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CLASSIFICATION OF POLLEN SURFACE PATTERNS OF MODERN PROTEACEAE USING SCANNING ELECTRON MICROSCOPE

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Abstract

The scanning electron microscopic study of pollen exine surface patterns of Proteaceae reveal 22 main pattern types. This study has manifested that many modern genera including nearly all those with large number of species were not pollen-morphologically homogeneous. Such genera often lack unique combinations of pollen characters that could distinguish them from other genera of the family. At species level, micromorphological differences in the detail and distribution of surface pattern, pore structure, shape and size of pollen grains have been found to exist.

Introduction

The family Proteaceae, owing to its phytogeographic and phylogenetic position have received intense interest in recent years. It is an ancient Gondwanan family that has left extensive fossil record over the past 110 million years or so. There is reasonable belief that the record stretches back to the Upper Cretaceous, the earliest pollen grains referred to the family Proteaceae with any reliability are being Senonian in age (Martin, 1981).

Proteaceae with 75 genera, is divided into 5 subfamilies (Johnson & Briggs, 1975), and is mainly confined to the southern hemisphere. The centre of concentration approximately 66% of known species is Australian and 25% of the species are found in South Africa. Only 9% of the modern species are widely distributed in the areas of Asia, New Zealand, New Caledonia, Papua Guinea, Fiji, South and Central America (Good, 1964). All the 7 genera now in the northern hemisphere are also found in Southern hemisphere (Martin & Memon, in press). One introduced genus is represented in Pakistan (Beg & Khan, 1974).

Some palynologists like Cookson & Erdtman (1952), Van Zindern Baker (1953) have described the pollen morphology of modern Proteaceae in piece-meal fashion, using the traditional optical microscope. In the present communication the pollen exine surface pattern of 148 species, representing 73 genera of modern Proteaceae, using the scanning electron microscope is described.

Material and Method

The acetolysed and glycerine jelly preserved pollen material of 142 species (collected by Dr. A.R.H. Martin) was taken from the Department of Botany, University of Sydney, Australia. However, pollen of *Embothrium coccineum*, *Franklandia triaristata*, *Garnieria spathulifolia*, *Lambertia uniflora* and *Neorites kerediana* were collected from the National Herbarium of N.S.W., Australia and pollen grains of *Selumerodendron austrocaledonicum* were received from Professor Leroy of Paris.

The acetolysed and glycerine jelly preserved pollen material was thoroughly washed in distilled water and then small drops of pollen suspension were allowed to evaporate onto the top of small pieces of coverslips (8 x 6 mm). Dried pollen material of some species was also smeared onto the top of coverslips in a drop of distilled water. After the evaporation of water the coverslips with pollen grains on top of them were glued on the specimen stubs (10 mm long and 8 mm diameter) with Tarzan's grip fixative. The specimen stubs were then put in a high vacuum chamber rotatory device (Dynavc, model CE 12/14, unit No. B 5900, Australia) and coated first by a thin layer of carbon (c. 50 Å) and then by a gold layer (c. 200-250 Å) on the carbon layer. Finally, the edges of coverslips were cemented by a silver electronic paint to avoid charging effects. Then the specimen stubs were examined in JEOL, model JSM U3 (Japan) scanning electron microscope. Photography was carried out at 15 KV accelerating beam voltage in zoom steps under magnification from 1,000-10,000. Usually, 20,000 or even more magnifications were used for sharp focusing. All pollen grains were photographed in three different orientations i.e. whole grain, surface pattern and aperture details.

Terminology & Classification

For the detailed description of pollen grains, Erdtman's terminology (1952, 1969) has been used. However, some terms have also been borrowed from Faegri & Iversen (1974); Kremp (1965); Norem (1958) and Wodehouse (1935). Some terms previously described by these authors have been amended and a few new terms have been made necessary for describing the detailed surface ornamentation of pollen grains.

Erdtman's N.P.C. system of classification (1969) was used and all the pollen grains under consideration fall into formulae 224 and 344 except *Beauprea*, which falls into 243. However, the grouping of the pollen grains is exclusively based on the type of surface patterns.

Following new terms and amendments were used (Text Fig. 1):

Contextum: Tectum reticulate, muri interwoven by thread-like tectal elements (Adj. Contextate).

Stranded. Tectal elements strongly interwoven forming rope-like muri (1-a).

Non-stranded. Tectal elements slightly twisted but not exactly interwoven (1-b).

Convallis: Tectal elements (insulae or cristae) forming a valley or depression more or less enclosed from all sides (Adj. convallate, 2, top arrow).

Eufossa: Furrow incising the textum deeply (adj. eufossulate, 3).

Suprafossa: Furrow superficially appearing on tectum (Adj. suprafossulate, 4).

Suprafova: Perforation which does not pass through tectum (Adj. suprafoveolate, 5-b).

Fova: Tectal perforation less than or equal to 1.0 μm diameter. This term has been flexibly used, depending upon the width of tectum between two adjacent perforations (Adj. foveolate, 5-a).

Retipilum: Reticulum formed by the heads of pila, appearing as beaded tectum (Adj. retipilate, 6).

