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# Global biostratigraphic comparison and correlation of an early Cisuralian palynoflora from Bolivia

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This paper presents new data about Early Permian (Cisuralian) strata, palynostratigraphy and absolute dating from the Copacabana Formation in central Bolivia. Recent stratigraphic and palynologic data from marine and transitional rocks at Apillapampa refine the age of Cisuralian palynomorphs in South America. Twelve samples interbedded with five volcanic ashes (processed and productive) yielded 94 palynomorph species arranged in two informal palynoassemblages: the lower assemblage *Vittatina costabilis* corresponds to one sample near the base of the Copacabana Formation and the upper *Lueckisporites virkkiae* assemblage occurs in overlying marine and coal-bearing transitional intervals. Ages were also independently refined by a modern review of conodonts, fusulinids, along with those U–Pb radiometric ages (Isotope Dilution Thermal Ionization Mass Spectrometry [ID-TIMS] of zircon-bearing interbedded tuffs). These data suggest that the lower marine member of the Copacabana Formation at this location is Asselian and Sakmarian. *Lueckisporites virkkiae* is a key species of palynomorph utilised in South American and global Permian biostratigraphic reconstructions. Hence, a thorough global comparison of these palynofloras and correlations is addressed in this contribution, considering first appearances of mainly cosmopolitan diagnostic taxa. Correlations are established with many similar Permian palynofloras, some also constrained with radiometric data, in South America (Brazil, Uruguay and Argentina) and elsewhere.

**Keywords:** *Lueckisporites virkkiae*; palynostratigraphy; correlations; Cisuralian; Copacabana Formation; Bolivia

## Introduction

The late Paleozoic stratigraphic succession in the central Andes reflects (a) fairly continuous Pennsylvanian–Permian deposition, (b) a change from cold water to warmer water settings (paleolatitudinal shift) and (c) a key system for western Gondwana correlations. Furthermore, these rocks have generated discussions regarding faunal and floral endemism versus cosmopolitanism related to Gondwana's sea-level changes, paleolatitudinal positions and paleoclimates. Late Paleozoic resolution for different biostratigraphic proposals, paleogeographic barriers or shared subaqueous conduits in the Peru-Bolivia Basin remains poorly defined (cf. Azcuy et al. 2007).

The Apillapampa section near Cochabamba (Figures 1 and 2) represents a Pennsylvanian paleohighland that separated largely carbonate deposition in western and northern Bolivia from siliciclastic-dominated environments to the south (di Pasquo and Grader 2012a; di Pasquo et al. 2012). This paleohigh was subsident during the Early Permian when the Copacabana Formation was deposited and interbedded with over 30 ash beds (Figure 3). Twelve palynologically productive samples and five recently dated volcanic ashes refine the age of the Copacabana Formation at Apillapampa to the Asselian–Sakmarian and its Coal

Member to the Sakmarian–?Artinskian (Henderson et al. 2009; Figure 4). Two main palynoassemblages were recognised by di Pasquo and Grader (2012a), with *Vittatina* and *Lueckisporites* as significant taxa. These studies emphasise differential regional Permo-Carboniferous subsidence and changing post-glacial sedimentation regimes (Grader et al. 2008), but involve problematic near-field, apparently time-transgressive Bolivian–Argentinean–Brazil–Uruguay stratigraphic correlations. The palynofloras are here considered for first appearances of taxa, overall species associations and the relative proportions of major spore-and-pollen groups. These are compared with similar and radiometrically constrained Permian palynozones, in Brazil (Iannuzzi et al. 2007; Mori et al. 2012), Uruguay (Beri et al. 2011) and Argentina (Césari 2007; Césari et al. 2011). Such comparison is extended to other dated Permian palynological zones or informal assemblages outside South America. These data are useful to understand the biostratigraphic importance of diagnostic taxa present at Apillapampa. These assemblages are predominantly composed of terrestrial miospores related to gymnosperms (conifers, cordaites and pteridosperms), with significant contributions from lower vascular plants (variably pteridophytes, sphenophylls and
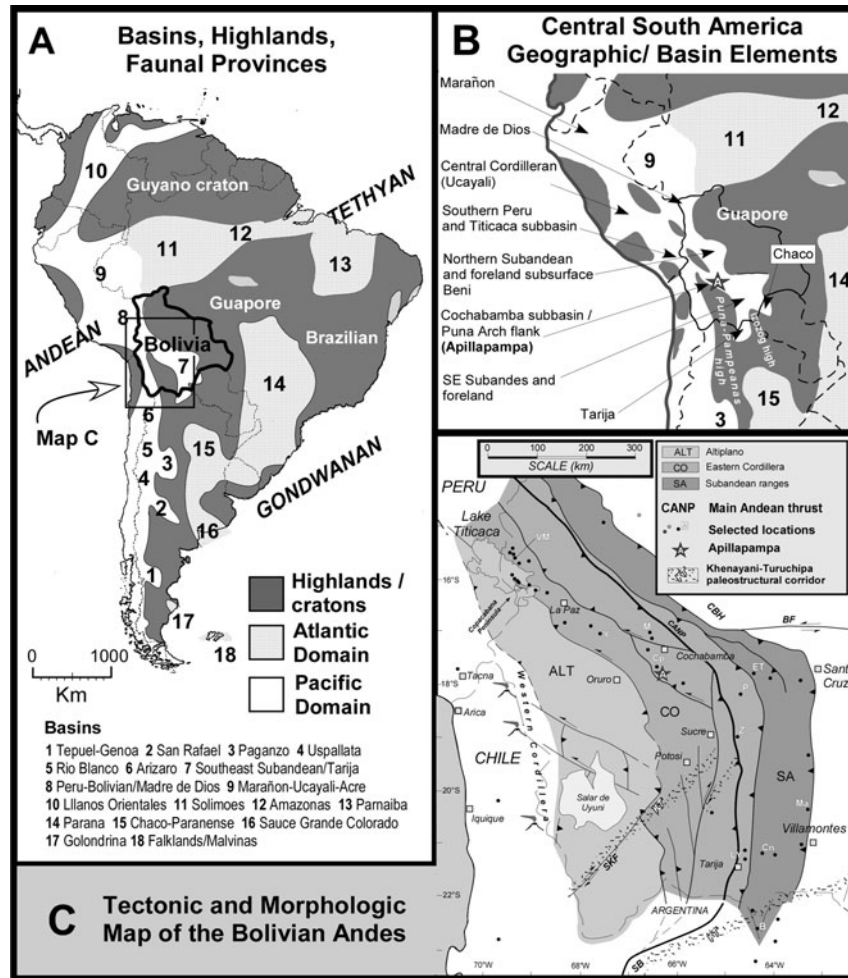
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Figure 1.   (A) Late Paleozoic map of South American showing major basins modified after Azcuy et al. (2007). The Peru–Bolivian master basin (numbers 7 and 8) is considered a single Permo-Carboniferous Basin with areas of differential subsidence (subbasins), as delineated in Figures 1(B) and 2 (Kley et al. 1999; Grader et al. 2003, 2008). (B) Differentiated Permo-Carboniferous paleogeographic nomenclature of the Peru–Bolivia Basin extending into northern Argentina and Paraguay (Tarija and Chaco basins). (C) Tectonic and morphologic map with major cities and Permo-Carboniferous outcrop locations. Late Cenozoic faults are shown with Paleozoic paleogeographic elements, which are illustrated after Sempere (1995). Structural and paleogeographic elements: BF, Boomerang Fault; CBH, Chaparé Buttress (i.e. Chaparé Basement high); SB, Susques Buttress. Locations include: VM, Villa Molino; Y, Iglesiani; M, Morochata; Cp, Capinota; ET, El Tunal; P, Pasorapa; Z, Zudañez; MA, Macharetí; LY, La Yesera; Cn, Canaletas.

lycophytes). An earlier inception *in Bolivia* of several groups of plants characteristics of the *Glossopteris* Flora recorded in South America based on this palynological record is here documented and discussed.

**Geologic setting**

Although this paper focuses on Permian rocks, the known time-transgressive nature of many Paleozoic Formations in the Bolivian Andes requires a review of Carboniferous paleogeography. The Pennsylvanian–Permian Titicaca Group of northern and central Bolivia (Dunbar and Newell 1946; Chamot 1965) records a late Paleozoic Andean marine transgressive to regressive red bed megasequence across the Gondwanan plate margin and Peru-Bolivia Basin

(Figures 1 and 2). Mixed carbonates and clastics occur through the entire sequence, but the distribution of demonstrably time-transgressive Copacabana carbonates thin to a feather edge and cross-paleogeographic boundaries from north to south (Grader et al. 2003, 2007, 2008). Cool to warm water, carbonate-bearing rocks with North American and Pacific faunal association are represented by the Tarma, Copacabana and Ene Formations in Peru, and the Yaurichambi, Copacabana and Chutani Formations in northern and central Bolivia (Díaz-Martínez 1999; Grader et al. 2000, 2003, 2008 and references therein). As summarised in Figure 2, the lower Titicaca Group has been correlated to coldwater, mostly resedimented glacigene clastic rocks of Bolivia's southeast Subandes and Tarija Basin (and Chaco-Parana Basin). These rocks have been
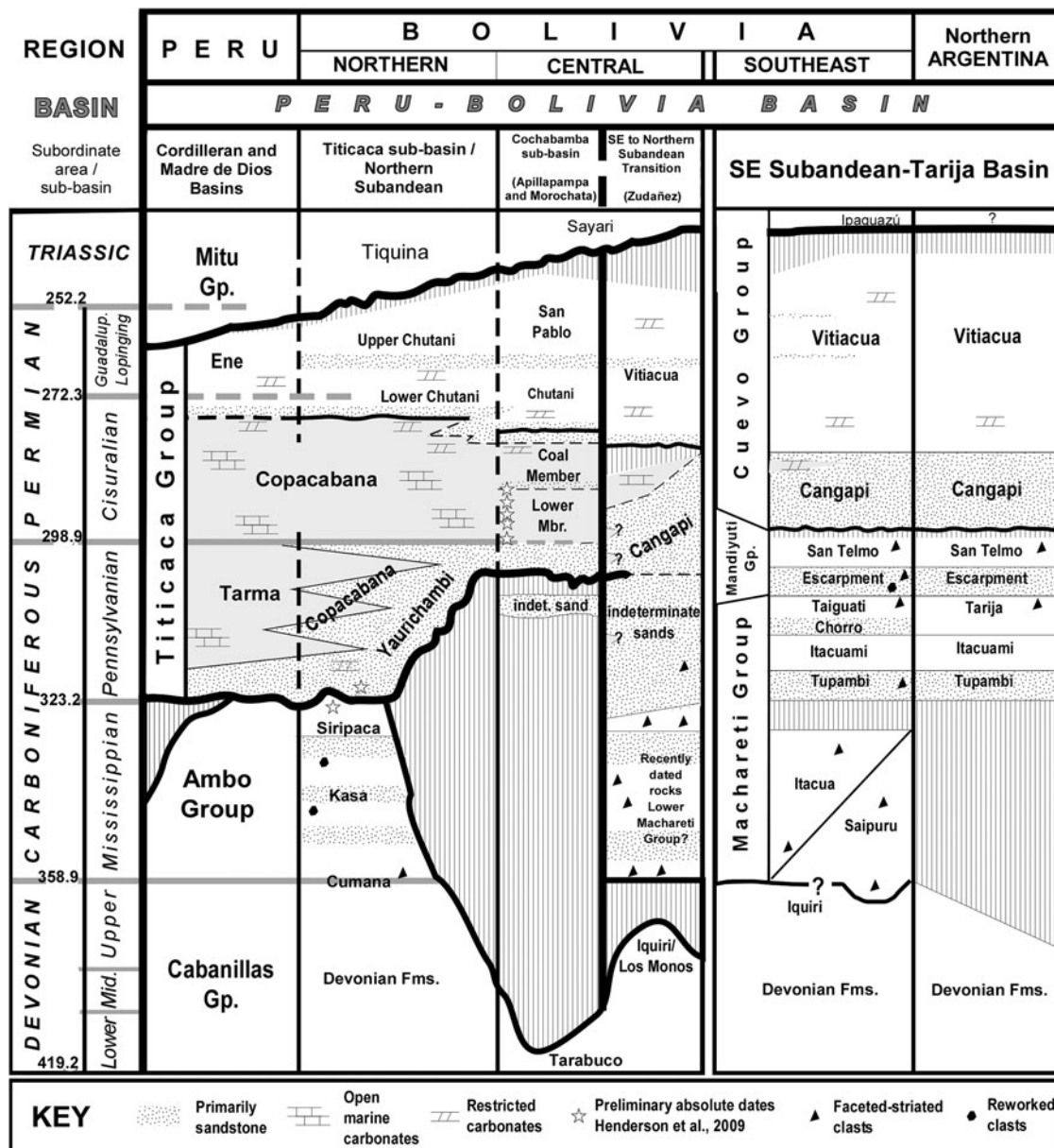
Figure 2.    Correlation of the Copacabana Formation and Coal Member in central Bolivia, with a regional relationship to Late Paleozoic rocks of southern Peru, Bolivia and northern Argentina. Geologic time is according to the International Commission on Stratigraphy 2013. Correlation shows a Cisuralian position for the Coal Member and a late Cisuralian through Early Triassic (?) designation for the Chutani and Vitiacua Formations (Chamot 1965; Sempere et al. 1992, 2002; Grader 2003; Grader et al. 2007, 2008). Northern to central Bolivia is modified after Sempere (1995) and Díaz-Martínez (1999). Southeastern Bolivia and northern Argentina are modified from di Pasquo (2003, 2007a, 2007b), Starck and del Papa (2006) and Azcuy et al. (2007).

differently interpreted (Sempere 1995; Suárez-Soruco 2000; Azcuy et al 2007; di Pasquo 2007a; Anderson 2011) in their relationship to each other and in their connection with Gondwana glaciations. Likewise Permian rocks in central and southern Bolivia with *Lueckisporites* have until recently not been subjected to re-evaluation of age or association with global deglaciation.

Deposited in a backarc basin, stratigraphic patterns of the Copacabana Formation are summarised in Figure 2.

Regional Pennsylvanian–Permian sequences were defined by Grader et al. (2008); Permian depositional cycles and abundant ash beds at Apillapampa are illustrated in Figure 4. The Chutani Formation (Oviedo 1962) overlies the Copacabana Formation at Lake Titicaca and includes alternating feldspathic sandstones, calcareous siltstones, dolostones and volcanics. Most authors suggest that this unit was deposited during the Upper Permian and Lower Triassic (Sempere et al. 2002), as confirmed by the
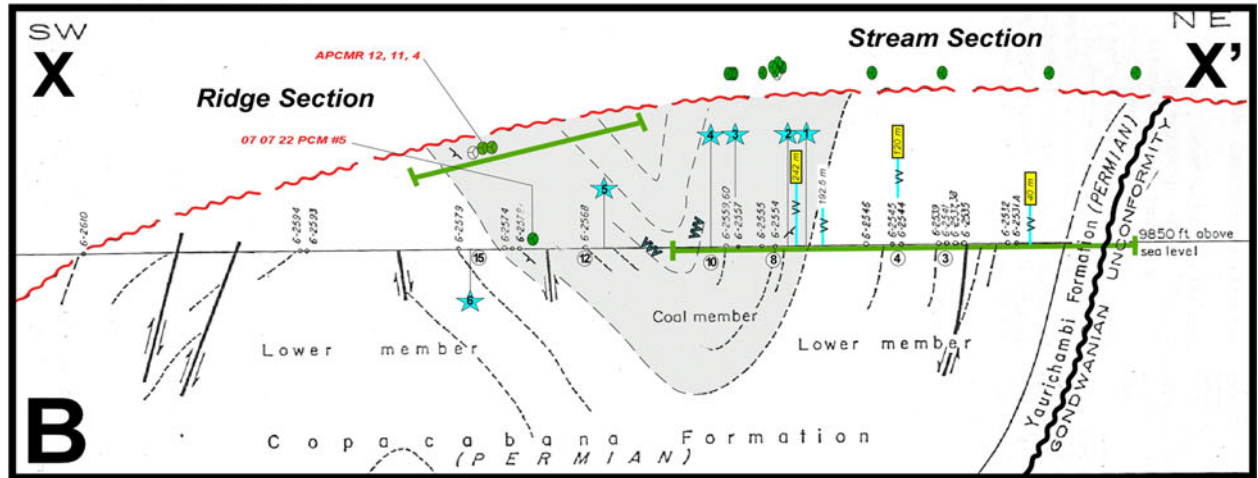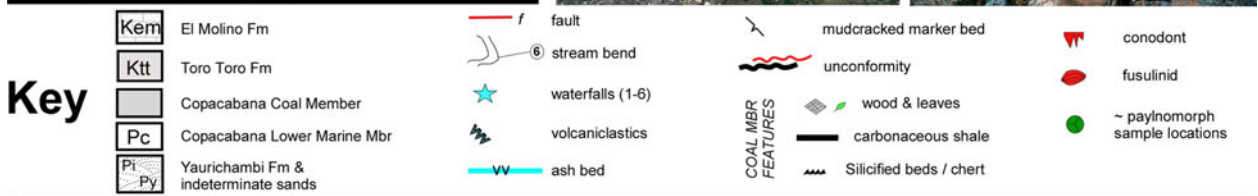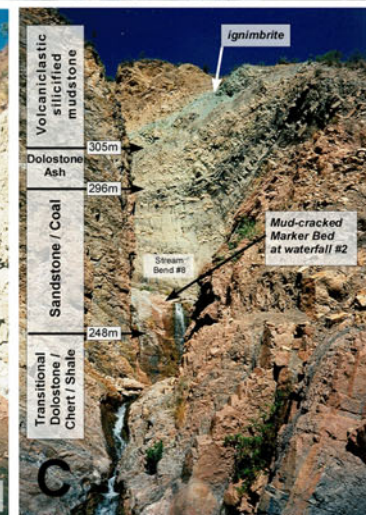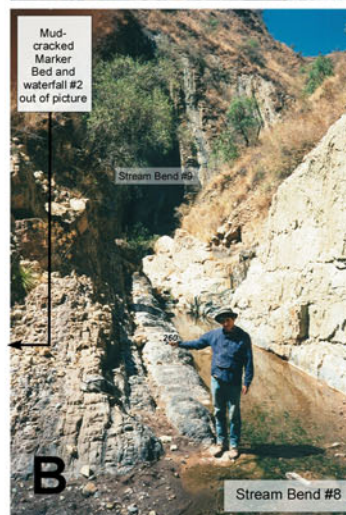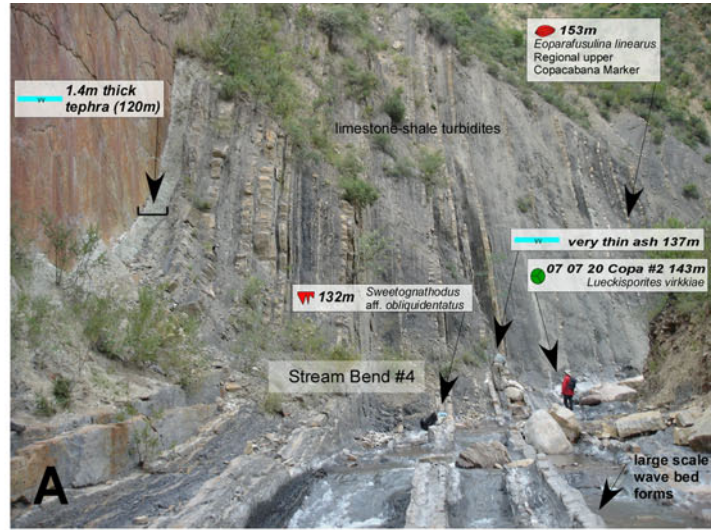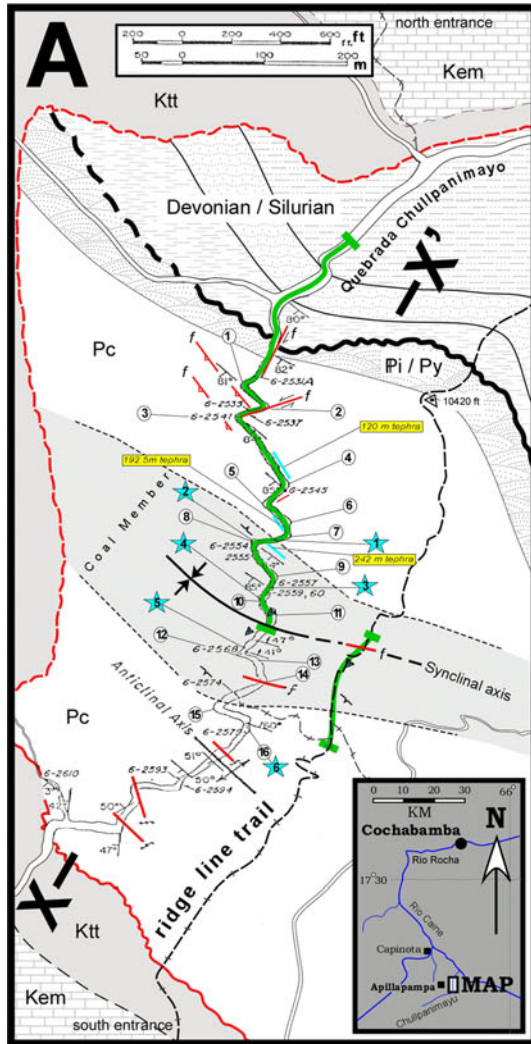
presence of plant fossil remains such as fragments of *Glossopteris*, *Asterotheca* and *Pecopteris* found in the calcareous San Pablo Member (Iannuzzi et al. 2004; Vieira et al. 2004). The upper Titicaca Group (upper Permian Chutani Formation) and part of the correlative Cuevo Group in southeastern Bolivia (upper Cangapi and Vitiacua Formations) were influenced by air-fall tephra and early Pangean rifting (Sempere 1990, 1995; Sempere et al. 1992, 2002). Although the Cangapi Formation is thought to be older at Lake Titicaca and in Peru, transition through marine facies correlative to the Vitiacua Formation is partially time-correlative with the upper (Cisuralian) Copacabana Formation in southern Bolivia, where the Copacabana was not deposited (Azcuy et al. 2007).

