

Lower/Middle Ordovician (Arenigian) shallow-marine trace fossils of the Pochico Formation, southern Spain: palaeoenvironmental and palaeogeographic implications at the Gondwanan and peri-Gondwanan realm

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Abstract

Nineteen ichnospecies belonging to thirteen ichnogenera (*Archaeonassa*, *Catenichnus*, *Cochlichnus*, *Cruziana*, *Didymaulichnus*, *Diplichnites*, *Gordia*, *Lingulichnus*, *Lockeia*, cf. *Monocraterion*, *Planolites*, *Ptychoplasma*, and *Rusophycus*) occur in the Pochico Formation (Arenigian) in the Aldeaquemada section, Sierra Morena, southern Spain, just above the Armorican Quartzite. They belong to the archetypal *Cruziana* ichnofacies, indicating a lower shoreface-upper offshore zone. The low degree of sediment reworking may be due to a high rate of sedimentation. The trace fossil assemblage, rich in large *Cruziana*, is typical of the Armorican Quartzite that developed on the margins of Gondwana and peri-Gondwanan microcontinents. The distribution of ichnofauna during the Early Ordovician was partly palaeogeographically controlled, although ichnological data from the literature point to paths of migration between Gondwana, Baltica and Laurentia. Differences between the ichnofauna of Gondwana and Baltica could be conditioned by facies (clastics in Gondwana and carbonates in Baltica) causing a taphonomic filter, because *Cruziana* requires diversified clastic deposits for preservation. The ichnofauna would also be influenced by trophic group amensalism between filter feeding and deposit feeding fauna, the former prevailing in Baltica and the latter in Gondwana.

Keywords: Ichnofossils, Arenigian, clastic sediments, Gondwana, peri-Gondwana, Iberia

Resumen

Se presenta el análisis sedimentológico/icnológico de los materiales de la Formación Pochico (Arenigian) de la sección de Aldeaquemada, Sierra Morena, Sur de España, provincia de Jaén, justo por encima la Cuarcita Armoricana. Se han reconocido diecinueve icnoespecies pertenecientes a trece icnogéneros (*Archaeonassa*, *Catenichnus*, *Cochlichnus*, *Cruziana*, *Didymaulichnus*, *Diplichnites*, *Gordia*, *Lingulichnus*, *Lockeia*, cf. *Monocraterion*, *Planolites*, *Ptychoplasma*, y *Rusophycus*). Las características icnológicas junto con los rasgos sedimentológicos permiten asignarlas a las icnofacies arquetípicas de *Cruziana*, comunes de las zonas de shoreface inferior a offshore superior. El grado de bioturbación relativamente bajo puede estar relacionado con una alta tasa de depósito. La asociación registrada, dominada por grandes *Cruziana*, es típica de la Cuarcita Armoricana desarrollada en los márgenes de Gondwana y peri-Gondwana. La distribución de icnofósiles del Ordovícico temprano posee, en gran medida, un control paleogeográfico, aunque datos icnológicos procedentes de la literatura indican la existencia de migraciones entre Gondwana, Baltica y Laurentia. Las diferencias entre las asociaciones de Gondwana y Báltica pueden estar asociadas a las diferentes facies, con el dominio de materiales clásticos en Gondwana y de carbonatados en Báltica, causando un filtro tafonómico ya que el potencial de conservación de *Cruziana* es mucho mayor en las facies clásticas heterolíticas. A estos factores habría que añadir las estrategias de alimentación asociadas, diferenciando entre filtradores y aquellos que se alimentan de las partículas existentes en el sedimento, los primeros podrían verse favorecidos en Báltica y los segundos en Gondwana.

Palabras clave: Icnofósiles, Arenigiense, sedimentos clásticos, Gondwana, peri-Gondwana, Iberia

1. Introduction

Arenigian shallow-marine clastic sediments of Western Europe, North Africa, South America and some parts of North America are characterized by abundant trace fossils, including large *Cruziana*, an ichnogenus first described from such deposits in Bolivia (d'Orbigny, 1842). Trace fossils of these facies are largely associated with quartzitic sandstones, in France and on the Iberian Peninsula largely attributed to the Armorican Quartzite (Grès Armoricaïn) (Gutiérrez-Marco *et al.*, 2002). The Armorican Quartzite, dated mostly to Arenigian, was deposited in several disconnected basins supplied from local sources (Torsvik and Cocks, 2011). The Armorican Quartzite and associated deposits rich in quartzite sandstones may be considered as a facies deposited in shallow seas in the margin part of Gondwana and peri-Gondwanan microcontinents in the stage of rifting and early drift of Avalonia (Gutiérrez-Alonso *et al.*, 2007). This area was a southernmost part of Gondwana and was situated near the South Pole during the Early Ordovician (e.g., Cocks and Torsvik, 2002).

Although a general ichnological characterization of the Armorican Quartzite is lacking to date, trace fossils are an important feature of this facies. They have been described in several sections and areas on the Iberian Peninsula (e.g., Delgado, 1886a, b; Bouyx, 1966; Baldwin, 1975, 1977a, b, c; Crimes and Marcos, 1976; Kolb and Wolf, 1979; Pickerill *et al.*, 1984; Romano, 1991; Neto de Carvalho, 2006; Sá *et al.*, 2011) and in France (Rouault, 1850; Lebesconte, 1883, 1886; Durand 1984, 1985a, b; Fortey and Owens, 1999).

In this paper, we describe a trace fossil assemblage in one section of the Armorican Quartzite facies, just on the transition of the Armorican Quartzite *sensu stricto*, and overlying heterolithic facies of the Pochico Formation in the Aldequemada section (Cimbarra section in Rey and Hidalgo, 2004), Central Iberian Zone (Fig. 1). Its palaeoenvironment is interpreted in the Gondwanan and peri-Gondwanan context. Considering that the Pochico Formation is ichnologically almost unexplored, a discussion of the more general ichnological features of this facies based on the literature serves to support our interpretation. Collected trace fossils are housed in the Department of Stratigraphy and Palaeontology, Faculty of Sciences, University of Granada (label Aq).

2. Geological setting

During the Early Ordovician, the Iberian Massif formed part of the northwest margin of Gondwana (e.g., Von Raumer *et al.*, 2003). The studied area is located in the southernmost part of the Iberian Massif, in the Central Iberian Zone, according to a subdivision into different zones (Fig. 1A) based on different stratigraphic-tectonic-metamorphic features (Julivert *et al.*, 1972). The studied outcrop is located in the Cascada de la Cimbarra, in the Sierra Morena Mountains (Fig. 1B), province of Jaen, 2.5 km south of Aldequemada

village by the El Negrillo pool of the Guarrizas River (GPS co-ordinates: N38°23.150'; W003°22.474'; ±9 m). Additional material was observed in the surroundings, especially at the bottom of the valley near this site, where nearly horizontal beds offered other in situ occurrences (GPS co-ordinates: N38°23.136'; W003°22.332'; ±8 m). Both localities are within the Despeñaperros Natural Park.

