CLASSIFICATION OF POLLEN SURFACE PATTERNS OF FOSSIL PROTEACEAE, USING SCANNING ELECTRON MICROSCOPE

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Abstract

The scanning electron microscopic study of 41 Australian fossil pollen species, attributed to the family Proteaceae, has revealed 11 main surface pattern types, 9 of these patterns are common to the pollen of modern Proteaceae; however, 2 surface patterns i.e. scabro-rugulo-foro-gemmate and scabro-gemmo-ornate are exclusively present in the fossil Proteaceae. The surface patterns in the fossil Proteaceae, appearing first in the Upper Cretaceous and extending to the Pliocene, reach greatest diversification in the Eocene with a subsequent decline taking place from Oligocene to Pliocene. A new species Proteacidites biporatus is also described.

Introduction

The fossil pollen history exhibits a major radiation in the Palaeocene to Eocene, and the greatest majority of records are from these periods. But the abundance and variety of forms was much less in the Oligocene to Pliocene periods. Though the correctness of assignment of some fossil forms to the family Proteaceae is doubted, nonetheless, there is a reasonable belief that the fossil record stretches back to the Upper Cretaceous. The earliest pollen grains with reliability referred to Proteaceae belong to Senonian age (Martin, 1981).

Pollen morphology of fossil Proteaceae has remained the focus of attention to many palynologists. Cookson (1950) and validated by Couper (1953) established 3 form genera Banksiaoidites, Beaupreaoidites and Proteacidites. Cookson (1950, 1954), Cookson & Pike (1953), Couper (1953, 1960), Dettmann & Playford (1968), Harris (1965, 1966, 1972), McIntyre (1968), Stover & Evans (1973), Stover & Partridge (1973) and Martin (1973) described fossil proteaceous pollen from southern hemisphere. Germeraad et al., (1968) reported Proteacidites dehaani from Tertiary deposits of tropical area of Colombia, Jain et al., (1973) have described Proteacidites subscabratus from India, and Wang (1982) has reported Proteacidites partitus, P. bullatus and P. rennelus from Late Cre-
taceous to Early Tertiary deposits of China. Some fossil forms of supposed Proteaceae have also been reported from the northern hemisphere (Anderson, 1960; Druggs, 1967; Leffingwell, et al., 1970; Samoilich, 1967 etc.) far outside the present geographical range of modern Proteaceae. The proteaceous species described by Leffingwell, et al., (1970) have been excluded from Proteaceae (Memon, 1983).

Martin (1973) has attempted to ascertain the validity of certain proteaceous palynomorphs as indicators of the occurrence of fossil Proteaceae, and to establish more homogenous taxonomic groupings. Martin & Harris (1974) have proposed two new form genera *Cranwellipollis* and *Propylipollis* to receive certain species excluded from Proteaceae. These new genera were based on pore characters rather than shape, exine sculpture etc. used by Cookson (1950) and Couper (1953) for establishing *Proteacidites*.

Though considerable progress has been made in piecemeal fashion towards the study of fossil Proteaceae by the traditional optical microscope, nonetheless, it was worth studying these forms by the scanning electron microscope. The present study is confined to the pollen surface pattern types of Australian fossil Proteaceae.

**Material & Method**

Fossil pollen species were picked from the following sedimentary rock samples of Australia:

4. Bore near Edicara at 280.4—283 m. ‘Wilkatana’ Formation, Middle of Upper Eocene, S. Aust.
8. Tarpeena Bore 1, 335 ft., Otway Basin, Knight Formation, Middle Eocene, Vict. Aust.
9). Nerriga, Eocene, N.S.W. Aust.

10). Warburn No. 1 Bore, W.C.I.C. Eocene, N.S.W., Aust.

Pollen material was treated by modifying Faegri & Iversen (1964) method, and the picking of the pollen grains and scanning electron microscopy was carried out by modifying Leffingwell & Hodgkin (1971) method. Photography was carried out as described by Memon (1984).

