

What do latest Famennian and Mississippian miospores from South American diamictites tell us?

M. Streel · M. V. Caputo · J. H. G. Melo · M. Perez-Leyton

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Abstract Cores from shallow boreholes penetrating the Mississippian Poti Formation, in the western margin of the Parnaíba Basin, contain dark grey diamictites which are extremely rich in well-preserved palynomorphs. Eighty-eight miospore taxa have been identified, and almost half of these are obviously reworked. The presence of these early Late Viséan-age diamictites might possibly contradict the accepted climatic implications of the Paraca Flora, which is also recorded in the Poti Formation. However, a time span of ca. 4 Ma, corresponding to almost the entire Late Viséan, probably allowed the warmer-climate Paraca Flora to exist between the early Late Viséan and Serpukhovian ice ages. Cores from a deep borehole penetrating the upper Cabeças strata of latest Famennian age, in central Parnaíba Basin, contain tillites and varve-like rhythmites, usually laminated siltstones and sandstones, with scattered clasts. Forty-one miospore taxa have been identified from these diamictites and associated siltstones, most of which (70 %) were reworked from Middle and Upper Devonian sediments. An

18-m-thick diamictite section in the lower portion of the Itacua Formation at Bermejo, southeast Bolivia, was reported to display the three successive Strunian miospore zones (LL–LE–LN) established in Western Europe, and thus interpreted as a composite that records several deglaciation events occurring over 3 million years. However, we challenge the presence of the three successive Strunian miospore zones in the Bolivian diamictites which for us correspond only to parts of the LE and LN zones. In Western Europe, the same shorter interval of the miospore zonation corresponds to a period of lower sea-surface palaeotemperatures based on oxygen isotopes from conodont apatite ($\delta^{18}\text{O}_{\text{phosph}}$) as well as a conspicuous sea-level change. Conodont data suggest a much shorter time span (100,000 years) for the highest LE and the LN interval encompassing the Hangenberg and Dreher Sandstones. On the other hand, the Itacua Formation (Bolivia), sampled 33 m and 58 m above the base of the formation, more likely testifies to multiple glacial–interglacial events featuring a superposition of latest Famennian and Mississippian diamictites.

M. Streel (✉)
Department of Geology, University of Liège,
Sart-Tilman B18,
BE 4000 Liège 1, Belgium
e-mail: Maurice.Streel@ulg.ac.be

M. V. Caputo
Centro de Geociências, Faculdade de Geologia,
Universidade Federal do Pará,
Av. Perimetral s/n,
66075-110 Belém-PA, Brazil

J. H. G. Melo
Petrobras/Cenpes/Pdgeo/Bpa,
Av. Horácio Macedo 950, I. Fundão,
21941-915 Rio de Janeiro, RJ, Brazil

M. Perez-Leyton
Calle Charcas N° 651,
Santa Cruz de la Sierra, Bolivia

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Introduction

Late Devonian- and Mississippian-age diamictites have been described from several regions of South America. However, controversy has arisen regarding their actual age and different climatic versus sedimentological interpretations. We present here two miospore-based case studies focusing, respectively, on early Late Viséan and latest Famennian diamictites of the Parnaíba Basin (northeastern Brazil), together with a re-evaluation of a previously described Famennian Bolivian diamictite.

Middle Mississippian glacial deposits of the Parnaíba Basin

In the Parnaíba Basin, the Poti Formation contains evidence of glacial and periglacial deposition in the Paleozoic outcrop belt of the basin's western margin, as well as periglacial deposition on the southeastern margin (Caputo et al. 2008). The formation consists of two superposed units. The lower unit comprises sandstones and rare conglomerates, whereas the upper one is primarily argillaceous. Diamictites with striated pebbles are observed to grade laterally into distal mudrock successions.

The lower stratigraphic boundary of the Poti Formation (Fig. 1), with the underlying Longá Formation (Strunian to early Late Tournaisian; cf. Grahn et al. 2001), seems to be conformable in outcrops, but, in fact, corresponds to a parallel unconformity as demonstrated by palynological studies (Melo and Loboziak 2000). Its upper boundary is likewise unconformable, with the overlying Piauí Formation (Middle Pennsylvanian; Dino and Playford 2002a), the basal conglomerate of which consists of a large number of quartz, quartzite, and sandstone boulders, enclosed within a sandy matrix without any preferential orientation. Many of these clasts resulted from the erosion of the Poti Formation.

Clasts in the Poti diamictites are mainly characterised by angular quartz grains, mica-schist, quartzite, gneiss, sandstone pebbles, and boulders disseminated within a compact silty-argillaceous, micaceous, and sometimes calciferous massive matrix. The relative abundance of basement clasts, in sandstones and diamictites along the outcrop belt of the Poti Formation, indicates that the primary source for these rock fragments was the Central Brazilian Shield.

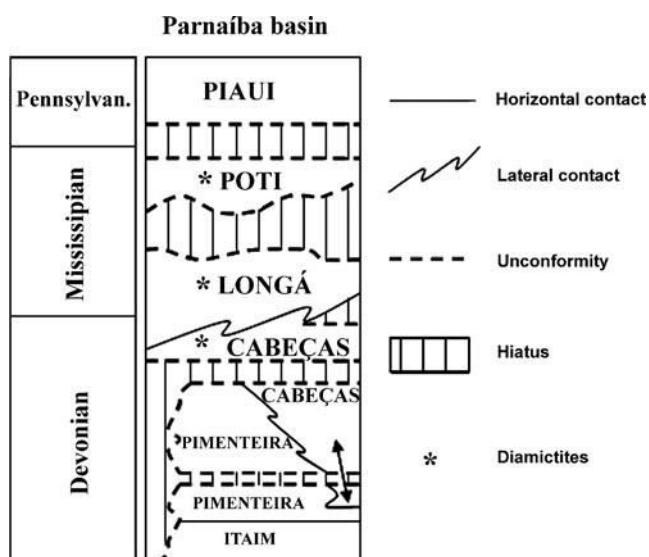


Fig. 1 Lithostratigraphy of the Parnaíba Basin (redrawn from Caputo et al. 2008)

Kegel (1954) dated the basal portion of the formation as early Carboniferous, based on several species of the bivalve *Edmondia*, and Dolianiti (1954) attributed the upper unit to the early Carboniferous based on macrofloral evidence. Using sporomorph evidence, Müller (1962) considered the formation to be Mississippian in age, Andrade and Daemon (1974) dated it as Viséan, and Melo and Loboziak (2000) assigned the Poti Formation to the early Late Viséan, correlating it with two successive West European palynozones, namely, the *Perotrilites tessellatus*–*Schulzospora campylopelta* (TC) and *Raistrickia nigra*–*Triquitrites marginatus* (NM). Melo and Loboziak (2003) referred the Poti Formation to the early Late Viséan Mag palynozone, erected by them in the Amazon Basin (upper Faro Formation and equivalent parts of the Oriximiná Formation).

Based on the fossil megaflora, which is dominated by pteridosperms, with some arboreal lycopsids and associated sphenopsids, Iannuzzi and Pfefferkorn (2002) assigned a Late Viséan age to the Poti Formation. This megaflora is related to the Paraca floral kingdom and consists of a warm to temperate climate floral belt (between 30° and 60°S) with a circum-Gondwanan distribution that developed within a non-glacial context, extending from northern South America to Australia, during the Late Viséan and Early Serpukhovian.

Miospores from the Tocantins River diamictites

Cores from shallow boreholes penetrating the Mississippian Poti Formation, drilled for the construction of a dam on the Tocantins River (western margin of Parnaíba Basin), include sandstones, siltstones, and dark grey diamictites. Palynomorphs were extracted from 30 samples taken from seven shallow wells drilled through diamictite sections ca. 26 m thick (Fig. 2). All samples proved extremely rich in well-preserved palynomorphs, and each prepared slide contains several thousand miospores. Both Devonian and Mississippian miospores are present, not only in the diamictites, but also in samples collected from silty strata above the diamictites.

Eighty-eight miospore taxa were identified from the diamictites and associated siltstones. Of these, 15 taxa (17 %) (Table 1) are Late Viséan markers such as *Schulzospora* sp. and *Raistrickia nigra*; 37 taxa (42 %) (Table 1) could be Late Viséan, but are also known from the Mississippian or even the latest Famennian (annotated species list 1); 35 taxa (41 %) are obviously reworked (Table 2): 18 (22 %) from the Tournaisian or Upper Devonian and 17 taxa (19 %) from the Upper or Middle Devonian. Most of the acritarchs observed are presumably reworked from the Devonian, except some morphologically simple acanthomorphs and ver-yhachids, which could be Carboniferous. Melo and Loboziak (2003) assigned the Poti Formation assemblages

| S101 20,56-20,66 (5) 28,16-28,27 (6) | S103 11,26 (1) 24,14 (2) 27,68 (3) 29,62 (4) | S202 12,71,12,83 (12) 20,05 (13) 22,94 (14) 32,16 (15) 33,77 (16) | S203 14,53-14,63 (17) 16,86 (18) 19,30 (19) 22,81 (20) 23,86 (21) | S204 16,60 (22) 32,32 (23) 34,50 (24) 58,93 (25) | S205 12,87-12,96 (26) 25,88 (27) 40,29 (28) 40,85 (29) 56,66 (30) | S208 11,77-11,91 (7) 18,35 (8) 35,36 (9) 38,15 (10) 44,65 (11) |
|--|--|--|--|--|--|---|
|--|--|--|--|--|--|---|

Fig. 2 Studied samples from the Tocantins River shallow boreholes drilled in the Upper Viséan of the Parnaíba Basin. S Shallow borehole identification. No. of palynological slide shown in parentheses

to the Late Viséan *Cordylosporites magnidictyus* (Mag) palynozone, which is now re-assigned to the *Reticulatisporites magnidictyus* Zone following the latest taxonomic review of the eponymous species (Dino and Playford 2002b).

