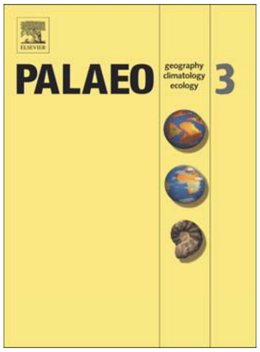

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Was the latest Devonian glaciation a multiple event? New palynological evidence from Bolivia

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ABSTRACT

Assemblages of acritarchs, prasinophytes, and miospores were recovered from the uppermost Iquiri and lower portion of the Itacua formations in southeast Bolivia. Analysis of the diverse and somewhat abundant well-preserved palynomorph assemblage indicates a Late Devonian (late Famennian) age for both formations, and further subdivision in ascending stratigraphic order into the ?VCo, LL, LE, and LN miospore biozones of Western Europe. The presence of age-diagnostic miospore taxa from South America and North America indicates contemporaneous glaciation events between these two regions. The results from close sampling of the diamictite facies of the Itacua Formation at the Bermejo West section, Bolivia, correlate the latest Famennian spore inceptions used to define the Euramerica miospore biozone sequence (LL, LE, and LN zones). The Itacua Formation diamictite sequence examined is relatively thin compared to other diamictite sequences in Bolivia. Furthermore, the miospore biozones represent an estimated duration of three million years, whereas orbitally-forced glacial-interglacial events (e.g., Ruddiman, 2001) are of the

Milankovitch frequency range of between 20,000 to 400,000 years. Therefore, it seems most likely that a number of glacial/interglacial events are represented, rather than a single glacial episode.

Highlights

- Miospores and acritarchs recovered from the Iquiri and Itacua formations, Bolivia.
- Analysis indicates ?VCo, LL, LE, and LN miospore biozones (Late Devonian).
- Age-diagnostic miospores indicate contemporaneous glaciation in N. and S. America.
- Miospores indicate it is unlikely diamictites deposited during one glacial episode.

Keywords: Late Devonian, glaciation, South America, palynology

Introduction

Caputo et al. (2008) identified three glacial episodes in Upper Devonian and Lower Mississippian strata in South America. These are based on a variety of sedimentologic, stratigraphic, and paleontologic data. The first glacial episode, interpreted from diamictites in Peru, Bolivia, and Brazil, occurred during the latest Famennian (Strunian). The second and third glacial episodes are younger and occurred during the late mid to early late Tournaisian and late Viséan, respectively.

There is increasing interest in the emerging record of this latest Famennian glaciation (as reviewed in Caputo et al., 2008; Isaacson and Díaz-Martinez, 1995; Isaacson et al., 2008; Vavrdóva et al., 1991), especially now that recent evidence includes an unequivocal record for a lower latitude glaciation in the Appalachians (~45°S, see discussion in Brezinski et al., 2008, 2009). To this can be added two poorly dated reports of ?Late Devonian diamictites from equatorial Africa (as summarized by Isaacson et al., 2008). The age of the South American and Appalachian diamictites is unequivocally latest Famennian based on the presence in both areas of the distinctive and age-diagnostic miospore taxon *Retispora lepidophyta*, which thus places them within the Strunian interval. The reported dates from the diamictites are based on spot palynological samples, and are generally attributed to the LE/LN spore zones of Higgs et al. (1988).

Compared to individual Quaternary glaciations, the duration of the Strunian (ca. 3 million years; Streel et al., 2006; Trapp et al., 2004) is very long.

To better understand the distribution of glacial-interglacial cycles within the Strunian, a series of closely spaced palynological samples were taken at one meter intervals from the Itacua Formation, a diamictite exposed in the Rio Lajas, Bermejo, Santa Cruz Department, Bolivia. This diamictite has previously been palynologically studied by Perez-Leytón (1991) and Díaz-Martínez et al. (1999 and references therein), where it has been attributed to the LE spore zone. Di Pasquo (2007a, b) also sampled the Itacua Formation, but at a locality some 500 km to the south at Balapuca (Fig. 1) on the Rio Bermejo (in Tarija Department), and concluded that it was Carboniferous in age. The palynology of the sub-diamictite interval (Huamampampa to Iquiri formations) from the Bermejo section in the Rio Lajas, has been studied by Troth et al. (2011).

Location, stratigraphy, and methods

The Bermejo West section is located along the Rio Lajas, approximately 80 km southwest of Santa Cruz, Bolivia (Fig. 1). It is not the same locality as figured by Díaz-Martínez et al. (1999, Fig. 5), which is a structural repeat and located further east. At the Bermejo West location, the uppermost 3 m of the Iquiri Formation, consisting of shale with some sandstone layers was sampled, as was the overlying Itacua Formation, which consists of more than 18 m of diamictites and sandstone lenses (Fig. 2). The diamictite lithology includes a range of dropstone clasts of variable size and different types. Most of these are sandstones and unsuitable for palynological recovery. However, a large (~2 m), 'exotic' dropstone block of deformed sediment that includes thin beds of dark-coloured shales, and is located approximately seven meters above the base of the Itacua Formation was successfully sampled (Fig. 2). The contact between the Iquiri and Itacua formations at the Bermejo West locality is sheared, with local differential movement along what is interpreted to be an unconformity, disconformity, or hiatal surface.

The three samples (1-3) from the top of the Iquiri Formation yielded a well-preserved, diverse, and abundant acritarch, prasinophyte, and miospore assemblage (Fig. 3). The 18 productive samples (4-21) from the lower Itacua Formation also yielded a diverse and abundant acritarch, prasinophyte, and miospore assemblage, albeit of somewhat different composition (Fig. 3). Above these levels, the lithologies are entirely sandstone and unsuitable for palynological recovery. Three samples (35-37) from the 'exotic' sedimentary block within the Itacua Formation also yielded a diverse and abundant palynomorph assemblage (Fig. 3).

