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Classification of *Acanthaceae*

R. W. SCOTLAND[1] & K. VOLLESEN[2]

Summary. The classification of *Acanthaceae* is discussed relative to recent molecular studies, pollen morphology, corolla aestivation and other potentially informative morphological homologues. The major pollen types of *Acanthaceae* are illustrated in the form of scanning electron micrographs. A three-item analysis of 11 morphological homologues is provided. A new classification of *Acanthaceae* is presented in addition to a list of generic synonymy.

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INTRODUCTION

Lindau (1895) is the most recent taxonomic treatment of *Acanthaceae* that accounts for all genera (Appendix 1). The lack of such a classification since Lindau (1895) reflects the extent of the task, the regional basis of many accounts, the lack of agreement as to the major sub-divisions, and a lack of consensus concerning the exact limits of the family. Bremekamp (1965) presented a classification of *Acanthaceae* (Appendix 2) that differed from that of Lindau (1895) in some important respects. However, a major limitation with Bremekamp's (1965) classification was that a list of group membership was not provided for many taxa.

Recent published molecular studies (Hedren *et al.* 1995; Scotland *et al.* 1995; McDade & Moody 1999) highlight the aspects of disagreement between Lindau (1895) and Bremekamp (1965). These studies have largely converged on a topology of *Acanthaceae* that supports some taxa recognized by Lindau (1895) and others recognized by Bremekamp (1965). In this paper, we review recent literature and provide a list of currently accepted genera of *Acanthaceae* in a new classification (Appendix 3). The list of genera is modified from Brummitt (1992) with the addition of new genera published since that time. We also list generic synonyms (Appendix 4). A new classification is needed, not only to provide a context for future research but also to consolidate recent research.

Figures 1A and 1B illustrate the major divisions of the Lindau (1895) and Bremekamp (1965) classifications. Lindau (1895) recognized four subfamilies (Fig. 1A), three of which comprise genera that do not possess retinaculate fruits (*Nelsonioideae, Thunbergioideae, Mendoncioideae*). *Mendoncioideae* and *Thunbergioideae* represented two very similar subfamilies of climbing plants separated on the basis of the capsular fruits of *Thunbergioideae* or the drupaceous fruits of *Mendoncioideae.* Lindau's (1895) *Acanthoideae,* comprising genera with retinaculate fruits, was subdivided into two groups based on corolla aestivation patterns (*Imbricatae* and