The Cortaderas Formation of the Rio Blanco Basin (Argentina), also contains glacial deposits. Pérez-Loinaze (2007) defined the Late Viséan MQ (*magnidictyus*–*quasi-gobbetti*) palynozone here, which she considered to be correlative of the Mag palynozone of Brazil. The age of the MQ Zone is now constrained by radiometric data (335.99 \pm 0.06 Ma; cf. Césari et al. 2011) which fits with a latest Holkerian or earliest Asbian age determination, according to the Carboniferous time scales of Menning et al. (2006) and Ogg et al. (2008), respectively.

Azcuy and di Pasquo (2005) recorded a low-diversity miospore assemblage from the Ambo Formation, Pongo de Mainique (Peru), which they compared with the early Late Viséan Mag Zone of northern Brazil. The authors stressed the poor preservation of the Peruvian palynoflora and the apparent absence of *Reticulatisporites magnidictyus* in the uppermost part of the Ambo Formation. The first occurrence of small *Schopfipollenites* spp. (attributed to *S. ellipsooides* by Azcuy and di Pasquo 2006) within the uppermost Ambo strata might imply possible correlation with the inception of true *S. ellipsooides* in the AT Zone of Eastern Canada and the NC Zone in Western Europe (the latter corresponding to the Viséan–Serpukhovian transition).

However, identical small praecolpates from the older Mag Zone of Brazil—likewise assigned to *S. ellipsooides* by Loboziak et al. (1991), but later redesignated as *Schopfipollenites* sp. (Loboziak et al. 1998; Melo and Loboziak 2003), have recently undergone taxonomic revision (G. Playford and J.H.G. Melo, in preparation). It is now concluded that the Viséan representatives of *Schopfipollenites* reported from South America are actually distinct from, and thus not necessarily coeval with, *S. ellipsooides*. Moreover, these small forms are now recorded, together with *Reticulatisporites magnidictyus*, from the very base of the Mag Zone in some Amazon Basin sections (G. Playford and J.H.G. Melo, in preparation), and, therefore, are not restricted to the higher parts of the zone as previously indicated (Loboziak et al. 1998).

Lastly, the local absence of *Reticulatisporites magnidictyus* is not age diagnostic per se, because the species also occurs erratically within some Mag sections of northern Brazil (S. Loboziak and J.H.G. Melo, unpublished data).

Furthermore, it is also known to range into Early Serpukhovian-age sections of South America, North Africa, and Australia (Dino and Playford 2002b; Fasolo et al. 2006; Hyam et al. 1997; Loboziak et al. 2000a; Melo et al. 1999; Pérez-Loinaze 2007). Therefore, local non-occurrences of *R. magnidictyus* in the Upper Viséan of South America can be best ascribed to ecofaciologcal constraints, and, thus, are probably devoid of stratigraphic significance.

In view of the palynological data, and together with the early Late Viséan (late Holkerian to late Asbian) radiometric dating of the Mag Zone (=MQ Zone) diamictites in north-western Argentina, it seems evident that a time span of ca. 4 Ma (corresponding to nearly the entire Late Viséan; cf. Bruckschen and Veizer 1997) allowed the warmer-climate Paraca Flora (Iannuzzi and Pfefferkorn 2002) to exist between the early Late Viséan and Serpukhovian ice ages (Césari et al. 2011).

Latest Famennian glacial deposits of the Parnaíba Basin (Fig. 1)

Sediments deposited under glacial and periglacial conditions in the Parnaíba Basin make up the upper Cabeças section of latest Famennian age. The Cabeças Formation is overlain by the Longá Formation, both conformably (in sites where the lowest Longá strata are end-Devonian transgressive marine shales) and unconformably (in places where the Longá Formation is entirely Tournaisian in age). The upper Cabeças beds, which are placed in the Famennian LVa (*lepidophyta-vallatus*) Zone, and are equivalent to the upper part, or the entire Western European LN (*lepidophyta-nitidus*) Zone (Melo and Loboziak 2001, 2003), contain massive polymict diamictites with subrounded to angular, striated and polished outsized clasts immersed in a silty and clayey matrix (Caputo 1985; Loboziak et al. 1993). The lower Cabeças beds (chiefly sandstones with minor shaly interbeds) are dated as early to late Famennian (Grahn et al. 2006).

The upper Cabeças/lower Cabeças boundary seems to correspond to a relatively minor (3rd to 4th order) unconformity, which thus accounts for the apparent absence of at least the LL Zone (locally also encompassing the VCo and VH zones), unless coeval Famennian sediments are palynologically barren or contain only non-diagnostic palynofloras. However, in parts of the western margin of the Parnaíba Basin where the lower Cabeças sandstone is absent, the

Table 1 Tocantins River shallow drills (Parnaíba). Mississippian recorded species and chronostratigraphy

(See also Figs. 3 and 4)

| | | |
|---|--|----------------------------------|
| ? <i>Cristatisporites inordinatus</i> 3c | (Menendez and Azcuy) Playford, 1978 | ? Late Visean–early Namurian |
| ? <i>Rotaspora</i> sp. 3k | | ? Presumed late Visean at least |
| ? <i>Schopfipollenites</i> 4abc | | ? Late Visean–late Carboniferous |
| ? <i>Spelaeotriletes ybertii</i> | (Marques-Toigo) Playford and Powis, 1979 | ? Late Visean to lower Permian |
| ? <i>Tripartites</i> sp. 4g | | ? Presumed late Visean at least |
| <i>Retusotriletes</i> ? <i>mirabilis</i> | | Late Visean |
| <i>Anapiculatisporites</i> cf <i>semisentus</i> 3a | Playford, 1971 | Late Visean |
| <i>Cingulizonates</i> sp | | ? Presumed late Visean at least |
| <i>Ductilispora corrugata</i> 4d | Perez-Lonaze, 2005 | Late Visean |
| <i>Indotriradites</i> sp cf <i>I. dolianitii</i> 3f | Loboziak et al., 1999 | Late Visean |
| <i>Raistrickia nigra</i> 3j | Love, 1960 | Late Visean–basal Namurian |
| <i>Schulzospora</i> sp. 3l | | Late Visean to Pennsylvanian |
| <i>Spelaeotriletes arenaceus</i> 4e | Neves and Owens, 1966 | Late Visean to early Westphalian |
| <i>Spinozonotriletes hirsutus</i> | | Late Visean–early Namurian |
| <i>Tumulispora</i> sp. aff <i>Lophozonotriletes muricatus</i> | | Late Visean |
| ? <i>Lycospora pusilla</i> | (Ibrahim) Somers, 1972 | Visean to Pennsylvanian |
| <i>Procoronaspora butterworthii</i> 3h | Staplin, 1960 | Visean |
| <i>Densosporites pseudoannulatus</i> 3d | Butterworth and Williams, 1958 | Visean–Namurian |
| <i>Densosporites triangularis</i> 3e | Kosanke, 1950 | Visean–Namurian |
| <i>Dibolisporites microspicatus</i> 4f | Playford, 1978 | Visean |
| <i>Raistrickia</i> cf <i>ponderosa</i> 4k | Playford, 1964 | Mississippian (Cheverie Fm) |
| <i>Secarisporites remotus</i> 3m | Neves, 1961 | Visean |
| <i>Thymospora cymbiformis</i> 4h | Playford and Satterthwait, 1988 | Visean |
| ? <i>Anulatisporites orbiculatus</i> 3b | (Waltz) Playford, 1963 | Mississippian |
| ? <i>Rugospora polyptycha</i> | Neves and Ioannides, 1974 | Mississippian |
| <i>Colatisporites decorus</i> | (Baradwaj and Venkatachala) Williams, 1973 | Mississippian |
| <i>Cristatisporites aculeatus</i> | | Mississippian (Horton Gr) |
| <i>Grandispora uncata</i> | (Hacquebard) Playford, 1971 | Mississippian (Horton Gr) |
| <i>Indotriradites variabilis</i> | | Mississippian? |
| <i>Lophozonotriletes dentatus</i> 3g | Hughes and Playford, 1961 | Mississippian |
| <i>Perotrilites perinatus</i> 4l | Hughes and Playford, 1961 | Mississippian |
| <i>Raistrickia clavata</i> 3i | Hacquebard, 1957 emend Playford, 1964 | Mississippian |
| <i>Schopfites angustus</i> 4i | Playford, 1964 | Mississippian (Horton Gr) |
| <i>Spelaeotriletes cabotii</i> | Utting et al., 1989 | Mississippian |
| <i>Tumulispora variverrucata</i> 4j | (Playford) Staplin and Jansonius, 1964 | Mississippian |
| <i>Vallatisporites</i> ? <i>agadesi</i> | Loboziak and Alpren, 1978 | Mississippian |
| ? <i>Raistrickia strumosa</i> | Playford, 1976 | BP–PC |
| <i>Auroraspora corporiga</i> | Higgs et al., 1988 | VI–PC |
| <i>Ceratosporites</i> sp. A | in Van der Zwan, 1979 | Mid Tournaisian–Visean |
| <i>Crassispora maculosa</i> | (Knox) Sullivan, 1964 | VI–Namurian A |
| <i>Kraeuselisporites hibernicus</i> | Higgs, 1975 | HD–CM |
| <i>Mooreisporites</i> sp. | in Melo and Loboziak, 2003 | BP–PC? |
| <i>Spelaeotriletes balteatus</i> | (Playford) Higgs, 1975 | BP–NM |
| <i>Spelaeotriletes obtusus</i> | Higgs, 1975 | VI?–BP |
| <i>Spelaeotriletes resolutus</i> | Higgs, 1975 | VI?–BP |
| <i>Spinozonotriletes impensus</i> | Higgs et al., 1988 | HD–PC |
| <i>Velamisporites lacertosus</i> | Playford, 1971 | Late Tournaisian |