Samples were prepared using standard palynologic techniques that included sieving the organic residue at 20 µm (e.g., Wood et al., 1996). Rather than recording the relative abundance of taxa, their presence or absence per sample are given in Figure 3, and the relative sense of abundance for the miospores and acritarchs/prasinophytes is discussed in relation to the composition of the various palynomorph assemblages.

Composition of the palynomorph assemblage

The palynomorph assemblage recovered from the 21 samples of the uppermost Iquiri and lower Itacua formations, as well as the three samples from the 'exotic' sedimentary block within the Itacua Formation, are all well preserved and reasonably diverse (Fig. 3). Although the total number of genera and species of miospores is greater than those of the acritarchs and prasinophytes, the acritarchs and prasinophytes are more abundant and diverse in the individual samples. Megaspores (including *Ancyrospora* spp. and *Hystricosporites* spp.) are also present in many of the samples, especially towards the top of the section. Whereas the preservation of the palynomorphs is very good, it is variable. In addition, many of the acritarch and prasinophyte species show a wide range of morphological variation.

Acritarch and prasinophyte assemblage

A total of 38 species of acritarchs and prasinophytes assigned to 29 genera of acritarchs and prasinophytes were recovered from the 21 samples of the Iquiri and Itacua formations, and the three samples of the 'exotic' sedimentary block (Fig. 3). The prasinophytes recorded are: *Cymatiosphaera ambotrocha* (Plate I, fig. 14), *Cymatiosphaera* cf. *C. perimembrana, Dictyotidium* cf. *D. craticulum, Duvernaysphaera angelae, Duvernaysphaera radiata* (Plate I, fig. 19), *Maranhites mosesii* (Plate I, fig. 18), *Muraticavea munificus, Polyedryxium pharaonis,* and *Pterospermella pernambucensis* (Plate I, fig. 21). Leiospheres (*Leiosphaeridia* spp.) and tasmanitids (*Tasmanites* spp.), also considered to be prasinophytes, were likewise recovered from both formations, as well as the 'exotic' sedimentary block, but because of their simple morphology and lack of biostratigraphic value, they are not included in any discussion or species counts. For the sake of simplicity, the term acritarchs will be used when referring to all organic-walled microfossils thought to be algal microplankton, i.e., the acritarchs and prasinophytes.

As is evident in Figure 3, the diversity of the acritarch assemblage is fairly consistent in all three samples of the uppermost Iquiri Formation. In terms of abundance, *Baltisphaeridium distentum, Pyloferites pentagonalis* (Plate I, fig. 16), *Umbellasphaeridium saharicum* (Plate I, fig. 20), and *Veryhachium polyaster* are the dominant species. These are followed by *Gorgonisphaeridium discissum, Gorgonisphaeridium* cf. *G. winslowii, Hapsidopalla* sp. A, *Maranhites mosesii, Pterospermella pernambucensis,* and *Tyligmasoma alargada*. The remaining taxa all are rare, with only a few specimens recorded in each sample.

The diversity of the acritarch assemblage for the 18 samples of the lower Itacua Formation is also fairly consistent throughout the section (Fig. 3). The main difference in the acritarch assemblages between the two formations is the first appearance in the Itacua Formation of *Baltisphaeridium* sp. A, *Daillydium pentaster* (Plate I, fig. 17), *Ecthymapalla* sp. A, *Gorgonisphaeridium ohioense* (Plate I, fig. 12), *Leiofusa* sp. A, *Navifusa bacilla, Tornacia* sp. A, and *Polyedryxium pharaonis*, all of which occur rarely throughout the section.

There is, however, a change in the dominant acritarch taxa between the Iquiri and Itacua formations. In the 18 samples of the Itacua Formation, *Pterospermella pernambucensis, Umbellasphaeridium saharicum, Veryhachium polyaster,* and the *Veryhachium trispinosum* complex are the four dominant taxa and are generally very abundant throughout the sampled Itacua Formation. They are followed by *Baltisphaeridium distentum*, *Gorgonisphaeridium discissum, Duvernaysphaera radiata*, *Gorgonisphaeridium* cf. *G. winslowii*, *Pyloferites pentagonalis,* and *Stellinium micropolygonale,* which are considered to be common taxa, and *Exochoderma arca*, which has a fair occurrence throughout the section. The remaining taxa are all considered rare, although they may show an increase in abundance in several samples.

In the three samples (35-37) from the 'exotic' sedimentary block within the Itacua Formation, diversity and abundance is low in samples 35 and 36. Furthermore, the preservation of the specimens is not particularly good in these two samples. However, in sample 37, preservation is excellent, and diversity and abundance are both high. The most abundant species is *Umbellasphaeridium saharicum,* followed by a group of species that are all of nearly the same abundance. These are *Duvernaysphaera radiata*, *Gorgonisphaeridium discissum, Maranhites mosesii*, *Veryhachium polyaster,* and the *Veryhachium trispinosum* complex.

Miospore assemblage

A total of 51 species assigned to 33 genera of spores were recorded from the 21 samples of the Iquiri and Itacua formations, and the three samples of the 'exotic' sedimentary block within the Itacua Formation. The three samples of the upper Iquiri Formation contain a low diversity spore assemblage in which only 10 species were recovered. *Cristatisporites triangulatus* (probably reworked), *Rugospora radiata* (Plate I, fig. 6), and *Verruciretusispora loboziakii* occur in all three samples, whereas *Ancyrospora* spp., *Geminospora lemurata,* and *Diaphanospora angusta* occur in two of the three samples. *Verruciretusispora loboziakii* is the most abundant species from this assemblage.

