Palynology of the Late Carboniferous from the Tarija Basin, Argentina: A systematic review of monosaccate pollen genera

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With 3 plates, 7 text-figures and 1 table

Abstract

This paper presents the results of a systematic analysis of pollen genera from the Late Carboniferous Escarpment and San Telmo Formations, Tarija Basin, Argentina. This study is preceded by a comparative discussion of the palynological evidence related to the evolution of the earlier gymnosperms from both the equatorial belt and Gondwana. Different taxonomic criteria used in the classification of monosaccate pollen grains are also analyzed. Twenty-one species are described and illustrated. A re-examination mainly of several species of genera *Cannanoropollis*, *Potonieisporites*, and *Caheniasaccites* based on the critical analysis of their original diagnosis, provided identifying characters that were also tabulated for each species. Thus, *Caheniasaccites flavatus* BOSE & KAR has been emended and its synonymy proposed. Abundant reworked Devonian and probably Lower Carboniferous material of spores and microplankton are present in the studied assemblage. The systematic study of pollen grains, that represent with certainty the indigenous material, suggests a Late Carboniferous age. Their stratigraphic distribution in South America is summarised in a diagrammatic format.

Key words: Pollen grains, Taxonomy, Escarpment and San Telmo Formations, Late Carboniferous, Argentina.

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Introduction

Since the early part of the twentieth century, many geologists, such as BODENBENDER (1906), BONARELLI (1914, 1921), SCHLAGINTWEIT (1937), have recognized clastic sequences in the northeastern part of Salta Province, which were reported as "Perm-Triassic". ARIGÓS & VILELA (1949) and PADULA & REYES (1958) have mainly contributed to the arrangement of the stratigraphic units from Sierras Subandinas, allowing the correlation with the Bolivian "Permian" units. Later, REYES (1972) and MINGRAMM et al. (1979) summarized the literature on the Bolivian and Argentinean sequences and proposed a Lower and Upper Carboniferous age for the Macharetí and Mandiyutí Groups, respectively, which was based on unpublished palynological information obtained from Yacimientos Petrolíferos Fiscales of Argentina (YPF) and Bolivia (YPFB).

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More recently, the advent and refinement of plate tectonic and sequence stratigraphic concepts, and related aspects of global eustasy, have renewed the interest among geologists. Several papers with new stratigraphic, tectonic and paleogeographic interpretations of the Tarija Basin have also been published: ARAMAYO FLORES (1989), SUÁREZ SORUCO (1989), SEMPERE (1990, 1995), STARCK et al. (1993 a, b), LÓPEZ GAMUNDÍ & ESPEJO (1993), STARCK (1995), ISAACSON & MARTÍNEZ (1995), TANKARD et al. (1995).

Some stratigraphic researches about Devonian and Late Palaeozoic deposits from this basin include lists of palynomorphs that are used to infer the age of the strata involved and/or to propose informal palynological assemblages. Only a few papers are published (MENÉNDEZ 1968, LOBO BONETA 1975, LOBO BONETA et al. 1977, AZCUY & LAFFITTE 1981, KIMYAI 1983, VOLKHEIMER et al. 1983, SUÁREZ SORUCO & LOPEZ PUGLIESSI 1983, SUÁREZ SORUCO & LOBO BONETA 1983, AZCUY et al. 1984, AZCUY 1985, AZCUY & OTTONE 1987, LOBO BONETA 1989, VAVRDOVÁ et al. 1991, 1993, OTTONE et al. 1996). The majority are unpublished reports of YPF and YPFB.

Palynological researchs that include systematic analysis of palynomorphs, are scarce for the Devonian and Lower Carboniferous sequences (MENÉNDEZ & PÖTHE DE BALDIS 1967, PÖTHE DE BALDIS 1974, 1979, VOLKHEIMER et al. 1986, MACGREGOR 1984, BARREDA 1986b, PÉREZ LEYTON 1991, WOOD 1994, 1995, OTTONE 1996, OTTONE & ROSSELLO 1996). Furthermore, only two papers are known to deal with the palynology of Lower Permian deposits (Copacabana Formation; COUSMINER 1965, OTTONE et al. 1998).

This present paper, for the first time, deals with the systematic analysis of Late Carboniferous pollen grains from Tarija Basin, Argentina. The pollen grains are the most important autochthonous group recovered from Escarpment and San Telmo Formations. Mainly three groups of palynomorphs were recognized: pollen grains, spores and acritarchs. The systematic description of monosaccate pollen grains included a critical analysis and discussion of the main criteria used in their classification. The other groups include abundant recycled material mainly of Devonian and probably Early Carboniferous origin.

The assemblage studied consists of moderately preserved pollen grains obtained from the boundary between Escarpment and San Telmo Formations (Mandiyutí Group), Sierras Subandinas (Salta Province, Argentina), from which it is established a Late Carboniferous age for this section. A correlation with Late Palaeozoic palynofloras elsewhere in South America (Brazil, Uruguay, and Argentina) is figured.

Geological setting

During the Late Palaeozoic, the Tarija Basin extended from northwestern Argentina beyond the latitude of the Titikaka Lake, located at the boundary between Bolivia and Peru. This oil-prone basin has been affected by Tertiary deformation, and its filling was involved in the well-known Subandean fold and thrust belt (BELLOTI et al. 1995).

In northwestern Argentina, outcrops of these Late Palaeozoic rocks are mostly restricted to the Sierras Subandinas (MINGRAMM et al. 1979) and the eastern part of Cordillera Oriental (STARCK et al. 1993a). Their presence have also been reported in subsurface further east beneath the present foreland basin filling (Chaco Salteño Plain; MINGRAMM et al. 1979, BELLOTI et al. 1995), see Text-fig. 1.

The Carboniferous deposits overlay Lower Palaeozoic rocks unconformably. This unconformity is attributed to the well-known Chanic phase that occurred during the latest Devonian, and it is also linked with eustatic episodes spanning the Lower-Middle Carboniferous (STARCK et al. 1993 a, b). Lithostratigraphic studies allow the definition of two Groups, named Macharetí (Tupambi and Tarija Formations) and Mandiyutí (Escarpment and San Telmo Formations) separated by an unconformity (REYES 1972, FERNÁNDEZ GARRASINO 1979), see Text-fig. 2.

The Escarpment Formation is an essentially sandy unit, with scarce conglomeratic and pelitic levels. It begins with stacked channel sandstone units occupying deeply incised palaeovalleys. Maximum thickness is about 500 m. The succeeding San Telmo Formation has a more varied lithology, composed of alternating beds of very fine sandstones, mudstones and bright red diamictites. Thickness varies up to 400 m in the Sierras Subandinas (Text-fig. 3). Psammitic rocks at the base of the Cuevo Group (Cangapi Formation) rest unconformably over the San Telmo Formation, which change transitionally to calcareous layers of the
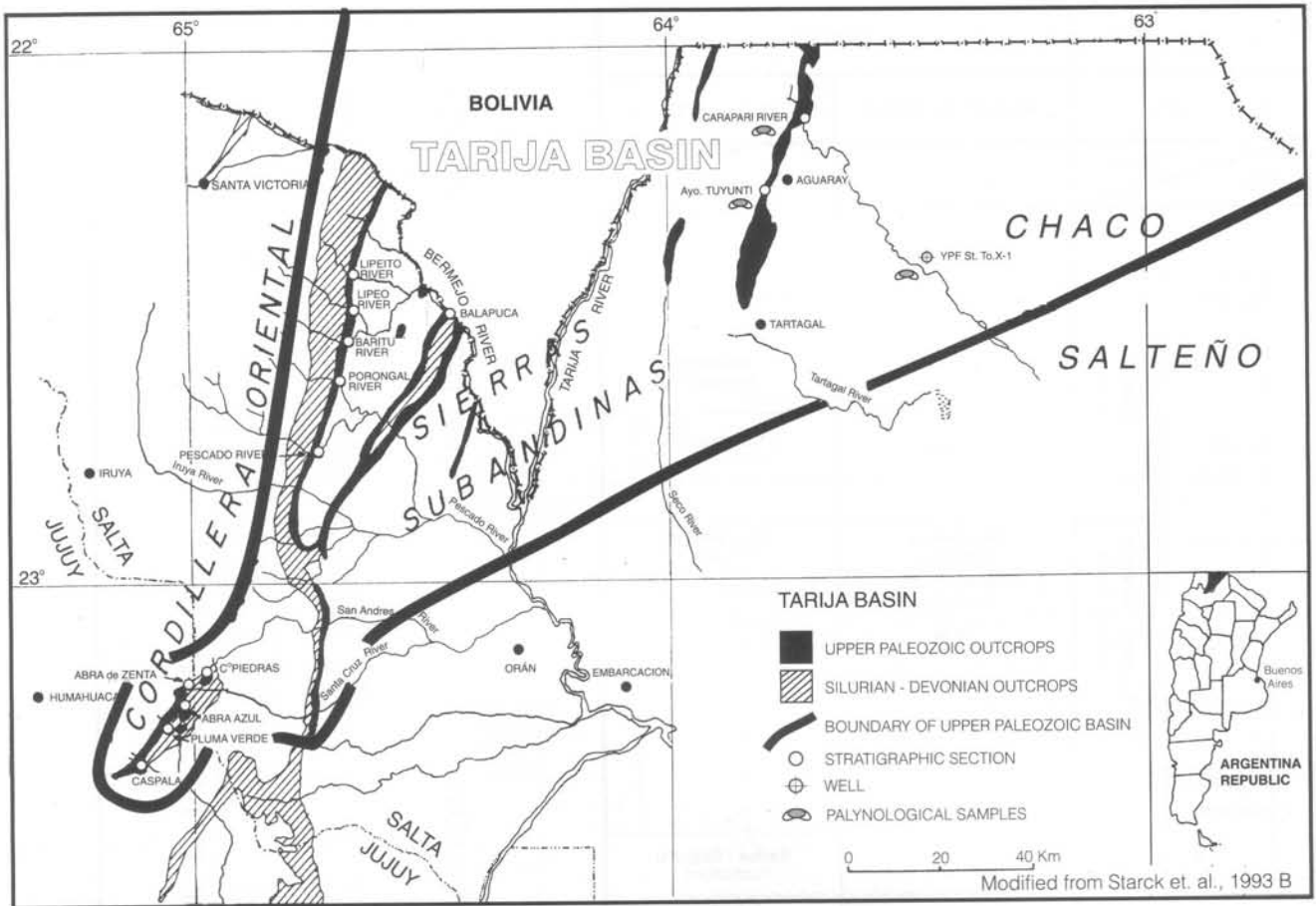
Text-fig. 1. Geologic map showing the Tarija Basin of Argentina and location of the Caraparí Section.

overlying Vitiacua Formation (STARCK et al. 1993a) (see Text-fig. 2). Detailed geological information about Late Palaeozoic sequences is summarized in STARCK (1995) and AZCUY & DI PASQUO (1998). The stratigraphic succession ends with sandstones of Tertiary (Tranquitas and Chaco Formations) age, separated by an erosional unconformity from the Late Palaeozoic sequence (BELLOTI et al. 1995, HERNANDEZ et al. 1996).

Methods

Palynological material studied herein belongs to a Carboniferous succession outcropping along the Caraparí River, Aguaragüe range, between 22° and 22°4' south and 64° and 63°45' west, related to the southern edge of the Tarija Basin (see Text-fig. 1).

Detailed lithostratigraphical analysis of the Caraparí River sections (Escarpment and San Telmo Formations), allowed the collection of a considerable number of palynological samples, but only six were productive (see Text-fig. 3). In order to separate palynomorphs, standard methods (VOLKHEIMER & MELENDI 1976, PLAYFORD 1977) have been used. Many samples were screened through a 25 μm mesh and mounted in unstained glycerine jelly. Five to ten slides were prepared from each of > 25 μm residues. Many samples were oxidized by nitric acid and/or hydrogen peroxide but the colour of the palynomorph exines was observed in the samples not oxidized.

All samples, spore residues, and slides have been housed with the prefix BAFC-Pl (Buenos Aires Facultad Ciencias, Palinología), in the Laboratory of Palynology, Department of Geology, University of Buenos Aires, Argentina. Palynomorph recognition was made using a binocular transmitted light microscope Orthoplan Leitz No. 4303017, with 1000 × maximum magnification. The photomicrographs were taken with a Leitz Orthomat Camera. Specimens are denoted by a prefix (BAFC-Pl) followed by the slide number and the England Finder (EF) reference.

