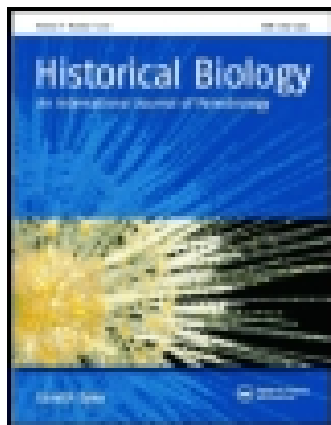


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Sol Noetinger^a, Mercedes Di Pasquo^b, Peter Isaacson^c, Guillermo Aceñolaza^d & María del Milagro Vergel^d

^a Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Angel Gallardo 470, C1405DJR Ciudad Autónoma de Buenos Aires, Argentina

^b CICYTTP-CONICET, Dr. Matteri y España SN, E3105BWA Diamante, Entre Ríos, Argentina

^c University of Idaho, Moscow, Idaho, 83844, USA

^d INSUGEO-CONICET Sede Miguel Lillo, Miguel Lillo 205, 4000 San Miguel de Tucumán, Argentina

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Integrated study of fauna and microflora from the Early Devonian (Pragian–Emsian) of northwestern Argentina

Sol Noetinger^{a*}, Mercedes Di Pasquo^b, Peter Isaacson^c, Guillermo Aceñolaza^d and María del Milagro Vergel^d

^aMuseo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Av. Angel Gallardo 470, C1405DJR Ciudad Autónoma de Buenos Aires, Argentina; ^bCICYTTP-CONICET, Dr. Matteri y España SN, E3105BWA Diamante, Entre Ríos, Argentina; ^cUniversity of Idaho, Moscow, Idaho, 83844, USA; ^dINSUGEO-CONICET Sede Miguel Lillo, Miguel Lillo 205, 4000 San Miguel de Tucumán, Argentina

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The Devonian System in northern Argentina has been broadly analysed, but details of its lithologies, biostratigraphy and fossil content have not been presented in a comprehensive study. We performed the first integrative analysis of the palynological and macrofossil content from the Pescado Formation at the Zenta Range, Argentina. We define a new species of cryptospore and extend the stratigraphic record of the ichnogenus *Psammichnites* isp. for South America. The stratigraphic ranges of the palynomorphs suggest a time span from the ?late Lochkovian to Pragian–earliest Emsian, but the co-occurrences of key invertebrates narrow the age of the beds to the late Pragian and early Emsian. Moreover, sedimentary analysis indicates a proximal shoreface–foreshore depocenter during this time range for the Zenta region. The contraction phase of the basin during the middle Pragian and Emsian is evidenced by the presence of sand bodies at the top of the column and the higher supply of terrigenous components. During this regression event, a low diversity Malvinokaffric Realm brachiopod assemblage occurs, with dominance of *Australospirifer hawkinsi*. The predominance of the latter species during this event is coeval with the first decline of the Malvinokaffric Realm in the neighbouring Paraná basin.

Keywords: palynology; trace fossils; invertebrates; palaeoenvironment; Early Devonian; northwestern Argentina

1. Introduction

Northwest Argentina has a complete geological history that ranges from the Precambrian to Holocene, including sedimentary basins with distinctive origins and subsidence scenarios. The sedimentary rocks exceed a thickness of 10 km Devonian deposits and are well exposed in the Subandean Range, the eastern part of the Eastern Range and are also present in the subsurface of the eastern Chaco-Salteño Plain (Starck 1999) (Figure 1). Along the Subandean mountains, the Zenta Range covers a surface of over 15,000 km² in between the provinces of Salta and Jujuy, reaching 5000 m elevation. Even though this range is one of the most important physiographic units in the region, it was not until recently that the area was accessible through the opening of a new road, making its survey possible (Aceñolaza et al. 2003; Vergel et al. 2008a; Aráoz 2009; Noetinger and Di Pasquo 2010a, 2010b; Di Pasquo et al. 2011).

Despite the fact that the Zenta Range was part of the Malvinokaffric Realm during the Lower Devonian (Boucot 1988; Meyerhoff et al. 1996), little is known yet about the local invertebrate fauna (Starck 1999; Tortello and Aceñolaza 2008). Palynological and invertebrate studies have proven not only to be one of the most reliable tools to determine the relative age and to correlate beds but also to

provide insight into depositional palaeoenvironments. Furthermore, trace fossils can provide important clues on the environment of particular sequences (Pemberton et al. 1992). When studied together with body fossils and the sedimentary features, they become remarkable factors enabling a comprehensive conceptualisation of strata.

As part of a multidisciplinary project to characterise the Zenta Range, a detailed palaeontological sampling of several sections was performed. Variably preserved associations of invertebrate fauna, palynology and trace fossils were found interbedded in Silurian-Devonian deposits of the area. This work presents the first integrative analysis for the Zenta Range (S23°14', W 65°2, 37', 4435 m, Figure 1) featuring palynology with invertebrate fauna and trace fossils. Taxa integration would help refine the age of the beds taking into consideration that there are no other proxies such as conodonts or graptolites preserved in the Silurian-Devonian of northwestern Argentina (Alvarez et al. 2003). The results of this study aim to extend the regional sedimentary and palaeogeographical framework, to better understand events with continental implications such as the demise of the Malvinokaffric fauna, which is known to have its first collapse during the early Emsian in the neighbouring Paraná Basin in Brazil (Bosetti et al. 2012).

*Corresponding author. Email: noetinger@macn.gov.ar

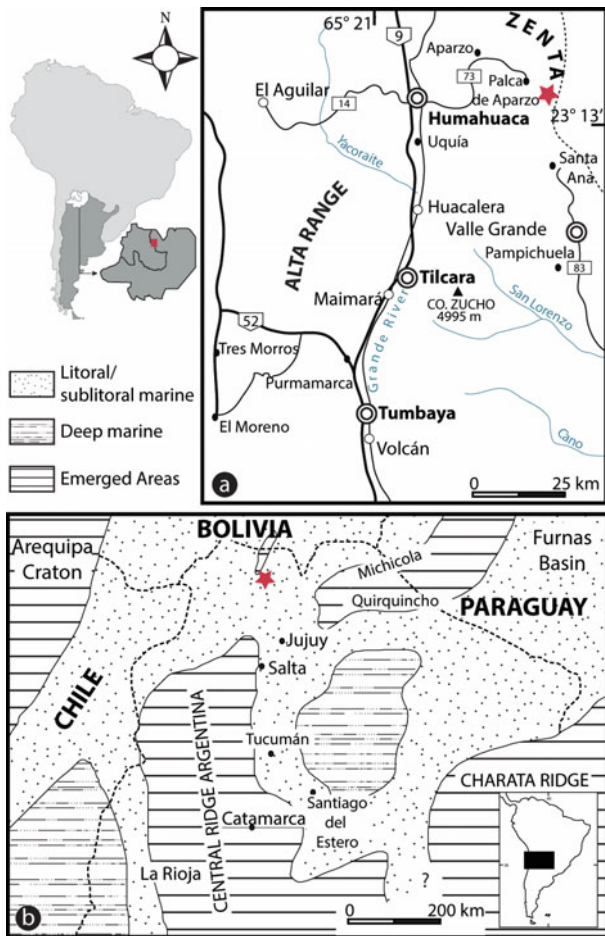


Figure 1. (Colour online) (a). Detail of the area and location of the studied section. (b). Palaeogeographical scheme of northwestern Argentina during the Silurian-Devonian (modified from Aceñolaza et al. 1999).

2. Geological setting

The stratigraphic units of Late Silurian to Devonian from northern Argentina and southern Bolivia have been assigned to supersequence hierarchies by Starck (1995, 1999; Figure 2). This includes a Silurian-Jurassic tectonic-stratigraphic interval that is divided into two units separated by a regional unconformity at the end of the Devonian. The Silurian-Devonian one comprises the Cinco Picachos, Las Pavas and Aguaraquí Supersequences, characterised by stacked, kilometre scale, coarsening-upward shale and sandstone facies bounded by first-order flooding surfaces. Under this scheme, the Cinco Picachos Supersequence includes, conformably over the Silurian Lipeón Formation, the Lower to Middle Devonian Baritú and Porongal formations. The Las Pavas Supersequence is represented by the Pescado and Piedras formations and the Aguaraquí Supersequence, by the Los Monos Formation (Starck et al. 1993).

