

LIFE IN THE LATE PALEOZOIC ICE AGE: TRACE FOSSILS FROM GLACIALLY INFLUENCED DEPOSITS IN A LATE CARBONIFEROUS FJORD OF WESTERN ARGENTINA

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ABSTRACT—The early Late Carboniferous rocks of the Guandacol Formation in western Argentina preserve the glacial to postglacial transition. In the study area, this unit has been divided in three intervals: 1) a lower diamictitic interval; 2) a middle interval chiefly composed of mudstone, and 3) an upper sandstone-dominated interval. The lower interval records infill of a fjord incised into the underlying Ordovician limestone. The middle and upper intervals reflect postglacial sedimentation. Four ichnotaxa, occurring as both discrete and compound trace fossils, are documented from the lower and middle intervals of the Guandacol Formation. *Diplopodichnus biformis* and *Cruziana diplopoda* n. isp. occur in the thinly bedded stratified diamictite in the upper section of the lower interval. These deposits record sedimentation from debris flows with dropstones reflecting overprinting of ice-rafting and rain-out processes. *Cruziana* cf. *problematica* and *Rusophycus carbonarius* are present in very-fine to fine-grained sandstone layers interbedded with dropstone-bearing mudstone in the lower section of the middle interval. These deposits record the interplay of suspension fall-out sedimentation, ice-rafting, rain-out processes, and storm waves. The presence of linguliformean brachiopods in coeval beds nearby strongly suggests marine influence and that brackish-water conditions prevailed during the early phase of the transgression. Harsh paleoenvironmental conditions may explain the small size of the trace fossils and the low ichnodiversity in comparison to that expected in fully marine environments. The morphology of the trace fossils as bilobate ridges and furrows ornamented with scratch marks indicates that the structures were produced by arthropods, most likely trilobites and/or notostracans. Although the possibility that different ichnotaxa have resulted from changes in burrowing behaviors can not be completely disregarded, the fact that distinct *Cruziana* ichnospecies display non-overlapping facies distribution may suggest their production by different arthropods.

INTRODUCTION

THERE IS a growing interest in the late Paleozoic Ice Age and its deposits in Gondwana (López Gamundí and Buatois, 2010). In particular, studies in South America have focused on sedimentologic, stratigraphic, and biostratigraphic aspects. However, the nature of glacially influenced ecosystems has been hardly explored. In part, lack of studies may be due to the low preservation potential of body fossils in areas adjacent to glaciated margins, such as modern fjords (e.g., Aitken, 1990). Trace fossils are relatively abundant in some of these Gondwanan upper Paleozoic deposits (see review by Buatois et al., 2010). Because trace fossils are in situ evidence of animal-substrate interactions, they may serve as a proxy to reconstruct paleoenvironmental conditions in these Gondwana glacial settings.

The Guandacol Formation contains excellent exposures of the early Late Carboniferous glacial episode that is well represented in the Andean basins of western and northwestern Argentina (e.g., Limarino et al., 2002; Pazos, 2002a; Marensi et al., 2005). In this paper we document bilobate trace fossils present in glacially influenced deposits of this formation that are filling a fjord in the Cuesta de Huaco area. Biogenic structures are present in a wide variety of lithologies, including mudstone, very fine- to fine-grained sandstone with current and combined-flow ripples, and granule conglomerate and very coarse-grained sandstone deposited from debris flows. This lithologic variability allows us to discuss the roles of variation in behavior, substrate (both grain size and consolidation degree) and producer on trace fossil morphology.

Finally, we evaluate the paleoenvironmental significance of this ichnofauna.

STRATIGRAPHIC FRAMEWORK AND PALEOENVIRONMENTAL SETTING

General stratigraphy and architecture.—The studied deposits represent part of the infill of the Upper Carboniferous to Upper Permian Paganzo Basin of western Argentina (Fig. 1.1); a foreland basin created through the subduction of the Pacific plate beneath the western continental margin of Gondwana. The Paganzo Basin may have evolved to a rift system during the Permian (Ramos, 1988). The Protoprecordillera, a north-south trending topographic high, separated the mostly marine Calingasta-Uspallata and Río Blanco basins on the west from the continental to marginal-marine deposits of the Paganzo Basin on the east. Paleotopography and physiography in the Paganzo Basin was complex, with sedimentation taking place in a number of sub-basins separated by internal basement highs (Azcuy and Morelli, 1970; Desjardins et al., 2009). The eastern boundary of the basin is defined by the cratonic Pampean arch. In general, the Paganzo Basin is subdivided into two main areas: an eastern zone dominated by continental environments, and a western one with increased participation of marginal-marine environments (Limarino et al., 2002).

The Carboniferous-Permian succession in the Cuesta de Huaco area consists of the Guandacol, Tupe, and Paquia formations (Limarino et al., 1986). The Guandacol Formation, which contains the trace fossils analyzed in this paper,

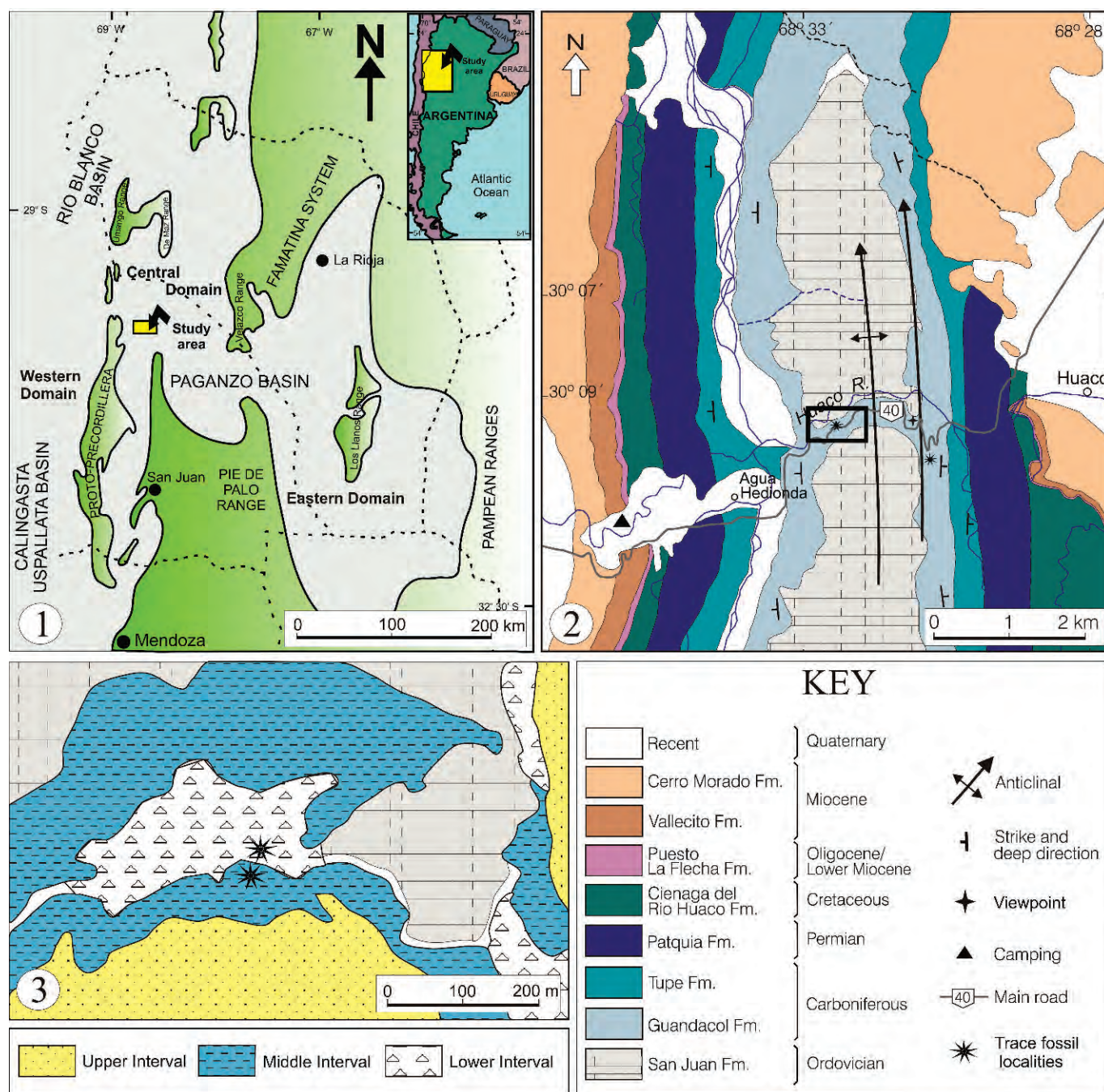


FIGURE 1—Location and geological maps of the study area. 1, general map of the Paganzo Basin (after Limarino et al., 2002); 2, geological map of the Cuesta de Huaco area; 3, detailed map of the paleovalley area near Rio Huaco on the west flank of the Huaco anticline (see insert in 2).

unconformably overlays the Ordovician limestone of the San Juan Formation (Figs. 1.2, 2). The Guandacol Formation records the glacial and postglacial conditions in the westernmost part of the Paganzo Basin. The basal deposits of the Guandacol Formation fill several paleovalleys incised in the Ordovician limestone. One such valley is well exposed near Rio Huaco on the west flank of the Huaco anticline (Figs. 1.2, 1.3, and 3.1), with some other valleys preserved east of the viewpoint on the east flank of the anticline (Fig. 1.2). In this latter region erosive features are common, including whale-backs (Fig. 4.1), striated blocks (Fig. 4.2), half-moon striations (Fig. 4.3), and wedge-shaped striations (Fig. 4.4). Also, glacial deposits resting on top of an irregular surface cut into

the Ordovician limestone in the Agua Hedionda Anticline (López Gamundí and Martínez, 2000; Pazos, 2002a). Outside the paleovalleys, the basal contact is relatively planar to locally irregular, representing interfluvial zones (Fig. 3.2, 3.3). Another paleovalley downcuts into the San Juan Formation and the metamorphic basement in the nearby Quebrada de Los Pozuelos (Marensi et al., 2005).

Sedimentary facies.—The Guandacol Formation in this area has been divided into three intervals: 1) a lower diamictitic interval; 2) a middle interval chiefly composed of mudstone, and 3) an upper sandstone-dominated interval (Fig. 2). Whereas the lower interval records glacial conditions, the middle and upper intervals reflect postglacial sedimentation.

