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# Middle Devonian microfloras and megafloras from western Argentina and southern Bolivia: their importance in the palaeobiogeographical and palaeoclimatic evolution of western Gondwana

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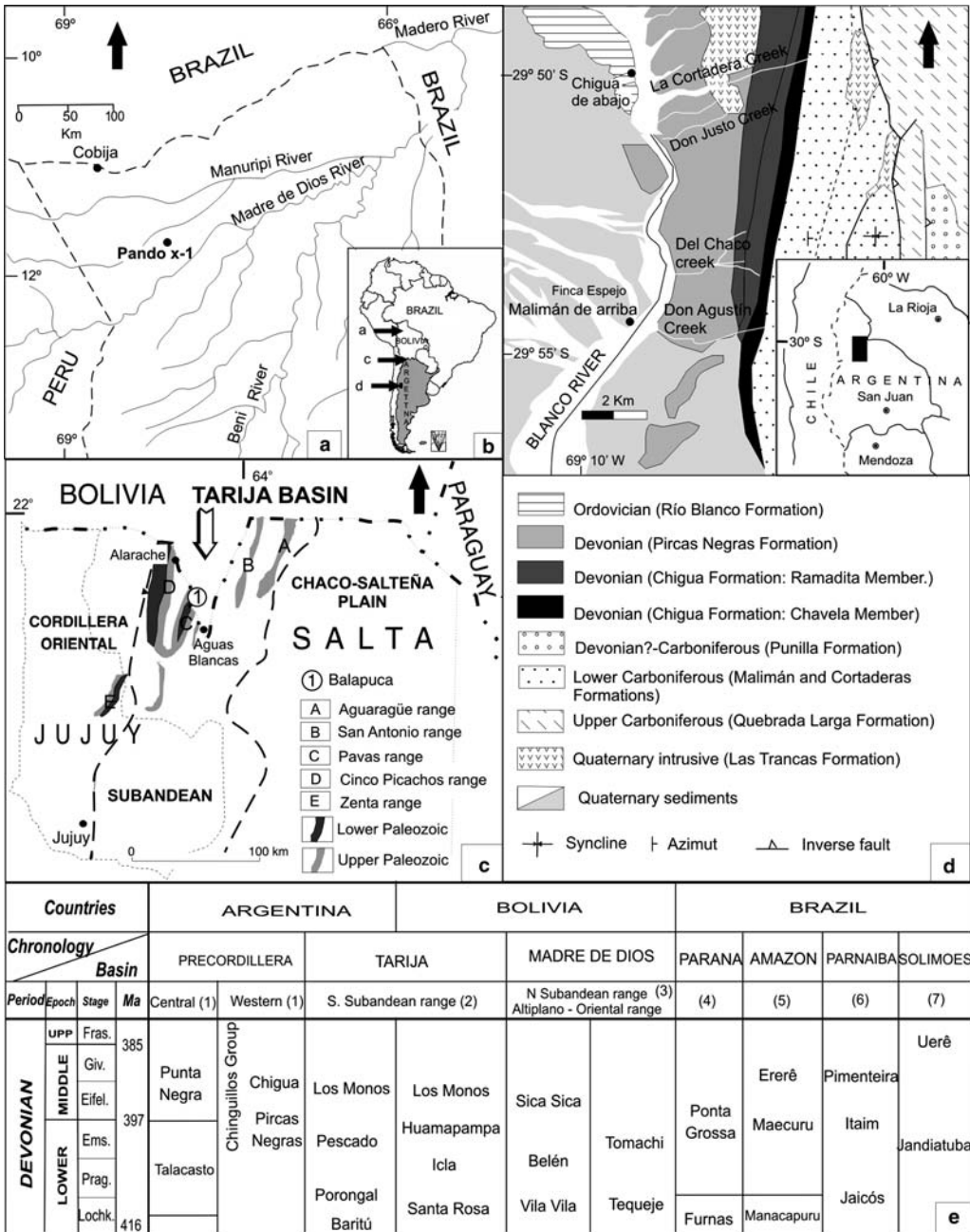
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**Abstract:** The study of microfloras and megafloras from western Argentina and southern Bolivia presented here extends our knowledge of the biodiversity and succession of floristic events during the Middle Devonian, and hence improves the current biostratigraphy. Among floral remains, species attributable to ‘*Haplostigma*’ are mostly recorded from the same *Grandispora pseudoreticulata* and other palynomorph-bearing sections at Balapuca (southern Bolivia) and Del Chaco and La Cortadera creeks in the Precordillera of Argentina. The northernmost record of *Grandispora pseudoreticulata* is recorded from a third palynoassemblage from the Pando x-1 corehole of northern Bolivia. A great similarity among all these assemblages (notably abundant *Grandispora pseudoreticulata*) suggests the identification of terrestrial connections, or at least proximity, of these local areas and other regions in South America during the Givetian. Comparison with other contemporary Gondwanan palynofloras shows cosmopolitan species (e.g. *Geminospora lemurata*, *Samarisporites triangulatus*, *Archaeozonotriletes variabilis*, *Chelinospora concinna*) along with some others with more restricted distribution (e.g. *Grandispora pseudoreticulata*, *Leiotriletes balapucensis*, *Acinosporites ledundae*). This pattern defines an Afro-South American Subrealm, which most likely results from the effects of palaeolatitude and, in a lesser way, local palaeoenvironmental conditions. On the other hand, such a level of cosmopolitanism supports previous palaeogeographical reconstructions where a narrow Rheic Ocean was developed between Euramerica and the northern parts of Africa and South America.

**Supplementary material:** Stratigraphical and geographical distributions of selected species recorded from Middle and Late Devonian Argentina, Bolivia and Brazil microfloras are available at: <http://www.geolsoc.org.uk/SUP18335>.

The microfloras and megafloras from southern Bolivia and western Argentina have recently provided important evidence to extend knowledge on the biodiversity and succession of floristic events during the Middle Devonian, and therefore contribute to the improvement of our current biostratigraphy. This contribution aims to present for the first time a record of both plant and palynological assemblages from Balapuca located on the Bolivian side of the Bermejo River (San Telmo–de las Pavas Range), and Del Chaco Creek, in the Volcán Range of the Precordillera of Argentina. Both outcrops contain plants attributed to ‘*Haplostigma*’ Seward 1932 and mostly continental palynomorphs with many species of *Grandispora*. The Pando x-1 Borehole in northwestern Bolivia has provided scarce specimens of *Grandispora pseudoreticulata* from one core sample. These new records allow an update of the palaeogeographical and stratigraphical

distribution of selected *Grandispora* and ‘*Haplostigma*’ species based on comparison with coeval or similar floras from Gondwanan South America and beyond (Figs 1–3; see Supplementary Material). In addition, it enables an evaluation of the degree of endemism of these palaeofloras and hence the identification of when terrestrial connections between these areas existed. Also analysed is the interaction of the main factors that controlled the development of these floras such as palaeoclimate, palaeoenvironment and palaeogeography. In this sense, some taphonomical features are analysed and discussed considering the previous palaeoenvironmental interpretations. Finally, a palaeobiogeographical region is proposed based on the correlation of the assemblages involved and the stratigraphical and geographical distribution of *Grandispora pseudoreticulata* and ‘*Haplostigma*’ for the Middle and Late Devonian of Western Gondwana.



**Fig. 1.** (a–d) Location maps of the studied localities: (a) Pando x-1 borehole; (b) the three localities in South America; (c) Balapuca; and (d) La Cortadera and Del Chaco creeks. (e) Correlation of Devonian units of Argentina, Bolivia and Brazil. References: (1) Rubinstein (1999, 2000); (2) Starck (1996, 1999), Suárez Soruco (2000); (3) Díaz Martínez (1999), Suárez Soruco (2000); (4) Dino (1999); (5) Melo & Loboziak (2003), Grahn (2003); (6, 7) Grahn *et al.* (2003). Absolute time dates after Gradstein *et al.* (2004). Note that there are relatively huge differences between this scale and the one proposed more recently by Menning *et al.* (2006), where the Emsian–Eifelian boundary is dated at 392 Ma and the Givetian–Frasnian at 381 Ma.

