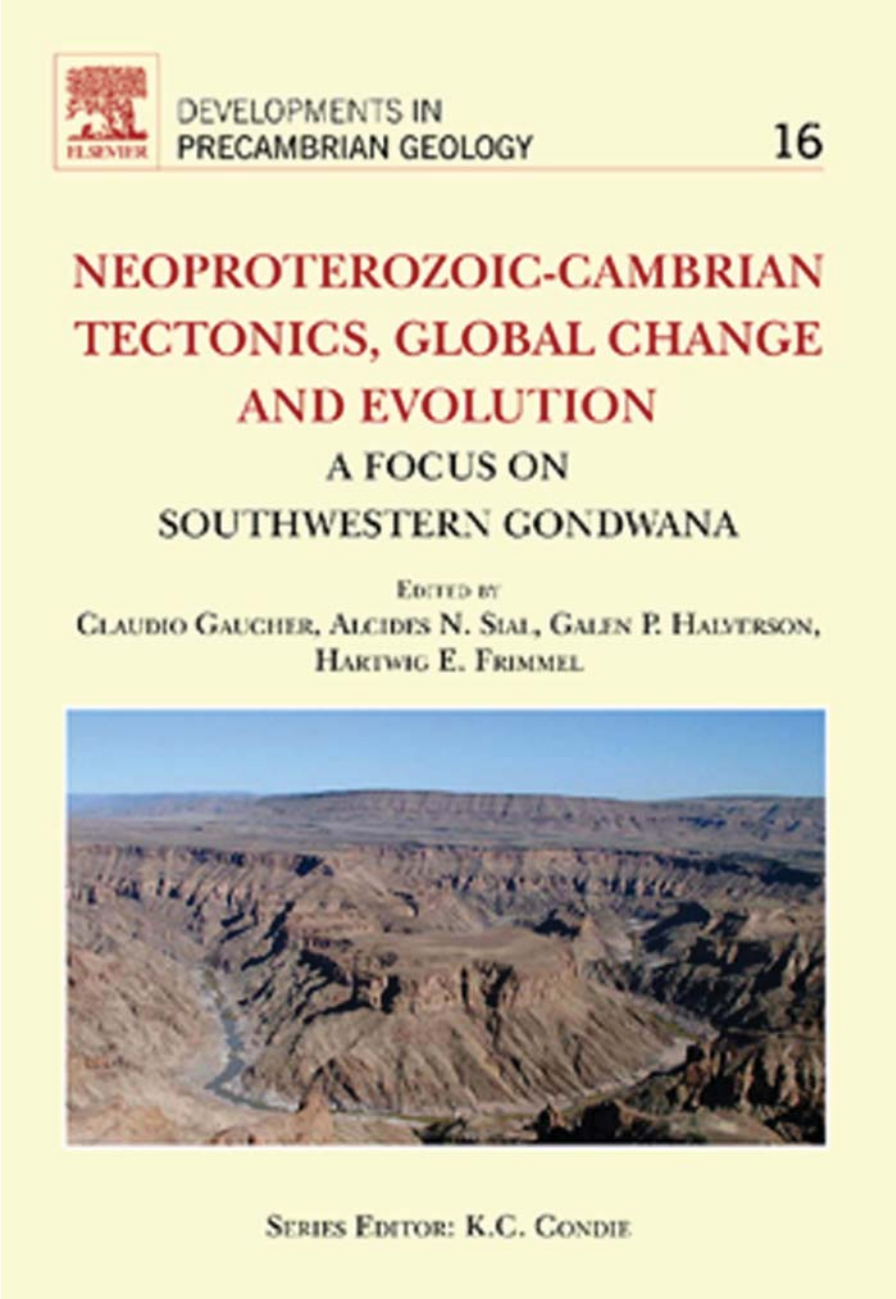
Provided for non-commercial research and educational use only.
Not for reproduction, distribution or commercial use.

This chapter was originally published in the book *Developments in Precambrian Geology*, published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who know you, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:
http://www.elsevier.com/locate/permissionusematerial

From Guillermo F. Aceñolaza, Gerard J.B. Germs and Florencio G. Aceñolaza, Trace Fossils and the Agronomic Revolution at the Neoproterozoic-Cambrian Transition in Southwest Gondwana. In: K.C. Condie, editor: Developments in Precambrian Geology, Vol 16, Neoproterozoic-Cambrian Tectonics, Global Change and Evolution: Focus on South Western Gondwana, Claudio Gaucher, Alcides N. Sial, Galen P. Halverson and Hartwig E. Frimmel.
The Netherlands: Elsevier, 2010, pp. 339–347.
ISBN: 978-0-444-53249-7
© Copyright 2010 Elsevier BV.

Author's personal copy

CHAPTER 9.3

Trace Fossils and the Agronomic Revolution at the Neoproterozoic-Cambrian Transition in Southwest Gondwana ☆

Guillermo F. Aceñolaza[1], Gerard J.B. Germs[2] *and* Florencio G. Aceñolaza[1]

Contents

9.3.1. Introduction 339
9.3.2. Trace Fossils in Northwest Argentina (South America) 340
9.3.2.1. General aspects of the Puncoviscana Formation *s.l.* 340
9.3.2.2. Lower Cambrian trace fossils 340
9.3.3. Trace Fossils of the Nama Group 342
9.3.3.1. Ediacaran (lower Nama Group) trace fossils (ca. 550–543 Ma) 343
9.3.3.2. Early Cambrian (upper Nama Group) trace fossils (ca. 540–530 Ma) 344
9.3.4. Trace Fossils of the Vanrhynsdorp Group (ca. 550–535 Ma) 344
9.3.5. Conclusions 345
Acknowledgements 347

9.3.1. Introduction

The Ediacaran-Cambrian transition represents an eventful period in the evolution of life on Earth. At this particular time, not only did the demise of the soft-bodied Ediacaran biota occurred, but also the explosive diversification of organisms known as the 'Cambrian explosion' (see Chapter 9.1). During the same time period, a considerable increase in the disruption of sediments known as the 'agronomic revolution' occurred, when shallow marine Ediacaran 'matgrounds' were largely replaced by the Early Cambrian better ventilated 'mixgrounds' (Seilacher and Pflüger, 1994).