The Baritú Formation (Figure 3) consists of indurated silicified quartz sandstone, with subaqueous cross-bedding stratification and subordinated dark grey to black, fissile shales (Padula et al. 1967). Noetinger and Di Pasquo (2010a) found spores, acritarchs and chitinozoans in the latter. Among the chitinozoans, *Angochitina chupaci* Paris and Laufeld and *Hoegisphaera* cf. *H. glabra* Staplin attributed the marine assemblage to the Lochkovian. The Baritú Formation is conformably followed by the Porongal Formation (Figure 3), composed of conglomerates with minor sandstones, greywackes and siltstones which transitions to the fine-grained, dark green–grey greywackes and grey, whitish and yellowish micaceous sandstones of the Pescado Formation (Cuerda and Baldi 1971; Antelo Perez 1983). These sandstone beds have abundant cross-stratification structures, while bioturbation

Countries			ARGENTINA			BOLIVIA		
Chronology			TARIJA				MADRE DE DIOS	
Basin			TARIJA				MADRE DE DIOS	
Geographic units			Supersequences (1)	Chaco-Salteño Plain (2)	Eastern Range (2)	Southern Subandean	Northern Subandean Altiplano - Eastern Range (3)	
Period	Stage	Ma						
DEVONIAN	Frasnian	382.7	Aguaraquí	Jollin		Iquirí		
	Givetian			Tonono	Los Monos	Los Monos	Sica Sica	
	Eifelian		Las Pavas	Michicola	Pescado	Huamampampa		Tomachi
	Emsian	393.3		Rincón	Piedras	Icla	Belén	
	Pragian				Porongal	Santa Rosa	Vila Vila	
SILURIAN	Lochkovian	419.2	Cinco Picachos	Caburé	Baritú	Tarabuco		
	Pridoli	423		Copo	Lipeón	Kirusillas	Catavi	Tequeje
	Ludlow							

Figure 2. Stratigraphic correlation of the local units with others from northern Argentina and southern Bolivia (Starck et al. 1993; Starck, 1999; Díaz Martínez, 1999; Suárez Soruco, 2000). Age (Ma): Gradstein et al. (2012).

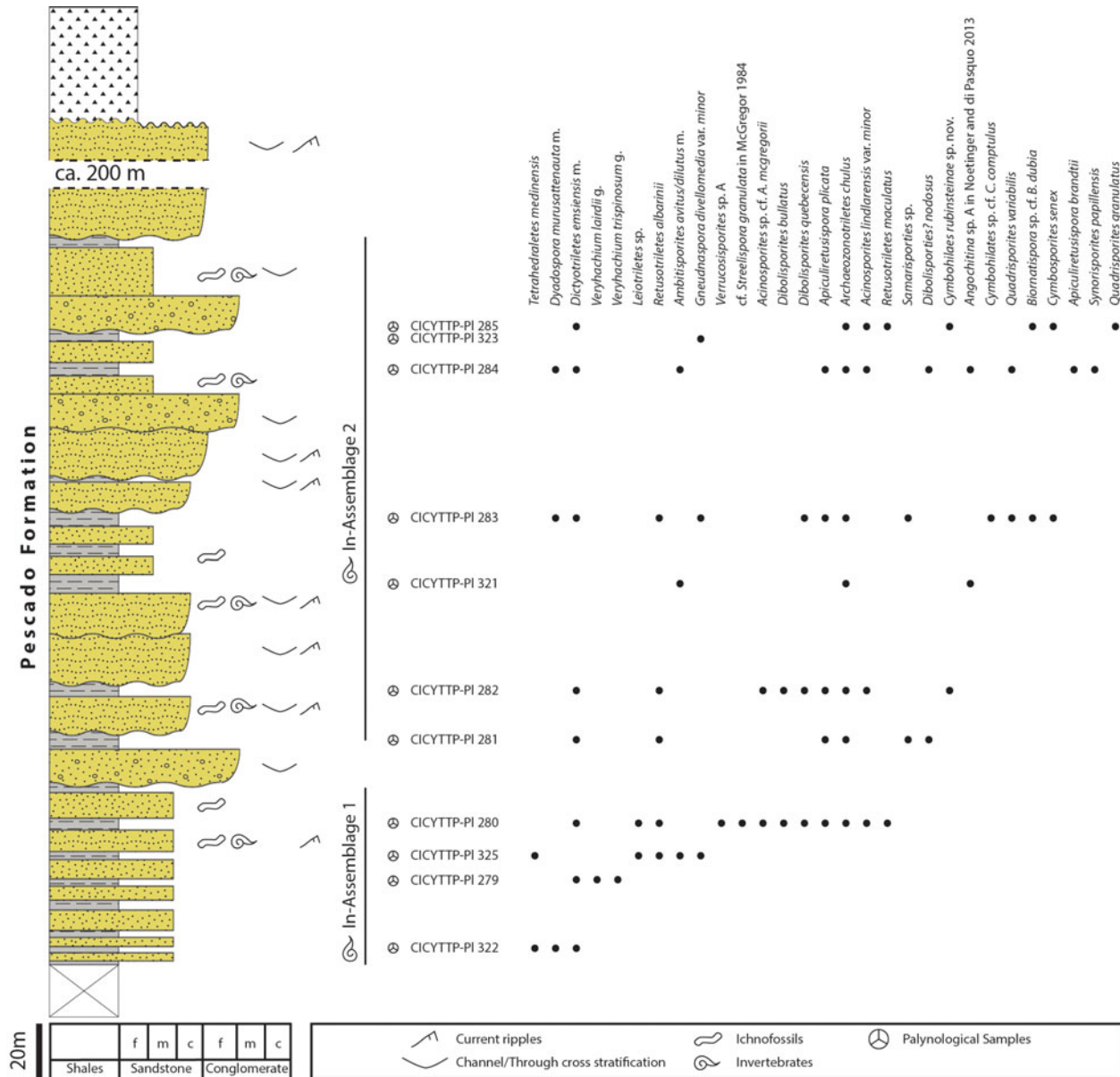


Figure 3. (Colour online) Composite lithologic log of the Pescado Formation at Abra Azul with sampling levels and stratigraphic distribution of palynological species and the invertebrate assemblages recorded in the locality.

is recognisable in several of the different lithologies. Noetinger and Di Pasquo (2010a) assigned a Middle Devonian age to the latter. In this same unit, Antelo Perez (1983) stated the presence of invertebrates such as *Australospirifer antarcticus*, *Proboscidina arcei*, *Australocoelia tourtelotti*, and *Notiochonetes falklandica* and the trace fossil *Zoophycos*. Some of the latter are also recognised in the Piedras Formation (Cuerda and Baldi 1971; Suárez Riglos 1975; Vistalli 1989; Rubinstein 2014) which starts with a polymictic conglomerate followed upward by dark green to black shales (Padula et al. 1967; Aceñolaza et al. 1999).

The late Palaeozoic sedimentary succession, the Machareti and Mandiyuti groups, occurs unconformably above the Silurian-Devonian (Starck et al. 1993). The Early Pennsylvanian BC Zone of the Tarija Formation was identified in the northern part of this area (Di Pasquo and Vergel 2008; Vergel et al. 2008a, 2008b; Di Pasquo et al. 2011). This important gap between the Devonian and the Pennsylvanian rocks confirms the erosion by glacial systems described in other localities of the Tarija Basin (Di Pasquo 2003, 2007) and other western basins of South America (e.g. Azcuay et al. 2007; Limarino et al. 2014).

3. Material and methods

3.1 Studied locality

The locality (Figures 1, 3) occurs over a covered section with brown-greenish shales and fine sandstones with invertebrates and abundant bioturbation (ca. 60 m). A polymictic conglomerate marks the base of the Porongal Formation (Figure 4a). Towards the top of this unit, the succession is characterised by consolidated medium and coarse-grained sandstones bearing current generated features (e.g. cross-bedded stratification). These sandstones are interbedded with grey shale, siltstone and fine-grained sandstone beds bearing bioturbation and invertebrates. Three sandstone packages with linear to slightly sinuous crests ripples (Figure 4b,c) mark the end of the succession over which the diamictites of the Tarija Formation unconformably rest (Di Pasquo and Vergel 2008; Di Pasquo et al. 2011).

3.2 Palaeontology

A total of 15 samples were collected, with 11 being productive (Figure 3). Standard palynological methods using HF and HCl digestion were performed to obtain organic residues from the samples (Playford 1977) in both the Department of Geology of the Natural and Pure Sciences Faculty (University of Buenos Aires) and the Laboratory of Palynostratigraphy and Palaeobotany of the CICYTTP (*Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción*, Entre Ríos). The residues were sieved through 25 µm mesh and mounted on standard microscope slides with glycerine jelly. The identification of palynomorphs and their illustrations was undertaken using trinocular transmitted light microscopes and videocameras (*Leitz Orthoplan* with *Motic* (2.0 MB), *Nikon Eclipse 80i* with *Pax-it* (3.1 MB) and *Nikon Eclipse E200* with *Labomed* (5.0 MB)). Some of the measurements of the recovered palynomorphs were carried out through the software “AnalyzingDigitalImages v. 11”. The position of illustrated specimens in the respective slides, quoted under the CICYTTP PI acronym (Repository), is based on England Finder coordinates. The thermal alteration index (TAI) of the organic material is stipulated following Utting and Wielens (1992).

