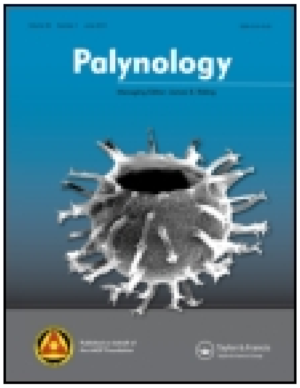


Palynology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tpal20

The palynology of the Lower Permian (Asselian-?Artinskian) Copacabana Formation of Apillapampa, Cochabamba, Bolivia

Mercedes M. di Pasquo [a] & George W. Grader [b]

[a] Laboratorio de Palinoestratigrafía y Paleobotánica, CICYTTP-CONICET, Dr. Matteri y España SN, Diamante (E3105BWA), Entre Ríos, Argentina

[b] Department of Geological Sciences, University of Idaho, 825 W 7th Street, Moscow, Idaho, 83844-3022, USA

Accepted author version posted online: 04 May 2012.Version of record first published: 05 Nov 2012.

To cite this article: Mercedes M. di Pasquo & George W. Grader (2012): The palynology of the Lower Permian (Asselian-?Artinskian) Copacabana Formation of Apillapampa, Cochabamba, Bolivia, Palynology, 36:2, 264-276

To link to this article: http://dx.doi.org/10.1080/01916122.2012.677644

Palynology
Vol. 36, No. 2, December 2012, 264–276

The palynology of the Lower Permian (Asselian–?Artinskian) Copacabana Formation of Apillapampa, Cochabamba, Bolivia

Mercedes M. di Pasquo[a]* and George W. Grader[b]

[a]*Laboratorio de Palinoestratigrafía y Paleobotánica, CICYTTP-CONICET, Dr. Matteri y España SN, Diamante (E3105BWA), Entre Ríos, Argentina;* [b]*Department of Geological Sciences, University of Idaho, 825 W 7th Street, Moscow, Idaho 83844-3022, USA*

The palynostratigraphy of the lower and Coal members of the Copacabana Formation from Apillapampa, central Bolivia was investigated. Twelve samples yielded abundant and diverse, moderately well-preserved pollen and spores. One new spore species, *Dictyotriletes cousmineri*, is described and 52 species are recorded for the first time in Bolivia. Two species each of acritarchs and scolecodonts are also present. The lowermost assemblage yielded *Vittatina* and taxa such as *Pakhapites ovatus* and *Marsupipollenites striatus*, which are characteristic of the Asselian–Early Artinskian *Vittatina costabilis* Zone of the Paraná Basin, Brazil. The uppermost assemblage is defined by the appearance of several species of *Lueckisporites*, together with species of *Vittatina*, *Lunatisporites*, *Pakhapites*, *Hamiapollenites*, *Corisaccites*, *Mabuitasaccites*, *Striomonosaccites*, *Striatoabieites*, *Striatopodocarpites* and *Weylandites*. Abundant monolete and trilete spores with subordinate pollen grains are present in the Coal Member. Those species suggest correlation to the Middle Artinskian–Wuachiapingian *Lueckisporites virkkiae* Zone of the Paraná Basin. Highly variable associations of gymnosperms occur in the lower member whereas pteridophytes, sphenophylls and lycopods are dominant in the overlying Coal Member. These groups of plants characterised terrestrial landscapes along marine margins during the Early Cisuralian, and confirm the widespread distribution of the *Glossopteris* flora during the Permian in Gondwanaland. Preliminary radiometric data from interbedded tuffs suggest an Asselian–Sakmarian age for the marine Copacabana Formation and a Sakmarian–?Artinskian age for the overlying Coal Member. These new data are highly significant in terms of Permian correlations in central South America.

Keywords: biostratigraphy; Bolivia; Copacabana Formation; Early Permian; palaeoecology; palynology; taxonomy

1. Introduction

The chronostratigraphy and palaeogeography of Late Palaeozoic sedimentary rocks in the Peru–Bolivia Basin are important for correlations within Gondwana. Palynology, micropalaeontology and radiometric dating provide new insights into the palaeogeography and glaciation/deglaciation of the area. Grader et al. (2003, 2008) summarised the palaeontology, palaeoecology and stratigraphy of the Upper Carboniferous to Lower Permian (Bashkirian–Artinskian) Titicaca Group in Bolivia. Azcuy et al. (2007) correlated South American Carboniferous and Permian biostratigraphical units, with a detailed review of the palynology. Upper Palaeozoic strata in the Peru–Bolivia Basin at Apillapampa near Cochabamba in central Bolivia were mapped, measured and sampled (Figures 1–3). The goals of this study are to improve correlations of the Copacabana Formation with coeval South American units using palynology, to refine the palaeoecology of this unit and to update the list of palynomorph taxa from the Coal Member of Cousminer (1965).

2. Stratigraphy and palaeontology

Apillapampa is a classic locality near Cochabamba in central Bolivia known for the fossiliferous Titicaca Group of Permian age (Chamot 1965; Cousminer 1965). Palaeozoic rocks are preserved in a narrow strip which is coincident with NW–SE trending folds and thrusts (Servicio Geológico de Bolivia 1:100,000 Capinota geological map). Permian strata overlie various Silurian and Devonian formations and are overlain by Mesozoic conglomeratic valley fill deposits. Late Permian–Jurassic rifting resulted in intense truncation, regional erosion and karstification of the Copacabana Formation on uplifted palaeovalley shoulders (Sempere et al. 2002; Grader 2003). Rift and later arc-associated variegated, heterolithic transitional to marine Mesozoic formations are present and