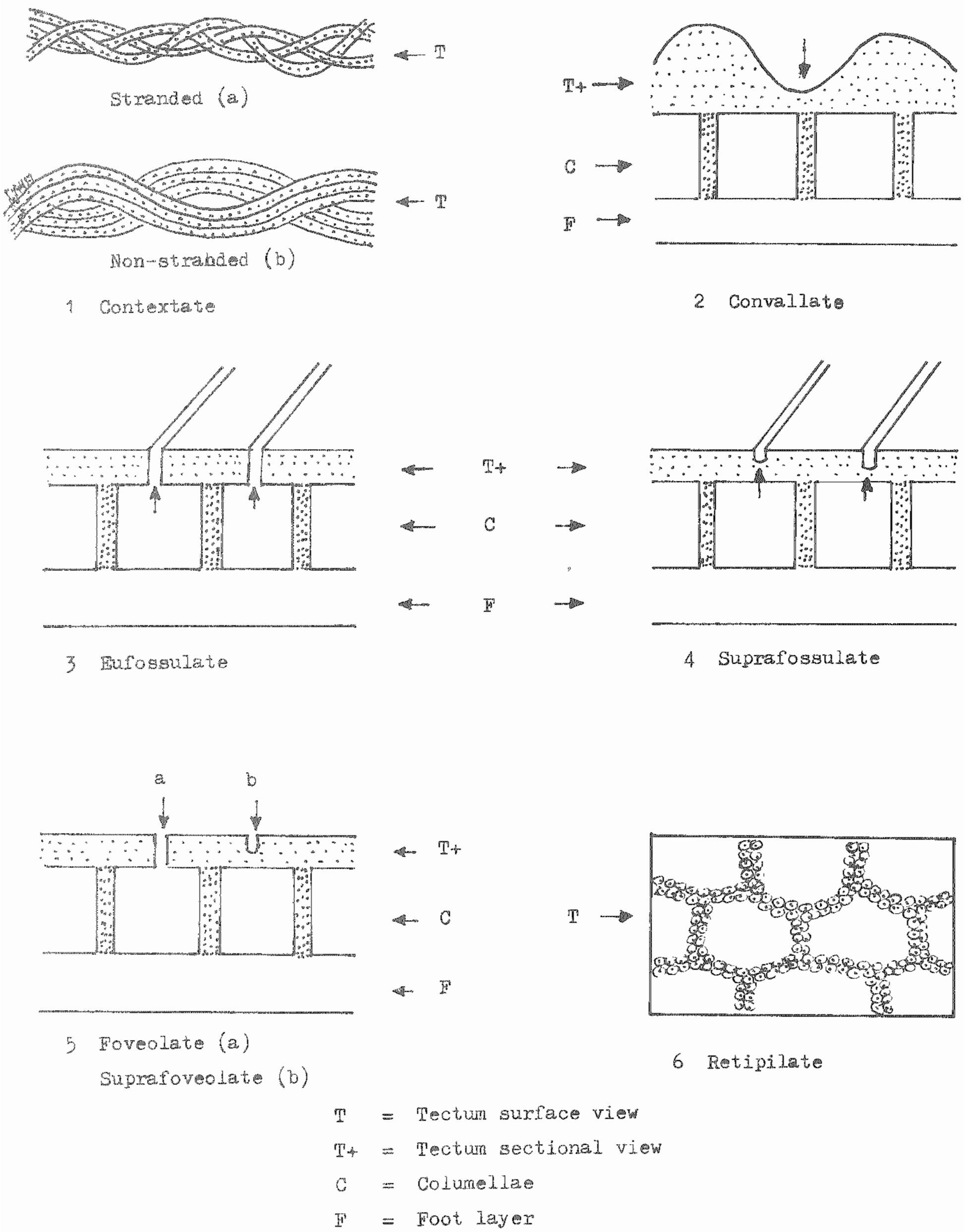
Suprascabrae: Tectal elevations (insluae, rugulae, scabrae, etc.) subdivided into minute processes (Adj. suprafossulate).

Results

Description of surface patterns is based on the observation of the whole pollen grain. The number on the right side of each species refers to the voucher specimen numbber. The specimens are lodged in the palynological collection at School of Biological Sciences, the University of Sydney, Australia; pollen of the species marked with (*) were taken from the Herbarium sheets lodged at National Herbarium of N.S.W., Australia.

I. *Clavate:* Fig. 1, A.

Clavae 1.6-7.2 μm long, 1.0-6.0 μm diameter, uniformly distributed; some clavae laterally and terminally fused and some forming narrow bridges among themselves; nanoverrucae and verrucae, 0.1-1.3 μm diameter, occationally present on foot layer.



Text Fig. 1. New terms and amendments used for the classification of pollen surface patterns of modern Proteaceae.

Franklandia fucifolia R. Br. 829
F. triaristata Benth. 996

II. *Reticulo-foveolate:*

A. Tectum beaded. Fig. 1, B.

Reticulum heterobrochate, muri 0.4-1.2 μm wide, lumina 0.4-3.0 μm in long axis; foveae 0.05-0.3 μm diameter; supratectal nanoverrucae 0.1-0.3 μm diameter, also occasionally present.

i. Reticulum reduced to foveae towards middle of distal pole and totally eliminated around pore areas.

Athertonia (Hicksbeachia) diversifolia (Sleum.) Johnson & Briggs 831

ii. Reticulum slightly reduced to foveae towards distal pole and pore areas, foveae also intermixed with lumina.

Grevillea shuttleworthiana Meissn. 751
Hicksbeachia pinnatifida F.v. Muel. 830

B. Tectum contextate, muri stranded. Fig. 1, C.

Reticulum heterobrochate, muri 0.3-0.7 μm wide, lumina 0.4-0.8 μm in long axis, reduced to foveae, 0.1-0 2 μm diameter, towards distal pole. foveae also occasionally intermixed with lumina; some tectal elements rising in more or less rounded or slightly elongated terminations comparable to verrucae or bacula respectively.

Petrophile fucifolia Kn. 125

C. Tectum contextate, muri non-stranded. Fig. 1, D.

Reticulum heterobrochate, muri 0.2-1.4 μm wide, lumina 0.3-2.0 μm in long axis, reduced to foveae, 0.1-0.2 μm diameter towards middle of distal pole and pore areas, foveae also intermixed with lumina; supratectal nanoverrucae, 0.1-0.5 μm diameter also present.

Serruria linearis Salisb. ex Kn. 1533
S. vallaris Kn. 536[s]
Triunia (Helicia) youngiana (F. v. Muel.) Johnson & Briggs. 1381

D. Tectum scabrate. Fig. 1, E.

Reticulum heterobrochate, muri 0.3-2.0 μm wide, lumina 0.4-2.0 μm in long axis, more or less confined to proximal pole and equator; foveae 0.1-0.3 μm diameters, mainly confined to distal pole, also intermixed with lumina; supratectal nanoverrucae 0.1-0.4 μm diameter, also present.

i. Tectum gently scabrate.

Isopogon dawsonii R.T. Bak. 1462
Kermadecia rotundifolia Brongn. & Gris. 833

ii. Tectum strongly scabrate.

