Pak. J. Bot., 17 (1): 87–106, 1985.

IMPLICATION OF POLLEN SURFACE PATTERN FOR SPECIES AND GENERIC-LEVEL CLASSIFICATION IN PROTEACEAE

HAROON R. MEMON

Department of Botany,
University of Sind, Jamshoro, Sind, Pakistan.

Abstract

Much parallelism in the gross characters of pollen of the family Proteaceae was found and many genera with large number of species were not pollen-morphologically homogeneous. Such genera often lack unique combinations of pollen characters which could distinguish them from other genera of the family. At species level, micromorphological differences and distribution of surface pattern, shape and size of pollen have been found to exist. Some tribes or subtribes with a small number of genera despite homogeneity in their pollen morphology could not be segregated from one another because invariable overlaping of surface pattern, shape an size of pollen grains was present throughout the family. However, on the basis of micromorphological study of the species examined, some inconsistencies were pointed out and alternative relationships have been suggested in correlation with the infrafamilial classification.

Introduction

The family Proteaceae owing to its southern hemisheric distribution pattern and phylogenetic position have remained the focus of attention. Johnson & Briggs (1963) giving the evidence on the internal phylogeny of Proteaceae, put forward a scheme of probable relationship within this well-developed and isolated family. Considering the findings and interpretations of Haber (1960, 1961, 1966 cited in Johnson & Briggs 1975) and Venkata Rao (1957, 1960, 1961, 1971 cited in Johnson & Briggs, 1975) to be confused and misleading. Johnson & Briggs (1975) revised their own work outlining the phylogenetic and taxonomic conclusions and have discussed many adaptive and morphological trend in the family.

The remarkable architecture of pollen exine is known to be distinctive for different taxa and each species retains its specific statistic which can be characterised on the bases of pollen morphology. Erdtman (1963) segregated two South American genera *Abolboda* and *Orectanthe* from the family Xyridaceae and referred them to a special family Abolbodaceae solely on the bases of pollen morphological characters. The pollen morphology

of family Proteaceae has revealed a wide spread heterogeneity and many genera including nearly all those with large number of species often lack unique combinations of pollen characters that could distinguish them from other genera of the family. Although some tribes and subtribes with a small number of genera show homogeneity in their pollen morphology, nonetheless, they could not be separated from one another because invariable overlaping of surface pattern, shape and size of pollen grains was present throughout the family (Memon, 1984a). In the present communication an attempt has been made to correlate the pollen surface pattern including shape and size for species- and generic-level with the infrafamilial classification proposed by Johnson &Briggs (1975).

Method

The preparation of pollen material for scanning electron microscopic study is described in Memon (1984a).

Results

Terms used for surface pattern are from Memon, 1984a; and shape and size of pollen are based on generic diagnosis. Voucher specimens are lodged in the palynological collection at School of Biological Sciences, University of Sydney; pollen of the species marked with (*) were taken from Herbarium sheets lodged at National Herbarium of N.S.W.; Vouch. spec. refers to voucher specimen.

I. SUBFAMILY *PERSOONIOIDEAE.*

Name of tribe, subtribe, genus and species	Vouc. spec.	Type of surface pattern	Shape class	Size class
i. BELLENDEAE				
Bellendena montana R.Br. (Monotypic)	580	Scabro-rugulo-foveolate	Oblate	Rather small
ii. PERSOONIEAE				
a) Persooniinae				
Acidonia angustifolia (Benth.) J. & B.	1559	Rugulo-foveolate	Oblate	Medium
Garnieria spathulifolia (Br. & Gr.) Br. & Gr.	(*)	Foveo-verrucose	Oblate to peroblatoid	Medium

Persoonia oblongata A. Cunn.	733	Scabro-foveolate	Oblate to oblate-spheroidal	Medium
P. linearis Andr.	1471	Verrucose		
Pycnonia saccata (R. Br.) J. & B.	1577	Subpsilate	Oblate to oblate-spheroidal	Medium
Toronia toru (A. Cunn.) J. & B.	1221	Foveo-verrucose	Subpsilate	Medium
b) Placosperminae				
Placospermum coriaceum White & Francis	837	Foveolate	Oblate (-suboblatoid)	Medium
II. SUBFAMILY *SPHALMIOIDEAE.*				
Sphalmium racemosum Brigs, Hayland & Johnson (Monotypic)	1662	Reticulo-foveolate	Oblate	Medium
III. SUBFAMILY *PROTEOIDEAE.*				
i. CONOSPERMEAE				
a) Cenarrheninae				
Agastachys odorata R. Br. (Monotypic)	582	Foveo-verrucose	Suboblate	Medium
Beauprea balansae Br. & Gr.	953	Reticulo-foveo-gemmate	Oblate	Medium
B. spathulifolia Br. & Gr.	823	Reticulo-foveo-verrucose		
B. elegans Br. & Gr.	1494	Reticulo-foveolate		
Beaupreopsis paniculata Virot. (Monotypic)	955	Rugulo-foveolate	Oblatoid	Small
Cenarrhenes nitida de la Bill. (Monotypic)	581	Scabro-rugulo-foveolate	Suboblate, oblate or oblatoid	Rather small
Symphionema montanum R. Br.	1452	Reticulo-foveolate	Oblatoid	Small to medium
S. paludosum R. Br.	160	–do–		

