

# Pennsylvanian megaspores from northeastern border of the Paraná Basin, Brazil: Correlation with Indian Gondwana megaspores

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## ABSTRACT

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Analysis of sediments from Campinas and Monte Mor, municipalities of the State of São Paulo, Brazil, has revealed the presence of new megaspores in addition to the known taxa. Trilete, alete, azonate and gulate dispersed fossil megaspores were recorded from the lower and middle levels of the Itararé Group from the northeastern border of the Paraná Basin (Lower Pennsylvanian) of Campinas municipality (Upper Bashkirian-Lower Moscovian) and of Monte Mor municipality (Kazimovian). Twenty-four species of megaspores recovered from one or both of these localities have been systematically analyzed and the synonymy of four previously described megaspores has been discussed.

The present study of megaspores from Campinas reveals the presence of the taxa *Banksisporites dijkstae*, *B. endosporitiferus*, *B. utkalensis*, *Biharisporites spinosus*, *Bokarosporites psilatus*, *B. rotundus*, *Duosporites perversus*, *Duosporites* sp. a, *Lagenicula horrida*, *Lagenicula* sp., *L. nudus*, *L. rugosus*, *Lagenoisporites* cf. *L. hispanicus* and *Lagenoisporites* sp. The megaspores from Monte Mor includes the taxa *Bokarosporites rotundus*, *Duosporites* sp. b, *Lagenoisporites nudus*, *L. rugosus* and *L. cf. L. hispanicus*. The taxa *Bokarosporites rotundus*, *B. psilatus*, *Banksisporites utkalensis*, *B. endosporitiferus*, *B. dijkstae* and *Biharisporites spinosus* are also known from the Permian of India. *Banksisporites tenuis* previously detected in Campinas and Monte Mor localities is also a species which is shared with India. The presence of these taxa in the Pennsylvanian of the Paraná Basin, Brazil indicates their appearance in the Carboniferous. While all of them persisted up to the Permian, some like *Biharisporites spinosus*, *Banksisporites tenuis* and *B. utkalensis* extend up to Triassic and Early Cretaceous as well. The presence of these megaspores both in India and in Brazil indicates the occurrence of common ancestral heterosporous early land plants. An attempt has been made to interpret the palaeogeographic distribution pattern of some of the megaspores which appeared earlier in Brazil as compared to India, suggesting the floral migration from Brazil towards India.

**Key-words**—Megaspores, Pennsylvanian, Paraná Basin, Permian, Palaeogeographic distribution, Brazil, India.

पराना द्रोणी, ब्राज़ील की पूर्वोत्तर सीमा से प्राप्त पेन्सिल्वेनियाई स्थूलबीजाणु: भारतीय गोडवाना स्थूलबीजाणुओं के साथ सहसंबंध

सांद्रा इंको मुने, रजनी तिवारी एवं मैरी ई सी बर्नान्डीज-डी-ऑलीवीरा

## सारांश

साओ पॉलो, ब्राज़ील के राज्य की कैंपीनस एवं माटे मोर नगर पालिकाओं से अवसर्दों के विशेषण सेचात टैक्सा के अतिरिक्त नवीन स्थूलबीजाणु प्रसूतों का पता चला है। कैंपीनस नगरपालिका (ऊपरी बशकिरियाई निचले मास्कोवियाई) व माटे मोर नगरपालिका (काज़ीमोवियाई) की पराना द्रोणी (निचले पेन्सीलवेनियाई) की पूर्वोत्तर सीमा से प्राप्त इतारैर समूह के निचले व मध्य स्तरों से विअरीय, अरहीन एज़ोट एवं गुलेट परिक्षित स्थूलबीजाणु अभिलिखित किए गए थे। इनमें से एक या दोनों उपवर्तितों से प्राप्त किए गए स्थूलबीजाणुओं की बौबीस जातियां क्रमबद्ध रूप से विश्लेषित की गई हैं तथा पूर्व में वर्णित चार स्थूल बीजाणुओं की समानार्थकता पर विचार-विमर्श किया गया है।

कैंपीनस से प्राप्त स्थूलबीजाणुओं का मौजूदा अध्ययन बैंकसीस्पोराइटिस डिक्स्ट्री, बी. एंडोस्पोराइटीफेरस, वी. उत्कलेन्सिस, बिहारीस्पोराइटिस स्पिनोसस, बोकारोस्पोराइटिस सिलेटस, बी. रोटंडस, ड्योस्पोराइटिस पर्वरसस, ड्योस्पोराइटिस जाति ए, लगेनीकुला हॉर्सड, लगेनीकुला जाति, एल. नुडस, रुगोसस, लगेनोइस्पोराइटिस तुल्य, एल. हिस्पेनीकस एवं लगेनोइस्पोराइटिस जाति टेक्सा की मौजूदगी बयां करता है। माटे मोर से प्राप्त स्थूलबीजाणु में बोकारोस्पोराइटिस रोटंडस, ड्योस्पोराइटिस जाति बी, लगेनोइस्पोराइटिस न्युडस, एल. रुगोसस, एल. तुल्य एल. हिस्पेनीकस सन्निहित है। बोकारोस्पोराइटिस रोटंडस, बी. सिलेटस, बैंकसीस्पोराइटिस उत्कलेन्सिस, बी. एंडोस्पोरिटिफेरस, वी. डिक्स्ट्री व बिहारीस्पोराइटिस स्पिनोसस टैक्सा भारत के पर्मियन से भी ज्ञात हैं। कैंपीनस एवं माटे मोर उपवास्तियों में पूर्व में पाई गई बैंकसीस्पोराइटिस टेन्युइस जाति भी भारत का अंश है। पराना द्रोणी के पेन्सीलवेनियन में इन टैक्सा की विद्यमानता कार्बनिफेरस में उनके रूप इंगित करती हैं जब कि ये समस्त पर्मियन तक निरंतर रहे, तथा बिहारीस्पोराइटिस स्पिनोसस, बैंकसीस्पोराइटिस टेन्युइस एवं बी. उत्कलेन्सिस ट्राइएसिक व प्रारंभिक क्रिटेशियस तक विस्तीर्ण रहे। भारत व ब्राज़ील दोनों में इन स्थूलबीजाणुओं की विद्यमानता सामान्य मूल विषमबीजाणु की प्रारंभिक स्थलीय पेड़-पौधे इंगित करती हैं। ब्राज़ील से भारत की ओर बनस्पति-जात अभिगमन सुझाते हुए कुछेक स्थूलबीजाणुओं के पुराभौगोलिक वितरण प्ररूप की व्याख्या करने का प्रयास किया गया है जो पहले ब्राज़ील में तदोपरांत भारत में दिखे।

**संकेत-शब्द—**स्थूलबीजाणु, पेन्सीलवेनियाई, पराना द्रोणी, पर्मियन, पुराभौगोलिक वितरण, ब्राज़ील, भारत।

## Megáscores Pensilvanianos da margem nordeste da bacia do Paraná, Brasil: Correlação com megásporos Gondvânicos Indianos

### RESUMO

Análises dos sedimentos de Campinas e Monte-Mor municípios do estado de São Paulo, Brasil, revelaram a presença de novos megásporos além dos taxa já conhecidos. megasporos fósseis dispersos tipo Trilete, alete azonate e gulate foram observados a partir dos níveis inferiores e médios do Grupo Itararé da margem nordeste da Bacia do Paraná (Pensilvaniano inferior) do município de Campinas (Bashiriano Superior e Moscoviano Inferior) e do município de Monte Mor (Kazimoviano). Vinte e quatro espécies de megásporos recuperados de uma ou ambas as localidades foram sistematicamente analisadas e as sinônimas de quatro megásporos descritos anteriormente tem sido objeto de discussão.

O presente estudo dos megásporos de Campinas revela a presença dos taxa *Banksisporites dijkstrae*, *B. endosporitiferous*, *B. utkalensis*, *Biharispores spinosus*, *Bokarospores psilatus*, *B. rotundus*, *Duosporites perversus*, *Duosporites sp. a*, *Lagenicula horrida*, *Lagenicula sp.*, *L. nudus*, *L. rugosus*, *Lagenoisporites cf. L. hispanicus* e *Lagenoisporites sp.*. Os megásporos de Monte Mor incluem os taxa *Bokarospores rotundus*, *Duosporites sp. b*, *Lagenoisporites nudus*, *L. rugosus*, *L. cf. L. hispanicus*. O taxon *Bokarospores rotundus*, *B. psilatus*, *Banksisporites utkalensis*, *B. endosporitiferous*, *B. dijkstrae* and *Biharispores spinosus* são também conhecidos do Permiano da Índia; *Bankesisporites tenuis* previamente detectado nas localidades de Campinas and Monte Mor é também uma espécie compartilhada com a Índia. A presença destes taxons no Pensilvaniano da Bacia do Paraná, Brasil indica o seu aparecimento no Carbonífero e, embora todas elas persistiram até o Permiano, alguns como *Biharispores spinosus*, *tenuis Banksisporites e utkalensis B.* estenderam-se até o Triássico e o eocretáceo também. A presença destes megásporos tanto na Índia quanto no Brasil indica a ocorrência de plantas terrestres primitivas heterósporas ancestrais comuns. Esforços tem sido feitos para interpretar o padrão de distribuição paleogeográfica de alguns dos megásporos que aparecem mais cedo no Brasil do que na Índia, sugerindo a migração da flora do Brasil para lá.

**Palavras-chave—**Megásporos, Pensilvaniano, bacia do Paraná, permiano, distribuição palaeogeográfica, Brasil, Índia.

### INTRODUCTION

The Late Palaeozoic Paraná Basin extends from Brazil to Uruguay, Argentina and Paraguay. It is an intracratonic interior sag basin, the subsidence of which was controlled by subduction along the western margin of Gondwana (Milani *et al.*, 1994). The most extensive lithological succession of late Palaeozoic Gondwana glaciation is in the Itararé Group of Paraná Basin (Rocha-Campos *et al.*, 2008). The sedimentary

succession has a maximum subsurface thickness of ~1400 m and extends over a total area greater than 1 million sq km (Fig. 1). The clastic conglomeratic rocks of this succession were interpreted as tillites for the first time by Derby(1888), a few decades after their preliminary identification in India (Blanford *et al.*, 1856) and in South Africa(Sutherland, 1870). The Brazilian rocks were immediately correlated with them (Rocha-Campos *et al.*, 2008). The lithostratigraphic division of the Itararé Group is not yet entirely solved: meanwhile in

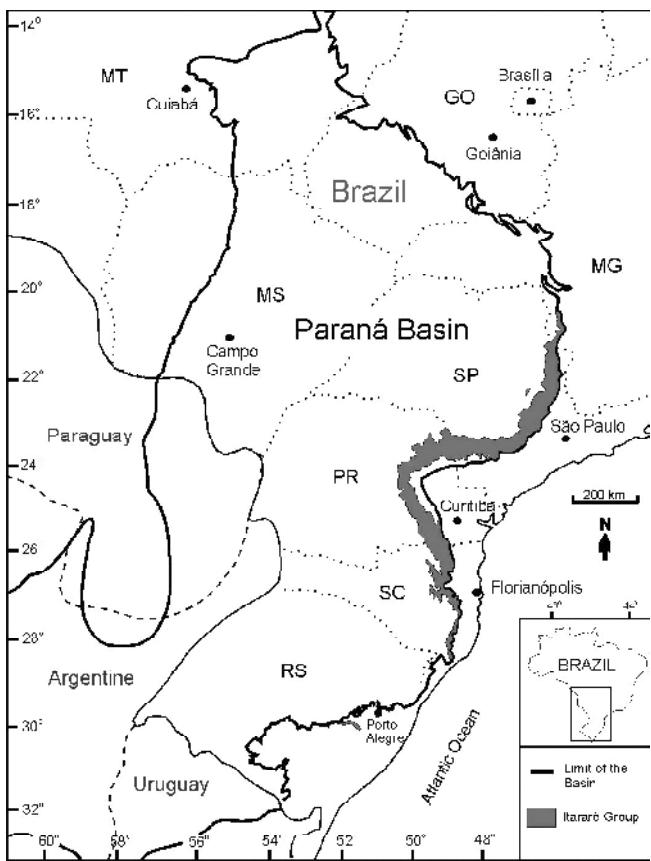


Fig. 1—Right border of Paraná Basin showing outcrop of Itararé Group.

the eastern outcrop band (Paraná and Santa Catarina states), the group has been subdivided into three formations. There is no generally accepted stratigraphic subdivision of the thick northeastern section in the State of São Paulo (Rocha-Campos, 1967; Rocha-Campos *et al.*, 2008). Distinct diamictite beds occur intercalated with sandstones, siltstones, shales and rhythmites in outcrops and in the subsurface of the Itararé Group as well. The relative proportions of these components vary according to their environmental settings. Stratigraphic thickness and lateral extent in the outcrop are also highly variable. The thickness of diamictite beds varies from tens of meters to a maximum of 150 m (Rocha-Campos *et al.*, 2008). Recurrent sets of analogous sedimentary lithofacies in outcrops and in the subsurface, plus other palaeoclimatic evidence (e.g., coal beds), support the interpretation that the glacial sedimentary cycles in the Itararé Group were probably controlled by climatic factors, as well as by a combination of glacial-isostatic, glacial-eustatic, and tectonic factors that remain poorly constrained (Rocha-Campos *et al.*, 1976, 2000, 2008; Tomio, 2004), Fig. 1. The palaeontological contents of these strata include both macro and microfossils of invertebrates, vertebrates and plants. The interglacial events in this sedimentary sequence are documented by several levels of Pre-Glossopterid and Proto-Glossopterid floras. However, fossil data (such as marine

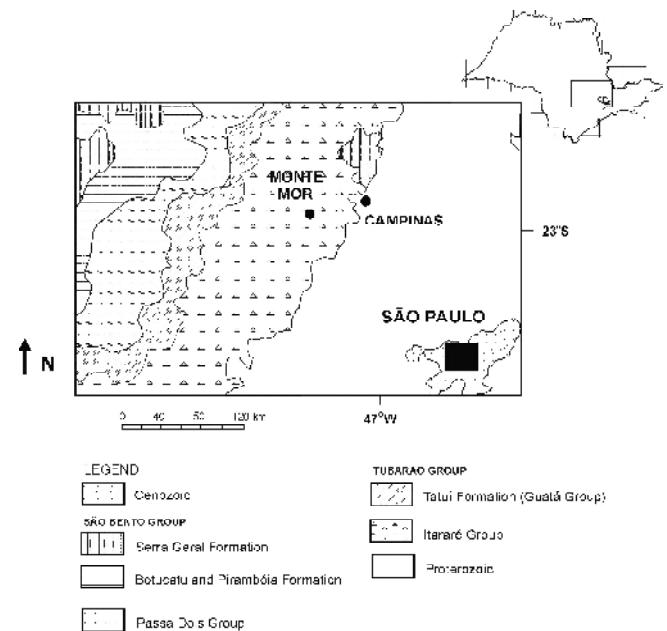


Fig. 2—Geological map of Campinas and Monte Mor areas showing location of the outcrops (Modified from IPT, 1981).

invertebrates and correlatable horizons) useful for correlation and for an accurate age calibration are scarce in these deposits. At present, the microfossils (megaspores and palynomorphs) seem to be the best biostratigraphic tools for this basin.