A comprehensive summary on fossils, stratigraphy and paleoenvironmental information about the Titicaca Group is presented by Grader et al. (2000, 2008). The regionally common Copacabana to Chutani–Vitiacua unconformity or rarely observed Copacabana Coal Member transition is thought to occur in the upper Cisuralian (Artinskian or Kungurian; Chamot 1965; Cousminer 1965; Figure 4). Azcuy et al. (2007) reviewed and correlated Carboniferous and Permian biostratigraphic units of South America; the Copacabana/Chutani or Cangapi/Vitiacua transition was placed in the Cirsuralian as shown in Figure 2.

### Apillapampa Reference Section, Bolivia

Apillapampa is a classic stratigraphic locality near Cochabamba in central Bolivia known for early palynology work (Cousminer 1965) and high-quality Permian microfossils, invertebrates and plant remains (Chamot 1965) from the Copacabana Formation (Figures 1–4). Downslope turbidites with abundant abraded to whole invertebrates including crinoid calices, bryozoans, corals, brachiopods, bivalves, gastropods, and rare trilobites and cephalopods represent the main environment of deposition of the lower member. Metre-scale turbidite successions often have basal cross-bedded crinoid grainstones overlain by thin, lower energy carbonate lime mudstone/

wackestone and thin to thick laminated to burrowed, to fully bioturbated shale (distal ramp background sedimentation). The sandy tephra unit at 120 m (Figures 3 and 4) overlies a resistant fossiliferous mudstone unit, with abundant *Zoophycos* sp., in turn overlain by thin- to medium-bedded wackestone, packstone, grainstone and laminated to bioturbated dark shale. This suggests that the tephra was deposited as an airfall event in relatively deepwater. *Zoophycos* sp. is also known to occur in abundance in well-dated Artinskian, upper Copacabana units all around Lake Titicaca (Grader et al. 2008). This unit also contains conodonts and small foraminifera, and fusulinids (Figure 4). The Coal Member overlies marine Copacabana strata and is here broken into four new lithosomes, including discovery of 45 m of uppermost volcaniclastics and silicified mudstones that share facies with the Vitiacua Formation. Low plant diversity (primarily lycophytes, *Dizeugotheca branisae*, *Pecopteris* sp. and new sphenopsids) occur in the Coal Member (Chamot 1965; Cousminer 1965; Iannuzzi et al. 2008).

### Materials and methods

Twelve shale and limestone samples interbedded with isotopically dated ash beds were studied in detail by di Pasquo and Grader (2012a) for palynology (Figure 4). The quantitative distribution (percentages) of all the taxa recorded along the studied interval with their botanical affinities and the percentages of the major botanical groups per sample are described in di Pasquo and Grader (2012a). Global stratigraphic ranges of biostratigraphically useful taxa (and others select data) recorded at Apillapampa are shown in Figure 5. The geographic distribution of the palynoassemblages compared with the Apillapampa palynofloras is depicted in Figure 6. These are supported by a data source presented in Chart 1(A)–(D), Supplementary Online Material. Full authority for these species (in alphabetical order into four major groups) together with the remaining species cited in the text is presented in Appendix 1. Important or frequent taxa discussed herein are illustrated in Figures 7–9.

Figure 3.    (Colour online) (A) Geologic map of Apillapampa and Quebrada Chullpanimayo modified after original surveyed map and sample locations of Chamot (1965) and Cousminer (1965). Located stratigraphic sections, key physical and structural features are shown. (B) Cross section modified after Chamot (1965) showing relationship of classic northern stream section to new ridge section, stream bends and water falls (numbered), select ash beds and previous sample points from Chamot (1965). Palynology samples taken from the continuous stream section (di Pasquo and Grader 2012a) are shown in Figure 5 in relationship to the same physical features. Location of laterally correlative samples from the southern syncline limb is shown in relationship to the mudcracked marker bed, which occurs near the base of the Coal Member. (A) Chullpanimayo stream bend #4 showing limestone and shale of highly fossiliferous, vertically bedded Copacabana Formation turbidites in the basal Pc5 Sequence (shaley marine ramp lithozone). View is to the south; up-section is to the right; Charles Henderson and Vladimir Davydov for scale. Photograph taken during medium water level, March 2007. (B) Oscar Arispe standing on coal bed at 260 m (Figure 4) at stream bend #8, above waterfall #2 during low water in October 1997. The sandy mudcracked marker bed occurs below. (C) View of waterfall #2 and stream bend #8. Shows transition to the lithosomes of the Copacabana Coal Member above the marine lower member. A thick ignmimbrite marks the end of coaly and carbonate rocks and the beginning of sandstones and cherty mudstone of Vitiacua Formation association.
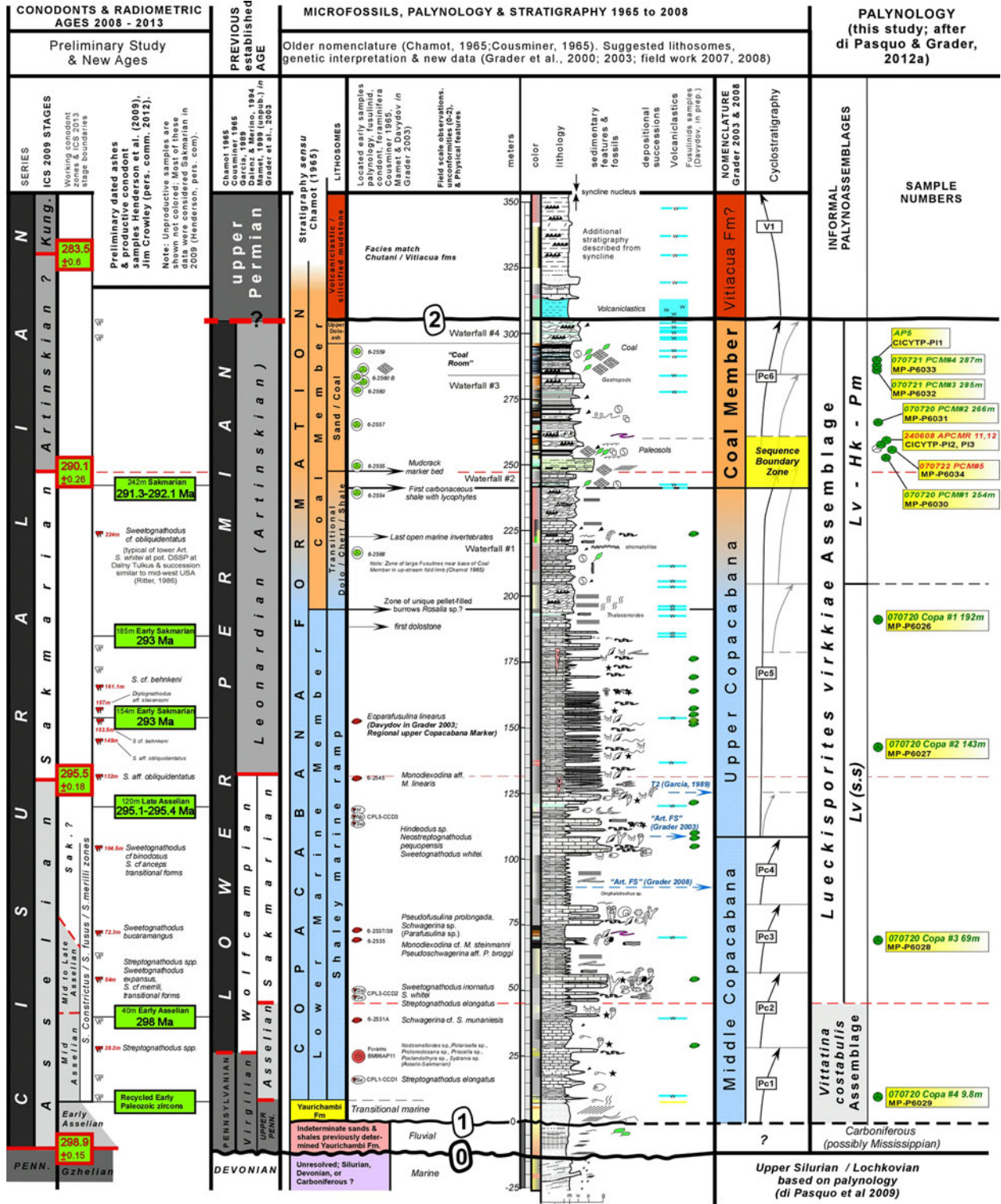
Figure 4. (Colour online) Stratigraphic section of the Copacabana Formation at Apillapampa with basal Yaurichambi Formation and indeterminate Carboniferous clastics above angular unconformity with Devonian rocks (di Pasquo et al. 2009). Preliminary new absolute ages from Henderson et al. (2009). Detailed ages after J. Crowley (personal communication, 2013). Palynology sample locations of di Pasquo and Grader (2012a); Devonian rocks dated by di Pasquo et al. (2009). Lv (s.s.), *sensu stricto*; Lv Hk-Pm, *Hamiapollenites karroensis–Polypodiisporites mutabilis*. Wood, leaves, paleosols are shown below and above the mudcracked marker bed and sequence boundary zone near waterfall #2. Seven third-order shallowing-upward cycles are shown. Coals and carbonaceous shales are better developed between waterfalls #3 and #4. Original nomenclature and ages of Chamot (1965) are compared with regional Copacabana nomenclature of Grader et al. (2003), lithosomes identified here and new conodont and radiometric ages.
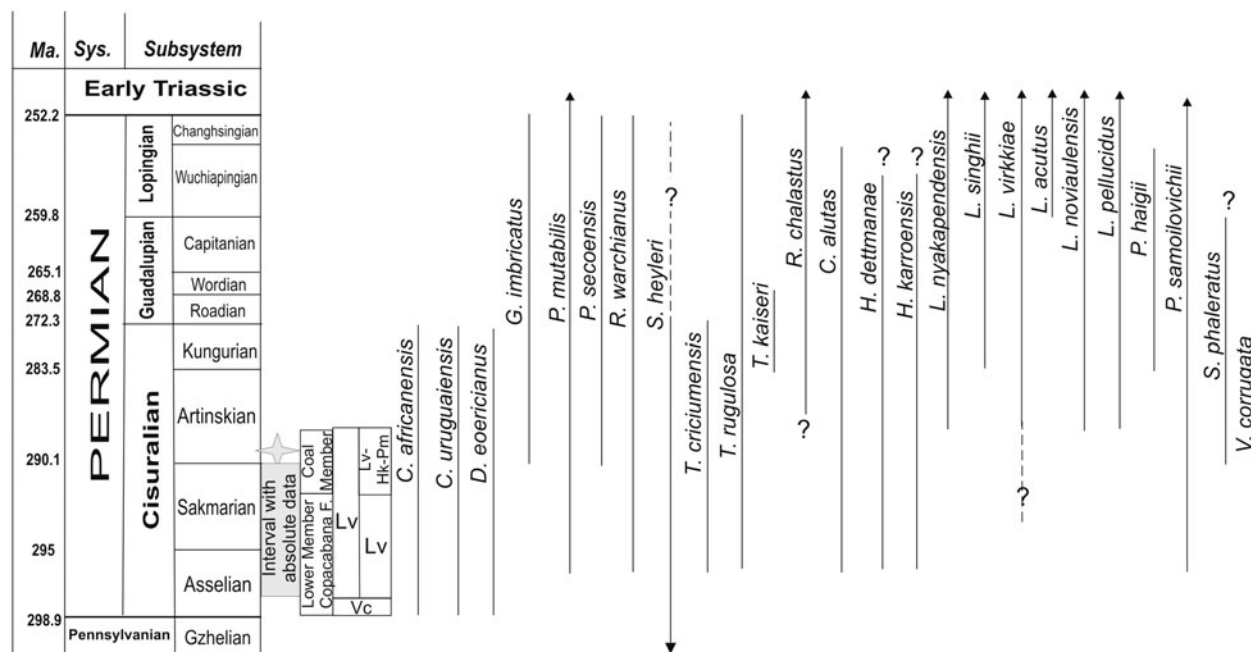
Figure 5.    Global stratigraphic ranges of biostratigraphically useful taxa and others selected recorded in the Vc and Lv assemblages at Apillapampa. References are included in Figure 6 and Chart 1(A)–(D), Supplementary Online Material. The interval of absolute data is after Henderson et al. (2009). Geologic time is according to the International Commission on Stratigraphy 2013.

## Previous paleontological information and age determinations of the Copacabana Formation in Bolivia

Knowledge of Late Carboniferous and Early Permian microfloras of South America has expanded significantly as a result of detailed investigations in (1) Argentina (Tarija, Paganzo, Uspallata-Iglesia, San Rafael, Chaco-paraná, Colorado and Tepuel-Genoa basins), (2) Brazil (Paraná, Amazonas and Parnaíba basins), (3) Paraguay and Uruguay (Paraná/Chacoparaná Basin) and (4) Peru and Bolivia (Peru-Bolivian Basin), including investigations in the Southeast Subandean/Tarija and Madre de Dios basins (Figure 1). However, biostratigraphic correlations (Azcuy et al. 2007; Grader et al. 2008) need to be reconciled with recent radiometric data (Henderson et al. 2009) in Bolivia (Figures 4, 5 and 10, Chart 1(A)–(D), Supplementary Online Material).

Biostratigraphic comparison between different taxonomic groups in the Copacabana Formation in Bolivia has led to age uncertainties as the unit is time-transgressive (Figures 2 and 4; Grader 2003). For the Permian part of the Copacabana Formation, this has included Wolfcampian (Asselian–mid-Sakmarian) conodont *Neogondolella bisselli–Sweetognathodus whitei* and fusulinid *Pseudosch-wagerina texana* Assemblage Zones (Sakagami et al. 1986, 1991; Suárez-Riglos et al. 1987; Sakagami and Mizuno 1994). The Coal Member was previously thought to be part of the Artinskian (Leonardian) stage as determined by fusulinids (*Eoparafusulina gracilus*

Subzone), conodonts (*Neostreptognathous pequopensis–Sweetognathodus behnkeni* Assemblage Zone) and small foraminifera (*Frontinodosaria–Robuloides*), as well as Wolfcampian–Leonardian/Artinskian(?) palynomorphs (Cousminer 1965; Suárez-Riglos et al. 1987; Dalenz-Farjat and Merino-Rodo 1994).

