



## Late Famennian Phytogeographic Provincialism: Evidence for a Limited Separation of Gondwana and Laurentia

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1 Text-Figure and 3 Plates



Allemagne  
Massif schisteux rhéan  
Devonien  
Corals  
Tabulata  
Paléogéographie

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### Phytogeographischer Provinzialismus im späten Famennium: Nachweis einer beschränkten Separation von Gondwana und Laurentia

#### Zusammenfassung

Acritarchen und Prasinophytenzysten sind Palynomorphe, die als marines Mikroplankton angesehen werden; sie weisen einen deutlichen Provinzialismus auf. Das Erkennen von Provinzen nach ausgewählten, Temperatur-empfindlichen Morphotypen mag dazu beitragen Paläokontinentallagen und Paläobreiten zu definieren. Die Verteilung des spätdevonischen Acritarchen *Umbellasphaeridium saharicum* wurde verwendet, um eine Mikroplanktongemeinschaft hoher Breitenlage zur Frasn/Famenne-Zeit auszuscheiden. *Umbellasphaeridium saharicum* dominiert im peruvianischen und bolivischen Palynospektrum des Spätdevons und tritt in vielen Lokalitäten West-Gondwanas auf, sowie auch in vermutlich südlichsten Teilen von Laurussia. Weitere palynologische Daten sind notwendig, um das restriktive Vorkommen dieses morphologisch klar zu unterscheidenden Morphotypes zu bestätigen wie auch seine Abwesenheit in spätdevonischen warmen bis tropischen Klimagürteln.

#### Abstract

Acritarchs and prasinophyte cysts are palynomorphs considered to be marine microplankton, and they reveal a distinct provincialism. Recognition of provinces, based on selected temperature-sensitive morphotypes, may help define paleocontinent positions and paleolatitudes. Distribution of the Late Devonian acritarch, *Umbellasphaeridium saharicum*, has been used to distinguish a high-latitude microplankton community in Frasnian and Famennian time. *Umbellasphaeridium saharicum* is dominant in Peruvian and Bolivian Late Devonian palynospectra and present in numerous western Gondwana localities, as well as in the presumed southernmost parts of Laurussia. Further palynological data are needed to confirm the restricted occurrence of this morphologically distinctive morphotype, and its absence in the Late Devonian warm to tropical climatic belts.

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## 1. Introduction

The distribution patterns of fossil marine microplankton cysts (acritarchs), cysts of fossil dinoflagellates (dinocysts) and of fossil phycmata of green prasinophycean algae represent an important tool for paleogeographic and paleoclimatic reconstructions. Many paleogeographic reconstructions are based on paleomagnetic data, and the potential of the non-megafaunal fossil record is still underestimated. In combination with other sedimentary data, such as development and occurrences of organic buildups, karst, glacial deposits, and temperature-sensitive calcareous algae (ROUX, 1991), fossil marine microplankton can be utilized for determination of global paleoclimatological variations and differentiation. This appears to be applicable to the Late Devonian.

Although the biological affinities of acid-resistant organic-walled microfossils attributed to the group Acritarcha are not yet well-established (SERVAIS et al., 1997), it appears that the majority of acritarchs represent abandoned cysts of unicellular marine green algae (COLBATH & GRENFELL, 1995; VAVRDOVA, 1996). The chemical composition of the polymeric and resistant wall, overall morphology, and a consistent presence of regular vesicle opening (aperture) are the most compelling arguments for their identification with resting stages of phytoplanktonic algae. Factors controlling the distribution of marine fossil microplankton are probably identical with those influencing the distribution pattern of phytoplankton in modern oceans.

Spatial distribution of recent oceanic microplankton depends on the mean annual temperatures of oceanic water masses, influenced by major currents and position of continental blocks. Major modern microplankton communities clearly show latitudinal control. Eight main planktonic bioprovinces in the Pacific Ocean (BROMWELL, 1977) form narrow, well-defined belts which parallel latitudes. The subarctic and subantarctic planktonic communities are confined to 50° and 60° latitude in each hemisphere.

The relation between acritarch biofacies and paleolatitudinal position was originally proposed by CRAMER (1971) and CRAMER & DIEZ (1972) in Silurian rocks. CRAMER's latitudinal model has been challenged (TAPPAN, 1980, FORTEY & MELLISH, 1992) and modified and complemented by many subsequent investigations (COLBATH, 1990; LE HERISSE & GOUVERNNEC, 1995).

Provincialism in acritarch distributions has been demonstrated in the Ordovician (LI JUN, 1987; TONGIORGI et al., 1995) and suggested in the Early Cambrian (FATKA & VAVRDOVA, 1998). Early Ordovician acritarch bioprovinces appear to reflect cold peri-Gondwanan and temperate Baltic and warm Australo-Laurentian provinces (TONGIORGI et al., 1995).

## 2. Late Devonian Acritarch Provincialism

Abundant and well-preserved palynomorphs recovered from the fine-grained clastic sequences in the Madre de Dios basin, northern Bolivia (Manuripi X-1 and Pando X-1 wells) yielded a large number of acritarch and prasinophyte taxa, with diverse miospores. Over 80 species of marine microfossils were identified (VAVRDOVA et al., 1996). The assemblages document intracratonic connections between Bolivian basins (Tarija-Titicaca basin) to sub-Saharan Devonian sequences from the Murzuq Basin, Libya and the Illizi basin, Algeria. Migration routes along the

northern rim of Gondwana, reaching to Appalachian regions have been suggested (WOOD, 1995; VAVRDOVA & ISAACSON, 1997).

