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On the pollen morphology and phylogeny of the Restionales and Poales

H. P. LINDER and I. K. FERGUSON

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Acetolysed pollen of the Restionaceae, Centrolepidaceae and allied families were studied by light microscopy, scanning electron microscopy and transmission electron microscopy, with special reference to the structure of the aperture and interapertural walls. It has been found that the Poales and Restionales share several features of exine stratification and aperture structure. These pollen characters were not found in the Centrolepidaceae, Hanguanaceae and Hydatellaceae. It was further found that both the Restionaceae and the Poaceae possess unique pollen wall characters, on the basis of which a phylogenetic hypothesis is presented.

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Although the orders Poales and Restionales are recognized by most recent authors (Thorne 1968, Takhtajan 1980, Cronquist 1981) the exact delimitations of several of the families of the Restionales are in doubt. Dahlgren & Clifford (1982) even question the distinction between the Poales and the Restionales.

The family limits within the Restionales have recently been in a state of flux. On largely anatomical grounds, Cutler & Shaw (1965) separated the Anarthriaceae and Ecdeiocoleaceae from the Restionaceae. Hamann (1975), separated the Hydatellaceae from the Centrolepidaceae. Most authors place the Hydatellaceae (comprising the genera *Hydatella* and *Trithuria*) in its own order, the Hydatellales, between the Cyperales and the Restionales in the superorder Commeliniiflorae (see also Dahlgren & Rasmussen 1983). The position of this family in the Commeliniiflorae is regarded as being somewhat dubious. The Joinvilleaceae were separated from the Flagellariaceae by Tomlinson & Smith (1970) largely on the basis of vegetative morphology and anatomy. They noted a close similarity between the Flagellariaceae, Joinvilleaceae and the Poaceae. Shaw (1965) placed *Hanguana* in its own

family, the Hanguanaceae, near the Xanthorrhoeaceae. The placing of the families in orders by the major authors since 1960 is summarized in Table I.

Due to the simplified nature of the monocot flowers, cryptic data has been of great importance in supra-generic classification. Embryological data has long been used extensively. Anatomical data was first employed by the Engler and Prantl school and is still valuable. Phytochemical data may be of importance (Harborne 1973, 1979), but needs to be extended and critically analysed. The pollen data has also not been fully employed. Erdtman (1952) in his survey of the pollen morphology of the Angiosperms described two main types of aperture in the Restionaceae and concluded that the pollen of the family is more or less similar to that of the Centrolepidaceae and Gramineae. Chanda (1966) has carried out the most significant and comprehensive study of the pollen morphology of the Centrolepidaceae, Restionaceae and Flagellariaceae using the method of light microscopy on acetolysed exines. Bortenschlager et al. (1966) studied *Hydatella* and *Trithuria* to extend Chanda's survey and noted how dissimilar their pollen was from the typical Restionaceae type. Chanda & Rowley (1967) investigated

Table 1. Families and orders in the study group as recognized by various authors since 1960

	Date of publication	Hamann 1964	Hutchinson 1973	Takhtajan 1980	Cronquist 1981	Dahlgren & Clifford 1982
Hydatellaceae	1976	Restionaceae	Juncaceae p.p.	Hydatellales	Hydatellales	Hydatellales
Centrolepidaceae	1856			Restionales	Restionales	Poales
Restionaceae	1810					
Anarthriaceae	1965					
Ecdeiocoleaceae	1965					
Joinvilleaceae	1970	?Flagellariaceae	Commelinaceae p.p.			
Flagellariaceae	1829					
Hanguanaceae	1965			Liliales p.p.	Liliales p.p.	
Poaceae	1895	Graminales	Graminales	Poales	Cyperales	

the structure of the apertures of several species of Restionaceae (*Restio* s.l., *Meeboldina*, *Ecdeiocolea*) and of *Joinvillea* in the Flagellariaceae s.l. using TEM. Ladd (1977) carried out a survey of the surface micromorphology of the pollen of the Restionales with the intention of locating characters on the basis of which fossil pollens might be assigned to extant families. Chanda & Ferguson (1979) in a study of the pollen of the Australian Restionaceae genera *Calorophus* and *Empodisma* illustrated the morphology of the apertures and the exine stratification of acetolysed and unacetolysed pollen grains. Nilsson (1982) provided a survey of the distribution of pollen characters in the monocots, but largely confined the survey to the various aperture types.

Linder (1984) examined the pollen morphology of the African species in detail. Problems in the interpretation of the aperture structure and wall stratification led to an extension of the study to the remaining families of the Restionales. In this paper we report on the results of this extended study, particularly on the implications for the classification of the families.

MATERIAL AND METHODS

Pollen was obtained from the Herbarium of the Royal Botanic Gardens, Kew (K) and acetolysed by the methods described by Erdtman (1969). For light microscopy the pollen was mounted in glycerol jelly, examined, measured and photographed with a Nikon LKe microscope with an apochromatic objective $\times 100$ and compensating eye-