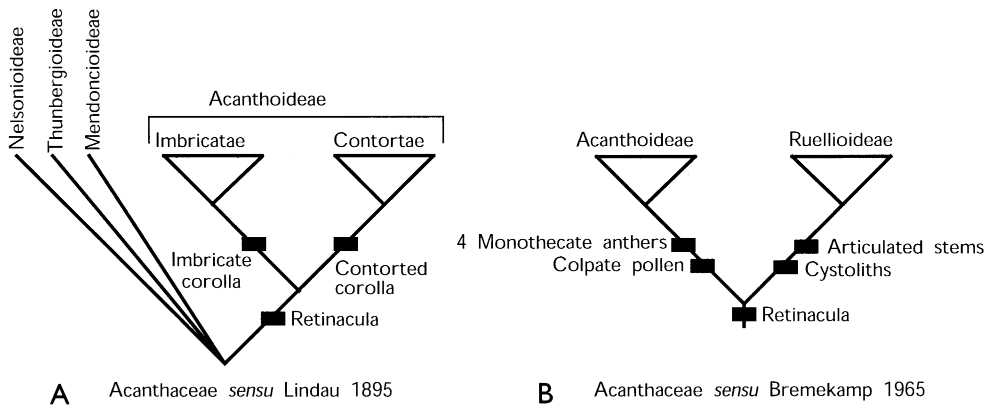


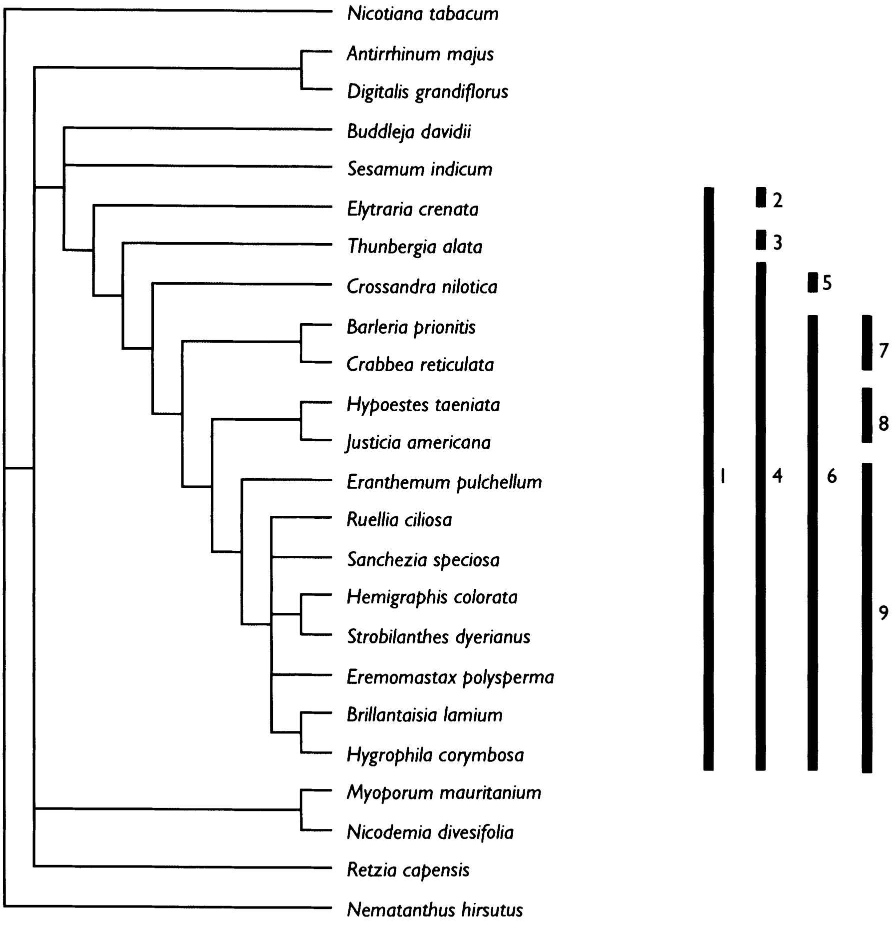
FIG. 1. Classifications of Acanthaceae. **A** Lindau 1895; **B** Bremekamp 1965.

Contortae). Further subdivisions (Appendix 1) were based primarily on pollen morphology. Bremekamp's (1965) *Acanthaceae* excluded genera that lack retinaculate fruits. He placed *Nelsonioideae* within *Scrophulariaceae*, recognized *Thunbergiaceae* and *Mendonciaceae* as distinct families and divided his restricted *Acanthaceae* into two groups (Fig. 1B) on the basis of presence and absence of cystoliths, articulated stems, monothecate anthers and colpate pollen (Fig. 1B). Further subdivisions (Appendix 2) were based primarily on pollen morphology.

MOLECULAR SYSTEMATICS OF ACANTHACEAE

To date, there have been four molecular systematic studies specifically addressing the higher level systematics of *Acanthaceae* (Hedren *et al.* 1995; Scotland *et al.* 1995; McDade & Moody 1999; McDade *et al.* 2000). The genes used for these studies were *rbc*L, *ndh*F, *trn*L-*trn*F and *trn*L-*trn*F combined with ITS, respectively. The *rbc*L data of Hedren *et al.* (1995), was re-analyzed by Scotland *et al.* (1995) but provided limited resolution within *Acanthaceae*. The strict consensus trees of Scotland *et al.* (1995), McDade & Moody (1999) and McDade *et al.* (2000) are shown in Fig. 2A – C respectively. The strict consensus tree of Scotland *et al.* (1995) and McDade *et al.* (2000) resolved *Acanthaceae sensu* Lindau (1895) as a group (Fig. 2A & C; group 1). These analyses demonstrated that there is no support for separating *Nelsonioideae*, *Thunbergia* and *Mendoncia* from *Acanthaceae* as proposed by Bremekamp (1965). The strict consensus tree of McDade & Moody (1999) resolved *Acanthaceae sensu* Lindau (1895) with the exception of *Elytraria* (*Nelsonioideae*) which remained unresolved (Fig. 2B). The analysis of Scotland *et al.* (1995) placed *Elytraria* and *Thunbergia* as successive sister taxa to *Acanthoideae sensu* Lindau (1995) (Fig. 2A; groups 2 and 3) and this was confirmed by the analysis of McDade *et al.* (2000) (Fig. 2C). The analysis of Scotland *et al.* (1995) did not include *Mendoncia* and therefore did not address its position. However, McDade & Moody (1999) and McDade *et al.* (2000) placed *Mendoncia* as sister taxon to *Thunbergia* (Fig. 2B & C; group 3) confirming the recent anatomical studies of Schönenberger & Endress (1998) on floral development, which showed that *Thunbergia*, *Mendoncia* and *Pseudocalyx* are a natural group based upon the shared possession of woody bristles on the anthers, lack of an endothecial cell layer, elongated connective tips and poricidal opening of the thecae. Furthermore, Schönenberger & Endress (1998) showed that *Mendoncia* initially possesses two ovary locules and four ovules, in common with many members of *Acanthaceae*, but later in development forms a 1 – 2 seeded drupe. This confirmed the view of Brummitt (1989) that separating *Mendoncia* from *Acanthaceae* on the basis of possession of a drupaceous fruit was mistaken.

