ABHANDLUNGEN DER GEOLOGISCHEN BUNDESANSTALT
Abh. Geol. B.-A. | ISSN 0016–7800 | ISBN 3-85316-02-6 | Band 54 | S. 213–237 | Wien, Oktober 1999
North Gondwana: Mid-Paleozoic Terranes, Stratigraphy and Biota | Editors: R. Feist, J.A. Talent & A. Daurer

Late Devonian (Famennian) Glaciation in Western Gondwana: Evidence from the Central Andes

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South America
Andes
Gondwana
Devonian
Famennian
Glaciation
Sedimentology
Chronostratigraphy
Climatology

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Oberdevonische (Famennium) Vergletscherung im westlichen Gondwana: Hinweise aus den zentralen Anden

Zusammenfassung

Der Beginn der hauptsächlichen spätpaläozoischen Vereisung in Gondwana ist stratigraphisch gut dokumentiert im Westteil des Superkontinents, der während des Devon und einem Teil des Karbon in hohen Breiten lag. Kürzliche Fortschritte in der Untersuchung glazialer mariner Sedimente und ihrer paläoklimatischen Bedeutung, zusammen mit revidierten älteren Altersangaben (spätes Devon bis Mississippium) verschiedener südamerikanischer Einheiten, die früher als pennsylvanisch angesehen wurden, erbringen weitere Erkenntnisse über die spätdevonische Vereisung im westlichsten Gondwana (Bolivien und Peru). Das Alter von Schichten mit Beleg von Vereisung ist durch Invertebraten- und Palynomorphen-Biostratigraphie eingegrenzt. Spätpaläozoische Vereisungszentren begannen sich während des Oberdevon im westlichen Gondwana (nördliches Südamerika und Nordafrika) zu bilden und wanderten zum östlichen Gondwana im Laufe des Karbon.

Abstract

The beginning of the main late Paleozoic glaciation in Gondwana presents a good stratigraphic record in the western sector of the supercontinent, which was at high latitudes during the Devonian and part of the Carboniferous. Recent advances in the study of glacial marine deposits and their paleoclimatic significance, together with the revised older (Late Devonian–Mississippian) ages of several South American stratigraphic units previously considered to be Pennsylvanian, provide further evidence for the Late Devonian glaciation in westernmost Gondwana (Bolivia and Peru). The age of strata with evidence for glaciation is constrained by invertebrate and palynomorph biostratigraphy. Late Paleozoic glacial centers began to form during the Late Devonian in western Gondwana (northern South America and northern Africa), and shifted towards eastern Gondwana during the Carboniferous.

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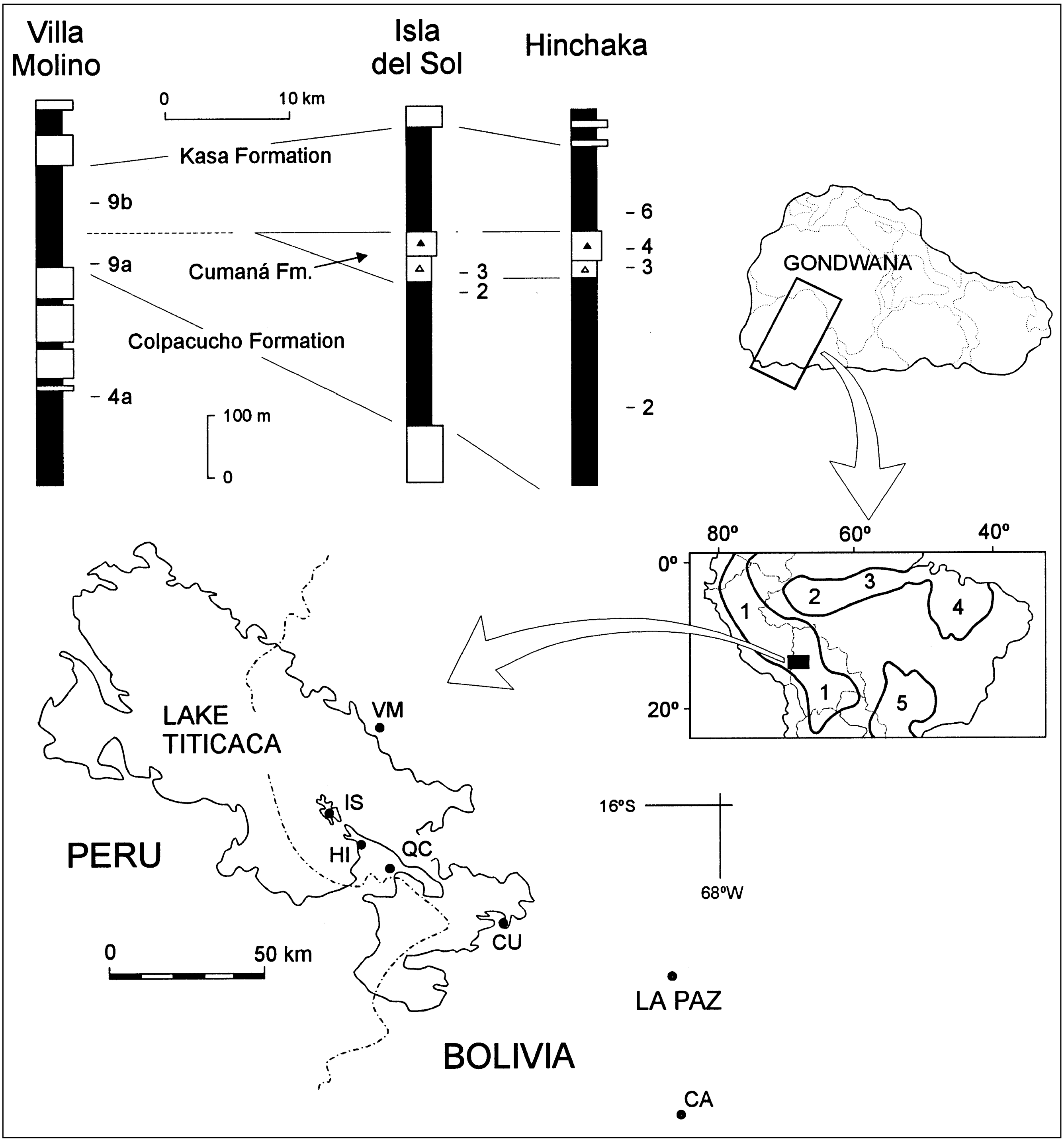
1. Introduction

Until recently, evidence for late Paleozoic glaciations described from sections in central and eastern Gondwana (India, Australia, Antarctica, and southern Africa; Text-Fig. 1) was much more abundant than what has been described from western Gondwana. This has led to a biased general agreement of the scientific community to assign the Gondwana glaciation the age inferred from the former areas, that is, Late Carboniferous (Pennsylvanian) and earliest Permian (e.g., DICKINS, 1993).

However, due to the progressive shift from low to high latitudes (warm to cold) of eastern Gondwana during this time (VEEVERS & POWELL, 1987; FRAKES et al., 1992), the glaciation events were younger on the eastern end of Gondwana, whereas on its westernmost end, the overall shift during the Carboniferous was from high to low latitudes (cold to warm; e.g., DÍAZ-MARTÍNEZ et al. [1993a, 1993b]). This gradual shift of the supercontinent took place during the late Paleozoic assemblage of Pangea,



Text-Fig. 1.
Location of study area within Gondwana, and of sections sampled for palynomorphs in western Bolivia (numbered ticks indicate location of samples mentioned in text and tables).
1 = Peru-Bolivia basin; 2 = Solimões basin; 3 = Amazonas basin; 4 = Parnaiba (Maranhão) basin; 5 = Paraná basin.
CA = Calamarca; CU = Cumaná; HI = Hinchaka; IS = Isla del Sol; MM = Villa Molino (road to Mina Matilde); QC = Quebrada Chamacani; Triangles = Cumaná Formation (filled = massive diamictites; open = shales with dropstones).

when Gondwana moved across the southern pole undergoing a clockwise rotation (TARLING, 1985; SCOTESE & BARRETT, 1990; POWELL & LI, 1994). The resulting stratigraphic record of paleoclimatic changes has an opposite arrangement on each end of the supercontinent, as described above. Therefore, the earliest records of the effects of glaciation in Gondwana are not in eastern Gondwana, but instead on its other end, that is, northern South America and western Africa, as already stated by many researchers (e.g., CAPUTO & CROWELL, 1985; VEEVERS & POWELL, 1987; CROWLEY & BAUM, 1992).

In South America, the late Paleozoic glacial record in Argentina and Brazil is already relatively well known (e.g., BIGARELLA et al., 1967; FRANÇA & POTTER, 1988; GONZÁLEZ, 1990; GONZÁLEZ-BONORINO, 1992; LÓPEZ-GAMUNDÍ et al., 1992; EYLES et al., 1993), whereas the evidence from the pre-Andean basins in the modern central and northern Andes (Bolivia, Peru, Ecuador, Colombia and Venezuela) is still relatively unknown, and it has not been widely published (mostly just in local journals and internal reports). Very few detailed paleoclimatic studies of the late Paleozoic record are available in the international geological literature from these latter countries, and this fact may be a major drawback for geoscientists in order to consider evidence for an older age of the Gondwana glaciations. The intention of this paper is to summarize some of the available paleoclimatic and biostratigraphic data on the beginning of the late Paleozoic (Gondwanan) glaciation in westernmost Gondwana, with special reference to the evidence from the Central Andean region (Bolivia, southern Peru and northern Argentina and Paraguay; Text-Fig. 1). Recent revisions of the age of the units that contain this evidence, as well as the recent advances in glacial marine sedimentology, urge for a revised interpretation of the age and significance of the onset of the late Paleozoic Gondwana glaciations.

2. Glacial Marine Sedimentation and its Paleoclimatic Significance

A review of the stratigraphic record of modern and ancient glaciations (HAMBREY & HARLAND, 1981; EYLES, 1993) demonstrates that the marine record of glaciations is much better preserved, and therefore much more abundant and frequent, than the terrestrial record. In general, the glacial record is composed predominantly of glacially influenced marine strata that accumulated on the margins of ice-covered areas (GONZÁLEZ-BONORINO & EYLES, 1995), frequently related to tectonic uplift (EYLES, 1993).