Spore diversity varies throughout the 18 samples of the Itacua Formation, and, except for sample 9, is highest in the uppermost six samples (16-21) analyzed. *Retispora lepidophyta* (Plate I, fig. 8), and *Verruciretusispora loboziakii* are, however, consistently present (16 samples), followed by *Geminospora* *lemurata* (11 samples) and *Rugospora radiata* (10 samples) respectively. The remaining spore species are generally rare throughout the section.

Two of the three samples of the 'exotic' sedimentary block contain the diagnostic species *Verrucosisporites nitidus*, allowing assignment of this clast to the LN Biozone. In addition, these three samples also contain numerous heavily ornamented acamerate specimens, which are also common throughout the highest nine samples studied.

Age of the palynomorph assemblages

The acritarchs, which are more diverse and abundant than the spores in nearly all of the samples examined, indicate that both the uppermost Iquiri and lower Itacua formations, as well as the 'exotic' sedimentary block within the Itacua Formation are Late Devonian (Famennian) in age, corroborating the miospore age determination. However, the miospores allow for a more detailed age assessment in terms of comparison to the Western European miospore biozones (Higgs et al., 1988). Although acritarch and miospore species that are restricted to the Late Devonian occur throughout the section, there are also many relatively long-ranging taxa recognized that could be either indigenous or reworked.

Significantly, there are no definitive Carboniferous miospore or marine phytoplankton species present in the samples examined. Particularly noteworthy is the absence of the miospore taxon *Neoraistrickia loganensis* (Winslow) Coleman and Clayton, 1987, which ranges from early mid to early late Tournaisian in various Euramerican and Gondwanan regions (Playford and Melo, 2009).

Acritarch assemblages

It must be noted that the taxonomy of many of the identified acritarch species is in a state of flux, and needing more detailed study. This paper, however, is not suitable for such a discussion. Therefore, where there is uncertainty in the literature as to taxonomic priority or problems associated with speciating morphologic continua, only one name for consistency is used, such as, for example, *Evittia geometrica* (Plate I, fig. 13) (Troth et al., 2011), *Exochoderma arca*, and *Pyloferites pentagonalis* (=*Multiplicisphaeridium escobaides* Cramer, 1964). The specimens of *Maranhites* are separated into two species, *Maranhites brasiliensis* and *Maranhites mosesii*, rather than considering whether previously named species might represent different ontogenetic stages of a single species (Gonzáles, 2009).

Although there are several acritarch species restricted to the Famennian, some of the recovered taxa are known from the literature to be either restricted to the Middle Devonian or lower, or only range into the Frasnian, but not the Famennian. In some of these cases, it is highly probable that the taxa are reworked, probably from the underlying Los Monos Formation (Eifelian-Frasnian; Ottone, 1996; Troth et al., 2011). Such taxa include *Ozotobrachion* cf. *C. furcillatus*, *Ammonidium* cf. *A. garrasinoi*, *Baltisphaeridium distentum*, *Dictyotidium craticulum*, *Gorgonisphaeridium discissum*, and *Veryhachium polyaster*. These taxa most likely represent reworking, and do not warrant an extension of their geologic range.

Samples 1-3 (uppermost Iquiri Formation)

The acritarch assemblages from these three uppermost Iquiri Formation samples are similar and although diverse, are not particularly abundant. The composition of the assemblages (Fig. 3) and the geologic ranges of the taxa are indicative of a Late Devonian age. Furthermore, the presence of *Horologinella quadrispina* (Plate I, fig. 11) and *Pyloferites pentagonalis* allow placement of these three samples in the Famennian.

Samples 4-21 (lower Itacua Formation)

Just as in the previous three samples from the upper Iquiri Formation, the acritarch assemblages from the 18 samples of the lower Itacua Formation also indicate a Late Devonian (Famennian) age based on the presence throughout the samples of *H. quadrispina* and *P. pentagonalis*. In addition, *Cymatiosphaera* *perimembrana, Daillydium pentaster, Gorgonisphaeridium ohioense,* and *Maranhites mosesii* are also present and all are recognized index species for the Late Devonian.

Diversity remains high in all of the 18 samples analyzed, with the main difference between the uppermost Iquiri and lower Itacua formations being the first appearance in the Itacua Formation of *Baltisphaeridium* sp. A, *Daillydium pentaster, Ecthymapalla* sp. A, *Gorgonisphaeridium ohioense, Leiofusa* sp. A, *Micrhystridium* sp. A, *Navifusa bacilla, Tornacia* sp. A, and *Polyedryxium pharaonis*.

Samples 35-37 ('exotic' sedimentary block within the Itacua Formation)

Two of the three samples from the 'exotic' sedimentary block contain a generally poorly preserved and somewhat low diversity acritarch assemblage. However, sample 37 contains a diverse, abundant, and well-preserved acritarch assemblage that closely resembles those from the Itacua Formation, and is clearly Late Devonian (Famennian) in age, based on the occurrence of *H. quadrispina* (all three samples) and *P. pentagonalis* (sample 37).

Acritarch assemblage summary

The acritarchs indicate a Late Devonian (Famennian) age. Except for such stratigraphically long ranging taxa as *Micrhystridium, Duvernaysphaera angelae,* and the *Veryhachium trispinosum* complex, none of the species recovered extend into the Carboniferous and the total assemblage from all 24 samples is very characteristic of the Upper Devonian, with some probable reworked Mid Devonian taxa also present.

Miospore assemblages

The miospore taxa, in contrast to some of the acritarch taxa, are taxonomically well established and allow for a more detailed age determination.