b) Conosperminae				
Conospermum stoechadis Endl.	754	Rugulo-foveolate	Prolate to oblatoid	Rather large to large
C. tenuifolium R. Br.	735	Foveolate		
Synaphaea favosa R. Br.	974	Foveolate	Oblatoid	Rather large to large
S. polymorpha R. Br.	616	–do–		
c) Dilobeiinae				
Dilobeia thouarsii Thouars (Monotypic)	959	Scabro-foveolate	Oblate to suboblate	Rather small
d) Petrophilinae				
Isopogan dawsonii R.T. Bak.	1462	Reticulo-foveolate	Oblate to oblatoid	Rather small to large
I. divergens R. Br.	1461	Reticulate		
Petrophile fucifolia Kn.	125	Reticulo-foveolate	Oblate	Rather small rather large
P. heterophylla Lindl.	1602	–do–		
P. semifurcata Lindl.	1565	–do–		
P. serruriae R. Br.	1500	–do–		
P. teritifolia R. Br.	637	–do–		
P. seminuda Lindl.	1498	Reticulate		
P. squamata R.Br.	1495	–do–		
e) Stirlingiinae				
Stirlingia tenuifolia Endl.	643	Scabro-rugulo-foveolate	Oblatoid	Rather small to large
II. FRANKLANDIEAE				
a) Adenanthinae				
Adenanthos barbigera Lindl.	644	Reticulo-foveolate	Oblate-spheroidal to oblate	Rather small

A. pungens Meissn.	1560	–do–		
b) Franklandiinae				
Franklandia fucifolia R. Br.	829	Clavate	Oblate-spheroidal	Large to very large
F. triaristata Benth.	996	–do–		
iii. PROTEEAE				
a) Aulacinae				
Aulax cneorifolia Kn.	575	Reticulo-foveo-spinulose	Suboblate	Medium
A. pinifolia (L.) Berg.	(*)	–do–		
Leucadendron concavum William	1524	Scabro-rugulo-foveolate	Oblate	Rather small to rather large
L. salignum Berg.	331[s]	Reticulo-foveolate		
b) Proteinae				
Diastella serphpyylifolia Salisb.	465[s]	Reticulate	Oblate to Peroblatoid	Small to medium
Faurea saligna Harv.	1343	Scabro-rugulo-foveolate	Oblatoid	Small to rather large
F. mcnaughtonii Phill.	1100	Scabro-foveolate		
Leucospermum cordifolium (Salsib. ex Kn.) Rourke	1511	Reticulo-foveolate	Oblatoid	Small to rather large
L. hypophyllocarpo-	*463*			
L. hypophyllocarpo-dendron (L.) Druce	463[s]	–do–		
L. alpinum (Salisb. ex Kn.) Rourke	1527	Foveolate		
Mimetes argentea Knight.	1531	Reticulo-foveolate	Oblatoid	Medium
M. fimbriaefolia Salisb.	464	Undulo-rugulo-foveolate		

Orothamus zeyheri Pappe. (Monotypic)	970	Scabro-rugulo-foveolate	Oblatoid	Rather small to medium
Paranomus bracteolaris Salisb. ex Kn.	1526	Foveolate	Oblatoid	Rather small to medium
P. capitatus (R. Br.)	1516	–do–		
P. reflexus (Phill. & Hutch.) Fourcade	538[S]	Reticulo-foveolate		
Protea nerifolia R. Br.	1542	Scabro-foveo-gemmate	Oblatoid	Small to medium
P. suzannae Phill.	1546	–do–		
P. tenex R. Br.	68[S]	–do–		
Serruria abrotanifolia Salisb. ex Kn.	1515	Reticulo-foveolate	Oblate to peroblate	Rather small to medium
S. elongata R. Br.	1519	–do–		
S. linearis Salisb. ex Kn.	1533	–do–		
S. pedunculata (Lam.) R. Br.	513[S]	–do–		
S. vallaris Kn.	536[S]	–do–		
Sorocephalus capitatus Rourke	1522	Foveolate	Oblate to oblatoid	Rather small
S. salsoloides R. Br.	973	–do–		
Spatalla curvifolia Rourke	1520	Reticulo-foveolate	Oblate to oblatoid	Small to medium
S. thyrsiflora Salisb. ex Kn.	1512	–do–		
S. caudata (Th.) R. Br.	515[S]	Foveolate		
S. nubicola Rourke	1523	–do–		
IV. SUBFAMILY *CARNARVONIOIDEAE*				
Carnarvonia araliaefolia F.v.M. (Monotypic)	957	Reticulo-foveolate	Oblate to oblate-spheroidal	Small