Studies of modern and ancient glacial marine depositional systems have had a considerable advance recently. Some of the most significant contributions are those of HAMBREY & HARLAND (1981), MOLNIA (1983), BORNHOLD & GUILCHER (1984), POWELL (1984), EYLES et al. (1983, 1985), DREWRY (1986), DOWDESWELL (1987), ANDERSON & MOLNIA (1989), POWELL & ELVERHØI (1989), DOWDESWELL & SCOURSE (1990), ANDERSON & ASHLEY (1991), and EYLES & EYLES (1992). These contributions contain discussions on facies analysis, modeling and interpretation of glacial marine sedimentary deposits and environments, and provide new concepts that are selectively utilized in our interpretations below. A few comments on the terminology and criteria necessary for the following discussion will be presented here, mostly following the above mentioned literature.

The term diamict (diamictite, if lithified) refers to an unsorted mixture of different clast sizes, from boulders to clay, regardless of its origin. It is a descriptive and nongenetic term, which refers to a common facies type, and which may have originated by one or more of different processes under a wide range of sedimentary environments and climates. Diamict(ite) facies are generally associated with highly competent transport agents such as ice, or mass transport due to gravity (slumps, slides, debris flows, colluvium, etc.), but there are also other possibilities for their origin. The term till (tillite, if lithified) refers to those materials deposited directly by a glacier or an ice-sheet, and with no further reworking by other transport means. It is a genetic term, and is usually limited to just a few subglacial facies associations: lodgement, deformation, ablation, and basal melt-out till(ite)s. The origin of a diamictite is commonly impossible to deduce from a single small outcrop, and detailed facies analysis is necessary in order to assess its depositional environment, including facies associations, sequences, geometries, lateral changes, and paleocurrents. Frequently, primary glacial sediments are reworked by nonglacial sedimentary processes in a glacially influenced environment, particularly rivers (glaciofluvial), lakes (glaciolacustrine), and continental shelves and slopes (glaciomarine or glacial marine).

As it is used today, the term glacial marine sedimentation is defined as the complex process that results in the accumulation of glacially eroded, terrestrially derived sediment within a variety of facies in the marine environment (MOLNIA, 1983; ANDERSON & ASHLEY, 1991). This sediment may be introduced into the marine environment by fluvial transport, by ice-rafting, as an ice-contact deposit, or by aeolian transport. An important consequence that follows from this definition is that glacial marine sedimentation takes place during or after glaciation, so that the record is necessarily synchronous with, or more frequently, slightly younger than the glaciation which caused it.

With regard to the paleoclimatic significance of the glacial record, the many factors that control the existence of basal meltwater in subglacial environments (such as thickness and flow velocity of the ice, geothermal heat, roughness of bedrock, mass balance, and mean surface temperatures) make it difficult or impossible to relate the basal thermal regime of a glacier or ice sheet to the climatic setting. Thus, we must be careful when trying to extrapolate too much information about the thermal regime of former ice sheets from subglacial deposits, and it has been recommended that the terms “dry-base“ and “wet-base“ be avoided (ANDERSON & DOMACK, 1991). Glacial marine sedimentology has undergone important advances and conceptual innovations during the last decades (see references above), including the interpretation of the paleoclimatic significance of this type of deposits (ANDERSON & ASHLEY, 1991). This means that previous interpretations of, and inferences from, the ancient glacial record may have to be considered with care, and that some of them may need revision.

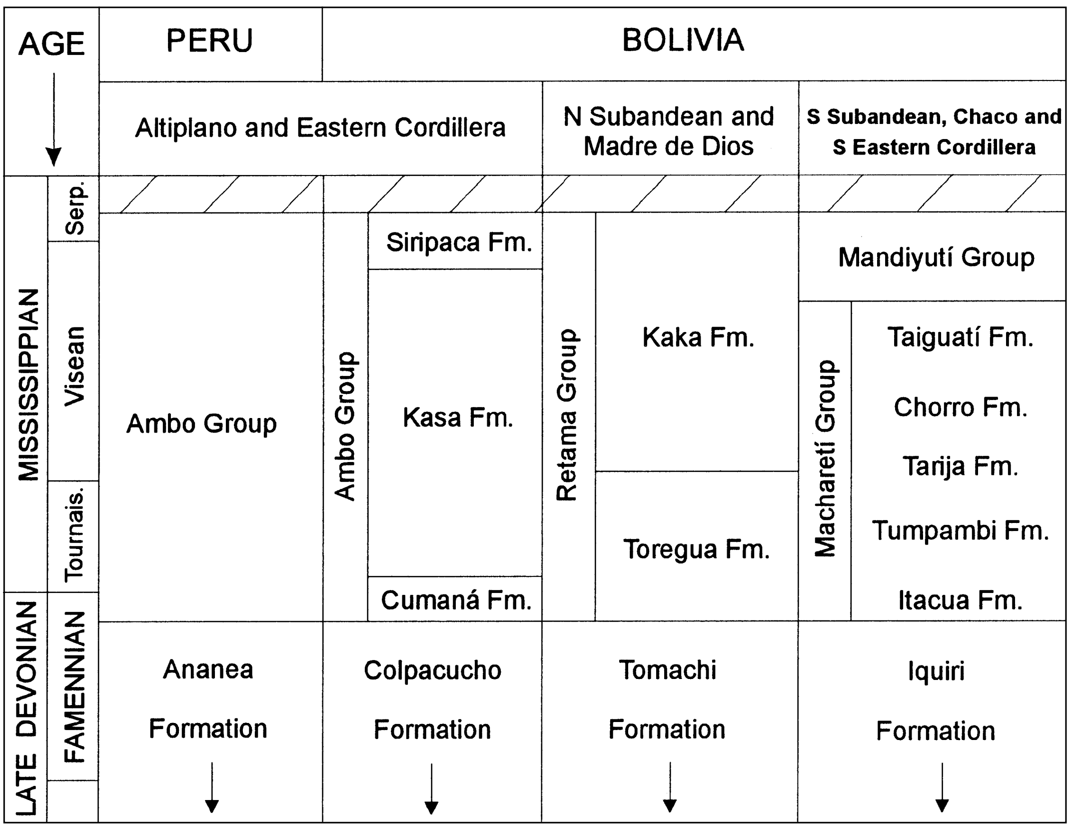
3. Stratigraphy of Glacial Marine Deposits in the Central Andes

3.1. Revised Carboniferous Chronostratigraphy

The age of the Carboniferous units in the Central Andes presenting evidence for glaciation has been recently revised (SEMPERE, 1993, 1995; DÍAZ-MARTÍNEZ, 1995a, 1996; SUÁREZ-SORUCO & DÍAZ-MARTÍNEZ, 1996), as new paleontological data has been made available. Former age assignments were mostly based on paleobotany and palynology, with biostratigraphic ages frequently correlated with units in Argentina, which in turn were frequently based upon correlation with central and eastern Gondwana (ARCHANGELSKY, 1971; ARCHANGELSKY & AZCUY, 1985; ARCHANGELSKY et al., 1987; GONZÁLEZ, 1997). A Pennsylvanian and/or Early Permian age has been frequently assigned to all these glacial deposits in Argentina (e.g., GONZÁLEZ, 1990; GONZÁLEZ-BONORINO, 1992; STARCK, 1995), and also directly applied to equivalent deposits in the Central Andean region (AZCUY, 1985; EYLES et al., 1995).

Plant communities migrated across western Gondwana during the late Paleozoic latitudinal shift of this supercontinent (IANNUZZI & RÖSLER, 1993, 1996). As a result, spore associations in the geological record also migrated with their corresponding source plant communities. This shift of plant communities and spore associations across Gondwana during the Carboniferous, results in the difficulty of assigning the same age for similar associations at different localities. Hence, other evidence has to be used for more confident age assignments than the use of spores alone, preferably with marine cosmopolitan organisms. During the last decade, micropaleontological studies and biostratigraphy of conodonts, algae and foraminifera in carbonate rocks located stratigraphically above the late Paleozoic glacial record in northern South America have set an upper (minimum) age limit for the glaciations in this part of Gondwana. In northern South America, carbonate and evaporite deposition at middle and tropical latitudes began in the earliest Pennsylvanian (Bashkirian), according to recent studies of conodont, small foraminifera and calcareous algae biostratigraphy (MERINO & BLANCO, 1990; MAMET, 1994, 1996).

All the sedimentary evidence for late Paleozoic glaciations in northern South America (westernmost Gondwana) underlies these carbonate and evaporite deposits, and therefore, all evidence for late Paleozoic glacially-related sedimentation in this part of Gondwana has to be older than Pennsylvanian (DÍAZ-MARTÍNEZ, 1995b, 1996), as displayed in Text-Fig. 2. This conclusion is important because it leads to older ages for the appearance of certain taxa (flora, fauna and palynomorphs) in western Gondwana. Such is the case of the *L. levis* brachiopod Zone, which was usually assigned a Namurian–Westphalian age, sometimes even younger. Recent revisions of its age in Australia indicate an older and more limited time range within the Namurian (mostly just Serpukhovian and earliest Bashkirian), based on absolute dating of interbedded tuffs (ROBERTS et al., 1995). Many authors (e.g., BRUNTON, 1985) have noticed the striking similarities and limited biogeographic distribution of the *L. levis* biozone along both ends of the southern Proto-Pacific (eastern Australia and western South America). It appears that this distribution just indicates the coincidence of both areas at similar southern latitudes during their opposite sense of latitudinal shift within Gondwana. Yet, in spite of all this evidence, the older age of many of the units containing evidence for the glaciations in western Gondwana is still not considered by many scientists in recent publications (e.g, VISSER & PRAECKELT, 1996; GONZÁLEZ, 1997; LÓPEZ-GAMUNDÍ, 1997; LÓPEZ-GAMUNDÍ & BREITKREUZ, 1997). At the same time, faunal zones are being revised, and new ones are being described, for the late Paleozoic sequences in Argentina (SIMANAUSKAS, 1996; SIMANAUSKAS & SABATTINI, 1997; TABOADA, 1997), and more biostratigraphic research is still needed in late Paleozoic sequences of other South American and African countries, where chronostratigraphic and biostratigraphic data is still very scarce.