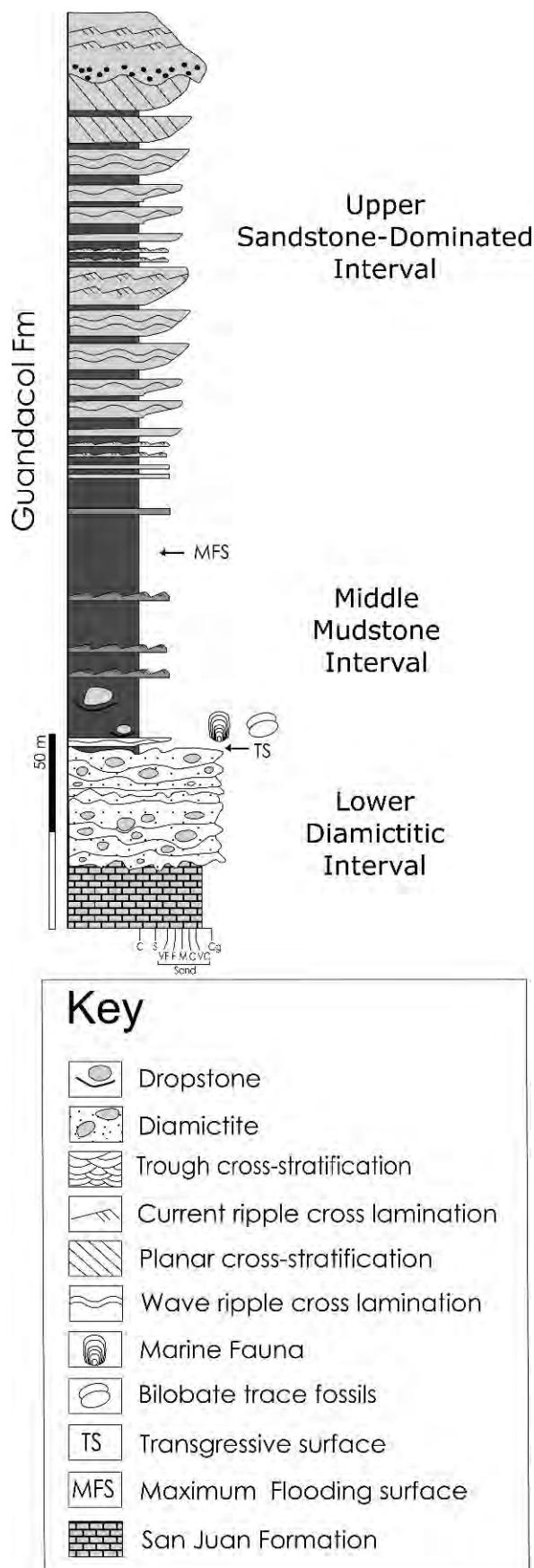


FIGURE 2—Stratigraphical section of the Guandacol Formation showing position of the studied interval and associated trace fossils (modified from Limarino et al., 2002 and Buatois et al., 2006).

The lower section comprises three types of diamictite facies (massive matrix-supported diamictite, stratified matrix-supported diamictite and thinly bedded stratified diamictite), which are replaced upwards by finer-grained deposits of the middle section (mudstone with interbedded sandstone facies). Only the latter two facies contain trace fossils. The four facies are described as follows:

The massive matrix-supported diamictite facies includes clasts up to 1 m in maximum diameter composed predominantly of limestone and shale derived from the underlying San Juan Formation (Ordovician) and Los Azules Formation (Late Ordovician) (Fig. 5.1). Locally clasts of granite, quartz, low-grade metamorphic rocks and migmatite have also been identified. The matrix is dominated by clay with minor proportions of silt and very fine-grained sand (Fig. 6.1). The massive matrix-supported diamictite is locally stratified in irregular thick beds up to 100 cm thick. No trace fossils are present in this facies. The massive and chaotic nature of these deposits suggests that they are true tillites (i.e., subglacial till accumulations). Specifically, this facies is interpreted as a lodgment till commonly filling glacial valleys incised in the San Juan Formation.

The stratified matrix-supported diamictite facies exhibits similar composition to the massive diamictite and is also matrix supported (Fig. 5.2). However, it is more organized than the previous type, showing poorly defined horizontal bedding and graded beds (Fig. 6.2). Beds are mainly tabular in shape and up to 80 cm thick. Trace fossils are absent in this facies. The stratified matrix-supported diamictite tends to overlie the massive matrix-supported diamictite, onlapping towards the wall of the paleovalley. The crude stratification, normal grading, and better sorting of these deposits indicate that they are resedimented diamictites chiefly resulting from cohesive subaqueous gravity flows and fluvial reworking of glacial deposits, rather than true tillites. Similar stratified deposits have been recognized in the Quebrada de Los Pozuelos, and interpreted as derived from a retrogradational morainal bank (Marensi et al., 2005).

The thinly bedded stratified diamictite facies is characterized by tabular beds, 0.6–15 cm thick. It is composed of matrix-supported fine-grained diamictite with clasts up to 3 cm in maximum diameter (Fig. 5.3, 5.4 and 5.5). Each diamictite bed is commonly draped by a thin veneer of mud (Fig. 6.3, 6.4). Commonly limestone and granite dropstones (up to 20 cm in diameter) disrupt the delicate stratification. *Diploplodichnus biformis* and *Cruziana diplopoda* n. isp. occur in this facies (trace-fossil assemblage 1). This facies marks the top of the valley infill and delineates sedimentation expansion towards the interfluvies. It records sedimentation from debris flows with dropstones reflecting overprinting of ice-rafting and rain-out processes. These debris flows were formed after the retreat of the glacier (Limarino et al., 2002).

The mudstone with interbedded sandstone facies consists of mudstone interbedded with thin layers of siltstone and very fine- to fine-grained silty sandstone with parallel lamination, ripple cross-lamination and asymmetric and near-symmetric ripples. Current ripple cross-lamination in the siltstone division is observed in thin section (Fig. 6.5). Limestone and granite dropstones are abundant (Fig. 5.6). Low-diversity suites of linguliform brachiopods (cf. *Oehlertella* sp.) occur in one bed in the Agua Hedionda section (Martínez, 1993). *Cruziana* cf. *problematica* and *Rusophycus carbonarius* are present in this facies (trace-fossil assemblage 2). These deposits characterize the lowermost part of the middle interval, and are present all across the study area. The dropstone-bearing

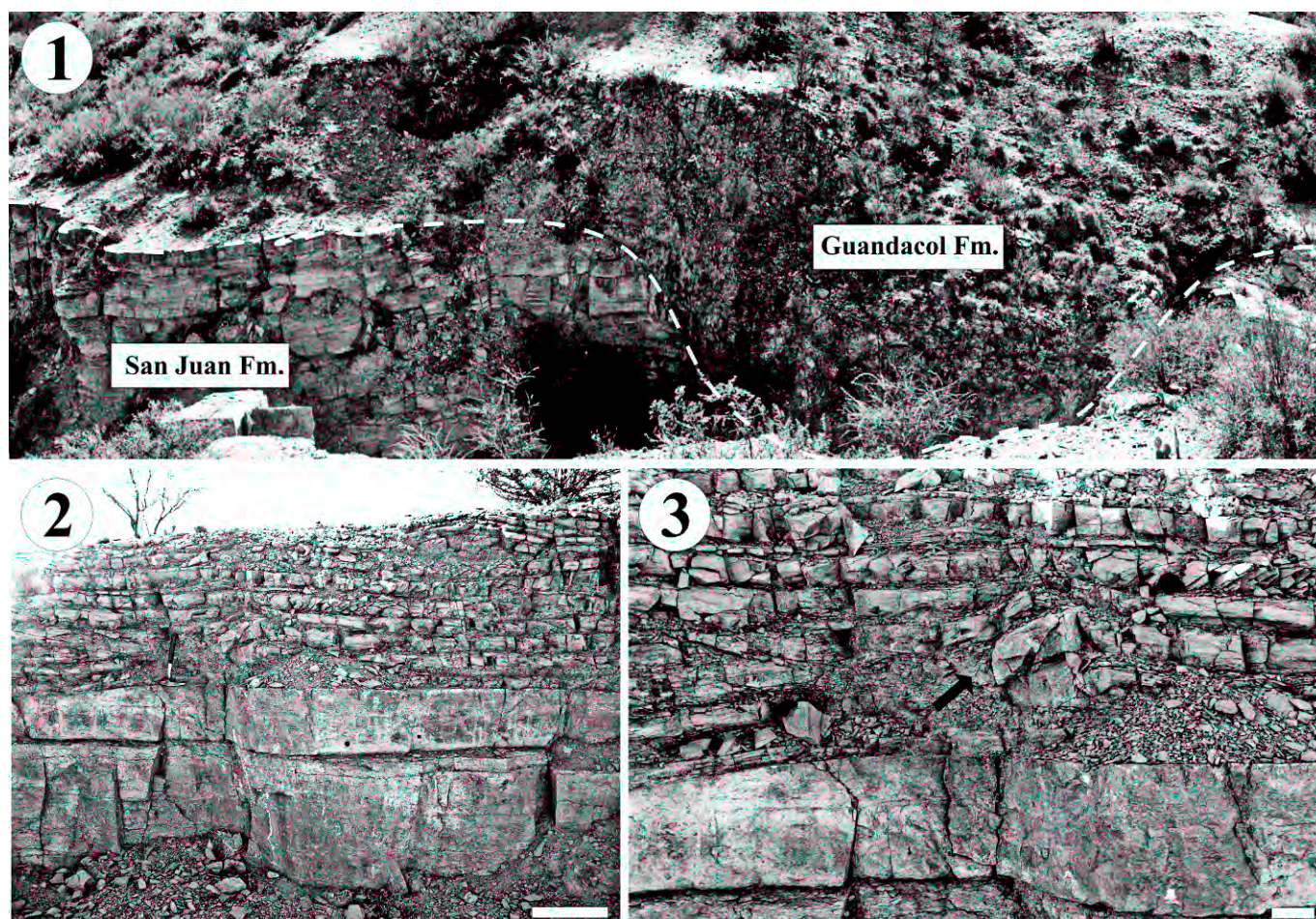


FIGURE 3—Different expressions of the contact between the Guandacol Formation and the underlying San Juan Formation. 1, paleovalley incised into the Ordovician limestone and filled with tillite, near Rio Huaco on the west flank of the Huaco anticline; 2, planar contact between the Guandacol and San Juan formations, the Guandacol Formation is represented by mudstone and interbedded combined-flow rippled sandstone, Viewpoint area, bar is 50 cm; 3, close-up of contact shown in 2, note limestone dropstone (arrow), bar is 10 cm.

mudstone records suspension fall-out sedimentation, ice-rafting, and rain-out processes. The near-symmetric ripples are interpreted as combined-flow ripples. The interbedded sandstone layers represent event beds, most likely due to storm deposition. The presence of current ripple cross-lamination in siltstone interbeds suggests that low-energy underflow currents played also some role in deposition. The mudstone with interbedded sandstone facies marks a basinwide transgressive event.

These dropstone-bearing deposits are overlain by unbioturbated black shale and marl that delineate the maximum flooding interval formed under sediment starvation and anoxic conditions (Limarino et al., 2002; Pazos, 2002a; Buatois and Mángano, 2003). The absence of dropstones suggests a major contraction of the ice bodies that would not have been in contact with the sea.

DEPOSITIONAL ENVIRONMENT

Glaciation affected the Paganzo Basin during the Namurian when alpine glaciers carved a number of valleys that drained away from the Protoprecordillera and the Pampean Arch (López Gamundí and Martínez, 2000; Limarino et al., 2002). In the Huaco area, paleocurrent measurements indicate ice flow from the southeast (Henry et al., 2008). The glacial stage is represented in the Huaco area by the lower diamictitic interval of the Guandacol Formation, more specifically by the

massive matrix-supported diamictite facies. These glacial valleys were flooded during deglaciation forming fjords affected by a strong discharge of freshwater associated with melting (Limarino et al., 2002; Buatois et al., 2006). In the Huaco area, this stage is illustrated by the fine-grained middle interval of the Guandacol Formation. Some of the resedimented diamictites may reflect the onset of transgression (Pazos, 2002a). These water bodies were filled during the subsequent regression mostly by deltaic progradation (upper sandstone-dominated interval of the Guandacol Formation) and subsequently by the establishment of fluvial systems, as recorded in the overlying Tupe Formation (Ottone and Azcuy, 1986; Desjardins et al., 2009).

SYSTEMATIC PALEONTOLOGY

Both discrete and compound trace fossils are described. Density of trace fossils on bedding planes (bedding-plane bioturbation index or BP-BI) is assessed following the categories established by Miller and Smail (1997) and applying the intersection-grid technique of Marenco and Bottjer (2010). Specimens are housed at the Invertebrate Fossil collection of the Instituto de Geología of the Universidad Nacional de San Juan. The synonym list is restricted to previous ichnologic work on the Guandacol Formation.