In the shallow marine Ediacaran deposits, trace fossil diversity is relatively low and dominated by horizontal simple trails and shallow burrows that display feeding strategies related to the exploitation of microbial matgrounds (Hagadorn and Bottjer, 1997, 1999; Jensen, 2003; Porada et al., 2008). This scenario changed in the Early Cambrian, when an explosive increase in trace fossil diversity occurred, followed by the onset of vertical bioturbation and the disappearance of a matground-based ecology. This increase in extent, tiering depth and complexity of bioturbation, determined biofabrics distribution and was strongly controlled by sedimentary fabrics (Droser and Li, 2001). During the Ediacaran, animals were already living on deep-sea floors. However, the ichnofaunas were poorly diverse, with a high proportion of undermat miners (Crimes, 2001; Seilacher et al., 2005). Simple horizontal, unbranched burrows, primitive systems and rare open meandering traces are recognised as a characteristic 'upper' Ediacaran set, while a more diverse branching burrow systems, resting traces and furrows represent some typical features of the pre-trilobite lower Cambrian strata (Jensen, 2003; McNaughton, 2007).

During the Early Cambrian a dramatic radiation of trace fossils behavioural programmes and sedimentary fabrics took place (Droser and Li, 2001). Even though the chronology of the Ediacaran-Early Cambrian transition

☆ Aceñolaza, G.F., Germs, G.J.B., Aceñolaza, F.G. 2009. Trace fossils and the Agronomic Revolution at the Neoproterozoic-Cambrian transition in Southwest Gondwana. In: Gaucher, C., Sial, A.N., Halverson, G.P., Frimmel, H.E. (Eds): Neoproterozoic-Cambrian Tectonics, Global Change and Evolution: a focus on southwestern Gondwana. Developments in Precambrian Geology, 16, Elsevier, pp. 339–347.

[1] Instituto Superior de Correlación Geológica (INSUGEO), Miguel Lillo 205, 4000 San Miguel de Tucumán, Argentina.
[2] University of Johannesburg, Private Bag X60, Oudtshoorn 6620, South Africa.

Developments in Precambrian Geology, Volume 16
ISSN 0166-2635, DOI 10.1016/S0166-2635(09)01624-7
© 2010 Elsevier B.V.
All rights reserved.

Author's personal copy

in South America is not completely understood, an early attempt of the onshore–offshore shift is probably represented in the rich ichnofauna of the remarkable Puncoviscana Formation of NW Argentina (Aceñolaza and Aceñolaza, 2005; Seilacher et al., 2005). Although the relative roles of environment and evolution in controlling the trace fossil record has been emphasised for the Ediacaran-Cambrian transition (McNaughton, 2007), a re-evaluation of the whole significance of the occurring trace fossil associations and their palaeoecological significance is still pending.

The aim of this contribution is to briefly discuss the trace fossil associations of the Puncoviscana Formation *s.l.* in northwest Argentina and of the Nama and Vanrhynsdorp groups in southern Africa, and to discuss their significance with regard to the 'agronomic revolution' trends, biodiversity and environmental shift during the Ediacaran to Early Cambrian transition.

9.3.2. Trace Fossils in Northwest Argentina (South America)

9.3.2.1. General aspects of the Puncoviscana Formation *s.l.*

The highly tectonised and metamorphosed siliciclastic strata – over 3,000 m thick – that underlies the more fossiliferous Cambro-Ordovician sequence in NW Argentina is named as the Puncoviscana Formation *s.l.* Trace fossil and geochronologic data support an agreed Ediacaran-Early Cambrian age for the fossiliferous strata in the unit. Even though widespread siliciclastics characterise this sequence, limestones, volcaniclastics and lava flows have also been mentioned, emphasising the complexity of facies and lithologies included in the basin (Aceñolaza and Aceñolaza, 2007). A detailed stratigraphical scheme with discussion on the chronological aspects of the basin is given in Chapter 6.

As stated earlier, trace fossils are a prime source of data for the chronological interpretation of the Puncoviscana Basin, and have been used with the sedimentological studies since the 1970s to interpret the ecology of the Puncoviscana Sea.

Although the classic model of Seilacher (1967) used the distribution of trace fossil associations in relation to bathymetry, later studies (e.g. Frey and Seilacher, 1980; Frey et al., 1990) have showed that environmental and ecological factors play an important role in the distribution of trace fossil associations. In addition, Crimes (1994) and Crimes and Fedonkin (1994) emphasised the importance of photic conditions and environmental energy in the general ecology of marine habitats. The significant diversification of infaunal burrowers driving the 'agronomic revolution' on shallow marine bottoms during the Ediacaran-Cambrian transition entailed the widespread demise of microbial mats at the sediment–water interphase.

Today, a complex palaeoenvironmental framework is inferred for the Ediacaran-Early Cambrian transition in the Puncoviscana basin, including shallow water wave-influenced strata, storm beds, haemipelagic clays, and relatively deep-ocean flysch-like shales and sandstones (Jezek, 1990). Trace fossil associations and the sedimentary characteristics suggest, for the whole basin, a shallow water sea deepening towards the west. The features referred above suggest that this slightly deeper-water environment was located below the storm wave base, mostly on the continental slope. There is not, however, clear evidence for truly deep off-slope oceanic settings in the Puncoviscana Basin (Aceñolaza and Aceñolaza, 2007).

9.3.2.2. Lower Cambrian trace fossils

The existence of exclusively Ediacaran trace fossils in the Puncoviscana Formation is not clear. The lack of an undisturbed stratigraphical succession, together with the absence of precise chronological elements and the structural complexity of the unit, preclude a clear chronostratigraphic understanding of the sequence.

Early Cambrian trace fossils of the Puncoviscana Formation were first recorded in the Sierra de La Ovejería, in the Catamarca Province of northern Argentina (Mirré and Aceñolaza, 1972), and later from other localities in Tucumán, Catamarca, La Rioja, Salta and Jujuy (Aceñolaza et al., 1999; Aceñolaza and Aceñolaza, 2005). Further sedimentological analysis associated to ichnological studies supported ecological interpretations that greatly contributed to the understanding of the Puncoviscana Basin and its fossils (Keppie and Bahlburg, 1999; Omarini et al., 1999; Sureda et al., 1999; Aceñolaza and Aceñolaza, 2001; Buatois and Mángano, 2003, 2004).