The poor recovery of organic material and therefore the low counts, prevents precise statistical analysis. Instead, an evaluation of basic relative abundance was conducted. Eight types of dispersed organic matter and palynomorph groups were identified including amorphous organic matter (AOM); structured phytodebris (SP), characterised by identifiable cuticles and wood; unstructured phytodebris (USP), known as gelified matter; black phytodebris (BP) or opaque clasts including charcoal; spores (SPO); cryptospores (CRY); and phytoplankton (PHY) comprising acritarchs and prasinophycean algae

and chitinozoans (CHI). This is a simplified scheme adapted from Tyson (1995) for the types of organic components and palynomorphs found in the analysed assemblages. A palynological marine index ($PMI = (-\text{Marine Richness (Rm)/Terrestrial Richness (Rt) + 1}) / 100$, (Helenes et al. 1998)) used as a substitute for terrestrial/marine ratio, was also calculated in order to support the interpretation of depositional environments. The applied values were following the analyses of De Araujo Carvalho et al. (2006), where the marine and terrestrial richness are expressed as number of specimens per genera per sample. High values of PMI are interpreted as indicative of normal marine depositional conditions.

In order to define different palynofacies and the palaeoenvironmental evolution of the succession, the percentages and composition of palynodebris and the palynomorphs and PMI were subjected to Q-mode cluster analysis. The frequency matrix was transformed as in Jaramillo (2008), by taking the square root of each value to minimise the effect of over abundant elements. The cluster analysis was conducted by the R base package, version 3.0.1 (R development Core Team 2013) based on the Complete Linkage algorithm using Horn dissimilarity index. The package *rioja* 0.8-5 (Juggins 2012) was used to perform a constrained cluster analysis (coniss algorithm, Horn dissimilarity index). The invertebrates and trace fossils studied herein were illustrated at the CICYTTP and are housed in the same institution.

4. Results

4.1 Palynology

The group of recovered palynomorphs (Figures 3 and 5) is fairly to poorly preserved (TAI -3 and 3+). It is composed of 24 spore and cryptospore species, two species of acritarchs, two Chlorophycean algae and one species of chitinozoans. The species identified are reported in the following list by major groups and alphabetical order. A new species and few not confidently assigned to specific level are further described separately.

Chitinozoans

Angochitina sp. A in Noetinger and Di Pasquo, 2013 (Figure 5a).

Cryptospores

Cymbophilates sp. cf. *C. comptulus* Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans and Wellman, 2007 (Figure 5b). *Dyadospora murusattenuata* morphon Strother and Traverse *sensu* Steemans Le Hérisse and Bozdogan, 1996 (Figure 5c).

Gneudnaspora divellomedia (Tchibrikova) Balme var. *minor*. Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans and Wellman, 2007 (Figure 5d).



Figure 4. (Colour online) (a). General view of the outcrop (b). Sandstone package of the Pescado Formation. The arrow indicates the location of sample CICYTTP-PI 321. (c) Detailed photo of the oscillatory ripple marks, indicating an upper shoreface setting.

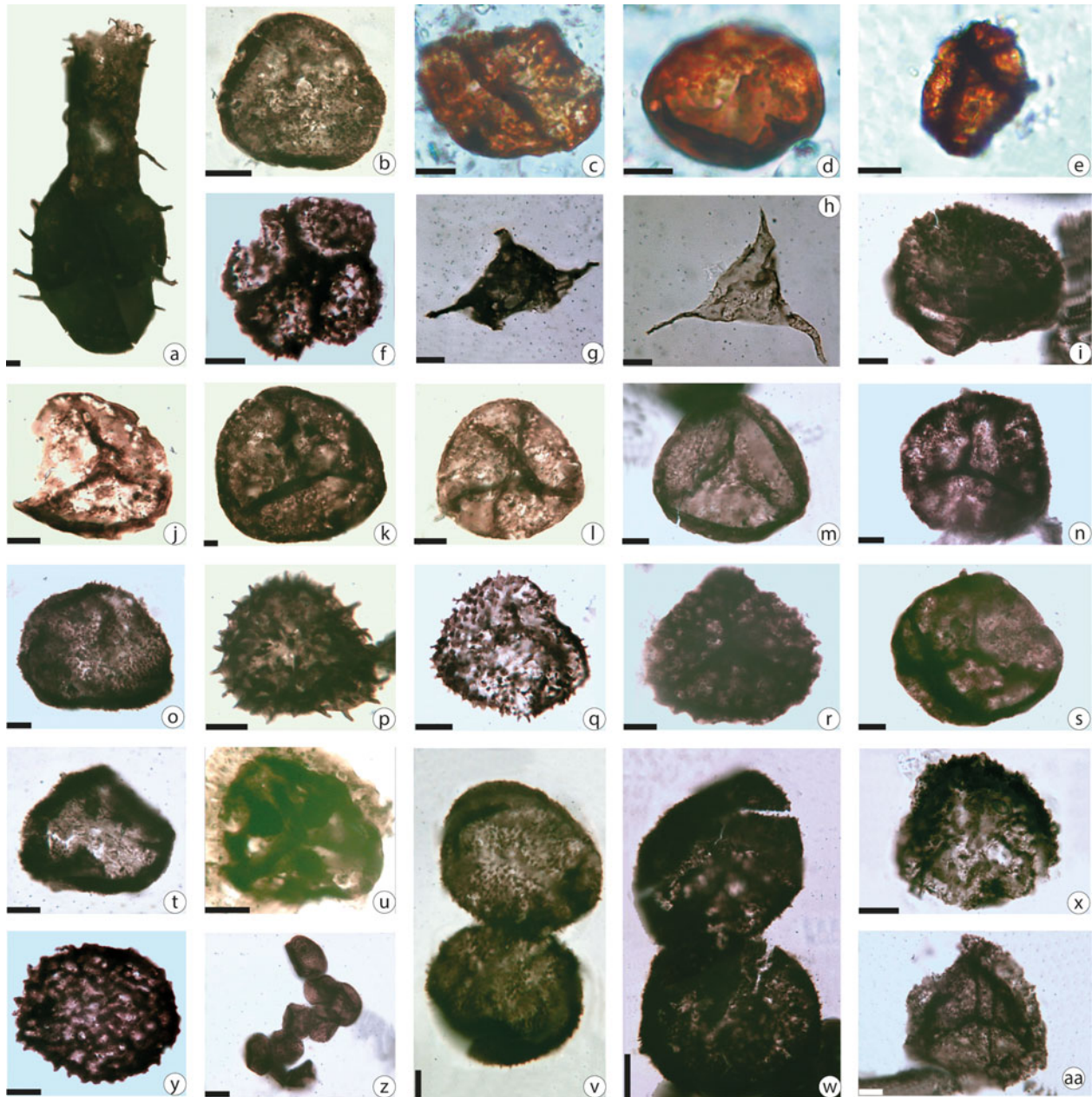


Figure 5. (Colour online) (a) *Angochitina* sp. in Noetinger and Di Pasquo 2013, CICYTTP 284 (1) M33. (b) *Cymbohilates* sp. cf. *C. comptulus*, CICYTTP 283 (1) T55/3. (c) *Dyadospora murusattenuata* morphon, CICYTTP 322 (1) Z51/4. (d) *Gneudnaspora divellomedia* var. *minor*, CICYTTP 323 (1) N22/4. (e) *Tetrahedraletes medinensis*, CICYTTP 322 (1) E30/2. (f) *Quadrifurcates variabilis*, CICYTTP 284 (1) Q51/3. (g) *Veryhachium lairdii* group, CICYTTP 279 (1) H45/2. (h) *Veryhachium trispinosum* group, CICYTTP 279 (1) O45/2. (i) *Acinosporites lindlarensis* var. *minor*, CICYTTP 280 (1) S39/3. (j) *Ambitisporites avitus/dilutus* morphon, CICYTTP 284 (1) F26/2. (k) *Apiculiretusispora brandtii*, CICYTTP 284 (1) P56. (l) *Apiculiretusispora plicata*, CICYTTP 284 (1) O27/2. (m) *Archaeozonotriletes chulus* var. *chulus*, CICYTTP 281 (2) V23/1. (n) *Cymbosporites senex*, CICYTTP 285 (2) B24. (o) *Dibolisporites bullatus*, CICYTTP 282 (2) E33. (p) *Dibolisporites? nodosus*, CICYTTP 284 (1) E50/2. (q) *Dibolisporites quebecensis*, CICYTTP 280 (1) D24/1. (r) *Dictyotriletes emsiensis* morphon, CICYTTP 283 (1) Y39. (s) *Retusotriletes albarinii*, CICYTTP 283 (1) R45/1. (t) cf. *Streelispora granulata* in McGregor 1984, CICYTTP 280 (1) B52/4. (u) *Synorisporites papillensis*, CICYTTP 284 (2) P50. (v) *Cymbohilates rubinsteinae* sp. nov., CICYTTP 285 (1) R36. (w) *Cymbohilates rubinsteinae* sp. nov., CICYTTP 282 (1) N60/2. (x) *Acinosporites* sp. cf. *A. mcgregorii*, CICYTTP 282 (1) O58/1. (y) *Biornatispora* sp. cf. *B. dubia*, CICYTTP 283 (1) R43/4. (z) *Verrucosisporites* sp. A., CICYTTP 280 (1) S39/4. (aa) *Samarisporites* sp., CICYTTP 281 (2) J31/2.