Discrete trace fossils.—Trace fossils are listed alphabetically.

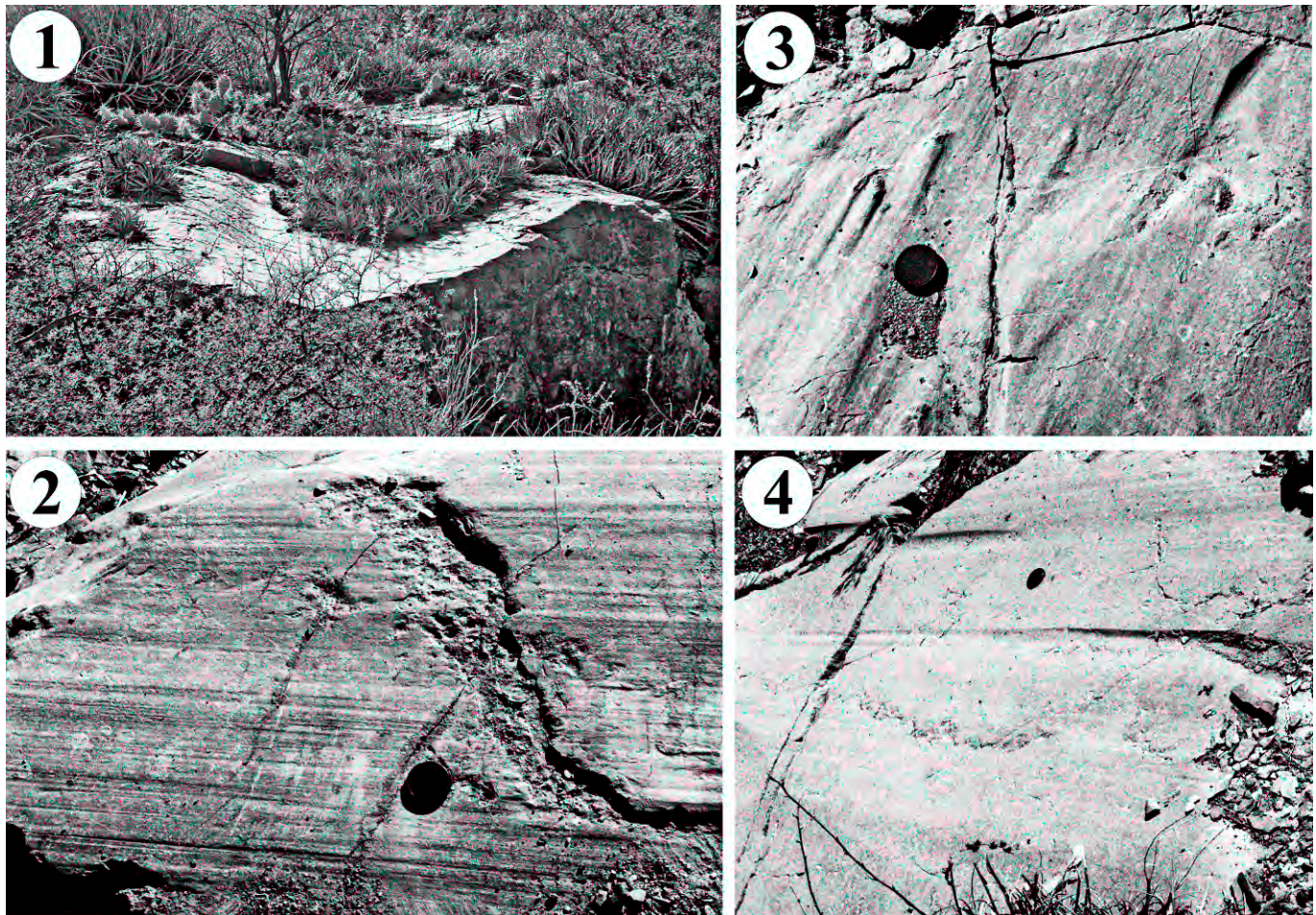


FIGURE 4—Erosive features indicative of glacial erosion near the base of the Guadacol Formation, east of the viewpoint. 1, whalebacks; 2, striated blocks; 3, half-moon striations; 4, wedge-shaped striations. Lens cap is 5.5 cm wide.

Ichnogenus CRUZIANA d'Orbigny, 1842
 CRUZIANA DIPLOPODA new ichnospecies
 Figures 7, 8.1–8.3, 9.1

Diagnosis.—Straight to curving, relatively small *Cruziana* showing fine transverse striae covering the lobes and irregular marginal ridges on either side of the central, main lobes. Structures display several morphologic variants showing narrower lobes and a wider median depression.

Etymology.—After its similarity with the arthropod ichnogenus *Diplopodichnus*.

Specimens.—Four slabs (INGEO-PI-NA°-1149, INGENO-PI-NA°-1154, INGENO-PI-NA°-1156, INGENO-PI-NA°-1160) containing 21 specimens.

Holotype.—Slab INGENO-PI-NA°-1149 (Fig. 8.1, lower specimen).

Description.—Horizontal, ribbon-like, relatively small bilobate trails preserved as positive hyporeliefs. Trails are straight to slightly curving displaying two subparallel lobes covered by faint, mostly transversal scratch marks or locally smooth. Irregular marginal ridges or levees are locally present in most of the specimens. Marginal ridges, present on one or both sides of the structure, are typically undulating and vary in width along the trace. Irregular marginal ridges are 0.5–2.1 mm wide. One specimen displays very locally a triple marginal ridge (Fig. 8.3, arrow). Some specimens are asymmetric terminating abruptly on one side of the structure (Fig. 8.3). Trace width is 5.8–9.2 mm, but commonly 6.4–6.8 mm. Lobes

range from 1.9–2.7 mm wide, typically closer to 2.2 mm. They are symmetrical and convex when the medial depression is small, and asymmetrical and flatter, inclining towards the medial axis in specimens with a wide medial depression (Fig. 8.1). Medial depression is between 0.1–2.6 mm wide, and is highly variable along individual specimens. Length is 21.9–167.3 mm. Scratch marks are very thin and form obtuse angles of 160°–180° on the lobes, showing a marked decrease at the medial depression. Specimens typically display variability in morphology from wider lobes with narrow axial depression into two narrower lobes separated by an irregular wide medial depression (Fig. 8.1), and ultimately into *Diplopodichnus* (tramline ridges, central depression > ridge width) (Fig. 7). In one large slab, structures seem to be oriented (Fig. 7), but the number of specimens is not large enough to warrant that this is not an artifact. Overlap among specimens occurs locally, although the density of trace fossils on the bedding plane is quite low (BP-BI of 2).

Remarks.—The presence of marginal ridges and the morphologic variation along the trail (i.e., gradation to two parallel narrow lobes separated by a wide medial depression) separate *Cruziana diplopoda* from *C. problematica* (for the later see Fillion and Pickerill, 1990, and Keighley and Pickerill, 1996). Another small form that displays intermittent marginal ridges is *Cruziana acadica* from the Upper Carboniferous of Eastern Canada (Keighley and Pickerill, 1996). However, *C. acadica* displays a more complex lobe morphology with smooth or

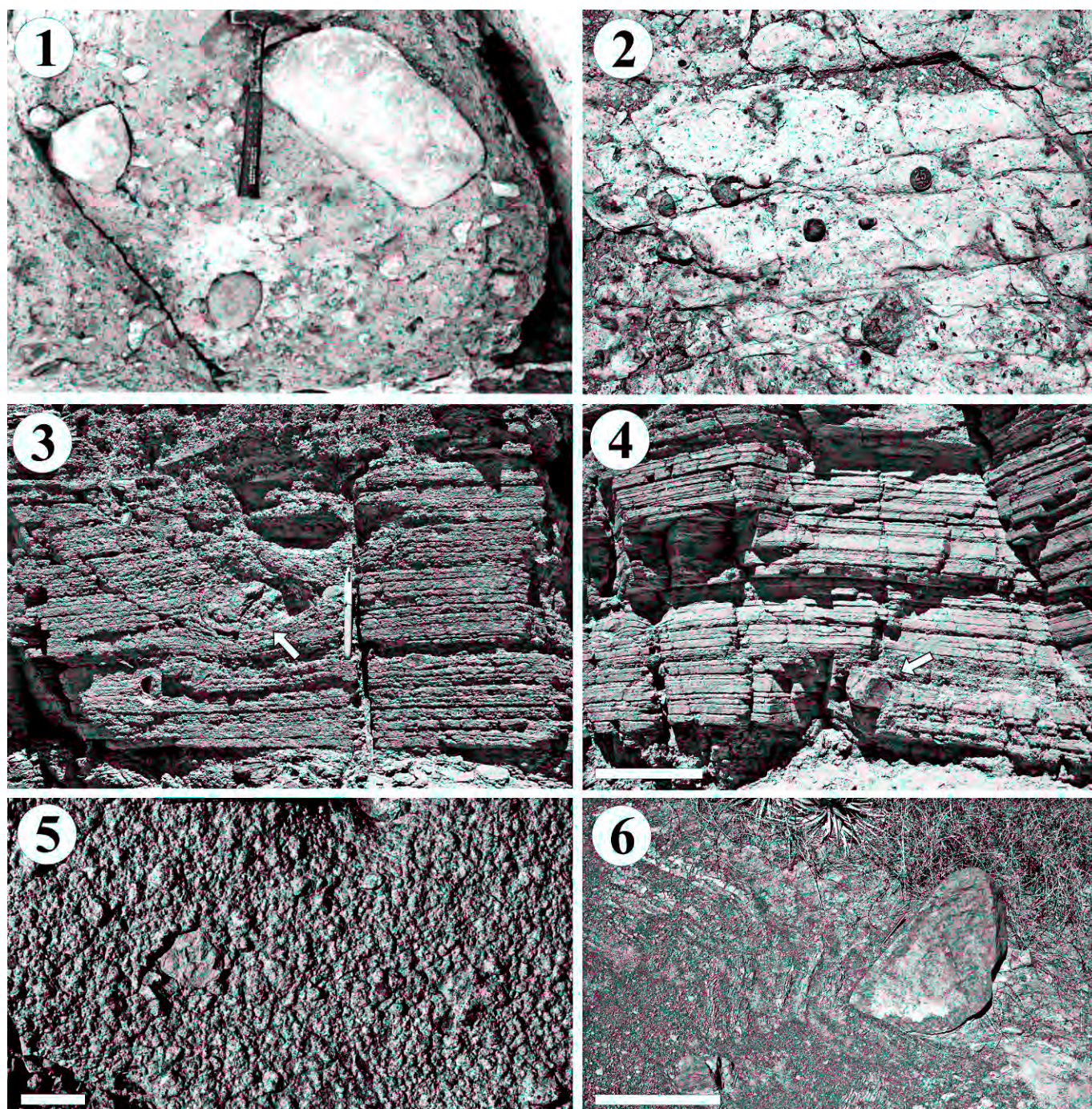


FIGURE 5—Sedimentary facies of the studied intervals in the Guandacol Formation, near Rio Huaco on the west flank of the Huaco anticline. 1, massive matrix-supported diamictite, note chaotic aspect, hammer is 33.5 cm long; 2, stratified matrix-supported diamictite, coin is 1.8 cm wide; 3, thinly bedded stratified diamictite, note thin bedding and dropstone (arrow), pen is 15 cm; 4, thinly bedded stratified diamictite, note dropstone (arrow), bar is 50 cm; 5, thinly bedded stratified diamictite, bedding-plane view, bar is 1 cm; 6, mudstone with a large dropstone, bar is 50 cm; 1–5, lower diamictitic interval; 6, lower part of the mudstone middle interval.

