ELSEVIER

Early Carboniferous palynoflora from the Ambo Formation, Pongo de Mainique, Peru

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Abstract

Six productive samples from the upper part of the Early Carboniferous Ambo Formation at Pongo de Mainique, Peru, are analyzed for 55 recognized miospore species of continental origin. One new morphospecies, *Cristatisporites peruvianus*, is described. An emended diagnosis is proposed for *Kraeuselisporites* together with lists of species that are accepted or rejected for this morphogenus. Five species are transferred to *Kraeuselisporites*: *K. explanatus* (Luber in Luber and Waltz, 1941 [Luber, A.A., Waltz, I.E., 1941. Atlas of microspores and pollen of the Paleozoic of U.S.S.R.. Tr. Tsent. Nauchno-Issled. Geol.- Razved. Inst. 139, 1107 (in Russian)]) nov. comb., *K. scorpius* (Balme and Hassell, 1962) nov. comb, *K. dolianitii* (Daemon, 1974) nov. comb., *K. reidii* (Foster, 1979) nov. comb., *K. daemonii* (Loboziak et al., 1999) nov. comb. A detailed analysis of the composition of the palynoflora allows its identification with the late Viséan *Cordylosporites magnidictyus* Palynozone, recently defined in the Amazon Basin in Brazil. Worldwide comparison of the Peruvian association indicates greater affinity with coeval palynofloras from Gondwana region (South America and North Africa) and North America. The greatest differences exist with European and Argentinean palynofloras, although the latter are still imperfectly known. The degree of similarity is likely to be determined by paleolatitude.
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1. Introduction

This contribution is the second of a planned series of palynological, paleobotanical and biostratigraphical studies related to Upper Paleozoic units in Peru. This study was carried out within the framework of a cooperation agreement between the Ricardo Palma University (Peru), the University of Buenos Aires (Argentina) and the University of Rio Grande do Sul (Brazil). The aim of this study is to contribute to the improvement of biostratigraphical knowledge of the Ambo Formation. Palynomorphs are listed, described and illustrated and the age, paleoenvironmental

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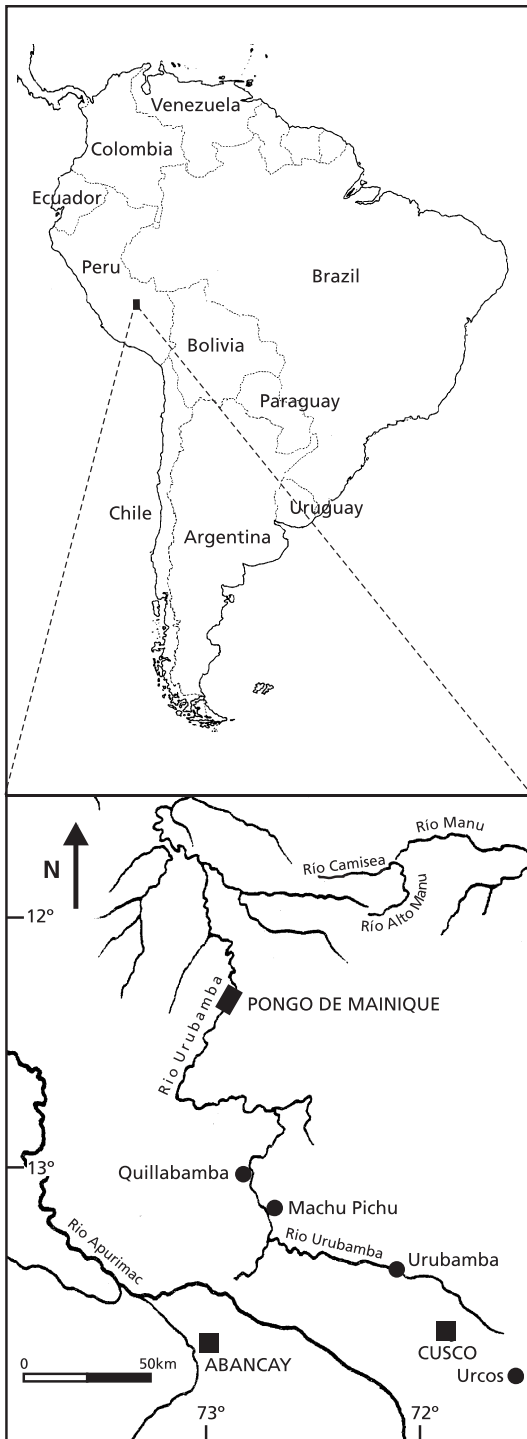
Fig. 1. Location of the Pongo de Mainique locality.

conditions and palynofloral comparisons are discussed. The correlation with other palynofloras of equivalent age, mainly from southern South America, the rest of Gondwana and Euroamerican continents, is considered.

The palynological material described in the present paper was collected in the Pongo de Mainique locality, which in local native language means "strong narrowness in the course of a river". Exposures at this locality (Lat. 12°20′ S, Long. 72°50′ W) represent one of the more complete stratigraphical sections of eastern Peru. Pongo de Mainique is located in the eastern edge of the Andean Range, about 450 km to the east of Lima and some 160 km to the northwest of Cusco, at the point where the Urubamba River leaves the last of the eastern spurs (Subandean Belt) of the Eastern Range, to enter to the Amazonian Plain (Fig. 1). There, the course of the river is very narrow until reaching in some places a width of around 50 m and crosses for 10–15 km vertical sedimentary sequence, ranging in age from Silurian to Tertiary.

2. Geological setting

The Late Paleozoic sedimentary rocks present in the Madre de Dios Basin are mainly siliciclastic with a smaller proportion of calcareous sediments. The latter belong chiefly to the Late Carboniferous–Early Permian. The Late Paleozoic sequence is subdivided into four formational units that in ascending stratigraphical order are: Ambo, Tarma, Copacabana and Ene Formations (Fig. 2).

The Ambo Formation has its type section in the neighborhood of the homonym locality, where outcrops attain approximately 700 m in thickness and are composed of quartzous sandstones, lutites, conglomerates and volcanic tuffites (Newell et al., 1949). Plant remains belonging to lycophytes, sphenophytes and pteridosperms were recovered and attributed to the Early Carboniferous.

The Ambo Formation at Pongo de Mainique is 822 m thick, and it unconformably overlies Devonian rocks of the Cabanillas Formation. The basal portion consists mainly of light grey, fine-grained sandstones that are superficially brown; less frequent are medium to coarse-grained sandstones. These fine- to coarse-grained layers have internal cross-stratification with

Region / Age		M.A.	PONGO DE MAINIQUE
PERMIAN	Early		Ene Formation
		299	Copacabana Formation
CARBONIFEROUS	Late — Step.	305	
	Late — Wes.	316	Tarma Formation
	Late — Nam.	320	
	Early — Serp.	327	
	Early — Vis.		Ambo Formation
	Early — Vis.	343	
	Early — Tour.	354	
DEVONIAN	S/L		Cabanillas Formation
			?

Fig. 2. Devonian–Permian stratigraphic sequence at the Pongo de Mainique, showing Carboniferous time scale after Menning et al. (2001).

lenticular geometry, and alternate with subordinate siltstones, light to dark grey lutites, sometimes with abundant pyrite, and thin laminated mudstone layers. A very thick band of light grey, pebbly sandstone with rounded clasts and pyrite, showing internal cross-stratification, forms the base of the unit. Calcareous deposits were not recorded. The palynomorphs analyzed below belong to this unit.

The type section of the Tarma Formation is located 2.5 km to the west of the homonym locality, and was described by Dunbar and Newell (1946). At Pongo de Mainique, the Tarma Formation, which is 237 m thick, conformably overlies the Ambo Formation, which is overlain by the Copacabana Formation. At the top of the Tarma Formation, the *Illinites unicus* Palynozone is recorded, which is considered to be Late Westphalian in age (Azcuy et al., 2002). The Copacabana Formation was defined by Cabrera La Rosa and Petersen (1936) in the slopes at Tiquina Strait, Lake Titicaca. At Pongo de Mainique, it consists mainly of 647 m, light to dark grey, micritic to bioclastic, compact limestones, containing fusuli-
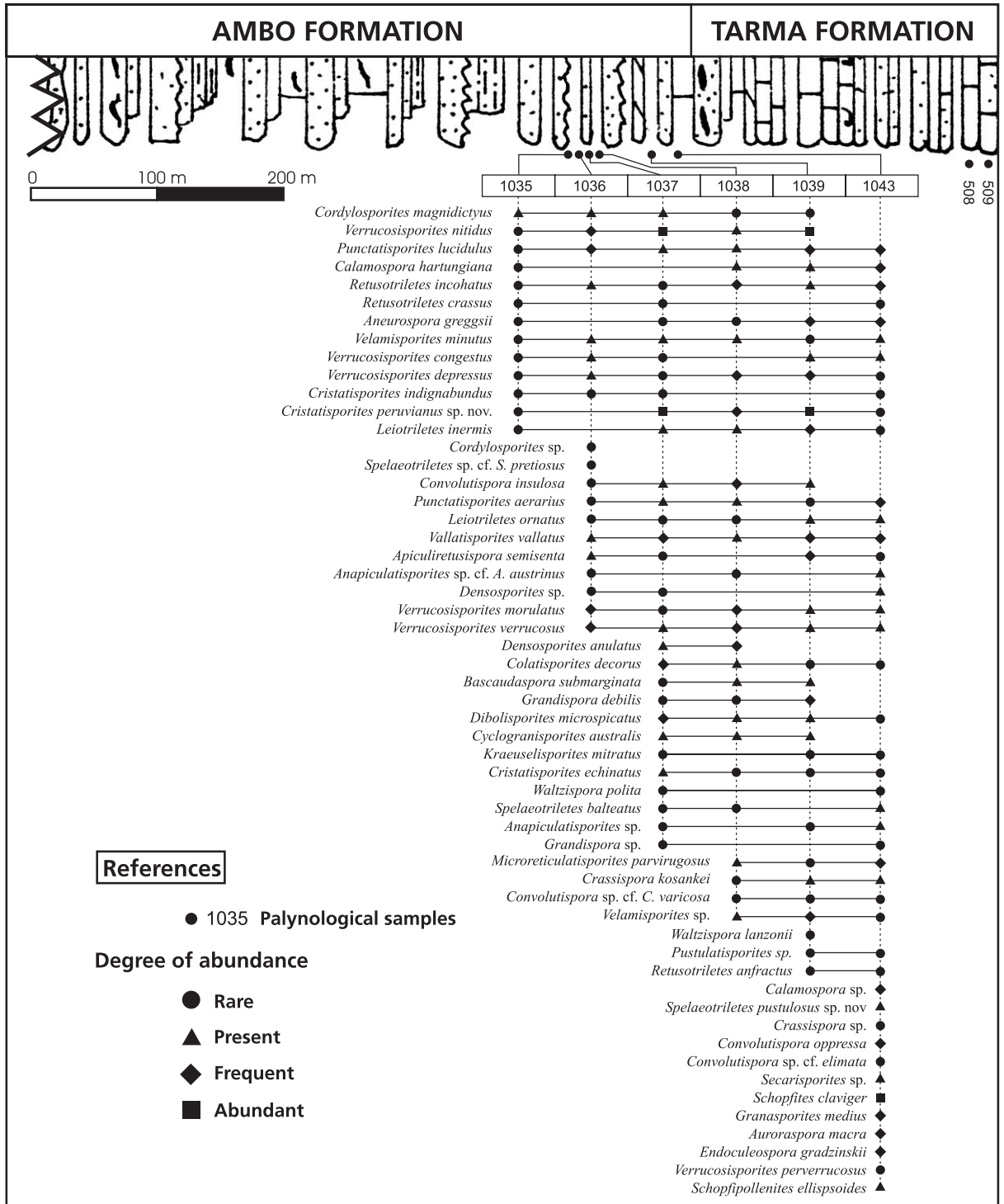
nids, brachiopods, pelecypods, bryozoans, and abundant fragments of fossils and chert nodules, in medium to thick beds. Interbedded are dark grey calcareous claystones, and light grey to brown dolostones in thin to medium layers. Their basal and upper contacts are conformable. Recently, Wood et al. (1999) analyzed palynomorphs and microfossils from this unit and assigned an Early–Middle Pennsylvanian age.

Above the Copacabana Formation, the Ene Formation is 168 m and consists mainly of minor limestones and dolostones interbedded within shales and sandstone layers. The sandstones are quartzose, white greyish to reddish brown in colour, fine- to very fine-grained, well bedded with cross-stratification. The claystones vary from brown to black or grey, with nodules and fragments of chert, in thin to medium layers with a weak odour of petroleum. The grey limestones are oolitic and occur with thin stromatolitic layers. The upper contact with the Oriente Group (Cretaceous) is unconformable.

3. Stratigraphy

The Carboniferous deposits of Peru are represented by two lithostratigraphical units, Ambo (Lower Carboniferous) and Tarma (Upper Carboniferous), which take their names from homonym localities in the Central Andes of that country. Although they have been named originally as "Groups" in Peru, without acknowledgement to the accepted norms or codes of stratigraphy, they have always been used as lithostratigraphical units without further internal subdivision. It is here proposed that they should be recognized with formational status. However, in the case of the Ambo Formation in Bolivia, some authors making reference to the deposits of the Lower Carboniferous have used the name Ambo with Group status, subdivided in three units: Cumaná, Kasa and Siripaca Formations (Díaz Martínez, 1991). If the Early Carboniferous sequences in Bolivia present sufficient lithostratigraphical differences to recognize three formational units, it would be desirable to consider the convenience of using the same established name to designate nondivisible sequences.