Early work on the 350-m-thick Copacabana Formation at Apillapampa was dated as Wolfcampian/Leonardian (Sakmarian and Artinskian), by paleontological means (Chamot 1965; Cousminer 1965), but newer biostratigraphic information indicates that these beds are Asselian–Sakmarian (Figure 4). Five U–Pb radiometric ages (ID-TIMS of zircon-bearing interbedded tuffs) documented recently by Henderson et al. (2009; James Crowley, personal communication) appear to support new and some previous microfossil ages suggesting that the lower member of the Copacabana Formation at this location is Asselian and Sakmarian. The uppermost dated ash at 242 m is late Sakmarian (291.6 ± 0.9 Ma; James Crowley, personal communication) and occurs near the base of the Coal Member (Figures 3–5). These authors referred also to the conodont *Sweetognathodus* lineage obtained from the lower marine member of this unit, and proposed that it evolved first in Bolivia (and possibly the midwest USA), restricted to a region near the paleo-equator during the Asselian based on the isotopic data (Figure 6).

Cousminer (1965) was the first to study the palynology of the Coal Member, and he recorded a total of 30 species,
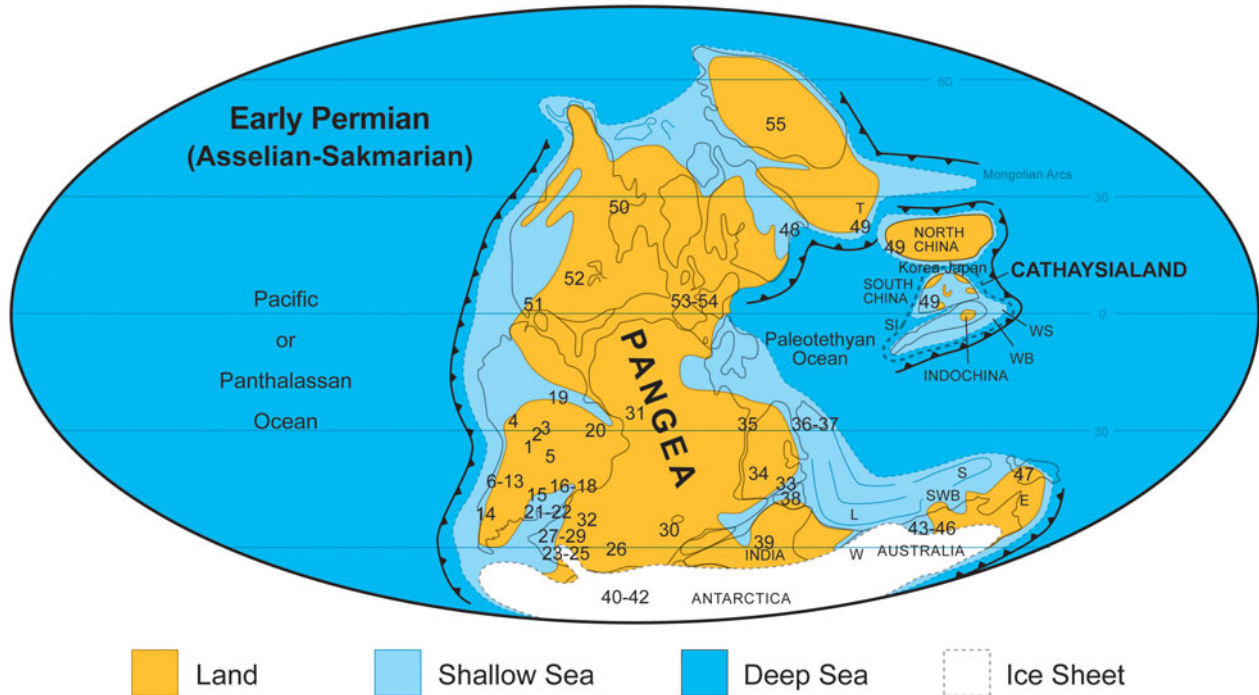
Figure 6. (Colour online) Geographic distribution of compared palynoassemblages with the Apillapampa palynofloras discussed in this contribution, based on the following *selected literature* (see Chart 1(A)–(D), Supplementary Online Material): 1, di Pasquo and Grader (2012a) and Cousminer (1965); 2, Sempere et al. (1992, 2002); 3, Beig et al. (1998) and Ottone et al. (1998); 4, Doubinger and Marocco (1981); 5, Muff et al. (1999), Pérez Loinaze, et al. (2010) and Pérez Loinaze, et al. (2010); 6, Césari and Gutiérrez (2001); 7, Balarino and Gutiérrez (2006); 8, di Pasquo et al. (2010); 9, Vergel (2008); 10, Gutiérrez et al. (2011); 11, Balarino et al. (2012) and Correa et al. (2012); 12, Gutiérrez, Correa, et al. (2010); 13, Pérez Loinaze, et al. (2010); 14, Gutiérrez et al. (2007); 15, Vergel (1993), Césari et al. (1995), Archangelsky and Vergel (1996) and Playford and Dino (2002); 16, Souza and Callegari (2004), Souza and Marques-Toigo (2005), Souza (2006), Mori et al. (2012), Mori and Souza (2012) and other papers; 17, Premoar et al. (2006); 18, Neregato et al. (2008); 19, Playford and Dino (2000a, 2000b); 20, Dino et al. (2002); 21, Beri et al. (2011 and its references); 22, Mautino et al. (1998a, 1998b); 23, Anderson (1977); 24, Stephenson and McLean (1999); 25, Modie and Le Hérissé (2009); 26, Nyambé and Utting (1997); 27, MacRae (1988); 28, Millsteed (1999); 29, Prevec et al. (2010); 30, Semkiwa et al. (1998, 2003); 31, Broutin et al. (1990); 32, Stephenson (2009); 33, Stephenson and Filatoff (2000a, 2000b), Stephenson and Osterloff (2002), Stephenson et al. (2003), Stephenson (2004, 2006, 2008) and Angiolini et al. (2006); 34, Broutin et al. (1995); 35, Eshet (1990a, 1990b); 36, Ghavidel-Syooki (1995) and Angiolini and Stephenson (2008); 37, Ghavidel-Syooki (1997); 38, Balme (1970); 39, Tiwari and Tripathi (1992); 40, Farabee et al. (1990); 41, Lindström (1995); 42, Lindström (1996), Lindström and McLoughlin (2007); 43, Backhouse (1991), Gilby and Foster (1988); 44, Foster (1979); 45, Foster (1982); 46, Foster and Waterhouse (1988); 47, Playford and Rigby (2008); 48, Dunn (2001, isotopically dated along with ammonites, conodonts, fusulinids); 49, Zhu et al. (2005); 50, Barss (1967); 51, Utting et al. (2004); 52, Wilson (1962); 53, Diéguez and Barrón (2005); 54, Clarke (1965); 55, Utting et al. (1997). Paleogeographic reconstruction after Metcalfe personal webpage (http://www-personal.une.edu.au/ ∼ imetcal2/web-data/Research/PalGeog/LEPerm.html). T, Tarim; WS, West Sumatra; SI, Simao; S, Sibumasu; WB, West Burma; L, Lhasa; SWB, South West Borneo. Black font numbers are referred to isotopically dated palynolocations.

most of which were designated with doubt. Moreover, a few of these species (*Granulatisporites trisinus*, *Krauselisporites splendens*, *Neoraistrickia* aff. *Neoraistrickia ramosa*, *Calamospora diversiformis* and *Triquitrites* aff. *Triquitrites tumulosus*) were not found by di Pasquo and Grader (2012a), who presented a detailed analysis of the stratigraphic distribution of 94 palynomorph taxa (Figures 4, 5 and 7–9, Appendix, Chart 1(A), Supplementary Online Material). In the first two samples of the lower member, *Vittatina costabilis* and *Lueckisporites virkkiae* are recognised, respectively. These two key taxa, as well as several other species of *Vittatina*, *Lueckisporites*, *Lunatisporites*, *Pakhapites*, *Hamiapollenites*, *Corisaccites*,

*Mabuitasaccites*, *Striomonosaccites*, *Striatoabieites*, *Striatopodocarpites*, *Weylandites*, and some trilete (e.g. *Cirratrirradites africanensis*) and monolete spores (e.g. *Polypodiisporites mutabilis*) document the Permian (Cisuralian) interval of this unit (Figure 5). They informally defined two main assemblages: the lower assemblage (LA) *Vittatina costabilis* (Vc) corresponds to the first sample, and the upper assemblage (UA) *Lueckisporites virkkiae* (Lv) corresponds to the remaining 11 samples comprising the Lower and Coal members, defined by the appearance of *Lueckisporites virkkiae* and other species of this genus at 69 m above the base of the Copacabana Formation. The stratigraphic distribution of

species allowed us to divide the Lv assemblage into the Lv (*sensu stricto*) and the Lv-Hk-Pm, *Hamiapollenites karrooensis-Polypodiisporites mutabilis* assemblages. The former corresponds to the Lower Member and the latter to the Coal Member of the Copacabana Formation (Figures 4 and 5, Chart 1(A), Supplementary Online Material). If we accept the absolute age data given by Henderson et al. (2009) as correct (and considering that the errors are likely less than ± 1 Ma, James Crowley, personal communication; see Figures 4 and 5), the appearance of *Lueckisporites virkkiae* at Apillapampa does not match its previous oldest known record recently obtained from the upper portion of the Rio Bonito Formation in the middle Artinskian (dated with zircons as 281.4 ± 3.4 Ma), in Brazil (Figures 5 and 10; Mori et al. 2012). Until the radiometric ages of Henderson et al. (2009) at Apillapampa are confirmed, two possible correlations of the Vc and Lv assemblages are presented herein. One is based on the radiometric (Asselian–Sakmarian–early Artinskian) data (Correlation 1 in Figures 10–12), and the other, on its biostratigraphic (ca. Artinskian–Kungurian) correlation (Correlation 2 in Figures 10–12), as previously proposed by Azcuy et al. (2007, based on Cousminer 1965) and di Pasquo et al. (2009). Hence, a comparison of these assemblages with other similar palynofloras from South America and elsewhere is shown in Figure 5 based on the presence of key taxa. Correlations are summarised in Figures 10–12.

### Correlation of the floral record at Apillapampa

Taeniate–striate pollen grains became increasingly prominent in the Early Permian globally. They represent a predominantly gymnospermous (cordaites, conifers and pteridosperms) vegetation, but with significant contributions from lower vascular plants, notably pteridophytes, sphenophytes and lycophytes. These groups of plants are represented by the palynological record at Apillapampa (di Pasquo and Grader 2012a). Comparing with other Permian assemblages, four species remain endemic in Bolivia (*Crustaesporites hessi*, *Dictyotriletes cousmineri*, *Lycospora variabila* and *Punctatisporites minutiarcus*); furthermore, there are new records of 52 species for Bolivia. The presence of *Marsupipollenites*, *Pakhapites*, *Striatoabieites* and *Striatopodocarpites*, among others, in the Apillapampa section, confirms the development of the *Glossopteris* Flora in Bolivia, although its plant remains have not been found in the lower member of the Copacabana Formation at this place (Figures 4, 5 and 10, Chart 1(A), Supplementary Online Material). The abundance of spores in the Coal Member of this section is in agreement with the occurrence of plant assemblages related to lower vascular plants (lycophytes, pteridophytes and sphenophytes; Iannuzzi et al. 2008). *Glossopteris* is absent in these plant assemblages. They represent the eponymous flora and this is supported on the basis of other species such as *Lycopodiopsis pedroanus* and *Dizeugoteca branisae* (Chamot 1965; Figure 4). *Glossopteris* occurs with species of *Pecopteris* and *Asterotheca* in the upper Chutani Formation at Lake Titicaca, Bolivia, which is Kungurian or younger (Iannuzzi et al. 2004, 2008; Vieira et al. 2004). The *Phyllotheca–Gangamopteris* (mid-Sakmarian) and *Glossopteris–Brasilodendron* (late Sakmarian) floral zones from Brazil (Iannuzzi and Souza 2005) suggest correlation with the upper Apillapampa palynoassemblage (Figure 10). These Brazilian floral zones occur above an important gap with no plant remains over the Late Pennsylvanian Pre-*Glossopteris* Flora (Iannuzzi et al. 2010).

### Correlation with other Permian assemblages from Bolivia, Peru and Paraguay

Azcuy et al. (2007) documented the previous information on Permian assemblages from Bolivia and Peru, which is still limited. Rare late Cisuralian to Guadalupian/Lopingian fossils of the Vitiacua Formation (Figure 2) in southern Bolivia include basal stomatolites and fish teeth, a microflora in lower calcareous-shaly rocks, pectin bivalves and the fish *Coelacanthus* cf. *granulatus* (Sempere et al. 1992). Although sparse in fossils, the Vitiacua Formation is thought to be marine and regionally correlative to the following units: The Chutani Formation (Bolivia), the Ene and Ampay Formations (Perú), the Irati Formation (Brazil) and the Whitehill Formation (Ecca Group) in the Karroo Basin in South Africa (Sempere et al. 1992; Grader 2003; Figures 1, 6 and 10–12). Volcaniclastics and cherty shales above the unconformity with the Coal Member at Apillapampa are thought to be Vitiacua facies (Figure 4).

Palynologically, important species also recognised by Sempere et al. (1992) in the Vitiacua Formation are *Lueckisporites virkkiae*, *Lunatisporites noviaulensis*, *Vitreisporites pallidus*, *Corisaccites alutas*, *Weylandites* sp. cf. *W. magmus*, as well as others not recorded herein, such as *Cycadopites* sp., *Striatoabieites* sp., *Alisporites parvus*, *Lunatisporites taeniaeformis*, *Protohaploxypinus enigmaticus* and *Protohaploxypinus varius*. It is likely that this assemblage could be younger than the UA (Lv), although many of these taxa are long ranging (Figures 5 and 10, Chart 1(A), Supplementary Online Material). New palynological information obtained from shales and limestones of the lower Vitiacua Formation at Yesera and Canaletas (Figure 1(C)) was recently presented by di Pasquo and Grader (2012b) indicating a possible correlation with the Lv assemblage based on their common miospore species (e.g. *Lueckisporites virkkiae*, *Polypodiisporites mutabilis* and *Reticuloidosporites*
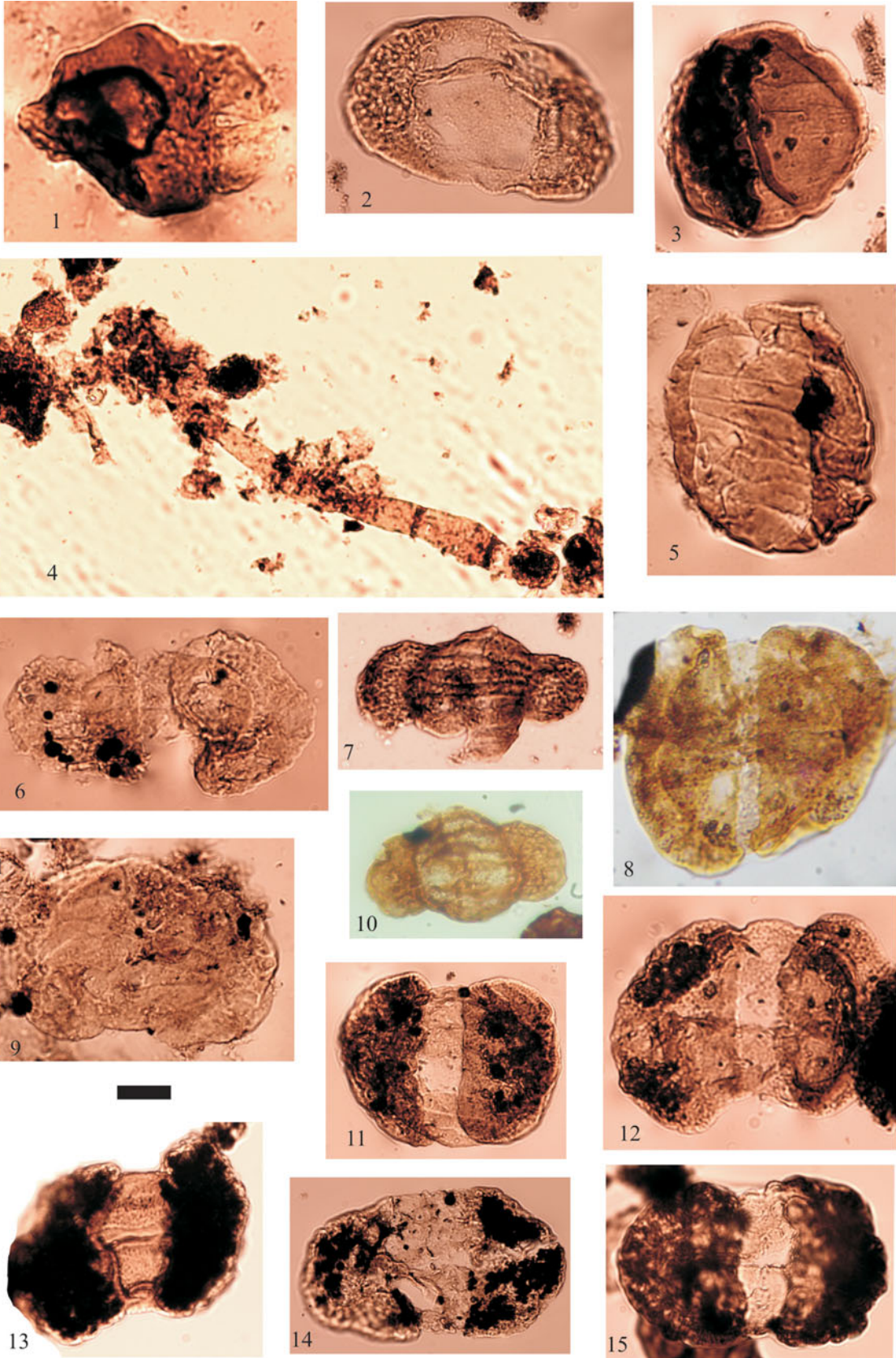
*warchianus*). Radiometric data from interbedded ash beds at both localities are under study.

