ARTICLE IN PRESS
PALAEO-05563; No of Pages 18
Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2010) xxx–xxx
Contents lists available at ScienceDirect
Palaeogeography, Palaeoclimatology, Palaeoecology
journal homepage: www.elsevier.com/locate/palaeo

Devonian sea-level change in Bolivia: A high palaeolatitude biostratigraphical calibration of the global sea-level curve

Ian Troth [a,b,*], John E.A. Marshall [a], Andrew Racey [b], R. Thomas Becker [c]

[a] School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, European Way, Southampton, SO14 3ZH, UK
[b] BG Group, 100 Thames Valley Park, Reading, RG6 1PT, UK
[c] Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität, Corrensstr. 24, D-48149, Münster, Germany

ARTICLE INFO

Available online xxxx

Keywords:
Bolivia
Chaco basin
Devonian
Goniatites
Malvinokaffric
Palynomorphs

ABSTRACT

During the Devonian Period the cool water Malvinokaffric Realm was located at high palaeolatitudes in the southern hemisphere. The Realm is defined by its highly endemic marine benthic fauna, which makes extra-Malvinokaffric correlations problematic. Investigation of the Devonian palynomorphs from an extensive regional sub-surface dataset (24 wells) in the Chaco Basin, Bolivia, reveals the presence of a number of stratigraphically restricted and regionally correlative epiboles (peak abundances) of the distinctive palynomorphs *Bimerga bensonii, Crucidia camirense, Evittia sommeri, Petrovina connata* and *Ramochitina magnifica*. These palynomorph epiboles were then located at outcrop by a high-resolution palynological investigation (225 samples) of two Bolivian outcrop localities in the Chaco Basin: Bermejo, Santa Cruz Department and Campo Redondo, Chiquisaca Department. The important *Evittia sommeri* epibole in the basal Los Monos Formation is related to a marine transgression that is present in both these outcrop sections. Additional chronostratigraphic control on this marine transgression comes from the occurrence of rare goniatites in the base of the Huamampampa Formation at Campo Redondo, which are at least early Eifelian in age (post Chotěc Event). Based on the goniatite together with spore data, the marine transgression with *Evittia sommeri* in the basal Los Monos Formation can be tentatively assigned to the Mid Devonian (mid-late Eifelian) Kačák Event.

The presence of a datable Malvinokaffric goniatite has shown that key spore taxa which are used zonally in both Laurussia and Gondwana do not all have coincident first occurrences in both areas. Furthermore, despite the appearance of some cosmopolitan elements in the microflora, Mid and Late Devonian spore assemblages in Bolivia are distinct from other regions in being relatively impoverished in both progymnosperm and lycopod spores. This floral difference is attributable to the Malvinokaffric Realm continuing to retain a distinctive cool climatic signature throughout this interval. However, the sporadic occurrences of extra-Malvinokaffric macrofauna in restricted stratigraphic intervals of the Middle Devonian in South America and South Africa are significant. The oldest known occurrence of the extra-Malvinokaffric brachiopod *Tropidoleptus* in Bolivia is coincident with the late Eifelian basal Los Monos Formation transgression. Hence there was a relationship between influxes of this fauna and marine transgressions, i.e. temporary periods of reduced climatic gradient.

The migration of Devonian spores, and particularly heterosporous spores, between Gondwana and Laurussia clearly occurs during the Mid and Late Devonian. This is at variance with models claiming a wide Rheic Ocean during much of the Devonian.

1. Introduction

Detailed age dating and correlation is now well established for the Devonian (Bultynck, 2000), especially through the combination of conodont and goniatite biostratigraphy (Becker and House, 2000). These correlations underpin other studies in geochemistry, sedimentology, palaeontology, and palaeoecology that have allowed a hierarchy of Devonian events to be established (House, 2002). These events encompass sea-level changes, extinctions, anoxia and climatic perturbations (e.g. Walliser, 1996). Whilst many of the events are known to be geographically widespread, none of them has been definitively proven to be truly global in nature, because both conodonts and goniatites, which are used to date the events, are restricted to the lower palaeolatitude areas of Laurussia and northern Gondwana (30°N–45°S, e.g. Becker and House, 2000; Charpentier,

* Corresponding author. BG Group, 100 Thames Valley Park, Reading, RG6 1PT, UK. Tel.: +55 21 3820 8127; fax: +55 21 2279 3851.
E-mail addresses: Ian.Troth@bg-group.com (I. Troth), jeam@noc.soton.ac.uk (J.E.A. Marshall), rbecker@uni-muenster.de (R.T. Becker).

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doi:10.1016/j.palaeo.2010.10.008

1984). Consequently, it has not been possible to undertake detailed work that establishes the presence of these events at higher palaeolatitudes. This is significant because many of the myriad of explanations for the different Devonian biotic events (e.g. McGhee, 1996) involve changes in the Devonian Earth System that would be present, and in some instances of greater magnitude, at high latitude. An excellent example is the significance of climatic cooling during the Frasnian–Famennian mass extinction (e.g. Joachimski and Buggisch, 2002). Therefore being able to determine the global limits of these events is of some importance.

During Emsian to late Eifelian times the area encompassing Antarctica, the Falkland Islands, the southern two thirds of South America, and sub-Saharan Africa was at a high southern hemisphere palaeolatitude (Boucot, 1988; Meyerhoff et al., 1996; Scotese, 2001). This area is known as the Malvinokaffric Realm, (Boucot, 1975; Fig. 1) and is characterized by cool to cold water marine faunas that were highly endemic and dominated by brachiopods, bivalves and trilobites (Boucot, 1988). Notable to the Malvinokaffric fauna, however, is the scarcity/absence of warm-water indicators, e.g. corals, some sponges and bryozoans, conodonts and goniatites (Boucot and Racheboeuf, 1993) which makes any extra-Malvinokaffric correlations problematic. Irrespective, this has not stopped some authors from using the Devonian sea-level curve as a primary correlation tool (e.g. Cooper, 1986 in South Africa), although its usage has never been adequately tested at high palaeolatitudes due to a lack of precise biostratigraphic control.

The Malvinokaffric correlation problem has long been recognised (e.g. Barrett and Isaacson, 1988). In an attempt to make correlations with Laurussia, rare records of the extra-Malvinokaffric brachiopods *Tropidoleptus* and *Rhipidothyris* from Bolivia, Brazil and South Africa have been utilised. These occurrences are generally regarded as being Mid Devonian or younger in age (Boucot and Theron, 2001; Boucot et al., 1983; Fonseca and Melo, 1987; Isaacson and Sablock, 1990). The extinction of Malvinokaffric trilobites (e.g. Feist, 1991) and the appearance of these cosmopolitan brachiopods at high palaeolatitudes is also interpreted as an indicator for the Mid Devonian, specifically the late Eifelian demise of the Malvinokaffric Realm (Boucot, 1988; Meyerhoff et al., 1996). However, conodont and goniatite occurrences from the region are rare following the supposed demise of the Malvinokaffric Realm with only a handful of documented records (Kullmann, 1993 and references therein; Hünicken et al., 1988; Over et al., 2009), including significant goniatite discoveries from Bolivia (Babin et al., 1991;Hünicken et al., 1980).

Some success with extra-Malvinokaffric Devonian correlations has been achieved through the application of palynology, particularly the study of spores in Brazil (e.g. Melo and Loboziak, 2003 and references therein). Palynological studies in South America are also commercially important as the Devonian rocks provide the source (e.g. Los Monos Formation), reservoir (e.g. Huamampampa Formation) and seal to the gas province of the Chaco Basin (Wiens, 1995) which encompasses eastern Bolivia, northern Argentina and northern Paraguay.

This contribution includes sub-surface data including a regional palynological dataset generated from 24 wells in central/southern Bolivia and northern Argentina. This sub-surface data set was integrated with studies of selected outcrop sections in Bolivia (Fig. 2) to provide a new synthesis of Devonian stratigraphy and sea-level change and how it might relate to contemporary changes at lower palaeolatitudes.

2. Devonian geology of Bolivia

In Early Devonian times, much of Bolivia formed an intracratonic foreland basin (Isaacson and Díaz-Martínez, 1995) along the western margin of Gondwana (Fig. 1). During the Devonian Gondwana was both slowly rotating and moving northwards relative to Laurussia, with which it eventually collided during closure of the Rheic Ocean. However, there is no consensus as to the timing of this closure with models proposing that there was either a narrow Devonian Rheic Ocean with Laurussia–Gonwana interaction (Cocks and Torsvik, 2006; Golonka, 2002) or a very wide ocean with no continental interaction (Keppie, et al., 2008; Nance et al., 2010). The Devonian sediments in the Subandean Thrust Belt comprise a clastic dominated sequence with a pre-Tertiary thrusting thickness of approximately 2 km. Five major units can be recognised (Fig. 3; e.g. Isaacson, 1977a) which are, from oldest to youngest; the Santa Rosa, Icla, Huamampampa, Los Monos and Iquiri Formations. These are all mainly shallow water marine clastic deposits that span the Lochkovian to Frasnian interval as dated herein. The overlying Itacua Formation comprises diamictites of glacial origin and has been dated as latest Famennian in age (Wicander et al., in press) and are thus correlative with palynologically dated Cumaná Formation diamictites in the Altiplano of western Bolivia (Díaz-Martínez et al., 1999).

Summaries of previous stratigraphic studies on the Devonian of Bolivia are given in Davila and Rodriguez (1967), Isaacson (1977a,b) and Racheboeuf et al. (1993). The utility of palynology in resolving

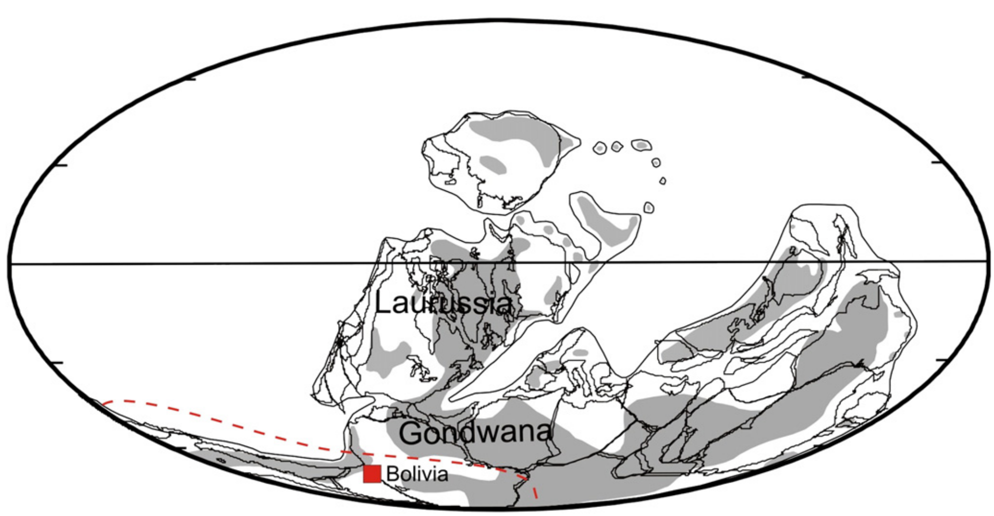

Fig. 1. Early Devonian paleogeography from Scotese (2001). The approximate extent of the Malvinokaffric Realm in the southern hemisphere is marked by the dashed line, with the red square representing the position of Bolivia during this interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Fig. 2. Outline map of Bolivia showing the Devonian sections sampled in this study (black squares). Some major cities (black circles) are also marked. Superimposed is the Chaco Basin (shaded), of which the exposed part is subdivided into the Subandean Thrust Belt (STB) and the Chaco Basin Foreland Fold Belt (CBFFB).

stratigraphic issues in Bolivia was highlighted by McGregor (1984) in his investigation of the Santa Rosa to Huamampampa Formations. The use of palynology for correlation purposes in Bolivia has continued

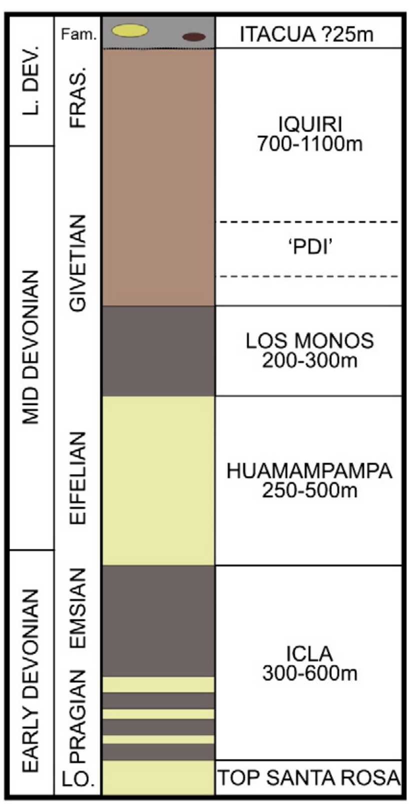

Fig. 3. A generalised Devonian lithostratigraphy in the Subandean Fold Belt. The precise recognition of the Devonian stage boundaries is problematic due to the scarcity of conodonts and goniatites; hence the stages can only be applied in a broad sense. Although regional in extent throughout the Chaco Basin, the Phytoclast Dominated Interval (PDI) is palynologically defined and has no obvious lithostratigraphic expression. Consequently, the PDI has not been recognised as a formal lithostratigraphic unit.