Basin		TARIJA	
Country		ARGENTINA	BOLIVIA
Age \ Region		S. Subandinas	S. Subandinas
UPPER PERMIAN	Cuevo Group	↑? Vitiacua Formation	↑? Vitiacua Formation
LOWER PERMIAN		Cangapi Formation	Cangapi Formation
UPPER CARBONIF.	Mandiyuti Group / Machareti Group	San Telmo Formation / Escarpment Formation / Tarija Formation / Tupambi Formation	San Telmo Formation / Escarpment Formation / Taiguati Formation / Tarija / Chorro Formations / Tupambi Formation
LOWER CARBONIF.			Itacua / Saipurú Formations
DEVONIAN		Los Monos Formation	Iquirí Formation

Text-fig. 2. Stratigraphic distribution of the Late Paleozoic lithostratigraphic units from Tarija Basin.

An approach to the evolution and taxonomy of monosaccate pollen grains

During the study of the Late Carboniferous palynomorphs identified in beds belonging to Escarpment and San Telmo Formations, it was necessary to review the diagnostic features of several genera and species of dispersed pollen grains, particularly those of monosaccate type.

Taxonomy of primitive saccate grains have been historically developed following two different pathways: one that related to the natural classification of plants and the connection to reproductive parts bearing pollen grains, while the other is developed as morphotaxonomy that is based only on the morphological characters of dispersed pollen grains.

The natural taxonomy began with the study of Late Carboniferous cordaitalean reproductive parts bearing pollen grains, described by RENAULT (1879). These reproductive structures were named as *Cordaianthus*, as well as the isolated grains from the same sediments. Later, FLORIN (1936) recorded the presence of grains with similar features, from Permian deposits without *Cordaianthus* fructifications but rich in coniferal debris, for which the binomial name *Pollenites cardaitiformis* was proposed.

However, as cited by POORT et al. (1996), it was necessary for a century to elapse before the zoidogamy concept, described by RENAULT (1896) in fossil gymnosperms, would attract researchers attention once again. This fertilization mechanism, strongly linked to the morphology of the pollen wall, occurred through the release of motile antherozoids, which has also been recognized in all extant cycadophyte genera and *Ginkgo*.
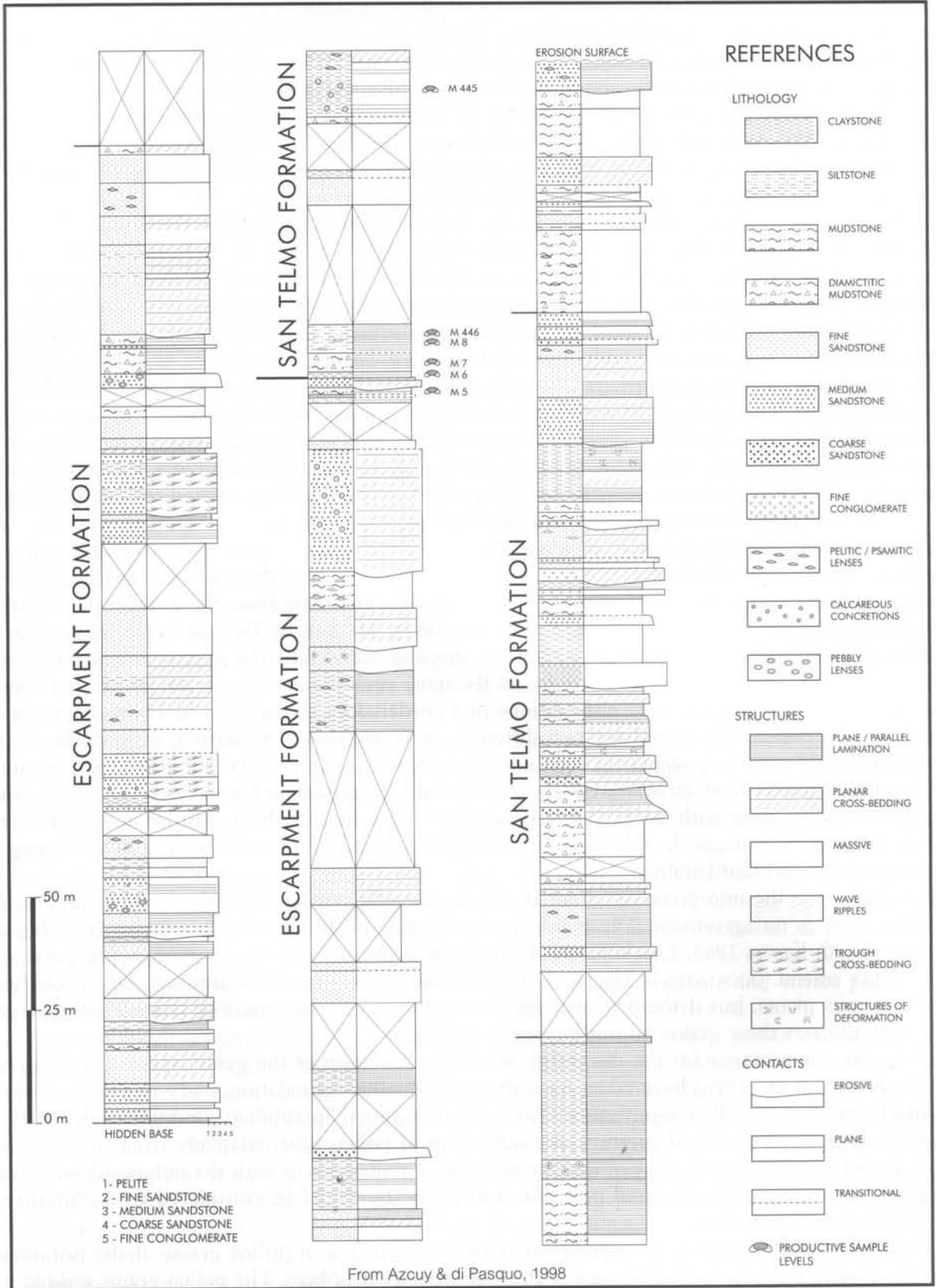
Text-fig. 3. Lithostratigraphic profile of the Mandiyutí Group in the Caraparí river section (Sierras Subandinas).

The characteristics pointing out zoidogamy in extant gymnosperms are: 1) motile antherozoids that are released by wall decay from a proximal position, 2) distal leptoma for the outgrowth of a haustorial pollen tube with an exclusively nutritive function, and 3) ovules with pollen chamber. In the case of the extinct gymnosperms considered as zoidogamous, the features to be taken into account for the recognition of their reproductive strategy are more controversial. Fossil evidences allow three possibilities to be considered: a) existence of only a proximal laesura able to release internally produced motile antherozoids, b) occasional recognition of a thinner distal area (cappula or sulcus) with possibility of outgrowing of a non functional pollen tube and c) presence of both proximal aperture and distal leptoma.

a) The first condition is the most significant and has been recognised in the pollen grains of some Cordaitales, Pteridospermales and more recently Coniferales. MILLAY & TAYLOR (1974) analyzed the morphology and evolution of Late Carboniferous saccate pollen grains, obtained from sporangia of Cordaitales. They recognized haptotypic features and proximal marks that probably have been functional (e. g. *Felixipollenites* MILLAY & TAYLOR 1974, early Pennsylvanian). In the Pteridospermales, "pollen grains" coming from male fertile structures of lyginopterid type (e. g. *Feraxotheca* MILLAY & TAYLOR 1977), show a similar morphology to that of the trilete spores of many ferns (MILLAY et al. 1978, TAYLOR & MILLAY 1979, STIDD et al. 1985). The presence of a pollen chamber in their corresponding ovules suggests zoidogamy. More recently, POORT et al. (1996, 1997) and POORT & VELD (1997), a zoidogamicous fertilization in some fossil Coniferales has also been demonstrated. POORT & VELD (1997), studying the morphology and ultrastructure of *Potonieisporites novicus* BHARDWAJ 1954, which has been related to Late Carboniferous/Early Permian *Walchia*, *Ernestiodendron* and *Otovicia* genera, redefined the prepollen concept.

b) The second character has been observed in a Late Pennsylvanian pteridosperm pollen grain, *Vesicaspora* (SCHEMEL) WILSON & VENKATACHALA 1963, which has developed distal sulcus, bisected by a leptoma, showing an absence of haptotypic features and a pollen tube emerging from the distal surface (ROTHWELL 1972, MILLAY & TAYLOR 1974, TAYLOR & TAYLOR 1993). MILLAY & TAYLOR (1974) have also studied *Florinites* (Middle Pennsylvanian) pollen grains in situ and established the generic emendation, in which diagnosis they took into account its alete trait as the most evolutionary Pennsylvanian cordaitalean pollen grain character. Nevertheless, these observations in a cordaitalean related to a functional leptoma for the outgrowth of a pollen tube may have two different interpretations. The former, improbable, is that the pollen tube would serve as a carrier for immotile gamete cells, so it would be interpreted as a gymnosperm with a siphonogamy reproductive strategy, then comparable to the extant Coniferales. The latter consists in a haustorial pollen tube with an exclusively nutritive function and the release of motile antherozoids through proximal wall decay. In this case the zoidogamous condition is consistent with all-known extinct Pteridospermales and Cordaitales.

c) Concerning the interpretation about of the functionality of both proximal and distal pollen grain apertures, there is no agreement. The majority corresponds to dispersed pollen grains (e. g. *Jugasporites* LESCHIK emend. KLAUS 1963, *Lueckisporites* POTONIÉ & KLAUS emend. KLAUS 1963, *Vestigisporites* BALME & HENNELLY emend. JANSONIUS & HILLS 1976), and if the stress is put in the leptoma they would belong to siphonogamous plants, but if the proximal aperture is functional they must be considered zoidogamous. Then, in both cases these grains do not qualify as prepollen.

Of greatest importance for the discussion about the evolution of the gymnosperms, is the prepollen concept. POORT et al. (1996) have taken back the zoidogamous fecundation study in fossil gymnosperms and redefined the prepollen significance. After these authors "prepollen condition: release of motile antherozoids through proximal aperture; no outgrowth of pollen tube; relatively large size (Late Palaeozoic)". Therefore, a change in the germination polarity of pollen grains with the outgrowth of a haustorial pollen tube emerging from the distal pole (ROTHWELL 1972), would be considered an evolutionary stage more evolved than prepollen.

The evidences cited above are representative of the evolution of pollen grains of the primitive gymnosperms during the Late Carboniferous in the Northern Hemisphere. The pollen grains yielded by male organs with cordaitalean, pteridosperm and conifer affinities would have evolved mainly following three steps, recently mentioned by POORT et al. (1996):

1) The only presence of a functional aperture in the proximal surface, such as occurs in the pteridophytes, is considered as a primitive character and these grains qualify as prepollen.

2) Pollen grains with a thinning of an area on the distal surface that permits the outgrowth of a haustorial pollen tube with only nutritive function added to the ability of release motile antherozoids through the proximal surface. Both characters suggest an intermediate pollen grain type with a change in the germination polarity although a clearly functional distal aperture (fertilization strategy) is still lacking. The a) and b) cases correspond to a zoidogamicous fecundation.

3) The third stage, still without Late Palaeozoic fossil evidences, consists in the development of a well-defined distal aperture with the outgrowth of a pollen tube that serves as a carrier for immotile gametes. This feature is indicative of siphonogamy fertilization and probably it would be related to the thickening of the proximal surface (cappa) and the lack of pollen chamber in the ovules.

In Late Palaeozoic deposits from Gondwana, the record of reproductive male organs bearing pollen grains is rather scarce. The fructification records are few, mostly isolated impressions, so that the establishment of their affinity with primitive gymnosperms is difficult, particularly if female organs are absent. Better known male fructifications of Carboniferous gymnosperms in Gondwana belong to sporangia bearing spores. An example of the latter is *Obandotheca* (ERWIN et al. 1994) from the late Early Carboniferous of Peru, which is a primitive gymnosperm whose male fructifications still do not produce pollen grains. This genus shows a microsporangiate branch system and is associated with ovulate organs attributed to the Pteridospermopsida. The reproductive structures are preserved as compression/casts and are referred as parts of a whole plant. Although the spores have not been found in situ, the sporangia of *Obandotheca* occur surrounded by a mass of localized concentrations of coalified spores in which trilete mark or other diagnostic features are obscure.

Male fructifications associated with fronds of *Botrychiopsis* have been described from the Late Carboniferous of Argentina. ARTABE et al. (1987) illustrated impressions and compressions of microsporophylls bearing pollen sacs that in turn contain monocolpate pollen grains. The morphology of this genus is compared with some Triassic corystosperms (*Zuberia-Pteruchus*) suggesting a pteridosperm affinity. CÉSARI & LIMARINO (1988) described similar fructifications also related to *Botrychiopsis*, which are interpreted as pollen sacs but without mentioning if the sacs bear pollen or spores. Other findings of male fructifications from the Late Carboniferous of Argentina preserved as impressions, are associated with *Fedekurtzia* (ARCHANGELSKY 1981, ARCHANGELSKY & ARCHANGELSKY 1988, GUTIERREZ 1994, CARRIZO & AZCUY 1995). Only sporangia? or pollen sacs have been recognized in them without the discovery of pollen grains.