In the present communication, trilete, alete, azonate and gulate dispersed fossil megaspores have been recorded from the lower and middle levels of the Itararé Group from the northeastern border of the Paraná Basin (Lower Pennsylvanian) of the Campinas municipality (Upper Bashkirian-Lower Moscovian) and of the Monte Mor municipality (Kazimovian), São Paulo State, Brazil. Twenty-four species of megaspores from both localities have been systematically analyzed. Additionally, the synonymy of four megasporite taxa, viz. *Banksisporites labiosus*, *Sublagenicula tripartites*, *Lagenoisporites scutiformis* and *Setosporites* sp. has been discussed. Besides, an attempt has been made to correlate the Pennsylvanian megaspores of the northeastern border of the Paraná Basin, Brazil with the megaspores of Indian Gondwana basins.

## GEOLOGY OF THE AREA

Bandeirantes Highway outcrop located at 96 km from São Paulo City (Campinas Municipality) and Volpe Ranch (Monte Mor Municipality) in the State of São Paulo (Fig. 2), both localities Pennsylvanian in age, are situated at different stratigraphic levels of the Itararé Group. They correspond to interglacial floras of the northeastern border of the Paraná Basin, and were sampled for megaspores and palynomorph studies.

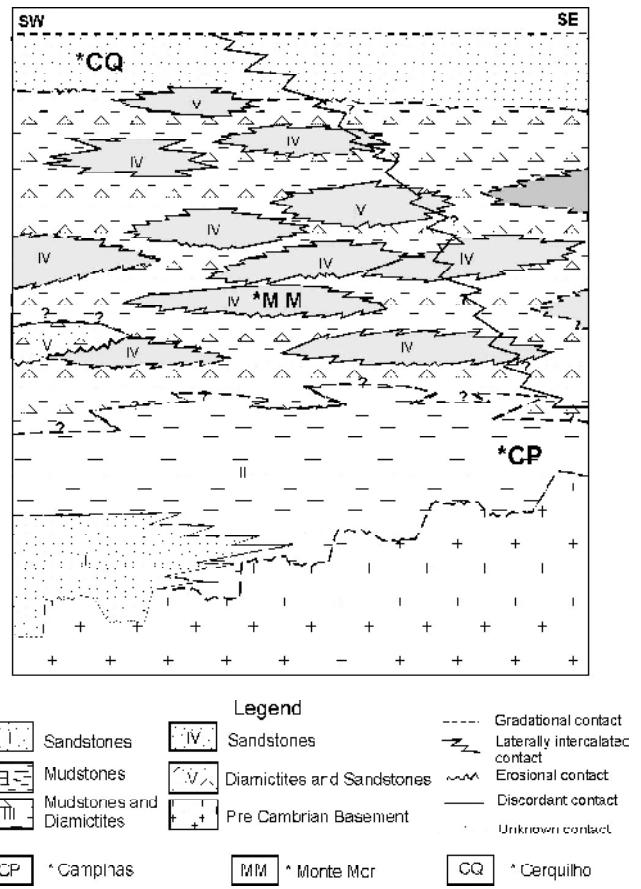


Fig. 3—Seven lithostratigraphical informal units of the Itararé Group in ascending order (Souza Filho, 1986), including the levels of the localities.

In a detailed geological mapping of the Pennsylvanian area including Campinas and Monte Mor localities, Souza Filho (1986) recognized the following informal lithostratigraphic units in ascending order: Unit I- fining-upward granulate sandstones; Unit II- mudstones; Unit III- mudstones and diamictites; Unit IV- sandstones; Unit V- diamictites and sandstones; Unit VI- sandstones with wave marks and Unit VII-red diamictites (Fig. 3). According to Souza Filho (1986), the outcrop located at 96 km on the Bandeirantes Highway is part of Unit II. It is composed of massive and stratified mudstones and rhythmite beds in the lower portion and siltstones and shales in the upper portion. The Unit II directly overlies the Pre-Cambrian basement and its lithology is laterally indented with that of Unit I, having a gradational contact with Unit III. The lithology of Unit II can be interpreted as distal subaqueous fan facies developed on high angles slopes or under glacial erosion and retreat of the glacier fluxes in a marine coastal area. The lithological column section of this outcrop (Amaral & Ricardi-Branco, 2004) shows intercalated massive mudstones and fine sandstones in the lower and the upper

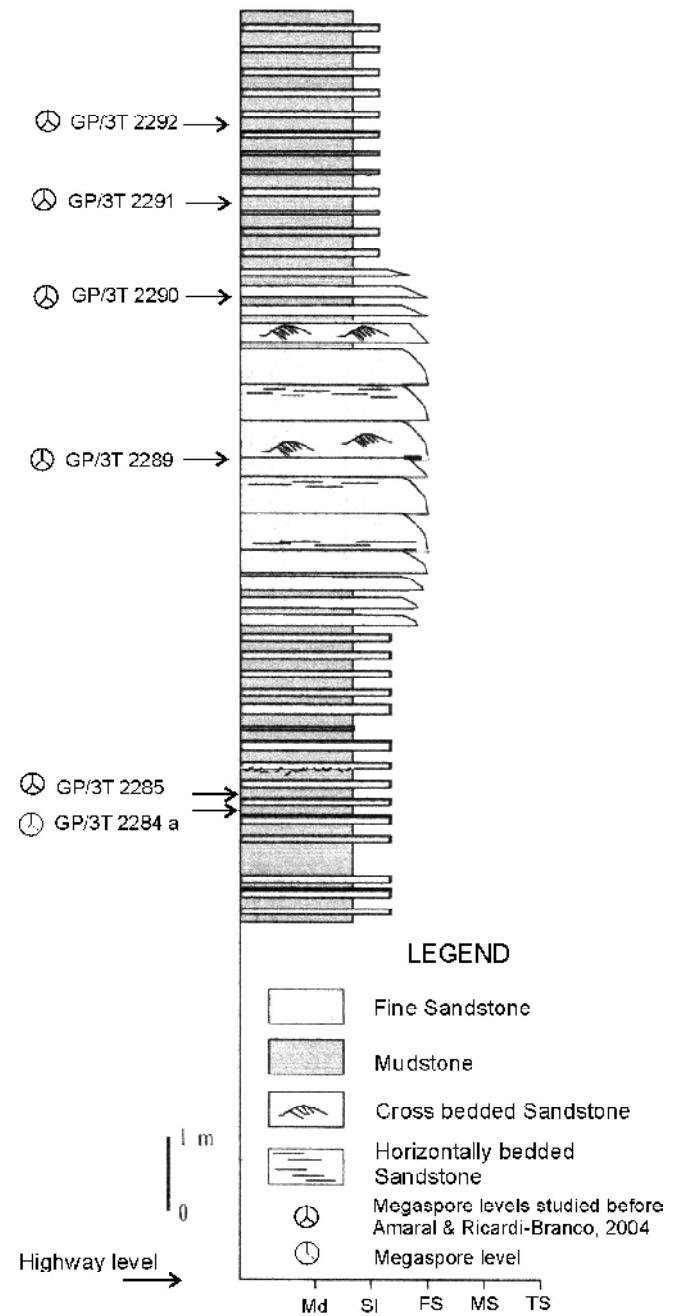


Fig. 4—Columnar section of the exposed levels of the outcrop located at 96 km on the Bandeirantes Highway, Campinas (São Paulo State), showing the megaspore levels of previous and present studies (modified from Amaral & Ricardi-Branco, 2004).

portions, respectively, with cross-bedded sandstones in the middle portion (Fig. 4).

The Monte Mor area, with its carbonaceous sediments is included in Unit IV (Souza Filho, 1986) and consists of conglomeratic sandstones, medium to fine grained sandstones, conglomeratic mudstones and coal beds. The Monte Mor area

corresponds to a facies of deltaic lobes with wave cross-bedded sandstones including deposits of proximal deltaic front or tidal plain and fluvial channels of deltaic plains, under a supraglacial facies of till of ablation flux and a subglacial facies with tillites and pebble pavements. In the Monte Mor facies of deltaic lobes, the mudstones with coal, muddy sandstones and greyish mudstones are rich in organic material (coal and plant remains) that were deposited on a flood plain continental environment, in a final sequence of pro-delta facies before the installation of a new glacial phase. The Volpe Ranch outcrop is located at the 22°56'47" S latitude and 47°18'56" W longitude, on the left margin of a creek, at 20 m from the mine entrance. The columnar section shows the fossiliferous levels in the lower portion of the exposition from where the megaspores of present study were recovered (Fig. 5).

The outcrop is composed of an alternate disposition of shales, carbonaceous mudstones, coal, siltstones and fine sandstone beds underlying a diamictite bed. Originally, these lower sedimentary beds and the upper tillite/diamictite beds of the Itararé Group were designated as Itu Formation (Barbosa & Almeida, 1949) and Elias Fausto Formation (Barbosa & Gomes, 1958), respectively.

### BIOSTRATIGRAPHY OF THE AREA

An improved scheme of the megafloristic succession of the Late Carboniferous to Early Permian palaeofloras from the northeastern Paraná Basin (State of São Paulo) was proposed by Bernardes-de-Oliveira *et al.* (2005). The lowermost of the five recognized megafloras of the Itararé Group corresponds to a tundra-like vegetation equivalent to the “*Dwykea-Sublagenicula-Calamospora Association*” (=DSC Association) found in Campinas (96 km, Bandeirantes Highway). It is mainly represented by lycopsid megaspores: *Lagenoisporites brasiliensis*, *Lagenoisporites sinuatus*, *Banksisporites tenuis*, *Calamospora* sp. and some bryophytes. The fossils were preserved in coastal glacial or cold interglacial rhythmites close to the base of the outcrop of Itararé Group. The palynoflora includes the *Ahrensisporites cristatus* Interval Zone (Souza, 2006) which indicates a Late Bashkirian to Kasimovian age.

The Volpe Ranch, in Monte Mor Municipality, Paraná Basin corresponds to the type-locality of the third megafloral succession level, namely “*Paranocladus-Ginkgophyllum-Brasilodendron Association*” (=PGB Association). The megaflora records the appearance of conifers (as indicated by abundance of *Paranocladus dusenii*, *Paranospermum* and less frequent representatives of the *Buriadia*-type), lycophytes (*Brasilodendron*, *Bumbudendron*), *Ginkgophyllum*-like leaves, *Noeggerathiopsis*, many species of the seed genera *Samaropsis* and *Cordaicarpus* and rare specimens of *Nothorhacopteris*, *Botrychiopsis*, *Koretrophylloites* and *Sphenophyllum*.

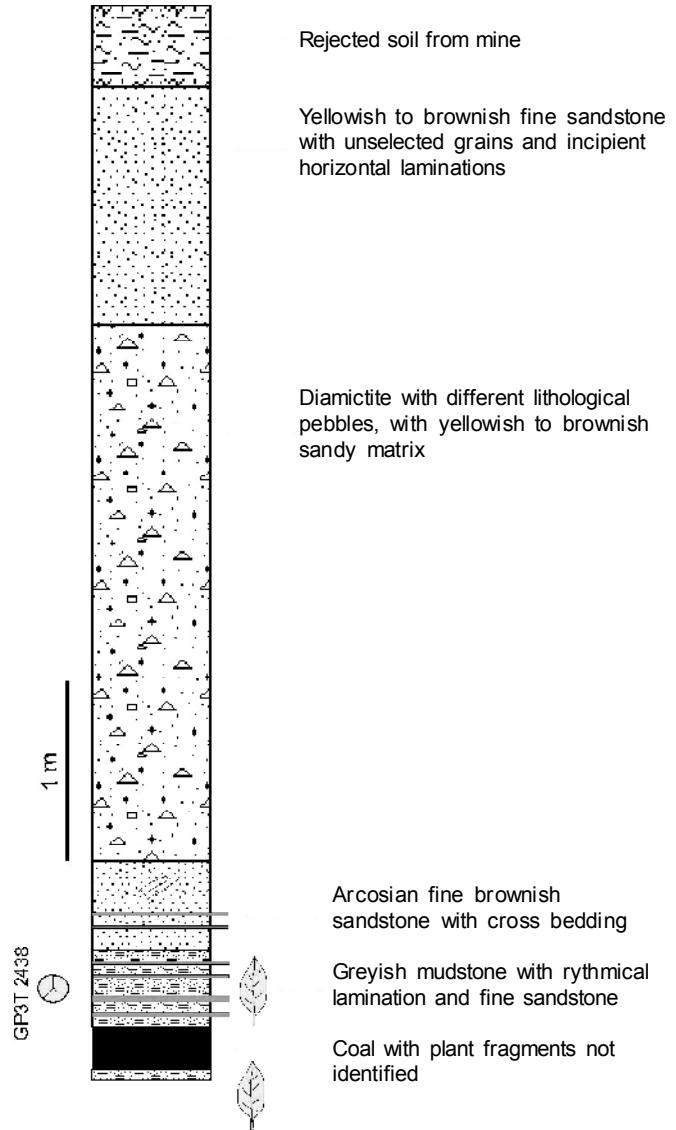


Fig. 5—Columnar section of the exposed levels on the creek margin at the Volpe Ranch, in Monte Mor.

The Pennsylvanian Monte Mor taphoflora was first studied by Millan (1972, 1974, 1976, 1977a, b, c, 1978, 1979a, b, 1980, 1981a, b, 1985) and revised by Mune (2005) and Mune and Bernardes-de-Oliveira (2007). The megaflora corresponds to the “Taphoflora A” of Rösler (1978) proposed for the Paraná Basin. It may further be correlated with the *Kräusecladus-Astrotheca* Phytozone of Argentina proposed by Carrizo and Azcuy (2006) who considered it to be of Upper Pennsylvanian (Kasimovian) - Cisuralian (Asselian) age. The palynological contents of Monte Mor were included in *Ahrensisporites cristatus* Interval Zone by Souza (2006). However, Mune and Bernardes-de-Oliveira (2009) on the basis of presence of *Scheuringipollenites maximus* suggested correlation with the *Crucisaccites monoletus* Interval Zone of Souza (2006). Based

Trindade (1970)	Mune (2005)
<i>Calamospora</i> sp.	= <i>Calamospora</i> sp.
<i>Trileites endosporitiferus</i> (Singh, 1955) Potonié, 1956	= <i>Banksisporites endosporitiferus</i> (Singh, 1953) Tewari & Maheshwari, 1992 emend. Glasspool, 2003
-----	= <i>Banksisporites tenuis</i> (Dijkstra, 1955b) Glasspool, 2003
-----	= <i>Banksisporites vulgatus</i> (Dijkstra, 1955b) emend. Glasspool, 2003
<i>Duosporites trivalis</i> (Dijkstra, 1955) Trindade & Sommer, 1966	= <i>Banksisporites indicus</i> (Singh, 1953) emend. Glasspool, 2003
<i>Trileites labiosus</i> (Dijkstra, 1955) Trindade, 1957	= <i>Banksisporites labiosus</i> (Dijkstra, 1955b) Glasspool, 2003
<i>Lagenoisporites scutiformis</i> Trindade, 1970	= <i>Lagenoisporites scutiformis</i> Trindade, 1970
<i>Lagenoisporites brasiliensis</i> (Dijkstra, 1955) Trindade, 1967	= <i>Sublagenicula brasiliensis</i> (Dijkstra) Dybová-Jachowicz et al., 1987 emend. Glasspool 2003
<i>Lagenoisporites sinuatus</i> (Dijkstra, 1955) Trindade, 1957	= <i>Sublagenicula brasiliensis</i> (Dijkstra) Dybová-Jachowicz et al., 1987 emend. Glasspool, 2003
<i>Lagenoisporites tripartites</i> Trindade, 1970	= <i>Sublagenicula tripartites</i> (Trindade, 1970) comb. nov.
<i>Setosisporites</i> sp.	= <i>Setosisporites</i> sp.