(Blieck, et al., 1996; Grahn, 2002; Limachi et al., 1996; Ottone, 1996; Perez-Leytón, 1991; Racheboeuf et al., 1993), with recent work integrating palynological and other data to construct a Devonian sequence stratigraphic model (Albariño et al., 2002; Miranda et al., 2000, 2003).

3. Materials and methods

The sub-surface samples analysed comprise more than 1500 drill-cutting samples from a line of 24 wells extending along section over 600 km in length from the area of Santa Cruz in eastern Bolivia to the southern extension of the Chaco Basin in northern Argentina.

Two main outcrop localities were investigated in the southern Sub-Andean Thrust Belt: Bermejo in Santa Cruz Department and Campo Redondo in Chiquisaca Department (Fig. 2). The Bermejo section (also known as Lajas) is located 80 km SW of Santa Cruz on the Samaipata road (UTM 20 K 429876 7994666) and has been studied previously by Isaacson (1977a), Perez-Leytón (1991) and Wood (1994, 1995, 1997, 2004). The section studied is exposed along the banks of the Rio Lajas immediately south of the parallel road section that lies between kilometre posts 80 and 82. This is more continuous and better exposed than the road section, with seasonal floods ensuring clean rock surfaces. A 1.2 km thick continuous section was measured in the river, comprising the uppermost Huamampampa, Los Monos and Iquiri Formation interval. A total of 145 palynological samples (CGH 1-145) were taken from mudstones/shales through this entire section, with the highest sampling density across the Huamampampa/Los Monos boundary. Twenty kilograms of bioclastic limestone from a concretion in the Los Monos Formation was processed for conodonts but proved barren.

The section at Campo Redondo (UTM 20 K 0359902 7864249) is located 3 km west of Padilla, on the Rio Sillani where the Icla/Huamampampa interval is exposed. Approximately 560 m of section was sampled for palynology (CMR 1-77). This section was selected because it is the type locality of the goniatite *Tornoceras bolivianum* Hünicken et al. (1980). Consequently, by studying this section it was possible to integrate the palynological record with both the lithostratigraphy and the age based on this diagnostic goniatite.

The palynology samples were processed using standard HCl and HF preparation techniques (e.g. Phipps and Playford, 1984) with a sieve mesh size of 15 μm being used. No oxidative methods were employed and preservation was generally good to excellent. The palynomorph abundances were determined quantitatively with 10 g rock samples being spiked with modern *Lycopodium* spore tablets (methodology as per Stockmarr, 1971).

4. Results

4.1. Sub-surface wells

Investigation of this large dataset (1500 drill cuttings, samples from 24 wells, 225 outcrop samples) revealed the presence of a number of distinct and regionally correlative palynological events. From these, four epiboles (*sensu* Brett and Baird 1997, when a fossil becomes abundant within the local assemblage through a short stratigraphic thickness and hence time duration) were chosen. These epiboles were first recognised in the wells and subsequently located in the outcrop sections. Fig. 4 shows the position of these epiboles in selected wells (those with unthrusted sections) and demonstrates clearly that they are both regional in extent and occur at consistent positions with respect to each other. In addition, two intervals characterized by distinctive palynofacies were also recognised as being particularly useful in sub-surface correlation. These were the prasinophyte peak and the Phytoclast Dominated Interval (PDI). The palynomorphs that define the epiboles are illustrated in Fig. 5.

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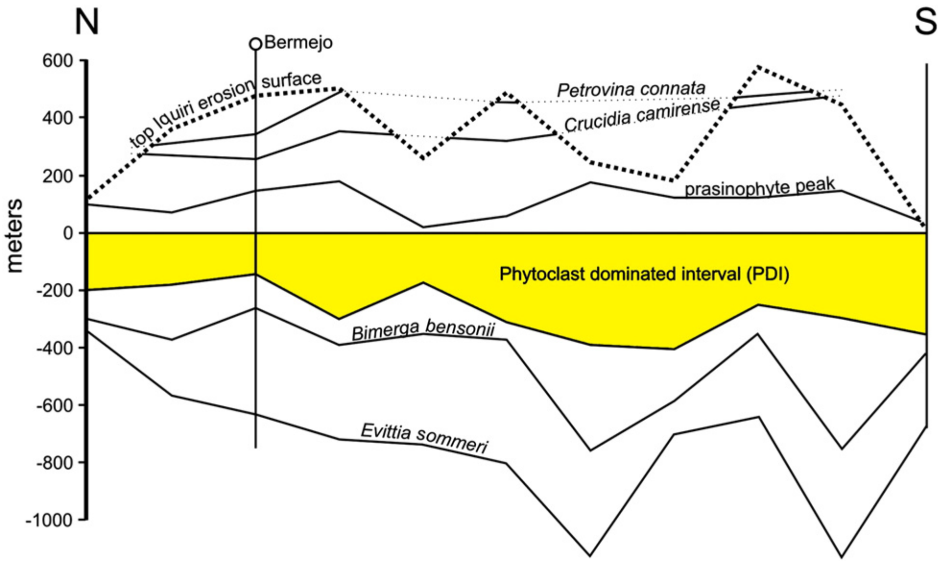

Fig. 4. Devonian palynomorph epiboles along a 500 km north–south sub-surface transect in the Subandean Thrust Belt (STB), extending south from Santa Cruz in central Bolivia into northern Argentina. Also shown is the PDI (Phytoclast Dominated Interval) and the overlying peak of prasinophytes. Note the consistent positions of the palynomorph epiboles and the PDI with respect to each other. The top Iquiri erosion surface (beneath the sub-Itacua Formation diamictite) is cut down to very different levels along the transect line and this erosion is frequently of sufficient magnitude to remove the *Petrovina* and *Crucidia* epiboles. The location of the Bermejo field section is shown. These robust stratigraphic relationships have formed the basis of an important regional Devonian sub-surface biostratigraphic framework which has had productive applications for the oil industry in the tectonically disrupted STB. The section is drawn on the top of the PDI. This major palynofacies change is a very easy datum to recognise within cuttings samples.

4.1.1. *Evittia sommeri epibole*

This acritarch epibole is the most significant event both in terms of magnitude and commercial importance. Importantly, it occurs in shales of the Los Monos Formation immediately above the sandstones of the Huamampampa Formation and hence can be used to recognise the top of this reservoir in the sub-surface. The *Evittia sommeri* epibole is characterized by a significant influx of the eponymous acritarch (Fig. 5H) through a short interval of section (characteristically <50 m) where it is the most distinctive component in a marine assemblage that is otherwise dominated by algal leiospheres (prasinophytes). The abundance of *E. sommeri* progressively rises to a maximum and then equally rapidly declines uphole/upsection to an assemblage dominated by leiospheres and *Duvernaysphaera* spp. *Evittia sommeri* has a very distinctive morphology and is unlikely to be confused with other taxa. The only other *Evittia* species recorded from the Devonian of Bolivia is *E. geometrica* (Fig. 6K) which is restricted to the uppermost Iquiri Formation and differs morphologically from *E. sommeri* in possessing a distinctive spinose ornamentation on the processes (compare the Famennian *E. sommeri* in Loboziak et al., 1997). In the sub-surface the *E. sommeri* epibole is usually very marked but can appear different in both relative abundance and thickness. This may be a consequence of its recovery from drill cuttings. Although these integrate/composite the lithologies over a 3 m interval they are normally only investigated at 30 m or sometimes 10 m intervals. This can have the effect of only partially sampling the full range and, in particular, of missing the acme both in terms of maximum relative abundance and depth. In addition, the basal Los Monos Formation is palynologically rich and occurs immediately above the Huamampampa Formation which is effectively barren of palynomorphs. This can give a long cavings tail extended range to *E. sommeri* and even the artefact of a distinctive second acme within this barren section. Given that the sub-surface data is entirely sourced from cutting samples it is difficult to assess the relative magnitude of the *E. sommeri* acme across Bolivia and northern Argentina. But it would appear to be more conspicuous in central Bolivia.

4.1.2. *Bimerga bensonii epibole*

This acritarch epibole is much less distinctive than that of *Evittia sommeri* because *Bimerga bensonii* (Fig. 5I) does not dominate the assemblage to the same extent. However, it co-occurs with an acme of the chitinozoan *Cladochitina varispinosa* (Fig. 5G) which is significantly more abundant and hence more conspicuous, albeit ranging through a longer stratigraphic interval. The epibole of both taxa marks a distinctive level in the middle part of the Los Monos Formation; an interval otherwise characterized by impoverished palynomorph assemblages.

4.1.3. *Prasinophyte peak*

This is a distinctive interval where the palynomorphs are dominated by prasinophytes together with acritarchs and a relatively lower proportion of terrestrial spores. The prasinophytes are mainly simple leiospheres but *Lophosphaeridium* and *Hemiruptia legaultii* can be very abundant. Towards the base of the interval there can be an epibole of *Veryhachium trispinosum*.

4.1.4. *Phytoclast Dominated Interval (PDI)*

This event differs from the acritarch epiboles in being a distinctive interval that is dominated by terrestrial phytoclasts and was identified in this study regionally throughout Bolivia and northern Argentina. Since the interval is palynofacies defined, and has no obvious lithostratigraphic expression, it cannot be formally recognised as a lithostratigraphic unit. This contrasts with the palynological epiboles which can be formalised by recognising unique stratigraphically restricted palynomorphs. The PDI is defined by an assemblage dominated by phytoclasts and spores of land plant origin including megaspores. However, leiospheres, rare chitinozoans and acritarchs occur in reduced numbers, indicating the PDI is still pervasively marine. The PDI is 200–300 m thick and is overlain by a unit rich in prasinophytes and marine palynomorphs (Fig. 4) that represents a time of relatively high marine productivity.

The PDI has a very distinctive top within the wells and is easily recognised within cuttings samples by an influx of terrestrial spores and phytoclasts. Hence it is the preferred datum for Fig. 4. Its base is not so easily defined from cuttings samples as it is so rich in organic matter that its cavings tail can very much dominate the underlying interval that has a much lower content of largely marine palynomorphs.