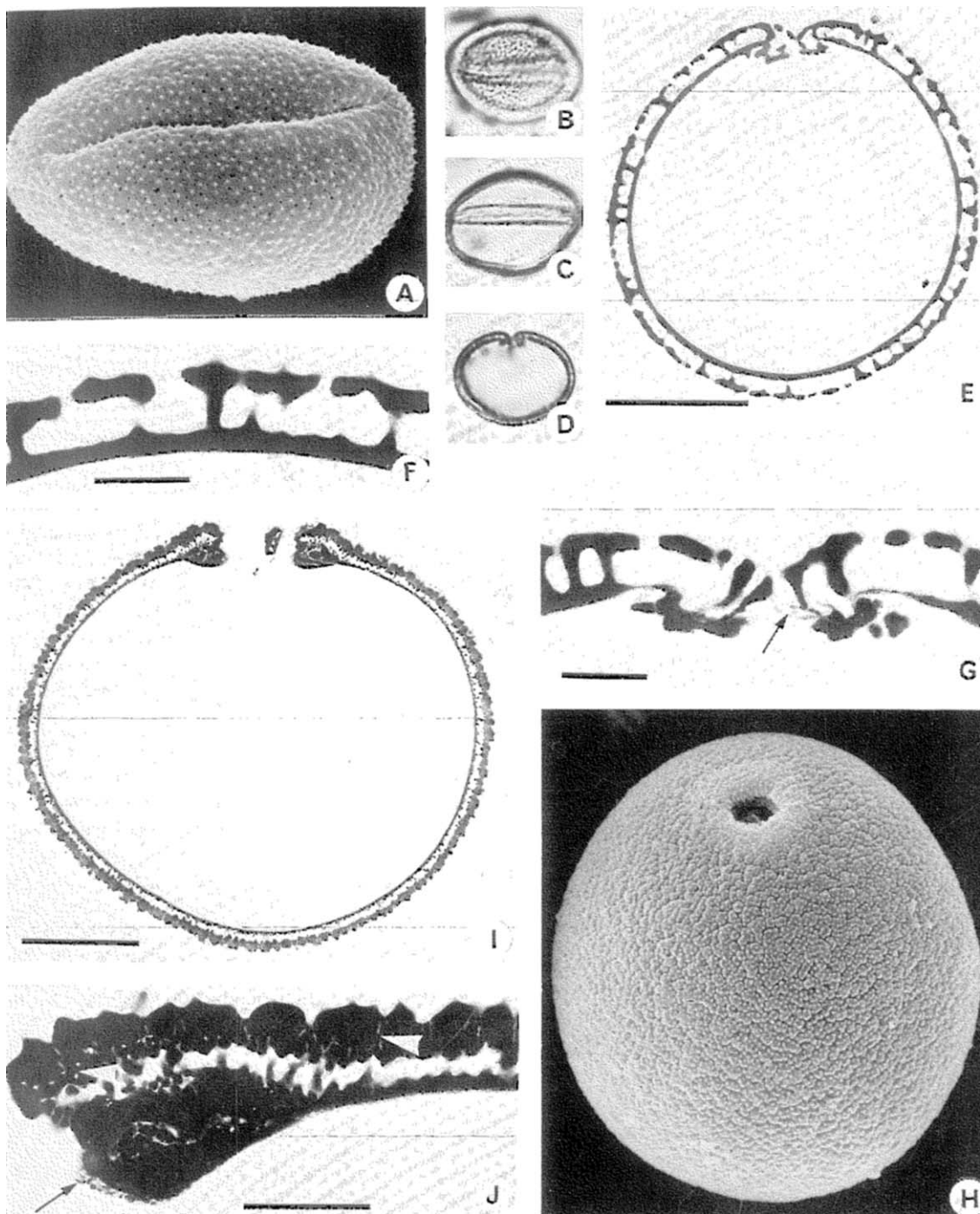
pieces $\times 10$. For scanning electron microscopy (SEM) the acetolysed pollen was critical point dried in a Balzers Union CPD using 100% ethanol as the exchange liquid or air dried from 100% ethanol. The specimens were sputter coated with platinum and examined in a Jeol T20 and a Jeol 35 SEM. The inner morphology of the walls and apertures were studied from material prepared by freeze sectioning similar to the method described by Muller (1973). For transmission electron microscopy (TEM) the acetolysed exines were embedded and stained by the methods similar to those described by Skvarla (1966), sectioned with a diamond knife and examined with a Jeol 100S TEM.

The terminology follows that previously used by Nilsson (1982), Chanda (1966) and Chanda & Rowley (1967).

Specimens examined

Anarthria prolifera R.Br., AUSTRALIA, Young s.n. (K). — *Brizula drummondii* Benth., AUSTRALIA, Swan River, Western Australia, Morrison s.n. (K). — *Centrolepis aristata* Roem. et Sch., AUSTRALIA, Kelmscott, Western Australia, Morrison s.n. (K). — *Flagellaria gigantia* Hook.f., FIJI, Viti Levu, Tholo North, Degener 14309 (K). — *Hanguana* sp., PAPUA NEW GUINEA, Lake Daviumbu, Brass 7925 (K). — *Lepyrodia scariosa* R.Br., AUSTRALIA, Mount Coolum, Moreton Distr., Queensland, Clemens s.n. (K). — *Poa pratensis* L., GREAT BRITAIN, Royal Botanic Gardens, Kew, Harley s.n. (K). — *Restio bifidus* Thunb., SOUTH AFRICA, Pringle Bay,

Fig. 1. A–G. *Trithuria macranthera*. (A) Tilted distal view of monosulcate pollen grain with spinulate ornamentation. SEM $\times 4400$. B–D Light micrographs. All $\times 1000$. (B) Distal polar view, high focus showing ornamentation and sulcus. (C) as (B) but lower focus showing sulcus. (D) Equatorial view, optical section showing sulcus and columellae. (E) Thin section of whole pollen grain showing



sulcus. TEM $\times 4000$. (F) Detail of exine stratification showing foot layer, distinct, widely spaced columellae and punctate tectum with spinules. TEM $\times 14000$. (G) Detail of aperture showing infolded sulcus margins and traces of endexine (arrow). TEM $\times 12500$. H-I. *Poa pratensis*. Showing pollen aperture Type (i) (graminoid). (H) Tilted equatorial view of whole pollen grain showing ulcus

and exine ornamentation. SEM $\times 3700$. (I) Thin section of whole pollen grain showing ulcus with operculum and margins of aperture with thickened foot layer and presence of endexine. TEM $\times 3800$. (J) Detail of aperture showing granular endexine (arrow) and intraexinous cavities (arrow head). TEM $\times 18000$. Scale line E, I = $5\ \mu\text{m}$, F, G, J = $1\ \mu\text{m}$.