Text-Fig. 2.
Lithostratigraphy of the Late Devonian and Early Carboniferous (Mississippian) stratigraphic record in the Peru-Bolivia basin (Central Andes; see location in Text-Fig. 1). The age of the units has been revised according to DÍAZ-MARTÍNEZ (1995a, 1995b, 1996), ISAACSON & DÍAZ-MARTÍNEZ (1995), and SEMPERE (1995). Note there is no vertical scale.

3.2. Late Devonian and Early Carboniferous Stratigraphy

The total composite accumulated thickness of the Paleozoic record in the Central Andes of Bolivia and Peru (Peru-Bolivia basin; Text-Fig. 1) may easily exceed 15 km (DALMAYRAC et al., 1980). This composite Paleozoic sequence has only a few stages missing. There are also three major unconformities within this sequence: mid-

Cambrian, Late Ordovician and mid-Carboniferous. These unconformities delineate four main tectonosedimentary cycles (SUÁREZ-SORUCO, 1989; SEMPERE, 1995): Brazilian (up to mid-Cambrian), Tacsarian (Late Cambrian–Late Ordovician), Cordilleran (Silurian–Mississippian) and Subandean (Pennsylvanian–Early Triassic). Each cycle records a different tectonic setting, in all cases related to the active margin of western Gondwana. In this paper we will concentrate on the description of the glacial record present in the upper part of the Cordilleran cycle (Late Devonian and Mississippian), which coincides with the Villamontes supersequence of SEMPERE (1995).

The Cordilleran cycle represents the gradual filling of a foreland basin, associated with transpression, tectonic uplift and deformation to the west and south, along the margin of Gondwana (ISAACSON & DÍAZ-MARTÍNEZ, 1995; SEMPERE, 1995). Most of the sediment input came from the active margin of the basin, with subsidence rates reaching 100 m/My, whereas its passive margin to the northeast underwent progressive flooding due to flexural subsidence, and much smaller subsidence rates. For the Paleozoic, this basin is called the Peru-Bolivia basin by SEMPERE (1995). Its southern and southwestern part enters Argentina and Paraguay, where it has been called the Tarija or Chaco-Tarija basin (Text-Fig. 1).

Text-Fig. 2 summarizes the lithostratigraphy of the Upper Devonian and Mississippian record in Bolivia, northwestern Argentina and Paraguay, and southeastern Peru. For the Devonian, it consists of off-shore and near-shore shallow marine siliciclastic sediments deposited under storm and wave influence from a southwestern tectonically-active source (MONTEMURRO, 1994; DÍAZ-MARTÍNEZ, 1995; DÍAZ-MARTÍNEZ et al., 1996). At latest Devonian to earliest Carboniferous time, an elongated uplifted area separated a western (Altiplano) basin from an eastern (Subandean and low plains) basin. This may have been a forebulge or a transpressive uplift (DÍAZ-MARTÍNEZ, 1995a; SEMPERE, 1995). As a result of this uplift within the basin, the Mississippian record in the Altiplano (Lake Titicaca area) maintained a similar style of deposition, but with a local eastern source. In contrast, the Mississippian record to the east of this uplift (modern Subandean area and Madre de Dios and Chaco plains) changed its style from being the passive margin of the foreland basin in the Silurian and Devonian, to being a deeper basin (below storm wave-base) with frequent sediment instability and resedimentation (slumps, debris flows, turbidites), and development of submarine channels draining towards the northwest (REQUENA & SADUD, 1994; EYLES et al., 1995; MORETTI et al., 1995; SEMPERE, 1995). This Mississippian paleogeographic reconstruction is important for two reasons. First, it implies that the Macharetí and Mandiyutí Groups of the Chaco basin and southern Subandean area are coeval and can be correlated with the Retama Group of the northern Subandean region (see Text-Fig. 2). Therefore, the Pennsylvanian age of the Macharetí and Mandiyutí Groups is paleogeographically unsustainable, as it would mean that the submarine paleochannels observed in seismic sections and field outcrops would drain downslope into the shallow water carbonate ramp of the Copacabana Formation, already well established since the early Bashkirian in SE Peru, and W and NW Bolivia (MAMET, 1994, 1996; ISAACSON et al., 1995; SEMPERE, 1995). Second, the aforementioned Mississippian paleogeographic reconstruction explains the recycled character of many of the Devonian palynomorphs found in the Retama Group and mixed with the Mississippian ones, with these latter providing the true age (AZCUY & OTTONE, 1987).

No sedimentologic studies have been undertaken on the equivalent Peruvian Late Devonian and Mississippian units (Ananea Formation and Ambo Group; Text-Fig. 2) in order to assess their sedimentary environments and paleogeographic and paleoclimatic significance with regard to the Gondwana glaciations. The Ananea Formation was defined by LAUBACHER (1974) to include the mid Silurian to Devonian siliciclastic sediments present in the Eastern Cordillera of Peru, and consisting of dark shales and schists with thin interbeds of quartzite. No reference has been made to the presence of any evidence for glaciation in the Ananea Formation, although there are no detailed descriptions of its facies. In contrast, the Ambo Group in the Eastern Cordillera of Peru is described by LAUBACHER (1977) as containing sandstones and shales with "tilloid-looking microconglomerates" towards the top, in conjunction with plant remains and coal beds. The equivalent unit (upper member of the Kasa Formation) at nearby sections in the southern (Bolivian) part of Lake Titicaca was studied in detail (DÍAZ-MARTÍNEZ et al., 1993b; DÍAZ-MARTÍNEZ, 1995b), concluding that these diamictites are interbedded within deltaic sequences, and resulted from gravity flows in delta front settings. Hence, due to the scarcity of detailed studies of the Late Devonian and Mississippian units in Peru, no confident evidence can be described yet for the Gondwana glaciation in this country. Nevertheless, because time-equivalent units in adjacent western and northern Bolivia contain this evidence, the possibility should not be discarded, and future detailed sedimentological and biostratigraphic studies must be pursued to corroborate the potential.

In the northern Bolivian Altiplano (Lake Titicaca area and south of La Paz), clear evidence for glaciation of a nearby source area has been described for the 100m-thick glacial marine diamictites and shales with dropstones of the Famennian Cumaná Formation (DÍAZ-MARTÍNEZ & ISAACSON, 1994). Evidence includes striated and faceted clasts, both as dropstones and within debris flows, the latter also with outsized granitoid boulders that reach 4 m in diameter (Text-Figs. 3 and 4). No tillites (glacier-contact deposits) have been described, although the glacigenic character of the clasts is unquestionable. The underlying Colpacucho Formation (Frasnian–Famennian) also contains isolated dropstones and dropstone accumulations (dumped from icebergs) in its upper part (Text-Fig. 3). The overlying Kasa Formation (Tournaisian–Visean) consists of a complex deltaic progradational sequence exceeding 1 km in thickness. Diamictite beds within the Kasa Formation are interpreted as gravity flows resulting from rapid progradation of braid-delta fronts, probably as a result of sudden water and sediment discharges related with terrestrial proglacial environments (DÍAZ-MARTÍNEZ, 1995a).

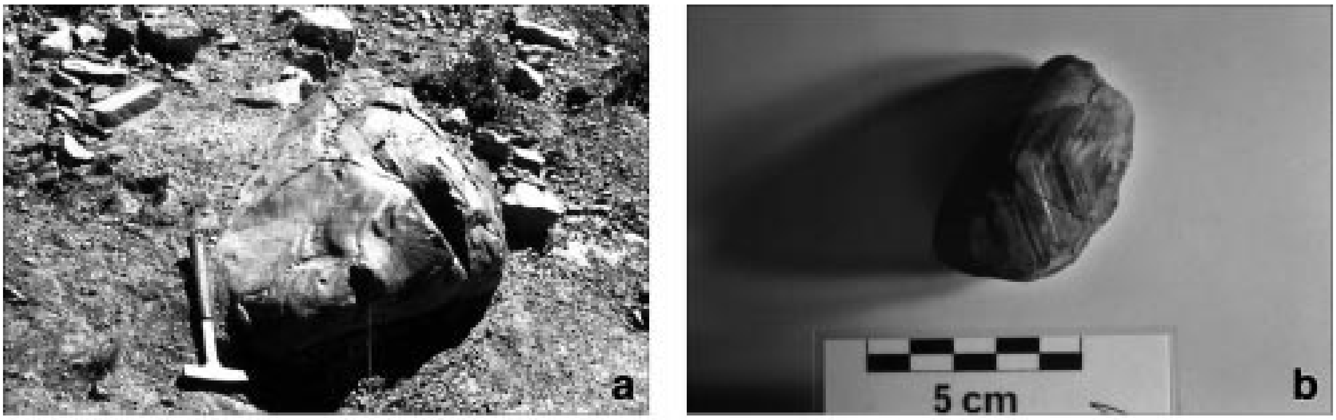
The Subandean region and the low-land plains (Madre de Dios and Chaco) of southeastern Peru, eastern Bolivia and northwestern Argentina and Paraguay also present evidence for glaciation of the source area in the late Paleozoic. Beginning in Famennian time, and during most of the Mississippian (following the revised ages mentioned above; Text-Fig. 2), sedimentation to the east of the Eastern Cordillera consisted of gravity-driven submarine processes such as slides, slumps, debris flows, and turbidity currents, resulting from sediment failure and redeposition. These units have been thoroughly studied due to their economic importance, both as hydrocarbon source rocks and as hydrocarbon reservoirs (ARDAYA, 1989;

Text-Fig. 3.
a,b) Sandstone clasts as dropstones.
c) Discontinuous conglomerate bed, probably as a result of dumping from an iceberg.
d) Rounded sandstone clast and angular granitoid clast.
e) Large (>4 m) granitoid clast in the foreground, and other clasts of variable composition and size in the background.
a, b and c are found within the shales and siltstones of the upper member of the Late Devonian Colpacucho Formation; d and e are found within the diamictites of the late Famennian Cumaná Formation.
All outcrops at Quebrada de Chamacani, except c, at Hinchaka, both locations at Copacabana Peninsula, northern Altiplano, Bolivia (see location in Text-Fig. 1).

