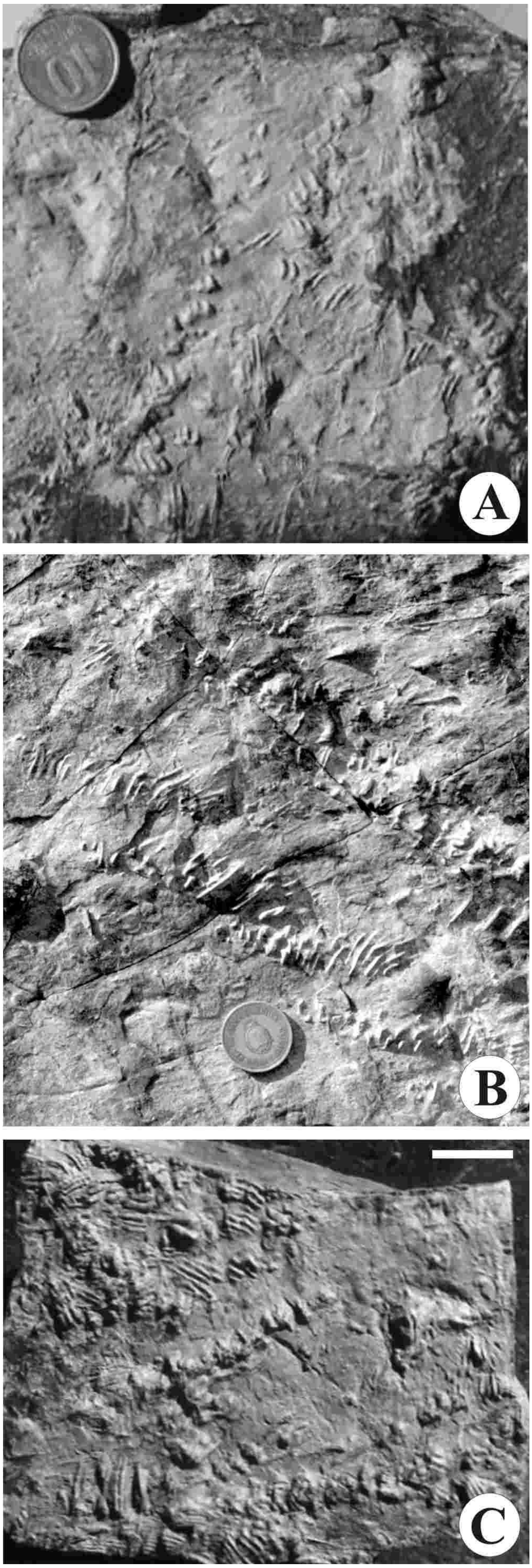

Figure 3. ***Dimorphichnus*** **aff.** ***D. quadrifidus.*** **A,** PIL 14953. Quebrada de Moya. **B,** Field photograph / *fotografía de campo*. Angosto del Morro de Chucalezna. **C,** PIL 15180. Quebrada de Moya. Coin / *moneda*: 1.8 cm. Scale bar / *escala*: 1 cm.

(1985, 1990) to consider specimens lacking pusher impressions as monomorphichnoid preservational variants of *Dimorphichnus*. Variations in the number of claw impressions of specimens from the Alfarcito Member suggest an undertrack preservational bias. Specimens previously included either in *Dimorphichnus* or *Monomorphichnus* by Borrello (1966), Aceñolaza and Manca (1982), Fernández and Lisiak (1984), Mángano *et al*. (1996) and Aceñolaza and Aceñolaza (2002, 2003) have been reassessed by Mángano and Buatois (2003) (see Remarks on *M. multilineatus*). *Dimorphichnus* is regarded either as a grazing structure (pascichnion) (Seilacher, 1955, 1985, 1990; Crimes, 1970; Fillion and Pickerill, 1990) or as resulting from trilobites moved by oscillatory currents (Osgood, 1970). The Seilacherian model of active stroke (rakers) and relaxation (pushers) impressions seems to best explain the morphology.
Occurrence. This ichnospecies occurs sporadically in the Quebrada de Moya, Angosto del Morro de Chucalezna, Quebrada de Casa Colorada and Quebrada de Rupasca sections.

Ichnogenus ***Diplichnites*** Dawson, 1873
Diplichnites isp.

Material. Five specimens in outcrop.

Description. Straight to, more rarely, curved trackways composed of two parallel rows of similar elongate to subcircular tracks. Imprint width is 0.5-1.1 mm. Imprint length is 3.9-5.6 mm. Maximum observed length of trackway is 59.7 mm. Preserved in positive hyporelief or negative epirelief in very fine- to fine-grained sandstone.
Remarks. Dawson (1873) proposed the ichnogenus *Diplichnites* for trackways in Carboniferous deltaic deposits of Canada, which were believed to be produced by crustaceans, annelids or myriapods. However, Seilacher (1955) applied this name to Cambrian shallow-marine trilobite trackways of Pakistan. Subsequently, Osgood (1970) and Briggs *et al*. (1979, 1984) suggested restricting *Diplichnites* to non-trilobite trackways. The present trend is to apply this name regardless of the tracemaker identity and depositional environment, and based strictly on trackway morphology (Mángano *et al*., 2002a). No ichnospecific assessment is provided due to uncertainty in the taxonomy of *Diplichnites*. Previous records of *Diplichnites* in lower Paleozoic rocks of

northwestern Argentina (*e.g.* Aceñolaza and Aceñolaza, 2002, 2003) have been re-evaluated in a recent review by Mángano and Buatois (2003). *Diplichnites* is a locomotion trace (repichnion) recording walking in a direction parallel to the body axis produced by undifferentiated multi-legged arthopods (Buatois *et al.*, 1998). In the Alfarcito Member, however, the common association of *Diplichnites* with *Cruziana* and *Rusophycus* of comparable size suggests most likely the walking activities of a trilobite producer. Arthropod trackways attributed to euthycarcinoids have been recently recorded from the Casa Colorada Member at the Quebrada de Rupasca section (Vaccari *et al.*, 2004).

Occurrence. This ichnospecies is relatively rare and occurs in the Quebrada del Abra Blanca, Quebrada de Moya and Angosto del Morro de Chucalezna sections.

Ichnogenus ***Gyrolithes*** de Saporta, 1884
?***Gyrolithes*** isp.
Figure 4.A

Material. One slab (PIL 14177) containing one specimen.

Description. Very shallow, corkscrew-shaped spiral, consisting of a single whorl and oriented perpendicular to bedding. Burrow width is 2.6-3.4 mm. Spiral diameter is 9.6-9.9 mm. Preserved in positive hyporelief in very fine-grained sandstone.

Remarks. *Gyrolithes* is very common in Cambrian strata (*e.g.*, Fritz, 1980; Fedonkin, 1981, 1983; Liñán, 1984; Crimes and Anderson, 1985; Hein *et al.*, 1991; Jensen, 1997; Jensen and Grant, 1998; Stanley and Feldmann, 1998). The specimen from the Alfarcito Member somewhat resembles the typical Cambrian ichnospecies *G. polonicus* Fedonkin 1980, which is characterized by being small and very shallow, having a few whorls, and the absence of terminal expansion, scratch marks and carapace impressions (Jensen, 1997). Partial preservation and lack of additional specimens prevent a more definite assessment. *Gyrolithes* is interpreted as a feeding trace (fodinichnia) produced by different kinds of crustaceans and polychaetes. Cambrian representatives are commonly regarded as produced by polychaetes (*e.g.* Stanley and Feldmann, 1998).

Occurrence. This ichnotaxon is very rare in the Angosto del Morro de Chucalezna section.

Ichnogenus ***Gyrophyllites*** Glocker, 1841
Gyrophyllites isp.
Figures 4.C-F

Material. One slab (PIL 14912) containing one specimen and approximately 20 specimens studied in the field.

Description. Radial structures having unbranched leaf-like, oval, petaloid lobes radiating from a vertical shaft. Five lobes are invariably present. Width of radial structure is 53.2-65.5 mm. Width of vertical shaft is 2.5-6.7 mm. Preserved as negative epirelief at the top of very fine- to fine-grained sandstone.

Remarks. Similar structures recorded in outcrops of the Santa Rosita Formation in Quebrada de Huamahuaca have been referred to as *Brooksella* and interpreted as medusoid body fossils by Moya *et al.* (1986). However, Brooksella is now regarded as a trace fossil (Rindsberg, 2000). *Gyrophyllites* is distinguished from other radial trace fossils, most notably from *Glockerichnus* Pickerill 1982, by its unbranched leaf-like lobes radiating from a vertical shaft (*cf.* Uchman, 1998). The presence of only a few lobes, invariably five, and the oval, petaloid morphology distinguish radial structures of the Alfarcito Member from other formally defined ichnospecies of *Gyrophyllites*. Furthermore, whereas *Gyrophyllites* is usually preserved as positive hyporelief, the specimens in the Alfarcito Member are preserved as negative epirelief. *Gyrophillites* is interpreted as a feeding trace (fodinichnion) produced by worm-like organisms.

Occurrence. This ichnospecies is relatively rare and occurs in the Quebrada de Moya section.

Ichnogenus ***Monomorphichnus*** Crimes, 1970
Monomorphichnus multilineatus Alpert, 1976
Figure 4.B

Material. Four slabs (PIL 14905, 15182, 15196 and 15197) containing four specimens and approximately ten additional specimens studied in the field.

Description. Ridges are grouped into sets of three to six subparallel, straight to slightly curved, subequal scratch marks. Scratch marks are either flat or deep and highly convex. Sets are commonly parallel or slightly oblique between them, although some relatively deep specimens show sets of scratch marks that tend to converge to a point. Ridge length is 11.3-33.8 mm and width is 0.5-2.1 mm. Maximum scratch mark depth is 2.2. mm. Preserved as positive hyporeliefs in fine- to very fine-grained sandstone.