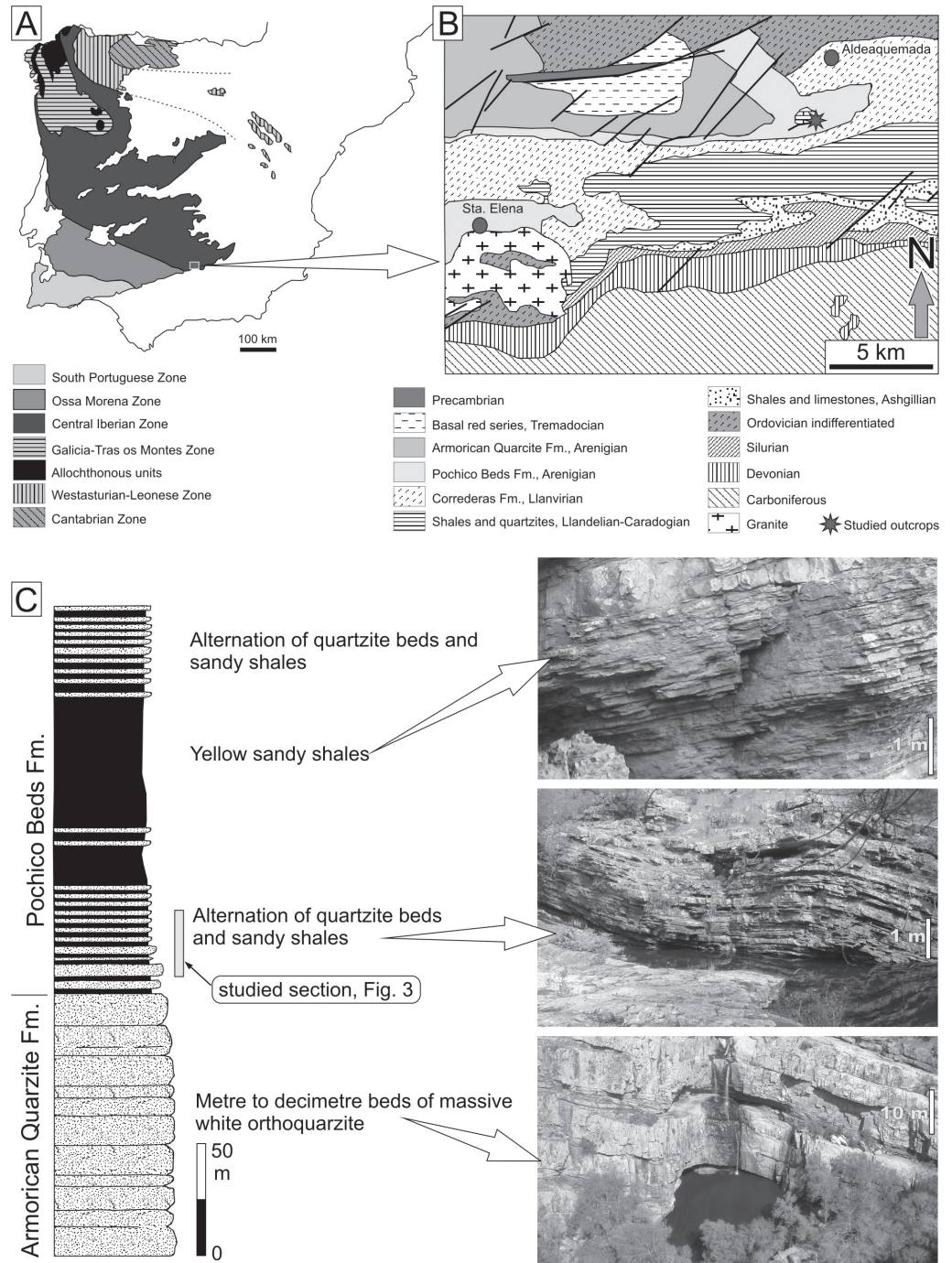
The Lower/Middle Ordovician in the Aldequemada area comprises two lithostratigraphic units: the Armorican Quartzite Formation and the Pochico Formation (Fig. 1C). The Armorican Quartzite in the Central Iberian Zone is up to 500 m thick and composed of white orthoquartzites. The lower part of the Armorican Quartzite Formation is not outcropping in the studied area, but its upper member, about 200 m thick, with beds ranging from 30 cm to 12 m, is identified in the Aldequemada area and described by Rey and Hidalgo (2004) and Lillo *et al.* (in press). Top beds of this member display wavy bedding, cross-stratification and the trace fossil *Cruziana*.

The Pochico Formation, around 200 m-thick in the studied area, is made up of alternating quartzites, quartz sandstones, sandy shales, siltstones and mudstones. Stratal stacking allows three members to be distinguished (Tamain, 1972). According to Gutiérrez-Marco *et al.* (2013), the Pochico Formation probably corresponds to the Dapingian sequence *sensu lato* in the southern part of the Central-Iberian Zone in Spain, being in this case the Middle Ordovician in age (Bergström *et al.*, 2009). The Lower Member (Pochico Alternations Member) is around 60 m thick and features a series of quartzite beds alternating with finer sediments, showing wavy-bedding (Fig. 2A), horizontal lamination (Fig. 2D), wave ripple cross-lamination and locally low angle cross-stratification (Fig. 2E). The Middle Member (Yellowish Pochico Sandstone Member) contains about 100 m thick sandy shales with wavy-bedding and locally hummocky cross-stratification. A few horizons show distinct cracks (Fig. 2F). In the Middle Member, lingulid horizons have been recorded and related to short catastrophic events (Emig and Gutiérrez-Marco, 1997). The Upper Member or Pochico Quartzite Intercalations Member (50 m thick) is characterized by numerous quartzite beds intercalated with finer clastics, similar to the first member. Most of these rocks are characterized by the low degree of sediment reworking and primary structures are usually clearly visible.

This study is focused on sedimentological and ichnological features at the transition between the Armorican Quartzite Formation and the Pochico Formation, where a 29 m-thick section was measured bed by bed (Fig. 3). These formations contact with a conformity showing gradual lithological transition. According to Matas-González *et al.* (2009), the Lower Member of the Pochico Formation was deposited on a siliclastic shelf dominated by storms.

Trace fossils were rarely mentioned from the Armorican Quartzite and the Pochico Formation (especially the lower

Fig. 1.- Geological setting. A, Iberian Peninsula and subdivisions of the Iberian Massif according to stratigraphic, tectonic and metamorphic features. The studied area is located in the southernmost part of the Central Iberian Zone. B, Detailed geological setting of the studied outcrop (GPS co-ordinates: N38°23.150'; W003°22.474'; ±9 m). C, Aldeaquemada section and illustrations of the lithological formations appearance in the field. Note location of the studied profile as a bar.



member) of the study area, which is covered by the Geological Map of Aldeaquemada (862, 1:50,000; a second edition still in press is unavailable, see Lillo *et al.*, in press). Rey and Hidalgo (2004) mention large and small *Cruziana* and *Skolithos* from the lower part of the Pochico Formation in the study region. In the surrounding areas, trace fossils have been described in the Pochico Formation, including *Cruziana furcifera*, *C. goldfussi*, *C. rugosa*, *Rusophycus* *isp.*, *Didymaulichnus rouaulti*, *Arthropycus* *cf. harlani* and *Daedalus halli* (Pérez Regodón, 1966; Butenweg, 1968; Poupon, 1971; Tamain, 1972). In nearby areas, covered by the surrounding Geological Maps 838 (Santa Cruz de Mudela), 840 (Bienservida), and 787 (Alhambra), other ichnotaxa, such as *Cruz-*

iana *cf. lefevbrei*, *Didymaulichnus lyelli*, *Monocraterion* *isp.*, *Monomorphichnus* *isp.*, *Bergaueria* *isp.* and *Isopodichnus* *isp.*, are mentioned in the map explanations.

3. Systematic palaeontology

Ichnogenus *Archaeonassa* Fenton and Fenton, 1937a *cf. Archaeonassa* *isp.* (Fig. 4A)

Material: One loose slab in the field.

Description:

Epichnial, shallow furrow, 2-3 mm wide, with narrow levees. Its course is slightly to strongly winding with occasional loops. The loops measure 15-30 mm across.