Montemurro, 1989; Requena & Sadud, 1994; Eyles et al., 1995; Moretti et al., 1995; Sempere, 1995; Peters et al., 1997). Their lithofacies present strong lateral changes, and they sometimes exceed 1 km in thickness. As with the Cumaná Fm., evidence for glaciation of the source area consists of striated and faceted clasts, as well as outsized granitoid boulders, both as dropstones and within debris flows and other resedimented deposits. This evidence is present in most of the units of the Macharetí and Mandiyutí groups.

Seismic sections in the Chaco Basin, and outcrops in the southern Subandean and southern Eastern Cordillera of Bolivia, display wide submarine channels flowing together and joining towards the north and northwest (towards southeastern Peru), and with source areas located to the southwest, south and east (Starck et al., 1993; Requena & Sadud, 1994; Eyles et al., 1995; Moretti et al., 1995; Sempere, 1995). This suggests that the glaciated areas for the Late Devonian and Mississippian were located both along the active margin of Gondwana (southwestern Bolivia and northwestern Argentina) and towards the interior (Paraguay and western Brazil).

The only confirmed late Paleozoic glacially-striated pavements in the Central Andes have been found at the base of the Tarija Formation in the Eastern Cordillera of northwestern Argentina (Starck et al., 1993; Starck, 1995, p. 258), corresponding to the southwestern tip of the Paleozoic Peru-Bolivia Basin. In addition to the striated pavements, with ice flow oriented towards the northwest, evidence mentioned by these authors also includes dropstones, and the true tillite character of the diamictites (lodgement till). The precise age of the sediments directly overlying the striated pavement has not yet been assessed.



Text-Fig. 4.
Glacially-striated clasts from the diamictites of the late Famennian Cumaná Formation.
a) Sandstone clast with several families of striations on its upper and lower faces (Quebrada Sikukuyu, western flank of Calamarca syncline, south of La Paz).
b,c) Striated sandstone clasts (Hinchaka, Copacabana Peninsula).
See locations in Text-Fig. 1.

Text-Fig. 5.
View of the Late Devonian section at the Bermejo River, in the Sub-Andean zone of the Andes, west of Santa Cruz de la Sierra, Bolivia.
Notice the synsedimentary (or glaciotectonic?) deformation of the uppermost interbedded sandstones and siltstones of the Late Devonian Iquiri Formation (light color), just below the diamictites of the Itacua Formation (dark color), which include large resedimented sandstone blocks.

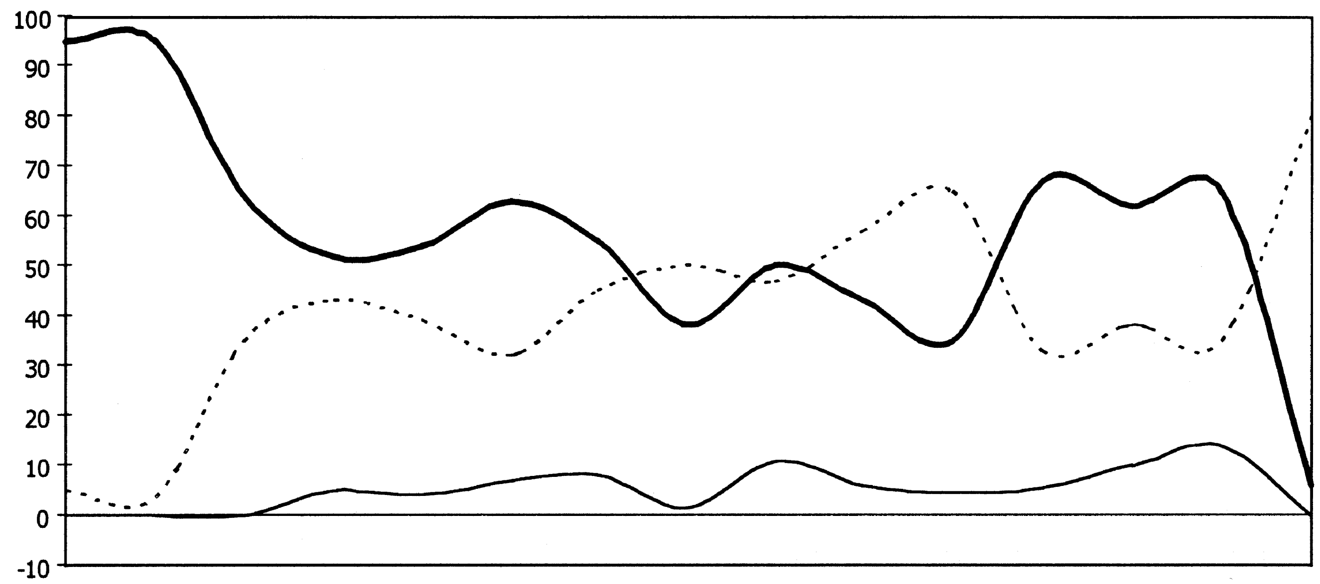
4. Palynomorph Biostratigraphy and Evidence for a Late Devonian Age of Glaciation

Biostratigraphic assessment of the units presenting evidence for glaciation in Bolivia is based on the presence of poorly preserved but distinctive and well-diversified assemblages of organic walled microfossils, including miospores, marine microphytoplankton, rare chitinozoans and scolecodonts. The sections studied of the Cumaná Formation are located in the Lake Titicaca area, western Bolivia, namely at Isla del Sol and Copacabana Peninsula. Preliminary palynological data suggest that these deposits can be correlated with the late Famennian LE (*Retispora lepidophyta – Indotriradites explanatus*) palynozone (Vavrdová et al., 1993). To support the rather scarce data, additional samples were investigated from other sections in the Altiplano, Eastern Cordillera, and Madre de Dios basin in northern Bolivia (Vavrdová et al., 1996).

Palynological data were utilized in the reconstruction of the sedimentary paleo-environment in Bolivia during the Devonian. Age-significant species such as *Retispora lepidophyta* (Kedo) Playford have contributed to the recognition of correct chronological position of siliciclastic units with otherwise limited paleontological record (Lobo-Boneta, 1989). A comprehensive outline of previous palynological research has been given by Ottone (1996) and by Rubinstein (1997).

The oldest Devonian sediments encountered in the Pando X-1 well (Madre de Dios basin) were laminated mudstones of the Tequeje Formation, at 1914 m, which yielded assemblages of palynomorphs which indicate an open-marine, off-shelf environment. Palynomorphs of marine origin attain 95% of recovered palynomorphs (chitinozoans were abundant and well-preserved at this level). Most characteristic were, among others, *Cingulochitina serrata* Taugourdeau and Jekhowsky, *Angochitina filosa* Eisenack and *Urochitina loboi* Volkheimer et al. (Dufka in Vavrdová et al., 1996). Age significant species of miospores and of marine microplankton indicated Lochkovian and possibly latest Silurian age of the assemblage.

The upper part of the Tequeje Formation has been palynologically assessed by Ottone and Rosello (1996). These authors assigned a Middle and Late Devonian (Givetian–Frasnian) age to the palynomorph assemblages, which exhibit a marine/terrestrial ratio of palynomorphs indicating a shallow, marginal marine facies. Miospores,



Sample	P38	P37	P34	P29	M56	M55	M54	M50	M48	M42	M41	M38	M29	P13	P9
Depth (m)	1932	1914	1764	1559	1468	1469	1465	1438	1433	1410	1406	1400	1381	1123	1095
Formation	TEQUEJE			TOMACHI				TOREGUA							

Text-Fig. 6.
Quantitative assessment of palynomorphs of terrestrial and marine origin from Pando X-1 (P samples) and Manuripi X-1 (M samples) well cores. Thick line represents acritarch and prasinophyte phycomata percentage, dotted line represents miospore percentage, and thin line represents percentage of *Umbellasphaeridium saharicum* JARDINÉ et al. (see details in VAVRDOVÁ et al., 1996).

such as *Geminospora lemurata* BALME and *Acinosporites ledundae* OTTONE indicate, according to OTTONE and ROSELLO (1996), a Middle Devonian age of the upper part of the Tequeje Formation. The same sedimentary environment persisted through deposition of the Tomachi Formation. Generally equal number of terrestrial spores and pollen, and marine algal cysts have been recovered from this formation (Text-Fig. 6), together with abundant chitinozoans and terrestrial plant debris, such as cuticles and tracheids. Occasional blooms of prasinophyte algae (genera *Maranhites*, *Tasmanites*, and *Hemiruptia*) mark the black shale horizons with abundant degraded organic matter. According to PETERS et al. (1997), the organic-rich Tomachi Formation sediments are prime hydrocarbon source rocks in the Madre de Dios Basin.

The relatively stable sedimentary conditions were drastically changed during the Famennian, in which hiatuses, transgressions and regressions and massive recycling mark more dynamic paleoclimatic conditions, probably reflected as local sea level glacio-eustatic oscillations. Late Famennian diamictites of the Cumaná Formation, in the Altiplano, and the Toregua Formation, in the Madre de Dios basin, yielded palynological associations with unusually rich and diverse associations of miospores, implying the presence of a humid lycophyte-pterophyte vegetation. These units yielded the following genera: *Ancyrospora*, *Hystricosporites*, *Retispora*, *Indotriradites*, *Convolutispora*, *Grandispora*, *Knoxisporites*, and *Tumulispora*, among others (Table 1). Unicellular marine microplankton are represented by the genera *Pterospermella*, *Exochoderma*, *Umbellasphaeridium*, *Duvernaysphaera*, *Gorgonisphaeridium*, *Schizocystia*, and *Maranhites* (Table 2).

Sequences influenced by presumed paleoclimatic cooling are marked by an increase of phytoplankton productivity and diversification of assemblages of acritarchs following the interval with predominant *Umbellasphaeridium saharicum* JARDINÉ et al. Favorable conditions for phytoplankton growth are suggested by the unusual size of specimens, in the range of 100-150 micrometers (for example, *Exochoderma irregularis* WICANDER, Plate 2, Figs. 1 & 2). Phytoplankton assemblages contain cosmopolitan forms, such as *Veryhachium pannuceum* WICANDER, *Veryhachium roscidum* WICANDER, *Stellinium micropolygonale* STOCKMANS and WILLERE, *Unellium winslowiae* RAUSCHER, as well as undescribed endemic taxa. The characteristic species, *Umbellasphaeridium saharicum* JARDINÉ et al. prevails among the marine microplankton.