*Terminology:* For detailed description of pollen surface pattern types, Erdtman's terminology (1952, 1969) has been used. However, some terms were borrowed from Faegri & Iversen (1964); Kremp (1965); Norem (1958) and Wodehouse (1935). Some terms previously described by these authors were amended and some new terms were made necessary for describing the detailed surface ornamentations of pollen grains (Memon, 1984).

**Results**

Description of surface pattern is based on the observation of whole grain.

I. *Reticulo-foveolate:*

A. Tectum more or less beaded to striate. Fig. 1, A.

Reticulum heterobrochate, muri 0.5–2.0 \( \mu \text{m} \) wide, lumina 1.1–1.7 \( \mu \text{m} \) in long axis; foveae 0.2–0.6 \( \mu \text{m} \) diameter; reticulum slightly reduced towards distal pole and pore area; foveae intermixed with lumina; foot layer seeming to be slightly verrucose; reticulum slightly tending towards striate.

*Proteacidites reticulanus* Cookson 1950.

B. Tectum more or less scabrate. Fig. 1, B.

Reticulum heterobrochate, muri 0.5–1.5 \( \mu \text{m} \) wide, lumina 0.5–1.5 \( \mu \text{m} \) in long axis, reduced to foveae, 0.1–0.4 \( \mu \text{m} \) diameter.


C. Tectum more or less fossulate. Fig. 1, C.

Reticulum heterobrochate, muri 0.4–2.0 \( \mu \text{m} \) wide, lumina 0.4–2.0 \( \mu \text{m} \) in long axis; foveae 0.1–0.6 \( \mu \text{m} \) diameter, in some species tectum slightly tending towards convolute.
Beaupreidites elegansiformis Cookson 1950.

Propylipollis (Proteacidites) reticuloscapatus Harris, 1965, emend. Martin & Harris, 1974.


D. Tectum flat and smooth. Fig. 1, D.

Reticulum heterobrochate, muri 0.3–2.0 μm wide, lumina 0.3–5.0 μm in long axis; foveae 0.1–0.4 μm diameter; suprafoveae present in some species; reticulum reduced almost to foveae towards middle of distal pole and pore area.

Propylipollis (Proteacidites) tripartitus Harris, 1972, emend. Martin & Harris, 1974.

Proteacidites adenanthoides Cookson 1950.
P. biporatus sp. nov. (see at the end of results).
P. callosus Cookson 1950.
P. kopiensis Harris 1972.

E. Reticulum uneven in elevation, muri irregular-shaped. Fig. 1, E.

Reticulum heterobrochate, muri 0.3–1.4 μm wide, lumina 1.0–5.0 μm in long axis; foveae 0.1–0.7 μm diameter, mainly confined to muri and also occasionally occurring in foot layer.


II. Reticulate:

A. Tectum smooth and flat. Fig. 1, F.

Reticulum heterobrochate, muri 0.3–1.4 μm wide, lumina 1.0–10.0 μm in long axis; foot layer in some species scabrate and foveolate in others.

Proteacidites grandis Cookson 1950.

B. Tectum tending towards striate to slightly non-stranded contextate, columellae thick apparently rounded and protruding in lumina. Fig. 1, G.

Reticulum heterobrochate, muri 0.7–1.8 μm wide, lumina 1.5–9.0 μm in long axis.
Fig. 1.  

A. Reticulo-foveolate
B. - do -
C. - do -
D. - do -
E. - do -
F. Reticulate
G. - do -
H. - do -

A. Proteacidites reticulatus
B. P. sipplatus
C. Beaufreidites elegansiformis
D. Proteacidites adenanthoides
E. P. alveolatus
A. P. grandis
B. P. confragosus
C. P. ornatus

(Unless otherwise stated all magnifications are X 10,000)
Proteacidites confragosus Harris 1972.