V. SUBFAMILY *GREVILLEOIDEAE*

i. ORITEAE

Neorites kerediana (*) L.S. Smith. (Monotypic)		Reticulo-foveolate	Oblate to oblatoid	Small to rather small
Orites excelsa R. Br.	1444	Scabro-rugulo foveolate	Oblate (-iod)	Small to medium
O. fiebrigii (Perkins) Diel. ex Sleum.	968	–do–		

ii. KNIGHTIEAE

a) Cardwelliinae

Cardwellia sublimis F.v.M. (Monotypic)	957	Reticulo-foveolate	Oblate-spheroidal	Medium

b) Knightiinae

Darlingia darlingiana (F.v.M.) Johnson (F.v.M.) Johnson	958	Scabro-rugulo-foveolate	Oblatoid	Small to medium
D. ferrugiana F.M. Bailey	825	–do–		
Eucarpha deplanchi (Vieill. ex Br. & Gr.) J. & B.	1585	Scabro-rugulo-foveolate	Oblate to oblatoid	Small to medium
E. strobilina (R. Br.)	1003	–do–		
Knightia excelsa R. Br. (Monotypic)	834	Reticulo-foveolate	Oblate	Rather small to medium

iii. EMBOTHRIEAE

a) Buckinghamiinae

Buckinghamia celsissima F.v.M. (Monotypic)	727	Rugulo-foveolate	Oblatoid	Medium

Opisthiolepis heterophyllus L.S. Smith (Monotypic)	838	Foveolate	Oblate	Rather small
b) Embothriinae				
Embothrium coccineum Forst. (Monotypic)	1447	Subscabro-baculate	Oblatoid	Medium to large
Oreocallis wickhmiana W. Hill & F.v.M.	736	Rugulo-foveolate	Oblate to suboblate (-iod)	Medium to large
Telopia speciosissima R. Br.	240	Foveolate	Oblate	Medium
T. truncata R. Br.	1208	Foveo-verrucose		
c) Lomatiinae				
Lomatia myricoides (Gaertn. f.) Domin.	765	Reticulo-foveolate	Oblate (-iod) to suboblate	Rather small to medium
L. polymorpha R. Br.	799	–do–		
L. silaifolia (Sm.) R. Br.	53	–do–		
d) Stenocarpinae				
Stenocarpus heterophyllus Br. & Gr.	1556	Reticulo-foveolate	Oblate to oblatoid	Rather small to medium
S. salignus R. Br.	1501	Foveolate		
Stangea linearis Meissn.	839	Reticulo-foveolate	Oblatoid	Rather small to medium
iv. GREVILLEEAE				
Finschia chloroxantha Diel.	828	Rugulo-foveolate	Oblate to peroblate	Large
Grevillea shuttleworthiana Meissn.	751	Reticulo-foveolate	Oblate	Rather small to very large

G. brownii Meissn.	1453	Foveolate		
G. australis R. Br.	499	Scabro-rugulo-foveolate		
G. acacioides Gardner (M)	1443	Scabro-foveo-gemmate		
G. alpina Lindl.	1589	Undulo-rugulo-foveolate		
G. lanigera A. Cunn.	249	–do–		
G. striata R. Br.	1442	–do–		
G. floribunda R. Br.	774	Undulo-fovoelate		
G. laurifolia Sieb. & Schult.	753	–do–		
G. punicia R. Br.	1469	–do–		
G. robusta R. Br.	1509	–do–		
G. sessilis White & Francis	1586	–do–		
G. thelemanniana Endl.	1465	–do–		
G. buxifolia R. Br.	9	Undulo-rugulo-verrucose		
G. crithmifolia R. Br.	1621	Cristo-foveolate		
G. dielsiana Gardner (M)	1583	–do–		
G. pinnatifida Bailey	1575	–do–		
G. pyramidales A. Cunn.	1606	–do–		
G. acanthifolia A. Cunn.	1547	Foveo-ornate		
G. synaphae R. Br.	1485	Verrucose		
Hakea lorea R. Br.	1201	Foveolate	Oblate to suboblate	Medium to very large
H. dactyloides Cav.	740	Reticulo-foveo-gemmate		
H. glabella R. Br.	1554	Undulo-foveolate		
H. purpurea Hook.	1135	Undulo-rugulo-foveolate		
H. tephrosperma R. Br.	1474	Undulo-foveo-verrucose		
H. eucalyptoides R. Br.	1464	Foveo-ornate		
H. multilineata	1445	–do–		

Meissn.				
H. microcarpa R. Br.	691	Subscabro-baculate		
v. HELICIEAE				
a) Heliciinae				
Helicia glabriflora F.v.M.	584	Scabro-rugulo-foveolate	Oblate to suboblate or oblatoid	Small to rather small
H. australasica F.v.M.	1567	Scabro-foveolate		
Xylomelum angustifolium Kipp.	1572	Foveo-verrucose	Oblate or peroblate to suboblate	Medium to rather large
X. pyriforme J.E. Smith	49	Subscabro-baculate		
b) Hollandaeinae				
Hollandaea sayerana F.v.M. (Monotypic)	832	Scabro-rugulo-foveolate	Oblate to suboblate	Small to medium
c) Triuniinae				
Triunia youngiana (F.v.M.) J. & B.	1381	Reticulo-foveolate	Oblate	Rather small
vi. MACADAMIEAE				
a) Floydiinae				
Floydia praealta (F.M. Bailey) J. & B. (Monotypic)	966	Reticulo-foveolate	Oblate	Rather small
b) Gevuininae				
Gevuina avellana Mol.	961	Reticulo-foveolate	Oblate to oblate-spheroidal	Medium

