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, provincia de Jaén, justo por encima la Cuarcita Armoricana. Se han reconocido diecinueve icnóspecies 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. Las diferencias entre las icnofacies 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, Arenigieno, 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 Armorican) (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 Aldeaquemada 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 Aldeaquemada 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 Aldeaquemada 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 Aldeaquemada 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 (Tainaud, 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 siliciclastic shelf dominated by storms.

Trace fossils were rarely mentioned from the Armorican Quartzite and the Pochico Formation (especially the lower
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 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, Archaeonassa cf. harlani and Daedalus halli (Pérez Regodón, 1966; Buteinweg, 1968; Poupon, 1971; Tamain, 1972). In nearby areas, covered by the surrounding Geological Maps 838 (Santa Cruz de Mudela), 840 (Bienvenida), and 787 (Alhambra), other ichnotaxa, such as Cruziana 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.
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 (Fenton and Fenton, 1937a; Buckman, 1994; Stanley and Flemmann, 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 approximately 20 mm deep. The cylinders are thinly to thickly lined with mudstone or siltstone.

Remarks:
Some of specimens of the type ichnospecies *Catenichmus 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 domiclhnion 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 (Gluszek, 1995), an interpretation that can also be extended to occurrences in marine settings.

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 30º, 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. goldfussii* and *C. rugosa*, and considered the remaining ichnospecies to be taphonomic variations of these three ichnospecies. The separation of *Cruziana goldfussii* (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).
**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 ichnospecies. 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 trace maker 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.
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 riming 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 domicnichon 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 Schlirf 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 ichno-species. 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.
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.

*Planolites* 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 con-
tains 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 inter-
sect.

Remarks:
*Ptychoplasma excelsum* was known so far from the Carbon-
iferous of USA (Fenton and Fenton, 1937b; Rindsberg, 1994).
The Arenigian occurrence extends its stratigraphic range. *Pty-
choplasma* is interpreted as the locomotion and feeding trace
of bivalves, and occurs in various marine and non-marine en-
vironments (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 trilo-
bites 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, al-
though 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 ich-
nogenera, 19 ichnospecies), dominated by *pascichnia* (*Ar-
chaeonassa, Cruziana, Gordia, Planolites*) and repichnia (*Co-
chlichnus, Didymaulichnus, ?Diplichnites, Ptychoplasma*),
the presence of domicichnia (*Catenichnus, Linguulichnus*, 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 *Cruz-
iana* ichnofacies in particular, which in open shelf sediments
points to the lower shoreface-upper offshore, where deposit
feeding persists (Pemberton et al., 2001). In the Lower Pal-
eaeozoic sediments, a reversal of ichnofacies can occur, i.e., the
*Cruziana* ichnofacies may occur in tidal flat heterolithic sedi-
ments, 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 (Du-
rand, 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. How-
ever, 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). Never-
theless, 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 nu-
tritional, 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 Polland 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 (Zylińska, 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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