Leucospermum hypophyllocarpodendron (L.) Druce. 463[s]
Neorites kerediana L.S. Smith. (*)
Serruria elongata R. Br. 1519

E. Tectum more or less fossulate. Fig. 1, F.

Reticulum heterobrochate, muri 0.3-1.8 μm wide, lumina 0.4-2.0 μm in long axis, reduced to foveae, 0.1-0.3 μm diameter towards distal pole and pore areas, foveae also occastionally intermixed with lumina; supratectal nanoverrucae 0.1-0.5 μm diameter, also present in some species.

i. Tectum slightly fossulate and luminal floor roughened.

Adenanthos barbigera Lindl. 643
A. pungens Meissn. 1560
Mimetes argentea Kn. 1531
Petrophile teretifolia R. Br. 637
Sphalmium (Orites) racemosum (C.T. White) Briggs, Hayland & Johnson. 1662

ii. Tectum suprafossulate.

Floydia (Macadamia) praealta (F.M. Bailey) Johnson & Briggs. 966
Paranomus reflexus (Phill. & Hutch.) Fourcade. 538[s]
Spatalla thyrsiflora Salisb. ex Kn. 1523

iii. Tectum eu-and suprafossulate.

Gevunia (Kermadecia) vitiensis (Turr.) Johnson & Briggs. 852
Knightia excelsa R. Br. 834
Leucadendron salignum Berg. 331[s]
Lomatia polymorpha R. Br. 799
Serruria abrotanifolia Salisb. ex Kn. 1515

F. Tectum smooth, lumina more or less elongated. Fig. 1, G.

Reticulum heterobrochate, muri 0.3-1.0 μm wide, lumina 0.4-1.3 μm in long axis, intermixed with foveae, 0.1-0.3 μm diameter, slightly reduced towards distal pole and pore areas; supratectal nanoverrucae 0.1-0.4 μm diameter, also present.

Carnarvonia araliaefolia F. v. Muel. 824
Leucospermum cordifolium (Salisb. ex Kn.) Fourcade. 1511
Serruria pedunculata (Lam.) R. Br. 513[s]

G. Tectum flat and smooth. Fig. 1, H.

Reticulum heterobrochate, muri 0.2-2.5 μm wide, lumina 0.4-4.2 μm in long axis, intermixed with foveae, 0.1-0.3 μm diameter (in some species), and totally reduced to foveae (in other species), towards middle of distal pole; supratectal nanoverrucae 0.1-0.4 μm diameter, also present in some species.

i. Reticulum more or less uniformly distributed and very slightly reduced towards distal pole and pore areas.

Gevuina avellana Mol. 961
Lomatia myricoides (Gaertin. f.) Domin. 765
Petrophille heterophylla Lindl. 1602
P. serruriae R. Br. 1500
Spatalla curvifolia Rourke. 1520

ii. Reticulum almost reduced to foveae, towards middle of distal pole and pore areas.

Lomatia silaifolia (Sm.) R. Br. 53
Virotia (Macadamia) rousselii (Sleum.) Johnson & Briggs. 967

iii. Reticulum latimurate and slightly reduced towards pore areas.

Sleumerodendron austrocaledonicum (Brongn. & Gris.) Virot. 1660

iv. Reticulum latimurate and reduced to foveae or almost totally eliminating towards distal pole and pore areas.

Cardwellia sublimis F. v. Muel. 957

v. Reticulum latimurate, lumina dentate, more or less uniformly distributed.

Stenocarpus heterophyllus Brongn. & Gris. 1556

vi. Nanoverrucae thickly and irregularly present.

Symphionema paludosum R. Br. 160

vii. Tectum slightly tending towards non-stranded contextum.

Symphionema montanum R. Br.

III. *Reticulate:*

A. Tectum contextate, muri stranded. Fig. 1, I.

Reticulum heterobrochate, muri 0.4-1.0 μm wide, lumina 0.3-3.0 μm in long axis, more or less uniformly distributed.

i. Some tectal units rising vertically in more or less rounded or elongated terminations.

Petrophile semifurcata Lindl. 1565

ii. Tectum more or less uniform in elevation.

Petrophile seminuda Lindl. 1498

B. Tectum stratified into two-layered reticulum. Fig. 1, J.

Reticulum hetrobrochate, muri 0.3-1.0 μm wide, lumina 0.4-2.7 μm in long axis, some muri of outer-layered reticulum (see a) bridging over partially obscure innerlayered reticulum (see b).

