

# SIGNIFICANCE OF THE CRETACEOUS-TERTIARY SPORE GENUS *CYATHEACIDITES* IN TRACING THE ORIGIN AND MIGRATION OF *LOPHOSORIA* (FILICOPSIDA)

by M. E. DETTMANN

**ABSTRACT.** Detailed study of the type species *Cyatheacidites annulatus* Cookson ex Potonié 1956, based upon type material from the Tertiary of Kerguelen (southern Indian Ocean), reveals morphological concurrence with the Cretaceous *C. tectifera* Archangelsky and Gamero 1965. Two other Cretaceous *spora dispersae* morphotypes are described and allocated to *Cyatheacidites*: *C. archangelskyi* nom. nov. (pro *Muricingulatisporis annulatus* Archangelsky and Gamero 1966) and *C. botuliformis* sp. nov. The set of diagnostic characters of *C. annulatus*—broad cingulum, cavate/stratified sclerine, prominent protuberances on contact faces, distal foveolae, and scabrate sculpture—is confined, among living ferns, to spores of *Lophosoria quadripinnata* (Gmel.) C. Chr. Affiliation of *Cyatheacidites* with *Lophosoria* implies a broad austral distribution of the latter during the Cretaceous and Tertiary, in contrast to its present restriction to South and central America.

Primary radiation, dated as earliest Cretaceous (Berriasian), was centred in a southern Gondwanic region adjacent to the proto South Atlantic Ocean. Migration, north to central America and east to Australia, was possibly triggered by climatic/habitat changes associated with fragmentation of Gondwana; routes to Australia were probably via Antarctica. Throughout its history, *Lophosoria* was associated with a variety of plant communities, ranging between temperate rain forest and open habitats.

The stratigraphic utility of dispersed spores is discussed in relation to climatic, topographic, sedimentological, and palaeoecological factors, and the effects of these on plant migration.

*CYATHEACIDITES* has had a chequered taxonomic history, having been proposed (Cookson 1947) before the guidelines of the Botanical Code were widely accepted by palynologists for Tertiary dispersed spore taxa. Its likely affiliation, too, was the subject of some controversy (Erdtman 1958) due to an incorrect identification of the extant *Lophosoria quadripinnata* spores (Knox 1938) with which *C. annulatus* Cookson ex Potonié was compared. Gastony and Tryon (1976), in accepting this affiliation, indicated a broader austral distribution during the Tertiary of *Lophosoria* than its current restriction to South and central America.

The present study of *L. quadripinnata* spores, and of the type and other material of *Cyatheacidites*, reaffirms an earlier, Cretaceous, history of *Lophosoria* as indicated by Archangelsky and Gamero (1965). A review of the fossil dispersed spore occurrences has also been undertaken to decipher more fully the history of *Lophosoria* and the nature of the floras with which it was associated. In the course of this review other questions emerged. One relates to the sometimes unjustified emphasis placed on cryptogam spores in stratigraphic correlation; others to whether we can model past climates and ecological ranges of plant groups on present-day criteria.

*Lophosoria* is a monotypic genus of 'tree' ferns confined to South and central America. It prefers cool moist habitats, with an opportunistic trait of invading disturbed sites such as road cuts, landslips, cutover forest, and burned areas (Tryon and Tryon 1982). In the tropics it inhabits cloud forests, paramo thickets, and grasslands at altitudes between 1000 and 3000 m. In south-eastern Brazil it is found as low as 500 m, and in its southernmost range (Chile, Argentina, and Juan Fernandez Islands) from sea level to 1000 m (Tryon and Tryon 1982).

As summarized by Tryon and Tryon, systematic affiliation of *Lophosoria* is uncertain; they

follow Pichi-Sermolli (1970, 1977) and place it alone in the Lophosoriaceae. Its relationships to other cyatheoid-dicksonioid tree ferns are also unclear; Tryon and Tryon indicate a closer affiliation to the Dicksoniaceae, in particular to *Cibotium*, on chromosome, stem, and petiole characters. Spore characters are, moreover, considered to ally *Lophosoria* to south-east Asian and western Malaysian species of *Cibotium* (Gastony 1982; Gastony and Tryon 1976). Comparative morphology of the spores, however, is largely confined to external features discernible by scanning electron microscopy; detailed studies have yet to be undertaken on wall stratification and structure by means of light and transmission electron microscopy.

Cyatheoid and dicksonioid ferns are known from at least the Jurassic. Abundant foliage attributed to *Dicksonia*, *Coniopteris*, and other genera is believed to signify the importance and widespread occurrence of the Dicksoniaceae in Jurassic and Cretaceous floras. The Cyatheaceae, too, have been traced to the Jurassic and are known largely from structurally preserved stems and occasional fertile foliage. *Lophosiorhachis japonica*, a petrified rachis described by Nishida (1982) from the Early Cretaceous (Aptian) of Japan, shares some anatomical features with *Lophosoria*. The species had previously (Nishida and Hara 1979) been affiliated with *Metaxya*, which, although anatomically similar to *Lophosoria*, has distinct petiole, spore, and chromosome characters. To date, *Lophosoria* foliage has not been recognized in the fossil record.

## MATERIALS AND METHODS

### Extant *L. quadripinnata* spores

Herbarium material was kindly provided by Dr A. F. Tryon of the Harvard University Herbaria. Catalogue details are: Killip & Garcia 33939, Colombia.

Two separate preparations were made, one using warm 2% potassium hydroxide for 2 min., the other following Erdtman's (1960) method of acetylosis followed by chlorination. Spores treated by the latter method were found to be considerably swollen (with equatorial diameters increased by more than 30%) and the morphological features of their outer sculptine somewhat disorganized. Gastony (1974) and Tryon (pers. comm.) have also remarked upon the detrimental effects of acetylosis on *L. quadripinnata* spores. Thus, the descriptions are based exclusively on the KOH preparations.

### Fossil *Cyatheacidites* spores

The type and other species described below are based on specimens recovered from Cookson's (1947) Kerguelen material and from other austral localities as follows:

*Kerguelen, southern Indian Ocean.* Waterfall Gorge, near Port Jeanne d'Arc, sample 85a, British Australian New Zealand Antarctic Research Expedition, 1929-1931 (BANZARE) Collection. Lignite and fine-grained, mid brown carbonaceous sandstone (see Cookson 1947). Age: Miocene (Nougier 1970).

*James Ross Island, Antarctic Peninsula.* The following samples discussed by Dettmann and Thomson (in press) have provided figured specimens:

1. D.3006.2, c. 1 km north of Lewis Hill. Light grey sandstone, Whisky Bay Formation (Lewis Hill Member). Age: late Albian.
2. D.8303.3, Crame Col. Calcareous siltstone with carbonaceous laminae. Age: Santonian-Campanian.
3. 8665, east side of Lachman Crags. Fine- to medium-grained sandstone. Age: Campanian.

*Victoria, Otway Basin.* Frome Broken Hill Co. Pty Ltd (FBH), Port Campbell No. 2 well (38° 36' 03" S., 142° 59' 20" E.), core 13, 7680-7694 ft (2340.9-2345.1 m). Medium grey siltstone, Belfast Mudstone. Age: Turonian (Taylor 1964).

Sample processing followed techniques outlined by Phipps and Playford (1984). Mineral digestion with warm 50% hydrofluoric acid was followed by 2-3 min. oxidation with warm nitric acid or Schulze solution. Soluble humic acids were then removed with weak (1-2%) potassium or ammonium hydroxide. Residues were mounted in glycerine jelly (lightly stained with Safranin O) under no. 0 glass coverslips for examination in transmitted light and photographic documentation with Ilford Pan F film. Specimens selected for SEM examination were gold-plated and photographed with Kodak Tri-X 35 mm film using Philips 505 and Cambridge Stereoscan 600 instruments.

Kerguelen and Victorian specimens are housed in the Museum of Victoria and are designated by registered catalogue numbers prefixed 'P'. Extant spores of *L. quadripinnata* and the James Ross Island specimens are

deposited in the micropalaeontological collection of the Department of Geology and Mineralogy, University of Queensland; catalogue numbers of that institution are prefixed 'Y'. Slide locations of all figured specimens are specified by preparation/slide number and mechanical stage coordinates as per standard 'England Finder' slide.

### DESCRIPTIVE PALYNOLOGY

Detailed descriptions are of homospores produced by the extant *L. quadripinnata*, and of morphologically similar miospores attributed to the form genus *Cyatheacidites* and obtained from Cretaceous and Tertiary sediments of various locations in the southern hemisphere (cited in the foregoing section).

#### Spores of *Lophosoria quadripinnata* (Gmel.) C. Chr.

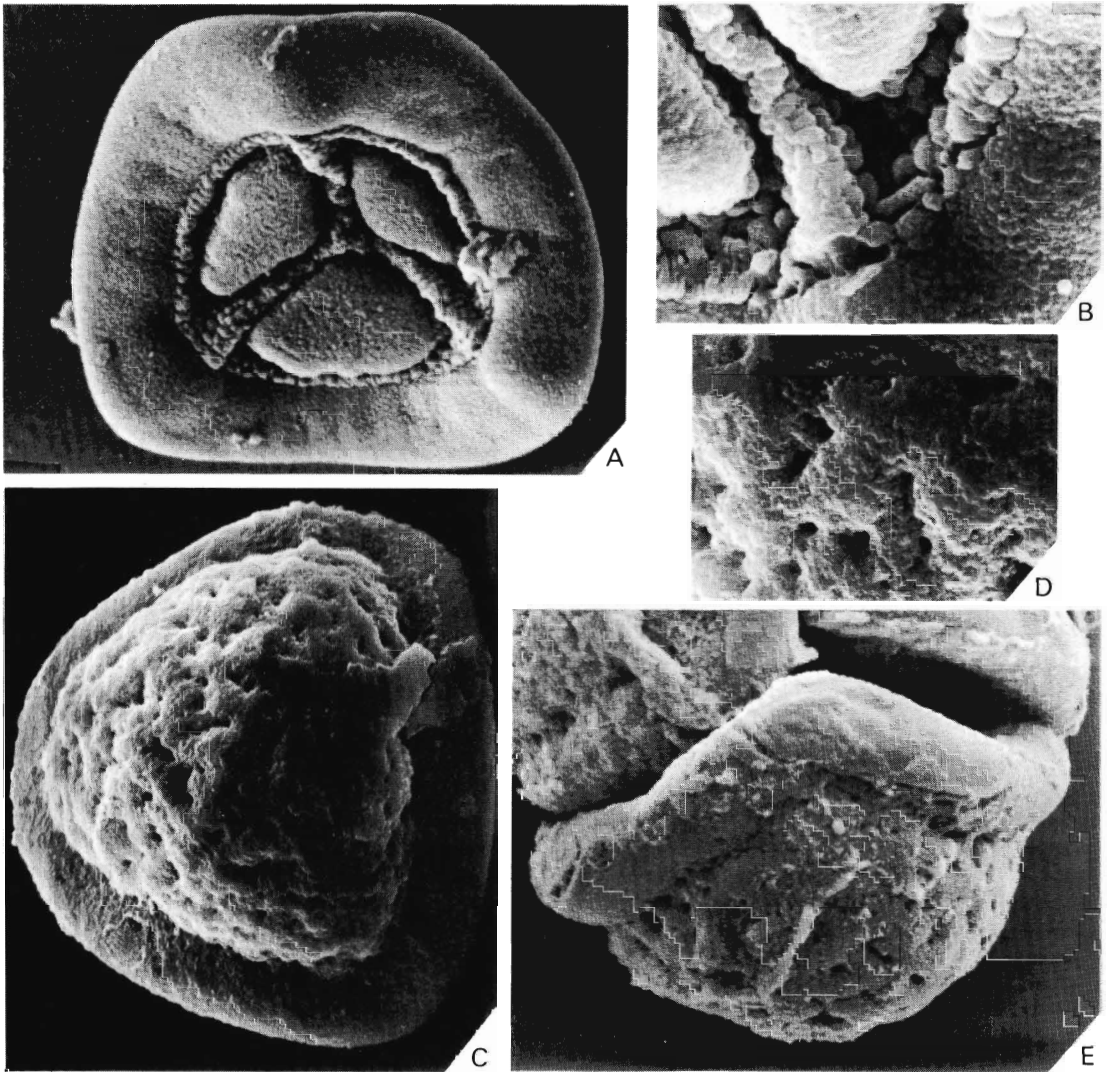
Plate 13, figs. 1-10; text-figs. 1A-E, 2A

*Description.* Spores radial, trilete, biconvex, the proximal surface pyramidal, distal surface hemispherical. Amb convexly subtriangular to subcircular. Sclerine stratified, consisting of smooth, homogeneous, 0.75-1.0  $\mu\text{m}$ -thick inner layer (intexine) that is closely adherent proximally to, but often separated distally from, the outer sculptine. Sculptine 2.5-4.5  $\mu\text{m}$  thick, thicker equatorially where a cingulum 8-12  $\mu\text{m}$  wide is developed. Cingulum normally of uniform width; occasionally constricted in radial regions; internal hollow duct sinuously circumscribes cingulum's inner margin in equatorial plane. Sculptine with scabrate to microreticulate sculpture, the positive elements composing a faintly resolvable, extremely thin, outermost (?perinous) layer that is closely adherent to the thick, coarsely sculptured layer of sculptine (?exoexine). Inner sculptine foveolate distally, the foveolae 1-2  $\mu\text{m}$  in diameter, spaced 2-6  $\mu\text{m}$  apart, 2-3  $\mu\text{m}$  deep, sometimes communicating internally to form vermiculate to negative reticulate subsurface pattern; pits at inner margin of cingulum communicate with cingulum duct, intersecting it at right angles. Proximal surface with a conspicuous, straight-sided, flat-topped pad on each contact area; pads occupy up to 80% of contact area, triangular or irregularly scalloped in basal outline, and with fine, deep pits, overlain by finely scabrate outermost sclerine. Remainder of proximal surface with scabrae and/or grana up to 1  $\mu\text{m}$  in diameter. Laesurae straight, extending to inner margin of cingulum and enclosed with membranous fimbriate to granulate lips, 2-4  $\mu\text{m}$  high.

*Dimensions.* Overall equatorial diameter 55 (64) 72  $\mu\text{m}$ , spore-cavity diameter 38 (43) 48  $\mu\text{m}$  (50 specimens); polar diameter 38 (42) 46  $\mu\text{m}$  (18 specimens).

*Remarks.* The spores of *L. quadripinnata* are morphologically complex and the stratification of the thick, highly refractive sculptine is difficult to resolve under the light microscope. The outermost scabrate sculpture may represent a very thin perinous layer that envelops and is closely adherent to the thick sculptured exoexine (text-fig. 2A). Support for the perinous nature of the outermost sculptine is provided by its variable development. It is absent to incompletely represented on immature spores (Pl. 13, fig. 8), and thicker and composed of more densely arranged scabrae that sometimes obscure the underlying foveolae on mature spores (Pl. 13, figs. 9 and 10) (cf. Tryon and Tryon 1982). Moreover some spores possess globular bodies, regarded by Lugardon (1981) as of perine derivation and the counterpart of orbicules or Ubisch bodies in pollen (Pl. 13, fig. 10). These globular bodies and the scabrate sculptine in which they are incorporated may reflect tapetal deposition, which, from the material examined, apparently continued after sculptural maturity of the exoexine. Gastony and Tryon (1976) and Tryon and Tryon (1982) inferred that the perine is represented only on mature spores, by the irregular granulate deposit that overlies the finely scabrate sculptine. They noted that this deposit is neither continuous nor is it inflatable when treated with warm 1N sodium hydroxide, a technique developed by Gastony (1974) for distinguishing the perine in cyatheaceous and other fern spores. If their concept of the perine is correct, then the underlying exine would be regarded as three-layered, the outermost scabrate layer and the underlying thick, heavily sculptured, cingulate layer representing the exoexine that envelops and is distally detached from the intexine.