G. vitiensis (Turr.) J. & B.	852	–do–		
Sleumerodendron austrocalifdonicum (Br. & Gr.) Virot.	1660	Reticulo-foveolate	Oblate	Medium
c) Hicksbeachiinae				
Athertonia diversifolia (Sleum.) J. & B.	831	Reticulo-foveolate	Oblatoid	Medium
Heliciopsis artocarpoides Sleum.		Reticulate	Oblate (-iod) to suboblate (-iod)	Medium to large
Hicksbeachia pinnatifida F.v.M. (Monotypic)	830	Reticulo-foveolate	Oblatoid	Small to medium
Virotia rousselii (Sleum.) J. & B.	967	Reticulo-foveolate	Oblate to oblatoid	Small to medium
Malagasia alticola (Capuron) J. & B.	816	Scabro-rugulo-foveolate	Oblate	Rather small
d) Lambertiinae				
Lambertia multiflora Lindl.	965	Rugulo-foveolate	Oblate to oblatoid	Small to medium or rather small
L. uniflora R. Br.	(*)	Foveo-spinulose		
L. formosa	5	Foveo-verrucose		
e) Macadamiinae				
Brabeium stellatifolium L.	70[s]	Scabro-rugulo-foveolate	Oblate-spheroidal	Medium
Macadamia whelani F.M. Bailey	1008	Foveolate	Oblate	Small to medium
Panospis rubescens Pitt.	971	Scabrate	Oblatoid	Rather small to medium

f) Roupalinae

Kermadecia rutundifolia Br. & Gr.	833	Reticulo-foveolate	Oblate (-iod)	Medium to large
Roupala brasiliensis Kl.	838	Scabro-foveolate	Oblatoid	Small to medium

vii. BANKSIEAE

a) Banksiinae

Banksia serratifolia Salisb.	722	Foveolate	Suboblate	Small to medium
B. aspilinifolia Salisb.	91	Rugulo-foveolate		
B. collina R. Br.	245	–do–		
Dryandra nivea R. Br.	1557	Rugulo-foveolate	Oblate	Medium to large
D. serra R. Br.	1571	Scabro-rugulo-foveolate		

b) Musgraveinae

Austromuellera trinervia C.T. White (Monotypic)	822	Scabro-rugulo-foveolate	Oblate	Rather small
Musgravea stenostachya F.v.M.	835	Scabro-rugulo-foveolate	Oblatoid	Rather small

Discussion

Although the micromorphological study of pollen surface pattern, shape and size of Proteaceae has demonstrated striking diagnostic features similar to the floral, chromosomal and vegetative characters of the family, these features show some inconsistencies with the taxonomic classification of the family into subfamilies, tribes and subtribes. However, some genera retain individually unique surface pattern (e.g. *Aulax* – reticulo-foveo-spinulose, *Franklandia* – clavete, *Panopsis* – scabrate, *Pycnonia* – subpsilate), and some tribes and subtribes with a small number of genera show homogeneity in their pollen surface pattern, though other characters such as shape and size range of pollen do not distinguish them from other members of the family. For example, the tribe Banksieae of subfamily Grevilleoideae produces biporate and bilateral pollen with foveolate, rugulo-foveolate and scabro-rugulo-foveolate surface patterns, which are phylogenetically

more or less close to each other (Memon, 1984c). This is a distinctive combination of characters though biporate and bilateral pollen grains are also produced by *Embothrium* of the tribe Embothrieae (Grevilleoideae), and surface patterns similar to Babksieae are wide spread throughout the family. Similarly, the subtribe Buckinghamiinae of tribe Embothrieae producing foveolate and rugulo-foveolate pollen resembles the pollen of subtribe Conosperminae (Conospermeae) in pollen surface pattern and more or less in shape except that the pollen of the latter subtribe are bigger than those of the former subtribe.

It was also noted that some subtribes or tribes despite the homogeneity in their pollen morphology, could not be segregated from other subtribes or tribes of the family. For example the subtribe Peterophilinae of tribe Conospermeae (Proteoideae) produces oblate to oblatoid, small to large-sized pollen with reticulo-foveolate and reticulate surface patterns, but such pattern and other features are wide spread throughout the family (see results).

In view of this, it could be concluded that pollen morphology cannot be solely used as the base of taxonomic classification of the family Proteaceae. However, if it is accepted that pollen morphology shows evolutionary sequences comparable to those in other organs, then it may need to be given as much weight as any other morphological character. On this assumption, in the light of pollen morphology of the species examined, some inconsistencies and alternative relationships have been suggested in correlation with the recent taxonomic classification proposed by Johnson & Briggs (1975).