Table 1 (continued)

(See also Figs. 3 and 4)

| | | | |
|------------------------------------|---|-----------|-------------|
| <i>Cordylosporites mariae</i> | (Winslow) Playford and Satterthwait, 1985 | LE–Visean | |
| <i>Cordylosporites spathulatus</i> | (Winslow) Playford and Satterthwait, 1985 | LE–NM | As early as |
| <i>Tumulispora rarituberculata</i> | (Luber) Playford, 1990 | LL–Visean | Uppermost |
| <i>Vallatisporites vallatus</i> | Hacquebard, 1957 | LN–NM | Famennian |
| <i>Vallatisporites verrucosus</i> | Hacquebard, 1957 | LE–NM | |

Reference to figures in the first column

Table 2 Tocantins River shallow drills

Reworked species

| | | | |
|---|---|------------------------------------|--|
| Latest Famennian–Tournaisian | | | |
| <i>Auroraspora macra</i> | Sullivan, 1968 | LL–Pu | |
| <i>Endoculeospora gradzinskii</i> | Turnau, 1975 | LE–CM | |
| <i>Indotriradites explanatus</i> | (Luber) Playford, 1991 | LE–PC | |
| <i>Plicatispora scolecophora</i> | (Neves and Ioannides) Higgs et al., 1988 | LL–CM | |
| <i>Raistrickia minor</i> | (Kedo) Neves and Dolby, 1967 | LL–PC | |
| <i>Retusotriletes crassus</i> | Clayton et al., 1980 | LN–CM | |
| <i>Retusotriletes incohatus</i> | Sullivan, 1965 | ?VH–HD? | |
| <i>Spelaeotriletes crustatus</i> | Higgs, 1975 | LL–PC | |
| Late–latest Famennian | | | |
| <i>Retispora lepidophyta</i> | (Kedo) Playford, 1976 | LL–LN | |
| <i>Leiotriletes struniensis</i> | Moreau-Benoit, 1979 | VCo–LN? | |
| <i>Rugospora radiata</i> | (Jushko) Byvsheva, 1985 | VCo–LN | |
| Late Frasnian–mid. Tournaisian | | | |
| <i>Cyrtospora cristifer</i> var A | (Luber) Van der Zwan, 1979 | Early Famennian–mid. Tournaisian | |
| <i>Retusotriletes planus</i> | Dolby and Neves, 1970 | Late Frasnian–PC | |
| Late Frasnian–Famennian | | | |
| ? <i>Teichertospora torquata</i> | (Higgs) McGregor and Playford, 1990 | IVc–LN | |
| <i>Cornispora varicornata</i> | Staplin and Jansonius in Staplin, 1961 | Late Frasnian–early Famennian | |
| <i>Cyrtospora cristifera</i> var. <i>biloba</i> | (Luber) Van der Zwan/(Kononenko) B.& H. | Famennian | |
| <i>Geminospora piliformis</i> | Loboziak et al., 1988 | BJ–IVc | |
| <i>Samarisporites</i> sp. E | in Streel and Loboziak, 1987 | BJ–IVc | |
| Mid.–Late Devonian | | | |
| <i>Ancyrospora</i> sp. | | Mid.–Late Devonian | |
| <i>Brochotriletes foveolatus</i> | Naumova, 1955 | BZ | |
| <i>Camarozonotriletes?</i> <i>concavus</i> | Loboziak and Streel, 1989 | AD | |
| <i>Corystisporites multispinosus</i> | Richardson, 1965 | AD–TA | |
| <i>Cymbosporites catillus</i> | Allen, 1965 | AD–IVc | |
| <i>Cymbosporites cyathus</i> | Allen, 1965 | AD–IVc | |
| <i>Grandispora douglastownense</i> | McGregor, 1974 | AP–AD | |
| <i>Grandispora mammillata</i> | Owens, 1971 | ADLem | |
| <i>Grandispora megaformis</i> | (Richardson) McGregor, 1973 | AP–AD | |
| <i>Grandispora permulta</i> | (Daemon) Loboziak et al., 1999 | AD | |
| <i>Grandispora protea</i> | (Naumova) Moreau-Benoit, 1980 | AP–AD | |
| <i>Grandispora pseudoreticulata</i> | (Menendez and Pothe de Baldis) Ottone, 1996 | Mid. Devonian–early Carboniferous? | |
| <i>Grandispora velata</i> | (Eisenack) Playford, 1971 | APVel | |
| <i>Hystricosporites</i> sp. | | Mid.–Late Devonian | |
| <i>Samarisporites eximius</i> | (Allen) Loboziak and Streel, 1989 | APVel–TA | |
| <i>Samarisporites praetervisus</i> | (Naumova) Allen, 1965 | APVel–TA | |
| <i>Samarisporites triangulatus</i> | Allen, 1965 | TA–early Famennian | |

