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## **Abstract**

Unusual fossil macrofloras from South America (Peru, Bolivia, Brazil), Africa (Niger), India, and Australia are distinctly different from both the Early and Late Carboniferous floras of Gondwana. These floras can be correlated with each other based on macrofloral and palynologic composition, and dated as Late Visean to earliest Serpukhovian through palynologic data from several floras and isotopic data from Australia. The floras are dominated by pteridosperm foliage and characterized by the occurrence of tree-lycopsids, and represent a warm-temperate, frost-free floral belt in Gondwana that reached from 30°S to as far as 60°S that existed directly before the onset of the major episode of the Carboniferous glaciation. The plants lived during an interval of very warm climate as indicated by the width and extent of the floral belt, conditions that facilitated the migration of plants into this area from other parts of the globe. The term Paracal floral realm is redefined and extended to include all of these Late Visean-earliest Serpukhovian floras throughout Gondwana.

## **Comments**

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# A Pre-Glacial, Warm-Temperate Floral Belt in Gondwana (Late Visean, Early Carboniferous)

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*Unusual fossil macrofloras from South America (Peru, Bolivia, Brazil), Africa (Niger), India, and Australia are distinctly different from both the Early and Late Carboniferous floras of Gondwana. These floras can be correlated with each other based on macrofloral and palynologic composition, and dated as Late Visean to earliest Serpukhovian through palynologic data from several floras and isotopic data from Australia. The floras are dominated by pteridosperm foliage and characterized by the occurrence of tree-lycopsids, and represent a warm-temperate, frost-free floral belt in Gondwana that reached from 30° to as far as 60° South that existed directly before the onset of the major episode of the Carboniferous glaciation. The plants lived during an interval of very warm climate as indicated by the width and extent of the floral belt, conditions that facilitated the migration of plants into this area from other parts of the globe. The term Paraca floral realm is redefined and extended to include all of these Late Visean-earliest Serpukhovian floras throughout Gondwana.*

## INTRODUCTION

Two different fossil floras have been recognized in the Carboniferous of Gondwana (Archangelsky et al., 1987; Anderson et al., 1999), one characterized by small-to-medium sized lycopsids in the Early Carboniferous and another impoverished flora with *Nothorhacopteris* and *Botrychiopsis* in the Late Carboniferous. Both floras have been interpreted as representing “plant life around the ice sheet” (Anderson et al., 1999, p. 153). “Between these two floras there is a relative blank in Gondwana (to be clarified with improved correlations) with inclement conditions (at least in eastern ‘Australia’) exacerbated by major volcanic activity” (Anderson et al., 1999, p. 153; parentheses by original authors). This blank now is being filled with an analysis and synthesis of plant assemblages from the middle of the Carboniferous of Gondwana that belong to neither of the aforementioned floras. These specific floras are characterized by the occurrence of a combination of forms known, in part, from other Carboniferous climatic belts. Only recently have sufficient data become available to correlate these floras and date them based on palynology, marine invertebrates, and isotope ages. Therefore, it is now possible to recognize a warm temperate floral belt

within Gondwana that is of late Visean age, predating the onset of the Carboniferous glaciation across Gondwana.

The floras under consideration have been found in South America (Peru, Bolivia, and Brazil), Africa (Niger), India, and Australia, and have been described variously as Early (= Mississippian) or Late (= Pennsylvanian) Carboniferous (Alleman, 1985). Their unusual species composition made them enigmatic or at least problematic. The Peruvian floras have been interpreted as representing a distinct, warm temperate floral belt for which the term Paraca floral realm was coined (Alleman and Pfefferkorn, 1988). This interpretation is revised here and extended to the other floras under consideration using recent comparisons between Carboniferous floras from Peru and Bolivia (Iannuzzi et al., 1998, 1999) and an analysis of western Gondwana floral changes (Pfefferkorn, 1997; Iannuzzi and Rösler, 2000). “Paracas” is the name of the peninsula where this type of flora was first recognized. The word “Paraca” designates a sandstorm in the area, and is used to mark the difference between the locality and the generalization derived from it.

## MATERIALS AND METHODS

The authors have collected macrofloras in Peru, Bolivia, and Brazil, and have studied material in museum collections that included material from Niger (Africa). The major collections used for comparison were: Museo de Historia Natural of the Universidad Ricardo Palma, Lima, Peru; Universidade de São Paulo, São Paulo, Brazil; Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; Museo de Historia Natural de Cochabamba, Cochabamba, Bolivia; Laboratoire de Paleobotanique, Université de Paris-VI, Paris, France; and the Smithsonian Institution, Washington, DC, USA. Comparisons with material from India and Australia have relied on the published literature (see appendices). The senior author investigated palynomorphs from Brazil and Bolivia, and compared this material with the publications from other continents. Tables 1 and 2 list the geographic and stratigraphic occurrences of macrofloras and palynofloras, respectively.

The macrofloras of the Paraca floral realm (Alleman and Pfefferkorn, 1988) cannot be compared simply based on their taxonomic lists. This is because various investigators in different countries have used different taxonomies due to the perception that these floras were unique in each localized area. Other problems originate from differ-

**TABLE 1**—Geographic and stratigraphic occurrences of macrofloras of the Paraca floral realm and their age assignments.

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PERU: Ambo Formation, Paracas Peninsula (Fuchs, 1990; Steinmann, 1929; Berry, 1922a, b; Seward, 1922; Gothan, 1928; Read, 1938; Jongmans, 1954; Doubringer and Alvarez-Ramis, 1980; Alleman, 1985; Alleman and Pfefferkorn, 1988, 1991; Erwin et al., 1994; Alleman et al., 1995; Pfefferkorn, 1997; Iannuzzi et al., 1998, 1999); Ambo Formation, Carhuamayo (Jongmans, 1954). *Previous age assignments*: Visean (Doubringer and Alvarez-Ramis, 1980); Early Carboniferous (Azcuay, 1990); both based on palynology.

BOLIVIA: Siripaca Formation, Copacabana Peninsula, Altiplano (Suárez-Soruco, 1974; Azcuay and Suárez-Soruco, 1993; Iannuzzi et al., 1993, 1998, 1999). Kaka Formation, northern Subandean area (Suárez-Soruco, 1974; Azcuay and Ottone, 1987). *Previous age assignments*: Late Visean to early Serpukhovian based on macro-flora (Iannuzzi et al., 1993b, 1998, 1999) and palynology (Azcuay, 1990; Azcuay and Ottone, 1987).

BRAZIL: Poti Formation, Parnaíba Basin, northeastern Brazil (Dolianiti, 1954; Dolianiti, 1980). *Previous age assignments*: Tournaisian to Visean (Daemon, 1974; Loboziak et al., 1992) based on palynology. Macro-flora has been found only in the upper part of the formation and is restricted to the late Visean as shown by additional palynological studies (Iannuzzi et al., 1993a; Iannuzzi and Scherer, 1996; Melo et al., 1998).

NIGER (Africa): Guézouman Formation, lower part of Togora Group, Air Mountains (DeRouvre, 1988). *Previous age assignment*: Late Visean to earliest Serpukhovian for part of the section containing the megaflora (Coquel et al., 1995) based on palynology.

INDIA: Wallarama Bed (member C) of Fenestella Shale Formation, Kashmir Basin, NW Himalayas (Singh et al., 1982; Tripathi and Singh, 1985; Pant and Srivastava, 1995). *Previous age assignments*: The Wallarama Bed (member C) of the Fenestella Shale Formation lies stratigraphically between two members that contain marine faunas indicating an age interval that ranges from middle Visean to Bashkirian.

AUSTRALIA: Mount Johnstone and Italia Road Formations, Gresford Block, Sydney Basin; McInnes Formation, Myall Block, Sydney Basin (Rigby, 1973, 1985; Morris, 1975, 1980, 1985; Retallack, 1980). This flora corresponds to the *Sphenopteridium* flora or enriched *Nothorhacopteris* flora, respectively of Retallack (1980) and Morris (1985). *Previous age assignments*: Roberts et al. (1993, 1994, 1995) using the SHRIMP method on single zircon crystals from volcanic tuff layers which occur above and below the plant fossil bearing horizons in the Mount Johnstone Formation (Visean [V3a] age) and above in the McInnes Formation (earliest Serpukhovian age).

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ences of preservation in various lithologies that reflect differences in ecologic, sedimentologic, and taphonomic settings and processes. Two taxonomic changes that are central to the argument presented herein have been made and have been presented in Appendix 1.

A working synonymy has been established for the plant macrofossils. Appendix 2 presents for each area a list with an interpretation of those taxa that are present, and a second list that provides all taxa reported in the literature. Taxonomy is more uniform in the palynologic literature, and Appendix 3 presents the occurrence of palynomorphs in the different countries.

### STRATIGRAPHY

Figure 1 presents nine stratigraphic columns from the six countries/areas where Paraca-type floras have been recognized. The stratigraphic correlation is based on palynomorphs and macrofloras. The lithologic signatures indicate the occurrence of climatically sensitive rocks including glacial deposits, coal beds, eolian deposits, and extensive marine carbonates. Isotopic ages have been determined in the two Australian columns and are indicated with asterisks (provided in the caption). In Brazil, Peru, and Bolivia (columns 1, 2, 4), and in part of Australia (Mount Johnstone and Italia Formations in the Sydney Basin, column 8), the *Nothorhacopteris* flora (N) occurs in an interval that contains thin coal seams. On the Indian Subcontinent and in Australia (columns 6, 7, 8), this flora is found below glacial deposits. Thus, indicators of cold climate occur at the bottom of the sections (Late Devonian to Tournaisian) in columns 1–4 while glacial deposits are seen in the upper parts of the sections (Late Carboniferous) in columns 6–8. Carbonates show the opposite trend (columns 1, 3, 4, 6, 7).

### MACROFLORA

Three higher taxonomic groups comprise the megafloras of the Paraca floral belt—lycopsids, sphenopsids, and pteridosperms. Lycopsids and sphenopsids are represented by fewer species than pteridosperms but can dominate in specific ecological settings and contribute to the characterization of these floras. Fern-like foliage existed during this time interval in several unrelated plant groups—ferns, progymnosperms, pteridosperms, and early cycads. The term pteridosperms is used here informally for all families of gymnosperms with fern-like foliage. To date, not all of the leaves from the Paraca-type floras can be attributed to a higher taxonomic group with certainty. However, it is clear that a majority belonged to the pteridosperms based on the constant presence of pteridosperm reproductive organs in all of the more intensively studied floras (Erwin et al., 1994; Morris, 1985; Retallack, 1980). Therefore, the term pteridosperms is used with the caveat that one or several of these forms may have to be re-assigned to a different taxonomic group in the future. Ranges of the stratigraphically most important macroflora taxa are plotted in Figure 2. The occurrence of the common genera in the different areas is shown in Table 3.

Similarity indices (Jacquard and Otsuka) show that the macrofloras from the late Visean are quite similar to each other, while they are different from both the Early and Late Carboniferous floras from Argentina (Table 4). The Argentinian floras were chosen for comparison because they are the best known from Gondwana for these two time intervals.

### Lycopsids

The Paraca lycopsids range in size from trees to small herbs. The largest stems reach diameters of up to 25 cm. Leaf cushions that have an infrafoliar bladder occur

TABLE 2—Geographic and stratigraphic occurrences of palynofloras of the Paraca floral realm and their previous age assignments.

SOUTH AMERICA: Biozone XII, Poti Formation, Parnaíba Basin, and Faro Formation, Amazonas Basin, northern and northeastern Brazil (Daemon, 1974; Iannuzzi and Scherer, 1996; Melo et al., 1998); Kaka Foramtion, Retama Group, of northern Bolivia (Azcuy and Ottone, 1987); Ambo Group of southern Peru (Doubinger and Alvarez-Ramis, 1980; Azcuy, 1990); all considered Visean in age based on palynological correlations.