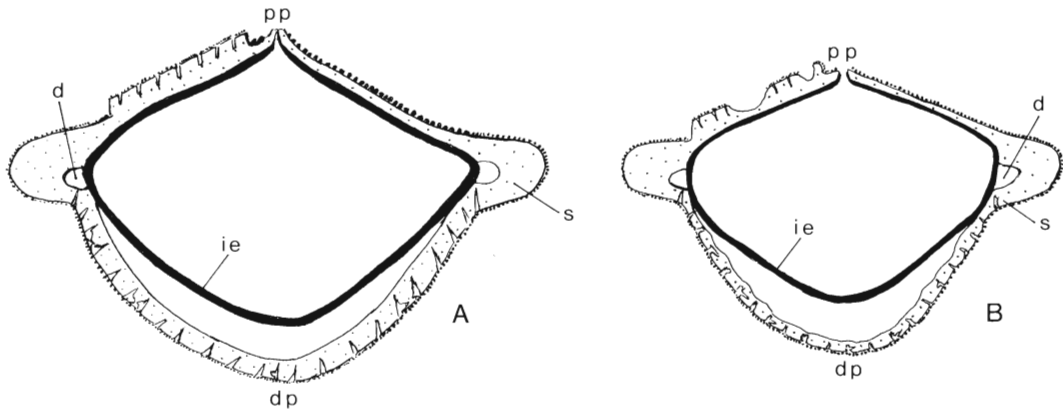
A different interpretation of the wall stratification of *L. quadripinnata* spores was presented by



TEXT-FIG. 1. Spores of *Lophosoria quadripinnata* (Gmel.) C. Chr. All Harvard University Herbaria specimen tag, Killip and Garcia 33939, Colombia. A, B, proximal surface ( $\times 1000$ ) and sculptural detail ( $\times 2500$ ); B579/S1, 033/1, Y.4839. C, D, distal surface ( $\times 1000$ ) and sculptural detail ( $\times 2500$ ); B579/S1, M31/1, Y.4840. E, lateral view of specimen in tetrad,  $\times 1000$ ; B579/S1, 033/1, Y.4841.

Erdtman (1957) and Erdtman and Sorsa (1971), who envisaged a thick, cingulate perine distally detached from a thinner, stratified exine. The perine layer as depicted by Erdtman (1957, figs. 133 and 134) equates with the pitted, cingulate exoexine and the closely adherent thin, scabrate layer; the thinner, two-layered wall shown by Erdtman may represent the single-layered intexine that is distally detached from the exoexine (see text-fig. 2A). A study of sculptine ontogeny using optical, scanning electron, and transmission electron microscopy is clearly necessary to ascertain the wall stratification and the nature of its component layers.

The function of the cingulum's internal duct is speculative, but possibly relates to dispersion. Gastony and Tryon (1976) emphasized the large size of *L. quadripinnata* spores, quoting a size



TEXT-FIG. 2. Interpreted polar sections of (A) *Lophosoria quadripinnata* (Gmel.) C. Chr. spores; and (B) *Cyatheidites annulatus* Cookson ex Potonié. Note: pp = proximal pole, dp = distal pole, s = sculptine, ie = intexine, d = cingulum duct; sections show lips cut of proximal contact-area sculpture (left) and laesurate lips (right).

range of 70–100  $\mu\text{m}$  similar to that reported by Heusser (1971); the specimens studied herein are smaller, ranging from 55 to 72  $\mu\text{m}$ .

Gastony and Tryon (1976, see also Tryon and Tryon 1982) illustrated the variable configuration of the proximal pads and the form and extent of the distal foveolae. Included among their illustrations are specimens taken from material erroneously identified by Tschudy and Tschudy (1965, figs. 73 and 74) as *Alsophila* sp. Other descriptions and line-drawings were provided by Knox (1938), who incorrectly captioned her figures (75a, b) as *Cyathea vestita*, and by Erdtman (1957) and Erdtman and Sorsa (1971). Morbelli (in Markgraf and D'Antoni 1978, pl. 2, fig. 27) illustrated, without description, a specimen from Argentina, the proximal sculpture of which consists of irregular coalescent verrucae and muri, and in which the cingulum is of uneven width. Archangelsky and Gamberro (1965) noted that Brazilian and Chilean specimens illustrated by Erdtman (1957) differed in proximal sculptural features and suggested that polymorphism may exist amongst *L. quadripinnata* spores. This could be determined by examining specimens from the species' known geographical and ecological range.

*Comparison.* The distinctiveness of *L. quadripinnata* spores was emphasized by Gastony and Tryon (1976) who concluded that their external morphology is unique amongst living ferns. According to Gastony (1982) and Tryon and Tryon (1982), the closest morphological analogues are found in south-east Asian and western Malaysian species of *Cibotium*, viz. *C. arachnoideum* (C. Chr.) Holtt., *C. barometz* (L.) J. Sm., and *C. cumingii* Kze. All are cingulate, have a thin scabrate perine (which, however, is readily inflated by hot alkali treatment), and prominent raised pads on the contact faces. They differ in having coarse distal ridges, orientated more or less parallel to the amb. As for *L. quadripinnata* spores the sclerine stratification has not yet been ascertained precisely.

#### Genus *CYATHEACIDITES* Cookson ex Potonié 1956 emend.

*Emended diagnosis.* Spores radial, trilete, cingulate. Sclerine stratified; inner layer thin, attached proximally but separated distally from thicker outer sculptine. Proximal surface with positive sculptural elements clustered or coalescent on contact faces adjacent to laesurae. Distal surface with foveolate or foveo-reticulate to rugulo-reticulate sculpture. Sculptine surface with additional fine scabrae or grana.

*Type species.* *C. annulatus* Cookson ex Potonié 1956 (designated by Potonié 1956, p. 62).

*Other species.* *C. (al. Muricingulatisporis) archangelskyi* nom. nov. (for *M. annulatus* Archangelsky and Gamarro 1966a, p. 204, pl. 2, figs. 4–8); *C. botuliformis* sp. nov.; *Cyatheacidites* sp. 1 of Kotova 1983, p. 889; pl. 7, figs. 3 and 4; *Cyatheacidites* sp. 2 of Kotova 1983, p. 889; pl. 7, figs. 5 and 6.

*Remarks and comparison.* Cookson (1947), in following the coenotype system of classification and nomenclature, first proposed the name in the trinomial designation *Trilites (Cyatheacidites) annulata*. The name *Cyatheacidites* was used to denote the spores' morphological resemblance to what Cookson believed were *Cyathea vestita* spores, but which were, in fact, *L. quadripinnata* spores (see reference to Knox 1938 above). She was later (1957, p. 41) persuaded by contemporary opinion to abandon the coenotype system and referred the spores to *C. annulata* thereby implying a relationship to *Cyathea*, a relationship that Erdtman (1958) quickly contested. Potonié (1956) had meanwhile resolved the problem by validating *Cyatheacidites* as a form genus and selecting a nomenclatural type.

The above diagnosis follows Stover and Partridge (1973, p. 247), but specifies the distal sculpture and the finely scabrate surficial features which are here considered as generically diagnostic.

The cavate sclerine distinguishes *Cyatheacidites* from *Cingulatisporites* Thomson 1953, *Polypodia-ceoisporites* Potonié ex Potonié 1956, and *Muricingulatisporis* Krutzsch 1959. *Densoisporites* Weyland and Krieger 1953 and *Lundbladisporea* Balme 1963 have a cavate sclerine, but the wall layers are widely separated equatorially and their sculptural features are distinct.

#### *Cyatheacidites annulatus* Cookson ex Potonié 1956

Plate 13, figs. 11–15; Plate 14, figs. 1–7; Plate 15, figs. 1–7; text-fig. 2B

- 1947 *Trilites (Cyatheacidites) annulata* Cookson, p. 136, pl. 15, figs. 53–55.  
 1956 *Cyatheacidites annulata* Cookson ex Potonié, p. 62, pl. 8, figs. 81 and 82.  
 1957 *Cyathea annulata* Cookson; Cookson, p. 45, pl. 9, figs. 4 and 5.  
 1965 *Cyatheacidites tectifera* Archangelsky and Gamarro, p. 163, pl. 2, figs. 1–11.  
 1969 *Cyathidites* Couper; Mechkova, p. 16, fig. 4.  
 1983 *Cyatheacidites* sp. 1 Bratzeva, p. 912, pl. 7, figs. 1 and 2.  
 ?1983 *Cyatheacidites* sp. 2 Bratzeva p. 912, pl. 7, figs. 3 and 4.  
 non 1983 *Cyatheacidites tectifera* Archangelsky and Gamarro; Truswell, p. 143, pl. 1, fig. 21.

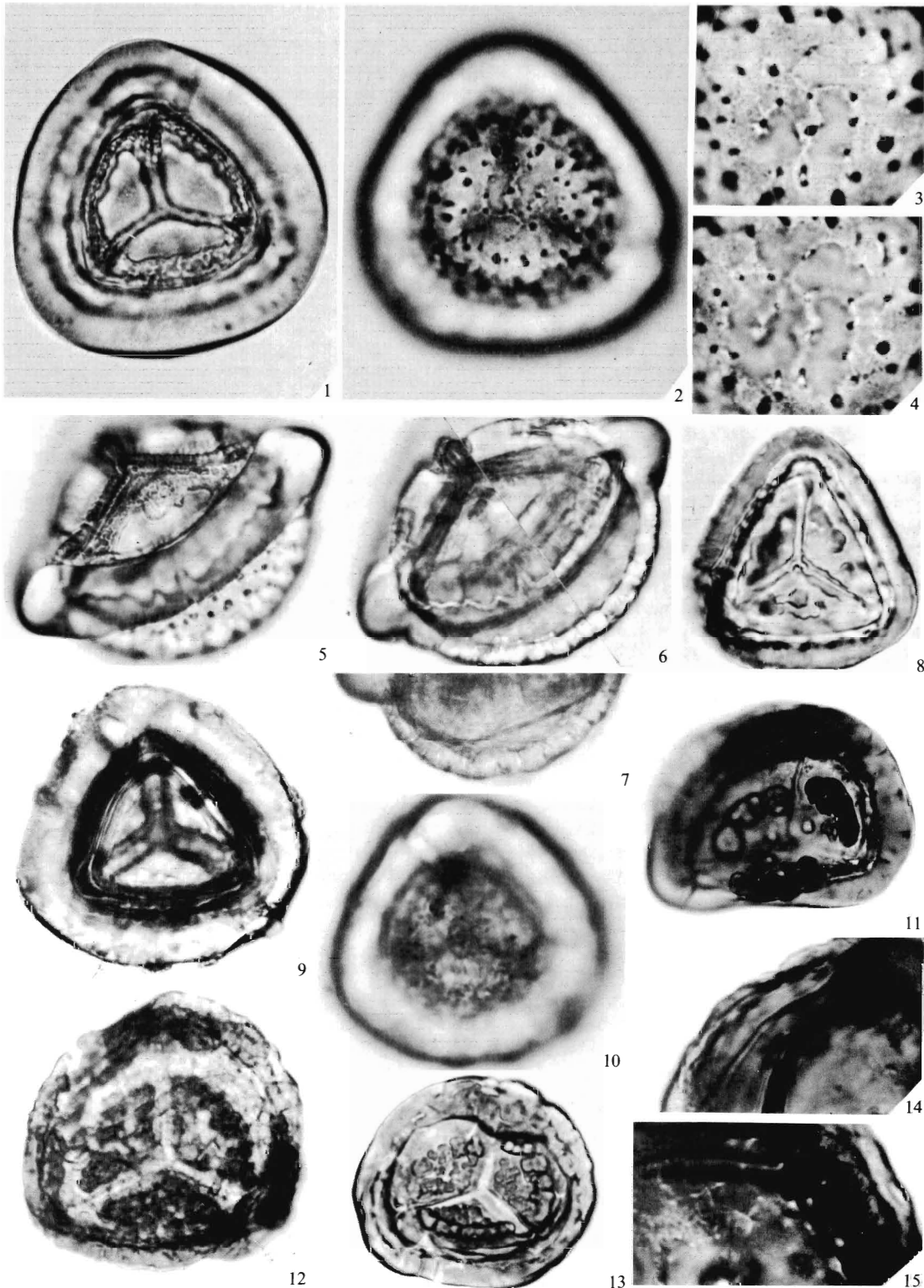
*Diagnosis.* Spores radial, trilete; biconvex to plano-convex, the distal surface strongly arched. Amb subcircular to convexly subtriangular. Sclerine stratified; inner layer (intexine) 1.0–1.5  $\mu\text{m}$  thick, homogeneous, usually distally detached from sculptine. Sculptine 3–4  $\mu\text{m}$  thick, thicker at equator where a cingulum of uniform to uneven width (6–8  $\mu\text{m}$  wide) is developed; cingulum broadly rounded in profile, with internal duct 2–3  $\mu\text{m}$  in diameter circumscribing inner margin of cingulum

#### EXPLANATION OF PLATE 13

All figures  $\times 750$  unless otherwise specified.

Figs. 1–10. Spores of *Lophosoria quadripinnata* (Gmel.) C. Chr.; all Harvard University Herbaria specimen tag, Killip and Garcia 33939, Colombia. 1, proximal view; B579/2, P29/3, Y.4842. 2–4, distal view and distal sculptural detail ( $\times 1250$ ), high and low foci; B579/2, M34/0, Y.4843. 5 and 6, lateral aspect, high and sectional foci, showing internal duct at inner margin of cingulum; B579/2, 033/4, Y.4844. 7, lateral aspect, optical section of distal sculptine showing detached inner layer; B579/1, U18/0, Y.4845. 8, proximal view of immature specimen; B579/1, L24/1, Y.4846. 9 and 10, mature specimen, sectional focus, showing cingulum duct and globular bodies embedded in outermost granulate deposit; and distal focus, showing granulate deposit obscuring foveo-reticulate sculpture; B579/1, H28/4, Y.4847.

Figs. 11–15. *Cyatheacidites annulatus* Cookson ex Potonié 1956; all Kerguelen Island, Waterfall Gorge, sample 85a. 11, neotype, proximal view, off-polar aspect, showing proximal sculpture and cingulum duct on right; B411/8, L39/1, P181685. 12, polar view of corroded specimen; B411/6, M36/0, P181686. 13, proximal view; B411/5, 037/0, P181687. 14 and 15, distal sclerine, sectional and surface foci ( $\times 1250$ ); B411/10, M30/2, P181688.