Third column: Miospore zonation after Streel et al. 1987 and Higgs et al. 1988

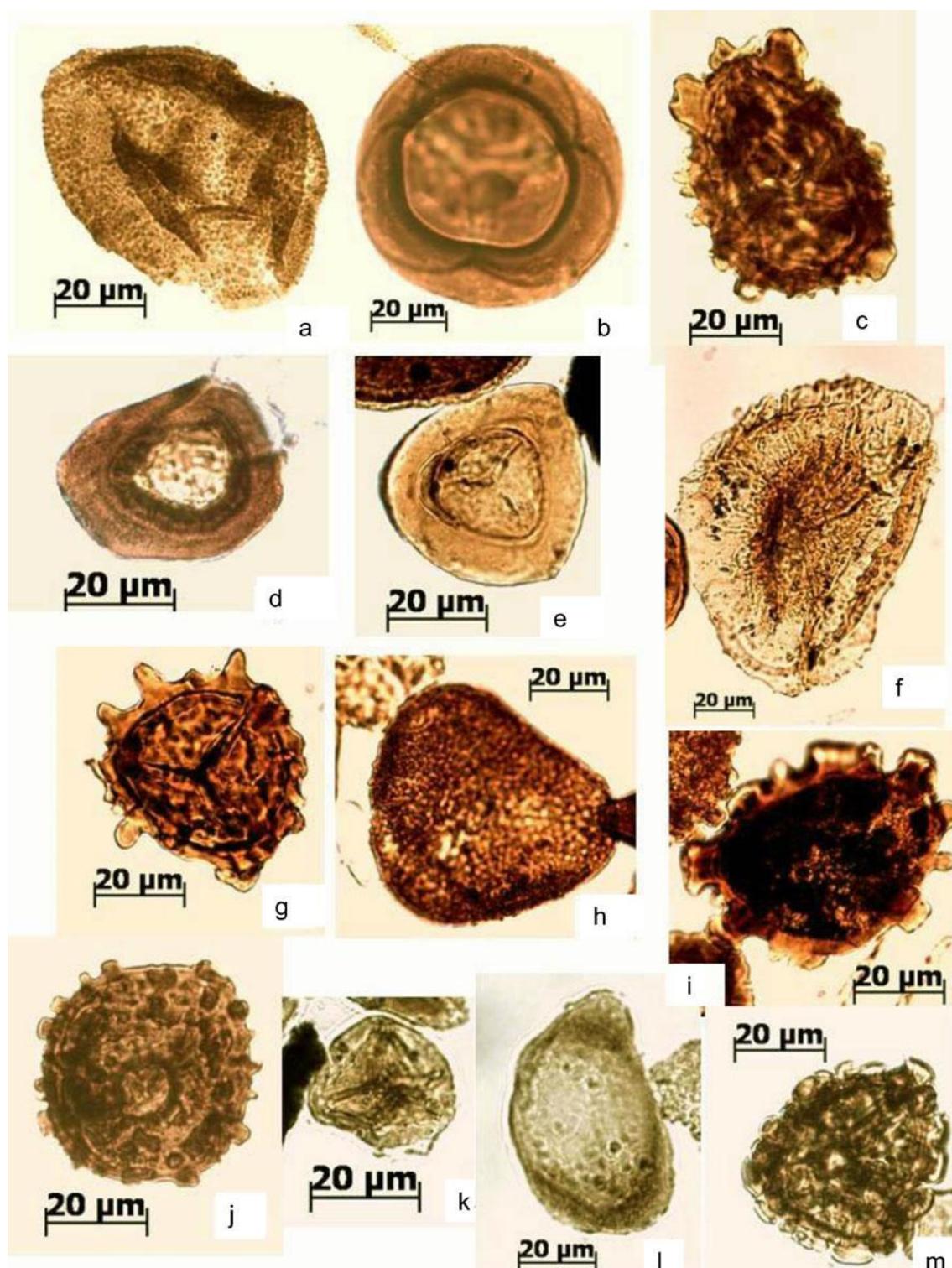


Fig. 3 See annotated species list No. 1. All specimens located by sample, slide number and England-Finder coordinates in annotated species lists. **a** *Anapiculatisporites* cf. *semisentus* Playford, 1971. **b** ?*Anulatisporites* cf. *A. orbiculatus* (Waltz) Playford, 1963. **c** ?*Crisatisporites inordnatus* (Menendez and Azcuy) Playford, 1978. **d** *Densosporites pseudoannulatus* Butterworth and Williams, 1958.

e *Densosporites triangularis* Kosanke, 1950. **f** *Indotriradites* sp. cf. *I. dolianitii* Loboziak et al., 1999. **g** *Lophozonotriletes dentatus* Hughes and Playford, 1961. **h** *Procoronaspora butterworthii* Staplin, 1960. **i** *Raistrickia clavata* Hacquebard, 1957 emend Playford, 1964. **j** *Raistrickia nigra* Love, 1960. **k** *Rotaspora* sp. **l** *Schulzospora* sp. **m** *Secarisporites remotus* Neves, 1961

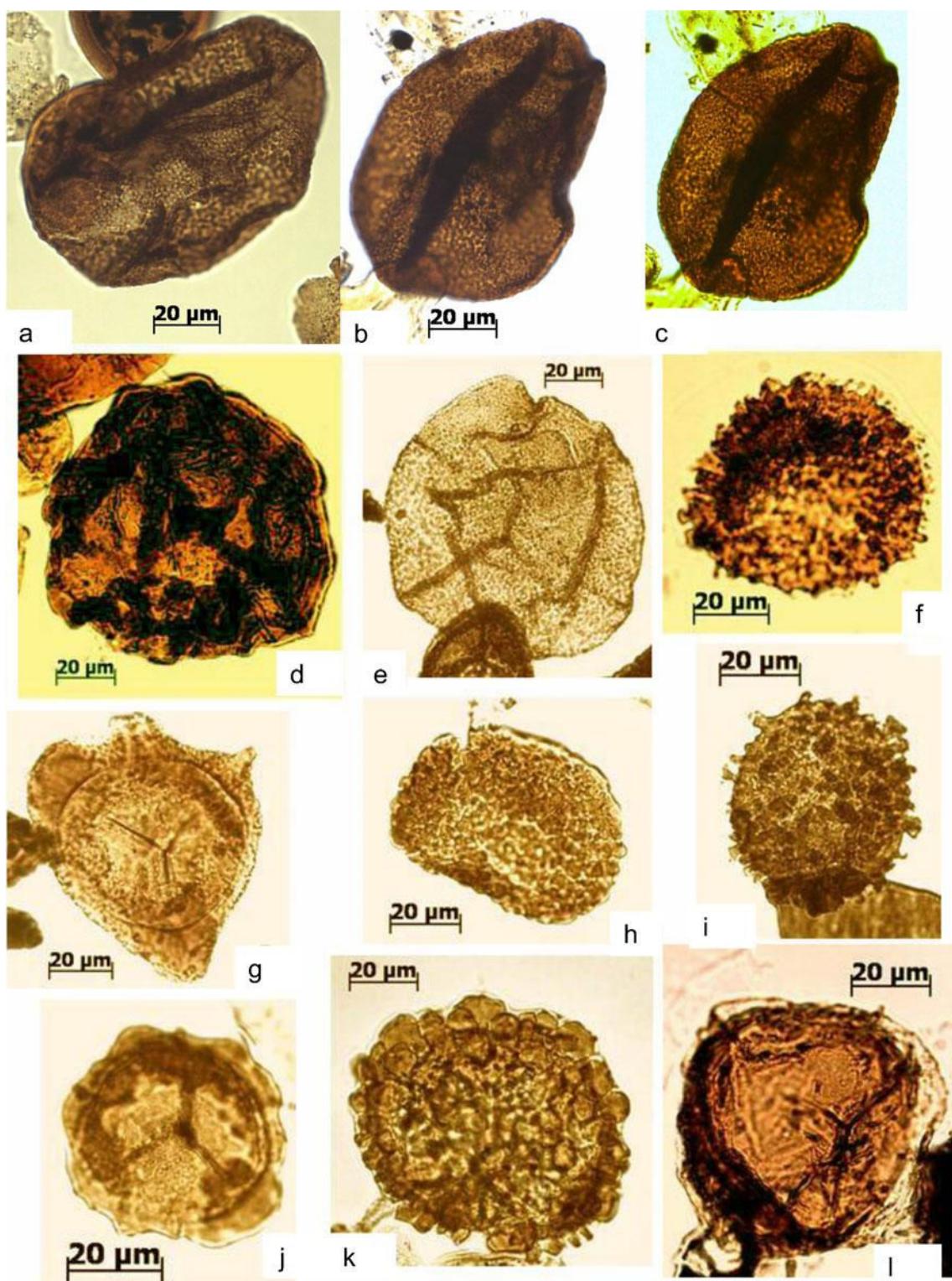


Fig. 4 See annotated species list No. 1. All specimens located by sample, slide number and England-Finder coordinates in annotated species lists. **a–c** *Schopfipollenites?* sp. **d** *Ductilispora corrugata* Pérez-Loinaze, 2005. **e** *Spelaeotriletes arenaceus* Neves and Owens, 1966. **f** *Dibolisporites microspicatus* Playford, 1978. **g** *Tripartites?* sp.

h *Thymospora cymbiformis* Playford and Satterthwait, 1988. **i** *Schopfites augustus* Playford, 1964. **j** *Tumulispora variverrucata* (Playford), Staplin and Jansonius, 1964. **k** *Raistrickia* cf. *R. ponderosa* Playford, 1964. **l** *Perotrilites perinatus* Hughes and Playford, 1961

upper Cabeças glaciogenic strata rest erosionaly on increasingly older rocks (Devonian through Precambrian; Loboziak et al. 2000b). Varve-like rhythmites, usually laminated siltstones and very fine sandstone couplets with scattered clasts, are known from well cores within diamictites and associated shales (Carozzi et al. 1975, pl. XVI.E-F; Caputo 1985, fig. 13; Caputo and Crowell 1985, fig. 11; Strel et al. 2001, pl. 1.A, pl. 2).

Miospores from the well 1-TM-1-MA diamictites (Figs. 1, 5)

The investigated material comes from four samples of core 16 in well 1-TM-1-MA, about 200 km east of the Tocantins River. One of these samples (Caputo 1985; Caputo and Crowell 1985, fig. 11E) is a laminitite (varve-like rhythmite) composed of alternating white, very fine sandy layers and dark grey silty layers, each being approximately 0.5 mm thick. Eight layers were macerated separately (Strel et al. 2001). The diamictites and associated siltstones yielded at

least 41 miospore taxa, most of which (29, i.e. 70 %) are reworked from Middle or Upper Devonian sediments. Among the other 12 taxa, *Vallatisporites vallatus* has the youngest first occurrence, at the base of the latest Famennian LVa (*lepidophyta-vallatus*) Zone. The other 11 taxa could also be latest Famennian, but they are known elsewhere to range down into the Famennian. Curiously enough, the reworked Middle Devonian miospores are found only in the diamictite samples, whereas the reworked Late Devonian miospores occur both in the diamictites and laminites.

We propose that the LVa Zone miospores represent the local vegetation of a deltaic and coastal environment that was locally disrupted by advancing lobes of the contemporary ice cap (Carozzi 1980). LVa Zone miospores were distributed on the subaqueous fans and mixed with miospores reworked from underlying Frasnian shales of the upper Pimenteira Formation. Reworked Middle Devonian miospores might have originated from normal and glacial erosion of lower parts of the Pimenteira Formation (Loboziak et al. 2000a).