AFRICA: Talak, Guézouman and Tchinezogue Formations, Tim Mersoï Basin, Niger (Coquel et al., 1995); biozones M6 and M7, Issendjel and Assekaïf Formations, Illizi Basin, Algeria (Lanzoni and Magloire, 1969); Collenia unit, Assedjefar Formation, Rhadames Basin, Cyrenaica Platform, Libya (Coquel and Massa, 1993); Saudi Arabia (Clayton, 1995); Doubayat Group, Syria (Ravn et al., 1994). All late Visean–earliest Serpukhovian based on palynological correlation and in a few cases intercalation with marine faunas, Basins of Illizi and Rhadames (Coquel and Massa, 1993).

AUSTRALIA: Italia Road Formation, Gresford Block, Sydney Basin (Playford and Helby, 1968); Mount Johnstone and Wallaringa Formations, Gresford Block, Sydney Basin (Morris, 1985); McInnes Formation, Myall Block, Sydney Basin (Roberts et al., 1995); Medusa Formation? and pre-Grant units, Bonaparte Gulf Basin (Morris, 1985; Jones and Truswell, 1992). Assemblages from Gresford Block in the Sydney Basin are dominated by *Grandispora maculosa* microflora (Kemp et al., 1977); all late Visean age of units based on isotope SHRIMP method (Roberts et al., 1993, 1994, 1995). Assemblages in the McInnes Formation are equated with those from *Spelaotriletes ybertii* zone (Kemp et al., 1977; Roberts et al., 1995), considered earliest Serpukhovian in age based on isotope SHRIMP method (Roberts et al., 1993, 1994, 1995) and palynological correlation (Kemp et al., 1977; Jones and Truswell, 1992; Roberts et al., 1995). Assemblages from the Bonaparte Gulf Basin are late Visean to earliest Serpukhovian in age based on stratigraphic correlation and faunistic data from underlying units (Morris, 1985; Jones and Truswell, 1992).

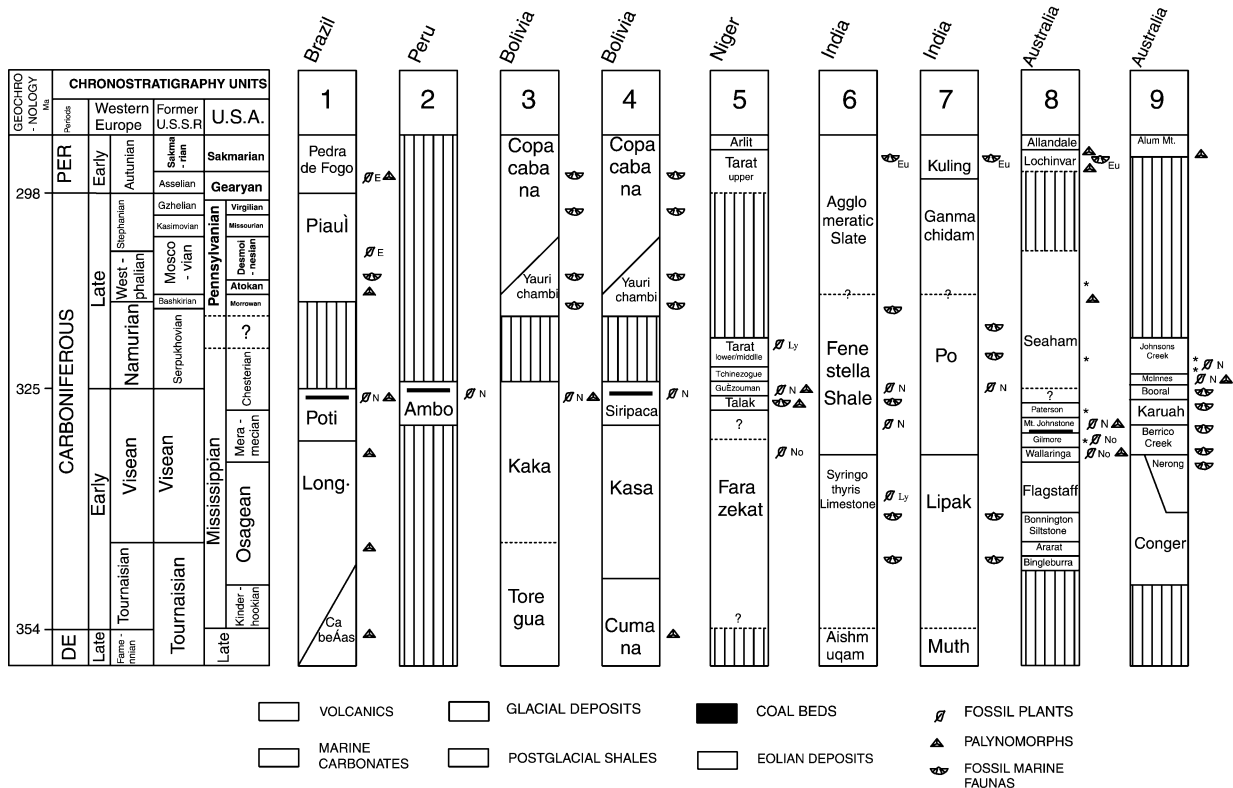


FIGURE 1—Stratigraphic columns and their correlation for areas under consideration: 1—Parnaíba Basin, Brazil; 2—Paracas Peninsula, Peru; 3—northern Subandean of Bolivia; 4—Bolivian Altiplano; 5—Tim Mersoï Basin, Niger; 6—Kashmir Basin, Indian Subcontinent; 7—Spiti Basin, India Subcontinent; 8—Sydney Basin, Australia; 9—Stroud-Gloucester Syncline, Myall Block, Australia. The ages and correlations between chronostratigraphic units follow Jones (1996) for column 8 and 9, and the authors' interpretation of floral relationships for the other columns. Additional letters and symbols used: E—Euramerican-type Flora; N—*Nothorhacopteris* Flora (= enriched *Nothorhacopteris* or *Sphenopteridium* complex in eastern Australia); No—older *Nothorhacopteris* flora of Australia; Ly—assemblages dominated by small lycosids; Eu—marine *Eurydesma* fauna; \*—numerical isotope ages (given here in sequence from top to bottom; in column 8 in Ma 310, 321, 329, 332; in column 9 in Ma 321, 323); hatched areas indicate stratigraphic gaps. Stratigraphic columns modified after: 1—Góes and Feijó, 1994; Melo et al., 1998; Iannuzzi et al., 1998; 2—Iannuzzi et al., 1998; 3, 4—Díaz-Martínez, 1995, 1999; 5—Coquel et al., 1995; 6, 7—Tripathi and Singh, 1985; 8, 9—Roberts et al., 1995.

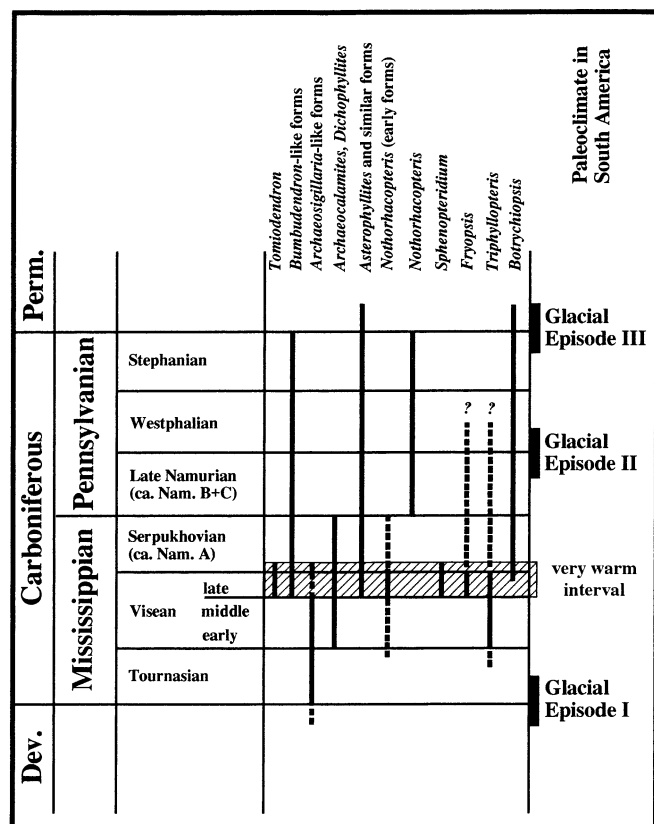


FIGURE 2—Stratigraphic ranges of selected fossil plants in the middle part of the Carboniferous of Gondwana. Hatched interval represents the late Visean—(?) earliest Serpukhovian floras of the Paraca Floral Belt. Glacial episodes in South America after López-Gamundí, 1997.

among the lycopsids with a lepidodendroid phyllotaxy (without vertical rows). These taxa can have a ligula like *Tomiodendron* (Alleman and Pfefferkorn, 1988) or none, like *Pseudobumbudendron* (Pant and Srivastava, 1995) and *Bumbudendron* (Archangelsky et al., 1981). The forms belonging to *Tomiodendron* are normally of tree size. Lycopsid stems often are preserved in decorticated states that can impart the appearance of high systematic diversity. Other types of lycopsids are those with a simple sigillaroid phyllotaxy often referred to as *Archaeosigillaria* or *Lepidosigillaria*. In the floras studied here, these latter forms occur only in India and Australia. These forms are found regularly in older strata in Argentina (Sessarego and Césari, 1989), Africa (Lejal-Nicol, 1987), and India (Singh et al., 1982).

The genus *Tomiodendron* is of special importance. This genus was established in the Angara floral realm of Siberia where it is common throughout the Early Carboniferous. The genus was first recorded from Peru by Alleman and Pfefferkorn (1988) who demonstrated that the co-occurrence of ligule and infrafoliar bladder in a leaf cushion without a leaf scar typified the genus (Fig. 3). This genus is characterized by vertically elongated diamond-shaped leaf cushions that can be close together or further apart, and are arranged in two intersecting sets of oblique rows. The appearance of the stem surface is quite variable depending on the position on the trunk, differing degrees of decortication, and the grain size of the entombing rock.

TABLE 3—Occurrences of common genera of plant macrofossils in different areas of the late Visean circum-Gondwana Paraca floral realm.

	Peru	Bolivia	Brazil	Niger	India	Australia
<i>Tomiodendron</i> <sup>1</sup>	O*	O*	—	O	cf	cf
<i>Archaeocalamites</i>	O	O	cf	O	O	O
<i>Nothorhacopteris</i>	O*	O*	O	O*	O*	O*
<i>Triphylopteris</i>	O*	O*	O	O*	O*	O*
<i>Sphenopteridium</i>	O*	O*	cf	—	—	O*
<i>Diplothemia</i>	O*	O*	O	—	cf	—
<i>Fryopsis</i>	O*	—	—	O*	—	O*

<sup>1</sup> First genus listed is a lycopsid, the second one a sphenopsid, all others are pteridosperms. Data used from own observations and literature cited in Table 1 and Appendix 2.

The fact that the presence of a ligule was not recognized earlier indicates that previous workers studied mostly weathered material. This opinion has been corroborated by the inspection of older collections from Paracas (in Heerlen and Bonn) by one of the authors. The Peruvian species was described originally by Gothan (1928), and the formal taxonomic transfer to *Tomiodendron* can be found in Appendix 1.

The Angara flora from which *Tomiodendron* was first described has been interpreted to represent a warm temperate climate (Meyen, 1968; Durante, 2000). The fact that *Tomiodendron* is a monocaulous (Meyen, 1982) or minimally branched tree (pers. observ.) indicates that few

TABLE 4—Similarity matrix based on the number of shared genera of macrofloras from the Paraca floral realm. The macrofloras have been clustered by continents, and reproductive form genera were removed because they are rare. SA—South American floras (= Peruvian + Bolivian + Brazilian floras); AF—African flora (= Niger flora), I—Indian floras (= Panjad-Kashmir floras); AU—Australian floras (= floras from Mount Johnstone Fm. and equivalents units). The floras under consideration also are compared with macrofloras found in Early (E.C.) and Late Carboniferous (L.C.) from Argentina. Two distinct similarity indices were applied (Jaccard and Otsuka index) based on data presented in Appendix 2.