On the other hand, the paleobotanical (Iannuzzi and Pfefferkorn, 2002) and palynological (Azcuy,

AMBO FORMATION   **TARMA FORMATION**

	1035	1036	1037	1038	1039	1043

509
508

0   100 m   200 m

Cordylosporites magnidictyus
Verrucosisporites nitidus
Punctatisporites lucidulus
Calamospora hartungiana
Retusotriletes incohatus
Retusotriletes crassus
Aneurospora greggsii
Velamisporites minutus
Verrucosisporites congestus
Verrucosisporites depressus
Cristatisporites indignabundus
Cristatisporites peruvianus sp. nov.
Leiotriletes inermis
Cordylosporites sp.
Spelaeotriletes sp. cf. *S. pretiosus*
Convolutispora insulosa
Punctatisporites aerarius
Leiotriletes ornatus
Vallatisporites vallatus
Apiculiretusispora semisenta
Anapiculatisporites sp. cf. *A. austrinus*
Densosporites sp.
Verrucosisporites morulatus
Verrucosisporites verrucosus
Densosporites anulatus
Colatisporites decorus
Bascaudaspora submarginata
Grandispora debilis
Dibolisporites microspicatus
Cyclogranisporites australis
Kraeuselisporites mitratus
Cristatisporites echinatus
Waltzispora polita
Spelaeotriletes balteatus
Anapiculatisporites sp.
Grandispora sp.
Microreticulatisporites parvirugosus
Crassispora kosankei
Convolutispora sp. cf. *C. varicosa*
Velamisporites sp.
Waltzispora lanzonii
Pustulatisporites sp.
Retusotriletes anfractus
Calamospora sp.
Spelaeotriletes pustulosus sp. nov
Crassispora sp.
Convolutispora oppressa
Convolutispora sp. cf. *elimata*
Secarisporites sp.
Schopfites claviger
Granasporites medius
Auroraspora macra
Endoculeospora gradzinskii
Verrucosisporites perverrucosus
Schopfipollenites ellipspoides

References

● 1035   **Palynological samples**

Degree of abundance

●   **Rare**

▲   **Present**

◆   **Frequent**

■   **Abundant**

1991) data obtained from the Ambo Formation in the localities of Paracas and Pongo de Mainique allowed the first authors to correlate the upper part of this unit with the Siripaca Formation of comparable age. Nevertheless, other authors (Suárez Soruco and Díaz Martínez, 1996; Díaz Martínez, 1999; Díaz Martínez et al., 1999) have extended the correlation between the Ambo "Group" to units of the southern Subandean Belt of Bolivia and northern Argentina, i.e., to the Macharetí and Mandiyutí Groups. This attempt at correlation has been rejected on the evidence of palynological data from those groups as discussed by di Pasquo et al. (2001) and di Pasquo (2002, 2003).

4. Material and methods

Azcuy et al. (2002) illustrated the outcrop of Pongo de Mainique with the distributions of the Ambo, Tarma, Copacabana and Ene Formations documented. In the case of the Ambo Formation a significant number of palynological samples were collected throughout the unit; six yielded palynomorphs from the uppermost part, last 100 m (Fig. 3). The state of preservation of the miospores varies from highly carbonized to good or excellent. Downward from sample 1027, sample levels are still productive but display a degree of carbonization that prevents any taxonomic identifications. Samples 1035 to 1043 were collected from a 100 m interval. Samples 1043 and 508 from Tarma Formation are separated by 224 m of section without samples (Azcuy et al., 2002). In both cases the degree of miospore preservation was fairly good.

Standard methods of palynomorph recovery have been used. The slides have been housed with sample numbers from the Laboratory of Palynology of Petroperú S.A., in the Laboratory of Palynology, Department of Geology, University of Buenos Aires, Argentina. Palynomorph identifications were made using a Leitz Orthoplan binocular transmitted light microscope No. 871080, with 1000× max-

imum magnification. The photomicrographs were taken with a Pixera digital camera. Coordinates of specimens are denoted by an England Finder (EF) reference.

5. Identified miospores

An annotated species list in alphabetical order is firstly presented. New species, forms classified in open nomenclature and *Kraeuselisporites* are described in detail following the scheme introduced by Potonié and Kremp (1954). Where necessary, remarks on taxonomy and morphology, and occurrences are also included for the other taxa. Morphological terminology is mainly in accordance with the glossary provided by Punt et al. (1994). The stratigraphical distribution of taxa with their relative abundance in each sample is shown in Fig. 3. The worldwide geographical distribution of selected taxa is presented in Fig. 4, where a list of selected palynological literature is included; the worldwide stratigraphical range is displayed in Fig. 5. Finally, reworked palynomorphs were found scarcely in most of the samples and are listed in the Discussion.

5.1. Annotated species list

Anapiculatisporites sp. cf. *A. austrinus* Playford and Satterthwait 1986 (Plate II, 7).

Aneurospora greggsii (McGregor, 1964) Steel in Becker et al., 1974 (Plates I, 14; II, 1).

Apiculiretusispora semisenta (Playford, 1971) Massa et al., 1980 (Plate II, 2, 3).

Auroraspora macra Sullivan 1968 (Plate VII, 7).

Bascaudaspora submarginata (Playford, 1964) Higgs et al., 1988 (Plate V, 3, 6).

Calamospora hartungiana Schopf in Schopf et al., 1944 (Plate I, 8).

Colatisporites decorus (Bharadwaj and Venkatachala, 1962) Williams in Neves et al., 1973 (Plate VII, 9, 10).

Fig. 3. Composite stratigraphic log of the Ambo and Tarma Formations showing lithologies and sampling horizons in the Pongo de Mainique section. Occurrence and frequency of miospore taxa identified in samples of the reference section are marked with a symbol. The range of frequency, based on the number of specimens per species in each sample, is the following: circle—1–2 specimens; triangle—3–5 specimens; rhombus—6–13 specimens, and square—more than 14 specimens.

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|	Latest Devonian					Early Carboniferous					Late Carb/Early Perm				
	E	SA	NA	Af	Au	E	SA	NA	Af	Au	E	SA	NA	Af	Au
Leiotriletes ornatus	x					x		x	x	x					
Retusotriletes incohatus	x	x		x		x	x	x	x						
Retusotriletes crassus	x		x			x		x	x						
Aneurospora greggsii	x		x			x									
Apiculiretusispora semisenta			x				x		x	x					
Verrucosisporites nitidus	x	x			x	x	x	x	x	x					
Convolutispora insulosa		x						x		x					
Convolutispora oppressa	x	x		x		x	x								
Bascaudaspora submarginata	x					x		x	x						
Kraeuselisporites mitratus						x	x		x						
Cristatisporites echinatus	x					x	x	x	x						
Spelaeotriletes balteatus						x	x	x	x						
Spelaeotriletes sp. cf. *S. pretiosus*						x	x	x	x						
Endoculeospora gradzinskii	x					x									
Colatisporites decorus						x	x	x	x						
Punctatisporites aerarius	x					x		x	x			x			
Densosporites anulatus	x		x			x	x	x			x		x	x	
Vallatisporites vallatus	x	x	x			x	x	x	x			x			
Auroraspora macra	x	x	x			x	x	x	x	x	x	x			
Schopfites claviger						x	x	x	x	x					
Waltzispora lanzonii						x									
Anapiculatisporites sp. cf. *A. austrinus*						x			x						
Dibolisporites microspicatus						x			x						
Verrucosisporites congestus						x	x	x							
Verrucosisporites depressus						x	x	x							
Verrucosisporites morulatus						x		x	x						
Convolutispora sp. cf. *C. elimata*									x						
Convolutispora sp. cf. *C. varicosa*						x			x						
Cordylosporites magnidictyus							x		x	x					
Microreticulatisporites parvirugosus								x	x						
Cristatisporites peruvianus sp. nov.						x									
Grandispora debilis									x						
Velamisporites minutus						x	x	x	x						
Leiotriletes inermis						x	x	x			x				
Waltzispora polita						x	x	x	x	x	x	x	x	x	x
Verrucosisporites perverrucosus						x					x				
Verrucosisporites verrucosus							x				x	x	x		
Cristatisporites indignabundus						x	x				x				
Schopfipollenites ellipsoides						x	x	x	x		x	x	x	x	
Punctatisporites lucidulus												x			x
Calamospora hartungiana											x	x	x	x	
Retusotriletes anfractus												x			
Granasporites medius											x	x	x		
Cyclogranisporites australis												x			
Crassispora kosankei											x	x	x		

Fig. 4. Worldwide geographical and stratigraphical distribution of Peruvian taxa based on selected palynologicaI papers listed in a continental order: **Europe (E)**: Avchimovitch et al. (1988), Clayton and Turnau (1990), Clayton et al. (1977, 1978, 1980), Doubinger and Rauscher (1966), Higgs (1996), Higgs et al. (1988, 1992, 2000), Neves and Ioannides (1974), Smith and Butterworth (1967), Turnau (1975, 1978), Van der Zwan (1980a). **South America (SA)**: Azcuy (1975a,b), Azcuy and Ottone (1987), Daemon (1974), di Pasquo (2002, 2003), di Pasquo et al. (2003a,b), Loboziak et al. (1991, 1992, 1998), Melo and Loboziak (2000, 2003), Melo et al. (1999), Playford and Dino (2000), Playford et al. (2001), Vavrdová et al. (1993). **North America (NA)**: Bharadwaj and Venkatachala (1962), Braman and Hills (1977), Clayton et al. (1998), Playford and McGregor (1993), Ravn (1991), Utting (1987a, 1991); Utting et al. (1989). **Africa (Af)**: Abdesselam-Rouighi and Coquel (1997), Attar et al. (1980), Clayton (1995), Coquel and Latreche (1989), Coquel and Moreau-Benoit (1986), Coquel et al. (1988, 1995), Loboziak and Alpern (1978), Loboziak et al. (1990), Massa et al. (1980). **Australia (Au)**: Playford (1971, 1976, 1978, 1991), Playford and Helby (1968), Playford and Satterthwait (1985, 1986, 1988).

Fig. 5. Chronostratigraphic distribution of selected species recognized in samples from the Ambo Formation.

(*Remarks*: The Peruvian specimens show close affinity with the original specimens illustrated by Bharadwaj and Venkatachala (1962) and *Colatisporites decorus* variant A Van der Zwan, 1980b).

Convolutispora insulosa Playford, 1978 (Plate III, 7, 8). (*Remark*: It was identified as *Verrucosisporites* sp. cf. *V. gobbettii* Playford 1962 by Ravn, 1991, p. 100, pl. 4, fig. 10).
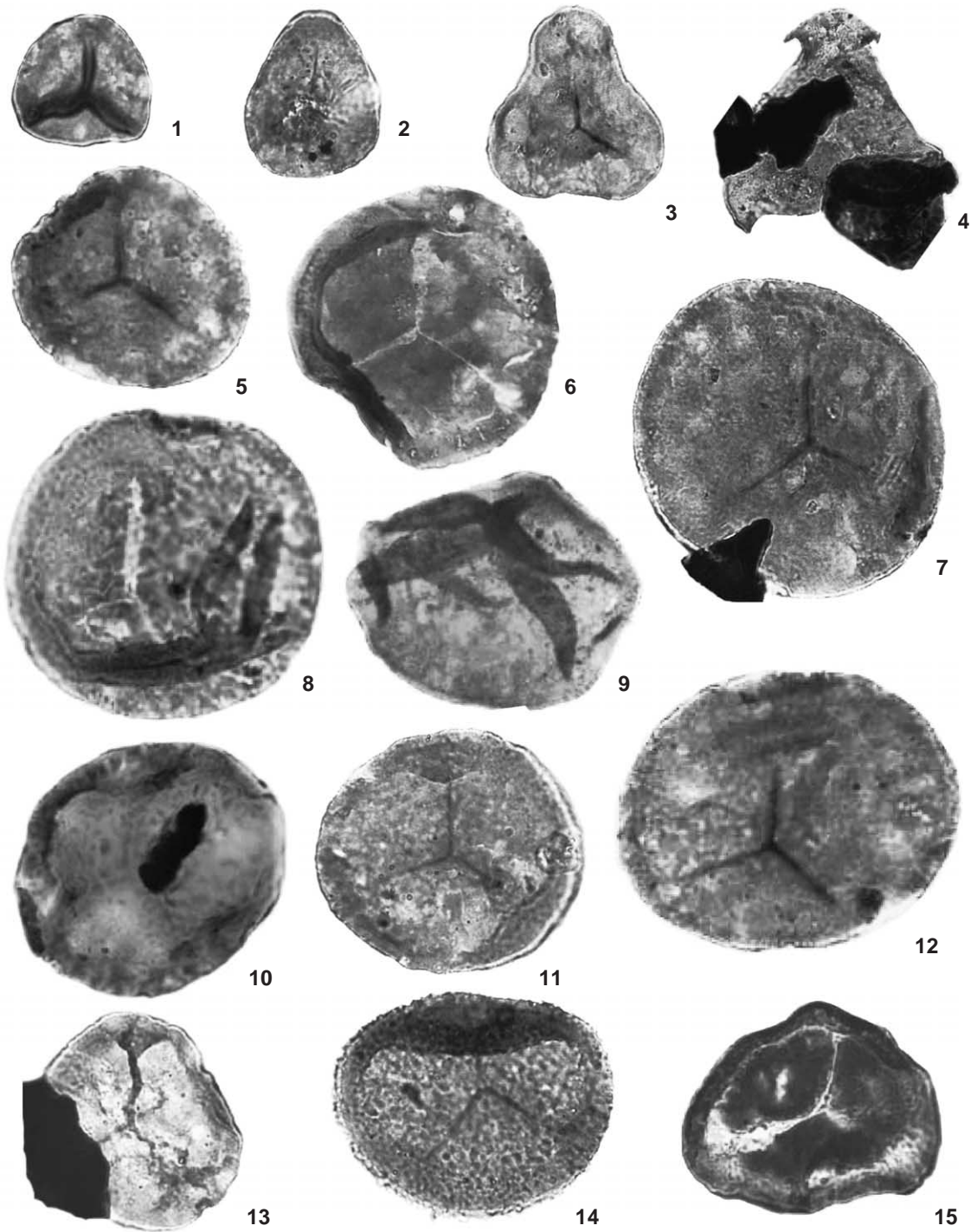
Convolutispora oppressa Higgs 1975 (Plate III, 12).