In the Villa Molino (Mina Matilde, Figure 1(C)) section, Beig et al. (1998) identified palynomorphs of continental origin, including *Calamospora plicata*, *Punctatisporites gretensis*, *Kraeuselisporites splendens*, *Laevigatosporites vulgaris*, *Lueckisporites* sp., *Monosaccites* sp., *Crustaesporites hessii*, *Vittatina costabilis*, *Vittitina subsaccata*, *Striates* sp., *Bisaccites* sp. and verrucate palynomorphs. These pollen and spores were interpreted as Sakmarian (in agreement with Grader et al. 2003), based on palynology from the Copacabana Formation at Angosto del Beu (Ottone et al. 1998). However, *Lueckisporites*, which occurs at Villa Molino, is absent in the Angosto del Beu, where the significant taxa are *Hamiapollenites insolitus* and *Pakhapites fusus* suggesting an older Asselian age for the latter (Figures 6 and 10, Chart 1(A), Supplementary Online Material). Bisaccate pollen grains and 'Wolfcampian' dates were also reported at Morochata with complex facies changes in what appears to be part of the Coal Member (García 1989; Grader 2003).

Sempere et al. (2002) reported two palynologic assemblages from the Permian Vitiacua Formation at Iglesiani in the Eastern Cordillera of Bolivia (Figures 1 (C) and 6). The first one contains *Hamiapollenites karrooensis*, *Tornopollenites toreutos*, *Lueckisporites virkkiae*, *Corisaccites alutas*, *Protohaploxypinus enigmaticus*, *Taeniaesporites* sp. (sp. 1 of Jardiné), *Weylandites lucifer* (as *Paravittatina cincinnata*), *Punctatisporites gretensis* and numerous acritarchs including a species of *Micrhystridium*. The second has *Corisaccites alutas*, *Lueckisporites virkkiae*, *Weylandites* sp. and numerous specimens of *Botryococcus*, suggesting a littoral marine paleoenvironment attributed to the Mid to Late Permian. Whereas *Tornopollenites toreutos* is a significant species originally described from the Early Permian of USA (Morgan 1972), it was recently identified at the following times and locations (Figures 1(A) and 6): (1) late Guadalupian of the Amazon Basin (Playford and Dino 2000b) and Parnaíba Basin (Dino et al. 2002) in Brazil; (2) late Cisuralian *Lueckisporites virkkiae* Zone to Guadalupian in Paraguay (Muff et al. 1999; Pérez Loinaze, Césari, et al. 2010); (3) the late Cisuralian–early Guadalupian La Veteada Formation of the Paganzo Basin

(Gutiérrez et al. 2011) and (4) the Late Permian of the Colorado Basin (offshore) Argentina (Balarino 2008). Dino et al. (2002) correlated the assemblage found in Pedra do Fogo Formation in the Parnaiba Basin with the *Tornopollenites toreutos* Biozone of the Amazonas Basin (Figures 10 and 12). These basins share important taxa with the UA (Lv) at Apillapampa, such as *Lueckisporites virkkiae*, *Corisaccites alutas*, *Hamiapollenites karrooensis*, *Hamiapollenites dettmannae*, and other species of *Vittatina*, *Striatoabieites* and *Striatopodocarpites* (Chart 1 (A),(B), Supplementary Online Material). It is also interesting that *Hamiapollenites karrooensis* is restricted to the upper subzone of the Vc Zone in the Paraná Basin (Souza and Marques-Toigo 2005), while it appears later in the Amazonas and Parnaiba basins (Figure 10). However, it is recorded earlier in the Coal Member of the Copacabana Formation (Figures 4 and 5). The lack of isotope information from the Vitiacua Formation at Iglesiani and Amazon, Parnaíba and Paraguay assemblages prevents a more accurate correlation among them and with the Apillapampa assemblage. However, the absence of *Tornopollenites toreutos* at Apillapampa could support that there is no correlation with the Iglesiani assemblages (Figures 10 and 12).

Doubinger and Marocco (1981) described an assemblage from the upper part of the Copacabana Formation (Ampay Formation/Coal Member correlative) at the Nevado Ampay (Perú, Figures 1 and 6) composed of 40 species dominated by trilete spores, subordinate monolete spores and pollen grains attributed to the Artinskian. Among the important taxa also recognised in the Apillampampa assemblages are (Chart 1(A), Supplementary Online Material) *Retusotriletes nigritellus*, *Brevitriletes cornutus*, *Horriditriletes ramosus*, *Lycospora variabila*, *Reticuloidosporites warchianus*, *Striatosporites heyleri*, *Hamiapollenites karrooensis*, *Hamiapollenites* cf. *gabonensis* (quite similar to *Hamiapollenites dettmannae*), *Protohaploxypinus enigmaticus* and *Striatoabieites* cf. *multistriatus*. Doubinger and Marocco (1981) proposed a correlation with the assemblage studied by Cousminer (1965) whereas Azcuy et al. (2007) suggested a possibly more accurate correlation with the *Hamiapollenites karrooensis* Subzone of the Vc Zone (Souza and Marques-Toigo 2005) in the Paraná Basin. However, the

Figure 7.    (Colour online) Selected species present in the LA Vc (1–5) and UA Lv (6–15) at Apillapampa. 1 and 5, scale bar = 10 μm; 2, 3 and 6–13, scale bar = 15 μm; 4 and 15, scale bar = 30 μm. 1. *Klausipollenites* sp. cf. *Klausipollenites vestitus* Jansonius, MP-P6029-c, T55/1; 2, *Chordasporites endroedi* MacRae, MP-P6026-a, O39/4; 3, *Vittatina costabilis* Wilson, MP-P6029-c, D44/0; 4. *Reduviasporonites chalastus* (Foster) Elsik, MP-P-6031-b, S42/0; 5. *Pakhapites ovatus (* Bose and Kar) García, MP-P6028-a, F50/3; 6. *Lueckisporites nyakapendensis* Hart, MP-P6028-a, R48/3; 7. *Hamiapollenites dettmanae* Segroves, CICYTTP-Pl 1(1 + 25), M41/4; 7. *Corisaccites alutas* Venkatachala and Kar, MP-P6032-b. K39/3; 9. *Lunatisporites acutus* Leschik, MP-P6028-a, J55/4; 10, *Hamiapollenites karrooensis* (Hart) Hart, CICYTTP-Pl 1(2 + 10), Q41; 11. *Lunatisporites noviaulensis* (Leschik) Foster, MP-P6026-c, U51; 12 and 13. *Lueckisporites virkkiae* (Potonié and Klaus) Klaus, 12-MP-P-6027-b-L51/4, 13-MP-P6026-a, O43/0-1; 14. *Lunatisporites pellucidus* (Goubin) Helby emend. de Jersey, MP-P-6027-b, D57; 15. *Lueckisporites singhii* Balme, MP-P6026-c, Q42/1.
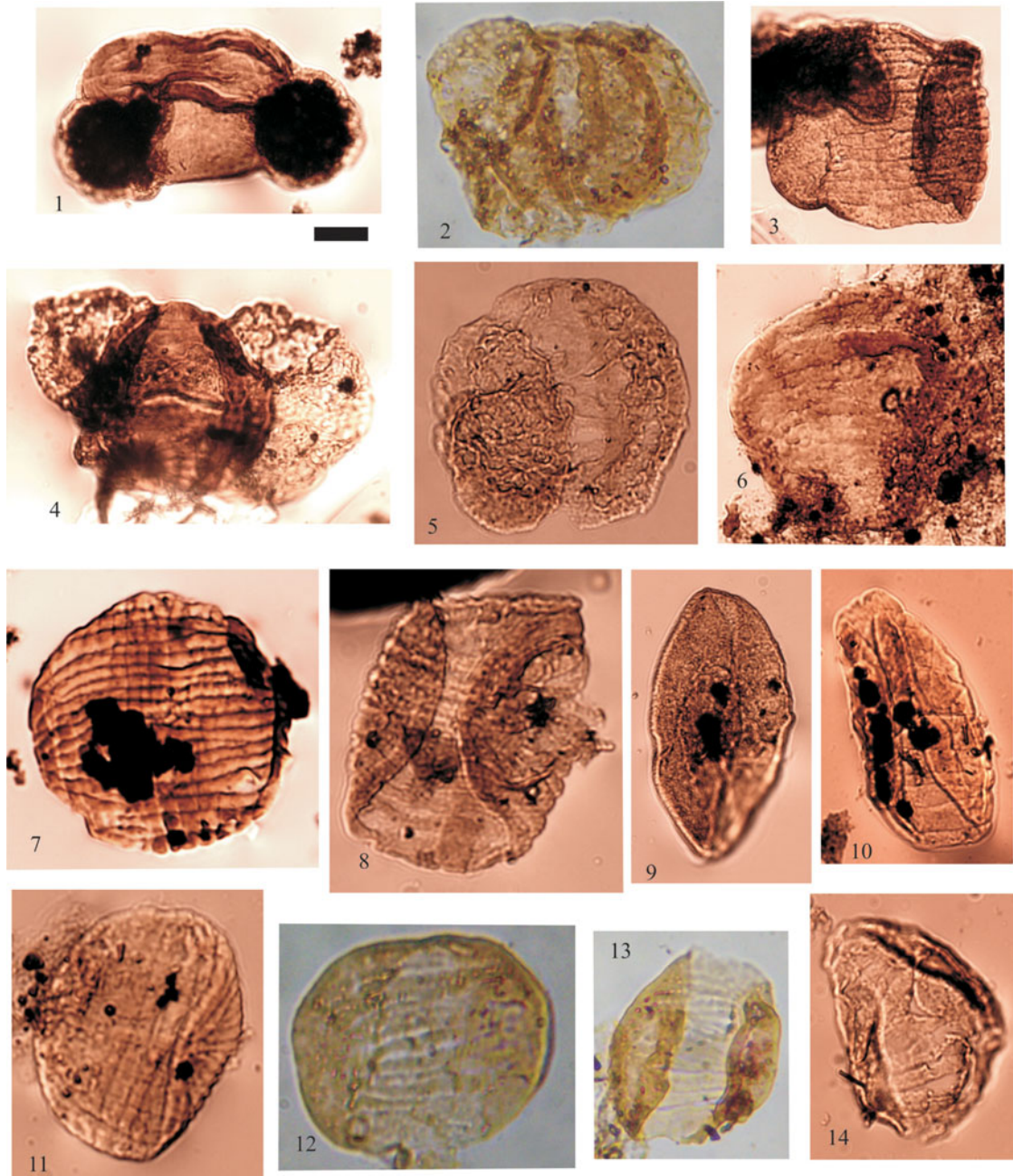
Figure 8.   (Colour online) Selected species present in the UA Lv at Apillapampa. 1 and 2, scale bar = 20 μm; 3, 4, 6, 9, 10, 13 and 14, scale bar = 15 μm; 5, 7, 8, 11 and 12, scale bar = 10 μm. 1. *Protohaploxypinus haigii* Foster, MP-P-6027-c, S44/4; 2. *Protohaploxypinus samoilovichii* (Jansonius) Hart, MP-P6032-b, Q38/3; 3. *Striatoabieites multistriatus* (Balme and Hennelly) Hart, MP-P6026-a, L44/1; 4. *Striatopodocarpites phaleratus (* Balme and Hennelly) Hart, MP-P6026-c, V58; 5. *Protohaploxypinus rugatus* Segroves, MP-P6026-c, M60/1; 6. *Vittatina corrugata* Marques-Toigo, MP-P6028-c, P47/3; 7. *Weylandites lucifer* (Bharadwaj and Srivastava) Foster, MP-P6027-c, S42/1; 8. *Vittatina subsaccata* Samoilovich, MP-P6026-c, J59/4; 9. *Cycadopites cymbatus* (Bame and Hennelly) Segroves, MP-P6026-c, O41/4; 10. *Pakhapites fusus* (Bose and Kar) Menéndez, MP-P6028-c, W44/1; 11. *Weylandites magmus* Bose and Kar, MP-P6028-d, V44/2; 12. *Vittatina saccata* (Hart) Jansonius, MP-P6032-b, K39/3; 13. *Pakhapites fasciolatus* (Balme and Hennelly) Hart, MP-P6032-b, M33; 14. *Marsupipollenites striatus* (Balme and Hennelly) Hart, MP-P6028-a, F60/4.

low frequency of *Lueckisporites* sp. suggests that it is close to the basal Lv Zone (Figure 10). Considering that no radiometric age is available for the Nevado Ampay assemblage, and that the age of the Apillapampa UA Lv is late Asselian–Sakmarian, an older Sakmarian age for the Peruvian assemblage is likely.
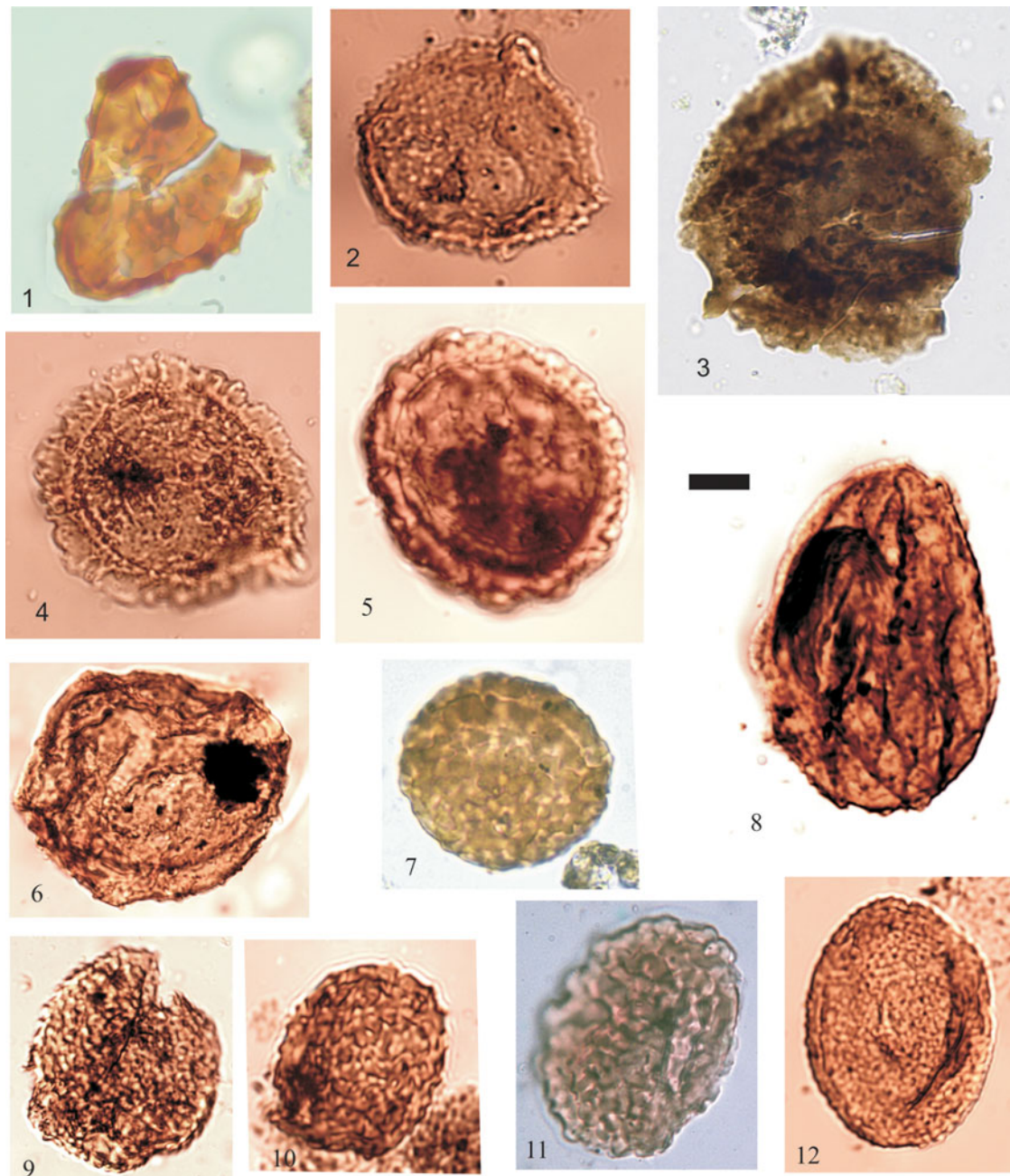
Figure 9.    (Colour online) Selected species present in the UA Lv at Apillapampa. Scale bar 10 μm. 1. *Triquitrites* sp. cf. *Triquitrites kaiseri* Playford and Rigby, CICYTTP-Pl 2(+25), U50/3; 2. *Cristatisporites morungavensis* (Días Fabricio) Picarelli and Días Fabricio, MP-P-6032-b, Y48/2; 3. *Gondisporites* sp. cf. *Gondisporites imbricatus* Segroves, CICYTTP-Pl 2(+25), L45/1; 4. *Cirratriradites africanensis* Hart, MP-P-6032-b, R34/2; 5, *Thymospora criciumensis* Quadros, Marques-Toigo and Cazzulo-Klepzig, MP-P-6032-b, E44/1; 6, *Lycospora variabila* Cousminer, MP-P-6030-b, L49/4; 7. *Thymospora rugulosa* Mautino, Vergel and Anzótegui, CICYTTP-Pl 5(Mer1), Y41/4; 8. *Striatosporites heyleri* (Doubinger) emend. Playford and Dino, MP-P6034-b, S44/2; 9. *Reticuloidosporites warchianus* Balme, CICYTTP-Pl 1(1), F49/1; 10. *Polypodiisporites mutabilis* Balme, MP-P-6030-b, K46/2; 11. *Polypodiites secoensis* Mautino, Vergel and Anzótegui, MP-P6033-a, P41/3; 12. *Leschikisporis chacoparanaense* Vergel, MP-P6032-b, G33/3.

## Correlation with other Permian South American palynofloras and palynozones

Mid-Pennsylvanian palynofloras in South America have generally yielded rare specimens of several bisaccate taeniate pollen grains, mainly species of *Protohaploxypinus*–*Striatoabieites*–*Striatopodocarpites*, while the Cisuralian sequences are composed of small to large amounts of diverse bisaccate and non-saccate taeniate taxa such as the

Figure 10. Litho- and palynostratigraphic correlation of the Permian of the Apillapampa assemblages (di Pasquo and Grader 2012a), with others in South America discussed in this contribution. For references see Figure 6 and Chart 1A-D (supplementary online material). Two different biostratigraphic correlations are proposed for the Apillapampa assemblages: one is based on isotopic data after Henderson et al. (2009, see interval of absolute age under the star) corresponding to the Correlation 1, and the other, the Correlation 2 is based on relative ages given by diagnostic taxa (biostratigraphic dating). Chronology after Cohen et al. (2013). See text for other radiometrical data from South America (Argentina, Brazil, Uruguay) and outside SAM.