Petrophile squamata R. Br. 1495

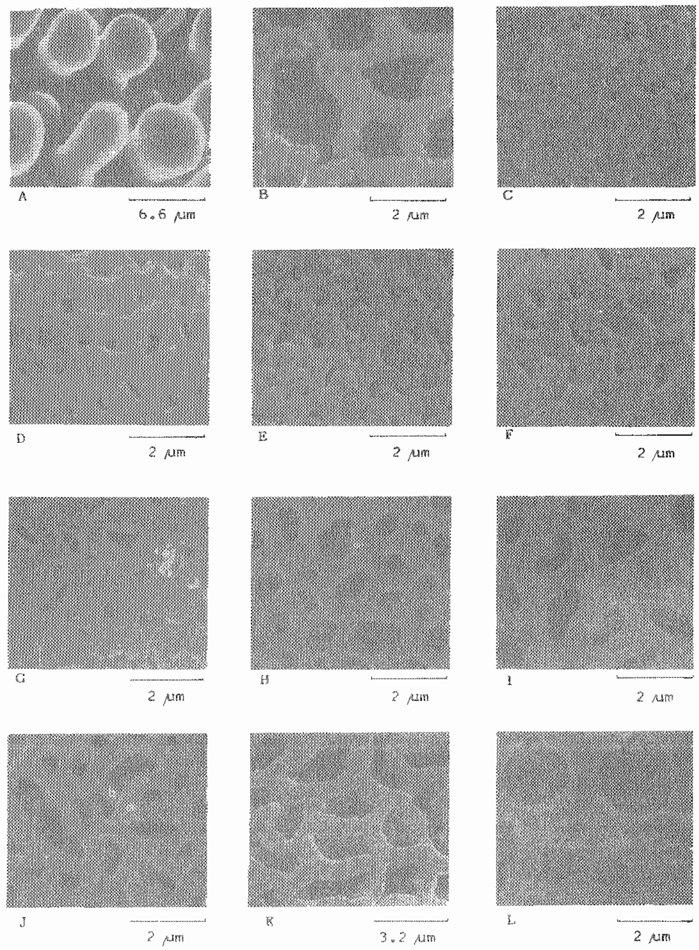


Fig. 1.	A.	Clavate	*Franklandia triaristata* x3000
	B.	Reticulo-Foveolate	A. *Hicksbeachia pinnatifida*
	C.	– do –	B. *Petrophile fucifolia*
	D.	– do –	C. *Seruuria linearis*
	E.	– do –	D. *S. elongata*
	F.	– do –	E. *Lomatia Polymorpha*
	G.	– do –	F. *Leucospermum cordifolium*
	H.	– do –	G. *Spatalla curvifoila*
	I.	Reticulate	A. *Petrophile seminuda*
	J.	– do –	B. *P. squamata*
	K.	– do –	C. *Heliciopsis artocarpoides* x6000
	L.	– do –	D. *Diastella serpyllifolia*

(Unless otherwise stated all magnifications are X 10,000)

C. Tectum smooth and flat. Fig. 1, K.

Reticulum heterobrochate, muri 0.3-1.4 µm wide, lumina 0.4-4.4 µm in long axis.

i. Muri more or less tube-like, columellae quite deep.

Heliciopsis artocarpoides Sleum. 963
H. terminalis (Kurz.) Sleum. 964

ii. Muri wavy and uneven in elevation.

Isopogan divergens R. Br. 1461

iii. Luminal floor scabrate.

Isopogan fletcheri F. v. Muel. 1466

D. Luminal floor verrucose. Fig. 1, L.

Reticulum hetrobrochate, muri 0.3-0.7 µm wide, lumina 0.4-1.0 µm in long axis, reduced towards apertures, some foveae 0.1-0.2 µm diameter, also present around pores; luminal nanoverrucae 0.1-0.5 µm diameter, almost fill whole luminal area.

Diastella serpyllifolia Salisb. 465^{s}

IV *Reticulo-foveo-gemmate:* Fig. 2, A.

Reticulum heterobrochate, muri 0.2-0.8 µm wide, lumina 0.4-1.0 µm in long axis; reduced to foveae, towards apertures, and also intermixed with foveae, 0.1-0.2 µm diameter; supratectal gemmae 0.5-3.0 µm diameter, more or less uniformly distributed.

i. Tectum beaded.

Hakea dactyloides Cav. 740

ii. Tectum flat and more or less convallate.

Beauprea balansae Brongn. & Gris. 953

V. *Reticulo-foveo-verrucose:* Fig. 2, B.

Reticulum heterobrochate, muri 0.3-1.4 μm wide, lumina 0.4-1.2 μm in long axis, intermixed with foveae, 0.1-0.2 μm diameter, reduced towards aperture areas; supratectal verrucae 0.8-4.3 μm diameter, more or less uniformly distributed.

Beauprea spathulifolia Brongn. & Gris. 823

VI. *Reticulo-foveo-spinulose:* Fig. 2, C.

Reticulum heterobrochate, muri 0.2-1.6 μm wide, lumina 0.4-1.7 μm in long axis, intermixed with foveae, 0.1-0.2 μm diameter; supratectal spinules 0.2-1.7 μm long, arranged in groups of twos, threes, fours or occasionally single; supratectal nanoverrucae and occasionally verrucae, 0.1-1.0 μm diameter, also present.

Aulax cneorifolia Kn. 575
A. pinifolia (L.) Berg. (*)

VII. *Foveolate:*

A. Tectum contextate. Fig. 2, D.

Foveae 0.1-0.8 μm diameter, occurring in the middle of funnel-shaped tectal depressions, slightly reduced in size and number towards middle of distal pole and pore areas; supratectal nanoverrucae 0.1-0.5 μm diameter, also occasionally present.

i. Muri non-stranded.

Leucospermum alpinum (Salisb. ex Kn.) Rourke. 1527
Paranomus bracteolaris Salisb. ex Kn. 1526
P. capitatus (R. Br.) Kn. 1516

ii. Muri more or less stranded.

Sorocephalus capitatus Rourke. 1522
S. salsoloides R. Br. 973

B. Tectum smooth, flat or slightly uneven in elevation. Fig. 2, E.

Foveae 0.1-0.6 μm diameter, more or less uniformly distributed, supratectal nanoverrucae and rarely verrucae, 0.1-1.5 μm diameter, also present.

i. Tectum flat.

Grevillea brownii Meissn. 1453
Hakea lorea R. Br. 1201
Spatalla nubicola Rourke. 1512

ii. Foveae occurring in more or less funnel-shaped tectal depressions, some foveae interconnected by fossae.

Conospermum tenuifolium R. Br. 735
Spatalla caudata (Th.) R. Br. 515*s*
Spatalla caudata (Th.) R. Br. 515^{s}
Synaphaea favosa R. Br. 974

iii. Tectum slightly uneven in elevation, foveae interconnected by suprafossae or eufossae or both.

Stenocarpus salignus R. Br. 1501

iv. Tectum slightly tending towards rugulate.

Banksia serratifolia Salisb. 722
Macadamia whelani F.M. Bailey. 1008
Placospermum coriaceum White & Francis. 837
Telopea speciosissima R. Br. 240

VIII. *Rugulo-foveolate:* Fig. 2, F.

Rugulae 0.3-1.7 μm wide; foveae 0.1-0.6 μm diameter, mainly confined to fossae, also occasionally occurring in rugulae; rarely supratectal bacula 0.5 μm long also present.

i. Rugulae poorly developed, fossae deep.

Banksia collina R. Br. 245
Buckinghamia celsissima F. v. Muel. 727
Finschia chloroxantha Diel. 828

ii. Rugulae poorly developed, fossae shallow.