Three stratigraphic sections have been studied for palynology in the Lake Titicaca area (Text-Fig. 1): Isla del Sol (IS-2 and IS-3), Hinchaka (HI-2, 3, 4 and 6), and Villa Molino (formerly also known as Mina Matilde; MM-4a, MM-4b and MM-9a). Palynological assemblages recovered from the Cumaná Formation diamictite (samples IS-3 and HI-2) were generally very poorly preserved. Associations of a low abundance of organic microfossils contained oxidized and degraded miospores and other palynomorphs. The poor preservation precludes the differentiation of specimens coeval with the origin of the diamictite and older recycled forms (Plate 1, Fig. 1). Characteristic is a frequent occurrence of algal coenobia (*Tetraletes* and *Quadrisporites*). Age-diagnostic species, *Retispora lepidophyta* (KEDO) PLAYFORD and *Umbellasphaeridium saharicum* JARDINÉ et al. dominate the assemblage. *Indotriradites explanatus* (LUBER) PLAYFORD and representatives of the genera *Raistrickia, Punctatisporites*, and *Convolutispora* are relatively common. The frequent occurrence of fragmentary plant debris, fungal remains, scolecodonts, and of chitinozoans indicates a high energy, shallow marine sedimentary paleo-environment. The composition of the acritarch and prasinophyte associations generally suggests a Late Devonian age. An absence of the index species *Verrucosisporites nitidus* PLAYFORD, which appears in sample 4a of the Villa Molino section, and is characteristic of early Tournaisian assemblages, suggests assignment to the LE palynozone (HIGGS

Table 1.
Selected miospores from the Colpacucho and Cumaná Formations at the Hinchaka, Isla del Sol and Villa Molino (Mina Matilde) sections. See location in Text-Fig. 1.

	Hinchaka				Isla del Sol		Villa Molino (Mina Matilde)		
	HI-2	HI-3	HI-4	HI-6	IS-2	IS-3	4a	9a	9b
Ancyrospora sp.								X	
Baculatisporites fusticus Sullivan		X	X		X	X	X		
Convolutispora flexuosa Hacquebard							X		
C. vermiformis Hughes & Playford	X						X	X	X
Corbulispora cancellata (Waltz) Bharadwaj & Venkatachala							X	X	
Cordylosporites marciae Playford & Satterwait	X						X	X	X
Cyrtospora cristifer (Luber) Van der Zwan								X	X
Densosporites spitsbergensis Playford				X					X
Dibolisporites distinctus (Clayton) Playford									X
Emphanisporites spp.		X					X	X	
Grandispora spp.								X	
G. sp. aff. *G. pseudoreticulata* (Menéndez & Pothe de Baldis) Ottone								X	
Indotriradites explanatus (Luber) Playford	X	X	X		X	X	X	X	X
Knoxisporites literatus (Waltz) Playford			X				X		
Pustulatisporites dolbii Higgs et al.							X		
Raistrickia clavata (Hacquebard) Playford				X					X
R. macrura (Luber) Dolby & Neves		X			X	X	X	X	
R. spathulata (Winslow) Higgs		X							
Retispora lepidophyta (Kedo) Playford	X	X	X		X	X	X	X	
Retusotriletes rotundus Streel							X		
R. incohatus Sullivan					X	X	X	X	
Spelaeotriletes resolutus Higgs		X					X		
S. obtusus Higgs		X							X
Tumulispora rarituberculata (Luber) Playford								X	X
Vallatisporites pusillites (Kedo) Dolby & Neves								X	
Verrucosisporites nitidus Playford							X	X	X

& Streel, 1984; Richardson & McGregor, 1986). Plate I illustrates some palynomorphs from the Cumaná Formation diamictite. The following plates illustrate better preserved palynomorphs from the Villa Molino section, in which palynozone LN (*lepidophyta-nitidus*) assemblages have been described.

Palynomorph assemblages from the Cumaná Formation reveal close affinities to the Late Devonian microflora recovered from the Retama Group of the northern Subandean of Bolivia (Azcuy & Ottone, 1987). Closely similar are associations from the Itacua Formation of the southern Subandean region (Lobo-Boneta, 1989). Samples from the Itacua Formation, processed by Perez-Leyton (1990), contained palynomorphs which indicate assignment to the LE palynozone. Azcuy & Ottone (1987) proposed an Early Carboniferous age for palynological assemblages from the upper part of the Retama Group, and the presence of Late Devonian miospores (*Retispora lepidophyta* (Kedo) Playford) and acritarchs (*Umbellasphaeridium saharicum* Jardiné et al.), which were described as reworked.

The Devonian–Carboniferous transition has been identified in the Villa Molino section (Vavrdová et al., 1991). Here, the appearance of *Densosporites spitsbergensis* Playford and other species (such as *Dibolisporites distinctus* (Clayton) Playford, Plate 4, Fig. 5) are considered as index forms indicating an early Tournaisian age. Although most of the characteristic miospore species persist across the Devonian–Carboniferous transition (Playford, 1993), Tournaisian acritarch populations are generally of a lower abundance in the Villa Molino section. *Umbellasphaeridium saharicum* Jardiné et al. and *Maranhites mosesii* are rarely present as untypical forms (Plate 5, Fig. 2; Plate 2, Fig. 5). Apart from genera *Polyedryxium* and *Stellinium*, most of the Devonian microplankton species completely disappear.

5. Late Devonian Glaciation in Western Gondwana

In northern Brazil, glacial and periglacial conditions have been proposed by Caputo (1985) and Caputo &

Table 2.
Selected acritarchs and prasinophytes from the Colpacucho and Cumaná Formations at the Hinchaka, Isla del Sol and Villa Molino (Mina Matilde) sections; see location in Text-Fig. 1.

	Hinchaka				Isla del Sol		Villa Molino (Mina Matilde)		
	HI-2	HI-3	HI-4	HI-6	IS-2	IS-3	4a	9a	9b
Ammonidium sp.					X				
Arkonites bilixus Jardiné et al.		X			X				X
Crassiangulina tesselita Jardiné et al.		X				X	X	X	
Cruzidia camirense (Lobo Boneta) Ottone		X				X			
Cymatiosphaera cornifera Deunff						X		X	X
C. winderi Deunff								X	X
Duvernaysphaera radiata Brito		X		X	X	X		X	X
Estiastra rhytidoa Wicander et Wood		X			X	X			
Evittia cf. *granulata* Brito	X								
Exochoderma irregulare Wicander						X	X	X	X
Gorgonisphaeridium absitum Wicander									X
G. evexispinosum Wicander						X	X		
G. ohioense (Winslow) Wicander							X		X
G. separatum Wicander						X			
Maranhites brasiliensis Brito							X		
M. mosesii (Sommer) Brito		X	X				X	X	X
M. pulcher Brito							X		
Ovnia desertica Cramer & Díez	X	X							
Polyedrixium pulchrum Deunff									X
P. simplex Deunff									X
P. turritum Colbath									X
Pterospermella latibalteata Wicander			X		X	X	X	X	X
Schizocystia bicornuta Jardiné et al.	X		X				X		
Stellinium micropolygonale (Stockmans & Williere) Playford							X	X	X
Umbellasphaeridium deflandrei (Moreau-Benoit) Jardiné					X	X	X		
U. saharicum Jardiné et al.		X			X	X	X	X	
Unellium winslowiae Rauscher									X
Veryhachium pannuceum Wicander & Loeblich						X	X	X	
V. roscidum Wicander						X	X	X	X

CROWELL (1985) during deposition of Late Devonian units. The evidence includes faceted and striated pebbles, striated pavements, varved sediments, exotic blocks, and widespread distribution of diamictites. Glacial influence has been observed in the Solimões, Amazonas and Parnaiba basins (Text-Fig. 1). The Jaraqui Diamictite Member of the Jandiatuba Formation, in the Solimões basin, is interpreted as deposited in a glacial marine environment, and has been dated as Famennian and Tournaisian (QUADROS, 1988; CAPUTO & SILVA, 1990; EIRAS et al., 1994). The Curiri Formation of the Curuá Group in the Amazonas Basin, also consists of glacial marine diamictites and shales deposited during the late Frasnian to mid Famennian interval (DAEMON & CONTREIRAS, 1971; CUNHA et al., 1994). The Cabeças Formation of the Canindé Group, in the Parnaiba Basin, consists of late Givetian to mid-Famennian sandstones, shales and diamictites (GÓES & FEIJÓ, 1994). Miospores isolated from the uppermost Cabeças Formation in the central Parnaiba Basin (LOBOZIAK et al., 1992, p. 225) allowed recognition of two interval zones (LE and LN) of latest Devonian age, corresponding to the Hangenburg shales in Germany. All these deposits in Brazil prove the existence of glaciers in many of the terrestrial land areas of northern South America during the Late Devonian.

In the African continent, in addition to an earlier Late Ordovician and Early Silurian glaciation recorded in its western and northern regions, the late Paleozoic glaciation also left its imprint. Evidence for Late Devonian and Early Carboniferous glaciation is present in the northern half of the continent in the countries of Niger, Egypt, Sudan and the Central African Republic (LANG et al., 1990; CENSIER et al., 1995). Beginning in the mid Carboniferous, the glaciation centers shifted towards southern Africa, manifesting themselves first in Zaïre, Gabon and Angola, then in Mozambique and Zimbabwe, then in Namibia and Botswana, and finally in South Africa during the Early Permian (CENSIER et al., 1995).

6. Conclusion

The evidence from Brazil and northern Africa, together with the evidence described above in this paper from Bolivia and adjacent countries, demonstrates that the beginning of the Late Paleozoic glaciation of Gondwana took place in westernmost Gondwana earlier than in other parts of the continent. The Late Devonian and Early Carboniferous (Mississippian) age of the main glaciation in northern South America and northern Africa predates its progressive shift to central and southern Gondwana in the mid to late Carboniferous, and its final shift to eastern Gondwana in the earliest Permian.