striated lobate pods which are absent in *C. diplopoda* (cf. Keighley and Pickerill, 1996, fig. 2A and p. 274). *Cruziana diplopoda* may display a wide medial furrow almost the size of the lobes, but lobes are irregular and commonly asymmetric, and tend to be inclined towards the medial line. Intergradations with *Diplopodichnus biformis* (i.e., compound structure *Cruziana diplopoda*-*Diplopodichnus biformis*) occur where lobes became symmetrical paired ridges separated by a distance equal or greater than the width of individual ridges (i.e., tramline-like morphology). However, appendage imprints or

striations may be locally present in *D. biformis* (cf. Brady, 1947; Keighley and Pickerill, 1996; Buatois et al., 1998). Additionally, the structure typically becomes shallower (i.e., less relief on the sandstone sole), indicating a change in burrowing behavior. While *Cruziana* is considered an endogenic, interfacial structure, *Diplopodichnus* is best regarded as an epigenic structure created by moving on poorly cohesive sediment (cf. Keighley and Pickerill, 1996; Buatois et al., 1998). The producer of *C. diplopoda* dived deeper into the substrate producing convex, well-developed lobes. Structures preserved as epichnial furrows

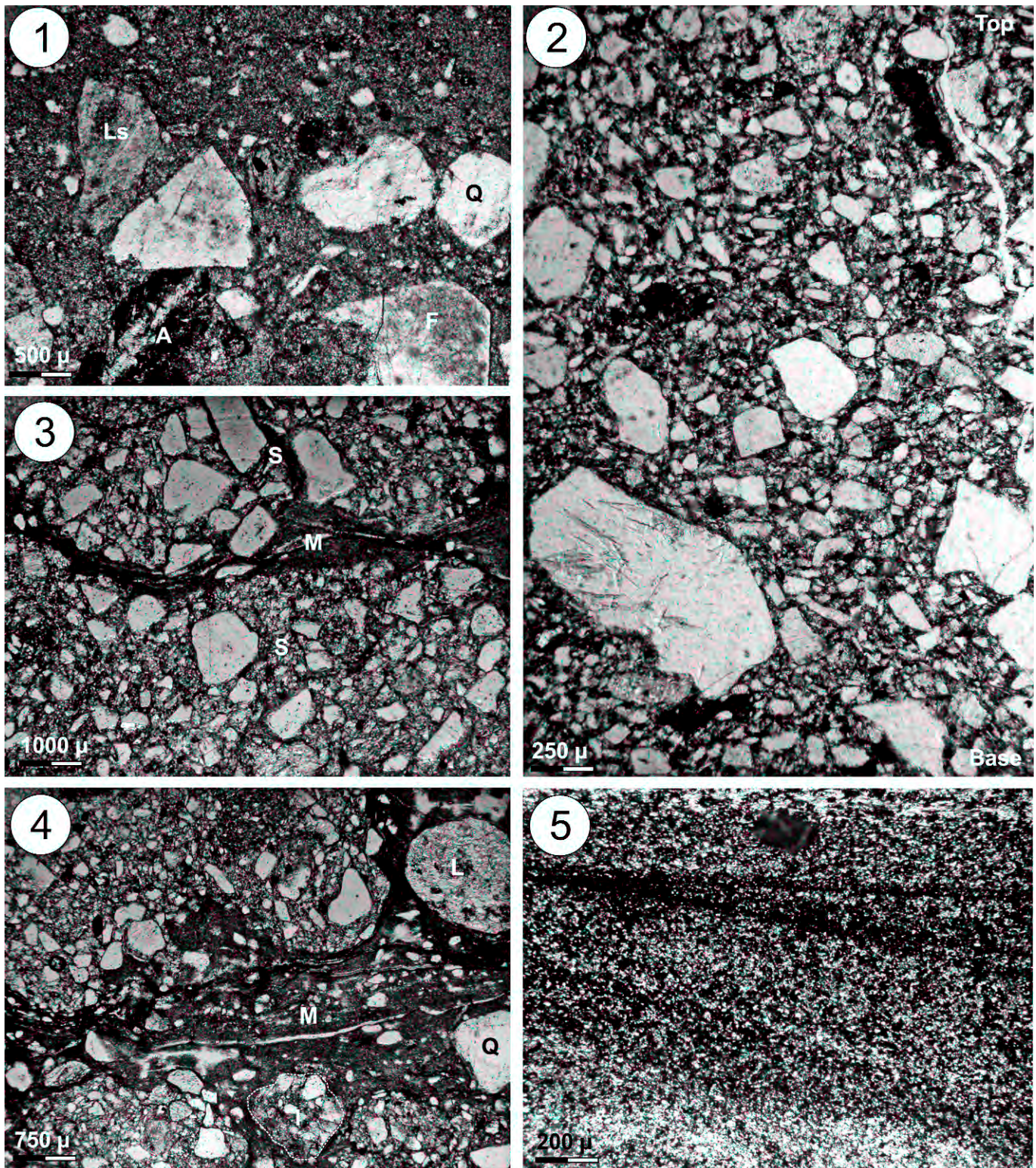


FIGURE 6—Thin-section photographs showing microscopic features of the matrix in the different types of diamictites and microstructures present in very fine-grained sandstone. 1, general aspect of massive matrix-supported diamictite, note sand-sized clasts (Q=quartz, F=feldspar and Ls=sedimentary lithic fragments) floating in a clayey matrix lacking any evidence of microstratification; 2, stratified matrix-supported diamictite exhibiting a microscopic normal-grading structure; 3, thinly bedded stratified diamictite showing thin veneers of mud (M) that separate sandy-rich layers (S); 4, thinly bedded stratified diamictite exhibiting intraclasts (I, white dotted line), quartz (Q) and lithic fragments (L), the muddy layer (M) shows evidence of soft-sediment deformation; 5, siltstone belonging to the interbedded mudstone and sandstone facies showing small sets of ripple-cross lamination indicating the activity of low-energy bottom currents (underflow currents).

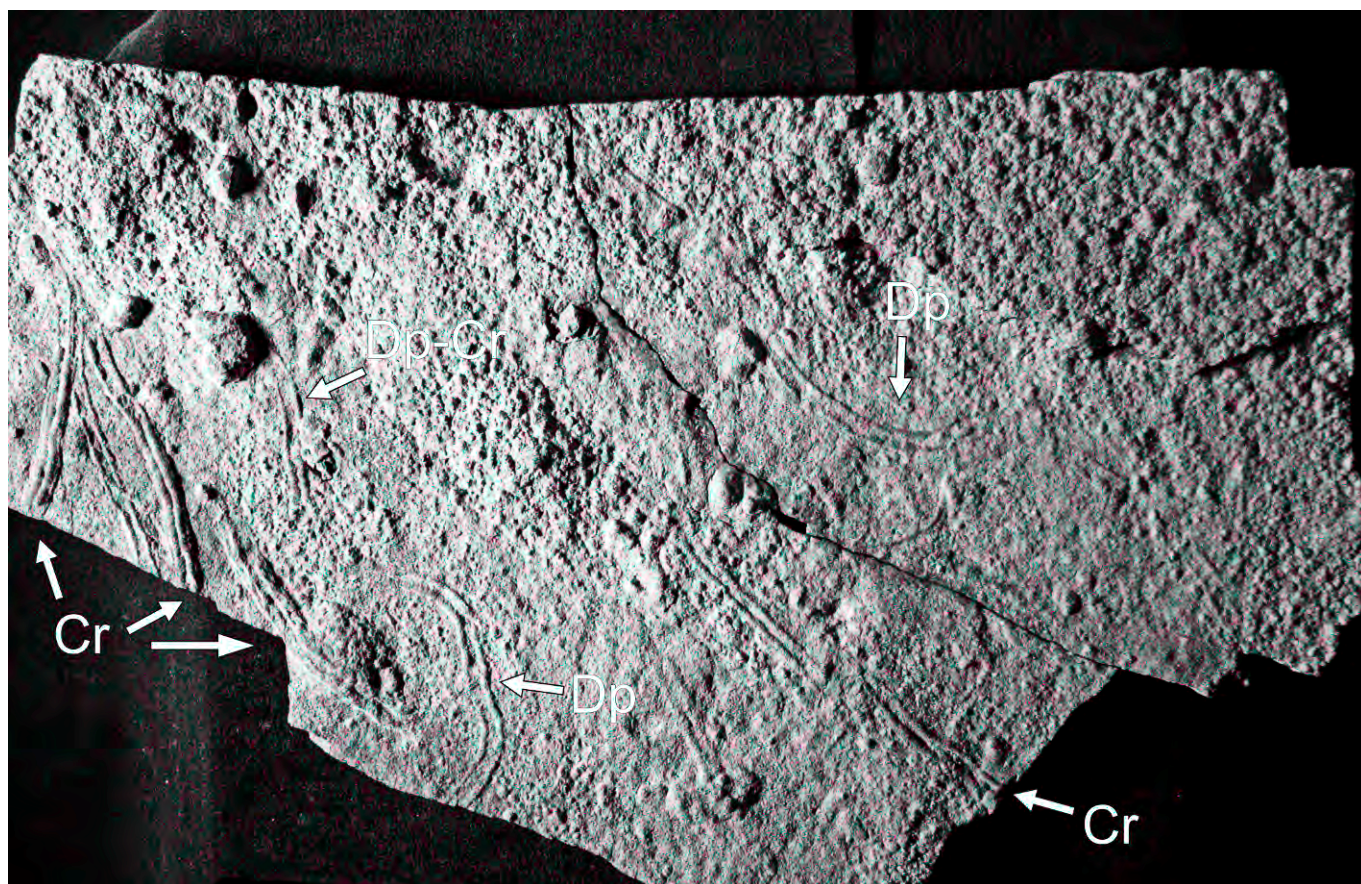


FIGURE 7—Slab INGEO-PI-NA°-1149 from the sandy debris-flows of the lower diamictite interval. *Cruziana diplopoda* (Cr), *Diploplodichnus biformis* (Dp), and compound trace fossils are present with associated dropstones, $\times 0.7$.

and ridges on the top of some of these beds, although most likely the product of the same tracemakers do not display the complex morphology of *C. diplopoda*, and are best regarded as *D. biformis*. Scratch marks on lobes are interpreted as the work of walking legs as the main burrowing tools. Specimens exhibiting marginal ridges most likely record the passive drawing of a skeletal part through the sediment, such as a carapace margin.

Some ribbon-like structures show local absence of scratch marks (i.e., “smooth lobes”). Absence of striations is interpreted as the deleterious result of substrate control (i.e., coarse grain size) on preservation of fine morphologic features. However, with careful inspection under horizontal light, faint transversal striations can be locally detected in almost all specimens analyzed. Following Young (1972) and Jensen (1997), bilobate structures displaying local, poorly preserved scratch marks are herein considered taphonomic variants of *C. diplopoda* rather than ichnospecies of the ichnogenus *Didymaulichnus* (contrary to previous assignments, see synonymy).

Distribution.—This ichnotaxon occurs in monospecific and paucispecific assemblages in matrix-supported fine-grained diamictite interpreted as debris-flow deposits (i.e., thinly bedded stratified diamictite facies) in the lower diamictite interval. Biogenic structures are directly associated to dropstones (see Taphonomy).