Caledon Division, Parker 4759 (K). — *R. dispar* Mast., SOUTH AFRICA, Houw Hoek Mountains, Caledon Division, Burchell 8068 (K). — *Trithuria macranthera* Stapf, AUSTRALIA, Swan River, Western Australia, Morrison s.n. (K).

The material cited in Linder (1984) was also consulted.

RESULTS

General pollen morphology

The pollen throughout most of the taxa investigated is spheroidal to oblate occasionally urn or pitcher shaped with a large variation in size between taxa, being about 12 µm in equatorial diameter in some taxa, as for example *Trithuria* (Fig. 1A) to about 65 µm in some species of Restionaceae (e.g. *Calorophus*). In general the pollen grains are solitary, but Bortenschlager et al. (1966) also record some tetrads in *Hydatella*. The apertures, with the exception of *Trithuria* and *Hanguana*, are ulcerate. The pollen of *Trithuria* is monosulcate (Fig. 1D) while that of *Hanguana* is inaperturate. The tectum surface may be almost smooth, verrucate to somewhat rugulate to rugulate. Almost throughout the group the pollen has microverrucate, spinulate or granular supracteal ornamentation.

Aperture types

Four different types of ulcerate apertures are recognized in the material studied in this investigation. Previously these have been grouped into 'graminoid' with a small pore with or without an annulus and 'centrolepidoid' with a large pore, by Chanda (1966) and Ladd (1977). Chanda did, however, recognize transitional forms, which Johnson & Briggs (1981) in their reinterpretation disregarded.

Type (i) (graminoid).—Figs. 1H–I, 2A–I. The borders of the apertures are precisely defined by a distinct annulus raised by a marked thickening of the foot layer. This thickening is distinctly lamellated (Figs. 1I, J, 2B). An operculum is present in the ulcus in the Poaceae, Ecdeiocoleaceae (Fig. 1I) and Anarthriaceae (Fig. 2C) but appears to be absent from the Flagellariaceae, Joinvilleaceae and Restionaceae. A very thin layer of endexine (nexine 2 of Chanda & Rowley, 1967) covers the ulcus and extends some distance under the margins (Figs. 1J, 2B, C). This is usually ruptured during acetolysis.

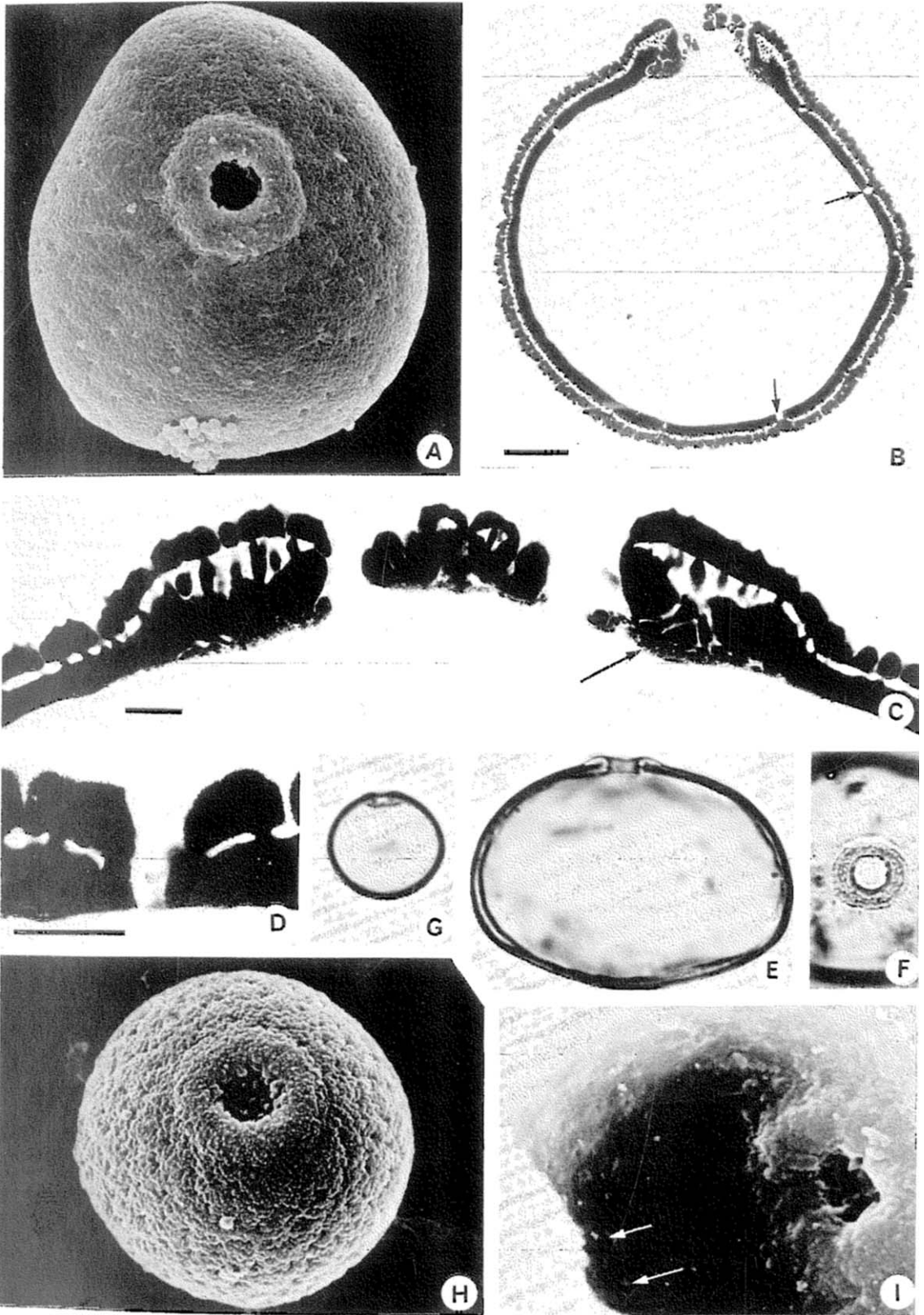
This type of aperture corresponds with the 'graminoid' aperture in the strict sense of the previous workers cited above. It occurs throughout the Poa-