Beaupreopsis paniculata Virot. 955
Dryandra nivea R. Br. 1557
Lambertia multiflora Lindl. 965
Oreocallis wickhamiana W. Hill & F. v. Muel. 736

iii. Rugulae well-developed, foveae confined to more or less deep eufossae.

Banksia asplenifolia Salisb. 91
Beauprea elegans Brongn. & Gris. 1494

iv. Rugulae strongly coarser, fossae deep.

Acedonia (Persoonia) angustifolia (Benth.) Johnson & Briggs. 1559
Conospermum stoechadis Endl. 754

IX. *Scabro-rugulo-foveolate:*

A. Tectum even or slightly uneven in elevation, sometimes discontinuous, rugulae occasionally subdivided into scabrae. Fig. 2, G.

Scabrae 0.1-1.0 μm diameter, intermixed with rugulae, 0.2-1.2 μm wide, foveae 0.1-0.4 μm diameter, mainly confined to fossae.

i. Tectum smooth, pattern fine and more or less uniformly distributed.

Austromuellera trinervia C.T. White. 822
Musgravea stenostachya F. v. Muel. 835

ii. Tectum coarser and uneven in elevation, foveae usually confined to fossae.

Darlingia darlingiana (F. v. Muel.) Johnson. 958
D. ferruginea F. v. Muel. 825

iii. Tectum slightly coarser, foveae more or less uniformly distributed.

Brabeium stellatifolium Lindl. 70[s]
Eucarphs (Knightia) strobilina (RBr.) Johnson & Briggs. 1003
Dryandra serra R. Br. 1571
Helicia glabriflora F. v. Muel. 584

iv. Tectum discontinuous, separated by irregular eufossae, foveae irregular-shaped.

Bellendena montana R. Br. 580
Faurea saligna Havr. 1343
Hollandaea sayerana (F. v. Muel.) L.S. Smith. 832
Orites fiebrigii (Perkins) Diels ex Sleum. 968
O. excelsa R. Br. 1444
Orothamus zeyheri Pappe & Hook. 970

v. Rugulae indistinct, subdivided into scabrae, supratectal nanoverrucae densely and irregularly distributed.

Cenarrhenes nitida de la Bill. 581
Eucarpha (Knightia) deplanchei (Veill. ex Brongn. & Gris.) Johnson & Briggs. 1585
Grevillea australis R. Br. 499
Leucadendron concavum Williams. 1524
Stirlingia tenuifolia Endl. 643

B. Tectum much coarser and uneven in elevation. Fig. 2, H.

Scabrae 0.4-1.0 μm diameter, intermixed with rugulae, 0.3-1.1 μm wide, foveae 0.1-0.4 μm diameter, mainly confined to fossae.

Malagasia (Macadamia) alticola (Capuron) Johnson & Briggs. 916

X. *Scabro-foveolate:* Fig. 2, I.

Scabrae 0.1-0.8 μm diameter; foveae 0.1-0.2 μm diameter, mainly confined to fossae, also occasionally occurring in scabrae; supratectal nanoverrucae 0.1-0.5 μm diameter also present.

i. Scabrae well-developed and more or less isodiametric.

Dilobeia thouarsii Thouars. 959
Helicia australasica F. v. Muel. 1567
Roupala brasiliensis Kl. 838

ii. Scabrae, fossae and foveae poorly developed.

Faurea mcnaughtonii Phill. 1100
Persoonia oblongata A. Cunn. 733

XI. *Scabro-foveo-gemmate:*

A. Scabrae more or less isodiametric, foveae mainly confined to equators and pore areas. Fig. 2, J.

Scabrae 0.1-0.5 μm diameter, confined to poles; foveae 0.1-0.2 μm diameter, supratectal nanogemmae and gemmae 0.2-1.0 μm diameter irregularly distributed.

Protea neriifolia R. Br. 1542
P. Suzannae Phill. 1546
P. Tenex R. Br. 68[s]

B. Scabrae irregular-shaped, intermixed with foveae. Fig. 2, K.

Scabrae 0.3-0.8 μm diameter, slightly tending towards rugulae; foveae 0.1-0.3 μm diameter, mainly confined to fossae; supratectal nanogemmae and gemmae 0.4-1.4 μm diameter sparsely distributed.

Grevillea acaciodes Gardener (MS). 1443

XII. *Undulo-rugulo-foveolate:* Fig. 2, L.

Undulation gentle; rugulae 0.2-1.3 μm wide; foveae 0.1-0.3 μm (occasionally up to 0.5 μm) diameter, more or less uniformly distributed.

Grevillea alpina Lindl. 1589
G. lanigera A. Cunn. 249
G. striata R. Br. 1442
Mimetes fimbriaefolia Salisb. 464

XIII. *Undulo-foveolate:*

A. Tectum gently undulate. Fig. 3, A.

Undulation gentle; foveae 0.1-0.9 μm diameter, more or less uniformly distributed; supratectal nanoverrucae and rarely verrucae 0.1-1.0 μm diameter, also present.

i. Distribution of surface pattern more or less uniform.