Convolutispora sp. cf. *C. elimata* Playford 1978 (Plate IV, 3).

Convolutispora sp. cf. *C. varicosa* Butterworth and Williams 1958 (Plate IV, 7).

Cordylosporites magnidictyus (Playford and Helby, 1968) Melo and Loboziak, 2000 (Plate IV, 6, 8, 9).

Crassispora kosankei (Potonié and Kremp, 1955) Bharadwaj, 1957 emend. Smith and Butterworth, 1967 (Plate IV, 10, 11).

Cristatisporites echinatus Playford 1963 (Plate V, 9, 12).

Cristatisporites indignabundus (Loose, 1934) Potonié and Kremp, 1954 emend. Staplin and Jansonius, 1964 (Plates V, 10 and VI, 1, 2).

Cyclogranisporites australis Azcuy 1975a (Plate II, 4).

Densosporites anulatus (Loose, 1934) Schopf et al., 1944 (Plate V, 4, 7).

Dibolisporites microspicatus Playford 1978 (Plate II, 8, 11, 12).

Endoculeospora gradzinskii Turnau 1975 (Plate VII, 5, 6).

(*Remarks*: The Peruvian specimens show a diffuse and irregular central body, and the laesurae are not visible. *Endoculeospora rarigranulata* var. *densigranulata* Staplin 1960 is closely comparable to this species, but differs in having a more distinct and less dense central body and ornamentation apparently restricted to grana. The features observed in *A. macra* (without visible ornamentation) and *E. gradzinskii* (with minute ornamentation) appear to confirm the *Auroraspora* morphon proposed by Van der Zwan, 1980b).

Granasporites medius (Dybová and Jachowicz, 1957) Ravn et al., 1986 (Plate II, 5, 6).

(*Remark*: This species corresponds to *Cyclogranisporites* sp. di Pasquo et al., 2003a, p. 284, pl. 3, G).

Grandispora debilis Playford 1971 (Plate VII, 3).

Leiotriletes inermis (Waltz in Luber and Waltz, 1938) Ischenko, 1952 (Plate I, 2).

Leiotriletes ornatus Ischenko 1956 (Plate I, 1).

Microreticulatisporites parvirugosus Staplin 1960 (Plate III, 13, 14).

Punctatisporites aerarius Butterworth and Williams 1958 (Plate I, 7, 12).

Punctatisporites lucidulus Playford and Helby 1968 (Plate I, figs. 5, 6).

(*Remark*: Identified as *Punctatisporites resolutus* Playford 1971 by Souza et al., 1997, pl. I, fig. 2).

Retusotriletes anfractus Menéndez and Azcuy 1969 (Plate I, 13).

Retusotriletes crassus Clayton in Clayton, et al., 1980 (Plate I, 15).

(*Remarks*: This species corresponds to *Retusotriletes* sp. A Higgs 1975, p. 395, pl. 1 figs. 9, 13;

Retusotriletes sp. A Higgs 1975 by Keegan, 1977, p. 548, Pl. 1 Figs. 4, 5; *Retusotriletes* sp. A Higgs 1975 by Clayton et al., 1977, p. 7, pl. 6 fig. 4;

Plate I.
Miospores from the Ambo Formation. All ×750.

1.   *Leiotriletes ornatus* Ischenko. BAFC-Pl 1043: E29/2.
2.   *Leiotriletes inermis* (Waltz) Ischenko. BAFC-Pl 1043: T58.
3.   *Waltzispora polita* (Hoffmeister, Staplin and Malloy) Smith and Butterworth. BAFC-Pl 1043: S46/3.
4.   *Waltzispora lanzonii* Daemon.BAFC-Pl 1039: S54/3.
5, 6.   *Punctatisporites lucidulus* Playford and Helby.
5.   BAFC-Pl 1043: U36/3.
6.   BAFC-Pl 1036: V57/2.
7, 12.   *Punctatisporites aerarius* Butterworth and Williams.
7.   BAFC-Pl 1043: P31/2.
12.   BAFC-Pl 1043: N46/2.
8.   *Calamospora hartungiana* Schopf, Wilson and Bentall. BAFC-Pl 1043: Q50/1.
9.   *Calamospora* sp. BAFC-Pl 1043: G54/3.
10, 11. *Retusotriletes incohatus* Sullivan.
10.   BAFC-Pl 1043: S61/2.
11.   BAFC-Pl 1043: G37.
13.   *Retusotriletes anfractus* Menéndez and Azcuy. BAFC-Pl 1043: L32.
14.   *Aneurospora greggsii* (McGregor) Streel *in* Becker, Bless, Streel and Thorez.BAFC-Pl 1043: K38/4.
15.   *Retusotriletes crassus* Clayton *in* Clayton et al. BAFC-Pl 1043: Q51.
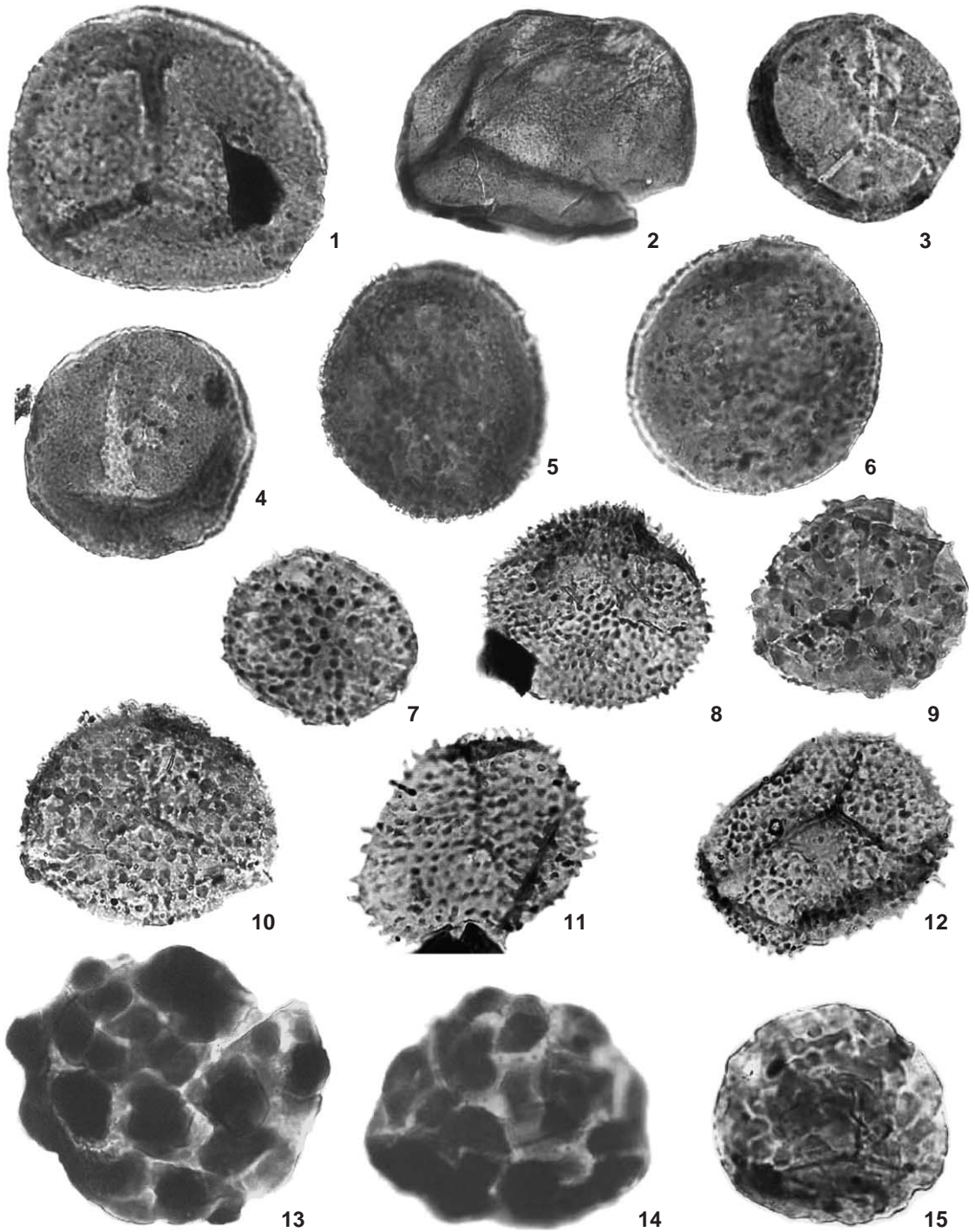
Retusotriletes sp. A Higgs 1975 by Utting, 1987b, p. 79, pl. 2, fig. 11).

Retusotriletes incohatus Sullivan 1964 (Plate I, 10, 11).

Schopfipollenites ellipsoides (Ibrahim, 1932) Potonié and Kremp, 1954 (Plate VII, 8).

(*Remark*: Utting (1987a) created *Schopfipollenites acadiensis* to include specimens clearly with the same characters of *S. ellipsoides* but somewhat smaller. On the other hand, Taylor (1978) and Taylor and Rothwell (1982), amongst others, stated that lamellar differentiation, development of distal grooves (which are generally obscured by folding) and grain size are function of maturity and cannot be reliably used for systematic purposes. There are in the literature some other examples of smaller specimens assigned to *S. ellipsoides* like the Peruvian ones, as cited by Coquel et al. (1988) from Libya, Loboziak et al. (1998) from Brazil and di Pasquo (2002) from Argentina. Therefore, *S. acadiensis* Utting (1987a, p. 38, pl. 5, figs. 7–11) and *Schopfipollenites* sp. Melo and Loboziak (2003, p. 192, pl. 7, fig. 6) are here regarded as junior synonyms).

Schopfites claviger Sullivan 1968 (Plate IV, 1, 2, 4, 5).

(*Remarks*: The criterion of Playford and Satterthwait (1986) is not followed to assign this species to the genus *Raistrickia* because of the absence of sculpture over almost all the proximal face. Nevertheless, in accordance with Playford (1991), the emendation proposed by Higgs et al. (1988) for *Schopfites claviger* Sullivan and *S. delicatus* Higgs are not accepted herein. The mentioned species, including also *S.* cf. *delicatus* Higgs et al., present ornamentation with a continuous gradation, as shown in Higgs et al. (1988, Fig. 30). Therefore, in order to avoid an artificial separation of these forms, they are considered herein as a single taxon. *Ceratosporites delicatus* (Higgs, 1975) Van der Zwan (1980a) is rejected, because it lacks a description and the illustration does not show ornamentation on the equator of the spore, a feature mentioned in the diagnosis of the species).

Spelaeotriletes balteatus (Playford, 1963) Higgs, 1996 (Plate VII, 1).

Spelaeotriletes sp. cf. *S. pretiosus* (Playford, 1964) Utting, 1987a (Plate VII, 2).

Vallatisporites vallatus Hacquebard 1957 (Plate VI, 10, 11).