DETTMANN, *Lophosoria*, *Cyatheacidites*

in equatorial plane. Sculptine surface scabrate; in some specimens, areas of the scabrate sculpture are eroded or detached as a thin membrane that may represent an outermost (?perinous) layer overlying more prominent proximal and distal sculpture. Distal surface with irregular foveolae 1–2  $\mu\text{m}$  in diameter, 2–3  $\mu\text{m}$  deep, spaced 2–4  $\mu\text{m}$  apart; foveolae interconnect beneath surface to form vermiculate to negative reticulate pattern. Those aligned adjacent to cingulum communicate with internal duct of cingulum. Proximal contact areas each with prominent, raised, flat-topped pads that are broadly triangular to irregular in basal outline, and finely pitted to fossulate in surface view. In some specimens, proximal sculpture is reduced, comprising discrete or coalescent verrucae and muri. Laesurae straight, extending to inner margin of cingulum and enclosed within membranous lips.

*Dimensions.* 1. Kerguelen specimens. Overall equatorial diameter 44 (57) 68  $\mu\text{m}$ , spore-cavity diameter 36 (42) 51  $\mu\text{m}$  (15 specimens); polar diameter 35 (37) 40  $\mu\text{m}$  (4 specimens).

2. Australian and Antarctic Peninsula specimens. Overall equatorial diameter 35 (54) 80  $\mu\text{m}$ , spore-cavity diameter 25 (42) 60  $\mu\text{m}$  (50 specimens); polar diameter 35 (38) 40  $\mu\text{m}$  (8 specimens).

*Type specimens.* Cookson's (1947 pl. 15, fig. 53) specimen was selected by Potonié (1956) as lectotype. The slide(s) containing this and other figured specimens (syntypes) have not been located, either in the Botany Department, University of Melbourne, where Dr Cookson carried out her investigation, or at the Museum of Victoria, the repository for much of Cookson's type material (pers. comm. Dr S. L. Duigan, Botany Department, University of Melbourne; Dr P. A. Jell, Museum of Victoria). A neotype is here designated to serve as the nomenclatural type. This and other Kerguelen specimens figured herein were recovered from a portion of the original sample from the type locality.

*Neotype.* Specimen P181685, Plate 13, fig. 11. Proximal off-polar aspect. Amb convexly subtriangular, 59  $\mu\text{m}$   $\times$  44  $\mu\text{m}$  in diameter. Laesurae 16  $\mu\text{m}$  long. Cingulum 6–8  $\mu\text{m}$  wide, faintly scabrate, hollow near its inner margin. Sclerine composed of 1  $\mu\text{m}$ -thick inner layer, distally detached from thicker (3–5  $\mu\text{m}$ ) sculptine. Sculptine pitted distally. Proximal surface with irregular coalescent verrucae and muri on each contact face.

*Type locality.* Kerguelen, Waterfall Gorge, near Port Jeanne d'Arc; sample 85a, BANZARE Collection. Age: Miocene (Nougier 1970).

*Remarks.* The description is based upon specimens recovered from the type locality and from Cretaceous sediments of James Ross Island, Antarctic Peninsula (Albian to Campanian) and the Otway Basin, Victoria (Turonian to Santonian). The Kerguelen specimens are compressed and in fair to poor preservation states, consistent with the condition of other palynomorphs in the sample. Except for their smaller size, the spores appear to be morphologically identical to those of Cookson (1947). The size discrepancy may well reflect differing preparation procedures. Cookson (1947, p. 130) used acetyolysis/chlorination followed by 5–10 % potassium hydroxide, and later indicated (1953, footnote to p. 463) that Kerguelen spores were enlarged by the treatment.

Cookson's illustrations (1947, pl. 15, figs. 54 and 55) clearly show a stratified sclerine, with the inner unsculptured layer distally detached from the sculptine. One specimen (pl. 15, fig. 54) shows that the cingulum carries a duct that circumscribes the spore body in the equatorial plane; distal pits adjacent to cingulum interconnect subsurface with this duct. These attributes are considered to be unrelated to preservational quality, being clearly exhibited by well-preserved Australian Tertiary specimens (Stover and Partridge 1973, pl. 13, figs. 5 and 6) and Cretaceous examples from Australia and Antarctica (Pl. 13, figs. 11 and 13; Pl. 14, figs. 1 and 5).

The scabrate surficial sculpture may denote a thin, outermost layer of the sculptine (text-fig. 2B). In some specimens, this scabrate layer is partially eroded or detached from the underlying sculptine as a thin membrane, and a perinous derivation is possible. The sculptural form of the contact areas is very variable; as described above, and is shown by specimens from the type locality and amongst individual populations from other samples. Similar variation is displayed by *C. tectifera* Archangelsky and Gamero 1965, here considered conspecific with *C. annulatus* Cookson ex Potonié 1956.

Archangelsky and Gamero (1965) distinguished *C. tectifera* from *C. annulatus* on the basis of size, stratigraphic occurrence, and the structure of the distal and equatorial exine. As noted above,



Cookson's (1947) measurements were taken from swollen specimens; the size range of the Kerguelen specimens examined (44–68  $\mu\text{m}$ ) approximates that specified (41–65  $\mu\text{m}$ ) for *C. tectifera*. *C. annulatus* and *C. tectifera* have comparable distal features; the distal tectate structure recorded by Archangelsky and Gamarro (1965, pl. 2, fig. 11) for *C. tectifera* is considered to reflect the subsurface communications of the pits and the undulate nature of the inner margin of the sculptine wall. Moreover, the equatorial columellate structure observed in *C. tectifera* by Archangelsky and Gamarro (1965, pl. 2, fig. 10) is represented in type and other examples of *C. annulatus* (Pl. 13, fig. 11; Pl. 14, fig. 5) and is interpreted to reflect the communications between the cingulum duct and adjacent distal pits. SEM and light microscopic analyses emphasize that Cretaceous and Tertiary examples described herein are morphologically comparable; thus discrimination on stratigraphic grounds cannot be upheld.

The specimen illustrated by Bratzeva (1983, pl. 7, figs. 1 and 2) as *Cyatheidites* sp. 1 is included within *C. annulatus*; the corroded example that Bratzeva (pl. 7, figs. 3 and 4) referred to *Cyatheidites* sp. 2 is questionably of the same specific affiliation. Truswell (1983) identified *C. tectifera* amongst recycled palynomorphs in Antarctic sediments; her specimen has distal rugulo-reticulate sculpture and is excluded from *C. annulatus*.

*Comparison and affinity.* From the above descriptions, it is evident that the spores of *Lophosoria quadripinnata* and the fossil spores attributed to *C. annulatus* share essentially the same morphological attributes, especially with respect to sclerine stratification, configuration, and sculpture. Both spore categories are comparable in constructional details of the cingulum and the contact area pads, in the nature and distribution of the fine surficial sculpture, and in the deeply pitted, distal sculptine. The extant spores, however, are larger, have a wider cingulum, a thicker sculptine, and coarser granules surrounding the contact area pads. The significance of these differences needs to be assessed from a wider sampling of *L. quadripinnata* spores representative of the species' geographical and ecological range.

*Distribution.* Widely distributed in the Cretaceous and Tertiary of southern Gondwana (text-figs. 3 and 4). Reported occurrences are summarized below:

AUSTRALIA: 1, Cretaceous. Middle Albian–Cenomanian, Eromanga Basin; Turonian–Santonian, Otway Basin (reported herein). 2, Tertiary. Late early Oligocene to possibly Pliocene, Gippsland, Otway, and Murray Basins (Harris 1971; Stover and Partridge 1973; Martin 1973; Harris and Morgan 1976); early Oligocene–Miocene, Tasmania (Harris 1971; Hill and Macphail 1983); Miocene, Queensland (Cookson 1957; for dating see Ewart *et al.* 1977); Pliocene, north-eastern New South Wales (Martin 1981).

SOUTH AMERICA: 1, Cretaceous. ?Barremian–Aptian, Argentina (Archangelsky and Gamarro 1965, 1967a; for further age discussions, see Archangelsky *et al.* 1981, 1984). 2, Tertiary. Paleocene–Eocene, Argentina (Archangelsky 1972, 1973a, b; Petriella and Archangelsky 1975; Gamarro and Archangelsky 1981); Eocene–early Oligocene, Chile (Cookson and Cranwell 1967; Fasola 1969).

ANTARCTICA: Cretaceous. Berriasian to possibly Barremian, Livingston and Snow Islands (Askin 1983); early Albian–Cenomanian and Santonian–Campanian, James Ross Island (Dettmann and Thomson, in press).

FALKLAND PLATEAU: 1, Cretaceous. ?Barremian–early Albian, Site 511 (Kotova 1983; for dating see Wise 1983; Krashennikov and Basov 1983). 2, Tertiary. Early Oligocene, Site 511 (Bratzeva 1983).

KERGUELEN: Tertiary, Miocene (Cookson 1947; Mechkova 1969; for dating see Nougier 1970).

SOUTH AFRICA: Cretaceous. Early Albian, Site 361 (McLachlan and Pieterse 1978; for dating see Proto Decima *et al.* 1978). This record is provisional.

*Cyatheidites archangelskyi* nom. nov.

Plate 14, figs. 8–12; Plate 15, figs. 11 and 12

1966a *Muricingulatisporis annulatus* Archangelsky and Gamarro, pp. 204–205, pl. 2, figs. 4–8.

1983 *Cyatheidites tectifera* Archangelsky and Gamarro; Truswell, p. 143, pl. 1, fig. 21.

*Diagnosis.* Spores radial, trilete; distal surface hemispherical, proximal surface pyramidal. Amb convexly subtriangular. Exine 3.0–3.5  $\mu\text{m}$  thick, stratified; innermost layer 0.75–1.0  $\mu\text{m}$  thick, occasionally detached in distal regions from sculptured, equatorially thickened sculptine, the outer,

finely scabrate surface of which may represent an extremely thin, closely adherent, perinous layer. Cingulum 4–6  $\mu\text{m}$  wide; profile more or less semicircular; narrow, internal duct circumscribes inner margin of cingulum in equatorial plane. Distal sculpture of low, sinuous, 2–5  $\mu\text{m}$  wide muri that anastomose or freely terminate to form foveo-reticulate surface pattern. Muri finely scabrate, flat-topped or (occasionally) rounded in sectional view; enclose lumina that are more or less subcircular and 1–2  $\mu\text{m}$  diameter adjacent to cingulum, and larger (2–5  $\mu\text{m}$  wide) and irregularly sinuous in distal polar region. Contact areas each with prominent, raised, flat-topped pad of triangular basal outline. The pads may be deeply pitted, displaying foveolate to irregularly reticulate surface pattern, or occasionally composed of discrete and partially fused verrucae and sinuous muri. Laesurae straight, extend to inner margin of cingulum, enclosed within membranous lips.

*Dimensions.* Overall equatorial diameter 40 (52) 60  $\mu\text{m}$ , spore-cavity diameter 32 (42) 48  $\mu\text{m}$  (15 specimens); polar diameter 32  $\mu\text{m}$ , 35  $\mu\text{m}$  (2 specimens).

*Remarks.* The finely scabrate, outermost surface of the sculptine resembles that of *C. annulatus* and may likewise represent an extremely thin, closely adherent, perinous layer. However, a distinct layer could not be resolved by  $\times 1000$  light microscopy. The distal foveo-reticulate sculpture is coarser in the polar region than adjacent to cingulum (Pl. 14, fig. 10). The form and extent of the proximal sculpture is very variable among the James Ross Island specimens (see Pl. 14, figs. 8 and 12) and also among the Argentinian specimens described by Archangelsky and Gamero (1966a, pp. 204–205, pl. 2, figs. 4–8) as *Muricingulatisporis annulatus*. On the basis of the sclerine stratification, construction, and sculpture the species is transferred to *Cyatheacidites* from *Muricingulatisporis* Krutzsch 1959. The latter genus has distinct proximal sculpture of narrow, sinuous, tangentially orientated, torus-like muri that circumscribe the laesurae; its wall stratification and fine surficial detail are unknown.

In referring *M. annulatus* Archangelsky and Gamero 1966 to *Cyatheacidites*, the epithet becomes a later homonym of the type species *C. annulatus* Cookson ex Potonié 1956. Accordingly Archangelsky and Gamero's species is renamed *C. archangelskyi* after Dr S. Archangelsky.

*Comparison.* *C. archangelskyi* is readily distinguishable from *C. annulatus* in having coarser foveolate to foveo-reticulate distal sculpture, a narrower cingulum, and a more consistently triangular amb.

*Distribution.* SOUTH AMERICA: Cretaceous, ?Valanginian–Aptian, Argentina (Archangelsky and Gamero 1966a, 1967a; for further age discussion see Archangelsky *et al.* 1981, 1984).

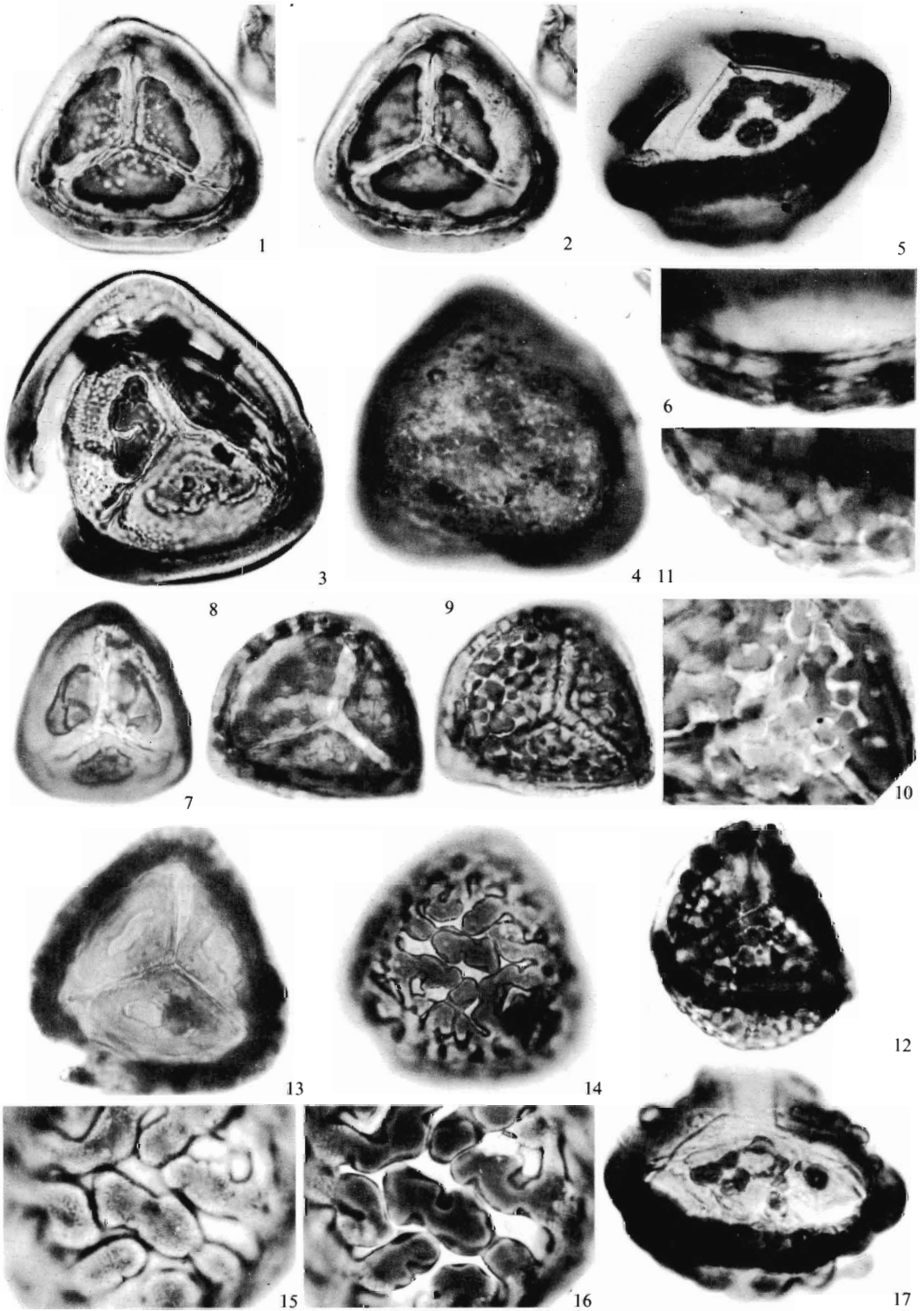
#### EXPLANATION OF PLATE 14

All figures  $\times 750$  unless otherwise specified.