Otsuka index:  $(c/n1 \times n2) \times 100$

Jaccard index:  $(c/n1 + n2 - c) \times 100$

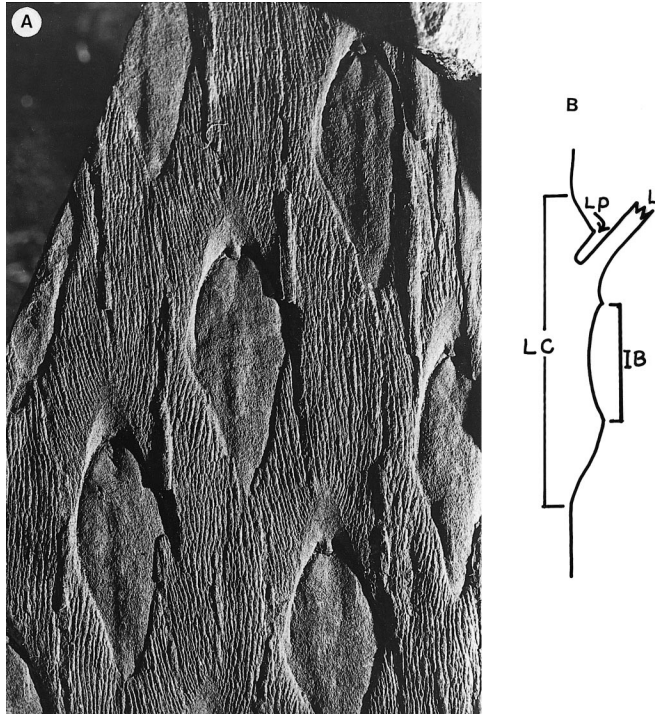
c = number of genera shared by assemblages 1 and 2

n1 = number of genera in assemblage 1

n2 = number of genera in assemblage 2

Results:

	Jaccard index					
	SA	AF	I	AU	E.C.	L.C.
Otsuka index						
SA	—	45	56	53	11	16
AF	9	—	27	42	0	15
I	6	6	—	36	21	18
AU	6	8	4	—	5	15
E.C.	2	0	3	1	—	17
L.C.	2	3	2	2	2,5	—



**FIGURE 3**—*Tomiodendron peruvianum* (Gothan, 1928) Pfefferkorn & Alleman comb. nov. (A) Stem surface seen from the inside; that is, leaves continue upward into the rock matrix along the upper curvature of the leaf cushion because there is no abscission layer or leaf scar. The ligule pit is filled with sediment and extending down and inward over the leaf cushion. The infrafoliar bladder is visible as an elongated, oval area in the center of the leaf cushions. Ambo Fm., Paracas, Peru, RPT-V-CP-013, scale 3:1. (B) Schematic cross section through one leaf cushion, L—leaf, Lp—ligule pit, IB—infrafoliar bladder, LC—leaf cushion. (RPT = Museo de Historia Natural, Universidad Ricardo Palma).

meristems were present, a feature restricted essentially to frost-free climates (Hallé et al., 1978). Alleman and Pfefferkorn (1988, 1991) made that point based on a number of observations. Besides the monocaulous habit, the combination of ligule and infrafoliar bladder is important. Ligules were present in many tree lycopsids of the Carboniferous that lived in the tropics but not in those known from cold climates (pers. observ.). Infrafoliar bladders show the opposite distribution, being typical of lycopsids from cool or cold climates but not known from the tropics. This pattern of occurrence and the combination of characters points at a plant that may have been tolerant of intermediate climatic conditions. In addition, stem diameters of tree lycopsids point in the same direction. Tropical forms have stem average diameters of 20–55 cm with maximum diameters of 1.2 m. The *Tomiodendron* stems of Paracas are intermediate with diameters of 7–25 cm, while forms from the cold climates of Gondwana have diameters of 1–4 cm (Alleman and Pfefferkorn, 1991).

#### Sphenopsids

The sphenopsids of the Paraca floral belt have small stem diameters, represent herbaceous or shrubby plants, do not have alternating ribs within the pith (= *Archaeocalamites* or *Paracalamites*), and are present in all floras

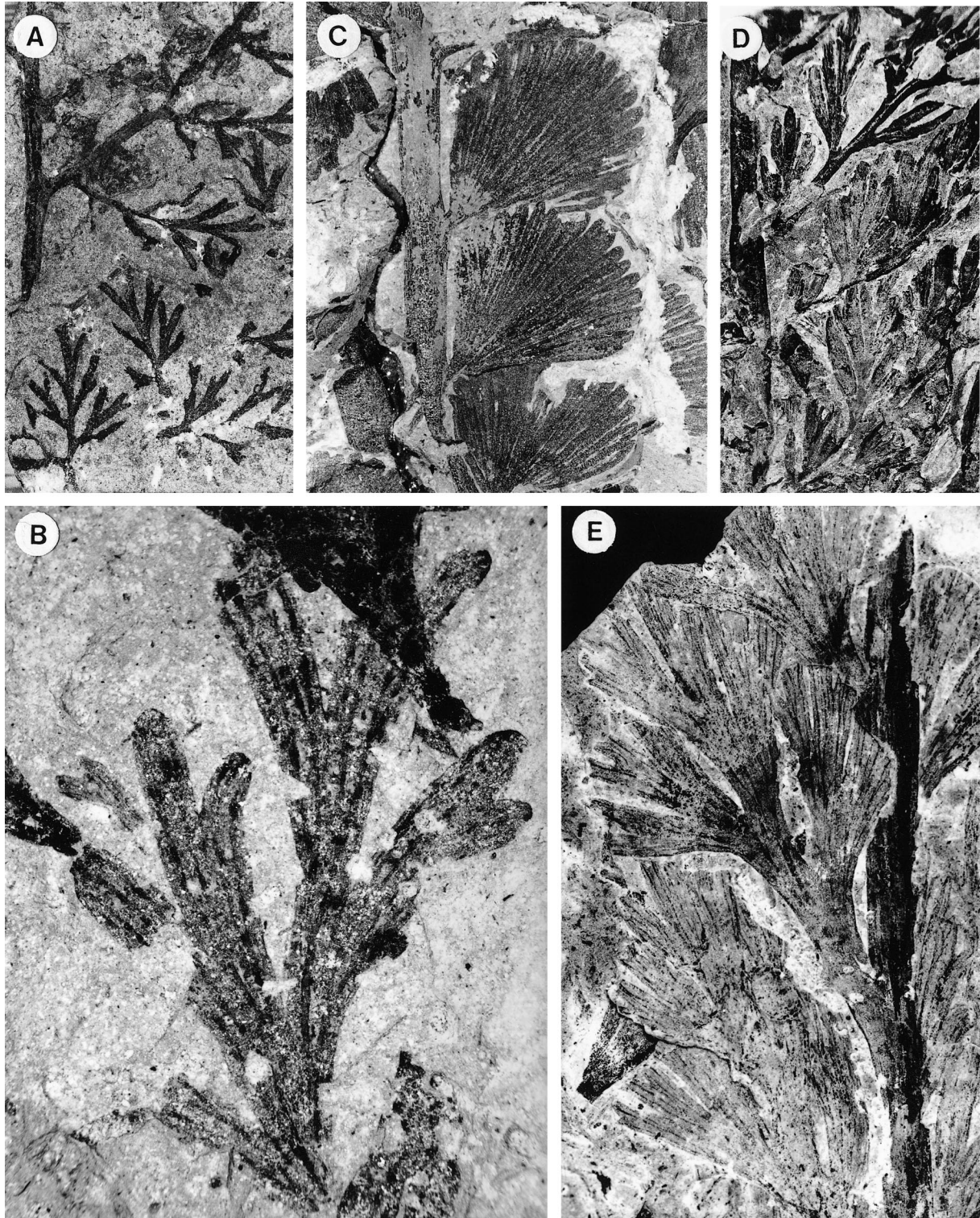
analyzed. The leaves are dichotomously divided into narrow lobes, each with a single vein (*Dichophyllites*). Stems of *Archaeocalamites* have been reported from middle to lower Viséan or even late Tournaisian strata in Africa (DeRouvre, 1988; Lejal-Nicol, 1985, 1987) and Australia (Morris, 1985). Thus, these taxa likely appeared in this part of Gondwana earlier than the interval under discussion. Sphenopsids with undivided leaves (*Asterophyllites* and similar forms) do occur rarely in Paraca-type floras, and have been reported from India (Høeg et al., 1955) and Australia (Morris, 1985; Morris, 1980). It appears that forms with undivided leaves occur for the first time in these parts of Gondwana in the late Viséan.

#### Pteridosperms

*Diplothmema gothanica*, *Nothorhacopteris*, *Triphylopteris*, and *Sphenopteridium* (Fig. 4A-E) are the most common and characteristic pteridosperms in these floras and represent, in part, endemic elements. *Nothorhacopteris* originally was known only from Late Carboniferous and Early Permian strata. Its range was later extended into the latest Early Carboniferous (DeRouvre, 1988; Tripathi and Singh, 1985; Azcuy and Suárez-Soruco, 1993; Iannuzzi et al., 1999; Roberts et al., 1993, 1994) based on material collected in Niger, India, Bolivia, and Australia. The one species of *Nothorhacopteris* identified from the Paraca floral realm, *N. kelaybelenensis* (Fig. 4C), has character states that distinguish it from species occurring in younger beds (i.e., *N. argentinica* in the Late Carboniferous—Archangelsky, 1983; Cúneo, 1990). The pinnules of *N. kelaybelenensis* are clearly petiolate, wedge-shaped (symmetrical or non-symmetrical), with well developed lateral margins, forming an angle of 80° to 120° between them (mean 90°). The distal margin is strongly crenulated, forming lobes that may have incisions themselves (Azcuy and Suárez-Soruco, 1993). The lamina is thick and subdivided into wedge-shaped segments with straight sides. The segments represent sharp folds that run into the incisions on margins between the lobes. *Nothorhacopteris kelaybelenensis* occurs in floras from Africa (Niger and Sinai; DeRouvre, 1988; Lejal-Nicol, 1987), India (Høeg et al., 1955; Pal and Chaloner, 1979), and Australia (Morris, 1975; 1980; 1985; Rigby, 1973; White, 1965).

A majority of these floras have been dated as Viséan based on palynology with the exception of the flora in the Farazekat Formation in Niger that was dated as basal Viséan/Tournaisian also using palynomorphs (Coquel et al., 1995). Hence, it follows that the genus *Nothorhacopteris* appeared in Gondwana around the beginning of the Viséan.

The forms of *Triphylopteris* (Fig. 4, D) that occur exclusively in the Paraca floral realm have unique characteristics. These are distinguished by possessing small pinnules with many lobes (the morphogenetically most developed pinnules have at least five lobes), which are distinctly separate at their attachment point. The venation is open dichotomous but not dense, making it distinct from other Euramerican and Gondwanan forms of similar appearance. These characteristics were emphasized in the diagnosis of the species *Triphylopteris boliviana* (Iannuzzi et al., 1993a) that occurs in the Siripaca Formation and at Paracas (Iannuzzi et al., 1998, 1999). Similar forms have



**FIGURE 4**—Selected species from the late Visean warm temperate floral belt in Gondwana. (A) *Diplothema gothanica* (Dolianiti) Iannuzzi nov. comb., Poti Fm., Brazil, DGM-682; scale 3:1. (B) *Diplothema gothanica* (Dolianiti) Iannuzzi nov. comb., Poti Fm., Brazil, DGM-1027; scale 11:1. (C) *Nothorhacopteris kelaybelenensis* Azcuy and Suárez-Soruco, 1993; Siripaca Fm., Bolivia, MP-Pb-3358a; scale 3:1. (D) *Triphyllopteris boliviana* Iannuzzi et al., 1993b; Siripaca Fm., Bolivia, GP/3T-1834; scale 2:1. (E) *Sphenopteridium* sp., Siripaca Fm., Bolivia, MHNC-059; scale 4:1. (D and E reprinted from Iannuzzi et al. (1999) with permission; DGM = Dept. Nac. Produção Mineral, Brazil; MP-Pb = Depto. Paleontología e Estratigrafía, Inst. Geociências, Universidade Federal do Rio Grande do Sul; GP/3T = Universidade de São Paulo).



been reported from Queensland (White, 1965; Rigby, 1973) and New South Wales (Morris, 1980).