Although most trace fossils were found in the Salta Province (NW Argentina), other material from Jujuy, Catamarca, Tucumán and La Rioja is important to complete the picture of the Puncoviscana Basin, and their significance for the Ediacaran-Early Cambrian strata in the SW margin of Gondwana.

The trace fossils of the Puncoviscana Formation *s.l.* are represented by the *Oldhamia* and *Nereites* ichnoassociations, named after the homonymus trace fossils (Aceñolaza and Durand, 1986; Aceñolaza et al., 1999; Aceñolaza and Alonso, 2001; Aceñolaza and Aceñolaza, 2005). The *Oldhamia* ichnoassociation is located on the western belt of the basin, while *Nereites* is found eastwards, with the shallower sedimentary facies represented in

Author's personal copy

the eastern belt. Some elements of these ichnological associations are restricted to one of them, although some forms are shared. These differences are still a matter of discussion, whether they correspond to particular ecological situations or if they represent different chronological levels within the same unit. Unfortunately, the intense multiphase deformations that affected these rocks do not allow reliable correlations of the units occurring in the basin.

Winding and meandering trace fossils are common both in the shallower eastern facies and in the deeper western facies of the Puncoviscana Basin. *Cochlichnus anguineus* represents one of the most common sinusoidal traces in the San Antonio de los Cobres, Campo Quijano, Cachi, Cuesta Muñano and Rio Corralito outcrops (Salta). It has a wide chronological record, and in NW Argentina it is mostly found associated with *Oldhamia*. Thick looping traces, up to 2 cm thick assigned to *Gordia marina* are recorded from the Abra Blanca and San Antonio de Los Cobres localities (Salta).

Archaeonassa is represented by an irregular shallow furrow bound by sub-angular crests or levees and slightly meandering. It is interpreted as produced by a gastropod-like organism and its generic name has been considered as a broad definition for many associated forms (Yochelson and Fedonkin, 1997; Jensen, 2003). *Archaeonassa fossulata* has been recognised in several localities of Salta. Bilobed smooth traces as *Didymaulichnus lyelli* are recorded in San Antonio de Los Cobres (Salta); while complex meandering ornamented traces are represented by *Neonereites uniserialis* and *Nereites biserialis* (Figure 9.3.1I).

One of the most striking ichnospecies of the Puncoviscana Formation is *Nereites saltensis* (Figure 9.3.1G), a meandering form with a semi-elliptic/circular outline sometimes displaying a central furrow defining two poorly marked lobes (Aceñolaza and Durand, 1973). This ichnogenus has been re-evaluated by Benton (1982) and Uchman (1995), supporting its interpretation as a worm burrow. More recently, a re-assignment of *Nereites saltensis* to *Psammichnites saltensis* was proposed by Seilacher et al. (2005) on the basis of a single specimen, while Aceñolaza and Aceñolaza (2006) re-evaluated abundant and type material that supports its original designation to the ichnogenus *Nereites*.

Among unbranched meandering burrows, *Helminthopsis abeli, Helminthopsis tenuis* and *Helminthoidichnites tenuis* (Figure 9.3.1H) represent the most common trace fossils occurring in the Puncoviscana Formation, while a slightly systemic meandering pattern can be seen in *Helminthoraphe* isp. (Figure 9.3.1E) and *Taphrelminthopsis* isp., which are associated with the earlier mentioned trace fossils.

The occurrence of scratch marks is important in the evolutionary history of early life, as it indicates that organisms already had mineralised appendages close to the Ediacaran-Early Cambrian transition. The sclerotisation of the appendages gave this group of organisms a comparative advantage with respect to soft-bodied forms, allowing them to move, hunt and dig more efficiently. Some forms included in this group are those assigned to *Monomorphichnus*, where *M. lineatus* is a common trace fossil in the strata of the Puncoviscana Formation at Muñano, El Alisal and Río Corralito (Salta). Associated with these arthropod-related traces, *Diplichnites* and *Dimorphichnus* (*D. obliquus*) occur, which are characterised by both punctual and slightly elongated imprints on the sediments. Rare forms assigned to cf. *Protichnites* and/or '*Cloeophycus*' occur in Abra Blanca and San Antonio de los Cobres (Salta), and are characterised by an elongated furrow bound on both sides by incisions. '*Cloeophycus*' is considered a hardly understandable tool mark on the deeper-water setting of the Puncoviscana Formation, and represents an intriguing element to be analysed. Another unique trackway in the Puncoviscana Formation is *Tasmanadia* (*T. cachii*), a form characterised by series of appendage scratches on the upper surface of sandstones that represent the hopping displacement of an unknown animal.

Asaphoidichnus (*A. trifidus*) displays locomotion marks with three short final probes and was recorded from San Antonio de los Cobres and Cachi (Salta). Finally it is necessary to mention the record of *Oldhamia* (Figure 9.3.1D, J), with six different ichnospecies: *Oldhamia alata*, *O. antiqua*, *O. curvata*, *O. flabellata*, *O. geniculata* and *O. radiata*. Interpretations of this trace assign it to arthropod scraping marks on microbial mats (Aceñolaza and Durand, 1984), or feeding tubes of undermat miners (Seilacher, 2007). All these trace fossils are common in the sections of San Antonio de los Cobres, Muñano, Abra Blanca (Salta) and the Sierra de la Ovejería (Catamarca).

Resting traces are rare, and their taxonomical status is a matter of debate on the ichnological literature. *Multipodichnus* (*M. holmi*) has been described from the Quebrada del Toro (Salta), and is represented by a structure of a bent sculpture towards a central area that has been interpreted as a resting trace of some arthropod-like organism (Aceñolaza et al., 1999).