Samples 1-3 (?VCo Biozone)

The presence of the miospore *Rugospora radiata* and the absence of *Retispora lepidophyta* in samples 1-3 of the uppermost Iquiri Formation indicate that these samples fall within the Western European VCo-VH miospore biozones of Maziane et al. (1999). The base of the VCo Biozone is defined by the first occurrence of *Grandispora cornuta, Retusotriletes phillipsii,* and *Rugospora radiata*. The base of the succeeding VH Biozone is defined by the first appearance of *Apiculiretusispora verrucosa* and *Vallatisporites hystricosus* (Plate I, fig. 9). The first occurrence of *Retispora lepidophyta* defines the base of the succeeding LL Biozone.

The relatively impoverished assemblages from sample 1-3 lack all of the index species of the VCo and VH miospore biozones except for *Rugospora radiata*. *V. hystricosus* only occurs in samples from the Itacua Formation in which *R. lepidophyta* is also present and so it is impossible to distinguish the VH Biozone in the Bermejo section. Therefore, we tentatively assign samples 1-3 to the VCo Biozone.

Perez-Leyton (1991) assigned a single sample (M19) to the VCo Biozone. This assemblage included *R. radiata* but, as in the present study, lacked *Grandispora cornuta* and *Retusotriletes phillipsii*. In a detailed account of the palynostratigraphy of the Amazon Basin of Northern Brazil, Melo and Loboziak (2003) assigned the upper part of the Barreirinha Formation and the basal part of the overlying Curiri Formation to the VCo Biozone, based on much more diverse miospore assemblages than those recovered from Bermejo. Of note, is the inception of *Leiotriletes struniensis* (Plate I, fig. 1) within this biozone. Melo and Loboziak (2003) also recorded the first occurrence of *V. hystricosus* in the lower part of the Curiri Formation, enabling them to recognize the base of the VH Biozone. Furthermore, *Spelaeotriletes granulatus* (Plate I, fig. 7) appears for the first time at this level (Loboziak and Melo, 2002).

Assemblages from samples 1-3 are broadly comparable to the '*Verruciretusispora loboziakii* assemblage' described by Higgs et al. (2002) from a single sample from the Yiginli Formation in southeastern Turkey. However, in addition to common *V. loboziakii*, this assemblage includes *R. radiata, S. granulatus, L.*

struniensis, and *V. hystricosus*, on the basis of which Higgs et al. (2002) suggested a correlation with the VH Biozone.

Samples 4 and 5 (LL Biozone)

Samples 4 and 5 of the lower Itacua Formation also contain low diversity assemblages of miospores and are similar in composition to samples 1-3 of the uppermost Iquiri Formation. However, these two samples contain rare specimens of *Retispora lepidophyta,* which allows tentative assignment to the LL Biozone of Western Europe. There are, however, many compositional differences in this miospore assemblage and those of the LL Biozone of Western Europe. These include the absence of common ‘European’ taxa such as *Diducites versabilis, Knoxisporites literatus,* and *Vallatisporites* spp.

Samples 6-12 (LE Biozone)

The miospore assemblages present in these seven samples of the Itacua Formation are similar to those of samples 4 and 5, but with the addition of rare specimens of *Indotriradites explanatus* (Plate I, fig. 5) and an increase in the number of specimens of *Retispora lepidophyta,* such that their occurrence can be considered common in these samples. Both diversity and abundance of the miospores varies from sample to sample in this interval. The assemblages from these seven samples can be assigned to the LE Biozone, but the scarcity of *I. explanatus* means that the base of the zone could easily prove to be lower if more samples were available or more slides scrutinized, i.e., the Signor-Lipps effect (Signor and Lipps, 1982).

Samples 13-21 (LN Biozone)

The miospore assemblages from these nine samples of the Itacua Formation are somewhat similar to those in the previous samples. Diversity, however, is much higher in samples 13 and 16-21, but abundance is still not particularly high in any of these nine samples. The presence of rare specimens of *Verrucosisporites nitidus* (Plate I, fig. 2) allows the assignment of these samples to the LN Biozone, however, it is possible that the base of this biozone could be lower if more samples or slides were analyzed.

Except for a rare occurrence in sample 21, *Vallatisporites verrucosus* (Plate I, fig. 10), which appears in large numbers with *V. nitidus* in Europe and North America, is apparently absent in these samples. Furthermore, most specimens of *Verrucosisporites* recovered are ornamented with irregular verrucae and short ridges. Because these forms cannot be assigned with certainty to *V. nitidus*, they are provisionally listed here as *Verrucosisporites* cf. *V. nitidus*. *Tumulispora malevkensis*, a species typical of the LN Biozone in Europe, also occurs infrequently in these assemblages. Lastly, murornate ornamented acamerate specimens (mostly *Convolutispora* spp.) are also common throughout this interval.

Samples 35-37 (LN Biozone)

The miospore assemblage in these three samples of the 'exotic' sedimentary block within the Itacua Formation is very similar to those in samples 13-21. Based on the presence of *Verrucosisporites nitidus* in samples 35 and 37, *Verrucosisporites* cf. *V. nitidus* in all three samples, and murornate ornamented acamerate specimens (*Convolutispora* spp.), as well as almost all of the same miospore taxa occurring in samples 13-21, this 'exotic' sedimentary block is placed in the LN Biozone.

Miospore assemblage summary

Despite the rare occurrence, and sometimes lack of index species used to define the Late Devonian European miospore biozones, some stratigraphically-useful taxa from western Gondwana are present, permitting broad correlation with Western Europe for the sampled intervals of the uppermost Iquiri and lower Itacua formations at the Bermejo West locality. The presence of the aforementioned miospore taxa permit subdivision of the Bermejo West section into the ?VCo, LL, LE, and LN biozones of Western Europe (Higgs et al., 1988; Maziane et al., 1999).