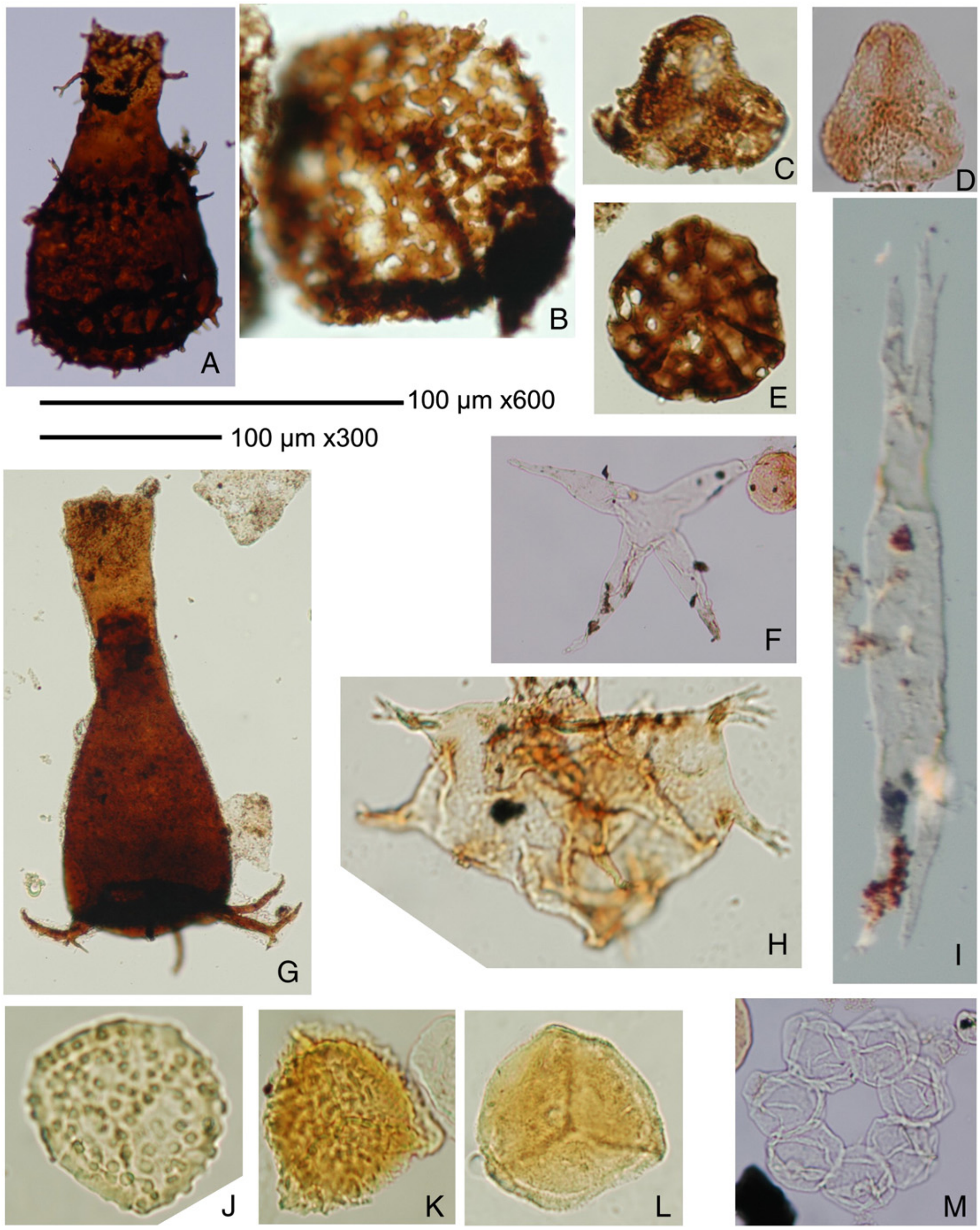

Fig. 5. (A) *Alpenachitina eisenacki*, CMR 48p, O44/2, x304. (B)? *Acinosporites acanthomammillatus*, CMR 66, Q13/2, x600. (C) *Lophotriletes devonicus*, CMR 40, V30, x600. (D) *Lophotriletes devonicus* CMR 69, Q25/3, x600. (E) *Emphanisporites annulatus*, CMR 34, U18/3, x600. (F) *Crucidia camirense*, CGH 122, Q20/3, x600. (G) *Cladochitina varispinosa*, CGH 76a, H13/1, x300. (H) *Evittia sommeri*, CMR 76, O9/2, x600. (I) *Bimerga bensonii*, CGH 78, O34, DIC, x600. (J) *Verrucosisporites bulliferus*, CGH 118, J15/2, x600. (K) *Cristatisporites triangulatus*, CGH 133, V16/3, x600. (L) *Geminospora lemurata*, CGH 138, V8, x600. (M) *Petrovina connata*, CGH 127, X19/4, x600.

4.1.5. *Crucidia camirense* epibole

This event is the short-lived epibole of the distinctive cruciform acritarch *Crucidia camirense* (Fig. 5F). As with *Bimerga bensonii*, *C. camirense* is much rarer in the palynological assemblage when compared with the *Evittia sommeri* epibole. However, it is a very distinctive acritarch that occurs over a very short interval and is therefore a significant and reliable marker species.

4.1.6. *Petrovina connata* epibole

This epibole is represented by the persistent occurrence of *Petrovina connata* (Fig. 5M) over a short stratigraphic range. *Petrovina connata* is morphologically distinct and occurs widely across Bolivia. But in contrast to the acritarch epiboles, which are defined using marine phytoplankton, the affinities of *Petrovina* (see Oliveira and Burjack, 1996) are with the hydrodictyacean algae (Chlorophyta, Chlorococcales). Extant hydrodictyacean algae are restricted to fresh water and a similar environment, or at least one with a strong fresh water influence is inferred for fossil forms (Batten, 1996).

4.2. The Bermejo section

The Bermejo section contains generally well-preserved assemblages of palynomorphs that vary from yellow to brown in colour with increasing age through the section. All the palynomorph epiboles recognised in the sub-surface together with the PDI and prasinophyte peak were identified in the same stratigraphic order in the Bermejo

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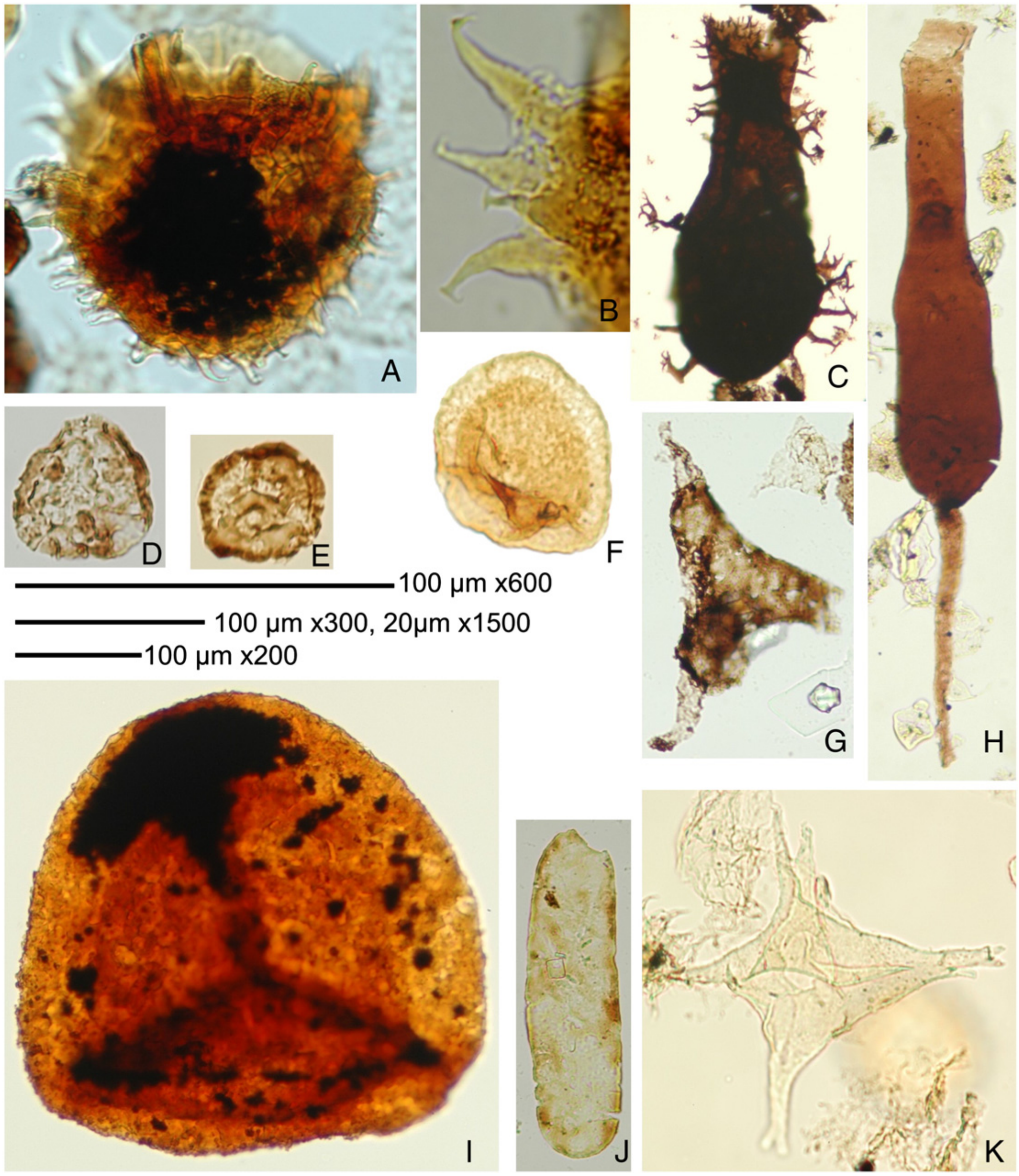

Fig. 6. (A) *Hystricosporites* sp, CGH119, V9/3, x600. (B) detail of bifurcate tipped sculpture on 6A, x1500. (C) *Ramochitina magnifica*, Bol 2–38, basal Belén Formation, Ayo Ayo to Caracato Road, Laz Paz, V38/1, x300. (D) *Synorisporites papillensis*, CMR45, R19, x600. (E) *Archaeozonotriletes chulus*, CMR40, V28/1, x600. (F) *Retispora lepidophyta*, BCG19, Y27/1, x600. (G) *Tyligmasoma alagarda*, CMR66, T15, x300. (H) *Urochitina bastosii*, CGH143 (chits), J13, x200. (I) *Contagisporites* cf. *optivus*, sub-surface PDI, Iquiri Formation, N34/4, x200. (J) *Navifusa bacilla*, *brasiliensa* morph, CMR68, U26/1, x300. (K) *Evittia geometrica*, BOL 7–14, L17, x600.

field section (Fig. 7). Moreover, as the stratigraphic position is known, the extent of the epiboles can be better constrained at outcrop since there is no loss of resolution through downhole contamination of the cuttings by cavings. The first appearances of some important cosmopolitan spores (*Geminospora lemurata*, *Cristatisporites triangulatus* and *Verrucosisporites bulliferus*) are also recorded (Figs. 5 and 7). These have been used to correlate the Devonian sections in Brazil with Western Europe (Melo and Loboziak, 2003), allowing the recognition, at a general level, of the Eifelian, Givetian and Frasnian stages within the section. The first occurrence of *G. lemurata* (Fig. 5L) is used to define the approximate base of the Givetian and this is coincident with the Los Monos/Iquiri Formation lithological boundary as it has a first occurrence some 10 m above the base of the Iquiri Formation.

The base of the Frasnian is tentatively placed between the first occurrences of *V. bulliferus* (Fig. 5J), which is early but not earliest Frasnian in northwestern Europe, and the late Givetian marker taxon *C. triangulatus* (Fig. 5K).

In outcrop at Bermejo the main Huamampampa Sandstone is quartz rich and has a well defined but irregular upper surface with abundant trace fossils and is interpreted as a condensation surface marking a hiatus. Above this level there is renewed deposition of sandstone but with a significant content of silt. This 'succio' or 'dirty' Huamampampa marks the upwards transition into (Fig. 8A and B) dark grey/black Los Monos Formation mudstones containing the *Evittia sommeri* epibole (Fig. 9) and the onset of a major marine transgression. Although the total stratigraphic range of *E. sommeri* is approximately 140 m (CGH 18 to CGH 57; Fig. 7), the thickness of the epibole is only 10 m (CGH 25 to CGH 29). Closer analysis of the epibole interval (Fig. 9) reveals a distinct spike in the abundance of *E. sommeri* in sample CGH 27 (a maximum of 12,900 specimens g^{-1}). *Evittia sommeri* dominates the microplankton assemblage at this level with an abundance that is greater (by 8700 specimens g^{-1}) than all the other acritarchs combined. The upper limit of *E. sommeri* is also characterized by the local epibole of the distinctive chitinozoan