Single dichotomised and radially arranged burrows and burrow networks are common in the Puncoviscana Formation *s.l.*, displaying a wide variety of trace fossils with frequent occurrences of *Palaeophycus* (*P. tubularis*, *Palaeophycus* isp.) and *Planolites* ispp. All of them have been recorded from the shallow and deeper settings of the basin in several localities of Jujuy, Salta, Catamarca and La Rioja. The presence of *Treptichnus* (*T. aequalternus* and *T. pollardi*) in Tucumán and Salta is regarded as the presence of unequivocal Cambrian trace fossils (Aceñolaza, 2004). Although it is very rare to find dichotomised burrows, large 'primitive networks' (comparable to *Thalassinoides*) have been mentioned in successions in San Antonio de los Cobres (Salta) which also includes a rich

Author's personal copy

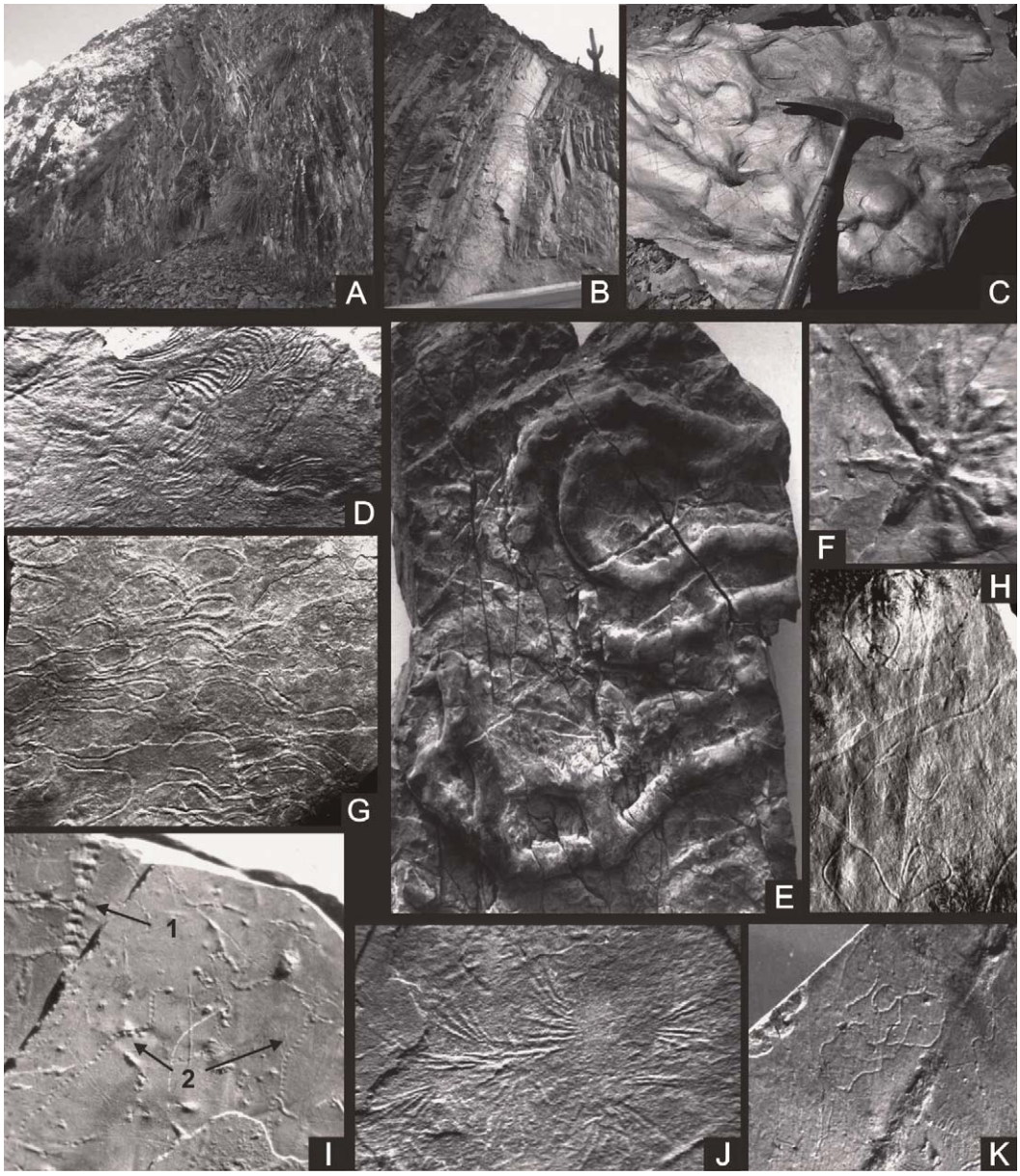


Figure 9.3.1 Ediacaran-Early Cambrian outcrops and trace fossils of the Puncoviscana Formation *s.l.* in NW Argentina. A- General view of the grey and greenish slates of Puncoviscana in Jujuy. B- Frontal view of an axis fold highlighting the strong deformation of the Puncoviscana Formation *s.l.* in the Andean Belt. C- Flute cast and sedimentary structures on the base of a sandstone bed in Salta. D- *Oldhamia curvata* from Quebrada del Toro, Salta Province (× 0.6). E- *Helminthoraphe* isp. (× 0.2). F- *Glockerichnus* isp. (× 1.5). G- *Nereites saltenis* from Salta Province (× 0.15; non-*Psammichnites saltensis* in Seilacher et al. 2005). H- *Helminthoidichnites tenuis* from Choromoro, Tucumán (× 0,6). I- 1: *Neonereites biserialis* (× 0.5); 2: *N. uniserialis* (× 0.5) from Salta. J- *Oldhamia radiata* from San Antonio de los Cobres, Salta Province (× 1.5). K- *Gordia* isp. from the Quebrada del Toro, Salta (× 2).

Oldhamia association. *Glockerichnus* (Figure 9.3.1F) has been described from Cachi (Salta), being represented by thick radially arranged burrows.

The co-existence of different tiering structures and the non-exclusively biomat-related feeding strategies require a more complex ecological structure for the Puncoviscana Formation than previously suggested (Buatois and Mángano, 2003; Aceñolaza, 2005).