Fig. 6—Comparative list of megaspores recorded by Trindade (1970) and Mune (2005) from Monte Mor (São Paulo State) locality.

on this evidence, Stephanian (Kasimovian-Gzhelian) age is proposed for the Monte Mor taphoflora which is younger than that of Campinas taphoflora.

#### CAMPINAS AND MONTE MOR MEGASPORE ASSEMBLAGES

In spite of the immense significance of the contribution of the lycopsids in the formation of the Gondwanan coal measures of the Itararé Group considering their macro- and microfossils constituents, megaspore studies have relatively been less emphasized. The megaspores of Late Palaeozoic sequence of the Itararé Group are not as diversified as the microspores (Trindade, 1959a, b, 1960, 1970; Alarcon & Bernardes-de-Oliveira, 1999; Amaral & Ricardi-Branco, 2004; Mune, 2005).

Whereas, Amaral and Ricardi-Branco (2004), while studying the Campinas material, have followed Dybová-Jachowics et al. (1979, 1987) for the classification of megaspore species, Mune (2005) has followed classification of Glasspool (2003) in her study of Monte Mor material. However, Glasspool's (2003) classification is only based on external characters. He has not considered the characters of mesosporium for specific diagnosis of megaspores. Recently, Jha and Tewari (2009) have emphasized the significance of study of mesosporium for categorization of megaspore species. Presently, both exosporium and mesosporium features have been taken into consideration for precise circumscription of species.

Amaral and Ricardi-Branco (2004) recorded five megaspore species from the outcrop located at 96 km on Bandeirantes Highway, Campinas Municipality, viz. *Sublagenicula brasiliensis* (Dijkstra) Dybová-Jachowicz et al., 1979 emend. Glasspool, 2003, (= *Lagenoisporites brasiliensis* (Dijkstra, 1955) Trindade, 1970); *Sublagenicula sinuata* (Dijkstra, 1955) Dybová-Jachowicz, 1979, (= *Lagenoisporites sinuatus* (Dijkstra, 1955) Trindade, 1957); *Trileites endosporitiferus* (Singh, 1953) Potonié, 1956, (= *Banksisporites endosporitiferus* (Singh, 1953) Tewari & Maheshwari, 1992 emend. Glasspool, 2003; *Trileites tenuis* (Dijkstra, 1955) Trindade, 1957, (= *Banksisporites tenuis* Dijkstra, 1955) Glasspool, 2003 and *Calamospora* sp. In the present study, in addition to these taxa, *Banksisporites dijkstrae* (Singh, 1953) Tewari & Maheshwari, 1992, *Banksisporites utkalensis* (Pant & Srivastava, 1961) Tewari & Maheshwari, 1992, *Biharisporites spinosus* (Singh) Bharadwaj & Tiwari, 1970, *Bokarosporites psilatus* Bharadwaj & Tiwari, 1970, *Bokarosporites rotundus* Bharadwaj & Tiwari, 1970, *Duosporites perversus* (Dijkstra, 1971) Piérart 1989, *Duosporites* sp. a, *Lagenicula horrida*, *Lagenicula* sp., *Lagenoisporites cf. L. hispanicus* (Dijkstra, 1955) Piérart, 1961, *Lagenoisporites nudus* (Nowak & Zerndt, 1936) Potonié & Kremp, 1955, *Lagenoisporites rugosus* (Loose, 1932) Potonié & Kremp 1955, *Lagenosporites* sp. have been recorded. Most of these megaspores are trilete, gulate while a few of them are alete.

The megaspores from Monte Mor have earlier been recorded by Trindade (1970), and Mune (2005) (Fig. 6). Mune

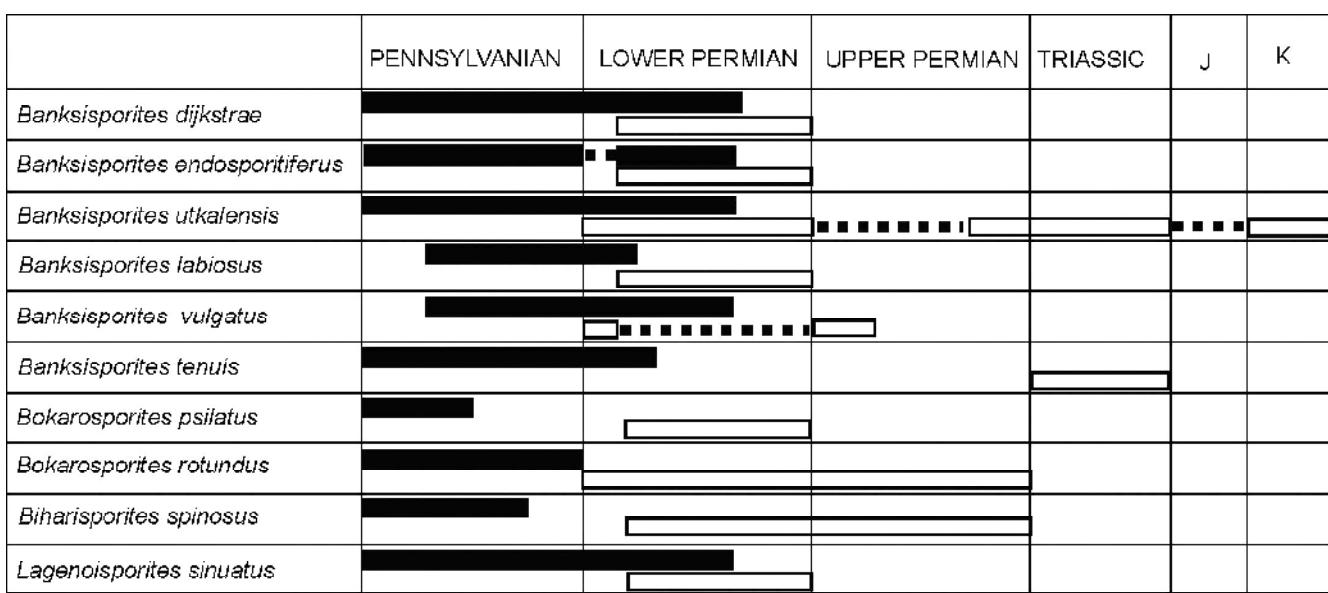


Fig. 7. Chronostratigraphical distribution of common species of megasporites between Brazil and India.

(2005) and Mune and Bernardes-de-Oliveira (2007) in their revision of Monte Mor material have registered the following taxa: *Banksisporites indicus* (Singh, 1953) emend. Glasspool 2003, *B. endosporitiferus* (Singh, 1953) Tiwari & Maheshwari, 1992 emend. Glasspool, 2003, *B. tenuis* (Dijkstra, 1955) Glasspool, 2003, *B. labiosus* (Dijkstra, 1955) Glasspool, 2003, *B. vulgatus* (Dijkstra, 1955) Glasspool, 2003, *Sublagenicula tripartites* (Trindade, 1970) Mune & Bernardes-de-Oliveira (2007) emend. *Sublagenicula brasiliensis* (Dijkstra 1955) Dybová-Jachowicz *et al.*, 1979 emend. Glasspool, 2003, *Lagenoisporites scutiformis* (Trindade, 1970), *Setosporites* sp. and *Calamospora* sp. Besides, these authors systematically analyzed and discussed the synonymies of the forms *Banksisporites indicus* (pars) (=*Banksisporites dijkstrae* (Singh, 1953) Tewari & Maheshwari, 1992), *Banksisporites indicus* (pars) (=*Banksisporites utkalensis* (Pant & Srivastava, 1961) Tewari & Maheshwari, 1992), *Sublagenicula brasiliensis* (Dijkstra, 1955) Glasspool, 2003 (pars) (=*Lagenosporites brasiliensis* (Dijkstra, 1955) Trindade, 1970), *Sublagenicula brasiliensis* (Dijkstra, 1955) Glasspool, 2003 (pars) (=*Lagenoisporites sinuatus* (Dijkstra, 1955) Trindade, 1957).

In addition to these megaspore species the present communication records for the first time, the taxa *Bokarosporites rotundus* Bharadwaj & Tiwari, 1970; *Duosporites* sp. b; *Lagenosporites* cf. *L. hispanicus* (Dijkstra, 1955) Piéart 1961; *L. nudus* (Nowak & Zerndt, 1936) Potonié & Kremp, 1955 and *L. rugosus* (Loose, 1932) Potonié & Kremp, 1955 from the Monte Mor Assemblage.

Based on the external features, exosporium and mesosporium characters, and comparison with the Indian material, twenty four species of trilete, alete, gulate and azonate megaspores have been recorded from Campinas and Monte Mor localities. List of Campinas megaspores from Upper Bashkirian-Lower Moscovian, includes the taxa *Bokarosporites rotundus* Bharadwaj & Tiwari, 1970, *Bokarosporites psilatus* Bharadwaj & Tiwari, 1970, *Banksisporites utkalensis* (Pant & Srivastava, 1961) Tewari & Maheshwari, 1992, *Banksisporites endosporitiferus* (Singh, 1953) Tewari & Maheshwari, 1992, *Banksisporites dijkstra* (Singh, 1953) Tewari & Maheshwari, 1992, *Banksisporites tenuis* (Dijkstra, 1955) Glasspool, 2003, *Biharisporites spinosus* (Singh) Bharadwaj & Tiwari, 1970, *Duosporites perversus* (Dijkstra, 1971) Piérart 1989, *Duosporites* sp.a, *Lagenicula horrida* Zerndt, *Lagenicula* sp., *Lagenoisporites rugosus* (Loose, 1932) Potonié & Kremp, 1955, *L. brasiliensis* (Dijkstra, 1955) Trindade, 1957, *L. sinuatus* (Dijkstra, 1955) Trindade, 1957, *L. nudus* (Nowak & Zerndt, 1936) Potonié & Kremp, 1955, *Lagenoisporites* cf. *L. hispanicus* (Dijkstra, 1955) Piérart, 1961 and *Lagenoisporites* sp. Of these, *Lagenoisporites rugosus*, *L. nudus*, *Lagenoisporites* cf. *L. hispanicus*, *L. brasiliensis*, *Bokarosporites rotundus* in addition to *Banksisporites vulgatus*, *Calamospora* sp. and *Duosporites* sp. b are also recorded from Kazimovian of Monte Mor. Additionally, taxonomical status of the taxa *Banksisporites labiosus*, *Lagenoisporites scutiformis* and *Sublagenicula tripartites* (Trindade, 1970) comb. nov. from the Monte Mor Assemblage has been discussed and occurrence of *Setosisporites* sp. remarked.

## MATERIAL AND METHODS

The megaspore assemblages have been recovered from carbonaceous shales of the lower most level of the Itararé Group (Westphalian) of Campinas and middle level of the same Group (Kazimovian) of Monte Mor, São Paulo State, Brazil. Samples were treated with concentrated hydroflouric acid for 5 to 10 days and then washed thoroughly with water. The specimens were then individually picked under low power binocular microscope. Some of them were photographed under SEM and studied for exosprium characters. Others were kept for one day in conc. nitric acid and potassium chlorate. They were again washed thoroughly with water followed by treatment with 5% potassium hydroxide. Differential controlled maceration in conc. nitric acid and potassium hydroxide revealed the mesosporium. Each specimen was photographed at this (wet/macerated) stage under transmitted light using a high power objective for details of ornamentation and mesosporium. The slides were finally mounted in canada balsam.

All the slides are deposited in the scientific collection of Institute of Geosciences, USP, São Paulo, Brazil.

## SYSTEMATICS

**Genus—CALAMOSPORA** Schopf *et al.*, 1944

**Type species—*Calamospora hartungiana*** Schopf *et al.*, 1944

*Calamospora* sp.

(Pl. 1.1-3)

### Regional Synonymy:

- 1970 - *Calamospora* sp. Trindade. Trindade, p. 468, fig. 26
- 2000 - *Calamospora* sp. Amaral, p.16, Plate. III, 1-2 and 5-6
- 2003 - *Calamospora* sp. Glasspool, p. 250.
- 2004 - *Calamospora* sp. Amaral & Ricardi-Branco, p. 259-260, fig. 3 (M-P)
- 2005 - *Calamospora* sp. Mune, p. 76-77, Plate XI, figs. 10, 12-15.
- 2007 - *Calamospora* sp. Mune & Bernardes-de-Oliveira, p. 434, fig. 10 (O).

**Description**—Two megaspores of oval to ellipsoidal outline, strongly plicate or folded, exine apparently smooth; triradiate and arcuate ridges not observed.

**Dimensions**—Overall size 900-1100 x 772-957 µm, size of folds 1070 x 17 µm.

**Comparison**—The specimen A7 (Pl. 1.1) resembles the specimen described by Trindade (1970, Fig. 26) in presence of large folds, although its contour is slightly triangular. The specimen A3 (Pl. 1.2, 3) compares well with the specimens described by Trindade (1970) and Amaral & Ricardi-Branco (2004) in overall morphology.

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (Amaral & Ricardi-Branco, 2004) and Monte Mor (São Paulo) (Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007); Rio Bonito Formation (Lower Permian): Charqueadas (Trindade, 1959b, 1964), Mina de Candiota (Dijkstra, 1955; Pant & Srivastava, 1962; Marques-Toigo *et al.*, 1975) (Figs 7, 8).

**Genus—BOKAROSPORITES** Bharadwaj & Tiwari, 1970

**Type species—*Bokarosporites psilatus*** Bharadwaj & Tiwari, 1970

*Bokarosporites psilatus* Bharadwaj & Tiwari, 1970

**Holotype—*Bokarosporites psilatus*** Bharadwaj & Tiwari, 1970, Pl.1, figs 1-3

(Pl. 2.8; Pl. 3.1, 3, 6; Pl. 5.1)

**Description**—Megaspores trilete, azonate, circular to subcircular in proximo-distal orientation; triradiate ridges well marked, tapering toward ends, arcuate ridges indistinct, contact area not visible, exosprium smooth, mesosporium thin, without cushions.

**Dimensions**—Overall size 1008-1563 x 1194-1354 µm, size of triradiate ridges 238-892 x 45-65 µm, width of arcuate ridges 48 µm(dry condition); overall size 600 x 450 µm, size of triradiate ridges 300 x 45 µm, width of arcuate ridges 15 µm, size of mesosporium 300 x 450 µm (wet condition).

**Comparison**—Megaspores are comparable with *Bokarosporites psilatus* (Bharadwaj & Tiwari, 1970, Plate I, 1, 4, 6-8) in shape, nature of triradiate ridges, smooth exosprium and mesosporium and absence of contact area.