*Sphenopteridium* represents a bipinnate leaf with a robust axis. The pinnules do not have an axis or clear midvein, and are irregularly and deeply subdivided into segments (Fig. 4E). Specimens that are essentially identical to the Australian material have been found in Peru and Bolivia (Iannuzzi et al., 1998, 1999), but have not been reported from Africa or India, to date (Table 3). Similar forms of *Sphenopteridium* are found in the Visean of the United Kingdom (Scott et al., 1994) but are restricted to the late Visean in Gondwana.

*Fryopsis* cf. *frondosa*, which is an Euramerican form, is rare but present in some floras (Table 3). It is restricted in Gondwana to the Paraca floral belt with the exception of only one record in the Jejenes Formation from the Upper Carboniferous strata of Argentina (Archangelsky et al., 1987; Vega, 1995; Iannuzzi, 1996).

Foliage of the *Diplothmema*-type is common in Carboniferous beds of all of South America (westernmost Gondwana) and were characterized by Césari (1987) who first described the Argentinian material. The forms of *Diplothmema* from Gondwana are different from those of Euramerica by having two veins in the last lobes of the pinnules (Fig. 4A, B) versus a single vein in the Euramerican forms. Two species of *Diplothmema* have been recognized in South America—*D. bodenbenderi* Césari (Césari, 1987) and *D. gothanica* (Dolianiti) Iannuzzi nov. comb. (Figs. 4A, B; see Appendix 1 for taxonomic transfer). The first species occurs in the Early and Late Carboniferous, while the second is restricted to the Early Carboniferous. Both species are characterized by tri- to quadripinnate fronds with a basal fork in the rachis and alternate pinnules that are highly dissected into lobes. The Early Carboniferous species, *D. gothanica*, is distinguished from *D. bodenbenderi* by pinnules that are straighter and wedge-shaped, with terminal lobes that tend to be undivided or rarely slightly lobed. Pinnules and pinna axes always depart at acute angles in a three-dimensional branching pattern. This species originally was described from the Poti Formation, Brazil (Dolianiti, 1954), but also is found in other floras in South America, Africa, and India (Appendix 2). However, it appears that forms of *Diplothmema* are absent from Australia during the late Visean. Thus, forms of *Diplothmema* similar to those described above seem to be restricted to western Gondwana and might have occurred first in a stratigraphic level slightly older (i.e., Early Visean/Tournaian) according to reports from Argentina (Carrizo and Azcuy, 1997) and India (Tripathi and Singh, 1985).

#### PALYNOFLORA

The palynofloras found in the same strata as the Paraca-type macrofloras are distinct from other palynomorph assemblages in the Carboniferous of Gondwana. Previous palynological studies of slightly older floras (Van Der Zwan, 1981; Clayton, 1985; Clayton et al., 1990) emphasized provincialism between Early Carboniferous assemblages from western Gondwana (Africa and South America) and those from eastern Gondwana (Australia). These results suggested the existence of two distinct microfloral realms, namely the *Spelaeotriletes balteatus* (= *Aratrisporites saharensis* microflora) and the *Granulatisporites*

*frustulentus* microfloras (Van Der Zwan, 1981; Clayton, 1985; Clayton et al., 1990). However, there are stronger similarities between the slightly younger Paraca-realm floras that point to a reduction in the degree of provinciality within the climatic belt. The microfloras that occur in the same strata as the macrofloras are described from Australia, India, Niger, Brazil, Bolivia, and Peru (Appendix 3). The stratigraphic occurrences of palynofloras reported from this interval are summarized in Table 5.

Microfloras of the Paraca floral belt are characterized by low diversity at the generic level when compared to contemporaneous Euramerica microfloras. Several Euramerican elements typical for this time interval including cingulate spores (e.g., *Lycospora*, *Densiosporites*), tripartite auriculate spores (e.g., *Triquitrites*, *Tripartites*), unornamented spores (e.g., *Waltzispota*), and ornamented monoletes (e.g., *Vestispota*) are absent or only rarely present. Quantitatively, there is a dominance of trilete spores that are smooth or minimally ornamented (e.g., *Punctatisporites*, *Calamospora*, *Retusotriletes*, *Apiculiretusispota*), with acavately ornamented forms (e.g., *Verrucosisporites*, *Reticulatisporites*) and cavate or pseudosaccate ones (e.g., *Grandispota*, *Spelaeotriletes*, *Auroraspora*) being less frequent, and cingulate or zonate forms (e.g., *Densiosporites*, *Rotaspota*, *Cristatisporites*, *Vallatisporites*, and *Radiizonites*) occurring only in small percentages (Appendix 3).

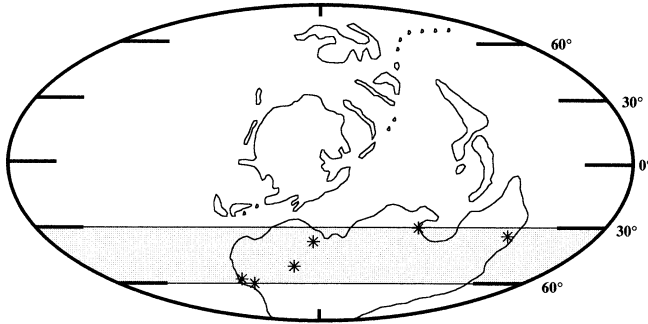
Some assemblages from Africa and the Near East have a larger percentage of cingulate and zonate palynomorphs. These assemblages correspond to the older part of the Visean (Coquel et al., 1988, 1995; Clayton, 1995). The first occurrences of Gondwana prepollen have been found in the other and slightly younger assemblages. The precolpate *Schopfipollinites* (*S. ellipsoides* and *S. cf. ellipsoides*) was reported from late Visean deposits in South America (Loboziak et al., 1991; Iannuzzi and Scherer, 1996; Melo et al., 1998), North Africa (Coquel et al., 1988), and Saudi Arabia (Clayton, 1995). The macroflora of the Poti Formation, northeastern Brazil, is associated with a *Schopfipollinites*-bearing palynological assemblage (Iannuzzi and Scherer, 1996). The youngest palynological assemblages of the interval under consideration are marked by first appearance of monosaccate pollen (*Potonieisporites* sp.; Roberts et al., 1995). The only Paraca-type macroflora analyzed from the McInnes Formation in eastern Australia is associated with an assemblage containing monosaccate pollen (= *Spelaeotriletes* (*Anabaculites*) *ybertii* Assemblage of Kemp et al. in Roberts et al., 1995).

Besides several cosmopolitan elements (i.e., *Auroraspora* spp., *Rotaspota* spp., *Waltzispota* 'sensu stricto' spp., *Diatomozonotriletes* spp., *Lycospora* spp.), a few endemic Gondwana forms occur over a large area and may be useful for intra-Gondwana biostratigraphic correlations, even though they are not always present in all assemblages analyzed. These are: *Verrucosisporites quasigobbetii* (Playford) Jones and Truswell (= *V. gobbetii*), *Grandispota maculosa* Playford and Helby, *Foveosporites appositus* Playford, *Indotriletes dolianitii* Morphon, and *Cordylisporites magnidictyus* (Playford and Helby) Melo and Loboziak (see Playford and Helby, 1968; Lanzoni and Magloire, 1969; Jones and Truswell, 1992; Loboziak et al., 1992; Clayton, 1995; Iannuzzi and Scherer, 1996; Loboziak et al., 1999; Melo and Loboziak, 2000). *Cordylisporites magnidictyus* is the most conspicuous endemic form due to its

**TABLE 5**—Occurrences of common genera and species of palynomorphs in different areas of the late Visean circum-Gondwana Paraca floral realm. SA = northern South America; AF: center and northern Africa and Near East; ID: Indian Subcontinent; AU: Australia. Symbols: X = present at specific level, cf. = presence at specific level doubtful, \* = present at generic level, — = form absent or not yet confirmed.

Taxa	SA	AF	ID	AU
<i>Acanthotriletes</i> sp.	X	X	—	X
<i>Anapiculatisporites amplus</i>	X	*	—	X
<i>A. concinnus</i>	X	X	—	X
<i>A. largus</i>	X	*	—	X
<i>A. semisentus</i>	X	X	—	X
<i>Apiculiretusispora multisetata</i>	X	X	*	*
<i>Aratrisporites saharaensis</i>	X	X	—	*
<i>Aurorasporamacra</i>	X	X	—	X
<i>A. solisorta</i>	X	X	—	X
<i>Brochotriletes diversifoveatus</i>	X	X	—	X
<i>Calamospora microrrugosa</i>	X	X	—	cf.
<i>Cingulizonates bilitatus</i>	X	X	—	—
<i>Corbulispora cancellata</i>	—	X	*	X
<i>Convolutispora balmei</i>	*	X	—	X
<i>C. harlandii</i>	*	X	—	X
<i>C. stigmoidea</i>	X	X	—	X
<i>C. vermiformis</i>	*	X	—	X
<i>Cordylosporites magnidictyus</i> (= " <i>R. magnidictyus</i> ")	X	X	—	X
<i>C. marciae</i>	*	X	—	X
<i>Crassispora</i> spp.	X	—	X	X
<i>Cristatisporites</i> spp.	X	X	X	X
<i>Densosporites claytonii</i> (= <i>D. variomarginatus</i> )	X	X	*	*
<i>Diatomozonotriletes fragilis</i>	X	X	—	*
<i>D. rarus</i>	X	X	—	*
<i>Dibolisporites distinctus</i>	—	X	*	X
<i>Endosporites micromanifestus</i>	*	X	—	X
<i>Foveosporites appositus</i>	X	X	—	X
<i>Grandispora maculosa</i>	X	X	—	X
<i>G. notensis</i>	*	X	—	X
<i>G. senticosa</i>	*	X	—	X
<i>Granulatisporites frustulensis</i>	X	*	—	X
<i>G. granulatus</i>	X	X	—	*
<i>Indotriradites dolianitii</i> Morphon.	X	X	—	X
<i>Knoxisporites literatus</i>	*	X	*	X
<i>K. cf. ruhlandi</i>	X	X	*	X
<i>Kraeuslisporites echinatus</i>	cf.	X	—	*
<i>Leiotriletes</i> spp.	X	X	X	X
<i>Lycospora</i> spp.	X	X	X	—
<i>Perotrilitis tessellatus</i>	X	X	—	—
<i>Pustulatisporites gibberosus</i>	cf.	X	—	—
<i>Radiizonates arcuatus</i> (= " <i>R. genuinus</i> ")	X	X	cf.	—
<i>Raistrickia clavata</i>	X	X	*	*
<i>R. pinguis</i>	*	X	*	X
<i>Retusotriletes crassus</i>	X	X	*	*
<i>Rotaspora ergonulii</i>	X	X	—	—
<i>Rugospora minuta</i>	X	X	—	—
<i>Schopfpollenites cf. ellipsoides</i>	X	X	—	—
<i>Spelaeotriletes arenaceus</i>	X	X	—	*
<i>S. balteatus</i>	X	X	—	*
<i>S. giganteus</i>	X	X	—	*
<i>S. owensii</i>	X	X	—	*
<i>S. pretiosus</i>	X	X	—	*
<i>S. triangulus</i> (= " <i>S. ybertii</i> ")	X	X	—	X
<i>Vallatisporites agadesensis</i>	X	X	*	—
<i>V. banffensis</i>	X	X	*	—
<i>V. ciliaris</i>	X	X	*	—
<i>V. splendens</i>	X	X	*	—
<i>V. vallatus</i>	X	X	*	—
<i>V. verrucosus</i>	X	X	*	—
<i>Velamisporites irrugatus</i>	—	X	—	X
<i>Verrucosiporites depressus</i>	X	X	—	*
<i>V. gobbetii</i>	X	X	—	*
<i>V. nitidus</i>	X	X	—	X
<i>V. quasigobbetii</i>	X	cf.	—	X
<i>Waltzisporea polita</i>	X	X	—	X
<i>W. planiangulara</i>	X	X	—	*

Data base from Coquel et al. (1977), Loboziak and Alpern (1978), Playford (1978), Playford and Powis (1979), Atar et al. (1980), Massa et al. (1980), Playford (1985), Playford and Satterthwait (1985), Coquel et al. (1988), Playford and Satterthwait (1988), Playford (1990), Loboziak et al. (1991), Ravn et al. (1994), Clayton (1995), Loboziak et al. (1998), Melo et al. (1998), Playford and Dino (2000a, b) and the other papers cited in Table 2 and Appendix 3.