CRUZIANA cf. PROBLEMATICA (Schindewolf, 1921)

Figure 9.2–9.4

Synonymy.—*Didymaulichnus alternatus* ACEÑOLAZA AND BUATOIS, 1991, p. 95–97, pl. 1:1; *Didymaulichnus lyelli*

ACEÑOLAZA AND BUATOIS, 1991, p. 95–97, pl. 1:3; *Didymaulichnus alternatus* ACEÑOLAZA AND BUATOIS, 1993, p. 186, 187, fig. 3c; *Didymaulichnus lyelli* ACEÑOLAZA AND BUATOIS, 1993, p. 187–189, fig. 3a; *Didymaulichnus lyelli* PAZOS, 2000, p. 27, 28, fig. 3c; *Didymaulichnus lyelli* PAZOS, 2002a, p. 477, 478, fig. 7c; *Didymaulichnus* PAZOS, 2002b, p. 625, 626, fig. 5a, c.

Specimens.—Seven slabs (INGEO-PI-NA°-1162, INGEO-PI-NA°-1163, INGEO-PI-NA°-1164, INGEO-PI-NA°-1165, INGEO-PI-NA°-1166, INGEO-PI-NA°-1167, INGEO-PI-NA°-1168), containing 44 specimens.

Description.—Horizontal, bilobate structures preserved as positive hyporeliefs, and negative epireliefs. Trails are straight to slightly curving. Trace width is 5.1–9.4 mm, but commonly are 5.5–8.1 mm. Median furrow is 0.4–3.2 mm wide. Length is 7.6–80.3 mm. Scratch marks covering the lobes are clearly visible and typically transverse or they curve outwards (convex anteriorly) from the medial axis forming a range in angles from about 100° at the center to 180° at the lobe margin. Lobes are symmetrical and convex. Some linear structures are composed of a succession of interconnected rusophysid structures (Fig. 9.2). Intergradations with *Rusophycus* are very common. Scratch marks are very thin and subequal, and in a few specimens they seem to be clustered forming transverse wrinkles (Fig. 9.3, center). Marginal ridges are absent. Overcrossing among specimens is common (BP-BI of 4; Fig. 9.3). Locally, specimens terminate in *R. carbonarius* (Fig. 9.3, center). Some linear structures may be envisaged to be composed of a succession of poorly defined, interconnected rusophysid forms (Fig. 9.3).

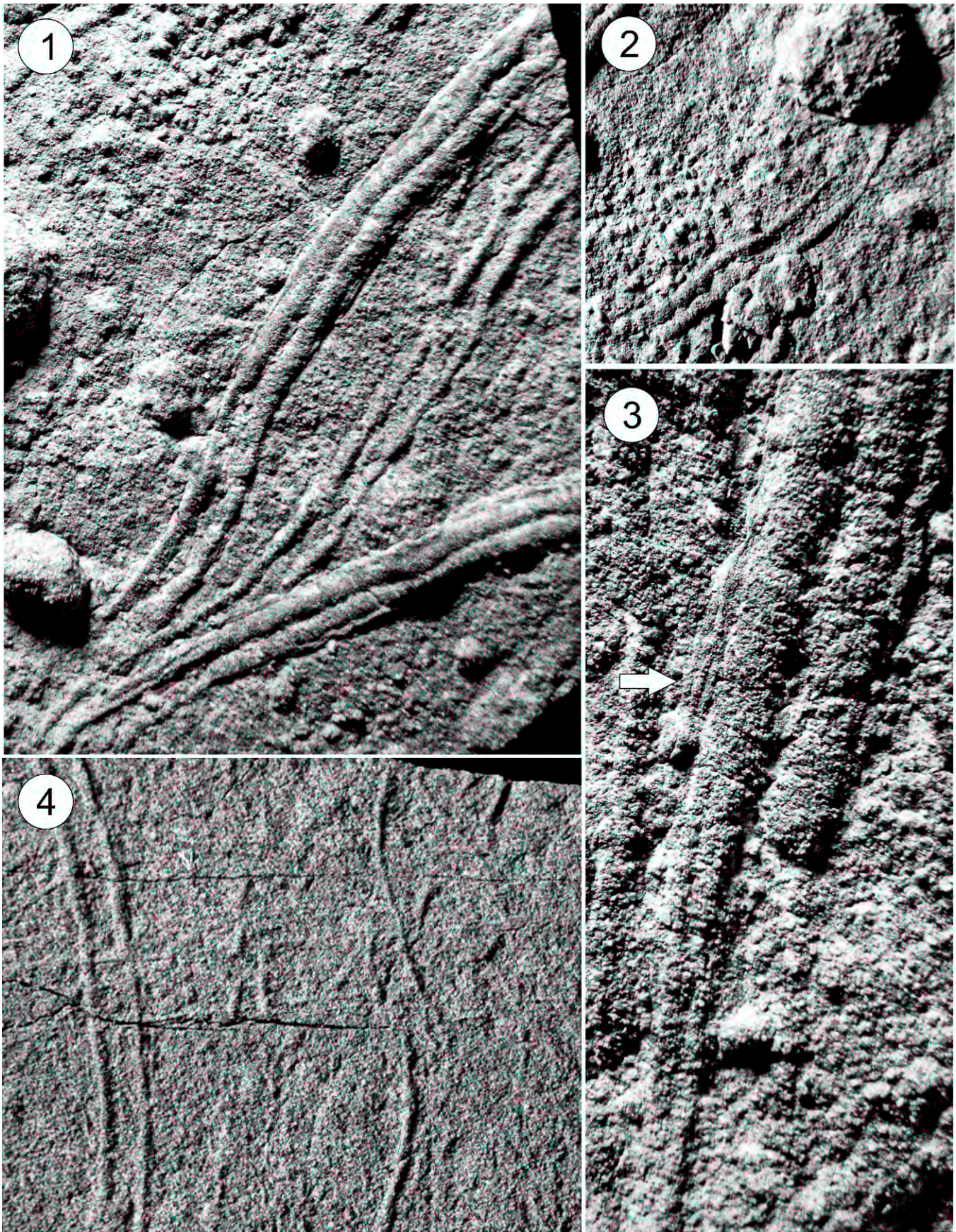


FIGURE 8—Trace fossils from the lower diamictite interval of the Guandacol Formation. 1, *Diplopodichnus biformis*–*Cruziana diplopoda* compound trace fossil with associated dropstone, $\times 2.2$, holotype is the lower specimen; 2, *Diplopodichnus biformis*–*Cruziana diplopoda* compound trace showing faint transverse scratch marks in bottom left and lacking marginal ridges, $\times 1.8$; 3, close up view of *Diplopodichnus biformis* transition to *Cruziana diplopoda* showing poorly preserved coarse scratch marks and triple marginal ridge (arrow), $\times 6.8$; 4, *Diplopodichnus biformis*, $\times 1.9$. 1–3, slab INGeo-PI-NA°-1149; 4, slab INGeo-PI-NA°-1158.

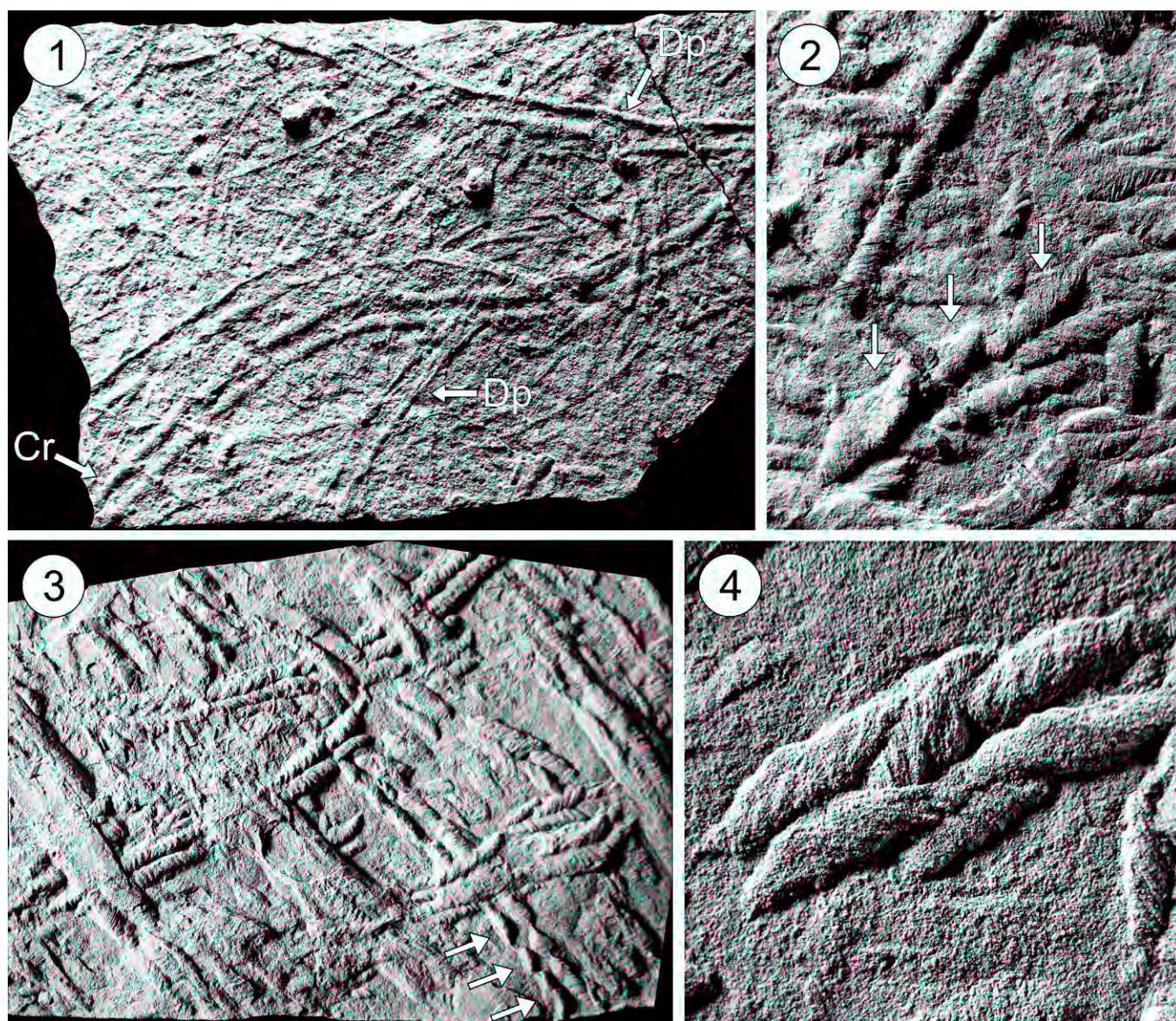


FIGURE 9—Trace fossils from the Guandacol Formation. 1, slab from the sandy debris-flows of the lower diamictitic interval showing a variation of *Cruziana diplopoda* (Cr) lacking marginal ridges and several *Diploplodichnus bififormis* (Dp) with associated dropstones, slab INGE0-PI-NA°-1154, $\times 1$; 2, three partially preserved specimens of *Rusophycus carbonarius* (arrows), slab INGE0-PI-NA°-1168, $\times 2$; 3, slab containing *Cruziana* cf. *problematica* with *Rusophycus carbonarius* (arrows)—*Cruziana* cf. *problematica* compound trace fossil, slab INGE0-PI-NA°-1166, $\times 0.7$; 4, close up of *Rusophycus carbonarius*—*Cruziana* cf. *problematica* compound trace fossil, slab INGE0-PI-NA°-1166, $\times 2.8$. 1, lower diamictitic interval; 2–4, middle mudstone interval.