Tetraedraletes medinensis Ströther and Traverse emend. Wellman and Richardson, 1993 (Figure 5e).

Algae

Quadrisporites granulatus (Cramer) Cramer and Diez, 1972.

Quadrisporites variabilis (Cramer) Ottone and Rosello, 1996 (Figure 5f).

Phytoplankton

Veryhachium lairdii group Servais, Vecoli, Li, Molyneux, Raevskaya and Rubinstein, 2007 (Figure 5g).

Veryhachium trispinosum group Servais, Vecoli, Li, Molyneux, Raevskaya and Rubinstein, 2007 (Figure 5h).

Spores

Acinosporites lindlarensis Riegel, 1968 var. *minor* McGregor and Camfield, 1976 (Figure 5i).

Ambitisporites avitus/dilutus morphon Steemans, Le Hérisse and Bozdogan, 1996 (Figure 5j).

Apiculiretusispora brandtii Streele, 1964 (Figure 5k).

Apiculiretusispora plicata (Allen) Streele, 1967 (Figure 5l).

Archaeozonotriletes chulus (Cramer) var. *chulus* Richardson and Lister, 1969 (Figure 5m).

Cymbosporites senex McGregor and Camfield, 1976 (Figure 5n).

Dibolisporites bullatus (Allen) Riegel, 1973 (Figure 5o).

Dibolisporites? nodosus Turnau, 1986 (Figure 5p).

Dibolisporites quebecensis McGregor, 1973 (Figure 5q).

Dictyotriletes emsiensis morphon Rubinstein, Melo and Steemans, 2005 (Figure 5r).

Leiotriletes sp.

Retusotriletes albarinii Di Pasquo and Noetinger, 2008 (Figure 5s).

Retusotriletes maculatus McGregor and Camfield, 1976.

cf. *Streelispora granulata* in McGregor, 1984 (Figure 5t).

Synorisporites papillensis McGregor, 1973 (Figure 5u).

4.1.1 Systematic palynology

Cryptospores

Genus. *Cymbohilates* Richardson emend. Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans and Wellman, 2007. Type species. *C. horridus* Richardson, 1996.

Cymbohilates rubinsteinae sp. nov. (Figures 5v–w)

2005 *Cymbohilates* sp. 1 Rubinstein et al. p. 12, Plate III (3) 2013 *Cymbohilates* sp. Noetinger and Di Pasquo, p. 117, Figure 5 (l)

Derivation of name: dedicated to Claudia V. Rubinstein.

Diagnosis: Hilate cryptospore. Amb subcircular. Distal and subequatorial areas densely ornamented with grana, spines, coni and biform elements that can be fused into a reticulum.

Holotype: CICYTTP PI 285 (1) R36 (Figure 6v)

Paratypes: CICYTTP 282 (1) N60/2 (Figure 6w); Noetinger and Di Pasquo (2013) CICYTTP PI 383 (1) C58/3 (Figure 5, l).

Description. Cryptospore hilate proximally. Circular to subcircular amb. Distal and subequatorial exospore sculptured with grana, spines, coni, baculae or biform elements densely packed which may or may not be fused in the base. Elements 1.1–2.5 μm high and 0.8–1.2 μm wide at base.

Remarks. Specimens are usually preserved as dyads.

Dimensions (seven specimens) 40–66 μm .

Comparison: *Cymbohilates baqaensis* Breuer et al. 2007 from the Pragian–Emsian of Saudi Arabia bears bacula that might be forked at the tip. *C. comptulus* Breuer et al. 2007 has the same kind of ornamentation but the elements are not fused at their bases and they are smaller in overall size. *Cymbohilates* sp. A in Mehlqvist et al. 2012 is smaller and has shorter elements.

Occurrence: Lochkovian from Brazil (Solimões Basin); Pragian–Emsian from the Chaco-Salteño Plain (north-western Argentina).

Spores

Anteturma **PROXIMEGERMINANTES** Potonié, 1970.

Turma **TRILETES** Reinsch emend. Dettmann, 1963.

Suprasubturma **ACAVATITRILETES** Dettmann, 1963.

Subturma **AZONOTRILETES** Lüber emend. Dettmann, 1963.

Infraturma **MURORNATI** Potonié and Kremp, 1954.

Genus. *Acinosporites* Richardson, 1965.

Type species. *A. acanthomammillatus* Richardson, 1965.

Acinosporites sp. cf. *A. mcgregorii* Di Pasquo and Noetinger, 2008 (Figure 5x).

Description. Amb subtriangular, interrational margins slightly convex, rounded vertices. Equatorial region darkened due to ornamentation concentration. Ornamentation on distal face comprises rugulae of 1 μm width up to 3 μm length and interspersed grana and spines. Dimensions (1 specimen) 43 μm .

Genus. *Biornatispora* Lele and Streele, 1969.

Type species. *B. dentata* (Streele) Lele and Streele, 1969.

Biornatispora sp. cf. *B. dubia* (McGregor) Steemans, 1989 (Figure 5y).

Description. Trilete mark indistinct. Amb subcircular to circular. Ornamentation on distal face consists of muri which anastomoses forming a reticuloid pattern with bacula and coni densely packed. Muri are 1.5–3 μm height and 2.4–2.6 μm wide at base. Lumina of the reticulum varies 3.3–3.6 μm in diameter. Exine 2.2–3.6 μm thick.

Dimensions (two specimens), 46–48 μm .

Infraturma **APICULATI** (Bennie and Kidston) Potonié, 1956.

Subinfraturma **VERRUCATI** Dybová and Jachowicz, 1957.

Genus. *Verrucosporites* (Ibrahim) emend. Smith and Butterworth, 1967.

Type species. *V. verrucosus* (Ibrahim) Ibrahim, 1933.