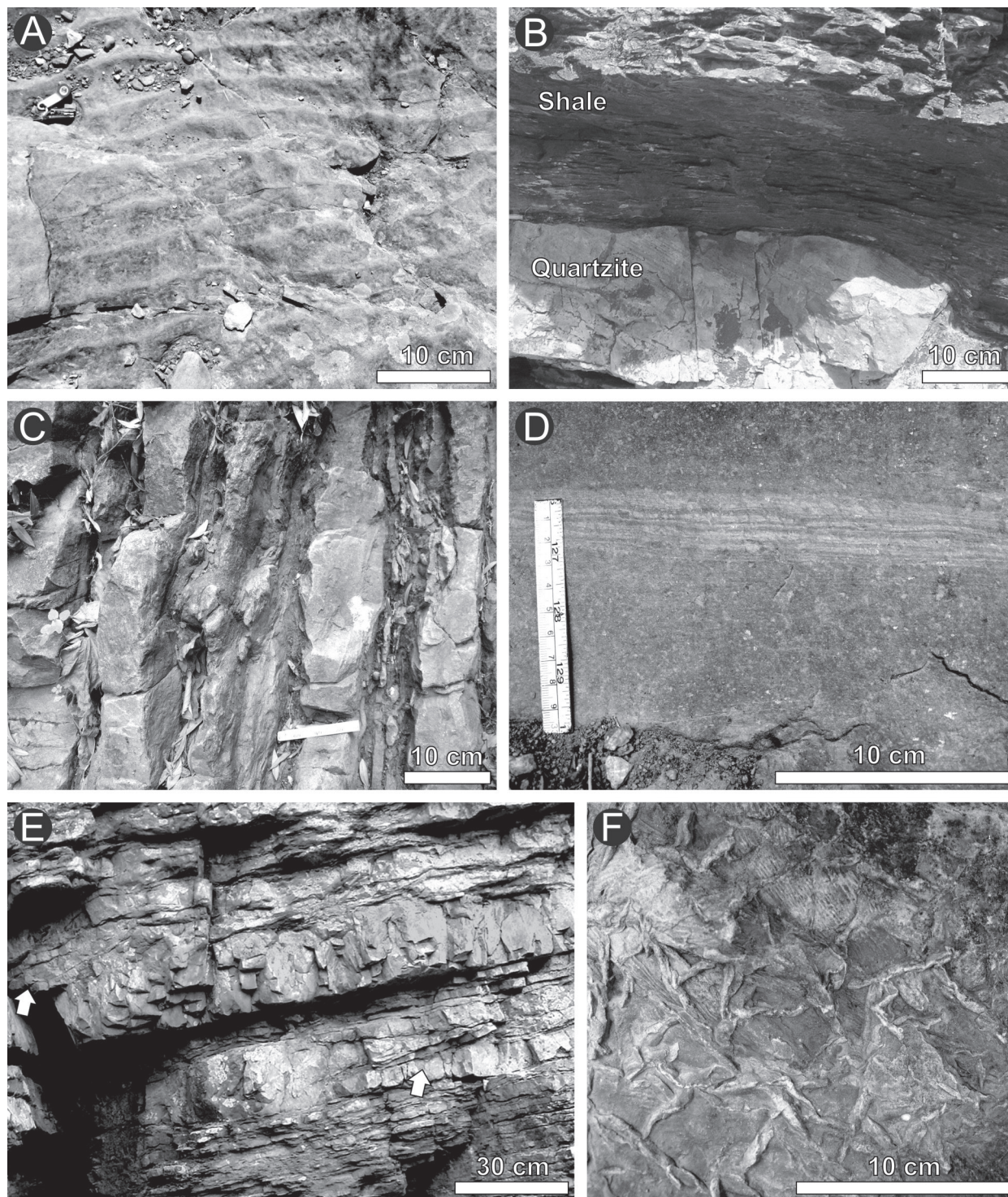


Fig. 2.- Sedimentary structures from the Aldeaquemada section. A, Wavy ripples on the top of beds of quartzite. B-C, Heterolithic quartzite-siltstone deposit. D, Beds of quartzite with parallel lamination. E, Low angle cross-stratification in sandstone beds. F, Cracks in upper surface of beds.

Remarks:

The winding course with occasional loops resembles *Helminthoidichnites* Fitch (Hofmann and Patel, 1989), which however does not display levees, when preserved as a furrow. Levees are typical of *Archaeonassa fossulata* Fenton and Fenton, 1937a, the type ichnospecies of *Archaeonassa*, which is interpreted as a crawling trail of gastropods (Fen-

ton and Fenton, 1937a; Buckman, 1994; Stanley and Feldmann, 1998) or crustaceans (Yochelson and Fedonkin, 1997; Mángano and Buatois, 2003). *A. fossulata* is larger and does not display loops as the described cf. *Archaeonassa* isp.

Ichnogenus *Catenichnus* McCarthy, 1979
Catenichnus isp. (Fig. 4B)

Material: About 10 specimens in the upper part of a quartzitic sandstone bed observed in the field.

Description:

U-shaped cylinder with divergent arms. The cylinder is of uniform diameter, which ranges from 7 to 11 mm among specimens. The structure is 11-60 mm wide and approximate-

ly 20 mm deep. The cylinders are thinly to thickly lined with mudstone or siltstone.

Remarks:

Some of specimens of the type ichnospecies *Catenichnus contentus* McCarthy, 1979 from the Permian of Australia, display poorly developed spreite, which are absent in the studied

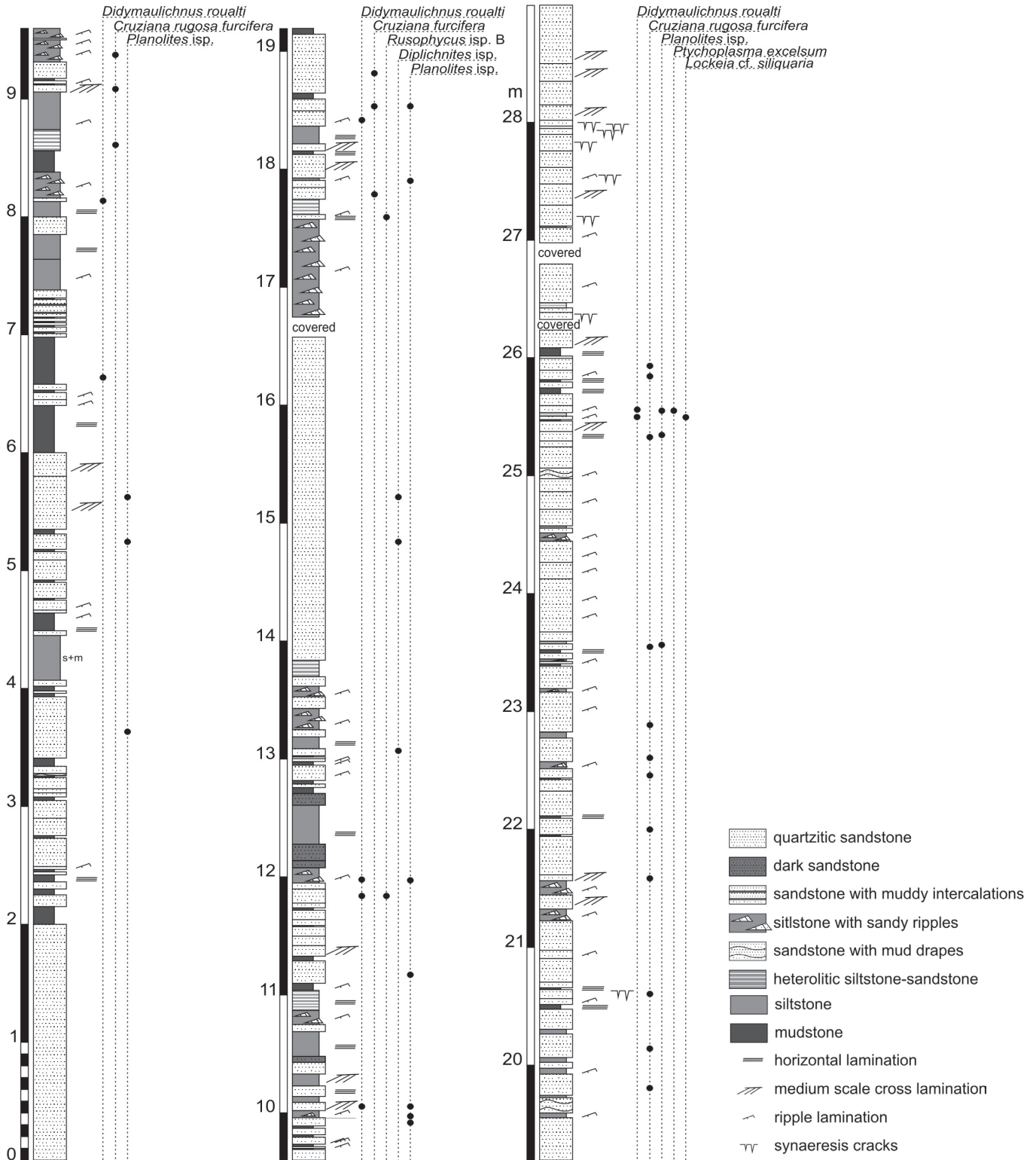


Fig. 3.- Profile of the Cascada de la Cimbarra outcrop with indication of sedimentary structures and ranges of selected trace fossils.

material. Trace fossils of this morphology, but without spreite, are also ascribed to *Arenicolites*, which however displays parallel arms (see Hofmann et al. 2011 for discussion). *Catenichnus contentus* can be interpreted as a domichnion produced by a suspension feeder (McCarthy, 1979). It occurs in moderate to high energy facies (Fillion and Pickerill, 1990). The same interpretation may be applied to *Catenichnus* isp. described here.

Ichnogenus *Cochlichnus* Hitchcock, 1858

Cochlichnus isp. (Fig. 7D)

Material: Two specimens observed in the field.

Description:

An epichnial, horizontal, regularly sinuous ridge. The ridge is 2 mm wide. The amplitude of the meanders attains 6-8 mm and the meanders are 2 mm high.

Remarks:

Cochlichnus occurs in a great variety of marine and non-marine environments. It is produced by many different invertebrates, including annelids and nematodes (see Fillion and Pickerill, 1990, for review). *Cochlichnus* from non-marine settings have been referred to scavengers or predators (Głuszek, 1995), an interpretation that can also be extended to occurrences in marine settings.

Ichnogenus *Cruziana* d'Orbigny, 1842

Cruziana furcifera d'Orbigny, 1842 (Fig. 5A-F)

Material: Six specimens collected, with numerous occurrences observed in the field.

Description:

Straight to loosely meandering bilobate ridges of uniform width ranging from 30 to 130 mm. The lobes of the ridges are semi-ellipsoidal in cross section and separated by a distinct V-shaped furrow. Their surface is densely covered by oblique distinct ridges, which are 0.5-2 mm wide. The ridges meet in the median furrow at an angle less than 30°, forming a V-shaped unidirectional pattern. In some specimens, narrow lateral ridges are observed (Fig. 5C).