Grevillea floribunda R. Br. 774

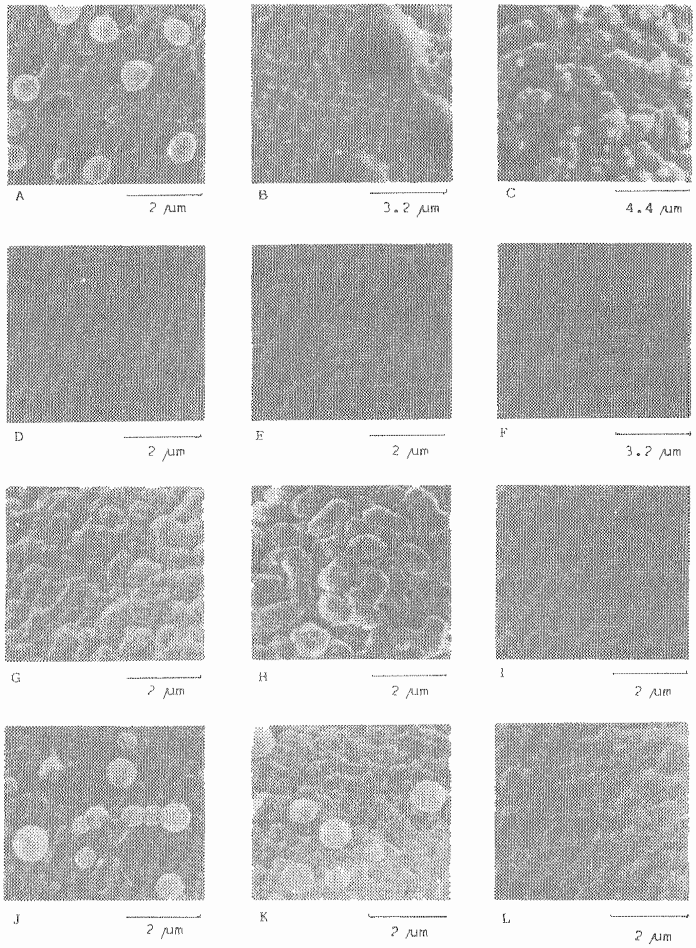


Fig. 2. A. Reticulo-Foveo-Gemmate *Hakea dactyloides*
B. Reticulo-Foveo-Verrucose *Beauprea spathulifolia* x 6000
C. Reticulo-Foveo-Spinulose *Aulax pinifolia* x 45000
D. Foveolate A. *Sorocephalus salsoloides*
E. – do – B. *Spatalla nubicola*
F. Rugulo-Foveolate *Bakksia aspienifolia* x 6000
G. Scabro-Rugulo-Foveolate A. *Darlingia ferrugiana*
H. – do – B. *Malagasia alticola*
I. Scabro-Foveolate *Helicia australasica*
J. Scabro-Foveo-Gemmate A. *Protea nerifolia*
K. – do – B. *Grevillea acaciodes*
L. Undulo-Rugulo-Foveolate *Mimetes fimbriaefolia*

G. laurifolia Sieb. & Schult. 753
G. punicea R. Br. 1469
G. thelemanniana Endl. 1465
Hakea glabella R. Br. 1554

ii. Tectum paraisopolar i.e. rugulo-foveolate towards distal pole and undulo-foveolate towards the rest area.

Hakea purpurea Hook. 1135

B. Tectum strongly undulate. Fig. 3, B.

Undulation strong; foveae 0.1-0.7 μm diameter, more or less uniformly distributed; supratectal nanoverrucae and rarely verrucae 0.1-1.3 μm diameter, also present.

Grevillea robusta R. Br. 1509
G. sessilis White & Francis. 1556

XIV. *Cristo-foveolate:* Fig. 3, C.

Cristae 0.5-2.5 μm wide, seeming to be subdivided into scabrae; foveae 0.1-0.4 μm diameter, irregularly distributed; supratectal nanoverrucae 0.1-0.4 μm diameter, irregularly distributed.

Grevillea crithmifolia R. Br. 1621
G. dielsiana Gardener. 1583
G. pinnatifida Bailey. 1575
G. pyramidalis A. Cunn. 1606

XV. *Foveo-spinulose:* Fig. 3, D.

Foveae 0.1-0.7 μm diameter; supratectal spinules 0.3-0.7 μm long, more or less uniformly distributed, rarely bacula 0.3-1.0 μm long also present.

Lambertia uniflora R. Br. (*)

XVI. *Subscabro-baculate:* Fig. 3, E.

Subscabrae poorly developed; supratectal bacula 0.5-1.5 μm long, 0.1-1.2 μm wide, more or less uniformly distributed, rarely gemmae and verrucae also present.

i. Tectum more or less flat.

Hakea microcarpa R. Br. 691

ii. Tectum uneven in elevation and suprafoveae also present.

Embothrium coccineum Forst. 1647
Xylomelum pyriforme J.E. Smith. 49

XVII. *Foveo-verrucose:* Fig. 3, F.

Foveae 0.1-0.5 μm diameter; supratectal nanoverrucae and verrucae 0.1-2.5 μm diameter, more or less uniformly distributed.

i. Verrucae slightly raised above tectum, and densely crowded towards middle of distal pole.

Xylomelum angustifolium Kipp. 1572

ii. Verrucae uniformly distributed, tectum slightly uneven in elevation.

Garnieria spathulifolia (Brongn. & Gris.) Brongn. & Gris. (*)
Toronia (Persoonia) toru (A. Cunn.) Johnson & Briggs. 1221

iii. Verrucae less in number and irregularly distributed.

Telopea truncata R. Br. (*)

iv. Verrucae tending to be fused apparently reticuloid or irregularly arranged, occurring on the top of irregular-shaped insulae.

Agastachys odorata R. Br. 582
Lambertia formosa J.E. Smith 5

XVIII. *Scabrate:* Fig. 3, G.

Scabrae 0.1-0.6 μm diameter, almost totally eliminating around pores; Supratectal nanoverrucae 0.1-0.4 μm diameter, also rarely present.

Panopsis rubescens Pitt. 971

XIX. *Verrucose:* Fig. 3, H.

Supratectal nanoverrucae and verrucae 0.2-1.0 μm diameter, more or less uniformly distributed.

Grevillea synapheae R. Br. 1485
Persoonia linearis Andr. 1471

XX. *Subpsilate:* Fig. 3, I.

Tectum subpsilate, slightly undulating, botryoidal, occasionally suprafoveae present; supratectal nanoverrucae and rarely verrucae, 0.1-1.0 μm diameter also present.

Pycnonia (Persoonia) saccata (R. Br.) Johnson & Briggs. 1577

XXI. *Undulo-foveo-verrucose:* Fig. 3, J.

Undulation gentle; foveae 0.1-0.3 μm diameter; supratectal nanoverrucae and verrucae 0.1-0.5 μm diameter, more or less uniformly distributed.

i. Tectum slightly tending towards rugulae, verrucae tending to fuse with each other.

Grevillea buxifolia R. Br. 9

ii. Tectum seeming to be slightly scabro-rugulo-foveolate, verrucae tending towards gemmae.