Although the majority of acritarchs of this age seem to show a worldwide distribution, endemic forms confined to local planktonic communities occur as well. VANGUESTAINE (in STREEL et al., 1988) compared the distribution of acritarchs from the Late Devonian subsurface material from Libya with 27 palynological associations from Laurentia, Europe, and Australia. VANGUESTAINE noted uneven distribution of phytoplankton forms and characterized the species as cosmopolitan, restricted, or endemic. He also recognized the Gondwanian bioprovince, marked by the presence of genus *Horologinella*, not found in the Euramerican province.

Acritarchs of Late Devonian age are still poorly documented. Despite the admittedly sparse data, four major groups of fossil microplankton taxa may be distinguished.

### 2.1. Ubiquitous Taxa

A majority of taxa within the Frasnian and Famennian association show a worldwide, cosmopolitan distribution. Among these, *Stellinium micropolygonale* (STOCKMANS et WILLIERE) PLAYFORD 1977, *S. comptum* WICANDER et LOEBLICH, 1977, *Gorgonisphaeridium absitum* WICANDER, 1974, *G. ohioense* (WINSLOW) WICANDER, 1974, *Navifusa bacillum* (DEUNFF) PLAYFORD, 1977, *Veryhachium downiei* STOCKMANS et WILLIERE 1962, and *Veryhachium polyaster* STAPLIN, 1961 are the most frequently recorded ubiquitous taxa. They are known from the sedimentary basins of South and North America, Saharan North Africa, Europe, China and Australia (LU LI CHANG & WICANDER, 1988; PLAYFORD, 1976, 1993).

### 2.2. Taxa Common to Western Gondwana and Eastern North America

Important links between the Late Devonian–Early Carboniferous sedimentary basins of the Appalachian region (Chagrin Shale and Cleveland Shale, Ohio, in WICANDER, 1974; Antrim Shale, Indiana, WICANDER & LOEBLICH, 1977) and western Gondwana are documented by the common presence of a large number of characteristic species such as *Acriora petala* WICANDER, 1974, *Barathrisphaeridium chagrinense* WICANDER, 1974, *Diaphrochroa ganglia* WICANDER, 1974, *Gorgonisphaeridium evexispinosum* WICANDER, 1974, *Exochoderma irregulare* WICANDER, 1974, *Orygmahapsis fistulosa* (COLBATH) COLBATH, 1977, *O. craticulum* COLBATH 1977, *Pterospermella latibalteata* WICANDER, 1974, *Puteosortum polyankistrum* WICANDER et LOEBLICH, 1977, *Veryhachium pannuceum* WICANDER et LOEBLICH, 1977, and *Veryhachium roscidum* WICANDER, 1974.

### 2.3. Gondwana-Wide Associations

Species confined to a peri-Gondwanan biogeographic province in the sense of VANGUESTAINE (in STREEL et al., 1988) include forms common to Bolivia, Peru, Brazil, Ghana, Algeria and Libya. *Crassiangulina tessellata* JARDINE et al., 1972, *Horologinella horologia* (STAPLIN) JARDINE et al., 1972, *H. quadrispina* JARDINE et al., 1972 and *Schizocystia bicornuta* JARDINE et al., 1972, among others, are characteristic.

### 2.4. Species Group Endemic to Western Gondwana

Although a need for biostratigraphic correlation of Upper Devonian rocks in South America has produced signifi-