Figs. 1–7. *Cyatheacidites annulatus* Cookson ex Potonié 1956. 1 and 2, proximal aspect, high and sectional foci; James Ross Island, c. 1 km north of Lewis Hill, sample D3006.2 (Whisky Bay Formation); X222/2, V53/1, Y.4848. 3, proximal focus of broken specimen showing scabrate surficial sculpture and partially detached innermost layer; James Ross Island, Crame Col, sample D8303.3; X202/1, D37/1, Y.4849. 4, distal view; locality as figs. 1 and 2; X222/2, X30/4, Y.4850. 5 and 6, oblique lateral view and optical section of distal sclerine ( $\times 1250$ ); James Ross Island, east of Lachman Crags, sample 8665; X213/1, W40/0, Y.4851. 7, proximal view; Otway Basin, south-eastern Australia, Port Campbell no. 2, 7680–7694 ft (2340.9–2345.1 m), Belfast Mudstone; F085/6, 039/2, P181689.

Figs. 8–12. *C. archangelskyi* nom. nov. 8–10, distal aspect, proximal and distal foci, and distal sculptural detail ( $\times 1250$ ); James Ross Island, c. 1 km north of Lewis Hill, sample D3006.2 (Whisky Bay Formation); X220/3, F26/4, Y.4852. 11 and 12, oblique lateral view and distal sculptine detail ( $\times 1250$ ); locality as figs. 8–10; X220/3, X44/0, Y.4853.

Figs. 13–17. *C. botuliformis* sp. nov. 13–16, holotype, distal aspect; proximal and distal foci (13 and 14) and high and low foci (15 and 16) of distal polar sclerine ( $\times 1250$ ); James Ross Island, east of Lachman Crags, sample 8665; X213/1, D53/0, Y.4854. 17, oblique lateral view; James Ross Island, c. 1 km north of Lewis Hill, sample D3006.2 (Whisky Bay Formation); X222/2, G27/0, Y.4855.



ANTARCTIC PENINSULA: Cretaceous. Early Albian–Cenomanian and Santonian–Campanian, James Ross Island (Dettmann and Thomson, in press). Recycled into Holocene sediments, Weddell Sea (Truswell 1983).

FALKLAND PLATEAU: Cretaceous. Barremian or Aptian–early Albian, Site 511 (Kotova 1983; for dating see Wise 1983, Krashennikov and Basov 1983).

*Cyatheacidites botuliformis* sp. nov.

Plate 14, figs. 13–17; Plate 15, figs. 8–10

1983 *Muricingulatisporis* sp. Baldoni and Archangelsky, p. 63, pl. 3, figs. 12–15.

**Diagnosis.** Spores radial, trilete, biconvex, the distal surface strongly arched. Amb convexly subtriangular to subcircular. Sclerine 4–6  $\mu\text{m}$  thick, stratified. Innermost layer thin (c. 0.75  $\mu\text{m}$  thick), homogeneous, sometimes partially separated from thicker sculptine. Sculptine 3–5  $\mu\text{m}$  thick, comprising outer, thin (0.5  $\mu\text{m}$ ), scabrate layer that overlies prominently sculptured, cingulate layer. Cingulum 7–8  $\mu\text{m}$  wide, semicircular in section; pierced by a narrow, internal, hollow duct that circumscribes cingulum's inner margin in equatorial plane. Distal sculpture of sinuous muri and occasional verrucae that have expanded, rounded crests (i.e. clavate-like in profile); elements 2–6  $\mu\text{m}$  wide, 4–6  $\mu\text{m}$  high, anastomose or freely terminate to form rugulate or rugulo-reticulate surface pattern. Lumina sinuously elongated (2–10  $\mu\text{m}$  wide, 5–20  $\mu\text{m}$  long), largest about distal pole. Proximal contact areas each with raised, flat-topped pad triangular in basal outline; pads sometimes with central lacunae or composed of discrete or partially fused muri and verrucae. Laesurae straight, extend to inner margin of cingulum, and enclosed within membraneous lips.

**Dimensions.** Overall equatorial diameter 48 (56) 68  $\mu\text{m}$ ; spore-cavity diameter 36 (44) 54  $\mu\text{m}$  (20 specimens); polar diameter 35, 40  $\mu\text{m}$  (2 specimens).

**Holotype.** Y.4854, Plate 14, figs. 13–16. Distal polar aspect. Equatorial diameter 58  $\mu\text{m}$ ; cingulum width 8  $\mu\text{m}$ . Proximal pads with central lacunae. Exine 4  $\mu\text{m}$  thick; muri 4–5  $\mu\text{m}$  wide, sinuous, with expanded crests. Laesurae 23  $\mu\text{m}$  long.

**Type locality.** James Ross Island, Antarctic Peninsula. Sample 8665, east side of Lachman Crags, Campanian.

**Etymology.** Latin *botulus*, sausage; Latin *forma*, shape.

**Remarks and comparison.** Except for their smaller size, the specimens described and figured by Baldoni and Archangelsky (1983) as *Muricingulatisporis* sp. are considered morphologically identical with *C. botuliformis* sp. nov. In possessing rugulo-reticulate sculpture, the species resembles *C. archangelskyi* but is readily distinguishable in having broader and higher muri, a wider cingulum, and coarser surficial sculpture of grana. *Cyatheacidites* sp. 2 of Kotova (1983, p. 889; pl. 7, figs. 5–7) is distally verrucate.

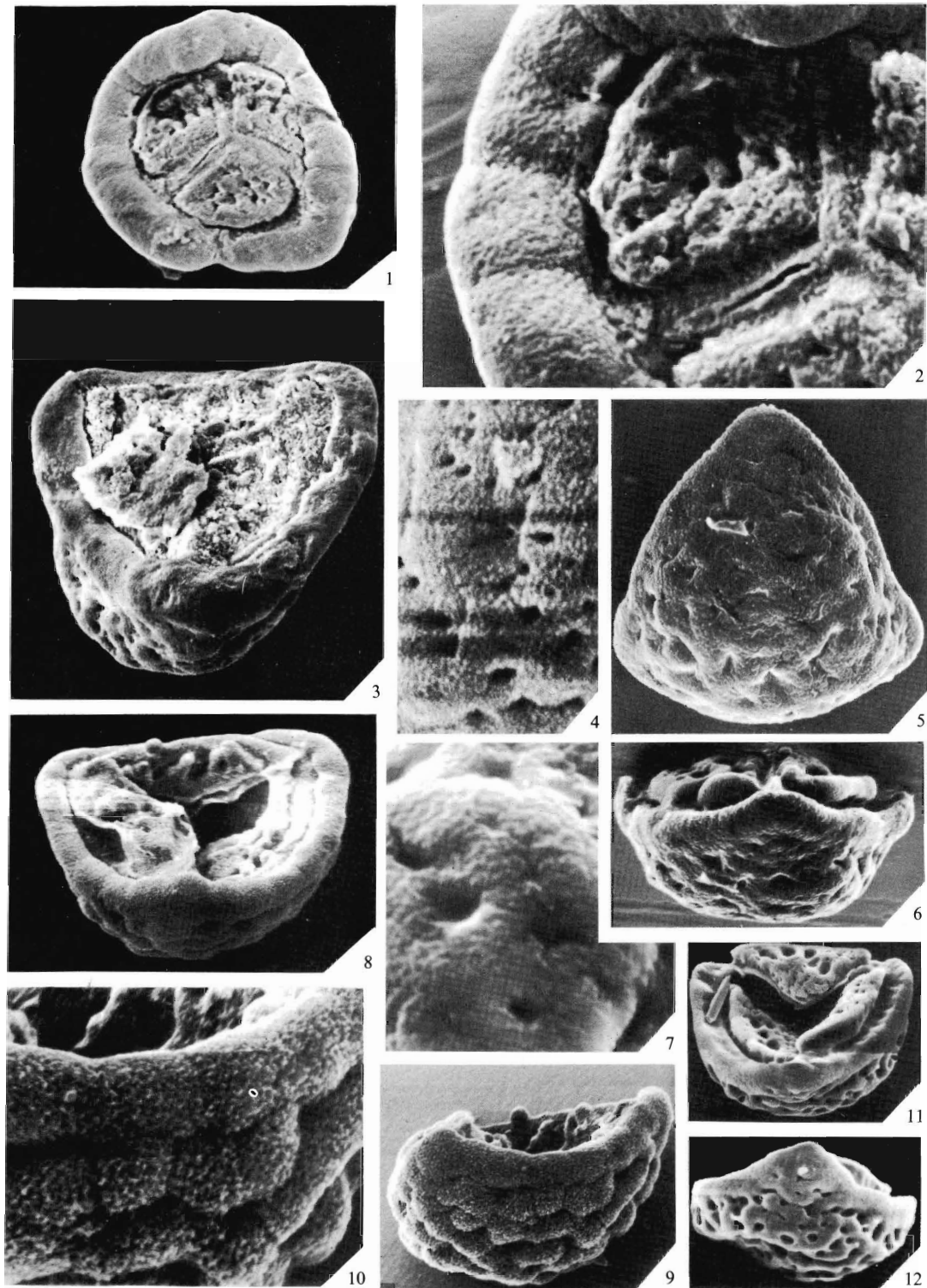
EXPLANATION OF PLATE 15

All figures  $\times 1000$  unless otherwise specified.

Figs. 1–7. *Cyatheacidites annulatus* Cookson ex Potonié 1956. 1 and 2, proximal surface and proximal sculptural detail ( $\times 2500$ ); Kerguelen Island, Waterfall Gorge, sample 85a; B411/S2, 033/0, P181690. 3 and 4, lateral view and distal sculptural detail ( $\times 2500$ ); locality as figs. 1 and 2; B411/S2, 032/4, P181691. 5–7, distal and lateral views, and distal sculptural detail ( $\times 2500$ ); James Ross Island, c. 1 km north of Lewis Hill, sample D3006.2 (Whisky Bay Formation); X222/S1, O38/3, Y.4856.

Figs. 8–10. *C. botuliformis* sp. nov. Off-polar and lateral views and disto-equatorial sculptural detail ( $\times 2500$ ); James Ross Island, c. 1 km north of Lewis Hill, sample D3006.2 (Whisky Bay Formation); X222/S1, M38/3, Y.4857.

Figs. 11 and 12. *C. archangelskyi* nom. nov. Off-polar and lateral views; James Ross Island, c. 1 km north of Lewis Hill, sample D3006.2 (Whisky Bay Formation); X222/S1, N39/3, Y.4858.



*Distribution.* ANTARCTIC PENINSULA: Early Albian–Cenomanian and Santonian–Campanian, James Ross Island.

SOUTH AMERICA: Berriasian–Valanginian, Magallanes Basin, southernmost Argentina and Chile (Baldoni and Archangelsky 1983; for dating see Riccardi 1977; Thomson 1982; Archangelsky *et al.* 1984).

## DISCUSSION

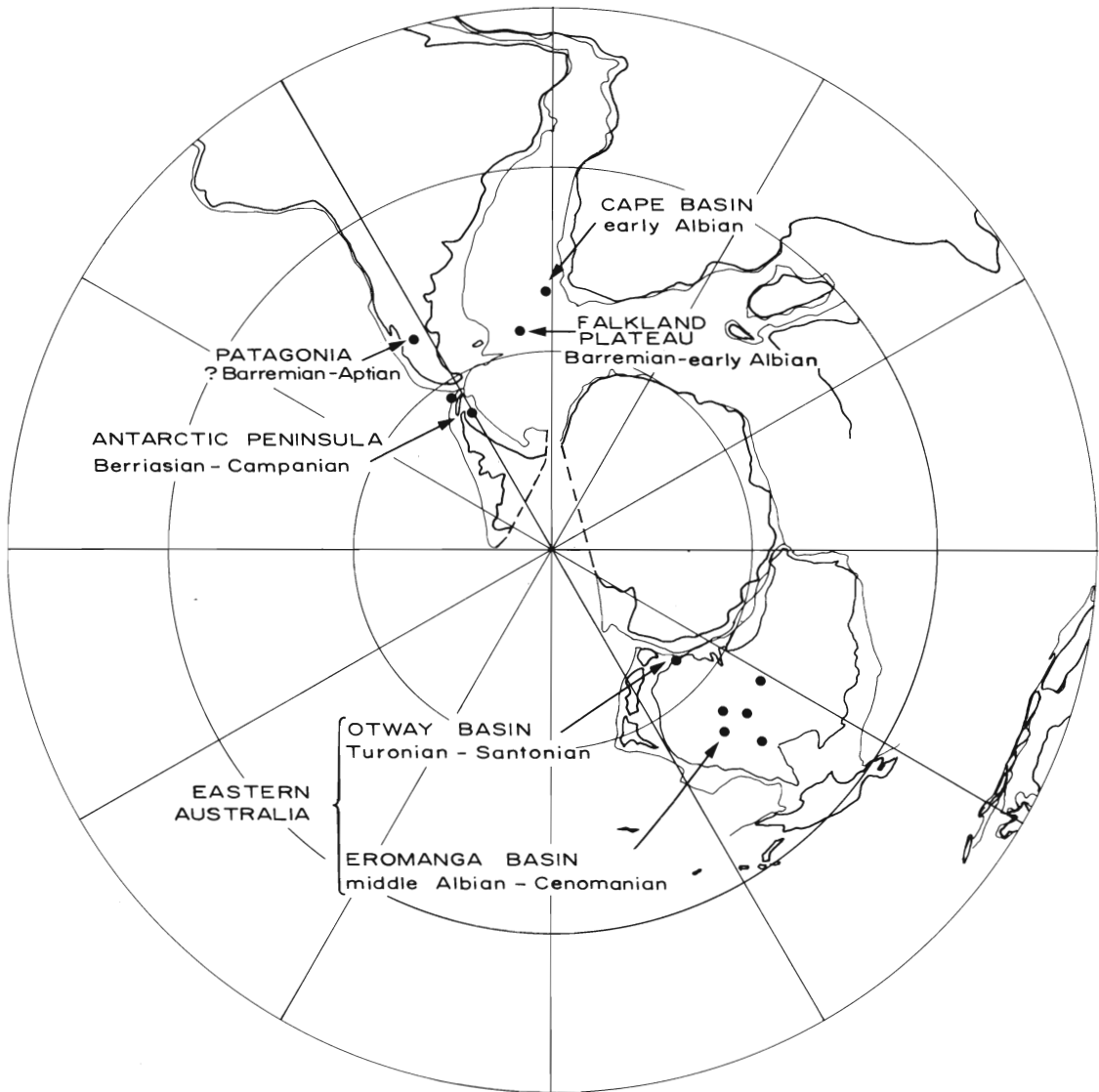
The present study demonstrates that *C. annulatus* is morphologically consonant with spores of the 'tree' fern *L. quadripinnata*. In size, wall thickness, and form and extent of the proximal protuberances, there are minor differences; these possibly relate to differing preparatory procedures, fossilization effects or to the small, and hence biased, sampling of the extant spores. Nevertheless, the set of morphological attributes comprising broad cingulum, distal foveolae, prominent protuberances on the contact faces, and finely scabrate surficial sculpture—regarded by Gastony and Tryon (1976) as peculiar to *L. quadripinnata* spores—implies a related origin of *C. annulatus*. The similarly constructed spores of *C. archangelskyi*, *C. botuliformis*, *Cyatheacidites* sp. 1 and *Cyatheacidites* sp. 2 of Kotova (1983), all differing only in distal sculptural detail, are also considered as allies of *Lophosoria*.