9.3.3. Trace Fossils of the Nama Group

The stratigraphy of the Nama Group and its depositional environments are described in Chapter 5.4 and shown in Figure 5.4.5. The trace fossils thus far identified in the Nama Group are shown in Table 5.4.1. Recent

Author's personal copy

studies have shown that these trace fossils (found in shallow marine deposits) warrant urgent re-examination (Seilacher et al., 2005; Jensen et al., 2006). Predominantly based on the occurrence of the trace fossils *Treptichnus pedum* and *Diplichnites*, the Ediacaran-Early Cambrian boundary has been established at the base of the Nomtsas Formation of the uppermost Schwarzrand Subgroup (Germs, 1972a,b, 1983; Crimes and Germs, 1982). This is in agreement with the ages of silicified ash beds in the Schwarzrand Subgroup (Grotzinger et al., 1995) (Figures 5.4.6 and 9.3.2). There is a possibility that the Ediacaran-Early Cambrian boundary may be within the Spitskop Member of the uppermost Urusis Formation of the Schwarzrand Subgroup (Jensen and Runnegar, 2005).

9.3.3.1. Ediacaran (lower Nama Group) trace fossils (ca. 550–543 Ma)

Trace fossils found in the Ediacaran Kuibis Subgroup and lower and middle Schwarzrand Subgroup are, as expected, generally sparse, small and display low diversity (Table 5.4.1). They are even sparser than as shown in Table 5.4.1 since trace fossils like *Archaeichnium* and *Bergaueria* (Seilacher et al., 2005) and *Buchholzbrunnichnus* (Germs, personal observations) are now considered to be most likely body fossils. *Skolithos*, reported by Crimes and Germs (1982), is now believed to be a body fossil (Crimes and Fedonkin, 1996) and it is generally accepted that vertical bioturbation (such as shown by *Skolithos*) is absent in the Ediacaran (Seilacher et al., 2005). However, vertical biogenic trace fossils occur in the Nudaus Formation of the northern Nama Group (Zaris sub-basin) and basal Huns Member of the Urusis Formation of the Schwarzrand Subgroup of the southern Nama Group (Witputs sub-basin) (Germs, personal observation). *Skolithos*-type trace fossils have probably also been found in the Kuibis Subgroup (Germs, 1972a,b).

Rare complex *Treptichnus* (*Trichophycus*)-type trace fossils occur in the Ediacaran Nasep Member (Germs, 1972b; Geyer and Uchman, 1995) and in the basal Huns Member (middle Schwarzrand Subgroup) (Jensen et al., 2000). This implies that *Treptichnus*-type trace fossils occur in Nama successions older than approximately 545 Ma (Figure 9.3.2). More recently the *Treptichnus*-type complex trace fossil *Streptichnus narbonnei* has been described

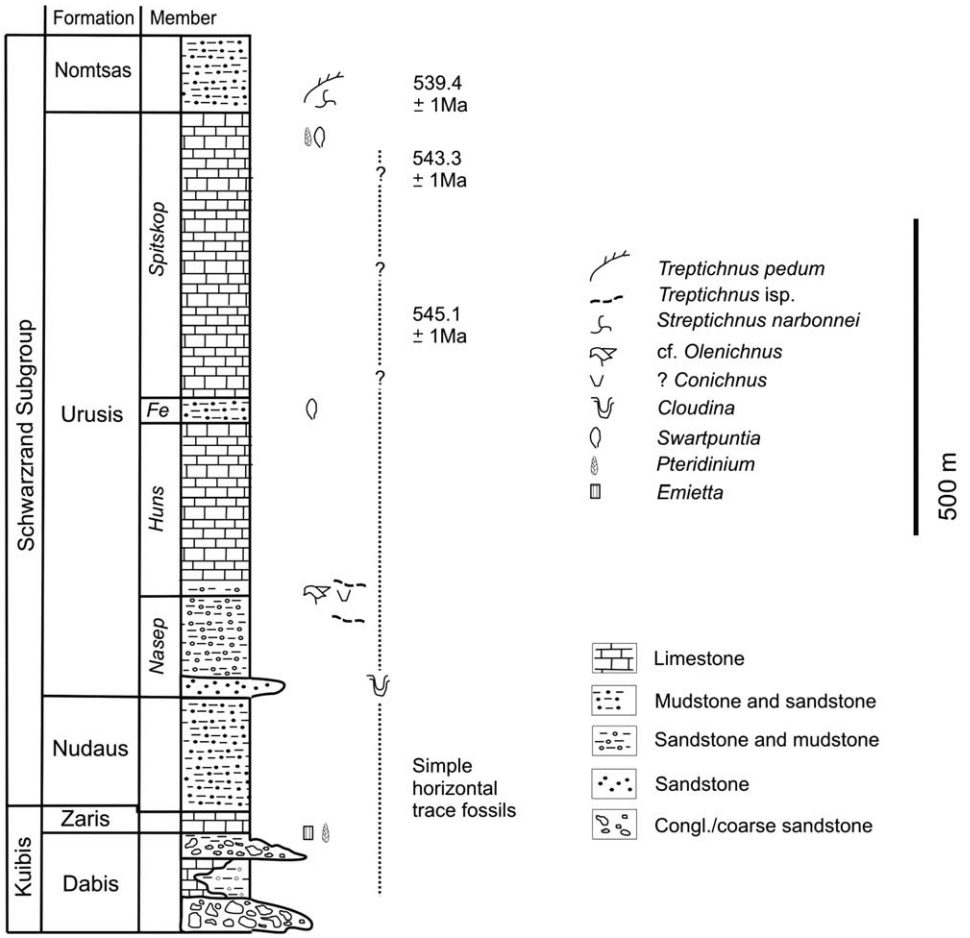


Figure 9.3.2 Generalised section of the Nama Group in the Witputs sub-basin (simplified from Germs, 1983), showing distribution of trace and body fossils. Fe- Feldschuhhorn (modified after Jensen and Runnegar, 2005).

Author's personal copy

from the Spitskop Member of the Urusis Formation (middle Schwarzrand Subgroup) (Jensen and Runnegar, 2005) (Figure 9.3.2).

Based on the radiometric date of 543 ± 1 Ma of a silicified ash bed in the Spitskop Member and the occurrence of the body fossil *Pteridinium carolinaense* in this member, a latest Ediacaran age has been assigned to the Spitskop Member (Grotzinger et al., 1995). However, the occurrence of *Streptichnus narbonnei* may be an indication that a part of the Spitskop Member may be Cambrian in age and that the Ediacaran-Early Cambrian boundary may be within the Spitskop Member and not at the base of the Nomtsas Formation (Jensen and Runnegar, 2005).