Furthermore, there are no taxa recorded which would suggest that any part of the sampled section is Carboniferous in age. The uppermost Iquiri and lower Itacua formations, as well as the 'exotic' sedimentary block within the Itacua Formation, are all late Famennian in age.

Environment of deposition

The presence of both acritarchs and prasinophytes in all the samples clearly indicates deposition in a marine environment. This is substantiated by the character of the sequence where the diamictite occurs entirely within a contemporary marine succession, but above a hiatus indicative of a drop in sea level during the glacial time interval. If it were deposited as a subglacial or proglacial outwash, then it would show characteristics such as internal deformation and overlie basement and/or striated pavements (Eyles and Eyles, 1992). Hence, it is interpreted as a glaciomarine deposit(s) that accumulated during a time of sea level rise, i.e., during a deglaciation event.

Implications for South American glaciation

Previous records of late Famennian age diamictites from South America were attributed (e.g., Isaacson et al., 1999; Melo and Loboziak, 2003 and references therein) an LE/LN age, i.e., the two latest Famennian zones grouped together. Significantly these previous results were based on spot samples. However, the results given here are from samples collected at both a higher resolution and at a regular spacing of one meter. These show that at Bermejo West, there is a sequence of latest Famennian spore inceptions that matches, in the correct stratigraphic order, those which define the sequence of Strunian miospore biozones recognized in Euramerica and Gondwana. This is very significant given that the sequence is thin relative to many coeval diamictite sequences in Bolivia (e.g., Díaz-Martínez et al., 1999), and it consists entirely of diamictite; characteristics which would normally be assumed to be the result of rapid deposition.

The Strunian has an estimated duration of three million years (Streel et al., 2006) and is represented by the LL Biozone at its base, then the LE Biozone, and finally by the LN Biozone at its top. Assuming the likely control of glacial-interglacial events at a Milankovitch frequency (i.e., from 20,000 to 400,000 years during the Quaternary), it is most unlikely that a single event spanned this entire Strunian time period. The diamictite sequence at Bermejo is therefore seen as a composite that represents several deglaciation events.

The large 'exotic' sedimentary block occurring within the Itacua Formation is very important in our interpretation of this sequence of diamictites. Lithologically, it is a deformed, bedded sandstone with shale intercalations, , and not itself a diamictite, but a dropstone within the diamictite. In terms of age, it is slightly younger (LN Biozone) than the incorporating sediment (LE Biozone) and is located just below the base of the former biozone (Fig. 2). It is considered to represents a unit of normally bedded sediment that was deposited on a marine shelf and was subsequently emplaced as a large block during the ?final Devonian deglaciation, undergoing soft sediment deformation. Its size, transport, and re-deposition in marine sediments imply active reworking by ice. Clearly, as re-deposited Strunian sediment, it would be most unlikely to have been lithified by burial compaction or cementation. Therefore, its survival as a coherent block suggests that it was transported in a frozen state.

There are two plausible explanations for the position of thelarge block two meters below the base of the LN Biozone, both of which are fully consistent with the palynological and stratigraphic evidence: 1) The actual base of the LN Biozone in the diamictites could be lower than the level identified; *V. nitidus*, the index species of the LN Biozone, is rare throughout this section and its lowest record may not represent the true base of its range. 2) The block of frozen sediment could have impacted on the Late Devonian seabed with sufficient momentum to sink into the unconsolidated diamictite and below the base of the LN Biozone.

Conclusions

Palynologic evidence indicates that the uppermost Iquiri and lower Itacua formations are both unequivocally Late Devonian (late Famennian) in age. Although the Itacua Formation has previously been considered as being possibly "Devono-Carboniferous" or "Early Carboniferous," the recovered acritarchs, prasinophytes, and miospores reported herein, definitely dictate a Late Devonian (Strunian) age. Both the miospore and acritarch and prasinophyte assemblages are generally well preserved and reasonably diverse. Whereas the acritarchs and prasinophytes are only able to provide an age of Late Devonian (Famennian), the miospores can refine the age further (late Famennian) and place, in ascending stratigraphic order, the two formations and 'exotic block' into the Euramerica miospore biozones ?VCo through LN.

The series of closely spaced palynological samples taken from the lower 18 m of diamictites and sandstone lenses of the Itacua Formation allows for correlation of this latest Famennian South American glaciation event with glaciation taking place at the same time in the Appalachian region of North America. The presence of age-diagnostic miospore taxa in the Bermejo West section constrains the time duration of sedimentation for this entire diamictite sequence, making it highly unlikely that a single episode of glaciation is represented. Rather, the sequence probably represents the final deglaciation at this location. The fact that the large 'exotic' sedimentary block occurring within the Itacua Formation is not a diamictite lithology, but rather a normally bedded sediment that is slightly younger (LN Biozone age) than the incorporating sediment (LE Biozone age) implies active reworking by ice and deposition as a frozen, or partially-frozen, block during transport. Immediately overlying the 'exotic' sedimentary block are diamictites of LN Biozone age, indicating the last deglaciation for which palynologic evidence at this location is preserved.

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Fig. 1. A. Outline map of Bolivia showing the sampled Devonian locality at Bermejo.