I. Subfamily Persoonioideae

Genera of subtribe Persooniinae (Persoonieae) show inconsistency in their pollen morphology. *Pycnonia* produces pollen with a unique surface pattern i.e. subpsilate; *Acidonia* produces rugulo-foveolate pollen grains; *Persoonia* produces pollen with scabro-foveolate and verrucose surface patterns; and *Garnieria* and *Toronia* produce foveo-verrucose pollen grains. Phylogenertically, the surface pattern of *Acidonia, G rnieria* and *Toronia* is close to each other (Memon, 1984c). *Persoonia* Producing two types of surface patterns comes fairly close to *Pycnonia.* Therefore, the subtribe Persooniinae may be considered carefully.

The unigeneric subtribe Placosperminae (Persoonieae), with *Placospermum* produces oblatoid, medium-sized and foveolate pollen grains. Venkata Rao (1971) has pointed out some primitive features in its inflorescence, flower and carpels. However, he has also stressed advanced features in its stamens, and occasional unisexuality, some advanced adaptations in the follicular fruit and occurrence of winged seeds. Johnson & Briggs (1975) have suggested that "in fact *Palcospermum* has much in common with

the *Garnieria* – *Persoonia* group, both in its very large chronosomes and in morphological features; it does indeed preserve the greatest number of primitive character-states in the family, but *Persoonia* and *Bellendena* R. Br. each preserves a few primitive features which have been modified in *Placospermum*". Pollen of *Placospermum* is undoubtedly primitive and lies near the base of evolutionary line of derivation (Memon, 1984c), and phylogenetically, its surface pattern is more or less close to *Garnieria, Toronia* and *Acidonia.* Besides, *Placospermum* also resembles these genera in shape and size of pollen and in basic chromosome number. Therefore, it is suggested that *Placospermum* may be grouped with *Garnieria, Toronia* and *Acidonia.*

II. Subfamily Sphalmioideae

The unigeneric subfamily Sphalmioideae with *Sphalmium,* producing oblate and medium-sized pollen with reticulo-foveolate surface pattern, resembles pollen grains of *Adenanthos barbigera, A. pungens, Mimetes argentea,* and more or less *Petrophile teretifolia,* and some species of *Isopogan, Leucadendron, Paranomus, Serruria* and *Spatalla* of subfamily Proteoideae, and *Floydia, Kermadecia, Knightia, Lomatia* and *Sleumerodendron* of subfamily Grevilleoideae. However, the above genera of subfamily Grevilleoideae except *Knightia,* which unlike *Sphalmium* and the other genera of the subfamily Proteoideae, have costae in their pores. Johnson & Briggs (1975) have stressed some similarities of *Sphalmium* to the subfamily Grevilleoideae in the folicles and wood anatomy. They have also stated that "*Sphalmium* has evidently had a long and not very successful evolutionary history since its divergence somewhere near the base of the 'line' which led to the Grevilleoideae". The pollen morphology adds very little evidence in placing *Sphalmium* in a more exact relationship with Grevilleoideae and Proteoideae, nonetheless, it is suggested that the taxonomic position of *Sphalmium* perhaps needs reconsideration.

III Subfamily Proteoideae

Adenanthos and *Franklandia* are quite inconsistent in the same tribe Franklandieae. The former genus produces semitectate and reticulo-foveolate pollen grains, whereas the the latter produces intectate and clavate pollen grains, which are absent in the other members of the family. Earlier, Johnson & Briggs (1963) and Venkata Rao (1971) have placed *Adenanthos* and *Franklandia* separately. Therefire, it is suggested that *Adenanthos* may be transferred perhaps to the tribe Proteae with which its pollen grains are consistent. (Venkata Rao, 1971, has put *Adenanthos* into a separate tribe Proteeae) and only *Franklandia* be left in the tribe Franklandieae, or perhaps it may be raised to the rank of a subfamily.

Pollen grains of a subtribe Cenarrheninae of tribe Conospermeae are quite inconsistent. *Symphionema* produces reticulo-foveolate pollen grains; *Agastachys* produces

pollen with foveo-verrucose surface pattern; *Beaupreopsis* produces pollen with foveolate surface pattern; and *Beauprea* unlike other genera of the entire family produces 3-colpoidate pollen with reticulo-foveo-gemmate, reticulo-foveo-verrucose and rugulo-foveolate surface patterns. Phylogenetically, the surface pattern of pollen of *Beaupreopsis* and *Agastachys* lie in one evolutionary line of derivation, *Beauprea* and *Symphionema* in the other, and *Cenarrhenes* in the third evolutionary line of derivation (Memon, 1984c). It is therefore suggested that this group of genera be reconsidered carefully.