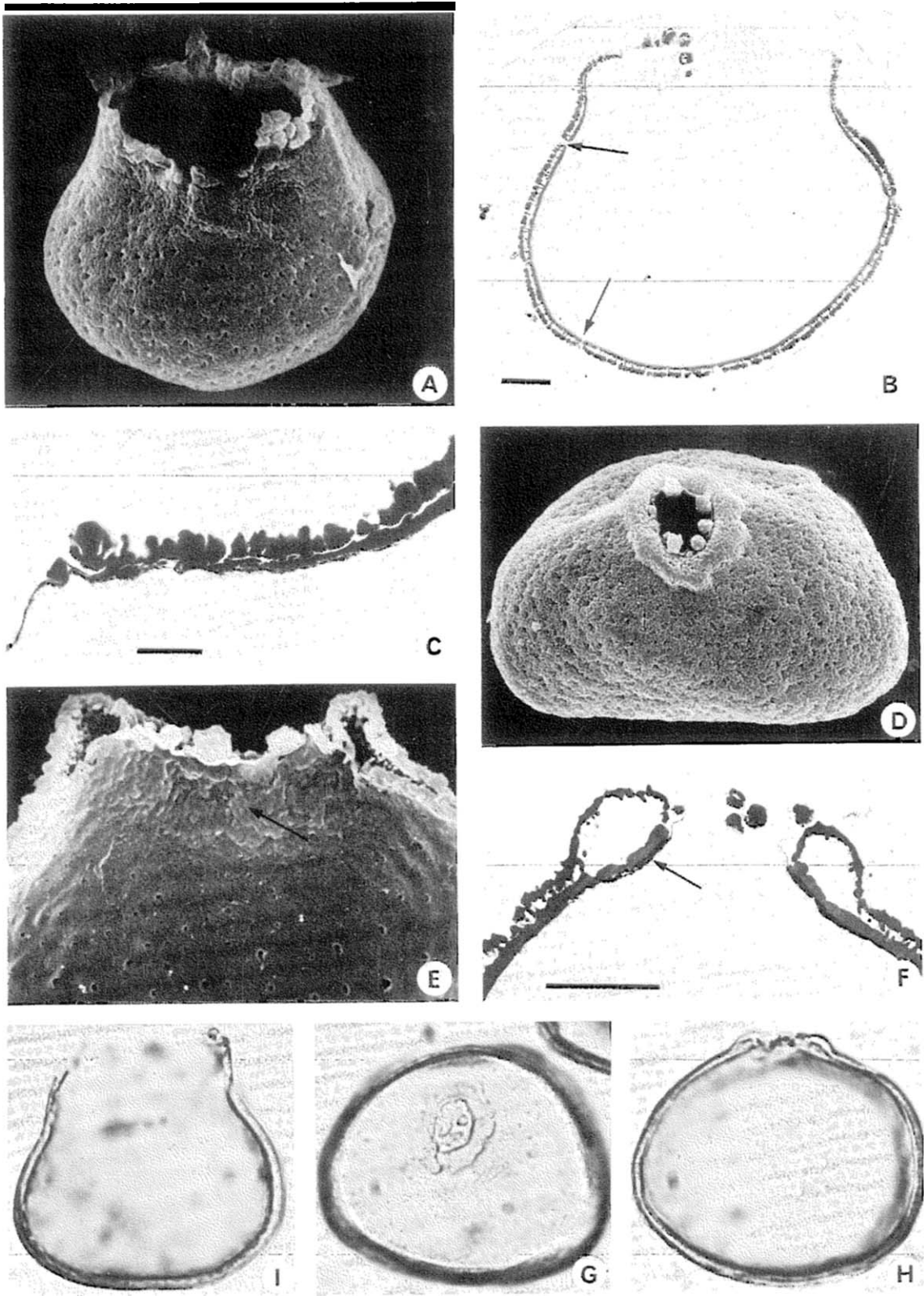
ceae, Flagellariaceae, Joinvilleaceae, Anarthriaceae, Ecdeiocoleaceae and in four genera of the Restionaceae (*Hopkinsia*, *Lyginia*, *Staberoha* and *Ischyrolepis*).

Type (ii) (African restioid).—Figs. 3D–H. The ulcus generally resembles *Type (i)*, and has a more or less defined margin which in many taxa may be somewhat irregular with coarse granules and some loose fragments of exine present which form an aperture membrane in unacetolysed pollen. The aperture margin is often somewhat raised, this is due not to a thickening of the foot layer as in *Type (i)*, but either to the separation of the foot layer and the tectum to form what may be termed a vestibulate annulus, or the whole exine may be raised (Linder 1984) to form the annulus. Often either the foot layer or the tectum is somewhat reduced in the margin of the aperture (Linder 1984). A very thin endexine occurs under the margins of the apertures and continues under the aperture membrane (Fig. 3F). Scrobiculi do not penetrate to the inner surface of this somewhat rugulate endexinous area (Fig. 3E).