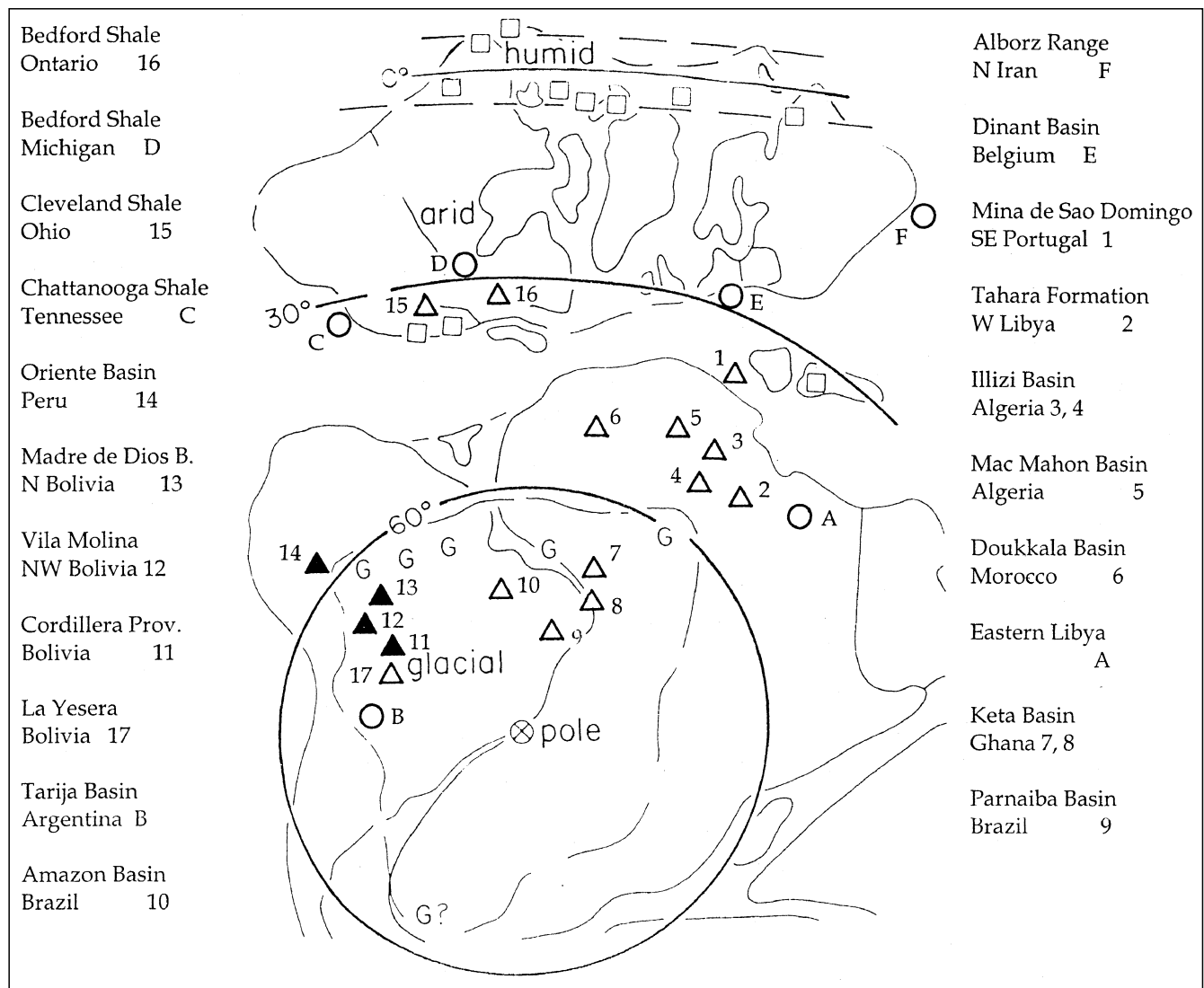
ficant new research on palynomorphs, species so far restricted to the western Gondwana region are still for the most part unknown. The palynological associations recovered in the Late Devonian Bolivian sequences and sub-surface samples reveal the presence of not yet described taxa of acritarchs. Other endemic forms are described by WOOD (1995) OTTONE (1996) and others.

### 3. *Umbellasphaeridium Saharicum* Bioprovince

In addition to taxa considered by VANGUESTAINE (in STREEL, 1988), the Famennian palynological associations from the intracratonic basins of southern America contain

a distinctive species of sphaeromorphic acritarch with characteristically expanded radial appendages. Defined by JARDINE et al. (1972) in Saharan Algeria, the genus *Umbellasphaeridium* now comprises three species and several undescribed forms. Umbrella-like expansions of the tubular processes and a firm, robust vesicle wall enables the preservation of *Umbellasphaeridium saharicum* even in assemblages strongly affected by various degradational processes.

WOOD (1984) described a recurrent species association of *Umbellasphaeridium saharicum*, *U. deflandrei*, *Stellinium octoaster*, *Navifusa bacillum* and *Maranhites brasiliensis* complex with stratigraphically important fossil miospore species *Retispora lepidophyta* (KEDO) PLAYFORD (1976). WOOD noted that *Umbella-*



Text-Fig. 1. The high-latitude *Umbellasphaeridium saharicum* acritarch bioprovince (from HECKEL & WITZKE, 1988, Fig. 4C), showing selected localities with Frasnian/Famennian age acritarch assemblages.

G = possible areal extent of glaciation. Circles (A-F) are localities with the genus *Umbellasphaeridium* present. Closed triangles indicate localities with *U. saharicum* as a frequent to dominant element of the taxa; open triangles indicate localities in which *U. saharicum* is present.

1 = Phyllite-quartzite Formation, Mina de Sao Domingos, SE Portugal (CUNHA & OLIVEIRA, 1989); 2 = Tahara Formation, Ghadamesh Basin, western Libya (MOREAU-BENOIT, 1984); 3 = Gazelle Formation, Illizi Basin, Algeria (JARDINE et al., 1972); 4 = Djebel Illerena Formation, Illizi Basin, Algeria (ATTAR et al., 1980); 5 = McMahan Basin, Algeria (LANZONI & MAGLOIRE, 1969); 6 = Doukkala Basin, central-west Morocco (RAHMANI-ANTARI, 1990); 7 = Takoradi Sandstone, Keta Basin, Ghana (BAR & RIEGEL, 1974); 8 = Well 10-1, Keta basin, Ghana (AANAN-YORKE, 1974); 9 = Longá Formation, Parnaiba Basin, Brazil (DAEMON, 1974); 10 = Curuá Formation, Amazon Basin, Brazil (DAEMON, 1974); 11 = Itacua Formation, Cordillera Province, (LOBO-BONETA, 1989); 12 = Colpacucho Formation, Vila Molina (Mina Matilde), Lake Titikaka, NW Bolivia (Vavrdova et al., 1991); 13 = Tomachi and Toregua Formations, Madre de Dios Basin, N Bolivia (Vavrdova et al., 1996); 14 = Oriente basin, Peru (WOOD, 1984); 15 = Cleveland Shale, Ohio (WOOD, 1984, MOLYNEUX et al., 1984); 16 = Bedford Shale, Ontario (WOOD, 1984).