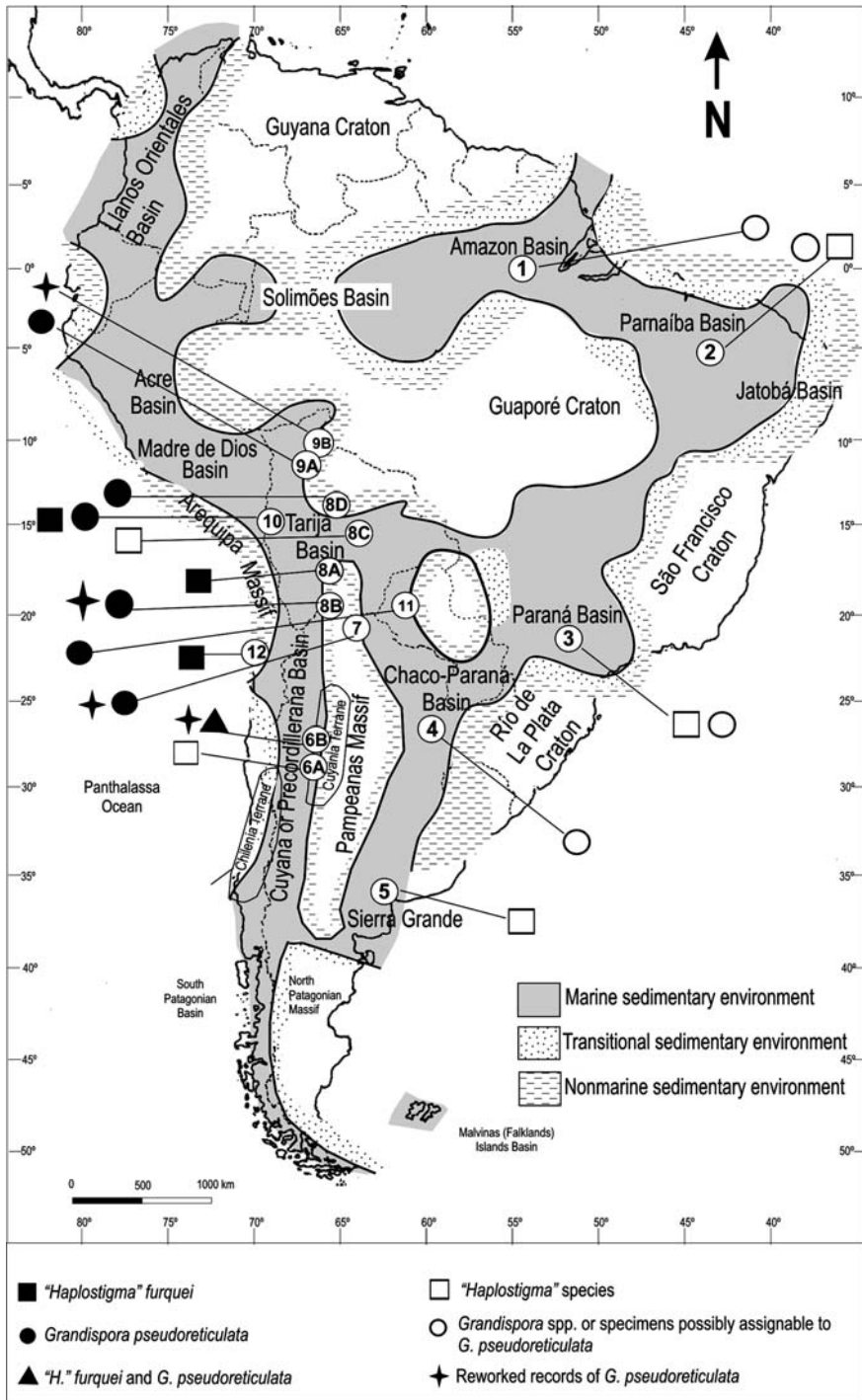


Fig. 2. Location of known occurrences of *Grandispora pseudoreticulata* and species of '*Haplostigma*' recorded in South America on a palaeogeographical reconstruction modified from Cuerda & Baldi (1971) and Melo (1989). Key: 1, Amazon Basin (Melo & Loboziak 2003). 2, Parnaíba Basin, Pimenteira Formation (Suárez Riglos 1975; Rodríguez *et al.* 1995). 3, Paraná Basin, Ponta Grossa Formation (Kräusel 1960; Daemon *et al.* 1967). 4, Chaco-Paraná Basin (Antonelli &

## Summary of stratigraphy and palaeontology

The stratigraphical development, palaeontological content, facies and palaeoenvironments of the Devonian of southern Bolivia, northern Argentina and the western Precordillera of Argentina are of such an extent that numerous studies are still required to understand the geological history of each of the regions and the group in general. The Devonian rocks in northern Argentina are exposed in the Sub-Andean and Santa Barbara mountains plus in the subsurface of greater part of the Chaco-Salteña and the Chaco-Paranense Plains (Fig. 1c, e). They comprise essentially marine sedimentary rocks of the Tarija Basin that extends to central Bolivia and northwestern Paraguay. These marine deposits would have been interconnected with other neighbouring marine rocks registered in the Arizaro (northern Chile and the Puna of Argentina) and the Madre de Dios (northern Bolivia and southern Peru) basins together with other basins in eastern Argentina and Brazil based on common palaeontological content (Fig. 2; see Grahn 2005). In general terms, the very extensive lateral distribution of the carbonaceous mudstones has sourced the deposits of petroleum and gas that mainly occur in the Sub-Andean Bolivian region (e.g. Starck 1999). For this reason this particular basin has been extensively studied for petroleum exploration. Many multidisciplinary works based on subsurface and surface information have been carried out by different oil companies, although published accounts are less numerous (e.g. Suárez Soruco 2000; Dalenz Farjat *et al.* 2002; Albariño *et al.* 2002; Alvarez *et al.* 2003).

Inevitably the number of Middle and Late Devonian palaeobotanical and palynological records from different areas around the world is very variable. For South America these are still few in comparison to those from North America and Europe. For northern Argentina, there are a few publications on Devonian microfloras that contain systematic descriptions and illustrations of spores, acritarchs and chitinozoans, notably Volkheimer *et al.* (1986), Barreda (1986), Ottone (1996), Grahn & Gutierrez (2001) and Grahn (2002). Menéndez & Pöthe de Baldis (1967) and

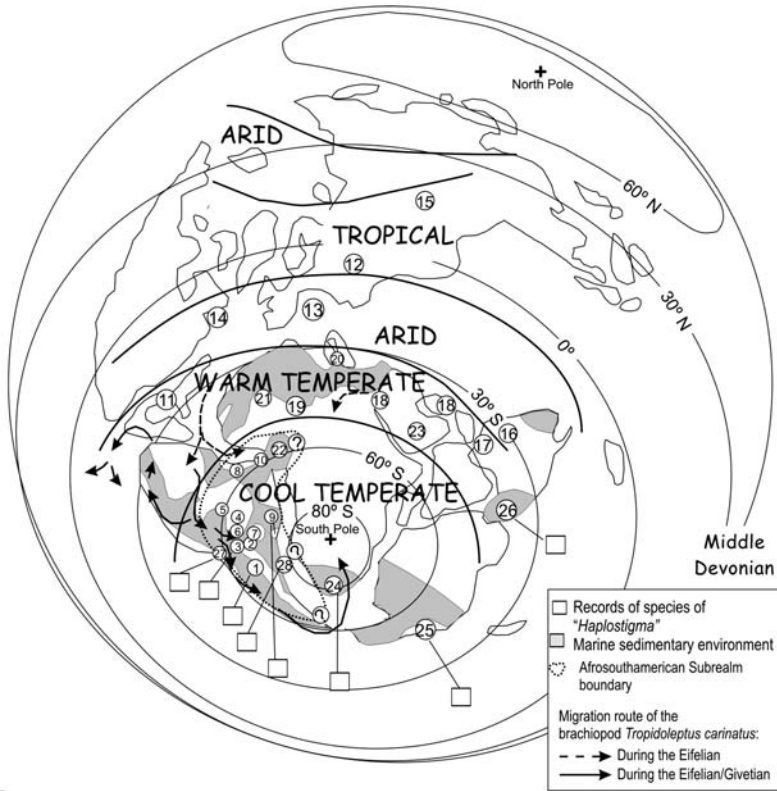
Pöthe de Baldis (1974, 1979) described and illustrated palynomorphs found in the Picuiba Borehole from northwestern Paraguay. For southern Bolivia, there are several stratigraphical, biostratigraphical and palaeobiogeographical contributions, some of which were illustrated; these include Lobo Boneta (1975), Suárez Soruco & Lobo Boneta (1983), Kimyai (1983), McGregor (1984), Wood (1984, 1994, 1995), Pérez Leyton (1990, 1991), Racheboeuf *et al.* (1993), Blicek *et al.* (1996), Grahn (2002, 2005) and di Pasquo (2005, 2007a, b). For northern Bolivia there are publications by Vavrdová *et al.* (1993, 1996), Ottone & Rossello (1996), Vavrdová & Isaacson (1999) and Díaz Martínez *et al.* (1999). Both Suárez Soruco & Lobo Boneta (1983) and Limachi *et al.* (1996) proposed biostratigraphical schemes for the Devonian to Permian based on lists of species but without illustration. Melo (2005) presented new palynostratigraphical results from some Devonian units in Bolivia but included neither lists nor illustrations of palynomorphs. Some of these works need to be revised; none of them are sufficiently detailed to understand the evolution of the microfloras in this region of Gondwana and cannot be applied with certainty to new localities or compared with other microfloras of more distant regions.

Plant occurrences in the Devonian of northern Argentina and Bolivia are rarely documented: Suárez Soruco (1988) contains illustrations, while other reviews lack them (Suárez Riglos 1975; Archangelsky 1993). The Bolivian material of the genus '*Haplostigma*' has not been revised previously and very few illustrations of the specimens were included in Branisa (1965) and Suárez Soruco (1988).

In the Precordillera Range in San Juan Province, northwestern Argentina, Devonian deposits belonging to the Chinguillos Group (Pircas Negras and Chigua formations, see Figs 1, 2), are present to the east of the Blanco River, in the western slope of the Punilla and Volcán ranges of the Cuyana or Precordillera Basin (Padula *et al.* 1967). The Chigua Formation (c. 700 m) overlies the Pircas Negras Formation with a thrust contact and is separated by an angular unconformity from the overlying Malimán Formation (Early Viséan; Amenábar 2006, 2007b). The Chigua Formation is divided

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**Fig. 2.** (Continued) Ottone 2006). 5, Sierras Australes, Lolén Formation (Cingolani *et al.* 2002). 6, Cuyana or Precordillerana Basin; 6A, Punta Negra Formation (Baldis & Peralta 2000); 6B, Chigua Formation (Gutiérrez 1996; Amenábar *et al.* 2006) and Malimán Formation (Early Viséan; Amenábar 2006) as a reworked form. 7, Tarija Basin, Los Monos (Middle Devonian) (Ottone 1996) and Macharefí and Mandiyutí Goups (Late Carboniferous; see di Pasquo & Azcuy 1997; di Pasquo 2003) as a reworked form. 8A, Huamampampa Formation (Finca Carlazo; Branisa 1965). 8B, Los Monos Formation, Balapuca (di Pasquo 2007a) and Itacua formations (Early Viséan; di Pasquo 2007b). 8C, Huamampampa, Los Monos, Iquirí formations (Campo Redondo (Suárez Riglos 1975), Lajas (Wood 1995)). 8D, Los Monos, Iquirí formations (Bermejo River, Santa Cruz; Pérez Leyton 1991). 9, Madre de Dios Basin: 9A, Pando x-1 Borehole (this contribution); 9B, Kaka Formation (Serpukhovian; Azcuy & Ottone 1987) as a reworked form. 10, Vila Molino, Titicaca lake (Vavrdová & Isaacson 2000) and Sica Sica (Branisa 1965). 11, Picuiba Borehole (Menéndez & Pöthe de Baldis 1967). 12, El Toco Formation (Antofagasta region; Moisan & Niemeyer 2005).