Fig. 8—Stratigraphical and Geographical distribution of megaspores from Campinas and Monte Mor taphofloras (Itararé Group) in Paraná Basin Brazil and Indian Gondwana horizons. Data sources: 1= Amaral & Ricardi-Branco (2004); 2= Mune & Bernardes-de-Oliveira (2007); 3= Trindade (1970); 4= Dijkstra (1955); 5= Ricardi-Branco *et al.* (2002); 6= Tewari & Maheshwari (1992); 7= Trindade & Sommer (1966); 8= Trindade (1964); 9= Trindade (1959a, b); 10= Trindade (1960); 11= Pant & Srivastava (1962); 12= Marques-Toigo *et al.* (1975); 13= Cauduro & Zingano (1965); 14= Bortoluzzi & Veiga (1981); 15= Bharadwaj & Tewari (1970); 16= Glasspool (2003); 17= Trindade (1962); 18= Trindade (1966); 19= Arai & Rösler (1984); 20= Tewari *et al.* (2009a, b); 21= Banerji *et al.* (1978); 22= Tewari *et al.* (2004); 23= Srivastava & Tewari (2004); 24= Jha & Tewari (2003); 25= Tewari & Jha (2007); 26= Tewari *et al.* (2007); 27= Kar (1968); \* = Present study; ● = Referred before.



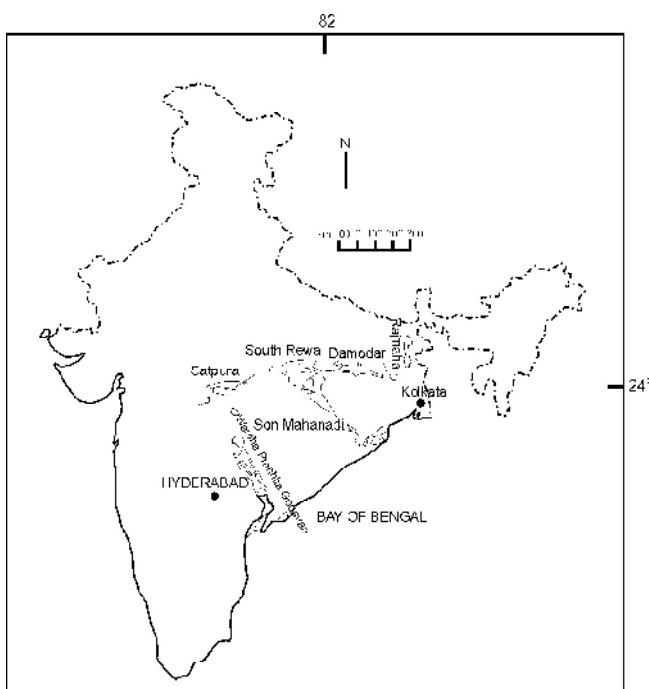


Fig. 9—Geographic location of Indian Gondwana basins.

*Geographic and Stratigraphic Distribution*—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (present study). India- Damodar Basin, Barakar Formation (Early Permian) (Bharadwaj & Tiwari, 1970) (Figs 7, 8).

**Bokarosporites rotundus** Bharadwaj & Tiwari, 1970

**Holotype**—*Triletes rotundus* Singh, 1953, Plate 2, Fig. 9

(Pl. 3.7, 9, 12; Pl. 4.3)

**Description**—Megaspores trilete, azonate, circular to subcircular in proximo-distal orientation; triradiate ridges well marked, tapering toward ends, bound by distinct arcuate ridges, contact area distinct, exosprium laevigate; mesosprium thin, transparent, spherical, almost 3/4 of the spore diameter, devoid of cushions.

**Dimensions**—Overall size 536-1226 x 689-923 µm, size of triradiate ridges 483-499 x 34-52 µm (dry condition); overall size 851 x 811 µm, size of triradiate ridges 220-431 x 69-106 µm, width of arcuate ridges 57 µm, size of mesosprium 534 x 709 µm (wet condition).

**Comparison**—Megaspores are comparable with *Bokarosporites rotundus* (Bharadwaj & Tiwari, 1970, Plate I, 9-14) in shape and nature of exosprium and mesosprium.

*Geographic and Stratigraphic Distribution*—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas and Monte Mor (São Paulo) (present study). India - Damodar Basin, Karharbari and Barakar formations (Early Permian) (Bharadwaj

& Tiwari, 1970; Tewari & Maheshwari, 1992); Wardha Basin, Barakar Formation (Early Permian) (Tewari *et al.*, 2004); Satpura Basin, Barakar Formation (Early Permian) (Srivastava & Tewari, 2004); Barren Measures Formation (Bharadwaj & Tewari, 1970); Godavari Graben, Raniganj Formation (Late Permian) (Jha & Tewari, 2003; Tewari & Jha, 2007; Tewari *et al.*, 2007); Mahanadi Basin, Raniganj Formation (Late Permian) (Tewari *et al.*, 2009a) (Figs 7, 8).

**Genus**—**BANKSISPORITES** Dettmann, 1961 emend.  
Banerji *et al.*, 1978

**Type species**—*Banksisporites pinguis* (Harris) Dettmann, 1961

*Banksisporites utkalensis* (Pant & Srivastava, 1961) Tewari and Maheshwari, 1992

**Holotype**—*Triletes utkalensis* Pant & Srivastava, 1961,  
Plate 31, Figs, 18-21

(Pl. 2.9,11; Pl. 3.5; Pl. 4.2,4-6,8,9,13; Pl. 5.2,5-7,9,10,15,17, 19,20)

**Regional Synonymy:**

1970 - *Duosporites trivalis* (Dijkstra) Trindade & Sommer, 1966.

Trindade, p. 468-469, figs 17-21.

2003 - *Banksisporites indicus* (Singh, 1953) emend. Glasspool, p.236-237

2005 - *Banksisporites indicus* (= *B.dijkstae* Singh, 1953) emend. Glasspool 2003. Mune, p. 81-82.

2007 - *Banksisporites indicus* (= *B.dijkstae* Singh, 1953) emend. Glasspool 2003. Mune & Bernardes-de-Oliveira, p. 434.

**Description**—Megaspores trilete, azonate, circular to subcircular in proximo-distal orientation, triradiate ridges straight to wavy, ¾ spore radius long, end up at distinct arcuate ridges; exosprium verrucate, verrucae uniformly distributed, visible in dry condition; mesosprium distinct, thin, spherical, ¾ of spore diameter, devoid of cushions.

**Dimensions**—Overall size 900-1081 x 737-1314 µm, size of triradiate ridges 237-436 x 31-65 µm, width of arcuate ridges 64 µm (dry condition); size of verrucae 9-11 x 11 µm (dry condition); overall size 649-1558 x 605-1499 µm, size of triradiate ridges 225-689 x 41-138 µm, width of arcuate ridges 30-82 µm, size of verrucae 8-12 x 11-16 µm, size of mesosprium 221-1248 x 170-1214 µm (wet condition).

**Comparison**—Megaspores are comparable in shape, nature of exosprium and mesosprium with *Banksisporites utkalensis* (Tewari & Maheshwari, 1992, Plate 2.7, Plate 6.1, 7).

*Geographic and Stratigraphic Distribution*—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (present study) and Monte Mor (São Paulo) (Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007); Rio Bonito Formation

(Lower Permian): Charqueadas (Trindade, 1959b, 1964), Mina de Candiota (Dijkstra, 1955; Pant & Srivastava, 1962; Marques-Toigo *et al.*, 1975; Glasspool, 2003), Barro Branco (Dijkstra, 1955; Trindade, 1959b, 1960; Pant & Srivastava, 1962; Glasspool, 2003); Palermo Formation: São Sepé (Cauduro & Zingano, 1965; Bortoluzzi & Veiga, 1981). India – Damodar Basin, Karharbari (Bharadwaj & Tiwari, 1970) and Barakar formations (Early Permian) (Bharadwaj & Tiwari, 1970; Tewari & Maheshwari, 1992); Wardha Basin, Barakar Formation (Early Permian) (Tewari *et al.*, 2004); Satpura Basin, Barakar Formation (Early Permian) (Srivastava & Tewari, 2004); Godavari Graben, Raniganj Formation (Late Permian) (Jha & Tewari, 2003; Tewari & Jha, 2007; Tewari *et al.*, 2007); Mahanadi Basin, Raniganj Formation (Late Permian) (Tewari *et al.*, 2009a); Jabalpur Formation (Early Cretaceous) (Tewari *et al.*, 2009b) (Figs 7, 8).

**Banksisporites dijkstrae** (Singh, 1953) Tewari & Maheshwari, 1992

**Holotype**—*Triletes indica* Singh, 1953, Plate 1, Fig. 3

(Pl. 3.2, 13; Pl. 4.1, 7; Pl. 5.8)

#### Regional Synonymy:

2005 - *Banksisporites indicus* (pars = B. Dijkstrae Singh, 1953) Glasspool 2003. Mune, p. 81-82.

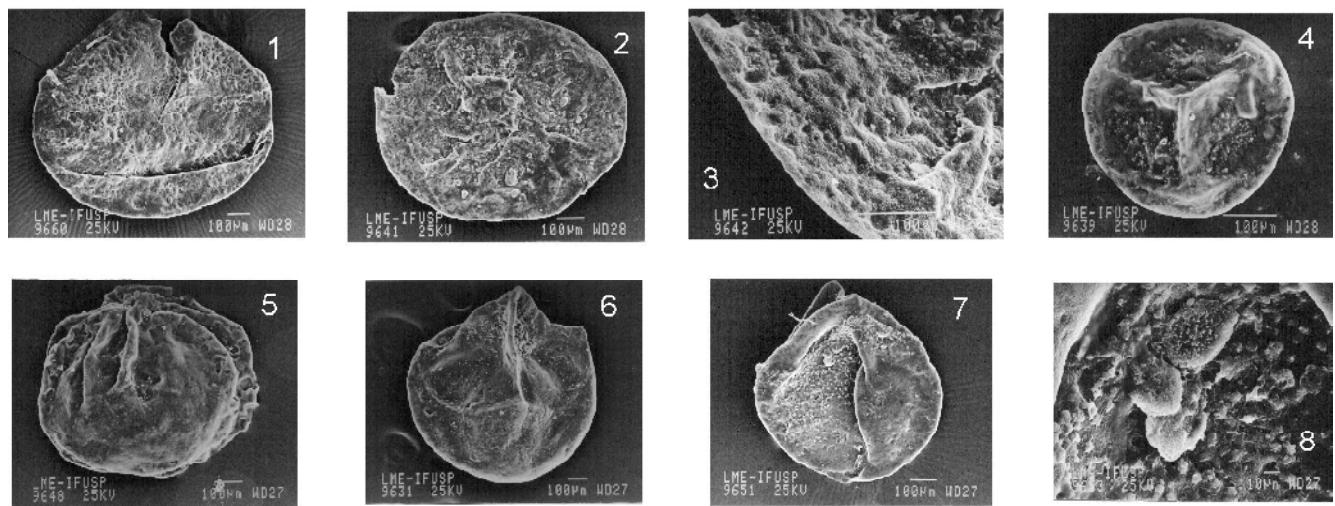
2007 - *Banksisporites indicus* (pars = B. Dijkstrae Singh, 1953) Glasspool 2003. Mune & Bernardes-de-Oliveira, p. 434.

**Description**—Megaspores trilete, azonate, circular in proximo-distal orientation; triradiate ridges well defined, straight to wavy, 2/3 to 3/4 of the spore radius, tapering at ends, ending up at arcuate ridges in wet condition, arcuate ridges not defined in dry condition; exosprium verrucate, verrucae closely set, differential maceration in concentrated HNO<sub>3</sub> and KOH reveals thin, subcircular mesosporium, mesosporium devoid of cushions.

**Dimensions**—Overall size 1075-1150 x 1130-1287 µm, size of tri-radiate ridges 273-679 x 36-84 µm, width of arcuate ridges 30 µm, size of verrucae 3 x 4 µm (dry condition); overall size 750-1044 x 600-1080 µm, size of triradiate ridges 195-558 x 15-75 µm, width of arcuate ridges 30-60 µm, size of verrucae 7-16 x 7-16 µm, size of mesosporium 600-861 x 525-862 µm (wet condition).

**Comparison**—In presence of granulate exosprium and mesosporium the present megaspores resemble *Banksisporites dijkstrae* (see Srivastavaesporites dijkstrae Bharadwaj & Tiwari, 1970, Plate 2.13-15).

**Geographic and Stratigraphic Distribution**—Brazil-Paraná Basin, Itararé Group (Pennsylvanian): Campinas (present study) and Monte Mor (São Paulo) (Trindade, 1970; Mune & Bernardes-de-Oliveira 2007; present study); Rio Bonito Formation (Lower Permian): Charqueadas (Trindade, 1959b, 1964), Mina de Candiota (Dijkstra, 1955; Pant & Srivastava, 1962; Marques-Toigo *et al.*, 1975), Barro Branco (Dijkstra, 1955; Trindade, 1959a, 1960; Pant & Srivastava, 1962; Glasspool, 2003); Palermo Formation, São Sepé (Cauduro &



**PLATE 1**  
Brazilian Pennsylvanian megaspores from northeastern margin of Paraná Basin.

1. *Calamospora* sp., specimen A7, Slide No. GP 3E 9172 and stub B.
2. *Calamospora* sp., specimen A3, Slide No. GP/3E 9172 and stub A.
3. Detail from 2, showing sculpture of the surface.
4. *Banksisporites vulgatus* (Dijkstra) emend. Glasspool 2003, specimen B11, Slide No. GP/3E 9172 and stub A.
5. *Banksisporites tenuis* (Dijkstra) emend. Glasspool 2003, specimen B14, Slide No. GP/3E 9172 and stub B.
6. *Lagenoisporites brasiliensis* (Dijkstra) Trindade, specimen A1, Slide No. GP/3E 9172 and stub A.
7. *Lagenoisporites brasiliensis* (Dijkstra) Trindade, specimen A8, Slide No. GP/3E 9172 and stub A.
8. Detail from 7, showing verrucate structures on the surface.

Zingano, 1965; Bortoluzzi & Veiga, 1981). India – Damodar Basin, Barakar Formation (Early Permian) (Bharadwaj & Tiwari, 1970; Tewari & Maheshwari, 1992) (Figs 7, 8).

**Banksisporites tenuis** (Dijkstra, 1955) Glasspool, 2003

**Holotype**—*Triletes tenuis* Dijkstra, 1955, Plate III. Fig. 17

(Pl. 1.5; Pl. 4.12)

#### Regional Synonymy:

1964 - *Triletes (Triletes) tenuis* (Dijkstra) Trindade. Trindade, p. 16-17, Est. I, fig. 4, Est. II, fig. 9, Est. III, fig. 17, Est. VI, fig. 29, Est. VIII, fig. 38, Est. IX, figs 40-41.

2003 - *Banksisporites tenuis* (Dijkstra) Glasspool. Glasspool, p. 243-244.

2004 - *Triletes tenuis*. Amaral & Ricardi-Branco, p. 259, figs 3 E-H.