Remarks. *Monomorphichnus* is a controversial *ichnogenus* (see Remarks on *Dimorphichnus* cf. *D. quadrifidus*). As discussed above, Mángano and Buatois (2003) noted that if *Monomorphichnus*-type material turns out to be *Dimorphichus*-like, there will be many structures presently included in *Monomorphichnus* (*e.g., M. multilineatus*) that are not easy to relocate in *Dimorphichnus* or in other available ichnogenera, requiring the erection of a substitute ichnotaxon. Accordingly, *Monomorphichnus* is retained temporarily to embrace sets of monomorphic scratch marks that exhibit distinctive morphology and cannot be placed in other arthropod-produced ichnogenera. Mángano

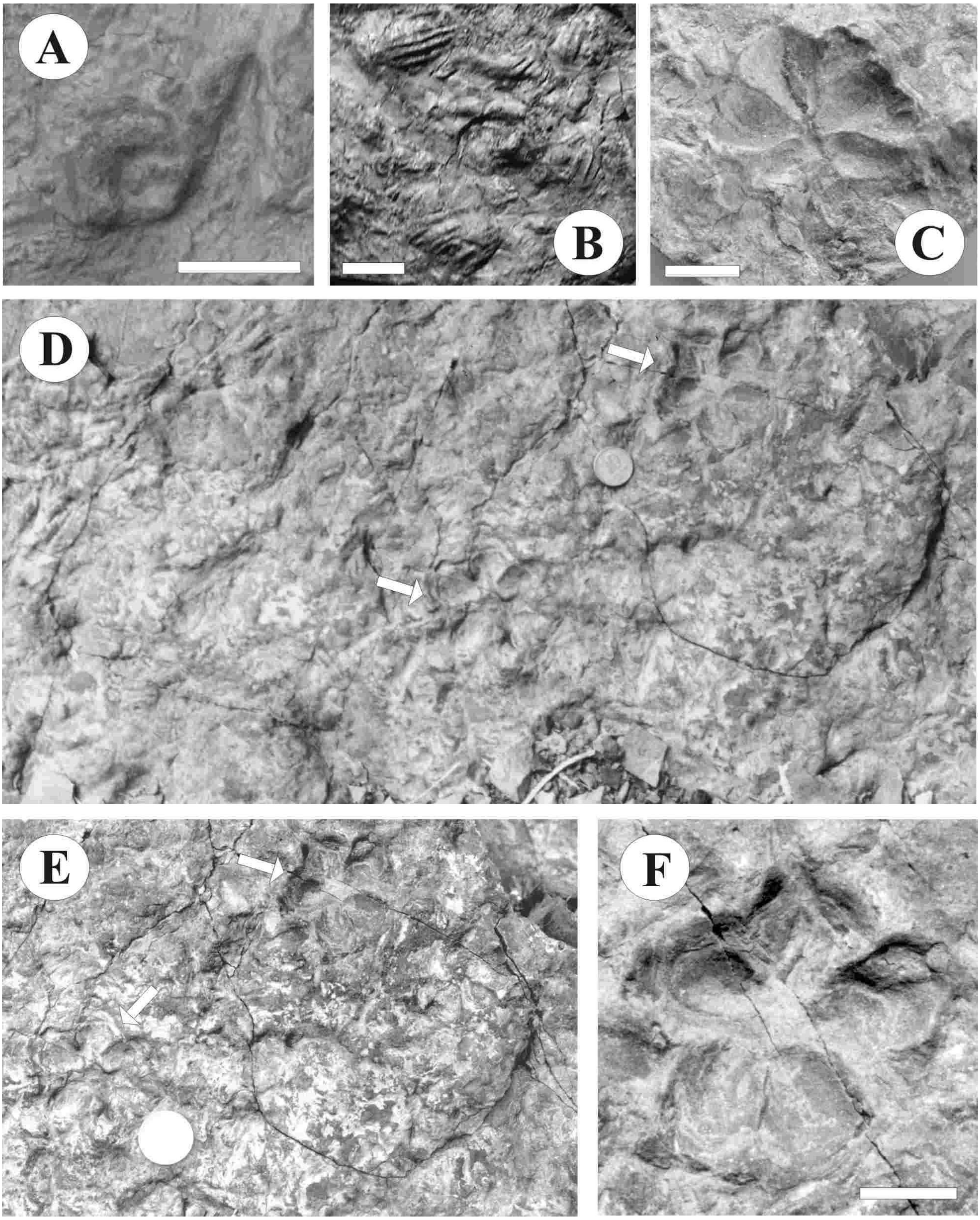

Figure 4. Trace fossils of the Alfarcito Member / *Trazas fósiles del Miembro Alfarcito.* **A, ?*Gyrolithes*** isp. PIL 14177. Angosto del Morro de Chucalezna. **B, *Monomorphichnus multilineatus.*** PIL 15182. Angosto del Morro de Chucalezna. **C, *Gyrophyllites*** isp. PIL 14912. Quebrada de Moya. **D, *Gyrophyllites*** isp. Bioturbated layer at the top of a hummocky cross-stratified sandstone. Arrows indicate two well preserved specimens, but the whole surface is covered by ***Gyropyllites*** isp. / *Tope bioturbado de una capa de estratificación entrecruzada hummocky. Las flechas indican dos ejemplares bien preservados, pero la totalidad de la superficie está cubierta por Gyropyllites isp.* Quebrada de Moya. Field photo. **E,** Close-up of the same layer showing distinct ***Gyrophyllites*** isp. specimens (arrows). Field photo / *Vista de detalle de* **Gyrophyllites** *isp. Quebrada de Moya. Fotografía de campo.* **F,** Close-up of ***Gyrophyllites*** isp. Quebrada de Moya. Field photograph / *Vista de detalle de* **Gyrophyllites** *isp. Fotografía de campo.* Scale bar / *escala*: 1 cm. Coin / *moneda*: 1.8 cm.

and Buatois (2003) reviewed specimens assigned to *Monomorphichnus* in the lower Paleozoic of northwest Argentina. These authors noted that *Monomorphichnus bilinearis* described by Mángano *et al*. (1996, fig. 12.B) is most likely a fragment of a shallow rusophycid structure. Also, the specimen figured as *Monomorphichnus* isp. by Aceñolaza and Manca (1982, fig. 2.3) is actually a pavement of superimposed, partially preserved shallow *Cruziana*. Mángano and Buatois (2003) found that *M. multilineatus* is equivalent to the specimen figured as *Monomorphichnus*-type Aceñolaza and Aceñolaza (2003). Fillion and Pickerill (1990) interpreted *M. multilineatus* as the result of powerful strokes of multidigitated appendages, presumably the exites. Although the number of scratches forming each set was not considered in the original diagnosis of *M. multilineatus* by Alpert (1976), the material from the Alfarcito Member clearly has a lower number of scratch marks than the type specimens. Additionally, the central mark is not always deeper than the outer marks, as occurs in *M. multilineatus*.

Occurrence. This ichnotaxon occurs sporadically and has been recorded in the Quebrada de Rupasca, Angosto del Morro de Chucalezna and Quebrada de Moya sections.

Ichnogenus ***Palaeophycus*** Hall, 1847
Palaeophycus striatus Hall, 1852
Figure 5.A

Material. One slab (PIL 14913) containing one specimen.

Description. Straight, horizontal, unbranched, thinly-lined, cylindrical to subcylindrical burrows having thin, relatively continuous, parallel, longitudinal striae. Burrow diameter is 2.4-3.5 mm. Maximum length observed is 38.7 mm. Striae are 0.1-0.3 mm wide and 3.5-8.9 mm long. Burrow-fill is similar to the host rock and structureless. Burrow collapse is absent. Although straight, the specimen displays a sharp change of orientation. Preserved as full relief in very fine-grained sandstone.

Remarks. The taxonomy of *Palaeophycus* has been addressed by Pemberton and Frey (1982) and by Keighley and Pickerill (1995). *Palaeophycus* is distinguished from *Planolites* by the presence of wall linings and by a burrow-fill identical to the host rock (Pemberton and Frey, 1982), and from *Macaronichnus* by the active burrow-fill of the latter (Clifton and Thompson, 1978; Curran, 1985). *Palaeophycus striatus* is distinguished from the other ichnospecies of *Palaeophycus* by its parallel and continuous striae (Pemberton and Frey, 1982). *Palaeophycus* is interpreted as dwelling structures (domichnia) of suspension feeders or predators, such as polychaetes (Osgood, 1970; Pemberton and Frey, 1982).

Occurrence. This ichnospecies is rare and has been found only in the Angosto del Morro de Chucalezna section.

Palaeophycus tubularis Hall, 1847
Figures 3.B, 6.B and 7.A

Material. Seven slabs (PIL 14596, 14598, 14906, 14913, 14915, 15158 and MPEF-IC-394) containing approximately 50 specimens and approximately 200 specimens studied in the field.

Description. Straight to slightly curved, horizontal, unbranched, thinly-lined, smooth-walled cylindrical to subcylindrical burrows. Burrow diameter is 2.0-9.5 mm. Maximum length is 54.0 mm. Burrow-fill is similar to the host rock and massive. Burrow collapse is absent. Preserved as full relief in fine- to very fine-grained sandstone.

Remarks. *Palaeophycus tubularis* is distinguished from the other ichnospecies of *Palaeophycus* by its thin wall and the absence of ornamentation. Mángano and Buatois (2003) noted that most specimens from lower Paleozoic strata of northwestern Argentina referred to as *Planolites* isp. (*e.g.* Aceñolaza and Fernández, 1978; Aceñolaza, 1978; Fernández and Lisiak, 1984) exhibit a thin lining and infill similar to the host rock. Accordingly, they have been reassigned to *Palaeophycus tubularis*. Horizontal, curved structures recorded as *Palaeophycus* cf. *P. tubularis* by Aceñolaza and Nieva (2003, fig. 6.F,H) are most likely syneresis cracks. The ethologic interpretation of *P. tubularis* is similar to that of *P. striatus*.

Occurrence. This ichnospecies is abundant in the Quebrada del Abra Blanca, Quebrada de Moya, Angosto del Morro de Chucalezna, Quebrada de Casa Colorada and Quebrada de Rupasca sections.

Ichnogenus ***Phycodes*** Richter, 1850
?***Phycodes*** isp.
Figure 6.C

Material. One slab (PIL 14601) containing one specimen and an additional specimen studied in the field.

Description. Horizontal branching burrow system, consisting of a few tubes (3 to 4) apparently branching from nearly the same point in a proximal position. Burrow diameter is 3.9-5.2 mm. Maximum burrow system length observed is 35.6 mm. Preserved as full relief in very fine-grained sandstone.

Remarks. Although these structures seem to be morphologically close to *Phycodes*, partial preservation prevents a more definite assessment. The ichnotaxonomy of *Phycodes* has been recently addressed by Seilacher (2000). *Phycodes* is interpreted as a feeding trace (fodinichnion) most likely produced by annelids (Seilacher, 1955; Osgood, 1970).