**Fig. 3.** Middle Devonian palaeogeographical map (modified from Isaacson & Sablock in Wood 1995) with palaeoclimatological zones (based on Scotese *et al.* 1999) showing the marine deposits with the migration route of the brachiopod *Tropidoleptus carinatus* (after Fonseca & Melo 1987) and the location of known Middle Devonian palynological assemblages, some of which contain *Grandispora pseudoreticulata* and other endemic species of the Afro-South American Subrealm. Key. Argentina: 1A, Chigua Formation (Amenabar 2007a, b, 2009); 1B, Villavicencio Formation (Rubinstein & Steemans 2007); 1C, Talacasto Formation (Le Hérisse *et al.* 1997); 1D, Punta Negra Formation (Rubinstein 1999, 2000). 2, Los Monos Formation (Barreda 1986; Ottone 1996). Bolivia: 3, Los Monos Formation (di Pasquo 2007a). 4, Limachi *et al.* (1996), Pérez Leyton (1991). 5A, Tomachi Formation (Vavrdová *et al.* 1996); 5B, Ottone & Rossello (1996). 6, Kimyai (1983), McGregor (1984), Blicek *et al.* (1996). Paraguay: 7, Menéndez & Pöthe de Baldis (1967), Pöthe de Baldis (1974, 1979). Brazil: 8, Maecurú, Ererê and Barreirinha formations (Melo & Loboziak 2003; Loboziak & Streele 1995); Jandiutuba and Uerê formations (Quadros 1988; Grahn *et al.* 2003). 9A, Ponta Grossa Formation (Loboziak & Streele 1995; Dino 1999; Quadros 1999); 9B, Daemon *et al.* (1967; biozones correlated to Dino 1999); 9C, Oliveira (1997); 10, Pimenteira Formation (Rodríguez *et al.* 1995). Old Red Sandstone Continent: 11, McGregor (1979), McGregor & Camfield (1976, 1982), Richardson & McGregor (1986), Ravn & Benson (1988). Pomerania: 12, Turnau (1996). France: 13, Le Hérisse & Deunff (1988). Canada: 14, Braman & Hills (1992), Cloutier *et al.* (1996). Russia: 15, Avchimovitch *et al.* (1993). Australia: 16, Hashemi & Playford (2005). 17, Colbath (1990), Playford & Dring (1981), Balme (1988). Iran: 18, Ghavidel-Syooki (1994, 2003), Hashemi & Playford (1998). Libya: 19A, Moreau-Benoit (1979, 1980), Loboziak & Streele (1989), Steemans *et al.* (2007a); 19B, Paris *et al.* (1985), Streele *et al.* (1988). Tunisia and Libya: 20, Loboziak & Streele (1995). Algeria: 21, Moreau-Benoit *et al.* (1993). Ghana: 22, Bär & Riegel (1974). Saudi Arabia: 23A, Loboziak (2000); 23B, Breuer *et al.* (2007b); 23C, Marshall *et al.* (2007). Records of species of 'Haplostigma' in the rest of Gondwana: 24, Karoo Basin, South Africa (Anderson & Anderson 1985). 25, Antarctica (Edwards 1990; McLoughlin & Long 1994). 26, Australia, New South Wales (McLoughlin & Long 1994). 27, El Toco Formation, Antofagasta, Chile (Moisan & Niemeyer 2005). 28, Lolén Formation, Sierras Australes, Argentina (Cingolani *et al.* 2002).

into two members, the lower Chavela (marine) and the upper Ramadita (marine–continental) (see Baldis & Peralta 2000). The lithology mainly consists of shales with concretions and calcareous lenses with subordinate sandstone layers, with rock colours

varying from green to brown. The succession is rich in fossiliferous levels, including flora and marine invertebrates. The latter include the trilobites *Punilaspis argentina* Baldis and *Phacops chavelai* Baldis & Longobucco, the cephalopods *Tornoceras*

*baldisi* Leanza and *Orthoceras* sp., and the cnidarian *Conularia* sp. (e.g. Furque 1956, 1963; Baldis & Sarudiansky 1975; Baldis & Longobucco 1977), whilst the palaeoflora is composed of the herbaceous lycophytes '*Haplostigma*' *furquei* Frenguelli and ?*Cyclostigma* sp. (Frenguelli 1952, 1954; Gutierrez 1996; Gutierrez & Archangelsky 1997). New palynological data from Devonian deposits of the Malimán area are presented by Amenábar (2006, 2007a, b, 2009) and Amenábar *et al.* (2006, 2007) (see also Supplementary Material). There are other few recent palynological contributions from the Precordillera Range of western Argentina but those with illustrated lists of palynomorphs include Le Hérisse *et al.* (1997), Rubinstein (1993, 1999, 2000) and Rubinstein & Steemans (2007). It is emphasized that the Precordillera has suffered strong tectonic activity not only during the Middle to Late Palaeozoic but also during the Andean Orogeny (cf. Alonso *et al.* 2005). This would be the main reason for poor preservation (or absence) of organic matter in most of the Devonian sediments and the difficulty of finding more complete sections.

Most of the palynological references mentioned above are part of the database (see Supplementary Material), along with others from Brazil, Africa, Antarctica, Australia and the rest of the world. It is also interesting to note that, in the Gondwana region, faunas and floras contain significant numbers of cosmopolitan taxa which allow correlation with palaeo-equatorial assemblages (e.g. Streef & Loboziak 1996). But a quite variable degree of regional microflora and some disparities in the vertical range of species may have some palaeogeographical and palaeoclimatic meaning, which is discussed later.

### Description of studied material

The characteristics, comparisons and age of the palynoassemblages collected from three localities are summarized as follows (see Figs 1–6).

#### *Balapuca* section (22°31'00"S, 64°26'00"W)

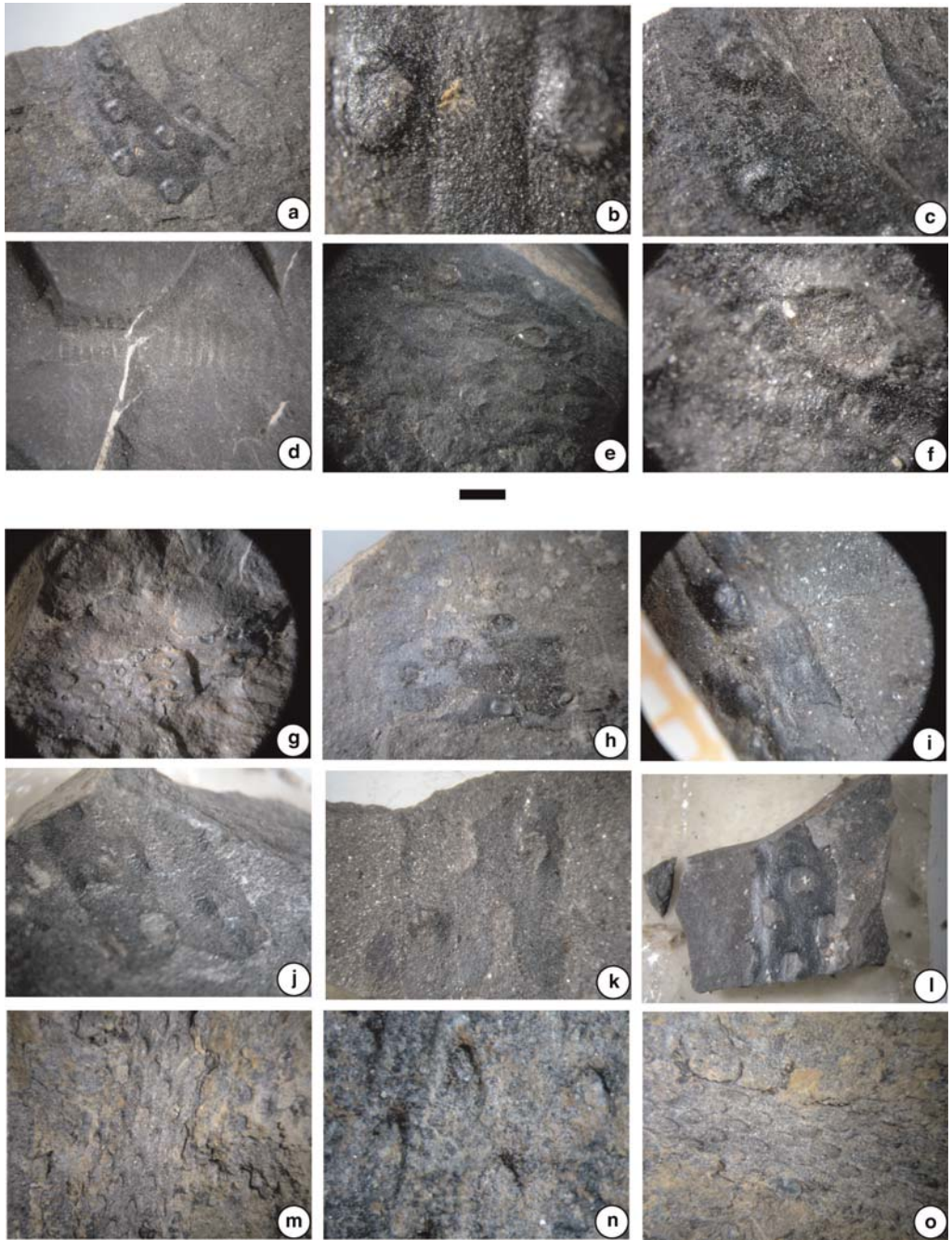
Recently, di Pasquo (2005, 2007a, b) published detailed stratigraphical and palynological information from the Middle Devonian Los Monos and the Lower Carboniferous Itacua Formations at Balapuca (Fig. 1). The upper section of the Los Monos Formation, c. 50 m thick, appears to be unconformable below the Itacua Formation (early Viséan) and is mainly composed of mudstones interbedded with sandstones representing tempestite and normal shelf deposits. According to di Pasquo (2005), the stratigraphical distribution of the species found in the Los Monos Formation at Balapuca enabled recognition of two assemblages composed of abundant plant debris (cuticles, tracheids, other brown to black