2005 - *Banksisporites tenuis* (Dijkstra) Glasspool 2003. Mune, p. 78-80, plate XI, figs 18-19.

2007 - *Banksisporites tenuis* (Dijkstra) Glasspool 2003. Mune & Bernardes-de-Oliveira, p. 434, fig. 10 (P).

**Description**—Megaspore identified in wet condition, trilete, azonate, circular to subcircular in proximo distal orientation, triradiate ridges straight,  $\frac{3}{4}$  spore radius long, end up at distinct arcuate ridges; folds present on contact area in wet condition, exosporium scabrate, mesosporium, thin, spherical,  $\frac{3}{4}$  of spore diameter, devoid of cushions.

**Dimensions**—Overall size 914 x 894  $\mu\text{m}$ , size of triradiate ridges 430-447 x 69-73  $\mu\text{m}$ , width of arcuate ridges 62  $\mu\text{m}$ , size of mesosporium 765 x 495  $\mu\text{m}$ .

**Comparison**—Megaspore is comparable in shape, scabrate exosporium and nature of triradiate and arcuate ridges with *Banksisporites tenuis* (Pant & Srivastava, 1961, Plate XVIII, 18, 36).

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (present study), Buri (São Paulo) (Trindade, 1959a, 1960; Trindade & Sommer, 1966; Bharadwaj & Tewari, 1970, Glasspool, 2003) and Monte Mor (Trindade & Sommer, 1966; Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007); Rio Bonito Formation (Lower Permian): Mina de Candiota (Dijkstra, 1955), Barro Branco (Dijkstra, 1955; Trindade 1959a, 1960; Pant & Srivastava, 1962; Glasspool, 2003); Palermo Formation: São Sepé (Cauduro & Zingano, 1965; Bortoluzzi & Veiga, 1981). India – Damodar Basin, Barakar Formation (Early Permian) (Bharadwaj & Tiwari, 1970) (Figs 7, 8).

**Banksisporites endosporitiferus** (Singh, 1953) Tewari and Maheshwari, 1992 emend. Glasspool, 2003

**Holotype**—*Triletes endosporitiferus* Singh, 1953, Plate 2, Fig. 6

(Pl. 5.11)

#### Regional Synonymy:

1970 - *Triletes (Triletes) endosporitiferus* (Singh 1953) Potonié 1956. Trindade, p. 468, fig. 22 and 24.

2004 - *Triletes endosporitiferus*. Amaral & Ricardi-Branco, p. 256.

2005 - *Banksisporites endosporitiferus* (Singh, 1953) Tewari & Maheshwari, 1992 emend. Glasspool 2003 - Mune, p. 77-78.

2007 - *Banksisporites endosporitiferus* (Singh, 1953) Tewari & Maheshwari, 1992 emend. Glasspool 2003 - Mune & Bernardes-de-Oliveira, p. 434.

**Description**—Megaspore identified in wet condition, trilete, azonate, circular in proximo-distal orientation, triradiate ridges straight,  $\frac{3}{4}$  spore radius long, end up at distinct arcuate ridges, widest at contact rims; contact area distinct, exosporium thick, finely verrucate to granulate, mesosporium, thin, subcircular,  $\frac{3}{4}$  of spore diameter, devoid of cushions.

**Dimensions**—Overall size 1125 x 1200  $\mu\text{m}$ , size of triradiate ridges 375 x 90  $\mu\text{m}$ , width of arcuate ridges 75  $\mu\text{m}$ , size of mesosporium 1050 x 900  $\mu\text{m}$ .

**Comparison**—In presence of fine ornamentation, nature of arcuate ridges and mesosporium the present megaspore resembles *Banksisporites endosporitiferus* (Bharadwaj & Tiwari, 1970, Plate III, 2).

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (present study), Buri (São Paulo) (Trindade, 1959a, 1960; Trindade & Sommer, 1966; Bharadwaj & Tewari, 1970, Glasspool, 2003) and Monte Mor (Trindade & Sommer, 1966; Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007); Rio Bonito Formation (Lower Permian): Mina de Candiota (Dijkstra, 1955), Barro Branco (Dijkstra, 1955; Trindade 1959a, 1960; Pant & Srivastava, 1962; Glasspool, 2003); Palermo Formation: São Sepé (Cauduro & Zingano, 1965; Bortoluzzi & Veiga, 1981). India – Damodar Basin, Barakar Formation (Early Permian) (Bharadwaj & Tiwari, 1970) (Figs 7, 8).

**Banksisporites vulgatus** (Dijkstra 1955) Glasspool, 2003

**Holotype**—*Triletes vulgatus* Dijkstra 1955, P. 6, Plate I, Figs 1-4

(Pl. 1.4)

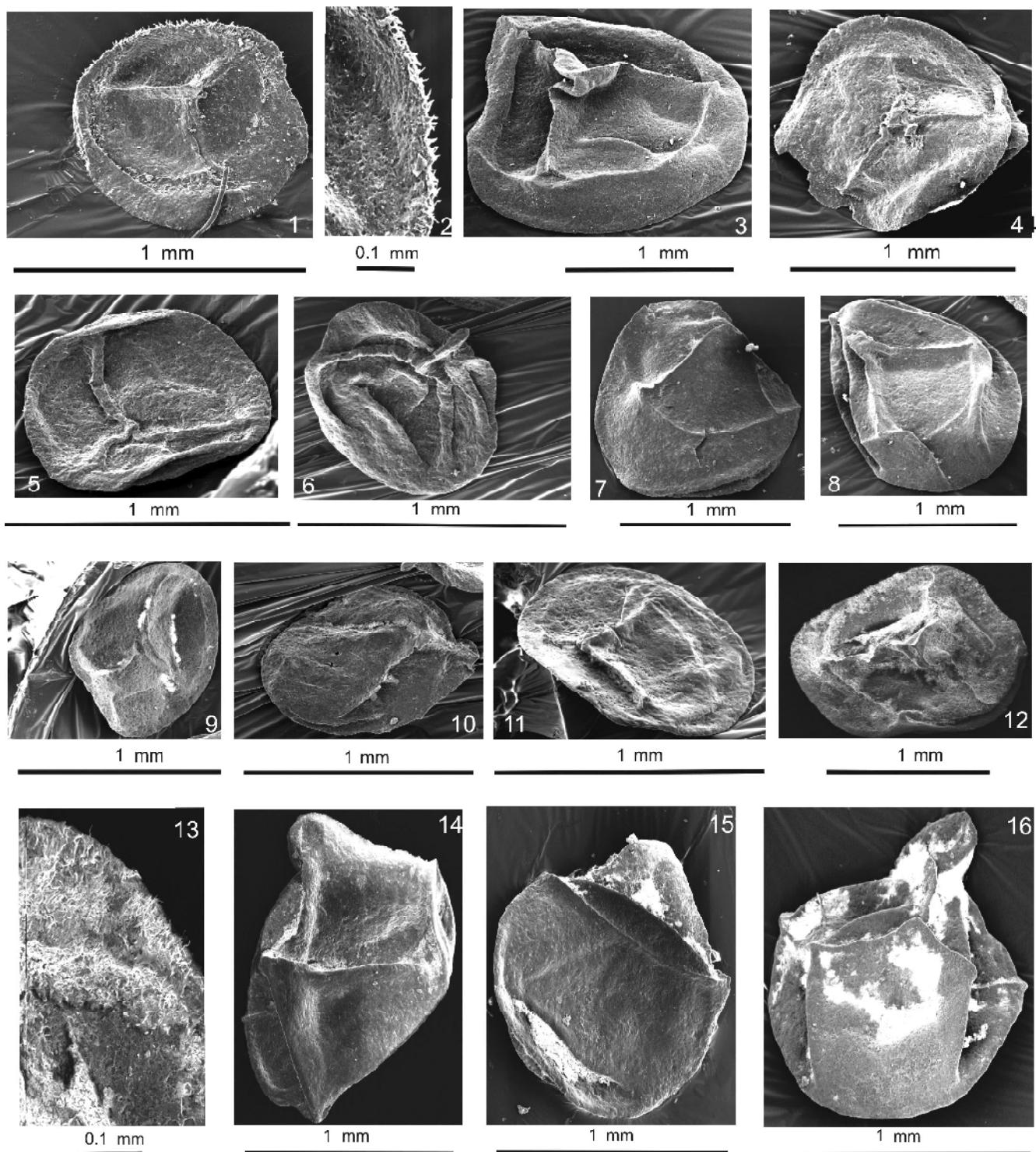
#### Regional Synonymy:

2003 - *Banksisporites vulgatus* (Dijkstra) Glasspool, 2003, p. 244.

2005 - *Banksisporites vulgatus* (Dijkstra) emend. Glasspool, 2003. Mune, p. 80-81, plate XI, figs 16-17.

2007 - *Banksisporites vulgatus* (Dijkstra) emend. Glasspool, 2003. Mune & Bernardes-de-Oliveira p. 434.

**Description**—Small megaspore, devoid of gula, outlines rounded, flattened in proximo-distal orientation. Triradiate ridges almost as long as the radius, increase in height towards



## PLATE 2

Brazilian Pennsylvanian megaspores from northeastern margin of Paraná Basin.

1. *Biharisporites spinosus* (Singh) Bharadwaj & Tiwari.
2. Part of megaspore in 1 enlarged to show spines.
3. *Lagenoisporites sinuatus* (Dijkstra) Trindade.
4. *Lagenoisporites cf. hispanicus* (Dijkstra) Piérart.
- 5, 7. *Lagenoisporites rugosus* (Loose) Potonié & Kremp.
6. *Lagenoisporites* sp.
8. *Bokarosporites psilatus* Bharadwaj & Tiwari.
- 9, 11. *Banksisporites utkalensis* (Pant & Srivastava, 1961) Tewari & Maheshwari.
10. *Duosporites perversus* (Dijkstra) Piérart.
12. *Lagenicula horrida* Zerndt.
13. Detail from megaspore in 12 enlarged to show spines.
14. *Lagenoisporites brasiliensis* (Dijkstra) Trindade.
- 15, 16. *Lagenoisporites nudus* (Nowak & Zerndt) Potonié & Kremp.

the apex. Arcuate ridges narrow and poorly defined. Contact surface slightly concave, shows small pores when observed under optical stereomicroscope and globules of similar size under SEM. Exine brown.

**Dimensions**—Diameter 367 µm; length of triradiate ridges 143–168 µm, width of triradiate ridges 10 µm, height of triradiate ridges 16 µm; width of arcuate ridges 11 µm, height of arcuate ridges 14 µm.

**Comparison**—The studied specimen is comparable with *Trileites* (=*Banksisporites*) *vulgatus* Dijkstra (1955, p. 6, Plate I, 1-4) in shape and size. As noted by Dijkstra (1955), specimens of this species resemble abortive forms of *T. brasiliensis*, which are, however, devoid of a neck (gula). This author also reported certain similarities between *T. vulgatus* and *T. nitens*. *T. nitens*, however, differs in larger dimensions and relatively short triradiate ridges. Trindade (1959), while studying the Charqueadas (RS) megaspores proposed the merge of *Trileites vulgatus* Dijkstra (1955) with *Trileites (Trileites) vulgatus* (Dijkstra) Trindade as suggested earlier by Trindade (1957). In 1960, Trindade made a revision of the genus *Trileites* in Brazilian Gondwana and following Potonié (1956), retained this designation for circular to subtriangular megaspores that show straight triradiate ridges reaching almost the equator and smooth to finely granulate or wrinkled exine. He included *T. vulgatus* Dijkstra 1955 in this category. The genus *Trileites* Potonié is distinguished from *Lagenoisporites* (Potonié & Kremp, 1954) Dybová-Jachowicz *et al.* 1979 in absence of gula. Pant and Srivastava (1962) proposed a new combination for the species *T. vulgatus*, within the genus *Duosporites vulgatus* Hoeg *et al.*, 1955, provided an emended diagnosis, based on observations of internal features (mesosporium) viewed under transmitted light in macerated megaspores. Glasspool (2003) recombined the epithet *vulgatus* in the genus *Banksisporites*, based on the following arguments: (a) trilete rays which do not exceed the equator, i.e. the boundary between the proximal and distal sides; (b) are not observable under transmitted light and absence of internal characteristics typical of *Duosporites*; (c) concave contact surface and (d) the height of the trilete rays which decreases from the apex to the arcuate ridges. This is the first record of the typical Early to Middle Permian species in Monte Mor Assemblage.

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian) Monte Mor, São Paulo (Mune & Bernardes-de-Oliveira, 2007); Rio Bonito Formation (Lower Permian): Barro Branco Bed, Criciúma, SC (Dijkstra, 1955; Trindade, 1959a, 1960; Pant & Srivastava, 1962; Trindade & Sommer, 1966; Glasspool, 2003), Charqueadas (Trindade 1959b, 1960, 1964), RS; Candiota (Dijkstra, 1955; Pant & Srivastava, 1962; Marques-Toigo *et al.*, 1975 and Trindade & Sommer, 1966) and Butiá, RS (Dijkstra, 1955; Trindade, 1960; Trindade & Sommer, 1966); Palermo Formation (Lower Permian) - Argilito de São Sepé, RS (Cauduro & Zingano, 1965; Bortoluzzi & Veiga, 1981). India - Damodar Basin, Karharbari Formation

(Lower Permian), Glasspool, 2003 and Barren Measures Succession (Early-Late Permian), Kar, 1968; Glasspool, 2003). (Figs 7, 8).

***Banksisporites labiosus*** (Dijkstra, 1955) Glasspool, 2003

**Regional Synonymy:**

1970 - *Trileites (Trileites) labiosus* (Dijkstra 1955) Trindade 1957. Trindade, p. 467, fig. 16.

2003 - *Banksisporites labiosus* (Dijkstra 1955) comb. nov. Glasspool, p. 239 and plate I, 1.

2005 - *Banksisporites labiosus* (Dijkstra 1955) Glasspool. Mune, p. 82.

2007 - *Banksisporites labiosus* (Dijkstra 1955) Glasspool. Mune & Bernardes-de-Oliveira, p. 434.

**Remarks**—The genus *Banksisporites labiosus* has not been recovered in the present study. Trindade (1970), analyzing the Monte Mor material, identified *Trileites (Trileites) labiosus* (Dijkstra, 1955). Trindade as a symmetrical, subtriangular megaspore with triradiate ridges spanning two thirds of the radius of the spore, indistinct arcuate ridges and finely punctate psilate exine. Glasspool (2003: 239) analyzed the species *Triletes labiosus* Dijkstra 1955 as a trilete spore distinguished by small auricles present at the intersection of trilete rays and arcuate ridges, and recombined this species with *Banksisporites labiosus*. The genus *Triletes* has been used only for forms that are not well defined. The Monte Mor forms are better defined and agree with the generic specifications of *Banksisporites* (Dettmann, 1961) Glasspool, 2003.

**Geographic and Stratigraphic Distribution**—Brazil - Itararé Group (Pennsylvanian)- Monte Mor, São Paulo (Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007); Rio Bonito Formation (Early Permian); Charqueadas (Trindade, 1959b, 1960, 1964), RS; Barro Branco BedSC (Dijkstra, 1955; Trindade, 1959a; Trindade, 1960; Pant & Srivastava, 1962; Glasspool, 2003). India – Barakar Formation (Bharadwaj & Tiwari, 1970; Glasspool, 2003) (Figs 7, 8).