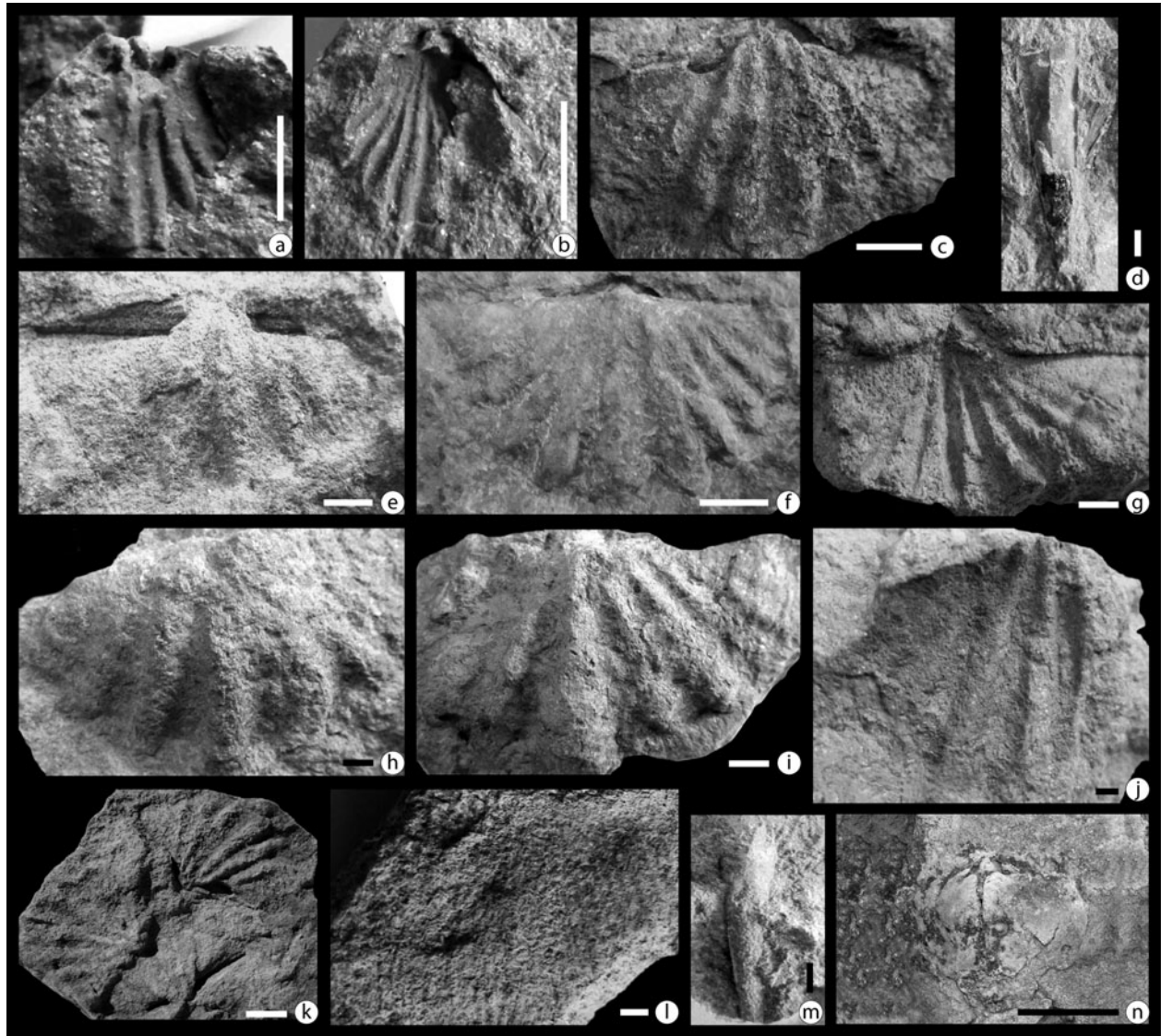


Figure 6. Invertebrate fossil fauna. (a, b) *Australocoelia palmata*. (a) Impression of interior of brachial valve, CICYTTP-In19. (b) Impression of exterior of brachial valve, CICYTTP-In20. (c) *Australospirifer hawkinsi*. Mould of pedicle valve interior, CICYTTP-In10. (d) *Bolitheca?* sp., CICYTTP-In17, $\times 2.2$. (e–j) *Australospirifer hawkinsi*. (e) Mould of pedicle valve interior, CICYTTP-In11. (f) Mould of brachial valve interior, CICYTTP-In12. (g) Mould of brachial valve exterior, CICYTTP-In13. (h) Mould of brachial valve interior, CICYTTP-In14. (i) Mould of brachial valve exterior, CICYTTP-In15. (j) Mould of brachial valve exterior, showing growth lamellae, CICYTTP-In16. (k) Accumulation of disarticulated and abraded *Australospirifer* valves as a lag deposit in shoreface higher energy setting, just above (2 m) ripples marks in Figure 4(c). (l) *Australostrophia mesembria*. Mould of valve exterior, CICYTTP-In21. (m) '*Hyolithes*' sp., CICYTTP-In18 $\times 2.9$. (n) *Meristelloides riskowskii*. CICYTTP-In23. Scale bar = (a–b) 2.5 mm; (c–n) 10 mm.

Verrucosporites sp. A (Figure 5z)

Description. Circular to rounded triangular amb. Laesurae accompanied by labra 0.8–1.6 μm wide, reaching three quarters of the spore radius. Exine bearing discrete small verrucae 0.5–1.5 μm wide and 0.4–0.8 μm high. Sculptural elements have polygonal or irregular shape in plan view. Ornamentation sharply reduced in contact areas.

Dimensions (seven specimens): 13.5–18.8 μm .

Remarks. The specimens found are part of the cluster shown in the figure. The most particular feature is the exceptional small size.

Subturma ZONOTRILETES Waltz in Luber and Waltz, 1938.

Infraturma ZONATI Potonié and Kremp, 1954.

Genus. *Samarisporites* Richardson, 1965.

Type species. *S. orcadensis* (Richardson) Richardson, 1965.

Samarisporites sp. (Figure 5aa).

Description. Radial trilete zonate spore. Amb subtriangular with convex sides and pointed apices. Trilete mark distinct. Central area strongly subtriangular clearly separated from the zona. The ornamentation on distal face consists of low conic.

Remarks. *Samarisporites* sp. is similar to cf. *Samarisporites* sp. Streel in Mortimer 1967, but the muri are not observable in this specimen.

Dimensions: (one specimen) 65 µm.

4.2 Invertebrates

Disarticulated, abraded and randomly oriented moulds of shells comprise the low diversity invertebrate fauna (Figure 6). Species are described or compared by major groups in alphabetical order as follows.

Brachiopods

Australocoelia palmata Morris and Sharpe, 1846 (Figures 6a,b).

Remarks. Only one brachial valve was found, exceptionally small, compared to the numerous specimens found in Bolivia, described and illustrated by Isaacson (1977a). Of 40 representative *A. palmata* specimens measured from the Devonian of Bolivia, Isaacson (1977b, p. 174) found only two with equivalent widths to the Zenta specimen. Therefore, the Zenta specimen is a juvenile.

Australospirifer hawkinsi Morris and Sharpe, 1846 (Figures 6c,d–j)

Description. Large shell, pauciplicate and few plications, numbering from 5 to 11. Biconvex with a smooth but deep sulcus and high fold. Lateral plications are rounded and high, with rounded interspaces of similar shape. The Zenta specimens range from 28 mm to 68 mm width.

Remarks. This is the most abundant brachiopod found at this locality. Isaacson (1977b) described the taxon in Bolivia and concluded that *A. hawkinsi* (Morris and Sharpe 1846, p. 276, Plate 11, Figure 1) had name priority over *A. antarcticus* (Morris and Sharpe 1846, p. 276, Plate 11, Figures 2 and 3). The similarity of these specimens with the ones reported in Bolivia by Isaacson (1977b) makes the assignment possible despite the lack of internal and hinge feature details (e.g. deltidial plates and nature of the cardinal process) in the recovered specimens. The reported Bolivian specimens range from 18 mm to 64 mm width (Isaacson 1977b, p. 181).

Australostrophia mesembria Clarke, 1913 (Figure 6l).

Remarks. Represented by a very poorly preserved shell fragment and it is distinguished from other larger Bolivian shells, because of its large, flat, parvicostellate shell.

Meristelloides riskowskii Branisa, 1965 (Figure 6n).

Remarks: Only a brachial valve interior found. Specimen shows portion of cardinal plate with fused crural plates. Strong, tapering median septum, triangular in cross

section. This taxon occurs commonly in the “big shell assemblage” that includes *A. hawkinsi* in the lower Icla and Belén formations (Isaacson 1977b, Figure 2) reaching the Middle Devonian of Bolivia. Interestingly, these taxa occur in the Santari Sandstone Member of the Sica Sica Formation concurring with *Tropidoleptus carinatus*.

Hyoliths

Two very small specimens of hyoliths were found representing juveniles of larger specimens known in Bolivia. *Bolitheca?* sp. (Figure 6d).

Remarks. Small internal mould with relatively flat side with a faintly ornamented, tapering shell.

‘*Hyolithes*’ sp. (Figure 6m).

Remarks. The small internal mould found is similar to ‘*Hyolithes*’ *steinmanni* because of its unornamented subrounded and tapered shell.

4.3 Trace fossils

Trace fossils are distributed all along the section (Figures 3 and 7) with a generally low density. Some sectors associated to the dark-coloured fine sandstones in the lower and middle part of the sequence display increasing degrees of bioturbation with partial mottling of strata. Weathering of the outcrops, particularly of fine sandstones, facilitates the recognition of the cross sections of ichnofossils. Sandier levels in the upper part of the sequence enhance morphological characters preserving, in some traces, delicate forms. Nine ichnospecies were recognised within the strata and are described or compared in alphabetical order as follows.

Archaeonassa fossulata Fenton and Fenton, 1937 (Figure 7d).

Remarks. Represented on top of the sandstones in the middle and upper part of the sequence. It is regularly seen in the rippled surfaces associated to other grazing burrows and trails as *Helminthoidichnites*, *Helminthopsis* and *Psammichnites*. Trace is characterised by a trail composed by two parallel levees separated by a flat to concave central zone. Total width of trace reaches up to 2 cm. Levees display oblique elements while central zone partially shows faint transverse corrugations. *Archaeonassa* is mostly interpreted as a gastropod trail (Buckman 1994).

Cruziana isp. (Figure 7c)

Remarks. Mid-size *Cruziana* isp. (up to 7 cm wide) were found in the middle and upper sector of the sequence associated to cross-bedded sandstones and preserved as convex hyporelief. Although Palaeozoic *Cruziana* is mostly interpreted as trilobite produced traces, notostracan brachiopods, aglaspids and even vertebrates were also considered (Shone 1979; Fillion and Pickerill 1990; Minter and Lucas 2009). The lack of detailed morphological aspects precludes a closer definition on the taxonomy of these forms.