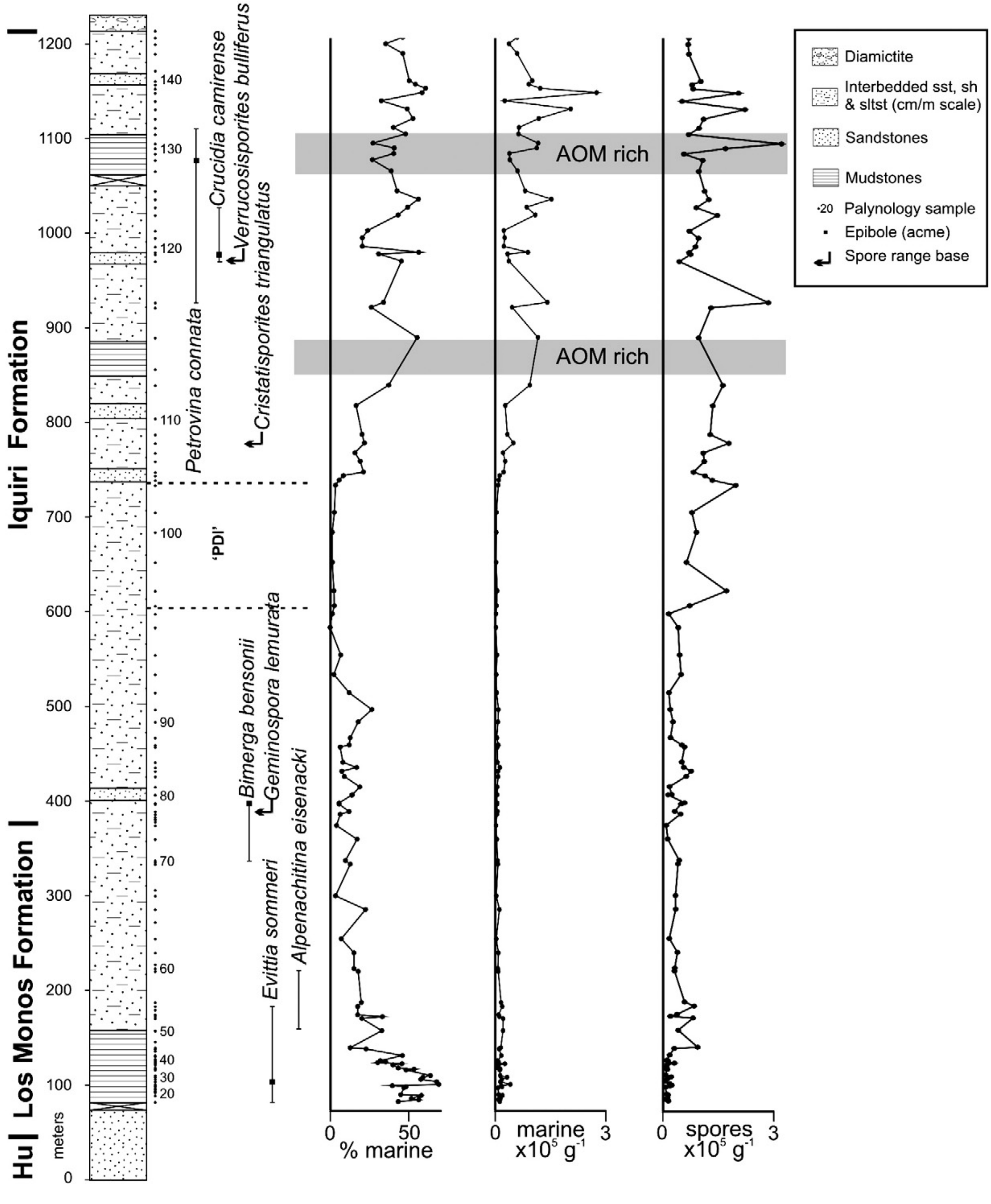

Fig. 7. A simplified log of the measured Devonian section in the Rio Lajas at Bermejo, Santa Cruz Department. All of the sub-surface palynomorph epiboles and the PDI are present in the section and in the same stratigraphic order as originally identified in the sub-surface (Fig. 3). The abundances of marine (acritarchs, prasinophytes and chitinozoans) and terrestrial (spores) are shown as palynomorphs g^{-1} rock together with % marine palynomorphs. This shows the generally low palynomorphs content of the Los Monos and lower Iquiri Formation with a dominance of marine forms particularly through the mudstones of the *Evittia sommeri* event. A significant reduction in the absolute numbers of marine palynomorphs and a greater increase in the terrestrial spores defines the PDI (Phytoclast Dominated Interval where, in fact, the dominant component are phytoclasts of land plant origin rather than spores). Spore abundance remains high through the upper part of the Iquiri Formation where it is paralleled by an increase in marine palynomorphs. There are two intervals of black mudstone within the Iquiri Formation that are dominated by AOM. The inceptions of some key cosmopolitan spores (*Geminospora lemurata*, *Cristatisporites triangulatus* and *Verrucosisporites bulliferus*) and the distinctive chitinozoan *Alpenachitina eisenacki* are shown since these taxa permit the broad recognition of the Eifelian, Givetian and Frasnian stages at Bermejo. Hu is the Huamampampa Formation.

Alpenachitina eisenacki (Fig. 5A). The stratigraphic overlap between the two taxa is also an important marker in recognising the top of the *E. sommeri* epibole in the sub-surface and hence proximity to the Huamampampa Formation reservoir.

The Iquiri Formation in the Bermejo section is overlain by diamictites of the Itacua Formation (Díaz-Martínez et al., 1999). These contain the distinctive spore *Retispora lepidophyta* (Fig. 6F; Perez-Leytón, 1991; Wicander et al., in press) and are latest Famennian in age. In the uppermost part of the Iquiri Formation there is the inception and acme of *Urochitina bastosi* (Fig. 6H) at CGH 141 (1160 m) indicating an age no younger than Frasnian (Grahn and Melo, 2002). This occurs 50 m beneath the overlying latest Famennian

Fig. 8. (A) the Huamampampa/Los Monos Formation contact at Bermejo. (B) note the eroded and bioturbated surface at the top of the Huamampampa Formation which is interpreted as a disconformity. There is a clear lithological change from quartzitic sandstones to siltstones across the disconformity, with the siltstones gradually grading into dark grey mudstones containing the *E. sommeri* epibole (out of view to the left of the picture in (A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Itacua Formation (Wicander et al., in press). Therefore there is a significant hiatus or condensation of the long interval of Famennian time (15 my; Kaufmann, 2006). In this context it is noteworthy that the alleged occurrence of the goniatite *Sporadoceras* from Belén of northwest Bolivia (Babin et al., 1991), a strictly Middle to Uppermost Famennian genus, is in fact based on a somewhat homeomorphic

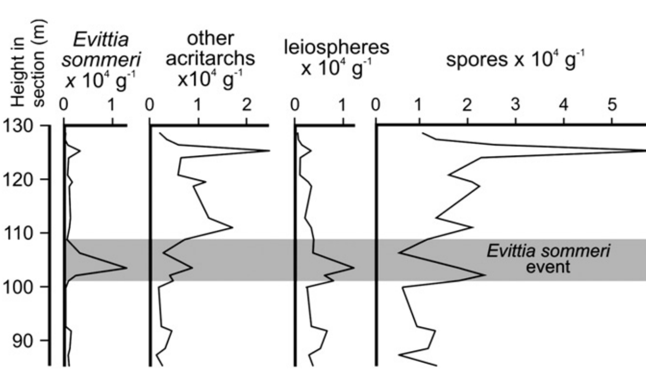

Fig. 9. Palynomorph abundances in the basal Los Monos Formation (CGH 18–CGH 39) at Bermejo. The abundance of *E. sommeri* increases dramatically above the background values in samples CGH25–CGH29 with this 10 m stratigraphic interval representing the *E. sommeri* epibole. The peak abundance of *E. sommeri* is in CGH 27 (12,900 specimens g^{-1}).

Givetian maenioceratid species. Therefore, there is, as yet, little evidence for any significant interval of Famennian section.

4.3. Campo Redondo

Palynomorphs are present through the uppermost Icla to basal Los Monos Formation in the Campo Redondo section (Figs. 10 and 11). In general these palynomorphs are somewhat poorly preserved with degraded and thinned walls, are generally brown or black in colour (i.e. a greater level of thermal maturity) but remain identifiable. The section at Campo Redondo is in part correlative with that studied by McGregor (1984) at Tarabuco some 65 km to the west. However, it has proved difficult to directly relate the two sections because McGregor (1984) did not provide a detailed thickness-scaled lithostratigraphic log. The lower part of the Campo Redondo section (below the log in Fig. 10) was only spot sampled and palynomorph recovery was somewhat sporadic with the lithologies being dominated by siltstones and fine sandstones. In the lower part of the Icla Formation there is an epibole of the distinctive chitinozoan *Ramochitina magnifica*. *Ramochitina magnifica* is well known and is the nominate taxon of the *R. magnifica* zone of Grahn (2005) with occurrences in Argentina, Paraguay and Brazil in addition to Bolivia (pers. obs., and Vavrdová et al., 1996). It is also known from the basal Fox Bay Formation in the Falkland Islands (Marshall pers. obs.) and has also been figured as *Angochitina* sp. A from the Horlick Formation of Antarctica (Kemp, 1972). The zone is attributed an Early Devonian, Pragian age based on correlation with spore assemblages from South America (Grahn, 2005; Rubinstein et al., 2005).

The palynomorph assemblages from the uppermost Icla Formation are generally dominated by psilate prasinophytes (leiospheres) and land-derived spores, together with long ranging acritarchs such as *Navifusa bacilla* (as the *N. 'brasiliensis'* morph, Fig. 6J; see Fatka and Brocke, 2008) and *Tyligmasoma (Triangulina) alagarda* (Fig. 6G). The accompanying spore assemblage in these lowest samples (CMR 1-19) comprises a very simple assemblage of small smooth-walled spores together with rarer apiculate spores and taxa such as *Synorisporites papillensis* (Fig. 6D) and *Archaeozonotriletes chulus* (Fig. 6E). Morphologically more complex spores are also present. These include rare specimens of *Dictyotriletes subgranifer* (Fig. 11H) and *Dictyotriletes* sp. A of McGregor (1984) (Fig. 11D) in samples CMR 9-13 and 34. Within the sequence the first significant spore inception is *Emphanisporites annulatus* (Fig. 5E) in sample CMR 33. Approximately coincident is the inception of zonate/camerate spores, *Grandispora* sp. (Fig. 11C) in sample CMR 34. Specimens of *Grandispora* are very rare (much less than 1%) and are usually present as single examples within preparations that otherwise contain several thousand palynomorphs. Many of the excellently preserved specimens of *Grandispora* in subsequent samples were picked from wet kerogen residues. However, their occurrence is persistent in these younger samples and represents a genuine inception and occurrence. They slowly become more abundant and diverse up-section but generally still occur only as single specimens of each morphotype. The next inception up-section is the spore *Lophotriletes devonicus* (Fig. 5C) in CMR 40 which is then present in most overlying samples.

There is an influx of the chitinozoan *Alpenachitina eisenacki* (Fig. 5A) in sample CMR 48. Such an abundance of a particular chitinozoan in a single sample is quite characteristic of their distribution in Bolivia based on the high resolution outcrop sampling performed during this study, i.e., relatively high abundances through short stratigraphical ranges (pers. obs.).

Above this level, and through the interval with goniatites (CMR 51-60), the lithologies become coarser siltstone and sandstones (Huamampampa Formation) and palynomorphs are not preserved. Adequate palynomorph preservation then returns within an intra-Huamampampa Formation shale interval from samples CMR 60 to 69. In these younger samples, the spore assemblage is more complex with

Please cite this article as: Troth, I., et al., Devonian sea-level change in Bolivia: A high palaeolatitude biostratigraphical calibration of the global sea-level curve, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2010), doi:10.1016/j.palaeo.2010.10.008

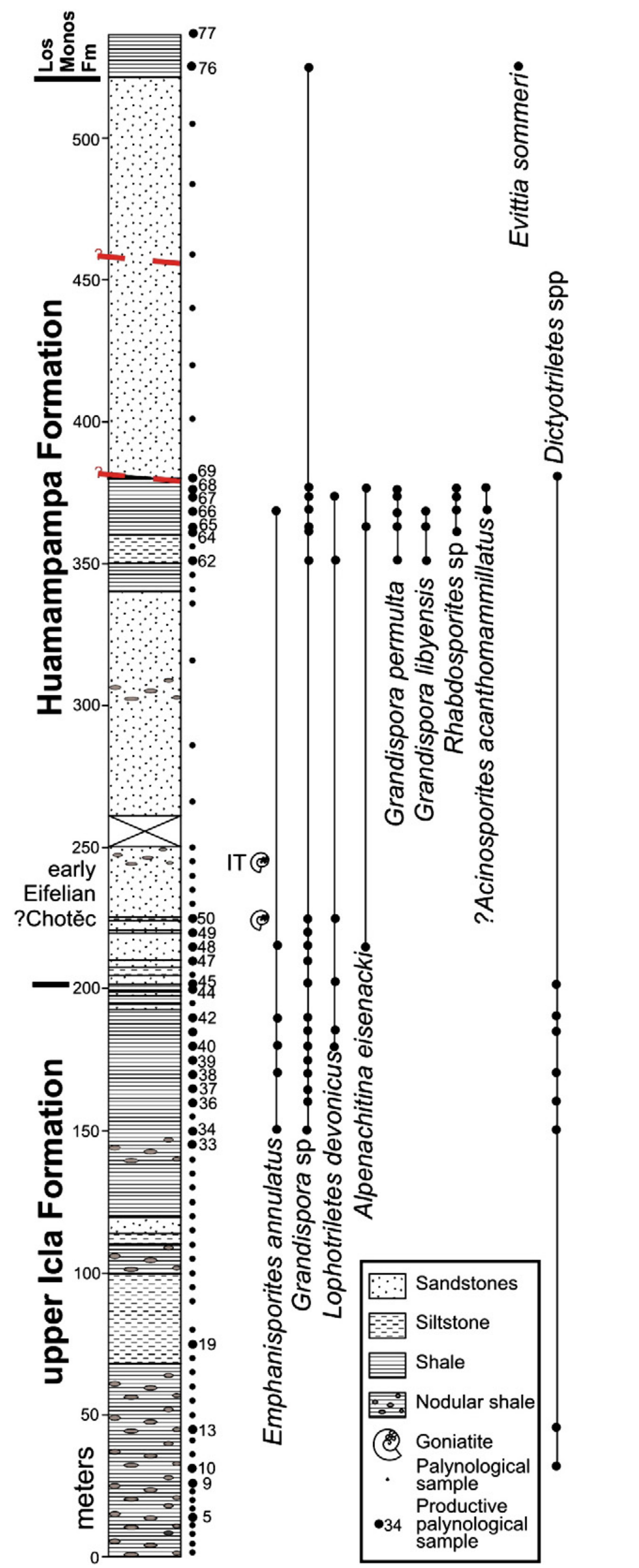

Fig. 10. A log of the upper Icla/basal Los Monos Formation interval at Campo Redondo, Chiquisca Department. There is some faulting in the section, but structural repetition is not an issue because fault displacements appear to be minor. Correlation with the basal Los Monos Formation at Bermejo is achieved as the *Evittia sommeri* epibole is present (as rather poorly preserved specimens) in a mudstone interval at the top of the section. Note that the sequence of first occurrences of important floral elements recorded in this section is similar to those reported from the correlative sections in South America, North Africa and Arabia (Loboziak and Streel, 1995). The original goniatite discovery by Hünicken et al. (1980) is thought to be approximately at the level of sample CMR50, although this horizon could not be located at the outcrop.