Aulax and *Leucadendron* are quite inconsistent in the subtribe Aulacinae (Proteeae). The former genus produces pollen with a unique surface pattern i.e. reticulo-foveo-spinulose in the family, whereas the latter genus produces reticulo-foveolate and scabro-rugulo-foveolare pollen grains. These genera stand apart cytologically and morphologically (Johnson & Briggs, 1975), and are linked together by possession of unisexual flower (a character that could have evolved independently), clustering of unit inflorescence in *Aulax* and the strobiliform inflorescence and lygnified fruiting bracts of *Leucadenfron* and similarity in leaf form. Earlier, Johnson & Briggs (1963) has treated both *Aulax* and *Leucadendron* separately. Venkata Rao (1971) has put *Aulax* in a unigeneric tribe Aulaceae on the bases of its spherical pollen grains and a supposedly unique inflorescence type in the female plants, and *Leucadendron* into a separate unigeneric subtribe Leucadendrinae. Though, phylogenetically, the surface pattern (i.e. reticulo-foveo-spinulose) of *Aulax* and some species of *Leucadendron* (i.e. reticulo-foveolate) lie in the same evolutionary line of derivation, but still other species of *Leucadendron* produce scabrorugulo-foveolate pollen grains and lie in a separate evolutionary line of derivation (Memon, 1984c). The present findings support the earlier interpretation and classification proposed by Johnson & Briggs (1963) and Venkata Rao (1971).

The subtribe Proteinae (Proteeae) is inconsistent in its pollen morphology. *Protea* produces scabro-foveo-gemmate pollen grains; *Faurea* and *Orothamus* produce pollen with scabro-rugulo-foveolate surface pattern; *Mimetes* produces reticulo-foveolate and undulo-rugulo-foveolate pollen grains; *Diastella* produces reticulate pollen grains; and *Leucospermum, Paranomus, Serruria, Sorocephalus* and *Spatalla* produce pollen with reticulo-foveolate and foveolate surface patterns. Phylogenetically, *Faurea, Orothamus* and *Protea* lie in the same evolutionary line, though *Protra* produces an advanced type of surface pattern (Memon, 1984c); *Diastella, Serruria* and some species of *Leucospermum, Mimetes, Paranomus* and *Spatalla* lie in one evolutionary line of derivation, and *Sorocephalus* and some species of *Leucospermum, Mimetes, Paranomus* and *Spatalla* lie in the other (Memon, 1984c). Johnson & Briggs (1975) have pointed out a wide range of ecological and habit types in the subtribe Proteinae, and have also added that adaption has occurred in the inflorescence and flower. In view of the inconsistency in pollen grains and evolutionary sequence, the subtribe Proteinae perhaps needs a careful reconsideration.

IV. Subfamily Carnarvonioideae

The unigeneric subfamily Carnarvonioideae, with *Carnarvonia* producing oblate to oblate-spheroidal and small-sized pollen with reticulo-foveolate surface pattern, resembles *Leucospermum cordifolium* and *Serruria pedunculata* of subtribe Proteinae (Proteeae, Proteoideae) except that the pollen of *Carnarvonia* are smaller. However, phylogenetically, the surface pattern of *Carnarvonia* is close to 14 genera of subfamily Proteoideae, and 18 genera (10 of tribe Macadamieae) of the subfamily Grevilleoideae (see results). Earlier, Johnson & Briggs (1963) had put *Carnarvonia* in the subfamily Grevilleoideae without assigning a tribal position. Venkata Rao (1971) has placed *Carnarvonia* into the tribe Macadamieae. In view of this, the author considers the classification of Venkata Rao (1971) more appropriate, or perhaps *Carnarvonia* may be treated in a unigeneric tribe of the subfamily Grevilleoideae.

V. Subfamily Grevilleoideae

Neorites and *Orites* are inconsistent in the same tribe Oriteae. The former genus produces pollen with reticulo-foveolate surface pattern, whereas the latter produces scabro-rugulo-foveolate surface pattern. Phylogenetically, the surface pattern of these genera lie apart, both lying in different evolutionary lines of derivation (Memon, 1984c). Pollen-morphologically, *Neorites* is close to *Knightia* of the subtribe Knightiinae (Knightieae), and *Orites* has similar pollen to *Darlingia* and *Eucarpha.* Therefore, it is suggested that *Neorites* be transferred from the tribe Oriteae to the tribe Knightieae and subtribe Knightiinae with *Knightia,* and *Darlingia* and *Eucarpha* be transferred from tribe Knightieae and subtribe Knightiinae to the tribe Oriteae with *Orites.*

Pollen grains of *Helicia* and *Xylomelum* of the subtribe Heliciinae (tribe Helicieae) are inconsistent in the same subtribe. The former genus produces scabro-rugulo-foveolate and scabro-foveolate surface patterns and small to rather small-sized pollen with oblate to suboblate or oblatoid shape, whereas the latter genus produces foveo-verrucose and subscabro-baculate surface patterns and small to medium-sized pollen with oblate or peroblatoid to suboblate shape. The surface pattern of *Helicia* phylogenetically, lies in one direction of evolutionary line, and of *Xylomelum* in the other and separate line of derivation (Memon, 1984c). However, the pollen of *Helicia* are more similar to *Hollandaea* of subtribe Hollandaeinae in surface pattern, shape and size and in number of chromosomes. Venkata Rao (1971) has pointed out some primitive features in the inflorescence and flower of *Xylomelum,* which are similar to *Darlingia* and *Orites,* while its sessile anthers are similar to *Hicksbeachia.* He has also maintained that the fruit of *Xylomelum* is largest in the family. Pollen grains of Xylomelum resemble Lambertiinae (a unigeneric subtribe of tribe Macadamieae) which produces oblate to oblatoid, small to medium or rather large-sized pollen grains with rugulo-foveolate and foveo-verrucose surface patterns,