Velamisporites minutus (Neves and Ioannides, 1974) Ravn, 1991 (Plate VII, 4).
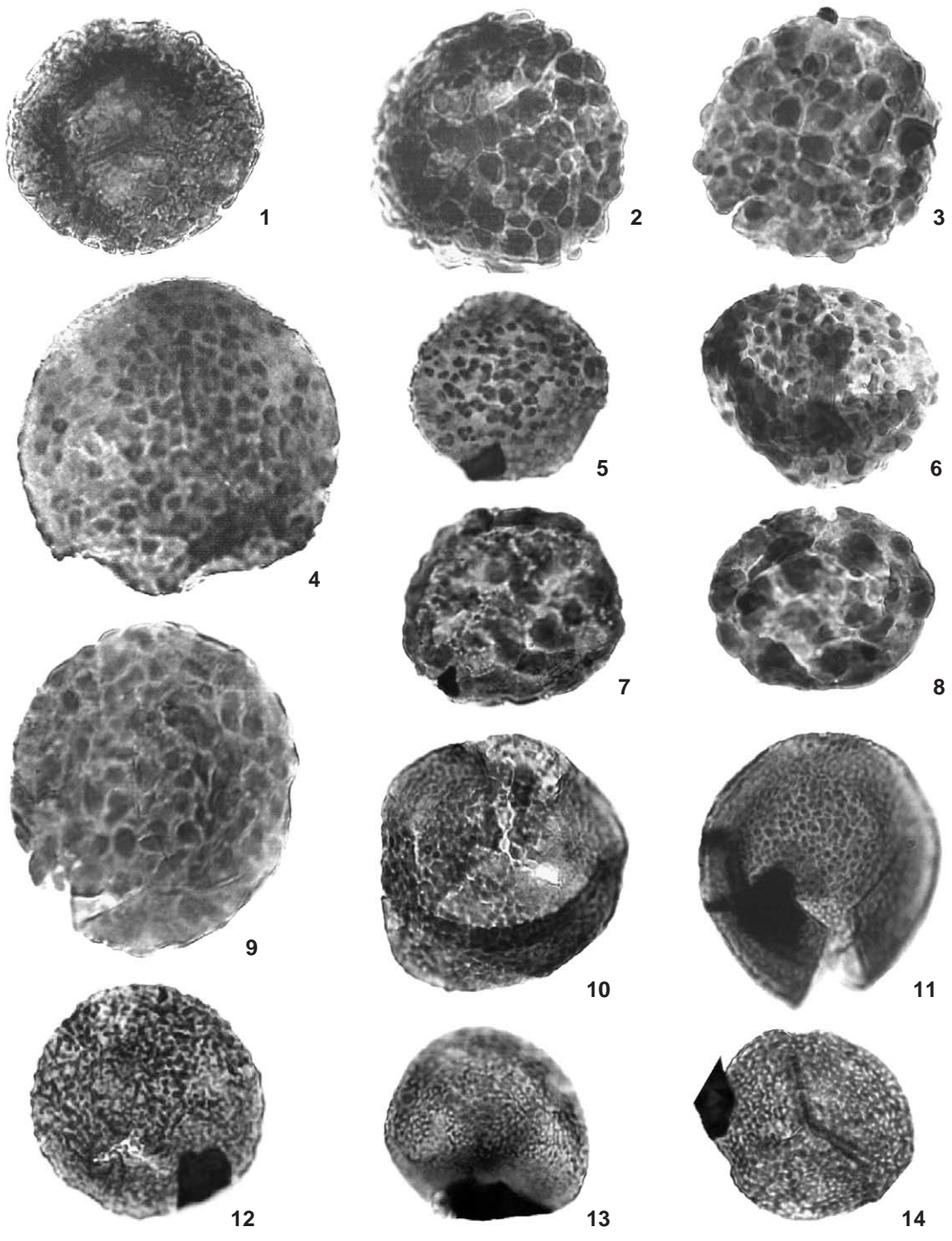
Verrucosisporites congestus Playford 1964 (Plate II, 13, 14).

(*Remark*: We follow the criterion of Turnau et al. (1994) that established an arbitrary separation for three species of this genus, *Verrucosisporites*

Plate II.

Miospores from the Ambo Formation. All ×750.

1.   *Aneurospora gregsii* (McGregor) Steel in Becker, Bless, Steel and Thorez. BAFC-Pl 1043: N32/5.
2, 3.   *Apiculiretusispora semisenta* (Playford) Massa, Coquel, Loboziak and Taugourdeau-Lantz.
2.   BAFC-Pl 1036: G40/2.
3.   BAFC-Pl 1039: P43/3.
4.   *Cyclogranisporites australis* Azcuy. BAFC-Pl 1037: O34/3.
5, 6.   *Granasporites medius* (Dybová and Jachowicz) Ravn, Butterworth, Phillips and Peppers.
5.   BAFC-Pl 1043: Q36.
6.   BAFC-Pl 1043: O56.
7.   *Anapiculatisporites* sp. cf. *A. austrinus* Playford and Satterthwait. BAFC-Pl 1043: Q52/4.
8, 11, 12. *Dibolisporites microspicatus* Playford.
8.   BAFC-Pl 1037: V49/1.
11.   BAFC-Pl 1037: H50/3.
12.   BAFC-Pl 1037: O33/2.
9.   *Pustulatisporites* sp. BAFC-Pl 1039: H34/1.
10.   *Anapiculatisporites* sp. BAFC-Pl 1039: D55/2.
13, 14. *Verrucosisporites congestus* Playford.
13.   BAFC-Pl 1036: T39/4.
14.   BAFC-Pl 1035: W62.
15.   *Verrucosisporites perverrucosus* (Loose) Potonié and Kremp emend. Smith. BAFC-Pl 1043: G66/2.

depressus Winslow 1962, *Verrucosisporites nitidus* Playford 1964, and *V. congestus* Playford 1964, based on the basal diameter of its warts).

Verrucosisporites depressus Winslow 1962 (Plate III, 10, 11).

Verrucosisporites morulatus (Knox, 1950) Potonié and Kremp, 1955 emend. Smith and Butterworth, 1967 (Plate III, 5, 6).

(*Remark*: This species corresponds to *Verrucosisporites nodosus* Sullivan and Marshall, 1966, p. 269, pl. 1, figs. 20, 21).

Verrucosisporites nitidus Playford 1964 (Plate III, 2, 3).

Verrucosisporites perverrucosus (Loose, 1934) Potonié and Kremp, 1955 emend. Smith, 1971 (Plate II, 15).

Verrucosisporites verrucosus (Ibrahim in Potonié et al., 1932) Ibrahim, 1933 (Plate III, 4, 9).

Waltzispora lanzonii Daemon 1974 (Plate I, 4).

Waltzispora polita (Hoffmeister et al., 1955) Smith and Butterworth, 1967 (Plate I, 3).

5.2. Systematic descriptions

Anteturma **Proximegerminantes** Potonié 1970.
Turma **Triletes** Reinsch emend. Dettmann 1963.
Suprasubturma **Acavatitriletes** Dettmann 1963.

Subturma **Azonotriletes** Luber emend. Dettmann 1963.
Infraturma **Laevigati** Bennie and Kidston emend. Potonié 1956.
Morphogenus ***Calamospora*** Schopf, Wilson and Bentall 1944.

Calamospora sp. (Plate I, 9).
Description: Trilete spore acavate, amb originally circular, laesurae indistinct, exine 3 μm thick, chagrinate to microgranulate, frequently folded.
Dimensions (4 specimens): Equatorial diameter 53–56.8 μm.
Remarks: A thicker and more microgranular exine are the features that distinguish this form from *Calamospora hartungiana*.

Spore sp.
Remark: It is interesting to note that almost all samples contained numerous specimens resembling *Cycadopites*, but one complete specimen was found that enabled us to identify this form as of *Calamospora*-type spore, displaying a short trilete mark on the proximal face. Both proximal and distal faces are still attached to each other at one end of the spore, and are folded giving the appearance of *Cycadopites*-type pollen grain.

Plate III.
Miospores from the Ambo Formation. All ×750.

1.   *Secarisporites* sp. BAFC-Pl 1043: P40/2.
2, 3.   *Verrucosisporites nitidus* Playford.
2.   BAFC-Pl 1037: L63.
3.   BAFC-Pl 1037: E54/2-4.
4, 9.   *Verrucosisporites verrucosus* (Ibrahim) Ibrahim.
4.   BAFC-Pl 1036: J36/4.
9.   BAFC-Pl 1037: U60/1.
5, 6.   *Verrucosisporites morulatus* (Knox) Potonié and Kremp emend. Smith and Butterworth.
5.   BAFC-Pl 1043: N52.
6.   BAFC-Pl 1036: M30.
7, 8.   *Convolutispora insulosa* Playford.
7.   BAFC-Pl 1039: P42/3.
8.   BAFC-Pl 1039: P46.
10, 11.   *Verrucosisporites depressus* Winslow.
10.   BAFC-Pl 1038:H 43/1-2.
11.   BAFC-Pl 1039: H41/3-4.
12.   *Convolutispora oppressa* Higgs. BAFC-Pl 1043: N58.
13, 14.   *Microreticulatisporites parvirugosus* Staplin.
13.   BAFC-Pl 1043: U53/1.
14.   BAFC-Pl 1043: J53/4.

Infraturma **Apiculati** Bennie and Kidston emend. Potonié 1956.
Subinfraturma **Nodati** Dybová and Jachowicz 1957.
Morphogenus *Anapiculatisporites* Potonié and Kremp 1954.

Anapiculatisporites sp. (Plate II, 10).

Description: Spores trilete; amb rounded subtriangular; margin slightly irregular. Laesurae straight, ca. 4/5 of spore radius, obscured by thin lips. Distal exine covered by blunt and tapering coni, 1 to 2 μm wide
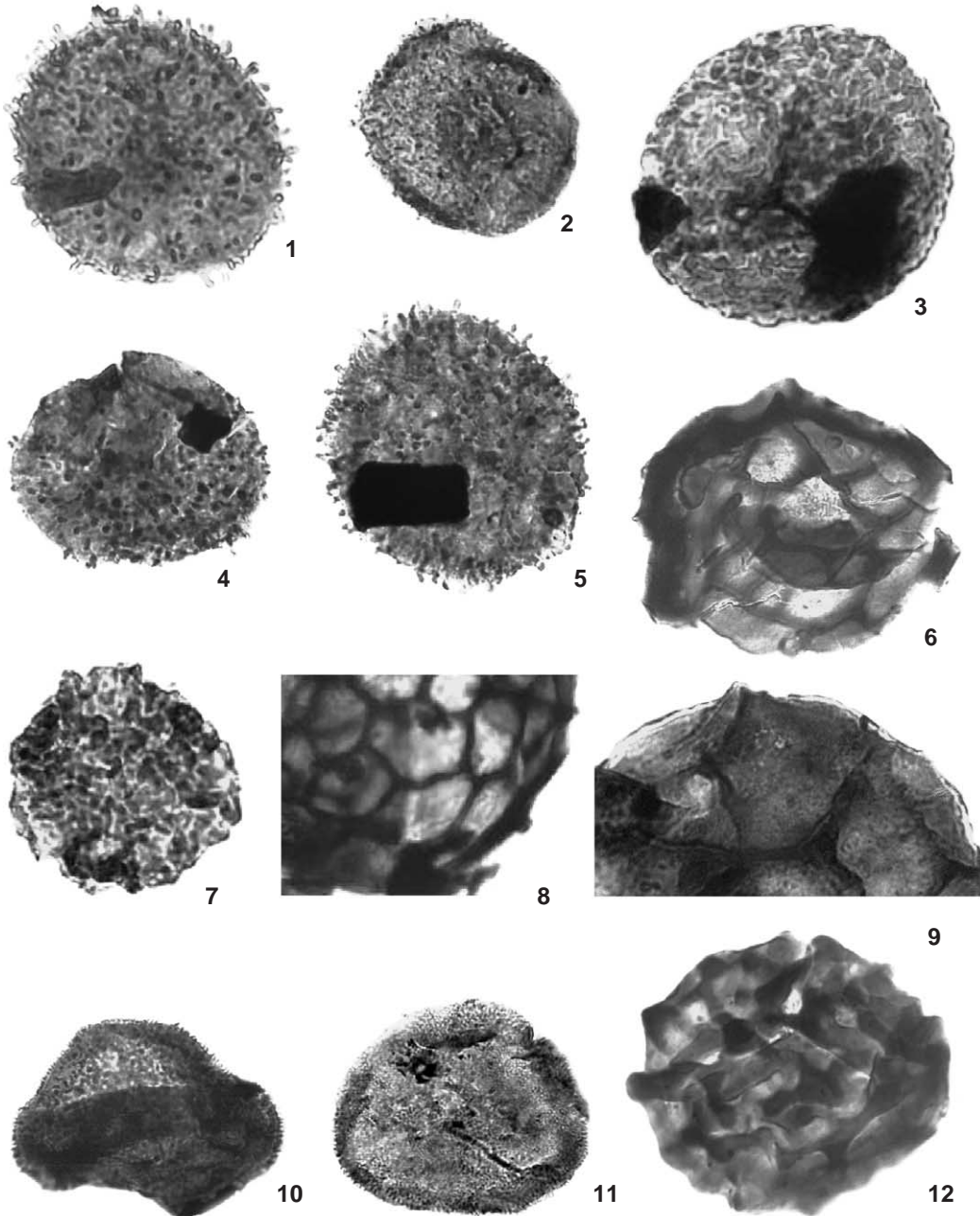
and high; spaces between coni generally somewhat wider than basal diameters. Proximal face laevigate.

Dimensions (6 specimens): Equatorial diameter 40–60 μm.

Remarks: *Anapiculatisporites redactus* Playford, 1978 and *A. austrinus* Playford and Satterthwait, 1986 differ from this species in being both smaller size and in having an ornamentation composed of delicate spinae or coni respectively, more widely spaced on both species. The scarcity of specimens prevents a more positive assignment.

Morphogenus ***Pustulatisporites*** Potonié and Kremp 1954.

Pustulatisporites sp. (Plate II, 9).

Description: Spores trilete acavate; amb rounded subtriangular; margin slightly irregular. Laesurae straight, almost reach the equator of the spore. Distal exine covered mainly with taper coni, 2 to 3.5 μm wide and up to 4.6 μm high; subordinate coni with blunt and well-rounded apices are present. Ornament irregularly distributed and occasionally few elements may be fused. Proximal face laevigate.

Dimensions (1 specimen): Equatorial diameter 43 μm.

Remarks: *Pustulatisporites pustulatus* Potonié and Kremp 1954 differs from the species described above in having less apiculate elements, which are irregularly distributed and more often fused.

Subinfraturma **Verrucati** Dybová and Jachowicz 1957.

Morphogenus ***Secarisporites*** Neves 1961.

Secarisporites sp. (Plate III, 1).