phytoclasts) and amorphous organic matter; the proportion of major palynological groups (spores, acritarchs, prasinophytes, chitinozoans) is variable in different samples but spores are always dominant over the microplankton. In assemblage 1 (A1) the dominant elements are of continental origin, with many specimens of diverse species of *Grandispora* associated with scarce marine palynomorphs, represented by acritarchs (*Leiosphaeridia*, *Navifusa*) and chitinozoans. Additionally, fragmented moulds of hyolithes, crinoid stems (see Fig. 4d) and trilobites plus the lycophytes referred to '*Haplostigma*' *furquei* (BAFC-Pb 16999 to 17003; BAFC-PI 1281) by di Pasquo (2007a) were recorded. The plant remains are composed of fragmented carbonaceous compressions and impressions of the herbaceous stems (Fig. 4). This section is composed of dark siltstones interbedded with bioturbated rippled sandstones and is interpreted as deposited on a shallow marine shelf.

The overlying assemblage 2 (A2) (BAFC-PI 1268 and 1269) is slightly more diverse, with abundant phytoclasts (tracheids, cuticles, charcoal) and many specimens of *Grandispora* and megaspores attributed to *Biharisporites* along with rare prasinophytes and acritarchs (generally spheroidal forms without processes) and chitinozoans. Only plant remains appeared with the palynomorphs in a black diamictitic deposit with a mudstone matrix that includes clasts of the underlying unit (see di Pasquo 2007a). This section was probably deposited in the same marginal palaeoenvironment as A1 but invertebrate fossils were not recovered. Di Pasquo (2007a) attributed A1 to the late Eifelian mainly based on the absence of *Geminospora lemurata* and other related species that first appear in the Givetian, and A2 to the early late Givetian to the base of the Frasnian, due to the presence chiefly of *Samarisporites triangulatus* and its correlation to the *optivus*–*triangulatus* Biozone Richardson & McGregor (1986), and the *Trg* Zone of Melo & Loboziak (2003) (Fig. 6).

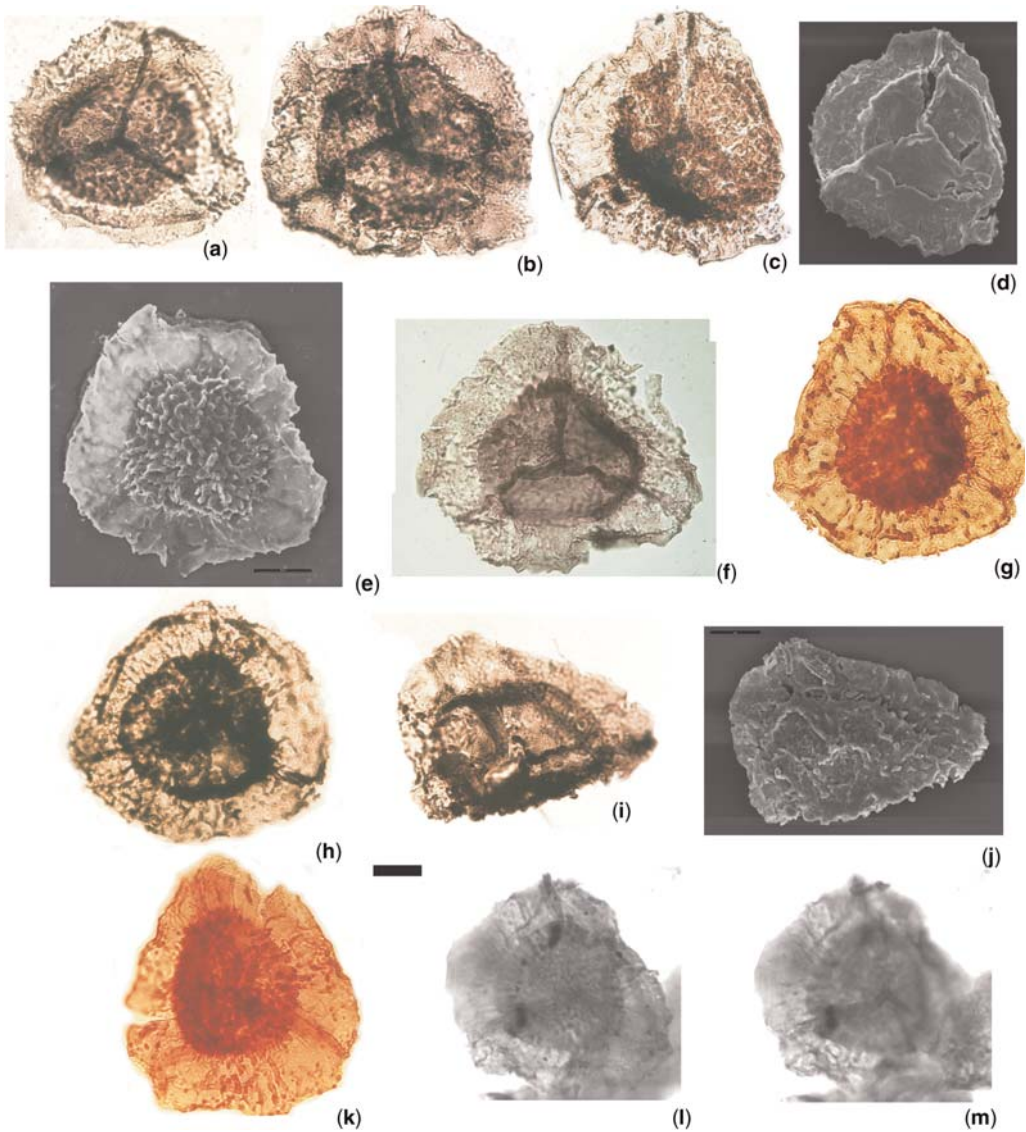
#### *Pando x-1* Borehole (11°36'07"S, 67°56'45"W)

Vavrdová *et al.* (1996) provided the first palynological study of this completely cored drilling located in northern Bolivia (see Figs 1, 2). More than 60 samples from the Devonian to Permian section of this borehole were collected by M.d.P. during a field trip to Bolivia in 2000 with permission of Pluspetrol S.A. This yielded 59 productive samples from which 26 levels between 1929–1932 m and 1203–1206 m correspond with certainty to the Devonian. They include 14 samples that cover the section between 1559.30 and 1189.09 m that was not sampled by Vavrdová *et al.* (1996). Preliminary examination of all the samples enabled the recognition only at 1260/63 m deep



**Fig. 4.** '*Haplostigma*' species from Bolivia and Argentina. (a) '*Haplostigma*' sp. BAFC-Pb 17003. Scale bar 3.3 mm. (b) Detail of the scars rib and furrows of (a). Scale bar 0.6 mm. (c) Detail of the disposition of the scars of (a). Scale bar 1.3 mm. (d) Impression of transported crinoid stem. Scale bar 3 mm. (e) '*Haplostigma*' sp. BAFC-Pb 16999. Scale bar 3.8 mm. (f) Detail of the scar of (e). Scale bar 1.4 mm. (g) '*Haplostigma*' sp. BAFC-Pb 17000. Scale bar 3.5 mm. (h) Detail of the scars in the counterpart of (g). Scale bar 1.7 mm. (i) Detail of the scars, ribs and furrows from part of (g). Scale bar 1 mm. (j, k) Part and counterpart '*Haplostigma*' sp. BAFC-Pb 17002. Scale bar 3.1 mm. (l) '*Haplostigma*' sp. BAFC-Pb 17001. Scale bar 0.3 mm. (m–o) '*Haplostigma*' sp. from Precordillera, BAFC-Pb 16998. (m, o) Scale bar 3.1 mm. (n) Detail of the phyllotaxis and scars. Scale bar 7.5 mm.





**Fig. 5.** *Grandispora pseudoreticulata* (Menéndez & Pöthe de Baldis) Ottone. (a, c–f). Precordillera (Chigua Formation, La Cortadera Creek): (a) BAFC-PI 1656 (1): H23; (c, d) BAFC-PI 1505; (e, f). BAFC-PI 1655(SEM) Q44. (b) Precordillera (Chigua Formation, Del Chaco Creek), BAFC-PI 1780 (1): J25/4. (g) Precordillera (Malimán Formation, La Cortadera Creek), reworked specimen. BAFC-PI 1508 (4): P44. (h–j). Los Monos Formation (Balpuca, San Telmo Range, Tarija department): (h) BAFC-PI 1269(1): Y35/2; (i, j). BAFC-PI 1269 (SEM) J45/2. (k) Itacuamí Formation (Tuyunti Creek, Salta), reworked specimen. BAFC-PI BAFC-PI 1154 (1): Y39/4. (l, m). Pando x-1 Borehole, Bolivia. BAFC-PI 1534 (5): M61/1. Scale bar 20  $\mu$ m.