---

*Corresponding author. Email: medipa@cicyttp.org.ar

ISSN 0191-6122 print/ISSN 1558-9188 online

http://dx.doi.org/10.1080/01916122.2012.677644
http://www.tandfonline.com

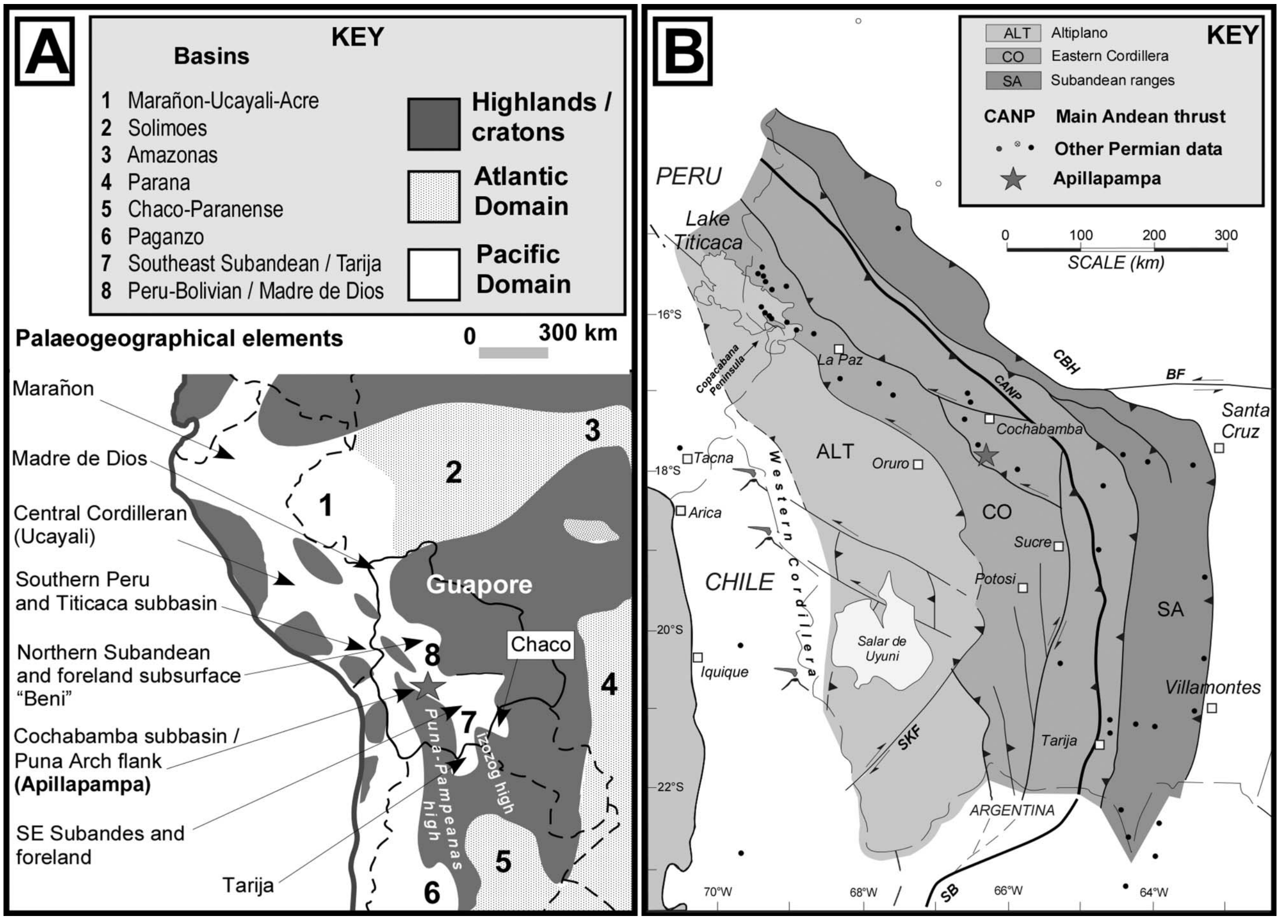


Figure 1. (A) Map of west-central South America illustrating the major Late Palaeozoic sedimentary basins modified after Azcuy et al. (2007). The Peru–Bolivian master basin (numbers 7 and 8) is considered to be a single Permo-Carboniferous Basin with areas of differential subsidence and partitioning (Kley et al. 1999; Grader et al. 2003, 2008). Some palaeogeographical and geographical elements of the greater Peru–Bolivian Basin are shown extending into northern Argentina and Paraguay (the Tarija and Chaco basins). The Central Andean faunal province was influenced by West Texas and Tethyan elements, and separated from the Gondwanan faunal province during the Permo-Carboniferous. (B) Tectonic map of west-central South America with major cities and some Permo-Carboniferous outcrop locations, illustrating the location of Apillapampa in the Cordillera Oriental. Late Cenozoic faults together with some Palaeozoic palaeogeographical elements are illustrated (after Sempere 1995). BF = Boomerang Fault; CBH = Chaparé Buttress (i.e. the Chaparé Basement high); SKF = Khenayani Fault System; SB = Susquess Buttress.

include carbonates, green tuffs and aeolian rocks. These rocks in Bolivia represent similar proto-Andean back-arc depositional environments that indicate upper Permian–Jurassic axial rifting along the active Gondwanan/Pangaean margin (Sempere et al. 2002).

At Apillapampa, Devonian rocks crop out below the steeply dipping Permian Titicaca Group along Quebrada Chullpanimayu (Figure 3). Thin Carboniferous successions may also be present. The stream is a complex system of riffles, waterfalls and sharp bends that follow or cross-cut strike, dip or faults. The succession was measured by Chamot (1965) and is illustrated in Figure 3 with the sample points of Cousminer (1965). Thick Silurian/Devonian siliciclastic foreland marine deposits referable to the Tarabuco and Santa Rosa formations were sampled at 80 and 18 m below the Gondwanan Unconformity of Chamot (1965) together with the overlying sandstones (Figure 3). Di Pasquo et al. (2009) documented the Late Lochkovian *Urochitina loboi* Zone in both samples. Overlying this are approximately 13 m of ?Carboniferous red continental sandstones and some darker shales with palaeosols and plant fragments, attributed to the Yaurichambi Formation by Chamot (1965). These beds may be related to the Viséan or younger sandstones and mudstones of central Bolivia (see Zudañez in Figure 2). One sample collected from this interval was palynologically barren. The overlying Copacabana Formation includes fossiliferous limestones and marls interbedded with evaporites, cherts, sandstones, shales and tuffs. Henderson et al. (2009) studied conodonts and fusulinids and dated the

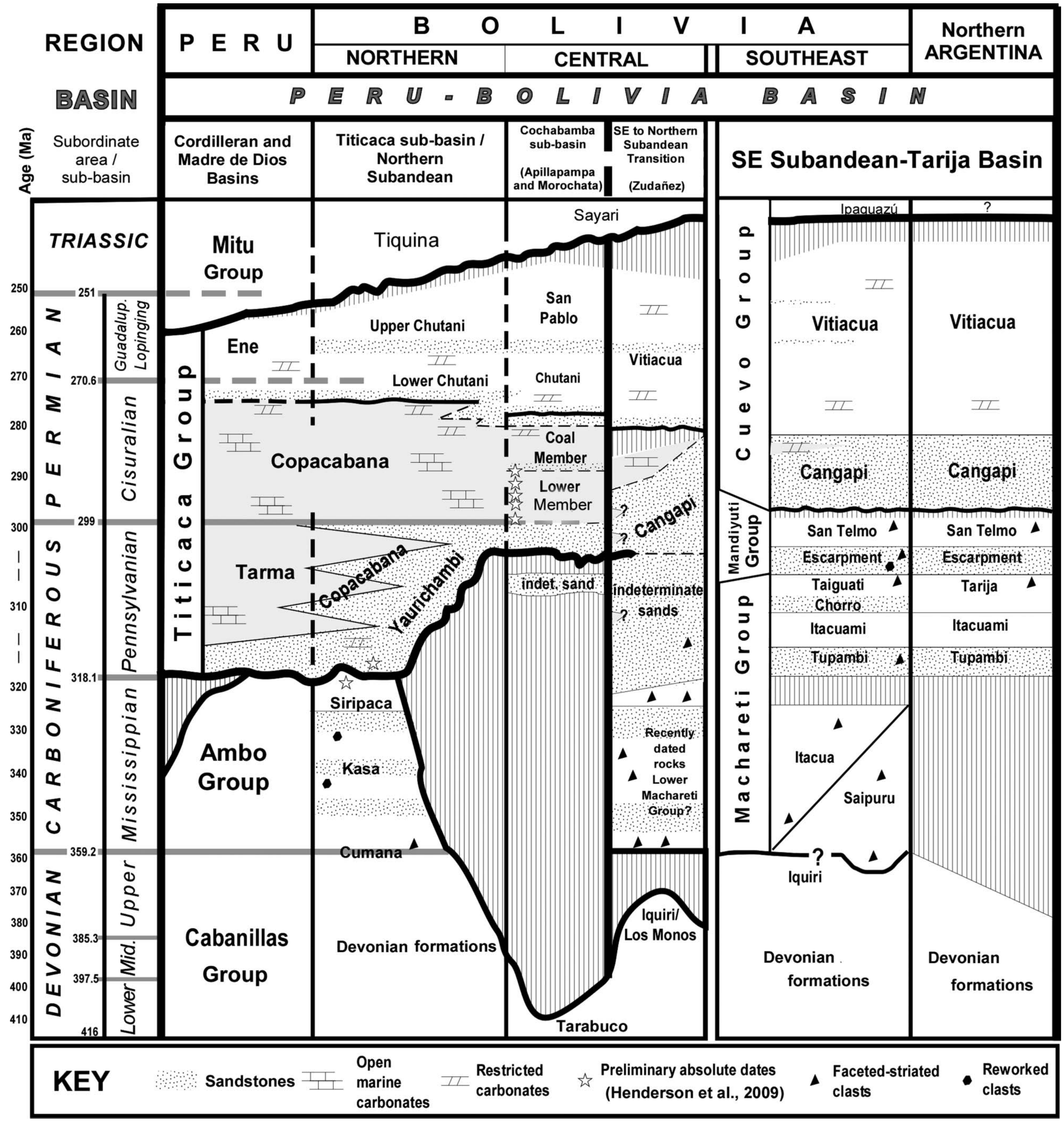


Figure 2. Correlation of the Copacabana Formation and the Coal Member in central Bolivia with their regional chronostratigraphic relationships to the Late Palaeozoic rocks of southern Peru, Bolivia and northern Argentina. These correlations show a Cisuralian age for the Coal Member and a Late Cisuralian–?Early Triassic age for the Chutani and Vitiacua formations (Chamot 1965; Sempere et al. 1992, 2002; Grader 2003; Grader et al. 2007, 2008). The northern and central Bolivian columns are modified after Sempere (1995) and Díaz-Martínez (1999). The southeastern Bolivian and northern Argentinian columns are modified after di Pasquo (2003, 2007a, b), Starck and del Papa (2006) and Azcuy et al. (2007). Some previous pan-Bolivian Permo-Carboniferous correlations that include the Macharetí and Mandiyutí groups are significantly different to those shown here, placing many of these units into the Mississippian (Sempere 1995; Díaz-Martínez 2002; Díaz-Martínez and Iannuzzi 2005). To begin to resolve Carboniferous correlations, units in the central part of the Peru-Bolivian Basin are based on early to recent invertebrate and palynology studies, including new sedimentologic and radiometric evidence (Henderson et al. 2009; Anderson et al. 2010). The star symbols indicate the locations of the ash-dated material of Henderson et al. (2009; V. Davydov, personal communication, 2009) and are consistent with earlier Permian ages at Apillapampa (Chamot 1965) and mid-Carboniferous ages at Lake Titicaca.

interbedded tuffs at Apillapampa, confirming an Asselian–Sakmarian age for the lower Copacabana Formation and a Sakmarian–?Artinskian age for the overlying Coal Member. Iannuzzi et al. (2008) also reviewed the flora. The palynomorphs described by Cousminer (1965) were obtained from six samples of the Coal Member (although only one was significantly diverse), and most of those species were recognised herein (Table S1, see online supplementary material). Cousminer (1965) found that 64% of the palynomorph assemblage were pteridophytes and 21% were gymnosperm pollen grains, resembling the Permian palynofloras of Australia.