**Genus—BIHARISPORITES** Potonié, 1956 emend.  
Bharadwaj & Tiwari, 1970

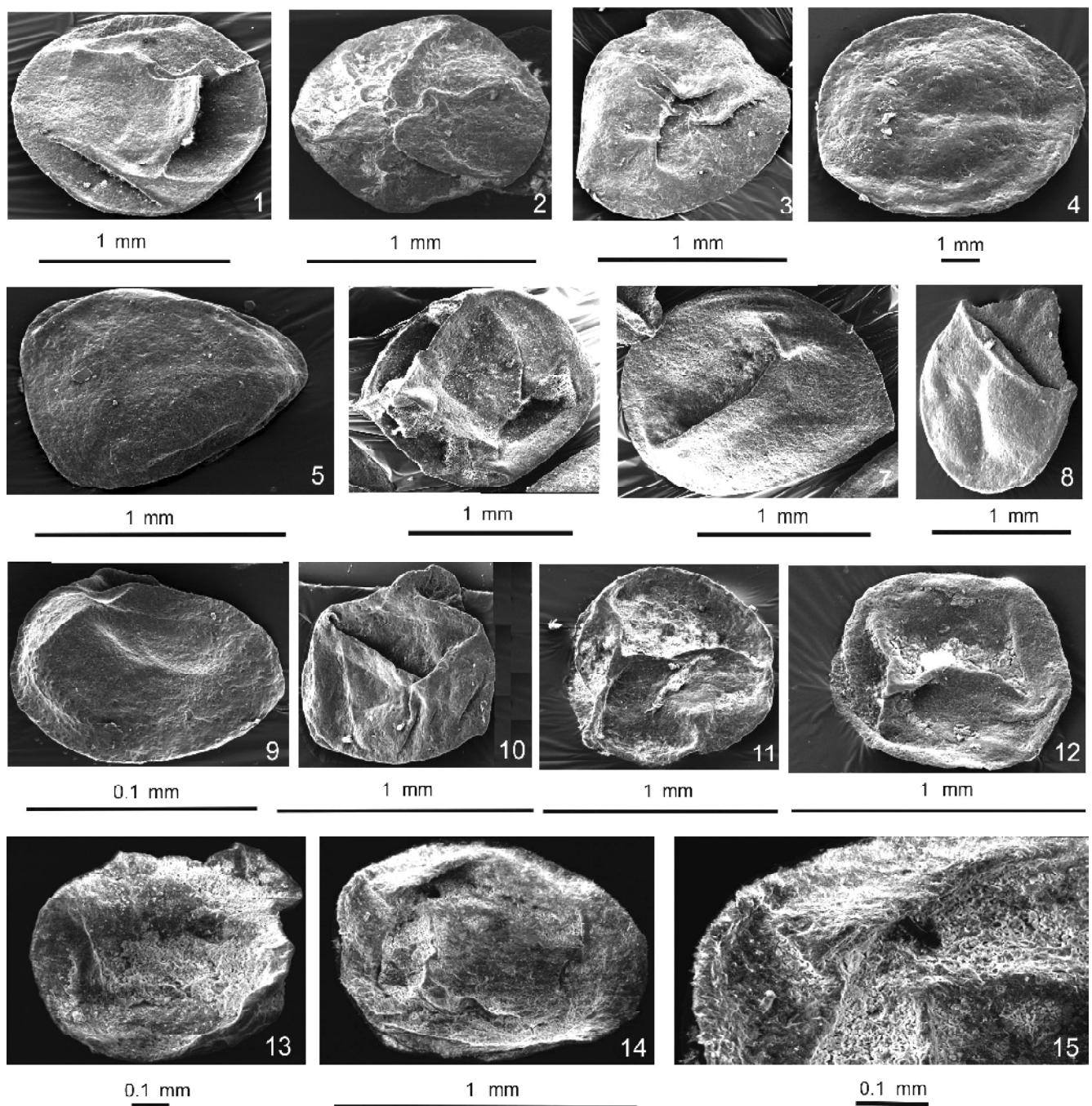
**Type species—*Biharisporites spinosus*** (Singh) Bharadwaj & Tiwari, 1970

***Biharisporites spinosus*** (Singh) Bharadwaj & Tiwari, 1970

**Holotype—*Triletes spinosus*** Singh, 1953 Plate 1, Fig. 1

(Pl. 2.1,2; Pl. 3.14, 15; Pl. 4.11)

**Description**—Megaspores trilete, circular, azonate; triradiate ridges distinct, straight to sinuous, more than 3/4 spore radius long, ending up at arcuate ridges, arcuate ridges



## PLATE 3

Brazilian Pennsylvanian megaspores from northeastern margin of Paraná Basin.

- 1, 3, 6. *Bokarosporites psilatus* Bharadwaj & Tiwari.  
 2, 13. *Banksisporites dijksterae* (Singh) Tewari & Maheshwari.  
 4. *Duosporites* sp.a.  
 5. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari.  
 7, 9, 12. *Bokarosporites rotundus* Bharadwaj & Tiwari.  
 8. *Lagenoisporites* sp.  
 10. *Lagenoisporites rugosus* (Loose) Potonié & Kremp.  
 11. *Duosporites perversus* (Dijkstra) Piérart.  
 14. *Biharisporites spinosus* (Singh) Bharadwaj & Tiwari.  
 15. Detail from 14 enlarged to show spines.

well defined, contact area circular in dry condition, triradiate and arcuate ridges not clear in wet condition, exosporium spinate, spines distinct, more prominent on margin, sparser on the remaining part of spore body, tips of spines pointed, mesosporium thin, transparent, subspherical, devoid of cushions.

**Dimensions**—Overall size 737-1531 x 777-1096 µm, size of triradiate ridges 120-533 x 42-70 µm, width of arcuate ridges 36-82 µm, length of spines 6-34 µm, width of spines at base 6-15 µm, width of spines at apex 1-8 µm (dry condition); overall size 854 x 783 µm, length of spines 20-21 µm, width of spines at base 11-13 µm, width of spines at apex 8-9 µm, size of mesosporium 700-795 x 623-700 µm (wet condition).

**Comparison**—Megaspores are comparable in shape, nature of exosporium and nature of mesosporium with *Biharisporites spinosus* (Bharadwaj & Tiwari, 1970, Plate VIII, 15; Plate IX, 2, 4, 5; Tewari & Maheshwari 1992, Plate V, 5).

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (present study). India - Damodar Basin, Barakar Formation (Early Permian) (Bharadwaj & Tiwari, 1970; Tewari & Maheshwari, 1992); Barren Measures Formation (Bharadwaj & Tiwari, 1970; Glasspool, 2003); Godavari Graben, Raniganj Formation (Late Permian) (Jha & Tewari, 2003; Tewari & Jha, 2007); Mahanadi Basin, Raniganj Formation (Late Permian) (Tewari *et al.*, 2009a) (Figs 7, 8).

**Genus—DUOSPORITES** Høeg *et al.*, 1955 emend.

Bharadwaj & Tiwari, 1970

**Type species—*Duosporites congoensis*** Høeg *et al.*, 1955

*Duosporites perversus* (Dijkstra, 1971) Piérart, 1989

**Holotype—*Duosporites perversus*** Dijkstra, 1971 Plate III, figs 1-2

(Pl. 2.10; Pl. 3.11)

**Description**—Two megaspores identified under SEM in dry condition, could not be recovered after treatment with concentrated HNO<sub>3</sub>, trilete, oval or rounded in outline, azonate; triradiate ridges distinct, straight to slightly wavy, two ridges extend up to arcuate ridges, while third tends to extend beyond them (Pl. 3.11), arcuate ridges clear in one specimen (Pl. 3.11) where almost merged with margin and not visible in the other specimen (Pl. 2.10), exosporium apparently verrucate.

**Dimensions**—Overall size 1288-1322 x 894-1384 µm, size of triradiate ridges 335-699 x 36-71 µm, width of arcuate ridges 112-125 µm.

**Comparison**—Megaspores are comparable in shape, nature of exosporium, nature of triradiate ridges and in having indistinct arcuate ridges in one of the specimens with *Duosporites perversus* (Piérart, 1989; Pl. 3.1, 2).

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (present study) (Fig. 8)

***Duosporites* sp. a**

(Pl. 3.4)

**Description**—Megaspore identified under SEM in dry condition, trilete, triangular in outline, azonate; triradiate ridges distinct, straight, extending up to margin, arcuate ridges indistinct, apparently merged with margin, contact area indistinct, exosporium apparently verrucate.

**PLATE 4**  
Brazilian Pennsylvanian megaspores from northeastern margin of Paraná Basin.



1. *Banksisporites dijkstrae* (Singh) Tewari & Maheshwari; 1, GP/3E9073b; Slide No. 1; 7, GP/3T2284a; Sl. No. 4.
2. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari. GP/3T2284a, Slide No. 8a.
3. *Bokarisporites rotundus* Bharadwaj & Tiwari; GP/3T2284a; Slide No. 10e.
4. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari. GP/3T2284a, Slide No. 14d.
5. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari. GP/3T2284a, Slide No. 9a.
6. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari. GP/3T2284a, Slide No. 8b.
7. *Banksisporites dijkstrae* (Singh) Tewari & Maheshwari; 1, GP/3E9073b; Sl.No.1; GP/3T2284a; Slide No. 4.
8. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari. GP/3T2284a, Slide No. 5.
9. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari. GP/3T2284a, Slide No. 2b.
10. *Lagenoisporites* sp.; GP/3T2284a; Slide No. 10d.
11. *Biharisporites spinosus* (Singh) Bharadwaj & Tiwari; GP/3T2284a; Slide No. 20.
12. *Banksisporites tenuis* (Dijkstra) Glasspool; GP/3T2284a; Slide No. 1.
13. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari. GP/3T2284a, Slide No. 10c.
14. *Duosporites* sp.b; GP/3E9073b; Slide No. 2b.
15. *Lagenicula horrida* Zerndt; GP/3T2284a; Slide No. 13a.
16. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3E9073b; Slide No. 2a.
17. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 13b.
18. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 6a.
19. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 14a.
20. *Lagenoisporites nudus* (Nowak & Zerndt) Potonié & Kremp; GP/3T2284a; Slide No. 19.

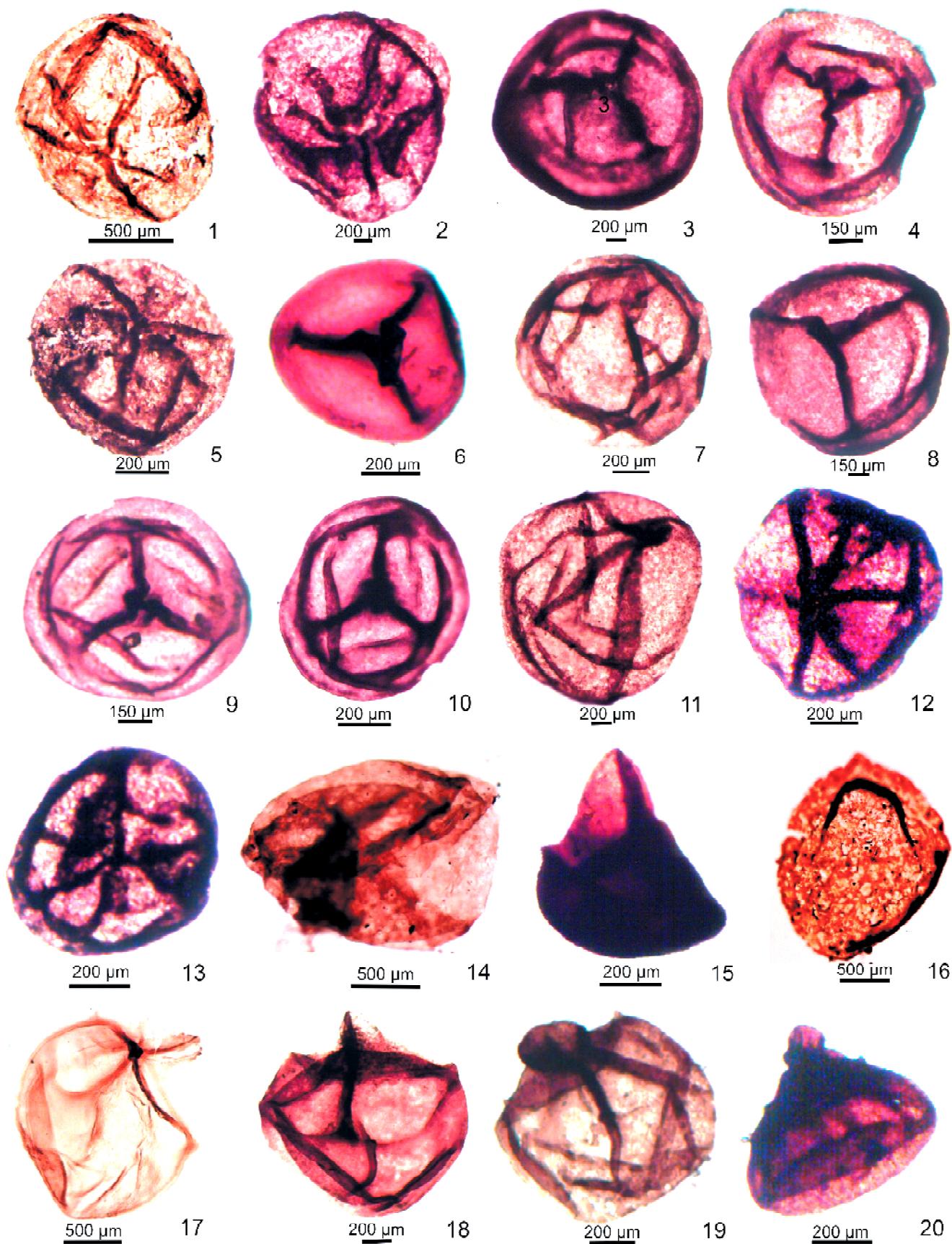


PLATE 4

**Dimensions**—Overall size 1496 x 1067 µm, size of triradiate ridges 395-932 x 53-66 µm, size of verrucae 6-10 x 7-11 µm.

**Remarks**—Since the megasporite was identified in dry condition its mesosporite could not be studied. However, since it is comparable in shape, nature of exosporite and nature of triradiate ridges with the genus *Duosporites* it is not given a specific status here and is designated as *Duosporites* sp. a.

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (present study) (Fig. 8).

#### *Duosporites* sp. b

(Pl. 4.14)

**Description**—Megaspores identified in wet condition, trilete, triangular in outline, azonate; triradiate ridges distinct, straight, extending up to margin, arcuate ridges and contact area indistinct, apparently merged with margin, exosporite apparently verrucate, mesosporite triangular, hyaline with folds, cushions, if present not visible due to folds.

**Dimensions**—Overall size 820-1368 x 619-1849 µm, size of triradiate ridges 138-969 x 30-191 µm, size of verrucae 12 x 12 µm, size of mesosporite 660-1651 x 420-1174 µm.