**FIGURE 5**—Map of Visean continental positions showing the location of floras from west to east in Peru, Bolivia, Brazil, Niger, Indian Subcontinent, and Australia. Position of continents is taken from Plate Tracker v. 1.0.19 (Eldridge et al., 2000) for the latest Visean (330 m.y.)

ubiquitous and exclusive occurrence in the Gondwana assemblages from the late Visean and its highly diagnostic characteristics (Playford and Helby, 1968; Melo and Loboziak, 2000). Playford (1990) previously has emphasized the biostratigraphic importance of this form for intra-Gondwana correlations. Identical specimens from central and northern Africa, the Near East, and northern South America have been reported as *Reticulatisporites* spp. (p. ex *R. cancelatus*) or *Dictyotriletes* spp. by several palynologists (for synonymy see Melo and Loboziak, 2000).

#### DISCUSSION

To interpret the phytogeography of the Paraca-type floras, their distribution must be plotted on the paleogeographic maps of the late Visean (Fig. 5), and these must be considered relative to the motion of the continents throughout the Carboniferous. In addition, global climatic changes must be considered because floral belts will differ significantly in glacial, interglacial, and very warm times (Pfefferkorn, 1995, 1997).

During the Carboniferous Period, the continent of Gondwana experienced a large clockwise rotation that moved western Gondwana (South America and Africa) from higher to lower latitudes (Scotese et al., 1979; Scotese and McKerrrow, 1990; Eldridge et al., 2000). Simultaneously, eastern Gondwana (Australia, India, Antarctica) was moving from lower to higher latitudes. The sedimentary sequence found in these two areas, western and eastern Gondwana, have been used as confirmation of these plate motions based on paleoclimatically sensitive lithologies preserved therein. Marine carbonates, as indicators of relatively warm waters, essentially are restricted to the Early Carboniferous in Australia, while in South America they are restricted to the Late Carboniferous and Permian (Fig. 1; Veevers and Powell, 1987; Scotese and Barret, 1990; Díaz-Martínez et al., 1993).

The succession of floras in eastern and western Gondwana also supports the inverse latitudinal changes in these two areas. In Australia, floras occur from the Tournaisian through the middle Visean (ages following Roberts et al., 1993, 1994) with forms that are closely related taxonomically to Euramerican forms (Morris, 1985), those known from the tropical belt. Remarkable is the presence of *Stigmara*-like rhizomes (Rigby, 1992) and tree ferns (Morris, 1985), both of which are indicators of tropical or subtropical climates. The

Paraca-type flora is first encountered in the late Visean but stratigraphically higher beds of glacial origin preserve a flora characterized by *Botrychiopsis* and *Dichophyllites* (Rigby, 1985; Retallack, 1999). The succession of microfloras in Australia shows a decline in diversity (Kemp et al., 1977) paralleling that of the megaflores.

The opposite floral pattern occurs in the central part of South America (Peru to Brazil). Floras of low diversity, consisting of small-statured plants, occur in the Tournaisian and early Visean (pers. observ.). Microfloras are known from this interval that are low in diversity with few Euramerican representatives (Daemon, 1974; Loboziak et al., 1991, 1992; Melo et al., 1998). The Paraca-type macrofloras occur toward the end of the Early Carboniferous (late Visean—earliest Serpukhovian?). In the contemporaneous microfloras there is an increase in diversity and endemism observable (in comparison with the tropical belt) as compared to older floras. Finally, among the plant fossils of the Late Carboniferous there are, again, some Euramerican forms that indicate a warm climate, including *Pecopteris* (Dolianiti, 1972), *Neuropteris*, and *Lobatopteris* (Odreman and Wagner, 1979). The microfloras of this Late Carboniferous interval are quite diverse and show a high degree of endemism (Lima and Sundaram, 1982; Di Pasquo and Azcu, 1997; Groves et al., 1997). A similar sequence of mega- and microfloristic changes to those reported from central South America has been found in central Africa (Lejal-Nicol, 1985; Coquel et al., 1988).

According to some of the most widely accepted paleogeographic reconstructions (Scotese et al., 1979; Bambach et al., 1980; Scotese and McKerrrow, 1990; Scotese, 1997; Eldridge et al., 2000), the continental positions during the late Visean and early Serpukhovian place the Paraca-type floras in a belt of equal latitude in western and eastern Gondwana, extending from approximately 30° to 60° South (Fig. 5). The occurrence of these Late Visean Gondwana floras in one latitudinal belt is not unexpected even though the width of 30° is a surprise. The specific climatic belts that are expected at these latitudes under present day conditions (interglacial within a cold interval) range from subtropical through temperate to subpolar. Thus, one would expect a gradient of floras with increasing latitude or at least some latitudinal zonation from 30°–60° S. The floras observed and those identified from the literature show astonishing uniformity over a large range of latitude. This would be expected during a non-glacial, very warm time interval (Pfefferkorn, 1995) when climatic belts become wider. During very warm times it is not unusual to have warm temperate conditions at 60° South or North (Pfefferkorn, 1995). However, the conclusions presented herein do not depend on the width of the belt or the reconstructions used. The validity of the Paraca Floral Realm should be consistent even if the belt should turn out to be narrower than here assumed. It should be noted, though, that Scotese (2000) reconstructs a paleoclimatic map for the latest Lower Carboniferous—earliest Late Carboniferous with a similarly wide warm temperate climatic belt based on climate-sensitive sedimentary rocks.

Climatic regimes that show similarities over a wide latitudinal belt allow for the dispersal of plants adapted to this climate assuming that there are no other barriers. Thus, the same taxa can be found from west to east Gondwana as appears to be the case for species of *Nothorhacop-*

*teris*, *Triphylopteris*, and *Sphenopteridium* (Table 3). Nevertheless, differences in the macrofloras exist specifically between the western part (South America, Africa, India) and the eastern part (Australia) of Gondwana. The floral provincialism between these two regions is expressed at the taxon-specific level, for instance by the presence of *Diplomthema* only in western Gondwana and *Dactylophyllum* only in eastern Gondwana (Morris, 1975, 1980).

The provincialism of microfloras suggested between parts of western and eastern Gondwana during the earliest Early Carboniferous (Clayton, 1985; Coquel et al., 1995) also occurs among the microfloras analyzed here. The provincialism is visible in the very common occurrence of cingulo-zonate forms in western Gondwana and the presence of *Aratrisporites saharensis* only in parts of western Gondwana. Nevertheless, the predominance of smooth spores or those with little ornamentation, and the presence of forms of *Reticulatisporites magnidictius*, demonstrate a unity of the microfloras that parallels the one observed in macrofloras during the latest Early Carboniferous.

When the Paraca-type flora only was known from Peru, it was possible to claim that this flora either was ecotonal between major floral belts (Amerosinian and Gondwana) or that it represented a special environment that existed only on or near the west coast of Gondwana. With the recognition of this floral type throughout Gondwana, these hypotheses are not longer valid. To make the floras ecotonal (representing a transition between adjacent larger ecologic areas), one would have to find two widespread fossil floras of identical age on either side of a narrow belt. However, a combination of worldwide climate change, floral migration, and origination of endemic forms better explains the origin of the Paraca-type flora.

It also could be asked if and how Walter's (1985) biomes (see also Ziegler, 1990) could be applied to the interpretation of Paraca-type flora. Applying the fossil data to that of Walter's (1985) descriptions, the Paraca-type flora falls within his biome V, the warm-temperate vegetational zone, which has "scarcely any or no winter" based on the occurrence of tree lycopsids and some endemic tropical forms (e.g., *Archaeocalamites*).

Several climatic fluctuations occurred during the Carboniferous Period that are reflected in the distribution of biota. The effects were largely parallel between land, as seen in plant assemblages, and in the oceans, as seen in the distribution of invertebrates (Raymond, 1985; Rowley et al., 1985; Raymond et al., 1985). The latest Devonian-earliest Tournaisian was characterized by global cooling that is documented by alpine-type glacial deposits in West-Gondwana (Caputo and Crowell, 1985; Diaz and Isaacson, 1994). During the later Tournaisian and the early and middle Visean, the overall climate became warmer, which allowed major diversification of floras on a global level (Raymond, 1985; Rowley et al., 1985; Raymond et al., 1985). An identical pattern of diversification is observed in marine faunas (Raymond et al., 1989, 1990; Kelley and Raymond, 1991). The overall pattern seems to be that worldwide climatic conditions gradually became warmer during the Early Carboniferous up until just before the beginning of the glacial episode near the Visean/Serpukhovian boundary.

The late Visean to perhaps earliest Serpukhovian in Gondwana corresponds to the high point of global warming in the Early Carboniferous. This global warming was

expressed by the elevation of mean temperatures in higher latitudes, as indicated by the expansion of brachiopod genera and terrestrial plants from the tropics to middle and high latitudes (Dolianiti, 1954; Rowley et al., 1985; Raymond et al., 1990). The floras analyzed here represent the vegetational communities of the mid-latitudes of the southern hemisphere between approximately 30° and 60° south. The common presence of tree lycopsids and pteridosperms with a tree habit has been used as an indicator for frost-free climate (Pfefferkorn, 1997).

For western South America, López-Gamundí (1997) described three glacial episodes between the latest Devonian and earliest Permian (Fig. 2). He also described stratigraphic intervals with coals and carbonaceous shales following each of these glacial episodes. The coal-bearing interval in the late Visean and the Paraca floral realm correspond well with this stratigraphic sequence of events. An important paleofloristic implication is the recognition of stratigraphical and compositional differences between floras of the Paraca realm and the *Nothorhacopteris-Botrychiopsis* flora (sensu Anderson et al., 1999) found in the Upper Carboniferous deposits from Argentina. Recently, Iannuzzi and Rösler (2000) have demonstrated clearly that two entirely distinct successive floras dominated by *Nothorhacopteris* occurred in South America during the Carboniferous. The older one, late Early Carboniferous in age, corresponds to floras discussed here from Peru, Bolivia, and northeastern Brazil. The younger one is encountered in Argentinian and southern Brazilian strata dated as Late Carboniferous. This latter flora is distinguished by the presence of more advanced gymnosperm groups that are present in the macroflora (cordaitalean and ginkgoalean foliage, shoots, and seeds) and in the palynoflora (mono- and bisaccate pollen grains). It appears that the Argentinian *Nothorhacopteris-Botrychiopsis* flora existed during the coal-bearing postglacial interval following the Glacial Episode II of López-Gamundí (1997), while the Paraca floral belt developed sometime after Glacial Episode I and before Glacial Episode II (Fig. 2).

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## APPENDIX 1

## SYSTEMATIC PALEOBOTANY

*Tomiodendron peruvianum*

(GOTHAN, 1928) PFEFFERKORN &amp; ALLEMAN comb. nov.

Fig. 3

Basionym: *Lepidodendron peruvianum*, GOTHAN, 1928, p. 294–295, Pl. 13, fig. 2

Synonymy.- (Only recognizable, photographically figured specimens from Peru are listed)

1922 *Lepidodendron rimosum*, BERRY, p. 24–26, Pl. 8, fig. 1,2 (but not 3)1922 *Lepidodendron obovatum*, BERRY, p. 26–27, Pl. 1, fig. 51929 *Lepidodendron peruvianum*, STEINMANN, p. 29–31, Fig. 231938 *Lepidodendron peruvianum*, READ, p. 402–403, Fig. 41954 *Lepidodendropsis peruvianum*, JONGMANS, p. 206–207, Pl. 20, fig. 15

This species is characterized by elongated diamond shaped leaf

cushions, the lack of a leaf scar, i.e. the leaf remained attached or rotted off, and the combined presence of ligula and infrafoliar bladder. Alleman and Pfefferkorn (1988) recognized that *Tomiodendron* is present at Paracas but did not propose a formal taxonomic transfer of this species which is presented here.