The nature of the contact between the Coal Member and the underlying lower member of the Copacabana Formation was discussed by Chamot (1965), and has been investigated here. A transitional upper Copacabana unit is defined between 195 m and 248 m, where dolostone and nodular chert are common below true carbonaceous shale-bearing intervals. At the base of this transitional unit, a thick interval of distinctive pellet-filled burrows occurs above dolomitised limestones, shales and a thick *Thalassinoides*-burrowed tephra bed. This unit includes the first appearance of plant stems, the first stromatolitic facies, the last interval of open marine invertebrates and the first carbonaceous shale with lycophyte trunks. The transitional unit ends below a clearly intertidal mud-cracked sandy marker bed at the top of waterfall 2 at 248 m, with palaeosols and abundant plant-bearing intervals above. The mud-cracked marker unit, the pellet-filled burrows and the blue ignimbrite beds beginning at 305 m can be traced throughout the syncline, allowing a correlation to a steep ridge line above Quebrada Chullpanimayu (Figure 3; Iannuzzi et al. 2008).

Grader (2003) suggested a gradational contact between the primarily marine Copacabana Formation and the volcanogenic, cherty 'tonstein' carbonaceous shale, and thin coal-bearing beds of the Coal Member. The latter is better defined between the first carbonaceous shale with significant leaf impressions and carbonised lycophyte trunks at ~242 m and a thick black coaly interval at ~297 m between waterfalls 2 and 4 (Figure 3). Finally, the Coal Member occurs below a highly angular unconformity with the Cretaceous Toro Toro and El Molino formations (Figures 2 and 3).

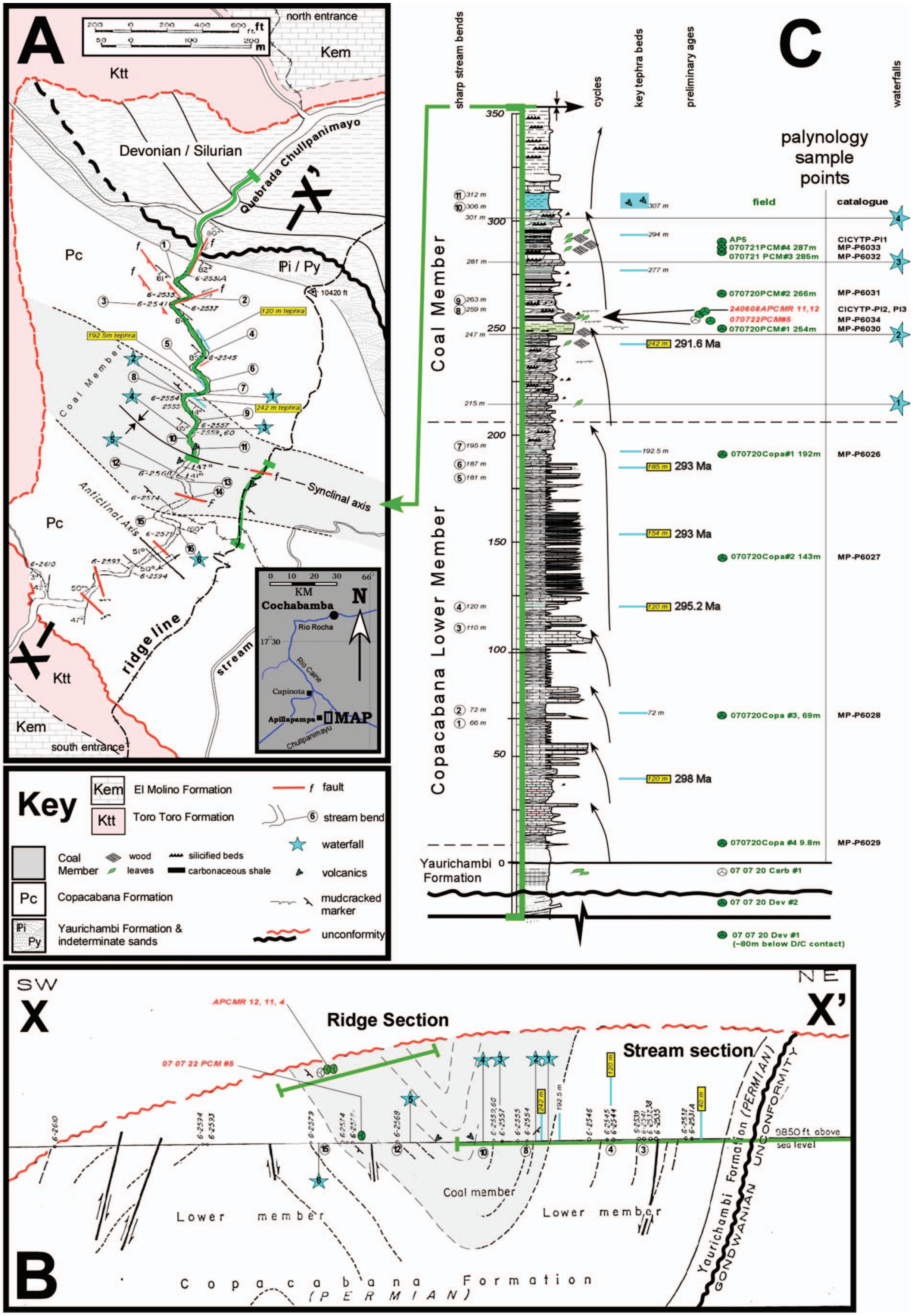
3. Materials and methods

Geological mapping, stratigraphical measurements and preliminary sampling for palynology and plant fossils focused primarily on the Coal Member at Apillapampa and was undertaken by E. Díaz-Martínez, G. Grader and R. Iannuzzi in 2008 (Figure 3). Earlier fieldwork by C. Henderson, V. Davydov and others in 2007 sampled the Devonian through Lower Permian marine strata.

A standard palynological preparation procedure using HF and HCl digestion without oxidation was used on 15 samples. Additionally, two dark grey indurated claystones from the Tarabuco/Santa Rosa Formation and two grey indurated mudstones (PCM2 and COPA1 from the Copacabana Formation, Figure 3) were processed using the sodium hexametaphosphate method of Riding and Kyffin-Hughes (2004) and Riding et al. (2007). A good result was obtained for the two Copacabana Formation samples, although this produced less palynomorphs than the acid digestion. The Tarabuco/Santa Rosa Formation samples yielded sparse chitinozoans and leiosphaerid acritarchs. They were therefore treated with the standard acid digestion technique and yielded abundant and diverse acritarchs, prasinophytes, spores, cryptospores, chitinozoans and scolecodonts. The organic concentrates from both the acid and non-acid treatments were sieved using a 10 μm mesh to remove fine material, and the microscope slides were mounted with glycerine jelly. The fluorescence of palynomorphs was studied for some samples to aid identification or to highlight morphological features affected by preservational effects. Many palynomorphs have been altered, and exhibit extinguished fluorescence (i.e. are black). However, spores and pollen grains occasionally exhibit bright yellow to orange colours and rare specimens of *Botryococcus* show weak orange to red colours. Two species were selected to illustrate the different autofluorescence intensities of palynomorphs. A striate bisaccate pollen grain *Hamiapollenites karroensis* exhibits a weak yellow colour, and *Botryococcus brauni* shows yellow to extinguished fluorescence and a cup morphology not visible under transmitted light. The palynomorphs are listed in the Appendix and Table S1 of the online supplementary material for this paper.

4. Palynology

Twelve samples from the Copacabana Formation proved palynologically productive and these have allowed the systematics of Early Permian taeniate pollen and spores of Cousminer (1965) to be updated. The palynomorph species recognised in this study are listed in the Appendix (see online supplementary material). *Dictyotriletes cousmineri* sp. nov. is formally described below and is illustrated in Plate 1. A full systematic treatment (including photographic illustrations in Plates 1–10) of the remainder of the palynoflora is given in the online supplementary material. The quantitative distributions of the palynomorphs as percentages are outlined in Table S1 of the online supplementary material pertaining to this paper (see also Table 1). The key index species allow comparison