In the Early Permian of Argentina, male conifer cones (*Ferugliocladus*) have been found. These consist of small structures with helical disposed microsporophylls (ARCHANGELSKY & CÚNEO 1987, ARCHANGELSKY 1996). The maceration of samples bearing exclusively seeds yielded mainly monosaccate pollen grains of *Cannanoropollis* type. Male organs of glossopterids are frequent in all Gondwana regions. These fructifications are commonly composed of microsporangiate clusters that have bisaccate and striate pollen grains (PANT & NAUTIYAL 1960, SURANGE & MAHESHWARI 1970, GOULD & DELEVORYAS 1977).

The absence of well-preserved primitive gymnosperm prepollen and pollen grains with a continuous occurrence in the Late Carboniferous, prevents the recognition of morphological changes that would determine the evolution of monosaccate pollen grains within Gondwana. The overwhelming majority of described pollen grains from Gondwana areas are dispersed and consequently, their botanical affinities are poorly known. Hence, validation of diagnostic features to distinguish genera and species, is more arbitrary.

Thus parataxonomy or morphotaxonomy, may be necessary for naming dispersed pollen grains having characteristics similar to those of known biological affinity. For dispersed monosaccate pollen grains of *Cordaianthus* type, the name *Florinites* is proposed by SCHOPF, WILSON & BENTALL (1944) following a parataxonomic classification. Its diagnosis, later emended by MILLAY & TAYLOR (1974), is based on a number of morphological features such as symmetry, body shape, development of saccus to body attachment, in this case suggested as distal, and the presence of a trilete mark on the proximal face.

TAYLOR & DAGHLIAN (1980) found pollen grains of *Felixipollenites* in different stages of maturity based on the arrangement and position of the pollen sacs in the cordaitalean male cone *Gothania lesliana*. An
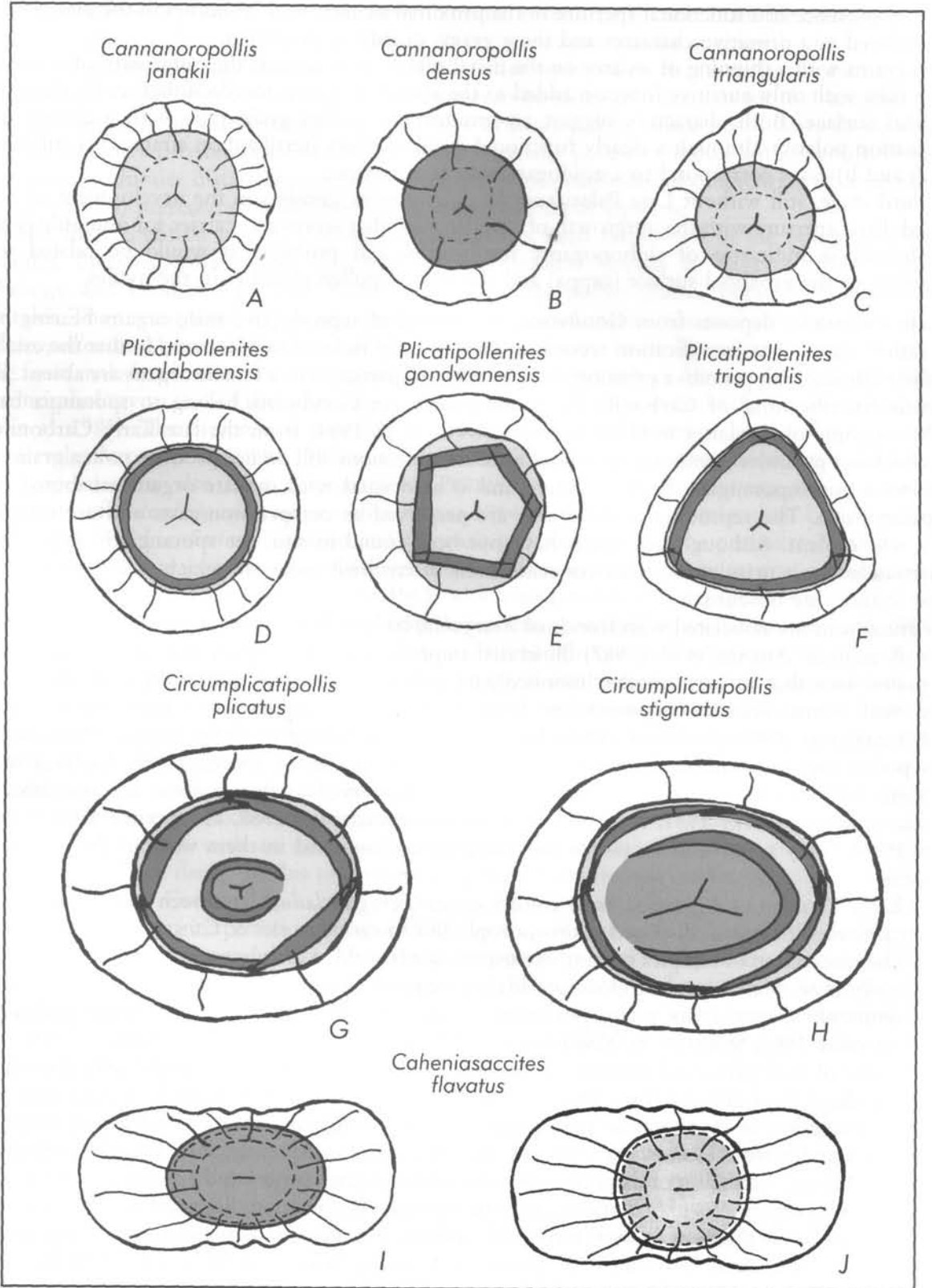
Text-fig. 4. Diagrams showing identifying characters of monosaccate pollen grain species considered for the present study.
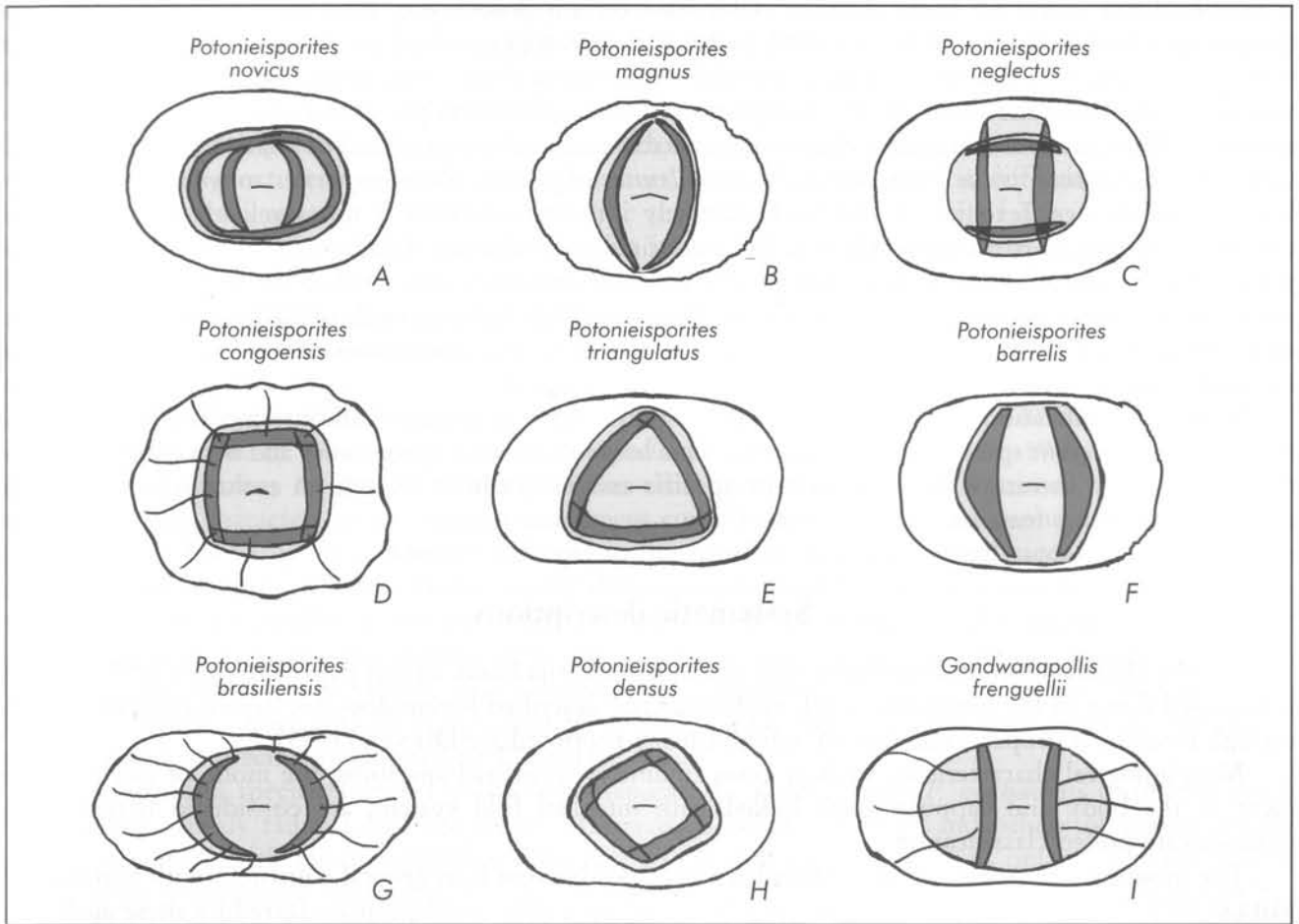
Text-fig. 5. Diagrams showing identifying characters of monosaccate pollen grain species considered for the present study.

interesting morphologic feature observed in mature pollen grains of this genus within sporangium, is the presence of grains with both radial or bilateral symmetry and the variety of suture configuration which were attributed to high range of variation in tetrad configuration.

The dispersed saccate pollen grains parataxonomical classification in their different condition has been and still continues to be a matter of discussion. Two important schemes of classification have been proposed: one is based on the aperture or germinal area, which can be functional proximally (prepollen concept, CHALONER 1970, POORT et al. 1996) or distally (true pollen). Taken together, they have deep phylogenetic implications (see above). Among the pioneering researchers that have contributed with many investigations to increase this concept, it is necessary to mention RENAULT (1896), ERDTMAN (1947), PANT (1954), POTONIÉ & KREMP (1954) and LESCHIK (1955).

The other scheme is based on the pattern of saccus attachment to the body. However, its evolutional and taxonomical value is uncertain. This concept was proposed by HART (1965) and utilized mainly by DIBNER (1971, 1973). The latter author proposed a new parataxonomic classification system based on this feature, in order to establish three infraturma with a number of subinfraturma in each one. Recently, GUTIERREZ (1993) discussed in detail this classification scheme and included monosaccate pollen grains recognized in Gondwana basins, mainly from Argentina and Brazil. The application of either the germinal areas or the exine layers attachment as taxonomic criteria, relies on the type of preservation which may preclude a correct evaluation of the features.

A diagnostic element with taxonomical value but, which is difficult to consider because of the flattening generally registered in dispersed pollen grains, is the intexinal fold system used widely in their classification.

It is considered useful by some authors to separate certain genera, e.g. *Plicatipollenites* LELE 1964 and *Circumplicatipollis* OTTONE & AZCUY 1988, and also their component species. Another group of diagnostic features with specific value has been used with different criteria: shape of the grain, shape of the central body and the thickness of the intexine. The recognition of these characters presents varied possibilities in their appraisal. Those cited first are more clearly recognizable and can be considered of relatively positive specific value (e.g. *Cannanoropollis triangularis*, *Plicatipollenites trigonalis*, *Potonieisporites congoensis*, *P. triangulatus*, *P. densus*; see Text-figs. 4 and 5). Conversely intexine thickness is not a reliable criterion in the separation of species particularly when it has a continuous gradation. Additionally, corrosion and/or bad preservation commonly distort it so that its specific value should be restricted to the specimens, which do not show any other reliable diagnostic features. There are other features, such as the presence or absence of saccus radial folds, proximal apertures and the absolute and relative dimensions of the total grain, body and saccus that can only be considered as complementary characters.

In every classification based only on morphological criteria, specimens with intermediate features occur between two different species (and also genera). This has created large synonymies and new combinations in the palynological literature. A more accurate specific assignment must include an evaluation of diagnostic and complementary features.