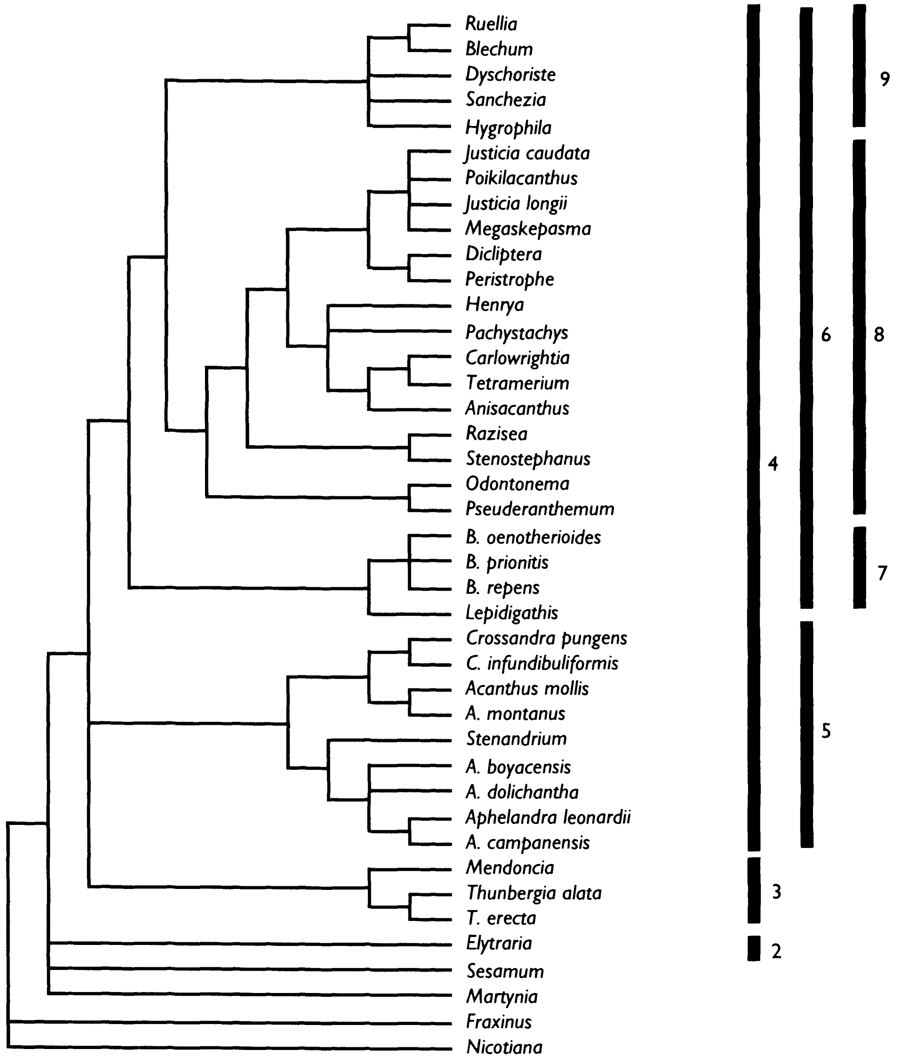
Scotland *et al.* (1995) and McDade *et al.* (2000) confirmed that genera with retinaculate fruits are a monophyletic group (Fig. 2A & C; group 4). Furthermore, within this group, Scotland *et al.* (1995) and McDade *et al.* (2000) demonstrated that the *Acanthoideae sensu* Bremekamp (1965), which lack cystoliths and possess four monothecate anthers and colpate pollen (Fig. 2A & C; group 5), are the sister group to all genera with retinacula and cystoliths (Fig. 2A & C). All analyses