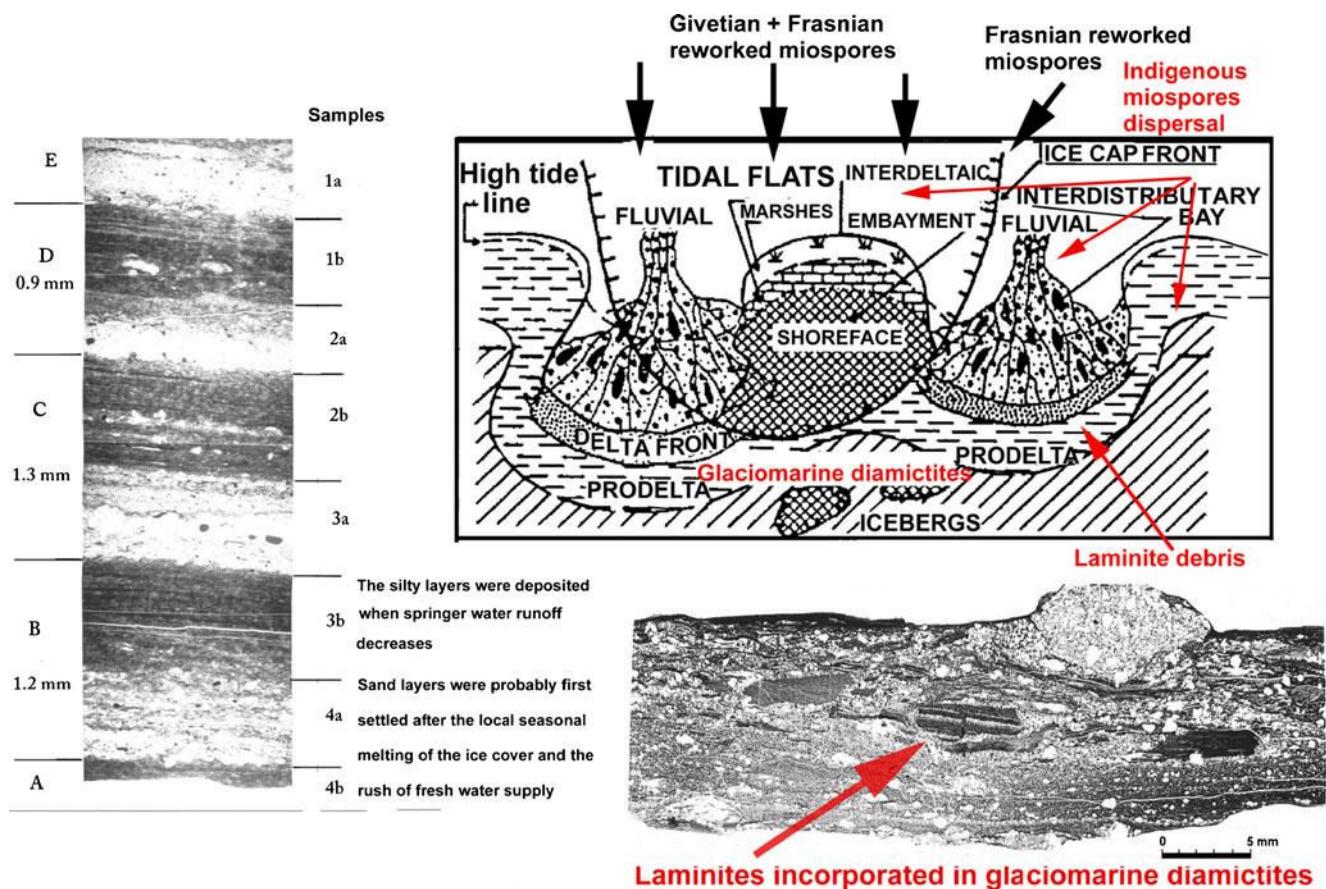


Fig. 5 Latest Famennian glacial deposits of the Parnaíba Basin. The Famennian LVa (*lepidophyta-vallatus*) Zone is characterised lithologically by massive polymict diamictites. The upper Cabeças glaciogenic strata rest erosionaly on increasingly older rocks. Varve-like rhythmites of this

unit (usually laminated siltstones and very fine sandstone couplets with scattered clasts) are known from well cores within tillites and associated shales (Carozzi et al. 1975, pl. XVI.E-F; Caputo 1985, fig. 13; Caputo and Crowell 1985, fig. 11; Strel et al. 2001, pl. 1.A, pl. 2)

In the Parnaíba Basin, the LVa Zone characterises latest Famennian-age strata of the upper Cabeças and basal Longá formations in several wells (Grahn et al. 2001, 2006; Loboziak et al. 1992) and outcrops along the Tocantins River valley (Loboziak et al. 2000b). Famennian (pre-Strunian) sandstones of the lower Cabeças Formation are preserved below the LVa diamictite section of well 1-TM-1-MA.

However, in some other localities of the western Parnaíba Basin, the Cabeças glaciation has removed the entire lower Cabeças sandstone plus varied sections of the underlying Pimenteira Formation (which spans the latest Eifelian through earliest Famennian; *fide* Grahn et al. 2001, 2006). Near Colinas do Tocantins village, in the western outcrop area (Tocantins State, north-central Brazil), the Cabeças tillites rest directly on the Precambrian metamorphic basement and are succeeded by black shales of the basal Longá Formation (Loboziak et al. 2000b).

Reworked palynomorphs may provide a reliable proxy for the source area of sediments (Strel and Bless 1980), and their occurrence in diamictites has been emphasised for many years in Argentina (di Pasquo and Azcuy 1997; di Pasquo 2007b). Although glacio-marine rhythmites have been described in the Carboniferous of Argentina (del Papa and di Pasquo 2007; Milana and Lopez 1998), no palynomorph analysis for the individual sandy and silty layers has yet been provided.

A quantitative palynological analysis of laminites from well 1-TM-1-MA shows a miospore/miospore + acritarch ratio ranging from 40 to 70 %. The palynomorph concentrations (number of specimens per gram of rock) suggest some rhythmicity as miospores progressively decrease from 4 to 2.5 k in the silty layers and from 2.5 to 1 k in the very fine sandy layers before another cycle starts. This could result from the changing intensity of freshwater currents entering the basin, causing glacio-lacustrine sediments to be deposited from subaqueous fans and related turbidity currents (Ponciano and Della Favera 2009), as well as from the calving of icebergs (Carozzi 1980). Therefore, living parent plants dispersing spores may have coexisted with glacially derived sediments at the margin of some lobes of the contemporaneous ice cap and perhaps even on the debris covering the glacier (Caccianiga et al. 2011).

Are latest Famennian diamictites multiple glacial-interglacial events?

Wicander et al. (2011), working on a 18-m-thick diamictite section in the lower part of the Itacua Formation at Bermejo (Río Lajas, Santa Cruz, southeast Bolivia), recognised three successive Late Devonian miospore zones established in Western Europe: LL (*lepidophyta-literatus*), LE (*lepidophyta-explanatus*), and LN (*lepidophyta-nitidus*). They concluded that the diamictite sequence was a

composite representing several deglaciation events. The diamictites are within a marine succession, and overlie a hiatus coincident with the Itacua/Iquiri Formation boundary, indicative of a lowering of sea-level during the glacial maximum (Wicander et al. 2011). The diamictites were thus interpreted as glaciomarine deposits that accumulated during a time of rising sea-level, *i.e.* during a deglaciation event.

In Brazil at least, the succession of LE–LN zones is not easily recognised. Instead, that interval is characterised by the successive Rle (*R. lepidophyta*, with, *i.a.*, *Indotriradites explanatus* and *Vallatisporites verrucosus*) and LVa (*lepidophyta–vallatus*) zones (Melo and Loboziak 2001, 2003). The Rle is considered to possibly represent an impoverished variant (ecofacies?) of the LVa in places where *Verrucosporites nitidus* and *Vallatisporites vallatus* are absent. It should be noted that *V. nitidus* is not always easily identifiable (Turnau et al. 1994), and the single specimen illustrated by Wicander et al. (2011, fig. 5, fig. 2) is unconvincing because its rather widely spaced verrucae sometimes exceed 8 μm in maximum diameter and do not form the negative reticulum diagnostic for this species.

Wicander et al. (2011) furthermore state that the recognition of the LL Zone in the Bermejo sequence is only tentative. They accept that it could also be the LE Zone, because of the scarcity of miospores. The same holds true for the three poorly palyniferous samples assigned to the VCo Zone at the base of the diamictites. This provisional assignment was due to the absence of *Retispora lepidophyta* and the occurrence of *Rugospora radiata*, a species also occurring in the *R. lepidophyta* range.

This lack of definitive zone assignment also applies to the miospore-poor sample M19 of Perez-Leyton (1991), at the base of the same diamictite interval at Bermejo (Río Lajas area), assigned by him to the VCo Zone. It should be noted that *R. lepidophyta* is not abundant in the youngest part of the LN Zone in Western Europe, and the same applies to some uppermost LVa sections of northern Brazil (J.H.G. Melo, personal observations).