B. Sketch map of the Bermejo West section.

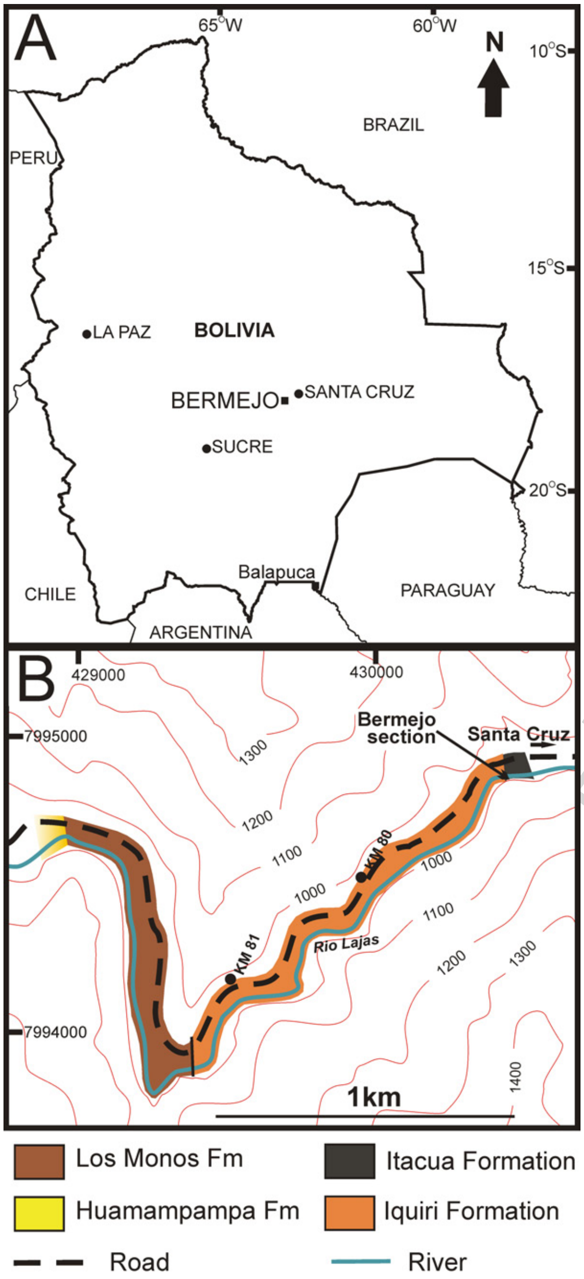


Fig. 2. Stratigraphic section at Bermejo West, showing formations, lithologies, thicknesses, sample numbers, and spore biozones.

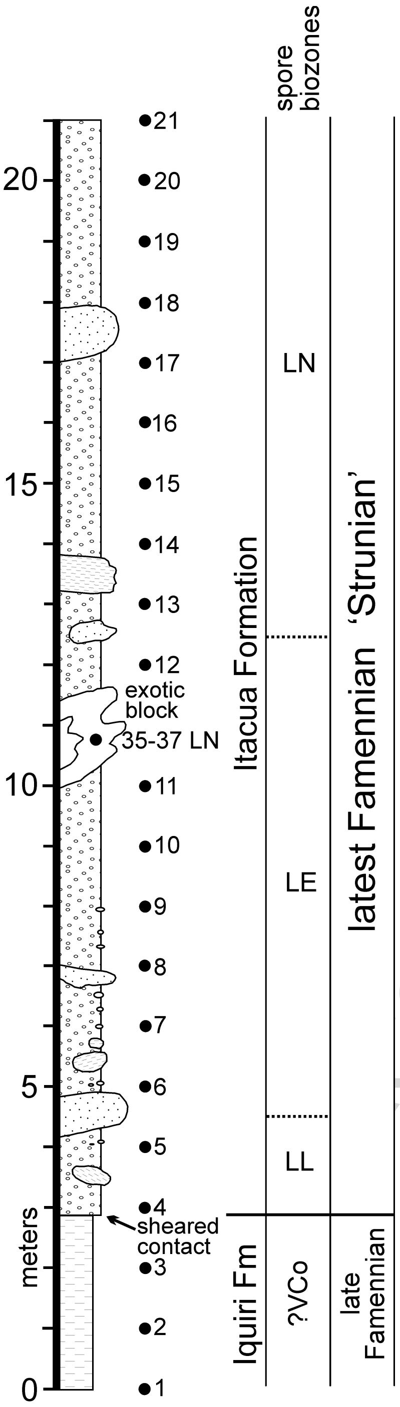
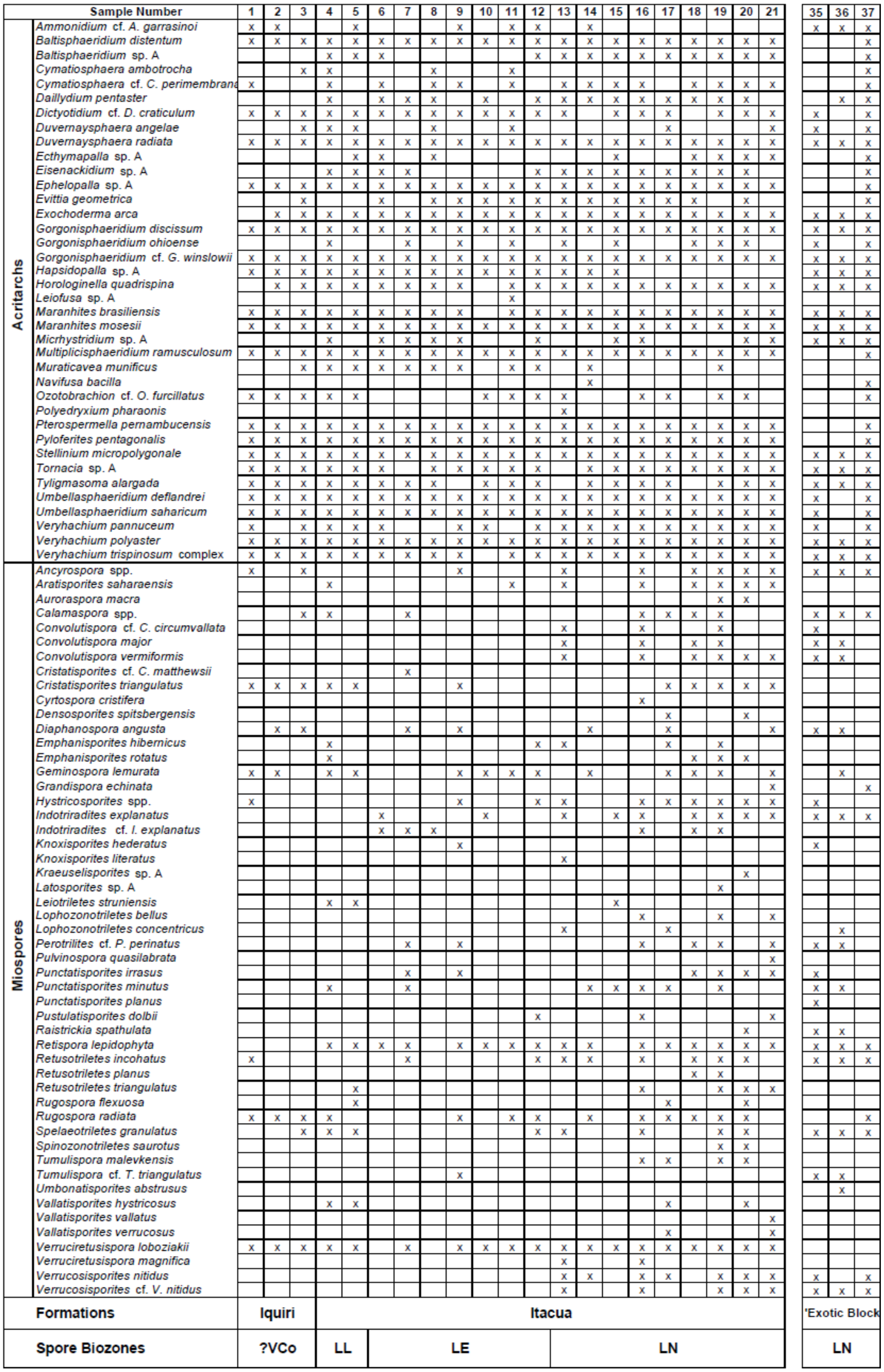