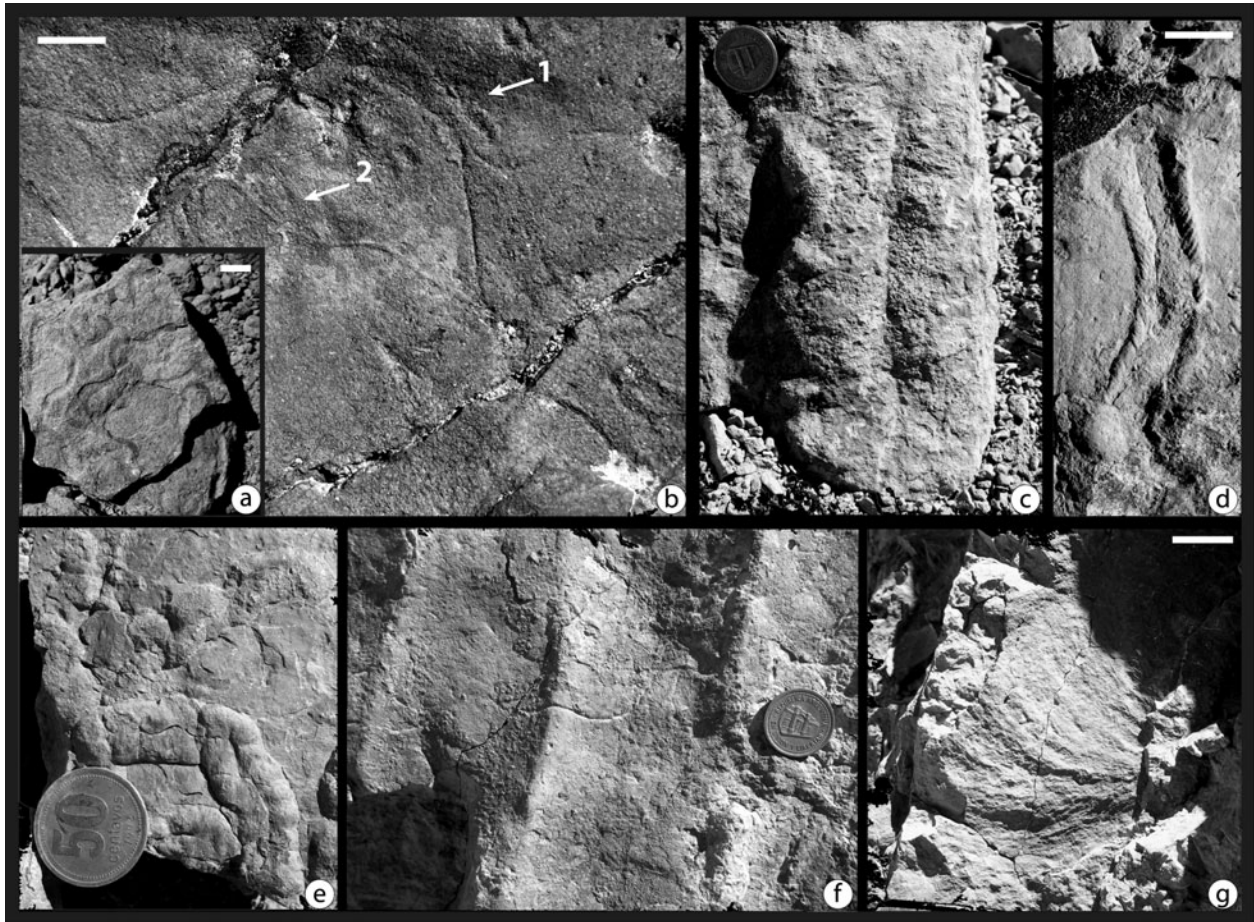


Figure 7. Lower Devonian trace fossils of Zenta Range. (a) *Helminthopsis abeli* on the surface of sandstone bed of the middle part of the section (scale 20 mm). (b1) Superficial phantom assigned to *Psammichnites* isp. (b2) *Helminthoidichnites tenuis* (scale 10 mm). (c) Rusophyciform convex hyporelief – lower view – of *Cruziana* isp. (d) Epichnial trace assigned to *Archaeonassa fossulata* (scale 20 mm). (e, f) Sinuous traces of *Psammichnites* isp. with the median sinusoidal ridge on the upper surface (Coin diameter 25 mm). (g) Spreite structure assigned to *Zoophycos* isp. in the dark grey sandstones of the middle part of the sequence (scale 50 mm).

Helminthoidichnites tenuis (Fitch), 1850 (Figure 7b 2).

Remarks. It was recognised on top of the thick sandstone levels in the upper part of the section as small and delicate winding traces. Identified material is represented by gently curved, irregularly winding burrows preserved as positive and negative hyporeliefs. Width ranges from 1 to 2.5 mm, being common the record of a restricted size range on a same surface. Some representatives of *Helminthoidichnites* can be compared to *Helminthoida* and *Gordia*, but morphology and meandering patterns distinguish the different forms from each other (e.g. Pickerill et al. 1987; Hofmann and Patel 1989).

Helminthopsis abeli (Książkiewicz), 1977. (Figure 7a)

Remarks. Common form in the middle and upper part of the sequence within the greyish fine sandstones. Represented by a loosely meandering trace preserved as a convex epirelief 2.8–6.5 mm in diameter, recording lengths up to 250 mm. Diameter of trace is constant along this unornamented trace. The winding and sinusoidal

pattern is slightly variable resembling Książkiewicz's type material.

Lockeia amygdaloides (Seilacher), 1953.

Remarks. Not a very common trace, it occurs on the sole of sandstone layers as ovoid shaped knobs preserved as convex hyporelief and concave epirelief. As expected, populations of *Lockeia* are monospecific, and the almond-shaped morphology supports this ichnospecific assignation. *Lockeia* is mostly interpreted as resting trace of pelecypods (e.g. Vossler and Pemberton 1988), and have contributed to the general knowledge of life history, ecology and ethology of bivalves (Kim 1994).

Palaeophycus tubularis Hall, 1847.

Remarks. Represented by endichnial horizontal to sub-horizontal lined burrow up to 1.2 cm wide. Even though they are not abundant, these are commonly associated to the fine to medium sandstones of the middle and upper sector of the sequence. *Palaeophycus* is a facies-crossing trace probably produced by polychaetes or annelids

(Pemberton and Frey 1982; Fillion 1989; Fillion and Pickerill 1990).

Psammichnites isp. (Figure 7b 1, e–f)

Remarks. Represented by horizontal sinuous traces characterised by a distinct median dorsal structure preserved as a groove. Traces are common on the surface of sandstones in the middle and upper part of the sequence associated with other grazing trails. Width of trace is quite regular, reaching up to 3 cm, with frequent preservation of faint transverse knobs on the upper surface of trace. Median groove is clearly preserved and is interpreted as the siphon-like device trace of producer organism (Mángano et al. 2002).

Zoophycos isp. (Figure 7g)

Remarks. Common in the dark greyish sandstones of lower and middle sector of the sequence. These are quite abundant and nicely preserved as full-relief spreite structure and as cross sections of helicoid spirals. Ichnofossil variety is low in the *Zoophycos*-bearing levels. Diameters reach up to 22 cm, and no central tube is clearly recognised. *Zoophycos* is a controversial trace assigned to an unknown deposit-feeding organism with a need of ichnotaxonomic revision (Olivero 2007; Seilacher 2007).

4.4 Age assessment and correlation

4.4.1 Palynology

The occurrence of *Dictyotriletes emsiensis* morphon in this association supports a correlation with the *Dictyotriletes emsiensis* Interval Zone (Ems) attributed to the latest Lochkovian through Pragian to early Emsian (Melo and Loboziak 2003; Melo 2005) (Figure 8). The inception of species such as *Acinosporites lindlarensis*, *Dibolisporites bullatus* and *D. quebecensis* in the sample CICYTTP-PI 280 indicates the beginning of the Pragian. This age is also supported with species such as *Apiculiretusispora brandtii* and *Cymbosporites senex* among others.

McGregor (1984) described an Emsian palynoflora from the Icla Formation, in Bolivia, containing *Emphanisporites annulatus*, *Dibolisporites* spp. *Apiculatasporites microconus*, spores close to or conspecific with *Acinosporites lindlarensis* var. *lindlarensis* and zonate spores. The absence of *E. annulatus* and the presence of *Dictyotriletes emsiensis* suggest an age not younger than middle Emsian.