A
north entrance
Kem
Ktt
Devonian / Silurian
Quebrada Chullpanimayo
X'
Pc
Pi / Py
10420 ft
120 m tephra
192.5m tephra
242 m tephra
Coal Member
Synclinal axis
Anticlinal Axis
ridge line
stream
X
south entrance
KM
Cochabamba
N
Rio Rocha
17°30
Rio Caine
Capinota
Apillapampa
MAP
Chullpanimayu
Key
El Molino Formation
Toro Toro Formation
fault
stream bend
waterfall
Coal Member
wood
leaves
silicified beds
carbonaceous shale
volcanics
Copacabana Formation
mudcracked marker
Yaurichambi Formation & indeterminate sands
unconformity
C
sharp stream bends
cycles
key tephra beds
preliminary ages
waterfalls
palynology sample points
field
catalogue
Coal Member
Copacabana Lower Member
Yaurichambi Formation
242 m 291.6 Ma
185 m 293 Ma
154 m 293 Ma
120 m 295.2 Ma
120 m 298 Ma
AP5
070721PCM#4 287m CICYTP-PI1 MP-P6033
070721 PCM#3 285m MP-P6032
070720PCM#2 266m MP-P6031
240608APCMR 11,12 CICYTP-PI2, PI3
070722PCM#5 MP-P6034
070720PCM#1 254m MP-P6030
070720Copa#1 192m MP-P6026
070720Copa#2 143m MP-P6027
070720Copa #3, 69m MP-P6028
070720Copa #4 9.8m MP-P6029
07 07 20 Carb #1
07 07 20 Dev #2
07 07 20 Dev #1 (~80m below D/C contact)
SW
NE
X
X'
Ridge Section
Stream section
APCMR 12, 11, 4
07 07 22 PCM #5
9850 ft. above sea level
Coal member
Lower member
Lower member
Yaurichambi Formation (PERMIAN)
GONDWANIAN UNCONFORMITY
Copacabana Formation (PERMIAN)
B

with similar assemblages from South America (di Pasquo et al. 2009). Selected descriptions, synonymy lists and occurrences of the species encountered in this study are included in the online supplementary material pertaining to this paper. Further occurrences are documented in the literature on South America and adjacent regions (e.g. Lindström 1995, 1996; Mautino et al. 1998a, 1998b, 1998c; Azcuy and di Pasquo 2000; Playford and Dino 2000a, 2000b; Azcuy et al. 2002; di Pasquo et al. 2003a, 2003b, 2010; Balarino and Gutiérrez 2006; Félix et al. 2006; Premaor et al. 2006; Neregato et al. 2008; Stephenson 2008; di Pasquo 2009; Gutiérrez et al. 2010; Mori and Souza 2010; Souza et al. 2010). Specific Pennsylvanian and Permian palynological records from Bolivia are separately documented in Table S1 in the online supplementary material.

Dispersed organic particles identified herein include amorphous organic matter (AOM), structured phytodebris such as identifiable cuticles and tracheids, unstructured phytodebris (gelified matter) of non-woody plant remains and resinite, brown and black phytodebris (or opaque clasts including charcoal) and palynomorphs. The simplified scheme adapted from Batten (1996) was used to calculate relative percentages. These results allow the characterisation of different palynofacies which are used in palaeoenvironmental interpretation (Figure 4).

5. Systematic palaeontology

Anteturma PROXIMEGERMINANTES Potonié 1970
Turma TRILETES (Reinsch) Dettmann 1963
Suprasubturma ACAVATRILETES Dettmann 1963
Subturma AZONOTRILETES (Luber) Dettmann 1963
Infraturma MURORNATI Potonié & Kremp 1954

Genus *Dictyotriletes* Naumova emend. Potonié & Kremp 1954

Type species. *Dictyotriletes bireticulatus* (Ibrahim) Potonié & Kremp 1955

Dictyotriletes cousmineri sp. nov.
Plate 1, figures 1–4

Holotype. Plate 1, figures 1, 2.
Paratypes. Plate 1, figures 3, 4.
Type locality. Chullpanimayu Creek, Apillapampa, Bolivia (Figure 3). The sample is from the Coal Member of the Copacabana Formation and is of Cisuralian (Early Permian) age.
Derivation of name. This species is dedicated to Harold Cousminer.
Description. Spores radial, trilete. Amb subcircular to oval or subtriangular. Laesurae simple and straight, almost reaching the equator. Exine equatorial and distally ornamented with an irregular reticulum; muri ca. 1.5–2.5 μm wide exhibiting an irregular thickness, ca. 2 μm high, enclosing irregular to oval luminae, ca. 1–6 μm in maximum diameter. The equator appears to be thickened due to the reticulum.
Dimensions. Equatorial diameter 25–40 μm.
Remarks. This species only occurs in one sample and mainly in the <25 μm fraction.
Comparisons. *Dictyotriletes aules* Rigby in Rigby & Heckel 1977 differs from *Dictyotriletes cousmineri* sp. nov. by having laesurae-bearing lips and a different reticulate ornamentation.

6. Results and conclusions

6.1. Assemblage characteristics and biostratigraphical implications

The moderately rich and diverse palynofloras recovered from the Copacabana Formation at Apillapampa allows the systematic classification of Early Permian taeniate pollen and spores by Cousminer (1965) to be updated. Twelve samples were productive and these yielded 94 species. These comprise 28 spore species (20 trilete and 8 monolete) and 58 pollen species (18 monosaccate, 8 bisaccate non-striate, 31 bisaccate striate and 1 colpate). Acritarchs (2 species) and scolecodonts (2 species) are also present (Table 1). Many palynomorphs are moderately well preserved and are light yellow to light orange in colour. They are Thermal Alteration Index (TAI) 1+ and 2 on the scale of Utting et al. (1989). Others are highly pyritised (both framboidal and euhedral), especially in the lower member of the Copacabana Formation, and these are often difficult to classify.

A comparison of the present study and Cousminer (1965) indicates that sample MP-P6032 is the most similar to sample BOGOC 6-2560 of Cousminer (1965). This is the most diverse sample from the Coal Member (Figure 3). Fifty-two species are recorded from Bolivia for the first time and one new species is

Figure 3. (A) A geologic map of Quebrada Chullpanimayo canyon near Apillapampa, Bolivia with the location of stratigraphic sections, key physical and structural features and a cross-section. Modified from Chamot (1965) and Cousminer (1965). (B) Cross-section modified from Chamot (1965) showing the relationship of the classic northern stream section to the newly measured ridge section high above the stream. (C) Stream stratigraphic section showing the location of sample points, significant waterfalls, sharp bends in the stream bed (numbered) and selected tephra beds with preliminary SHRIMP ages after Henderson et al. (2009). This section starts in the north in the Devonian, crosses a major unconformity and ends in the centre of the syncline.

Table 1. The percentages of the major botanical groups in each sample from the Copacabana Formation at Apillapampa, Bolivia.

	MP-P6029	MP-P6028	MP-P6027	MP-P6026	MP-P6030	MP-P6034	CICYTTP-Pl2	CICYTTP-Pl3	MP-P6031	MP-P6032	MP-P6033	CICYTTP-Pl1
Pteridophytes	2.6	1.7	3.4	1.1	7.3	45.8	41.5	51.4	40.4	21.3	48.3	36.8
Lycophytes	2.6			2.3	5.5	15.9	15.4	44.3	23.9	13.0	6.9	14.8
Lepidodendrales					77.3	7.5	0.8		0.9	3.1		3.2
Sphenophytes		1.7	1.7	1.1	5.5	9.3			1.8	5.1	7.8	9.0
Gymnosperms	28.2	20.7	49.2	27.3	0.9	14.0				12.6	12.9	3.2
Glossopterids	7.7	19.0	6.8	13.6					0.9	5.9		4.2
Corystosperms, Peltasperms	23.1	24.1	13.6	11.4	1.8	1.9	0.8		1.8	12.6	6.0	7.1
Cordaites, Conifers	12.8	20.7	25.4	40.9	1.8	1.9			0.9	7.1	6.0	8.7
Freshwater algae (mainly *Botryococcus*)	10.3	3.4					38.5	4.3	27.5	16.9	8.6	
Reduviasporonites	7.7	8.6				2.8			1.8	2.4	3.4	12.9
Deusilites tenuistriatus	2.6					0.9	3.1					
Scolecodonts	2.6			2.3								

described. Three of the thirty species recorded by Cousminer (1965) are endemic; these are *Crustaesporites hessi*, *Lycospora variabila* and *Punctatisporites minutiarcus*. Five species noted by Cousminer (1965) were not observed in this study; these are *Calamospora diversiformis*, *Granulatisporites trisinus*, *Krauselisporites splendens*, *Neoraistrickia* aff. *N. ramosa* and *Triquitrites* aff. *T. tumulosus*.

Lueckisporites virkkiae and *Vittatina costabilis* first appear in the lowermost two samples of the lower member of the Copacabana Formation. These key taxa indicate the Permian interval, as do the genera *Corisaccites*, *Hamiapollenites*, *Lueckisporites*, *Lunatisporites*, *Mabuitasaccites*, *Pakhapites*, *Striatoabieites*, *Striatopodocarpites*, *Striomonosaccites*, *Vittatina* and *Weylandites*, and some monolete spores such as *Polypodiisporites mutabilis*. It is therefore possible to define two main assemblages: a lower assemblage (LA) corresponding to sample MP-P6029 at 9.8 m and an upper assemblage (UA) corresponding to the overlying samples from 69 to 287 m, based mainly on the appearance of the key forms *Lueckisporites virkkiae* and *Lueckisporites* spp. (Figure 3).

The lower assemblage (MP-P6029) is characterised by relatively sparse monosaccate and bisaccate non-striate pollen grains and several species of striate pollen such as *Marsupipollenites striatus*, *Pakhapites ovatus*, *Vittatina costabilis* and *V. vittifera* (Table S1, online supplementary material). These are the typical markers for the Asselian to mid-Artinskian *Vittatina costabilis* Zone of the Paraná Basin (Souza and Marques-Toigo 2005), and the *Pakhapites fusus*-*Vittatina subsaccata* Zone of western Argentina (Césari and Gutiérrez 2001).