Hakea tephrosperma R. Br. 1474

XXII. *Foveo-ornate:* Fig. 3, K.

Ornamentation curvimurate, muri 0.1-4.5 μm wide, lumina anastomosing; foveae 0.1-0.5 μm diameter, confined to luminal floor, occasionally occurring in muri, supratectal nanoverrucae and verrucae 0.5-1.0 μm diameter, also present, supratectal columellae (arrow) also observed.

i. Tectum irregularly ornate, luminal floor scabrate.

Grevillea acanthifolia A. Cunn. 1547

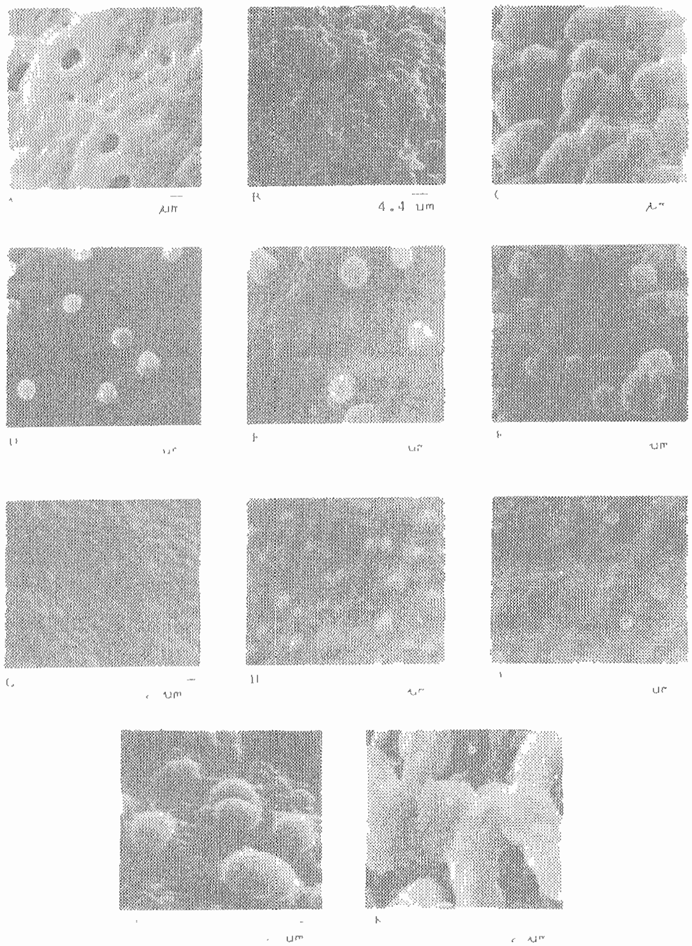


Fig. 3.	A.	Undulo-Foveolate	A. *Hakea purpurea*
	B.	– do –	B. *Grevillea sessilis* x 45000
	C.	Cristo-Foveolate	C. *G pyramidales*
	D.	Foveo-Spinulose	*Lambertia uniflora*
	E.	Subscabro-Baculate	*Hakea microcarpa*
	F.	Foveo-Verrucose	*Toronia toru*
	G.	Scabrate	*Panopsis rubescens*
	H.	Verrucose	*Grevillea synapheae*
	I.	Subpsilate	*Pycnonia saccata*
	J	Undulo-Foveo-Verrucose	*Hakea tephrosperma*
	K.	Foveo-Ornate	*H. eucalyptoides* x 6000

ii. Tectum two-layered i.e. outer mural layer (see a) connected by short supratectal columellae with inner layer (see b).

Hakea eucalyptoides R. Br. 1464
H. multilineata Meissn. 1445

Discussion

Although the scanning electron microscope has revealed micromorphological details of surface patterns of pollen grains, which are not resolved either by the transmission electron microscope or by an optical microscope, the sectional study of the exine cannot be as accurately studied by the scanning electron microscope as by the transmission electron microscope. The real advantage of the scanning electron microscope in the sectional study of exine lies in the realm of middle magnitude structures in three dimensions. However, the optical microscope is very useful for basic study of pollen morphology, especially for studying the details of aperture.

It was noted that the surface pattern of pollen grains was more completely analysed by the scanning electron microscope than the optical microscope which exaggerates some features or does not reach the full depth of focus of exine sculpture. For example, exine with contextate tectum seem to be smooth to the optical microscope viz, *Petrophile fucifolia, P. seminuda, Serruria linearis, S. elongata* etc. (Fig. 1–C, I, D, E respectively), and foveae occurring in the middle of contextate tectal depressions look like the meshes of reticulum to the optical microscope viz, *Sorocephalus salsoloides, Paranomus bracteolaris* (Fig. 2-D, F; 4–C respectively).

In majority of pollen grains the nature of some supratectal elements (viz. nanogemmae, nanoverrucae, nanospinules) is uncertain. Whether they are developed from the upper part of exine or are ubisch bodies (orbicules, Heslop-Harrison, 1968) derived from the tapetum is not clear. Echlin (1973) has suggested that ubisch bodies although generally uniform in morphology are sometimes verrucae or spinules, exhibiting a greater similarity to the pollen exine.

The study of pollen exine surface pattern of modern Proteaceae reveals that many genera including nearly all those with large number of species (eg. *Grevillea* & *Hakea*) are not pollen-morphologically homogeneous. Such genera often lack unique combinations of pollen characters that could distinguish them from other genera of the family. At the species level, micromorphological differences in the detail and distribution of surface pattern, pore structure, shape and size of pollen have been found to exist. In some instances these features appear to be of diagnostic value. For example, the pollen of *Franklandia fucifolia* and *F. triaristata* (Fig. 4–A, B) are clavate, but the pollen and clavae of the latter species are much bigger than those of the former. In other instances, the sample size is yet too small to confirm whether it could be of diagnostic value. For example, the pollen of *Paranomus bracteolaris* and *P. capitatus* are oblate, small-sized with foveolate and contextate tectum, but the foveae (Fig. 4–C) are bigger in former species than those of tn latter (Fig. 4–D).

Certain genera possess unique surface pattern, but they are not distinguished by other characters such as pore structure, shape and size of pollen grains from other genera of the family. For example, *Aulax* produces reticulo-foveo-spinulose (Fig. 2–C) pollen, but its pore structure, size and shape range fall into the range of other genera.