Acknowledgements

Acknowledgement is made to the donors of the Petroleum Research Fund, administered by the American Chemical Society. The Bolivian Geological Survey (SERGEOMIN), the National Oil Company of Bolivia (YPFB) and the French Overseas Research Institute (ORSTOM) kindly helped with field logistics and data acquisition.

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Manuskript bei der Schriftleitung eingelangt am 2. Oktober 1998

Plate 1

Palynomorphs from the Isla del Sol section (Late Famennian).

Figs. 1,2: ***Retispora lepidophyta*** **(Kedo) Playford, 1979.**
Fig. 1: Sample IS-2, slide 2, 16 × 125.
Size 66 µm.
Fig. 2: Sample IS-2, slide 5, 8.7 × 129.
Size 70 µm.

Fig. 3: ***Pterospermella latibalteata*** **Wicander, 1974.**
Sample IS-3, slide 3, 5 × 119.5.
Size 55 µm.

Fig. 4: ***Cruzidia camirense*** **Ottone, 1996.**
Sample IS-3, slide 5, 22 × 108.8.
Size 75 µm.

Fig. 5: ***Umbellasphaeridium saharicum*** **Jardiné et al., 1972.**
Sample IS-2, slide 2, 17 × 127.
Size 76 µm.

Fig. 6: ***Retispora lepidophyta*** **(Kedo) Playford, 1979.**
Sample IS-3, slide 3, 5 × 143.
Size 45 µm.

Fig. 7: ***Umbellasphaeridium deflandrei*** **(Moreau-Benoit) Jardiné et al., 1972.**
Sample IS-2, slide 8, 15.8 × 120.5.
Size 54 µm.

Fig. 8: **Algal coenobium.**
Sample IS-2, slide 1, 15.5 × 120.6.
Size 40 µm.

All specimens in plates are stored in the Collections of the Geological Institute, Academy of Sciences in Prague (No. IS 1-25).

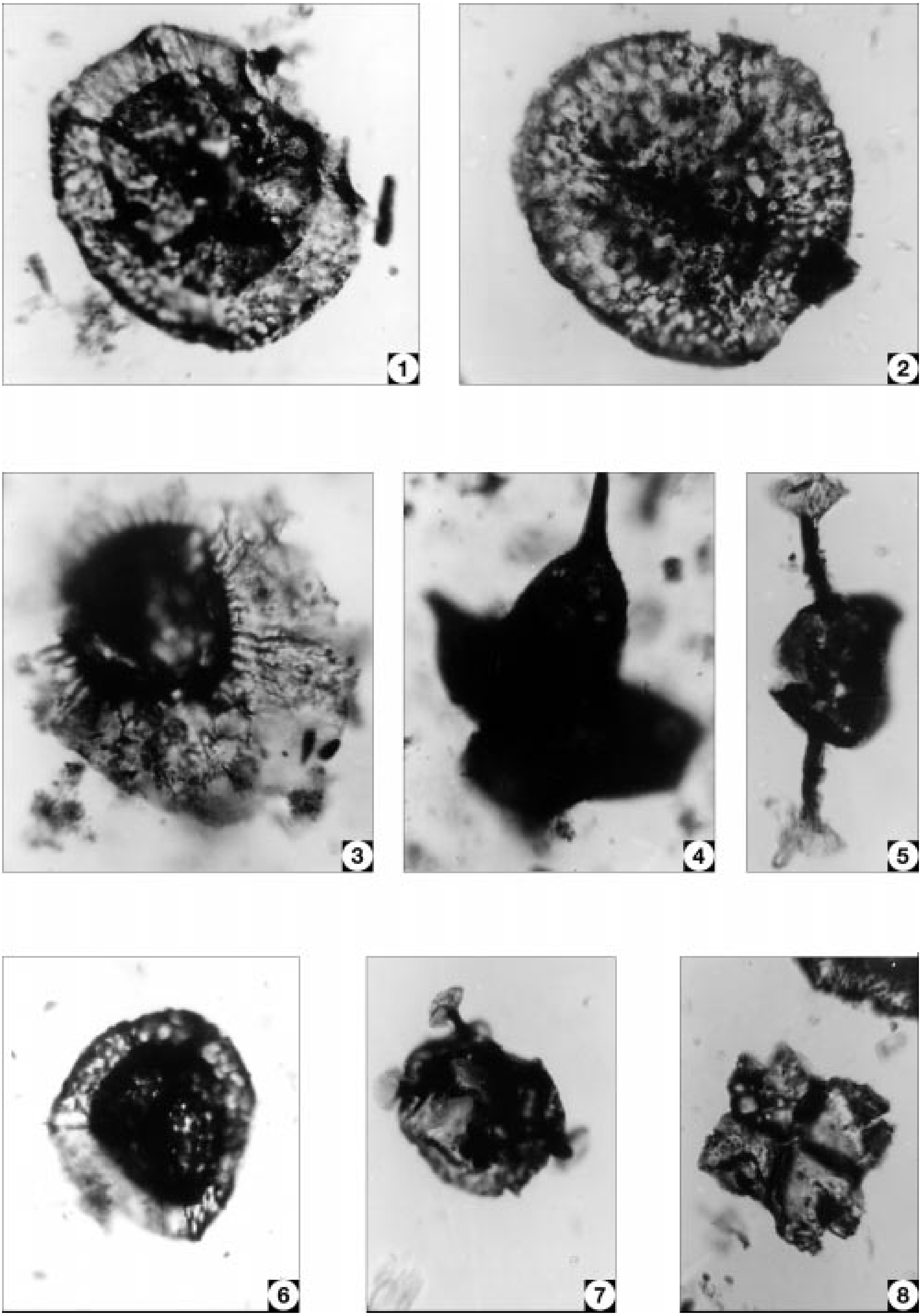
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Plate 2

Palynomorphs from the Villa Molino section (LN palynozone).

Figs. 1,2: ***Exochoderma irregulare* WICANDER, 1974.**
Fig. 1: Sample MM-4A, slide 3, 20 × 119.4.
Size 145 µm.
Fig. 2: Sample MM-4A, slide 12, 9.2 × 115.
Size 110 µm.

Fig. 3: ***Maranhites brasiliensis* BRITO, 1965.**
Sample MM-4A, slide 8, 23.5 × 112.

Fig. 4: ***Umbellasphaeridium saharicum* JARDINÉ et al., 1972.**
Sample MM-4A, slide 6, 8.8 × 131.
Size 70 µm.

Fig. 5: ***Maranhites mosesii* (SOMMER) BRITO, 1967.**
Sample MM-4A, slide 6, 14.5 × 104.5.
Size 61µm.

Fig. 6: ***Stellinium micropolygonale* (STOCKMANS et WILLIERE) PLAYFORD, 1977.**
Sample MM-4A, slide 12, 5 × 121.
Size 62 µm.

All specimens in plates are stored in the Collections of the Geological Institute, Academy of Sciences in Prague (No. IS 1-25).

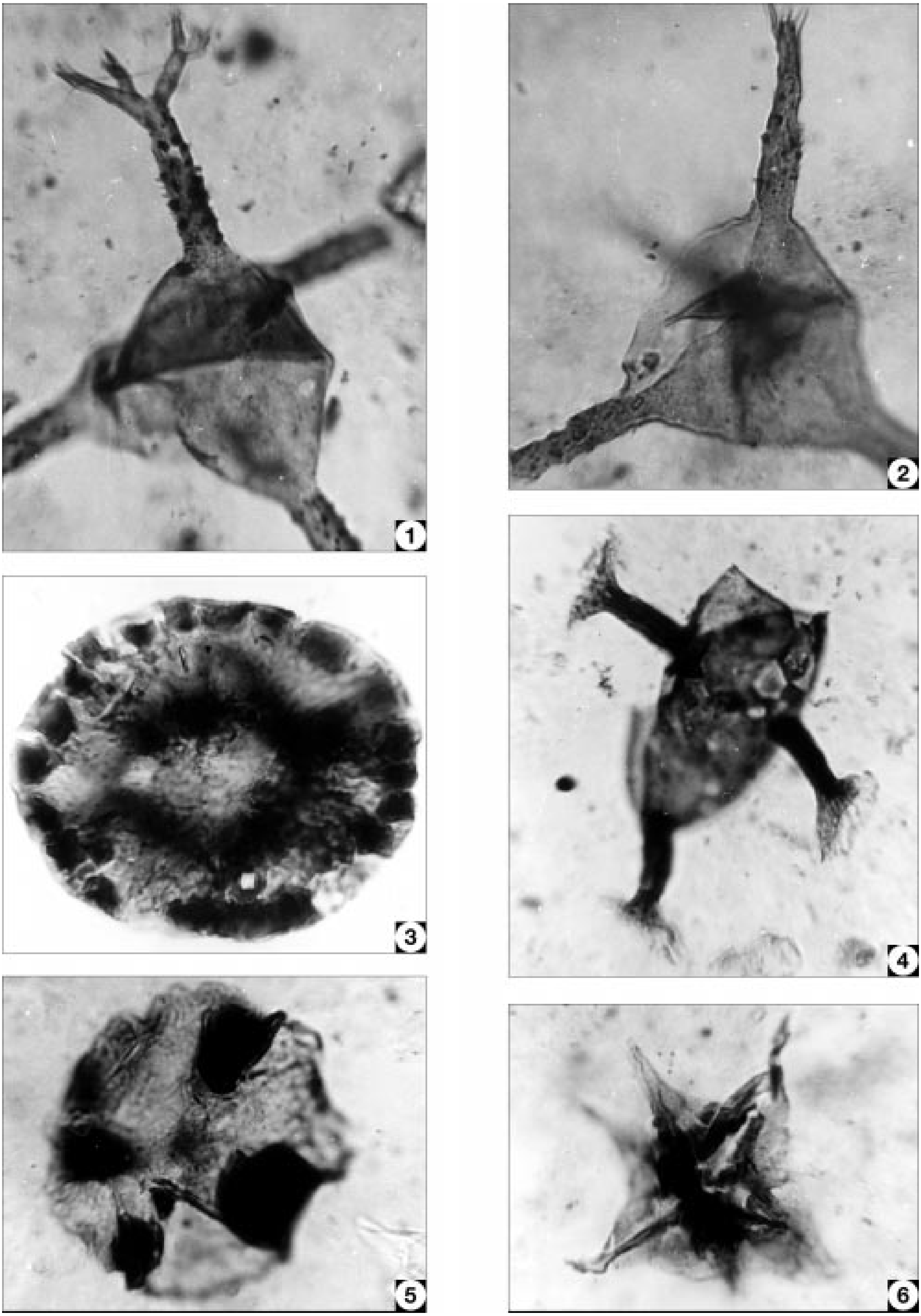

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Plate 3

Palynomorphs from the Villa Molino section (LN palynozone).