*Diplothmema gothanica* (DOLIANITI) IANNUZZI comb. nov.

Fig. 4, A, B

Basionym: *Adiantites gothanica* DOLIANITI, 1954, p. 11–16, pl. I, fig. 1–5, pl. II, fig. 1–3;

Holotype: pl. I, fig. 1

*Adiantites gothanica* was synonymized with *Diplothmema bodenbenderi* by Césari (1987) pointing out the similarities of these two taxa. This conclusion is correct in the sense that both taxa belong to the same genus. However, they should be treated as separate species because their character states can be consistently distinguished as outlined in the text. Therefore, the formal nomenclatural transfer is presented here. The Early Carboniferous species, *D. gothanica*, is distinguished from *D. bodenbenderi* by pinnules that are straighter, wedge-shaped, with terminal lobes that tend to be undivided or rarely slightly lobed. Pinnules and pinna axes are always inserted at acute angles in a three-dimensional branching pattern.

## APPENDIX 2

## Plant Macrofossil Data

[Alternate names used in the literature are given in angular parentheses]

Part I, a—Common plant macrofossils from Paracas, Peru. Data from Fuchs (1900); Steinmann (1929); Berry (1922a, b); Seward (1922); Gothan (1928); Read (1938); Jongmans (1954); Doubinger and Alvarez (1980); Alleman and Pfefferkorn (1988); Erwin et al. (1994); Iannuzzi et al. (1998) and our own observations.

## LYCOPSIDS

*Tomiodendron peruvianum* [*Lepidodendron*, *Lepidodendropsis*]  
*Cyclostigma pacifica* [*Sigillaria*]

## SPHENOPSIDS

*Archaeocalamites radiatus* [*Calamites*, *Paracalamites*]

## PTERIDOSPERMS

*Nothorhacopteris kellybelenensis* [*Rhacopteris*]  
*Triphylopteris boliviana*  
? *Sphenopteridium intermedium*  
*Fryopsis frondosa*  
*Paulophyton* sp. [*Rhodea*, *Rhodopteridium*]  
*Aneimites* sp.  
*Diplothmema gothanica* [*Sphenopteris*]  
*Oclloa cesariana*  
*Obandothea laminensis*

Part I, b—Plant macrofossils taxa described or mentioned from Paracas, Peru, by Fuchs (1900) I; Steinmann (1910) II; Berry (1922a, b) III–IV; Seward (1922) V; Gothan (1928) VI; Steinmann (1929) VII; Read (1938) VIII; Jongmans (1954) IX; Doubinger & Alvarez (1980) X; Alleman & Pfefferkorn (1988) XI; Erwin et al. (1994) XII; Alleman & Pfefferkorn (1997) XIII; Iannuzzi et al. (1998) XIV; Iannuzzi & Pfefferkorn (this paper) XV

\* denotes species for which this is the type locality

\*\* after the name indicates that a specimen from Paracas was figured

## LYCOPSIDS

*Archaeosigillaria kidstoni* Kräusel & Weyland X\* *Asolanus* (?) *minimus* Gothan VI\*\*, VII*Bothrodendron* (?) sp. V\*\*\*\* *Bothrodendron* " *pacificum* Steinmann VI\*\*, VII\*\*



*Cyclostigma* sp. X  
 \**Cyclostigma pacifica* (Steinmann) Jongmans IX\*\*, X\*\*  
 \**Cyclostigma pacifica* var. *decorata* Jongmans X  
 cf. *Enigmophyton* sp. X  
*Knorria* sp. III, VI\*\*  
*Lepidodendron* sp. V\*\*  
 \**Lepidodendron lissoni* Steinmann VI\*\*, VII\*\*  
*Lepidodendron obovatum* III\*\*  
 \**Lepidodendron peruvianum* Gothan VI\*\*, VIII\*\*  
*Lepidodendron rimosum* Sternberg III\*\*  
*Lepidodendron sternbergii* Brongniart I  
*Lepidodendron* cf. *veltheimi* II  
*Lepidodendron* cf. *volkmanni* II  
 ?*Lepidodendropsis* sp. IX, X  
 \**Lepidodendropsis lissoni* (Steinmann) Jongmans IX\*\*  
 \**Lepidodendropsis peruviana* (Gothan) Jongmans IX\*\*  
*Lepidophyllum* sp. III, X  
*Lepidostrobus* sp. III  
 Licópodo sp. A XI  
 Licópodo sp. B XI  
 Licópodo sp. C XI  
 Licópodo sp. D XI  
 Licópodo sp. E XI  
*Sigillaria tessellata* Brongniart I  
*Stigmaria* sp. III  
*Stigmaria ficoides* Brongniart I  
*Sublepidodendron mirabili* (Nathorst) Hirmer X  
*Tomiodendron* sp. X\*\*, XIV  
 \**Tomiodendron peruvianum* (Gothan) Pfefferkorn & Alleman XV\*\*

#### SPHENOPSIDS

*Archaeocalamites* sp. IX, X  
*Archaeocalamites radiatus* Brongniart II, X  
 fructification of *Archaeocalamites*? X  
 \**Clamites peruvianus* Gothan VI\*\*, VII\*\*, VIII\*\*  
*Calamites suckowii* Brongniart I, III\*\*  
*Calamostachys* sp. III  
*Paracalamites* sp. XIV  
*Sphenophyllum* sp. X  
*Sphenophyllum davyi* Bureau X

#### PTERIDOSPERMS

\**Adiantites bassleri* Read VIII\*\*  
 \**Adiantites peruvianus* (Berry) VIII\*\*  
 \**Adiantites whitei* (Berry) VIII  
*Anisopteris circularis* (Walton) Hirmer X\*\*  
 \**Aphlebia australis* Read VIII\*\*  
*Baiera pluripartita* Sch. I  
*Diplothemema* cf. *bodenbenderi* XIV  
*Diplothemema gothanica* (Dolianiti) Iannuzzi XV\*\*  
 \**Eremopteris peruvianus* Berry III\*\*, VII  
 \**Eremopteris whitei* Berry III\*\*, VII  
*Nothorhacopteris kellybelensis* XIV  
 \**Oclloa cesariana* XII\*\*  
 \**Obandotheca laminensis* XII\*\*  
*Palmatopteris furcata* III\*\*  
*Paulophyton* cf. *sommeri* XIV  
*Rhabdocarpus* sp. II  
*Rhacopteris circularis* Walton VI\*\*, VII\*\*  
*Rhacopteris* cf. *cuneata* Walkom VIII\*\*, IX\*\*  
*Rhacopteris ovata* (McCoy) Walkom VIII\*\*  
*Rhodea* sp. VI, VII\*\*  
*Rhodea filifera* II  
*Sphenopteridium* cf. XIV  
*Sphenopteridium hissaricum* Savizkaja X  
*Sphenopteridium noeldeki* Daber X  
*Sphenopteridium schimperii* Goepfert X  
*Sphenopteris* sp. V\*\*  
*Sphenopteris affinis* = *Sphenopteris furcata* II  
*Sphenopteris hartlebeni* Dunker I  
 \**Sphenopteris paracasica* Gothan VI\*\*, VII\*\*, VIII\*\*, X\*\*  
 \**Sphenopteris whitei* (Berry) Jongmans IX\*\*, X

\**Trachyphyton neglegibile* Gothan VI\*\*, VII  
*Triphyllopteris boliviana* XIV *Triphyllopteris collombiana* (Schimper) X\*\*  
*Vojnowskyia* sp. X

Part II, a—Plant macrofossils from Titicaca, Bolivia. Data from Iannuzzi et al. (1993b); Iannuzzi et al. (1998); Iannuzzi et al. (1999) and our own observations.

#### LYCOPSIDS

*Tomiodendron* sp. [*Lepidodendropsis*]  
 “*Lepidodendropsis*” sp.  
*Pseudobumbudendron* sp.  
 ?*Porostrobus* sp.

#### SPHENOPSIDS

*Archaeocalamites radiatus* [*Paracalamites*]

#### PTERIDOSPERMS

*Nothorhacopteris kellybelensis* [*Rhacopteris*]  
*Triphyllopteris boliviana*  
 ?*Sphenopteridium intermedium*  
*Paulophyton sommeri*  
*Diplothemema bodenbenderi*

Part II, b—Plant macrofossil taxa described or mentioned from Copacabana Peninsula, Bolivia, by Oviedo (1965) I; Suárez-Soruco (1974) II; Archangelsky (1993) III; Azcuy & Suárez-Soruco (1993) IV; Iannuzzi et al. (1993) V; Iannuzzi, Pfefferkorn et al. (1998) VI; Iannuzzi et al. (1999) VII

#### LYCOPSIDS

*Lepidodendropsis* sp. III, V  
*Lepidodendron* sp. I  
 Lycophyta “forma A” VI, VII  
 Lycophyta “forma B” VI, VII  
 cf. *Tomiodendron* sp. VI, VII  
 Reproductive structure of Lycophyta “forma A” VI, VII  
 Reproductive structure of Lycophyta “forma B” VI, VII

#### SPHENOPSIDS

*Calamites* sp. I  
*Paracalamites* sp. III, V, VI, VII  
 Reproductive structure of Sphenophyta “forma A” VI, VII  
 Reproductive structure of Sphenophyta “forma B” VI, VII

#### PTERIDOSPERMS

*Diplothemema* cf. *D. bodenbenderi* (Kurtz) Césari (1986) VI  
*Diplothemema bodenbenderi* (Kurtz) Césari (1986) VII  
*Neuropteris* sp. I  
*Nothorhacopteris* cf. *szajnochai* (Kurtz) Azcuy & Suárez-Soruco (1984) III  
*Nothorhacopteris argentinica* Archangelsky (1983) III  
*Nothorhacopteris kellybelensis* Azcuy & Suárez-Soruco (1993) IV, V, VI, VII  
*Nothorhacopteris szajnochai* (Kurtz) Azcuy & Suárez-Soruco (1984) III  
 Pteridophylla VI, VII  
*Paulophyton* cf. *P. sommeri* Dolianiti (1954) VI  
*Paulophyton sommeri* Dolianiti (1954) VII  
 Reproductive structure of Pteridospermophyta VI, VII  
*Rhacopteris* cf. *ovata* sp. II  
*Rhodea* sp. III  
 cf. *Sphenopteridium* sp. VI  
 ?*Sphenopteridium intermedium* (Feistmantel) Rigby (1973) VII  
*Triphyllopteris boliviana* Iannuzzi, Rösler & Suárez-Soruco (1993) IV, V, VI, VII

*Triphylopteris* aff. *T. collombiana* (Schimper) Jongmans (1954) III

Part III, a—Common plant macrofossils from Parnaíba Basin, Brazil. Data from Dolianiti (1954, 1980); Rigby (1969); Leguizamón and Archangelsky (1981); Rocha-Campos and Archangelsky (1985); Césari (1986); Sessarego and Césari (1989); Iannuzzi (1994); Iannuzzi et al. (1998), and our own observations.

#### LYCOPSIDS

"*Lepidodendropsis*" sp.

#### SPHENOPSIDS

*Archaeocalamites* sp. [*Paracalamites*]

#### PTERIDOSPERMS

*Nothorhacopteris* cf. *N. kellybelenensis* [*Rhacopteris*]  
*Triphylopteris alvaro-albertoi* [*Fedekurtzia*]  
 ?*Sphenopteridium* sp.  
 ?*Fryopsis* sp. [*Cardiopteridium*, *Botrychiopsis*]  
*Paulophyton sommeri* [*Rhodea*]  
*Paulophyton* sp. 1  
*Kegelidium lamegoi* [*Paulophyton*]  
*Aneimites* sp. [*Sphenopteris*, *Adiantites*, *Triphylopteris*, *Eusphenopteris*]  
*Diplothmema gothanica* [*Sphenopteris*, *Adiantites*]  
*Diplothmema* cf. *D. bodenbenderi*  
 ?*Stamnostoma* sp.