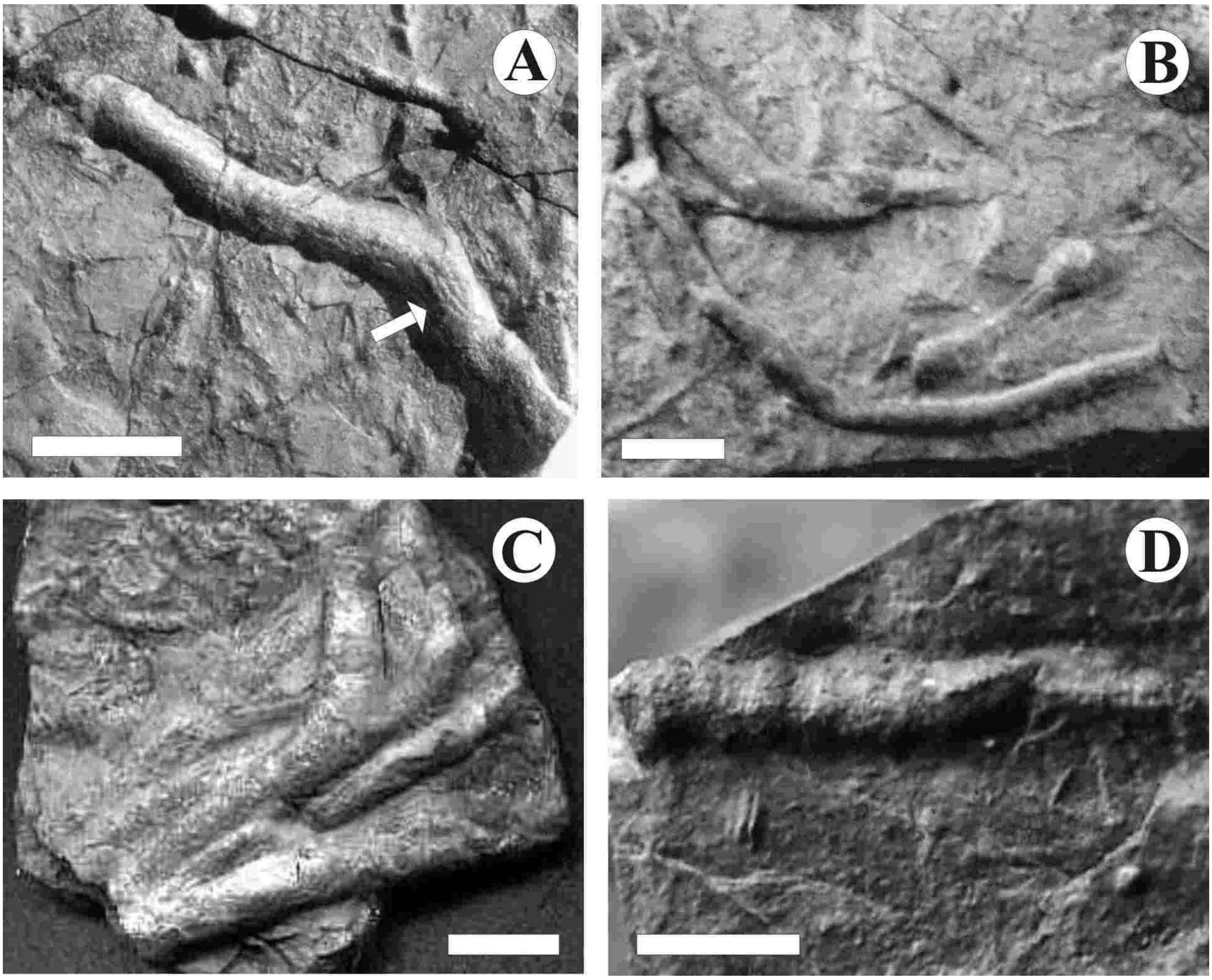

Figure 5. Trace fossils of the Alfarcito Member / *Trazas fósiles del Miembro Alfarcito*. **A, *Palaeophycus striatus*.** Arrow indicates striae / *la flecha indica estrías*. PIL 14913. Angosto del Morro de Chucalezna. **B, *Palaeophycus tubularis*.** PIL 14915. Angosto del Morro de Chucalezna. **C, ?*Phycodes*** isp. PIL 14601. Angosto del Morro de Chucalezna. **D, *Planolites reinecki*.** PIL 15185. Quebrada de Moya. Scale bar / *escala*: 1 cm.

Occurrence. Although relatively common in other Cambrian-Ordovician units of Cordillera Oriental, in the Alfarcito Member this ichnotaxon has only been found in the Angosto del Morro de Chucalezna section.

Ichnogenus ***Planolites*** Nicholson, 1873
Planolites reinecki Ksiazkiewicz, 1977
Figure 6.D

Material. One slab (PIL 15185) containing one specimen.

Description. Horizontal trace fossil having both subtle, regularly spaced, longitudinal striae and transverse annulae. Wall is absent. Length is 34.8 mm and width is 3.6-4.5 mm. Preserved as full relief in very fine-grained sandstone.

Remarks. A similar specimen (PIL 11956) from Sierra de Cajas, assigned to *Planolites* isp. by Aceñolaza and Fernández (1978), displays distinct regular annulae and local striae and was referred to *Planolites reinecki* by Mángano and Buatois (2003). Furthermore, specimens assigned to *Plagiogmus* by Aceñolaza and Fernández (1978) and Aceñolaza (1978) were compared with *Planolites reinecki* by Mángano and Buatois (2003). This ichnospecies was also documented from the Upper Tremadocian Rupasca Member in the Angosto del Ferrocarril (Chucalezna) section (Mángano and Buatois, 2003). *Planolites reinecki* is distinguished from other *Planolites* ichnospecies by having both tranverse annulae and longitudinal striae (Stanley and Pickerill, 1994; Uchman, 1998). *Planolites constriannulatus* Stanley and Pickerill 1994 was regarded as a junior synonym of *P. reinecki* by Uchman (1998). *Planolites reinecki* is interpreted as a feeding structure (fodinichnion) of deposit-feeder annelids, moving by peristaltic contractions and actively filling the structure. (Stanley and Pickerill, 1994).

Occurrence. This ichnotaxon has been found only in the Quebrada de Moya section.

Ichnogenus **Rusophycus** Hall, 1852
Rusophycus carbonarius Dawson, 1864

Material. Two slabs (PIL 14906 and 15186) containing two specimens and approximately 10 specimens studied in the field.

Description. Small, relatively shallow, bilobate structures; the lobes are commonly parallel and juxtaposed to resemble a coffee bean or slightly oblique to gape at the anterior end, leaving a triangular central zone. Central furrow is typically well defined. Some lobes are smooth while others are covered by very fine scratch marks. Scratch marks are perpendicular to slightly retroverse towards the posterior zone. No marginal marks or impressions in the axial region are present. Trace width is 2.2-6.6 mm and length is 3.2-7.4 mm. Preserved as positive hyporeliefs in fine- to very fine-grained sandstone.

Remarks. Similar small, juxtaposed, coffee bean-like cubichnia have been traditionally assigned to *Rusophycus didymus* (Salter, 1853). However, *R. didymus* is a problematic ichnotaxon. The holotype comes from strata regarded as Precambrian in age (Crimes *et al*., 1977) and some authors considered that the specimen is probably of inorganic origin (Pickerill, in Mángano *et al*., 1996). Mángano and Buatois (2003) included in *R. carbonarius* specimens described by Ramos (1973) as *R. bilobatus*. Some of the specimens of the Alfarcito Member are associated with *R. moyensis*. Although they may be considered as ontogenetic variations of *R. moyensis*, they are placed in *R. carbonarius* because they lack the diagnostic features of *R. moyensis*, such as coxal marks, cephalic marks and marginal spine marks. *Rusophycus carbonarius* is interpreted as resting traces (cubichnia) probably produced by small trilobites.

Occurrence. This ichnospecies is common in the Quebrada de Moya, Angosto del Morro de Chucalezna and Quebrada de Rupasca sections.

Rusophycus moyensis Mángano, Buatois
and Muñiz Guinea, 2002b
Figures 6.A-F

Material. 32 slabs (PIL 14879 to 14906, 14952, 14960, 15180 and MPEF-IC-396) containing approximately 180 specimens and more than three hundred additional specimens studied in the field. Possible epichnial examples are in PIL 15189 and 15190. A transition with a fragmentary specimen of *Cruziana* is present in PIL 15190.

Description. Elongate, coffee-bean shaped bilobate structures with a central depressed area that may be either smooth or display up to eight subquadrate coxal impressions. Lobes can converge at the anterior part defining a close central depression or they may gape anteriorly. Lobes are typically covered by transverse scratch marks at the anterior part shifting to more retroverse, and commonly thinner scratch marks at the posterior part. Genal and pleural spine impressions are occasionally present. Total length is 2.9-42.6 mm (about 70% of specimens measured are within the 12.0-23.0 mm range). Trace width is 1.9-23.1 mm. Maximum depth is 4.5 mm, but commonly less than 2.0 mm. Clusters of nested individuals are relatively common. Preserved as positive hyporeliefs and possibly as negative epireliefs in fine- to very fine-grained sandstone.

Remarks. *Rusophycus moyensis* was erected by Mángano *et al*. (2002b). This ichnospecies is close morphologically to *R. polonicus*. The author of *Rusophycus polonicus* has been matter of disagreement in the ichnological literature (see for contrasting opinions Gámez-Vintaned, 1995 and Stanley and Pickerill, 1998). This disagreement is based on the confusing history of the erection of the ichnotaxon. Although Orlowski *et al*. (1970) did not provided a formal diagnosis and explicitly stated that the new form was not designated formally at that moment, they figured (Pl. 3b-d) and mentioned "*Rusophycus* new species" recognizing the identity of the new ichnotaxon. In the same volume Seilacher (1970, p. 473) formally defined *Cruziana polonica* for rusophycid forms, including in the synonym list specimens published by Radwanski and Roniewicz (1963). The problem is further complicated by the fact that although the name *R. polonicus* has been used in recent decades, the taxon may actually be a *nomen nudum* (as outlined by Gamez-Vintaned, 1995) and in this sense may be a non-available name. Incidentally, it should be noted here that the correct name for the ichnospecies is *Rusophycus polonicus* and not *R. polonica* as indicated by Aceñolaza (2003). The suffix icus is the correct termination for *Rusophycus* ichnospecies, while ica is the appropriate for ichnospecies of *Cruziana*.