Description: Spores trilete, acavate, anisopolar. Amb circular to oval. Laesurae straight accompanied by flattened lips, 3.5 μm wide. Their ends are not visible because of the strong subequatorial sculpture of the proximal face. Contact areas laevigate. Distal face and subequatorial proximal surface bearing closely spaced and low narrow-based warts, 1.5 to 3.8 μm wide, 1.5 to 2.5 μm high with a strong flattened apical expansion, 2.3 to 7.5 μm wide. In plan view, the warts appear separated by narrow striae or sometimes they are fused.

Dimensions (4 specimens): Equatorial diameter 38–51 μm.

Remarks: A partly comparable species is *Convolutispora mellita* Hoffmeister et al. (1955), which displays ribs with flattened expansions but is clearly distinguished from the Peruvian material because it lacks laevigate contact areas.

Subinfraturma **Murornati** Potonié and Kremp 1954.

Morphogenus ***Cordylosporites*** Playford and Satterthwait 1985.

Cordylosporites sp. (Plate IV, 12).

Description: Spores trilete, amb subcircular and margin irregular. Laesurae simple, straight, 2/3 to 3/4 of spore radius. Exine sculptured with a coarse, imperfect reticulum. Muri smooth, 3.5 to 4 μm high and wide; baculate or conate supramural projections, 3 to 8 μm high, 5 to 8 μm basal width, are frequent in muri junctions. The thickness of exine is 4.6 μm.

Dimensions (1 specimen): Equatorial diameter 62.6 μm.

Plate IV. Miospores from the Ambo Formation. All ×750.

1, 2, 4, 5.	*Schopfites claviger* Sullivan.
1.	BAFC-Pl 1043: K52/3.
2.	BAFC-Pl 1043: S60/4.
4.	BAFC-Pl 1043: M51/4.
5.	BAFC-Pl 1043: M44/3.
3.	*Convolutispora* sp. cf. *C. elimata* Playford. BAFC-Pl 1043: N50.
6, 8, 9.	*Cordylosporites magnidictyus*. (Playford and Helby) Melo and Loboziak.
6.	BAFC-Pl 1036: W46.
8.	BAFC-Pl 1035: N41/1.
9.	BAFC-Pl 1037: C53/1.
7.	*Convolutispora* sp. cf. *C. varicosa* Butterworth and Williams. BAFC-Pl 1036: O61.
10, 11.	*Crassispora kosankei* (Potonié and Kremp) Bharadwaj *emend*. Smith and Butterworth.
10.	BAFC-Pl 1043: G53.
11.	BAFC-Pl 1039: O42/1.
12.	*Cordylosporites* sp. BAFC-Pl 1036: D39/4.
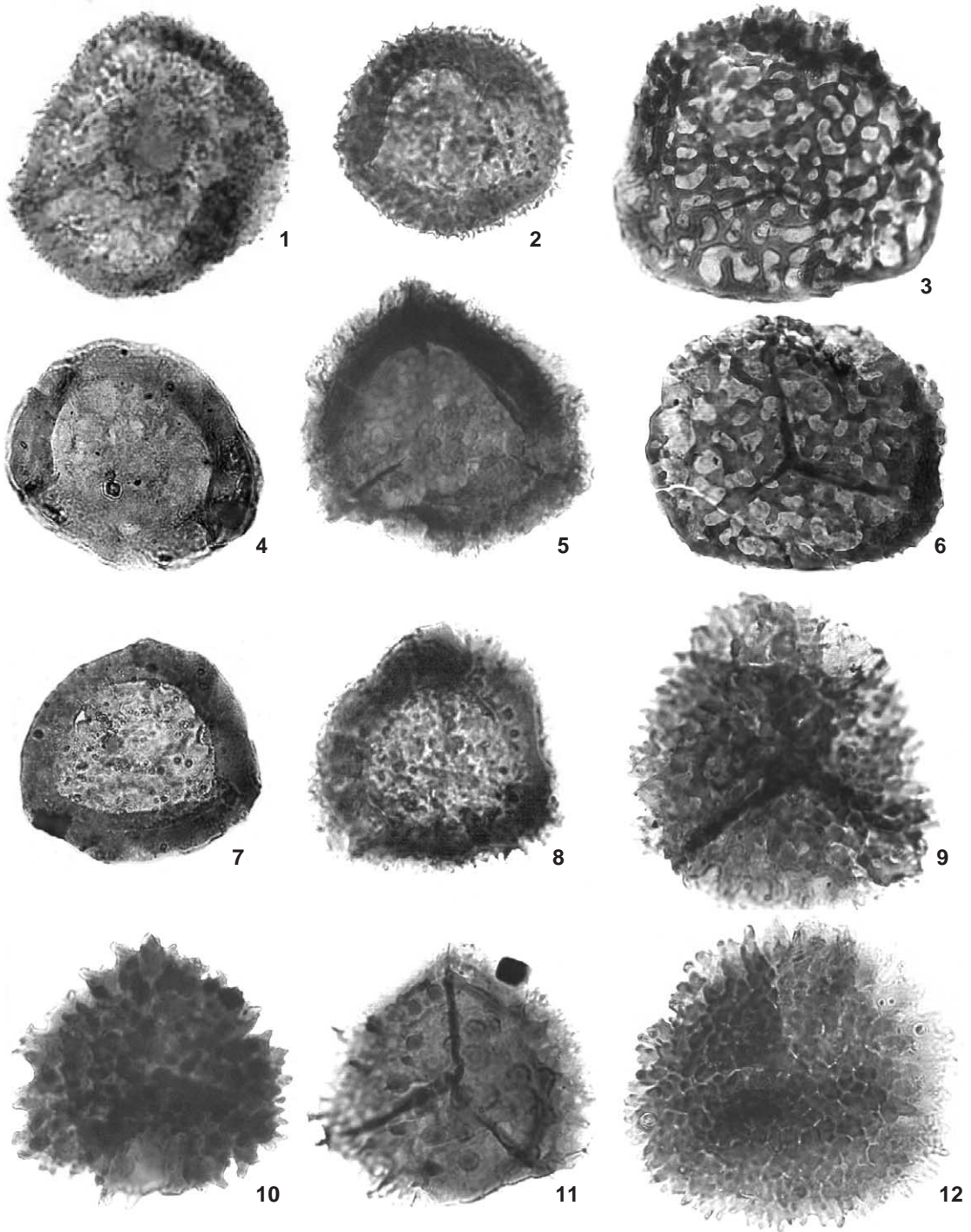
Remarks: The specimens illustrated as ?*Dictyotriletes trivialis* Naumova in Kedo by Van Veen (1981, pl. 3, fig. 3) and *Corbulispora* sp. Ravn (1991, pl. 11, figs. 10–13) resemble the one here described, but as they were not described a better comparison is not possible. *Cordylosporites papillatus* (Naumova) Playford and Satterthwait, 1985 differs from the Peruvian form by the presence of almost perfect to perfect reticulum and a greater development of the projections on the muri. *Reticulatisporites rudis* Staplin (1960, pl. 2, fig. 23) is similar but differs because of the lack of projections in the junctions of rugulae and by possessing a well-defined reticulum. The specimens illustrated by Smith (1971, pl. XVIII, figs. 13–15) as *Verrucosisporites perverrucosus* Loose emend. Smith also present some similarity although the size of rugulae-warts and their projections are clearly smaller. The lack of more specimens does not allow a more precise taxonomic assignment.

Suprasubturma **Laminatitriletes** Smith and Butterworth 1967.

Subturma **Zonolaminatitriletes** Smith and Butterworth 1967.

Infraturma **Crassiti** Bharadwaj and Venkatachala emend. Smith and Butterworth 1967.

Morphogenu*s* ***Crassispora*** Bharadwaj 1957 emend. Keegan and Penney, 1978.

Crassispora sp. (Plate V, 1, 2).

Description: Spores trilete, amb circular, equatorial margin irregular. Laesurae somewhat flexuous, accompanied by dark lips, 3.5 μm wide, almost reaching the equator. Cingulum more or less regular in width, 5–6 μm wide. Distal face and cingulun densely ornamented with pointed apiculate elements, some of them biform, up to 3 μm high and wide. Proximal face laevigate.

Dimensions (2 specimens): Equatorial diameter 45–56.5 μm.

Remarks: This species is similar to *Crassispora kosankei* (Potonié and Kremp, 1955) Bharadwaj, 1957 emend. Smith and Butterworth, 1967, but the sculpture in the former presents some biform elements, and the elements are generally larger. *Crassispora scrupulosa* Playford 1971 is also comparable but is larger and possesses biform elements with more verrucate bases, which support two or more minute coni or spinae (setose verrucae), features not observed in *Crassispora* sp.

Infraturma **Cingulicavati** Smith and Butterworth 1967.

Morphogenu*s* ***Densosporites*** Berry 1937 emend. Butterworth et al., 1964.

Densosporites sp. (Plate V, 5, 8).

Description: Spores trilete, camerate, cingulizonate; amb subtriangular; equatorial margin almost smooth.

Plate V.

Miospores from the Ambo Formation. All ×750.

1, 2.　　　*Crassispora* sp.
1.　　　　BAFC-Pl 1043: S61/3.
2.　　　　BAFC-Pl 1043: K44.
3, 6.　　　*Bascaudaspora submarginata* (Playford) Higgs, Clayton and Keegan.
3.　　　　BAFC-Pl 1037: W26/4.
6.　　　　BAFC-Pl 1039: R63.
4, 7.　　　*Densosporites anulatus* (Loose) Schopf, Wilson and Bentall.
4.　　　　BAFC-Pl 1037: U58/2.
7.　　　　BAFC-Pl 1037: Q33/1-3.
5, 8.　　　*Densosporites* sp.
5.　　　　BAFC-Pl 1043: C57/2.
8.　　　　BAFC-Pl 1036: S47/2.
9, 12.　　*Cristatisporites echinatus* Playford.
9.　　　　BAFC-Pl 1037: D35/1.
12.　　　　BAFC-Pl 1038: W28/1.
10.　　　*Cristatisporites indignabundus* (Loose) Potonié and Kremp *emend*. Staplin and Jansonius. BAFC-Pl 1043: R30/2-4.
11.　　　*Kraeuselisporites mitratus* Higgs. BAFC-Pl 1043: N28.
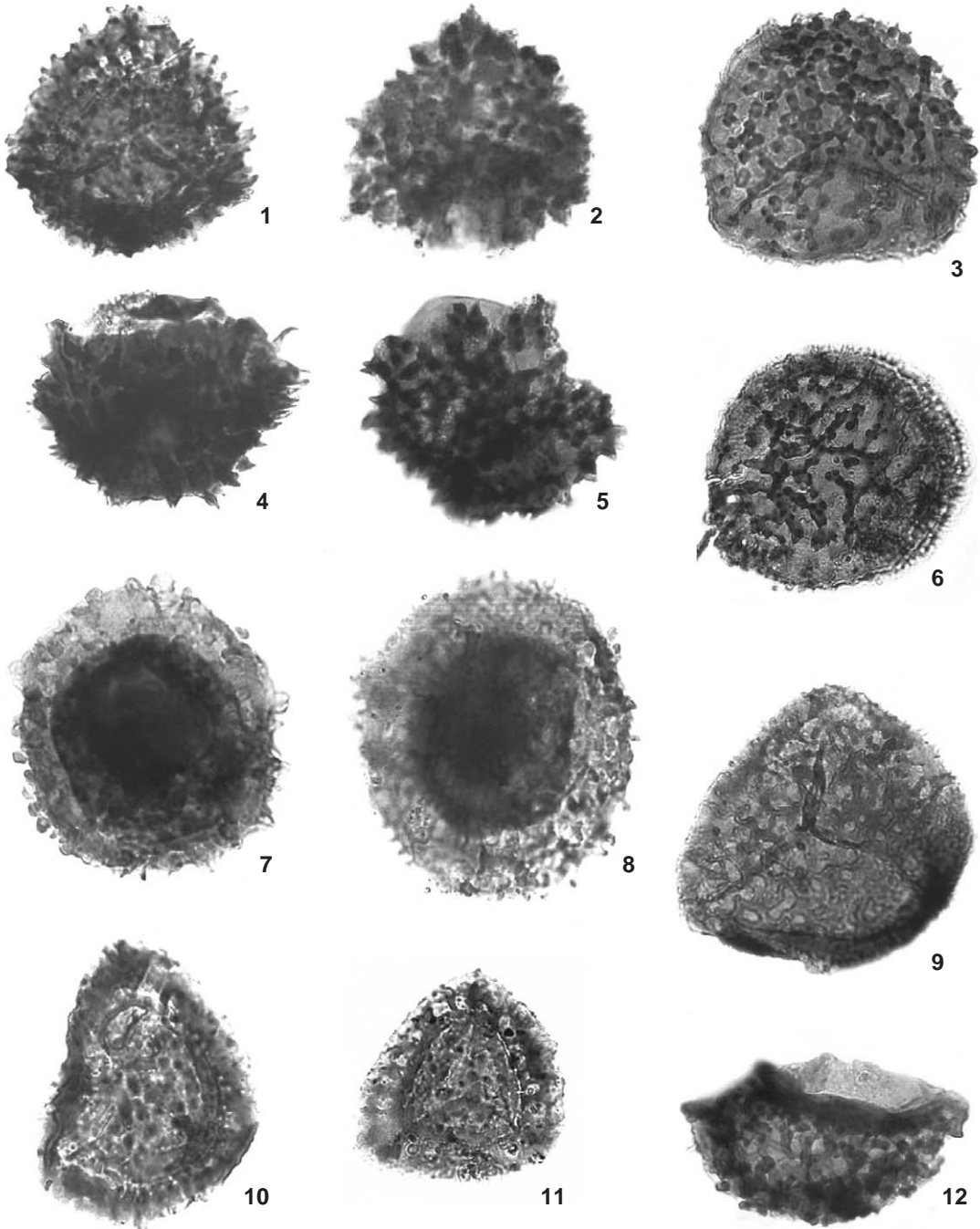
Laesurae straight, reaching the internal border of the cingulum, sometimes indistinct. Distal and proximal central area translucent with small grana and coni up to 2.3 μm high and wide. The cingulizona is more or less uniform in width and reaches ca. 1/2 of spore radius. The thickest inner zone corresponds to the cingulum whose external edge is irregular and ill-defined, with a narrow, more translucent zone outwards. The cingulizona bears scattered coni and some punctuations.