A = Eastern Libya (STREEL et al., 1988); B = Los Monos Formation, Tarija Basin, Argentina (OTTONE, 1996); C = Chattanooga Shale, Tennessee (REAUGH, 1978); D = Bedford Shale, Michigan (WOOD, 1984); E = Geirud Formation, Central Alborz Range, N Iran (GHAVIDEL-SYOOKI, 1994); F = Dinant Basin, Belgian Ardennes, (MARTIN, 1985).

*sphaeridium saharicum* displays a distinct southern hemisphere endemism.

Occurrences of *Umbellasphaeridium saharicum* are plotted in Text-Fig. 1 to illustrate the common environmental conditions in the peri-Gondwanan belt rimming the margin of the paleocontinent; this distribution largely corresponds to the *Coryphidium bohemicum* bioprovince in the Early Ordovician. The presence in the glacially influenced sequences at the eastern shore of Lake Titicaca suggest the assignment to the cold, high-latitude oceanic regions. The bioprovince, originally proposed by WOOD (1984), is complemented by a new record in Portugal (CUNHA & OLIVEIRA, 1989) and occurrences of *Umbellasphaeridium* sp. (MARTIN, 1985; GHAVIDEL-SYOOKI, 1994) are considered herein as characteristic for the marginal areas outside of the *Umbellasphaeridium saharicum* bioprovince.

Text-Fig. 1 presents a map of the high-latitude *Umbellasphaeridium saharicum* acritarch bioprovince, which includes sixteen localities with assemblages of acritarchs of Frasnian/Famennian age. Associations of Early to Middle Devonian age and forms of *U. saharicum* presumably recycled into Early Carboniferous sequences are not included. The bioprovince ranges from SE Portugal across the Saharan Africa (western Libya, Algeria, Morocco) to Gulf of Guinea, Brazil, Bolivia, Peru and eastern North America. Marginal regions not included within the bioprovince are characterized by the occurrence of *U. deflandrei* (MOREAU-BENOIT) JARDINE et al. (sensu lato) without *U. saharicum*. These regions include eastern Libya, Argentina, Michigan, Tennessee, Belgium and Iran. At present, data are insufficient to decide if the absence of *U. saharicum* is caused by paleoclimatological or other factors. *U. saharicum* and other representatives of the genus were not reported from the low-latitude, warm to tropical "belt" ranging from western Canada (Alberta, Great Slave Lake region, Saskatchewan) to Poland, Siberia, and Australia (NAUTIYAL, 1977; PLAYFORD, 1993).

Selection of taxa representing the warm climatic belt is very difficult. Some taxa are mentioned by NAUTIYAL (1977) that occur in Western Gondwana as well. This could be a result of the region's movement to lower latitudes by later Devonian time (ISAACSON & DÍAZ-MRTÍNEZ, 1995). One very distinctive acritarch, *Craterisphaeridium sprucegrovense* (STAPLIN) TURNER, 1986 occurs in western Canada (NAUTIYAL, 1977), in the Dinant Basin, Belgium, and NW China

(Xinjiang, LI CHANG & WICANDER, 1988), and in NE Libya, North Africa (VANGUESTAINE in STREEL et al., 1988).

#### 4. Comparison with the Miospore Record

Siliciclastic sediments from the Tarija-Titicaca basin and from Brazil have provided rich, diversified and well preserved terrestrial palynomorphs, which show a uniform vegetation closely similar to coeval assemblages of predominantly homosporous plants from North Africa and Euramerica (STREEL et al., 1990; LOBOZIAK et al., 1992; OTTONE, 1996). Comparison of characteristic miospore taxa from numerous drill holes has not supported existence of a wide ocean separating the paleocontinent Gondwana from Laurentia and the Armorican terranes (STREEL et al., 1990). Important vegetational bioevents, shown by the first occurrences of age-significant index species, arose in the same order of succession in all these areas. This allows an application of Devonian palynozones defined in southern Euramerica to Upper Devonian rocks of Western Gondwana.

#### 5. Conclusions

The latest Devonian distribution of *Umbellasphaeridium saharicum* is remarkably similar to the megafossil-based Malvinokaffric Realm of the Early Devonian (ISAACSON & SABLACK, 1990), in that an endemic province that apparently paralleled high latitudes contained a restricted (highly endemic) fauna. A notable exception for the Late Devonian province is that it extends into eastern North America and North Africa, two regions assumed to be much more temperate. Yet, it appears that high latitude-generated, cooler water currents controlled acritarch distribution. In the absence of well-developed megafaunal communities at this time (as well as paleomagnetic information), it appears that insight into paleo-oceanographic surface current circulation, relative to continental positions, will be dependent upon organic microfossil distribution data.

#### Acknowledgments

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## Plate 1

Acritarchs and prasinophytes from the Vila Molina section.  
Latest Famennian, Lake Titicaca, NW Bolivia.

Fig. 1: *Umbellasphaeridium saharicum* JARDINE et al., 1974.  
× 1000.