9.3.3.2. Early Cambrian (upper Nama Group) trace fossils (ca. 540–530 Ma)

The trace fossils of the Nomtsas Formation (uppermost Schwarzrand Subgroup) and Fish River Subgroup are generally larger in size, more complex and slightly more diversified than the trace fossils occurring in the underlying Ediacaran sediments. '*Phycodes*' *pedum* occurs widespread and some complex trace fossils occur in these successions especially in the Fish River Subgroup (Crimes and Germs, 1982; Geyer and Uchman, 1995; Geyer, 2005; Table 5.4.1). Most of the trace fossils thus far found in the Fish River Subgroup have been found in the Rosenhof Member (Gross Aub Formation). The trace fossils in the Rosenhof Member are *Trichophycus pedum*, *Trichophycus pollardi*, *Paleophycus*, *Gordia*, *Skolithos* and *Enigmatichnus* (Crimes and Germs, 1982; Geyer and Uchman, 1995; Geyer, 2005). Geyer and Uchman (1995) and Geyer (2005) consider some trace fossils like *Phycodes* to belong to *Trichophycus* whereas, for example Jensen and Runnegar (2005) and Buatois et al. (2007) consider them to belong to *Treptichnus*. There is much dispute about the taxonomical status of *Trichophycus*, *Phycodes* and *Treptichnus*; and discussions are focused on fine morphological characters and the nature of the burrow (Erdogan et al., 2004; Aceñolaza and Aceñolaza, 2007).

The diverse ichnoassemblages of the Fish River Subgroup are indicative of an earliest Cambrian pre-trilobite age (Geyer, 2005). They comprise traces of deposit feeders as well as others that were probably created by suspension feeders and agrichnial farmers (Geyer, 2005). The trace maker of *Enigmatichnus* was probably an arthropod (Crimes and Germs, 1982).

9.3.4. Trace Fossils of the Vanrhynsdorp Group (ca. 550–535 Ma)

The stratigraphy of the Vanrhynsdorp Group and its depositional environments are discussed in Chapter 5.4 and shown in Figure 5.4.8. The Ediacaran-Cambrian boundary has not yet been pinpointed in the Vanrhynsdorp Group. The boundary may occur at the base of the Arondegas Formation or more likely at the base of the Besonderheid Formation of the Knersvlakte Subgroup. Future dating of silicified volcanic ash beds in the Gannabos and Besonderheid Formations most probably will make it possible to determine where this important boundary is stratigraphically located in the Vanrhynsdorp Group.

The Vanrhynsdorp Group is emerging as a key succession for documenting ichnodiversity, ichnostratigraphy, body size and burrowing behaviour among infaunal metazoans across the Ediacaran-Cambrian boundary (Buatois et al., 2007; Almond et al., 2008). The trace fossils thus far described from the Vanrhynsdorp area are shown in Figures 5.4.8 and 9.3.3. Much progress has recently been made with the study of trace fossils by Buatois et al. (2007) and Almond et al. (2008). The Vanrhynsdorp Group is considered to be a slightly deeper-water unit that correlates to the Nama Group (Germs and Gresse, 1991; Gresse and Germs, 1993; Figure 5.4.3). Even though, precise correlation of the Nama and Vanrhynsdorp successions remains disputable.

No trace fossils have yet been found in the basal Flaminkberg Formation. Narrow straight to curved horizontal burrows of *Helminthopsis* are associated with microbial dark mudstones of the younger Hoedberg Formation (Kwanous Subgroup) (Gresse, 1992; Buatois et al., 2007; Almond et al., 2008; Figure 9.3.3A). According to Buatois et al. (2007) and Almond et al. (2008) this trace fossil is characteristic of inshore as well as deeper water in the Ediacaran Period. More data are required to ascertain whether these *Helminthopsis*-bearing successions are latest Ediacaran or Early Cambrian in age.

Large 1–2.3 cm-wide horizontal burrows occur in the heterolithic upper Gannabos Formation of the Knersvlakte Subgroup (Gresse, 1992; Buatois et al., 2007; Almond et al., 2008; Figure 9.3.3B). This unidentified type of trace fossil (*Planolites*?) is also associated with microbial wrinkle marks and is characteristic for an offshore storm-influenced marine environment.

Buatois et al. (2007) and Almond et al. (2008) provisionally assigned an Ediacaran age to the Hoedberg, Arondegas and Gannabos formations based on the apparent absence of *Treptichnus*-type burrows which characterise comparable storm dominated shelf-facies in the Early Cambrian. If correct, this implies that infaunal large-bodied metazoans appeared before the end of the Ediacaran (Almond et al., 2008).