Finally, considering that the absence of *V. nitidus* is not necessarily age-diagnostic, we conclude that samples 35–37 (within the exotic block) do not contain the same miospore assemblage as recorded in samples 13–21 (within the “LN” sequence) of Wicander et al. (2011, p. 80). Almost 18 taxa unrecorded in the exotic block are present in the “LN” sequence, but again absent in the “LE” sequence. Therefore, there is no need to resort to soft sediment deformation to explain the lower position of the exotic block in relation to samples 13–21.

In our view, the multiple glaciations and interglacials suggested by Wicander et al. (2011) in the Bermejo diamictites, and supposedly extending through the entire latest Famennian (or Strunian), have not been convincingly demonstrated.

Do the Itacua diamictites represent two superposed glacial events?

Di Pasquo (2007a, b, c) described three samples spaced 1–3 m apart within the Itacua Formation (about 15 m thick) at a locality some 500 km to the south of Bermejo (Santa Cruz), on the Río Bermejo (Balapuca, Department of Tarija, near the Argentina–Bolivia border). She concluded that the entire section was Mississippian in age, and that all the Devonian miospores (66 % of the total palynoflora) were reworked.

Perez-Leyton (1990) illustrated several miospore taxa from the Saipuru (now Itacua) Formation at Bermejo (Santa Cruz), some of which were not published in his 1991 paper. His samples M12 and M13 were from 33 and 58 m, respectively, above the base of the formation, i.e. from stratigraphic levels considerably higher than the 18-m section studied by Wicander et al. (2011) at the same locality and were tentatively attributed to the LE Zone (due to the absence of *V. nitidus*). However, subsequent revision by us has demonstrated the presence of some Mississippian miospores in this palynoflora (see Fig. 6 and annotated species list 2).

Therefore, the Itacua Formation of Bolivia could testify to a succession of glacial–interglacial events, causing Mississippian diamictites to rest directly on latest Famennian ones (Suárez-Soruco and Lobo-Boneta 1983), as also noted in the Solimões Basin of northern Brazil. In the latter, Middle to early Late Tournaisian (PC-age; fide Loboziak et al. 1995), crudely stratified diamictites occur in the upper part of the Jaraqui Member of the Jandiatuba Formation (Eiras et al. 1994). Clasts are randomly oriented and consist of angular to rounded quartz, shale, sandstone, and igneous pebbles. Some diamictite layers are highly deformed and show significant dips. These Tournaisian strata rest disconformably on underlying latest Famennian diamictites and older, non-glaciogenic rocks of the Jandiatuba and Uerê formations (Caputo et al. 2008).

Comparison with European miospore zonation, bathymetry, and geochemical data (Fig. 7)

In recent years, detailed geochemical data have been obtained from Upper and Uppermost Famennian and Lower Tournaisian strata in several localities of central and southern Europe. The data comprise carbon isotope analyses of micrites ($\delta^{13}\text{C}_{\text{carb}}$) and sedimentary organic matter ($\delta^{13}\text{C}_{\text{org}}$), as well as oxygen isotopes from conodont apatite ($\delta^{18}\text{O}_{\text{phosph}}$). The latter was interpreted in terms of sea-surface palaeotemperatures by Kaiser et al. (2008). With the aid of refined conodont stratigraphy (Kaiser et al. 2009), these data have been correlated with both the lithological successions and inferred sea-level changes of the Rhenish Massif (Germany), and can also be correlated with the miospore zonation of the Rhenish Massif and the Ardennes in Belgium (Strel et al. 2000, Higgs et al., in preparation). The

results are summarised in Kaiser et al. (2011) and reproduced here with some modifications (Fig. 7).

These data provide the opportunity to test the hypothesis of the duration, and possible multiple character of the end-Devonian glaciation. In terms of bathymetry, one should note that the major drop in sea-level at the Hangenberg Sandstone level in Germany is confined to the uppermost LN Zone (LN* Zone, characterised by more than 50 % of specimens of *Retusotriletes* and *Apiculiretusispora*; after Higgs et al. 1993). Such major drop in sea-level has no equivalent record elsewhere in the uppermost Famennian and lowermost Tournaisian.

In the uppermost part of the LE Zone, the Brewer Sandstone might correspond to an earlier sea-level fall of lesser magnitude. On the other hand, the two *Retispora lepidophyta* zones below the Brewer Sandstone correspond to times of rather high sea-surface palaeotemperatures, which would be unexpected during an ice age. Additionally, a cooling episode (with low sea-surface palaeotemperatures) at the “Dasberg/Fontin Event” level, around the VCo/VH Zonal boundary, does not correspond to any major sea-level fall. Therefore, it is unlikely that multiple glacial–interglacial events could have persisted for the 3 Ma duration of the combined Strunian LL–LE–LN time interval as suggested by Wicander et al. (2011). The glacial event might as well be characterised by the high LE and LN zones, i.e. by the upper part only of the Strunian.

A much shorter duration of time (100,000 years) has been proposed by Sandberg and Ziegler (1996) for the sequence enclosing the Hangenberg and Brewer Sandstones (Strel 1999, text-fig. 5). The recognition of the LN Zone in the Hangenberg Black Shale (HBS), which overlies the Brewer Sandstone, is based on poorly diversified and scarce palynofloras (Higgs and Strel 1994), in which *Verrucosisporites nitidus* is an erratic component. Even in Ireland (Higgs et al. 1988), where the LN Zone has been defined, *V. nitidus* (usually represented by more finely verrucate variants) is also rather sparse in the basal part of the biozone. Therefore, it is possible that the transitional LE–LN interval, although poorly defined, could correspond to a much shorter duration than the duration accepted for the Strunian.

Conclusions

1. The local absence of *Reticulatisporites magnidictyus* and the presence of small praecolpates (*Schopfipollenites* sp.) in the Tocantins River diamictites are palynological features previously noted in the Viséan Ambo Formation of Peru (and also in some Amazon Basin sections of northern Brazil), and do not necessarily imply a Latest Viséan age for these glaciogenic rocks of the Poti Formation. Moreover, the 4 Ma duration of the entire Late Viséan,