Systematic descriptions

For the classification of dispersed pollen grains from Tarija basin, in this paper DIBNER's (1973) scheme is followed down to the infraturma level, as the material described herein does not depict a variation broad enough to allow a proper validation of subinfraturma proposed by DIBNER (1973).

Morphological characteristics such as grain symmetry, proximal apertures, the mode of saccus attachment to the body and cappula shape linked with intexinal fold system, are considered herein in the monosaccate pollen classification.

The monosaccate pollen grains terminology employed herein is in general consistent with that used by MILLAY & TAYLOR (1974), with the exception of the terms sulcus and leptoma referred by these authors to the saccus corpus attachment (roots) and distal area bisected by a well-defined line, respectively. Instead, the broad (or less restricted) term cappula referred to a distal area of thinner exine (KREMP 1974) is considered in this paper with an only descriptive sense. It consists in a distal area (thinner or not) delimited by the roots sometimes associated with an intexinal fold system, but without fertilization value.

The identifying characters proposed for the monosaccate species recovered from Escarpment and San Telmo Formations are tabulated in Text-figs. 4 and 5 showing graphical criteria for the recognition and differentiation between species.

The geographical distribution and stratigraphic range of different taxa described herein are based on the previous records from South America (Argentina, Brazil and Uruguay) and are documented in Text-fig. 6. Occurrences mentioned for some taxa, should not be regarded as the complete range for all Gondwana, but rather as an example of their presence.

<div style="text-align:center">

Anteturma Variegerminantes POTONIÉ 1970

Turma Saccites ERDTMAN 1947

Subturma Monosaccites (CHITALEY) POTONIÉ & KREMP 1954

Infraturma Dipolsacciti HART emend. DIBNER 1971

Genus *Cannanoropollis* POTONIÉ & SAH 1960

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1964a *Parasaccites* BHARADWAJ & TIWARI, p. 143.
1964 *Virkkipollenites* LELE, p. 157.

Type species: *Cannanoropollis janakii* POTONIÉ & SAH 1960.

Botanical affinity: Coniferophyta-Coniferopsida (STAPLIN et al. 1967); Coniferopsida and Corda-itopsida (POTONIÉ 1967); Coniferales-Cordaitales (VERGEL 1986); Coniferopsida-Ferugliocladaceae (AR-CHANGELSKY & CÚNEO 1987).

Discussion: The authors accept FOSTER's (1975) consideration of *Parasaccites* as a synonym of *Cannanoropollis*. The precise position of saccus detachment (proximally-distally subequatorial para-condi-tion) is not of distinct generic significance. Moreover, such a characteristic is difficult to identify. This criteria involves two aspects: a botanical one, like the real taxonomic value of this feature; the other practical is related clearly to the identification of this feature whose light morphological expression implies difficulties in the task of its recognition, even in moderately well preserved material. As such, only occasionally it is possible to observe a subequatorial proximal and distal saccus detachment in para-condi-tion, so it is preferred to reserve this subtle trait for specific distinctions. Some authors principally from India, prefer the generic status of *Parasaccites* based on the presence of para-condition (TIWARI et al. 1989, TIWARI & RAM-AWATAR 1989, VIJAYA & TIWARI 1992, TIWARI & TRIPATHI 1992, GUTIERREZ 1993).

An examination of type species *Cannanoropollis janakii* POTONIÉ & SAH 1960 and *Parasaccites korbaensis* BHARADWAJ & TIWARI 1964a indicates that they cannot be distinguished meaningfully. In turn, the unique character for its logical arrangement could be the so-called para-condition, described by BHARADWAJ & TIWARI (1964a), which is referred to the equal proximal and distal saccus attachment. This feature has not been described in the *C. janakii* diagnosis, presumably because it was not present. On the other hand, it is not possible to recognize this character on the photomicrographs figured by POTONIÉ & SAH (1960: pl. 2, figs. 15, 16). Furthermore, *C. janakii* is not included in the six species retained in *Parasaccites* by TIWARI et al. (1989), after a careful re-examination of twenty-two species assigned to this genus. In addition, other authors (LELE 1964, FOSTER 1979, GUTIERREZ 1993) have observed the lack of para-condition in specimens assigned to *C. janakii*.

The remaining specific features available to separate *C. janakii* from *P. korbaensis* (proximal mark, saccus width, saccus radial folds, the width of saccus to corpus overlap, and others of minor specific value), are similar with minor variability. The two species can be distinguished only if it is possible to determine the symmetrical saccus attachment. Finally, *C. korbaensis* (BHARADWAJ & TIWARI) FOSTER 1975 is restricted to specimens showing symmetrical saccus attachment. The specimens not showing para-condition will have to be transferred to *C. janakii*.

The authors propose the following features to distinguish *Cannanoropollis*:
a) Grains with original radial symmetry.
b) Saccus detachment proximally equatorial-subequatorial and distally subequatorial.
c) Distal roots delimiting cappula more or less circular or polygonal.
d) Distal intexinal fold system absent.
e) Presence of radial arranged saccus folds.
f) Proximal mark mainly trilete (sometimes visible).

Cannanoropollis densus (LELE) BOSE & MAHESHWARI 1968

Plate 1, figs. 3, 6; Text-fig. 4B

Synonymy: see AZCUY & GUTIERREZ (1985).

1986 *Cannanoropollis* cf. *densus* – BARREDA, pl. 1, figs. 2, 3.

Holotype: *Virkkipollenites densus* LELE, 1964; pl. 2, fig. 19.
Type locality: Talchir Beds, South Rewa Basin, India.

Identifying characters: Pollen monosaccate, amb subcircular, margin crenulate. Central body thick, outline subcircular. Saccus attachment proximally equatorial and distally subequatorial. Cappula subcircular. Radially arranged saccus folds, common.

Dimensions (27 specimens): Overall equatorial diameter 153.1(104.4–81.2) 75.4 µm; corpus diameter 92.8 (63.8) 46.4 µm.

Remarks: Although it was not possible to measure the intexine thickness, all specimens studied here show a dark and dense central body which is in conformity with *C. densus*. The specimens described by BARREDA (1986a) are included in this species as the absence of a trilete mark has not been considered significant to exclude them.

Occurrence: Lower Permian, (India): LELE 1964, TIWARI 1965; (Africa): BOSE & MAHESHWARI 1968; UTTING 1976; (Australia): FOSTER 1979.

Cannanoropollis janakii POTONIÉ & SAH 1960
Plate 1, figs. 1, 2; Text-fig. 4A

Synonymy: see LELE (1964), FOSTER (1979) and OTTONE & AZCUY (1989).

1996 *Cannanoropollis korbaensis* – GARCÍA, pl. 1, fig. 1.

Holotype: POTONIÉ & SAH, 1960; pl. 2, fig. 15.
Type locality: Cannanore Beach, Malabar Coast, India.

Identifying characters: Pollen monosaccate, amb subcircular, crenulate to smooth peripheral margin. Central body poorly distinct to well-defined, subcircular. Body-saccus attachment proximally equatorial and distally subequatorial with cappula subcircular. Trilete mark is observed in many specimens. Radial folds are common.

Dimensions (45 specimens): Overall equatorial diameter 145 (104.4) 90.5 µm; corpus diameter 99.8 (75.4) 48.7 µm.

Remarks: The specimens described herein do not display the para-condition, and are similar to the type material described by POTONIÉ & SAH (1960).

Occurrence: Upper Carboniferous-Lower Permian, (Australia): JONES & TRUSWELL 1992. Lower Permian, (India): POTONIÉ & SAH 1960, BHARADWAJ & TIWARI 1964a, LELE 1964, TIWARI 1965; (Africa): BOSE & MAHESHWARI 1968; (Australia): FOSTER 1975, 1979. Upper Permian, (Australia): DE JERSEY 1979; (Antarctica): LINDSTRÖM 1995, 1996.

Cannanoropollis triangularis (MEHTA) BOSE & MAHESHWARI 1968
Plate 1, fig. 4; Text-fig. 4C

1993 *Cannanoropollis* sp. cf. *C. triangularis* – GUTIERREZ, p. 187, pl. 4, fig. 2.

Holotype: *Hymenozonotriletes triangularis* MEHTA, 1944; pl. 1, fig. 1.
Type locality: Pali, South Rewa Gondwana Basin, India.

Identifying characters: Pollen monosaccate, amb subtriangular, margin undulate. Central body oval to subcircular, outline distinct. Saccus detachment proximally equatorial, distally subequatorial. Cappula oval-subcircular. Radial folds on saccus present.

Dimensions (8 specimens): Overall equatorial diameter 104.4 (89.3) 75.4 µm; corpus diameter 75.4–51 µm.

Remarks: *C. triangularis* differs from other species of *Cannanoropollis* by its triangular outline. The forms described under *Cannanoropollis* sp. cf. *C. triangularis* (GUTIERREZ 1993) conform to the diagnostic features of this species.

Occurrence: Lower Permian, (India): MEHTA 1944, POTONIÉ & LELE 1961; LELE 1964, MAITHY 1964; BHARADWAJ & SALUJHA 1964; (Africa): BOSE & MAHESHWARI 1968.

Cannanoropollis sp.
Plate 1, fig. 5

Description: Pollen monosaccate, amb oval, margin crenulate. Central body oval to subcircular. Roots proximally slightly subequatorial and distally nearer to the polar region with distinct radial folds,

and distally subequatorial. Cappula subcircular. Marked radial saccus folds and trilete mark frequently present.

Dimensions (87 specimens): Overall diameter 226 (133.4–116) 88.2 µm; corpus diameter 162 (92.8–87) 58 µm.

Remarks and comparisons: The central body development varies with respect to the saccus width. Our specimens have similar size range as those described by Potonié & Sah (1960), Lele (1964) and Azcuy & Gutierrez (1985).

Occurrence: Gondwana distribution in Azcuy & Gutierrez (1985).

Plicatipollenites trigonalis Lele 1964

Plate 1, fig. 10; Text-fig. 4F

Synonymy: see Lele (1964), Ottone & Azcuy (1990) and Gutierrez (1993).

Holotype: Lele 1964; pl. 2, fig. 13.
Type locality: Talchir Beds, South Rewa Basin, India.

Identifying characters: Pollen monosaccate, amb subcircular to subtriangular, margin smooth. Central body subtriangular with distinct outline. The distal body fold system consists of three continuous and peripheral elements with triangular arrangement. Triangular cappula. Roots proximally equatorial and distally subequatorial following the shape of the intexinal folds. Thin radially orientated saccus folds are frequent.

Dimensions (5 specimens): Overall diameter 134.6–98.6 µm; corpus diameter 98.6 (77.7) 58 µm.

Remarks: *P. trigonalis* differs from *Potonieisporites triangulatus* Tiwari by its radial symmetry. For other comparisons see Gutierrez (1993).

Genus *Potonieisporites* Bhardwaj emend. Bharadwaj 1964a

Type species: *Potonieisporites novicus* Bhardwaj 1954.

Botanical affinity: Pteridospermales (Potonié 1967); Coniferopsida, Voltziales (Bharadwaj 1964b, Staplin et al. 1967, Nygreen & Bourn 1967, Rothwell 1982; Taylor 1982, Clement-Westerhof 1984); Coniferales (Vergel 1986); Coniferales, Lebachiaceae (Florin 1938–1945, Mapes 1981, Mapes & Rothwell 1984, Poort & Veld 1997).

Generic remarks: Several species attributed to *Potonieisporites* Bhardwaj emend. Bharadwaj 1964a have been described in many palynological papers, without separating clearly the diagnostic features from the complementary ones and without emphasizing the important relationship between the roots, which are the result of the attachment of the saccus to the body, and the corpus fold system. Based on the relationship of these features, different types of cappula and fold systems can be recognized, and their evaluation leads to the differentiation of species.

The following criteria are used herein for the recognition of this genus:
a) Grains with originally bilateral symmetry.
b) Saccus detachment proximally equatorial and distally subequatorial.
c) Distal roots delimiting different shapes of cappula, which can be associated with a more or less distinct intexinal fold system.
d) Distal intexinal fold system sometimes composed of a peripheral fold and/or of two or more elements with several shapes and arrangements that border and protect a probable germination area.
e) Frequently radially arranged saccus folds are absent.
f) Proximal mark mainly monolete or dilete (sometimes visible).

Potonieisporites barrelis Tiwari 1965

Plate 2, figs. 3, 4; Text-fig. 5F

Synonymy: see Gutierrez (1993).

1971 *Potonieisporites jayantiensis* – Lele & Karim; pl. 2, figs. 17, 18.

Holotype: BHARADWAJ & TIWARI 1964 b; pl. 2, fig. 31.
Type locality: Borehole G1, Korba Coalfield, India.