This evidence implies a broad austral distribution during the Cretaceous and Tertiary of *Lophosoria* as compared to its present-day restriction to southern and central America. Diversification during the Cretaceous is also indicated by the occurrence of several morphotypes of *Cyatheacidites*; of these, the widely distributed *C. annulatus* has the greatest stratigraphic range with a continuum of spatially disjunct records from the Neocomian to the latest Tertiary in southern Gondwanan regions (see text-figs. 3–5). A review of the geographic distribution with reference to time and postulated continental movements would be expected to provide information on the timing and centre of origin and subsequent migration of the plants that produced *Lophosoria*-like spores. The composition and palaeoecology of associated plant communities may also be inferred from the spore-pollen assemblages containing *Cyatheacidites*. Inferences drawn from these data must be treated with caution since there is as yet only sketchy knowledge of the Cretaceous–Tertiary spore-pollen successions in each of the component land masses of the former southern Gondwana assembly. For instance, little is known of middle to Late Cretaceous assemblages of Western Australia and southern South America and few data exist on Cretaceous palynofloras from eastern Antarctica. Late Cretaceous records from southern South Africa and many of the southern deep sea drilling sites are also meagre. Similarly for the Tertiary there are major gaps in the floral records of southern South America, Antarctica, Western Australia, and the intervening oceanic regions. A further limitation relates to the precision and basis of dating of disparate sequences. Age evidence based on long distance correlation of one or several 'key' spore/pollen species may be suspect and, in a synthesis of this nature, uncritical acceptance of spore/pollen-based datings merely begs the question. First appearances and ranges of 'key' species or indeed associations are possibly indicative of particular environments or plant habitats which in disparate geographic areas may not be coeval.

Moreover, the absence of spore-pollen taxa in a sequence may not necessarily signify extinction of the parent plant within the region. With fluctuations in base-level and/or climate, plant communities may respond by latitudinal or altitudinal migration away from the depositional site. Under these circumstances, spores with low dispersal capability shed by plants with a preference for dry-land habitats may escape fossilization.

### *Temporal and Spatial Distribution of Cyatheacidites*

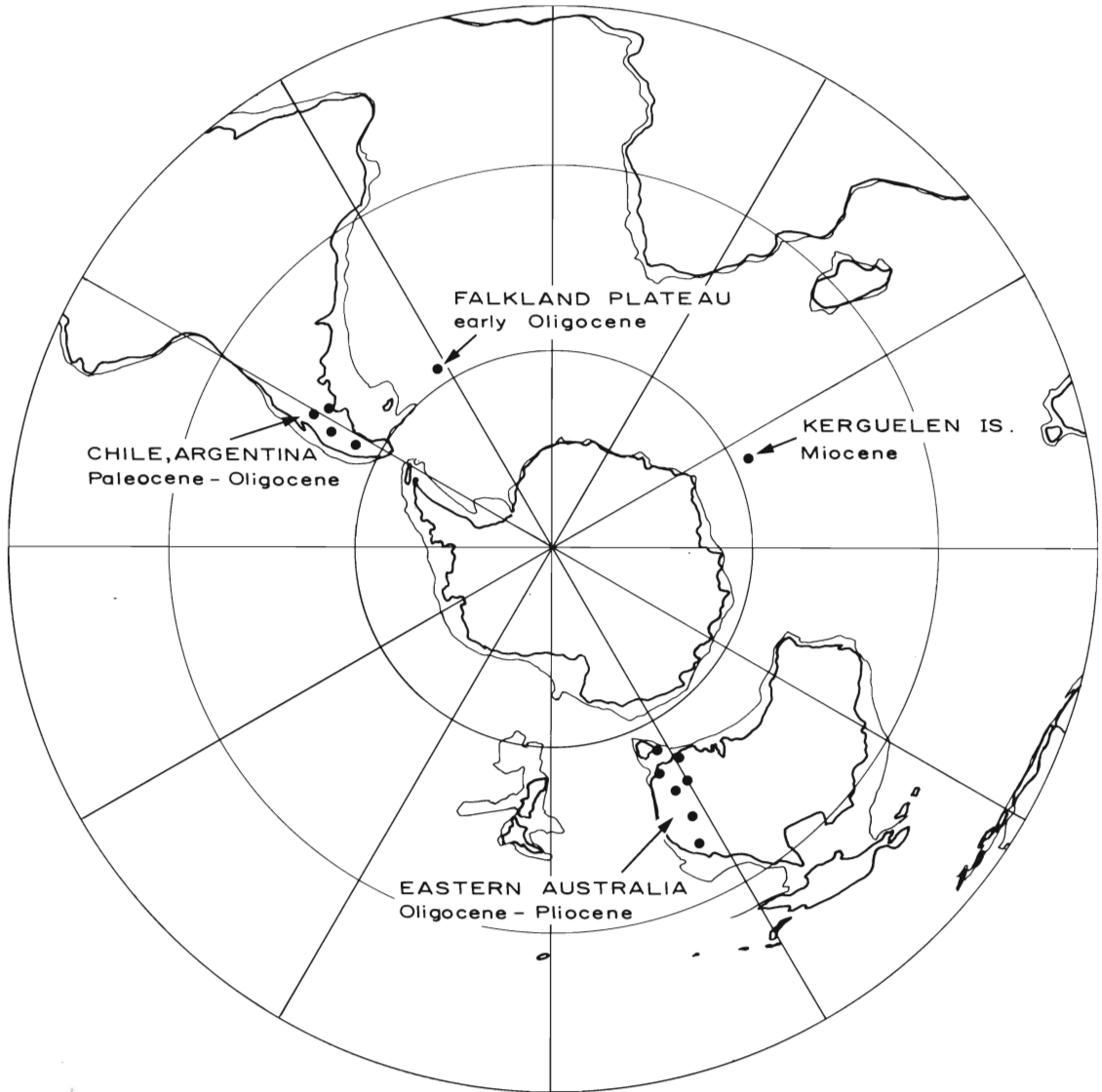
Except for a Pleistocene–Holocene record from Colombia (van der Hammen and Gonzales 1960), *Cyatheacidites* is known only from southern Gondwanic regions. The Cretaceous and Tertiary plots (text-figs. 3 and 4) denote two distribution regions diametrically opposite the present South Pole. Oldest occurrences are in the Western Hemisphere, in southern South America, the Antarctic Peninsula, and on the Falkland Plateau. It is here, too, that the genus has greatest diversity, being represented by up to five distinct morphotypes. Of these *C. annulatus* appears earliest in the Neocomian of the Antarctic Peninsula (Askin 1983) and the Falkland



TEXT-FIG. 3. Cretaceous distribution of *Cyatheacidites annulatus* Cookson ex Potonié 1956. Map is South polar Lambert equal-area for the earliest Cenomanian (adapted from Smith *et al.* 1981, Map 28, with modification after De Wit 1977).

Plateau (Kotova 1983); in southern South America the incoming of *C. annulatus*, *C. archangelskyi*, and *C. botuliformis* is also dated as Neocomian (Archangelsky and Gamero 1965, 1966a; Baldoni and Archangelsky 1983; Archangelsky *et al.* 1984).

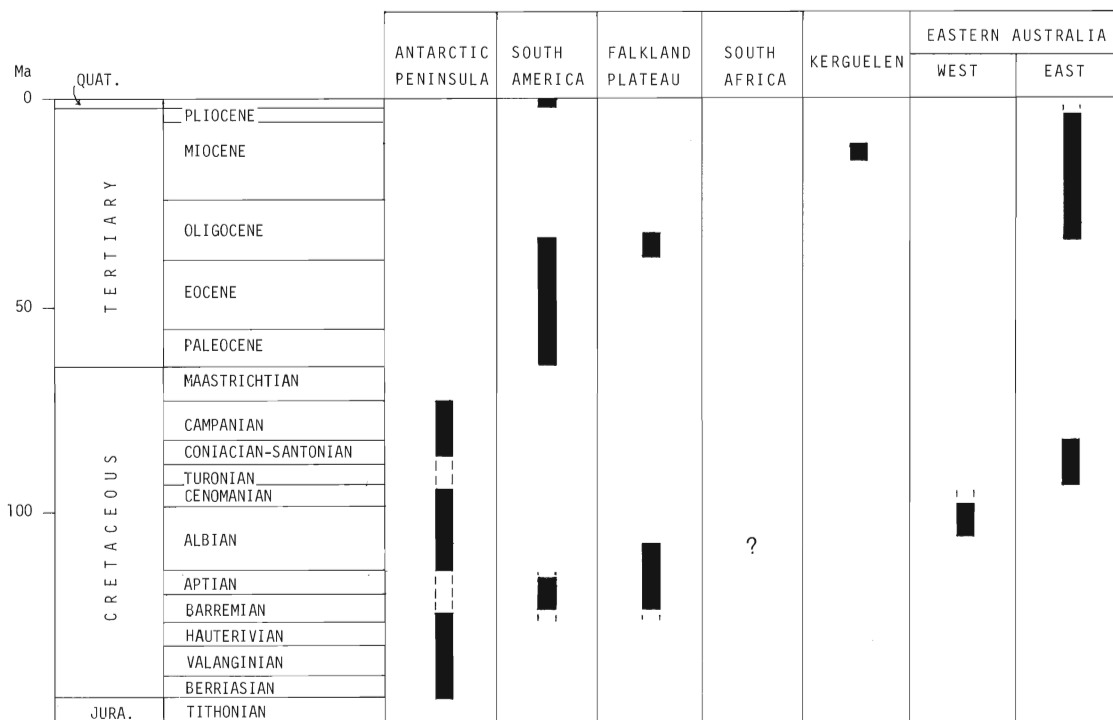
The Antarctic, Livingston and Snow Islands material studied by Askin (1983) includes marine outcrops of the Byers Formation from which Tithonian, Berriasian, and Valanginian invertebrate faunas have been recorded (see Smellie *et al.* 1980). According to Askin, the oldest occurrence of *C. annulatus* is associated with a Berriasian fauna and the dinoflagellate *Hystrichogonyaulax serrata* (Cookson and Elsenack) Stover and Evitt, which, in Australia, has a Tithonian-Berriasian range (Helby *et al.* in press). Stratigraphically higher records are from sediments that overlie Valanginian faunal occurrences; associated dinoflagellates include



TEXT-FIG. 4. Tertiary distribution of *Cyatheacidites annulatus* Cookson ex Potonié. Map is South polar Lambert equal-area for the late Eocene (adapted from Smith *et al.* 1981, Map 16).

*Aptea attadalica* (Cookson and Elsenack) Davey and Verdier, a species that Helby *et al.* (in press) accord a Hauterivian–early Albian range in Australia. Collectively, the faunal and dinoflagellate evidence indicates that the range of *C. annulatus* observed by Askin is Berriasian to at least Hauterivian (see text-fig. 5). A range into the Barremian was argued by Askin on the basis of long-distance spore correlation (of *C. annulatus* and *Polypodiaceoisporites elegans* Archangelsky and Gamarro) with the terrestrial Baquero Formation in Patagonia; as discussed below and noted above, such correlation on cryptogam spores may not be reliable for age assessment, and hence Askin's Barremian dating must not be treated unreservedly. Elsewhere on the Antarctic Peninsula, on James Ross Island, the species ranges from early Albian to at least Campanian. The specimens documented herein and by Dettmann and Thomson (in press) are from a collection of outcrop samples dated from associated marine faunas and dinoflagellates (Dettmann and Thomson, in press) as early Albian to





TEXT-FIG. 5. Summarized stratigraphic and geographic distribution of reported occurrences of *Cyatheacidites annulatus* Cookson ex Potonié and *Lophosoria quadripinnata* (Gmel.) C. Chr. spores. Time scale after Harland *et al.* (1982). Broken lines indicate inferred and/or unconfirmed age-ranges; ? indicates tentative record.

Cenomanian and Santonian to Campanian (see text-fig. 5); sediments of Turonian and Coniacian age were not identified in the material studied. Two other species of *Cyatheacidites* occur in Antarctic Peninsula sediments: *C. archangelskyi* in early Albian to Cenomanian and Santonian to Campanian of James Ross Island and as remanié in Holocene sediments of the Weddell Sea (Truswell 1983); and *C. botuliformis* in early Albian to early Cenomanian and Santonian to Campanian of James Ross Island.

In the Magallanes Basin, southernmost Chile and Argentina, *C. botuliformis* occurs in the Springhill Formation (dated as Berriasian on the basis of ammonites: Riccardi 1977; Thomson 1982). To the north, in southern Argentina, Cretaceous *Cyatheacidites* was initially documented as *C. tectifera* (= *C. annulatus*) and *M. annulatus* (= *C. archangelskyi*) by Archangelsky and Gamarro (1965, 1966a) from the terrestrial Baquero Formation, dated as Barremian–Aptian solely on plant fossil evidence. The stratigraphical distribution of these two species was later detailed by Archangelsky *et al.* (1984; see also Pöthe de Baldi and Ramos 1980) from neighbouring areas in several, essentially non-marine, subsurface sequences in which *C. archangelskyi* appears first, and *C. annulatus* second. Both species and *C. botuliformis* have stratigraphical significance with reference to the palynological zones defined by Archangelsky *et al.* (1981, 1984). Zone-datings were largely from ‘mean-age’ analyses of spore-pollen taxa documented outside Argentina, from sparse associated dinoflagellate evidence (Seiler 1979; Archangelsky and Seiler 1980), and from spore-pollen correlation into the marine, faunally dated sequences of the Magallanes and Neuquen Basins. The ranges given for the species, viz. *C. botuliformis*—Berriasian–Valanginian, *C. archangelskyi*—Valanginian–Aptian, and *C. annulatus*—Barremian–Aptian, cannot be regarded as unequivocal; detailed analyses of associated dinoflagellates will be important in this regard. Nevertheless, it seems clear that *C. annulatus* has later inceptions in Argentina than in Antarctica, and that possible allies of *Lophosoria*, as represented by *C. botuliformis*, were established in southernmost South America during earliest Cretaceous, Berriasian, time. Numerous Tertiary records exist of *C. annulatus* from southern South America, many in marine strata. In Argentina the species is known from the Palaeocene and Eocene (Archangelsky 1972, 1973a, b; Petriella and Archangelsky 1975; Gamarro and Archangelsky 1981),

and in Chile from the Eocene and early Oligocene (Cookson and Cranwell 1967; Fasola 1969). To the north, in the eastern Cordillera of Colombia, van der Hammen and Gonzales (1960) reported spores similar to *L. quadripinnata* from a radiocarbon-dated late Pleistocene–Holocene lake sequence.