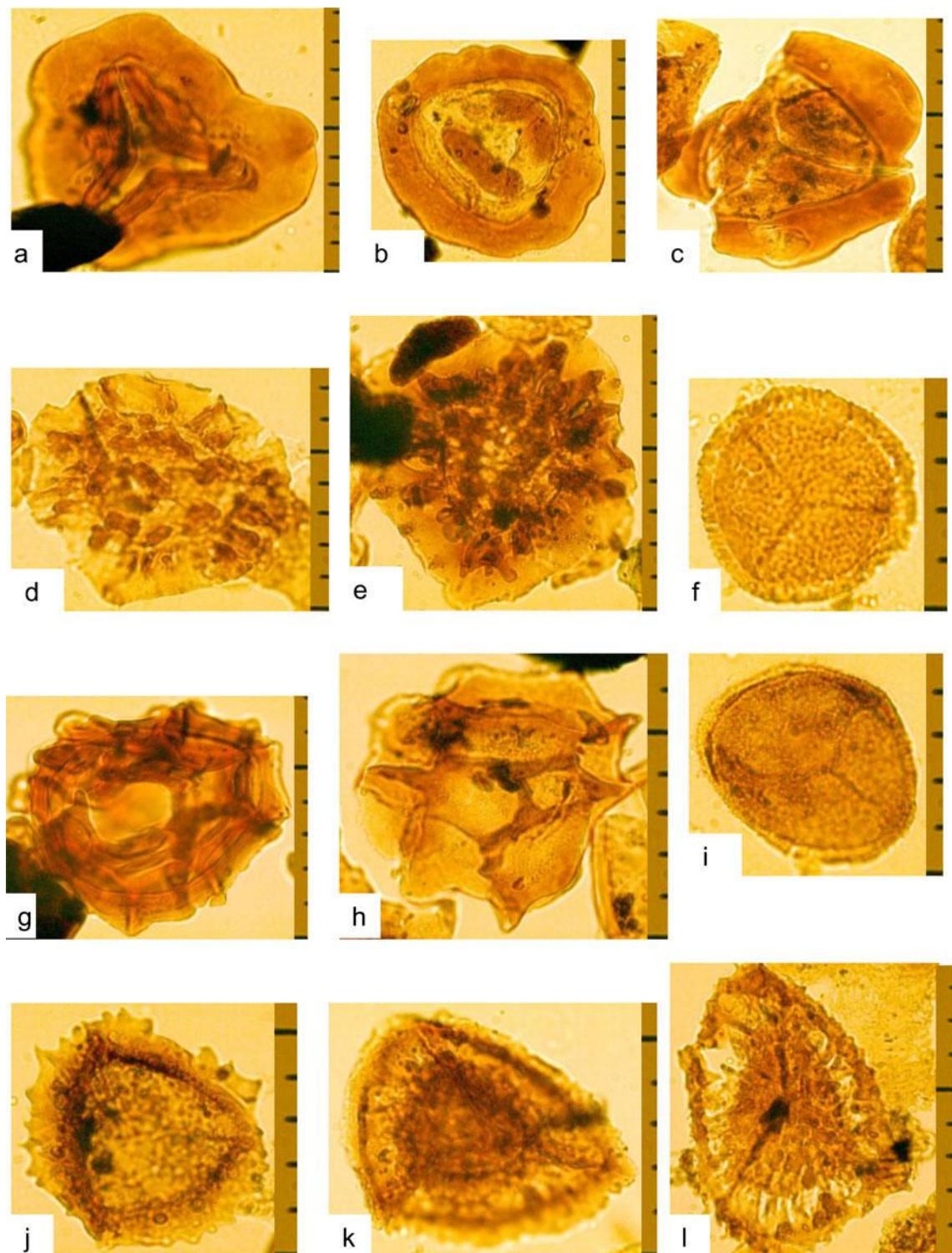
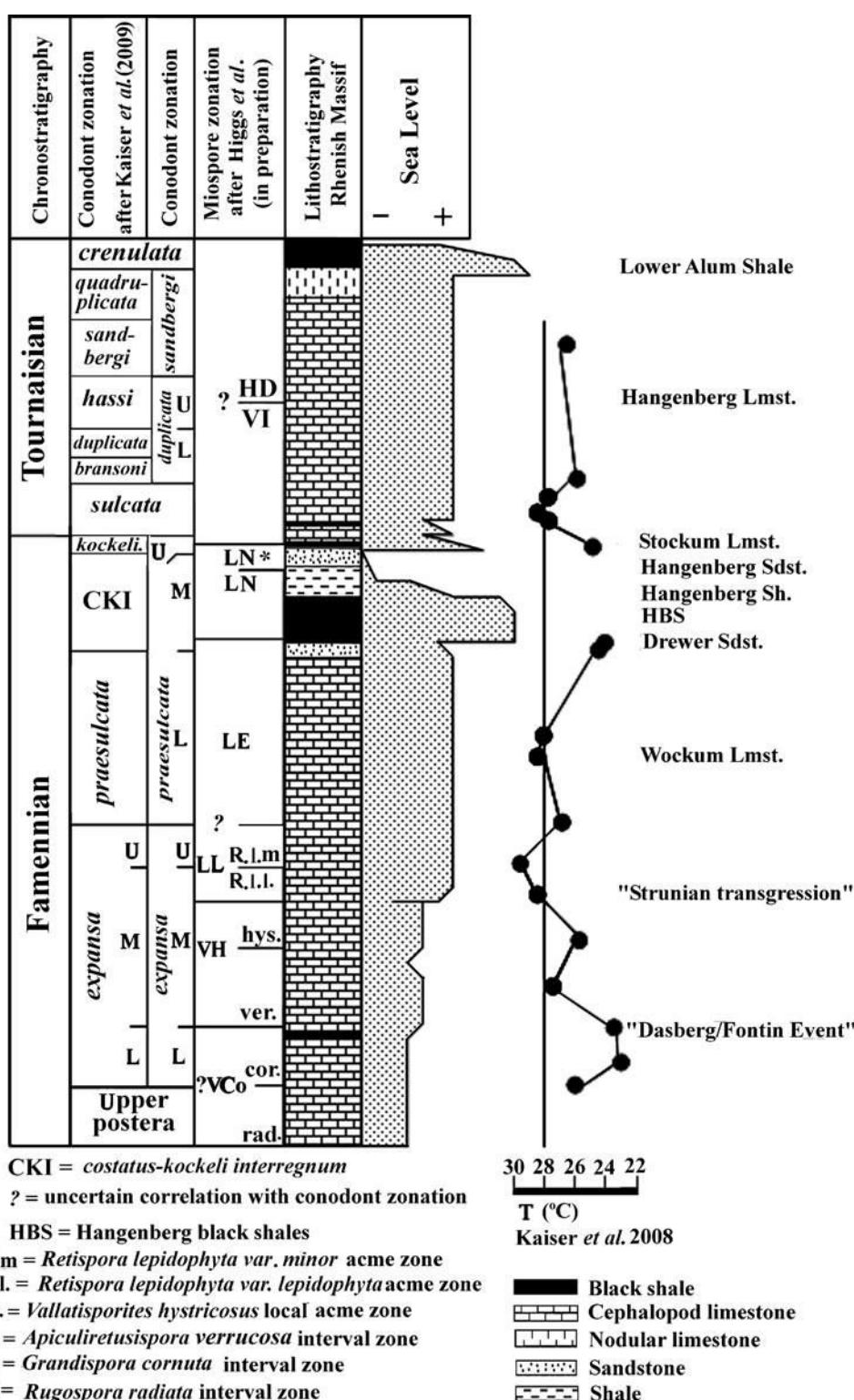


Fig. 6 See annotated species list No. 2. All specimens located by sample, slide number and England-Finder coordinates in annotated species lists. **a** *Murospora* cf. *M. aurita* (Waltz) Playford, 1962. **b** *Lophozonotriletes concentricus* (Byvsheva) Higgs et al., 1988. **c** *Lophozonotriletes triangulatus* (Ischenko) Hughes and Playford,

1961. **d, e** *Cristatisporites* sp 1 in Perez-Leyton, 1991. **f, i** *Spelaeotriletes resolutus* Higgs, 1975. **g, h** *Dictyotriletes flavus* Keegan, 1977. **j** *Indotriradites* cf. *I. mitratus* Higgs, 1975. **k, l** *Vallatisporites banffensis* Staplin and Jansonius, 1974. Scale bar 10 m μ

Fig. 7 Comparison of European miospore zonation, bathymetry, and geochemical data. Oxygen isotopes from conodont apatite ($\delta^{18}\text{O}_{\text{phosph}}$) are interpreted in terms of sea-surface palaeotemperatures by Kaiser et al. (2008). With the aid of refined conodont stratigraphy (Kaiser et al. 2009), these data have been correlated with lithological successions and inferred sea-level changes in the Rhenish Massif (Germany), and with the miospore zonation of the Rhenish Massif and the Ardennes in Belgium (Higgs et al., in preparation). Note the major sea-level fall at the Hangenberg Sandstone level, confined to the uppermost LN Zone. That sea-level fall has no equivalent record elsewhere in the uppermost Famennian and lowermost Tournaisian. In the uppermost part of the LE Zone, the Dreher Sandstone might correspond to an earlier sea-level fall of lesser magnitude. On the other hand, the two *Retispora lepidophyta* zones below the Dreher Sandstone correspond to times of rather high sea-surface palaeotemperatures, which would be unexpected during an ice age



and the early Late Viséan age of the Mag Zone (dated radiometrically in northwestern Argentina), pose no serious contradiction to the climatic implications of the Paraca Flora. These warmer-climate plant assemblages may have thrived during the fairly long interglacial separating the early Late Viséan and Serpukhovian ice ages

2. Among the 30 % of presumably autochthonous miospores found in diamictites and other associated sediments of well 1-TM-1-MA, *Vallatisporites vallatus* has the youngest known first occurrence. It is suggested that the autochthonous latest Famennian palynoflora, characteristic of the LVa (*lepidophyta*–*vallatus*) Zone, could

- thus represent the local vegetation developed in deltaic and coastal environments, which were locally disrupted by ice lobes originating from the contemporaneous ice cap (Fig. 5)
3. A 18-m-thick diamictite section in the lower part of the Itacua Formation (Bolivia) was interpreted by Wicander et al. (2011) to be the result of multiple glacial–interglacial events recurrent during the 3 million years of duration of the combined LL–LE–LN zones. This hypothesis does not fit palaeoclimatic and eustatic evidence from Western Europe, where the standard miospore zonation has been compared to sea-surface palaeotemperature estimates based on oxygen isotopes from conodont apatite ($\delta^{18}\text{O}_{\text{phosph}}$) as well as to sea-level changes. It is concluded that sea surface temperatures remained rather warm for most of the *R. lepidophyta* biochron, except during a major sea-level fall (documented by the Hangenberg Sandstone) restricted to the uppermost LN Zone. These data suggest a much shorter depositional time span (100,000 years) for the lower part of the Itacua Formation than previously considered, corresponding to the upper LE–LN zonal span in Western Europe, and LVa Zone in South America. On the other hand, higher parts of the Itacua Formation contain Mississippian miospores, thus indicating a probable superposition of latest Famennian and Mississippian diamictites, as also noted in the Solimões Basin of northern Brazil
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Annotated species list 1 (All slides housed in the palynological slide collection of the Biostratigraphy and Palaeoecology Sector of PETROBRAS Research Centre (CENPES/DIVEX/SEBIPE), Rio de Janeiro, Brazil)

Anapiculatisporites cf. *A. semisentus* Playford 1971. Fig. 3a. Ref. 1/W62

As indicated by Playford (1971), the distal sculpture of *A. semisentus* is too uniform in size and distribution for it be considered as belonging to *Apiculiretusispora* (Strel) Strel 1967. The species is recorded as *Apiculiretusispora semisentata* (Playford 1971) Massa et al. 1980 in the highest part of the Ambo Formation in Peru (Azcuy and di Pasquo 2005). The species is known from Bonaparte wells (Bonaparte Basin) in Western Australia where it is dated as Viséan (by conodonts) and late Viséan (by Foraminifera) (Playford 1971, p. 7)

? *Anulatisporites* cf. ? *A. orbiculatus* (Waltz) Playford 1963. Fig. 3b. Ref. 22/P61-4

A single specimen which fits rather well with the description given by Playford (1963) except that it also shows a very distinct *curvatura perfectae*, a feature never (to our knowledge) observed in densospores. *A. orbiculatus* is known from the Mississippian of Eastern Europe and Spitsbergen.