Dimensions (6 specimens): Equatorial diameter 40.6–70 μm; cingulizona width 9 to 14 μm.

Remarks: The scarcity of specimens prevents a better comparison. *Densosporites granulosus* Kosanke 1950 differs because of the absence of coni in the polar area and a slightly pronounced zone beyond the cingulum. *Cingulizonates landesii* (Staplin, 1960) Staplin and Jansonius, 1964 possesses a minutely granulose proximal face and a more distinct zone.

Morphogenus ***Kraeuselisporites*** Leschik 1955 emend.

1964 *Indotriradites* Tiwari, pp. 251–252.

Type species: *K. dentatus* Leschik, 1955.

Emended diagnosis: Trilete spores, acamerate or camerate, zonate to slightly cingulizonate. Amb sub-triangular. Margin entire, smooth to slightly sculptured. Trilete suturae with or without labra may extend up to the margin of the spore. Intexine smooth. Proximal face laevigate or occasionally with markedly reduced sculpture. Distal face sculptured mainly with discrete apiculate elements and occasionally with grana, baculae or verrucae interspersed. The ornamentation of the zona may be reduced in size and density. A slightly darkened inner portion of the zona may be present.

Remarks: Although *Kraeuselisporites* has been discussed many times in the literature and many authors have proposed emendations, the present emended diagnosis is based on the existence of a zona independently of the degree of adhesion of the layers of the exine.

The emendation proposed by Jansonius (1962) focused on the presence of a trilete mark, a feature originally interpreted as alete by Leschik (1955) in the original diagnosis.

The later emendation of Scheuring (1974) limited the genus to acamerate forms whereas Segroves (1970) and Balme (1970) accepted the interpretation of Jansonius (1962) and in addition, proposed to include both acamerate and camerate forms. In the present emendation, the use of the latter term includes camerate forms in the sense of Neves and Owens (1966), where the loosening of the exoexine is also known as "cavate", if restricted to only the equatorial zone, and "pseudosaccate" if it reaches the distal zone (according to Grebe, 1971). Owens et al. (1976) followed the emendation of Scheuring (1974), although the evidence of loosening of the exine layers led them to assign *Kraeuselisporites* to the Infraturma Cingulicamerati Neves and Owens, 1966.

Plate VI.
Miospores from the Ambo Formation. All ×750.

1, 2.	*Cristatisporites indignabundus* (Loose) Potonié and Kremp *emend*. Staplin and Jansonius.
1.	BAFC-Pl 1043: L53/1.
2.	BAFC-Pl 1043: R30/2-4.
3, 6, 9, 12.	*Cristatisporites peruvianus* sp. nov. Azcuy and di Pasquo.
3.	BAFC-Pl 1037: G35/3.
6.	BAFC-Pl 1039: D29/4.
9.	BAFC-Pl 1039: J59/2
12.	BAFC-Pl 1043: W53/1.
4, 5.	*Grandispora* sp.
4.	BAFC-Pl 1043: E30/2.
5.	BAFC-Pl 1037: G35/1-2.
7, 8.	*Spelaeotriletes pustulosus* sp. nov. Azcuy and di Pasquo.
7.	BAFC-Pl 1043: R58/4.
8.	BAFC-Pl 1043: S34/1.
10, 11.	*Vallatisporites vallatus* Hacquebard.
10.	BAFC-Pl 1036: N54/2.
11.	BAFC-Pl 1036: V47/1-2.
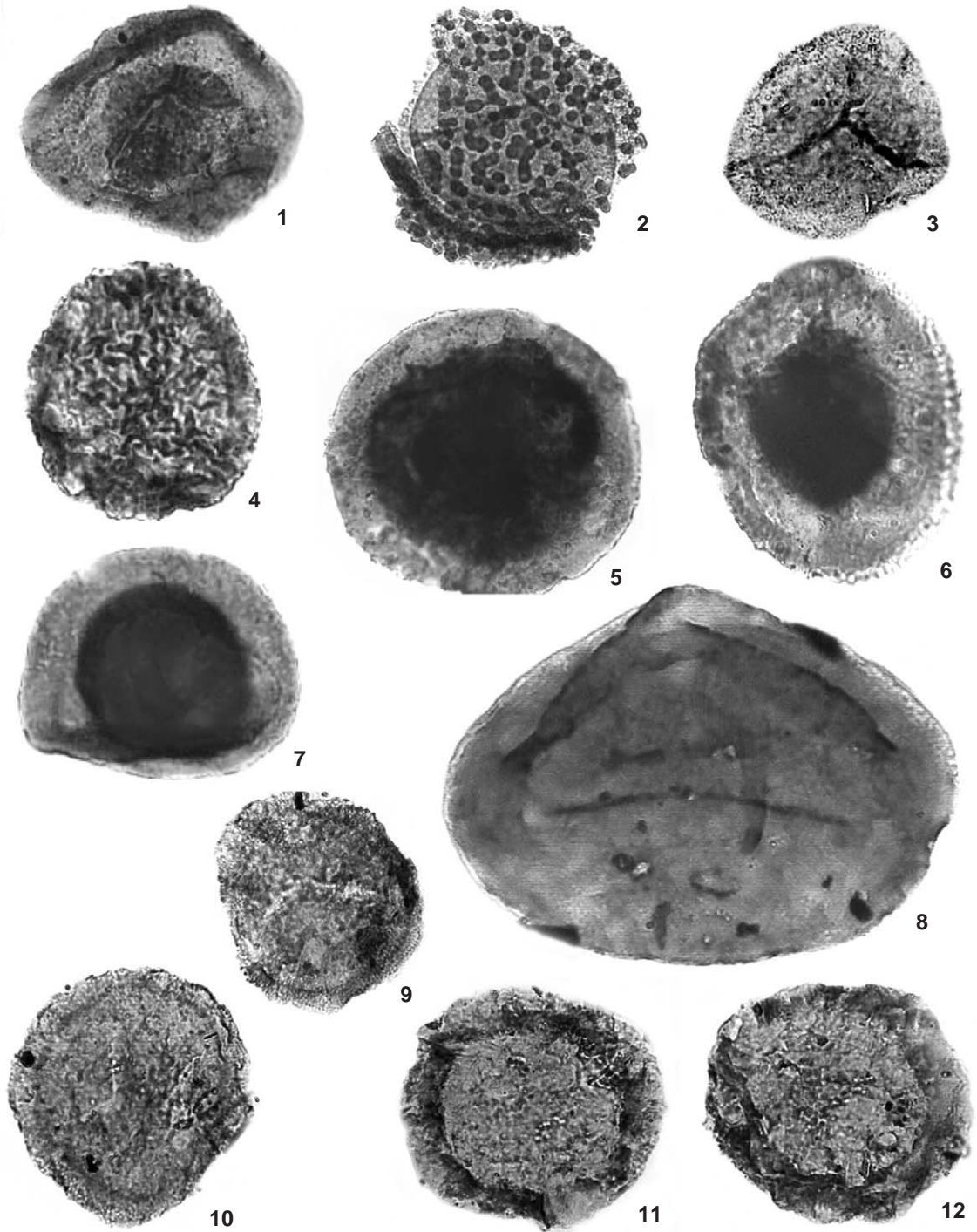
Because of its similar morphology, *Indotriradites* Tiwari 1964 has been a subject of intense discussions in order to justify its separation from *Kraeuselisporites*. Based on its diagnosis, the greatest and almost only difference from the latter comprises the presence of a central body, sometimes with semilunar folds. This feature suggests the separation of both layers of the exine. In this sense, Foster's (1979) proposed emendation of the genus to emphasize its camerate condition is insufficient to separate it from *Kraeuselisporites*, in our opinion. The present emendation is further confirmed by the recognition of specimens of the same species showing acamerate and camerate structure (sometimes partially) in the same association. Therefore, *Indotriradites* is here considered to be a junior synonym of *Kraeuselisporites*. *Comparisons*: Although *Grandispora* Hoffmeister et al. 1955 emend. Neves and Owens, 1966 is distinguished from *Kraeuselisporites* by the different degree of cameration and the mainly distal apiculate sculpture, the former is also separated by the lack of a zona and by the variable thickness of the exoexine, seen as a marginal thickening or limbus in the sense of Higgs et al. (2000).

Cingulizonates Dybová and Jachowicz 1957 emend. Butterworth et al. in Staplin and Jansonius, 1964 differs from *Kraeuselisporites* by the presence of a well-defined cingulum in the inner part of the cingulizona and granulose or verrucose ornamentation in the central distal face.

Cristatisporites Potonié and Kremp 1954 emend. Butterworth et al. in Staplin and Jansonius, 1964 differs from *Kraeuselisporites* by the presence of an apiculate and/or verrucose setose ornamentation developing crests on the distal face. The variable development of the cingulizona and the distinctive ornamentation shown in its frequently stellate amb provide further criteria to distinguish the genus.

In addition, all these genera differ from *Vallatisporites* Hacquebard 1957 mainly because of the absence of the typical vacuolation developed in the cingulizona of the latter genus.

Species here transferred to *Kraeuselisporites*:

Kraeuselisporites explanatus (Luber in Luber and Waltz 1941) nov. comb.
Basionym: *Zonotriletes explanatus* Luber in Luber and Waltz, Trudy tsent. Nauchno-issled geologo-razv. Inst. 105, 45 pp., 1941; p. 10, pl. 1, fig. 4.

Kraeuselisporites scorpius (Balme and Hassell, 1962) nov. comb.
Basionym: *Hymenozonotriletes scorpius* Balme and Hassell, Micropaleontology 8, 1–28, 1962; p. 16, pl. 3, figs. 8–11.

Kraeuselisporites dolianitii (Daemon, 1974) nov. comb.
Basionym: *Hymenozonotriletes dolianitii* Daemon, Annales Academia Brasiliera Sciênces, 46, 549–587, 1974; p. 572, pl. 8, figs. 7, 8.

Kraeuselisporites reidii (Foster, 1979) nov. comb.
Basionym: *Indotriradites reidii* Foster, Geological Survey of Queensland, Publication 372, Paleontological Paper 45, 244 pp., 1979; p. 55, pl. 16, figs. 6–9.

Plate VII.
Miospores from the Ambo Formation. All ×750.

1.   *Spelaeotriletes balteatus* (Playford) Higgs. BAFC-Pl 1038: E31/1.
2.   *Spelaeotriletes* sp. cf. *S. pretiosus* (Playford) Utting. BAFC-Pl 1036: U46/3.
3.   *Grandispora debilis* Playford. BAFC-Pl 1037: M43/1.
4.   *Velamisporites minutus* (Neves and Ioannides) Ravn. BAFC-Pl 1043: P66/3.
5, 6.   *Endoculeospora gradzinskii* Turnau.
5.   BAFC-Pl 1043: O36/3.
6.   BAFC-Pl 1043: M32/3.
7.   *Auroraspora macra* Sullivan. BAFC-Pl 1043: W39/2.
8.   *Schopfipollenites ellipsoides* (Ibrahim) Potonié and Kremp. BAFC-Pl 1043: U36/3.
9, 10.   *Colatisporites decorus* (Bharadwaj and Venkatachala) Williams *in* Neves, Gueinn, Clayton, Ioannides and Neville.
9.   BAFC-Pl 1037: E27/2.
10.   BAFC-Pl 1037: S56/2.
11, 12.   *Velamisporites* sp.
11.   BAFC-Pl 1039: E54.
12.   BAFC-Pl 1039: Q61/2.

Kraeuselisporites daemonii (Loboziak et al., 1999) nov. comb.

Basionym: *Indotriradites daemonii* Loboziak et al., Review of Paleobotany and Palynology, 107, 17–22, 1999; p. 20, pl. 1, figs. 1–5.

Species here accepted:

1963 *Kraeuselisporites cuspidus* Balme; p. 19, pl. 5, figs. 9–11.

1968 *Kraeuselisporites kuttungensis* Playford and Helby; p. 112, pl. 11, figs. 6, 7.

1970 *Kraeuselisporites splendens* (Balme and Hennelly) Segroves; p. 65, pl. 9, figs. FH.

1970 *Kraeueselisporites rallus* Balme; p. 337, pl. 4, figs. 9–13.

1970 *Kraeueselisporites wargalensis* Balme; p. 338, pl. 4, figs. 14–17.

1975 *Kraeuselisporites fasciatus* Higgs; p. 400, pl. 6, figs. 13, 14.

1975 *Kraeuselisporites mitratus* Higgs; p. 4001, pl. 6, figs. 18–20.

1975b *Kraeuselisporites volkheimerii* Azcuy; p. 130, pl. 24, figs. 155–158.