Remarks.—Relatively small, simple *Cruziana* with transverse to nearly transverse scratch marks are traditionally included in *C. problematica* (e.g., Schindewolf, 1921; Bromley and Asgaard, 1979; Fillion and Pickerill, 1990; Schlirf et al., 2001; Minter et al., 2007a). Although there is a considerable variability within what has been called *C. problematica* in the literature, the analyzed material displays some features that are unknown in this ichnospecies. In particular, scratch marks are not always transversal and locally they have a tendency to cluster, forming transverse wrinkles (Fig. 9.3, center). The name *C. problematica* is preferred over *C. tenella* for reasons of nomenclatural stability (Mángano et al., 2002). Although considerably larger in size, some studied specimens show similarities with ribbon-like type *C. stromnessi* (Trewin, 1976, fig. 4Eb). However, variability of *C. stromnessi* is significantly larger than variability in the analyzed material (cf. Trewin, 1976, fig. 3).

Scratch marks covering the lobes are interpreted as the work of endopodites that served as the main burrowing tools. Although scratch marks are extraordinarily preserved in many specimens, claw morphology is not discernible. Contrastingly, several slabs exhibit specimens with almost completely smooth lobes as in *Didymaulichnus*. In fact, specimens previously assigned to *Didymaulichnus* in the studied unit (Aceñolaza and Buatois, 1991, 1993; Pazos, 2000, 2002a, 2002b) are now relocated in *Cruziana*. In many cases, scratch marks were only locally detected after casting the trace fossils, suggesting that careful inspection is required to avoid misidentification and overestimation of ichnodiversity. The type specimen of *Didymaulichnus lyelli* comes from the Lower Ordovician of northwest France (Rouault, 1850). In this unit, *D. lyelli* is associated with a wide variety of *Cruziana* ichnospecies. It is likely that specimens included in *D. lyelli* in the Ordovician of France are poorly preserved ichnospecies of *Cruziana*. If this is

the case, the ichnogenus *Didymaulichnus* is invalid. Specimens subsequently assigned to *Didymaulichnus* may either belong in *Cruziana*, if the presence of scratch marks is demonstrated, or may represent a still unnamed ichnogenus characterized by smooth bilobate hyporeliefs, most likely recording the locomotion structures of mollusks or arthropods in unstabilized soft substrates (e.g., Davis et al., 2007). One of the specimens in slab INGE-PI-NA°-1166 (Fig. 9.3, lower right) is particularly revealing as it resembles *D. alternatus* (see Aceñolaza and Buatois, 1993, fig. 3C), suggesting a clear substrate control in the morphology of these structures. Locally the ribbon-like structures consist of a succession of interconnected rusophysids or end up in a specimen of *Rusophycus carbonarius*, thus being intergradational with this ichnospecies (see Compound trace fossils). In terms of behavior, this move-stop strategy is most likely related to feeding activities rather than pure locomotion.

Considering the similar size ranges of *C. diplopoda* and *C. cf. problematica*, it may be argued that they represent different burrowing techniques. *Cruziana diplopoda* may record a tail-down or opisthocline burrowing position and *C. cf. problematica*, a head-down or prosocline burrowing position. However, the fact that *C. diplopoda* seems to be restricted to the lower diamictite levels is suggestive of a different producer. In addition, no intergradations between *C. diplopoda* and *C. cf. problematica* have been observed in the studied material. Nevertheless, based on available evidence, the possibility that both ichnospecies of *Cruziana* may have been produced by the same arthropod cannot be completely disregarded.

Distribution.—This ichnotaxon forms well-developed pavements within the very-fine to fine-grained sandstone (mudstone with interbedded sandstone facies) of the middle mudstone interval.

DIPLOPODICHNUS BIFORMIS (Brady, 1947)

Figures 7, 8.2, 8.4, 9.1

Synonymy.—*Diplopodichnus* PAZOS, 2002b, p. 625, 626, fig. 5d; *Didymaulichnus* PAZOS, 2002b, p. 625, 626, fig. 5b.

Specimens.—Eleven slabs (INGEO-PI-NA°-1149, INGE-PI-NA°-1150, INGE-PI-NA°-1151, INGE-PI-NA°-1152, INGE-PI-NA°-1153, INGE-PI-NA°-1154, INGE-PI-NA°-1155, INGE-PI-NA°-1157, INGE-PI-NA°-1158, INGE-PI-NA°-1161) containing 40 specimens.

Description.—Straight to sinusoidal trails consisting of two parallel ridges separated by a flat, wide, median furrow and preserved as positive hyporeliefs or negative epireliefs. Median furrow is equal in width or typically wider than lateral ridges. Total trace width is 2.9–6.2 mm. Individual lateral ridges are typically 0.8–1.6 mm wide. Median furrow is 1.2–3.7 mm wide. Length is 12.2–118.2 mm. Trails are straight to open sinusoidal. In many cases, the trail has segments in which only one ridge is preserved. This is particularly the case where the course of the trail is winding, the ridge in the concave part of the curve being the only one recorded (Fig. 8.4, right). Most specimens are smooth. However, a few specimens exhibit subtle, nearly transverse imprints or scratch marks covering the parallel ridges. Overlapping of specimens locally occurs, although assemblages are typically not dense (typically BP-BI of 2), although one stratigraphic level displays a BP-BI of 3 (Fig. 9). Intergradations with *C. diplopoda* are observed in at least two stratigraphic levels.

Remarks.—Tramline forms with a central depression equal or wider than individual ridges are herein included in *D. biformis*, following Keighley and Pickerill (1996) and Buatois et al. (1998). Some specimens exhibit faint imprints or

striations, particularly those displaying gradation with *C. diplopoda*. However, symmetrical subparallel ridges and the wider median furrow are considered diagnostic of *Diplopodichnus* (Keighley and Pickerill, 1996; Buatois et al., 1998). Some morphologic variants of *C. diplopoda* exhibit a wide central depression almost similar in width to the lobe width. In these cases, however, lobes are typically not symmetrical; they are quite irregular in shape (i.e., do not display a “tramline” morphology, see Fig. 8.1). Moreover, they tend to be slightly inclined towards the medial axis of the structure. Although locally grading with *C. diplopoda* forming paucispecific assemblages, *D. biformis* typically occurs forming monospecific assemblages in several stratigraphic levels. *Diplopodichnus biformis* forming continuous, relatively straight courses most likely records locomotion structures (repichnia). Single trails may record a sort of undertrack-fallout effect resulting from the animal balance being slightly displaced towards one side and generating a deeper ridge.

Distribution.—This ichnotaxon occurs in matrix-supported fine-grained diamictite interpreted as debris-flow deposits (i.e., thinly bedded stratified diamictite facies) of the lower diamictite interval.

RUSOPHYCUS CARBONARIUS (Dawson, 1864)

Figure 9.2–9.4

Specimens.—Four slabs (INGEO-PI-NA°-1162, INGE-PI-NA°-1164, INGE-PI-NA°-1166, INGE-PI-NA°-1167) containing seven specimens.

Description.—Bilobate, heart-shaped trace fossils preserved as positive hyporeliefs. Structures are typically elongated (i.e., length larger than width). Lobes parallel, forming commonly an anterior V-shaped gap, and slightly tapering backwards. However, a few specimens show posterior lobes pointing backwards and forming a small V-shaped gap (Fig. 9.4, lower left specimen). Lobes can be completely smooth or display perpendicular to oblique scratch marks. Width is 5.8–7.0 mm. Length is 6.6–11.3 mm, but typically 9.1–9.3 mm. Specimens are commonly aligned forming linear structures (Fig. 9.2, 9.4). *Rusophycus carbonarius* displays transitions to *C. cf. problematica*.

Remarks.—*Rusophycus carbonarius* is the preferred name to characterize small, coffee-bean to heart-shaped simple rusophycid structures with transverse to oblique scratch marks (Mángano and Buatois, 2003). Similar structures were previously included in *R. didymus*, but the later is most likely an inorganic structure (Keighley and Pickerill, 1996). However, as outlined by Schlirf et al. (2001), the location of the type material of *R. carbonarius* is at present unknown. Bromley and Asgaard (1979) included small rusophycids associated to *C. problematica* in *R. eutendorfensis* (Bromley and Asgaard, 1979). However, specimens assigned to *R. eutendorfensis* described by these authors differ from the Cuesta de Huaco specimens in exhibiting a quite complex ornamentation involving transverse and longitudinal scratch marks, very much mimicking trilobite mode of construction using biramous appendages (cf. Bromley and Asgaard, 1979, fig. 17). Moreover, Schlirf et al. (2001) reviewed Linck (1942) original description of *R. eutendorfensis*, and found that this ichnotaxon is characterized by being mostly smooth and elongate, displaying longitudinal striations on its lobes (Schlirf et al., 2001). In any case, the specimens analyzed herein are characterized by a simple ornamentation involving V-shaped or transverse striations covering the totality of the lobes. No longitudinal scratch marks have been detected in the analyzed material clearly separating it from *R. eutendorfensis*.

Distribution.—This ichnotaxon occurs in the very-fine to fine-grained sandstone (Mudstone with interbedded sandstone facies) of the middle mudstone interval, where it is commonly gradational with *C. cf. problematica*.

Compound trace fossils.—A trace fossil is described as compound when it contains two or more intergradational ichnotaxa (Pickerill, 1994; Pickerill and Narbonne, 1995; Minter et al., 2007b). Compound trace fossils are present in both the thinly bedded debris-flow deposits of the lower diamictitic interval and the very fine- to fine-grained sandstones of the middle mudstone interval. The first contains the compound trace fossil *Diplopodichnus biformis*–*Cruziana diplopoda* in which the width of the medial furrow decreases as each ridge widens internally to develop a convex lobe morphology, and maintaining a fairly constant total trace width (Figs. 7, 8.1, 8.2, and 8.3). This transition is interpreted as the product of increasing burrowing depth, resulting in deeper lobes covered by distinct transversal to slightly oblique scratch marks (recording the sweeping action of the endopodites), and the appearance of marginal ridges (recording the dragging of a skeletal part). It could be argued that *C. diplopoda* involves the whole range of morphologic variability previously described (making unnecessary to invoke *D. biformis*). Many stratigraphic bedding planes, however, host smooth, tramline-like parallel ridges with no transition to *C. diplopoda*, making the assignment of this material to *Cruziana* inappropriate. Also, tramline-like epichnial grooves (i.e., negative epireliefs) present at several stratigraphic levels within the lower diamictite are best included in *Diplopodichnus* rather than in *Cruziana*, in the absence of ornamentation.

The very fine- to fine-grained sandstone contains the compound trace fossil *Rusophycus carbonarius*–*Cruziana cf. problematica*. This intergradation has been well-recorded in other occurrences of these ichnotaxa, and represents a start-stop motion of the animal which burrows a short distance before nestling into a resting position. There are a number of smooth interconnected specimens (probably reflecting substrate control, see Controls on trace-fossil morphology), in which the trail is composed of a string of tear drop-like shapes (Fig. 9.3, bottom right). Assignment to *Cruziana* or *Rusophycus* in these specimens is more a matter of opinion than a decision dictated by a morpho-ethologic analysis.

Intergradations between ichnotaxa demonstrate that the structures involved were undoubtedly produced by the same tracemaker. A more difficult question to answer is whether the structures present in the lower diamictitic interval (i.e., *D. biformis* and *C. diplopoda*) and those hosted in the fine-grained sandstone of the middle interval record activities of the same tracemakers under different environmental conditions. It is possible that the four ichnotaxa described resulted from different behaviors performed by one type of arthropod. However, the absence of *C. diplopoda* in the overlying sandstone levels and the absence of marginal ridges in *C. cf. problematica* both suggest production by different type of arthropods. An alternative explanation will involve modifications in the burrowing technique of the tracemaker in relation to different behavior (e.g., locomotion vs. feeding). Based on available data both hypotheses are worth investigation (see Potential tracemakers and Controls on trace-fossil morphology).