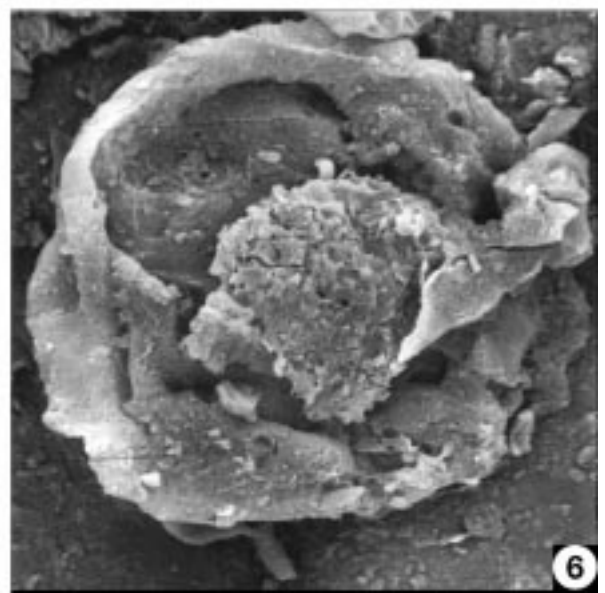
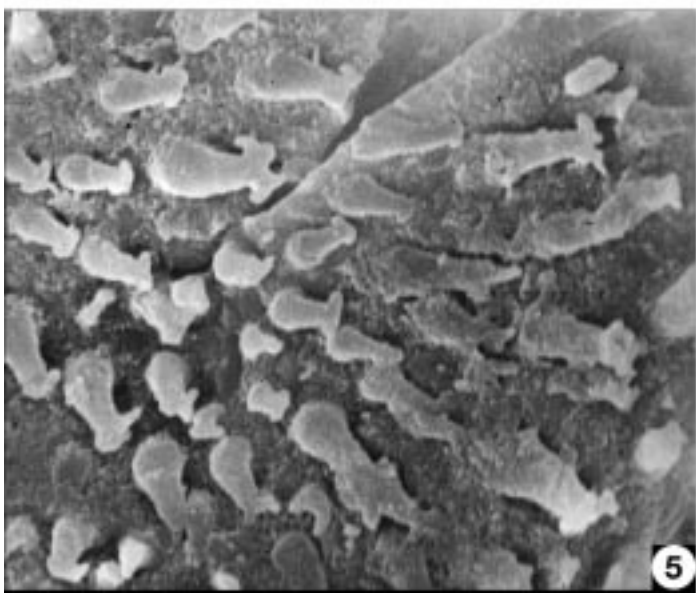
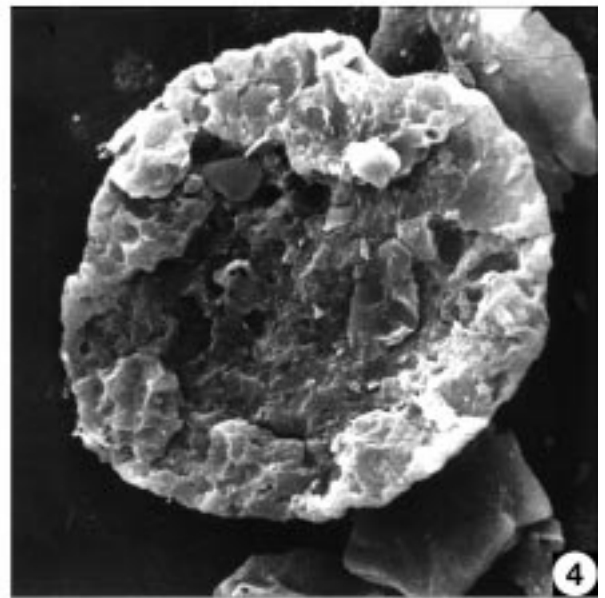
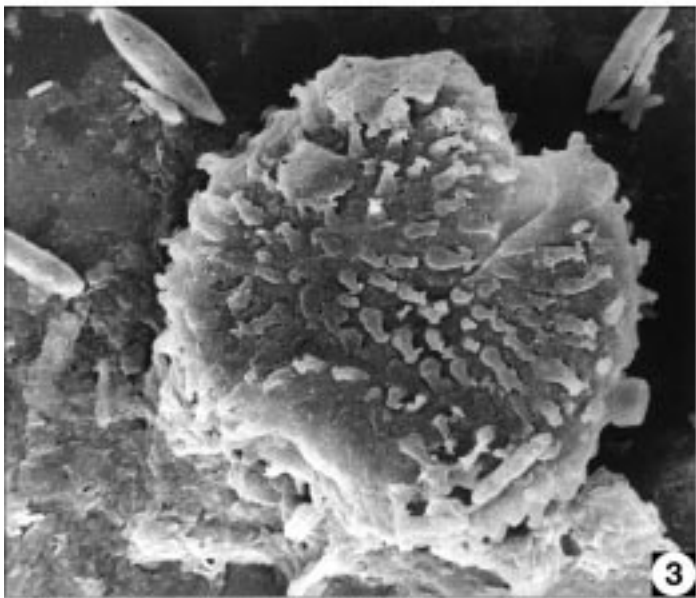
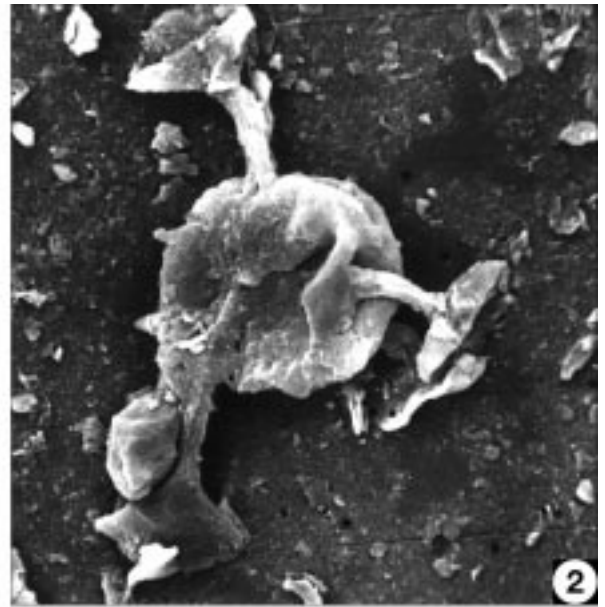
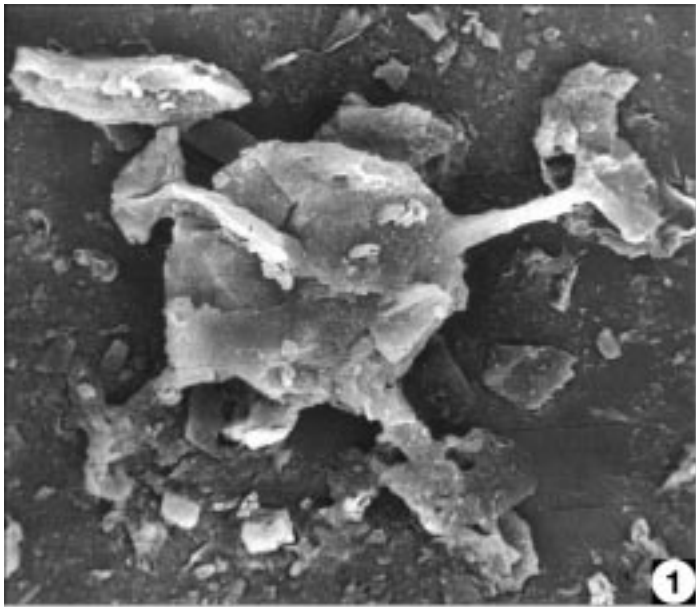
Fig. 2: *Umbellasphaeridium saharicum* JARDINE et al., 1974.  
× 1200.