Chanda (1966) did not critically distinguish the vestibulate annulus which is more easily demonstrated by thin sectioning (Linder 1984) and he regarded most of the African Restionaceae as having 'graminoid' apertures though he recognized a group with a 'transitional' type of aperture between his 'centrolepidoid' and 'graminoid' types. Ladd (1977) and Johnson & Briggs (1981) have oversim-

Fig. 2. A–F. *Anarthria prolifera*. Showing pollen aperture *Type (i) (graminoid)*. (A) Distal polar view of whole pollen grain showing aperture with raised margin and scrobiculate ornamentation. SEM $\times 2400$. (B) Thin section of whole pollen grain showing aperture with remnants of operculum and interapertural exine with scrobiculi (arrows). TEM $\times 2000$. (C) Detail of aperture showing operculum in thin section, note that the operculum is constructed of about 4 fused exine elements and is intermediate between Fig. 1, I and Fig. 3, F. aperture margins with thickened foot layer and presence of endexine (arrow); note columellate interstitium. TEM $\times 8500$. (D) Detail of scrobiculum. TEM $\times 17000$. (E) Equatorial view showing aperture in optical section. LM $\times 1000$. (F) Distal polar view showing aperture. LM $\times 1000$. G–I. *Flagellaria gigantea*. Showing pollen aperture *Type (i) (graminoid)*. (G) Equatorial view showing aperture in part optical section LM $\times 1000$. (H) Distal polar view of whole pollen grain showing raised aperture margin and scrobiculate interapertural exine. SEM $\times 3600$. (I) Inner view of pollen grain showing aperture and scrobiculi penetrating the interapertural exine. SEM $\times 7200$. Scale line B = 5 µm, C, D = 1 µm.





plified the aperture types and thereby rendered their terminology as inappropriate to describe most of the African Restionaceae.

Type (iii) (Australian restioid).—Figs. A–C, I. This third type of aperture has margins which in acetolysed preparations appear somewhat irregular with a loose ring of large, coarse granules and broken fragments being the remnants of a coarse granular aperture membrane in unacetolysed pollen (Chanda & Ferguson 1979). The foot layer, interstitium and tectum are attenuated towards the aperture. A thin layer of endexine similar to *Types (i) and (ii)* occurs under the aperture margins (Fig. 3C) and together with a very thin layer of ectexine attaches the coarse granules together to form the aperture membrane and attaches the granules to the edges of the aperture.

This type occurs in the non-African Restionaceae excluding *Lyginia* and *Hopkinsia*. The aperture type is termed 'restioid' by Chanda & Rowley (1967), but has been included in 'centrolepidoid' by Chanda (1966), Ladd (1977) and Johnson & Briggs (1981). The aperture of the Centrolepidaceae is quite distinct (described here as *Type (iv)*) and it is felt that the term 'centrolepidoid' should be reserved for that type. It is proposed that the terms

'African restioid' is used for *Type (ii)* and 'Australian restioid' for *Type (iii)*.

Type (iv) (centrolepidoid).—Figs. 4A–I. The margins of the ulcus in this type are not regularly defined (they sometimes may appear so due to rolling inwards as an artifact of acetolysed preparations, Ladd 1977, fig. 28) and the exine is continuous, unmodified and somewhat irregularly interrupted to form a large almost unstructured opening (Figs. 4A, H). There are no coarse granules or exine fragments surrounding the margins or forming an aperture membrane. Endexine is absent. In light microscopy and sometimes in SEM, as mentioned above, this aperture type is superficially similar to that of *Type (iii)* (Chanda 1966, plate 4: 4, 5, 6). However, the differences described in the present investigation are evident in combined SEM and TEM (Figs. 4A–B, E–F).

This type of aperture is restricted to the Centrolepidaceae and if a prefix is applied to apertures it must be referred to as 'centrolepidoid sensu stricto'. The similarity between *Types (iii) and (iv)* is superficial, and to use the term 'centrolepidoid' in the sense of Chanda (1966) and Ladd (1977) is misleading.