On the Falkland Plateau, Site 511, *C. annulatus* occurs consistently in a section (495–530 m) dated as Barremian–early Albian on rich and varied nannoplankton and invertebrate evidence (Wise 1983; Jeletzky 1983). A further record is at 547–548 m, regarded as Barremian on stratigraphic and scant planktic foraminiferal data (Krasheninnikov and Basov 1983; Jeletzky 1983); Goodman and Millioud (in Ludwig *et al.* 1983) suggested a Late Jurassic age on the basis of the dinoflagellate *Endoscrinium luridum* (Deflandre) Gocht which, however, could be reworked (Basov *et al.* 1983) across the hiatus between the Barremian and underlying Late Jurassic section. Three other species of *Cyatheacidites* have Cretaceous occurrences at Site 511 and all have first appearances stratigraphically above that of *C. annulatus*. *C. archangelskyi* ranges from Barremian or early Aptian to early Albian, and both *Cyatheacidites* sp. 1 and *Cyatheacidites* sp. 2 of Kotova (1983) from late Aptian to early Albian. All ranges quoted here and in the species distribution records are linked to the faunal evidence. They differ somewhat from Kotova's ranges as she used spore-pollen evidence exclusively to date her Site 511 assemblages. Her Assemblage III, containing initial appearances of *C. archangelskyi*, *Cyatheacidites* sp. 1, and *Cyatheacidites* sp. 2, is in fact of Barremian or Aptian–early Albian age, not entirely early Albian. Spore-pollen contents of the overlying mid to Late Cretaceous marine section penetrated at Site 511 are unreported. However, from the early Oligocene marine section, Bratzeva (1983) recorded *C. annulatus* (as *Cyatheacidites* sp. 1 and possibly *Cyatheacidites* sp. 2) in assemblages that contain an admixture of Palaeozoic, Mesozoic, and Tertiary taxa. Bratzeva argued that the better-preserved Tertiary forms are *in situ*, not reworked from older early Tertiary sediments; Goodman and Ford (1983) did not report reworking in associated dinoflagellate assemblages.

At nearby Site 327A, Harris (1977) reported, without illustration, *Cyatheacidites* from core 22 which contains coccoliths of the *Parhabdolithus angustus* Zone of middle Aptian to early Albian age (see Barker *et al.* 1977, p. 35). Harris suggested an Aptian age largely on spore-pollen evidence; Hedlund and Beju (1977) an Albian age on the basis of *Spiniferites cingulatus* (Wetzel) Lentin and Williams, a dinoflagellate now known to range into the Neocomian in the Southern Hemisphere (Morgan 1980). Bair and Hart's (1984) Albian determination is similarly based on inconclusive evidence. Underlying sediments are early Aptian according to coccolith and dinoflagellate determinations (Barker *et al.* 1977, p. 35; Hedlund and Beju 1977; Bair and Hart 1984).

At Site 361 in the Cape Basin, offshore South Africa, McLachlan and Pieterse (1978) recorded *C. annulatus* (as *C. tectifera*) from core 28 which is early Albian according to nannoplankton evidence (Proto Decima *et al.* 1978). Davey (1978) asserted a late Aptian age on dinoflagellates, several species of which he regarded as confined to the Aptian in France and Australia. Amongst these, *Dingodinium cerviculum* Cookson and Eisenack, *Muderongia* cf. *staurota* Sarjeant, and *M. tetracantha* (Gocht) Alberti have early Albian occurrences in marine, faunally dated sequences in Australia and Antarctica (Morgan 1980; Helby *et al.* in press; Dettmann and Thomson, in press), and the Site 361 assemblage is more consistent with an early Albian dating. McLachlan and Pieterse's record, however, must be regarded as provisional as the poorly focused specimen (pl. 3, fig. 14) does not clearly display the critical proximal and distal detail.

In the southern Indian Ocean, *C. annulatus* is known only from the Kerguelen Islands (Cookson 1947; Mechkova 1969). Here it occurs in lignites associated with basalts isotopically dated as Miocene (Nougier 1970).

In Australia *Cyatheacidites* has Cretaceous and Tertiary occurrences in eastern Australia, being represented solely by *C. annulatus*. It is as yet unrecorded amongst the scarce palynological data published from Cretaceous–Tertiary sequences of Western Australia. In eastern Australia, first appearances of *C. annulatus* are demonstrably diachronous from west to east, occurring first (middle Albian) in western regions of the Eromanga Basin and later (Turonian) in the Otway Basin of south-eastern Australia. Within the Eromanga Basin's Early to middle Cretaceous sequence, documented first appearances are in marine mudstones containing middle Albian foraminiferal and dinoflagellate assemblages of the *Hedbergella planispira* Zone and the *Canningiopsis denticulata* Zone respectively (Haig 1979; Helby *et al.* in press). The species ranges to the top of the overlying marine to terrestrial sequence that is truncated by a widespread unconformity; the Cenomanian dating of the uppermost terrestrial sediments is largely on spore-pollen evidence. To the south-east, in the Otway Basin sequence that virtually spans the Cretaceous, *Cyatheacidites annulatus* first appears in marginal marine sediments containing sparse dinoflagellates and arenaceous Foraminifera indicative of Taylor's (1964, 1971) Zonule B of Turonian age. Later occurrences are in the basal part of the succeeding foraminiferal Zonule A (Taylor *loc. cit.*) and equivalent dinoflagellate zone, the *Odontochitina porifera* Zone of Senonian, Santonian age (Taylor 1971; Dettmann and Playford 1969; Helby *et al.* in press).

In the Otway Basin, and the more easterly Gippsland Basin, *C. annulatus* is missing from succeeding Campanian through Eocene palynofloras, reappearing in the late early Oligocene and ranging into the Pliocene (Stover and Partridge 1973; Harris 1971). Its second incoming is consistent and apparently synchronous with reference to the well-defined planktic foraminiferal zones (see Abele *et al.* 1976) and thus serves as a useful biostratigraphic marker delineating the *Proteacidites tuberculatus* Zone (Stover and Partridge 1973) and equivalent *C. annulatus* Zone (Harris 1971).

To the north, in New South Wales, *C. annulatus* is thought to have a similar early Oligocene to Pliocene range, but occurs only sporadically in the largely non-marine sequences (Martin 1973, 1981; Harris and Morgan 1976). In Tasmania the species occurs in marine Miocene sediments (Harris 1971) and in a fluvial sequence that underlies early-middle Miocene basalts (Hill and Macphail 1983). The Queensland record by Cookson (1957) is probably early Miocene; the enclosing lignitic sediments underlie basalts dated as *c.* 22 m.y. (pers. comm. N. C. Stevens; see also Ewart *et al.* 1977).

From the above, it is evident that association of *C. annulatus* with *Lophosoria* implies a broad southern Gondwanic distribution of the latter during the Cretaceous and Tertiary (see text-figs. 3-5). Inception is dated as early Neocomian, Berriasian, for the Antarctic Peninsula. The later, Barremian, appearances on the Falkland Plateau and in Patagonia may imply early migration; the evidence for this needs to be supported by further comprehensive palynological documentation from well-dated pre-Barremian sequences within these regions. A possible spread to Site 361, offshore South Africa, during the early Albian is implied by a single, albeit tentative, record. Palaeogeographic maps (text-fig. 3; see also McLachlan and Pieterse 1978; Farquharson 1983) indicate that Site 361, Site 511, Site 327A, Patagonia, and the Antarctic Peninsula were in close proximity adjoining the Early Cretaceous euxinic sea of the embryonic South Atlantic Ocean.

Evidence for migration, possibly in an easterly direction, is indicated by the eastern Australian data. Here introductions were earlier (mid Albian) in western regions (Eromanga Basin) and later (Turonian) in the east (Otway Basin). It is noteworthy that no Cretaceous reports exist of *C. annulatus* from either the more easterly Gippsland Basin or the then cojoined New Zealand region (see text-fig. 3; Frakes *et al.* in press, maps 1-12).

Diversification of *Cyatheacidites* appears to have occurred soon after origination and was restricted to the 'cradle area', according incidentally with Simpson's (1953) evolutionary model. Of the Cretaceous species, only *C. annulatus* appears to persist into the Tertiary. In southern South America, a Palaeocene through early Oligocene range has been established. At similar latitudes, on the Falkland Plateau, the species may extend into the Oligocene; to the east, in the southern Indian Ocean, *C. annulatus*-producing plants were established on the Kerguelen Islands in Miocene times.

In eastern Australian southerly sequences there is a seemingly enigmatic absence of *C. annulatus* from Campanian to earliest Oligocene. This cannot be attributed to paucity of data, because the palynological succession of the latest Cretaceous to Early Tertiary has been rather thoroughly investigated. Perhaps regional extinction (in the Santonian) was followed eventually (in early Oligocene) by reintroduction during a second migratory phase. Alternatively, there may have been local displacements of the plant communities in response to changing ecological circumstances in the southern Australian region.

### *Palaeoecology*

An appreciation of the palaeoecology of *Cyatheacidites*-producing plants may be gained from knowledge of associated vegetation and the types of environments they inhabited. Cofossilized plant remains provide a perspective of the vegetation; the enclosing sediments reflect the interaction of physiographic/biotic processes at and around the depositional site. The vegetational interpretations must, however, be viewed with caution; they may be biased to the fortuitous set of circumstances involving dispersal of plant organs from within the watershed of the depositional site. The morphology of *Cyatheacidites* argues against long-distance wind dispersal and hence its presence in 'upland' vegetation remote from the depositional site is unlikely to be recorded; yet wind-borne spores/pollen from associates of the same vegetation may be preserved. The vegetational inferences are further constrained by incomplete published listings and by the inexactitude of assessing affinities of associated spore-pollen taxa. The palaeoecological interpretations given below and on Table 1 are admittedly tentative and have been drawn from broad assemblage characteristics coupled with generalized palaeoenvironmental and lithologic features of the enclosing sediments. Detailed lithotope/assemblage analyses have not been attempted (and indeed are mostly not feasible) from available published data.

*Early Cretaceous*. The oldest (Berriasian–Hauterivian or possibly Barremian) reported occurrences of *Cyatheidites* from the Shetland Islands, Antarctic Peninsula, are in marine deltaic and non-marine strata. The palynofloras contain frequent *Podocarpidites*, *Alisporites*, and *Callialasporites* associated with common and diverse filicean, lycophytic and moss spores; *Cyatheidites* is more common in the younger, Valanginian–Barremian assemblages that occur in terrestrial sediments (Askin 1983). The James Ross Island, early Albian, assemblages (Dettmann and Thomson, in press) are similar, except for lower frequencies of *Callialasporites* and lycophytic spores, more common *Microcachrydites antarcticus* and the presence of monosulcate angiospermous grains (*Clavatipollenites*). These occur in marine sediments deposited in submarine fan and slope apron settings in a back-arc basin (Thomson 1984). The palynological data thus indicate a vegetation with a strong component of the Podocarpaceae associated with bisaccate-producing pteridosperms. Diverse ferns including the Cyatheaceae, Dicksoniaceae, Osmundaceae, Schizaeaceae, Matoniaceae, Gleicheniaceae, and Pteridaceae, together with varied lycopods of the *Lycopodium clavatum*-type and a small bryophytic component, were also represented. Contributions from the Cheirolepidaceae (manifested by *Classopollis*) were low, and in the early Albian angiosperms were represented.

Megafloras reported from near Askin's Snow Island localities confirm the presence of ferns, cycadophytes, and conifers (Herández and Azcárate 1971). A more vivid picture of Early Cretaceous Antarctic vegetation is given by Jefferson (1983) in a preliminary account of megafloras from Alexander Island on the western side of the Peninsula. Here foliage of conifers, cycads, and ferns and occasional bryophytes and *in situ* wood of forest trees are preserved in a fluvial/lacustrine sequence thought to be of Barremian–early Albian age. Jefferson (1983, fig. 3) envisaged an open-canopied forest of notophyll (broad-leaved) podocarp-like trees with undergrowth of taeniopterids and ferns. Flood plain and lake margin communities of Ginkgoales and ferns allied to the Osmundaceae, Dicksoniaceae, and Matoniaceae are implied from facies associations of foliage remains. To Jefferson, the megafossil evidence, notably leaf architecture and wood structure, implied a warm temperate pluvial climate, despite the postulated high latitudes (70° S.) of the region during the Early Cretaceous. Axelrod (1984, 1985) argues that growth patterns are consistent with high polar and subpolar latitudes and rejects the necessity for a year-round photoperiod and a consequent reduction in the earth's obliquity as postulated by Jefferson (1983), Douglas and Williams (1982), and Williams and Douglas (1985). There are no palynological data from Alexander Island, but the strong lycophytic element of the *L. clavatum*-type in the Shetland and James Ross Islands palynofloras points to a cool-temperate moist climate. That element is well represented in the tropics, but is confined there mainly to high mountainous regions; at higher latitudes it more commonly occupies habitats at or near sea level (Tryon and Tryon 1982). The fern component reflected in the palynofloras also implies a temperate climatic regime.

In the Magallanes Basin, southernmost South America, a possible ally of *Lophosoria*, *Cyatheidites botuliformis*, occurs in Berriasian marine and terrestrial sequence from which plant megafossils and microfossils have been recorded (Archangelsky 1976; Baldoni 1979; Gamarro and Baldoni 1978; Baldoni and Archangelsky 1983). The flora was evidently similar to that of the Antarctic Peninsula, with strong representation of podocarpacean/araucarean conifers, the Bennettitales, and ferns. However, contrasting with coeval Shetland Islands palynofloras, hepatic spores and *Classopollis* are more frequent, and lycopod spores are neither common nor diverse. The evidence implies humid conditions (Baldoni and Archangelsky 1983), and a vegetation primarily of rain forest with minor development of sclerophyllous communities.

In more northerly regions of Santa Cruz Province and adjacent areas of Chubut, occurrences of *Cyatheidites* are within a mostly terrestrial sequence containing rich megafloras (Archangelsky 1963, 1965, 1967) and diverse spore-pollen assemblages (Archangelsky and Gamarro 1965, 1966a, b, c, 1967a, b; Archangelsky *et al.* 1981, 1983, 1984). These indicate a flora rich in pteridosperms, particularly the Bennettitales, strong representation of the Cheirolepidaceae, and varied podocarpacean/araucarean conifers. Lycopods appear to be sparse in the spore-pollen assemblages that indicate a highly diversified fern component of cyatheaceous, osmundaceous, schizaeaceous, and pteridaceous allies. Hepatic spores infer derivation from the Ricciaceae, Sphaerocarpaceae, and Anthocerotae, and are especially diverse in the older portion of the sequence referred to the 'Interulobites–Foraminisporis' Zone of Archangelsky *et al.* (1984). Within this zone occur occasional algal microfossils including *Microfosta evansii* Morgan, which in Australia is associated with shallow-water lake and marginal marine sediments. In the succeeding 'tectifera–corrugatus' Interval, algal microfossils include *Schizosporis reticulatus* Cookson and Dettmann of freshwater, chlorophycean affinity, and occasional dinoflagellates suggestive of ephemeral marine influence. Near the top of the sequence, in the 'Antulsporites–Clavatipollenites' Zone, sulcate angiospermous pollen occur infrequently. The presence of *Anemia*-like (*Appendicisporites* and some *Cicatricosisporites*) and *Lygodium*-like (*Concavissimisporites*) spores, common *Classopollis*, and infrequent coniferous saccate pollen imply a warmer climatic regime than existed to the south in the Magallanes Basin/Antarctic Peninsula region. The Santa Cruz/Chubut plant fossils, which accumulated landward

of the embryonic South Atlantic coast, reflect a mosaic of plant communities with dry-zone elements, including cheirolepidacean gymnosperms and possibly some schizaeaceous/pteridaceous ferns occupying dry and/or coastal habitats adjacent to more mesic conifer-fern-bennettitalean communities. From cuticular evidence, Archangelsky (1967) inferred seasonality, support for which may be provided by conspicuous palynofloral representation of the Ricciaceae and Sphaerocarpaceae. Members of these groups today occupy seepage areas, ponds, and river banks, particularly in semi-arid and desertic regions (Scott 1982).