C. Tectum convolute and more or less vermiculate. Fig. 1, H.

Reticulum heterobrochate, muri 0.5–1.5 μm wide, lumina 0.7–8.2 μm in long axis; reticulum coarser towards equators and reduced around pores, sometimes to the extent of narrow clefts (arrow).

Proteacidites ornatus Harris 1972.

III. Reticulo-foveo-verrucose: Fig. 2, A.

Reticulum heterobrochate, muri 0.5–1.4 μm wide, lumina 0.5–1.2 μm in long axis; intermixed with foveae, 0.1–0.4 μm diameter; suprarectal verrucae 0.8–3.4 μm diameter; tectum slightly fossulate.

Beaupreaidites verrucosus Cookson 1950.

IV. Rugulo-foveolate: Fig. 2, B.

Rugulae 0.3–2.0 μm wide; foveae 0.1–1.2 μm diameter; rugulae poorly to strongly developed; fossae shallow to deep; in some species foveae confined to more or less deep eufossae.

Banksieaeidites elongatus Cookson 1950.
Proteacidites granulatus Cookson 1950.
P. pachypolus Cookson & Pike 1953.

V. Scabro-rugulo-foveolate:

A. Tectum smooth to slightly coarser, more or less even in elevation, sometimes subdivided into scabrae. Fig. 2, C.

Scabrae 0.2–1.0 μm diameter, intermixed with rugulae, 0.2–1.3 μm wide; foveae 0.1–0.7 μm diameter, mainly confined to fossae; ekstexine of Proteacidites amolosexinus easily strips off.

Proteacidites amolosexinus Dettmann & Playford 1968.
P. obscursus Cookson 1950.
P. varius Harris 1972.
P. wilkatanaensis Harris 1972.

B. Tectum much coarser, incised by short and discontinuous rugulae in one species and superficially two-levelled in other. Fig. 2, D.

Scabrae 0.3–1.0 μm diameter, intermixed with rugulae, 0.3–1.0 μm wide; foveae 0.1–1.0 μm diameter, mainly confined to fossae, occasionally occurring in rugulae or central protrusion.


C. Rugulae subdivided into subrugulae and scabrae. Fig. 2, E.

Scabrae 0.3–0.7 μm diameter, intermixed with rugulae, 0.8–2.5 μm wide, subdivided into subrugulae 0.3–0.6 μm wide; foveae 0.1–0.5 μm diameter, occurring more or less in funnel-shaped tectal depressions.

Proteacidites fromensis Harris 1972.

VI. Scabro-foveolate: Fig. 2, F.

Scabrae 0.2–1.0 μm diameter; foveae 0.1–0.3 μm diameter; in some species scabrae poorly developed and in others well-developed and more or less isodiametric.

Proteacidites similis Harris 1972.
P. subscaibratus Couper 1953.

VII. Foveo-spinulose: Fig. 2, G.

Foveae not very clear, supratectal spinules 0.2–1.0 μm long; tectum seeming to be slightly scabrate in one species and verrucose in other.

Propylipollis (Proteacidites) concretus Harris 1972, emend. Martin & Harris 1974.
Fig. 2. A. Reticulo-foveo-verrucose:  
B. Rugulo-foveolate:
C. Scabro-rugulo-foveolate
D. - do -
E. - do -
F. Scabro-foveolate
G. Foveo-spinulose:
H. Foveo-verrucose:  

Beaupreacidites verrucosus
Proteacidites granulatus
A. Propylipollis parus
B. Proteacidites rectomarginis × 6000
C. P. fromensis
P. similis
Propylipollis latrobensis
Proteacidites tenalexinus
VIII. *Foveo-verrucose*: Fig. 2, H.

Foveae 0.1–0.2 μm diameter; suprarectal verrucae 0.1–0.7 μm diameter, uniformly distributed; tectum slightly undulating.