1975b *Kraeuselisporites malanzanensis* Azcuy; p. 28, pl. 23, figs. 149–150.

1976 *Kraeuselisporites echinatus* Owens et al.; p. 148, pl. 1, figs. 1–6.

1976 *Kraeuselisporites ornatus* (Neves) Owens et al.; p. 153, pl. 2, figs. 2–4.

1988 *Kraeuselisporites zosteriformis* Playford and Satterthwait; p. 7, pl. 4, figs. 1–7.

Species here rejected:

1970 *Kraeuselisporites niger* Segroves; p. 65, pl. 9, figs. C–E.

1970 *Kraeuselisporites enormis* Segroves; p. 67, pl. 8, fig. G; pl. 9, figs. A–B.

1975 *Kraeuselisporites hibernicus* Higgs; p. 400, pl. 6, figs. 11, 12.

1988 *Kraeuselisporites tedantus* Playford and Satterthwait; p. 7, pl. 3, figs. 9–19.

Kraeuselisporites mitratus Higgs 1975 (Plate V, 11).
Remarks: The Peruvian specimens do not show a distinct exinal separation. As suggested by Higgs et al. (1988), *Kraeuselisporites* sp. A Owens et al. (1976, p. 154, pl. 2, figs. 5, 6) is here considered to be a junior synonym of *K. mitratus*.

Morphogenus **Cristatisporites** Potonié and Kremp 1954 emend. Butterworth et al., 1964.

Cristatisporites peruvianus sp. nov. (Plate VI, 3, 6, 9, 12).

1980a ?*Cristatisporites colliculus* Playford 1971; Van der Zwan, pl. 30, figs. 1–5.

1988 *Bascaudaspora collicula* (Playford, 1971) Higgs et al., pl. 7, figs. 15–17.

Holotype: BAFC-Pl **1039**, J59/2, Plate VI, 9.

Paratypes: BAFC-Pl 1043, W53/1, Plate VI, 12; BAFC-Pl 1039, D29/4, Plate VI, 6; BAFC-Pl 1037, G35/3, Plate VI, 3.

Type locality: Pongo de Mainique, Ambo Formation, Madre de Dios Basin, Perº (Lower Carboniferous).

Diagnosis: Spores radial, trilete, cingulate, cavate; amb subtriangular to subcircular. Laesurae simple or bordered by labra with curvaturae perfectae or imperfectae at their ends. Cingulum narrow, bearing biform elements fused in the equatorial region. Proximal exoexine microgranular or smooth; equator and distal face with galeae and coni fused forming rugulae which give it a beady appearance. These rugulae may be branched or anastomosed into an irregular reticulum.

Derivatio nominis: Referred to the country of provenance.

Description: Spores radial, trilete, cingulate, cavate; amb subtriangular to subcircular. Equatorial margin slightly serrated because of the projection of low sculptural elements. Laesurae frequently masked by the ornamentation, simple or accompanied by thin lips, something sinuous, up to 2.3 çm wide, reaching almost the spore margin with curvaturae perfectae or imperfectae. Intexine thin, smooth, sometimes not visible, conformable with spore amb. Cingulum narrow, 3.57 çm wide, not always uniform, bearing biform elements which may be fused at the equator. Proximal exoexine flattened, microgranular or smooth. Equatorial and distal exoexine with galeae and coni with fused bases defining an imperfect reticulum (beady appearance), with short and long rugulae, relatively loosely spaced, up to 2.3 mm wide. The apical end of the mammillate elements reach 0.8 to 3 çm in height. Rugulae of irregular disposition, two or three times their width apart, which can delimit luminae of irregular to oval outline and of variable size (up to 9 çm in greatest

diameter). The frequent lateral views show the strong convexity of the distal face.

Remarks: The specimens described and illustrated by Van der Zwan (1980a, p. 228229, pl. XXX, figs. 1–5) as ?*Cristatisporites colliculus* and by Higgs et al. (1988, p. 65, pl. 7, figs. 1517) as *Bascaudaspora collicula* (Playford, 1971) Higgs et al., 1988 display the features observed in the Peruvian material (e.g., ornamentation composed of biform elements and setose warts which may be fused forming crests or rugulae that can branch or anastomose into an imperfect reticulum). The occurrence of these diagnostic characters has been recognized in a large number of specimens, which justifies the establishment of a new taxon. It is however interesting to point out that Playford and Satterthwait (1988) state that the specimens described by Van der Zwan (1980a) as ?*C. colliculus* are different from the Australian ones in having crests that delimit a reticulate pattern on the distal face.

Dimensions (58 specimens): Equatorial diameter 45(55–60)70 μm.

Comparisons: *Cristatisporites colliculus* Playford (1971, pl. 14, figs. 1, 2; pl. 15, figs. 1–6) is considered to be a closely related species but differs from the Peruvian one by its dense distal sculpture of cones forming short crests and the presence of discrete cones in variable proportions, which rarely delimit a reticulum. *Bascaudaspora submarginata* (Playford, 1964) Higgs et al. (1988, pl. 7, figs. 19, 20) differs clearly from *C. peruvianus* sp. nov. by its predominance of luminae into an almost perfect reticulum and the absence of sculpture on the muri. The former was considered by Van der Zwan (1980a) as at one end of the *Dictyotriletes submarginatus* morphon, transitional with *C. colliculus*. Nevertheless, the specimens illustrated by Van der Zwan (1980a, pl. XXVII, fig. 2; pl. XXVIII, figs. 4–5; pl. XXIX, fig. 4) as *D. submarginatus* could also be included in *C. peruvianus* sp. nov. *Acinosporites microconicus* Playford and Satterthwait 1985 differs from *Cristatisporites peruvianus* sp. nov. in having an ornamented proximal face and a more perfect reticulum on the distal surface.

Occurrence: Early Carboniferous (Ireland): Van der Zwan, 1980a; Higgs et al., 1988.

Morphogenus *Grandispora* Hoffmeister, Staplin and Malloy 1955 emend. McGregor, 1973.

Grandispora sp. (Plate VI, 4, 5).

Description: Spores trilete, pseudosaccate; amb subtriangular. Strongly projecting spines on the equator. Laesurae indistinct. Intexine distinct, thin and conformable with the amb. Distal ornamentation composed of wide-based, stout spines and mammoids, up to 8.2 çm high and 4.5 çm wide. Elements discrete, densely to moderately spaced; sometimes the tips of spines are slightly curved. Proximal face usually smooth.

Dimensions (3 specimens): Equatorial diameter 5960 çm; pointed coni 2.3 to 4.5 çm in basal width, and 3.5 to 8.2 μm high.

Remarks: *Grandispora acuta* (Kedo, 1963) Byvscheva (1980), discussed by Higgs et al. (2000) is similar to the Peruvian species but the latter possesses a denser ornamentation and narrower-based apiculate elements.

Suprasubturma **Pseudosaccitriletes** Richardson, 1965.
Infraturma **Monopseudosacciti** Smith and Butterworth 1967.
Morphogenus *Spelaeotriletes* Neves and Owens 1966.

Spelaeotriletes sp. (Plate VI, 7, 8).

Description: Spores trilete, pseudosaccate; amb subcircular to oval. Elements of ornamentation are well seen on the equatorial margin. Laesurae indistinct to distinct, simple and straight, extending to the margin of the central body. Intexine fairly well defined, smooth, dark and more or less conformable with the amb. Exoexine proximally smooth. Sculpture on distal and equatorial surface consisting predominantly of rounded verrucae, closely spaced coni and occasional baculae, occasionally fused. Basal width and height of verrucae and coni 2.5 to 3 μm.

Dimensions (4 specimens): Equatorial diameter 45.2–54.5 μm.

Remarks: The specimens assigned as *Spelaeotriletes* sp. are distinguished from the other species of the genus by the strong projection of their wart-like sculpture and rounded cones on the margin, the dense central body and the subcircular amb.

Morphogenus *Velamisporites* Bharadwaj and Venkatachala 1962.

Velamisporites sp. (Plate VII, 11, 12).

Description: Spores trilete, pseudosaccate; amb more or less circular. Equatorial margin wavy. Laesurae

poorly distinguishable. Intexine smooth, slightly eccentric and somewhat lighter in colour than the exoexine, which appears thinly folded. The folds are conspicuous on the distal face and have a faintly radial arrangement.

Dimensions (8 specimens): Equatorial diameter 40–63.8 μm.

Comparisons: This material possesses the generic features for assignment to *Velamisporites*, but is distinguished from other species of the genus by its type of folding. *Velamisporites australiensis* (Playford and Helby, 1968) di Pasquo et al., 2003b is superficially similar, but *Velamisporites* sp. differs in having a dense and fine, radially arranged folding mainly on the exoexine, and lacks microgranulation.

6. Discussion

6.1. Palynological antecedents and composition of the palynoflora

Only two brief palynological contributions and one summary have been previously published from the Ambo Formation. The first one consists of a list of illustrated species, almost all reported in open nomenclature, from a locality exposing a littoral facies at Paracas about 130 km to the south of Lima (Doubinger and Alvarez Ramis, 1980). The authors suggested that the association was probably of Viséan age. The second is a contribution based on the Pongo de Coñec locality, located about 200 km to the southeast of the locality studied here (Aliaga López, 1985). The palynomorphs were only recognized at generic level and attributed as a whole to the Mississippian s.l. Finally, the summary is a list of eight species that mentions forms not recorded in previous studies (Azcuy, 1991), assigning an Early Carboniferous age.

The palynoflora of Pongo de Mainique is composed of 55 species, mostly defined at species level, of which only one is new: *Cristatisporites peruvianus* (Fig. 3). The assemblages are generally abundant, diverse and variably preserved except for levels 1035 and 1036 which yielded less than 100 specimens each. Tracheid fragments are abundant in almost all the samples, but other land-derived palynodebris such as cuticles are less frequent.

The quantitative distribution of the palynoflora was calculated on the basis of the total number of counted specimens, which reached 772 in the six samples. The percentages for the parent plants sources of the groups of palynomorphs are as follows: Lycophyta (23.8%), Pteridophyta (51.2%), Sphenophyta (8.8%), Pteridospermaphyta (0.6%), Spores with unknown botanical affinity (15.5%), reworked spores (0.9%), reworked microplankton (2.6%). Spore sp. is frequently registered and is considered in the quantitative assessment as a member of the Sphenophyta group.

Scarce acritarchs and other algal cysts are represented by *Veryhachium trispinosum* (Eisenack) Deunff, *Veryhachium downiei* Stockmans and Willière, *Gorgonisphaeridium* sp., *Umbellasphaeridium deflandrei* (Moreau-Benoit) Jardine et al., *Palacanthus* sp., *Maranhites insulatus* Burjack and Oliveira, *Quadrisporites granulatus* (Cramer) Ströther and some typically Devonian spore species like *Grandispora* sp. cf. *G. mammillata* Owens, *Retispora lepidophyta* (Kedo) Playford and *Emphanisporites hibernicus* McGregor, which are poorly represented at some sampled horizons. All of these palynomorphs have been considered as reworked, and therefore are neither described nor illustrated in this study. Figs. 4 and 5 show the geographical and stratigraphical distribution, and age range of selected species found in the Ambo Formation, some of which correspond to long-ranging forms that appear in the latest Devonian or Tournaisian.

The Peruvian assemblage is exclusively composed of spores with only one exception, the praecolpate pollen grain *Schopfipollenites ellipsoides*, that appears in sample 1043 (located immediately below the contact with the Tarma Formation). The greatest percentage of spores includes forms characteristic of the Early Carboniferous, although some other species appear in the latest Devonian whilst others persist into the Late Carboniferous and Early Permian (Fig. 4). The most abundant species in the whole assemblage, i.e., those represented by more than 17 recorded specimens, include: *Leiotriletes inermis*, *Punctatisporites lucidulus*, *Punctatisporites aerarius*, *Calamospora hartungiana*, *Retusotriletes incohatus*, *Aneurospora greggsii*, *Verrucosisporites nitidus*, *Verrucosisporites depressus*, *Verrucosisporites morulatus*, *Verrucosisporites verrucosus*, *Cristatisporites peruvianus* sp. nov., *Convolutispora insulosa*, *Vallatisporites vallatus*, *Dibolisporites microspicatus* and *Microreticulatisporites parvirugosus*. *Cordylosporites magnidictyus* is infrequent and relatively badly preserved in all levels with

exception of sample 1043. With respect to this level, other characteristic forms which occur in relative abundance (more than 8 specimens) include: *Calamospora* sp., *Convolutispora oppressa*, *Schopfites claviger*, *Granasporites medius*, *Auroraspora macra* and *Endoculeospora gradzinskii* (Fig. 3).

6.2. *Cordylosporites magnidictyus* Palynozone (Mag) Melo and Loboziak 2003

Recently, Melo and Loboziak (2003) carried out an exhaustive analysis of a large number of productive samples from Devonian–Early Carboniferous subsurface sections in the Amazon Basin, and proposed 17 new interval palynozones. The association here analyzed for the Ambo Formation shares with the *Cordylosporites magnidictyus* Palynozone of Melo and Loboziak, the following species in addition to the homonym species: *Schopfites claviger*, *Schopfipollenites ellipsoides*, *Waltzispora polita*, *Verrucosisporites nitidus*, *Velamisporites minutus*, *Vallatisporites vallatus*, *Spelaeotriletes balteatus*, *Spelaeotriletes pretiosus*, *Colatisporites decorus*, *Auroraspora macra* and *Kraeuselisporites mitratus*. Assignment to this Palynozone is therefore suggested for the Pongo de Mainique samples. It is however important to note that the appearance of the praecolpate pollen grain *Schopfipollenites ellipsoides*, at the top of the Ambo Formation, is not associated with *Cordylosporites magnidictyus* (Fig. 3) as observed in the Viséan basins of Brazil (Melo et al., 1999). This fact could have an additional stratigraphical meaning, similar to that proposed by Utting (1987a) for Viséan palynofloras of Canada.