The Site 511, Falkland Plateau, Early Cretaceous sequence is marine, comprising Barremian to late Aptian coquinoid siltstones and mudstones intercalated within Barremian and early Albian claystones (Wise 1983). Barremian to early Aptian palynofloras are dominated by *Classopollis* with common *Vitreisporites*, infrequent araucarean/podocarpacean pollen, and rare fern spores (Kotova 1983). Here the Cheirolepidaceae may have occupied coastal, tidally influenced sites as well as dry inland areas under a warm climatic regime. In the late Aptian to early Albian assemblages, which contain initial appearances of angiospermous pollen, *Classopollis* remains dominant, but frequencies decline; and there is increased diversity and numerical representation of *Cyatheidites* and other fern spores. This microfloral change is associated with lithological and faunal changes that accompanied a shift from deposition in the inner neritic zone to the outer neritic or upper bathyal zone in the 'Falkland' sea (Jeletzky 1983) prior to the initiation of free exchange with the Indian Ocean (Basov and Krashennikov 1983). The spore-pollen associations imply diversification of habitats. Angiosperms were introduced as were hydropterid ferns (indicated by *Crybelosporites*) which prefer standing non-saline water or intermittently wet situations. The Gleicheniaceae, reflected by diverse spore taxa, may have ranged into open heathlands and areas wooded by podocarps and araucarean conifers. *Cyatheidites*-producing ferns diversified within this range of habitats.

At nearby Site 327A, *Cyatheidites* is reported from sapropelic claystones with interbeds of micritic limestone of middle Aptian to early Albian age. Associated assemblages contain abundant *Classopollis*, common pteridospermous pollen and fern spores, together with occasional araucarean and podocarp pollen (Harris 1977; Bair and Hart 1984; Hedlund and Beju 1977). As for Site 511, the florule reflects a strong cheirolepidacean component together with pteridosperms and a moderately diverse fern element.

At site 361, in the Cape Basin off South Africa, the early Albian vegetation was primarily cheirolepidacean adjacent to the silled basin in which sapropelic-rich shales accumulated. Ryan *et al.* (1978) indicated a humid coastal climate and a mangrove habitat for at least some of the *Classopollis*-producing plants. Rare fern spores, including a tentative record of *Cyatheidites*, and podocarpacean/araucarean pollen reflect a small contribution from mesic dry land vegetation.

These Early Cretaceous occurrences of *Cyatheidites* are from areas bounding the euxinic sea of the embryonic South Atlantic Ocean between palaeolatitudes of *c.* 70°–55° S. *Cyatheidites* was introduced during opening of the South Atlantic, an event diachronous from oldest (Late Jurassic) in the south to youngest (mid Cretaceous) in the north (Farquharson 1983). On the Falkland Plateau, Aptian diversification of *Cyatheidites* is coincident with angiosperm inception, habitat diversification, and initial disruption of oceanic barriers.

The plant fossil data from the juvenile South Atlantic region emphasize pronounced vegetation zonation ordered across the latitudes, with temperate podocarp-like rain forests to the south (Antarctic Peninsula/Magallanes Basin) and coastal mangrove and/or xeric cheirolepidacean communities on the Falkland Plateau and the Cape Basin. Between these extremes, mesic araucarean/podocarpacean/bennettitalean forests and mangrove/xeric cheirolepidacean communities coexisted in Patagonia. *Cyatheidites*-producing ferns may have ranged into a variety of habitats, from rain forest to heathland where moisture requirements were sufficient.

The dominance of *Classopollis* on the Falkland Plateau and in the Cape Basin is especially notable. According to Vakhrameev (1981, 1982), frequencies of 50–80% would infer tropical climates, and hence a steep climatic gradient to Antarctica, a circumstance hinted at by Crame (1984) on faunal evidence. It also implies warmer Early Cretaceous climates than exist today within that latitudinal range.

For most of the early Cretaceous the Antarctic Peninsula was tempered by oceanic influences of the Pacific. Atmospheric circulation over the more northerly areas of the euxinic sea may have been irregular and influenced by a superheating effect off the adjacent continental areas. With progressive widening of the South Atlantic, oceanic influences may have lessened the climatic gradient. Increased conifer and fern representation and a reduction of the cheirolepidacean component in the late Aptian to early Albian Falkland vegetation may express some climatic moderation.

*Mid to Late Cretaceous.* By middle Albian times *Cyatheidites*-producing ferns occupied western areas of the Eromanga Basin in eastern Australia. Here there were broad, low-relief areas exposed after partial retreat of

TABLE 1. Summary of Cretaceous and Tertiary vegetation types (as inferred from spore/pollen and megafloral evidence) associated with *Cyatheacidites*-producing ferns; relationships of vegetation to inferred terrains, contemporaneous sediments, and palaeolatitudes.

Vegetation	Sediments	Terrain	Palaeolatitude
QUEENSLAND, TAMBORINE MTN. (Mioc.): temp. <i>Nothofagus</i> rain forest	Lignitic clays	Volcanism and associated uplift New England plateau	35° S.
NEW SOUTH WALES, E. MURRAY BASIN (early Oligoc.-Plioc.): temp. <i>Nothofagus</i> rain forest (replaced in Plioc. by araucarian closed forest + Compositae/grasslands) and Myrtaceae forests	Terr. clays, sands, gravels	Low relief riverine valley; marine influence in Mioc.	Mioc. 35–40° S. Oligoc. 45–50° S.
SE. AUSTRALIA, GIPPSLAND AND OTWAY BASINS (early Oligoc.-Plioc.): cool and warm temp. and subtrop. rain forests of <i>Nothofagus</i> , Cunoniaceae/ <i>Quintinia</i> , and Myrtaceae/Elaeocarpaceae. Swamps with Restoniaceae/Epacridaceae/Gleicheniaceae	Mar., marg. mar., and terr. clays, silts, and coals	Coal swamps and coastal deltas; high relief hinterland; widening of seaway between S. Australia and Antarctica	Mioc. 40–45° S. Oligoc. 50–55° S.
KERGUELEN I. (Mioc.): cool temp. podocarp/araucarian rain forest; dicksoniaceae ferns; angiosp. herbs incl. grasses, <i>Gunnera</i>	Lignites, sandstones	Volcanic activity on emergent island	55° S.
FALKLAND PLATEAU (Oligoc.): cool temp. rain forest of <i>Nothofagus</i> and Podocarpaceae; presence Myrtaceae, chenepods	Diatomaceous-radiolarian ooze	Circumpolar current established prior to opening Drake Passage	55–60° S.
SOUTH AMERICA, S. CHILE AND ARGENTINA (late Paleoc.-Oligoc.): temp. rain forests of <i>Nothofagus</i> and Podocarpaceae	Mar. and terr. muds, silts, sands, and coals	Coastal and coal swamps adjacent southern Pacific and Atlantic Oceans	55–60° S.
SOUTH AMERICA, S. CHILE AND ARGENTINA (early-late Paleoc.): mangrove, trop. rain forest, mossy forest, <i>Araucaria</i> woodland, and sclerophyll communities	Mar. and terr. muds, silts, sands, and coals	Coastal and coal swamps adjacent southern Pacific and Atlantic Oceans	55–60° S.
JAMES ROSS I. (Santon.-Campan.): temp. podocarp/araucarian rain forest; introduction <i>Nothofagus</i> ; tree and ground ferns incl. Schizaeaceae	Mar. vol./clastic clays, silts, sands	Rugged magmatic arc adjacent southern Atlantic	70° S.
SE. AUSTRALIA, OTWAY BASIN (Turon.-Santon.): rain forests as above, but less diverse ferns incl. Schizaeaceae	Marg. mar. silts, clays, sands	Initial invasion of sea into rift valley between S. Australia and Antarctica	60° S.
JAMES ROSS I. (middle Albian-Cenoman.): rain forest of podocarps/araucareans; diverse ferns; early angiosp.; some Cheirolepidaceae	Marg. mar. vol./clastic silts, sands, and conglomerates	Rugged magmatic arc adjacent southern Atlantic; volcanism and tectonism	70° S.
E. AUSTRALIA, EROMANGA BASIN (middle Albian-Cenoman.): rain forest of podocarps/araucareans + heathland/aquatic fern/hepatic communities; early angiosp.; increased Cheirolepidaceae in Cenomanian	Mar., marg. mar., and terr. muds, silts, sands, minor coals	Late Albian sea withdrawal and development of riverine system; low relief landscape	50–55° S.

JAMES ROSS I. (early Albian): temp. rain forest of podocarps/araucareans/taeniopterids; diverse ferns and lycopods ( <i>L. clavatum</i> -type); early angiosp.	Mar. volc/clastic muds and minor congl.	Magmatic arc adjacent southern Atlantic; volcanism and tectonism	70° S.
SOUTH AFRICA, CAPE BASIN (early Albian): dominantly mangrove/xeric cheirolepidacean vegetation. Provisional record <i>Cyatheacidites</i>	Organic-rich muds, silts	Initial connection Cape-Angola Basins; tectonism; rugged terrain	50° S.
FALKLAND PLATEAU (Aptian-early Albian): mangrove/xeric Cheirolepidaceae and mesic araucareans; heathland and aquatic ferns; early angiosp.	Organic-rich shales, nanochalks	Displacements in 'Falkland' sea; deposition outer neritic to upper bathyal	55° S.
FALKLAND PLATEAU (Barrem.-early Aptian): dominantly mangrove/xeric Cheirolepidaceae	Organic-rich shales and chalks	Shallow 'Falkland' sea; inner neritic/littoral deposition	55° S.
SOUTH AMERICA, SANTA CRUZ AND CHUBUT (?Barrem.-Aptian): xeric Cheirolepidaceae + mesic araucareans/podocarps/Bennettitales; diverse ferns and hepatics; early angiosp.	Terr. silts and sands.	Lake/river system inland from 'Falkland' sea	55-60° S.
SOUTH AMERICA, MAGALLANES BASIN (Bertias.): rain forest of podocarps, araucareans, Bennettitales + dry-zone Cheirolepidaceae; diverse ferns and hepatics	Mar. and lacustrine silts	Coastal lake adjacent southern 'Atlantic'	65° S.
SHETLAND IS. (Bertias.-Barrem.): rain forest of podocarps, cycadophytes, taeniopterids; diverse ferns and lycopods ( <i>L. clavatum</i> -type)	Marg. mar. and terr. volc/clastic shales and silts	Adjacent southern 'Pacific' and 'Atlantic' coasts; volcanic and tectonic activity	70° S.

the sea which had formerly (during the Aptian) inundated much of the continent, isolating two northern islands from the large conjoined southern Australia/eastern Antarctica landmass (see Frakes *et al.* in press). The middle Albian sea withdrawal was associated with profound vegetational changes involving modification to the formerly widespread podocarp/araucarean rain forests and invasion of newly exposed coastal areas by angiosperms and diverse fern/hepatic communities (Dettmann 1981). Palynofloras from marine and marginal marine argillaceous sediments deposited within the shallow middle Albian sea indicate strong representation of *Microcachrys*-like podocarps and lesser contributions from araucarean, cheirolepidacean, and pteridospermous gymnosperms. Angiosperms were sulcate- and tricolpate-producing forms, and ferns/hepatics included Schizaeaceae, Cyatheaceae, Osmundaceae, Hydropteridae, Anthocerotae, Ricciaceae, Sphaerocarpaceae, and perhaps Riellaceae. Many of the cryptogam spores may have derived from heathland and aquatic communities that colonized coastal sites. Warm temperate conditions, indicated by associated faunas (Day 1969), are consistent with the vegetational evidence.

After brief flooding by the Toolebuc Sea during late middle to early late Albian times, the sea finally withdrew and a broad riverine system developed. Palynofloras of the late Albian to Cenomanian paralic to terrestrial sequence contain abundant and varied fern and hepatic spores. Associated gymnospermous pollen are mostly podocarpacean and araucarean; *Classopollis* and angiospermous pollen are sometimes locally common, but pteridospermous pollen is infrequent (Dettmann 1981). This implies that a mosaic of plant communities, each with distinct hydrological and nutrient requirements, coexisted in the area. Refugia of podocarp/araucarean rain forest persisted and there was extensive sclerophyllous/heathland vegetation of Cheirolepidaceae and ferns. Lagoons and intermittently wet areas supported diverse hydropteridean/hepatic associations adjacent to habitats occupied by early angiosperms. This admixture of mesic, dry-zone, and aquatic vegetation is consistent with warm temperate climates; within this realm, *Cyatheidites*-producing ferns may have ranged between mesic forest and open heathland habitats.

*Cyatheidites* has not been observed in coeval sediments of the dominantly fluvial sequence that accumulated in the then more southerly rift valley (Otway Basin) situated between south-eastern Australia and eastern Antarctica. During Cenomanian to Turonian times the sea invaded this rift and deposition for the remainder of the Late Cretaceous was in marginal marine and marine environments. Occasional specimens of *Cyatheidites* occur within the lower Turonian to Santonian part of this sequence. Associated are, abundant gymnospermous pollen pointing to strong representation of *Microcachrys*-like conifers, *Lagarostrobos*, *Dacrydium*, and *Araucaria*. Cycad-like pollen are infrequent and *Classopollis* is virtually absent. Angiospermous pollen, including early triporate types, are represented together with cyatheaceous, gleicheniaceous, and osmundaceous fern spores. However, schizaeaceous types are rare, in marked contrast to their common occurrence in the underlying Albian to Cenomanian sequence. The palynological data imply a rain forest vegetation, composed largely of podocarp conifers with araucarias and tree ferns (Dettmann 1981) suggestive of cool to mild temperatures and high humidities.

On the Antarctic Peninsula (James Ross Island), late Albian to Cenomanian and early Senonian occurrences of *Cyatheidites* are in marine volcanoclastic sediments deposited in a back-arc basin to the east of the emergent magmatic arc (Farquharson 1983). The climax vegetation of the late Albian to Cenomanian flora appears to have been similar to that of the Eromanga Basin, eastern Australia, as evidenced by common representation of podocarpacean and araucarean pollen. *Classopollis* and both sulcate and tricolpate angiospermous pollen occur infrequently, together with abundant filicean spores indicating the presence of the Cyatheaceae, Gleicheniaceae, Schizaeaceae, Dicksoniaceae, Osmundaceae, and Pteridaceae. *Cyatheidites*-producing ferns were possibly associated with these groups within and fringing the rain forest. The rarity of hydropteridean ferns and hepatic spores possibly points to lack of suitable habitats on the rugged terrain of the source region (Farquharson 1983). This contrasts with the riverine landscape in the Eromanga Basin, where, as emphasized above, hydropteridean ferns and hepatics flourished under what was also a warm, but possibly less humid, temperate climatic regime.