2A

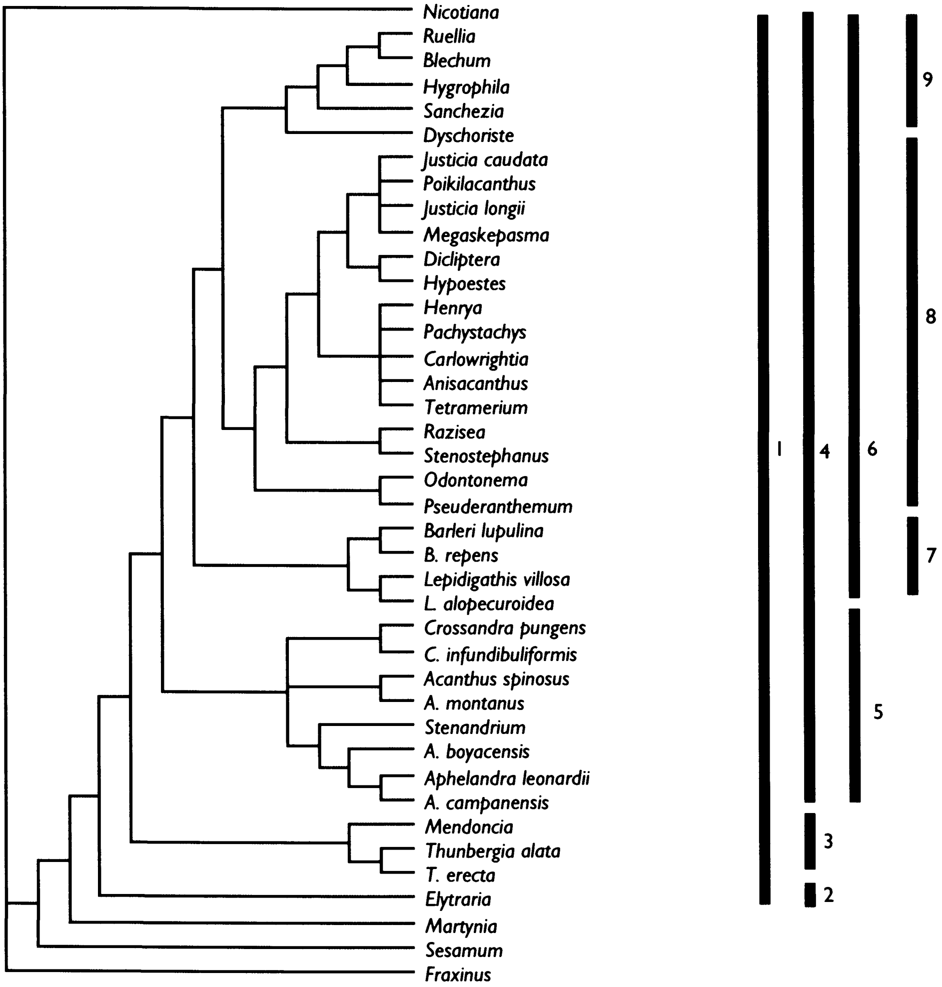
FIG. 2. Molecular studies of *Acanthaceae*. **A** Strict consensus tree of *ndh*F study from Scotland *et al.* (1995); **B** Strict consensus tree of *trn*L- *trn*F study from McDade & Moody (1999); **C** Strict consensus tree of combined analysis of *trn*L- *trn*F and ITS from McDade *et al.* (2000).

distinguished three taxa (Fig. 2A – C; groups 7 – 9) within group 6 that correspond to those taxa with left-contort (group 9), quincuncial (group 7) and ascending-cochlear (group 8) aestivation patterns (Scotland *et al.* 1994). This is in support of Bremekamp's (1965) *Justicieae* (group 8), Lindau's (1895) *Barlerieae* (group 7) and Lindau's (1895) *Contortae* less *Barlerieae* (group 9). The level of congruence between the analyses of Scotland *et al.* (1995), McDade & Moody (1999), McDade *et al.* (2000) from different molecular data sources, coupled with the congruence between these analyses and morphological data shows that several high-level groups within *Acanthaceae* are extremely well corroborated.



2B

These analyses therefore provide support for a broad concept of *Acanthaceae* which includes those genera that lack retinacula (Fig. 2A & C; group 1). There is strong support for a group including *Mendoncia* and *Thunbergia* (Fig. 2B & C; group 3) and for a group comprising genera with retinacula (Fig. 2A & C; group 4). A group comprising genera that possess retinacula, four monothecate anthers and 3-colpate pollen but lack cystoliths (Bremekamp's *Acanthoideae*) is supported (Fig. 2B & C; group 5). A group comprising genera that possess retinacula and cystoliths is also supported (Fig. 2A & C; group 6). Resolution within those taxa that possess



2C

cystoliths and retinacula (group 6) supports *Barlerieae sensu* Lindau (1895) (group 7), *Contortae sensu* Lindau (1895) less *Barlerieae* (group 9) and *Justicieae sensu* Bremekamp (1965) (group 8).