**Remarks**—Megaspores are comparable in shape, nature of exosporite, nature of triradiate ridges and nature of mesosporite with the genus *Duosporites*. However, cushions are not visible. Hence, it is not given a specific status here and is described as *Duosporites* sp.b

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Monte Mor (SP) (present study) (Fig. 8).

**Genus**—**LAGENICULA** (Bennie & Kidston, 1886) Zerndt, 1934, Potonié and Kremp, 1954 emend. Spinner, 1969

**Type species**—*Lagenicula horrida* Zerndt, 1934

*Lagenicula horrida* Zerndt, 1934

**Holotype**—*Lagenicula horrida* Zerndt, 1934, Taf. 28, Fig. 1

(Pl. 2.12, 13; Pl. 4.15)

**Description**—Megasporite identified under SEM in dry condition, lageniculate / gulate, trilete, subcircular in outline, triradiate ridges distinct, straight to slightly wavy, extend up to arcuate ridges, raised into neck like projection-gula along with arcuate ridges and contact area, polar axis longer than equatorial axis, exosporite spinate.

**Dimensions**—Overall size 1059 x 1481 µm, size of triradiate ridges 491-634 x 27-29 µm, width of arcuate ridges 87 µm, length of gula 163 µm, width of gula at base 176 µm, width of gula at apex 46 µm, length of spines 6-9 µm, width of spines at base 1-2 µm, width of spines at apex 0.3-0.9 µm.

**Remarks**—Megaspore is comparable in presence of spinate exosporite and gula with *Lagenicula horrida* Zerndt (Zerndt, 1934, Plate XXVIII, 2, 5). However, splitting of gula into three subtriangular segments (Zerndt, 1934, XXVIII, 1, 3, 4; Potonié & Kremp, 1955, Plate IV, 20) is not seen. This is probably due to the preservation of megaspore in a dorsoventrally compressed position.

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (present study) (Fig. 8).

#### PLATE 5

Brazilian Pennsylvanian megaspores from northeastern margin of Paraná Basin.



1. *Bokarosporites psilatus* Bharadwaj & Tiwari; GP/3T2284a; Slide No. 10a.
2. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 18.
3. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 7.
4. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 8b.
5. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 14e.
6. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 10b.
7. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 14f.
8. *Banksisporites dijkstrae* (Singh) Tewari & Maheshwari; GP/3T2284a; Slide No. 12.
9. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 15.
10. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 16.
11. *Banksisporites endosporitiferus* (Singh) Tewari & Maheshwari; Slide No. GP/3T2284a.
12. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 8c.
13. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 6b.
14. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 17.
15. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 14b.
16. *Lagenoisporites rugosus* (Loose) Potonié & Kremp; GP/3T2284a; Slide No. 2a.
17. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 14c.
18. *Lagenoisporites* sp.; GP/3T2284a; Slide No. 9b.
19. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 9c.
20. *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari; GP/3T2284a; Slide No. 19.

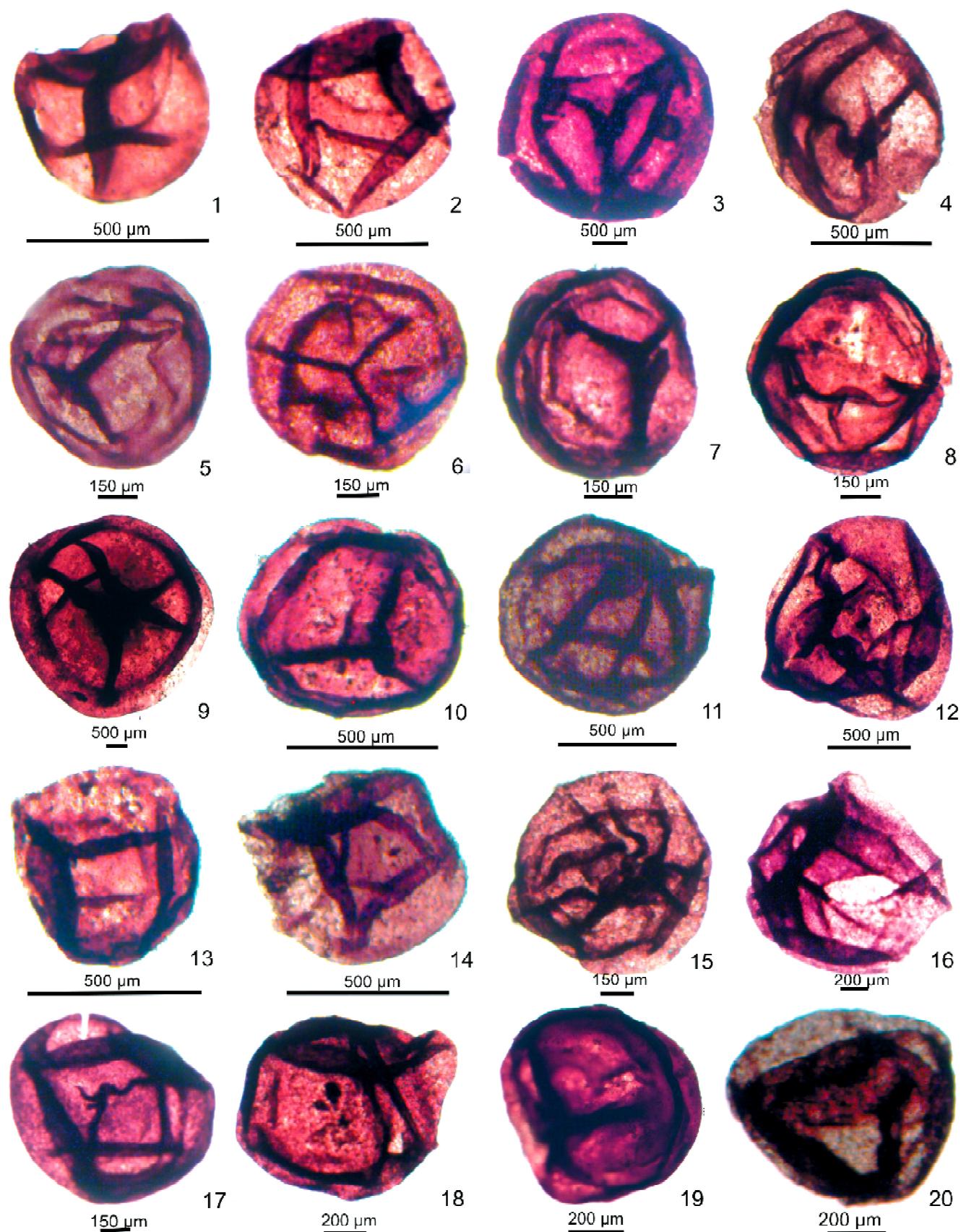


PLATE 5

***Lagenicula* sp.**

**Description**—Megaspore identified in wet condition, lageniculate / gulate, trilete, oval in outline, triradiate and arcuate ridges not clear, neck like projection-gula present, polar axis longer than equatorial axis, exosporium spinate, spines small, mesosporium subcircular, folded, without cushions.

**Dimensions**—Overall size 696-854 x 570-783  $\mu\text{m}$ , length of gula 330  $\mu\text{m}$ , width of gula at base 330  $\mu\text{m}$ , width of gula at apex 30  $\mu\text{m}$ , length of spines 2-3  $\mu\text{m}$ , width of spines at base 2-3  $\mu\text{m}$ , width of spines at apex 3  $\mu\text{m}$ , size of mesosporium 750 x 570  $\mu\text{m}$ .

**Remarks**—In presence of spines and gula the megaspore is comparable with the genus *Lagenicula* (Zerndt, 1934; Spinner, 1983). However, since the gula does not split into three subtriangular segments (Zerndt, 1934, Plate XXVIII, 1, 3, 4; Potonié & Kremp, 1955, Plate IV, 20, text-fig. 35), triradiate and arcuate ridges are not clear and the spines are too small, its inclusion in *Lagenicula horrida* and *L. crassiaculeata* (Zerndt, 1934) – the spinate species of *Lagenicula* is not possible. Hence, specific circumscription is not given here.

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (present study) (Fig. 8).

**Genus—LAGENOISPORITES** Potonié & Kremp, 1955**Type species—*Lagenoisporites rugosus* (Loose, 1932)**  
Potonié and Kremp, 1955

***Lagenoisporites rugosus* (Loose, 1932)** Potonié and Kremp, 1955

**Holotype—*Sporogonites rugosus* Loose, 1932, Pl. 20, Fig. 59**

(Pl. 2.5, 7; Pl. 3.10; Pl. 4.16-19; Pl. 5.3, 4, 12-14, 16)

**Description**—Megaspores lageniculate / gulate, trilete, subcircular in outline, triradiate and arcuate ridges distinct, straight to slightly wavy, extend up to arcuate ridges, gula formed by raising or expansion of triradiate ridges and part of contact area, less prominent, polar axis longer than equatorial axis, exosporium laevigate, mesosporium subcircular, hyaline, folded, without cushions.

**Dimensions**—Overall size 625-1279 x 750-1121  $\mu\text{m}$ , size of triradiate ridges 476-618 x 40-79  $\mu\text{m}$ , width of arcuate ridges 20-79  $\mu\text{m}$ , length of gula 100-559  $\mu\text{m}$ , width of gula at base 199-754  $\mu\text{m}$ , width of gula at apex 46-235  $\mu\text{m}$ , (dry condition); overall size 691-1595 x 648-1568  $\mu\text{m}$ , size of triradiate ridges 267-813 x 54-164  $\mu\text{m}$ , width of arcuate ridges 67-115  $\mu\text{m}$ , length of gula 129-440  $\mu\text{m}$ , width of gula at base 243-574  $\mu\text{m}$ , width of gula at apex 106-292  $\mu\text{m}$ , size of mesosporium 647-1430 x 556-1133  $\mu\text{m}$  (wet condition).

**Remarks**—Megaspores are comparable in shape, laevigate exosporium and presence of gula with *Lagenoisporites rugosus* (Potonié & Kremp, 1955, Plate IV, 22; Piéart, 1962 Plate III, 9). Mesosporium has not been reported by earlier authors. Asubcircular, hyaline mesosporium without cushions is recorded in the megaspores studied presently. Since the external characters are similar to *Lagenoisporites rugosus*, megaspores with mesosporium are included in this taxon.

**Geographic and Stratigraphic Distribution**—Brazil-Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) and Monte Mor (São Paulo) (present study) (Fig. 8).

***Lagenoisporites sinuatus* (Dijkstra, 1955)** Trindade, 1959a

**Holotype—*Triletes sinuatus* Dijkstra, 1955;** Plate III, Fig. 44  
(Pl. 2.3)

**Regional Synonymy:**

1970 - *Lagenoisporites sinuatus* (Dijkstra) Trindade. Trindade, p. 466, figs 6-8.

2004- *Sublagenicula sinuata* (Dijkstra) Dybová-Jachowicz et al. 1979. Amaral & Ricardi-Branco, p. 259, figs I-L.

**Description**—Single megaspore identified under SEM in dry condition, lageniculate/gulate, trilete, subcircular in outline, triradiate ridges distinct, undulate,  $\frac{3}{4}$  spore radius long, extend up to arcuate ridges, arcuate ridges and contact area distinct, gula formed by raising or expansion of triradiate ridges, less prominent, exosporium smooth to granulate.

**Dimensions**—Overall size 1288 x 1384  $\mu\text{m}$ , size of triradiate ridges 335-636 x 69-71  $\mu\text{m}$ , width of arcuate ridges 112-125  $\mu\text{m}$ , length of gula 132  $\mu\text{m}$ , width of gula at base 320  $\mu\text{m}$ , width of gula at apex 37  $\mu\text{m}$ .

**Comparison**—Megaspores are comparable in shape, nature of exosporium, undulate, triradiate and presence of gula with *Lagenoisporites sinuatus* (Trindade, 1959a, Plate II, 3, 5-6; 1959b, Plate V, 24-28; 1962, Plate II, 3-4).

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (Amaral & Ricardi-Branco, 2004; present study), Buri (São Paulo) (Trindade, 1959a) and Monte Mor (Trindade & Sommer, 1966; Trindade, 1970); Rio Bonito Formation (Lower Permian): Charqueadas (Trindade, 1964), Mina do Leão (Trindade, 1962), Mina de Candiota (Dijkstra, 1955; Pant & Srivastava, 1962; Marques-Toigo et al., 1975), Barro Branco (Dijkstra, 1955; Trindade 1959a, 1960; Pant & Srivastava, 1962); Palermo Formation: São Sepé (Cauduro & Zingano, 1965; Bortoluzzi & Veiga, 1981). India—Barakar Formation (Bharadwaj & Tiwari, 1970) (Figs 7, 8).

***Lagenoisporites cf. L. hispanicus*** Piérart, 1961

(Pl. 2.4)

**Description**—Megaspore identified in dry condition, lageniculate, trilete, subtriangular in outline, triradiate ridges distinct, straight, extend up to arcuate ridges, arcuate ridges almost merged with margin, contact area distinct, gula well marked, formed by swelling of part of trijunction (of triradiate ridges), exosporium laevigate.

**Dimensions**—Overall size 1027 x 1189 µm, size of triradiate ridges 417-466 x 25-26 µm, length of gula 85 µm, width of gula at base 159 µm, width of gula at apex 72 µm.

**Comparison**—Megaspore is comparable in shape, laevigate exosporium and presence of gula with *Lagenoisporites cf. L. hispanicus* (Piérart, 1961, Plate IV, 2-4, Plate V, 2-4, Piérart, 1965, Plate VI, 2, 4, 6, 7).

**Geographic and Stratigraphic Distributions**—Brazil-Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) and Monte Mor (São Paulo) (present study) (Fig. 8).

***Lagenoisporites nudus*** (Nowak & Zerndt, 1936) Potonié and Kremp, 1955

**Holotype**—*Lagenicula nuda* Nowak & Zerndt, 1936 Plate 1, Fig. 6

(Pl. 2.15, 16; Pl. 4.20)

**Description**—Megaspores lageniculate, trilete, oval to subcircular in outline, triradiate ridges distinct in dry condition, raised to form dome-shaped gula, gula prominent, polar axis longer than equatorial axis, arcuate ridges and contact area not visible, exosporium smooth, mesosporium opaque, apparently without cushions, filling entire spore cavity.

**Dimensions**—Overall size 1209-1250 x 1107-1150 µm, size of triradiate ridges 99-227 x 55 µm, length of gula 243-330 µm, width of gula at base 270-850 µm, width of gula at apex 53-100 µm, (dry condition); overall size 1260-1838 x 975-1840 µm, length of gula 300-320 µm, width of gula at base 330-800 µm, width of gula at apex 75-160 µm, size of mesosporium 975-1760 x 975-1392 µm (wet condition).

**Remarks**—Megaspores are comparable in shape, nature of exosporium and presence of gula with *Lagenoisporites nudus* (Piérart, 1963, Plate I, 7). However, mesosporium has not been reported by previous authors.

**Geographic and Stratigraphic Distribution**—Brazil-Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) and Monte Mor (São Paulo) (present study) (Fig. 8).

***Lagenoisporites scutiformis*** Trindade, 1970

**Holotype**—*Lagenoisporites scutiformis* Trindade, 1970, Fig. 12

## Regional Synonymy:

1970 - *Lagenoisporites scutiformis* Trindade. Trindade p. 466, figs 9-12.