**Abbreviations**: (this study) Vc, *Vittatina costabilis*; Lv, *Lueckisporites virkkiae*; (Chacoparaná) PL, *Potonieisporites - Lundbladispora* (Vergel 1993), (Tarija) TB, *Marsupipollenites triradiatus-Lundbladispora braziliensis* (di Pasquo 2003), (Paraná) Pre-Gl, Pre-*Glosssopteris*, Ph-Ga, *Phylloteca-Gamgamopteris* Flora, Gl-B *Glossopteris-Brasilodendron* Flora, Po-Gl, *Polysolenoxylon-Glossopteris*.

Figure 11. Litho- and palynostratigraphic correlation of the Permian of the Apillapampa assemblages (di Pasquo and Grader 2012a), with others elsewhere. Main palynological events of some key species discussed in this contribution are included. For references see Figure 6 and Chart 1A-D (supplementary online material). Two different biostratigraphic correlations are proposed for the Apillapampa assemblages: o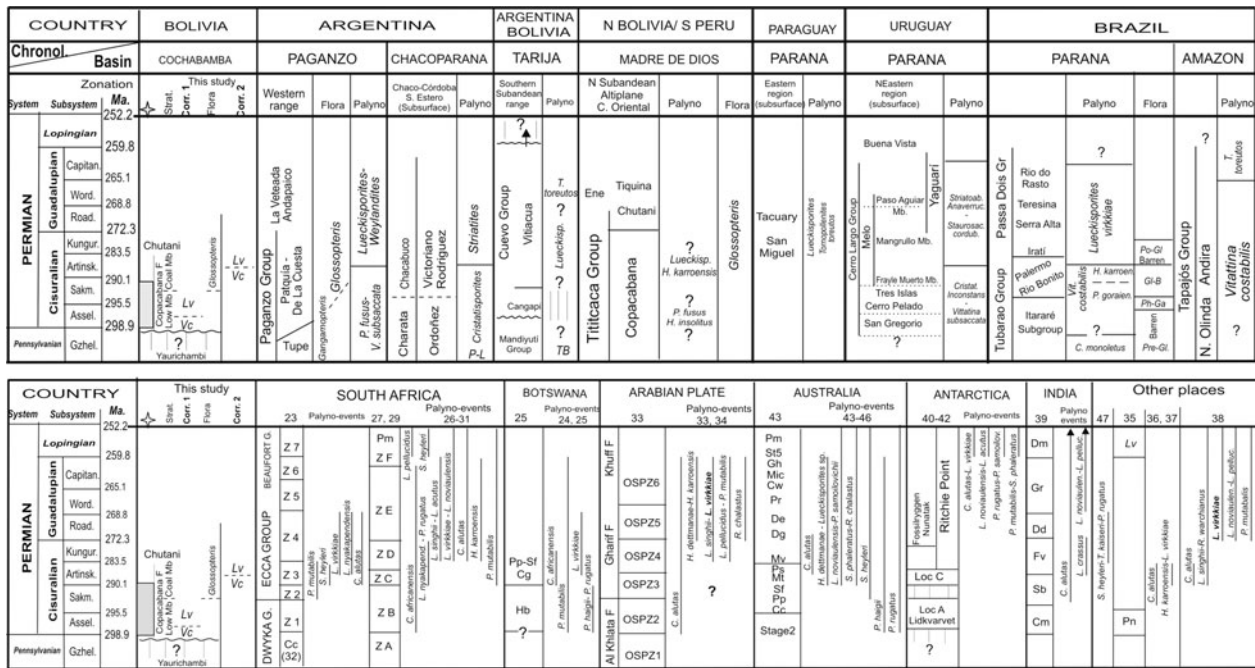ne is based on isotopic data after Henderson et al. (2009, see interval of absolute age under the star) corresponding to the Correlation 1, and the other, the Correlation 2 is based on relative ages given by diagnostic taxa (biostratigraphic dating). Chronology after Cohen et al. (2013). See text for other radiometrical data.

**Abbreviations**: (this study) Vc, *Vittatina costabilis*; Lv, *Lueckisporites virkkiae*; (23) Cc, *Converrucosisporites confluens*; (27-29) Pm, *Protohaploxypinus microcorpus*; (25) Hb, *Hamiapollenites bullaeformis*; Cg, *Cyclogranisporites gondwanensis*; Pp-Sf, *Platysaccus papillonis-Striatopodocarpites fusus*; (43) Cc, *Converrucosisporites confluens*; Pp, *Pseudoreticulatispora pseudoreticulata*; Sf, *Striatopodocarpites fusus*; Mt, *Microbaculispora trisina*; Ps, *Praecolpatites sinuosus*; Mv, *Microbaculispora villosa*; Dg, *Dulhuntyspora granulata*; De, *Didecitriletes ericianus*; Pr, *Protohaploxypinus rugatus*; Pm, *Protohaploxypinus microcorpus*; Cw, *Camptotriletes warchianus*; Mic, *Microbaculispora* sp. A; Gh, *Guttulapollenites hannonicus*; St5, Stage 5; Pm, *Protohaploxypinus microcorpus*; (39) Cm, *Crucisaccites monoletus*; Sb, *Scheuringipollenites barakarensis*; Fv, *Protohaploxypinus "Faunipollenites" varius*; Dd, *Densipollenites densus*; Gr, *Gondisporites raninganjensis*; Dm, *Densipollenites magnicorpus*; (35) Pn, *Potonieisporites novicus*; Lv, *Lueckisporites virkkiae*.

above cited and *Vittatina*, *Lueckisporites*, *Hamiapollenites*, *Lunatisporites*, *Pakhapites* and *Illinites*, among others. In this context, the appearance of species of *Vittatina costabilis*, *Pakhapites fusus* and *Lueckisporites* particularly *Lueckisporites virkkiae* was considered as the key species used to define biostratigraphic schemes of mid-Artinskian to Capitanian age (Figures 5, 6 and 10–12, Chart 1, Supplementary Online Material). Recently, some of these palynozones were calibrated with radiometric dates in Argentina (Césari et al. 2011), Brazil (Iannuzzi et al. 2010; Mori et al. 2012) and Uruguay (Beri et al. 2011).

### Palynozones radiometrically dated from western Argentina

The base of the *Pakhapites fusus – Vittatina subsaccata* (FS) Zone Césari and Gutiérrez (2001) in western Argentina (Figures 1(A) and 6) is defined by the appearance of *Pakhapites fusus* and the increase in striate pollen grains, especially of *Vittatina*, the index species *Converrucosisporites confluens* and the first appearance of *W. lucifer*. This zone is equivalent to the base of the *Gangamopteris* Phytozone (see Césari et al. 2011). A basaltic horizon interbedded in the lower part of the La

| COUNTRY | BOLIVIA | ARGENTINA | | | BOLIVIA-PERU | URUGUAY | BRAZIL | | AMAZON | SOUTH AFRICA | | | BOTSWANA | ARABIAN PLATE | AUSTRALIA | ANTARCTICA | INDIA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chronol. / Basin | COCHABAMBA | PAG. | CHACOP | TARIJA | MADRE DE DIOS | PARANA | PARANA | | AMAZON | KAROO | | | | | | | |
| Zonation — System / Subsystem / Ma. | This study — Strat. Corr.1 Flora Corr.2 | Palynozones | | | | | Palynozones | Flora | | Palynozones | | | | | | | |
| PERMIAN — Lopingian | 252.2 | | | | | | ? | T. toreutos | | Zone 7 / Pm | | | | | Pm St5 Gh Mic Cw Pr De Dg | Fossilryggen Nunatak / Ritchie Point | Dm |
| Lopingian | 259.8 | | | | | | | | | Zone 6 / Zone F | | | | | | | Gr |
| Guadalupian — Capitan. | 265.1 | | Lueckisporites-Weylandites | Striatites | T. toreutos | | Striatoab. Anaverruc. - Staurosac. cordub. | Lueckisporites virkkiae | | Zone 5 / Zone E | OSPZ6 | | | | Mv Ps Mt Sf Pp Cc | | Dd |
| Word. | 268.8 | | | | | | | | | Zone 4 / Zone E | OSPZ5 | | | | | Loc C | Fv |
| Road. | 272.3 | Chutani / Glossopteris (Lv Vc) | | | Lueckisp. | | | | | Zone 4 / Zone D | OSPZ4 | Pp-Sf Cg | | | Stage2 | Loc A Lidkvarvet | Sb |
| Cisuralian — Kungur. | 283.5 | | | | Lueckisp. H. karroensis | | Vit. costabilis — H. karroen. / P. goraien. | Po-Gl Barren | | Zone 3 / Zone C | OSPZ4 | | | | | | |
| Artinsk. | 290.1 | Copacabana F. Low Mb Coal Mb (Lv Vc) | P. fusus- V. subsaccata | Cristatisporites | ? | | Cristat. Inconstans - Vittatina subsaccata | Gl-B / Ph-Ga / Barren | Vittatina costabilis | | Zone 2 / Zone B | OSPZ3 | Hb | | | | Cm |
| Sakm. | 295.5 | | | | P. fusus H. insolitus | | | | | Zone 1 / Zone B | OSPZ2 | | | | ? | | |
| Assel. | 298.9 | Yaurichambi | P-L | | TB | | ? / C. monoletus | Pre-Gl | ? | Cc(32) / Zone A | OSPZ1 | | | | | | |
| Pennsylvanian — Gzhel. | | | | | | | | | | | | | | | | | |

Figure 12.    Summary of the two global palynostratigraphic correlation of the Apillapampa assemblages (Vc and Lv) with other Permian palynozones or palynofloras in South America and elsewhere discussed in this contribution.

Colina Formation provided a geochronological datum ranging from 308 ± 6 to 293 ± 6 Ma (K/Ar method) with a maximum age of 298–301 Ma for the first glossopterid remains from this unit (see Césari 2007). Characteristic taxa are *Hamiapollenites fusiformis*, *Hamiapollenites insolitus*, *Vittatina subsaccata*, *Barakarites rotatus*, *Striatoabieites multistriatus*, *Marsupipollenites striatus*, *Latusipollenites quadrisaccatus*, *Granulatisporites* cf. *trisinus*, *Kraeuselisporites sanluisensis*, *Lophotriletes rarus*, *Lophotriletes cursus* and *Brevitriletes cornutus* (see shared species in Chart 1, Supplementary Online Material).

The upper boundary of the FS Zone is not clearly defined, but the appearance of *Lueckisporites* spp. marks the base of the overlying *Lueckisporites–Weylandites* (LW) Zone (Figure 10). This zone is characterised by the dominance of striate pollen (*Vittatina* and *Marsupipollenites*) and the appearance of *Alisporites splendens*, *Lueckisporites brasiliensis*, *Lueckisporites latisaccus*, *Lueckisporites stenotaeniatus*, *Lueckisporites virkkiae*, *Protohaploxypinus rugatus*, *Scheuringipollenites medius*, *Staurosaccites cordubensis*, *Striatoabieites anaverrucosus*, and *Striatopodocarpites solitus* (Chart 1, Supplementary Online Material). Recent studies on Argentina Permian assemblages from Río Francia (Gutiérrez, Correa et al. 2010), La Veteada (Gutiérrez et al. 2011) and Andapaico Formations (Correa et al. 2012; Balarino et al. 2012) have incorporated new elements to LW Biozone, some of which are in common with the Apillapampa assemblages (e.g. *Caheniasaccites flavatus*, *Latusipollenites quadrisaccatus*, *Potonieisporites lelei*, *Scheuringipollenites circularis*, *Scheuringipollenites maximus*, *Illinites unicu* and *Pakhapites ovatus*, see Chart 1, Supplementary Online Material).

The radiometric dating of the section bearing the LW Zone in the Yacimiento Los Reyunos Formation varies between $^{40}$Ar/$^{39}$Ar age of 282 ± 13 and 266 ± 5 Ma

from volcaniclastic samples of the Toba Vieja Gorda member. This spans the Artinskian to Capitanian (e.g. Césari 2007). A palynological correlation between the Argentinian LW Biozone, the *Lueckisporites virkkiae* Interval Biozone from Brazil and Assemblage Zone 3 from South Africa is possible (Figures 10–12, Chart 1, Supplementary Online Material) and supported by other radiometric data (e.g. Stollhofen et al. 2000; Santos et al. 2006). Gulbranson et al. (2010) have dated radiometrically the SI-3 (Patquía Formation and equivalent units) that has been traditionally assigned a Permian age based on the occurrence of *Gangamopteris* and *Glossopteris* megaflora. An age of 296.09 ± 0.085 Ma was obtained just above the levels of these *Glossopteris* occurrences. The middle and upper strata of SI-3 have been interpreted as recording the long-term Permian aridification trend, recognised in Pangaean deposits worldwide (Parrish 1993), also confirming an Early Permian age for the appearance of glossopterid elements in western Argentina (Figure 10).

### Palynozones without absolute datings from eastern Argentina

The *Cristatisporites* (CZ) and *Striatites* (SZ) Zones of the Chaco-Paraná Basin (e.g. Vergel 1993; Césari et al. 1995; Archangelsky and Vergel 1996) from Argentina are attributed (by palynological comparison and correlation) to the early Cisuralian and late Cisuralian to Guadalupian, respectively (Figures 1(A), 6, 10 and 12). The CZ shares with the Apillapampa palynofloras many species of the genera *Vittatina*, *Weylandites*, *Pakhapites*, *Mabuitasaccites*, *Striomonosaccites* and *Marsupipollenites*, among others (Chart 1, Supplementary Online Material). The SZ is characterised by the appearance of *Lueckisporites virkkiae* and other species of this genus

among other striate pollen grains. No radiometric data are available. The correlation of these zones with the Apillapampa palynofloras and globally is shown in Figures 10–12.

### Palynozones radiometrically dated from Uruguay

The *Cristatisporites inconstans*–*Vittatina subsaccata* (ISZ) and *Striatoabieites anaverrucosus*–*Staurosaccites cordubensis* (ACZ) Zones (Beri et al. 2011) of Uruguay span the early Cisuralian to Guadalupian (Figures 1(A), 6, 10 and 12, Chart 1, Supplementary Online Material). The Asselian–Artinskian ISZ is dominated by apiculate and cingulicavate trilete spores and monosaccate pollen grains of the genera *Anapiculatisporites*, *Brevitriletes*, *Converrucosisporites*, *Kraeuselisporites*, *Murospora*, *Barakarites*, *Mabuitasaccites* and *Striomonosaccites*. Recently, Beri et al. (2011) have recorded few specimens of *Lueckisporites* sp. in this zone. Conversely, the ACZ has fewer spores and a dominance of bisaccate pollen grains, both taeniate and non-taeniate, including a high diversity of *Lueckisporites* species, with several first appearances of taxa (e.g. *Lueckisporites brasiliensis*, *Lueckisporites crassus*, *Staurosaccites cordubensis* and *Lunatisporites paliensis*). Recent radiometric data have yielded an age no older than Artinskian for this zone (Rocha-Campos et al. 2006). The correlation of these zones with the Apillapampa palynofloras and globally is shown in Figures 10–12.

### Palynozones radiometrically dated from Paraná Basin in Brazil

In the Paraná Basin (Brazil, Figures 1(A) and 6), the *Vittatina costabilis* (VcZ) Interval Zone (Souza and Marques-Toigo 2005; Mori et al. 2012) is marked by the appearance of the polyplicate genus *Vittatina* and *I. unicus*, bisaccate taeniate species of *Protohaploxypinus* (e.g. *Protohaploxypinus rugatus* and *Protohaploxypinus goraiensis*) and a granulate spore *Converrucosisporites confluens*, a key taxon for the Pennsylvanian–Cisuralian boundary, which is not recorded in the Apillapampa assemblages. The VcZ was subdivided into two subzones, *Protohaploxypinus goraiensis* and *Hamiapollenites karrooensis*. Diagnostic species of the former subzone, regarded as Early Permian (Sakmarian/Artinskian) in age, are recorded in the studied material such as *I. unicus*, which are stratigraphycally restricted to this subzone (Figures 10 and 12, Chart 1, Supplementary Online Material). Diagnostic species of the subsequent subzone are *Hamiapollenites karrooensis* and *Striatopodocarpites fusus*. The *Protohaploxypinus goraiensis* Subzone was recently re-dated (SHRIMP U-Pb 291 ± 1.3 Ma) by Simas et al. (2012) based on isotopic ages from the tonstein of

Candiota and Faxinal coalfields, and previous isotopic data provided for the *Hamiapollenites karrooensis* Subzone of VcZ (ID-TIMS U-Pb 285.4 ± 8.6 Ma) were also discussed in the article. According to the last Geologic Time Scale (Cohen et al. 2013) followed in this paper, these ages correspond to the upper Sakmarian and Artinskian, respectively (Figure 10). *Hamiapollenites karrooensis* occurs in the Coal Member at Apillapampa (Figure 5, Chart 1, Supplementary Online Material), and it is recognised in the Cisuralian of northern Gondwana (e.g. Doubinger and Marocco 1981; Ghavidel-Syooki 1997; Playford and Dino 2000b; Dino et al. 2002; Chart 1, Supplementary Online Material). In Oman and Saudi Arabia, Stephenson (2008) recorded this taxon in small numbers in sparse assemblages within the Oman-Saudi Arabia Palynozone 4 (OSPZ4) Biozone attributed to the Artinskian–Kungurian, but it becomes common at the base of OSPZ5 (mid-Roadian–mid-Wordian), and persists into the middle part of the OSPZ5. *Hamiapollenites andiraensis* (here as *Hamiapollenites dettmannae*) also found in the Coal Member at Apillapampa was considered by Playford and Dino (2000b) to be the characteristic of the *Vittatina costabilis* Zone of the Amazonas Basin (Figures 5 and 10–12, Chart 1, Supplementary Online Material), associated with species of *Vittatina* and *Lueckisporites*. In Oman and Saudi Arabia, *Hamiapollenites dettmannae* after Stephenson (2008) was first recorded marking the base of the OSPZ5 Biozone (Stephenson 2006); common at the base of OSPZ5 and persists into OSPZ6 (Chart 1, Supplementary Online Material).