Author's personal copy

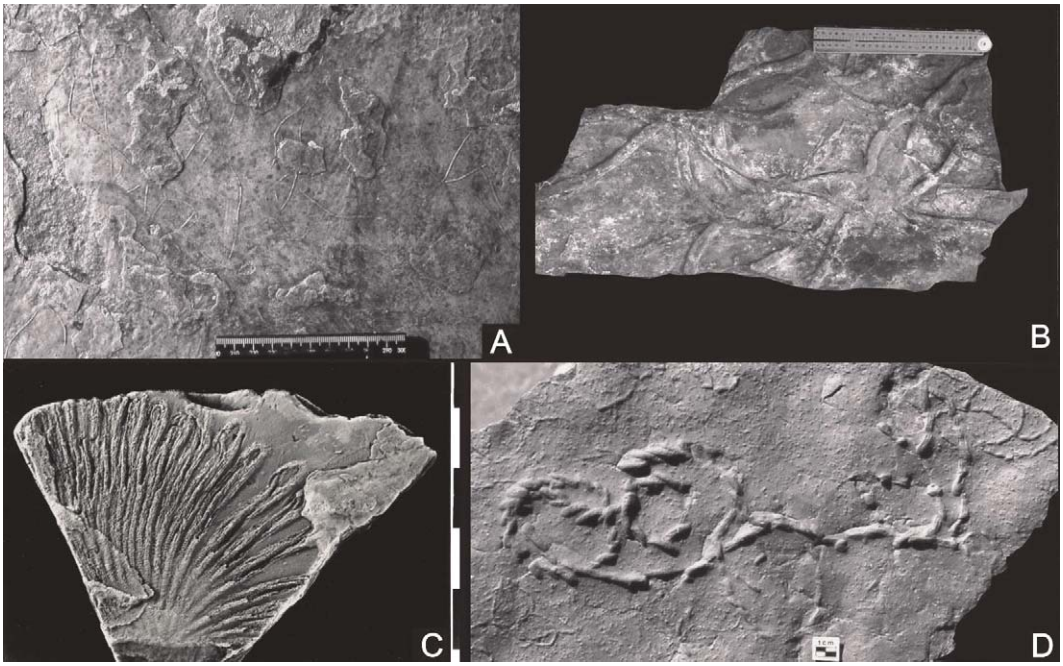


Figure 9.3.3 Ediacaran-Early Cambrian trace fossils from South Africa. A- *Helminthopsis* ichnoguild, horizontal burrows, Hoedberg Formation, Vanrhynsdorp Group. B- *Planolites* isp., Gannabos Formation, Vanrhynsdorp Group. C- *Oldhamia geniculata*, Besonderheid Formation, Vanrhynsdorp Group (scale segments to the right are 1 cm). D- *Treptichnus pedum*, Kalkgat Formation, Vanrhynsdorp Group (Photographs supplied by J.E. Almond).

Complex sub-horizontal burrow systems of the distinctive Cambrian ichnofossil *Oldhamia geniculata* (Figure 9.3.3C) occur in the distal, finely laminated mudrocks of the Besonderheid Formation of the middle Knersvlakte Subgroup (Gresse, 1992; Buatois et al., 2007; Almond et al., 2008). This trace fossil is also known from the Early Cambrian of Argentina (Seilacher et al., 2005). The Vanrhynsdorp *Oldhamia* systems are associated with wrinkle marks and show a sophisticated foraging behaviour of the trace maker. The successions of the overlying upper Knersvlakte and the Klipbak subgroups contain prolific low diversity trace fossil assemblages, dominated by *Treptichnus*-type trace fossils (Germs, 1983; Gresse, 1992; Almond et al, 2008). The presence of *Treptichnus pedum* (Figure 9.3.3D), as well as the absence of unequivocal arthropod scratch burrows such as *Rusophycus/Cruziana*, suggests an earliest Cambrian age for the Vanrhynsdorp successions overlying the Besonderheid Formation (Buatois et al., 2007; Almond et al., 2008).

The Vanrhynsdorp treptichnids display considerable preservational, morphological and hence behaviour, plasticity with frequent intergradations between *Treptichnus pedum* and other treptichnid ichnospecies within the same burrow system (Buatois et al., 2007; Almond et al., 2008). Transitions with *Curvolithus–Saerichnites–Arthrophycus* and *Cruziana* morphs have been observed (Buatois et al., 2007; Almond et al., 2008). Buatois et al. (2007) and Almond et al. (2008) consider the identity and arthropod origin of *Monomorphichnus* reported from the Klipbak Formation controversial (Germs, 1983).

9.3.5. Conclusions

Thus far, definitive Ediacaran fossils have not yet been found in the Puncoviscana Formation, even though geochronological data includes indisputable Ediacaran strata in the basin (Aceñolaza and Aceñolaza, 2005, 2007). This is in contrast to the Nama and Vanrhynsdorp groups, where such deposits are well exposed and contain trace fossils (Germs, 1972b, 1983; Crimes and Germs, 1982; Almond et al., 2008).

The Late Ediacaran trace fossil assemblages of the lower Nama and lower Vanrhynsdorp groups are similar to Ediacaran trace fossils elsewhere in the world: generally sparse, very low in diversity and dominated by small, fairly simple horizontal burrows generated in a shallow marine to offshore depositional environment (Crimes and Germs, 1982; Buatois et al., 2007; Almond et al., 2008; Table 5.4.1; Figure 9.3.3A). Unnamed, up to 2.5 cm-wide trace fossils occurring in the probable Ediacaran, Gannabos Formation (Vanrhynsdorp Group; Figure 9.3.3B) suggest that large metazoans appeared prior to the Cambrian (Buatois et al., 2007; Almond et al., 2008).

In contrast, the latest Ediacaran middle and upper Nama Group contains complex *Treptichnus*-type trace fossils which occur in the Nasep Member and lower Spitskop Member of the Urusis Formation (Schwarzrand Subgroup)

Author's personal copy

(Germs, 1972b; Geyer and Uchman, 1995; Geyer, 2005; Jensen et al., 2000). In other words, as shown by the Nama Group, treptichnid-type trace fossils already occur in ca. 546 Ma old successions, that is, prior to the Cambrian (Figure 9.3.2). It is not yet certain if the newly described *Treptichnus*-type *Streptichnus narbonnei* from the Spitskop Member is Ediacaran (Grotzinger et al., 1995) or Early Cambrian in age (Jensen and Runnegar, 2005; Figure 9.3.2).

The earliest Cambrian trace fossil assemblages of the uppermost successions of the Nama and Vanrhynsdorp groups display a higher, but still relatively low, diversity of trace fossils dominated by *Treptichnus* (Crimes and Germs, 1982; Almond et al., 2008) (Table 5.4.1, Figures 9.3.2, 9.3.3D and 5.4.8). The treptichnid-dominated assemblages of the uppermost Nama and Vanrhynsdorp groups are predominantly associated with reddish shallow marine sandy deposits. *Diplichnites* and ?*Monomorphichnus* sparsely occur in more distally deposited finer clastic sediments of these uppermost successions (Crimes and Germs, 1982; Germs, 1983).