POTENTIAL TRACEMAKERS

The morphology of the trace fossils as bilobate ridges and furrows ornamented with scratch marks clearly indicates that all structures were produced by arthropods. Most likely candidates are branchiopod crustaceans, in particular notos-

tracans, and/or trilobites. In fact, trilobite segmentation and burrowing technique best fit some fine morphologic details of *C. diplopoda*, while the relatively simple morphology of *C. cf. problematica* resembles structures commonly attributed to other non-trilobite arthropods (e.g., notostracans). Branchiopod crustaceans radiated during the Silurian–Devonian (Wills, 1998), being marine in their origin, although today they are almost totally restricted to freshwater settings. Based on studies of extant species, notostracans are able to crawl and plunge into the sediment to collect organic detritus with their anterior endopodites, or occasionally scavenge some animal remains (Fryer, 1988a, 1988b). Several occurrences of relatively small rusophycids (*R. eutendorfensis*, *R. carbonarius*, *R. furcosus*) and cruzianids (*C. problematica*) in continental deposits have often been attributed to notostracan branchiopods (e.g., Bromley and Asgaard, 1979; Schlirf et al., 2001; Minter et al., 2007a; Gand et al., 2008). Bromley and Asgaard (1972) observed *Lepidurus arcticus* in modern ponds of Greenland plowing into silt in search for food and producing a double furrow with a basal striated surface comparable to *C. problematica* (see also Bromley and Asgaard, 1972, fig. 3). More recently, Gand et al. (2008) documented structures included in the ichnogenus *Acripes*, and interpreted them as trackways of notostracans akin to modern structures produced by *Triops cancriformis*. It is clear from these examples that extant notostracans can produce both epigenic trackways and also endogenic plowings. Some shallow *D. biformis* found in the lower diamictite may have been produced as epigenic structures similar to those described above. However, the Cuesta de Huaco material is dominated by endogenic structures. No semicircular carapace impressions are present in the Cuesta de Huaco material, although its absence could be well explained as a preservational bias (i.e., the semicircular carapace impression being toponomically shallower than the burrowing legs producing the bilobate structure at the sandstone-siltstone interface). On the other hand, marginal ridges in *C. diplopoda* are adjacent to the lobes, and could not be produced by a notostracan semicircular carapace. Anostracan branchiopods have also been considered potential tracemakers of bilobated structures, particularly *Rusophycus* (e.g., Seilacher, 2007, pl. 11). However, extant anostracans of the genus *Branchinecta* stays mostly stationary on the substrate feeding by scraping the substrate with their endopodites rather than plowing through it (Fryer, 1966, 1983, 1985), most likely producing superficial scratch marks rather than endogenic bilobate structures (Minter et al., 2007a; Minter and Braddy, 2009). Conchostracans (“clamp shrimps”) is another primitive crustacean group that is often found in fresh and brackish-water environments. Conchostracans are bivalved and their legs do not extend further from the carapace. Contrary to anostracans and notostracans, they can completely enclose their bodies within the bivalved carapace. Laboratory studies indicate that when burrowing, conchostracans produce a microturbidity current that mobilizes the sediment and generates a microdepression or a winding furrow in the mud (Tasch, 1964). Although modern observations are limited, these structures do not resemble the analyzed material.

Ostracods are well-represented in many upper Paleozoic North American localities, but their fossilized remains have not been reported in the Guandacol Formation or in any other correlative unit in the Paganzo Basin. Moreover, ostracod leg movement is longitudinal rather than oblique or transversal, as observed in the analyzed material and the shell can not be opened flat (Bromley and Asgaard, 1972).

Isopods are a very successful eumalacostracan group, today inhabiting a wide range of marine, brackish and freshwater settings. Unquestionable members of the group are known from Upper Carboniferous marine rocks (Schram, 1979). Modern studies using both isopods and amphipods have produced a number of epireliefs, such as simple furrows, single furrows with levees on either side, as well as ribbon structures showing three positive lobes (Uchman and Pervesler, 2006). Unfortunately, no casts of epichnial structures were produced. However, the hyporeliefs that could be expected based on the description and photos of the lower surface of the structures (cf. fig. 4 in Uchman and Pervesler, 2006) are not similar to the bilobate ornamented structures described herein. In any case, the ichnogenus *Isopodichnus* which has been used in the past to refer to small bilobate hyporeliefs (now included in the ichnogenus *Cruziana* and *Rusophycus*) has often been attributed to isopods (e.g., Pollard, 1985; Gingras et al., 2008). Whether extinct isopods were able to burrow in a trilobite-like way remains an open question.

A significant morphologic element of *C. diplopoda* is the presence of marginal ridges. This morphologic feature could be produced by the genal or pleural spines of a trilobite. Although trilobites are extremely rare in the upper Paleozoic of Gondwana, the trilobite genus *Australosutura* is known from the upper Namurian to lower Westphalian of the Tepuel-Genoa Basin in southern Argentina, and is preserved in postglacial facies immediately overlying the diamictite (Amos et al., 1960). This genus is also known from the Visean Bayou Manard Member of the Moorefield Formation in North America as well as the Westphalian of the Kuttung series in New South Wales, Australia (Amos et al., 1960; Ormiston, 1966; Hahn et al., 2001). Functional analysis of *Australosutura* reveals morphologic features of a soft bottom dweller. This genus is characterized by a strongly inflated cephalon and glabella, raised double eyes, high positioning of the eyes and the presence of short genal spines close to the body contour. The presence of genal spines almost attached to the body allows production of marginal ridges of *C. diplopoda*, and suggests *Australosutura* as a potential tracemaker candidate, at least for this ichnotaxon (and intergradational *Diplopodichnus bififormis*). The only recovered complete specimen of *Australosutura gardneri* measures 20.0 mm between the genal spines, which is about twice the average width of the cruzianids from the Guandacol Formation. However, four specimens of *A. gardneri* from Australia show smaller size (maximum width between genal spines 12.0–17.0 mm). Morphologic features of *C. diplopoda*, including its plowing nature, are reminiscent of trilobite behavior. The fact that trilobite remains have been found in coeval and similar facies makes it plausible to envisage these organisms as the most likely producers of *C. diplopoda*, suggesting that trilobites inhabited brackish-water fjord settings during the Late Carboniferous. The other bilobate structures of the Guandacol Formation displaying a simpler bilobate morphology, in particular *C. cf. problematica* and *R. carbonarius*, could have been produced by non-trilobite makers, as discussed above. The fact that *C. diplopoda* is never intergradational with *C. cf. problematica* points out to different tracemakers. However, the possibility of the same producer moving within different substrate and using different burrowing techniques can not be completely ruled out.

CONTROLS ON TRACE-FOSSIL MORPHOLOGY: THE INTERPLAY OF BEHAVIOR AND SUBSTRATE

Trace fossil morphology is controlled by both intrinsic (anatomy of the producer and behavior) and extrinsic factors

(substrate). Grain size and substrate consistency are significant controls on trace-fossil preservation in the Cuesta de Huaco succession. The very fine- to fine-grained sandstone interbedded with mudstone preserves exquisite scratch marks poorly visible or absent in specimens preserved in the coarser-grained, thinly bedded, stratified diamictite. Although preservation of fine morphologic details is limited in the diamictite facies, the fact that biogenic structures are preserved in such a coarse-grained lithology is in itself exceptional, opening a window to paleoecologic information on Paleozoic fjords. Sedimentary facies within this lower interval record the severe conditions of fjord sedimentation. Bedding surfaces displaying *C. diplopoda* and *D. bififormis* most likely record snapshots of animal activity following debris-flow sedimentation events. Subsequent dropstone fall-out and higher rates of debris-flow deposition may have only provided time for short-term bioturbation events.

In contrasting, the overlying fine-grained sandstone facies are characterized by a higher bedding-plane trace-fossil density (BP-BI of 4) and provide clues for a more complex taphonomic pathway. Linear structures produced by interconnected rusophycid structures are typically smooth and display evidence of soft sediment deformation (i.e., bulgy, asymmetrical lobes) suggestive of very soft, water-rich substrate (Fig. 9.3). However, specimens of *C. cf. problematica* and *R. carbonarius* cross-cutting these structures display exquisitely preserved morphologic details suggesting a later stage of formation when the sediment was partially dewatered and firmer (Fig. 9.2, 9.3). In short, bedding planes with *C. cf. problematica* and *R. carbonarius* record palimpsest surfaces, involving changes in substrate consistency and most likely the recurrent feeding activities, of a low-diversity arthropod community.

Assessment of biodiversity based on ichnodiversity is not straightforward and may be misleading. The question of whether the diamictite trace-fossil assemblage 1 (*Cruziana diplopoda*–*Diplopodichnus bififormis*) actually records the same producers as the fine-grained sandstone trace-fossil assemblage 2 (*Cruziana cf. problematica*–*Rusophycus carbonarius*) is worth exploration, although no definite answer can be provided. Seilacher (1970, 1985, 1990, 1992) proposed that in the case of trilobite-produced *Cruziana*, a “tail-down” body position would allow any pleural spines (or genal spines, Crimes, 1970) to drag along the substrate producing marginal ridges along either side of the *Cruziana*. Slightly tilted organisms would result in ridges being present on only one side of the structure. The “tail-down” body position also produces fainter scratch marks due to the use of the smaller posterior legs for excavation and the occasional delicate imprints of posterior exopodites. This opisthocline (i.e., “tail-down”) body position would explain *C. diplopoda* and transitions to *D. bififormis*. On the contrary, if the organism is burrowing in a “head-down” position, the spines do not drag in the sediment and more conspicuous scratch marks record the movement of the stronger anterior walking legs. This prosocline (“head-down”) body position also results in an obtuse angle of the scratch marks to the medial furrow. A prosocline to isocline burrowing position combined with a frequent short-stop and keep-moving strategy could explain morphologic variability observed in the *C. cf. problematica*–*R. carbonarius* trace-fossil assemblage. Although this mode of construction was inferred based on trilobite-produced cruzianids, other arthropods may have developed convergent behavior (cf. Bromley and Asgaard, 1972). In fact, as previously stated, the lack of intergradation and the facies restriction of *C. diplopoda* and *D. bififormis* to the lower