diverse and more abundant specimens of *Grandispora* spp. including *G. velata*, *G. permulta* and *G. libyensis* (Fig. 11E, G and A–B). Also present is a persistent component of *Lophotriletes devonicus* (Fig. 5C), spores comparable to *Acinosporites acanthomammillatus* (Fig. 5B) and small camerate spores with an apiculate sculpture. These small camerate spores (Fig. 11F) are similar to specimens referred to various species of *Rhabdosporites*, *R.* sp. of Riegel (1973), *Rhabdosporites* 'small, perhaps new form' of Riegel (1974); *R. parvulus* of McGregor and Camfield (1976); *R. 'wernerii'* and *R. 'prumensis'* of Riegel (1982) both of which are *nomina nuda*, and *R. minutus* Tiwari and Schaarschmidt (1975). The latter has been formally adopted as a nominate species for the *Min* Sub-zone by Streel et al. (1987) and is becoming widely adopted (Al-Ghazi, 2007; Ashraf and Utescher, 1991; Bruer et al., 2007). However, it must be recognised that the type specimen (*R. minutus*, Tiwari and Schaarschmidt, 1975; pl. 21, Fig. 4a–d) is from the much younger Loogh Formation and hence of Givetian age and is regarded here as, in all probability, a specimen of *Geminospora lemurata* which is known to be abundant in this unit (Riegel, 1982 who referred it to *Geminospora antaxios*). *Alpenachitina eisenacki* also reoccurs in sample CMR 65. Above this shale interval, palynomorphs are absent until the mudstones/shales equivalent of the basal Los Monos Formation in sample CMR 76. This sample has a well preserved acritarch assemblage including a significant influx of *Evittia sommeri* which confirms its stratigraphical position at the base of the Los Monos Formation.

The horizon that previously yielded the goniatite *Tornoceras bolivianum* Hünicken et al. (1980) occurs approximately 20–25 m above the base of the Huamampampa Formation (Fig. 12). The holotype is preserved in dark-grey, fine-grained, silty limestone. Although the precise level and lithology of this first goniatite could not be located in the field, another goniatite was discovered by one of the authors (goniatite IT on Fig. 8) in a mid grey, calcareous nodule that was an estimated 15 m above the inferred level of the original find of *T. bolivianum*.

5. Discussion

5.1. Palynomorph epiboles

The *Evittia sommeri* epibole is a single, stratigraphically short-lived event (Fig. 9). It occurs across an interval at Bermejo that is relatively impoverished in terms of marine palynomorphs. Sedimentologically, the fining-up sequence (siltstone to mudstone) in the basal Los Monos Formation (Fig. 8) is consistent with a marine transgression. *Evittia sommeri* may have been an opportunistic species which took advantage of the changing environmental conditions. The increase in the abundance of preserved *E. sommeri* specimens may have been enhanced by sedimentological condensation, suggesting the epibole could represent an interval of reduced clastic input close to, or at, the maximum flooding surface of the basal Los Monos Formation marine transgression. Furthermore, given the restricted stratigraphic range of *E. sommeri* in Bolivia and northern Argentina (Fig. 9) the occurrence of this acritarch in a conspicuous mudstone interval at the top of the measured section at Campo Redondo, demonstrates that the same marine transgression occurs in both outcrop sections. The presence of goniatites and the inception of *Alpenachitina eisenacki* in the basal Huamampampa Formation permits additional chronostratigraphic constraints to be placed on this marine transgression (see Section 5.4).

The *Bimerga bensonii* and *Crucidia camirense* epiboles are regarded as not as significant palaeoenvironmentally and should be considered more as useful biostratigraphic markers. Morphologically, *Petrovina connata* has affinities with the fresh water hydrodictyacean algae and hence its occurrence in relative abundance in an otherwise transgressive marine palynological assemblage dominated by AOM (Fig. 7) is intriguing.

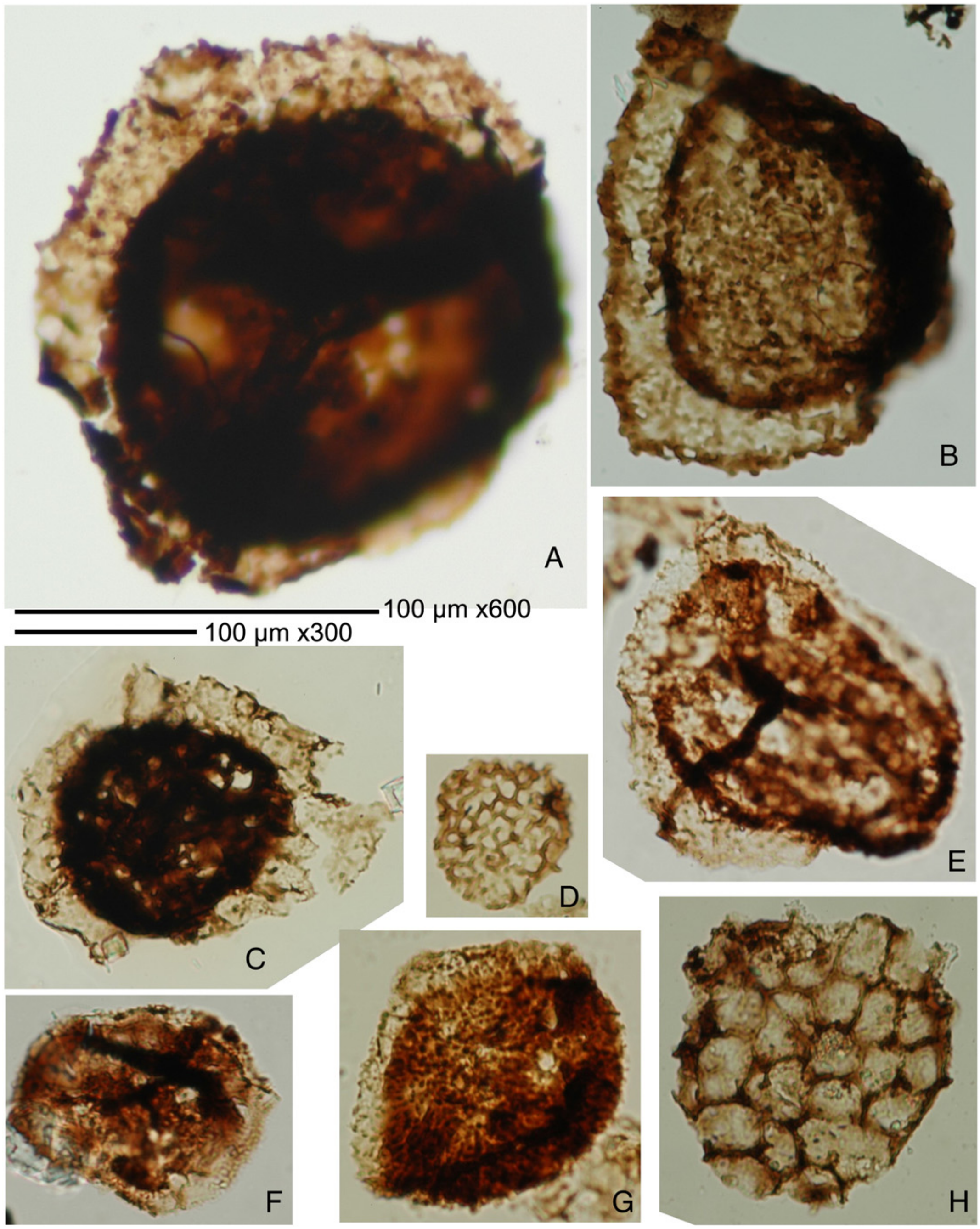

Fig. 11. (A) *Grandispora libyensis*, CMR 65p, W47/2, x300. (B) *Grandispora libyensis*, CMR 65p, M31/2, x600. (C) *Grandispora* sp., CMR 34, E26, x600. (D) *Dictyotriletes* sp. A of McGregor (1984), CMR 69.2, F19/3, x600. (E) *Grandispora velata*, CMR 68, G11/4, x600. (F) *Rhabdosporites* sp, CMR 64, S30/1, x600. (G) *Grandispora permulta*, CMR 69.2, V15/2, x600. (H) *Dictyotriletes subgranifer*, CMR 69.2, X23, x600.

The prasinophyte peak, although not containing any unique palynomorph, is distinctive through its position beneath the *Crucidia camirense* epibole and above the terrestrially dominated PDI. It usually contains a significant proportion of *Hemiruptia legaultii*, a simple leiosphere that is distinguished by its epitractal excystment. There is also an internal sequencing within the peak with the local abundance of *Veryhachium trispinosum* at the base. It is also identifiable from its assemblage of typical Iquiri Formation acritarchs and chitinozoa.

Lithologically, the PDI is indistinguishable from the bulk of the Iquiri Formation and is named only as an informal palynologically defined subdivision. At outcrop it is clearly within a marine influenced section as shown by the presence of pelmatozoan crinoids and starfish (both including articulated specimens) and trilobites (including intact moult exuviae). However, the relative increase in terrestrial plant derived phytoclasts and spores together with the presence of clastic granule layers is certainly very striking and its top is easily defined within sub-surface cuttings samples.

The four distinctive palynomorph epiboles have not yet been demonstrated beyond the Chaco Basin, but these taxa have been documented from broadly time equivalent sections in other regions. *Evittia sommeri* was originally recognised from northeastern Brazil (Brito; 1967, see Section 5.4), and has since been recorded in the Solimões Basin in western Brazil (Quadros, 1988). *Bimerga bensonii* has also been recorded from Ghana (Anan-Yorke, 1974; see also Wood, 1995) and *Crucidia camirense* from the Altiplano in western Bolivia (pers. obs.). *Petrovina connata* has also been reported in the

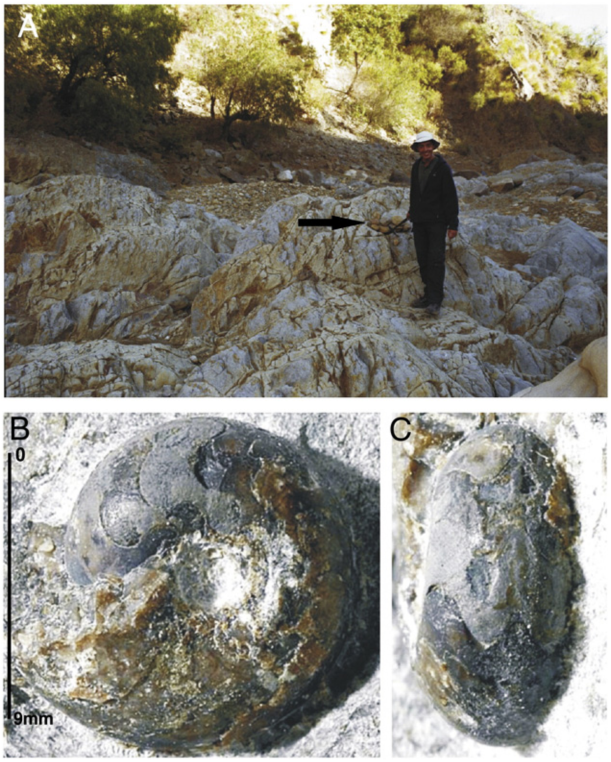

Fig. 12. A. the new goniatite bearing locality at Campo Redondo. The stone cairn to the left of I. Troth (arrowed) marks the level which yielded the second goniatite specimen (B, C) from the basal Huamampampa Formation. In terms of morphology, both this goniatite and the specimen figured in Hünicken et al. (1980) share greater affinity with *Mimotornoceras* than *Tornoceras* (the original generic assignment). *Mimotornoceras* is unknown beneath the Choteč Event level (early Eifelian), and because no other goniatite genera had reached a similar advanced level of septa morphology in the Emsian, the goniatite and hence the base of the Huamampampa Formation can only be early Eifelian in age.

Amazonas Basin, northern Brazil (Le Hérissé, 2001) and the holotype is from the Paraná Basin in southern Brazil (Oliveira and Burjack, 1996).