From the ichnofossil assemblages found in the Ediacaran Nama (Table 5.4.1) and Vanrhynsdorp (Figure 5.4.8) groups, it becomes evident that the increase in trace fossil diversity towards the Cambrian occurs more gradually than generally accepted. This has also been noted by Gehling et al. (2001). This more 'gradual' increase in trace fossil diversity from the Ediacaran to the Early Cambrian appears to apply also to body fossil diversity (Jensen et al., 1998). The relatively low diversity and apparent absence of trilobite tracks and trails probably indicate that the upper Nama and upper Vanrhynsdorp groups are of pre-trilobite age (Geyer, 2005; Almond et al., 2008), and that these successions accumulated prior to the acme of the 'agronomic revolution' and the 'Cambrian explosion', and that these events occurred gradually. Vertical bioturbation might have taken place during deposition of the Ediacaran lower and middle Nama groups which probably confirms the gradual evolution of these events.

The trace fossil diversity of the Cambrian Puncoviscana Formation is higher than that of the earliest Cambrian Nama and Vanrhynsdorp groups. Arthropod trace fossils as *Tasmanadia*, *Diplichnites*, *Monomorphichnus* and worm-like tracks and trails are quite common in the Puncoviscana Formation. Vertical bioturbation occurs both in the eastern shallow and western deeper part of the Puncoviscana Basin. The frequent occurrence of these trace fossils indicates that these fossiliferous levels of the Puncoviscana Formation may be younger than the uppermost lower Cambrian (pre-trilobite) successions of the Nama and Vanrhynsdorp groups and that the Puncoviscana Formation most likely accumulated during a time interval including 'trilobite' time. The trace fossil assemblages of the Puncoviscana Formation reflect the development of the true 'agronomic revolution' (Seilacher and Pflüger, 1994) or the 'Cambrian substrate revolution' (Bottjer et al., 2000).

The trace makers of the ichnofossils occurring in the Cambrian Puncoviscana Formation and in the Ediacaran and Cambrian Nama and Vanrhynsdorp groups, as elsewhere on Earth during that time, predominantly fed on or beneath the surface of biomats which occurred abundantly in the Puncoviscana, Nama and Vanrhynsdorp basins (Aceñolaza and Aceñolaza, 2001, 2007; Noffke et al., 2002a,b; Buatois and Mángano, 2004; Buatois et al., 2007; Almond et al., 2008). The biomats were formed by microbial communities and were a key element of the ecological structure of shallow and deep-water settings. They are characterised by wrinkle structures and elephant skin among other forms (e.g. Droser et al., 2002; Noffke et al., 2002b; McIlroy et al., 2005; Bailey et al., 2006). The occurrence of the trace fossil *Nereites* in shallow marine deposits of the Vingerbreek Member (Nudaus Formation, Schwarzrand Subgroup, Nama Group; Table 5.4.1, Chapter 5.4) and in the eastern shallow facies of the Puncoviscana Formation indicates that its trace maker had not yet moved to an offshore environment. The timing of this event is uncertain. More studies of the turbiditic Besonderheid Formation (Vanrhynsdorp Group) and deeper marine facies of the Puncoviscana Formation are needed to establish when this event took place.

The occurrence of *Oldhamia geniculata* (Figure 9.3.3C) in the Besonderheid Formation (Vanrhynsdorp Group) probably indicates a Cambrian age for this formation. Its occurrence in distal pro-delta deposits (probably distal turbidites) represents a step in the ecological onshore–offshore shift of its trace maker (Seilacher et al., 2005). The sparse occurrence of only one *Oldhamia* species (i.e. *Oldhamia geniculata*) in the Besonderheid Formation and the low trace fossil diversity of this formation contrasts with the higher trace fossil diversity of the Puncoviscana Formation which contains various *Oldhamia* ichnospecies (Figure 9.3.1D) associated with arthropod traces and probable early network systems comparable to *Thalassinoides* (Aceñolaza and Aceñolaza, 2005; Seilacher et al., 2005). The difference in diversity can most probably be ascribed to a difference in age, with a Puncoviscana Formation younger in age than the uppermost Cambrian successions of the Nama and Vanrhynsdorp groups.

It may also be explained by different environmental conditions. The general depositional environments of the Nama and Vanrhynsdorp groups are rather well known (Figures 5.4.5 and 5.4.8), but not those of the Puncoviscana Formation. More work is needed to identify the various depositional environments of the unit. A basic requirement for identifying those depositional environments is to have a good knowledge of the stratigraphy of the Puncoviscana Formation. Due to complex structural deformation and lack of chronological data the stratigraphy of the Puncoviscana Formation has not yet been unravelled. The Early Cambrian Guachos Formation is included in the Puncoviscana Basin, and represents a local environmentally controlled facies within the framework of the Ediacaran-Early Cambrian successions in northwest Argentina (Aceñolaza and Aceñolaza, 2005).

Author's personal copy

The eastern facies of the Puncoviscana Formation accumulated in a shallow marine setting, while there is no full consensus regarding the depositional setting of the western facies of the Puncoviscana Formation (Borrello, 1969; Aceñolaza, 2005). The generally accepted deep-water western facies of this formation is challenged in this publication. It is proposed herein that the Puncoviscana Formation was deposited in an overall shallow marine environment in a basin deepening towards the west. The occurrence of relatively deep-ocean flysch-like shales and sandstones indicate that the western Puncoviscana facies (García-Bellido and Aceñolaza, 2005) was generally deposited in deeper water than the Nama and Vanrhynsdorp (with the exception of the Besonderheid Formation) groups.

In the Vanrhynsdorp Group the multiple intergradations between *Treptichnus pedum* and different ichogenera, including other *Treptichnus* forms, cast serious doubts about the reliability of using *Treptichnus* ichnospecies, such as *Treptichnus pedum*, in biostratigraphic zonations of Ediacaran and lowermost Cambrian sediments (Buatois et al., 2007; Almond et al., 2008).

Finally, a re-examination of Ediacaran to Early Cambrian trace fossils is urgently needed from well-dated reference sections around the world, especially considering *Treptichnus pedum* and its evolutionary history.

ACKNOWLEDGEMENTS

The authors are indebted to J.C. Gutiérrez-Marco, D. García-Bellido and S. Jensen for the revision of the manuscript, and to J.E. Almond for the graphical assistance with photographs. The manuscript benefited from field discussions with P. Vickers-Rich and M. Fedonkin. This contribution was supported by the Universidad Nacional de Tucumán (CIUNT).