Identifying characters: Pollen monosaccate, amb subcircular to oval. Central body vertically arranged with a barrel to subhexagonal shape. Intexinal fold system composed of two more or less straight to vertically convex folds, which delimit a subrectangular cappula. Roots proximally equatorial and distally subequatorial.

Dimensions (9 specimens): Total horizontal grain diameter 150.8–101 μm; vertical diameter 116–67.3 μm; maximum horizontal corpus diameter 104.4–53.4 μm; vertical diameter 102.1–50 μm; saccus width 2.3 (7–21) 30.2 μm.

Comparisons: The holotype of *P. jayantiensis* LELE & KARIM 1971, does not appear to be distinct from *P. barrelis*. LELE & KARIM (1971) did not compare the two species, but from the interpretation of their diagnosis *P. jayantiensis* has a subhexagonal central body whereas *P. barrelis* has a barrel shaped central body. This subtle difference between the two species is not regarded here as useful in distinguishing species. Thus, *P. jayantiensis* LELE & KARIM 1971 is considered here as a junior synonym of *P. barrelis* TIWARI 1965.

Occurrence: Permian, (India): TIWARI 1965; LELE & KARIM 1971.

Potonieisporites brasiliensis (NAHUYS, ALPERN & YBERT) ARCHANGELSKY & GAMERRO 1979

Plate 2, figs. 1, 2; Text-fig. 5G

Synonymy: see ARCHANGELSKY & GAMERRO (1979), and GUTIERREZ (1993).

Holotype: *Vestigisporites brasiliensis* NAHUYS, ALPERN & YBERT 1968; fig. 59.
Type locality: Charqueadas, Rio Grande do Sul, Brazil.

Identifying characters: Pollen monosaccate, amb distinctly oval, periphery undulate. Central body longitudinally oval to subcircular. Distal intexinal fold system composed of two vertically semilunar folds or one more or less peripherally discontinuous. Roots proximally equatorial and distally subequatorial delimiting an horizontally oval to subcircular cappula. Abundant radially arranged saccus folds.

Dimensions (5 specimens): Total horizontal grain diameter 160.6–116 μm; vertical diameter 84.7–60.3 μm; maximum horizontal corpus diameter 82.4–54.5 μm; vertical diameter 73.1–51 μm; saccus width 5.8–40.6 μm.

Occurrence: Lower Permian, (Brazil): NAHUYS, ALPERN & YBERT 1968.

Potonieisporites congoensis BOSE & MAHESHWARI 1968

Plate 1, fig. 12; Text-fig. 5D

1984 *Potonieisporites* sp. cf. *P. densus* – LIMARINO et al., pl. 2, fig. 9.
1988 *Potonieisporites neglectus* – LIMARINO & CÉSARI, fig. 19.

Holotype: BOSE & MAHESHWARI 1968; pl. 12, fig. 2.
Type locality: South of Albertville, Luanda, Africa.

Identifying characters: Pollen monosaccate, amb subquadrangular to subcircular. Central body quadrangular or longitudinally subrectangular to suboval. Intexinal distal fold system more or less peripheral and continuous, composed of four elements. Saccus attachment proximally equatorial and distally subequatorial delimiting a quadrangular to rectangular cappula. Radial saccus folds and monolete mark present.

Remarks: The specimens from Caraparí River have characteristics similar to those specimens described from the Congo by BOSE & MAHESHWARI (1968), except for having a more peripheral fold system. According to GUTIERREZ (1993: p. 177), the specimen illustrated by LIMARINO et al. (1984: p. 341, pl. 2, fig. 9) as *Potonieisporites* sp. cf. *P. densus*, and later by LIMARINO & CÉSARI (1988: p. 127, fig. 19) as *Potonieisporites neglectus*, is included in *P. congoensis*.

Dimensions (10 specimens): Total horizontal grain diameter 139.2 (116) 100 μm; vertical diameter 121.8–92.8 μm; maximum horizontal corpus diameter 90.5 (78.9) 58 μm; vertical diameter 81.2 (69.6) 58 μm; saccus width 32.5 (17.4) 11.6 μm.

Potonieisporites densus MAHESHWARI 1967

Plate 2, fig. 6; Plate 3, fig. 2; Text-fig. 5H

Holotype: MAHESHWARI 1967; pl. 4, fig. 32.
Type locality: Bansloi Valley, Santhal Parganas, Bihar, India.

Identifying characters: Pollen monosaccate, distinctly oval, periphery smooth. Central body horizontally trapezoid to rhomboid, with distal infold system composed of four folds more or less following the amb of the central body. Saccus attachment proximally equatorial and distally subequatorial. Cappula trapezoid to rhomboid.

Dimensions (5 specimens): Total horizontal grain diameter 226–127.6 µm; vertical diameter 151–90.5 µm; maximum horizontal corpus diameter 160–83.5 µm; vertical diameter 81.2–69.6 µm; saccus width 11.6 (23.2) 46.4 µm.

Occurrence: Upper Carboniferous, (Argentina): GUTIERREZ 1993; GARCÍA 1996. Lower Permian, (Brazil): CAUDURO 1970.

Potonieisporites magnus LELE & KARIM 1971

Plate 2, figs. 5, 7; Text-fig. 5B

1987a *Potonieisporites brasiliensis* – VERGEL, pl. 1, fig. 15.

Holotype: LELE & KARIM 1971; pl. 2, fig. 16.
Type locality: Patharjore Nala, Jayanti Coalfield, Bihar, India.

Identifying characters: Pollen monosaccate, amb suboval, periphery smooth. Central body vertically oval, with one more or less peripheral fold, sometimes discontinuous, or two vertically semilunar folds, associated with the vertically elongated cappula. Roots proximally equatorial and distally subequatorial linked to the fold system. Monolete or dilete mark.

Dimensions (14 specimens): Total horizontal grain diameter 133.4 (127.6) 76.7 µm; vertical diameter 110.2–58 µm; maximum horizontal corpus diameter 87 (69.6) 39.4 µm; vertical diameter 98.6 (81.2) 48.7 µm; saccus width 34.8 (29) 6 µm.

Remarks: The specimen illustrated by VERGEL (1987a: pl. 1, fig. 15) as *Potonieisporites brasiliensis*, is transferred to this species, as previously noted by GUTIERREZ (1993: p. 178).

Potonieisporites neglectus POTONIÉ & LELE 1961

Plate 2, fig. 8, Plate 3, fig. 7; Text-fig. 5C

1980 *Potonieisporites* sp. – ARCHANGELSKY et al., pl. 1, fig. 12.

Holotype: POTONIÉ & LELE 1961; pl. 3, fig. 64.
Type locality: Goraia, South Rewa Gondwana Basin, India.

Identifying characters: Pollen monosaccate, amb oval to subrectangular. Central body longitudinally oval to subcircular with a well-defined distal intexinal fold system, composed of two pairs of elements more or less parallel to the major and minor axes. Saccus attachment proximally equatorial and distally subequatorial. Cappula with subrectangular shape transversely arranged, delimited by semilunar-shaped folds. Monolete or dilete mark present.

Dimensions (14 specimens): Total horizontal grain diameter 210 (140.4–116) 110.2 µm; vertical diameter 151 (104.4) 82.4 µm; maximum horizontal corpus diameter 130–67.3 µm; vertical diameter 120–67.3 µm; saccus width 38.3–5.8 µm.

Remarks: The specimen figured by ARCHANGELSKY et al. (1980: p. 49, pl. 1, fig. 12) as *Potonieisporites* sp. has diagnostic characteristics of *P. neglectus* and is therefore included in this species.

Potonieisporites novicus BHARDWAJ emend. POORT & VELD 1997

Plate 1, fig. 11; Text-fig. 5A

Synonymy: see BALME (1970) and GUTIERREZ (1993).

Holotype: BHARDWAJ 1954; Fig. 10.
Type locality: Saarkarbon, Germany.

Identifying characters: Pollen monosaccate (monosaccoid), amb elliptical to subcircular, outer margin smooth. Corpus longitudinally elliptical to subcircular, with one more or less peripheral and discontinuous fold. Roots proximally equatorial and distally subequatorial sometimes associated with two semilunar-shaped folds perpendicular to the long axis. Broadly oval cappula. Radial saccus folds less marked.

Dimensions (9 specimens): Total horizontal grain diameter 145–106.7 µm; vertical diameter 98.6–82.4 µm; maximum horizontal corpus diameter 84.7–71.9 µm; vertical diameter 77.7–60.3 µm; saccus width 29 (11.6–17.4) 9.3 µm.

Potonieisporites triangulatus TIWARI 1965
Plate 3, figs. 1, 4; Text-fig. 5E

Synonymy: see GUTIERREZ (1993).

Holotype: TIWARI 1965; pl. 4, fig. 83.
Type locality: Borehole G-101, Korba Coalfield, Bihar, India.

Identifying characters: Pollen monosaccate, amb oval. Central body subtriangular, outline distinct. Distally infold system composed of three peripheral elements. Subtriangular cappula associated with the fold system. Saccus attachment proximally equatorial and distally subequatorial. Monolete mark present.

Dimensions (6 specimens): Total horizontal grain diameter 160.4–125.3 µm; vertical diameter 124–87 µm; maximum horizontal corpus diameter 106.7–74.2 µm; vertical diameter 87–69.6 µm; saccus width 11.6–34.8 µm.

Genus *Gondwanapollis* LELE & MAITHY 1969

Type species: *Gondwanapollis ganjraensis* LELE & MAITHY 1969.
Botanical affinity: Gymnosperms? (GUTIERREZ 1993).

Generic remarks: This genus includes species with a proximally subequatorial and distally bilateral-transverse saccus attachment; which is related to the infold system. LELE & MAITHY (1969) and GUTIERREZ (1993) have discussed the other features in detail, which are accepted in this paper.

Gondwanapollis sp. cf. *G. frenguellii*
(CÉSARI) GUTIERREZ 1993
Plate 3, fig. 12; Text-fig. 5I

Holotype: *Potonieisporites frenguellii* CÉSARI 1984; pl. 1, fig.5.
Type locality: Mina La Victoria, Sierra de Maz, La Rioja Province, Argentina.

Description: Pollen monosaccate, amb oval, periphery smooth. Central body longitudinally oval, outline distinct. Intexinal distal fold system composed of two semilunar folds, vertically arranged. Saccus attachment proximally subequatorial and distally bilateral-transverse which is associated with the infold system. Cappula more or less subrectangular vertically arranged. Radial saccus folds present. Monolete mark present.

Dimensions (3 specimens): Total horizontal grain diameter 156.6–99.8 µm; vertical diameter 98.6–66.1 µm; maximum horizontal corpus diameter 100.9–52.2; vertical diameter 81.2–49.9 µm; saccus width 32.5-25.5 µm.

Comparisons: The specimens from Caraparí River are similar to those described by CÉSARI (1984) and GUTIERREZ (1993), both from Paganzo Basin. However, the small number of specimens available here prevent a more precise assignment.

Occurrence: Upper Carboniferous, (Argentina): CÉSARI 1984; VERGEL 1990, 1993, GUTIERREZ 1993, GARCÍA 1996.

Genus *Circumplicatipollis* OTTONE & AZCUY 1988

Type species: *Circumplicatipollis plicatus* OTTONE & AZCUY 1988.
Botanical affinity: Gymnosperms (OTTONE & AZCUY 1988); Cordaitopsida-Coniferopsida (OTTONE & AZCUY 1990).

Circumplicatipollis plicatus OTTONE & AZCUY 1988
Plate 3, fig. 11; Text-fig. 4G

Holotype: OTTONE & AZCUY 1988; pl. 1, figs. 1–3.
Type locality: Quebrada La Delfina, San Juan Province, Argentina.

Identifying characters: Pollen monosaccate, amb circular. Central body subcircular with two infold systems. The peripheral external fold system, consists distally of 4 or 5 wide elements, straight to more or less curved; the other system, proximally polar, consists of one more or less discontinuous fold that borders a subcircular denser area. Roots subequatorial weakly marked. Cappula broadly subcircular.
Dimensions (12 specimens): Total horizontal grain diameter 150.8 (140) 110.2 µm; vertical diameter 141.5 127.6) 78.9 µm; maximum horizontal corpus diameter 104.4 (98.6) 69.6 µm; vertical diameter 106.7–58 µm; saccus width 34.8 (23.2–17.4) 11.6 µm.

Circumplicatipollis stigmatus
(LELE & KARIM) OTTONE & AZCUY 1988
Plate 3, fig. 8; Text-fig. 4H

Synonymy: OTTONE & AZCUY 1988.

Holotype: *Plicatipollenites stigmatus* LELE & KARIM 1971; pl. 1, fig. 8.
Type locality: Jayanti Coalfield, Bihar, India.