The overlying *Lueckisporites virkkiae* (LvZ) Zone (Souza and Marques-Toigo 2005) is mainly characterised by the appearance of the genus *Lueckisporites* (*Lueckisporites virkkiae* and *Lueckisporites densicorpus*) and species of *Staurosaccites* and *W. lucifer*. These pollen grains, as well as species of *Protohaploxypinus*, *Striatopodocarpites*, *Striatoabieites*, *Lunatisporites* and *Marsupipollenites* (Chart 1, Supplementary Online Material), are dominant in this zone reaching up to 80% of the association. Some species of spores and monosaccate pollen grains of the former units are also present and two new species appearing within this zone are *Thymospora criciumensis* and *Convolutispora pintoi*, from levels within the Palermo and the Irati Formations, respectively. According to Souza and Marques-Toigo (2005), lithostratigraphic boundaries are not coincident with those of the main biohorizons (Figures 10 and 12). The VcZ includes the upper Itararé Subgroup and part of the Rio Bonito Formation. No significant biostratigraphic change has been recorded in these sections, despite lithological variations in the basin. The boundary between the *Vittatina costabilis* and *Lueckisporites virkkiae* Interval Zones is recorded in the upper Rio Bonito Formation and the lower Palermo Formation (Figures 10 and 12).

Recently, Mori and Souza (2010) observed certain guide species of the Vc and Lv zones together in the same samples. Considering the lithostratigraphic positions of the samples, these records were interpreted as a transitional stage between these two zones. Santos et al. (2006) presented a radiometric dating of the LvZ from the Irati Formation of the Paraná Basin that yielded SHRIMP U–Pb 278.4 ± 2.2 Ma (early Kungurian, under the current GTS2013 of Cohen et al. 2013). Palynomorphs and radiometric dating were obtained by Mori et al. (2012) from an outcrop section in southernmost Brazilian Paraná Basin, where the Permian Vc and Lv zones were identified. U–Pb dating in zircons from a volcaniclastic level interbedded in the coal strata was analysed through LA-MC-ICP-MS method, providing a new absolute age dating of 281.4 ± 3.4 Ma (late Artinskian after the GST2012 of Gradstein et al. and early Kungurian under the current GTS2013) for the basal Lv Zone. This was assumed as the oldest occurrence of the LvZ in Paraná Basin, which contains index species that are widespread in other Gondwana basins (Figures 6 and 10–12, Chart 1, Supplementary Online Material). The appearance of *Lueckisporites virkkiae* at Apillapampa is documented here as old as Asselian supported by the radiometric data (Figure 5) provided by Henderson et al. (2009). A correlation with the Vc Zone should be established (Correlation 1 in Figures 10 and 12). However, a better correlation between the Apillapampa palynofloras and the palynozonation of Paraná Basin is established with both upper Vc and Lv zones based on the first occurrence datum (FOD) of their diagnostic taxa (see Correlation 2 in Figures 10 and 12). This is also in agreement with di Pasquo et al. (2009) when no radiometric information was available.

Of particular importance is the appearance of several monolete spores in the Coal Member of the Copacabana Formation at Apillapampa, some of which were defined by Mautino et al. (1998b) in the continental section of the Melo Formation in Uruguay (*Convolutispora uruguaiensis*, *Thymospora rugulosa* and *Polypodiites secoensis*). These taxa are part of the ACZ (Figures 5, 10 and 12, Chart 1, Supplementary Online Material) and were also recorded in the Guadalupian Teresina and Rio do Rastro Formations (Figures 10 and 12, Chart 1, Supplementary Online Material) by Neregato et al. (2008). The latter authors also proposed two informal intervals into the LvZ, on the basis of the abundance of *Laevigatosporites vulgaris* and *Thymospora*. They highlighted the presence of lycophyte and sphenophyte stems, and glossopterid leaves as the megafossils associated to the palynoassemblages dominated by pteridophytes. Even though those assemblages are not time-correlative with the Apillapampa palynoflora, the presence of endemic long-ranged taxa in South America is reinforced, which in this case represented similar ecological environmental facies and local humid conditions (see di Pasquo and Grader 2012a).

## Palynozones without absolute datings from the Amazonas Basin in Brazil

Playford and Dino (2000a, 2000b) proposed two zones for the Permian of the Amazonas Basin in northern Brazil (Figures 1(A), 6, 10 and 12, Chart 1, Supplementary Online Material): *Vittatina costabilis* (Vc) (separated in two subzones/zones) and *Tornopollenites toreutos* (Tt) Zones, attributed to the Sakmarian–Capitanian and Capitanian–Lopingian, respectively. The first zone is correlated to the Vc and Lv Zones of Paraná Basin. Although some species of *Striatopodocarpites* and *Protohaploxypinus* appear in the Pennsylvanian of Amazonas Basin (Playford and Dino 2000b) as well as in the Pennsylvanian assemblage of the Pando borehole X-1 of northern Bolivia (di Pasquo 2009), and in western Argentina (Césari and Gutiérrez 2001), they are widely occurring in the Permian of Gondwana and elsewhere (e.g. *Striatopodocarpites cancellatus*, which is restricted to the Permian of Gondwana, see Chart 1, Supplementary Online Material). *Lueckisporites virkkiae*, *Hamiapollenites andiraensis* and *Hamiapollenites karrooensis* are introduced in the upper *Vittatina costabilis* Zone and are consistently present in the following *Tornopollenites toreutos* Zone. A correlation of both Vc and Lv assemblages of the Copacabana Formation is established with the lower (Correlation 1) or middle VcZ (Correlation 2 in Figures 10 and 12), sharing 19 species of a total of 39 (Figure 5, Chart 1, Supplementary Online Material).

## Global correlations

It is very important at this time to confirm or establish long-distance correlations to take into account that highly endemic palynofloras are more difficult to correlate when other paleontological or absolute data are not available. To make these correlations possible, it is also important to refine, update and unify systematic classification of species at the local scale before attempting to erect long-distance correlation schemes. In this sense, global Permian assemblages including those of Lower and Upper Permian boundaries show similar features to the Apillapampa assemblages sharing cosmopolitan taxa of rather long ranges (e.g. *W. lucifer*, *Vittatina costabilis* and *Striatopodocarpites cancellatus*), whereas others are diachronously short-ranging taxa in different regions (e.g. *Triquitrites kaiseri*, *Striatosporites heyleri* and *Lueckisporites virkkiae*; Figures 5, 10 and 11, Chart 1(A)–(D), Supplementary Online Material). Hence, mutual correlations of these palynofloras presented in Figures 10–12 are only

established by their given ages (some of these radiometrically constrained).

### Africa and Australia

Palynological studies of the Karoo Supergroup (Dwyka and Ecca groups) in South Africa have been undertaken by various workers in several of the contemporaneous Karoo basins of southwestern Gondwana (e.g. Falcon 1975; Anderson 1977; MacRae 1988; Millsteed 1999). These palynofloras were correlated with different locations in Africa (Figures 6 and 11, Chart 1, Supplementary Online Material), including Tanzania (Semkiwa et al. 1998, 2003) and Nigeria (Broutin et al. 1990). Anderson (1977) established three palynozones for the Pennsylvanian–Cisuralian Dwyka and Ecca groups, and a thorough taxonomical revision of palynomorph species (i.e. synonymies) was needed to permit correlation. This was partially done by subsequent work (e.g. Foster 1979) and a few more synonymies were also proposed by di Pasquo and Grader (2012a). Foster and Waterhouse (1988) suggested a correlation between zone 1 of the Dwyka tillite with the palynoassemblage subzone A of Falcon (1975) from glacigene sediments of the Lower Karoo in the mid-Zambezi Basin (Zimbabwe), as well as to the *Converrucosisporites confluens* Zone that occurs in marine beds of late Pennsylvanian–Asselian age in Australia (Figures 11 and 12). Backhouse (1991) suggests that this zone may be late Asselian to early Sakmarian in age (Figures 11 and 12) sharing with the Vc and Lv assemblages of the Copacabana Formation several taxa (e.g. *Brevitriletes cornutus*, *Horriditriletes ramosus*, *Cycadopites cymbatus*, *Marsupipollenites striatus*, *Striatoabieites multistriatus*, *Protohaploxypinus amplus* and *Pakhapites fasciolatus*). In the Sakmarian/Artinskian *Striatopodocarpites fusus* Zone, *Striatopodocarpites cancellatus* and *W. magmus*, and *Scheuringipollenites maximus* are shared. In the zones below the Roadian (Ufimian) *Protohaploxypinus rugatus* Zone, the species in common *W. lucifer* and *Corisaccites alutas* appear, and in the latter zone, the eponymous taxon first appears (Figure 11, Chart 1, Supplementary Online Material). Anderson (1977) indicated that the genus *Lueckisporites* is recorded in his upper zone 3 attributed to the Artinskian (Figure 11, Chart 1, Supplementary Online Material). Both *Converrucosisporites confluens* and *Striatopodocarpites fusus* Australian zones are tentatively correlated with the *Protohaploxypinus goraiensis* of the Brazilian VcZ, respectively (Figure 12), taking into account the stratigraphic ranges of *Converrucosisporites confluens* and *Striatopodocarpites fusus* in the Paraná Basin (see Souza 2006). None of these taxa are present at Apillapampa, although a correlation is established using other species in common (Figures 10–12, Chart 1(A)–(D), Supplementary Online Material).

Recently, Stephenson (2009) has recorded *Converrucosisporites confluens* in the Dwyka Group in Namibia (Figures 6 and 11, Chart 1, Supplementary Online Material), radiometrically dated latest Pennsylvanian (i.e. Gzhelian or Kasimovian), containing common elements with Apillapampa such as *Pteruchipollenites indarraensis*, *Cristatisporites* spp., *Lundbladispora braziliensis*, *Vittatina* spp. and in small numbers *Horriditriletes ramosus*, *Caheniasaccites flavatus*, *Cannanoropollis* spp., *Cycadopites cymbatus*, *Plicatipollenites* spp. and *Striatoabieites multistriatus*. A correlation with the lower assemblage of the Copacabana Formation discussed here is impeded due to their different radiometric ages, although they are quite similar assemblages (Chart 1, Supplementary Online Material). Conversely, *Converrucosisporites confluens* is recorded in the TB Zone of the Mandiyutí Group of the Tarija Basin in northern Argentina (di Pasquo 2003) similar to the Namibian microflora. However, infrequent common taxa and, especially, the absence of striate pollen grains in the former mark the difference between these two assemblages of probably similar age (Figure 12).

Absolute ages obtained from the Dwyka Group support a Late Carboniferous and an early Early Permian age for most of the glacial events in Western Gondwana in agreement with its regional equivalent Itararé Subgroup in Brazil (Stollhofen et al. 2000). Rhyolitic–andesitic volcanic tuffs present in the Dwyka Group of southern Africa were dated with U/Pb on zircons from tuffs about 400 m above the base of the Dwyka yielding an Asselian date of 297 ± 1.8 Ma (Bangert et al. 1999). The age of the top of the Dwyka has been similarly derived using zircon dates from tuffs in the lowermost beds of the overlying Prince Albert Formation (288 ± 3 and 289 ± 3.8, i.e. Artinskian). An absolute age of U–Pb zircon 270 ± 1 Ma (i.e. Roadian) was obtained from tuff beds of the Collingham Formation, in South Africa (Stollhofen et al. 2000), which overlies the Whitehill Formation. The distinctive black pyrite-rich mud horizon corresponding to the Whitehill Formation extends across into the Paraná Basin of South America in which the contemporaneous Irati Formation was deposited. Both contain the characteristic fauna of the fresh water *Mesosaurus* and dragonflies (de Wit et al. 2007). This distinctive geochemical marker is a true 'time line' for correlation (Faure and Cole 1999). Both the Whitehill and Irati shales have a very high total organic carbon content (up to 24% in condensed sections of the Irati) and a sulphur content as high as 8%, and bears the *Lueckisporites virkkiae* Interval Zone (partly equivalent to upper Zone 3 of Anderson 1977, see Figure 12). Considering that there is no marked diachronism between these two lithostratigraphical units, Souza (2006) proposed that the Irati Formation should likewise be regarded older than 270 Ma (Figures 10–12), confirming the Artinskian age proposed by Santos et al. (2006).

MacRae (1988) described Pennsylvanian to Late Permian palynomorph assemblages from subsurface northern Karoo basins of South Africa (Figure 6) and subsequently erected six palynozones, namely biozones A–F, in ascending order (Figure 11). Based on limited similarity of individual taxon ranges, a broad correlation of the zonation of MacRae (1988) with the Apillapampa assemblages is possible (Figures 11 and 12). The zone A is Late Pennsylvanian in age and zone B records the early Cisuralian based on palynostratigraphic comparisons. Even *Lueckisporites virkkiae* and *Corisaccites alutas* are not recorded by MacRae (1988), several species in common with the Apillapampa assemblages appear in the zone A (i.e. *Horriditriletes ramosus*, *Brevitriletes cornutus* and *Kraeuselisporites splendens*), and close to its top or the base of zone B are recorded *Marsupipollenites striatus*, *Striatoabieites multistriatus* and *W. lucifer*. Into the zone B, *Alisporites ovatus* and *Cirratriradites africanensis* appear; in zone D, *Chordasporites endroedii* and *Granulatisporites trisinus*; and at its top, *Striatopodocarpites cancellatus* are introduced (Chart 1, Supplementary Online Material).

Millsteed (1999) proposed three informal assemblages for the Artinskian of South Africa (Figure 6, Chart 1, Supplementary Online Material). The sporites assemblage shares with the Apillapampa palynofloras the spores *Didecitriletes eoericiana* and *Brevitriletes cornutus*, and in the Transition Assemblage appear *Lueckisporites nyakapendensis*, *W. lucifer*, *Striatopodocarpites cancellatus* and *Horriditriletes ramosus*.

Semkiwa et al. (1998, 2003) summarised assemblages from the Idusi and Mchuchuma Formations of the Ngaka coalfield in Tanzania (Figure 6, Chart 1, Supplementary Online Material). In general, in the upper part of the Idusi Formation the *Cannanoropollis–Plicatipollenites* assemblage contains abundant monosaccate pollen and trilete spores (*Horriditriletes ramosus*, *Punctatisporites* spp. and *Kraeuselisporites splendens*) tentatively assigned to the late Asselian to early Sakmarian. The lower part of the Mchuchuma Formation is defined by the *Scheuringipollenites* assemblage, mostly with non-taeniate disaccate pollen (*Scheuringipollenites ovatus* and *Scheuringipollenites maximus*), whereas in the upper part of the formation the *Scheuringipollenites–Protohaploxypinus* assemblage occurs with common to abundant taeniate disaccate pollen (*Protohaploxypinus amplus*, *Protohaploxypinus rugatus* and *Striatopodocarpites cancellatus*), rare to abundant trilete spores (*Horriditriletes ramosus*, *Brevitriletes cornutus*, *Cirratriradites africanensis*, *Kraeuselisporites splendens, Retusotriletes* spp and *Punctatisporites* spp.), monolete spores (*Laevigatosporites vulgaris* and *Polypodiisporites mutabilis* [ = *Polypodiisporites detritus* in di Pasquo and Grader 2012a]), non-taeniate disaccate pollen (*Scheuringipollenites ovatus*, *Scheuringipollenites maximus*, *Alisporites* spp.), rare monosaccate pollen (*Cannanoropollis*), rare monosulcate pollen (*Cycadopites cymbatus*), praecolpate pollen (*Marsupipollenites striatus*, *Pakhapites fasciolatus*), rare polyplicate pollen (*Vittatina*, *W. lucifer*) and rare algal species of *Tetraporina* and *Botryococcus* (all species in brackets are in common with the Apillapampa palynoflora; Figure 6, Chart 1, Supplementary Online Material). Based on comparisons with Zimbabwe (Falcon 1975) and Australia, Semkiwa et al. (2003) assigned the *Cannanoropollis–Plicatipollenites* assemblage to the Upper Dwyka Group, and the *Scheuringipollenites* and the *Scheuringipollenites–Protohaploxypinus* assemblages to the Middle Ecca Group, spanning a late Sakmarian age (Figure 11). Few of these taxa shared with the Apillapampa palynofloras are biostratigraphically useful to establish a possible correlation with other similar assemblages in South America (e.g. *Vittatina* spp., *W. lucifer*, *Marsupipollenites striatus* and *Pakhapites fasciolatus*) such as Vc Zone in Brazil and FS Zone in Argentina (Figures 10–12, Chart 1, Supplementary Online Material).

Modie and Le Herissé (2009) presented palynostratigraphic analysis of the Late Carboniferous to Permian core samples from two borehole sections, STRAT 1 and CKP 6, which penetrated the glacial to post-glacial and coal-bearing Lower Karoo sequence, Kalahari Karoo Basin, Botswana (Figure 6). They established the *Hamiapollenites bullaeformis* Zone, the *Cyclogranisporites gondwanensis* Zone and the *Platysaccus papilionis–Striatopodocarpites fusus* Zone, as local biozonation in ascending order of stratigraphy (Figures 11 and 12). They correlated the first zone to the Vc Interval Zone and the remaining two zones to the Lv Interval Zone of Souza (2006), in the Paraná Basin, especially due to the appearance of the eponymous taxon into the lower part of the second zone (Figure 11, Chart 1, Supplementary Online Material). Ages for these zones of Kalahari Karoo Basin were broadly equated to these Brazilian assemblages supported on comparisons with similar assemblages from previous Gondwana studies. Most important species in common to the Apillapampa assemblages are (36 of a total of 165 species, Chart 1, Supplementary Online Material) *Didecitriletes eoericianus*, *Horriditriletes ramosus*, *Cristatisporites morungavensis*, *Lundbladispora braziliensis*, *Polypodiisporites mutabilis*, *Cycadopites cymbatus*, *Lueckisporites virkkiae*, *Lunatisporites variesectus*, *Marsupipollenites striatus*, *Protohaploxypinus haigii*, *Protohaploxypinus rugatus*, *Striatopodocarpites cancellatus*, *W. lucifer*, *W. magmus*, *Pakhapites fusus* and *Pakhapites ovatus*. A broad correlation is established with the *Hamiapollenites bullaeformis* Zone, although the inception of *Lueckisporites virkkiae* in this region occurs in the next zone (Figures 11 and 12).