Remarks:

Delgado (1886) distinguished almost twenty ichnospecies of *Cruziana* from the Lower Palaeozoic of Portugal, yet Seilacher (1970) retained only *C. furcifera*, *C. goldfussi* and *C. rugosa*, and considered the remaining ichnospecies to be taphonomic variations of these three ichnospecies. The separation of *Cruziana goldfussi* (Rouault), distinguished from *C. furcifera* in terms of its finer and more continuous scratch marks (see Fillion and Pickerill, 1990 for discussion), is problematic because of transitional specimens. Also, the presence or absence of lateral ridges used to discern these two

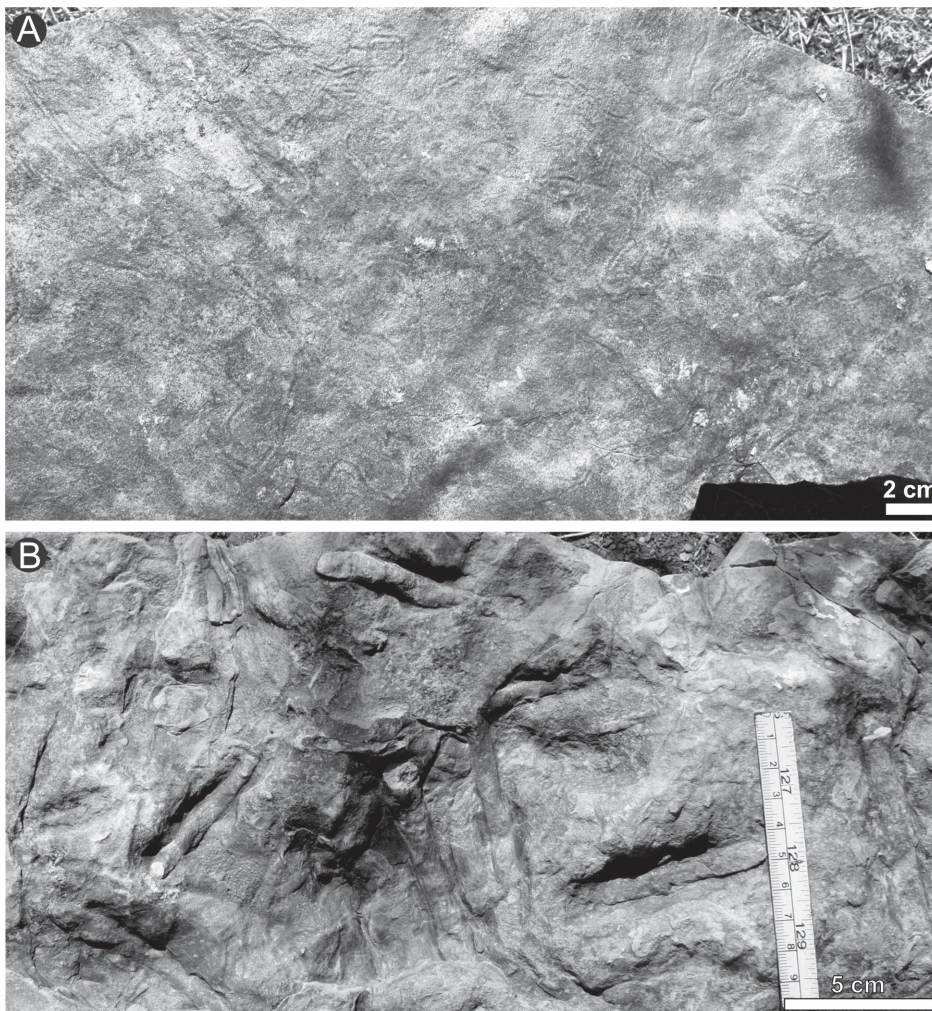


Fig. 4.- A, cf. *Archaeonassa* isp., epichnial semirelief on medium bed of sandstone. B, *Catenichnus* isp. drawing on unfocused photograph of hyporelief on medium bed of sandstone. Cascada de la Cimbarra, Pochico Formation (Lower/Middle Ordovician).

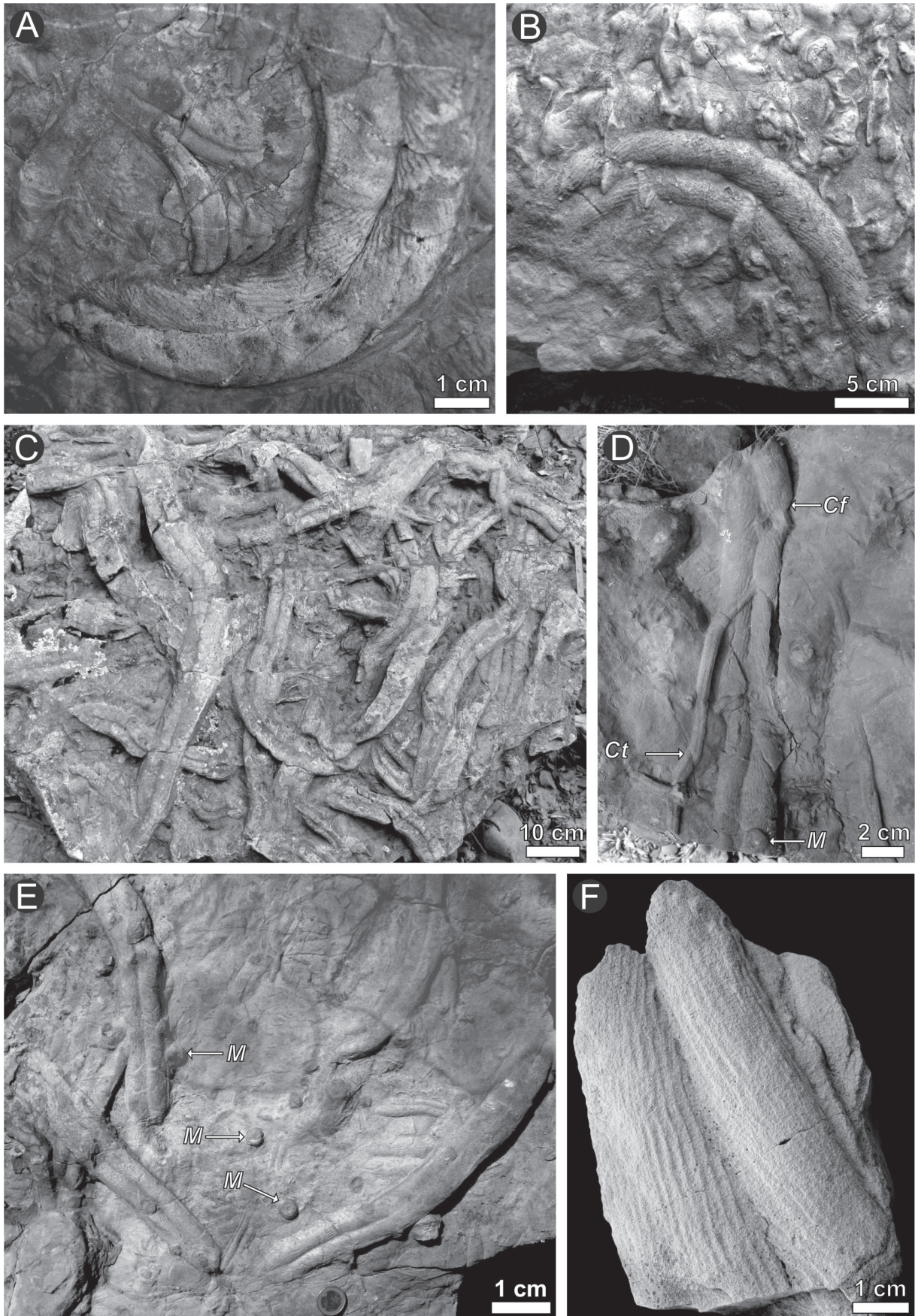


Fig. 5.- A-F, *Cruziana furcifera* d'Orbigny, 1842. Hypichnia with convex semirelief on medium to thick beds of sandstones. D, *C. furcifera* (Cf), *C. tenella* (Ct) and cf. *Monocraterion* isp. (M). E, *C. furcifera*, cf. *Monocraterion* isp. (M). Cascada de la Cimbarra, Pochico Formation (Lower/Middle Ordovician).

ichnotaxa, is problematic as they occur in the type material of both ichnospecies (Durand, 1985a). Therefore, Mángano and Buatois (2003) regarded *C. furcifera*, *C. goldfussi* and *C. rugosa* as subichnospecies of *C. rugosa* (respectively: *C. rugosa furcifera*, *C. rugosa goldfussi* and *C. rugosa rugosa*). However, many other authors retain them at the ichnospecies level (e.g., Aceñolaza and Milana, 2005; Neto de Carvalho, 2006) regarding that all the three ichnotaxa display distinctive morphological features (e.g., Egenhoff et al., 2007).