The upper assemblage is more diverse, especially due to the appearance of many striate pollen grains belonging to *Lueckisporites*, *Lunatisporites*, *Striatoabieites*, *Striatopodocarpites* and *Weylandites*. It is correlated to the *Lueckisporites virkkiae* Zone of Brazil (Souza and Marques-Toigo 2005) and the *Lueckisporites*-*Weylandites* zones of Argentina (Césari and Gutiérrez 2001); both these were attributed to the mid-Artinskian–Guadalupian (Souza et al. 2007). Analysis of the data herein to establish accurate correlations with similar assemblages in South America, together with the preliminary radiometric data of Henderson et al. (2009), is depicted in Figures 2 and 3.

6.2. Palaeoecology, palynofacies and palaeoenvironmental conclusions

The palynological data presented here differ from those of Cousminer (1965) who found that the palynofloras from the Coal Member are dominated by pteridophytes (64%) and that gymnosperm pollen

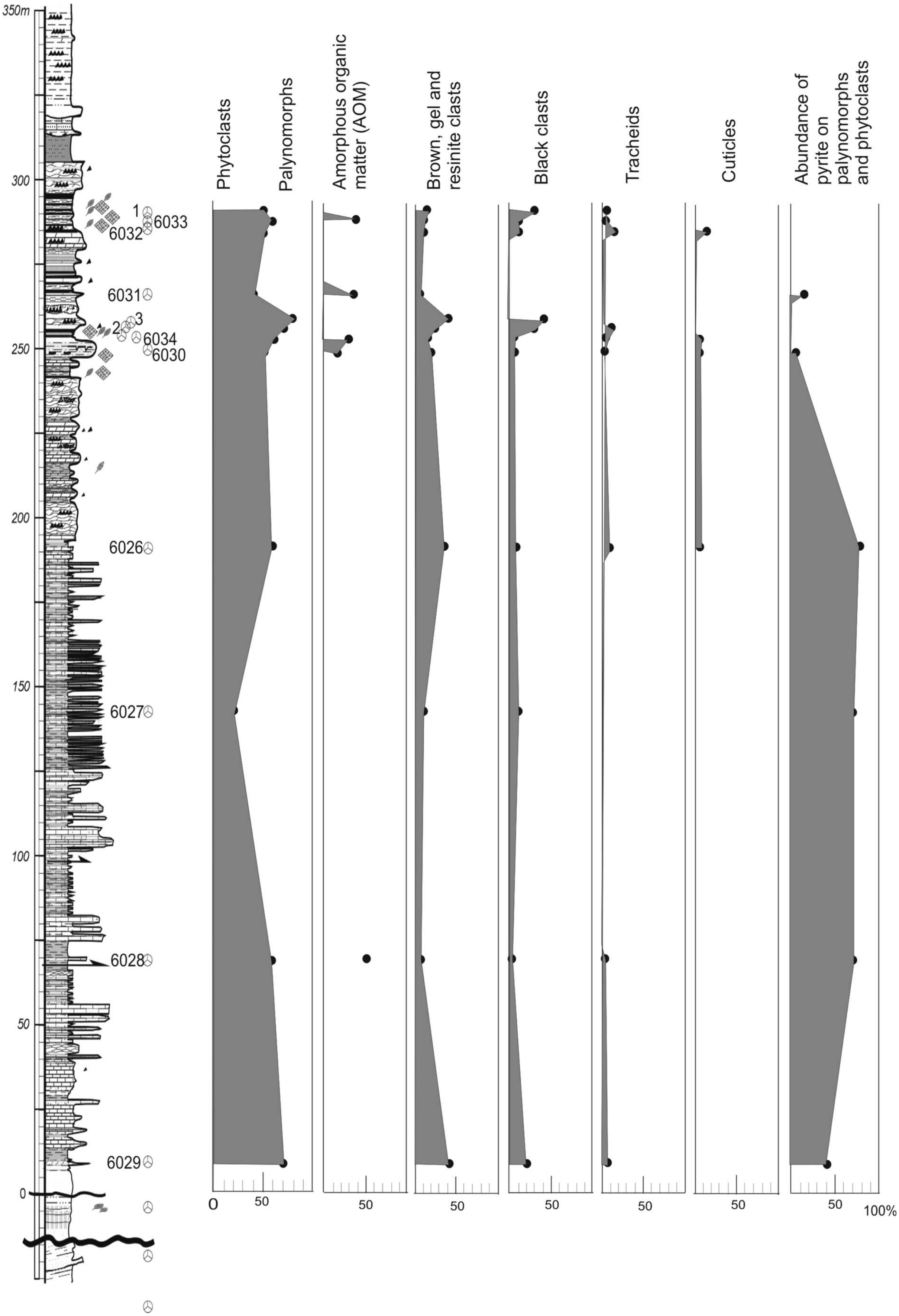


Figure 4. The relative abundances of palynodebris and palynomorphs in the Copacabana Formation at Apillapampa, Bolivia.

(21%) is subordinate. The lowermost four samples from the lower member of the Copacabana Formation are dominated by diverse gymnospermous pollen, including many species of striate pollen, whereas lower vascular plants and algal remains were dominant in the Coal Member (Figures 3, 4; Table 1). A predominantly varied gymnospermous composition characterises the lower assemblage of the Copacabana Formation with some algae and spores from lower vascular plants, notably lycopods, pteridophytes and sphenophylls. The upper assemblage indicates that taeniate-striate pollen grains are prominent in the lower member of Copabana Formation (samples MP-P6028 to MP-P6026) associated with marine ramp deposits (Figure 3). Lower vascular plants, especially lycophytes and pteridophytes, together with algae and some gymnospermous groups became the dominant groups in the Coal Member. These groups of plants confirm the widespread distribution of the *Glossopteris* flora during the Permian in Gondwana (Iannuzzi et al. 2004).

The parent plants of species of the lower assemblage are mainly gymnospermous (i.e. Coniferales, Cordaitales, Corystospermaceae/Peltaspermaceae and Glossopteridales), suggesting a lowland landscape bordering the Copacabana seaway with a hygro-mesophilous flora. These were probably associated with hygro-hydrophilous lycophyte and pteridophyte trilete spores from the forest understory. The frequent presence of the freshwater/brackish algae *Botryococcus* and *Reduviasporonites chalastus*, single specimens of undetermined acritarchs and scolecodonts and *Deusilites tenuistriatus* are consistent with cyclic littoral marine conditions into which miospores were transported. This assemblage is associated with the lowermost Yaurichambi to Copacabana Formation transition, where sandstones are sharply overlain by pyrite-bearing black shales and burrowed brachiopod wackestones overlain by marls and thin-bedded lime mudstones/wackestones. A change to restricted conditions is supported by the presence of pyrite in the exine of palynomorphs, suggesting bottom water anoxia (euhedral or anhedral pyrite) and euxinic conditions (framboidal pyrite), enhanced by the abundant input of plant-derived phytoclasts (Figures 3, 4; Table 1; Bajpai et al. 2001).

Palaeoenvironmental variability occurred in both the lower and upper assemblages, probably due to high-frequency cyclicity. A palaeoenvironmental change is present in the upper assemblage from the lower member to the Coal Member of the Copacabana Formation. Scolecodonts and the intense pyritisation

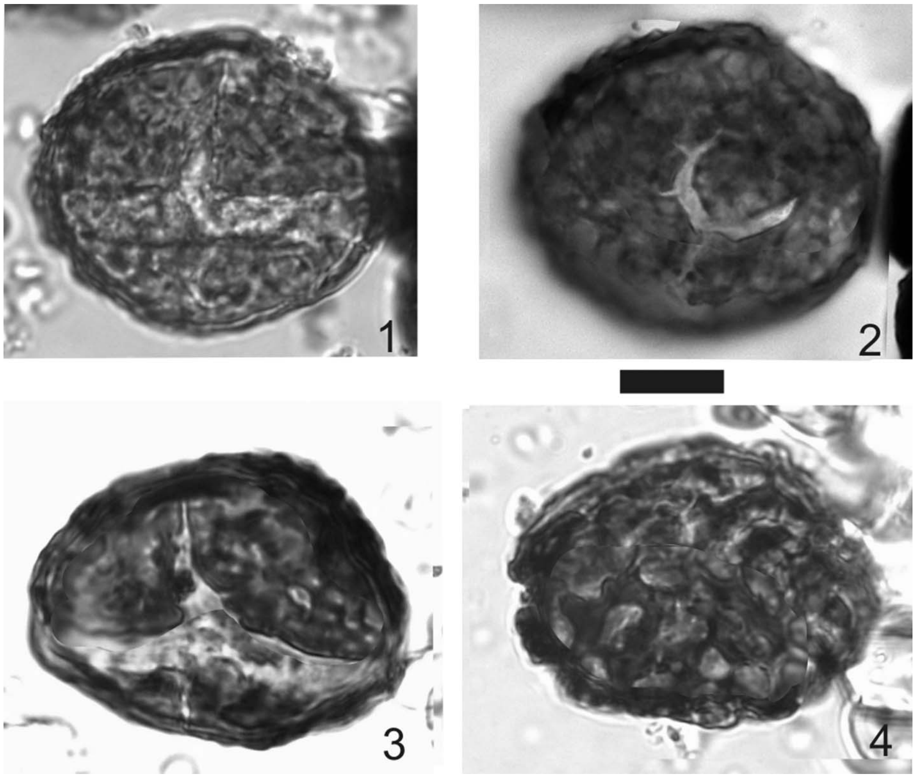


Plate 1. *Dictyotriletes cousmineri* sp. nov. Figures 1, 2. The holotype**:** 1 – proximal face; 2 – distal face, CICYTTP-Pl 3 (+10), Q28/4. Figure 3. A paratype - CICYTTP-Pl 3 (+10), R27/1. Figure 4. A paratype - CICYTTP-Pl 3 (+10), V62/2. The scale bar represents 10 μm.