(BAFC-PI 1534) of scarce specimens attributable to *Grandispora pseudoreticulata* (Fig. 5l, m). This assemblage would probably be akin to the Frasnian due to the presence of *Acinosporites eumammillatus* and several species of genera such as *Maranhites*, *Ancyrospora* and *Hystricosporites*. More detailed studies are in progress.

#### *La Cortadera and Del Chaco creeks* (29°53'S, 69°7'W)

Palynoassemblages from the Chigua Formation (Chavela Member), exposed in the eastern part of the Blanco River, Del Volcán Range, western Precordillera Argentina (Figs 1 and 2), were recently

SYSTEM	SERIE	REGION	Euroamerica A	Brazil B	Bolivia C	Bol-Arg D	Argentina (Precordillera) E	
DEVONIAN	LATE	FAMENNIAN	<i>lepidophyta-nitidus</i>	<i>R. lepidophyta</i> - <i>V. vallatus</i>	?	HIATUS	HIATUS	
			<i>pusillites-lepidophyta</i>	<i>R. lepidophyta</i>	<i>R. lepidophyta</i>			
			<i>flexuosa-cornuta</i>	<i>V. hystricosus</i> <i>R. radiata</i>	?			
			<i>torquata-gracilis</i>	<i>T. torquata</i> - <i>A. pseudocrista</i>				
		FRASNIAN	<i>ovalis-bulliferus</i>	<i>R. bricei-D. mucronatus</i> <i>V. bulliferus</i> - <i>G. piliformis</i>	Maranhites- Samarisporites			
			<i>C. optivus</i> - <i>C. triangulatus</i>	<i>S. triangulatus</i>				
	MIDDLE	GIVETIAN	<i>lemurata-magnificus</i>	<i>G. lemurata</i> - <i>Ch. ligurata</i>	<i>V. premnus</i> - <i>V. scurrus</i>	No information	A2	Palynoass. 3
			<i>devonicus-naumovii</i>	<i>G. permulta</i>				Palynoass. 2
		EIFELIAN	<i>velatus-langii</i>	<i>Grandispora</i> - <i>Samarisporites</i>	<i>pseudoreticulata</i>	<i>H.</i>	A1	?
	<i>douglastownense</i> - <i>eurapterota</i>							
	EARLY	EMSIAN	<i>annulatus</i> - <i>sextanti</i>	HIATUS	<i>Evittia sommeri</i> - <i>Emph. annulatus</i>			
			PRAGIAN	<i>polygonalis</i> - <i>emsiensis</i>	<i>D. emsiensis</i>	HIATUS		
		<i>breconensis</i> - <i>zavallatus</i>						
		LOCHKOVIAN	<i>micromatus</i> - <i>newportensis</i>		<i>Schisocystia</i> - <i>Dictyotriletes</i>			

Fig. 6. Summary correlation chart of the assemblages studied (D, E) from the Balapuca, La Cortadera and Del Chaco sections, with other Devonian biozones or assemblages of Euroamerica (A), Brazil (B) and Bolivia (C), and the stratigraphical ranges of selected spore species recovered. References: A, Richardson & McGregor (1986); B, Melo & Loboziak (2003); C, Suárez Soruco & Lobo Boneta (1983), Limachi *et al.* (1996); D, di Pasquo (2007a); E, Amenábar *et al.* (2006), Amenábar (2007b). Correlation chart modified from di Pasquo (2007a).

studied by Amenábar *et al.* (2006, 2007) and Amenábar (2007a, b, 2009). The Chigua Formation (Devonian) unconformably underlies the Carboniferous sediments of the Malimán Formation at La Cortadera Creek. But, in the Del Chaco Creek the top and base of the Devonian section are delimited by faults. The fossiliferous samples collected at La Cortadera (BAFC-PI 1505, 1656) were obtained from carbonaceous shales which also contain trilobites (e.g. *Punillaspis argentina* Baldis). The microflora has yielded more or less the same ratio of *Grandispora pseudoreticulata* and microplankton specimens. Amenábar (2007a, b, 2009) attributed the assemblage from La Cortadera Creek to the Middle Devonian (early Givetian), based on the range of key species that are recognized in the *D. devonicus*-*G. naumovii* (DN) and *G. lemurata*-*C. magnificus* (LM) Richardson & McGregor (1986) and the GS, Per and LLi Interval zones Melo & Loboziak 2003 (Fig. 6). This assemblage would represent the time between the A1 and A2 assemblages from the Los Monos Formation at Balapuca.

Samples from the Del Chaco Creek (BAFC-PI 1797, 1798, 1780) are characterized by miospores, acritarchs, prasinophytes and chitinozoans, with

many specimens of *Grandispora pseudoreticulata* (Fig. 5). Two assemblages are distinguished (Fig. 6): one obtained from shales (BAFC-PI 1797) is very rich in microplankton (A1) while the other (BAFC-PI 1780) has spores as the dominant element (A2). Lycophyte remains are present in fine sandstones interbedded within the section bearing the latter sample; they comprise mainly impressions of stems parallel to bedding planes at several levels (Fig. 4). The third level (BAFC-PI 1798) has very few palynomorphs so it is not considered further.

Assemblage 1 (A1) is characterized by high microplankton diversity (26 species = 72% of the total of the association) and spores as subordinate elements (10 species = 28%). Some biostratigraphically important spores are *Dictyotriletes emsiensis* Morphon, *Emphanisporites decoratus*, *Acinosporites hirsutus* and *Grandispora* spp. The *D. emsiensis* morphon has been recorded in the Talacasto Formation (Central Precordillera of Argentina), where the assemblage was attributed to the late Lochkovian-Emsian (Le Hérisse *et al.* 1997). In Brazil, it is recognized in the late Lochkovian-Emsian deposits from the Solimões (Rubinstein

et al. 2005), Paraná (Dino 1999) and Amazon basins (Melo & Loboziak 2003). According to Melo & Loboziak (2003) the *Grandispora/Samarisporites* spp. (GS) Interval Zone (late Emsian–early Eifelian) is characterized by the appearance of large spinose pseudosaccates/zonates spores of the genera *Grandispora*, *Samarisporites* and *Craspedispora*. Some species such as *Dictyotriletes emsiensis* are more typical of the Early Devonian but they do not persist into younger biozones. Thus, palynoassemblage 1 was attributed to the late Emsian–early Eifelian due to the co-occurrence of *Dictyotriletes emsiensis* morphon and species of *Grandispora* (Fig. 6).

In contrast, assemblage 2 (A2) is dominated by continental elements with 19 species of spores and five species of microplankton representing 79% and 21% respectively. Pseudosaccate spores of the genus *Grandispora* are especially dominant (e.g. *Grandispora mammillata*, *G. pseudoreticulata*) and other diagnostic spore species are *Acinosporites hirsutus*, *A. macrospinosus*, *A. acanthomammillatus*, *Corystisporites horridus*, *Dibolisporites* sp. cf. *D. eifeliensis* and *Leiotriletes balapucensis*. This level is correlated to the levels BAFC-PI 1505 and 1656 recorded from La Cortadera Creek on the basis of common species including some of those mentioned above. These taxa together with *Acinosporites hirsutus*, *A. macrospinosus*, *Acanthotriletes horridus* and *Grandispora mammillata* enable this assemblage to be assigned to the early Givetian and correlate to the *D. devonicus*–*G. naumovii* (DN) and *G. lemurata*–*C. magnificus* (LM) Zones Richardson & McGregor (1986) and the GS, Per and LLI Interval Zones Melo & Loboziak 2003 (see Fig. 6).

Considering the co-occurrence of trilobites comparable to those of the *Acanthopyge balliviani* zone (Eifelian or Emsian, according to different authors, see Baldis & Saurdiansky 1975) defined in Bolivia, with the cephalopod genus *Tornoceras* (Frasnian) in the Chigua Formation, Baldis & Saurdiansky (1975) suggested that the range of the unit would be from the Emsian–Eifelian boundary up to the Givetian–Frasnian boundary. Therefore, these authors indicated that the presence of *Tornoceras* could reduce the age range of *A. balliviani* and thus they propose a tentative Givetian age for the Chavela Member of the Chigua Formation.

## Methods

The plant specimens were studied with a stereo microscope under magnifications between  $\times 8$  and  $\times 50$ . The illustrations were taken with a Sony Cyber-shot DSC-P200 7.2 megapixel camera. Standard palynological isolation was carried out on

udstone samples to obtain the organic residues. They were extracted from crushed samples, treated first with hydrochloric acid and then hydrofluoric acid to remove carbonate, silica and silicates, respectively, and finally mounted on slides with glycerin jelly. Identification of the palynomorphs was undertaken using both Leitz Orthoplan and Nikon Eclipse 80i binocular transmitted light microscopes, with  $\times 1000$  maximum magnification. The photomicrographs were obtained with Motic (2.0 megapixels) and Pax-it (3.1 megapixels) video cameras. The illustrations are indicated by the BAFC-PI acronym followed by the England Finder reference. The microfossils were processed and deposited at the Department of Geology of the Faculty of Natural and Pure Sciences (University of Buenos Aires) under the prefix BAFC-PI (palynology) along with megafossils (BAFC-Pb for plants). Surface details of the spores were photographed under SEM with a Phillips series XL model 30 at the Natural Science Argentine Museum 'Bernardino Rivadavia' (MACN) of Buenos Aires (Argentina). The specimens were coated with a 200–300 Å gold-palladium film using a sputter-coater 'termo VG Scientific SC 7620'. Following SEM study, cover slips bearing the isolated spores were removed and mounted on slides with glycerin jelly to be re-illustrated under the light microscope.