5.2. The Campo Redondo goniatites

Goniatites are rare in the Devonian of Bolivia and are generally very poorly located both geographically and stratigraphically (i.e. described specimens have been acquired from street markets). They are also not easily placed within existing and known faunas from lower palaeolatitudes or easily correlated with the standard goniatite zonation. Hence, the discovery *in situ* of a second goniatite in the Campo Redondo section (Fig. 12) is significant. The earlier discovery (Hünicken et al., 1980) and its interpretation as late Givetian-early Frasnian age had caused some difficulties in correlation in what was palynologically considered to be an Emsian or early Eifelian sequence. For example, some interpretations (Racheboeuf et al., 1993, p.798) have introduced a significant hiatus within the Icla Formation beneath the level with this single goniatite. In addition, the goniatite became widely cited (e.g. Boucot, 1988) as evidence for an extra-Malvino-kaffric faunal incursion and hence indicated the breakdown of the faunal realm. The acquisition of the second specimen meant that it has been possible to investigate and compare the actual specimens of both goniatites in the context of increased knowledge of faunas that was not available to Hünicken et al. (1980).

Both specimens have strong similarities in suture pattern and the fact that both specimens come from the same locality and same overall part of a formation strongly suggests that the new smaller specimen is a juvenile of *Tornoceras bolivianum*. Assuming that this identification is correct, the juvenile and a re-examination of the holotype reveal several important features of the species, as follows:

- it has open umbilicate early whorls (Fig. 12B–C) which in post-embryonic *Tornoceras* are strictly involute
- the presence of a weakly developed ventral band on the median stages is unknown in true *Tornoceras*
- it has a rather shallow dorsal lobe, clearly visible on septal surfaces of the holotype (but not illustrated in Hünicken et al., 1980), a character that it shares with the Parodiceratinae or Pinacitidae (Foorditinae), but not the true Tornoceratinae
- the mature flank lobe is subangular whereas in *Tornoceras* it is always subrounded
- the dorsolateral saddle is very short in the juvenile which suggests that the flank lobe, not the lobe at the umbilical seam, is the lateral lobe (L of common terminology), a defining character of the Pinacitidae (Foorditinae) or Holzapfeloceratidae

Consequently, *T. bolivianum* clearly needs to be removed from *Tornoceras*. The listed characteristics and relatively expanding mature whorls suggest affinities with *Mimotornoceras* Klug (2002), which is known from the Eifelian of North Africa (Morocco, Algeria) and eastern North America (Ohio, *Foordites* sp. n. in House and Blodgett, 1982). This distribution is significant as it would provide a viable source for immigration into South America (cf. Isaacson and Perry, 1977 who suggested brachiopod migration from Libya). However, the adult conch on the larger specimen is so different from true *Mimotornoceras* that the introduction of a new genus appears inevitable. The Foorditinae (Pinacitidae), which includes *Mimotornoceras*, spread globally early in the Eifelian. But *Mimotornoceras* itself is not known from below the Choteč Event level (Fig. 13).

The morphology of both specimens is incompatible with an Emsian age when compared to the complete global ammonoid record for the Lower Devonian in that no known Emsian ammonoids have reached a similar advanced septal morphology. In all Emsian forms, the septa are still synclastic (laterally curved backwards, with a dominant flank lobe and lacking a prominent, wide inner flank saddle) even including the very rare forms with some additional lobes at the venter or near the umbilicus. Anticlastic septa, as found in this juvenile specimen from Bolivia, are not known to occur before the Mid Devonian, where they originated independently and at different times in several lineages (in the Eifelian: *Mimotornoceras*, Holzapfeloceratidae, Tornoceratidae, some Anarcestidae and from the Givetian: Maenioceratidae). There is also no ancestral Emsian form from which this South American species could have arisen independently. The ancestors of *Mimotornoceras* (*Foordites*) are also Eifelian in age. Therefore it would be possible that the first known ammonoid influx into South America occurred in conjunction with the Choteč Event which is the age of the first known *Mimotornoceras* in North Africa. The age of this level in Campo Redondo is therefore assigned to (at least) the early Eifelian and this is consistent with the inception of *Alpenachitina eisenacki* in CMR 48 some 10 m beneath the goniatite (see Section 5.3). The different (and much younger) original age determination of Hünicken et al. (1980) resulted from the advanced morphology of the adult specimen and homeomorphy with Givetian/early Frasnian tornoceratids, such as *Tornoceras arcuatum* or *Epitornoceras*.

The lithology that preserves the adult goniatite specimen from Campo Redondo is a dark grey limestone. It has been processed for conodonts and found to be barren. However, the overall lithological context is atypical of classic goniatite bearing lithologies, because it lies within the start of the regressive transition to the sandstones of the Huamampampa Formation. However, 30 m below the goniatite level there is a 45 m thick package (CMR33–CMR42) of dark grey upper Icla Formation shales rich in macrofossils including brachiopods, pelmatozoans and trilobites. This is tentatively proposed as

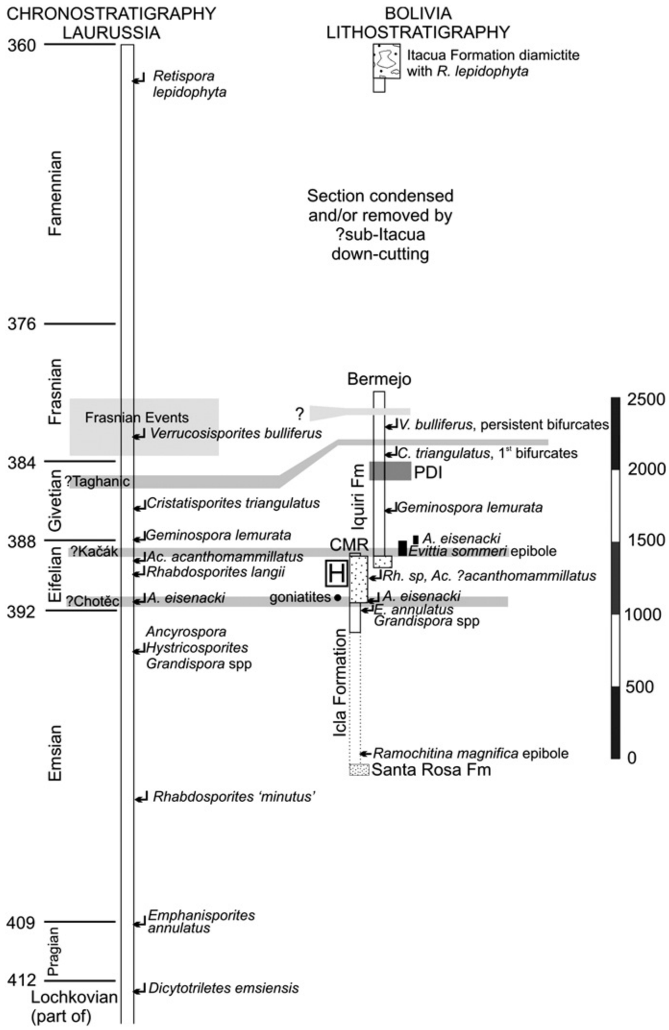

Fig. 13. A synthesis showing the bases of key palynological events in Laurussia and Bolivia. Laurussia is scaled to chronostratigraphy using the geochronological stage durations of Kaufmann (2006). Bolivia is scaled to stratigraphical thickness with the vertical scale adjusted so that the Choteč and Kačák Events act as tie-points between the two areas. Also shown are selected Devonian marine transgressive events from Laurussia and northern Gondwana (highlighted). The data from Bolivia is a composite of the Bermejo and Campo Redondo sections. The latter is continued down to the Santa Rosa Formation using an average sub-surface thickness from the epiboles of *Evittia sommeri* to *Ramochitina magnifica*. The correlation with Laurussia is based on the goniatites at the base of the Huamampampa Formation [H] in the Campo Redondo section and the first occurrence of *Alpenachitina eisenacki* (calibrated to the conodont zonation in the USA). Consequently there is relatively greater biostratigraphic and hence chronostratigraphic control in this interval. Note the absence of *Rhabdosporites langii* and the delayed first occurrences of *Emphanisporites annulatus*, *Ancyrospora* and *Hystricosporites* in Bolivia relative to Laurussia. The marine transgression associated with the *Evittia sommeri* epibole in the basal Los Monos Formation is tentatively correlated with the Kačák Event in Laurussia. However, the correlation of other Laurussian sea-level perturbations with the significant marine transgressions in the Icla and Iquiri Formations is more speculative due to lack of biostratigraphic precision.

representing the Choteč Event and is consistent with both the age of the goniatites and the *partitus* conodont zone inception of *A. eisenacki.*

5.3. The Campo Redondo palynomorphs: global comparisons

The pattern of inceptions within the Campo Redondo section parallels that reported by McGregor (1984) from the Tarabuco section. It also has a similar pattern to that reported in correlative sections in South America, North Africa and Arabia (e.g. Loboziak and Streel, 1995) which are characterized initially by an assemblage of morphologically simple spores which then rapidly increase in sculptural and morphological complexity through what is generally attributed to the late Emsian to early Eifelian interval.

In Campo Redondo *Emphanisporites annulatus* and *Grandispora* spp. have a near common inception in the uppermost Icla Formation (Fig. 10). This is 70 m below the goniatite locality which is now shown to be of early Eifelian age. In northwestern Europe (Fig. 13), the inception of *E. annulatus* is well constrained to the uppermost Pragian (Steemans, 1987; Streel et al., 1987) where it defines the base of the AB zone. The AB zone has been recognised widely in both South America (e.g. Loboziak and Melo, 2002) and North Africa (e.g. Loboziak et al., 1992) where, by correlation with northwestern Europe, its base is placed within the early Emsian. In Bolivia the base of this zone can now be seen to be nearly one stage and up to 17 my younger (time scale of Kaufmann, 2006) based on its goniatite-controlled first occurrence in the Campo Redondo section (Fig. 13).

In the German GSSP section (Riegel, 1982; Ziegler, 2000), where spores occur with both goniatites and conodonts, the first occurrence of *Grandispora* spp. is latest Emsian in age (Fig. 13). These latest Emsian spore assemblages are characterized by the presence of persistent but rare *Grandispora* (often referred to in older publications as either *Calyptosporites* or *Spinozonotriletes*). In Brazil the inception of these more complex spores is used to define the correlative *Samarisporites*/*Grandispora* assemblage zone (Melo and Loboziak, 2003). Although there are now much earlier unequivocal records of very rare specimens of *Grandispora* in the Lochkovian (earliest Devonian) of both Saudi Arabia (Steemans et al., 2007) and Brazil (Steemans et al., 2008) its significance here in the Emsian and Eifelian relates to its persistent presence.

The inception of *Grandispora* spp. In the GSSP section is, in fact, only a minor component of the major changes that occur in the latest Emsian palynofloras. This major change is the inception of the bifurcate (grapnel) tipped group of spores *Hystricosporites* and *Ancyrospora*. In Laurussia, the species of both these genera at this stratigraphical level are characterized by relatively short bifurcate tipped spines thus defining a very distinct assemblage (McGregor, 1982). Neither of these bifurcate tipped forms are known to occur at the same level in South America (Fig. 13). In fact, both genera have much later first occurrences and comprise the longer spined forms that characterize the much younger Laurussian spore assemblages (McGregor and Playford, 1992). In the Bermejo section bifurcate tipped spores have an inception some 600 m (sporadic from CGH 108, persistent at and above CGH 117, Fig. 6A, B) above the base of the Iquiri Formation and between the inceptions of *Geminospora lemurata* and *Cristatisporites triangulatus* and hence of mid/late Givetian age.

This apparent paucity of both *Ancyrospora* and *Hystricosporites* is also notable in Eifelian sections along the northern margin of Gondwana (Fig. 14), Morocco (Rahmani-Antari, 1990; Rahmani-Antari and Lachkar, 2001), Libya (Grignani et al., 1991; Massa and Moreau-Benoit, 1976), Algeria (Moreau-Benoit et al., 1993), Saudi Arabia (Loboziak, 2000; Loboziak and Streel, 1995) and Iran (Ghavidel-syooki, 2003). In all these areas the genera are only present sporadically in the Emsian/Eifelian interval where some typical Laurussian species (*A. nettersheimensis*, Loboziak and Streel, 1989; Moreau-Benoit et al., 1993) have been recognised. Apart from these early occurrences both taxa, as in Bolivia, only become common in the latter part of the Givetian.

In northwestern Europe the next major inception, above that of the bifurcate tipped spores, is *Rhabdosporites langii* (Fig. 13), a spore that originates from the aneurophytalean progymnosperms. This species then becomes a dominant element in most Laurussian mid and late Eifelian spore assemblages (e.g. Avkhimovitch et al., 1993; Marshall and Fletcher, 2002; Richardson and McGregor, 1986; Riegel, 1982). Despite this increase in abundance the taxon is apparently absent from the Eifelian in southern South America although it has a sporadic Givetian occurrence (Melo and Loboziak, 2003).