of palynomorphs and AOM together with miospores are indicative of marine depositional conditions with variable terrestrial input (Batten 1996). This is observed in the deeper water facies of the lower member (i.e. MP-P6028 at 69 m), although significant AOM also occurs in half the Coal Member samples. High levels of AOM, which are related to the decomposition of algal components due to its subcolloidal or spongeous aspect, and high grades of pyritisation are recorded in MP-P6028 supporting generally deeper marine conditions (Grader et al. 2000). This sample is from black distal ramp shales associated with downslope channelled crinoid grainstones and diverse coral, bryozoan and cephalopod-bearing deposits. Conversely, the overlying lower Copacabana samples MP-6027 and 6026 at 143 and 192 m contain significant black and brown phytoclasts and other non-woody plant remains, suggesting shallower marine conditions.

The Coal Member is dominated by lycophyte and pteridophyte spores and moderate levels of AOM, which are related to restricted marine and lagoonal conditions supporting the facies interpretations of Grader et al. (2000) and Iannuzzi et al. (2008) (Figures 3, 4; Table 1). Most of the few abundant species are restricted to single intervals, reflecting a local autochthonous to parautochthonous source of the microflora. These taxa include *Convolutispora uruguaiensis*, *Dictyotriletes cousmineri*, *Hamiapollenites dettmanae*, *Hamiapollenites karroensis*, *Lycospora variabila*, *Reduviasporonites chalastus* and *Thymospora rugulosa*. *Botryococcus brauni* and *Polypodiisporites mutabilis* are frequent to dominant species in most of the Coal Member samples (Table S1, online supplementary material). The appearances of *Lycospora variabila* and *Lundbladispora braziliensis* in samples MP-P6030 and MP-P6034 are associated with palaeosols and with the first occurrence of unequivocal lycopod logs and leaves in outcrops above and below the mud-cracked marker unit at $\sim$250 m (Figure 3). Samples MP-P6034, CICYTTP-Pl2 and CICYTTP-Pl3 are lateral interval equivalents with MP-P6030 in a sequence boundary zone, where carbonaceous shales become more common in the Coal Member. Pteridophytes and *Botryococcus* are dominant in sample CICYTTP-Pl2 in the ridge section, about 3 m above the mud-cracked marker bed where it contains rooted intervals. The influence of an oligotrophic water body (i.e. lacking plant nutrients and hence supporting few plants) with a primarily autochthonous microflora is proposed. However, CICYTTP-Pl2 occurs 10–20 cm above laminated dolomitic shale with woody stems, lycophyte debris, *Pecopteris* sp. and a sphenophyte (Iannuzzi et al. 2008), and is overlain by a palaeosol with equigranular fabric with organic fragments and rootlets. *Lycospora variabila* (related to the arborescent Lepidodendrales) is dominant in sample MP-P6030 above the mud-cracked marker bed in the stream section. It also suggests autochthonous microflora associated with palaeosols and plant fragments (Figures 3, 4; Table 1). Lycophytes, pteridophytes and sphenophytes, probably with Cordaitales and some Coniferales, therefore occupied more humid restricted areas of swamps, mires or mangrove-like transitional areas near to the Copacabana Sea (Calder et al. 1996).

Foster et al. (2002) linked the size of *Reduviasporonites chalastus* cells with palaeolatitude, with larger cells occurring in the palaeotemperate Permian of Australia, Arctic Canada, China and Russia and smaller cells being typical of the palaeotropical and palaeoequatorial Permian of northern Australia, western Europe and Saudi Arabia. According to Foster et al. (2002) the cell length and width ranges of 230 specimens are 18–220 μm and 9–127 μm, respectively, and the mean length to width ratio is 2.2. This trend may indicate palaeoenvironmental control on the growth and development of the organism that produced *Reduviasporonites chalastus*. The relatively large size of the *Reduviasporonites* cells in this study suggests a palaeotemperate climate. The maximum dimensions of chains of *Reduviasporonites* are 70 × 260 μm and the maximum and minimum ranges of discrete cells are 70 × 130 μm and 33–70 μm, respectively. This is in agreement with the palaeogeographical and palaeoclimatical reconstructions of Scotese et al. (1999) and Scotese (2003). The pteridosperms represented by the *Corystospermaceae*, *Glossopteridales* and *Peltaspermaceae* mainly produce striate pollen grains (Figures 3, 4; Table S1, online supplementary material) and are interpreted as being indicative of relatively low humidity or seasonally arid conditions. This open lowland vegetation is indicative of a palaeotemperate climate during the Cisuralian in Bolivia. In contrast, few specimens of striate bisaccate pollen grains such as *Protohaploxypinus amplus* and *Striatopodocarpites solitus* were recorded in the Pennsylvanian Copacabana Formation assemblage (di Pasquo 2009) in the Pando X-1 core, which includes evaporites and aeolianites. Di Pasquo (2009) explained this difference by invoking palaeoclimatic and palaeogeographical changes produced by northern movement or rotation of Gondwana during the Late Pennsylvanian and the Cisuralian (Díaz-Martínez and Isaacson 1995). Pennsylvanian assemblages from northern Argentina, Bolivia and Peru with rare to moderately common striate bisaccate pollen grains therefore indicate seasonally drier climates, in comparison to assemblages devoid of striate bisaccate pollen in northern Argentina and southern Bolivia that developed under more humid conditions (di Pasquo 2003, 2009). During the Permian, the ubiquitous striate bisaccate taxa indicate seasonally warmer climates, supporting both northward rotation of Gondwana into lower palaeolatitudes and the increased diversification of Copacabana invertebrates (Grader 2003). The mixed character of the biotas of the Central Andes suggest the influence of cold waters from Gondwana and warmer currents connected to tropical to equatorial environments in North Africa, North America and Europe (Newell et al. 1953; Iannuzzi and Rössler 2000; Scotese 2003).

Further work on the Copacabana Formation should help in the refinement of Permian correlations in Bolivia and central South America (Henderson et al. 2009) and improve the understanding of short-term cyclicity during the Permian deglaciation of Gondwana.

Acknowledgements

This contribution is one of a series on the Upper Palaeozoic lithostratigraphical units of Bolivia. The authors acknowledge the invaluable help of Paulo A. Souza (UFRGS), Gustavo Holfeltz (FCEN, UBA) and Renee Breedlovestout (University of Idaho) for processing most of the samples. We also thank Shirely Lopez and Sergeotecmin for help with logistics, Shirley and Nestor Jimenez for hospitality in La Paz and Ramiro Suárez-Soruco and Ricardo Céspedes for assistance at the Museum of Palaeontology, Cochabamba. Oscar Arispe accompanied us to Apillapampa and other sites in 1997 and 2007. We also thank the Arispe-Pérez family in La Paz. Fieldwork in 2007 and 2008 was concurrent with Peter Isaacson and Heidi Anderson's work in the southeasten Subandes. Work at Apillapampa and at Zudañez included Roberto Iannuzzi, Enrique Díaz-Martínez and Renee Breedlovestrout. Charles Henderson and Vladimir Davydov provided important contributions and collected samples at Apillapampa during a small flash flood in March 2007. This work is dedicated to the people of Bolivia. We acknowledge funding from Projects CGL2006-07376/BTE (2007–2009, granted to Enrique Díaz-Martínez) provided by the Instituto Geológico y Minero de España and PIP 5518 CONICET (2005–2007, granted to Mercedes di Pasquo) by the Consejo Nacional de Investigaciones Científicas y Técnicas. Moreover, Fulbright and CONICET gave Mercedes di Pasquo a research scholarship grant in 2009 to work in collaboration with Peter Isaacson and Heidi Anderson (University of Idaho), who are all excellent colleagues and friends. This study was also supported by funds from the University of Buenos Aires (UBACYT X 428, 2008-2010, granted to Mercedes di Pasquo) and we are grateful to FCEN, UI and CICYTTP, where the main part of this work was carried out.