Fig. 3. Occurrences of acritarch and miospore species within the uppermost Iquiri and Itacua formations, as well as the 'exotic' sedimentary block within the Itacua Formation. Only ‘presence’ (x) or ‘absence’ (blank) are given. Formation names and spore biozones are also shown.



	Sample Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	35	36	37
Acritarchs	*Ammonidium* cf. *A. garrasinoi*	x	x			x				x		x	x		x								x	x	x
	Baltisphaeridium distentum	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x
	Baltisphaeridium sp. A				x	x	x						x	x	x	x	x	x	x	x	x	x			x
	Cymatiosphaera ambotrocha			x	x				x			x													x
	Cymatiosphaera cf. *C. perimembrana*	x			x		x		x	x		x		x	x	x	x		x	x	x	x			x
	Daillydium pentaster				x		x	x	x		x		x	x	x	x	x	x	x	x	x			x	x
	Dictyotidium cf. *D. craticulum*	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x		x
	Duvernaysphaera angelae			x	x	x			x			x						x				x	x		x
	Duvernaysphaera radiata	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Ecthymapalla sp. A					x	x		x							x			x	x	x	x			x
	Eisenackidium sp. A				x	x	x	x					x	x	x	x	x	x	x	x	x				x
	Ephelopalla sp. A	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x
	Evittia geometrica			x			x		x	x	x	x	x	x	x	x	x	x	x		x				x
	Exochoderma arca		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Gorgonisphaeridium discissum	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Gorgonisphaeridium ohioense				x			x		x		x		x		x			x	x	x		x		x
	Gorgonisphaeridium cf. *G. winslowii*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Hapsidopalla sp. A	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x							x	x	x
	Horologinella quadrispina		x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Leiofusa sp. A											x												
	Maranhites brasiliensis	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Maranhites mosesii	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Micrhystridium sp. A				x		x	x	x	x			x			x	x				x	x	x	x	x
	Multiplicisphaeridium ramusculosum	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x
	Muraticavea munificus			x	x	x	x	x	x	x		x	x		x					x				
	Navifusa bacilla														x										x
	Ozotobrachion cf. *O. furcillatus*	x	x	x	x	x					x	x	x	x			x	x		x	x				x
	Polyedryxium pharaonis													x											
	Pterospermella pernambucensis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x
	Pyloferites pentagonalis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x
	Stellinium micropolygonale	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Tornacia sp. A	x	x	x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
	Tyligmasoma alargada	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x		x	x	x	x	x	x
	Umbellasphaeridium deflandrei	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
	Umbellasphaeridium saharicum	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
	Veryhachium pannuceum	x		x	x	x	x			x	x		x	x	x	x	x	x	x	x	x	x	x		x
	Veryhachium polyaster	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Veryhachium trispinosum complex	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Miospores	*Ancyrospora* spp.	x		x						x				x			x		x	x	x	x	x	x	x
	Aratisporites saharaensis				x							x		x			x		x	x	x	x			
	Auroraspora macra																			x	x				
	Calamaspora spp.			x	x			x									x	x	x	x			x	x	x
	Convolutispora cf. *C. circumvallata*													x			x			x			x		
	Convolutispora major													x			x		x	x			x	x	
	Convolutispora vermiformis													x			x		x	x	x	x	x	x	
	Cristatisporites cf. *C. matthewsii*							x																
	Cristatisporites triangulatus	x	x	x	x	x				x								x	x	x	x	x			
	Cyrtospora cristifera																x							
	Densosporites spitsbergensis																	x			x				
	Diaphanospora angusta		x	x				x		x					x			x				x	x	x	
	Emphanisporites hibernicus				x								x	x				x		x				
	Emphanisporites rotatus				x														x	x	x				
	Geminospora lemurata	x	x		x	x				x	x	x	x		x			x	x	x		x		x	
	Grandispora echinata																					x			x
	Hystricosporites spp.	x								x			x	x			x	x	x	x	x	x	x		
	Indotriradites explanatus						x				x			x		x	x		x	x	x	x	x	x	x
	Indotriradites cf. *I. explanatus*						x	x	x								x		x	x				
	Knoxisporites hederatus									x													x		
	Knoxisporites literatus													x											
	Kraeuselisporites sp. A																				x				
	Latosporites sp. A																			x					
	Leiotriletes struniensis				x	x										x									
	Lophozonotriletes bellus																x			x		x			
	Lophozonotriletes concentricus													x				x						x	
	Perotrilites cf. *P. perinatus*							x		x							x		x	x		x	x	x	
	Pulvinospora quasilabrata																					x			
	Punctatisporites irrasus							x		x									x	x	x	x	x		
	Punctatisporites minutus				x			x							x	x	x	x		x			x	x	
	Punctatisporites planus																						x		
	Pustulatisporites dolbii												x				x					x			
	Raistrickia spathulata																				x		x	x	
	Retispora lepidophyta				x	x	x	x		x	x	x	x	x	x		x	x	x	x	x	x	x	x	x
	Retusotriletes incohatus	x						x					x	x	x		x		x	x	x		x	x	x
	Retusotriletes planus																		x	x						
	Retusotriletes triangulatus					x											x			x	x	x			
	Rugospora flexuosa					x												x			x				
	Rugospora radiata	x	x	x	x					x		x	x		x		x	x	x	x	x				x
	Spelaeotriletes granulatus			x	x	x							x	x			x			x	x		x	x	x
	Spinozonotriletes saurotus																			x	x				
	Tumulispora malevkensis																x	x		x	x				
	Tumulispora cf. *T. triangulatus*									x													x	x	
	Umbonatisporites abstrusus																								x	
	Vallatisporites hystricosus				x	x											x			x				
	Vallatisporites vallatus																					x			
	Vallatisporites verrucosus																	x				x			
	Verruciretusispora loboziakii	x	x	x	x	x		x		x	x	x	x	x	x	x	x	x	x	x	x	x			
	Verruciretusispora magnifica													x			x								
	Verrucosisporites nitidus													x	x		x	x		x	x	x	x		x
	Verrucosisporites cf. *V. nitidus*													x			x			x	x	x	x	x	x
	Formations	Iquiri			Itacua																		'Exotic Block		
	Spore Biozones	?VCo			LL		LE							LN										LN		