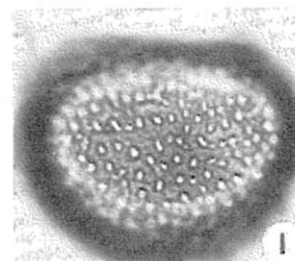
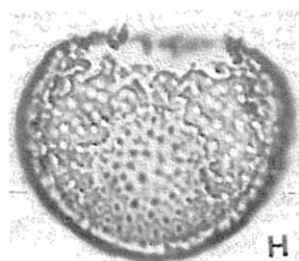
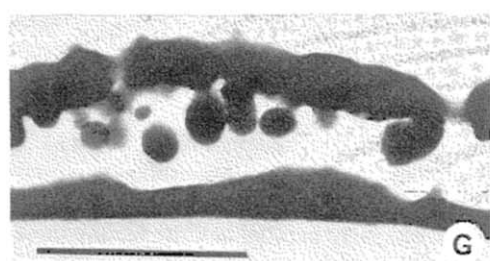
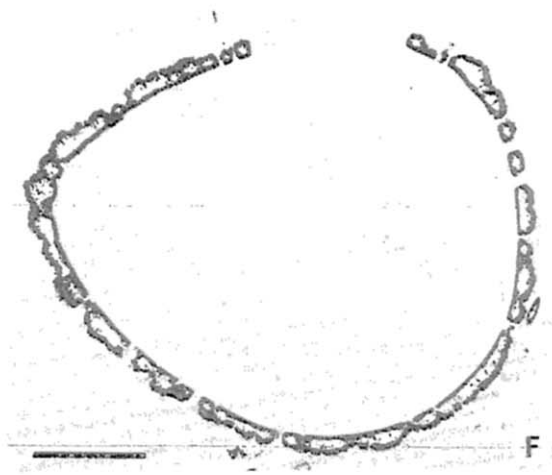
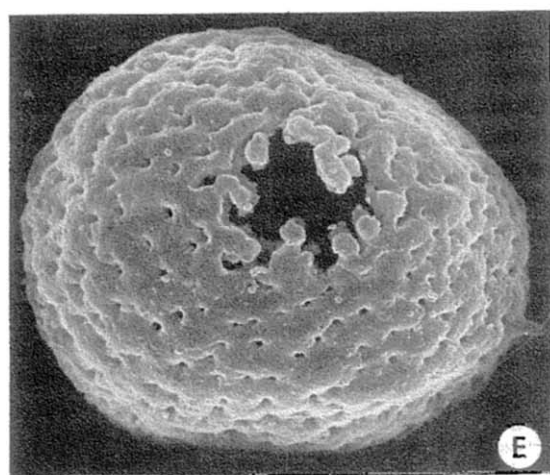
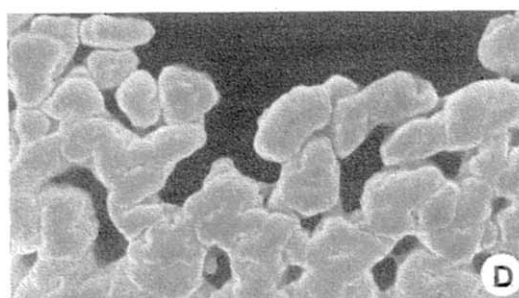
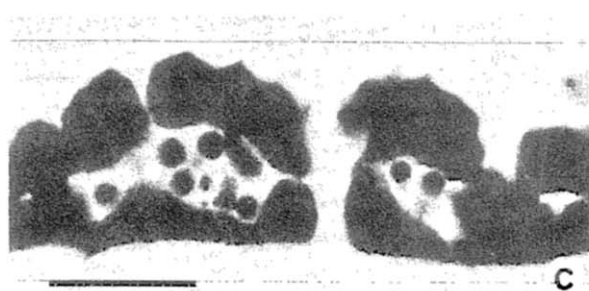
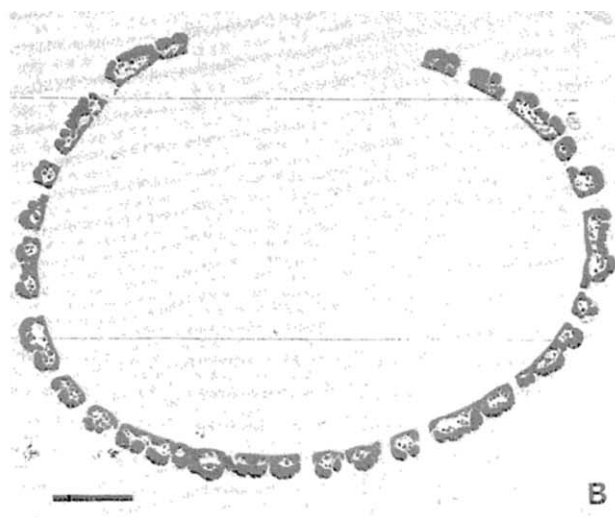
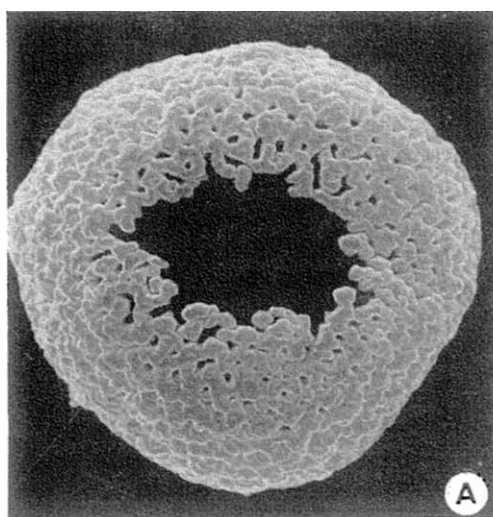
Heslop-Harrison (1977) reviews the occurrence of an additional stratum interposed between the foot layer and the intine particularly adjacent to and beneath the aperture. Skvarla & Larsen (1966) refer to this as endexine. Although this terminology is not the terminology used by Christensen & Horner (1974), Heslop-Harrison (1979) or Kress & Stone (1982) it is used in this work, because of the similarity in staining reaction to the stratum referred to as endexine in dicotyledons, and its resistance to acetolysis.

Interapertural exine

The general condition found is a well developed foot layer (Fig. 2B), columellate interstitium (Fig. 2C) and well developed tectum (Fig. 1I). All the layers are more or less equal in thickness (Fig. 2B). The inner surface of the tectum and the foot layer are more or less parallel (Fig. 2B) and the columellae are more or less uniform in height (Fig. 3B). Variation in surface ornamentation is the result of small differences in the thickness of the tectum.