## *Grandispora* and 'Haplostigma' species: commented records

A detailed taxonomic study of both *Grandispora pseudoreticulata* and the 'Haplostigma' species is beyond the scope of this paper and will be the subject of other contributions currently in preparation. This paper includes commented references about the presence of both taxa in South America and other related species illustrated from different Middle and Late Devonian assemblages of the rest of the world (see Figs 2 and 3). The Supplementary Material summarizes selected palynological references from the world based on selected species mainly from the Emsian to Frasnian of Argentina, Bolivia and Brazil, where the complete authority of species is included; if not, it is specified in the text.

### 'Haplostigma' spp. (Figs 1–4)

Several records of the lycopsid 'Haplostigma' Seward 1932 are known from South America and some other places of Gondwana (Figs 2 and 3); however, because of problems of nomenclature that still exist with the generic status, it is considered here with inverted commas. Plumstead (1967) suggested that the specimens illustrated by Seward

(1932, pl. XXIII, figs 2, 6, 7; pl. XXIV, figs 11, 13) from the Lower Witteberg Group, Cape Fold Belt of South Africa, were truly assignable to the type species '*Haplostigma irregularis*' (Schwarz) Seward 1932. She also added that the specimens should show evidence of a vascular strand and foliar appendages longer than 10 mm. This feature changes the diagnosis of the genus '*Haplostigma*'. Subsequently, Anderson & Anderson (1985) emended the genus '*Haplostigma*' based on the description of two different species, '*Haplostigma kowiensis*' (Plumstead) Anderson & Anderson 1985 and '*Haplostigma irregularis*' (Schwarz) Seward 1932, and included in the latter species the records of '*Haplostigma furquei*' Frenguelli 1952 emend. Gutierrez 1996 from the Middle to Late Devonian of the Precordillera, Argentina. The description noted the occasional forking of the axes as well as a central vascular trace that was sometimes evident and included the presence of appendages ('leaves') that would be found, rarely, as squat conical with an acute tip and diverging at 50–60° from the axis. Because of this emendation of Anderson & Anderson (1985) is unclear, the diagnosis of the genus still remains inconclusive (see also Cingolani *et al.* 2002).

The resemblance of '*Haplostigma furquei*' to '*Haplostigma irregularis*' is remarkable, although a revision of the material is needed to confirm this in agreement with McLoughlin & Long (1994). In this context, the specimens illustrated here from the Los Monos Formation at Balapuca (Figs 1, 2 and 4; see also di Pasquo 2007a), resemble '*Haplostigma furquei*' and '*Haplostigma irregularis*' but they lack spiny lateral appendages due to fragmentation thus preventing a more precise assignment at this time. More material recently collected by M.d.P. from new localities in southern Bolivia is under study. Many of these specimens are very similar to the ones illustrated by Branisa (1965) as '*Haplostigma furquei*' from Finca Carlazo (east of Tarija city; pl. 51, figs 2, 3) and as '*Haplostigma*' cf. '*furquei*' from Sica Sica (pl. 50, figs 1–3). Finally, the revision of the records of '*Haplostigma furquei*' presented by Gutierrez (1996) is accepted here where the presence of this species is mentioned in the El Toco Formation, Angosturas range, Antofagasta, northern Chile. Moreover, recently Moisan & Niemeyer (2005) mentioned new findings of this taxon from the same place.

However, the specimens from the Precordillera of Argentina (Fig. 4) are somewhat similar to the 'Lepidodendroid fragments' from the Middle Devonian deposits of the Falkland Islands (Halle 1911) in the phyllotaxis and shape of the scars, but differ in the absence of any evidence of a leaf trace, and the axis is narrower. Seward & Walton's 'Lepidodendroid stems' (1922) from Halfway Cove (West Falkland) include the specimens found by Halle (1911), even

remarking on the resemblance between the specimens (Halle 1911, pl. 6, fig. 3) and theirs (Seward & Walton 1992, pl. XIX, fig. 2). Subsequently Archangelsky (1983) reassigned these specimens to his new species *Malanzania antiqua* (see also Gutierrez & Archangelsky 1997).

Other illustrated records are referred to as '*Haplostigma*' sp. by Cingolani *et al.* (2002) from the Givietian Lolén Formation (Ventana Range, Buenos Aires Province), '*Haplostigma baldisii*' Gutierrez & Archangelsky 1997 from the Chigua Formation (Precordillera) of Argentina, and '*Haplostigma lineare*' (Walkom) McLoughlin & Long 1994 from Beacon Orthoquartzite (Middle Devonian), Southern Victoria Land, Antarctica. The latter has grooves like '*Haplostigma furquei*' but bears fusiform leaf scars without preserved appendages. In contrast, Retallack (1995) described new records of this lycophyte from the same locality, but he assigned the stems to '*Haplostigma irregularis*'. Even though this report did not include photographs, a reconstruction of the plant showing the oval scars and short mucronate, keeled 'leaves' is pictured. '*Haplostigma irregularis*' was also illustrated by Kräusel (1960) from Ponta Grossa Formation (Middle Devonian), Paraná Basin, Brazil (see Figs 1–3). Other records are cited in the literature but they cannot be confirmed since they were not illustrated and the materials were not available. These are (see Figs 2, 3): '*Haplostigma irregularis*' from Pimenteira Formation, Parnaíba Basin (Suárez Riglos 1975); '*Haplostigma furquei*', from Huamampampa, Los Monos and Iquirí formations, at Campo Redondo (Suárez Riglos 1975) and Lajas (Wood 1995); and other localities of the central part of Bolivia (Suárez Soruco 1988).

The similarity between the herbaceous lycophyte '*Haplostigma furquei*' from Precordillera and Bolivia with '*Haplostigma irregularis*' from Brazil and South Africa and others from Antarctica and the Falklands Islands is remarkable (Anderson and Anderson 1985; Edwards 1990), although they still require detailed morphotaxonomical study. Due to the fact that none of the lycophyte-bearing Middle Devonian deposits cited above yielded paly-nomorphs and they may also continue into the early Frasnian, they are not trustworthily for detailed biostratigraphy. But, at least the records of both '*Haplostigma*' and *Grandispora pseudoreticulata* and other key taxa from the same stratigraphic levels at Balapuca or from interbedded ones in Del Chaco and La Cortadera creeks (see Figs 1, 2) enable a more accurate age for these plant assemblages. On the other hand, the mentioned similarity among those plant species or specimens should probably be enough to support a common origin for them during this time.

## Palynology

*Grandispora pseudoreticulata* (Menéndez & Pöthe de Baldis) Ottone 1996 is a trilete camerate spore distinguishable from others of the genus by its characteristic distal-polar exoexine sculpture of cones, spines and biform elements mostly fused to form concentric irregular, anastomosing ridges and mainly discrete on the flange (see Fig. 5). It was described for the first time as ‘*Hymenozonotriletes*’ *pseudoreticulatus* by Menéndez & Pöthe de Baldis (1967, pp. 168–169, pl. 1 figs C, D, E) and later reassigned by Ottone (1996) to *Grandispora*. Currently, the original specimens are lost, so it was not possible to directly compare our material. Nevertheless, we have revised slides from the ‘*Hymenozonotriletes*’ *pseudoreticulatus* zone of Suárez Soruco & Lobo Boneta (1983) from Bolivia provided by Lobo Boneta, and plenty of specimens of this species and the subsurface Devonian material from Argentina described by Ottone (1996). Additionally, M.d.P. collected surface and subsurface samples during several field trips to Bolivia, which have provided comparison specimens of this and related species.

*Grandispora pseudoreticulata* was illustrated from the Middle Devonian of Paraguay (Menéndez & Pöthe de Baldis 1967), Middle Late Devonian of Argentina (Ottone 1996; Amenábar *et al.* 2007b) and Bolivia (Ottone & Rosello 1996; Vavrdová & Isaacson 2000; di Pasquo 2007a). Unfortunately, the only record for this species outside South America was in a list, but not illustrated, by Bär & Riegel (1974) from the Middle Devonian of Ghana. The assemblage comprises some other species also cited by Menéndez & Pöthe de Baldis (1967) from the Middle Devonian of Paraguay (see Figs 2, 3). This taxon is used as a zonal index species in biostratigraphical schemes proposed for the Tarija Basin (di Pasquo 2007c), mainly that proposed by Limachi *et al.* (1996), who described the ‘*Hymenozonotriletes*’ *pseudoreticulatus* Zone, which in turn is correlated to the ‘*Haplostigma*’ zone Limachi *et al.* 1996, attributed to the Eifelian to early Frasnian and partially to the *Tropidoleptus carinatus* brachiopod zone Limachi *et al.* 1996 (late Givetian–Frasnian) (see Figs 2, 3, 6). Therefore, its stratigraphical range is well established as late Eifelian to early Famennian on the basis of the presence of Euramerican index species.

This species is also recognized as reworked in the Early Carboniferous (early Viséan) Malimán Formation (Río Blanco Basin, Argentina; Amenábar 2006, 2007b), from the Itacua Formation at Balapuca (overlying the Los Monos Formation; di Pasquo 2007b), the Serpukhovian Kaka Formation (Madre de Dios Basin, Bolivia; Azcuy & Ottone 1987; Fasolo *et al.* 2006), and in the Late

Carboniferous Macharetí and Mandiyutí Groups from the Tarija Basin (di Pasquo & Azcuy 1997; di Pasquo 2003; see Figs 2 and 5). *Grandispora pseudoreticulata*, as *Indotriradites variabilis* Pérez Loinaze (2005), from the Malimán and Cortaderas (Mississippian) formations, is here interpreted as a reworked form from the Devonian Chigua Formation (see Amenábar 2006). Evidence to support this interpretation is presented and discussed by di Pasquo and Azcuy (1997) and Amenábar (2006) and di Pasquo (2003, 2007b).