Cruziana is interpreted as the feeding trace of trilobites and/or other arthropods such as aglaspids, limulids or phyllo-pods, whereas *C. rugosa* is attributed exclusively to trilobites (e.g., Seilacher, 1970, 2007).

Cruziana imbricata Seilacher, 1970 (Fig. 8A)

Material: One slab containing two specimens.

Description:

A short, bilobate, hypichnial ridge, 8-20 mm long, 4-19 mm wide, 1-4 mm high. The lobes are covered by distinct, uniformly thick (1-2 mm wide), gently curved regularly distributed scale-like ridges, which meet in the median furrow at an angle of about 100° and form a V-shaped, unidirectional pattern in the median furrow.

Remarks:

The trace fossil was originally described as *Cruziana imbricata* Seilacher, 1970, which includes also forms that should be ascribed to *Rusophycus* (for the later see also Sá et al., 2011). *Cruziana imbricata* is common in the Arenigian in association the *Cruziana rugosa* group (Seilacher, 1970).

Cruziana rouaulti Lebesconte, 1883 (Fig. 6C)

Material: One collected specimen and a few specimens observed in the field.

Description:

This is a hypichnial bilobate ridge bounded with side ridges. The lobes are smooth, semi-circular in cross section, and show a wide median furrow. The whole structure is 11-18 mm wide. The side ridges are 1-3 mm wide.

Remarks:

This trace fossil was assigned to *Didymaulichnus* Young, 1972 (e.g., Crimes, 1970; Knaust, 2004), which mostly smooth, bilobate ridge. However, many authors ascribed it to *Cruziana* d'Orbigny (e.g., Neto de Carvalho, 2006; Seilacher, 2007). This is supported by the presence of scratches in well preserved specimens (Egenhoff et al., 2007). The strongly developed side ridges suggest a carapace of an arthropod. Crimes (1970) considered the discussed trace fossil as a trace of trilobites.

Cruziana rugosa d'Orbigny, 1842 (Fig. 6A-B)

Material: A few specimens documented in the field.

Description:

Hypichnial, bilobate ridge 90-100 mm wide, with transverse corrugations, covered by oblique, fine, comb-like ridges. The preserved fragments of ridges are 150-200 mm long.

Remarks:

The transverse corrugations are characteristic features of this subichnospecies. It is considered as a locomotion-feeding burrow of trilobites (e.g., Seilacher, 1970, 2007).

Specimen of *Cruziana rugosa* illustrated herein on Fig. 6 show only short fragment of up and down probing tracemaker work. Therefore, the resulted hypichnia (Fig. 6A) are similar to the rusophyciform of *Rusophycus marginatus* Bergström and Peel, 1988.

Cruziana tenella (Linnarsson, 1871) (Figs. 5D, 6C, 8A)

Material: Two collected slabs containing few specimens. A few additional specimens observed in the field.

Description:

Hypichnial bilobate, straight or slightly winding ridges, 2.5-8 mm wide. It displays faint, perpendicular striae in some specimens, while other specimens are smooth.

Remarks:

The perpendicular striae are most significant morphological features distinguishing this ichnospecies, even if some smooth forms occur in the same population of burrows. Presence of perpendicular striae or smooth surface (like *Didymaulichnus* isp.) on hypichnia depends on taphonomy. This is well visible in much larger *Cruziana furcifera* from the study area, where preservation of bioglyphs deteriorates along the bilobate ridge up to their disappearance. Additionally, specimens of *C. tenella* and part of specimens of *Cruziana rouaulti* (which is generally smooth) are of the same width; indeed, in some cases distinction between these two ichnospecies is problematic.

Cruziana tenella is known from the Cambrian (see Sadlok, 2010 for review), but also from the Grebes Nest Point Formation (Arenigian) of Newfoundland, where it was described under *Cruziana stromnessi* (Trewin, 1976). *Cruziana tenella* is commonly described under *Isopodichnus*, which is a locomotion and feeding trace of phyllopod crustaceans in non-marine environments (Pollard, 1985). It is widely accepted that *Isopodichnus* is a junior synonym of *Cruziana*, though some researches retain this name (e.g., Seilacher, 2007). The taxonomic relation between *C. tenella* and *Isopodichnus* is problematic (Jensen, 1997). In any case, *C. tenella* has a priority. It can be referred to the locomotion-feeding activity of small arthropods, including phyllopods for the non-marine variants.

Ichnogenus *Didymaulichnus* Young, 1972

Didymaulichnus lyelli (Rouault, 1850) (Fig. 6D)

Material: One slab containing mass occurrence specimens. A few single specimens in the field.

Description:

Hypichnial, straight to slightly winding, smooth bilobate ridge, 7-10 mm wide, with a narrow V-shaped median furrow, which is 1 mm wide. The ridge is bounded by thin, discontinuous bevels, about 1 mm thick. It occurs together with *Cruziana rouaulti* in some beds.

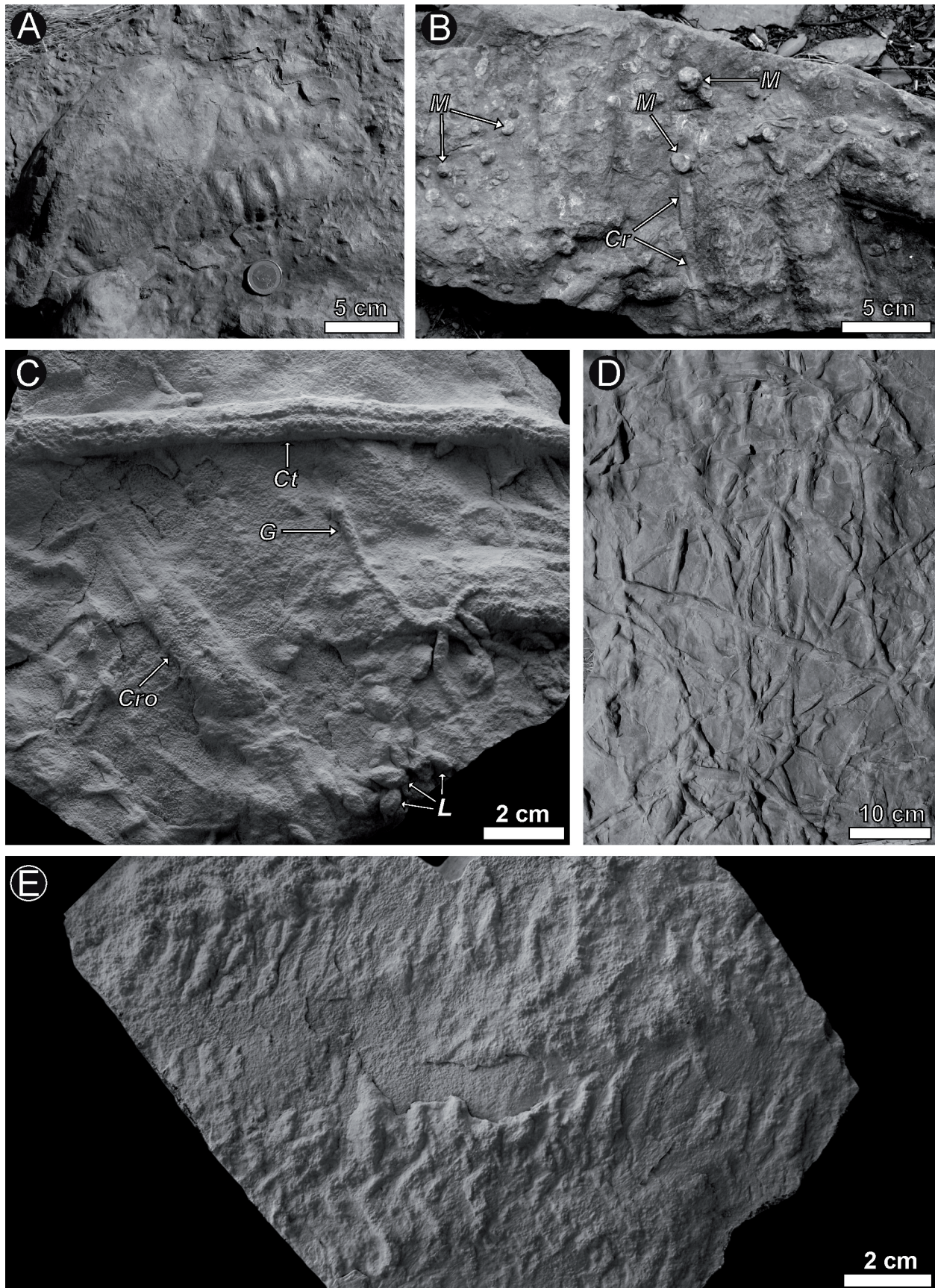


Fig. 6.- A, *Cruziana rugosa* d'Orbigny, 1842. B, *C. rugosa* (Cr) and cf. *Monocraterion* isp. (M). C, *Cruziana tenella* (Linnarsson, 1871) (Ct), *Cruziana rouaulti* Lebesconte, 1883 (Cro), *Gordia* isp. (G) and *Lockeia* cf. *siliquaria* James, 1879 (L). D, *Didymaulichnus lyelli* Rouault, 1850. E, ?*Diplichnites* isp. Hypichnial, concave semireliefs on medium beds of sandstone. Cascada de la Cimbarra, Pochico Formation (Lower/Middle Ordovician).