In fact, poorly preserved specimens of relatively large *R. moyensis* can be confused with poorly preserved *R. polonicus*. However, these two ichnotaxa can be distinguished when a significant collection is taken into consideration. Based on a small collection (PIL 14988 and 14989), Aceñolaza (2003, p. 579) advised that the name *R. moyensis* be abandoned with the argument that "the elements presented to justify the ichnotaxonomic independence of *R. moyensis* ....are all elements also represented in some degree in *R. polonica* (sic)". However, a more representative

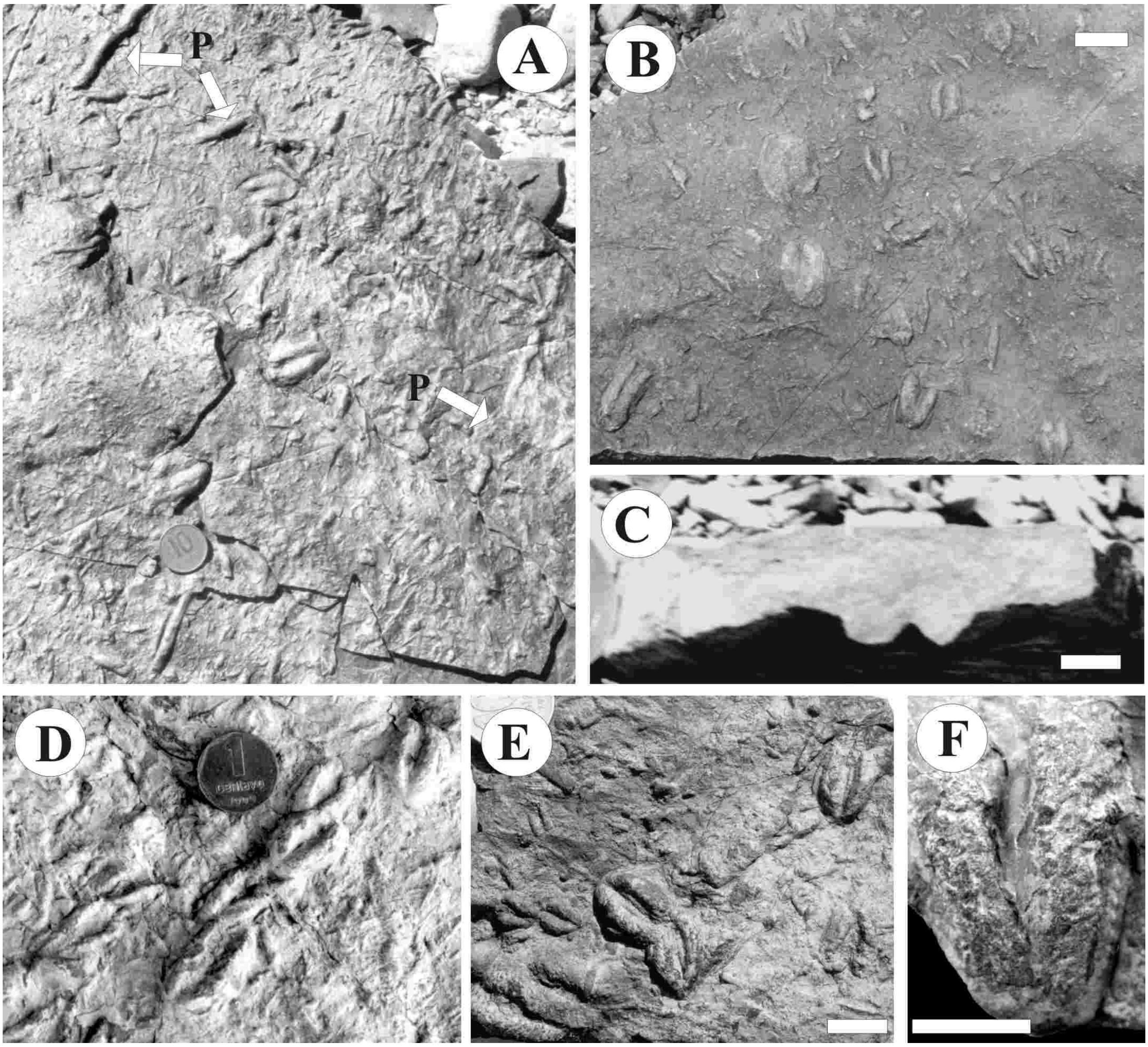

Figure 6. Trace fossils of the Alfarcito Member / *Trazas fósiles del Miembro Alfarcito.* **A, *Palaeophycus tubularis*** (P) and ***Rusophycus moyensis***. Field photograph / *fotografía de campo*. Quebrada de Moya. Coin / *moneda*: 1.8 cm. **B, *Rusophycus moyensis***. Field photograph / *fotografía de campo*. Quebrada de Moya. Scale bar /*escala*: 1 cm. **C, *Rusophycus moyensis*** in cross section at the base of a thin-bedded tempestite. Field photograph / *en sección vertical en la base de una tempestita finamente estratificada. Fotografía de campo*. Angosto del Morro de Chucalezna. Scale bar / *escala*: 1 cm. **D, *Rusophycus moyensis*.** Poorly preserved aligned specimens. Field photograph / *ejemplares alineados pobremente preservados. Fotografía de campo*. Quebrada de Moya. Coin / *moneda*: 1.5 cm. **E, *Rusophycus moyensis*.** Cluster of specimens of different sizes. PIL 14884 / *Agrupamiento de especímenes de diferentes tamaños. PIL 14884.* Quebrada de Moya. Scale bar / *escala*: 1 cm. **F, *Rusophycus moyensis*.** Delicate pleural spine impressions are present on the right. Angosto del Morro de Chucalezna / I*mpresiones de delicadas espinas pleurales presentes sobre la derecha.* Scale bar / *escala*: 1 cm.

sample of *R. moyensis* shows that compared with *R. moyensis*, *R. polonicus* commonly exhibits a more open and wider coxal area. Additionally, *R. polonicus* displays an oval outline, whereas *R. moyensis* exhibits a more pointed posterior end and is commonly more deeply excavated than the anterior part. *Rusophycus moyensis* also differs from *R. polonicus* in scratch mark ornamentation on lobes, morphology and frequency of pleural and genal spine impressions (only observed in about 10% of over 100 specimens studied), consistently smaller size range and mode of occurrence. All these morphologic features suggest differences in appendage morphology and resting attitude, most likely ultimately related to a different trilobite producer. An expanded notion of *R. polonicus* (*i.e.* presence of coxal marks, and marginal spines) as advocated by Aceñolaza (2003), would mean that many other *Rusophycus* ichnospecies (*e.g. Rusophycus carleyi*) would be assigned to *R. polonicus*, thus, decreasing the value of this ichnotaxon.

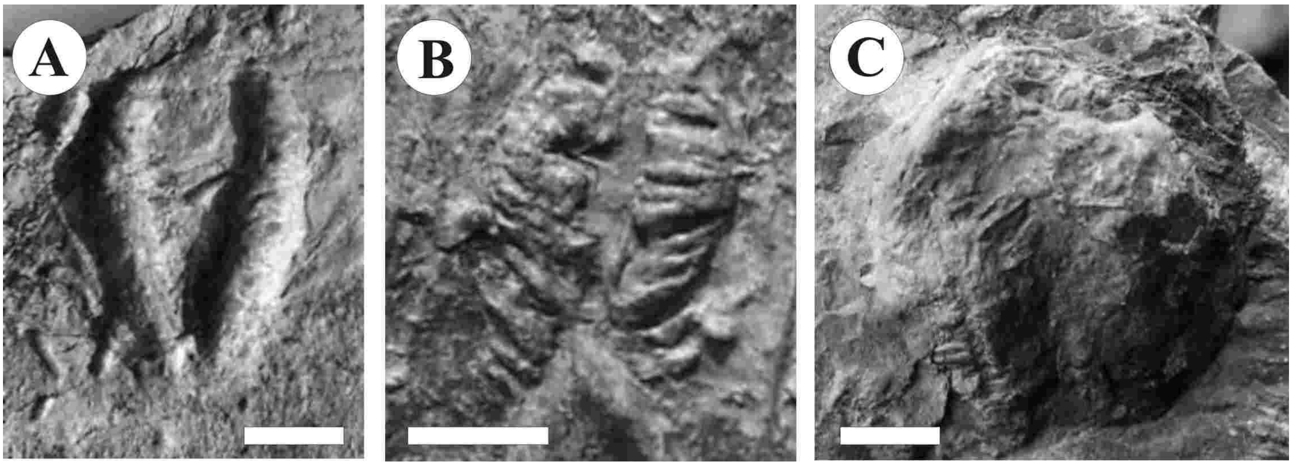

Figure 7. ***Rusophycus*** issp. of the Alfarcito Member. **A,** ***Rusophycus*** isp. ***A.*** PIL 15188. Angosto del Morro de Chucalezna. **B,** ***Rusophycus*** isp. B. PIL 15192. Angosto del Morro de Chucalezna. **C,** ***Rusophycus*** isp. C. PIL 15185. Quebrada de Moya. Scale bar / *Escala:* 1 cm.

Rusophycus moyensis may be transitional with short cruzianids, displaying conspicuous transversal endopodal scratch marks and a broad axial depression. As discussed by Mángano and Buatois (2003), specimens referred to as *Rusophycus* isp. by Aceñolaza and Aceñolaza (2003) most likely represent poorly preserved *R. moyensis*. The same holds true for specimens figured as *Rusophycus* isp. A by Aceñolaza (2003); the specimen figured as *Rusophycus* isp. B is too poorly illustrated to be evaluated. These stratigraphic levels in the Quebrada de Moya contain abundant *Rusophycus moyensis*. Specimens described as *R. polonica* (Seilacher 1970) by Aceñolaza (2003) seem to be a poorly preserved specimen of *R. moyensis*. In addition, the specimen described as cf. *Phycodes* isp. by Aceñolaza and Durand (1978), and reiterated as *Phycoides* (*lapsus calami*) by Aceñolaza (1978) and as *Phycodes* isp. by Aceñolaza and Aceñolaza (2003) is a compound specimen of a rusophycid structure and successive linear impressions of pleural spines produced by an inclined body when it attempted to exit the resting structure. This rusophycid structure was compared to *R. moyensis* by Mángano and Buatois (2003). Mángano *et al*. (2002b) and Mángano and Waisfeld (2004) noted that the latero-ventral morphology of *R. moyensis* suggests it was produced by olenids belonging to *Angelina* or *Leptoplastides*. This is also supported by the finding of the olenid *Angelina* on a slab bearing possible *R. moyensis* (Aceñolaza, 2003).