Fig. 3: *Gorgonisphaeridium evexispinosum* WICANDER, 1974.  
× 2500.

Fig. 4: *Maranhites* sp.  
× 1000.

Fig. 5: *Gorgonisphaeridium evexispinosum* WICANDER, 1974.  
× 7000.

Fig. 6: *Pterospermella latibalteata* WICANDER, 1974.  
× 1000.



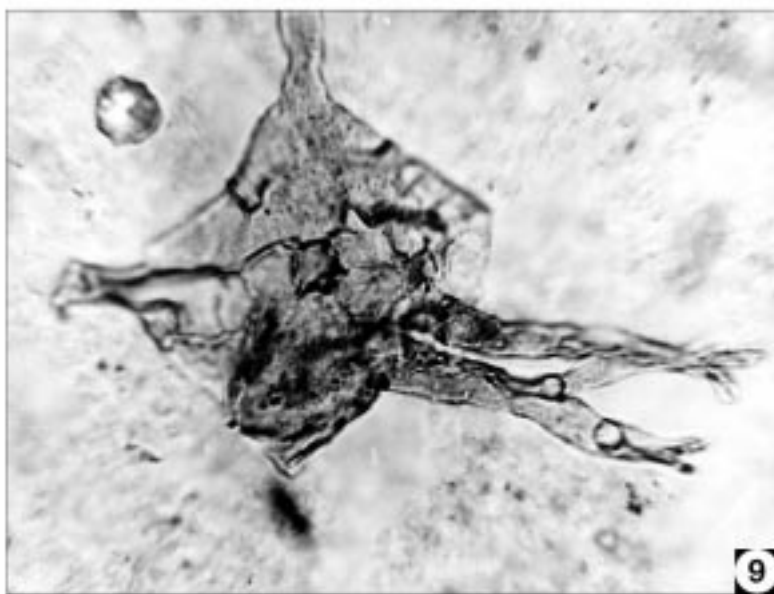
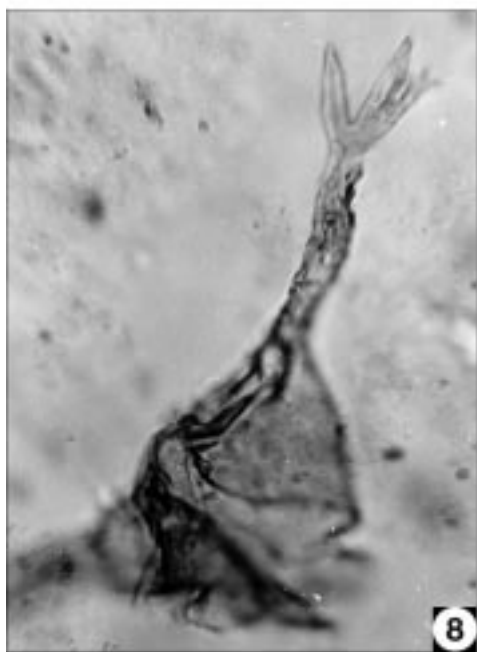
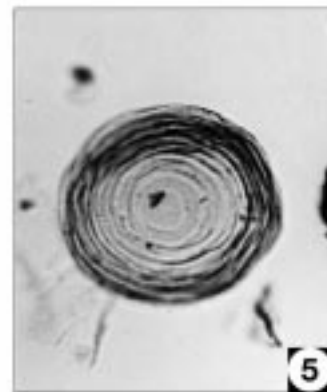
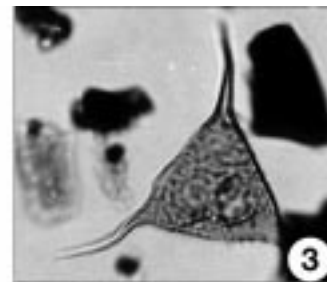
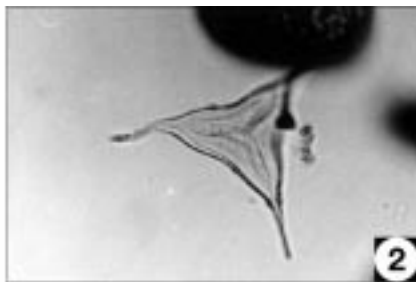
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## Plate 2