Identifying characters: Pollen monosaccate, amb subcircular to oval. Central body oval to subcircular with two infold systems. The peripheral external system, consists of distally one thin, more or less continuous fold, and the other system, proximally polar, is composed of an imperfect semilunar element that borders a broadly and oval shaped dense area. Roots subequatorial weakly marked. Cappula broadly oval.
Dimensions (11 specimens): Total horizontal grain diameter 200 (145–127.6) 122 µm; vertical diameter 140 (110.2) 92.8 µm; maximum horizontal corpus diameter 186 (92.8) 84.7 µm; vertical diameter 113.7 (81.2) 69.6 µm; saccus width 21 (17.4–11.6) 11.6 µm.
Comparisons: *C. stigmatus* differs from *C. plicatus* in having a thinner, ill-defined and more continuous external circumpolar fold and in showing a larger oval area bordered by proximal circumpolar fold.

Genus *Caheniasaccites* BOSE & KAR 1966

Type species: *Caheniasaccites flavatus* BOSE & KAR 1966.
Botanical affinity: Coniferophyta (POTONIÉ 1967, AZCUY 1978); Ferugliocladacea (ARCHANGELSKY & CÚNEO 1987, ARCHANGELSKY 1996).
Generic remarks: Several species of *Caheniasaccites* have been broadly recognized in the Gondwana basins, and the definition of the genus has not suffered modifications that question its validity. ARCHANGELSKY & GAMERRO (1979) emended the genus on the basis of the frequent presence of a monolete mark in their material. Because of the differential corrosion as mentioned by ARCHANGELSKY & GAMERRO (1979), we consider that the presence or absence of a proximal mark can not be considered as a diagnostic generic or specific feature.
The recognition of *Caheniasaccites* is considered here to be based on the following characteristics:

a) Pollen grain with bilateral symmetry.
b) Saccus laterally constricted from haploxylonoid to diploxylonoid.

c) Proximally and distally subequatorial attachment of the saccus.
d) Distal roots delimit a cappula from oval to circular or polygonal.
e) Infold system absent.
f) Presence of remarkable radial saccus folds.
g) Mainly monolete mark (sometimes visible).

Specific discussion: BOSE & KAR (1966) established three species in the genus, viz., *C. flavatus*, *C. elongatus* and *C. ovatus*. The differentiation between them is based on the morphology of the central body and cappula. Therefore, *C. flavatus* is described with both features horizontally oval, *C. ovatus* with both as subcircular and *C. elongatus* with horizontally oval central body and rectangular cappula. Amongst the species of this genus, those most cited within Gondwana are *C. ovatus* BOSE & KAR 1966 and *C. densus* LELE & KARIM 1971.

Text-fig. 6. Geographic and stratigraphic distribution of the different *taxa* described from Mandiyutí Group from the Tarija Basin and others of South America.
Abbreviations: PAM. = Pampeanas; FAMAT. (FAM.) = Famatina; PRECORD. (PR.) = Precordillera; DIAM. = Diamante; ALHUA. = Alhuampa; S.CRT. = San Cristobal; ORIENT. = Oriental; Sb. = Subbasin; S.C. = Santa Catarina; R.G.S. = Rio Grande do Sul; CL = Cerro Largo; M. = Melo; RN = Rio Negro.
References: 1. This paper; 2. AZCUY & LAFFITTE (1981); 3. OTTONE & AZCUY (1988); 4. MENÉNDEZ (1971); 5. AZCUY & JELIN (1980); 6. BARREDA (1986á); 7. AZCUY & GUTIERREZ (1984); 8. CÉSARI (1984); 9. CÉSARI & LIMARINO (1987); 10. VÁSQUEZ NÍSTICO & CÉSARI (1987); LIMARINO & CÉSARI (1988); 11. CÉSARI & VÁSQUEZ NSTICO (1988); 12. OTTONE (1989); 13. OTTONE & AZCUY (1986, 1989); OTTONE (1991); 14. OTTONE & AZCUY (1990); 15. GUTIERREZ & CÉSARI (1986); 16. CARRIZO (1992); 17. VERGEL & LUNA (1992); VERGEL et al. (1993); 18. LIMARINO et al. (1984); 19. GUTIERREZ (1993); 20. ACEÑOLAZA & VERGEL (1987); 21. AZCUY & GUTIERREZ (1985); 22. GARCÍA (1996); 23. GARCÍA & AZCUY (1987); 24. VERGEL (1987b, 1990, 1993); 25. VERGEL (1987a); 26. ARCHANGELSKY et al. (1980); 27. ARCHANGELSKY & GAMERRO (1979); RUSSO et al. (1980); 28. CÉSARI et al. (1995); 29. SOUZA et al. (1993); 30. YBERT (1975); 31. MARQUES TOIGO (1988, 1991); MARQUES TOIGO et al. (1989); 32. CAUDURO (1970); 33. DAEMON & QUADROS (1970); 34. PONS (1976); 35. BERI (1987); 36. VERGEL (1987c); 37. MARQUES TOIGO (1974).

Table 1. Measurements of specimens assigned to species considered herein as synonyms of *C. flavatus* Bose & Kar emend.

SPECIES		Horiz. Diam.	Vert. Diam.	H/V Coef.
C. flavatus	(holotype)	69	64	1.08
Bose & Kar	(isotype)	92	87	1.06
C. ovatus	(holotype)	58	54	1.07
Bose & Kar	(isotype)	55	55	1.00
C. ovatus	Bose & Kar emend. Gutierrez	30(50-70)75	30(50-70)75	(0.9-1.05)1.10
C. densus	Lele & Karim emend. Gutierrez	50-80	(45-50)60	1.15-1.35
C. flavatus	Bose & Kar emend.	76-126	58-110	1.03-1.56

The study of specimens assigned to *Caheniasaccites*, found in the Caraparí River section, needed a re-examination of the features used in the recognition of its species. The diagnosis of *C. flavatus* and *C. ovatus* distinguish the two species by the shape of the central body and cappula (Bose & Kar 1966: 85 and 87). The dimensions of the central body of both *C. flavatus* holotype and isotype provide the coefficient of horizontal/vertical central body diameters (H/V coef.) as 1.08 and 1.06, respectively, whereas the H/V coef. of *C. ovatus* holotype and isotype is 1.07 and 1, respectively (Table 1). It is evident that the H/V coef. of *C. ovatus* holotype is within the average of both H/V coef. of *C. flavatus*. This observation lets us conclude that the two species are synonymous. *C. flavatus* has priority.

The dense intexine was considered as a diagnostic feature of *C. densus* Lele & Karim 1971. In addition, this species shows a central body shape from circular to oval. It has been observed that the intexine thickness has a broad range of colour variation and it is difficult to measure its real thickness. The specimens of *C. densus* and *C. flavatus* depict continuous range of intexine variation that invalidates the distinction between the two species. *C. densus* Lele & Karim is considered here a junior synonym of *C. flavatus* Bose & Kar emend.

The central body shape in the Caraparí River specimens assigned to *C. flavatus* Bose & Kar emend., shows a continuous gradation from horizontally oval to circular with only some hundredths of variation of the H/V coef. of the central body diameters (Table 1 and Text-fig. 7). Similar difference in H/V coef. of central bodies was used by Gutierrez (1993: 192, Table 10), to distinguish *C. ovatus* Bose & Kar emend. Gutierrez from *C. densus* Lele & Karim emend. Gutierrez. Thus, the limited difference observed (see Table 1) between specimens of *C. ovatus* Bose & Kar emend. Gutierrez with less circular central body (H/V coef. = 1.10) and those of *C. densus* Lele & Karim emend. Gutierrez with less oval central body (H/V coef. = 1.15). For the species mentioned above the cappula shape conforms to the central body shape. Cappula being different from the central body shape can be considered at specific level (e.g. *C. elongatus*
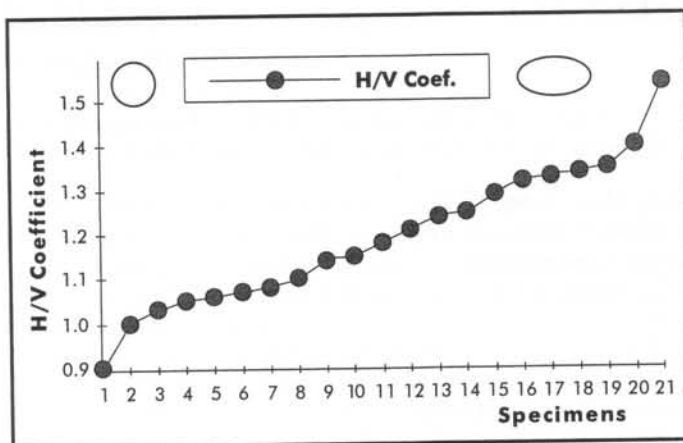
Text-fig. 7. Diagram showing specimens with continuous gradation from circular to oval of central bodies coefficient (H/V) assigned to *Caheniasaccites flavatus* Bose & Kar emend. Data after Table 1 including measured specimens from Caraparí river.

BOSE & KAR). Thus, the circular-oval shape of the central body and cappula and intexine thickness are not considered as diagnostic features at specific level in this genus.

Considering the above criteria *C. densus* LELE & KARIM emend. GUTIERREZ 1993, *C. ovatus* BOSE & KAR emend. GUTIERREZ 1993, *C. ellipticus* BOSE & MAHESHWARI 1968 (p. 45, pl. 10, fig. 1, pl. 9, fig. 7), *C. diffusus* LELE & MAITHY 1969 (p. 304, pl. 3, fig. 27) and *C. indicus* SRIVASTAVA 1970 (fig. 10), are considered junior synonyms of *C. flavatus* BOSE & KAR emend. *C. ellipticus* depicts, in both its diagnosis and illustration, the central body and cappula are oval-shaped, even though the text-fig. 8 (BOSE & MAHESWARI 1968) shows a cappula sketch as circular. *C. diffusus* LELE & MAITHY and *C. indicus* SRIVASTAVA have gradual or continuous range of central body shape, from circular to oval. Finally, the rest of species like *C. granulatus* LELE & CHANDRA 1974, *C. verrucosus* (GONZALEZ AMICON) GUTIERREZ 1993 and *C. elongatus* BOSE & KAR 1966 do not display any difficulties in the interpretation of their diagnosis.

Caheniasaccites flavatus (BOSE & KAR) emend.

Plate 3, figs. 5, 6, 10; Text-fig. 4I

Synonymy: *C. flavatus* is a senior synonym of the following species: *C. ovatus* BOSE & KAR 1966, *C. ellipticus* BOSE & MAHESHWARI 1968, *C. diffusus* LELE & MAITHY 1969, *C. indicus* SRIVASTAVA 1970, *C. densus* LELE & KARIM 1971, *C. densus* LELE & KARIM emend. GUTIERREZ 1993, *C. ovatus* BOSE & KAR emend. GUTIERREZ 1993.

1968 *Parasaccites ovatus* – KAR, pl. 2, fig. 46.
1989 *Caheniasaccites ovatus* – OTTONE & AZCUY, pl. 2, fig. 7.
1990 *Caheniasaccites ovatus* – OTTONE & AZCUY, pl. 2, fig. 5.
1993 *Caheniasaccites ovatus* – VERGEL et al., pl. 3, fig. 23.
1995 *Caheniasaccites ovatus* – CÉSARI et al., p. 87.
1996 *Caheniasaccites ovatus* – GARCÍA, pl. 2, fig. 5.
1996 *C. densus* – GARCÍA, pl. 2, figs. 3, 9.

Holotype: BOSE & KAR, 1966; pl. 26, fig. 4.
Type locality: Mabuita, Walikale region, Zaire, Africa.

Emended diagnosis: Pollen monosaccate, symmetry bilateral. Saccus laterally constricted from haploxylonoid to diploxylonoid. Central body longitudinally oval to circular with thin to thick intexine. Subequatorial saccus attachment, distally more overlapped than proximally. Distal roots marked by radial folds which define an oval to circular-shape cappula. Monolete mark sometimes present.

Remarks: The aim of the amendment is to prevent the proliferation of spurious species within *Caheniasaccites*. It includes grains with circular to oval central body and cappula shapes and with variable intexine thickness, which constitute gradual or continuous features in this genus.

Dimensions (14 specimens): Total horizontal grain diameter 200–79 µm; vertical diameter 111–40.6 µm; maximum horizontal corpus diameter 126–76.6 µm; vertical diameter 110.2–58 µm; horizontal saccus width 30.2 (23.2) 12.8 µm.

Occurrence: Lower Permian, (India): KAR 1968, LELE & MAITHY 1969, SRIVASTAVA 1970, LELE & KARIM 1971, LELE 1975, CHANDRA & LELE 1979; (Africa): BOSE & KAR 1966, BOSE & MAHESHWARI 1966, 1968.