In the Centrolepidaceae the interstitium is granular. The inner surface of the tectum and the foot layer are not regularly parallel and the tectum does

Fig. 3. A–C. 1. *Lepyrodia scariosa*. Showing pollen aperture *Type (iii) (Australian restioid)*. (A) Whole pollen grain showing urn shape, large ulcerate aperture with associated coarse granules. SEM $\times 1450$. (B) Thin section of whole pollen grain showing columellate interstitium, scrobiculi (arrows); the interstitium disappears towards the aperture where the foot layer and tectum run together and taper to aperture margin; coarse granules associated with aperture. TEM $\times 1400$. (C) Detail of aperture margin showing foot layer and tectum with a thin band of endexine extending across the aperture. TEM $\times 10000$. (I) Equatorial view, optical section showing shape and aperture. LM $\times 1000$. D–H. *Restio bifidus*. Showing pollen aperture *Type: (ii) (African restioid)*. (D) Distal polar view of whole pollen grain showing raised aperture margins and associated coarse granules. SEM $\times 2000$. (E) Inner view of pollen in aperture region showing structure of the raised aperture margins, coarse granules and structure of scrobiculi on inner surface; note the somewhat rugulate inner »endexinous« surface adjacent to the aperture (arrow) which no scrobiculi penetrate. SEM $\times 3600$. (F) Thin section through aperture showing structure of raised aperture margin; note dark staining endexine (arrow) tapering to a very fine membrane supporting the coarse apertural granules. TEM $\times 3500$. (G) Distal polar view showing aperture and granules. LM $\times 1000$. (H) Equatorial view showing aperture in optical section. LM $\times 1000$. B, F line = 5 μm . C line = 1 μm .



not vary in thickness. Here in thin section the tectum and foot layer meet in a regular pattern forming cushion-like cavities (Figs. 4B, C, F). In surface view this structure forms a rugulate or undulate surface. The constrictions between the 'cushions' are scrobiculate. These will be described and discussed further below.

In *Trithuria* (Hydatellaceae) the interstitium is columellate, but the inter-columellar spaces are relatively much wider than in other groups investigated. Also the columellae are much higher than the thickness of the foot layer (Figs. 1 E–F).

The Restionaceae, Anarthriaceae, Flagellariaceae and Joinvilleaceae have scrobiculi defined as pores which pass through the entire exine (i.e. sensu Chanda & Rowley 1967). The scrobiculi are frequently broadened on the inner surface of the foot layer (counter-sunk). In the marginal areas the scrobiculi are obscured by the endexine (Fig. 3E). These scrobiculi in the Restionaceae and the three associated families mentioned above appear as holes punched through the exine where no associated changes in the arrangement and thickness of the foot layer, interstitium or tectum occur (Figs 2D, 3D). In contrast the Centrolepidaceae scrobiculi of the (*Centrolepis* and *Brizula*) arise in areas where the exine is 'pinched off', the tectum and foot layer meeting together, attenuating and then closing of the interstitium (Figs. 4B, C, F).

In the Poaceae the tectum and foot layer are perforated by intra-exinous channels running parallel and at right angles to the outer surface (these seem very similar to the 'conspicuous small spherical intra-exinous cavities' described in Myristicaceae by Walker & Walker 1979). These channels

have not been observed in any of the other taxa (Fig. 1J) in this study or in the published TEM micrographs of Chanda & Rowley (1967) or of Skvarla & Rowley (1970). However, the presence of the channels can be seen in published TEM micrographs of a number of taxa of Poaceae by various workers including Rowley (1960, 1964), Larson et al. (1962) and Skvarla & Larson (1966). Christensen, Horner & Lersten (1972) and Christensen & Horner (1974) describe the ontogeny of the channels, while Heslop-Harrison (1979) comments on their presence in a review of the structure of the pollen of the Poaceae.

DISCUSSION

Trithuria and *Hanguana* are palynologically distinct from the Restionales/Poales/Cyperales 'group' by not being ulcerate. Nilsson (1982) shows that the ulcerate condition is almost restricted to this group, and Dahlgren & Rasmussen (1983) use it to characterize the group (i.e. as autapomorphy). The inaperturate condition of *Hanguana* is also found in the Zingiberales, Orchidales, Triuridales, and occasionally in several other orders, whilst the monosulcate condition of *Trithuria* is convincingly argued by Dahlgren & Rasmussen (1984) to be primitive in the monocots.

Trithuria exine stratification is different from that usually found in the Restionales/Poales. However, there is not as yet an adequate understanding of the variation in exine stratification within the monocots, and it is not possible to find any possible allies for the taxon on the basis of this character. This supports the results obtained by Hamann (1975), where he listed numerous embryological differences between the Centrolepidaceae and the Hydatellaceae. Cutler (1969) also showed anatomical differences between the two groups. From this it would appear that pollen data supports the separation of *Trithuria* in the Hydatellales, as suggested by Dahlgren & Clifford (1982).

Although the exine stratification of *Hanguana* has not been studied, Erdtman's (1952) observations (inaperturate, spinulose grains) have been confirmed. Palynological data supports Shaw's (1965) moving *Hanguana* out of the Restionales. Shaw (1965) also cites anatomical data (from Smithson 1957) to support this move. It is clear that *Hanguana* is not yet well enough understood to place it with confidence, but it would appear to be

Fig. 4. A–D, H–I. *Centrolepis aristata*. Showing pollen aperture Type (iv) (centrolepidoid). (A) Distal polar view of whole pollen grain showing irregularly defined ulcus. SEM $\times 2400$. (B) Thin section of whole pollen grain showing aperture as an abrupt interruption of the exine and the 'pinched off' structure of the scrobiculi. TEM $\times 2000$. (C) Detail of exine stratification showing scrobiculus and granular interstitium. TEM $\times 18600$. (D) Detail of margin of the ulcus. SEM $\times 14000$. E–G. *Brizula drummondii*. (E) Distal polar view of whole pollen grain showing ulcus. SEM $\times 3300$. (F) Thin section of whole pollen grain showing features of the ulcus and exine similar to (B). TEM $\times 2800$. (G) Detail of exine stratification showing granular interstitium. TEM $\times 26000$. (H) Whole pollen grain in equatorial view showing ulcus. LM $\times 1000$. (I) Whole grain in equatorial view showing scrobiculi. LM $\times 1000$. Scale line B, F = 5 μm , C, G = 1 μm .