The recovered association correlates to the *Dictyotriletes-Schizocystia saharica/S. pilosa* Zone of Lochkovian age proposed by Suárez Soruco et al. in Limachi et al. (1996, Figure 8). It includes species enclosed in the

GEOCHRONOLOGY			PALEOREGIONS							This study
Period	Epoch	Stage	SEA		EG	SWG		NWG		
			Euramerica	Russia	Australia	Brazil	Bolivia	Saudi Arabia/ Africa		
DEVONIAN	UPPER	Famennian	<i>lepidophyta-nitidus</i>	PLE PM <i>lepidophyta-explanatus</i>	<i>R.lepidophyta</i>	<i>R.lepidophyta</i> - <i>V.vallatus</i>	<i>R.lepidophyta</i>			
			<i>pusillites-lepidophyta</i>	LV LL <i>lepidophyta</i>		<i>R.lepidophyta</i>				
			<i>flexuosa-cornuta</i>	VF <i>C.variocornuta</i>	Microflora Brewer					
		<i>torquata-gracilis</i>	CZ VV <i>Limingsus</i>							
		Frasnian		<i>ovalis-bulliferus</i>	DE OG SD <i>G.extensa</i>	Spinozonotriletes sp.				
			BM BJ <i>optivus-triangulatus</i>							
	TC TA <i>lemurata-magnificus</i>									
	MIDDLE	Givetian		<i>devonic-naumovii</i>	<i>R.langii</i>	Ancyrospora sp.				
			AD <i>velatus-langii</i>							
		Eifelian	AP <i>douglastownense</i> - <i>euryptero</i>	<i>P.tortus</i>	<i>Aratrissporites</i> sp. <i>Hystriocporites</i> sp. <i>Brachozonotriletes</i> sp.					
	LOWER	Emsian	FD <i>annulatus-sexantii</i>	<i>R.clandestinus</i>						
			AB							
Pragian		PoW <i>polygonalis</i> - <i>emsiensis</i>								
	BZ <i>breconensis</i> - <i>zavallatus</i>									
Lochkovian	MN <i>micromatus</i> - <i>newportensis</i>									

Figure 8. (Colour online) Correlation chart of the most popular biozones based on palynofloras with the position of the assemblage studied herein (AA). Palaeoregions: SEA, southern Euramerica; EG, eastern Gondwana; SWG, southwestern Gondwana; NWG, northwestern Gondwana. References: Euramerica: Richardson and McGregor (1986); Strel et al. (1987). Russia: Avchimovitch et al. (1993); Byyscheva (1997). Australia: Playford (1985, 1991); Young (1996). Brazil: Melo and Loboziak (2003). Bolivia: Suárez Soruco and Lobo Boneta (1983); Limachi et al. (1996). Saudi Arabia/Africa: Breuer and Steemans (2013). Abbreviations: (Russia) OK, *C. optivus-S. krestovnikovii*; SD, *G. semilucensa-P. donensis*; OG, *A. ovalis-V. grumosus*; DE, *C. deliquescens-V. evlanensis*; VV, *C. vimineus-V. evlanensis*; CZ, *C. cristifer-D. zadonica*; VF, *D. versabilis - G. famenensis*; LV, *R. lepydophyta-A. verrucosa*; LL, *R. lepydophyta-K. literatus*; LM, *R. lepydophyta - T. mirabilis*; PLE, *V. pusillites-R. lepydophyta-I. explanatus*; PM, *V. pusillites-T. malevkensis*. (Saudi Arabia/ Africa) *rug-lib*, *rugulata-libyensis*; *lem-lan*, *lemurata-langii*; *tri-cat*, *triangulatus-catillus*. The invertebrate zonation (based on brachiopods and conularids) from Limachi et al. (1996) is shown in grey and with asterisks.

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Dictyotriletes emsiensis morphon, *Apiculiretusispora plicata* and *Retusotriletes maculatus*. Nonetheless, the appearance of species known to occur after the Pragian suggests an age younger than Lochkovian, at least from the sample CICYTTP-PI 280. The succeeding (*Emphanisporites annulatus*/*Evittia sommeri*) zone established for the Emsian by the latter authors was erected by taxa that are not present in this assemblage.

Even though the Pragian and early-middle Emsian miospore zones are absent in the Paraná Basin (Mendlowicz Mauller et al. 2009), the association shares the occurrence of several species such as *Retusotriletes maculatus*, *Synorisporites papillensis*, species of the *Dictyotriletes emsiensis* morphon and *Apiculiretusispora brandtii* amongst others. The latter occurs in the lower part of the Chapada Group unit (CGU) 2 of the Apucarana Subbasin in the northern part of the Paraná Basin in Brazil (Grahn et al. 2010). This part is correlated to the PoW Spore Zone from Euramerica, which ranges from the late Pragian to early Emsian, the time range proposed for the first decline of the Malvinokaffric fauna in the Paraná Basin (Bosetti et al. 2012).

In Euramerica, Richardson and McGregor (1986) defined the *Verrucosisorites polygonalis* – *Dictyotriletes emsiensis* Assemblage Zone of Pragian (Siegenian)–? earliest Emsian age (Figure 8). Despite the absence of *Verrucosisorites polygonalis*, the studied palynoflora share some species (e.g. *Dictyotriletes emsiensis*, *Apiculiretusispora plicata*, *A. brandtii*) with this zone. Both also have *Dibolisporites* spp. and scarce papillate spores as additional features.

Breuer and Steemans (2013) established the *Synorisporites papillensis*–*Cymbohilates baqaensis* Assemblage Zone covering the upper Pragian in northwestern Gondwana (Figure 8). Some of the most characteristic trilete spores concurrent with this association are *Apiculiretusispora plicata*, *Dictyotriletes emsiensis*, *D. subgranifer* (species related to the *Dictyotriletes emsiensis* morphon) and *Synorisporites papillensis*, whilst among the cryptospores *Gneudnaspora divellomedia* var. *minor* and *Cymbosporites comptulus* are present. Despite the fact that the latter are still a common element in the following Assemblage Zone *ovalis-biornatus* (upper Pragian–lower Emsian) defined by Breuer and Steemans (2013), there are only few species in common (e.g. *Biornatiospora dubia*, *Dibolisporites bullatus* and *Apiculiretusispora brandtii*) and the average size of the spores in northwestern Gondwana is much larger in comparison with the assemblage presented herein.

Only scarce and fragmentary specimens of chitinozoans were observed. *Angochitina* sp. A in Noetinger and Di Pasquo (2013) was described from the upper Pragian to the Emsian of the Chaco-Salteño Plain subsurface in Argentina. Grahn (2002) based on chitinozoans recognised an upper and lower division for the Icla Formation at

several localities in Bolivia, according to Racheboeuf et al. (1993). The lower unit yielded species such as *Ramochitina* sp., *R. magnifica*, *Pterochitina* sp., *Angochitina* aff. *A. comosa*, suggesting an early to late Pragian. The presence of *Ancyrochitina parisi*, an index species for the late Emsian (Volkheimer et al. 1986; Grahn et al. 2000; Noetinger and Di Pasquo 2013), in the upper Icla Formation supports a late Emsian–earliest Eifelian age for this part. Gaugris and Grahn (2006) have proposed the Interval range zone of *Ancyrochitina pachycerata*, dated as latest Pragian–pre-late Emsian age, for the Paraná Basin, characterised by *Ancyrochitina* species. Nonetheless, the preserved association in Zenta comprises mainly spores and cryptospores which make correlation to exclusively marine assemblages difficult.

4.4.2 Invertebrates and trace fossils

The Devonian in Bolivia has yielded the most abundant populations of *Australospirifer hawkinsi*. The latter, together with *Australocoelia palmata* and *Australostrophia mesembria* documents that the Zenta area was part of the Malvinokaffric Realm (Richter and Richter 1942; Boucot 1971, 1975; Isaacson, 1974 1977a, 1977b). The relative abundance of the different taxa varies in the sequence and we could recognise two assemblages: In-Assemblage 1 (Figure 3) composed of a low assortment of moulds of *Australocoelia palmata*, *Australostrophia mesembria* and hyoliths, and the In-Assemblage 2 (Figure 3), characterised by a dominance of *Australospirifer hawkinsi*, along with single specimens of two other taxa. All of the latter are known to range from the Pragian to Eifelian in Bolivia (Isaacson 1977a, 1977b; Racheboeuf et al. 1993; Blicek et al. 1996). Limachi et al. (1996) proposed several zones for the Silurian and Devonian of the latter country based on brachiopod fauna (Figure 8). Since terebratulid taxa, conspicuous in the upper Pragian(?)–lower Emsian beds in Bolivia, are scarce at Zenta, the fauna would be slightly above the *Scaphiocoelia* rich basal beds (Figure 8). *Australospirifer* survived during the Middle Devonian transgressive event (Isaacson and Díaz Martínez 1995) as well as *A. palmata*, that continues through the Eifelian–Givetian limit in the Paraná Basin in Brazil (Bosetti et al. 2012). During this event, the arrival of new immigrants from Africa precipitates the decline in diversity and abundance of the endemic Malvinokaffric brachiopods (Isaacson 1977a). *Meristelloides riskowskii* occur higher in the Zenta beds. This taxon has been quoted from the Icla, Belén, Sica Sica and probably in the Huamampampa formations of Bolivia (Isaacson 1977b; Figure 2).

Regarding the trace fossils, the outstanding preservation of *Psammichnites* isp. highlights the presence of the ichnogenus in the late middle Palaeozoic (Early Devonian), extending the time span record of the genus for South America.