- Fig. 1: *Navifusa bacillum* (DEUNFF) PLAYFORD, 1977.  
Murzuq Basin, Libya (Ashkidah Formation, sheet Sabha).
- Fig. 2: *Veryhachium pannuceum* WICANDER & LOEBLICH, 1977.  
Murzuq Basin, Libya (Ashkidah Formation, sheet Sabha).
- Fig. 3: *Veryhachium roscidum* WICANDER, 1974.  
Murzuq Basin, Libya (Ashkidah Formation, sheet Sabha).
- Fig. 4: *Umbellasphaeridium deflandrei* (MOREAU-BENOIT) ex JARDINE et al., 1972.  
Murzuq Basin, Libya (Ashkidah Formation, sheet Sabha).
- Fig. 5: *Chomotriletes vedugensis* NAUMOVA, 1953.  
Murzuq Basin, Libya (Ashkidah Formation, sheet Sabha).
- Fig. 6: *Gorgonisphaeridium ohioense* (WINSLOW) WICANDER, 1974.
- Fig. 7: *Umbellasphaeridium deflandrei* (MOREAU-BENOIT) ex JARDINE et al., 1972.  
Murzuq Basin, Libya (Ashkidah Formation, sheet Sabha).
- Fig. 8: *Exochoderma irregulare* WICANDER, 1974.  
Vila Molina section, NW Bolivia.
- Fig. 9: Gen. et sp. indet.  
Vila Molina section, NW Bolivia.

All × 1000.