Occurrence. This ichnospecies is abundant in the Angosto del Moreno, Quebrada de Moya, Angosto del Morro de Chucalezna and Quebrada de Rupasca sections.

Rusophycus isp. A
Figure 7.A

Material. One slab (PIL 15188) containing one specimen.

Description. Relatively small, shallow bilobate structure, with convex lobes that gape at the anterior end, leaving a wide central zone that is more than twice the width of the lobes. Lobes are mostly smooth, but locally covered by indistinct, oblique scratch marks. Maximum width is 22.7 mm and length is 34.0 mm. Preserved as positive hyporelief in fine- to very fine-grained sandstone.

Remarks. Lack of diagnostic characteristics and additional specimens preclude a more detailed analysis and ichnospecific assignment.

Occurrence. This ichnospecies was found in the Angosto del Morro de Chucalezna section.

Rusophycus isp. B
Figure 7.B

Material. Four slabs (PIL 15192 to 15195) containing four specimens.

Description. Relatively small, shallow bilobate structure, with lobes that are covered by transverse, fine scratch marks. General outline is subcircular to pointed towards the posterior part. No claw formula is detected. Central furrow is wide. Width is 12.7-23.4 mm and length is 17.0-33.8 mm. Preserved as positive hyporelief in fine- to very fine-grained sandstone.

Remarks. *Rusophycus* isp. *B* is occasionally associated with fragmentary specimens of *Cruziana* and *R. moyensis*. It is distinguished from the latter by its general outline, transverse scratch marks and absence of marginal and cephalic impressions. Although different from *R. moyensis*, the small number of specimens and lack of diagnostic characteristics preclude ichnospecific assignment.

Occurrence. This ichnospecies is rare and occurs in the Angosto del Morro de Chucalezna and Quebrada de Moya sections.

Rusophycus isp. C
Figure 7.C

Material. One slab (PIL 15185) containing one specimen.

Description. Poorly preserved, large, moderately deep bilobate structure, with lobes that are covered by robust, transverse scratch marks. General outline is subcircular. No claw formula is detected. Central furrow is wide and shallow. Width is 34.8 mm and length is 39.3 mm. Preserved as positive hyporeliefs in very fine-grained sandstone.
Remarks. Although rare and poorly preserved, this structure clearly differs from other rusophycid in the Alfarcito Member and records the activities of a relatively large arthropod. Absence of additional, better preserved specimens precludes an ichnospecific assignment.
Occurrence. This ichnotaxon has only been found in the Quebrada de Moya section.

Ichnogenus **Skolithos** Haldeman, 1840
Skolithos linearis Haldeman, 1840

Material. Over 80 specimens studied in the field.

Description. Straight, vertical, unbranched, cylindrical, endichnial burrows, typically 2.4-9.4 mm in width. Maximum length observed is 45.5 mm. Burrow walls are distinct and typically lined. Burrow-fill is structureless, commonly similar to the host rock. Preserved as full relief in fine- to very fine-grained sandstone.
Remarks. *Skolithos* consists of simple, unbranched, vertical burrows, and it has been historically distinguished from *Monocraterion* Torell 1870, by the funnel-shaped upper portion of the latter. However, Schlirf and Uchman (2005) noted that the lectotype of *Monocraterion tentaculatum* Torell, 1870 differs from *Skolithos* in showing clearly radiating tubular structures (see also Jensen, 1997), suggesting that *Monocraterion* should be only used for the type material. *Skolithos linearis* is characterized by being relatively small, typically straight and vertical (Alpert, 1974; Fillion and Pickerill, 1990). Although large specimens of *Skolithos* (cf. *Skolithos magnus* Howell 1944, in Aceñolaza and Aceñolaza, 2003) are common in lower Paleozoic rocks of northwestern Argentina, these straight burrows show a distinct lining and exhibit similar lengths to those of *S. linearis*. As previously noted, specimens commonly included in the local literature as *Bergaueria* are in many cases sections of *Skolithos* (*e.g.* Aceñolaza and Fernández, 1978; Aceñolaza, 1978; Fernández and Lisiak, 1984). *Skolithos* is interpreted as a dwelling structure (domichnion) produced by a wide variety of animals, including polychaetes and phoronids (Alpert, 1974).
Occurrence. This ichnospecies is abundant in the Quebrada del Abra Blanca, Quebrada de Moya, Angosto del Morro de Chucalezna, Quebrada de Casa Colorada and Quebrada de Rupasca sections.

Sedimentary facies and trace fossil distribution

Four main sedimentary facies have been recognized in the lower fine-grained interval of the Alfarcito Member, environmentally ranging from the lower offshore to the lower/middle shoreface (Buatois and Mángano, 2003). These facies are stacked forming regional, coarsening-upward parasequences that record short-term progradational episodes. The environmental zonation model of MacEachern *et al.* (1999) is adopted.

The *Lower Offshore facies* consists of laterally extensive, greenish gray, massive or thinly parallel-laminated mudstone units. Sharp-based, tabular, thin (0.5-2.0 cm), gray very fine-grained silty sandstone beds, with gradational tops, are interbedded occasionally. These interbedded sandstone layers contain combined-flow ripple cross-lamination and symmetric to near-symmetric ripple tops. Exceptionally, up to 12 cm-thick, very fine-grained sandstone beds, having a lower parallel-laminated interval, are present. Very thin layers (0.1-0.5 cm) of normally graded, coarse-grained siltstone are present locally. Sandstone/mudstone ratio is low (up to 1:10). Trilobites are locally abundant within the mudstone intervals. Bioturbation is very rare, commonly restricted to a few, simple burrows (*Palaeophycus tubularis*) on the base of the sandstone beds. These deposits blanket or interfinger with estuarine deposits. Depositional processes in the lower offshore mostly involved suspension fall-out in an overall low-energy setting. However, background deposition was punctuated by rare storm events, recorded by the interbedded sandstone and graded siltstone beds, which are interpreted as distal tempestites. Local presence of sandstone beds with oscillatory structures indicates deposition immediately above storm-wave base. Normally graded siltstone beds are commonly regarded as an extremely distal end member of storm sedimentation, recording currents capable of transporting sediment beyond the zone where oscillatory currents are dominant (*e.g.* Aigner, 1985; Brenchley *et al.*, 1993).

The *Upper Offshore facies* consists of parallel-laminated, yellowish green and gray mudstone interbedded with thin (1.0-5.0 cm) light gray, laterally extensive, erosive-based, very fine-grained silty sandstone beds with parallel lamination, combined-flow ripple cross-lamination and symmetrical to near-symmetrical ripples with rounded tops. Compared with the lower offshore and offshore transition facies, upper offshore deposits are the most variable. Micro-hummocky cross-stratification and planar lamination are present in some of the thin sandstone beds. Occasionally, laterally extensive, erosive-based, up to 26 cm-thick sandstone beds are present. These thicker sandstone units are internally more variable; most of them are entirely formed by combined-flow ripple cross-lamination and, more rarely, current ripple cross-lamination. In some cases, however, these beds display a lower massive interval and an upper parallel-laminated zone capped by symmetrical ripples. Gutter casts are locally present. Small load casts and tool marks are present on the bases of sandstone beds. Sandstone/mudstone ratio is low to rarely moderate (1:10 to 1:2). Upper offshore deposits display the most diverse trace fossil assemblages of the Alfarcito Member. Trilobite trace fossils (*Rusophycus moyensis*, *R. carbonarius*, *Rusophycus* isp., *Cruziana semiplicata*, *C. problematica*, *Cruziana* isp., *Dimorphichnus* aff. *D. quadrifidus*, *Diplichnites* isp., *Monomorphichnus multilineatus*) and other forms (*Palaeophycus tubularis*, *P. striatus*, *Bergaueria* aff. *B. hemispherica*, *Arthrophycus minimus*, ?*Gyrolithes* isp., ?*Phycodes* isp.) are preserved at the base of sandstone layers. *Archaeonassa fossulata* and *Diplichnites* isp. are present at the top of some sandstone beds. *Skolithos linearis* is present as endichnia in sandstone beds. This facies is commonly sandwiched between the lower offshore and the offshore transition facies. As in the case of the lower offshore facies, upper offshore deposits mostly record sediment fall-out in a low-energy setting. However, the increased proportion of thin, interbedded, erosive-based sandstone layers and gutter casts records alternation of more frequent and higher energy event deposition. The presence of micro-hummocky cross-stratification, combined-flow ripple cross-lamination, symmetrical to near-symmetrical ripples and gutter casts indicates deposition from storm flows and the sandstone beds are, therefore, interpreted as distal tempestites. The presence of ripples with rounded profiles suggests the action of relatively low oscillatory flow velocities that yield small vortices (Yokokawa *et al.*, 1995). Upper offshore deposits are more variable mostly due to the greater influence of storm activity (Pemberton *et al.*, 2001).