though *Xylomelum pyriforme* produces an advanced type of surface pattern (i.e. subscabro-baculate) than *Lambertia,* because this surface pattern is phylongenetically derived from rugulo-foveolate (Memon, 1984c) which is also produced by *Lambertia multiflora.* Besides, the number of chromosomes in both genera is 14 (Johnson & Briggs, 1975). In view of this, it is suggested that *Xylomelum* may be separated from the subtribe Heliciinae and grouped with *Lambertia* in subtribe Lambertiinae, and *Helicia* be left in the subtribe Heliciinae, or perhaps the unigeneric subtribe Hollandaeinae with *Hollandaea* may be amalgamated with subtribe Heliciinae.

Pollen grains of genera *Triunia* of subtribe Triuniinae (Tribe Helicieae), *Euplassa* (not examined here, but quoted from Walker & Doyle, 1975; Pl. 3, Fig. B, page 671), *Gevunia* and *Sleumerodendron* of subtribe Gevuininae (tribe Macadamieae) produce reticulo-foveolate and reticulate surface patterns, oblate to oblatoid and small to medium-sized pollen grains. In view of very close similarity in pollen morphology and phylogeny (Memon, 1984c) these tribes be reconsidered very carefully.

Panopsis seems to be inconsistent with *Brabeium* and *Macadamia* in the same subtribe Macadamiinae. The former genus produces oblatoid, rather small to medium-sized pollen with tectate-imperforate tectum and scabrate surface pattern, whereas the latter genera produce oblate-spheroidal and oblate, small to medium-sized pollen with tectate-perforate tectum and scabro-rugulo-foveolate and foveolate surface patterns. Phylogenetically, the exine structure and surface pattern of *Panopsis* are more advanced than *Brabeium* and *Macadamia* (Memon, 1984c). However, *Roupala* of subtribe Roupalinae (Tribe Macadamieae), producing oblatoid, small to medium-sized pollen with tectate-perforate tectum and scabro-foveolate surface pattern is phylogenetically more close to *Panopsis.* Earlier, Johnson & Briggs (1963) had treated both *Panopsis* and *Roupala* together in the same group. It is therefore suggested that the older classification of Johnson & Briggs be re-evaluated.

The genera of subtribe Hicksbeachiinae (Tribe Macadamieae) produce more or less homogeneous pollen grain i.e. oblate to oblatoid, small to large size with reticulate and reticulo-foveolate surface patterns, except that *Malagasia* producing pollen with scabro-rugulo-foveolate surface pattern is similar to *Brabeium* of subtribe Macadamiinae (Tribe Macadamieae). Phylogenetically, the surface pattern of *Malagasia* lies in one direction of evolutionary line and that of *Athertonia, Heliciopsis, Hicksbeachia* and *Virotia* in the other (Memon, 1984c). Johnson & Briggs (1975) have suggested that *Malagasia* is a split of *Macadamia,* therefore it may be grouped with *Macadamia* and *Brabeium* in the subtribe Macadamiinae of tribe Macadamieae.

Formation of new genera i.e. *Athertonia* J. & B. (*Hicksbeachia* F. Muell. as *H. diversifolia* (C.T. White) Sleum.), *Triunia* J. & B. (*Helicia* Lour., in part), *Eucarpha*

J. & B. (*Knightia* R. Br., in part), *Floydia* J. & B. (*Macadamia* F.v.M. as *M. praealta* (F. Muell.) F.M. Bailey), *Malagasia* J. & B. (*Macadamia* F.v.M. as *M. alticola* (Capuron) J. & B.), *Virotia* J. & B. (*Macadamia* F.v.M., in part), *Toronia* J. & B. (*Persoonia* J.E. Smith, as *P. toru* (A. Cunn.) J. & B.), *Acidonia* J. & B. (*Persoonia* J.E. Smith, in part) and *Pycnonia* J. & B. (*Persoonia* J.E. Smith, in part) by Johnson & Briggs (1975) is reasonably supported by pollen morphology, though *Athertonia diversifolia* and *Hicksbeachia,* and *Floydia* and *Virotia* have similar surface pattern, shape and size of pollen grains, but such overlaping of pollen characters is invariably present throughout the family.