Figs. 1,2: ***Tumulispora rarituberculata*** **(LUBER) PLAYFORD, 1991.**
Fig. 1: Sample MM-4A, slide 2, 24.2 × 117.
Size 61 µm.
Fig. 2: Sample MM-9A, slide 20, 19.2 × 110.5.
Size 90 µm.

Fig. 3: ***Spelaeotriletes resolutus*** **HIGGS, 1975.**
Sample MM-4A, slide 17, 18.7 × 96.3.

Fig. 4: ***Convolutispora flexuosa*** **HACQUEBARD, 1961.**
Sample MM-4A, slide 3, 7.5 × 105.

Fig. 5: ***Knoxisporites literatus*** **(WALTZ) PLAYFORD, 1963.**
Sample MM-4A, slide 20, 7.8 × 105.
Size 75 µm.

Fig. 6: ***Maranhites*** **sp. indet.**
Sample MM-4A, slide 2, 19 × 123.5.
Size 75 µm.

All specimens in plates are stored in the Collections of the Geological Institute, Academy of Sciences in Prague (No. IS 1-25).

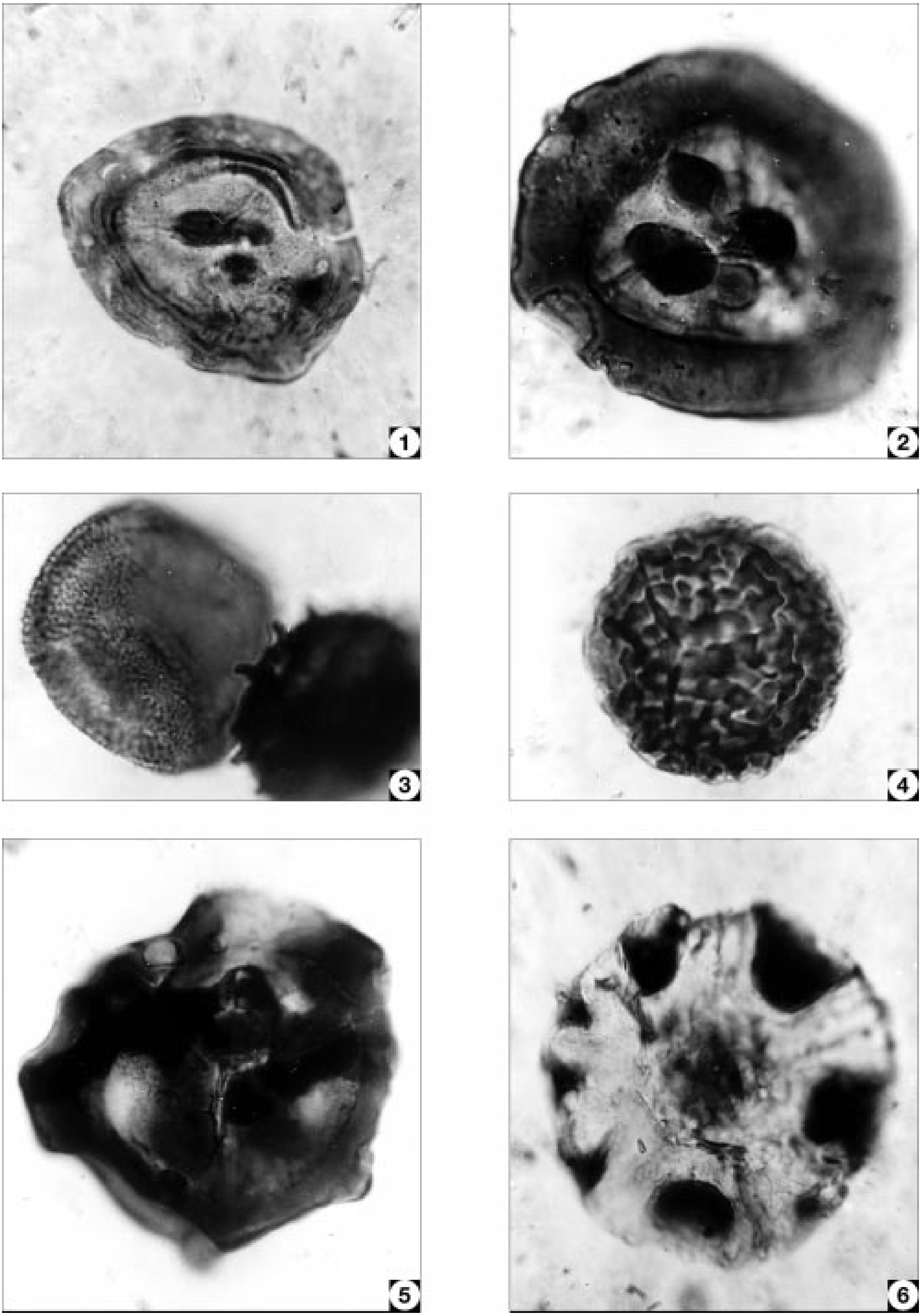
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Plate 4

Palynomorphs from the Villa Molino section (Devonian–Carboniferous transition).

Fig. 1: ***Grandispora* sp. indet. (?recycled).**
Sample MM-9A, slide 10, 3.2 × 133.4.

Fig. 2: ***Grandispora* sp. indet. aff. *G. pseudoreticulata* (Menendez et Pothe de Baldis) Ottone 1996.**
Sample MM-9A, slide 10, 26.2 × 130.2.
Size 100 µm.

Fig. 3: **Algal coenobium.**
Sample MM-4A, slide 6, 12.7 × 108.6.
Size 70 µm.

Fig. 4: ***Polyedrixium pulchrum*** Deunff, 1971.
Sample MM-9B, slide 2, 13.3 × 125.3.
Size 63 µm.

Fig. 5: ***Dibolisporites distinctus*** (Clayton) Playford, 1976.
Sample MM-9B, slide 1, 10.3 × 108.2.
Size 80 µm.

Fig. 6: ***Pustulatisporites dolbii*** Higgs, Clayton et Keegan, 1988.
Sample MM-4A, slide 8, 19.2 × 122.6.
Size 54 µm.

All specimens in plates are stored in the Collections of the Geological Institute, Academy of Sciences in Prague (No. IS 1-25).

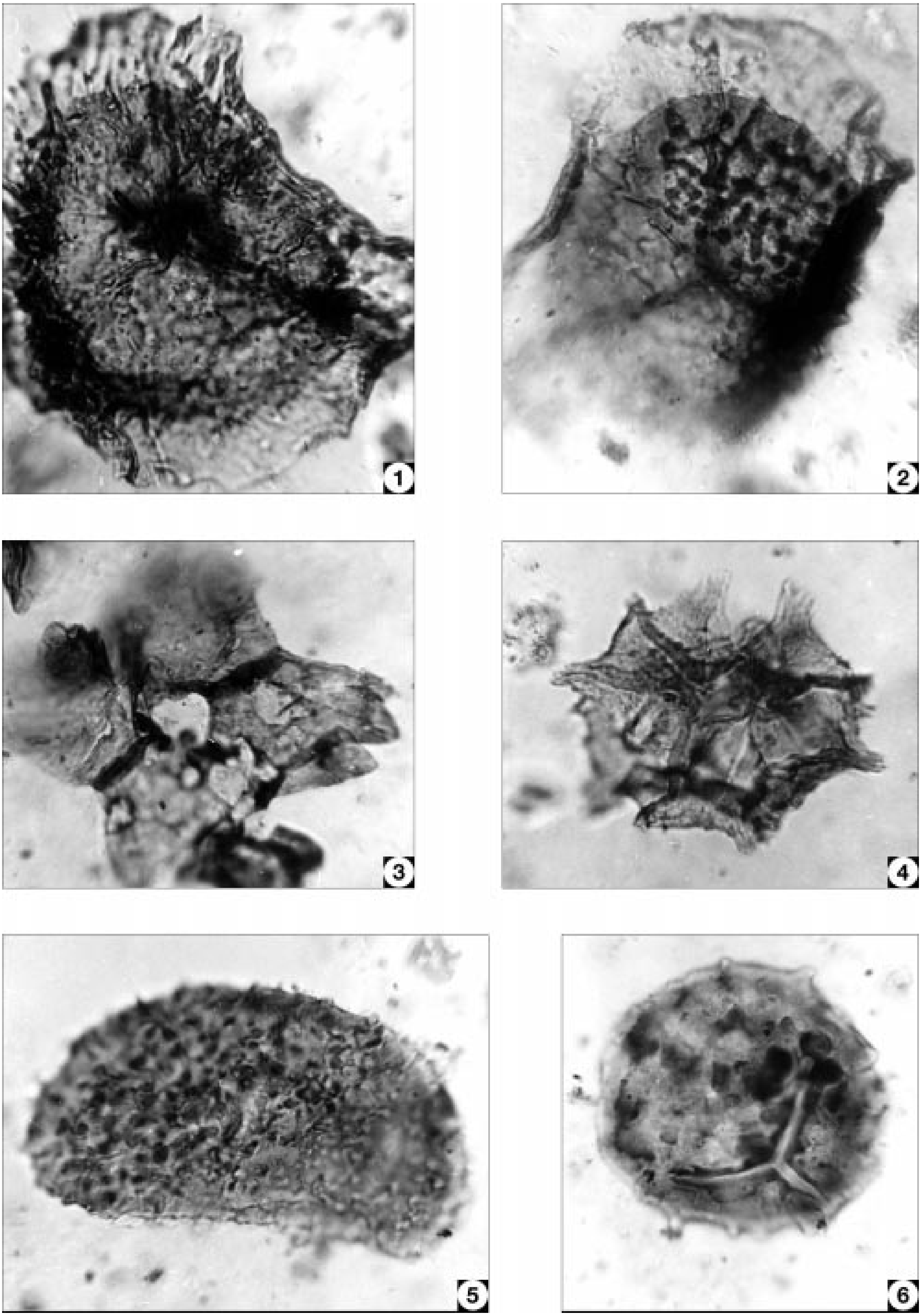
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Plate 5

Palynomorphs from the Villa Molino section (Devonian–Carboniferous transition).