Remarks:

Didymaulichnus is interpreted as a trail of gastropods (Glaessner, 1969; Hakes, 1976) or trilobites (Crimes, 1970; Bradshaw, 1981). *Didymaulichnus* is a common facies-crossing trace fossil in the Lower Palaeozoic (for a review see Fillion and Pickerill, 1990; Kumpulainen et al., 2006). *D. lyelli* is known from the Armorican Quartzite (Durand, 1985a).

Ichnogenus Diplichnites Dawson, 1873

?*Diplichnites* isp. (Fig. 6E)

Material: One specimen collected.

Description:

The trace fossil is composed of two parallel rows of hypichnial, irregular to more regular ridges, which are arranged obliquely to the main axis of the structure. Each row is 25-30 mm wide and separated by the median smooth part, about 20 mm wide. The whole structure is about 60 mm wide. The rows are composed of mostly straight ridges, which are 1-2 mm wide, 3-5 mm apart. Some of them appear to be outwardly bifid, but in others it is not evident due to poor preservation. In one row a wide V-shaped arrangement of the ridges is also present.

Remarks:

A bad state of preservation does not permit closer determination. One can consider it even as an undertrack of *Cruziana* or *Rusophycus*, but partial preservation of lower surface of the bed (lower part of Fig. 6E) excludes such a possibility. *Diplichnites* is interpreted as a locomotion trace of arthropods, typical of Palaeozoic-early Mesozoic shallow-marine, occasionally deeper-marine environments (Fillion and Pickerill, 1990).

Ichnogenus Gordia Emmons, 1844

Gordia isp. (Fig. 6C)

Material: One collected specimen.

Description:

Convex, hypichnial, subcylindrical ridge forming a loop. The ridge is about 3 mm wide and loop is about 20 mm wide. The ridge crosses *Didymaulichnus rouaulti*.

Remarks:

Formation of loops is typical of *Gordia* Emmons, 1844, which is a pascichnion formed by various organisms in different environments (e.g., Fillion and Pickerill, 1990; Geyer and Uchman, 1995). The described form is similar to *Gordia marina* Emmons, 1844, but fragmentary preservation does not permit a closer determination.

Ichnogenus Lingulichnus Hakes, 1976

?*Lingulichnus verticalis* Hakes, 1976 (Fig. 7B)

Material: Two specimens observed on a bedding plane of a loose slab.

Description:

Elliptical disc on a bedding surface, 15 mm wide and 22-29 mm long, with an external bevel rimming the disc. The bevel varies in width from 1 to 3 mm.

Remarks:

The discs are a typical bedding plane expression of *Lingulichnus*, which is a shaft, U-shaped when fully developed, with the elliptical cross-section. The bevel can be an expression of a thick lining. *Lingulichnus* is interpreted as a domichnion of lingulid brachiopods (Hakes, 1976; Zonneveld and Pemberton, 2003; Zonneveld et al., 2007).

Ichnogenus Lockeia James, 1879

Lockeia cf. *siliquaria* James, 1879 (Fig. 6C)

Material: Two collected slabs containing several specimens.

Description:

Lockeia cf. *siliquaria* occurs as amygdaloidal mounds, which are 3-4 mm wide and 7-8 mm long, up to 2-3 mm high, pointed on both sides, with a median longitudinal keel.

Remarks:

Stout forms of *Lockeia* have been ascribed to *L. amygdaloides* (Seilacher, 1953), and narrow forms to *L. siliquaria* James, 1879. However, Seilacher and Seilacher (1994) and Schirf et al. (2001) held them to be morphological variants of *L. siliquaria* James, because they occur in the same beds together with transitional forms between these two ichnospecies. This is the cubichnion produced mostly by bivalves (Seilacher and Seilacher, 1994) in various environments, but mostly shallow-marine settings.

Lockeia isp. (Fig. 7D)

Material: About 30 specimens in a loose slab observed in the field.

Description:

Amygdaloidal or drop-shaped mounds on the lower surface of sandstone beds, which are 16-27 mm wide and 27-60 mm long, pointed on one side (drop-shaped) or both sides.

Remarks:

Its larger size, occasional drop-shape and the absence of a keel are the features differentiating it from *Lockeia* cf. *siliquaria*.

Ichnogenus Monocraterion Torell, 1870

cf. *Monocraterion* isp. (Figs. 5D, E, 6B, 7A)

Material: Several slabs containing abundant specimens observed in the field.

Description:

Vertical to subvertical, straight, simple shafts crossing quartzitic sandstone bed, showing a steep conical upper part, filled with mudstone-siltstone. Only a part of the structure limited to the 20 cm thick host sandstone bed was observed. The conical part is up to 80 mm long and up to some 10 mm in diameter in the upper part. In horizontal section, the conical part is manifest on the upper bedding plane as a circular or oval disc-like structure, which is about 10 mm in diameter, with a centric or eccentric knob of various sizes and occasionally expressed concentric rings. The lower part is expressed on the bedding plane as oval to circular knobs.

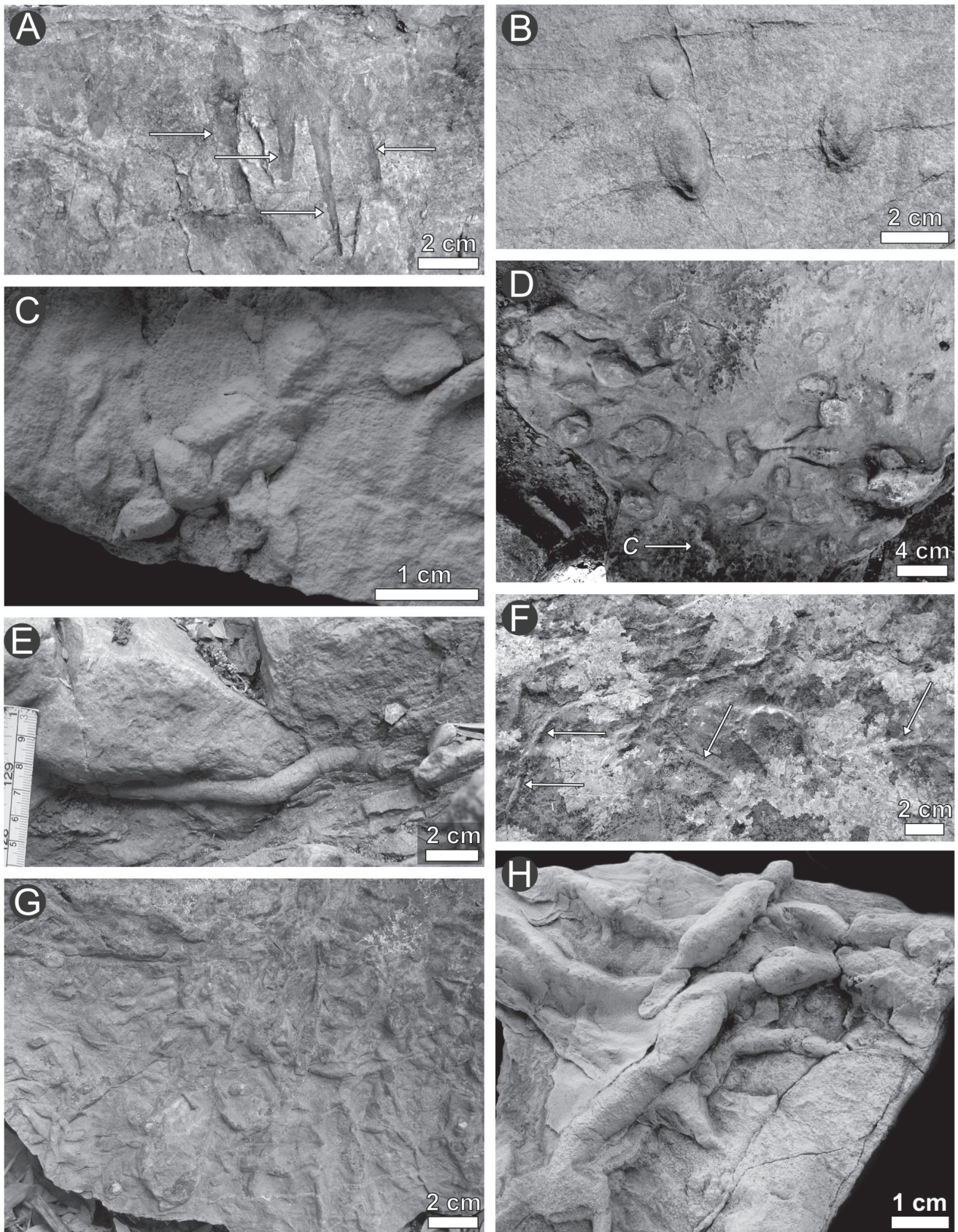


Fig. 7.- A, cf. *Monocraterion* isp. (arrowed), endichnia, full reliefs in medium bed of sandstone. B, ?*Lingulichnus verticalis* Hakes, 1976. C, *Lockeia* cf. *siliquaria* James, 1879. D, *Lockeia* isp. and *Cochlichnus* isp. (C). E, *Planolites beverleyensis* (Billings, 1862). F, *Planolites* isp. G, *Planolites montanus* Richter, 1937. H, *Ptychoplasma excelsum* Fenton and Fenton, 1937b. B, C, D, F-H, hypichnia, convex semireliefs on thin to medium beds of sandstones; E, endichnion in medium bed of sandstone. Cascada de la Cimbarra, Pochico Formation (Lower/Middle Ordovician).