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## Plate 3

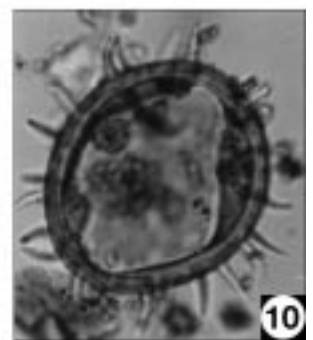
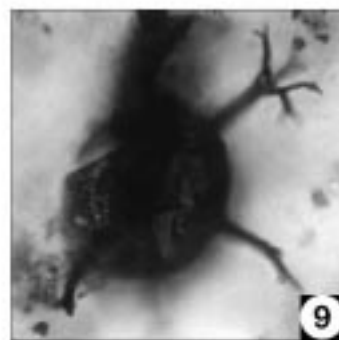
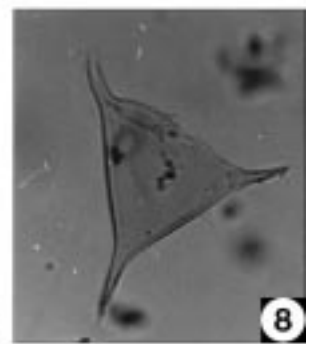
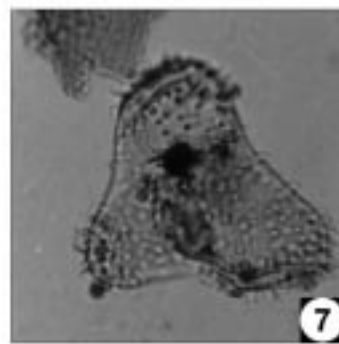
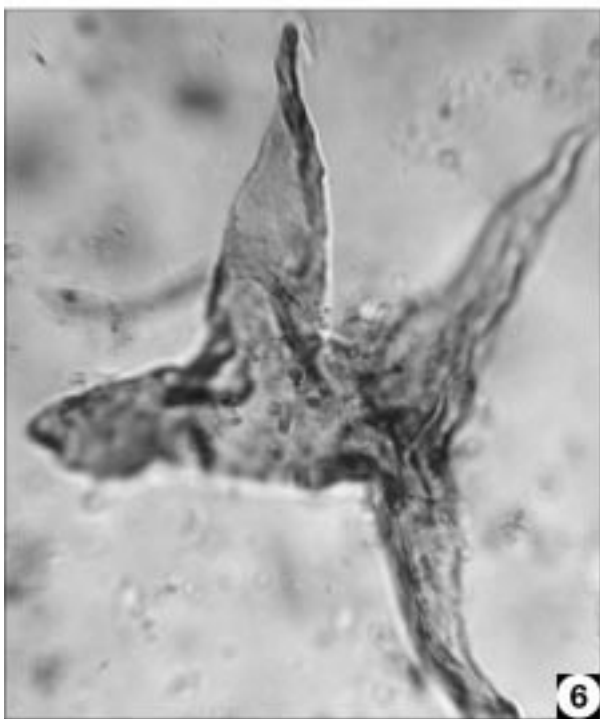
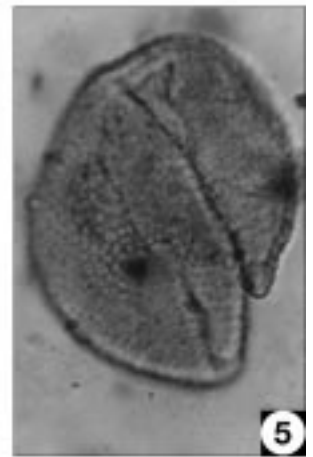
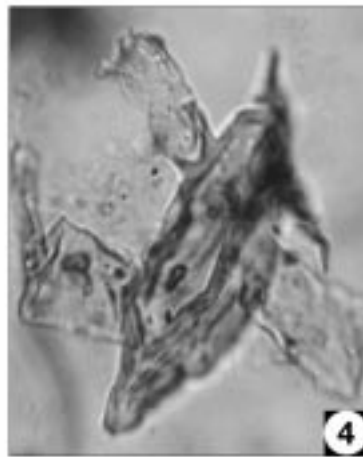
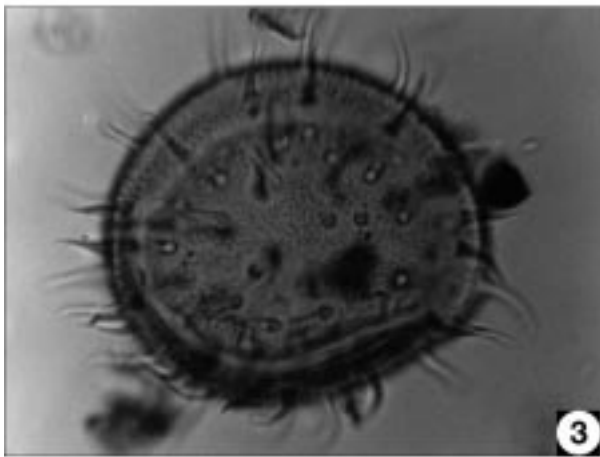
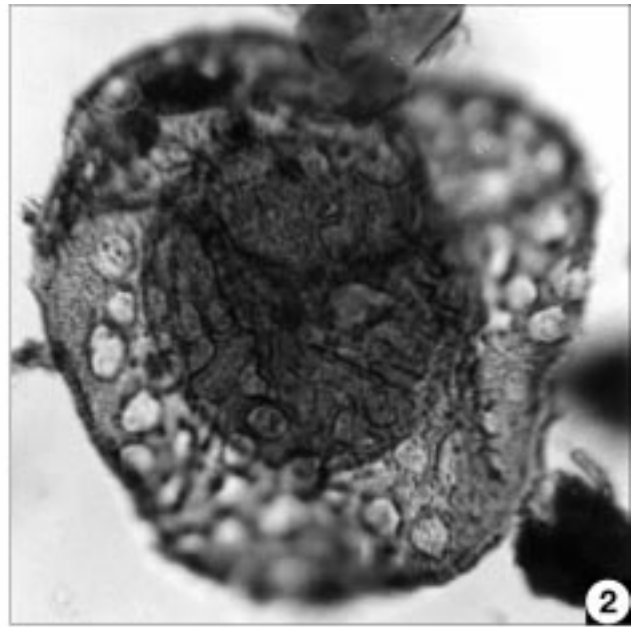
Palynomorphs from selected Late Devonian localities in Bolivia.

- Fig. 1: *Umbellasphaeridium saharicum* JARDINE et al., 1974.  
Calamarca, early Famennian.
- Fig. 2: *Retispora lepidophyta* (KEDO) PLAYFORD, 1976.  
latest Devonian of the Murzuq Basin, Libya.
- Fig. 3: *Barathrisphaeridium chagrinense* WICANDER, 1974.  
latest Devonian of the Murzuq Basin, Libya.
- Fig. 4: Gen. et sp. indet.  
Pando X-1 well, Madre de Dios Basin.
- Fig. 5: *Orygmahapsis fistulosa* (COLBATH), COLBATH, 1987.  
La Yesera.
- Fig. 6: *Horologinella quadrispina* JARDINE et al., 1972.  
Pando X-1 well, Madre de Dios Basin.
- Fig. 7: *Deltotosoma intonsum* PLAYFORD in PLAYFORD & DRING, 1981.  
latest Devonian of the Murzuq Basin, Libya.
- Fig. 8: *Veryhachium downiei* STOCKMANS et WILLIERE, 1962.  
latest Devonian of the Murzuq Basin, Libya.
- Fig. 9: *Diaphrochroa ganglia* WICANDER, 1974.  
Hinchaka, late Famennian.
- Fig. 10: *Gorgonisphaeridium ohioense* (WINSLOW) WICANDER, 1974.  
latest Devonian of the Murzuq Basin, Libya.

All × 1000.

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