IX. *Verrucose*: Fig. 3, A.

Suprarectal verrucae 0.1–0.4 μm diameter, more or less uniformly distributed.


X. *Scabro-rugulo-foveo-genmate*: Fig. 3, B.

Scabrae 0.3–1.0 μm diameter; rugulae 0.3–1.8 μm wide; foveae 0.1–0.5 μm diameter, usually occurring in insulae or sometimes in gemmae (arrow a); suprarectal gemmae 1.0–4.5 μm diameter; partial fusion of some gemmae results in an ornate pattern in one species, and gemmae connected with foot layer by short suprarectal columelle (arrow b) in other.


XI. *Scabro-genmo-ornate*: Fig. 3, C.

Scabrae 0.1–0.7 μm diameter, confined to foot layer; gemmae 1.0–3.5 μm diameter, c. 1.0–2.0 μm raised above the tectum; ornamentation with 1.2-2.5 μm wide muri.


*Proteacidites biporatus* sp. nov. Fig. 3, F-H.

*Material*: Moorlands Lignites member of the Renmark Beds, Late Eocene, South Australia.
Fig. 3.  A. Verrucose:  
B. Scabro-rugulose-foveo-gemmative:  
C. Scabro-gemmato-ornate:  
D. Surface pattern  
E. — do —  
F. Optical microscopy  
G. S.E. Microscopy  
H. Surface pattern

*Propyliopsis beddoesi*  
*P. tuberculiformis* X 6000  
*Cranwelliaopsis tortuosus* X 4000  
*Banksiellaedites arcuatius*  
*Propyliopsis annularis*  
*Proteacidites biporatus* (Holotype) X 1000  
— do — X 1200
**Description:** Pollen grains 2-porate, bilateral, plano-convex to biconvex or slightly concavo-convex, 43–(58)–70 μm long, 17–(21)–26 μm in breadth; pores more or less circular c. 1.5–4.0 μm diameter.

Exine 1.5–(2.6)–3.7 μm thick, semiectectate, ekteixine more or less as thick as endexine, tectum reticulo-foveolate; reticulum heterobrochate, muri 0.3–1.0 μm wide, lumina 0.3–2.0 μm in long axis, slightly reduced towards distal pole, and to foveae, 0.1–0.2 μm diameter towards pore area, foveae also intermixed with lumina; tectum slightly fossulate.

**Comparison:** The surface pattern of Proteacidites biporatus and P. adenanthoides Cookson (1950) is almost identical, but the endexine thickens below pore and then tapers with corrugations into tenuimarginate in the former species, whereas endexine gradually tapers into more or less blunt edges towards pore margin in the latter species.

**Holotype:** Specimen on slide No. Ry 1182, c. 70 μm long and 21 μm in breadth, deposited in the palynological collection of the Geological Survey of S. Australia.

**Discussion**

Though the scanning electron microscope greatly helps in resolving the micromorphological details of pollen exine surface patterns in comparison to optical microscope, the sectional study of exine can be accurately carried out by the transmission electron microscope (Memon, 1984). The scanning electron microscopic study suggests that the optical microscope exaggerates some features or does not reach the full depth of focus of surface pattern. For example, the surface pattern of Proteacidites stipitatus (Fig. 1, C.) is reticulo-foveolate with scabro-fossulate muri rather than granulate or tuberculate as described by Partridge (Stover & Partridge, 1973). Under the optical microscope the scabro-fossulate muri are exaggerated to granules or tubercles. Similarly, the surface pattern of Banksieaeidites arcuatus (Fig. 3, D.) and Propylpollis annularis (Fig. 3, E.) is scabro-rugulo-foveolate rather than puncto-reticulate as described by Stover (Stover & Partridge, 1973) for the former palynomorph, and reticulate as described by Cookson (1950) for the latter. Under the optical microscope the scabiae and rugulae are not easily detectable and the foveae are exaggerated to lumina of a reticulum.