? *Cristatisporites inordinatus* (Menendez and Azcuy) Playford 1978. Fig. 3c. Ref. 15/V50-4

A single specimen which fits rather well with the ornament description of *Ancistrospora inordinata* Menendez and Azcuy 1972 from the Late Viséan–Early Namurian from the Province of La Rioja (Argentina), although the radial amb and laevigate proximal surface is difficult to recognize on our specimen.

Densosporites pseudoannulatus Butterworth and Williams 1958. Fig. 3d. Ref. 1/G62-1

The species has a massive smooth cingulum that is wider than the cingulum of *D. annulatus*. *D. annulatus* first occurs near the base of the Viséan.

Densosporites triangularis Kosanke 1950. Fig. 3e. Ref. 21/F43-2

The species has a subtriangular amb and a cingulum with foveolate dissections.

Densosporites are known to be much more abundant in coals than in shales and therefore its first occurrence might be linked to facies. *Densosporites* become numerically important components from the TC Zone in the Late Viséan until the Pennsylvanian.

D. pseudoannulatus and *D. triangularis* are present in the Viséan and Namurian of Scotland.

Dibolispores microspicatus Playford 1978. Fig. 4f. Ref. 8/Y62

The species is described from Viséan sediment of the Drummond Basin (Queensland, Australia) and is identified in a few South American papers: i.e., in the highest part (Late Viséan?) of the Ambo Formation in Peru (Azcuy and di Pasquo 2005) and in the early? Viséan of the Tarija Basin (di Pasquo 2007a, b, c).

Ductilispora corrugata Pérez Loinaze 2005. Fig. 4d. Ref. 5/F47-1

Described from the Late Viséan-age Cortaderas Fm. in the San Juan province (Argentina)

Indotriradites sp. cf. *I. dolianitii* Loboziak et al. 1999. Fig. 3f. Ref. 7/L57

Species recorded from Late Viséan-age strata of North Africa, the Middle East and South America.

Lophozonotriletes dentatus Hughes and Playford 1961. Fig. 3g. Ref. 21/B45-4

Species recorded from the Mississippian of Spitsbergen. A badly preserved conspecific specimen is perhaps *Spinozonotriletes* sp. in Sessarego and Cesari (1989) from the El Raton Formation (an equivalent to the Maliman Formation) in western Argentina, a locality with well-documented megafloras thought to belong to the Viséan.

Perotrilites perinatus Hughes and Playford 1961. Fig. 4l. Ref. 25/D53-3

Species recorded from the Mississippian of Spitsbergen.

Procoronaspora butterworthii Staplin 1960. Fig. 3h. Ref. 20/R56-2

Species recorded from the Late Mississippian in Alberta, Canada.

Raistrickia clavata Hacquebard 1957 emend Playford 1964. Fig. 3i. Ref. 7/N53-1

Species recorded in the Euramerican and Gondwanan Mississippian.

Raistrickia nigra Love 1960. Fig. 3j. Ref. 2/F56

A Late Viséan to earliest Namurian species in Western Europe, and also known in Brazil.

Raistrickia cf. *R. clavata* in Duenas and Cesari (2005) in the Llanos Orientales Basin, Colombia, might be conspecific.

Raistrickia cf. *R. ponderosa* Playford 1964. Fig. 4k. Ref. 1/C59

This species is described as characteristic of the ?Viséan Cheverie Formation, Horton Group, Canada. Some specimens in our material show less dense and more verrucate ornaments as in the Namurian? *Verrucosporites quasigobetti* Jones and Truswell 1992.

Rotaspora sp. Fig. 3k. Ref. 5/F42-4

A single specimen. *Rotaspora* sensu stricto is known from the Namurian of Scotland and is first found in the Late Viséan in Western Europe.

Schopfipollenites? sp. Fig. 4a,b,c. Ref. 25/E57-2 and E58

Two forms with possible longitudinal furrows. Small praecolpates reminiscent of, and possibly conspecific with, the illustrated specimens have been previously reported from other Upper Viséan sections of South America, including the Faro Formation of the Amazon Basin in northern Brazil (Loboziaik et al., 1991, 1998; Melo and Loboziaik, 2003), the uppermost Ambo Formation in Peru (Azcuy and di Pasquo 2006), and in the partly coeval Kaka Formation in Bolivia (Fasolo et al. 2006).

Schopfites augustus Playford 1964. Fig. 4i. Ref. 1/D64-3

The species is described from the Mississippian undifferentiated Horton Group, Canada.

Schulzospora sp. Fig. 3l. Ref. 1/U46-4

The genus is known from the Late Viséan and Pennsylvanian of western Europe and is identified in a few South American papers: i.e., from the Upper Viséan Cortaderas Formation. (Pérez Loinaze, 2008) in the San Juan province, Argentina.

Secarisporites remotus Neves 1961. Fig. 3m. Ref. 24/M59-1

The species is described from the Namurian B and C of the southern Pennines, England. A close species, *S. undatus*, is described (Playford 1978) from Viséan sediment of the Drummond Basin, Queensland, Australia.

Spelaeotriletes arenaceus Neves and Owens 1966. Fig. 4e. Ref. 25/S50

A species described from the Namurian of England but generally accepted as ranging from Late Viséan to Early Westphalian.

Thymospora cymbiformis Playford and Satterthwait 1988. Fig. 4h. Ref. 26/S58-3

A Viséan monolete species with coarse verrucate to rugulate ornaments described from the Bonaparte Basin, Western Australia.

Tripartites? sp. Fig. 4g. Ref. 13/C52-2

A single specimen of unknown affinity. *Tripartites* might be inappropriate due to the presence of a well-rounded central area. True cingulate genera like *Murospora*, *Simozonotriletes*, *Cincturasporites*, or *Tendosporites* do not seem to fit any better. *Tripartites*-type miospores are known to first occur in the Late Viséan in western Europe.

Tumulispora variverrucata (Playford) Staplin and Jansonius 1964. Fig. 4j. Ref. 9/H46

Lophozonotriletes variverrucatus was described from the Mississippian of Spitsbergen.

Annotated species list 2 (slides housed in the palynological slide collection of the Palaeogeobiology, Palaeopalynology, Palaeobotany Research Unit, Department of Geology, University of Liège, Belgium.)

Cristatisporites sp 1 in Perez-Leyton 1991. Fig. 6d,e

Perez-Leyton 1990: pl. 10, fig 3, slide M12 : N28- 3; fig 4, slide M12: W44. Perez-Leyton 1991: pl. 2, figs. 9–10.

Palynozone M3 (Tournaisian) in Lanzoni and Magloire (1969): No. 3256.

Dictyotriletes flavus Keegan 1977. Fig. 6g,h.

Perez-Leyton 1990: pl. 9, fig. 14, slide M12: T41; fig. 15, slide M12: G39.

BP-PC biozones in Higgs et al. (1988).

Indotriradites cf. *mitratus* (Higgs 1975) Higgs 1996. Fig. 6j. (M13:N29-4).

See another specimen in Perez-Leyton 1990: pl. 12, figs. 1–2, slide M13: M28.

PC biozone in Higgs et al. (1988).

Lophozonotriletes concentricus (Byvsheva) Higgs et al. 1988. Fig. 6b.

Perez-Leyton 1990: pl. 10, fig. 9, slide M13: H42-2.

LE-PC biozones in Higgs et al. (1988).

Lophozonotriletes triangulatus (Ischenko) Hughes and Playford 1961. Fig. 6c

Perez-Leyton 1990: pl. 10, figs. 10–11, slide M13: H31-4.

VI-PC biozones in Higgs et al. (1988).

Murospora cf. *M. aurita* (Waltz) Playford 1962. Fig. 6a.

Perez-Leyton 1990: pl. 10, figs. 13–14, slide M13: H42-4.

Mississippian in Karczewska and Turnau (1974). See also palynozones M4-5 (Viséan) in Lanzoni and Magloire (1969): No. 2894.

Spelaeotriletes resolutus Higgs 1975. Fig. 6 fi

Perez-Leyton 1990: pl. 11, fig 9, slide M13: X31-3; fig. 10, slide M12: P44-1; fig. 11, slide M13: F24-4.

VI-PC biozones in Higgs et al. (1988).

Vallatisporites banffensis Staplin and Jansonius 1974. Fig. 6 kl.

Perez-Leyton 1990: pl.12, figs 15–16, slide M13: R40; fig. 17, slide M12: T27; fig. 18, slide M12: F26-3. Perez-Leyton 1991: pl. 2, figs 27–30.

Palynozones L10-M3 in Lanzoni and Magloire (1969): No. 2891.