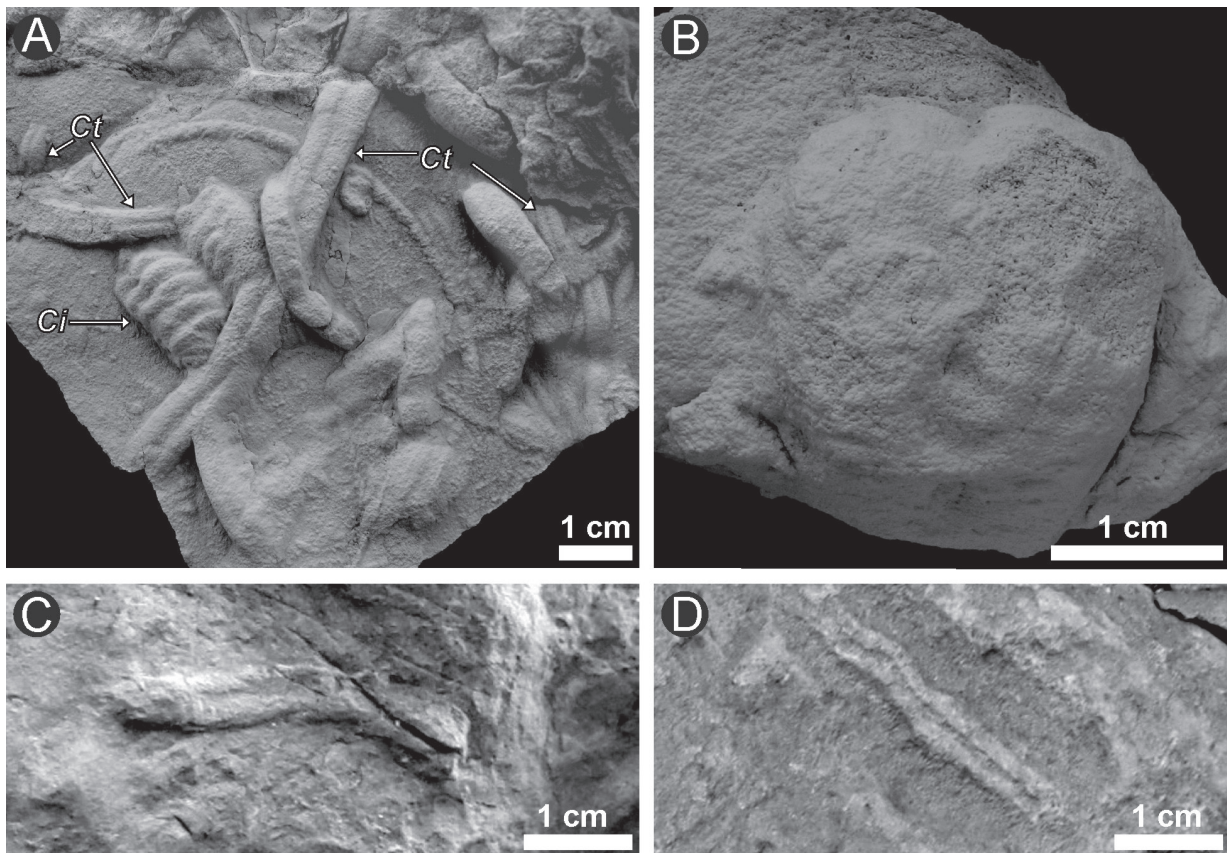


Fig. 8.- A, *Cruziana imbricata* Seilacher, 1970 (Ci) and *Cruziana tenella* (Linnarsson, 1871) (Ct); B, *Rusophycus* isp., hypichnia, convex semi-reliefs on thin beds of sandstones. C-D, epichnial bilobate ridges on rippled beds. Cascada de la Cimbarra, Pochico Formation (Lower/Middle Ordovician).

Remarks:

Validity of *Monocraterion* as a separate ichnogenus, considered by some authors as the same trace fossil as *Skolithos* Haldeman (interpreted as erosionally truncated *Monocraterion*) is confirmed (see Fillion and Pickerill, 1990); however, we follow the idea that it is better to separate these with funnel from these without funnel, if the erosional truncation is not evident. The type material displays some ridges running from the funnel, which pose certain unsolved taxonomic problems (Jensen, 1997). Therefore, the described material is determined as cf. *Monocraterion* isp. *Monocraterion* sensu lato is typical of shallow-marine, high-energy sandy facies and is interpreted as a domichnion of suspension-feeders or scavengers (e.g., Schlirf and Uchman, 2005).

Ichnogenus *Planolites* Nicholson, 1873

Planolites beverleyensis (Billings, 1862) (Fig. 7E)

Material: A few specimens documented in the field.

Description:

Hypichnial or endichnial, horizontal to oblique, unbranched curved or straight, smooth cylindrical structure, 6-12 mm in diameter, without distinct lining.

Remarks:

The diagnosis of *P. beverleyensis* "relatively large, smooth, straight to gently curved or undulate *Planolites*" (Pemberton and Frey, 1982) fits the described material well. *Planolites*

occurs in various marine and non-marine facies, and is produced by vermiform invertebrates of many phyla, which are interpreted as deposit-feeders that actively fill their burrows (e.g., Pemberton and Frey, 1982; Keighley and Pickerill, 1995).

Planolites montanus Richter, 1937 (Fig. 7G)

Material: A few specimens documented in the field.

Description:

Hypichnial, short, semi-cylindrical, smooth, straight to slightly curved ridges, 6-7 mm wide, up to 23 mm long. The ridges plunge into the bed.

Remarks:

This ichnospecies is characterized by common change of orientation on short distances, and what is manifested by short courses on bedding plains, while course of other ichnospecies of *Planolites* are more stable (Pemberton and Frey, 1982). This trace fossil reflects reworking of mudstone-sandstone interface.

Planolites isp. (Fig. 7F)

Material: A few specimens documented in the field.

Description:

Planolites isp. is a horizontal to subhorizontal, rarely oblique, unbranched gently curved, rarely straight, smooth cylindrical structure, without distinct lining. There are two dif-

ferent size classes: the smallest specimens are about 2 mm in diameter and larger ones about 4 mm in diameter.

Remarks:

The mostly horizontal course and the smaller size are the main differences from *P. beverleyensis*, whose diagnosis contains the phrase “relatively large...” (Pemberton and Frey, 1982).

Ichnogenus *Ptychoplasma* Fenton and Fenton, 1937b

Ptychoplasma excelsum Fenton and Fenton, 1937b (Fig. 7H)

Material: One collected specimen and a few observations in the field.

Description:

Hypichnial ridges 5-9 mm wide, with elongate, smooth mounds, some of which separated by more even segments. The mounds are amygdaloidal in cross section, 11-20 mm long, up to 9 mm high and only slightly wider than the even ridge. The overall course is winding; some segments intersect.

Remarks:

Ptychoplasma excelsum was known so far from the Carboniferous of USA (Fenton and Fenton, 1937b; Rindsberg, 1994). The Arenigian occurrence extends its stratigraphic range. *Ptychoplasma* is interpreted as the locomotion and feeding trace of bivalves, and occurs in various marine and non-marine environments (Uchman et al., 2011); however, *P. excelsum* is limited so far to shallow-marine settings (Rindsberg, 1994).

Ichnogenus *Rusophycus* Hall, 1852

Remarks:

Rusophycus is a resting trace of arthropods, mostly trilobites in Palaeozoic (Osgood, 1970), considered by Seilacher (1970) as *Cruziana*, but most authors keep these ichnogenera separate (e.g., Fillion and Pickerill, 1990, for discussion).