Part III, b—Plant macrofossil taxa described or mentioned from Poti Formation, Parnaíba Basin, by Dolianiti (1954 III, 1972 IV, 1980 V); Millan (1965) VI; Rigby (1969) VII; Leguizamón & Archangelsky (1981) VIII; Rocha-Campos & Archangelsky (1985) XIX; Césari (1986) X; Sessarego & Césari (1989) XI; Iannuzzi & Rösler (1993) XII; Iannuzzi, Pfefferkorn et al. (1998) XIII

#### LYCOPSIDS

*Cyclostigma brasiliensis* Dolianiti (1962) IV  
*Lepidodendropsis* sp. III, XII  
 ?*Ursodendron brasiliensis* (Dolianiti) Iannuzzi in Iannuzzi & Rösler (1993) XII

#### SPHENOPSIDS

cf. *Paracalamites* sp. XII, XIII

#### PTERIDOSPERMS

*Adiantites paracasica* (Gothan) Rigby (1969) VII  
*Adiantites gothanica* Dolianiti (1954) III  
*Adiantites oliveiranus* Dolianiti (1954) III  
*Adiantites santosi* Dolianiti (1954) III  
*Adiantites alvaro-albertoi* Dolianiti (1954) III  
*Botrychiopsis weissiana* (Kurtz) Archangelsky & Arrondo (1971) XIX  
*Cardiopteridium* sp. III  
*Cordaicarpus* sp. VI  
*Diplothmema* cf. *D. bodenbenderi* (Kurtz) Césari (1986) XIII  
*Diplothmema bodenbenderi* (Kurtz) Césari (1986) X  
*Eusphenopteris sanjuanina* (Kurtz) Césari (1986) X  
*Fedekurtzia argentina* (Kurtz) Archangelsky (1981) X, XI  
*Kegelidium lamegoi* Dolianiti (1954) III  
*Nothorhacopteris argentinica* Archangelsky (1983) XI  
*Nothorhacopteris* cf. *N. kellybelenensis* Azcuy & Suárez-Soruco (1993) XIII  
*Paulophyton sommeri* Dolianiti (1954) III, VIII  
*Rhacopteris* sp. V  
*Rhodea* sp. III  
 ?*Sphenopteris* sp. VII  
*Sphenopteris oliveiranus* (Dolianiti) Rigby (1969) VII  
*Sphenopteris santosi* (Dolianiti) Rigby (1969) VII

cf. *Sphenopteridium* sp. XIII  
*Sphenopteridium* sp. III  
 ?*Stamnostoma* sp. XII  
*Triphylopteris alvaro-albertoi* (Dolianiti) Rigby (1969) V, VII

Part IV, a—Common plant macrofossils from the Aire region of Niger. Data from De Rouvre (1984, 1985, 1988) and from observations of her collection.

#### LYCOPSIDS

*Tomiodendron* sp. [*Tomiodendron*, *Lepidodendropsis*, *Pseudolepidodendropsis*, *Ursodendron*]

#### SPHENOPSIDS

*Archaeocalamites radiatus* [*Paracalamites*]

#### PTERIDOSPERMS

*Nothorhacopteris* sp. [*Nothorhacopteris*, *Rhacopteris*]  
*Triphylopteris* sp. [*Triphylopteris*]  
*Fryopsis frondosa* [*Cardiopteris*]  
*Paulophyton* sp. [*Rhodea*]

Part IV, b—Plant macrofossil taxa described or mentioned from the Aire region of Niger by De Rouvre (1984 I, 1985a II, b III, 1988 IV)

#### LYCOPSIDS

*Lepidodendropsis rhombiformis* De Rouvre (1984) I, II, IV  
 cf. *Pseudolepidodendropsis klitzschi* Lejal-Nicol (1972) II, IV  
*Pseudolepidodendropsis nigeriensis* De Rouvre (1984) I, II, IV  
*Tomiodendron varium* (Radczenko) Meyen (1972) I, IV  
*Ursodendron wijkianum* (Heer) Radczenko (1960) I, IV

#### SPHENOPSIDS

cf. *Paracalamites australis* Rigby (1966) I

#### PTERIDOSPERMS

*Cardiopteris frondosa* Schimper (1869) II, IV  
*Cardiopteris hochstetteri* (Ettingshausen) Stur (1875) II, IV  
*Cordaites* sp. IV  
*Eremopteris artemisiaefolia* Schimper IV  
*Eremopteris elegans* (Ettingshausen) Lesquereux (1880) II, IV  
*Eremopteris intermedia* De Rouvre (1985) II, IV  
*Eremopteris missouriensis* Lesquereux (1879) II, IV  
*Lagenospermum tenuifolium* Nathorst IV  
*Nothorhacopteris argentinica* Archangelsky (1982) II, IV  
*Nothorhacopteris crenulata* De Rouvre (1985) II, IV  
*Paralitistrobos africanum* De Rouvre (1985b) IV  
*Paralitistrobos boureaui* De Rouvre (1985b) IV  
*Rhacopteris chubutiana* Archangelsky & Arrondo (1966) II, IV  
*Rhacopteris circularis* Walton (1926) II, IV  
*Rhacopteris* cf. *circularis* var. *afaraggii* De Rouvre (1985) II, IV  
*Rhacopteris ovata* (McCoy) Walkom (1934) II, IV  
*Rhacopteris semicircularis* Lutz (1933) II, IV  
*Rhacopteris szajnochai* Kurtz (1921) II, IV  
 cf. *Rhodea fluitans* Daber (1959) II, IV  
*Sphenopteridium dissectum* (Goepfert) Schimper (1874) II, IV  
*Sphenopteridium pachyrrhachis* (Goepfert) Schimper (1879) II, IV  
*Sphenopteris pseudofurcata* Kidston (1923) II, IV  
*Sphenopteris teiliana* Kidston (1889) II, IV  
*Triphylopteris alvaro-albertoi* (Dolianiti) Rigby (1969) II, IV  
*Triphylopteris collombiana* Schimper (1869) II, IV  
*Triphylopteris gothani* Daber (1959) II, IV

Part V—Common plant macrofossils from Panjab-Kashmir region of India. Data from Gothan and Sahni (1937); Høeg et al. (1955); Pal (1978); Pal and Chaloner (1979); Singh et al. (1982); Pant and Srivastava (1995); Iannuzzi et al. (1999) and our interpretations. A critical list of taxa was published by Pant and Srivastava (1995).

**LYCOPSIDS**

*Archaeosigillaria* spp.  
*Cyclostigma* spp.  
 “*Lepidodendropsis*” spp.  
*Lepidosigillaria quadrata*  
*Pseudobumbudendron* spp.  
 ?*Tomiodendron* sp. [*Lepidodendropsis*]

**SPHENOPSIDS**

*Archaeocalamites radiatus*  
*Asterophyllites* sp.

**PTERIDOSPERMS**

*Nothorhacopteris* cf. *N. kellybelenensis* [*Rhacopteris*]  
*Triphylopteris* cf. *T. boliviana*  
 ?*Aneimites* sp. [*Sphenopteridium*]  
 ?*Diplothmema* sp. [*Rhodea*]  
*Rhodea* sp.  
*Sphenopteris* sp.

Part VI, a—Common plant macrofossils from New South Wales, Australia. Data from Rigby (1973); Morris (1975, 1980, 1985); Retallack (1980); Iannuzzi et al. (1999) and our interpretations.

**LYCOPSIDS**

*Cyclostigma australe*  
 “*Lepidodendropsis*” *steinmannii*  
 “*Sigillaria*” sp.  
*Tomiodendron* sp. [*Lepidodendropsis*]

**SPHENOPSIDS**

*Archaeocalamites radiatus* [*Calamites*, *Paracalamites*]  
*Asterophyllites* [*Stellothea*]

**PTERIDOSPERMS**

*Nothorhacopteris kellybelenensis* [*Rhacopteris*, *Pseudorhacopteris*]  
*Nothorhacopteris* sp. [*Rhacopteris*, *Pseudorhacopteris*]  
*Triphylopteris* cf. *T. boliviana* [*Sphenopteridium*]  
 ?*Sphenopteridium intermedium* [*Fedekurtzia*]  
*Fryopsis frondosa* [*Cyclopteris*, *Cardiopteris*]  
*Dactylophyllum digitatum*  
*Botrychiopsis* [*Triphylopteris*]

Part VI, b—Plant macrofossil taxa described or mentioned of “*Rhacopteris* Flora” from New South Wales, Australia, by Rigby (1969 I, 1973 II and earlier authors cited here); Morris (1975 III, 1980 IV, 1985 V); Retallack (1980) VI; Rigby (1985) VII; Iannuzzi et al. (1999) VIII

**LYCOPSIDS**

*Cyclostigma australe* Feistmantel (1890) I, III, IV, V  
 “*Lepidodendron veltheimii*” Sternberg (1828) II  
*Lepidodendropsis* sp. I  
 ?*Lepidodendropsis pacifica* (Steinmann) in Morris (1985) V  
*Lepidodendropsis peruviana* (Gothan) Jongmans (1954) V  
*Lepidodendropsis steinmannii* Jongmans (1954) III, IV, V  
 Lycopod gen. et sp. indeterminate VII

*Sigillaria* (*Subsigillaria*) group *Clathraria* sp. nov. in Morris (1975) III, IV  
 “*Subsigillaria*” sp. 1 V  
 “*Subsigillaria*” sp. 2 V

**SPHENOPSIDS**

“*Calamites*” *peruvianus* Gothan (1928) I, II, V  
*Dichophyllites peruviana* (Gothan) in Morris (1985) V  
 ?*Paracalamites* sp. III  
*Paracalamites peruviana* (Gothan) in Morris (1980) IV  
*Stellothea* aff. *S. robusta* Surange & Prakash (1960) IV

**PTERIDOSPERMS**

*Aphlebia diversiformis* (Etheridge Jr.) in Morris (1980) IV  
*Archaeopteris* sp. II  
*Archaeopteris wilkinsoni* Feistmantel (1879) II  
 ?*Adiantites robustus* Walkom (1934) IV  
*Aneimites austrina* Etheridge Jr. (1888) II  
*Aneimites ovata* (McCoy) Arber (1902) II  
 ?*Bergiopteris* sp. V  
*Botrychiopsis ovata* (McCoy) in Rigby (1985) and Morris (1985) V, VII  
*Botrychiopsis weissiana* (Kurtz) Archangelsky & Arrondo (1971) VI  
*Cardiopteris* cf. *C. frondosa* (Göeppert) Schimper (1869) II  
*Cardiopteris* cf. *C. polymorpha* (Göeppert) Schimper (1869) I, II  
*Cardiopteris frondosa* (Göeppert) Schimper (1869) III, IV, V, VI  
 [*Cyclopteris*] sp. II, VI  
*Dactylophyllum digitatum* (Etheridge Jr.) in Morris (1975) III, IV, V, VI  
*Dictyothalamus* sp. III, V  
*Fedekurtzia intermedia* (Feistmantel) Rigby (1985) VII  
*Fryopsis* sp. I  
*Gondwanidium plantianum* (Carruthers) Gerth (1932) II  
*Neuropteris valida* Feistmantel (1876) II  
*Neuropteris* (*Neuropteridium*) *valida* Feistmantel (1879) II  
 ?*Noeggerathia* sp. VI  
*Nothorhacopteris* cf. *N. argentinica* Archangelsky (1983) VII  
*Nothorhacopteris argentinica* Archangelsky (1983) VII, V  
*Nothorhacopteris* cf. *N. kellybelenensis* Azcuy & Suárez-Soruco (1993) VIII  
*Nothorhacopteris kellybelenensis* Azcuy & Suárez-Soruco (1993) VIII  
 “*Oopteris*” *argentinica* Geinitz (1876) VI  
*Oopteris ovata* McCoy (1847) II  
*Pseudorhacopteris ovata* (McCoy) Rigby (1973) II  
*Rhacophyllum diversiforme* Etheridge Jr. (1888) III  
*Rhacopteris digitata* Etheridge Jr. (1888) III  
*Rhacopteris* cf. *R. inaequilatera* (Göeppert) in Feistmantel (1878) II  
*Rhacopteris R. inaequilatera* (Göeppert) in Feistmantel (1879, 1890) II  
*Rhacopteris intermedia* Feistmantel (1878) I, II, VI  
*Rhacopteris ovata* (McCoy) Walkom (1934) I, II, III, IV, VI  
*Rhacopteris septentrionalis* Feistmantel (1879) I, II  
*Sphenopteridium* complex III, IV, V  
 ?*Sphenopteridium intermedium* (Feistmantel) Rigby (1973) II, VI, VIII  
 ?*Sphenopteridium cuneatum* Walkom (1934) II  
*Sphenopteris clarkei* Dun (1905) I  
*Triphylopteris* sp. I  
*Triphylopteris austrina* (Etheridge Jr.) in Morris (1975) III, IV  
*Triphylopteris* cf. *T. boliviana* Iannuzzi, Rösler & Suárez-Soruco (1993) VIII

## APPENDIX 3

## Palynological Data

Part I—Palynomorphs of South American assemblages. 1. Poti Fm., Parnaíba B.; 2. Ambo Gr., southern Peru; 3. Kaka Fm., North Subandean Bolivia. Data from Doubinger and Alvarez-Ramis (1980), Azcuy and Ottone (1987), Azcuy (1990), Iannuzzi (1994), Iannuzzi and Scherer (1996), Melo et al. (1998), Melo and Loboziak (2000). ? = species presence doubtful.