The *Offshore Transition facies* consists of regularly interbedded, parallel-laminated mudstone and thin to thick (0.5-60 cm, but commonly 12-20 cm) light gray, erosive-based, fine- to very fine-grained sandstone with hummocky cross-stratification, combined-flow ripple cross-lamination and/or symmetrical to near-symmetrical ripples at the top. Mudstone units are 3-20 cm thick, but commonly 8-15 cm thick. Sandstone beds are laterally extensive, but display thickness variation. Hummocky cross-stratification tends to be dominant in the thickest sandstone beds, whereas combined-flow ripple cross-lamination is dominant in the thinner beds. Amalgamation of hummocky beds is uncommon, but occasionally observed. Shell lags up to 10 cm-thick and intraclast layers are present at the base of hummocky beds. Hummocky laminae usually are mantled by mica; parting lineation is absent. Some hummocky laminae thicken over the crests of antiforms. Unidirectional climbing-ripple cross-lamination overlying a hummocky zone is present in a few beds. Combined-flow ripples with rounded profiles and interference ripples are commonly present at the top of hummocky beds. Convolute lamination and wrinkle marks, though present, are relatively rare. Gutter casts, both discrete and connected to the bed, are common and display a wide variety of morphologies. Sandstone/mudstone ratio is 1:1 to 1:2. Trilobite trace fossils (*e.g.*, *Rusophycus moyensis*, *Cruziana semiplicata*) are preserved at the base of sandstone layers, as well as other ichnotaxa (*e.g.*, *Palaeophycus tubularis*, *Bergaueria* aff. *B. hemispherica*). *Skolithos linearis* occurs as endichnia in sandstone beds. Simple horizontal burrows (*P. tubularis*) and radial trace fossils (*Gyrophyllites* isp.) occur locally at the top of sandstone beds. These deposits record the alternation of quiet-water sediment fall-out and combined and pure oscillatory flows. The presence of hummocky cross-stratification clearly points to a storm origin for the sandstone beds. The presence of mudstone separating the sandstone tempestites indicates deposition below the normal-wave base under low-energy conditions during fairweather. Gutter casts are believed to have formed by diverse erosional processes, such as oscillatory flows, unidirectional flows, vortex flows, and combined flows (Myrow, 1992). The association of gutter casts with tempestites suggests that storm flows were involved in their production (Kreisa, 1981; Aigner, 1985). Absence of parting lineation argues against significant traction transport along the depositional surface. The fact that hummocky laminae thicken over the antiforms suggests accretionary growth (Dott and Bourgeois, 1982; Brenchley *et al.*, 1986; Cheel and Leckie, 1993). Cross-lamination and ripples overlying the hummocky zone record temporary reworking by waves as storms waned (Dott and Bourgeois, 1982). Variations in thickness and character of hummocky cross-stratified strata can be explained in terms of proximal-distal trends (Dott and Bourgeois, 1982; Cheel and Leckie, 1993). Thinner discrete hummocky beds with rippled tops, separated by mudstone interbeds, represent storm reworking in offshore-transition settings. Offshore transition deposits are commonly characterized by a regular alternation of sandstones and mudstones (Pemberton *et al.*, 2001).

The *Lower/Middle Shoreface* facies is composed of light gray, amalgamated hummocky cross-stratified, fine-grained sandstone. Individual sandstone beds generally pinch out, but bedsets are laterally persistent. Sandstone beds are amalgamated and internal second-order erosion surfaces separating hummocky cross-stratified laminasets are present. Mudstone partings, a few millimeters to rarely 4 cm thick, occur occasionally between some hummocky cross-stratified units. Commonly hummocky cross-stratification occurs throughout the whole bed. Individual hummocky laminae are occasionally stacked forming thinning-upward laminasets. Parting lineation is absent. Some hummocky laminae thicken over the crests of antiforms. Interference and combine-flow ripples are occasionally preserved at the top of hummocky sandstones. Large scours, ball-and-pillows, pseudonodules and load casts are common at the base of thick sandstone packages. Trace fossils are very rare, although vertical burrows (*Skolithos linearis*) occur locally. Hummocky cross-stratification is regarded as produced from episodic storm-wave activity and wave-generated surges (*e.g.*, Bourgeois, 1980; Dott and Bourgeois, 1982; Hunter and Clifton, 1982; Walker and Plint, 1992; Brenchley, 1985; Cheel and Leckie, 1993). Thick, amalgamated beds displaying hummocky cross-stratification, such as those present in this facies, represent proximal storm beds and record high-energy oscillatory and combined flows during storms. These thick-bedded, amalgamated hummocky sandstones were formed by repeated storm events; wave erosion removed mud layers between sandstone beds, with the exception of locally preserved residual mud partings (Brenchley *et al.*, 1993). The scarcity or even absence of mudstone interbeds between storm sandstone layers indicates deposition above storm-wave base and continuous water agitation. Deep scours also indicate strong erosive flows whereas large load casts suggest rapid influx of sand. The fact that hummocky laminae thicken over the antiforms suggests accretionary growths (Dott and Bourgeois, 1982; Brenchley *et al.*, 1986; Cheel and Leckie, 1993). As noted by MacEachern and Pemberton (1992), differentiation between the lower and middle shoreface in high-energy settings may be very difficult due to the scarcity or direct absence of fairweather trace fossils and rapid variations in physical structures due to local conditions.

Discussion

Paleoecological and paleoenvironmental implications

Trace fossils are relatively diverse and abundant in the wave-dominated shallow-marine deposits of the Alfarcito Member, reflecting the establishment of shallow-marine conditions that terminated estuarine deposition in the area. Alternating and contrasting energy conditions due to repeated storm events were among the key controlling factors for trace fossil distribution and preservation. Storm events involve erosion followed by rapid deposition. The initial phase of rapid deposition is in turn followed by a waning phase and the re-establishment of fairweather sedimentation under lower energy conditions. Accordingly, these sedimentary events impose a stress factor on the benthic communities inhabiting wave-dominated, shallow-marine areas.

The ichnology of storm-influenced, shallow-marine successions has been addressed in a number of studies (*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). These authors noted that storm-influenced deposits display two contrasting trace fossil assemblages that reflect the behavioral response of the benthic fauna inhabiting two successive and different habitats. The resident, fairweather trace fossil assemblage records the establishment of a benthic community developed under stable and rather predictable conditions. This assemblage commonly belongs to the *Cruziana* ichnofacies and has been attributed to populations displaying K-selected or climax strategies (see also Bromley, 1996). By contrast, the storm-related trace fossil assemblage records colonization after storm deposition. This assemblage reflects the establishment of an opportunistic community displaying r-selected population strategies in an unstable, physically-controlled environment. Opportunistic colonizers are usually, though not always, represented by the *Skolithos* ichnofacies.

These two trace fossil assemblages have been recognized in the Alfarcito Member. The fairweather trace fossil assemblage is the most diverse and includes more varied behavioral strategies, representing an example of the *Cruziana* ichnofacies. Ethologically, this assemblage includes locomotion (*Archaeonassa fossulata*, *Cruziana semiplicata*, *C. problematica*, *Cruziana* isp. and *Diplichnites* isp.); resting (*Rusophycus moyensis*, *R. carbonarius*, *Rusophycus* issp. and *Bergaueria* aff. *B. hemispherica*); pascichnia (*Dimorphichnus* aff. *D. quadrifidus*); feeding (*Arthrophycus minimus*, ?*Gyrolithes* isp., *Gyrophyllites* isp., ?*Phycodes* isp. and *Planolites reinecki*); and dwelling (*Palaeophycus tubularis*, *P. striatus*) trace fossils. Most of these ichnotaxa are preserved at the base of sandstone layers. However, some occur at the top of the event beds (*Archaeonassa fossulata*, *Diplichnites* isp., *Gyrophyllites* isp.). Ichnotaxa preserved at the top of sandstone layers may record the activity of infaunal organisms that burrowed through the fairweather and waning mudstone down to the mudstone-sandstone interface (*Gyrophyllites* isp.). These structures are clearly part of the community that established under normal conditions after the storm disturbance. Other biogenic structures preserved at the top of event layers record the activity of vagile organisms that produce simple locomotion trails and trackways (*Archaeonassa fossulata*, *Diplichnites* isp.). This suite may reflect the activity of the first incomers after the storm, which may in fact have survived the mild effects of a storm in a distal setting. Distinction of pre- and post-storm assemblages in these cases is less straightforward.

The typical storm-related trace fossil assemblage in the Alfarcito Member is monospecific and includes vertical dwelling traces (*Skolithos linearis*), recording an example of the *Skolithos* ichnofacies. This assemblage occurs in low to moderate densities and records opportunistic colonization after storm deposition. Vertical burrows are preserved as relatively deep, endichnial structures that penetrate into storm-emplaced sandstone layers. Because these vertical burrows commonly do not occur in profuse densities, degree of bioturbation remains relatively low and internal physical structures of the tempestites (*e.g.* hummocky cross stratification, combined- flow ripple lamination) are well preserved. *Skolithos linearis* records a distinctive onshore-offshore trend. Specimens of *S. linearis* in distal settings (upper offshore) characteristically display smaller size and occur in even lower densities than those from more proximal environments (offshore transition and shoreface).

Integration of ichnologic and sedimentologic data allows reconstruction of proximal-distal trends in shallow-marine trace fossil assemblages along a nearshore-offshore transect (figura 8). High-energy conditions prevailed in lower and middle shoreface environments, commonly precluding the preservation of biogenic structures. Most shoreface beds are unbioturbated. Repeated storm-wave erosion precluded the establishment and/or preservation of the fairweather assemblage in the shoreface deposits. Shallow- to mid-tier biogenic structures were most likely removed by erosion due to deep scouring. Bioturbation is therefore restricted to vertical burrows (*Skolithos linearis*) of the *Skolithos* ichnofacies. This postdepositional assemblage records environmental changes related to episodic sedimentation, such as the input of organic particles that were kept in suspension in the water column by storm wave agitation.

Environmental conditions in the offshore transition are more variable and reflect the alternation of high-energy storm events and low-energy fairweather mudstone deposition. The storm-related *Skolithos* trace fossil assemblage is present, but alternates with the fairweather trace fossil assemblage illustrating an archetypal *Cruziana* ichnofacies. Hummocky sandstones having intensely bioturbated tops and covered by the radial feeding trace *Gyrophyllites* isp. are common in the offshore transition deposits. As previously discussed, these sandstone tops are palimpsest surfaces, recording the storm-related assemblage and the subsequent fairweather assemblage.

As in the offshore transition facies, upper offshore deposits display the alternation of the resident fairweather and storm-related colonization trace fossil assemblages. The fairweather trace fossil assemblage reaches a diversity maximum in the upper offshore (archetypal *Cruziana* ichnofacies). Undoubtedly, the less erosive nature of these more distally emplaced tempestites coupled with the overall lower energy of the upper offshore favor development and preservation of the fairweather suite. Additionally, there is a tendency for the preservation of shallow-tier trace fossils (*e.g. Arthrophycus minimus*). Additionally, preservation of trace fossils in upper offshore deposits may have been favored by the presence of abundant sandstone/mudstone interfaces. The *Cruziana* ichnofacies reaches a climax in the upper offshore deposits studied. Here, however, the storm-related assemblage becomes less and less distinctive, with some sandstone beds recording small and dispersed *Skolithos linearis* or occasionally only the presence of horizontal locomotion structures.

Trace fossils are scarce in lower offshore deposits. The storm-related trace fossil assemblage is not present and the fairweather assemblage is restricted to a few non-descript burrows, mostly *Palaeophycus tubularis* (representing the distal *Cruziana* ichnofacies). The scarcity of trace fossils in lower offshore facies probably reflects oxygen-depleted conditions. This hypothesis is also supported by the overall small size of the trace fossils studied, which suggests a stressed environment. Additionally, the lower abundance of sandstone interbeds may have inhibited preservation and visibility of biogenic structures.