Author biographies

MERCEDES M. DI PASQUO received her Ph.D. in 1999 from the University of Buenos Aires, Argentina for a thesis on Late Carboniferous palynofloras from northern Argentina and southern Bolivia. In 2002, she became a permanent researcher of CONICET and also works as a consultant to the oil industry. In 2009, Mercedes was made a Fulbright Research Fellow at the University of Idaho to work on Upper Palaeozoic palynofloral changes in Bolivia and Argentina during the Gondwanaland glaciation. During 2010, she became a senior researcher in charge of the Palynology and Palaeobotany Laboratory at CICYTTP in Diamante, Entre Ríos, Argentina, working on the Silurian–Permian palynofloras of South America and K/P of Antarctica. Recently, Mercedes began studies on the Devonian and Carboniferous boundary of Idaho and Montana and the Holocene of Entre Ríos Province. Mercedes is currently President of the *Asociación Latinoamericana de Paleobotánica y Palinología*.

GEORGE W. GRADER, JR. is a consulting carbonate stratigrapher with PRISEM Geoscience Consulting LLC. George received his BS in geology from Colby College and his M.Sc. and Ph.D. from the University of Idaho. His research has focused on the Devonian and Mississippian sedimentology and stratigraphy of the northern Rockies, and on the Carboniferous–Permian siliciclastics and carbonates of the central Andes. From 2003 to 2005, George worked for Washington State University and consulted on hydrological and environmental projects throughout the Pacific Northwest. Since 2006, he has been involved in projects on the Devonian and Mississippian stratigraphy of Idaho and Montana and the Palaeozoic stratigraphy of South America.

References

Anderson H, Grader GW, Di Pasquo M, Isaacson PE. 2010. Ice-proximal stratigraphy and active tectonics: an example from southern Bolivia. *Geological Society of America Abstracts with Programs* 42(3), 52.

Azcuy CL, di Pasquo MM. 2000. Palynology of the Late Carboniferous from the Tarija Basin, Argentina: a systematic review of monosaccate pollen genera. *Palaeontographica Abteilung B* 253, 103–137.

Azcuy CL, di Pasquo MM, Ampuero HV. 2002. Late Carboniferous miospores from the Tarma Formation. *Review of Palaeobotany and Palynology* 118, 1–28.

Azcuy C, Beri A, Bernardes-de-Oliveira MEC, Carrizo HA, di Pasquo MM, Díaz Saravia P, González C, Iannuzzi R, Lemos V, Melo JHG, Pagani A, Rohn R, Rodríguez Amenábar C, Sabattini N, Souza PA, Taboada A, Vergel MM. 2007. Bioestratigrafía del Paleozoico Superior de América del Sur: primera etapa de trabajo hacia una nueva propuesta cronoestratigráfica. *Asociación Geológica Argentina, Serie D: Publicación Especial* No. 11, 9–65.

Bajpai U, Kumar M, Shukla M, Anand-Prakash, Srivastava GP. 2001. Nature and composition of pyrite framboids and organic substrate from degraded leaf cuticles of Late Tertiary sediments, Mahuadanr Valley, Palamu, Bihar. *Current Science* 81, 102–106.

Balarino ML, Gutiérrez PR. 2006. Palinología de la Formación Tasa Cuna (Pérmico Inferior), Córdoba, Argentina: sistemática y consideraciones bioestratigráficas. *Ameghiniana* 43, 437–460.

Batten DJ. 1996. Chapter 26. Palynofacies. In: Jansonius J, McGregor DC, editors. Palynology: principles and applications. *American Association of Stratigraphic Palynologists Foundation* 3, 1011–1084.

Calder JH, Gibling MR, Eble CF, Scott AC, MacNeil DJ. 1996. The Westphalian D fossil lepidodendrid forest at Table Head, Sydney Basin, Nova Scotia: Sedimentology, paleoecology and floral response to changing edaphic conditions. *International Journal of Coal Geology* 31, 277–313.

Césari SN, Gutiérrez PR. 2001. Palynostratigraphy of Upper Paleozoic sequences in Central-Western Argentina. *Palynology* 24, 113–146.

Chamot GA. 1965. Permian section at Apillapampa, Bolivia and its fossil content. *Journal of Paleontology* 39, 1221–1124.

Cousminer HL. 1965. Permian spores from Apillapampa, Bolivia. *Journal of Paleontology* 39, 1097–111.

Dettmann ME. 1963. Upper Mesozoic microfloras from south-eastern Australia. *Procceedings of the Royal Society of Victoria* 77, 1–148.

di Pasquo MM. 2003. Advances sobre palinología, biostratagrafía y correlación de grupos Macharetí y Mandiyutí, Neopaleozoico de la Cuence Tarija, provincia de Salta, Argentina. *Ameghiniana* 40, 3–32.

di Pasquo MM. 2007a. Asociaciones palinológicas presentes en las Formaciones Los Monos (Devónico) e Itacua (Carbonífero Inferior) en el perfil de Balapuca, sur de Bolivia. Parte 1. Formación Los Monos. *Revista Geológica de Chile* 34, 98–137.

di Pasquo MM. 2007b. Asociaciones palinológicas presentes en las Formaciones Los Monos (Devónico) e Itacua (Carbonífero Inferior) en el perfil de Balapuca, sur de Bolivia. Parte 2. Formación Itacua e interpretación estratigráfica y cronología de las formaciones Los Monos e Itacua. *Revista Geológica de Chile* 34, 163–198.

di Pasquo MM. 2009. The Pennsylvanian palynoflora of the Pando X-1 Borehole, northern Bolivia. *Review of Palaeobotany and Palynology* 157, 266–284.

di Pasquo MM, Azcuy CA, Souza PA. 2003a. Palinología del Carbonífero Superior del Subgrupo Itararé en Itaporanga, Cuenca Paraná, Estado de São Paulo, Brasil. Parte 1: sistemática de esporas y paleofitoplancton. *Ameghiniana* 40, 277–296.

di Pasquo MM, Azcuy CA, Souza PA. 2003b. Palinología del Carbonífero Superior del Subgrupo Itararé en Itaporanga, Cuenca Paraná, Estado de São Paulo, Brasil. Parte 2: sistemática de polen y significado paleoambiental y estratigráfico. *Ameghiniana* 40, 297–313.

di Pasquo MM, Souza PA, Grader G, Díaz-Martínez E. 2009. Early Devonian and Permian (Titicaca Group) palynology from Bolivia: The Apillapampa section revisited for stratigraphic assessment. AASP 42nd Annual Meeting, Tennessee, East Tennessee State University. *The Palynological Society, Abstracts* 23.

di Pasquo MM, Vergel MM, Azcuy CL. 2010. Pennsylvanian and Cisuralian palynofloras from the Los Sauces area, La Rioja Province, Argentina: chronological and palaeoecological significance. *International Journal of Coal Geology, Special Issue: Hermann Pfefferkorn* 83, 276–291.

Díaz-Martínez E. 1999. Estratigrafía y paleogeorafía del Paleozoico Superior del norte de los Andes Centrales (Bolivia y sur del Peru). In: Macharé J, Benavides V, Rosas S, editors. *Boletín de la Sociedad Geológica de Peru* 5, 19–26.

Díaz-Martínez E. 2002. Revised older age of Late Paleozoic Glaciations in South America. 3rd European meeting on the Paleontology and Stratigraphy of Latin America, Toulouse, Extended Abstract. p. 40–43.

Díaz-Martínez E, Isaacson PE. 1995. Long-lived Phanerozoic crustal weakness and suture zone in the Central Andes of Peru and Bolivia. Geological Society of America, Annual Meeting, Seattle. Abstracts with Programs, Vol. 25.

Díaz-Martínez E, Iannuzzi R. 2005. Carboniferous paleogeography and paleoclimatology of western Gondwana: towards an integrated biostratigraphical approach. In: Pankhurst RJ, Veiga GD, editors. *Gondwana 12: Geological and Biological Heritage of Gondwana*. Academia Nacional de Ciencias de Argentina, Córdoba, Abstracts, 139.

Félix CM, Premoar E, Hermany G, Souza PA. 2006. Análise palinotaxonômica e bioestratigráfica da Subturma Monosaccites na Bacia do Paraná, Brasil. I: *Plicatipollenites* Lele 1964 e *Crucisaccites* Lele and Maity 1965. *Revista Brasileira de Paleontogia* 9, 63–72.

Foster CB, Stephenson MH, Marshall C, Logan GA, Greenwood PF. 2002. A revision of *Reduviasporonites* Wilson 1962: Description, illustration, comparison and biological affinities. *Palynology* 26, 35–58.

Grader GW. 2003. Carbonate-siliciclastic sequences of the Pennsylvanian and Permian Copacabana Formation, Titicaca Group, Andes of Bolivia [Ph.D. thesis]. [Moscow (ID)]: University of Idaho.

Grader GW, Isaacson PE, Rember B, Mamet B, Díaz-Martínez E, Arispe O. 2000. Stratigraphy and depositional setting of the late Paleozoic Copacabana Formation in Bolivia. *Zentralblatt Geologie und Paläontologie* 1(7/8), 723–741.