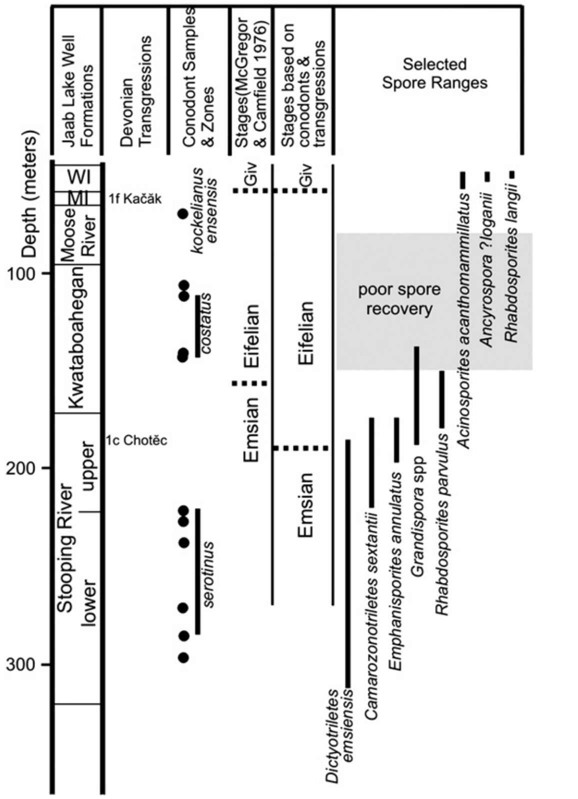

Fig. 14. Selected spore and conodont data from the Jaab Lake No. 1 well, Moose River Basin, Ontario, Canada. The distribution of spores and spore group common to sections in Bolivia shows parallel groups of inceptions. The conodont data shows similar ages to those determined from Bolivia. This contrasts with Western Europe where the spores have different inceptions. The positions of the Choteč and Kačák events are shown. Compiled from McGregor and Camfield (1976), Uyeno and Bultynck (1993) and Stoakes (1978). MI (Murray Island Formation), WI (Williams Island Formation).

The inception of *Alpenachitina eisenacki* in CMR 48 is notable because this taxon has a conodont dated inception in North America that is in the early Eifelian *partitus* Zone (Paris et al., 2000; Wright, 1980). *Alpenachitina eisenacki* displays a quite variable presence/absence within the section (Fig. 13). Its subsequent re-occurrence in abundance at a higher level in the Los Monos Formation is revealing as it means that its distribution is not simply controlled by evolutionary first appearance.

Grandispora spp. is more diverse in the samples (CMR 62–69) from the shale unit found within the Huamampampa Formation. This assemblage has been reported from Brazil (Melo and Loboziak, 2003) where it defines the *Per* assemblage zone, which succeeds the *Samarisporites*/*Grandispora* assemblage zone, and has been attributed an early Eifelian age. However, these zones have not been defined in contiguous sections, and lack conodont or goniatite age control. This intra-Huamampampa shale also has the first occurrence of the small species of *Rhabdosporites* that is generally referred to as *R. minutus*. As already noted, this has a first appearance in the uppermost part of the Emsian in Germany (Riegel, 1982; Tiwari and Schaarschmidt, 1975) and has been used to define the late Emsian *Min* sub-zone (Streel et al., 1987). However, its inception above the goniatite levels in the Campo Redondo section indicates that its first appearance is both different and later than that in Germany (Fig. 13). This is significant as it is a widely recognised form and has been used in the Arabian Plate (Al-Ghazi, 2007; Bruer et al., 2007; Loboziak, 2000; Loboziak and Streel, 1995) as a late Emsian index species.

Other systematic differences between South America and western Europe are also well known. For example, in northwestern Europe, *Dictyotriletes* has a well defined late Lochkovian first occurrence when it is used to define the E sub-zone of Streel et al. (1987) and occurs as populations with a low morphological diversity close to that of typical *D. emsiensis*. Whereas, in Brazil, *D. emsiensis* has a first occurrence as part of a diverse morphon of related forms and has an earlier inception that is dated as being within the Lochkovian (Rubinstein et al., 2005).

5.4. Laurussian analogue

Perhaps the most similar sequence of assemblages in Laurussia to that recorded from Bolivia is from the Jaab Lake well in northern Canada (Fig. 14 and McGregor and Camfield, 1976), a location that is palaeogeographically relatively close to South America (Fig. 15). In the Stooping River Formation there is the near coincident inceptions of *Emphanisporites annulatus* followed by *Grandispora* (as *G. ?macrotuberculata*) and then a form attributed to *Rhabdosporites parvulus* (i.e. *R. minutus*). There is also a similar overlap in both northern Canada and Bolivia of the last occurrence of *Dictyotriletes emsiensis* and *D. subgranifer* with the first occurrence of *E. annulatus*. Unfortunately a more detailed analysis is precluded by poor spore recovery through the overlying Kwataboahegan Formation. Acritarchs have also been monographed in a parallel study (Playford, 1977) but *Evittia sommeri* was not reported. The Jaab Lake well is also important because conodonts have now been documented in detail (Uyeno and Bultynck, 1993) from the section and provide information that was not available to McGregor and Camfield (1976). These show (Fig. 14) that late Emsian (*serotinus* Zone) conodonts occur through much of the Stooping River Formation followed by an approximately 45 m thick barren interval before the occurrence of *costatus* Zone conodonts (early but not earliest Eifelian) in the lower part of the Kwataboahegan Formation. This interval that is barren of conodonts includes the inception of *Emphanisporites annulatus* and *Grandispora* spp. and hence from comparison with spore assemblages from Europe was attributed a late Emsian age. However, sedimentological interpretation of the sequence (Stoakes, 1978; Uyeno and Bultynck, 1993) suggests that Transgressive Regressive Cycle (TRC) Ic of Johnson et al.

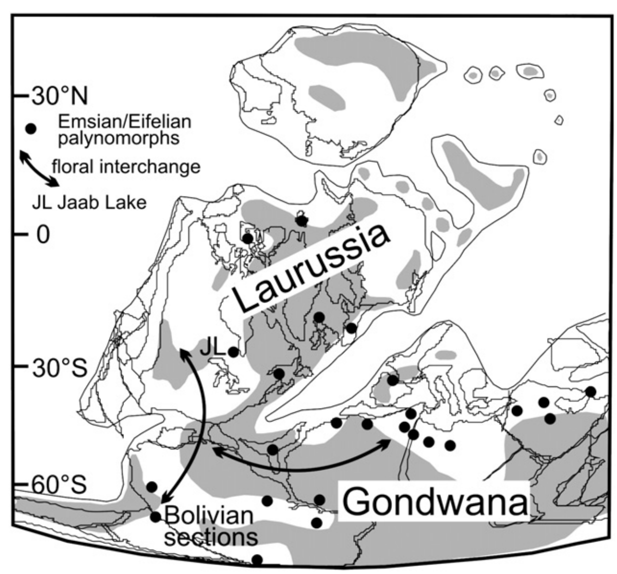

Fig. 15. Potential pathways for intra/extra-Gondwanan floral interchange during the Early/Mid Devonian collision of Laurussia and Gondwana. Localities in the former Gondwana and Laurussia land masses which have yielded Emsian/Eifelian spore assemblages are marked. The continental interaction may have permitted more climatically tolerant plants to begin moving between low palaeolatitutes (i.e. Laurussia) and higher palaeolatitudes (Malvinokaffric Realm). While the number of common elements between the Laurussian and Gondwanan spore assemblages did increase throughout the Devonian, the Malvinokaffric Realm appeared to retain a distinct floral signature at least until the Late Devonian. The Late Devonian spore record is, however, incomplete in the Sub-Andean due to erosion. From Scotese (2001).

Please cite this article as: Troth, I., et al., Devonian sea-level change in Bolivia: A high palaeolatitude biostratigraphical calibration of the global sea-level curve, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2010), doi:10.1016/j.palaeo.2010.10.008

(1985), i.e. the earliest Eifelian Choteč Event, occurs in the upper part of the Stooping River Formation (Fig. 14).

This interpretation of a somewhat younger age now gives a parallel pattern of spore inceptions with the conodont/goniatite chronostratigraphy in both Bolivia and Canada. A similar sequence of assemblages are also recovered from Gaspé, Canada (McGregor, 1973, 1977) but as these sections then lacked any independent age control they were again only dated through comparison with assemblages from western Europe. However, there are now some associated conodont and brachiopod assemblages (Uyeno and Lespérance, 1997) from related sections that suggest a somewhat younger age and are hence in accord with the age from Bolivia.

Clearly the rare occurrence of a Malvinokaffric goniatite tie-point in Bolivia has shown that key spore taxa that are used zonally in both Laurussia and Gondwana do not all have coincident inceptions in both areas. Some are earlier (*E. annulatus* in Laurussia, *D. emsiensis* in Gondwana), other later (*R. minutus*, *Ancyrospora* and *Hystricosporites* in Gondwana) whilst other are approximately synchronous (persistent *Grandispora* spp. although with much earlier sporadic records in Gondwana and the Arabian plate). Significantly the chitinozoan inceptions such as *Alpenachitina eisenacki* appear to be broadly coincident between the two areas.

5.5. Sea-level change: Bolivia and Laurussia

Based on the new goniatite data (Section 5.2), the Huamampampa Formation cannot be older than Eifelian. In addition, the inception of *Geminospora lemurata* (Figs. 7, 13) in the basal Iquiri Formation provides a latest Eifelian age constraint for the uppermost Los Monos Formation. Therefore, the marine transgression associated with the *Evittia sommeri* epibole is within the mid to late Eifelian interval.

In the Eifelian of Laurussia, there are two major transgressions (Fig. 13): the Choteč and the Kačák Events (Walliser, 1996) that occur within TRC Ic and If of Johnson et al. (1985). The best records of Devonian sea-level change come from carbonate dominated pelagic sections in Euramerica and northern Gondwana (e.g. Morocco) where the sediments although highly condensed are believed to be complete and contain excellent faunas of both conodonts and ammonoids. In contrast, the Bolivian formations are from a clastic neritic succession and although with a much higher sedimentation rate are heterolithic in lithology and hence inherently more difficult to interpret. Therefore emphasis is placed on the more obvious lithological changes and that these would represent the sea-level changes that are larger in magnitude from Euramerica and northern Gondwana. This situation is exactly analogous to the development of the Devonian sea-level curve where the greater magnitude events were the first to be recognised (e.g. Johnson et al., 1985) and are now being followed (e.g. Ver Straeten, 2009) by the identification and naming of an increasing number of second and third order events.

There are four significant marine transgressions in the Devonian of Bolivia that are identifiable by the replacement of the finely laminated heterolithic sandstone/mudstones by homogenous dark grey shale/mudstone deposition. These intervals are typically tens of metres thick or more. On this basis there is an inferred marine transgression in the upper Icla Formation above CMR 33 (Fig. 10) and coincident with the onset of a package of dark grey shales 60 m thick. This is tentatively proposed as representing the Choteč Event. Placing the Chotěc Event at this stratigraphic level is consistent with the early Eifelian age of the goniatites and the *partitus* Zone inception of *Alpenachitina eisenacki* in the basal Huamampampa Formation.

The next major transgression is that with *Evittia sommeri* in the basal Los Monos Formation. This stratigraphic interval is broadly time equivalent to the late Eifelian Kačák Event (late Ei 1 of Walliser, 2000). Hence, the basal Los Monos Formation is proposed as a correlative of this event. Within South America, this same Eifelian transgression is also recorded at the base of the Pimenteira Formation (Melo, 1988) in the sub-surface of the Parnaíba Basin, northeastern Brazil. Although the *E. sommeri* epibole has not yet been demonstrated at this level in the Parnaíba Basin, it is likely to be present, as samples from this interval in well 2-PM-1-Ma (Brito, 1967) yielded abundant specimens of *E. sommeri*. Evidently, *E. sommeri* can be found in a similar stratigraphic position across a large geographical area in South America (Peru and Argentina, pers. obs.) There are as yet unsubstantiated reports of *E. sommeri* from the Mid Devonian in Laurussia (Cramer, 1969). Assuming similar stratigraphic trends to Bolivia (i.e., a restricted stratigraphic range), locating *E. sommeri* (or its epibole) at the Kačák level in Laurussia would be the conclusive proof that the basal Los Monos Formation marine transgression is the Kačák Event (cf. Wood, 1995).

There are few distinct lithological changes that herald the deposition of the PDI, as this interval displays typical but variable Iquiri Formation facies of interbedded mudstones, siltstones and sandstones throughout. However, in the Bermejo section there are, at outcrop, rare layers that contain angular unsorted granules of quartz with minor feldspar indicating a proximal influence within the interval. The simple interpretation is that this terrestrial plant matter rich interval was related to a marine regression. The most obvious candidate correlative level in Euramerica would be that at the Ludlowville-Moscow Formation boundary (between sequences 4 and 5) in the Hamilton Group of New York State (Brett and Baird, 1996). This regression is now widely recognised across East-Central North America (Bartholomew and Brett, 2007). An alternative explanation is that the PDI records a climatic overprint of increased continental run-off during this thick (130 m), i.e. long interval in the Iquiri Formation.