Fig. 1: ***Umbellasphaeridium saharicum*** **Jardiné et al., 1972.**
Sample MM-4A, 3319, × 1000.

Fig. 2: ***Umbellasphaeridium*** **aff.** ***saharicum*** **Jardiné et al., 1972.**
Sample MM-9B, 3343, × 1000.

Fig. 3: ***Apiculiretusispora fructicosa*** **Higgs, 1975.**
Sample MM-9B, 3349, × 1000.

Fig. 4: ***Raistrikia macrura*** **(Luber) Dolby et Neves, 1970.**
Sample MM-9A, 3365, × 1000.

Fig. 5: **aff.** ***Grandispora lupata*** **Turnau, 1975.**
Sample MM-9B, × 1500.

Fig. 6: **Planctonic form, incertae sedis.**
Sample MM-9B, 3338, × 1000.

All specimens in plates are stored in the Collections of the Geological Institute, Academy of Sciences in Prague (No. IS 1-25).

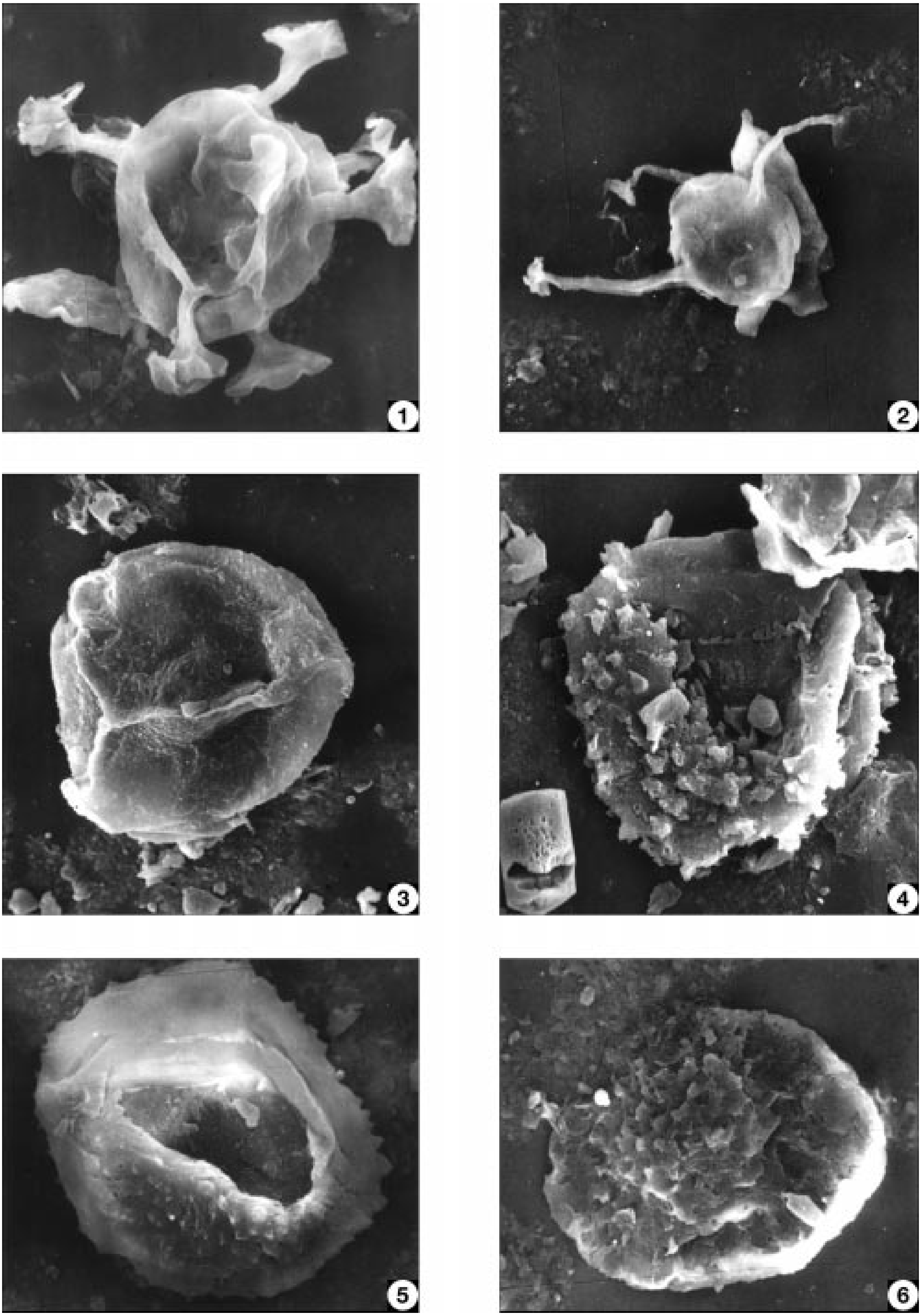
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Plate 6

Palynomorphs from the Villa Molino section (Devonian–Carboniferous transition).

Fig. 1: ***Convolutispora vermiformis* Hughes et Playford, 1961.**
Sample MM-9B, 3343, × 1400.

Fig. 2: ***Gorgonisphaeridium evexispinosum* Wicander, 1974.**
Sample MM-9B, 3367, × 1800.

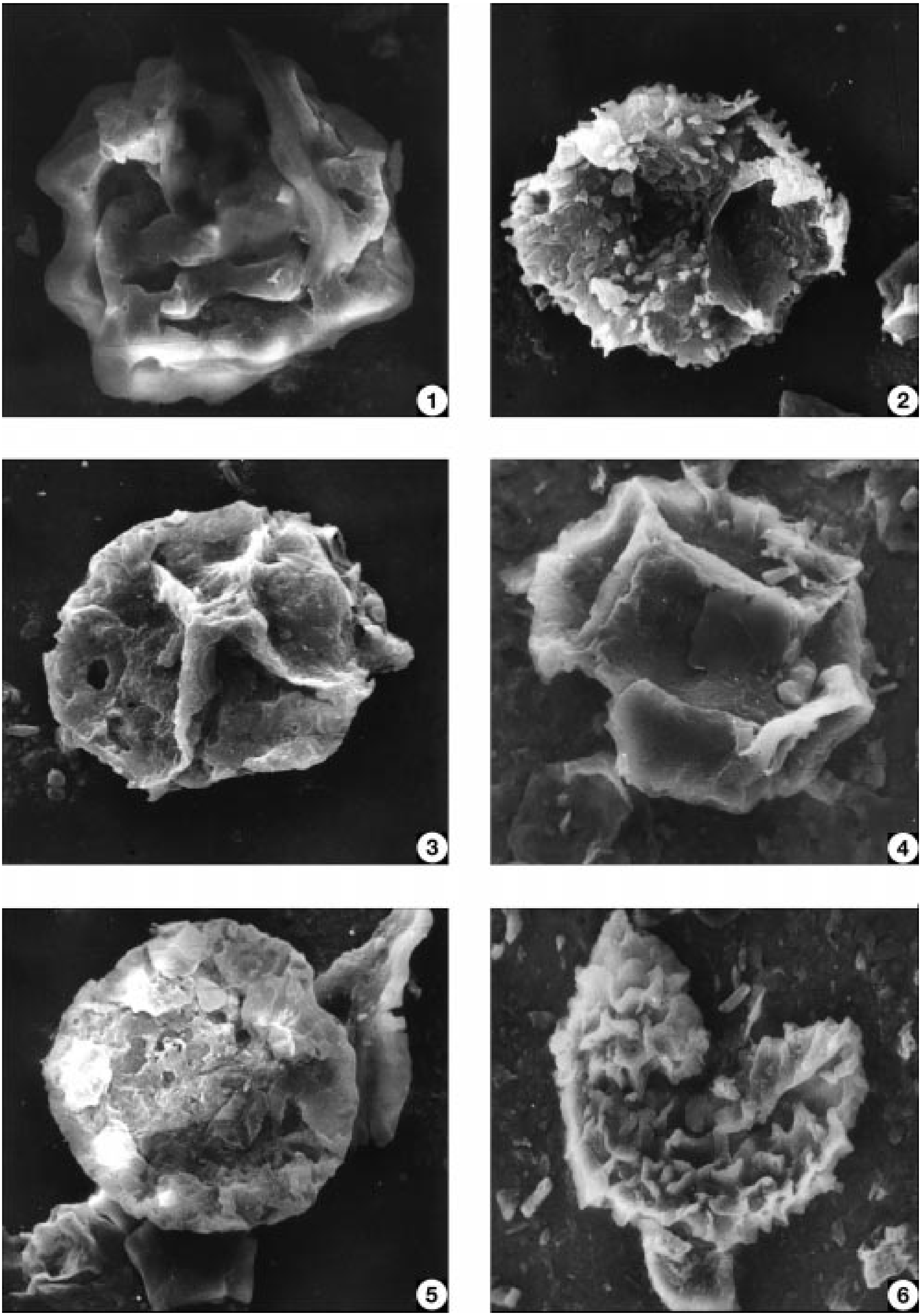
Fig. 3: ***Polyedrixium simplex* Deunff, 1955.**
Sample MM-9B, × 1000.

Fig. 4: ***Polyedrixium* aff. *decorum* Deunff, 1955.**
Sample MM-9B, × 1000.

Fig. 5: ***Maranhites* sp., indet.**
Sample MM-9B, 3342, × 1000.

Fig. 6: ***Rugospora minuta* Neves et Ioannides, 1974.**
Sample MM-9B, × 900.

All specimens in plates are stored in the Collections of the Geological Institute, Academy of Sciences in Prague (No. IS 1-25).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