Several species present in our assemblages show clear morphological characters allowing unambiguous identification (e.g. *Leiotriletes balapucensis*, *Archaeozonotriletes variabilis*, several species of *Apiculiretusispora*, *Geminospira lemurata*, *Samarisporites triangulatus*). Ravn & Benson (1988) and Breuer *et al.* (2007a) have also commented on the highly variable and intergradational complex of large miospores assignable to *Grandispora*. Ravn & Benson (1988) noted that many of the specimens recovered from the Emsian–Eifelian of Georgia (USA) resemble known species but were difficult to assign, so they were illustrated and left in open nomenclature. Breuer *et al.* (2007a) found a continuous morphological intergradation within a single form-species *Grandispora libyensis* in the Middle Devonian of Libya. This is also the case of *Grandispora pseudoreticulata* that intergrades especially with *G. mammillata* in our assemblages. Other similar or very similar species assigned to the genus *Grandispora* or allied genera such as *Samarisporites*, ‘*Calyptosporites*’ or ‘*Hymenozonotriletes*’, defined and illustrated from global the Middle to Late Devonian spore literature, are compared as described below (a–k; see also Supplementary Material).

(a) *Camptozonotriletes caperatus* McGregor and *Grandispora* cf. *protea* (Naumova) Moreau-Benoit in Cloutier *et al.* (1996, pl. 1, figs 5, 14) from the middle Frasnian Escuminac Formation, eastern Québec, Canada. These spores, along with *Grandispora douglastounense*, were recorded in the same level as other characteristic spores from the Emsian–Eifelian such as *Dictyotriletes emsiensis*, so these authors have interpreted all of them as reworked.

(b) *Perotriletes meonacanthus* var. *rugosus* Kedo in Turnau (1996, pl. 2, fig. 5) from western Pomerania assigned to the late Eifelian–mid Givetian (*Rhabdosporites langii* and *Aneurospora extensa* zones Avchimovitch *et al.* 1993) resembles *Grandispora mammillata*.

(c) ‘*Hymenozonotriletes*’ *domanicus* Naumova in Braman & Hills (1992, pl. 14, figs 14, 15, pl. 15, fig. 1) from the Givetian to Frasnian Imperial Formation of northwestern Canada. The sculpture on distal face forms a pseudoreticulum but not like *G. pseudoreticulata*.

(d) *Grandispora macrotuberculata* (Archangelskaya) McGregor 1973 in Melo & Loboziak (2003, pl. 4, fig. 9) and *Grandispora mammillata* Owens 1971 in Melo and Loboziak (2003, pl. 3, fig. 20) from the late Eifelian and *Auroraspora pseudocrista* Ahmed 1980 in Melo & Loboziak (2003, pl. 1, fig. 6) from the Frasnian–early Famennian of the Amazon Basin in Brazil.

(e) *Samarisporites eximius* (Allen) Loboziak & Streel (1989) in Rodrigues *et al.* (1995, pl. 1, fig. 2) and *Samarisporites praetervisus* (Naumova) Allen (1965) in Rodrigues *et al.* (1995, pl. 1, fig. 1) from Parnaíba Basin in Brazil, are considered here as likely records of *Grandispora pseudoreticulata* (see Fig. 2).

(f) *Samarisporites* sp. A and B in Daemon *et al.* (1967, pl. 1, figs 14, 15) from Paraná Basin in Brazil are also considered here as likely records of *Grandispora pseudoreticulata* (see Fig. 2).

(g) *Grandispora ?macrotuberculata* (Archangelskaya) McGregor 1973 in Boumendjel *et al.* (1988, pl. 2, fig. 3) from the Givetian Gazelle Formation, D'Illizi Basin, Sahara Algeria. In this assemblage the common species are *Geminospora lemurata*, *Grandispora inculta*, *Grandispora mammillata*, *Grandispora velata*, *Rhabdosporites parvulus*, *Samarisporites praetervisus*, *Emphanisporites annulatus*, *Emphanisporites rotatus* and some chitinozoans (e.g. *Ancyrochitina taouratinensis* Boumendjel, *Linochitina jardinei* Boumendjel, *Alpenachitina eisenacki* Dunn & Miller).

(h) *Camptozonotriletes leptohymenoides* Balme (1988, pl. 8, figs 1–4, size range 100–170 µm) from the early Frasnian Gneudna Formation, Carnarvon Basin, Western Australia. Balme (1988) noted that it is very close to *Grandispora pseudoreticulata*, being differentiated only by its apparently smaller size (85–114 µm). Scarce specimens of this species were recorded only from the lower half of this sequence, so Balme gave little significance to its apparent stratigraphical restriction. The close similarity of these species remains unresolved and it is important to compare material. This information would confirm the migration path of the parental plant eastwards during the latest Givetian to early Frasnian. Balme's assemblage has 44 species of which only the following are common to South America: *Ancyrospora langii*, *Emphanisporites annulatus*, *Emphanisporites rotatus*, *Geminospora lemurata*, *Cymbosporites hormiscoides*, *Gneudaspora divellomedia*, *Rhabdosporites langii*, *Samarisporites triangulatus*, *Verrucosisorites scurrus*. The Frasnian plant assemblages from Gneudna Formation are dominated by progymnosperms, but during the Givetian plant species are less known (see Balme 1988).

(i) *?Calyptosporites* sp. A in Paris *et al.* (1985, pl. 21, fig. 1) from the early Eifelian of Libya.

(j) Spores similar to *Grandispora pseudoreticulata* were recently studied by Wellman & Gensel (2004). These authors presented a detailed morphological study including SEM and TEM of the sporangia and spores of the enigmatic Lower Devonian (*douglastownense–eurypterota* Zone Richardson & McGregor 1986, late Emsian–earliest Eifelian) plant *Oocampsa catheta* Andrews *et al.*, which is considered intermediate between the trimerophytes and progymnosperms. In addition, they analysed dispersed spores assigned to *Grandispora douglastownense* and *Grandispora ?macrotuberculata* considered to possibly represent forms derived from *O. catheta*. They concluded that *G. douglastownense* and *G. ?macrotuberculata* are probably end members of the same spore complex and most likely are dispersed camerate spores produced by *Oocampsa catheta*.

(k) Another similar form (*Camptozonotriletes caperatus*) was illustrated with an SEM by Wellman (2006) but is different in possessing verrucate–vermiculate distal sculpture with many radial folds on the flange. *Camptozonotriletes caperatus* appears in the Pragian–Emsian *polygonalis–emsiensis* Zone Richardson & McGregor (1986).

As the inception of both *G. douglastownense* and *C. caperatus* occurred prior to *G. pseudoreticulata*, it would be interesting to investigate whether one of these taxa could be the ancestor of *G. pseudoreticulata* and related species of the late Eifelian South American microfloras. On the other hand, the abundant presence of *Grandispora pseudoreticulata* and 'Haplostigma' in the same stratigraphic levels at Balapuca, Del Chaco and La Cortadera creeks, leads us to speculate on a possible relationship among them.

## Approaches to Middle and Late Devonian palaeogeography and palaeobiogeography

Some previous palaeobiogeographical proposals for the Middle and Late Palaeozoic were summarized and updated by Wnuk (1996), who distinguished the Euramerican Realm and Gondwanan Realm, the latter including the South Gondwanan Temperate region. Wnuk provided a brief synthesis of previous palaeontological data to sustain the Middle and Late Devonian palaeobiogeographical scheme, but indicated that additional work on Middle and Late Devonian phytogeography is needed. The Gondwanan Realm encompasses the largest land area during the Palaeozoic and includes the continents of South America, Antarctica, Africa, India and Australia plus smaller regions such as Madagascar, Arabia, New Zealand and the peripheral Tibetan, Iranian, Turkish and China Plates (Li Xingxue 1986; see Fig. 3). Although the

Devonian floristic development of this realm is not well understood due to the uneven knowledge of its fossil record, Streele & Loboziak (1996) defined, for the Middle and Late Devonian, the Northern Euramerica and Southern Euramerica–Western Gondwana phytogeographical provinces. The former is based on the southern limit of *Archaeoperisaccus*, while the latter includes eastern Canada and western Europe based on the resemblance of its palynoassemblages.

Although most palynomorphs had a cosmopolitan distribution during the Devonian, Bär & Riegel (1974) suggested that provincialism would be recognized at the specific level for Gondwana. In this sense, Loboziak & Streele (1995) have shown that the miospore assemblages from western Gondwana are dominated, in the Middle Devonian, by some endemic forms such as *Camarozonotriletes? concavus*, *Craspedispora ghadamisensis*, *Grandispora libyensis* and *G. permulta*. The frequent association of *Grandispora pseudoreticulata* with other endemic but stratigraphically important spore species (e.g. *Grandispora daemonii*, *G. permulta*, *Leiotriletes balapucensis*, *Acinosporites ledundae*, *A. eumammillatus*, *Apiculiretusispora laxa*, *Apiculatisporis grandis*, *Retusotriletes paraguayensis*), as well as with the ‘*Haplostigma*’ flora (see Figs 2, 3), shows a certain degree of endemism of the floras mainly in South America (embracing Bolivia, Brazil, Paraguay, Chile, Peru and Uruguay) and northwestern Africa (e.g. Ghana). All these taxa allow the establishment of the Afro-South American (ASA) Subrealm as the southwestern part of the Gondwana palaeophytogeographic Province during the Middle and early Late Devonian. Its northeastern boundary may be situated somewhere between Ghana and North Africa as not all the characteristic species from the ASA Subrealm occur in those assemblages (see Loboziak & Streele 1995). In the same way, the current evidence sustains the point of view that the vegetation was not uniform worldwide even though herbaceous lycophytes were widespread during the Middle Devonian (see McLoughlin 2001). The ASA northwestern boundary should be established somewhere between Venezuela and Colombia and the rest of South America based on different megaflores of the former region, which Edwards & Benedetto (1985; see also Berry 1996) integrated to the Old Red Sandstone Continent. It provided the most diverse assemblages of Devonian plant fossils including lycophytes, trimerophytes and progymnosperms, but unfortunately nothing is known about the palynomorphs accompanying these floras (see Berry *et al.* 1993; Berry & Edwards 1995 and references therein).