Analysis of shallow-marine clastic deposits of the lower fine-grained interval of the Alfarcito Member shows that few ichnotaxa are restricted to particular zones of the nearshore to offshore transect. This case study reveals, therefore, the pitfalls of the checklist approach, as previously noted by Howard and Frey (1975). An integrated approach, which takes into account several characteristics, such as degree of bioturbation, abundance of individual ichnotaxa, ethological and ecological significance of the biogenic structures, ichnofabrics and tiering structure, is more useful to delineate environmental subdivisions of shallow-marine clastic successions (*e.g.* Buatois *et al.*, 2002).

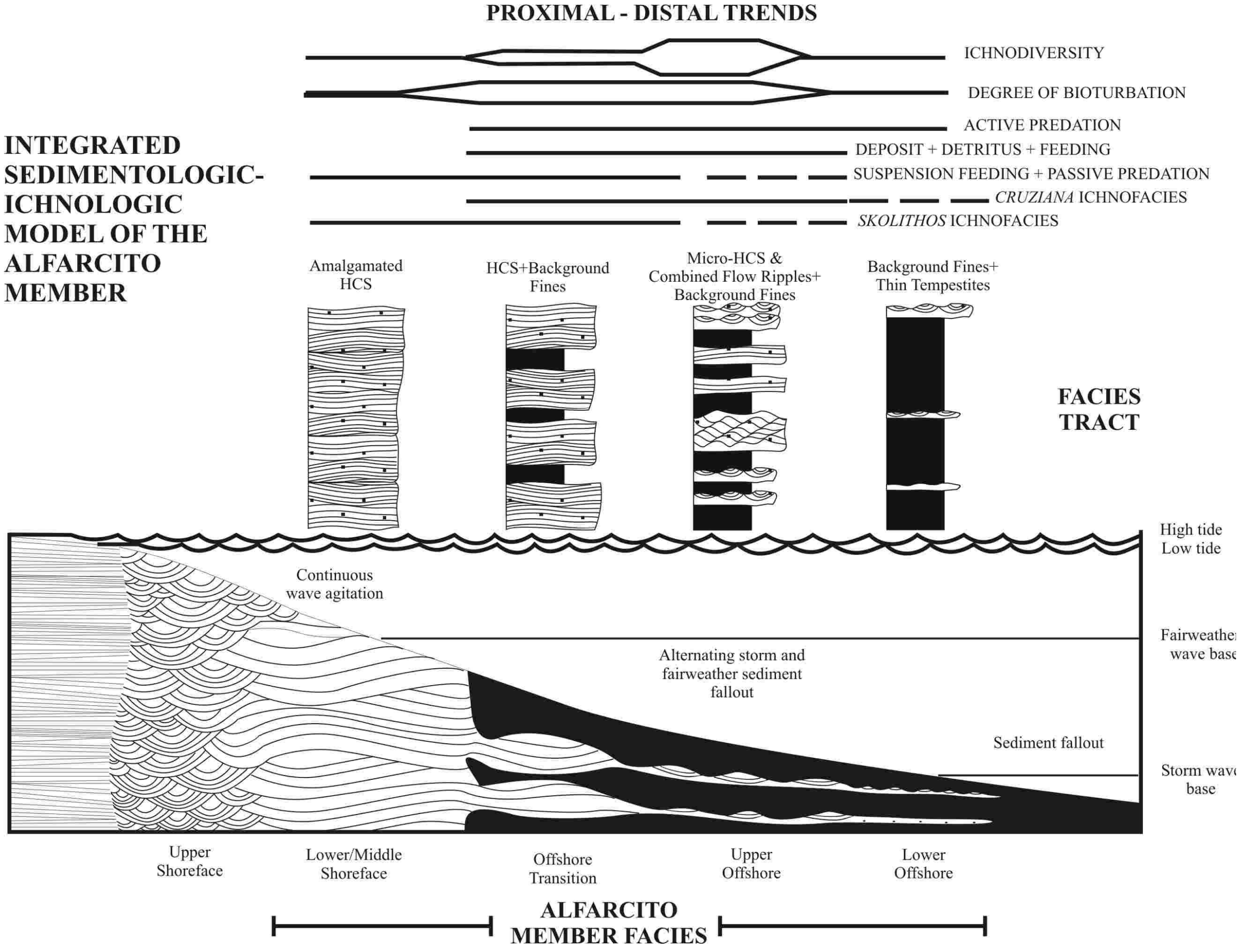

Figure 8. Integrated sedimentologic and ichnologic model of the lower fine-grained interval of the Alfarcito Member / *Modelo sedimentológico e icnológico integrado del intervalo inferior de grano fino del Miembro Alfarcito.*

MacEachern and Pemberton (1992) analyzed shoreface variability in the Cretaceous of the North American Western Interior Seaway and characterized three types of shoreface based on the intensity and frequency of storm events. This model has proved to be useful to characterize shoreface deposits in the stratigraphic record. The weakly storm-affected shorefaces (low energy) are characterized by relatively minor amounts of tempestites. These shorefaces are dominated by fairweather trace fossil assemblages and thin storm beds are commonly obliterated by biogenic reworking or thoroughly bioturbated. A transition from the *Cruziana* to the *Skolithos* ichnofacies is coincident with the lower to middle shoreface transition. Examples of ichnofaunas in weakly storm-affected shorefaces have been documented recently from the Upper Ordovician Santa Gertrudis Formation of northwestern Argentina (Mángano and Buatois, 2003), the Lower Pennsylvanian Morrow Sandstone of subsurface Kansas (Buatois *et al*., 2002), the Upper Carboniferous Hoyada Verde Formation of San Juan (Mángano *et al*., 2003) and the Miocene Chenque Formation of Patagonia (Buatois *et al*., 2003). The moderately storm-dominated shorefaces (intermediate energy) display an alternation of laminated storm beds and intensely bioturbated fairweather deposits, resulting in the so-called "Lam-Scram" pattern. These deposits commonly show the alternation of elements of the *Skolithos* ichnofacies as opportunistic pioneers colonizing sandstone tempestites and the *Cruziana* ichnofacies recording the activity of the fairweather resident community. Examples of ichnofaunas in moderately storm-dominated shorefaces are known from the Permian Rio Bonito and Palermo formations in southern Brazil (Netto, 1998; Buatois *et al*., 2001, 2005). The strongly storm-dominated shorefaces (high energy) commonly consist of amalgamated hummocky sandstones showing little or no bioturbation; only the deepest representatives of the post-storm *Skolithos* ichnofacies are present and development of the fairweather assemblage is inhibited. Examples of ichnofaunas in strongly storm-dominated shorefaces have been documented also from the Rio Bonito and Palermo formations (Netto, 1998; Buatois *et al*., 2001, 2005). Shoreface deposits from the Alfarcito Member compare favorably with the strongly storm-dominated type of MacEachern and Pemberton (1992).

Sequence stratigraphic implications

Integration of ichnologic data within a sequence stratigraphic framework allows delineation of wave-dominated parasequences, parasequence sets and alostratigraphic surfaces in the lower fine-grained interval of the Alfarcito Member. A wave-dominated parasequence coarsens upward, recording shoreline progradation (Van Wagoner *et al*., 1990). In terms of associated environmental factors, each parasequence reflects a progressive increase in hydrodynamic energy, degree of oxygenation, sand content, amount of organic particles in suspension, and mobility of the substrate (Pemberton *et al*., 1992; Mángano *et al*., 2002a). These environmental factors undoubtedly controlled vertical distribution of trace fossils in stratal packages of the Alfarcito Member. An idealized wave-dominated parasequence in the Alfarcito Member is characterized, from base to top, by a distal *Cruziana* ichnofacies (lower offshore), an archetypal *Cruziana* ichnofacies associated with a storm-related *Skolithos* ichnofacies (upper offshore to offshore transition) and a *Skolithos* ichnofacies (lower/middle shoreface). However, this ideal parasequence is the exception rather than the rule because not all subenvironments are represented in each parasequence. This is understood if individual parasequences are analyzed in the context of their stacking pattern (figura 9).

In the Alfarcito Member, regional parasequences are well developed recording short-term seaward migrations of the shoreline separated by drowning events. This is in marked contrast with the estuarine units, whose stratal packages are areally restricted to the paleovalley. The lowermost beds of the Alfarcito Member records the drowning of the underlying estuarine deposits. Open-marine deposits locally interfinger with the seaward face of the subtidal sandbar complex that characterizes the outer region of the estuarine valley (Buatois and Mángano, 2003). The passage from estuarine to open-marine conditions is commonly expressed by a low-energy flooding surface or, more appropriately, a drowning surface (sensu Posamentier and Allen, 1999) rather than an erosive wave ravinement surface (Buatois and Mángano, 2003). Zaitlin *et al*. (1994) suggested that wave ravinement surfaces are typically absent in tide-dominated estuaries. However, the local presence of channels scoured into the tidal sandbar complex and transgressive lags suggests some influence, albeit limited, of wave ravinement at the top of the estuarine unit. The transgressive systems tract at the lower interval of the Alfarcito Member is poorly developed. Only the lowermost strata of the Alfarcito Member are included in the transgressive systems tract; the bulk of this systems tract is preserved within the underlying incised valley. Transgressive strata culminate with the development of a maximum flooding surface that lies within lower offshore deposits at the lower interval of the Alfarcito Member. At this moment of depositional evolution, the Alfarcito sea reached its maximum depth, coastal plains were flooded and sediment was trapped in shoreline areas, resulting in condensation and starvation in offshore settings. Maximum flooding intervals are currently associated with oxygen-depleted conditions and display limited development of trace fossil assemblages. This condensed section is overlain by lower offshore to offshore transition deposits forming a progradational parasequence set, which represents a highstand systems tract that characterizes part of the lower interval of the Alfarcito Member.

Another sequence boundary is present at the top of this highstand package. This sequence boundary is a co-planar surface (flooding surface/sequence boundary), which marks the vertical replacement of a progradational to a retrogradational parasequence set. This retrogradational parasequence set represents the establishment of a transgressive systems tract that includes parasequences that environmentally range from upper to lower offshore deposits and reflects that the accommodation rate exceeds the rate at which sediment is supplied during deposition of this interval of the Alfarcito Member. A maximum flooding surface separates these transgressive deposits from the subsequent highstand. As in the case of the maximum flooding interval of the lower sequence, bioturbation is restricted and oxygen-depleted conditions were dominant. The lower parasequences in this progradational parasequence set include lower to upper offshore facies, while offshore transition and lower/middle shoreface deposits are restricted to the upper parasequences of the unit. The progressive shallowing reflected by stratal architecture is paralleled by vertical changes in trace fossil distribution as discussed above. Overall, the *Cruziana* ichnofacies is gradually replaced by the *Skolithos* ichnofacies.