In Nigeria (Figure 6), Broutin et al. (1990) studied a microflora of the Tarat Formation recording 30 miospores of Permian (Kungurian–Capitanian) Gondwanan and Euramerican affinities; the macroflora is represented by

Euramerican elements. This microflora shares 14 species with the Apillapampa assemblages, although no correlation is established (e.g. *Pakhapites fasciolatus*, *Lunatisporites noviaulensis*, *Lunatisporites acutus*, *Striatopodocarpites cancellatus*, *Lueckisporites virkkiae*, *Lueckisporites singhii*, *Corisaccites alutas*, *Vittatina costabilis*, *Hamiapollenites karrooensis* and *Vitreisporites pallidus*; Chart 1, Supplementary Online Material).

On the other hand, Late Permian assemblages in South Africa still have some species in common with the Apillapampa palynoflora (Chart 1, Supplementary Online Material). A recent study integrating mega and microflora from the New Wapadsberg Pass in South Africa (Figure 6) was presented by Prevec et al. (2010), who recorded a decrease in abundance and diversity of taeniate bisaccates just above the boundary of the *Protohaploxypinus microcorpus* Zone (Figure 11) and at the base of the Triassic. The number of multitaeniate bisaccate taxa (e.g. *Striatopodocarpites*) decreases, whereas taxa including *Protohaploxypinus microcorpus*, *Lunatisporites noviaulensis* and *Lueckisporites*, in addition to alete bisaccates (e.g. *Falcisporites*), assume dominance together with cavate (e.g. *Lundbladispora* and *Densoisporites*) and acavate spores. Several poorly preserved pollen grains attributed to cf. *Lunatisporites pellucidus* are also found, which is also present in the Latest Permian–Triassic of Australia (Foster 1982; Chart 1, Supplementary Online Material). Overall, Prevec et al. (2010) proposed an age assessment for the New Wapadsberg Pass assemblage based on a comparison with Australian palynostratigraphic zones that are calibrated against independently dated marine invertebrate zones, carbon-isotope stratigraphy and radio-isotopic dates (see Metcalfe et al. 2008).

The Permian–Triassic boundary in Australia can be placed in relation to the pollen-based *Protohaploxypinus microcorpus* Zone that has been dated independently as late (but not latest) Changhsingian in age (Metcalfe et al. 2008). It serves as the standard biostratigraphic zonation for the Southern Hemisphere (Lindström and McLoughlin 2007). This correlation supports a late Changhsingian (late Lopingian) age assignment for the palynoflora in accordance with the megafloral record. It is noticed that spores present in this zone are not recorded in the Apillapampa palynoflora except for *Columinisporites* sp. cf. *Columinisporites peppersii* (a junior synonym of *Striatosporites heyleri*, see Playford and Dino 2000a), while many pollen grains do (e.g. *Vitreisporites signatus*, *W. lucifer*, *Marsupipollenites striatus*, *Protohaploxypinus rugatus*, *Protohaploxypinus haigii*, *Protohaploxypinus amplus*, *Protohaploxypinus samoilovichii*, *Hamiapollenites dettmanae*, *Striatopodocarpites cancellatus*, *Alisporites ovatus*, *Striatoabieites multistriatus*, *Lunatisporites noviaulensis*, *Pteruchipollenites indarraensis* and rare *Lueckisporites* species) and the algal *Reduviasporonites chalastus* (Chart 1, Supplementary

Online Material). Most of these taxa are also recorded from the underlying zones in Australia (Figure 11). *Striatosporites heylerii* found in the Lv assemblage at Apillapampa (Figure 5, Chart 1, Supplementary Online Material) is a widespread geographically distributed taxon related to the Sphenophyta (Sphenophyllales) from Westphalian to Permian in Gondwana (see di Pasquo and Grader 2012a).

### Antarctica

Lindström (1995) also described some palynomorph assemblages from the Asselian–Sakmarian (Tastubian) of Antarctica (Figure 6), which compare favourably with those recognised from the Apillapampa assemblages (Figures 11 and 12). The most significant of the shared taxa (18 of 80) include (Chart 1, Supplementary Online Material) *Retusotriletes nigritellus*, *Horriditriletes ramosus*, *Brevitriletes cornutus*, *Marsupipollenites striatus*, *Scheuringipollenites maximus*, *Protohaploxypinus amplus*, *Striatopodocarpites cancellatus*, *Striatoabieites multistriatus*, *Pakhapites fasciolatus*, *W. magmus*, *Cycadopites cymbatus* and species of *Lunatisporites*.

Lindström (1996) documented younger Kazanian–Tatarian assemblages from Antarctica and common species with Apillapampa (17 of 66 species). They include (among others) *Scheuringipollenites maximus*, *Vitreisporites pallidus*, *W. lucifer*, *W. magmus*, *Protohaploxypinus rugatus*, *Corisaccites alutas*, *Striatopodocarpites cancellatus*, *Striatopodocarpites phaleratus*, *Striatoabieites multistriatus*, *Pakhapites fasciolatus*, *Cycadopites cymbatus*, *Brazilea scissa* and certain species of *Lueckisporites* (Chart 1, Supplementary Online Material). A correlation chart among different assemblages of Gondwana was also presented by Lindström (1996), here updated in Figures 11 and 12.

### West Papua

Playford and Rigby (2008) described a Kungurian–Roadian palynoflora from West Papua (Figures 6 and 11) containing 57 species and of these, 17 species are shared with the Apillapampa palynofloras (Chart 1, Supplementary Online Material). Miospores (e.g. *Triquitrites kaiseri* also recorded at Apillapampa) and freshwater or brackish phytoplankton species and paleobotanical elements are related to the *Glossopteris* floral affiliation (Gondwanan realm), although some minor components of both mega and microfloras are linked to the Cathaysian floral realm. These authors addressed the evidence of intermingling of northern or peripheral-Gondwanan realm with other floral realms (the so-called mixed floras), particularly the Cathaysian flora from the Southeast Asia realm (?) that corroborate the location of the West Papua region on the northeastern margin of Gondwana close to the Cathaysian landmasses (Figure 6).

### Oman and Saudi Arabia

The standard Permian palynozonation for the Arabian Peninsula (Figures 6 and 11) consists of a framework of six biozones for the uppermost Carboniferous to Middle Permian strata (e.g. Stephenson and Filatoff 2000a, 2000b; Stephenson and Osterloff 2002; Stephenson et al. 2003; Stephenson 2004, 2006, 2008). However, there is a lack of any remarkable similarities between taxa from the Arabian Peninsula, and hence only a limited comparison is possible (Chart 1, Supplementary Online Material). The lower five biozones (OSPZ1, 2, 3a, 3b and 3c) represent the palyniferous uppermost Carboniferous to Lower Permian sequence in Oman (Figure 6), and to some extent these are recognisable in successions in central and southern Saudi Arabia (Figure 11). OSPZ1, associated with the lowermost Al Khlata Formation and the Unayzah C member, is probably Ghezelian (Stephanian) in age. Common elements with the Apillapampa palynofloras are *Brevi-triletes cornutus*, *Calamospora microrugosa*, *Retusotri-letes nigritellus*, *Lundbladispora braziliensis* and several monosaccate pollen grains (Chart 1, Supplementary Online Material). OSPZ2 is Asselian–Sakmarian in age and is associated with the upper part of the Al Khlata Formation and the Unayzah B member. Common species are *Horriditriletes ramosus*, *Protohaploxypinus amplus*, *Striatoabieites multistriatus*, *Marsupipollenites striatus*, *Cycadopites cymbatus* and *Alisporites nuthallensis* (as *Alisporites ovatus* in di Pasquo and Grader 2012a), together with some species from the underlying zone. *Lycospora pusilla* is also present (a similar species *Lycospora variabila* is recorded at Apillapampa). OSPZ3 is subdivided into three sub-biozones and is associated with the Lower Gharif Member. Common taxa that appear in this zone are *Striatopodocarpites cancellatus*, *I. unicus* and *Corisaccites alutas*. The age is late Sakmarian, based on fusulinid evidence from the subsurface Haushi Limestone in central Oman, widely present towards the top of the Lower Gharif Member (Angiolini et al. 2006). Strikingly, there is a record (not illustrated) of few specimens assigned with doubts to *Lueckisporites virkkiae* in this unit (Figures 5 and 11, Chart 1(C), Supplementary Online Material), as well as others to *Corisaccites alutas* by Angiolini et al. (2006).

OSPZ4 was established based on the sporadically palyniferous Oman Middle Gharif Member where *Vittatina costabilis*, *Vittatina subsaccata* and several species of the underlying zones are shared with the Apillapampa palynoflora. OSPZ5 and 6 are based on the Oman Upper Gharif Member and Saudi Arabian Unayzah A member and basal Khuff clastics, attributed to the late Early to mid-Permian, which sporadically contain diverse and well-preserved pollen and spore assemblages. The older assemblages were designated by Stephenson et al. (2003) as OSPZ5, characterised by new appearances of species not described in OSPZ4 such as *Lueckisporites virkkiae* and *Reduviasporonites chalastus*, although previously described taxa (*Pteruchipollenites indarraen-sis*, *Alisporites ovatus*, *Corisaccites alutas* and *W. lucifer*) are also frequent. All of them are in common with the Apillapampa palynoflora (Figures 5 and 11, Chart 1(A)–(C), Supplementary Online Material).

Recently, these palynofloras were better described by Stephenson (2008), who recognised distinctive endemic palynomorphs not recognised at Apillapampa. Instead, Gondwanan taxa are recognised, such as *Hamiapollenites dettmannae* and *Hamiapollenites karrooensis* that are common in the lower part of OSPZ5; *Alisporites ovatus* appears close to the base of the OSPZ5, common throughout OSPZ5 and 6; *Corisaccites alutas* appears within the OSPZ3, locally common in the OSPZ4 and persists into the younger OSPZ6 (Figure 11, Chart 1(C), Supplementary Online Material). *Lueckisporites singhii*, *Lunatisporites noviaulensis* and *Lunatisporites* cf. *pellu-cidus* appear in the OSPZ6 with abundant *Reduviaspor-onites chalastus* and also some species from the OSPZ4 and 5 (Stephenson and Filatoff 2000b).

*Reduviasporonites chalastus* was re-evaluated by Foster et al. (2002), based on a comprehensive account of many specimens attributable to this taxon around the world. They proposed synonymies that showed it ranges from the Late Permian to Early Triassic (Capitanian to Griesbachian). After that study, new records extend the range to older Permian ages (Figures 6 and 11, Chart 1(C), Supplementary Online Material): (1) Roadian to Capitanian of Oman and Saudi Arabia (Stephenson et al. 2003), (2) mid-Permian and Triassic in Argentina (Balarino 2008) and (3) late Cisuralian of Paraguay (Pérez Loinaze, Ciccioli, et al. 2010). Hence, our Bolivian records from the Asselian–Sakmarian are the oldest at present (Figures 5 and 10–12).

Other Permian floras were described from the Arabian Peninsula by Broutin et al. (1995). The paleoflora of the Gharif Formation (Artinskian–Kungurian) has palyno-morphs of the *Protohaploxypinus microcorpus* Zone in Australia, whereas plant fossils of Gondwanan, Euramer-ican and Cathaysian affinities are present in the macroflora. Common and important palynomorphs in the Apillapampa assemblages (12 of 35, Chart 1(A)–(C), Supplementary Online Material) and mainly OSPZ5 Zone (Figures 11) are *Polypodiisporites* cf. *mutabilis*, *Vitreis-porites pallidus*, *Protohaploxypinus amplus*, *Lunatispor-ites* cf. *pellucidus*, *Lueckisporites virkkiae*, *Lueckisporites singhii*, *Corisaccites alutas*, *Striatoabieites multistriatus*, *Striatopodocarpites cancellatus* and *W. lucifer*.

### Israel

In Israel (Figure 6), Eshet (1990a, 1990b) defined for the Asselian the *Potonieisporites novicus* (Pn) Zone (Figure 11)

that shares with Apillapampa the monosaccate pollen grain species and *Vittatina costabilis*, *Reticuloidosporites warchianus*, *Krauselisporites splendens*, *Polypodiisporites mutabilis*, *Pteruchipollenites indarraensis* and *Striatoabieites multistriatus*. The Lopingian (Thuringian) *Lueckisporites virkkiae* Zone is defined by the eponymous species and the appearance of *Reduviasporonites chalastus*, *Lunatisporites noviaulensis*, *Lunatisporites acutus*, *Lunatisporites pellucidus* and *Vitreisporites pallidus* whereas *Lueckisporites singhii* appears in the Triassic (Figures 5 and 11, Chart 1(C), Supplementary Online Material).

### Iran

Ghavidel-Syooki (1997) presented an extensive study of the Cisuralian Zagros Basin in Iran (Figure 6) as part of the Gondwanan continent, and 58 species were recorded, of them 19 are shared with Apillapampa (e.g. *Horriditrileites ramosus*, *Corisaccites alutas*, *Cycadopites cymbatus*, *Pakhapites fusus*, *Pakhapites ovatus*, *Hamiapollenites karrooensis*, *Lueckisporites virkkiae*, *Marsupipollenites striatus*, *Striatopodocarpites cancellatus*, *Striatoabieites multistriatus*, *Strionomosaccites cicatricosus*, *Vittatina costabilis*, *Vittatina subsaccata* and *W. magmus*; Chart 1 (C), Supplementary Online Material). Although a precise age of the assemblages was not given, Ghavidel-Syooki (1997) referred that *Lueckisporites virkkiae*, *Corisaccites alutas* and *Hamiapollenites karrooensis* appeared since the Artinskian in South America, Africa and Australia (Figures 5, 10 and 11). Angiolini and Stephenson (2008) recorded an assemblage from the lower and middle Dorud Group, northern Iran, composed of monosaccate pollen grains and non-striate and striate pollen grains. Among the latter group, important taxa in common with the Apillapampa assemblages are *Corisaccites alutas*, *Vittatina costabilis* and species of *Striatopodocarpites* and *Protohaploxypinus*. This assemblage was attributed to the Asselian–Sakmarian on the basis of the content of invertebrate fossils interbedded with the palynoassemblage and it is correlatable to the Apillapampa palynofloras, although *Lueckisporites virkkiae* is not recorded (Figure 11, Chart 1(C), Supplementary Online Material).

### Pakistan

Although no corelation is possible with the late Cisuralian–Guadalupian assemblages from the Salt Range in Pakistan (Figure 6) described by Balme (1970), they share with the Apillapampa assemblages several important species (15 of 60 species), such as *Polypodiisporites mutabilis*, *Reticuloidosporites warchianus*, *Vitreisporites pallidus*, *Striatopodocarpites cancellatus*, *Lueckisporites virkkiae*, *Lueckisporites singhii*, *Lunatisporites pellucidus*, *Lunatisporites noviaulensis*, *Corisaccites alutas*, *Alisporites*

*ovatus*, *W. lucifer* and *Brazilea scissa* (Figure 11, Chart 1 (C), Supplementary Online Material).

### India

A close correlation with the Gondwana Sequence of India (Figure 6) is overwhelmingly limited despite several taxonomic and palynostratigraphic studies (e.g. Tiwari and Tripathi 1987, 1992; Vijaya and Tiwari 1992) as there is some noticeable degree of variation in its taxonomic nomenclature. However, many species are morphologically quite similar to the rest of Gondwanan microfloras (cf. Hart 1971). Tiwari and Tripathi (1992) compiled a species-determined composite palynozonation scheme based on stratigraphic distribution of key taxa (first and last occurrences, FO-LO data) obtained from previous studies undertaken in the Damodar Graben and several other pertinent basins of India. This work allows for a limited but important comparative analysis of the nine assemblage zones from the Pennsylvanian–Permian of India, and common species with the Apillapampa assemblages are as follows (13 of 180 species, Figures 11, Chart 1(C), Supplementary Online Material): *Horriditrileites ramosus*, *Potonieisporites magnus*, *Potonieisporites neglectus*, *Potonieisporites congoensis*, *Caheniasaccites flavatus*, *Plicatipollenites malabarensis*, *Scheuringipollenites maximus*, *Cycadopites cymbatus*, *W. lucifer*, *Corisaccites alutas*, *Striatoabieites multistriatus*, *Marsupipollenites striatus*, *Vitreisporites pallidus*, *Lunatisporites pellucidus*, *Lunatisporites noviaulensis* and certain species of *Vittatina*, *Striatopodocarpites* and *Lueckisporites* (*Lueckisporites crassus* Sinha). Correlations are shown in Figures 11 and 12.

### Kazakhstan

Dunn (2001) described a 50-m section containing the Carboniferous–Permian boundary in Kazakhstan (Figure 6). The boundary is based on fusulinids, ammonoids and conodonts. The section is characterised by abundant and diverse records of *Vittatina* and a variety of taeniate disaccate pollen grains, including the appearance in the latest Carboniferous of rare specimens of the *Scuttasporites* (*Lueckisporites*-like) group. The specimens illustrated by Dunn (2001, pl. 4, figs. 9–12) look quite different from the cosmopolitan species of *Lueckisporites* recorded during the Permian except for some resemblance to *Lueckisporites stenotaeniatus* recorded in the mid-late Cisuralian in Argentina, Brazil and Uruguay (see Gutiérrez, Balarino, et al. 2010), although this latter species is more diploxylonoid with larger sacci. Among the shared species with Apillapampa are *Vittatina costabilis*, *Vittatina vittifera*, *Vittatina simplex*, *Vittatina subsaccata*, *Potonieisporites novicus* and *I. unicus*, while species of *Calamospora*, *Punctatis-*

*porites*, *Limitisporites*, *Protohaploxypinus* and *Hamiapollenites* are similar but not the same. This assemblage was correlated to the *Limitisporites monstruosus*–*Vittatina costabilis* Zone of the Sverdrup Basin in the Canadian Arctic (Utting 1994), and it is possibly correlated to the Vc assemblage at Apillapampa (Chart 1(C), Supplementary Online Material).

### China

Zhu et al. (2005) presented a comparison of Permian palynological assemblages from Junggar and Tarim Basins (Figure 6) with ca. 60 species in each region, being the former part of the Angaran realm (Subangara area) during the Cisuralian, whereas the latter is related to the Euramerican realm mixed with Angaran floras especially since the Artinskian. Cosmopolitan species are shared with the Apillapampa assemblages (Chart 1(C), Supplementary Online Material), such as *Calamospora liquida*, *Calamospora microrugosa*, *Laevigatosporites vulgaris*, *Vittatina subsaccata*, *Vittatina costabilis*, *Vittatina vittifera*, *Cycadopites caperatus*, *Protohaploxypinus samoilovichii*, *Vitreisporites pallidus* and *Lueckisporites virkkiae*. An earlier appearance of the latter species was reported (not illustrated) by Gao (1984) from the Sakmarian of North China (Figure 5).