Subturma Disaccites COOKSON 1947

Infraturma Disaccitriletes LESCHIK 1956

Genus *Limitisporites* LESCHIK emend. SCHAARSCHMIDT 1963

Type species: *Limitisporites rectus* LESCHIK 1956.
Botanical affinity: Glossopteridales (GOULD & DELEVORYAS 1977); Coniferophyta (POTONIÉ & SCHWEITZER 1960, GREBE & SCHWEITZER 1962, CLEMENT-WESTERHOF 1984).

Limitisporites sp. cf. *L. rectus* LESCHIK 1956

Plate 3, fig. 9

Holotype: *Limitisporites rectus* LESCHIK 1956; pl. 21, fig. 15.
Type locality: Neuhof, bei Fulda, Germany.

Description: Pollen bisaccate, haploxylonoid, amb oval. Central body subcircular to longitudinally oval. The sacci are subspherical, horizontally expanded and laterally joined by a very thin exinal ridge. Distal roots of the sacci appear associated with the vertical infolds, which are straight to semilunar. These folds delimit a broadly rectangular cappula.

Remarks: The specimens studied herein displayed a secondary fold along the longitudinal axis, which created a general deformation of the grain. The rare occurrence of specimens prevented a more precise specific designation.

Dimensions (2 specimens): Total horizontal grain diameter 250–121.8 µm; vertical diameter 101–56.8 µm; maximum horizontal corpus diameter 168–63.8 µm; vertical diameter 92.8–55.7 µm; saccus horizontal diameter from distal root 81.2–34.8 µm; maximum vertical saccus diameter 83.5–61.5 µm; maximum horizontal cappula diameter 87–31.3 µm.

Occurrence: Upper Carboniferous, (Argentina): GARCÍA 1996; GUTIERREZ 1993. Lower Permian, (Argentina): GAMERRO & ARCHANGELSKY 1981, CÉSARI et al. 1995, GARCÍA 1996; (Brazil): DAEMON & QUADROS 1970, MARQUES TOIGO 1988.

Genus *Platysaccus* NAUMOVA ex POTONIÉ & KLAUS 1954

Type species: *Platysaccus papilionis* POTONIÉ & KLAUS 1954.
Botanical affinity: Coniferophyta (POTONIÉ & KREMP 1956, STAPLIN et al. 1967, BHARADWAJ 1975).

Platysaccus sp. cf. *P. trumpii* OTTONE 1989

Plate 3, fig. 3

Holotype: pl. 10, fig. 11.
Type locality: El Chiquerito Creek, Cerro Bayos, Mendoza Province, Argentina.

Description: Pollen bisaccate, diploxylonoid. Central body longitudinally oval. Sacci globe-shape hemispherical. Broad cappa and small vertically subrectangular to irregular cappula. Roots marked with radial folds.

Dimensions (3 specimens): Total horizontal grain diameter 174–107.9 µm; vertical diameter 69.6–39.4 µm; maximum horizontal corpus diameter 104.4–58 µm; vertical diameter 46.4–36 µm; horizontal saccus diameter from distal root 69.6–46.4 µm; maximum vertical saccus diameter 98.6–58 µm; horizontal cappula diameter 17.4 à 8.1 µm; horizontal cappa diameter 24.4 µm.

Remarks: The specimens illustrated by OTTONE (1989: pl. 10, figs. 11, 12) differ from Caraparí River specimens in having a more subcircular central body and a slightly greater coefficient of total horizontal grain/maximum horizontal corpus diameters.

Occurrence: Lower Permian (Argentina): OTTONE 1989.

Characteristics and age of the assemblage

The palynomorphs assemblage found in the Escarpment and San Telmo Formations (see Text-fig. 3), includes pollen grains (Cordaitopsida and Coniferopsida), spores (Pteridophyte and Algae) and microplankton (Acritarcha and Prasinophycea). Several spore species and almost all the acritarchs and prasinophytes are reworked elements (DI PASQUO & AZCUY 1997a). Many of these elements have already been described and illustrated by MENÉNDEZ & PÖTHE DE BALDIS (1967), PÖTHE DE BALDIS (1974, 1979), MACGREGOR (1984), BARREDA (1986b), PÉREZ LEYTON (1991), OTTONE (1996) from Devonian and Early Carboniferous beds of

Tarija Basin of Argentina, Paraguay and Bolivia. This reworked material seems to be related to a marginal setting of this southern part of the basin near the Michicola High (AZCUY & DI PASQUO 1998). Most palynomorphs exhibit similar preservation characteristics, especially in terms of spore colour making it difficult to differentiate the reworked population from the indigenous one. This could be the result of the proximity of the source of reworked material to the depositional centre (AZCUY & LAFFITTE 1981), added to a slightly burial of the Devonian/Early Carboniferous deposits. In contrast, the southern part of Bolivia corresponds to a deep depocentre in the Tarija Basin and no reworked material of this age has been reported in Carboniferous sequences (SUÁREZ SORUCO 1986, SEMPERE 1995).

In the interest of determining the age of the assemblage found in the Caraparí River, it was considered necessary to begin with the systematic analysis of pollen grains. This indicated the presence of 21 species of pollen grains, with a broad predominance of monosaccate pollen (91 %) over disaccate (9 %) and the absence of striate pollen grains.

The studied samples (see Text-fig. 3) occur at the boundary between Escarpment and San Telmo Formations. The age of these strata based on the palynomorphs assemblage is considered to be of the Upper Carboniferous (DI PASQUO & AZCUY 1997 b). The studied assemblage is correlated with the *Plicatipollenites* Superzone and within this, with the *Potonieisporites* Palynozone (AZCUY & JELIN 1980, AZCUY 1986). The absence of striated forms especially *Vittatina*, which is characteristic of the beginning of the Permian in the basins of Brazil and Argentina, suggests an age no younger than the Late Carboniferous.

Acknowledgements

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Explanation of plates

Plate 1

(Magnification × 500)

Specimens are denoted by a prefix (BAFC-Pl = Buenos Aires Facultad Ciencias, Palinología) followed by the slide number and the England Finder reference, EF.

Figs. 1, 2. *Cannanoropollis janakii* POTONIÉ & SAH 1960.
Fig. 1.   BAFC-Pl 446(2), EF: A26/3.
Fig. 2.   BAFC-Pl 446(5), EF: W30/4.
Fig. 3.   *Cannanoropollis densus* (LELE) BOSE & MAHESHWARI 1968, BAFC-Pl 446(5), EF: L33/4.
Fig. 4.   *Cannanoropollis triangularis* (MEHTA) BOSE & MAHESHWARI 1968, BAFC-Pl 446(3), EF: X21/0.
Fig. 5.   *Cannanoropollis* sp., BAFC-Pl 8 T, EF: T29/0.
Fig. 6.   *Cannanoropollis densus* (LELE) BOSE & MAHESHWARI 1968, BAFC-Pl 446(2), EF: K33/3.
Figs. 7, 8. *Plicatipolllenites malabarensis* (POTONIÉ & SAH) FOSTER 1975.
Fig. 7.   BAFC-Pl 446(5), EF: J18/0.
Fig. 8.   BAFC-Pl 446(3), EF: Z26/0.
Fig. 9.   *Plicatipollenites gondwanensis* (BALME & HENNELLY) LELE 1964, BAFC-Pl 446(h), EF: B30/2.
Fig. 10.   *Plicatipollenites trigonalis* LELE 1964, BAFC-Pl 445(5), EF: W28/0.
Fig. 11.   *Potonieisporites novicus* BHARDWAJ emend. POORT & VELD 1997, BAFC-Pl 446(4), EF: C50/1.
Fig. 12.   *Potonieisporites congoensis* BOSE & MAHESHWARI 1968, BAFC-Pl 445(1), EF: C24/0.

Plate 2

(Magnification × 500)

Figs. 1, 2. *Potonieisporites brasiliensis* (NAHUYS, ALPERN & YBERT) ARCHANGELSKY & GAMERRO 1979.
Fig. 1.   BAFC-Pl 446(4), EF: X27/1.
Fig. 2.   BAFC-Pl 446(1), EF: O34/2.
Figs. 3, 4. *Potonieisporites barrelis* TIWARI 1965.
Fig. 3.   BAFC-Pl 8 T, EF: N35/0.
Fig. 4.   BAFC-Pl 7 II, EF: P44/4.
Fig. 5.   *Potonieisporites magnus* LELE & KARIM 1971, BAFC-Pl 446(4), EF: Y49/0.
Fig. 6.   *Potonieisporites densus* MAHESHWARI 1967, BAFC-Pl 446(3), EF: Z26/4-Z27/3.
Fig. 7.   *Potonieisporites magnus* LELE & KARIM 1971, BAFC-Pl6-1, EF: X42/3.
Fig. 8.   *Potonieisporites neglectus* POTONIÉ & LELE 1961, BAFC-Pl 446(2), EF: D22/0.
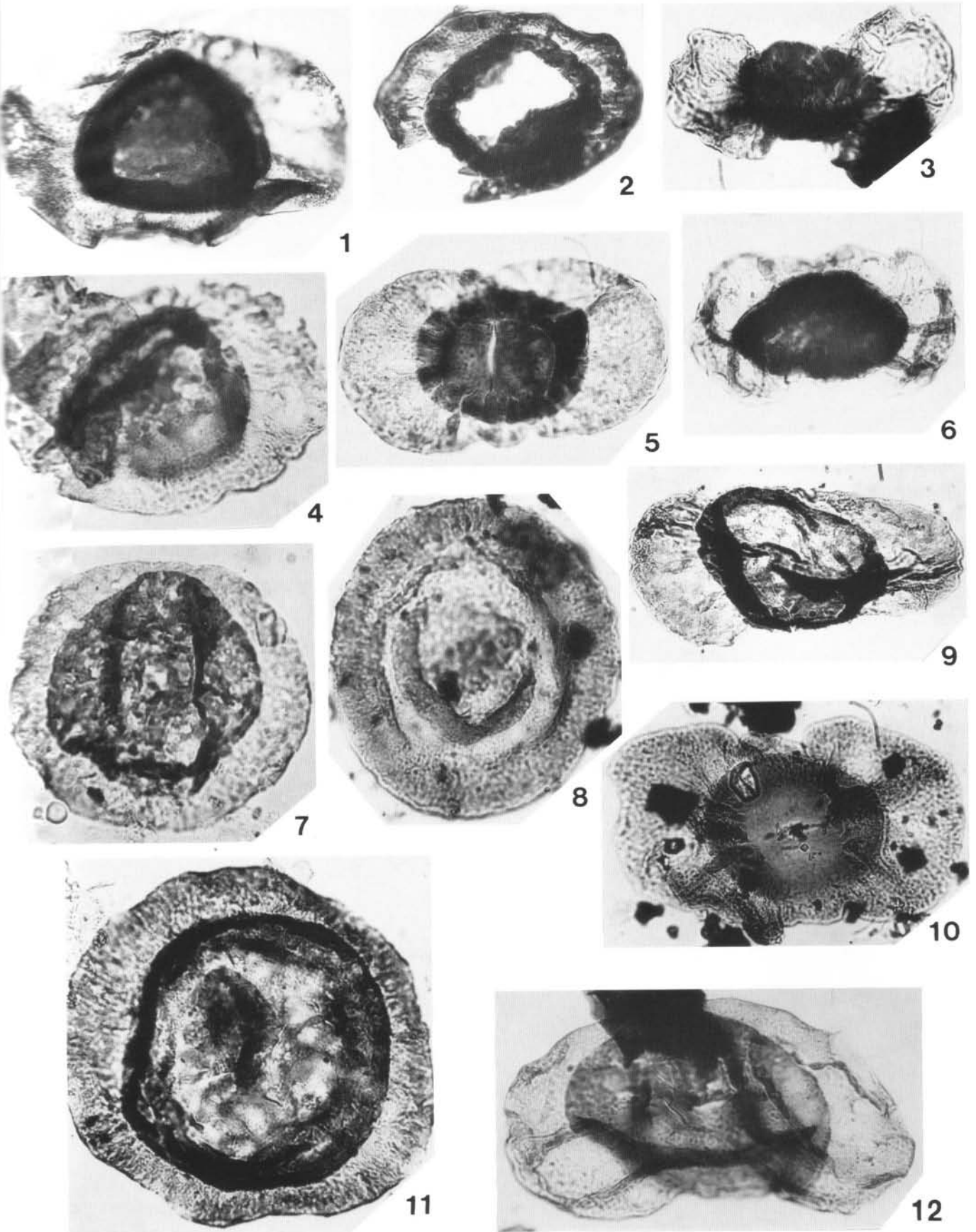
Plate 3

(Magnification × 500)