Embothrium a South American genus produces pollen with subscabro-baculate (Fig. 3, E) surface pattern, which is also found in the Australian genera (*Hakea* & *Xylomelum*), but *Embothrium* though 2-porate, is distinct from the Australian 2-porate genera (*Austromuellers, Banksia, Dryandra* & *Musgravea*) in surface pattern.

Beauprea (Fig. 4, E) a South Pacific genus is quite odd in Proteaceae in producing 3-colpoidate pollen, but shape, size and surface pattern do invariably occur in the other genera of the family.

Franklandia is the only genus which produces clavate surface pattern (Fig. 1, A) pollen grains with intectate exine, and the shape and size (over 100 μm) hardly match the other genera of the family.

Usually the surface pattern on both hemispheres of pollen grains is similar; but dissimilar pattern is also present in some species (eg. *Adenanthos pungens, Hakea purpurea, Serruria vallaris, Sphalmium racemosum* etc.).

Conclusion

Pollen grains of Proteaceae are usually 3-aperturate except that *Austromuellera, Banksia, Dryandra, Embothrium* and *Musgravea* are 2-porate. The 3-aperturate pollen grains vary from isopolar to para-isopolar, and are triquetrous (deltoid, subtriquetrous, less often triquetrous), semiangular or more or less circular. However, 2-aperturate pollen grains are bilateral, concavo-convex to plano-convex. Some species which mainly produce 3-aperturate grains may also produce a small percentage of pollen with 2 or 4-8 apertures. The shape of pollen grains varies from peroblate to oblate (-oid) or oblate spheroidal, the majority of them are oblate. Size also varies from small to medium or large and less often very large. The apertures are pores (usually circular or sometimes equatorially or meridionally elliptical), less often poroid, which may be I or Y-shaped (*Protea*). The pollen of *Beauprea* are always colpoidate (Fig. 4, E); pores of *Banksia, Grevillea, Hakea, Xylomelum* possess an expanded pore membrane c. 0.5-13 μm above the pore margin (Fig. 4, F).

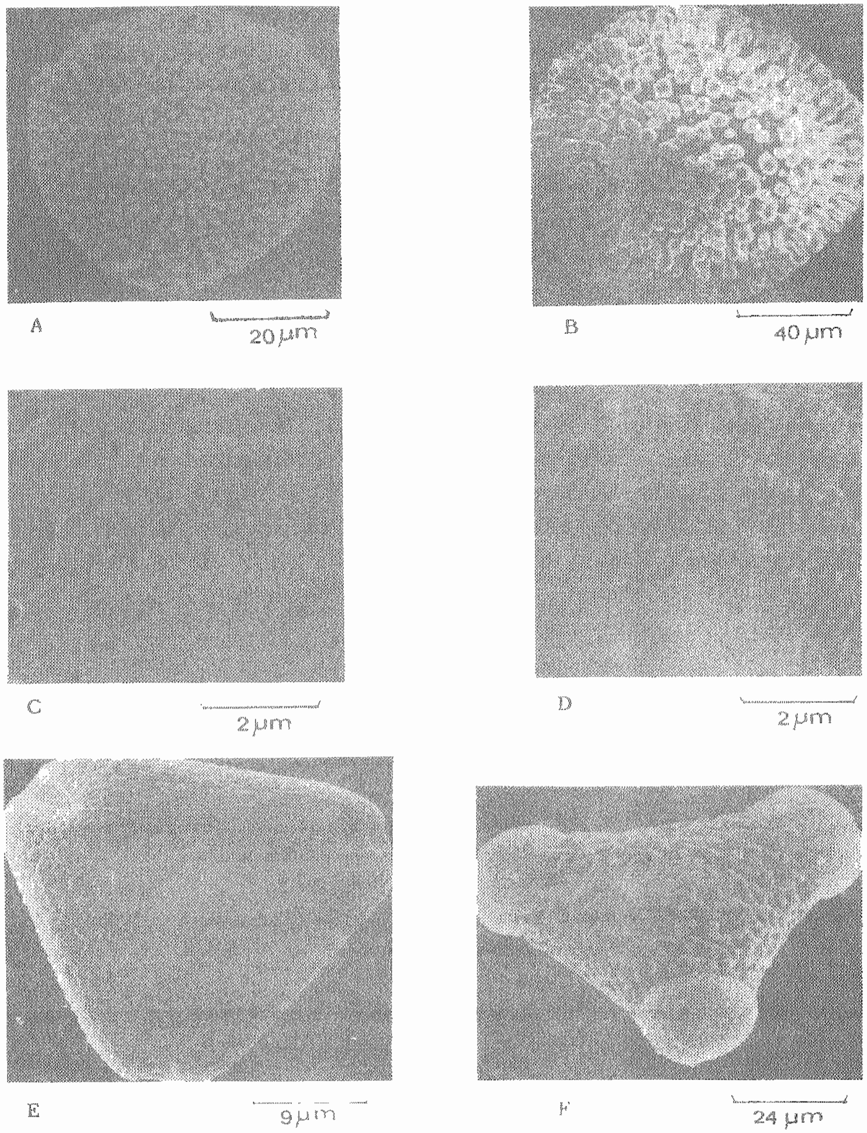


Fig. 4. A. *Franklandia fucifolia* x 1000
B. *F. triaristata* x 500
C. *Paranomus bracteolaris* x 3000
D. *P. capitatus* x 3000
E. *Beauprea elegans* x 2250
F *Hakea eucalyptoides* x 800 -

Exine thickness varies from 0.7-7.8 μm, but is usually ranging from 1.0-3.0 μm in thickness. Exine structure is usually tectate-perforate, but a small number of tectate-imperforate, semitectate and intectate (only in *Franklandia*) forms are also present in the family.

Pollen exine of modern Proteaceae reveals 22 main surface pattern types. The two commonest groups (i.e. reticulo-foveolate & reticulate, and foveolate, rugulo-foveolate, scabrorugulo-foveolate & scabro-foveolate) constitute about 80% of surface patterns of the family.

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