4.5 Composition of the assemblages and palaeoenvironmental considerations

Invertebrates occur in sandstone beds, generally disarticulated, abraded and randomly oriented, characterising a high energy depositional environment. The lower part of the succession is represented by the In-Assemblage 1 (Figure 3). Marek and Isaacson (1992) described Bolivia's hyoliths as living offshore in finer-grained siliciclastic sediments, concurring with pelagic fossils and few brachiopods. The presence of *Australocoelia* is not diagnostic since it is known to occur in a variety of depositional settings from the Devonian of Bolivia (Isaacson 1977b, p. 175). However, their small size implies shoreward transport (by storms) as well for the hyoliths.

The palynofacies of this section is dominated by BP with a peak of the PMI (Figure 9). This is concurrent with a high proportion of phytoplankton and the presence of fragmentary chitinozoans. The marine phytoplankton is exclusively represented by specimens of *Veryhachium* displaying traces of pyritisation. This genus occurs in many marine settings. However, most records show shallow marine occurrences (see Servais et al. 2007). This is in agreement with the deposition of pyrite in the specimens studied herein and the high proportion of BP.

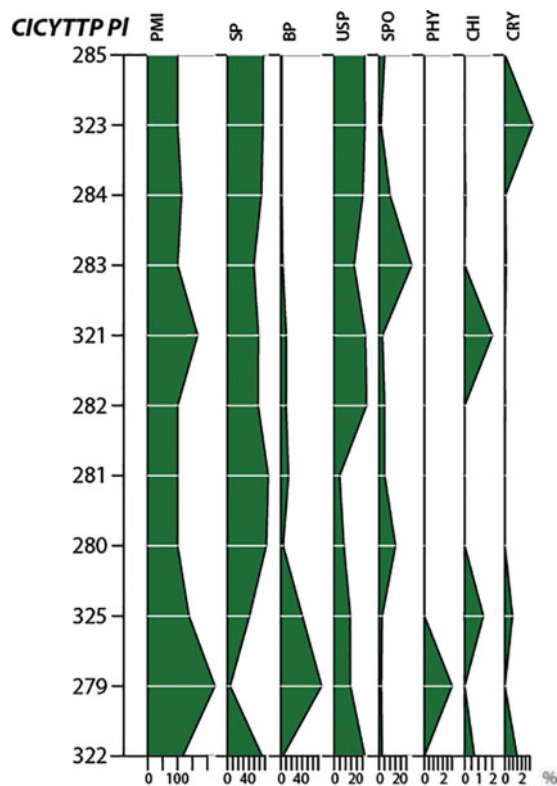


Figure 9. (Colour online) Abundance diagrams of PMI, SP, BP, USP, SPO, PHY, CHI and CRY.

Traces are dominated by horizontal feeding, dwelling, locomotion and resting forms, representing the activity of a mobile biota suggesting mid-energy environments, while higher energy vertically developed traces are less common. This further suggests infrequent sediment reworking by storms.

The integration of palynology, invertebrates and trace fossils, as well as the sedimentological evidence supports a restricted shoreface setting for the lower and middle part of the section.

The upper part of the sequence grades into a shallower and more oxygenated facies. It is characterised by the In-Assemblage 2. A single occurrence of *Australospirifer* (Figure 6k) is a shell lag related to shoreface-related currents, which is stratigraphically close to the intertidal-oscillatory ripples shown in Figure 4(b) and (c). Generally, the shoreface energy would require thick shells (i.e. *Australospirifer*), but they also are disarticulated and re-oriented post-mortem and transported by storms and normal waves. Similarly, smaller invertebrates have been transported shoreward to form a mixed assemblage together with larger, more robust shells (e.g. A fragment of *Australostrophia mesembria*, probably transported from the upper foreshore shoreward by storms, occurs with the larger spiriferids).

The palynofacies of this unit is characterised by an increase of SPO, USP and CRY. The latter agrees with the shallower settings proposed above. This regressive trend is mainly indicated by an abrupt disappearance of phytoplankton and a high input of USP, BP and SPO reaching the maximum concentration of the latter in the sample CICYTTP-PI 283. While the spores rapidly decrease, the succeeding sample (CICYTTP-PI 323) shows a high proportion of cryptospores. A foreshore setting with fluctuating supply of terrigenous material is interpreted for the top part of the succession.

Moreover, the constrained hierarchical clustering for the palynomorphs resulted in two main associations, A and B (Figure 10a). Albariño et al. (2002) recognised two transgressive events in the south Subandean and Chaco Plain in Bolivia and Argentina, a major one by the end of the Lochkovian and another one, of small scale, by the early Pragian. The association recovered from the lower beds, assembled in cluster A, does not have any diagnostic species that would undoubtedly assign the beds to the late Lochkovian. The peak of the palynological marine index (PMI) that clearly defined this group could either correspond to the late Lochkovian or early Pragian, although the invertebrates constrain the age to the Pragian. A Q-mode cluster analysis (complete linkage algorithm, Horn dissimilarity index) recognises two groups of samples as well, with similar composition: Cluster A' and Cluster B' (Figure 10b), with the exception of the sample CICYTTP-PI 322, which is included in the "younger" cluster.

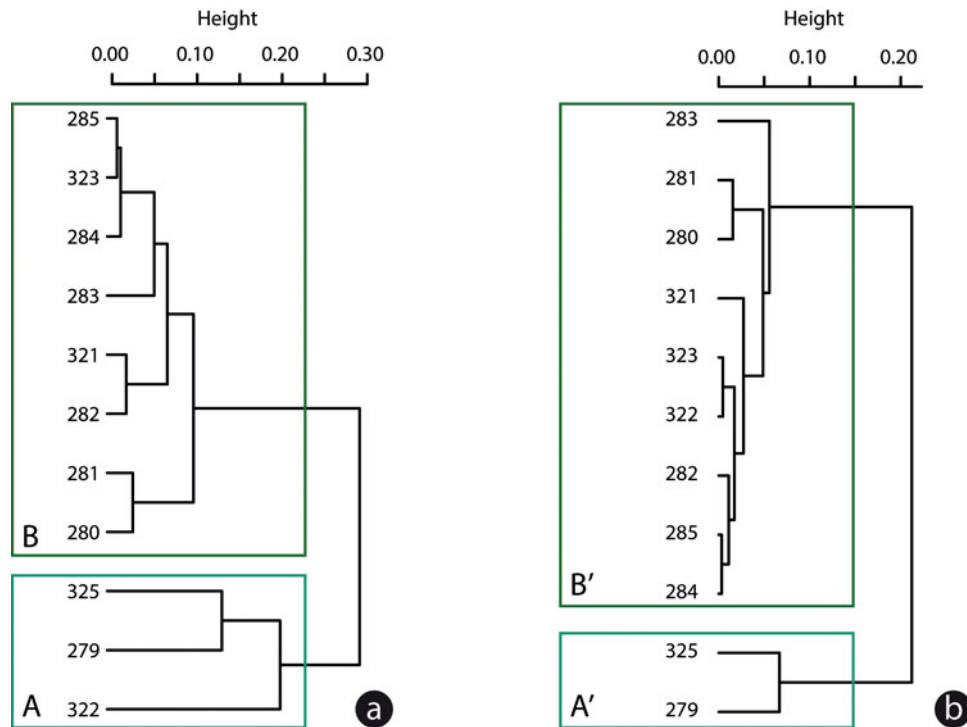


Figure 10. (Colour online) (a) Constrained cluster by sample order dendrogram plot derived from the Horn dissimilarity index using coniss algorithm resulted in two main associations, A and B. (b) Q-mode cluster analysis (complete linkage algorithm, Horn dissimilarity index) recognises two groups of samples as well, with similar composition: Cluster A' and Cluster B', with the exception of the sample CICYTTP-PI 322, which is included in the 'younger' cluster.

5. Concluding remarks

Most popular Devonian biostratigraphic proposals based on palynology such as the ones presented for Euramerica, Brazil and Bolivia are recognised, in part, in the palynological assemblage presented herein. The stratigraphic distribution of the palynomorphs suggests a time span from the ?late Lochkovian to Pragian–earliest Emsian, but the co-occurrences of *Australostrophia mesembria*, *Australospirifer hawkinsi* and *Australocoelia palmate* narrow the age of the Zenta beds to the late Pragian and early Emsian.

Even though Alvarez et al. (2003) proposed a continental–mixed environment for the Zenta region, the data presented in this study agree with the palaeoenvironmental interpretation by Noetinger and Di Pasquo (2010a). These authors suggest a proximal shoreface–foreshore depocenter in the late Lochkovian to Pragian. The contraction phase of the basin, proposed by Alvarez et al. (2003) during the middle Pragian and Emsian, is evidenced by the presence of sand bodies at the top of the column and the increased supply of terrigenous components. A noteworthy coeval regression event marks the first decline of the Malvinokaffric realm in the neighbouring Paraná Basin (Bosetti et al. 2012). During this period of time, in the Zenta region, the benthic fauna is dominated by

Australospirifer hawkinsi (In-Assemblage 2) which is known for their resistance to disturbance (Bosetti et al. 2012).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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