Evolutionary implications

Because most of the classical ichnologic models of storm-dominated shallow-marine seas are based on

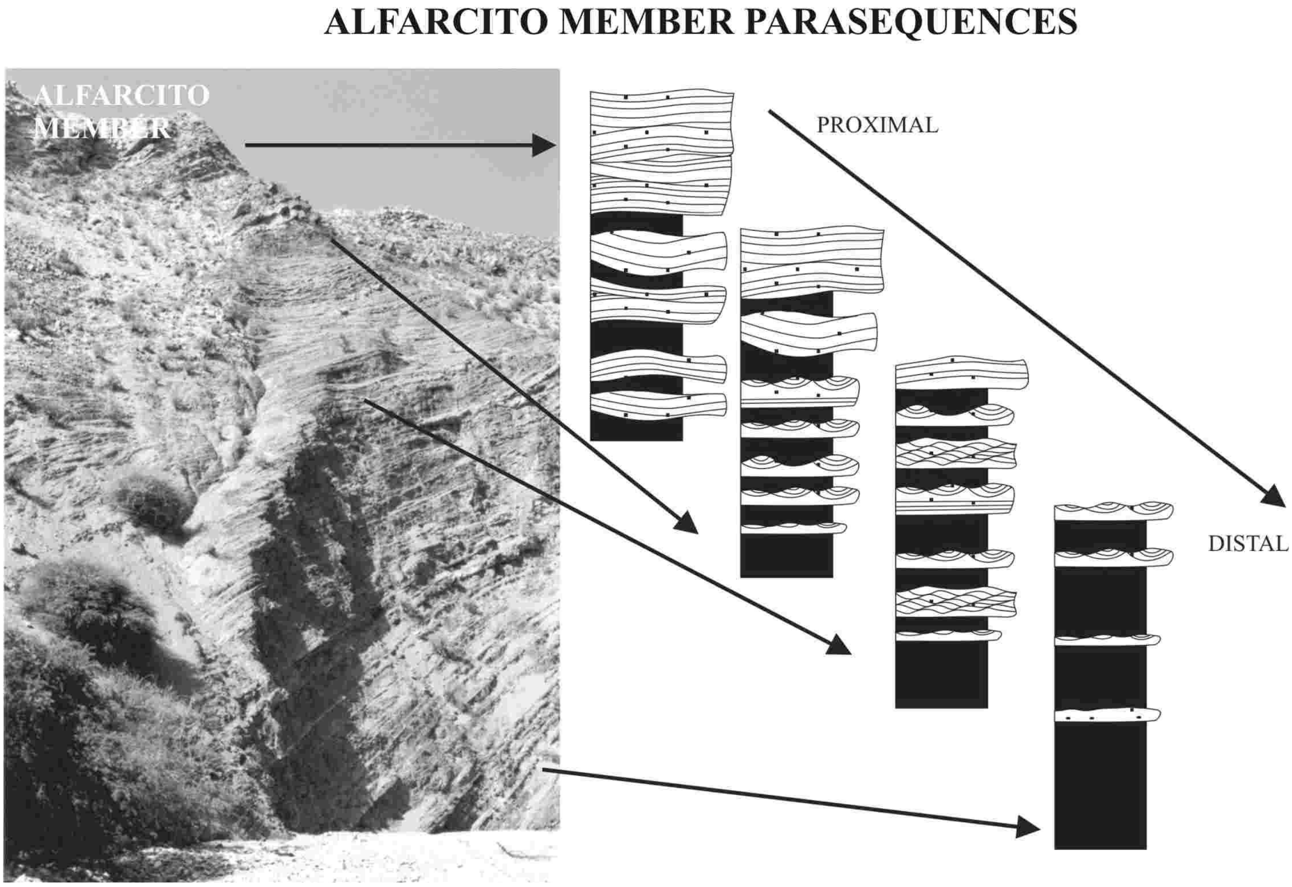

Figure 9. Proximal-distal trends in parasequences in the lower fine-grained interval of the Alfarcito Member. Parasequence stacking pattern reflects overall shoreline progradation. *Shoreface* deposits occur at the top / *Tendencias de proximalidad-distalidad en parasecuencias del intervalo inferior de grano fino del Miembro Alfarcito. El patrón de las parasecuencias refleja la progradación de la línea de costa. Los depósitos de* shoreface *se presentan hacia el tope.*

Mesozoic examples (*e.g.* MacEachern and Pemberton, 1992), the main peculiarities of the lower Paleozoic example are worth analyzing to evaluate evolutionary trends and secular changes in bioturbation in wave-dominated shallow-marine clastic rocks (cf. McIlroy and Logan, 1999).

Although there seems to be gross similarities between Paleozoic and Mesozoic shallow-marine ichnofaunas, some differences in both fairweather and storm-related trace fossil assemblages are apparent under closer inspection. While *Skolithos* is the dominant ichnotaxa in lower Paleozoic storm-related trace fossil assemblages, *Ophiomorpha* is the dominant trace fossil in their Mesozoic counterparts. The decline of *Skolithos* piperocks through the Paleozoic has been noted by Droser (1991). The replacement of *Skolithos* by *Ophiomorpha* in high-energy shallow-marine environments is most likely related to the Mesozoic radiation of decapod crustaceans (see Carmona *et al.*, 2004). However, this is certainly a long-term evolutionary trend because the storm-related *Skolithos* assemblage remains virtually unchanged during the lower Paleozoic. As noted by Mángano and Buatois (2003), opportunistic storm-related assemblages are less sensitive to evolutionary events than fairweather, climax ichnofaunas.

Mángano and Droser (2004) noted that while trilobite trails and trackways are dominant in Cambrian to Early Ordovician shallow-marine fairweather assemblages, Middle to Late Ordovician ichnofaunas generally show more varied behavioral patterns. Also, lower Paleozoic fairweather assemblages are dominated by shallower-tier structures than younger, particularly post-Paleozoic shallow-marine assemblages. An increase in burrowing depth and intensity through the Phanerozoic has been suggested (*e.g.* Thayer, 1979, 1983). In lower Paleozoic clastic rocks of northwestern Argentina, some temporal changes in fairweather ichnofaunas have been detected (Mángano and Buatois, 2003). Late Cambrian to early Tremadocian fairweather assemblages are dominated by shallow-tiered community structures, defining an essentially two-dimensional ichnofabric. By the late Tremadocian, three-dimensional ichnofabrics became more common and produced significant disruption of the primary sedimentary fabric, reflecting more efficient ecospace utilization by deposit feeders. This is clearly evidenced by upper offshore deposits of the Rupasca and Humacha members, which are characterized by the establishment of a pervasive *Trichophycus* ichnofabric.

The increase in depth and extent of bioturbation through geologic time has implications with respect to preservation of event layers. Wheatcroft (1990) noted that if the transient time (*i.e.* time required to advect the signal through the biologically active zone) is less than the dissipation time (*i.e.* time required to destroy the event bed), then some evidence of the event layer should be preserved in the stratigraphic record. The pristine preservation of thin tempestites in the Alfarcito Member most likely reflects the restriction of the benthic fauna to the uppermost tiers of the sediment and the absence of true sediment bulldozers in these ancient seas.

Biostratigraphic implications

Although most trace fossils display long temporal ranges, there are some ichnotaxa that reflect particular kinds of animals in which body morphology and behavior underwent closely related evolutionary transformations through geologic time (Seilacher, 2000). Accordingly, these trace fossils are useful in biostratigraphic studies. Recent research in Cambrian-Ordovician clastic rocks of northwest Argentina underscores the potential of the *Cruziana* and Arthrophycid stratigraphy proposed by Seilacher (1970, 1990, 1992, 1994, 1996, 2000).

The *Cruziana* stratigraphy is based on ribbon-like bilobate structures (*Cruziana*) and coffee bean-shaped structures (*Rusophycus*) identified at ichnospecies level; other trilobite ichnotaxa (*e.g. Dimorphichnus*) were added to the scheme subsequently (Seilacher, 1990). *Cruziana* ichnospecies are based on fine morphological features, particularly the so called 'claw formula' (*i.e.* the fingerprint left by the tips of the endopodites displaying groupings of claws or setae), and secondarily on the presence and morphology of exopodal brushings, pleural or genal spine impressions, and cephalic and coxal marks reflecting burrowing behavior. The attempt to establish a biostratigraphic zonation based simply on the size of *Cruziana* and *Rusophycus* (Aceñolaza, 2003, figure 4) is flawed because it ignores taxonomy at ichnospecies level and fails to reflect the complexities of trilobite trace fossils. The biostratigraphic utility of trilobite trace fossils in lower Paleozoic rocks of northwest Argentina has been discussed by Mángano and Buatois (2001, 2003). One of these biostratigraphically useful *Cruziana* ichnospecies is *C. semiplicata*, which is present in the Alfarcito Member (and coeval and slightly older units of Cordillera Oriental as well). *Cruziana semiplicata* ranges from the Upper Cambrian to the Tremadocian (Crimes, 1969, 1975; Baldwin, 1977; Fillion and Pickerill, 1990) and represents a valuable stratigraphic indicator in northwestern Argentina. *Rusophycus moyensis*, also present in the Alfarcito Member, is a local diagnostic element that also characterizes Upper Cambrian-Tremadocian strata of northwestern Argentina and is apparently absent in younger and older strata (Mángano *et al*., 2002b). Seilacher (1990) suggested a Middle Cambrian age for *D. quadrifidus*. *Dimorphichnus* cf. *D. quadrifidus* occurs in the younger Alfarcito Member. However, further material should be analyzed to extend the stratigraphic range of this ichnotaxon.

The Arthrophycid stratigraphy is based on the analysis of selected ichnotaxa (*i.e. Arthrophycus*, *Daedalus* and *Phycodes*) produced by worms of unknown taxonomic affinity and has been recently proposed by Seilacher (2000). *Arthrophycus minimus*, which occurs in the Alfarcito Member, is less complex and remarkably smaller than Ordovician and Silurian *Arthrophycus* ichnospecies. As noted by Mángano *et al*. (2005), it may be considered a primitive ichnospecies of *Arthrophycus*, a sort of link between the ichnogenera *Phycodes* and *Arthrophycus*.

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