Southern hemisphere fossil forms so far examined, belonging to form genera Banksieaeidites, Beaufreidites Cranwellipollis, Propylpollis and Proteacidites, attributed to the family Proteaceae, resemble modern pollen species in the range of shape, size and usually in surface pattern and pore structure. However, scabro-rugulo-foveo-gemmate (Fig. 3, B.) and scabro-gemmo-ornate (Fig. 3, C) surface patterns are not found in modern Proteaceae (Memon, 1984, and also see Fig. 4).
Fig. 4. Pollen surface patterns in relation to different geological periods of fossil Proteaceae (Left). Numbers on bars refer to the number of surface patterns occurring in each period and towards right it shows pollen surface patterns of modern Proteaceae. Numbers on bars refer to the number of species within that kind of surface pollen.
Pollen morphology of fossil Proteaceae has demonstrated two main groups of surface patterns: i.e. 1) reticulo-foveolate (Fig. 1, A-E) and reticulate (Fig. 1, F-H), and 2) rugulo-foveolate (Fig. 2, F), scabro-rugulo-foveolate (Fig. 2, C-E) and scabro-foveolate (Fig. 2, F), which together form a core surface pattern of the family (Fig. 4), appearing first in the Upper Cretaceous and extending to the Pliocene. In Palaeocene three new patterns i.e. 1) reticulo-foveo-verrucose (Fig. 2, A), 2) foveo-spinulose (Fig. 2, G) and 3) foveo-verrucose (Fig. 2, H) appeared. By the Eocene three additional surface patterns i.e. 1) scabro-rugulo-foveo-gemmate (Fig. 3, B), scabro-gemmo-ornate (Fig. 3, C) and 3) verrucose (Fig. 3, A) appeared and continued right up to the Miocene. Then from Oligocene to the Pliocene only core pattern was found (Fig. 4).

It is evident that the family Proteaceae underwent an apparent major burst of surface pattern diversification in the Palaeocene and especially in Eocene, with a subsequent decline taking place from the Oligocene to Pliocene. This may be because the early Tertiary Proteaceae had more generalised floral morphology, higher pollen cut and open pollination mechanism (Martin, 1981). The reason of decline of pollen grains from Oligocene may be because the Australian palynologists appear to have been a rather conservative in species making. Martin, (1981) has suggested that the considerable fall is also more than an artifact of the data. He further suggests that only the Pliocene and Pleistocene data seem to be seriously affected by the scarcity of these periods.

Conclusion

Pollen morphology of 41 Australian fossil Proteaceae has revealed 11 main surface pattern types, 9 of them are invariably found in the species of modern Proteaceae (Memon, 1984). However, scabro-rugulo-foveo-gemmate and scabro-gemmo-ornate surface patterns are exclusively present in the fossil forms. The two commonest group (i.e. 1-reticulo-foveolate & reticulate, and 2-rugulo-foveolate, scabro-rugulo-foveolate & scabro-foveolate) form a core pattern of the family Proteaceae.

It was noted that though majority of fossil forms manifest similar surface pattern which are grouped together, nonetheless, each species retains its individuality.

The surface pattern of fossil Proteaceae, appearing first in the Upper Cretaceous extending to Pliocene, reach its greatest variation in the Eocene with a subsequent decline taking place from Oligocene to Pliocene.

Cranwellipollis tortuosus, C. tuberculatus, Propyliopollis tuberculiformis, Proteacidites alveolatus, P. confraomus, P. leightonii, P. recanus and P. oratus could be identified on the bases of their surface pattern and more or less on shape. However, Banksieaedites being 2-porate, Beaurpseudites being 3-colpoidate, Proteacidites bioratus being reticulo-foveolate and 2-porate, and Proteacidites asperopolis being scabro-rugulo-
foveolate with polar protrusion, and *Proteacidites pachypolus* being rugulo-foveolate with polar protrusion could be segregated from the other fossil forms of Proteaceae.

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**References**