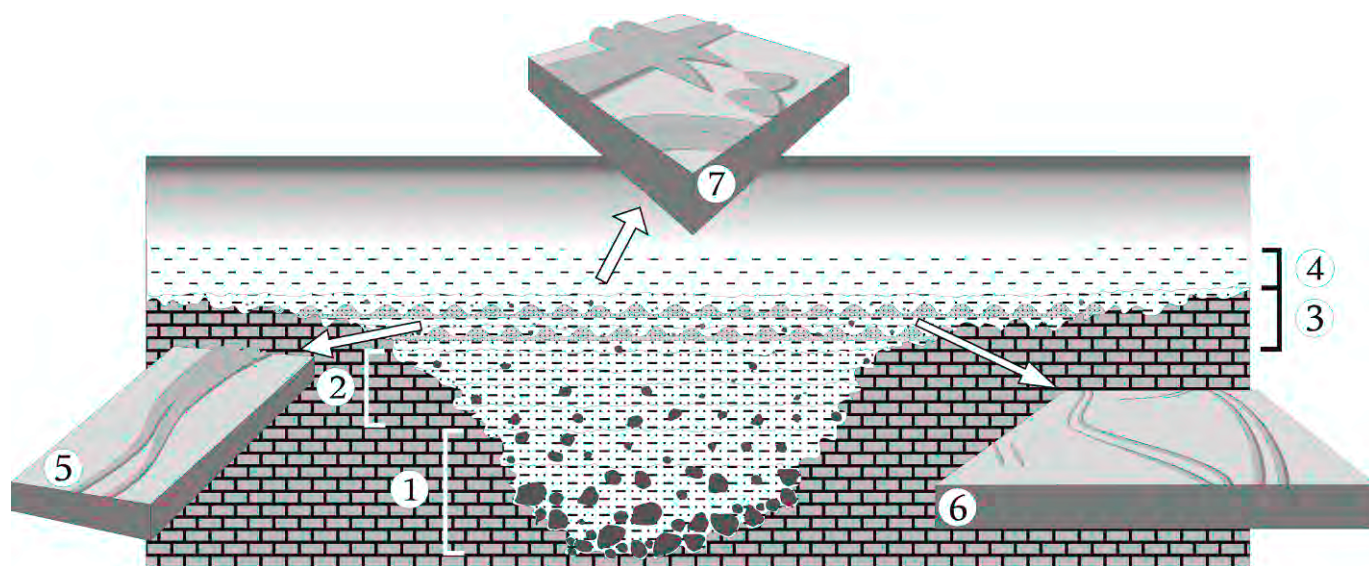


FIGURE 10—Incised valley reconstruction. Note that the San Juan Formation has been carved out (represented by the brick pattern) and the Guandacol Formation has been deposited as the valley infill. 1, massive matrix-supported diamictite facies; 2, stratified matrix-supported diamictite facies; 3, thinly bedded stratified diamictite facies; 4, mudstone facies with large dropstones; 5, *Diplopodichnus bififormis*–*Cruziana diplopoda* compound trace fossil; 6, *Diplopodichnus bififormis*; 7, *Cruziana cf. problematica* and *Rusophycus carbonarius*–*Cruziana cf. problematica* compound trace fossil. 1–3, lower diamictitic interval; 4, lower part of the middle mudstone interval.

diamictite, and of *C. cf. problematica* and *R. carbonarius* to sandstone of the middle mudstone interval is suggestive of more than one culprit rather than mere changes in burrowing techniques of a single producer.

IMPLICATIONS FOR PALEOENVIRONMENTAL RECONSTRUCTIONS

The trace fossil-bearing deposits of the Guandacol Formation were formed in a small fjord carved out by glacial retreat (Fig. 10). Transversal orientation with respect to the regional paleoshoreline and small size suggests side-entry valleys within the large-scale Guandacol fjord in the area. The lower diamictitic interval records the paleovalley infill. Massive matrix-supported diamictite filled the valley axis and represents lodgment till. These deposits are overlain by a stratified matrix-supported diamictite, onlapping towards the wall of the paleovalleys and recording subaqueous gravity flows and fluvial reworking of glacial deposits. The tops of the paleovalleys are filled with a thinly bedded stratified diamictite, which records sedimentation from debris flows overprinted by ice-rafting and rain-out processes. The middle mudstone with interbedded fine-grained sandstone interval represents the subsequent basinwide transgression. The upper sandstone-dominated interval is clearly regressive, and records deltaic progradation (Limarino et al., 2002; Pazos, 2002a).

Fjords include a wide variety of environmental stresses that affect benthic colonization, including extreme salinity dilution, high rates of sedimentation, variable degree of substrate consolidation, oxygen-depleted conditions, high water turbidity, and intense storm activity (Syvitski et al., 1987; Buatois and Mángano, 2011). In polar areas, seasonal light restriction and floating ice masses contributing to ice-rafted debris rainfall may be important stress factors. Salinity dilution is undoubtedly one of the most significant stress factors because fjords are characterized by strong meltwater discharge issuing from seasonal glacial melting. Increased precipitation and runoff during summer lead to reduced salinity (e.g., Feder and Keiser, 1980). As a result, most Cenozoic and Holocene

fjords, unless anoxic, are dominated by brackish-water ichnofaunas (Eyles et al., 1992; Corner and Fjalstad, 1993).

The nature of salinity conditions during deposition of the Guandacol Formation and similar units in Gondwana has been strongly debated (Buatois et al., 2010 and references therein). There is general agreement that melting of the ice caps released a significant amount of freshwater to fjord and related coastal areas (Buatois et al., 2001, 2006, 2010; Pazos, 2002b; Buatois and Mángano, 2003). In fact, freshwater conditions may have prevailed for some time in these fjords allowing the establishment of freshwater ichnofaunas dominated by grazing trails and arthropod trackways (Buatois et al., 2006, 2010). In the Cuesta de Huaco area, this ichnofauna occurs essentially above the maximum flooding surface and includes a combination of elements of the *Mermia* and *Scoyenia* ichnofacies (Buatois et al., 2006, 2010).

Interestingly, the combined *Mermia* and *Scoyenia* ichnofacies is absent in the lower diamictitic interval and the lowermost strata of the middle mudstone interval. Instead, the early transgressive deposits of the Guandacol Formation contain the distinctive monospecific or paucispecific trace-fossil assemblages of bilobate trails attributed to arthropods described in this paper. These assemblages are composed of facies-crossing ichnotaxa. *Diplopodichnus* has been almost exclusively recorded in continental to marginal-marine environments (Buatois et al., 1998), while simple cruzianids comparable to *C. problematica* and *R. carbonarius* are well-known ichnotaxa in both continental and shallow-marine deposits (Seilacher, 1970, 1992; Mángano and Buatois, 2003; Buatois and Mángano, 2007; Minter et al., 2007a). In fact, it should be noted that most *Cruziana* and *Rusophycus* ichnospecies display a relatively restricted paleoenvironmental range. A few ichnospecies, such as *Cruziana pascens*, *Rusophycus eutendorfensis* and *Rusophycus versans*, only occur in continental deposits, while most of them (e.g., *C. rugosa*, *C. semiplicata*, *C. omanica*) are present in marine or brackish-water settings, and some (e.g., *C. problematica*, *R. carbonarius*)

are present in both. Specimens assigned to *R. versans* in Upper Cambrian marine deposits of Poland (Sadlok and Machalski, 2010) belong in *R. moyensis* and *R. polonicus*.

Cruziana diplopoda described herein exhibits features compatible with the morphology of a trilobite, *Australosutura*. Trilobites have been traditionally considered marine organisms, but incursions in brackish-water settings, based on the presence of complex cruzianids, have been reported (e.g., Selley, 1970; Mángano and Buatois, 2003; Buatois et al., 2005). Ichnologic evidence from the lower intervals of the Guandacol Formation suggests that trilobites may have also inhabited the cold, diluted waters of fjords during the Late Carboniferous. Although morphologic variability of Guandacol bilobate structures could be explained in terms of body position and segmental variation in trilobites (cf. Seilacher, 1970), very simple structures, such as *C. cf. problematica* and *R. carbonarius* have proved to be the product of other arthropods, resembling a trilobite-like constructional mechanism. However, it is worth noting that marginal ridges, such as those present in *C. diplopoda*, seem to be uncommon in the freshwater ichnospecies of *Cruziana*. In addition, the presence of linguliformean brachiopods in coeval beds nearby strongly suggests that brackish-water conditions prevailed during the early phase of the transgression. Salinity changes due to influx of glacial meltwater to a marine influenced fjord may explain the small body size of organisms resulting in small trace fossils (Buatois et al., 2010).

High rates of sedimentation are persistent in fjord environment as a result of high fluvial input. In addition, mass-sediment transport, aeolian transport and input from wave and tidal erosion may also play significant role (Syvitski et al., 1987). As a result of high sedimentation rates and steep margins, fjords are strongly affected by sediment-gravity flows, most commonly turbidity currents and debris flows. Sudden influx of sediment affects the epifauna by subjection to flocculation and agglomerate rain, microturbidity flows due to biologic resuspension of unstable slope sediment, and disturbances due to major slides (Farrow et al., 1983). Bioturbation is commonly inhibited in the innermost zone of the fjord due to rapid sediment accumulation (Buatois and Mángano, 2011). Rapid sedimentation is also a limiting factor for larval settlement (Farrow et al., 1983).

Trace-fossil density is variable throughout the succession as a result of high sedimentation rates and high energy. Density of trace fossils is low (BP-BI of 2) in the debris-flow deposits of the lower diamictitic interval and relatively high (BP-BI up to 4) in the mudstone middle interval, which contains overlapping and cross-cutting *C. cf. problematica* and *R. carbonarius*. This pattern reflects different colonization windows as a result of contrasting sedimentation rates (Pollard et al., 1993). The debris flows were deposited very quickly allowing for short-term colonization by an opportunistic benthic fauna, while the mudstone mantling the very fine- to fine-grained sandstone was formed by slow suspension fall-out allowing for several successive colonization events recorded in a single bedding plane.

It may be argued that the presence of trace fossils in direct association with debris-flow deposits reflects colonization by doomed pioneers. In the doomed pioneer model (Föllmi and Grimm, 1990; Grimm and Föllmi, 1994), animals living in nearshore well-oxygenated settings are transported basinward into anoxic settings via sediment gravity flows. The doomed pioneers construct biogenic structures in completely anoxic sediments, but do not persist in such settings, dying from suffocation. However, there is no evidence of anoxia in these

deposits, and the fact that bilobate trace fossils are also present in the overlying interbedded mudstone and sandstone deposits indicates that the fjord bottom was well oxygenated during the early stages of the transgression, arguing against colonization by doomed pioneers.

CONCLUSIONS

The early Late Carboniferous Guandacol Formation at Cuesta de Huaco, Precordillera of western Argentina, records the glacial to postglacial transition. This formation has been subdivided into three intervals: a lower diamictitic interval; a middle mudstone-dominated interval, and an upper sandstone-dominated interval. While the lower interval records infill of a fjord incised into the underlying Ordovician limestone, the middle and upper intervals reflect postglacial sedimentation.

Four ichnotaxa are present in the lower and middle intervals of the Guandacol Formation. These occur as both discrete and compound trace fossils. *Diplopodichnus biformis* and *Cruziana diplopoda* n. isp. are present in the thinly bedded stratified diamictite in the upper section of the lower interval. This diamictite record deposition from debris flows with dropstones reflecting overprinting of ice-rafting and rain-out processes.

Cruziana cf. problematica and *Rusophycus carbonarius* are present in very-fine to fine-grained sandstone layers interbedded with dropstone-bearing mudstone in the lower section of the middle interval. Mudstone deposits record the interplay of suspension fall-out sedimentation, ice-rafting, rain-out processes and low-energy underflows, while the interbedded sandstone is interpreted as the product of storms.

Brackish-water conditions during the early phase of the transgression are indicated by the presence of linguliformean brachiopods in coeval beds nearby. Stress factors typical of brackish-water environments may be invoked to explain the small size of the trace fossils and the low ichnodiversity.

Based on morphologic evidence, arthropods are the putative producers of the biogenic structures analyzed. Trilobites are proposed as potential tracemakers of *Cruziana diplopoda*–*Diplopodichnus biformis* (lower diamictite interval) and notostracans (middle mudstone interval) of *Cruziana cf. problematica*–*Rusophycus carbonarius*. Alternatively, different ichnotaxa may have resulted from changes in body position and burrowing technique by the same tracemaker controlled by under different substrate conditions. However, absence of intergradations between *C. diplopoda* and *C. cf. problematica*, and facies distribution of these ichnotaxa militate against the hypothesis of a single kind of organism as producer of the range of arthropod structures described.

Contrasting trace-fossil density in the bedding planes analyzed is essentially a response to the interplay of sedimentation rates and energy. Density of trace fossils is low in the debris-flow deposits of the lower diamictitic interval and relatively high in the mudstone-dominated middle interval. This pattern reflects different colonization windows as a result of contrasting sedimentation rates. The debris flows were deposited quickly allowing for short-term colonization by an opportunistic benthic fauna, while the mudstone mantling the interbedded sandstone was formed by slow suspension fall-out allowing for successive colonization events on individual beds.

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