Plate I. Important miospore, acritarch, and prasinophyte taxa from the Bermejo West section, Bolivia. Specimens are located by sample and slide number (BGC15-1), collection (GC), and England-Finder coordinates. For example, BGC15-1(GC), O64/4 refers to sample BGC15, slide number 1 of Geoff Clayton collection, and England-Finder coordinates O64/4. All specimens are x500.

1. *Leiotriletes struniensis* Moreau-Benoit, 1979. BGC15-1(GC), O64/4.
2. *Verrucosisporites nitidus* (Naumova) Playford, 1964. BGC17-1(GC), H52/0.
3. *Tumulispora malevkensis* (Kedo) Turnau, 1978. BGC17-1(GC), Q52/0.
4. *Lophozonotriletes concentricus* (Byvscheva) Higgs, Clayton, and Keegan, 1988. BGC17- 1(GC), O51/4.
5. *Indotriradites explanatus* (Luber) Playford, 1991. BGC16-2(GC), R38/0.
6. *Rugospora radiata* (Jushko) Streel, 1974. BGC17-1(GC), U29/2.
7. *Spelaeotriletes granulatus* (Kedo) Moreau-Benoit, 1980. BGC16-2(GC), F49/0.
8. *Retispora lepidophyta* (Kedo) Playford, 1976. BGC16-1(GC), H33/1.
9. *Vallatisporites hystricosus* (Winslow) Byvscheva, 1985. BGC17-1(GC), Q59/2.
10. *Vallatisporites verrucosus* Hacquebard, 1957. BGC16-2(GC), R45/4.
11. *Horologinella quadrispina* Jardiné, Combaz, Magloire, Peniguel and Vachey, 1972. BGC12-1(RW), V21/2.
12. *Gorgonisphaeridium ohioense* (Winslow) Wicander, 1974. BGC9-1(RW), U23.
13. *Evittia geometrica* Brito, 1967. BGC3-1(RW), N8/3.
14. *Cymatiosphaera ambotrocha* Wicander and Loeblich, 1977. BGC19-1(RW), Q24/2.
15. *Umbellasphaeridium deflandrei* (Moreau-Benoit) Jardiné, Combaz, Magloire, Peniguel and Vachey, 1972. BGC11-1(RW), F18.
16. *Pyloferites pentagonalis* Quadros, 1999. BGC11-1(RW), T49.
17. *Daillydium pentaster* (Staplin) emend. Playford in Playford & Dring, 1981. BGC15-1(RW), T23.
18. *Maranhites mosesii* (Sommer) Brito, 1967. BGC16-1(RW), S39/1.
19. *Duvernaysphaera radiata* Brito, 1967. BGC11-1(RW), K48/2.

20. *Umbellasphaeridium saharicum* Jardiné, Combaz, Magloire, Peniguel and Vachey, 1974. BGC11-1(RW), R22/3.

21. *Pterospermella pernambucensis* (Brito) Eisenack, Cramer, and Díez, 1973. BGC13- 1(RW), G19.