Rusophycus isp. (Fig. 8B)

Material: One collected specimen and a few observations in the field.

Description:

An oval, bilobate hypichnion, 22 mm long, 23 mm wide, 7 mm high, which consists of two symmetrical lobes separated by an indistinct median furrow. The surface of the lobes is irregular. Incomplete ridges occur on the steep slope of one side. They display a wide V-shaped pattern.

Remarks:

General shape of the discussed specimen corresponds somewhat with *Rusophycus dispar* Linnarsson, 1869, although the bad state of preservation does not permit closer determination.

Epichnial bilobate ridge (Fig. 8C-D)

Material: Two specimens in the field.

Description:

Epichnial, smooth, bilobate, slightly curved ridges, with semi-circular lobes that are about 7 mm wide.

Remarks:

A closer determination is impossible because of fragmentary preservation. *Gyrochorte comosa* Heer, which is typically preserved as an epichnial bilobate ridge, displays oblique ribbing and is typically narrower (Gibert and Benner, 2002).

4. Discussion

4.1. Palaeoenvironmental aspects

The trace fossil assemblage is moderately diverse (13 ichnogenera, 19 ichnospecies), dominated by pascichnia (*Archaeonassa*, *Cruziana*, *Gordia*, *Planolites*) and repichnia (*Cochlichnus*, *Didymaulichnus*, ?*Diplichnites*, *Ptychoplasma*), the presence of domichnia (*Catenichnus*, *Lingulichnus*, cf. *Monocraterion*) and cubichnia (*Lockeia*, *Rusophycus*). This assemblage is typical of the *Cruziana* ichnofacies in general (e.g., Frey and Seilacher, 1980) and of the archetypal *Cruziana* ichnofacies in particular, which in open shelf sediments points to the lower shoreface-upper offshore, where deposit feeding prevails (Pemberton et al., 2001). In the Lower Palaeozoic sediments, a reversal of ichnofacies can occur, i.e., the *Cruziana* ichnofacies may occur in tidal flat heterolithic sediments, while the *Skolithos* ichnofacies is present in subtidal sand bars (Buatois and Mángano, 1999, 2004). Nevertheless, there are no signs of tidal environment. Instead, the presence of hummocky cross stratification indicates storm influences, which is consistent with previous observations (Rey and Hidalgo, 2004). The classic facies depth interpretation can therefore be applied. Furthermore, in Portugal, the Armorican Quartzite is interpreted as foreshore-upper offshore sediment (Neto de Carvalho, 2006). This does not necessarily apply to the Armorican Quartzite facies in other regions. For instance, *Cruziana*-rich facies are referred to tidal flats in NW Spain (Crimes and Marcos, 1976) and in the Armorican Massif (Durand, 1984, 1985a, b; Dabard et al., 2007; Vidal et al., 2011).

The presence of *Cruziana*, *Rusophycus* and other trace fossils attributed to trilobites would suggest normal salinity. However, the common occurrence cracks in the upper part of the section (Fig. 3) might be referred to salinity changes, as “syneresis” cracks (Burst, 1965). In this part of the section, the trace fossils are absent. Only in metre 20-21 of the section (Fig. 3) is *Cruziana* present together with the cracks. However, the latest investigations show that cracks of such type can be intrastratal cracks caused by shrinkage of sediments containing microbial structures (Harzim et al., 2013). Nevertheless, the relation of the cracks to microbial structures is not obvious in the investigated section.

The low degree of sediment reworking suggests a high rate of clastic sedimentation. The most abundant occurrences of trace fossils are in mudstone-sandstone intercalations, where sandstone prevails. Such sediments are probably the most nutritional, attracting deposit feeders, while the preservational potential is high due to lithological heterogeneity, especially on sandstone-mudstone interfaces. Most sandstone beds dis-

play well preserved primary sedimentary lamination. Not all sandstone-mudstone intercalations contain trace fossils (Fig. 3). Total bioturbation is confined to thin horizons. This may be attributed to a high rate of sedimentation, when the time available for colonization (colonization window sensu Polard *et al.*, 1993) of bedforms was insufficient.

Generally, trace fossil are relatively uncommon in pure quartzitic sandstones of the Armorican Quartzite facies (e.g., Kolb and Wolf, 1979). Sandstones with some admixture of finer fractions yield characteristic trace fossils, e.g., *Skolithos* and *Daedalus*, which are attributable to the *Skolithos* ichnofacies, indicating a high-energy environment above the fair-weather wave base. The associated heterolithic facies are characterized by abundant pascichnia, such as *Cruziana*, typical of the *Cruziana* ichnofacies.

4.2. Palaeogeographic background

The Lower Ordovician and Lower/Middle Ordovician trace fossils of the Gondwana and peri-Gondwanan zone are highly diverse. The Ordovician is an important time of biodiversification in shallow marine environments, which is also recorded in trace fossils (Mángano and Droser, 2004). So far, the highest ichnodiversity in the Ordovician (38 ichnogenera) comprises several formations of the Wabana and Bell Island groups in Newfoundland (Fillion and Pickerill, 1990). However, these formations differ from Armorican Quartzite facies formations in that they are composed mostly of shales or heterolithic rocks, except for the Redmans Formation, made up of massive quartzite similar to the Armorican Quartzite. This quartzitic formation yields scarce trace fossils – only *Cruziana furcifera* was described (Fillion and Pickerill, 1990).

The distribution of some Lower Ordovician trace fossils is controlled by different aspects, among others by palaeogeographical location. Foremost, these concerns trace fossils, which morphology depends largely from anatomy of trace-maker, such as *Cruziana* or *Rusophycus*. The *Cruziana rugosa* group is very common in the Iberian Peninsula, France, Wales, North Africa, southern Asia and South America, which represents the northern margin of Gondwana (e.g., Cocks and Torsvik, 2002). This group of trace fossils is generally absent in Laurentia (continental part of North America and Greenland) and Baltica (Eastern Europe and Scandinavia) (Seilacher and Crimes, 1969). Nevertheless, the palaeogeographical restriction is not strict. The *C. rugosa* group and other trace fossils, e.g., *Trichophycus venosus*, were reported from the Norwegian part of Baltica (Knaust, 2004) despite the fact that Baltica during the Ordovician was separated from Gondwana by the Tornquist Sea (e.g., Cocks and Torsvik, 2002).

Mixed Gondwanan-Baltic assemblages of trilobites, which are *Cruziana* trace-makers, have also been reported from the Cambrian of Poland (Żylińska, 2002). The possibility of pre-Ordovician paths of migration of ichnofaunas between Laurentia and Baltica palaeocontinents, based on *Rusophycus*, was mentioned by Stachacz (2012).

In other hand, the distribution of trace fossils in the Ordovician is also facies controlled (Mángano and Droser, 2004). Baltica, which during the Ordovician was closer to the Equator, is characterized by dominant condensed carbonate sedimentation, with numerous discontinuity surfaces (Cocks and Torsvik, 2005). The Baltica facies are rich in skeletal fossils and relatively scarce in trace fossils (Ekdale and Bromley, 2001, 2003; Dronov *et al.*, 2002; Dronov and Mikuláš, 2010), especially *Cruziana*, which is believed to be a palaeo-ichnozoogeographic marker. One can invoke an effect of antagonism between suspension feeders and deposit feeders, i.e. trophic group amensalism (Rhoads and Young, 1970), which is also applicable to trace fossils (Bromley, 1996; Buatois and Mángano, 2011). It is an open question if the trophic group amensalism, observed generally in a scale of habitat, can be extrapolated to whole continents. Probably, the stronger role was played by the taphonomic filter, as preservation of trilobite trace fossils is highest in heterolithic siltstone-sandstone deposits (Crimes, 1975; Goldring, 1985). The calcareous, commonly condensed sediments of Baltica are not suitable for preservation of trilobite burrows.

5. Conclusions

The described trace fossils belong to the archetypal *Cruziana* ichnofacies, indicating a lower shoreface-upper offshore zone. A high rate of sedimentation limited the colonization window of bedforms, causing a generally low degree of bioturbation.

The studied trace fossil assemblage has significant but not strict palaeogeographic implications in the Gondwana and peri-Gondwanan context. The trace fossil assemblages of *Cruziana* ichnofacies in the Armorican Quartzite facies (margins of Gondwana) are characterized by common large *Cruziana*, in this sense differing from the Baltica setting. Ichnofauna of Early Ordovician was palaeogeographically controlled, although trilobite related ichnotaxa typical of Gondwana can be found rarely in Baltica and Laurentia. The differences between the ichnofauna of Gondwana and Baltica may be influenced by the facies (clastics in Gondwana and carbonates in Baltica), mostly owing to the preservation potential of *Cruziana*, which is high in heterolithic clastic sediments.

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