Conclusion

The pollen morphology of Proteaceae has revealed much parallelism in the gross characters of pollen grains, and many genera including nearly all those with large number of species were not pollen-morphologically homogeneous. Such genera often lack unique combinations of pollen characters which could distinguish them from other genera of the family. However, some genera viz., *Aulax* producing pollen with reticulo-foveo-spinulose, *Franklandia* clavate, *Protea* scabo-foveo-gemmate, and *Pycnonia* subpsilate surface patterns could be separated from the other genera of the family. *Austromuellera, Banksia, Dryandra* and *Musqravea* producing 2-porare and *Beauprea* producing 3-colpoidate pollen grains could be distinguished from the other genera of the family. At species level, the micromorphological differences in the detail and distribution of surface pattern, shape and size of pollen grains have been found to exist.

A wide spread overlapping of pollen surface pattern, shape and size has resulted that one subfamily, tribe or even subtribe could not be separated from the other subfamily, tribe or subtribe on the bases of pollen morphology. Although some tribes and subtribes with a small number of genera show consistency in their pollen morphology, nonetheless, such characters are invariably present in the rest of the family.

On the bases of present findings and interpretations and to some extent supplemented by cytology and Johnson & Briggs's (1963) and Venkata Rao's (1971) classification, the following alternative relationships and suggestions are made in correlation with the infrafamilial classification put forwarded by Johnson & Briggs (1975).

In subfamily Persoonioideae the unigeneric subtribe Placosperminae (Tribe Persoonieae) with *Placospermum* be extended to multigeneric level, and *Acidonia, Garneieria* and *Toronia* instead of subtribe Persooniinae (Tribe Persoonieae) be grouped with *Placospermum* in the subtribe Placosperminae, and only *Persoonia* and *Pycnonia* be left in the subtribe Persooniinae.

In subfamily Proteoideae, *Adenanthos* be separated from tribe Franklandieae and transferred to the tribe Proteeae, and *Franklandia* be left alone, or the tribe Franklandieae be raised to the rank of a unigeneric subfamily "FRANKLANDIOIDEAE" with *Franklandia* similar to two other unigeneric subfamilies i.e. Carnarvonioideae and Sphalmioideae. *Leucadendron* of subtribe Aulacinae (Tribe Proteeae) be separated and put to its own unigeneric subtribe "LEUCADENDRINAE" of tribe Proteeae, and the subtribe Aulacinae with *Aulax* be treated as a unigeneric subtribe of the tribe Proteeae.

The unigeneric subfamily Carnarvonioideae with *Carnarvonia* be eliminated and instead, only a unigeneric tribe "CARNARVONIEAE" of subfamily Proteoideae be formed for *Carnarvonia,* or it may be placed in the tribe Macadamieae of subfamily Grevilleoideae.

In subfamily Grevilleoideae *Neorites* of tribe Oriteae and *Knightia* of subtribe Knightiinae (Tribe Knightieae) be treated together in the same subtribe Knightiinae, and *Darlingia* and *Eucarpha* be separated from subtribe Knightiinae and grouped with *Orites* in the tribe Oriteae. *Xylomelum* be separated from subtribe Heliciinae (Tribe Helicieae) and placed with *Lambertia* in the subtribe Lambertiinae (Tribe Macademieae), and only *Helicia* be left in the subtribe Heliciinae, or eliminating the unigeneric subtribe Hollandaeinae (Tribe Helicieae), *Hollandaea* and *Helicia* be treated together in the same subtribe Heliciinae of tribe Helicieae. *Panopsis* of subtribe Roupalinae (Tribe Macadamieae) be treated together either in subtribe Macadamiinae or Roupalinae. And *Malagasia* of subtribe Hicksbeachiinae (Tribe Macadmieae) be grouped with *Macadamia* and *Brabeium* in the same subtribe Macadamiinae of the tribe Macadamieae.

Acknowledgements

I wish to express my sincere thanks to Dr. A.R.H. Martin. School of Biological Sciences, University of Sydney, Australia, for extending facilities to carry out this research work and helping me with his valuable discussion and suggestions. I am also thankful to Dr. M.T.M. Rajput, Department of Botany, University of Sind, Pakistan, for critically reading the manuscript.

References

Erdtman, G. 1963. Palynology. In, *Advances in Botanical Research.* (Ed.) R.D. Preston, 1. 149–208. Hafner Pub. Co. New York & London.

Johnson, L.A.S. and B.G. Briggs. 1963. Evolution in the Proteaceae *Aust. J. Bot.*, 11: 21-61.

Johnson, L.A.S. and B.G. Briggs. 1975. On the Proteaceae – the evolution and classification of a southern family. *Bot. J. Linn. Soc.*, 70: 83-182.

Memon, H.R. 1984a. Classification of pollen surface pattern of modern Proteaceae, using scanning electron microscope, *Pak. J. Bot.*, 15: 205–229.

Memon, H.R. 1984c. Evolution of exine structure and surface pattern in Proteaceae. *Sind Uni. Res. Jour. (Sci. Ser.)* (in press).

Walker, J.W. and J.A. Doyle. 1975. The bases of angiosperm phylogeny: Palynology. *Ann. Miss. Bot. Garden.*, 62: 664–723.

Venkata Rao, C. 1971. *Proteaceae.* Botanical Monograph No. 6, New Delhi: C.S.I.R.