### North America

In the Atlantic provinces of Canada, striate saccate pollens (e.g. *I. unicus* and *Hamiapollenites*) first occur in the Late Pennsylvanian (Barss 1967; Barss and Hacquebard 1967). In the USA, Peppers (1964), Jizba (1962), Tschudy and Kosanke (1966), Habib (1966), Gupta and Boozer (1969) and others have shown the striate saccates (e.g. *Hamiapollenites*, *Illinites* and *Protohaploxypinus*), first occurring in the Late Pennsylvanian and/or Early Permian. Since the Asselian (Cisuralian), palynofloras from the USA (e.g. Wilson 1962; Morgan 1972) and Canada (e.g. Jansonius 1962) were also described including *Vittatina costabilis*, *Vittatina saccata* and *Vittatina simplex*, and some important taxa discussed here such as *Lueckisporites virkkiae* and *Tornopollenites toreutos* are known since the Artinskian (Utting and Piasecki 1995; Figures 5 and 6, Chart 1(C), Supplementary Online Material).

On the other hand, Barss (1972) discussed the age of the Tatonduk River section of Yukon, underlying Permian rocks dated as mid-Pennsylvanian on the bases of brachiopods and fusulinids (*Pseudostaffella*, *Fusulinella* and *Profusulinella*). Palynological assemblages recorded in this section are characterised by numerous striate saccate forms, and especially some common taxa with Apillapampa assemblages are *Lueckisporites virkkiae*, *Striatoabietites multistriatus?*, *Protohaploxypinus* cf.

*Protohaploxypinus samoilovichii*, *Striatopodocarpites* cf. *Striatopodocarpites cancellatus*, *Vittatina costabilis?*, *Vittatina simplex*, *Vittatina subsaccata* and *Vittatina vittifera*. These taxa should be attributed to the Permian. However, this is in conflict with the age suggested by the marine fauna (i.e. Late Pennsylvanian). In addition to these apparent discrepancies in age, an important factor in the study is the evidence of widespread reworking of Mississippian and Devonian miospores in the younger assemblages. This reworked material is almost always better preserved than the younger material. A study of whether there is also reworking of the marine fauna would be essential given that most of the palynologic species mentioned above are until now only recorded in the Permian (Barss 1972). We are not considering the appearances of these palynomorphs as being Pennsylvanian until this discrepancy is solved.

### Europe and Russia

Some species discussed here such as *Lueckisporites virkkiae* and others belonging to genera such as *Lunatisporites*, *Vittatina* (*Vittatina subsaccata*, *Vittatina vittifera*) and *Vitreisporites*, among others, were first described in the Permian of these regions (Figure 6; Utting and Piasecki 1995). *Vittatina* and *Illinites* appear in the Late and mid-Pennsylvanian, respectively, but are abundant mostly during the Early Cisuralian in Europe and Russia (Utting and Piasecki 1995). In the upper Artinskian, the inception of *Vitreisporites* and *Lunatisporites* occurred, whereas *Lueckisporites virkkiae* is introduced later in the Wordian (Guadalupian) age of the Russian Platform (Utting et al. 1997), Europe, Svalvard and Greenland (Utting and Piasecki 1995). This taxon is widely recorded up to the end of the Permian, where it is also used as the eponymous name for the latest Permian palynozone in several places in Europe (Klaus 1980; Diéguez and Barrón 2005; Figures 5 and 11, Chart 1(C), Supplementary Online Material).

### Final remarks and conclusions

Global Permian assemblages including lower and upper system boundaries show similar qualitative and quantitative features as the palynofloral assemblages observed in the Copacabana Formation at Apillapampa in central Bolivia. U–Pb geochronology (ID-TIMS of zircons) from four interbedded tuffs of the lower member confirmed new and some previous microfossil (conodonts and fusulinids) ages suggesting that the lower member of the Copacabana Formation at this location is Asselian and early Sakmarian (see Figure 4). The whole palynoassemblage is composed of 94 palynomorph species arranged in two informal palynoassemblages from 12 samples. The LA *Vittatina*

*costabilis* (Vc) corresponds to one sample at 9.8 m above the base of the Copacabana Formation, and the UA corresponds to where *Lueckisporites virkkiae* first appears at 69 m. Based on superposition above well-defined Sakmarian strata, the upper Coal Member of the Copacabana Formation may also be Sakmarian to early Artinskian (including one more ash sample datum, see Figure 4), although palynology suggests an Artinskian age (di Pasquo et al. 2009). The stratigraphic distribution of species supports here the subdivision of the Lv assemblage into the Lv (*sensu strictus*) and the Lv-Hk-Pm assemblages, each one corresponding to the Lower Member (marine environment) and the Coal Member (transitional) of the Copacabana Formation, respectively (Figures 4 and 5, Chart 1(A), Supplementary Online Material). Thorough global comparison of these palynofloras addressed in this contribution based on first appearances of mainly cosmopolitan diagnostic taxa allowed the establishment of correlations with other palynofloras of late Sakmarian and Artinskian ages (Figures 10–12, Charts 1(A)–(D), Supplementary Online Material). This is the case for the stratigraphically important species, *Lueckisporites virkkiae*, which is of particular interest because it is utilised in South American and global Permian biostratigraphic reconstructions (Figures 10–12). Therefore, from the biostratigraphic comparison (Correlation 2 in Figures 10–12), the LA should be correlated to the South American VcZ, FSZ, ISZ and CZ and the UA correlates to the LW, Lv, S and AC Zones, based on the appearance of key taxa such as *Lueckisporites virkkiae* and other spores, striate and bisaccate non-striate pollen grains that are exclusive of the latter zone (e.g. *Vittatina costabilis*, *Hamiapollenites karrooensis*, *Lunatisporites variesectus*, *Protohaploxypinus samoilovichii*, *Lundbladispora braziliensis*, *Polypodiisporites mutabilis*, *Thymospora criciumensis*, *Thymospora rugulosa*, *Convolutispora uruguaiensis* and *Convolutispora ordonensis*).

However, if we accept the age of this unit based on its isotopic data (Henderson et al. 2009), correlations must be established to the Asselian–Sakmarian palynozones (Correlation 1 in Figures 10–12). Therefore, the appearance of *Lueckisporites virkkiae* at Apillapampa is considered here the oldest record and does not match the previous oldest known record recently documented in Brazil, in the upper Rio Bonito Formation and dated as late Artinskian (281.4 ± 3.4 Ma, Mori et al. 2012; Figure 10). Similar radiometrically dated palynoassemblages bearing this taxon are also known from Argentina (Césari et al. 2011) and Uruguay (Beri et al. 2011). In addition, the appearance of *Scuttasporites (Lueckisporites*-type) group in the Carboniferous–Permian boundary in Kazakhstan (Dunn 2001; Figure 6), along with few doubtful records of *Lueckisporites virkkiae* in the Sakmarian of Uruguay (Beri et al. 2011) and Iran (Angiolini and Stephenson 2008; Figures 5, 6, 10 and 11), requires further taxonomic studies. Therefore, Bolivia could have been part of older centres of dispersion for some striate–taeniate pollen grains and monolete spores follow-

ing the Asselian. The information provided also supports that the plant remains belonging to the *Glossopteris* Flora recorded in the Coal Member of the Apillapampa section are slightly older than previously dated.

From this thorough biostratigraphic comparison, global stratigraphic ranges of several species (e.g. *Protohaploxypinus haigii*, *Striatopodocarpites phaleratus*, *Lueckisporites virkkiae*, *Lueckisporites nyakapendensis*, *Lueckisporites singhii*, *Lunatisporites noviaulensis*, *Lunatisporites acutus*, *Lunatisporites pellucidus*, *Hamiapollenites karrooensis*, *Hamiapollenites dettmanae* and *Reduviasporonites chalastus*) are extended here to the Asselian–Sakmarian (Figure 5).

We would like to stress that floral evolution and migration are subject to changing information. Explanations of the disagreement between the ages of the Apillapampa palynofloras containing *Lueckisporites virkkiae* (radiometrically dated) and the correlative palynozones from South America are likely related to palynofloral distribution and evolution during punctuated paleoclimatic and paleogeographic changes that require further review.

Furthermore, no basin in Gondwana seems to record a complete sedimentary record and, consequently, biostratigraphical succession is more complete in certain intervals and areas. Interval zones are established in stratigraphic horizons that represent limits of discontinuity. These stratigraphical horizons imply erosional events, which obliterate biostratigraphic succession. Thus, the true first appearances of certain taxa cannot be well correlated across all basins.

As cosmopolitan and endemic species recorded in the Apillapampa palynofloras are long ranged and their FODs are regionally or globally diachronic, two things are highlighted as conclusion: (1) a local biostratigraphic scheme is required for the Permian of Bolivia and Peru and (2) radiometric data are still required to establish accurate regional and global correlations.

## Supplementary material

Supplementary material can be accessed at http://dx.doi.org/10.1080/08912963.2014.910204

## Notes

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## Appendix 1. List of palynomorph species

This appendix lists all validly described palynomorph species by di Pasquo and Grader (012a), included in Chart 1 (Supplementary Online Material), some of which are mentioned in this contribution along with other species not present at Apillapampa, but discussed in the text (marked with an asterisk), with full author citations, listed alphabetically within four constituent groups.

## Pollen

*Alisporites ovatus* (Balme and Hennelly) Jansonius
*\*Alisporites parvus* de Jersey
*\*Barakarites rotatus* (Balme and Hennelly) Bharadwaj and Tiwari
*Caheniasaccites flavatus* Bose and Kar emend. Azcuy and di Pasquo
*Cannanoropollis densus* (Lele) Bose and Maheshwari
*Cannanoropollis janakii* Potonié and Sah
*Chordasporites endroedi* MacRae
*Corisaccites alutas* Venkatachala and Kar
*Crustaesaccites hessii* Cousminer
*\*Cycadopites caperatus* (Luber and Waltz) Hart
*Cycadopites cymbatus* (Bame and Hennelly) Hart
*Hamiapollenites dettmannae* Segroves
*\*Hamiapollenites fusiformis* Marques-Toigo emend. Archangelsky and Gamerro
*\*Hamiapollenites insolitus* (Bharadwaj and Salhuja) Balme
*Hamiapollenites karrooensis* (Hart) Hart
*\*Hamiapollenites* sp. cf. *Hamiapollenites gabonensis* Jardiné
*Illinites unicus* Kosanke emend. Jansonius and Hills
*Klausipollenites* sp. cf. *Klausipollenites vestitus* Jansonius
*Latusipollenites quadrisaccatus* Marques-Toigo
*Limitisporites* sp. cf. *Limitisporites luandensis* Bose and Maheshwari
*\*Lueckisporites brasiliensis* Cauduro
*\*Lueckisporites crassus* Sinha
*\*Lueckisporites densicorpus* Archangelsky and Gamerro
*\*Lueckisporites latisaccus* Archangelsky and Gamerro
*Lueckisporites nyakapendensis* Hart
*Lueckisporites singhii* Balme
*\*Lueckisporites stenotaeniatus* Menéndez
*Lueckisporites virkkiae* (Potonié and Klaus) Klaus
*Lunatisporites acutus* Leschik
*Lunatisporites noviaulensis* (Leschik) Foster
*\*Lunatisporites paliensis* Tiwari and Ram-Awatar
*Lunatisporites pellucidus* (Goubin) Helby emend. de Jersey
*\*Lunatisporites taeniaeformis* Jardiné
*Lunatisporites variesectus* Archangelsky and Gamerro
*Mabuitasaccites crucistriatus* (Ybert) Playford and Dino
*Marsupipollenites striatus* (Balme and Hennelly) Hart
*Pakhapites fasciolatus* (Balme and Hennelly) Hart
*Pakhapites fusus* (Bose and Kar) Menéndez
*Pakhapites ovatus* (Bose and Kar) García
*Peppersites ellipticus* Ravn
*Plicatipollenites malabarensis* (Potonié and Sah) Foster
*Plicatipollenites trigonalis* Lele
*Potonieisporites barrelis* Tiwari
*Potonieisporites congoensis* Bose and Maheshwari
*Potonieisporites densus* Maheshwari
*Potonieisporites lelei* Maheshwari
*Potonieisporites magnus* Lele and Karim
*Potonieisporites marleniae* Playford and Dino
*Potonieisporites neglectus* Potonié and Lele
*Potonieisporites novicus* Bhardwaj emend. Poort and Veld
*Protohaploxypinus amplus* (Balme and Hennelly) Hart
*\*Protohaploxypinus enigmaticus* (Maheshwari) Jardiné
*\*Protohaploxypinus goraiensis* (Potonié and Lele) Hart
*Protohaploxypinus haigii* Foster
*\*Protohaploxypinus microcorpus* (Schaarschmidt) Clarke
*Protohaploxypinus rugatus* Segroves
*Protohaploxypinus samoilovichii* (Jansonius) Hart
*\*Protohaploxypinus varius* (Bharadwaj) Balme
*Pteruchipollenites indarraensis* (Segroves) Foster

*Scheuringipollenites circularis* Césari, Archangelsky and Seoane
*Scheuringipollenites maximus* (Hart) Tiwari
*\*Scheuringipollenites medius* (Burjack) Dias-Fabricio
*\*Scheuringipollenites ovatus* (Balme and Hennelly) Foster
*\*Staurosaccites cordubensis* Archangelsky and Gamerro
*\*Striatoabieites anaverrucosus* Archangelsky and Gamerro
*Striatoabieites multistriatus* (Balme and Hennelly) Hart
*Striatopodocarpidites cancellatus* (Balme and Hennelly) Hart
*Striatopodocarpidites solitus* (Bharadwaj and Salhuja) Foster
*\*Striatopodocarpites fusus* (Balme and Hennelly) Potonié
*Striatopodocarpites phaleratus* (Balme and Hennelly) Hart
*Striomonosaccites cicatricosus* Archangelsky and Gamerro
*\*Taeniaesporites* sp. 1 of Jardiné
*\*Tornopollenites toreutos* Morgan
*Vitreisporites pallidus* (Reissinger) Nilsson
*Vittatina corrugata* Marques-Toigo
*Vittatina costabilis* Wilson
*Vittatina saccata* (Hart) Playford and Dino
*Vittatina* sp. cf. *Vittatina simplex* Jansonius
*Vittatina subsaccata* Samoilovich
*Vittatina vittifera* (Luber and Waltz) Samoilovich
*Weylandites lucifer* (Bharadwaj and Srivastava) Foster
*Weylandites magmus* (Bose and Kar) Bharadwaj and Dwivedi

## Spores

*Brevitriletes cornutus* (Balme and Hennelly) Backhouse
*\*Calamospora diversiformis* Balme and Hennelly
*Calamospora liquida* Kosanke
*Calamospora microrugosa* (Ibrahim) Schopf, Wilson and Bentall
*\*Calamospora plicata* (Luber and Waltz) Hart
*Cirratriradites africanensis* Hart
*\*Columinisporites* sp. cf. *Columinisporites peppersii* (as junior synonym of *Striatosporites heyleri*, see Playford and Dino 2000a)
*\*Converrucosisporites confluens* (Archangelsky and Gamerro) Backhouse
*Convolutispora ordonensis* Archangelsky and Gamerro
*\*Convolutispora pintoi* Dellazzana
*Convolutispora uruguaiensis* Mautino, Vergel and Anzótegui
*Cristatisporites morungavensis* (Dias Fabricio) Picarelli and Dias Fabricio
*Dictyotriletes cousmineri* di Pasquo and Grader
*Didecitriletes eoericianus* (Anderson) Millsteed
*Gondisporites* sp. cf. *Gondisporites imbricatus* Segroves
*\*Granulatisporites trisinus* Balme and Hennelly
*Horriditriletes ramosus* (Balme and Hennelly) Bharadwaj and Salujha
*\*Kraeuselisporites sanluisensis* Menéndez
*\*Kraeuselisporites splendens* (Balme and Hennelly) Segroves
*Laevigatosporites vulgaris* (Ibrahim) Ibrahim
*Leschikisporis chacoparanaensis* Vergel
*\*Lophotriletes cursus* Upshaw and Creath
*\*Lophotriletes rarus* Bharadwaj and Salhuja
*Lundbladispora braziliensis* (Pant and Srivastava) Marques-Toigo and Pons emend. Marques-Toigo and Picarelli
*Lundbladispora riobonitensis* Marques-Toigo and Picarelli
*\*Lycospora pusilla* (Ibrahim) Schopf, Wilson and Bentall emend. Somers
*Lycospora variabila* Cousminer
*\*Neoraistrickia* aff. *Neoraistrickia ramosa* Balme and Hennelly
*Polypodiisporites mutabilis* Balme
*Polypodiites secoensis* Mautino, Vergel and Anzótegui
*\*Punctatisporites gretensis* Balme and Hennelly
*Punctatisporites minutiarcus* Cousminer

*Reticuloidosporites warchianus* Balme
*Retusotriletes nigritellus* (Lüber) Foster
*Striatosporites heyleri* (Doubinger) emend. Playford and Dino
*\*Thymospora criciumensis* Quadros, Marques-Toigo and Cazzulo-Klepzig
*Thymospora criciumensis* Quadros, Marques-Toigo and Cazzulo-Klepzig
*Thymospora rugulosa* Mautino, Vergel and Anzótegui
*\*Triquitrites* aff. *Triquitrites tumulosus* Imgrund
*Triquitrites* sp. cf. *Triquitrites kaiseri* Playford and Rigby

## Algae

*Botryococcus braunii* Kützing
*Brazilea scissa* (Balme and Hennelly) Foster

*Reduviasporonites chalastus* (Foster) Elsik
*Tetraporina punctata* (Tiwari and Navale) Kar and Bose

## Acritarchs

*Deusilites tenuistriatus* Gutiérrez, Césari and Archangelsky

## Plant fossils

*Lycopodiopsis pedroanus* (Carruthers) Edwards [=*Brasilodendron pedroanum* (Carruthers) Chaloner, Leistikow, Hill]
*Dizeugoteca branisae* Arrondo