Knowledge about Devonian palynofloras related to floral assemblages from South Africa, the

Falkland Islands, Antarctica and Australia (see Anderson & Anderson 1985; Playford 1990; Edwards 1990; McGregor & Playford 1992) is still scarce. McGregor & Playford (1992) presented a detailed comparison between the microfloras from Canada and Australia with other parts of the world including western Gondwana. They suggested that enough similarities between these countries and the rest of world exist to sustain long-distance biostratigraphical correlation during the Middle and Late Devonian. But there are many qualitative dissimilarities between palynofloras recorded from Australia and the rest of the world, including South America, during this lapse that probably reflect phytogeographical–palaeoclimatic differences (see also Streele & Loboziak 1996). Recent palynological studies from Middle Devonian subsurface deposits in Saudi Arabia (Breuer *et al.* 2007b; Marshall *et al.* 2007) have shown several common species with Euramerica and the ASA Subrealm (e.g. *Geminispora lemurata*, *Samarisporites triangulatus*, *Dibolisporites eifelensis*, *Acinosporites acanthomammillatus*, *Verrucosporites scurrus*). However, the endemic species of the ASA Subrealm were not recorded in Saudi Arabia.

During the Middle Devonian this floral subrealm appears to have developed between 55°S and 75°S palaeolatitude based on the reconstruction of palaeoclimatic zones from Scotese *et al.* (1999; see Fig. 3). The co-occurrence of some Euramerican miospore species in the assemblages of a cooler ASA Subrealm sustains some terrestrial connection between the palaeoequatorial continent Laurussia with Gondwana, with the east–west Rheic Ocean almost closed or at least not so extensive, and with some land masses connecting both continents (see Fig. 3; e.g. Streele *et al.* 1990; Edwards 1990; McGregor & Playford 1992; Cloutier *et al.* 1996; Steemans *et al.* 2007a; Marshall *et al.* 2007). Recently, Steemans *et al.* (2007b) have presented new palynological evidence from Saudi Arabia that the same palaeogeographical scenario, with a narrow Rheic Ocean between Gondwana and Euramerica, existed at least since the Lochkovian. Scotese *et al.* (1999) explained that during the ‘Hot House’ periods, the warm and cool temperate belts extended to the pole and the polar climate zone did not exist. The development of relatively gradual climatic changes is supported by palaeontological records during the Middle Devonian (e.g. Streele & Loboziak 1996), such as the records of brachiopods like *Tropidoleptus carinatus* (e.g. Fonseca & Melo 1987), fossil plants like *Haskinsia* (see Cingolani *et al.* 2002) and several miospores and microplankton species. This scenario is concordant with, for example, the palaeogeographical reconstruction presented by Heckel & Witzke (1979) used by Streele *et al.* (1990) and Wood (1995) to

map Givetian–Frasnian phyto geography. A juxtaposition of Venezuela and eastern North America is also supported by Edwards & Benedetto (1985), due to the fact that both regions share the same flora (see also Berry *et al.* 1993). Later, Berry (1996) presented another explanation for this common origin of both floras: Venezuela (and Colombia) could have been a displaced terrane accreted to the north of South America during the collision of Laurussian and Gondwanan forming Pangaea. Even this interpretation could have been possible because, as was mentioned above, common palynomorphs are registered almost from the palaeoequator towards both poles. This fact reinforces that, at least during Middle Devonian time, Laurussia and Gondwana were connected and the main factor producing this subtle palaeobiogeographical distribution could have been the palaeolatitudinal climatic gradient (e.g. Streeel & Loboziak 1996). In fact, as already noted, the latter authors used several endemic taxa such as *Archaeoperisaccus* (e.g. Braman & Hills 1985; Streeel *et al.* 1990; Hashemi & Playford 2005) to delimit the Northern Euramerica phyto geographical province. The floral distribution of the northern hemisphere during the same time probably involved more than one endemic flora (see McGregor & Playford 1992; Berry 1996), and that appeared to be climatically influenced as well.

Other factors that influence the palaeobiogeographical distribution of plants relate to palaeogeography and the ability of plants to migrate short or long distances (homosporous *versus* heterosporous), to cross barriers (e.g. water bodies or mountains) and the time involved in this process. This subject was discussed extensively by Streeel *et al.* (1990), McGregor & Playford (1992), Steemans *et al.* (2007b) and Marshall *et al.* (2007). Even though the long-distance dispersion of plants is not easy, cosmopolitan species are evidence of this type of migration. For example, *Archaeozonotriletes variabilis* shows a slightly diachronic pattern as it first appeared in the late Eifelian of the Old Red Sandstones (cf. Richardson & McGregor 1986) and later in the Givetian–Frasnian of South America, Saudi Arabia, Libya and Australia and in the Frasnian of Russia. This diachronism in its range reinforces a stronger connection between western Europe and eastern Canada with northern South America and Africa, at least during the Givetian. It is also probable that changes in sea level (regressions) have favoured such connections at least for short times. In contrast, the dispersion of endemic species such as *Grandispora pseudoreticulata* must be controlled by the nature of the parent plant, i.e. heterosporous *versus* homosporous plants, with some palaeoenvironmental and

palaeoclimatic requirements, especially miospore dispersal (e.g. large size to be air-dispersed), that have prevented their migration over long distances (see also McGregor & Playford 1992).

### Palaeoenvironmental considerations

A close affinity among the microfloras from the Precordillera and the north of Argentina and southern Bolivia (Tarija Basin) is supported by several common palynomorph species, invertebrates and plant fossils, which reinforces a palaeogeographic connection between both areas during the Middle Devonian (see Fig. 3; Baldis 1967). Although palyniferous levels are scarce in Del Chaco Creek, the microplankton/spore ratio was useful to interpret palaeoenvironmental change along the Chavela Member (Amenábar 2009). This shows a tendency to more terrestrial input through the sequence from the late Early Devonian (Emsian–Eifelian) to the Middle Devonian (early Givetian). These palaeoenvironmental considerations are coincident with previous palaeontological records (see Baldis & Peralta 2000). Additional sedimentological studies and new palynological samples will permit and improve recognition of transgressive–regressive cycles in the Devonian of the Precordillera.

Albariño *et al.* (2002) and Alvarez *et al.* (2003) established for the Tarija Basin a general model of distribution of facies in a sequence–stratigraphic framework, integrating unpublished palaeontological and sedimentological data to correlate the successions. They concluded that wave-dominated marine siliciclastic platforms were developed during the Ludlow to Frasnian interval. The deposition would have been controlled by eustasy marked by at least three intervals of forced regressions as shown by sand bodies deposited basinward. It is significant that the Balapuca outcrop yielded both palynomorphs and plants from the same stratigraphic levels. These recent studies show that *Grandispora* species frequently dominate in some levels where the microplankton is scarce or absent. Scarce and fragmented marine macrofossils are indicated in A1 from Balapuca associated with the plant remains, supporting a shallow-water marine platform environment. This interpretation is compatible with the general framework presented by Albariño *et al.* (2002) where the late Emsian to late Givetian Balapuca section is located on the border of the basin, thus mostly representing marginal palaeoenvironments. Thus, on the basis of these data Figure 2 gives a more accurate delimitation of the emergent areas (i.e. continental or at least transitional areas) of the studied regions.



## Conclusions

Middle and Late Devonian (Eifelian to Frasnian) palynomorphs in Argentina, Bolivia and neighbouring areas include cosmopolitan species, such as *Geminospora lemurata*, *Samarisporites triangulatus*, *Archaeozonotrites variabilis* and *Chelinospora concinna*. Others with more restricted distribution include *Grandispora pseudoreticulata*, *Leiotrites balapucensis* and *Acinosporites ledundae*. Among the floral remains, species attributable to ‘*Haplostigma*’ are found from the same stratigraphic levels at Balapuca, Del Chaco and La Cortadera creeks. The northernmost record of *Grandispora pseudoreticulata* is from a third palynoassemblage of the Pando x-1 corehole of northern Bolivia.

‘*Haplostigma*’-bearing beds are dated accurately, based on associated palynoassemblages. These new records extend our knowledge of biodiversity and the succession of floristic events during the Middle Devonian, and hence give their biostratigraphic position.

A great similarity among these assemblages includes the co-occurrence of *Grandispora pseudoreticulata* and ‘*Haplostigma*’ species. This suggests that there were terrestrial connections between (or at least proximity of) these local areas and other regions in South America mainly during the Givetian.

We offer an improved interpretation of the current palaeobiogeographic knowledge of *Grandispora pseudoreticulata* and other endemic palynomorphs and associated ‘*Haplostigma*’ flora. The local distribution of these taxa allows the definition of the Afro-South American Subrealm; it most likely results from the effects of palaeolatitude and, to a lesser extent, to local palaeoenvironmental conditions (such as marine versus continental environments). On the other hand, the presence of cosmopolitan together with endemic species supports previous palaeogeographical reconstructions where a narrow Rheic Ocean was developed between Euramerica and the northern parts of Africa and South America.

More studies are needed in order to analyse the accuracy of the relatively restricted palaeogeographical distribution of all South American taxa. This will offer greater insight into the connection of this subrealm with its neighbouring regions. Additionally, it is important to define whether all ‘*Haplostigma*’ species found in southwestern Gondwana belong to the same taxon (‘*H. irregularis*?’). The recovery of its associated palynological assemblage (and its *in situ* spores) is also necessary.

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