During the mid. Senonian (Santonian-early Campanian) the forest vegetation of James Ross Island was possibly similar to that of the Otway Basin, south-eastern Australia. *Microcachrys*-like conifers, *Lagarostrobos*, *Dacrydium*, and *Araucaria* are indicated in the pollen record (Dettmann and Thomson, in press). Angiospermous pollen includes simple triporate, colporate, colpate, and sulcate types and there are diverse spores of cyatheaceous, osmundaceous, gleicheniaceous, schizaeaceous, dicksoniaceous, and lycophytic affinities. A temperate rain forest, with a more diverse fern component than the Otway Basin, is indicated. Moreover, on James Ross Island, occasional *Cyatheidites* occur in younger (mid-Campanian) assemblages that contain earliest occurrences of *Nothofagidites*, an association unknown from the Otway Basin Late Cretaceous sequence.

In summation, the source vegetation of microfloras associated with middle to Late Cretaceous occurrences



of *Cyatheidites* implies cool to warm temperate climates in palaeolatitudes of *c.* 70°–50° S. The parental plants possibly ranged from rain forest to heathland habitats.

*Tertiary.* Earliest Tertiary records of *Cyatheidites* are from Palaeocene to early Oligocene marine and terrestrial sequences of southern South America in Argentina and adjacent areas of Chile. For the early Palaeocene, Archangelsky (1973*b*) and Petriella and Archangelsky (1975) assumed tropical climates, a high-relief topography, and altitudinal zonation of the vegetation that comprised mangrove, tropical rain forest, mossy forest, *Araucaria* woodland, and sclerophyll communities. Within this flora, *Lophosoria* was envisaged to occur in the higher altitude, moist temperate forests of *Nothofagus* and *Araucaria*. Romero (1978), however, argued against significant altitudinal zonation and suggested that the temperate and tropical elements coexisted with a single composite vegetational community. With climatic cooling in the late Palaeocene and Eocene the tropical element was displaced by expansion of the temperate forests. A cyclic alternation of *Nothofagus* and podocarp pollen (including *Dacrydium*, *Lagarostrobos*, and *Podocarpus*) is believed to indicate an advance–retreat interplay between the two forest types in response to climatic fluctuations (Fasola 1969; Romero 1977). In the Chilean sequence, Fasola's pollen diagrams point to association of *Cyatheidites* with the gymnospermous element rather than with *Nothofagus*.

At a similar palaeolatitude, Site 511 on the Falkland Plateau, *Cyatheidites* occurs in the upper portion of a late Eocene to Oligocene sequence of siliceous radiolarian-diatomaceous oozes (Ryan *et al.* 1983). The oozes record establishment of a circumpolar current prior to the Oligocene, whilst climatic deterioration at the late Eocene/Oligocene boundary is reflected by profound alteration to benthic foraminiferal assemblages (Basov and Krasheninnikov 1983). The extremely low spore-pollen recovery from the oozes (Bratzeva 1983) may reflect the bathyal depositional situation remote from the source vegetation and/or reworking from older sediments. In the early Oligocene section, reworking is evidenced by a diverse component of Late Palaeozoic and Mesozoic forms, but there is no indication that the Cainozoic taxa were recycled. The early Oligocene spore-pollen associations containing *Cyatheidites* point to a vegetation containing *Nothofagus*, podocarpaceous conifers, together with diverse ferns and occasional myrtaceous, proteaceous, and chenopodiaceous angiosperms, and hence a vegetation closely allied to that which existed in southern South America.

The Kerguelen, Waterfall Gorge, occurrences of *Cyatheidites* are within Miocene lignites and fine-grained sandstones that contain taxonomically restricted spore-pollen assemblages. Although never common, *Cyatheidites* occurs more frequently in the sandstone lithologies, whereas *Trilites tuberculiformis* dominates the lignite assemblages. The parental vegetation included a strong component of conifers (*Lagarostrobos*, *Podocarpus*, *Microcachrys*, *Araucaria*). Fern spores are abundant, but taxonomically restricted; *T. tuberculiformis*, possibly of dicksoniaceous affinities, is the most prevalent form. Moss and lycophytic spores occur rarely and infrequent angiospermous pollen indicate a herbaceous vegetation of *Gunnera*, Graminae, and Compositae. Similar palynoassemblages occur in lignites from Dome Rouge; in several samples *C. annulatus* occurs commonly (Mechkova 1969) in contrast to its infrequent occurrence in the Waterfall Gorge material.

In eastern Australia, *Cyatheidites*-producing plants apparently retreated away from the source region of latest Cretaceous to early Oligocene sequences, reappearing in the latest early Oligocene and persisting into the Pliocene. In the Gippsland Basin, occurrences are in a thick, latest early Oligocene to Miocene coal sequence that accumulated adjacent to the coast; to the south and west, in Tasmania and the Otway Basin, *Cyatheidites* occurs in coeval sediments deposited in marine, marginal marine, and terrestrial environments. The vegetation surrounding these depositional areas was composed of subtropical, warm temperate, and cool temperate rain forest communities dominated respectively by Myrtaceae/Elaeocarpaceae, Cunoniaceae/*Quintinia*, and *Nothofagus*. These coexisted under high rainfall and were ordered along an altitudinal gradient (Kershaw and Sluiter 1982; Sluiter and Kershaw 1982; Hill and Macphail 1983). Swamp communities were envisaged to include Restionaceae, Gleicheniaceae, and Epacridaceae. *Lagarostrobos*, reflected by high pollen frequencies of *Phyllocladites mawsonii*, grew adjacent to the swamps or in the dry-land vegetation. Infrequency of *Cyatheidites* may indicate that the parent plant was a dry-land inhabitant; Hill and Macphail (1983) indicate a stream-bank niche in the Tasmanian Oligocene flora.

To the north, in New South Wales, *Cyatheidites* has patchy distribution in the largely terrestrial sequences deposited along the eastern edge of the Murray Basin (Martin 1973, 1984). The Oligocene to Miocene vegetation of this riverine area was apparently similar to that surrounding the coal-forming swamps in the Gippsland Basin, but an increase in the Myrtaceae/*Nothofagus* ratio in New South Wales suggested to Martin (1982) more substantial representation of the subtropical element that here occupied drier habitats (Martin 1984). *Cyatheidites* occurs in darker lithologies that contain higher frequencies of *P. mawsonii* and *Nothofagidites*. Thus, *Lophosoria* ferns may have been associated with *Lagarostrobos* and *Nothofagus* communities that, according to Martin (1984), occupied better watered habitats than the Myrtaceae.

Cool temperate *Nothofagus* communities occurred in southern Queensland during the early Miocene as evidenced by high frequencies of *Nothofagus* pollen in carbonaceous clays from Tamborine Mountain (Harris 1965). *Cyatheacidites* occurs in these clays (Cookson 1957) occurring between two lava flows ejected during uplift of the New England Plateau.

According to Sluiter and Kershaw (1982), *Nothofagus* rain forests contracted to coastal areas in Australia during late Miocene to Pliocene times and there was concomitant expansion of open vegetational communities. Known Pliocene occurrences of *Cyatheacidites* are few (Harris 1971; Martin 1981); associated spore-pollen assemblages include moderate frequencies of *Nothofagus* and podocarpacean/araucarean pollen.

Tertiary occurrences of *Cyatheacidites* indicate, therefore, association of the parent plant with rain forest vegetation in floras having a strong representation of southern conifers (*Araucaria*, *Dacrydium*, *Microcachrys*, and *Lagarostrobos*). In South America and Australia occurrence of these conifers, *Nothofagus*, and other angiosperms collectively indicate a series of rain forest communities that were ordered both latitudinally and altitudinally. On the Kerguelen Islands, stands of araucarean/podocarpacean conifers occurred with minor, largely herbaceous, angiosperms.

As for the Cretaceous, there is no clear evidence to suggest that the *Cyatheacidites*-producing ferns occupied permanently wet, swampy habitats. The spores are rarely common and are usually associated with a diversity of palynomorphs reflecting significant contributions from dry-land vegetation. The range of habitats indicated for Tertiary *Lophosoria* is within and fringing temperate rain forests between the latitudinal range of c. 60°–35° S.

## CONCLUSIONS

If degree of morphological uniqueness, stratigraphic continuity, and ecological compatibility can together be regarded as a reliable way of assessing dispersed spore affiliations, then there is little doubt, on the first two counts at least, that *C. annulatus* was shed by *Lophosoria* ferns. Primary radiation of *Lophosoria* may thus be dated as earliest Cretaceous (Berriasian), centred in a southern Gondwanan region encompassing the Antarctic Peninsula, Patagonia, and the Falkland Plateau adjacent to the proto South Atlantic Ocean. The Berriasian to early Albian appearance of several morphotypes, considered as allies of *Lophosoria*, indicates diversification soon after inception within the cradle area. This early phase of adaptive radiation was concomitant with initial disruption of oceanic barriers that foreshadowed opening of the South Atlantic; vegetational changes imply habitat diversification and climatic moderation. Reported earliest occurrences are in sequences that accumulated at or near sea level; an earlier inception in suitable habitats at higher altitudes is feasible, but unlikely to be preserved in the fossil record. Associated vegetation, as determined palynologically, denotes moist habitats fringing and within rain forest communities.

Migration eastwards to Australia occurred during the early Cretaceous and routes probably involved western Antarctica. The Campanian to early Oligocene hiatus in the otherwise continuous middle Albian to Pliocene record in Australia may possibly reflect short distance retreat away from the depositional areas or a second migratory wave into Australia, where ultimate extinction occurred at Pliocene or later time.

As for Australia the Kerguelen Miocene occurrences may also be associated with, as yet undated, dispersal from western Antarctica.

Today *Lophosoria* survives, at sea level, in the northern part of the cradle area (southern South America) and in similar cool humid habitats at higher altitudes in tropical South America and central America. The timing of this northern migration is uncertain, but may have been a Late Cretaceous or Tertiary event, involving routes along the Andean chain and the emergent island arc of central America. Van der Hammen and Gonzales's (1960) record indicates that *Lophosoria* was in Colombia during late Pleistocene/Holocene time.

Affiliation of the stem genus *Lophosoriachis* with *Lophosoria* (Nishida 1982) implies a spread to Japan during the Early Cretaceous. This affiliation may be questioned in so far as the stem characters of *Lophosoria* are not entirely definitive (Tryon and Tryon 1982). Moreover, *Cyatheacidites* is unknown from the Japanese Cretaceous (e.g. Takahashi 1974).

In reviewing the age and composition of spore-pollen assemblages associated with *Cyatheacidites*,

a series of questions emerged with broader biostratigraphic, phytogeographic, and palaeoclimatic connotations.

*Biostratigraphic implications.* The ages of the sequences containing initial and subsequent appearances of *Cyatheacidites* were, where possible, determined from independent pelagic-planktic fossil evidence (foraminiferids, ammonites, nannoplankton, dinoflagellates) and radiometric data. From this emerged a pattern of successively younger introductions of *Cyatheacidites* (see text-fig. 5), allowing the probable inception area and migration routes of *Lophosoria* to be inferred. The biostratigraphic implications are clear: long-distance correlation based upon first appearances of *Cyatheacidites* must be viewed with caution. In this connection the chronostratigraphic syntheses by Askin (1983) and Kotova (1983) for their respective Shetland Islands and Falkland Plateau assemblages, using the range of *C. annulatus* (*C. tectifera*) as observed in the terrestrial Baquero Formation, cannot be regarded as unequivocal. The Baquero assemblages are not securely dated, being based, at least in part, upon long-distance spore correlation. In Australia, *C. annulatus* cannot be used for time-stratigraphic correlation between Cretaceous sequences of the Otway and Eromanga Basins.

It further became apparent that other 'stratigraphically useful' species, especially those of cryptogam derivation, likewise have discordant stratigraphic ranges in separate areas, as previously noted by Dettmann (1981) for several Cretaceous zonal indices in the Otway and Eromanga Basins of Australia. This suggested to Dettmann migration of the parent plants in response to habitat availability. Clearly, the former is dependent upon the latter, and is controlled by climate, topography, and physical access of the plants to the region.

In the Australian Tertiary the second incoming of *C. annulatus* has been utilized biostratigraphically in the Gippsland and Otway Basins and in Tasmania. However, in New South Wales, *C. annulatus* occurs only rarely and its biostratigraphic usefulness has been questioned (Martin 1984). The climatic and topographic differences that existed between the two regions are reflected not only in the sediments (marine and coal sequences vs. riverine deposits) but also in the vegetation (Martin 1984).

*Phytogeographic implications.* The cradle area of *Lophosoria* seems likely to have been an important exchange region for many other taxa represented in past and present-day austral floras. Opening of the South Atlantic, which signalled climatic and topographic alteration, possibly triggered the southerly migration of angiosperms into austral regions along routes involving Antarctica (cf. Raven and Axelrod 1974). The pollen record emphasizes an earlier inception of *Clavatipollenites* in southern South America (?Barremian-Aptian) than in Australia (early Albian), and hence a migrational lag of some 10 m.y. Although its Antarctic incoming has not been pin-pointed, it is known from the early Albian of the Peninsula region (Dettmann and Thomson, in press). *Dacrydium*, *Lagarostrobos*, *Nothofagus*, the Proteaceae, and the Myrtaceae intermingled during Late Cretaceous and earliest Tertiary times on Antarctica, which thus served as an important distribution centre prior to separation from South America and Australia during the Early Tertiary. The Antarctic Peninsula may also have been a cradle area for some elements of austral floras. As the pollen record suggests, *Nothofagus* is one important element that may have an Antarctic origin.

*Palaeoecological and palaeoclimatic implications.* The palaeogeographic and stratigraphic occurrences of *Cyatheacidites* indicate that, soon after inception, *Lophosoria* spread over wide areas of southern Gondwana within a Cretaceous to Eocene latitudinal range of 70°–50° S. The palynofloras are consonant with temperate to tropical climates, with *Lophosoria* invading chiefly mesic habitats. *Lophosoria* maintained a similar latitudinal spread during the middle Tertiary but was displaced into somewhat lower latitudes (60°–35° S.) that supported temperate to subtropical rain forests. Its Pliocene or later extinction in Australia may be a consequence of decreased rainfall and increased seasonality. In South America *Lophosoria* has survived in its northernmost source region and appears there to have adapted successfully to progressively cooler habitats, a feature expressed by some long-resident temperate fern groups in other austral regions (Page and Clifford 1981). Climatic

cooling from Oligocene time is well recorded (Basov *et al.* 1983) and related to establishment of a circumpolar current and ice cap formation on Antarctica. The Cretaceous and Early Tertiary vegetational record suggests progressive climatic moderation associated with opening and enlargement of the South Atlantic Ocean. Whilst climatic models proposed for the Cretaceous (e.g. Barron and Washington 1982) signify warm polar seas, the predicted equator-to-pole temperature gradient is assumed to have been considerably less than that suggested by floral evidence within the proto South Atlantic region.

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