The inceptions of the spores *Cristatisporites triangulatus* and *Verrucosisporites bulliferus* provide broad age constraints for the two additional marine transgressions found in the Iquiri Formation. These spores provide late Givetian and early/mid Frasnian ages respectively for two very distinctive dark grey organic matter rich (AOM) mudstone/shale packages in the upper Iquiri Formation (Fig. 7). The late Givetian event is tentatively assigned to the Taghanic Onlap (TRC IIa1b, the post-Tully transgression, Aboussalam, 2003), whereas the Frasnian transgression is associated with the *Petrovina connata* epibole and is correlated to the marine transgression at the base of TRC IIc (Walliser, 1996). Although both events require additional external tie-points in order to be able to confirm these ages, broadly coeval marine transgressive intervals have been reported from the sub-surface of the Amazonas Basin (Grahn and Melo, 2002, 2004; Loboziak et al., 1996; Melo, 1988) and the Paraná Basin (Melo, 1988).

The record of Devonian sea levels is based around a structure of recognising and correlating transgressions. This is inevitable given that it is these levels that contain both the goniatites and most diverse conodont faunas. However, it should be noted that the record of regressions is equally of significance. The Huamampampa Formation can now be recognised as a time of distinct sea level fall that was sustained between the Choteč and Kačák events.

5.6. Implications for the demise of the Malvinokaffric Realm

The main evidence given for the demise of the Malvinokaffric Realm is the occurrence of extra-Malvinokaffric fauna in South America and South Africa. However, it has long been acknowledged that there is no sustained lithological evidence for a warmer climate, e.g. limestones in the Middle-Upper Devonian rocks of these regions (Boucot and Racheboeuf, 1993). Despite this paucity of lithological evidence a general climatic amelioration is often cited (e.g. May, 1996) as the cause for the Mid Devonian decline in biostratigraphic provincialism. However, the palynological epiboles identified in this contribution considerably clarify the character of the extra-Malvinokaffric excursions and reveals them to be discrete events rather than the permanent immigration of new warmer water taxa. In Bolivia, the oldest known occurrence of *Tropidoleptus* is in the *carinatus* Shale at Cha-Kjeri, Chiquisaca Department (Fig. 2; Isaacson, 1977a). Palynological investigation of this unit shows that it contains (pers. obs.) both abundant *Evittia sommeri* together with *Alpenachitina eisenacki* and is therefore a lateral equivalent to the basal Los Monos Formation. In Brazil, a *Tropidoleptus* dominated assemblage is also documented from the basal Pimenteira Formation in the Parnaíba Basin (Melo, 1988), which records the same marine transgression with accompanying *E. sommeri*. Hence, it is now possible to demonstrate a relationship between the occurrence of *Tropidoleptus* and the epibole of *E. sommeri*, (?Kačák Event marine transgression) in South America. This restricted distribution of *Tropidoleptus* (and also *Rhipidothyris*) has been noted previously (Boucot, 1999; Boucot et al., 1995; Isaacson and Perry, 1977) and was similarly explained by short-lived influxes of warmer water from lower palaeolatitudes coincident with marine transgressions. On the South American continent there is a distinct pattern of Devonian basins (e.g. Melo, 1988) separated by highs (arches) that during transgressions would be over-topped and allow migration of warmer water forms (Isaacson and Sablock, 1990).

In Laurussia, *Tropidoleptus* is known from Pragian and younger rocks. Because its appearances in South America appears to be coincident (at least in part) with marine transgressions, this taxon should, in theory, also be expected in the Lower Devonian of the Malvinokaffric Realm where periods of high sea-level with diverse faunas are recorded, i.e. the Icla Formation (Isaacson, 1977a,b; Sempere, 1995). However, *Tropidoleptus* is, so far, unknown from the Lower Devonian strata of South America and South Africa although present in North Africa (Boucot et al., 1983; Isaacson and Perry, 1977; Mergl et al., 2001). Jansen (2001) found *Tropidoleptus* in rocks of mid-late Siegenian age (Pragian) in southern Morocco in what are Old World Realm brachiopod faunas. This demonstrates that elements that were subsequently able to move south into the Malvinokaffric Realm were already established in Gondwana in the Early Devonian. This supports models (e.g., Fonseca and Melo, 1987) that propose it was the reduction in climatic gradient with associated sea level highs rather than palaeogeography that controlled their ability to move to higher Gondwana palaeolatitudes. Hence, at times of reduced climatic gradient, such as the *E. sommeri* event, these exotic forms were able to temporarily attain higher latitudes. However, their presence should not be inferred as necessarily marking the termination of the faunal realm. For example, some of the last members of the Malvinokaffric calmoniid trilobites survived the Kačák Event and ranged into the early and mid Givetian (Feist, 1991; Melo, 1988).

5.7. Palynomorph interchange across the Laurasian–Gondwana Interface

As shown here this floral interchange was highly selective with the more mobile and climate tolerant floral elements moving both north (*Dictyotriletes emsiensis* from the *D. emsiensis* morphon) and south (?*Grandispora* spp and *Emphanisporites annulatus*) with some elements (*Ancyrospora* and *Hystricosporites*) initially penetrating only into northernmost Gondwana where they remain a very minor component of the flora (Fig. 14). Other conspicuous northern spores such as *Rhabdosporites langii* (the spore of the aneurophytalean progymnosperms; Allen, 1980; Balme, 1995) never achieved this Eifelian dispersal either through a slightly later origination or being less environmentally tolerant. Subsequently, and as agreed by many authors (Hashemi and Playford, 2005; McGregor and Playford 1992; Streel and Loboziak, 1996), the number of common elements increases in the Gondwana and Laurussian spore floras.

Although *Geminospora lemurata* is present and indeed a persistent element within the excellent microfloras from the PDI it is still subordinate to the simple laevigate and apiculate spores that together with a plexus of coarsely sculptured spores (*Verrucosisporites scurrus*) continue to dominate the assemblage. This indicates that the flora was still overwhelmingly dominated by the less 'advanced' elements and was generally impoverished in both progymnosperms and lycopods. However, the flora remained open to the introduction of new taxa as shown by the successive inceptions of *Archaeozonotriletes variabilis*, *Chelinospora concinna*, *Cristatisporites triangulatus* and *Verrucosisporites bulliferus* which are well known in Laurussia, zonally significant, and have inceptions in the same sequence in both areas.

This paucity of *Geminospora lemurata* is in marked contrast to assemblages from Laurussia where it is frequently the dominant element in Givetian and Frasnian microfloras. *Geminospora lemurata* is known *in situ* from fossil archaeopteridalean progymnosperms (Allen, 1980). These are notable for having secondary wood and hence grew to be substantial trees (estimated at 25 m in height) and where the details are known are heterosporous with *Contagisporites* and *Biharisporites* identified (Allen, 1980) as the megaspore. These are relatively large propagules that can be in excess of 500 μm in diameter. During this study a megaspore (Fig. 6I) that can be attributed to *Contagisporites* (compare to Marshall, 1996) was found in the sub-surface Iquiri Formation. Hence it would appear that by the Givetian there is no substantive barrier between Laurussia and Gondwana that cannot be crossed by this relatively large propagule. This high palaeolatitude occurrence of *C. optivus* is supported by its contemporaneous occurrence in northern Gondwana (de Ville de Goyet et al., 2007).

These palynological and palaeobotanical similarities between Gondwana and Laurussia have long been recognised (e.g. Streel, 1974) and regarded as strong evidence for a narrow Rheic Ocean in the Mid and Late Devonian. Many Devonian palaeogeographic reconstructions (Fig. 15; Cocks and Torsvik, 2006; Dalziel et al., 1994; Golonka, 2002; Isaacson and Díaz-Martínez, 1995; Scotese, 2001; Torsvik and Cocks, 2004) support this narrow Rheic Ocean model as they show a progressive northward drift and clockwise rotation of Gondwana with the eventual collision of North and South America. These models are generally based on recognising similarities in Devonian sedimentary successions, the biogeographical distribution of their fossil content and the presence of climatically sensitive sediments. However, several more recent detailed reconstructions (e.g. Nance, 2008; Nance et al., 2010) for the Devonian show the presence of a wide (30° of palaeolatitude) Rheic Ocean with the eventual collision of North and South America only occurring during the Carboniferous. These kinematic reconstructions are based on detailed geochemical and geochronological studies within both the basement and cover sequences of the orogenic zones that resulted from the closure of the Rheic Ocean. The estimated width of this ocean at ~3000 km (Nance et al., 2010) would clearly prevent any long distance dispersal of plants with large spores so there is clearly a conflict between the evidence from the distribution of the spores and palaeogeographical reconstructions that have no evidence for major Gondwana–Laurussia interaction. However, there is some evidence for the earlier interaction of components of Gondwana and Laurussia. Much of this comes from the Acatlán Complex (now within Mexico and part of the Mixteca Terrane) where an episode of Early to Mid Devonian deformation has been recognised (Cawood and Buchan, 2007; Vega-Granillo et al., 2007; Yañez et al., 1991). The Acatlán Complex ultimately made contact with the North America continent south of Ouachita. At its simplest this collision may have been limited to microcontinent interaction rather than a continental scale collision. However, Permian reconstructions (Vega-Granillo et al., 2007) show a significant group of terranes trapped between North and South America. During the Palaeozoic, these terranes would, at different times, have been spread across the Rheic Ocean giving the shorter distances that would be required to successfully migrate the large (>500 μm) and inherently immobile megaspores of a heterosporous plant such as *Archaeopteris*. Clearly for the successful migration of such plants regressions may be more significant than transgressions as lower sea levels would increase the area of exposed shelf with the greater possibility of contiguous land masses. Another sub-aerial

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structure within the Rheic Ocean that could also provide a migration route for terrestrial plants was an Early-Mid Devonian volcanic arc (Keppie et al., 2008). This arc was then removed by Late Devonian subduction with only its erosional detritus preserved within younger sediments.

However, despite these selective interchanges the Laurussian fauna and flora was still unable to freely interchange with that of the Malvinokaffric Realm on a long term basis. Macrofaunas including elements with Malvinokaffric affinities are still recorded in South America into the mid Givetian (Melo, 1988) and the marine palynomorph assemblage also remained highly endemic throughout the Devonian with many taxa unique to the region (Grahn and Melo, 2005; Le Hérissé, 2001). Hence, the very limited extent of the faunal movements south from warmer waters by both brachiopods and goniatites suggests that the climatic gradient was normally sufficient to prevent this. The only interchange occurred during the special circumstances of the Devonian event levels when sea-levels and temperatures appeared to be at their maximum or when warming eventually reached even the high latitudes.

It has been shown that the climatic integrity and the distinct flora of the Malvinokaffric Realm was retained for much of the Devonian and, in fact, probably became more isolated with the onset of climatic cooling in the Famennian that ultimately led to the latest Devonian glacials. However, in most of Bolivia the late Frasnian and almost the entire Famennian has been truncated by erosive down-cutting related to the glaciation (Fig. 4). This truncation has removed much of the evidence for the history of the Late Devonian vegetation. In other areas, such as Brazil, the Late Devonian palynological record is a little better with the sequence, if complete, being very condensed through this interval (Grahn and Melo, 2002, 2004; Loboziak et al., 1996).

This contribution shows how the presence of a single goniatite has both polarized our interpretations of Malvinokaffric–Laurussian relationships and then following this re-interpretation has enabled a more realistic model for microfloral interchange between these continents. Realistically there are few opportunities to collect further goniatites within the Malvinokaffric Realm. Further progress is more likely to come from areas such as Morocco following integration of palynological studies with their now well established goniatite and conodont biostratigraphies. However, until now these goniatite faunas tend to be collected from flat lying desert exposures of deeply weathered rock and, as such, are the least likely conditions in which to recover palynomorphs. Importantly, the palynological assemblages from Morocco are not dissimilar to those found in Bolivia.

Acknowledgements

IT was in receipt of a NERC CASE studentship with BG Group. Grateful thanks for assistance are to M. Bond, E. Clarke, S. Smyth, M. Wakefield and R. Wrigley (BG Group, Reading); G. Beccar (BG, Santa Cruz); A. Ayavira (Repsol, Santa Cruz); M. Suarez-Riglos (NHM, Santa Cruz); Johnny Zambrano (Trinidad, Bolivia); S. Akbari and I. C. Harding, (Southampton). We have also had much fruitful discussion and advice from G. Wood, P. Isaacson, C. Brett, R. Wicander, T. Uyeno, J.H.M. Melo and Y. Grahn.

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Please cite this article as: Troth, I., et al., Devonian sea-level change in Bolivia: A high palaeolatitude biostratigraphical calibration of the global sea-level curve, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2010), doi:10.1016/j.palaeo.2010.10.008