Fig. 1.   *Potonieisporites triangulatus* TIWARI 1965, BAFC-Pl 445(1), EF: H37/1.
Fig. 2.   *Potonieisporites densus* MAHESHWARI 1967, BAFC-Pl 446(4), EF: G39/3.
Fig. 3.   *Platysaccus* sp. cf. *P. trumpii* OTTONE 1989, BAFC-Pl 446(5), EF: A53/3.
Fig. 4.   *Potonieisporites triangulatus* TIWARI 1965, BAFC-Pl 446(4), EF: J34/3.
Figs. 5, 6.   *Caheniasaccites flavatus* BOSE & KAR emend.
Fig. 5.   BAFC-Pl 446(4), EF: K27/0.
Fig. 6.   BAFC-Pl 446(5), EF: Y22/4.
Fig. 7.   *Potonieisporites neglectus* POTONIÉ & LELE 1961, BAFC-Pl 446(d), EF: X39/0.
Fig. 8.   *Circumplicatipollis stigmatus* (LELE & KARIM) OTTONE & AZCUY 1988, BAFC-Pl 446(1), EF: G41/0.
Fig. 9.   *Limitisporites* sp. cf. *L. rectus* LESCHIK 1956, BAFC- Pl 8 TT, EF: M23/2.
Fig. 10.   *Caheniasaccites flavatus* BOSE & KAR emend., BAFC-Pl 6-2, EF: U44/0.
Fig. 11.   *Circumplicatipollis plicatus* OTTONE & AZCUY 1988, BAFC-Pl 446(b), EF:T19/1.
Fig. 12.   *Gondwanapollis* sp. cf. *G. frenguellii* (CÉSARI) GUTIERREZ 1993, BAFC-Pl 446(5), EF: Y47/0-Y47/1.
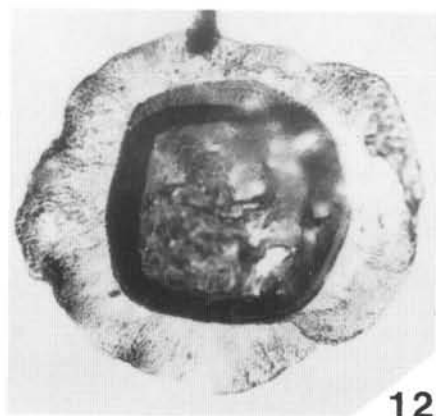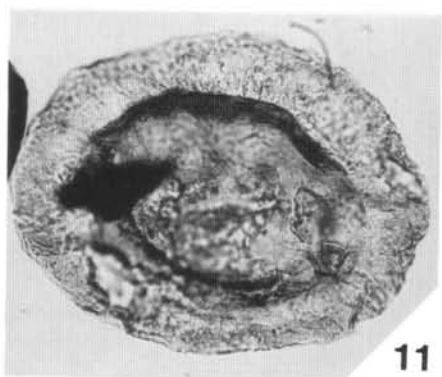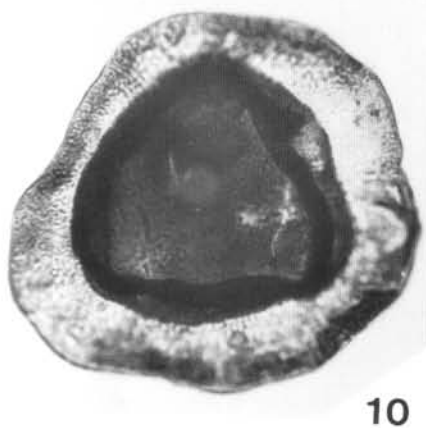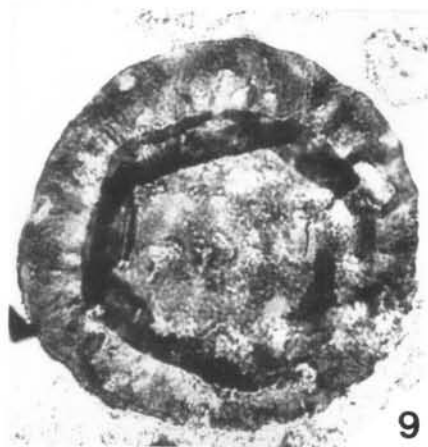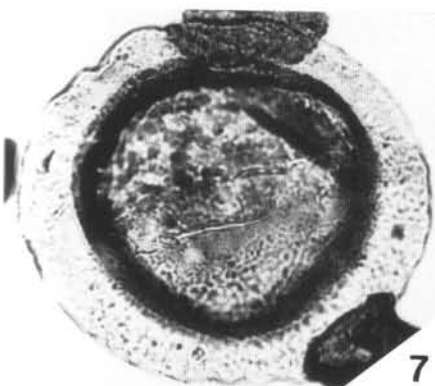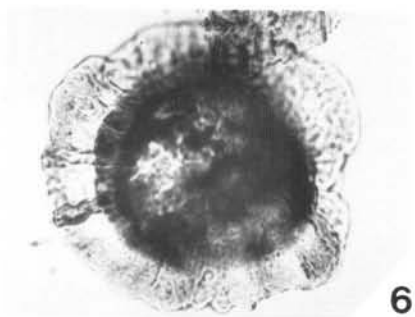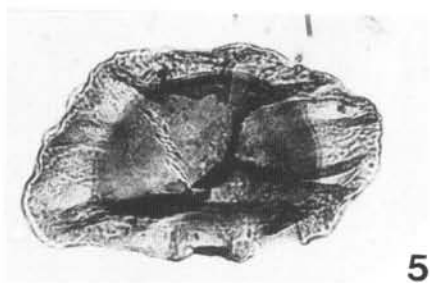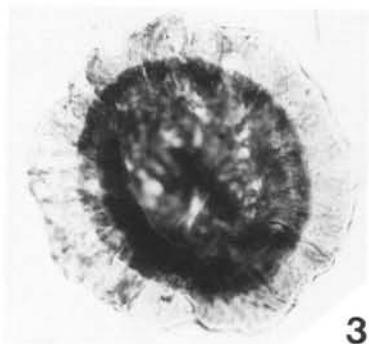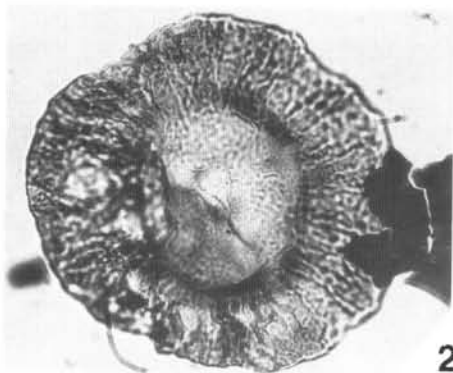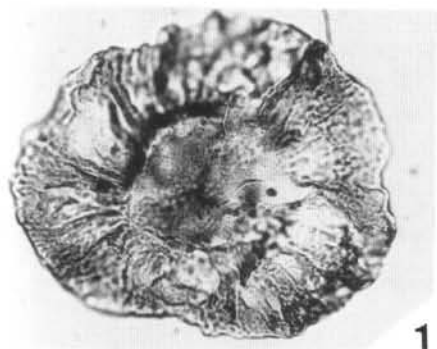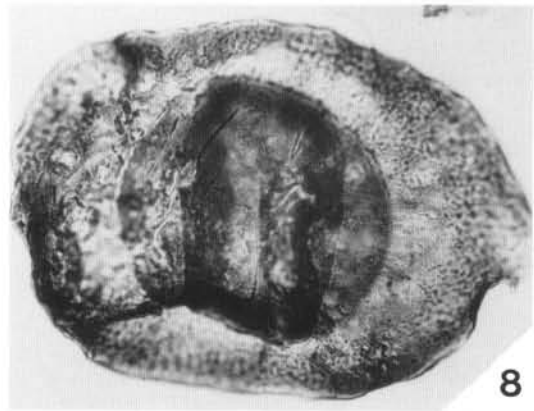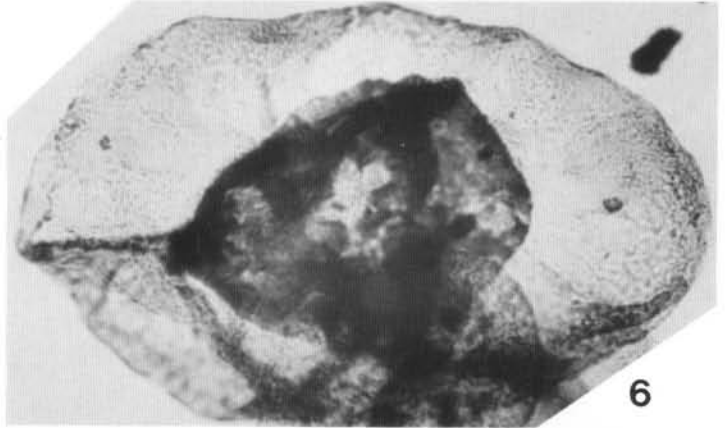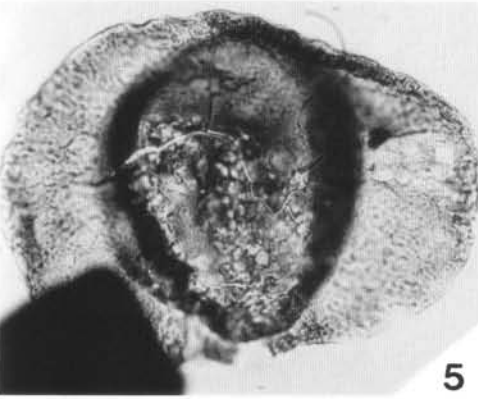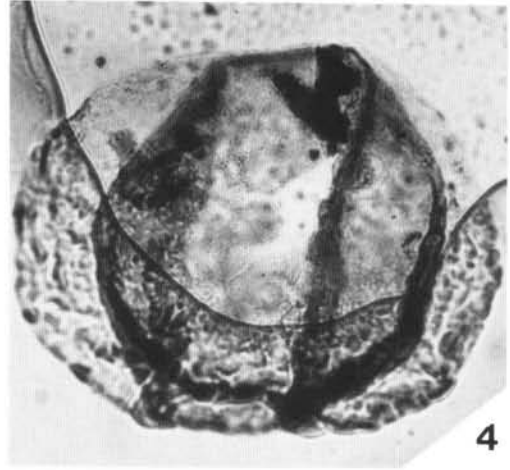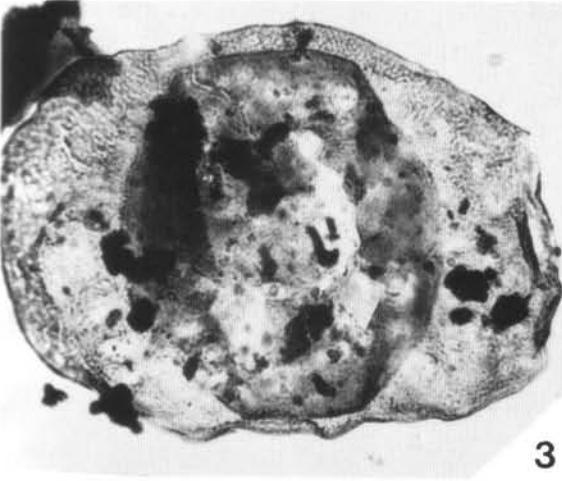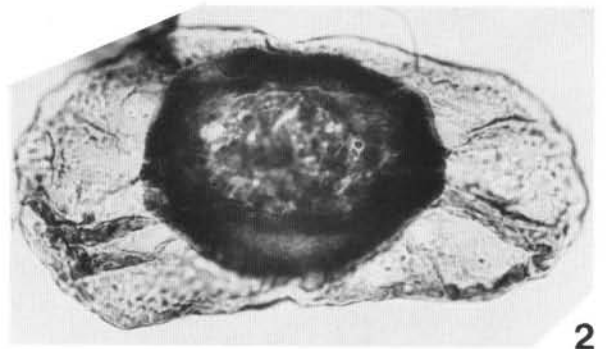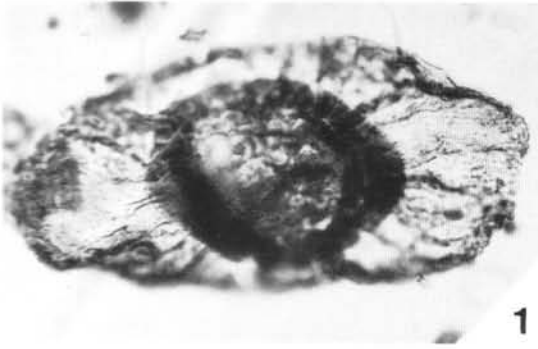
Azcuy, C. L. & di Pasquo, M.: Late Carboniferous monosaccate pollen genera.