6.3. Age of the palynoflora and paleoenvironmental significance

In agreement with the previous records of the selected species, shown in Fig. 5, the age of the assemblage is late Viséan. Palynological data from the middle and basal parts of the Ambo Formation is sparse due to the high degree of thermal maturity, making it difficult to establish with certainty the age of that part of the section. On the other hand, samples from the upper parts of the overlying Tarma Formation (samples 508 and 509, Fig. 3), about 250 m above the *Mag* Palynozone, have recently yielded another palynoflora (Azcuy et al., 2002), which is

comparable to the *Illinites unicus* Palynozone of Playford and Dino (2000), also defined in the Amazon Basin and assigned to the late Westphalian. Nevertheless, it is still uncertain if the barren layers between both palynozones represent a continuous interval of deposition or, on the contrary, if a hiatus exists between both units. The thickness of this section shown in Fig. 3 and the time scale based on radiometric ages used in Fig. 2 seem to support the first hypothesis.

With respect to the paleoenvironment, the palynoflora of the Ambo Formation is composed exclusively of continental elements (abundant spores and one praecolpate pollen grain) associated with abundant land-derived plant debris which suggest continental deposition. The botanical affinities attributed to the miospores show a strong predominance of Pteridophyta and subordinated Lycophyta and Sphenophyta (see percentages above), which suggests humid environmental conditions. Paleogeographic reconstruction of South America during the Late Devonian–Early Carboniferous (Azcuy and di Pasquo, 1999) locates the studied regions of Peru and the Amazon Basin at approximately the 50°S paleolatitude. This datum would suggest warm temperate conditions for the region where the parent flora was developed (Iannuzzi and Pfefferkorn, 2002).

On the other hand, data from this study and those reported by Azcuy et al. (2002) referred to associations of late Viséan and the late Westphalian age, respectively, imply alternative interpretations. In the light of the paleogeographic and paleoclimatic reconstructions presented by Scotese (2000) and considering the absolute ages proposed by Menning et al. (2001), shown here in Fig. 2, it is probable that the region of Pongo de Mainique experienced a drift towards the Equator during a period of about 18 m.a. that took it towards lower paleolatitudes, close to 30°S. This would have favored the deposition, in a marine paleoenvironment, of the first calcareous banks of the Tarma Formation, located only 50 m above sample 1043, which is at the top of the Ambo Formation. This evidence is in agreement (other than the difference of absolute ages with respect to other time scales) with the Serpukhovian paleoclimatic reconstruction after Scotese (2000), which locates the interval above the *Mag* Palynozone in the warm temperate belt next to

the limit with the arid belt around 35°S paleolatitude. It would therefore differ from the cold temperate conditions prevailing during the earliest Carboniferous in the southern part of Gondwana.

6.4. Distribution and correlation

The Early Carboniferous *s.l.* stratigraphical section in Fig. 4 allows one to draw some conclusions on the geographic distribution of the selected species from the Peruvian palynoflora in relation to different continents. The data which have been compiled from previous records of described species, in the bibliography available, show the following affinity percentages: Europe 66%; North America 57%; South America 54%; Africa 45% and Australia 30%. Considering that the age of the studied palynoflora is late Viséan, then it is evident that some proportion of the above mentioned percentages does not reflect the true degree of similarity of the various palynofloras. On the other hand, although the data are influenced by the variable number of studies made in each region, the greatest affinity appears to be with North Gondwana (Africa and South America), North America (Canada) and Australia, rather than with the colder Gondwana regions to the south and the warmer regions of Europe.

6.4.1. South America

Both the *Mag* and *Illinites unicus* Palynozones have been recognized in the valley of the Urubamba river (Azcuy et al., 2002) as well as in the Amazon Basin (Playford and Dino, 2002; Melo and Loboziak, 2003). Also, the geographic and stratigraphical distribution of the older *Mag* Palynozone is recognized in nearby localities of Brazil and Bolivia. In the first case, the Poti Formation of the Parnaiba Basin, recently studied by Melo and Loboziak (2000), yielded palynofloras from four wells which contained the following species in common with the Ambo Formation assemblage: *Cordylosporites magnidictyus*, *Waltzispora polita*, *Vallatisporites vallatus*, *Bascaudaspora submarginata*, *Verrucosisporites nitidus*, *Verrucosisporites congestus*, *Verrucosisporites depressus*, *Cristatisporites echinatus*, *Colatisporites decorus* and *Apiculiretusispora semisenta*. This assemblage was also assigned to the late Viséan by Melo and Loboziak (2000). In relation to the north

of Bolivia, the Kaka Formation of the Retama Group has yielded preliminary palynological data reported by Azcuy and Ottone (1987) from the Alto Beni river section. Although the species in common with the Peruvian association are few (*Apiculiretusispora semisenta*, *Verrucosisporites nitidus* and *Auroraspora macra*), the above mentioned authors attributed with some reservations the association from the Kaka Formation to the Viséan and made a comparison with the *Verrucosisporites* sp. 85 (=*V. nitidus*)–*Reticulatisporites magnidictyus* Palynozone, recorded by Suárez Soruco and Lobo Boneta (1983) from the subsurface of Bolivia. The late Viséan age of these Bolivian palynofloras was later confirmed on the basis of its association with a coeval macroflora, *Nothorhacopteris kellaybelenensis* (Azcuy and Suárez Soruco, 1993; Iannuzzi et al., 1998; Iannuzzi and Pfefferkorn, 2002; Iannuzzi et al., 2003).

6.4.2. Europe

A significant number of species present in the late Viséan Peruvian assemblage are common to Early Carboniferous associations of western Europe (Clayton et al., 1977; Higgs et al., 1988; Fig. 4). Populations from the two regions share the following species: *Leiotriletes ornatus*, *Leiotriletes inermis*, *Punctatisporites aerarius*, *Retusotriletes incohatus*, *Retusotriletes crassus*, *Waltzispora polita*, *Aneurospora greggsii*, *Verrucosisporites nitidus*, *Verrucosisporites congestus*, *Verrucosisporites depressus*, *Verrucosisporites morulatus*, *Verrucosisporites perverrucosus*, *Schopfites claviger*, *Convolutispora oppressa*, *C. varicosa*, *Bascaudaspora submarginata*, *Densosporites anulatus*, *Kraeuselisporites mitratus*, *Cristatisporites echinatus*, *Cristatisporites indignabundus*, *Spelaeotriletes balteatus*, *S. pretiosus*, *Endoculeospora gradzinski*, *Colatisporites decorus*, *Vallatisporites vallatus*, *Auroraspora macra* and *Velamisporites minutus*. Most of these species first appear in the Tournaisian, and some of them extend into the Viséan of Europe. However, only relatively few of the Viséan Peruvian species are shared with the coeval TC-NM Palynozones (Clayton et al., 1977): *Waltzispora polita*, *Bascaudaspora submarginata*, *Densosporites anulatus* and *Colatisporites decorus*. On the other hand, it should be stressed that *Schopfipollenites ellipsoides*, described from the Late Carboniferous of Europe (e.g., Smith and Butter-

worth, 1967; Turner and Spinner, 1993), has its earliest records in the late Viséan of Brazil (Loboziak et al., 1998; Melo et al., 1999; Melo and Loboziak, 2003), Libya (Coquel et al., 1988) and Canada (Utting, 1987a).

6.4.3. North America

The species common to the late Viséan of Canada and the Peruvian palynoflora are more numerous than those shared with Europe. Of the three biozones established by Utting (1987a), the NS and AT Biozones are correlated with *Mag* Palynozone recognized in Brazil and now also in Peru. The species in common are: *Verrucosisporites verrucosus*, *Verrucosisporites nitidus*, *Verrucosisporites morulatus*, *Auroraspora macra*, *Colatisporites decorus*, *Bascaudaspora submarginata*, *Leiotriletes inermis*, *Leiotriletes ornatus*, *Retusotriletes incohatus*, *Velamisporites minutus*, *Schopfites claviger*, *Spelaeotriletes pretiosus* and *Schopfipollenites ellipsoides*. It is interesting to note, in the Canadian associations, the absence of *Cordylosporites magnidictyus* and the presence of *Schopfipollenites ellipsoides*. The former is an exclusive species with provincial value in the late Viséan of the North Gondwana, more indeed in the floral Paraca realm (Alleman and Pfefferkorn, 1988; Iannuzzi and Pfefferkorn, 2002). The latter has not been previously recorded in the Early Carboniferous either of Europe or of Australia. In the late Viséan of Canada, Utting (1987a) uses the appearance of *Schopfipollenites ellipsoides* (called *S. acadiensis*) to define the AT Palynozone, whereas in Libya (Coquel et al., 1988), Saudi Arabia (Clayton, 1995), Russia (Reitlinger et al., 1996) and Peru (this work; Fig. 4), its appearance is contemporary thus confirming its stratigraphical value. In Brazil its association with *Cordylosporites magnidictyus* could mask this value.

6.4.4. Africa

In Africa the Early Carboniferous species shared with the Peruvian palynoflora are numerous: *Leiotriletes ornatus*, *Retusotriletes incohatus*, *Retusoletes crassus*, *Schopfites claviger*, *Cordylosporites magnidictyus*, *Punctatisporites aerarius*, *Apiculiretusispora semisenta*, *Waltzispora polita*, *Microreticulatisporites parvirugosus*, *Verrucosisporites nitidus*, *Verrucosisporites depressus*, *Verrucosisporites mor-*

ulatus, *Kraeuselisporites mitratus*, *Cristatisporites echinatus*, *Spelaeotriletes balteatus*, *Spelaeotriletes pretiosus*, *Colatisporites decorus*, *Vallatisporites vallatus*, *Auroraspora macra*, *Velamisporites minutus*, *Schopfipollenites ellipsoides*. Also the number of late Viséan common species is significant: *Retusotriletes incohatus*, *R. crassus*, *Verrucosisporites depressus*, *Apiculiretusispora semisenta*, *Colatisporites decorus*, *Cordylosporites magnidictyus*, *Spelaeotriletes balteatus*, *Waltzispora polita*, *Velamisporites minutus* and *Schopfipollenites ellipsoides* (Massa et al., 1980; Loboziak et al., 1986; Coquel et al., 1988, 1995; Clayton, 1995). The number of common species seems to show a strong relation between the North Africa basins with those of Peru and Brazil. However, the absence of certain North African taxa (e.g., *Aratrisporites saharensis* Loboziak et al., *Vallatisporites agadesi* Loboziak and Alpern, *Spelaeotriletes benghaziensis* Loboziak and Clayton, *Spelaeotriletes owensii* Loboziak and Alpern) in Peru prevents a closer correlation, yet all of them occur in the adjacent Amazon Basin of Brazil (Melo and Loboziak, 2003).

6.4.5. Australia

The degree of affinity between the Peruvian palynoflora and the assemblages of Australia is significant, as demonstrated by the number of common species: *Leiotriletes ornatus*, *Schopfites claviger*, *Cordylosporites magnidictyus*, *Apiculiretusispora semisenta*, *Waltzispora polita*, *Verrucosisporites nitidus*, *Auroraspora macra*, *Convolutispora insulosa*, *C. elimata*, *C. varicosa*, *Anapiculatisporites austrinus*, *Dibolisporites microspicatus* and *Grandispora debilis*. Except for *Verrucosisporites nitidus* and *Auroraspora macra*, which have their first records in the Late Devonian, the remaining species are all restricted to the Viséan (Playford, 1985, 1991; Playford and Satterthwait, 1986, 1988). *Cordylosporites magnidictyus*, a key species of the Gondwanan regions like South America, Africa and Australia, was selected by Melo and Loboziak (2003) to define a homonym palynozone. Originally it was described by Playford and Helby (1968) in Italy Road Formation of the eastern Australia, and attributed to the Westphalian as part of the *Grandispora maculosa* Palynoflora. Later, absolute dating studies using the SHRIMP method, carried out on

horizons from the Mt. Johnstone Formation (Roberts et al., 1993, 1995), confirmed the correlation of the upper part of this unit with the Italy Road Formation, thus modifying the age of the *G. maculosa* Palynoflora. Consequently both formations are now considered as of latest Viséan age.

Finally, and considering quantitative affinities for the late Viséan only, it is evident that the proportion of species common to the upper part of the Ambo Formation and Europe is restricted (4 spp.) probably as a result of Europe's lower paleolatitudinal position. North America (13 species) and Gondwana (21 species with Africa and 17 species with South America) present greater affinities, which must be attributed mainly to a roughly equivalent paleolatitudinal position of these regions. In the case of Australia (11 species), the quantitative differences seem to come partly from the endemic character of their palynofloras, in result of its relative isolation, and also of its lower paleolatitudinal position (Van der Zwan, 1981; Clayton, 1985, 1996; Playford, 1991; Li and Powell, 2001; Iannuzzi and Pfefferkorn, 2002). On the other hand, in higher paleolatitudes, preliminary palynological studies carried out in Argentina also show differences with relation to the present palynoflora (Césari and Limarino, 1995; Rodríguez Amenábar et al., 2003).

Acknowledgements

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