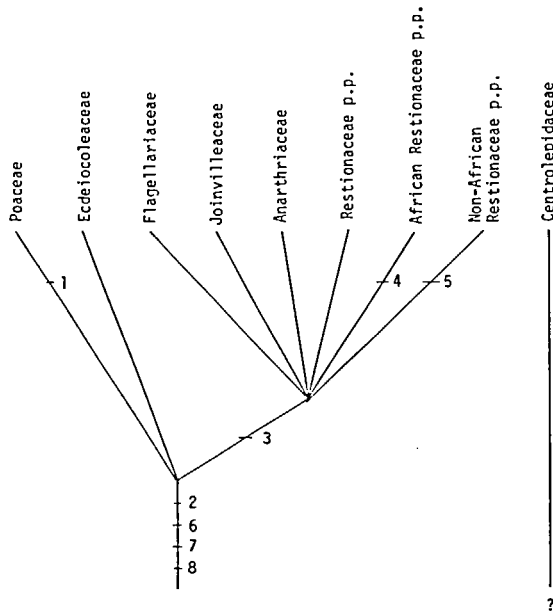


Fig. 5. Cladogram of the Poales and Restionales based on pollen data. Hanguanaceae and Hydatellaceae are not included. Characters used are: 1. Intra-exinous channels present; 2. Operculum or granules present; 3. Scrobiculi present; 4. Aperture type (ii); 5. Aperture type (iii); 6. Interstitium columellate; 7. Aperture type (i); 8. Aperture ulcerate.

out of place within the Restionales, contrary to the position taken by Dahlgren & Rasmussen (1983).

The Centrolepidaceae should probably also be excluded from the Poales/Restionales. Although the pollen grains are scrobiculate and ulcerate, the walls have a granular rather than a columellate interstitium, and the structure of the surface appearance is quite different. The 'scrobiculi', on a structural-positional argument, may not be homologous to those of the Restionales *sensu strictum*. Endexine is lacking, and it further differs by the construction of the aperture and the absence of a well defined margin. The aperture is more reminiscent of the type found in the Cyperales, and might even show similarities to the Limnocharitaceae (see Harley 1982). Dahlgren & Clifford (1982) and Dahlgren & Rasmussen (1983) regard the Centrolepidaceae and the Restionaceae as forming the core of the Restionales, but they can only unite them on the unisporangiate anthers and some embryological characters. Cutler (1969) indicated that there is no anatomical evidence for suggesting a close relationship. However, only an analysis tak-

ing all available data into account could resolve the correct position of the Centrolepidaceae.

The remaining families (Poaceae, Flagellariaceae, Joinvilleaceae, Anarthriaceae, Ecdeiocolaeaceae and Restionaceae) share a suite of characters which suggest that they are closely related. The structure of the pollen walls is similar, i.e. columellate, the ulcus has a more or less defined margin, endexine occurs under the margin, and exinous granules frequently occur associated with the apertures. However, the type of margin, the presence of scrobiculi and of intra-exinous channels and of an operculum in the ulcus allows the taxa to be separated as in Fig. 5.

The pollen grains of the Poaceae are characterized by intra-exinous channels which can be seen in both acetolysed and unacetolysed exines. We have not recorded them in any other taxa of the Restionales, and this appears to be a valuable pollen morphological character separating the Poales from the Restionales.

Ecdeiocolaea is curious. It possesses the typical 'graminoid' aperture (Chanda & Rowley 1967), with no intra-exinous channels visible in the TEM micrographs published by Chanda & Rowley (1967), and no scrobiculi (Ladd 1977, authors observation). The aperture is provided with an operculum (Johnson & Briggs 1981), a character shared with the Poaceae and Anarthriaceae. As an operculum does not appear to occur in the Cyperales (Erdtman 1952) which are probably the outgroup for the Poales/Restionales (Dahlgren & Rasmussen 1983), the presence of an operculum must be derived and secondarily lost in most of the families. The apertural ectexinous granules found in many of the other taxa are probably structurally homologous to the operculum.

The Restionales may be defined by the possession of scrobiculi *sensu strictum*. These may be very small, such as in *Flagellaria gigantea*, or clearly visible. Such a definition, however, excludes the Ecdeiocolaeaceae. In the African and Australasian taxa of Restionaceae different aperture margins have evolved by reduction of the Type (i) apertures. These views are consistent with the phylogeny of the family published by Johnson & Briggs (1981) and Linder (1984). The remainder of the taxa in the order only share a primitive character (i.e. a symplesiomorphy) consequently palynology does not resolve the relationships among the families of this order.

Ladd (1977) suggested that it might be difficult separating fossil pollen grains of the Poaceae, Centrolepidaceae and Restionaceae, but this work shows that by careful SEM and TEM work these problems can be resolved.

CONCLUSIONS

The study of the detailed structure of the exine in both the interapertural and the apertural regions of acetolysed pollen grains of Poales and Restionales by TEM and SEM produces data which may have important implications on the classification of families within these orders.

On palynological data it is suggested that the families Hanguanaceae, Hydatellaceae and Centrolepidaceae be excluded from the orders. The Poales and the Restionales can be distinguished palynologically. The Ecdeiocoleaceae appear to occupy a basal position between the Poales and the Restionales. This family certainly needs more detailed study. Although palynology is consistent with the current hypotheses on the phylogeny of the Restionaceae, it does not provide any data on the position of the Anarthriaceae within the Restionales, or on the distinction between the Flagellariaceae and the Joinvilleaceae. It does indicate that the Ecceioleaceae be excluded from the Restionaceae.

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