<i>Acanthotriletes</i> sp.	2
<i>Anapiculatisporites largus</i> Playford	2
<i>A. cf. semisentus</i> Playford	3
<i>Apiculiretusispora multisetata</i> (Luber) Butterworth & Spinner	1
<i>A. semisenta</i> (Playford) Massa et al.	1
<i>Aratrisporites saharaensis</i> Loboziak et al.	1
<i>Aurorasporamacra</i> Sullivan	1 3
<i>A. solisorta</i> Hoffmeister et al.	1
<i>Bascaudaspora submarginata</i> (Playford) Higgs et al.	1
<i>Brochotriletes diversifoveatus</i> Playford & Satterthwait	1
<i>Calamospora</i> sp.	1 3
<i>C. microrrugosa</i> Ibrahim	2
<i>Cingulizonates bialatus</i> (Waltz) Smith & Butterworth	1
<i>Colatisporites decorus</i> (Bharadwaj & Venkatachala) Williams in Neves et al.	1
<i>Convolutispora cf. mellita</i> Roffmeister et al.	3
<i>C. stigmioidea</i> Bharadwaj & Venkatachala	1
<i>Cordylosporites magnidictyus</i> (Playford & Helby) Melo & Loboziak	1 2? 3?
<i>C. spathulatus</i> (Winslow) Playford & Satterthwait	1
<i>Chomotriletes cf. multivittatus</i> Playford	3
<i>Crassispora</i> sp.	3
<i>Cristatisporites</i> sp.	3
<i>C. echinatus</i> Playford	1
<i>Densosporites cf. aculeatus</i> Playford	2
<i>D. anulatus</i> (Loose) Butterworth & Williams	1
<i>D. claytonii</i> Ravn et al.	1
<i>D. spinifer</i> Hoffmeister et al.	2
<i>D. spitsbergensis</i> Playford	1
<i>Diatomozonotriletes fragilis</i> Clayton in Neves et al.	1
<i>D. rarus</i> Playford	1
<i>Endosporites</i> sp.	2 3
<i>Foveosporites appositus</i> Playford	1
<i>Grandispora</i> sp.	3
<i>G. maculosa</i> Playford & Helby	1
<i>G. spiculifera</i> Playford	1
<i>Granulatisporites</i> sp.	2
<i>G. cf. crenulatus</i> Playford	3
<i>G. frustulensis</i> (Balme & Hassel) Playford	1 3
<i>Indotriradites daemonii</i> Loboziak et al.	1
<i>I. dolianitii</i> (Daemon) Loboziak et al.	1 2
<i>I. tedantus</i> (Playford & Satterthwait) Playford	1
<i>Knoxisporites</i> sp.	3
<i>K. cf. ruhlandi</i> Doubinger & Rauscher	2
<i>Leiotriletes inermis</i> Ischenko	2
<i>L. ornatus</i> Ischenko	2
<i>Lycospora noctuina</i> Butterworth & Williams	1
<i>L. pusilla</i> Butterworth & Williams	1
<i>Perotriletes tessellatus</i> (Staplin) Neville in Neves et al.	1
<i>Punctatisporites</i> sp.	1 2 3
<i>Pustulatisporites cf. gibberosus</i> Playford	1 3
<i>Radiizonates arcuatus</i> (= " <i>R. genuinus</i> ") Loboziak et al.	1 2
<i>Raistrickia clavata</i> Hacquebard emend. Playford	1 3?
<i>R. claviger</i> (Sullivan) Playford & Satterthwait	2
<i>R. ponderosa</i> Playford	1
<i>Retusotriletes incohatus</i> Sullivan	1 2
<i>R. crassus</i> Clayton et al.	1
<i>Rotaspora ergonulii</i> (Agrali) Sullivan & Marshall	1
<i>Rugospora minuta</i> Neves & Ioannides	2
<i>Schopfpolenites cf. ellipsoides</i> (Ibrahim) Potonié & Kremp	1
<i>Spelaeotriletes arenaceus</i> Neves & Owens	1 3?
<i>S. balteatus</i> (Playford) Neves & Owens	1 2
<i>S. benghaziensis</i> Loboziak & Clayton	1
<i>S. owensii</i> Loboziak & Alpern	1
<i>S. pretiosus</i> (Playford) Neves & Belt	1
<i>S. triangulus</i> Neves & Owens	1
<i>Vallatisporites agadesensis</i> Loboziak & Alpern	1 2

APPENDIX 3  
Continued.

## Part I—Continued

<i>V. banffensis</i> Staplin & Jansonius	1
<i>V. ciliaris</i> (Luber) Sullivan	1 2
<i>V. splendens</i> Staplin & Jansonius	1
<i>V. vallatus</i> Hacquebard	1
<i>V. verrucosus</i> Hacquebard	1
<i>Verrucosiporites cerosus</i> (Hoffmeister et al.) Butterworth & Williams	3
<i>V. congestus</i> Playford	1
<i>V. depressus</i> Winslow	1
<i>V. gobbetii</i> Playford	1
<i>V. morulatus</i> (Knox) emend. Smith & Butterworth	2
<i>V. nitidus</i> (Naumova) Playford	1 3
<i>V. perverrucosus</i> (Loose) Potonié & Kremp	2
<i>V. quasigobbetii</i> Jones & Truswell	1
<i>Waltzispora polita</i> (Hoffmeister et al.) Butterworth & Williams	1 2

## Part II—Palynomorphs of northern Niger assemblage; Guézouman Formation, Tim Mersoï Basin. Data from Coquel et al. (1995), Melo and Loboziak (2000).

<i>Acanthotriletes socraticus</i> Neves & Ioannides
<i>Anapiculatisporites tersus</i> Playford
<i>A. spinosus</i> (Kosanke) Potonié & Kremp
<i>Apiculatisporis variocorneus</i> Sullivan
<i>Apiculiretusispora multisetata</i> (Luber) Butterworth & Spinner
<i>Aratrisporites saharaensis</i> Loboziak et al.
? <i>Aurorasporamacra</i> Sullivan
<i>A. solisorta</i> Hoffmeister et al.
<i>Calamospora</i> sp.
<i>Calamospora liquida</i> Kosanke
<i>Cingulizonates bialatus</i> (Waltz) Smith & Butterworth
<i>C. capistratus</i> (Hoffmeister et al.) Staplin & Jansonius
<i>Corbulispora subalveolaris</i> (Luber) Sullivan
<i>Cordylosporites magnidictyus</i> (= " <i>R. cancellatus</i> ") (Playford & Helby) Melo & Loboziak
<i>Densosporites claytonii</i> Ravn et al.
<i>Grandispora inculta</i> Allen
<i>Kraeuselisporites ornatus</i> (Neves) Owens et al.
<i>Planisporites asperatus</i> Bharadwaj & Venkatachala
<i>Punctatisporites</i> sp.
<i>Pustulatisporites gibberosus</i> Playford
<i>Radiizonates arcuatus</i> (= " <i>R. genuinus</i> ") Loboziak et al.
<i>Rotaspora knoxii</i> Butterworth & Williams
<i>Rugospora minuta</i> Neves & Ioannides
<i>Spelaeotriletes arenaceus</i> Neves & Owens
<i>S. triangulus</i> Neves & Owens
<i>Vallatisporites agadesensis</i> Loboziak & Alpern
<i>V. ciliaris</i> (Luber) Sullivan
<i>V. communis</i> Sullivan
<i>Verrucosiporites depressus</i> Winslow
<i>V. nitidus</i> (Naumova) Playford
<i>V. variotuberculatus</i> Sullivan
<i>Waltzispora prisca</i> Kosanke

## Part III—Palynomorphs from Indian Subcontinent; Po Formation, Spiti Basin. Data from Khanna and Tiwari (1983).

<i>Apiculiretusispora</i> sp.
<i>Cingulatisporites</i> sp.
<i>Cirratriradites</i> sp.
<i>Corbulispora</i> sp.
<i>Crassispora</i> sp.
<i>Cristatisporites</i> sp.
<i>Densosporites</i> sp.
<i>Dibolisporites</i> sp.
<i>Hymenozonotriletes</i> sp.
<i>Knoxisporites</i> sp.
<i>Leiotriletes</i> sp.
<i>Lycospora</i> sp.
<i>Microreticulatisporites</i> sp.
<i>Phyllothecotriletes</i> sp.

APPENDIX 3  
Continued.

Part III—Continued

*Raistrickia* sp.  
*Retispora* sp.  
*Retusotriletes* sp.  
*Schulzospora* sp.  
*Simozonotriletes* sp.  
cf. *Tripartites* sp.  
*Vallatisporites* sp.

Part IV—Palynomorphs of Australian *Grandispora maculosa* assemblage; Italia Road, Wallaringa and Mt. Johnstone Formations, Sydney Basin. Data from Playford and Helby (1968), Kemp et al. (1977), Jones and Truswell (1992), Melo and Loboziak (2000).

*Anapiculatisporites* spp.  
*Apiculatisporis* sp.  
*Auroraspora macra* Sullivan  
*Auroraspora solisorta* Hoffmeister et al.  
*Convolutispora* sp.  
*Cordylotisporites magnidictyus* (Playford & Helby) Melo & Loboziak  
*Cristatisporites kuttungensis* (Playford & Helby) Jones & Truswell  
*Cyclogranisporites* sp.  
*Dibolisporites* sp.  
*Dictyotriletes* sp.  
*Foveosporites pellucidus* Playford & Helby  
*Granulati sporites* sp.  
*Grandispora maculosa* Playford & Helby  
*Laevigato sporites* sp.  
*Leiotriletes* sp.  
*Psomospora detecta* Playford & Helby  
*Punctatisporites lucidulus* Playford & Helby  
*P. subtritus* Playford & Helby  
*Raistrickia accinta* Playford & Helby  
*R. radiosa* Playford & Helby  
*Rattiganispora apiculata* Playford & Helby  
*Reticulatisporites asperidictyus* Playford and Helby  
*Retusotriletes* sp.  
*Rugospora australiensis* (Playford & Helby) Jones & Truswell  
*Stenozonotriletes* sp.  
*Verrucosisporites aspritis* Playford & Helby  
*V. italiaensis* Playford & Helby  
*V. quasigobbetii* Jones & Truswell

REMARKS ADDED IN PROOF: The following taxa were confirmed in Australia based on recent exam of specimens housed in the Australian Museum by one of the authors (RI): *Nothorhacopteris kellaibelensis*, *Triphyllopteris boliviana*, *Fryopsis frondosa* and *Tomiodendron* sp. The same author also confirmed the synonymy between South American and Australian specimens classified as *?Sphenopteridium intermedium*.

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