2005 - *Lagenoisporites scutiformis* Trindade, 1970. Mune, p. 82-83.

2007 - *Lagenoisporites scutiformis* Trindade, 1970. Mune & Bernardes-de-Oliveira, p. 434.

**Remarks**—This species earlier reported by Trindade (1970) from Monte Mor has not been recovered in the present assemblage. The specimens from Monte Mor show generic features as described by Dybová-Jachowicz *et al.* (1979) and specific characters of *L. scutiformis* Trindade, viz. pyramidal neck, apical prominence developed from the point of crossing of the arcuate and the triradiate ridges, i.e. presence of a hologula and a psilate exine. However, shape and other morphological features are not well-defined and require a re-examination and more accurate diagnostic boundaries which is only possible after study of the holotype and original material.

**Geographic and Stratigraphic Distribution**—Paraná Basin, Itararé Group (Pennsylvanian): Monte Mor, São Paulo (Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007); Rio Bonito Formation (Lower Permian): Figueira (Ricardi-Branco *et al.*, 2002) and São João do Triunfo, PR (Arai & Rosler, 1984) (Fig. 8).

***Lagenoisporites brasiliensis*** (Dijkstra, 1955) Trindade, 1970

**Holotype**—*Triletes brasiliensis* Dijkstra, 1955, Plate II, figs 34-40, Plate III, figs 41-42.

(Pl. 1.6-8; Pl. 2.14)

## Regional Synonymy:

1970 - *Lagenoisporites brasiliensis* (Dijkstra) Trindade. Trindade, p. 465-466, figs 1-5.

2003 - *Sublagenicula brasiliensis* (Dijkstra) Dybová-Jachowicz *et al.* emend. Glasspool. Glasspool, p. 274-277, Plate VI, figs 1-3.

2004 - *Sublagenicula brasiliensis* (Dijkstra) Dybová-Jachowicz *et al.* 1979. Amaral & Ricardi-Branco, p. 257-258, fig. 3A-D.

2005 - *Sublagenicula brasiliensis* (Dijkstra, 1955) Dybova Jachowicz *et al.* 1979 emend. Glasspool 2003. Mune, p. 83-86, plate XI, figs, 4-9, 11 and 20.

2007 - *Sublagenicula brasiliensis* (Dijkstra, 1955) Dybova Jachowicz *et al.* 1979 emend. Glasspool 2003, in Mune & Bernardes-de-Oliveira, p. 434, Fig. 10, M.

**Description**—Megaspore identified in dry condition, lageniculate, ellipsoidal in outline, triradiate ridges, arcuate ridges and contact area not clear, gula well marked, polar axis longer than equatorial axis, exosporium rugose.

**Dimensions**—Overall size 1515 x 1150 µm, length of gula 85 µm, width of gula at base 159 µm, width of gula at apex 72 µm.

**Comparison**—Megaspore is comparable in shape, nature of exosprium and presence of gula with *Lagenoisporites brasiliensis* (Trindade, 1959a, Plate I, 1,2; Plate III, 14,16, text-fig. 2; Trindade, 1962, Plate I, 3,4, Plate III,12,13; Plate IV,15).

**Geographic and Stratigraphic Distributions**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (São Paulo) (Amaral & Ricardi-Branco, 2004; present study), Buri (São Paulo) (Trindade, 1959a; Trindade & Sommer, 1966; Bharadwaj & Tewari, 1970) and Monte Mor (Trindade & Sommer, 1966; Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007); Rio Bonito Formation (Lower Permian): Charqueadas (Trindade, 1964), Mina do Leão and Butiá (Trindade, 1962; Trindade & Sommer, 1966), Mina de Candiota (Dijkstra, 1955; Pant & Srivastava, 1962; Marques-Toigo *et al.*, 1975), Arroio dos Ratos (Trindade & Sommer, 1966), Barro Branco (Dijkstra, 1955; Trindade 1959a, 1960; Trindade & Sommer, 1966; Pant & Srivastava, 1962); Palermo Formation: São Sepé (Cauduro & Zingano, 1965; Trindade & Sommer, 1966; Bortoluzzi & Veiga, 1981)(Fig. 8).

#### *Lagenoisporites* sp.

(Pl. 2.6; Pl. 3.8; Pl. 4.10; Pl. 5.18)

**Description**—Megaspores lageniculate/gulate, trilete, subcircular in outline, triradiate ridges distinct, thick, straight, one of them extend up to gula, arcuate ridges and contact area faint, less prominent, polar axis longer than equatorial axis, exosprium laevigate, mesosporium subcircular, hyaline, filling spore cavity, without cushions.

**Dimensions**—Overall size 884-1096 x 861-931 µm, size of triradiate ridges 315-579 x 21-70 µm, width of arcuate ridges 61 µm, length of gula 210-340 µm, width of gula at base 65-350 µm, width of gula at apex 59-70 µm, (dry condition); overall size 1595 x 1568 µm, size of triradiate ridges 626-813 x 87-164 µm, width of arcuate ridges 67-115 µm, length of gula 399 µm, width of gula at base 574 µm, width of gula at apex 292 µm, size of mesosporium 1347 x 1133 µm (wet condition).

**Remarks**—Megaspores are comparable in shape, presence of gula and thick triradiate ridges with *Lagenicula bulbata* Dijkstra (Piérart, 1989, Plate II, 5, 6). However, *Lagenicula bulbata* has spinate exosprium and the exosprium in the present specimen is laevigate which is a characteristic feature of the genus *Lagenoisporites*. Hence, the megaspores are being described presently as an indeterminate species of the genus *Lagenoisporites*.

**Geographic and Stratigraphic Distribution**—Brazil - Paraná Basin, Itararé Group (Pennsylvanian): Campinas (SP) (present study) (Fig. 8).

**Genus**—**SUBLAGENICULA** Dybová-Jachowicz *et al.*, 1979

**Type species**—*Sublagenicula nuda* (Nowak & Zerndt, 1936) Dybová-Jachowicz *et al.*, 1979

This generic designation is used for Late Palaeozoic megaspores which show a proximal expansion of exine named subgula, i.e. a gula that rises from the median portion of the proximal face to the apex as defined by Dybová-Jachowicz *et al.*, 1979.

***Sublagenicula tripartites*** (Trindade, 1970) Mune & Bernardes-de-Oliveira, 2007

**Holotype**—*Lagenoisporites tripartites* Trindade 1970, Figs 13-15

**Regional Synonymy:**

1970 - *Lagenoisporites tripartites* Trindade. Trindade, p. 467, figs 13-15.

2005 - *Sublagenicula tripartites* (Trindade, 1970) nov. comb. Mune, p. 86-87 (unpublished).

2007 - *Sublagenicula tripartites* (Trindade, 1970) nov. comb. Mune & Bernardes-de-Oliveira, p. 434.

**Remarks**—Trindade (1970), while analyzing the megaspores from Monte Mor, erected a new species *Lagenoisporites tripartites*. Her diagnosis was based on ten specimens, which is as following: “megaspores with neck opening near the apex, without prominence, sharp arcuate ridges, triradiate ridges 50 µm of length x 40 µm of width, three indentations in its equator coinciding with the extensions of the triradiate ridges”. The emended generic diagnosis by Dybová-Jachowicz *et al.*, 1979 includes a characteristic feature—the presence of a hologula. *Lagenoisporites tripartites* Trindade (1970, figs 13-15) shows just a “subgula”. Since “subgula” is a diagnostic character of the genus *Sublagenicula*, it is necessary to create a new combination. Therefore, a new combination, viz. *Sublagenicula tripartites* is being proposed here for the species *Lagenoisporites tripartites*.

**Geographic and Stratigraphic Distribution**—Paraná Basin, Itararé Group (Pennsylvanian): Monte Mor, São Paulo (Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007) (Fig. 8).

**Genus**—**SETOSISPORITES** (Ibrahim) Dybová-Jachowicz *et al.*, 1979

**Type species**—*Setosisporites hirsutus* (Loose, 1932) Ibrahim, 1933

***Setosisporites*** sp.

### Regional Synonymy:

- 1970 - *Setosisporites* sp. Trindade, p. 467, fig.25.  
 2005 - *Setosisporites* sp. Mune, p. 87.  
 2007 - *Setosisporites* sp. Mune & Bernardes-de-Oliveira, p. 434.

**Remarks**—Based on study of 25 megaspores, Trindade (1970) reported the presence of genus *Setosisporites* (Ibrahim, 1933) Potonié & Kremp 1954 emend. Dybová & Jachowicz *et al.* 1979 from fossil plant material of Volpe Ranch (Monte Mor, São Paulo). According to Trindade (1970), the characteristics of the megaspore are: “the presence of a neck present only at the proximity of the apex and the ornamentation of the capitate exine at both poles, proximal and distal”. These features are characteristics of *Setosisporites hirsutus* (Loose) Ibrahim 1933 and as description of Tewari *et al.* (2004) for Barakar Formation (Wardha Basin). Some megaspores of the present collection show these features. However, they are not good enough for systematical analysis. Presence of this genus has been reported as *Setosisporites* cf. *S. furcatus* in the Triunfo Member, Rio Bonito Formation (Lower Permian) of Paraná Basin by Ricardi-Branco *et al.* (2002).

**Geographic and Stratigraphic Distribution**—Paraná Basin, Itararé Group (Pennsylvanian): Monte Mor, São Paulo, (Trindade, 1970; Mune & Bernardes-de-Oliveira, 2007) (Fig. 8).

## DISCUSSION

Fig. 8 reveals the megaspore taxa recorded in the Pennsylvanian of the Campinas and Monte Mor (São Paulo State) assemblages of the Itararé Group from the northeastern margin of the Paraná Basin, Brazil.

An analysis of the megaspore assemblage and synonymies of some of them as proposed in this paper reveal that the megaspore taxa present in the Campinas Assemblage are: *Banksisporites dijkstrae*, *B. endosporitiferus*, *B. tenuis*, *B. utkalensis*, *Biharisporites spinosus*, *Bokarosporites psilatus*, *B. rotundus*, *Duosporites perversus*, *Duosporites* sp. a, *Lagenicula horrida*, *Lagenicula* sp., *Lagenoisporites brasiliensis*, *Lagenoisporites* cf. *L. hispanicus*, *L. nudus*, *L. sinuatus*, *L. rugosus*, *Lagenoisporites* sp. and *Calamospora* sp.

Based on SEM (for exosprium characters) and LM (for both exosprium and mesosprium characters) observations, the following megaspore taxa are recorded from the Monte Mor Assemblage: *Banksisporites dijkstrae*, *B. endosporitiferus*, *B. tenuis*, *B. utkalensis*, *B. labiosus*, *B. vulgatus*, *Bokarosporites rotundus*, *Duosporites* sp. b, *Sublagenicula tripartites*, *Lagenoisporites brasiliensis*, *Lagenoisporites* cf. *L. hispanicus*, *L. nudus*, *L. sinuatus*, *L. rugosus*, *L. scutiformis*, *Setosisporites* sp. and *Calamospora* sp.

Although the genera *Duosporites*, *Sublagenicula*, *Lagenicula*, *Setosisporites* and *Calamospora* occur in both

India and Brazil, some of their species are exclusively Brazilian in occurrence, viz. *Duosporites perversus*, *Duosporites* sp. a, *Duosporites* sp. b, *Sublagenicula tripartites*, *Lagenicula horrida*, *Lagenicula* sp., *Lagenoisporites brasiliensis*, *Lagenoisporites* cf. *L. hispanicus*, *L. nudus*, *L. rugosus*, *L. scutiformis*, *Lagenoisporites* sp., *Setosisporites* sp. and *Calamospora* sp. All these forms are restricted either to the Pennsylvanian or to the Pennsylvanian and the Lower Cisuralian of the Paraná Basin (Fig. 8). The taxa which occur both in Brazil and India are: *Banksisporites dijkstrae*, *B. endosporitiferus*, *B. utkalensis*, *B. labiosus*, *B. vulgatus*, *Bokarosporites psilatus*, *B. rotundus* and *Lagenoisporites sinuatus*. Hence they could be significant in biostratigraphical correlation between the two countries. Fig. 8 shows that the shared species extend from the Pennsylvanian to the Cisuralian in Brazil and from the Cisuralian/Guadalupian to the Lopingian or even to the Triassic and to the Cretaceous in India. The occurrence of these megaspores indicates that they appeared in the Late Carboniferous in Brazil and persisted there till the Early Permian. Megaspores are not documented in Brazil after the Early Permian. In Indian Gondwana, the appearance of megaspores is normally later than in Brazil and their records persist from the Early Permian till the Early Cretaceous, reflecting a long stratigraphical distribution.

The occurrence of species of the genera *Lagenicula*, *Lagenoisporites* (gulate), *Setosisporites* and *Cystosporites* (alete) has been recorded from different Gondwana basins of India, viz. *Lagenicula gondwanensis*, *L. barakarensis* (Pant & Mishra, 1986) are recorded from the Damodar and the South Rewa Gondwana basins, *Cystosporites indicus* and *Cystosporites* sp. (Trivedi, 1953) are recorded from the South Rewa Gondwana Basin; *Lagenoisporites* sp. and *Setosisporites hirsutus* (Tewari *et al.*, 2004) are recorded from the Wardha Basin from the Barakar Formation (Early Permian) and *Cystosporites* sp. (Tewari *et al.*, 2009b) is recorded from the Early Cretaceous of the Satpura Basin (Fig. 9). The common existence of these genera both in India and Brazil is indicated in Fig. 8. It is interesting to note that while on the one hand, Carboniferous megaspores are mostly laevigate, granulate and verrucate (some with small and sparsely distributed spines) on the other hand Permian megaspores show a variety of ornamentations on their exosporia, viz. coni, bacula, mamillate appendages, rods / rodlets, long, stout, simple, bifurcate and multifurcate spines and setae. Mesozoic megaspores are distinct in presence of reticulate exosprium (Tewari, 2008). However, mesosprium is either indistinct in them or absent. Besides being useful in taxonomy, tracing evolutionary history of early land plants and in identifying source vegetation, exosprium characters of megaspores like presence of spines and reticulations are helpful in interpretation of palaeoecology, since they indicate aquatic conditions (Collinson *et al.*, 1985; Dilcher *et al.*, 1992; Kar & Dilcher, 2002; Tewari *et al.*, 2009a, b). According to Dilcher *et al.* (1992) and Kar and Dilcher

(2002), presence of spines and apical prominence is inclined towards “increasing surface to volume ratio” and hence augments buoyancy. Furthermore, the spines aid in fertilization by adhering to microspores. According to Collinson *et al.* (1985) hairy surfaces help in aquatic dispersal and promote attachment of megaspores to the moist muddy surface of the ground. Affinity of the dispersed fossil megaspore is now well established with the lycopsids on the basis of widespread prevalence of heterospory in the group (Pant & Mishra, 1986). Besides, dispersed fossil megaspores are also comparable with the *in situ* megaspores of the lycopsids in presence of spines. Megaspores of *Isoetes* are similar to the genus *Duosporites* (Høeg *et al.*, 1955). The gulate and spinate megaspores of the present study reflect aquatic conditions and hence, could be affiliated with the water dwelling lycopsids.

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