Grader GW, Díaz-Martínez E, Davydov V, Montañez I, Tait J, Isaacson PE. 2007. Late Paleozoic stratigraphic framework in Bolivia: constraints from the warm water Cuevo Megasequence. In: Díaz-Martínez E, Rábano I, editors. 4th European Meeting on the Paleontology and Stratigraphy of Latin America, Madrid, Cuadernos del Museo Geominero, Instituto Geológico y Minero de España 8, 181–188.

Grader GW, Isaacson PE, Díaz-Martínez E, Pope MC. 2008. Pennsylvanian and Permian sequences in Bolivia: Direct responses to Gondwana glaciation. In: Fielding CR, Frank TD, Isbell JL, editors. The Late Paleozoic Gondwanan Ice Age: Timing, extent, duration and stratigraphic records. *Geological Society of America, Special Paper* 441, 143–159.

Gutiérrez PR, Balarino, ML, Beri, Á. 2010. Palynology of the Lower Permian of Paraná Basin, Uruguay. *Journal of Systematic Palaeontology* 8, 459–502.

Henderson CM, Schmitz M, Crowley J, Davydov V. 2009. Evolution and geochronology of the *Sweetognathus* lineage from Bolivia and the Urals of Russia; Biostratigraphic problems and implications for Global Stratotype Section and Point (GSSP) definition. *Permophiles, Newsletter of the Subcommission on Permian Stratigraphy* 53, 20.

Ianuzzi R, Rössler O. 2000. Floristic migration in South America during the Carboniferous: phytogeographic and biostratigraphic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 161, 71–94.

Iannuzzi R, Vieira CE.L, Guerra-Sommer M, Díaz-Martínez E, Grader GW. 2004. Permian plants from the Chutani Formation (Titicaca Group, northern Altiplano of Bolivia): 2. The morphogenus *Glossopteris*. Academia Brasileira de Ciências. *Anais* 76(1), 129–138.

Iannuzzi R, Breedlovestrout R, Grader GW, Díaz-Martínez E. 2008. Early Permian flora from Apillapampa, central Bolivia: New data. 12° Simposio de Paleobotánica y Palinología, Florianópolis, Boletín de resúmenes, 96.

Kley J, Monaldi CR, Salfity JA. 1999. Along-strike segmentation of the Andean foreland: causes and consequences. *Tectonophysics* 301, 75–94.

Lindström S. 1995. Early Permian palynostratigraphy of the northern Heimefrontfjella mountain-range, Dronning Maud Land, Antarctica. *Review of Palaeobotany and Palynology* 89, 359–415.

Lindström S. 1996. Late Permian palynology of Fossilryggen, Vestfjella, Dronning Maud Land, Antarctica. *Palynology* 20, 15–48.

Mautino LR, Anzótegui LM, Vergel MM. 1998a. Palinología de la Formación Melo (Pérmico Inferior) en Arroyo Seco, Departamento Rivera, República Oriental del Uruguay. Parte IV: Esporas. *Ameghiniana* 35, 67–79.

Mautino LR, Vergel MM, Anzótegui LM. 1998b. Palinología de la Formación Melo (Pérmico Inferior) en Arroyo Seco, Departamento Rivera, Uruguay. Parte V: Granos de pólen, acritarcas e incertae sedis. *Ameghiniana* 35, 299–314.

Mautino LR, Vergel MM, Anzótegui LM. 1998c. Palinología de la Formación Melo (Pérmico inferior) en Arroyo Seco, Departamento Rivera, República Oriental del Uruguay, Parte III. Especies nuevas. *Revista Española de Micropaleontología* 30, 107–110.

Mori ALO, Souza PA. 2010. Palinologia das formações Rio Bonito e Palermo (Permiano Inferior, Bacia do Paraná) em Candiota, Rio Grande do Sul, Brasil: novos dados e implicações bioestratigráficas. *Ameghiniana* 47, 61–78.

Neregato R, Souza PA, Rohn R. 2008. Registros palinológicos inéditos nas formações Teresina e Rio do Rasto (Permiano, Grupo Passa Dois, Bacia do Paraná): implicações biocronoestratigráficas e paleoambientais. *Pesquisas em Geociências* 35, 9–21.

Newell ND, Chronic J, Roberts TG. 1953. Upper Paleozoic of Perú. *The Geological Society of America, Memoir* 58, 1–230.

Playford G, Dino R. 2000a. Palynostratigraphy of upper Palaeozoic strata (Tapajós Group), Amazonas Basin, Brazil: Part One. *Palaeontographica Abteilung* 255, 1–46.

Playford G, Dino R. 2000b. Palynostratigraphy of upper Palaeozoic strata (Tapajós Group), Amazonas Basin, Brazil: Part Two. *Palaeontographica Abteilung B* 255, 87–145.

Potonié R. 1970. Synopsis der Gattungen der *Sporae dispersae*. V. Teil: Nachtrage zu allen Gruppen (Turmae). *Beihefte Geologischen Jahrbuch* 87, 1–222.

Potonié R, Kremp G. 1954. Die Gattungen der Paläozoischen *Sporae dispersae* und ihre Stratigraphie. *Beihefte Geologischen Jahrbuch* 69, 111–194.

Potonié R, Kremp GO. 1955. Die *Sporae dispersae* des Ruhrkarbons, ihre Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte, Teil I. *Palaeontographica Abteilung B* 98, 1–136.

Premaor E, Fischer TV, Souza PA. 2006. Palinologia da Formaçâo Irati (Permiano Inferior da Bacia de Paraná), em Montividiu, Goiás, Brasil. *Revista del Museo Argentino de Ciencias Naturales, nueva serie* 8, 221–230.

Riding JB, Kyffin-Hughes JE. 2004. A review of the laboratory preparation of palynomorphs with a description of an effective non-acid technique. *Revista Brasileira de Paleontologia* 7, 13–44.

Riding JB, Kyffin-Hughes JE, Owens B. 2007. An effective palynological preparation procedure using hydrogen peroxide. *Palynology* 31, 19–36.

Rigby JF, Heckel H. 1977. Palynology of the Permian sequence in the Springsure Anticline, Central Queensland. *Geological Survey of Queensland, Publication* 363, *Palaeontological Papers* 37, 1–76.

Scotese CR. 2003. *Paleomap Project*. http://www.scotese.com.

Scotese CR, Boucot AJ, McKerrow WS. 1999. Gondwanan paleogeography and paleoclimatology. *Journal of African Earth Sciences* 28, 99–114.

Sempere T. 1995, Phanerozoic evolution of Bolivia and adjacent regions. In: Tankard AJ, Suarez R, Welsink HJ, editors. Petroleum basins of South America, *American Association of Petroleum Geologists Memoir* 62, 207–230.

Sempere T, Aguilera E, Doubinger J, Janvier P, Lobo J, Oller J, Wenz S. 1992. La Formation de Vitiacua (Permien moyen à supérieur-Trias? inférieur, Bolivie du Sud): Stratigraphie, palynologie et paléontologie. *Nueus Jarburch Geologischen Paläontologie Ablandunghen* 185, 239–253.

Sempere T, Carlier G, Soler P, Fornari M, Carlotto V, Jacay J, Arispe, O, Cárdenas J, Rosas S, Jiménez N. 2002. Late Permian–Middle Cretaceous lithospheric thinning in Peru and Bolivia and its bearing on Andean-age tectonics. *Tectonophysics* 345, 153–181.

Souza PA, Marques-Toigo M. 2005. Progress on the palynostratigraphy of the Permian strata in Rio Grande do Sul State, Paraná Basin, Brazil. *Anais da Academia Brasileira de Ciências* 77, 353–365.

Souza PA, Vergel MM, Beri A. 2007. Pennsylvanian and Permian Palynostratigraphy of the Paraná/Chacoparaná Basins in Brazil, Argentina and Uruguay: an integrative analysis. In: Díaz-Martínez E, Rábano I, editors. 4th European Meeting on Paleontology and Stratigraphy of Latin American, Madrid, Instituto Geológico Minero de España. *Serie Cuadernos del Museo Geominero* 8, 285–290.

Souza PA, Félix CM, Pérez-Aguilar A, Petri S. 2010. Pennsylvanian palynofloras from the Itu rhythmites (Itararé Subgroup, Paraná Basin) in São Paulo State, Brazil. *Revue de Micropaléontologie* 53, 69–83.

Starck D, del Papa C. 2006. The northwestern Argentina Tarija Basin – stratigraphy, depositional systems and controlling factors in a glaciated basin. *Journal of South American Earth Sciences* 22, 169–184.

Stephenson MH. 2008. Spores and pollen from the middle and upper Gharif members (Permian) of Oman. *Palynology* 32, 157–182.

Utting J, Goodarzi F, Dougherty BJ, Henderson CM. 1989. Thermal maturity of Carboniferous and Permian rocks of the Sverdrup Basin. Canadian Arctic Archipielago. *Geological Survey Canada* 89–19, 1–20.