One issue that has not been addressed here is the position of the *Andrographideae* within these studies. This issue will be discussed more fully by Scotland *et al.* (in prep.). Figure 3 is a summary consensus tree from the *ndh*F analysis of Scotland *et al.* (in prep.) that demonstrates *Andrographideae* to be sister group to *Barlerieae sensu* Lindau (1895).

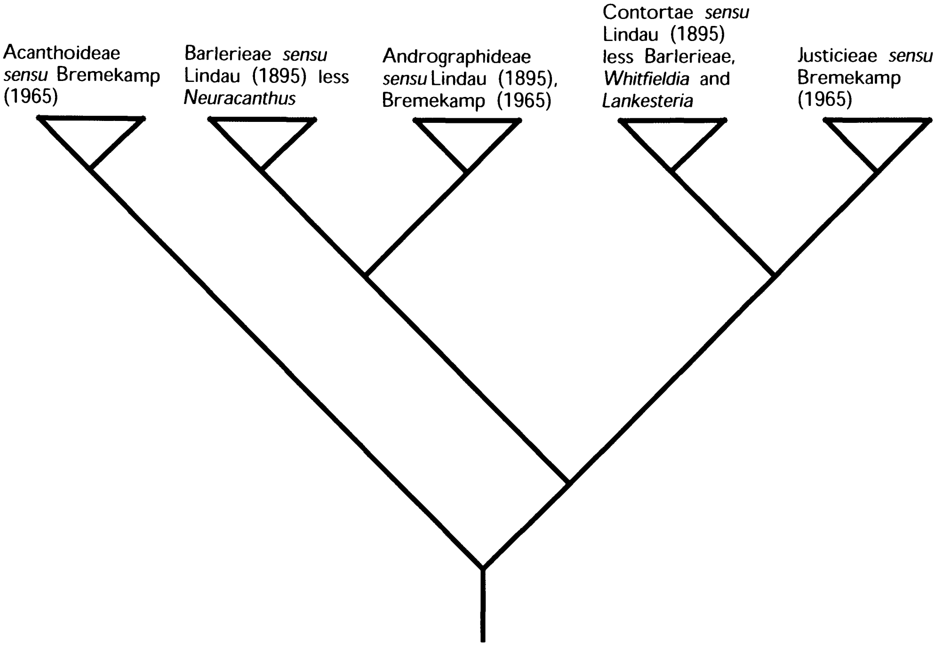


FIG. 3. Schematic strict consensus tree of *ndh*F sequence data from Scotland *et al.* (in prep.) showing the position of *Andrographideae* as sister group to *Barlerieae.*

COROLLA AESTIVATION

Corolla aestivation patterns are highly conserved across genera of *Acanthaceae* (Anderson 1863, 1867; Balkwill & Getliffe Norris 1988; Bentham 1876; Bremekamp 1965; Burkill & Clarke 1899 – 1900; Clarke 1885; Lindau 1893, 1895; Nees 1832, 1847; Scotland *et al.* 1994) and have been used extensively for the recognition of taxa. Within his subfamily *Acanthoideae,* Lindau recognized two major groups, *Contortae* and *Imbricatae,* based on corolla aestivation patterns (Fig. 1A). Lindau (1895) described his *Barlerieae* as having quincuncial aestivation but classified *Barlerieae* within a group including all taxa with retinacula, cystoliths and left-contort aestivation. All other taxa with imbricate aestivation formed *Imbricatae,* diagnosed by ascending-cochlear aestivation. Scotland *et al.* (1994) demonstrated explicitly that within *Acanthaceae sensu* Lindau (1895) there are at least five distinct corolla aestivation types; ascending-cochlear (Fig. 4A & F), left-contort (Fig.4 B) quincuncial (Fig. 4C), open (Fig. 4D) and descending-cochlear (Fig. 4E). The taxonomic distribution of these aestivation patterns are shown in Table 1. Schönenberger (1999) further showed that *Thunbergia* is polymorphic for corolla aestivation, containing mostly left-contort aestivation but also ascending-cochlear aestivation. Scotland *et al.* (1994) detailed corolla aestivation for 34 genera across the range of variation of *Acanthaceae.* One important feature that emerges from Scotland *et al.* (1994) is that the quincuncial aestivation pattern in *Barleria, Crabbea* and *Lophostachys* is distinct from left-contort

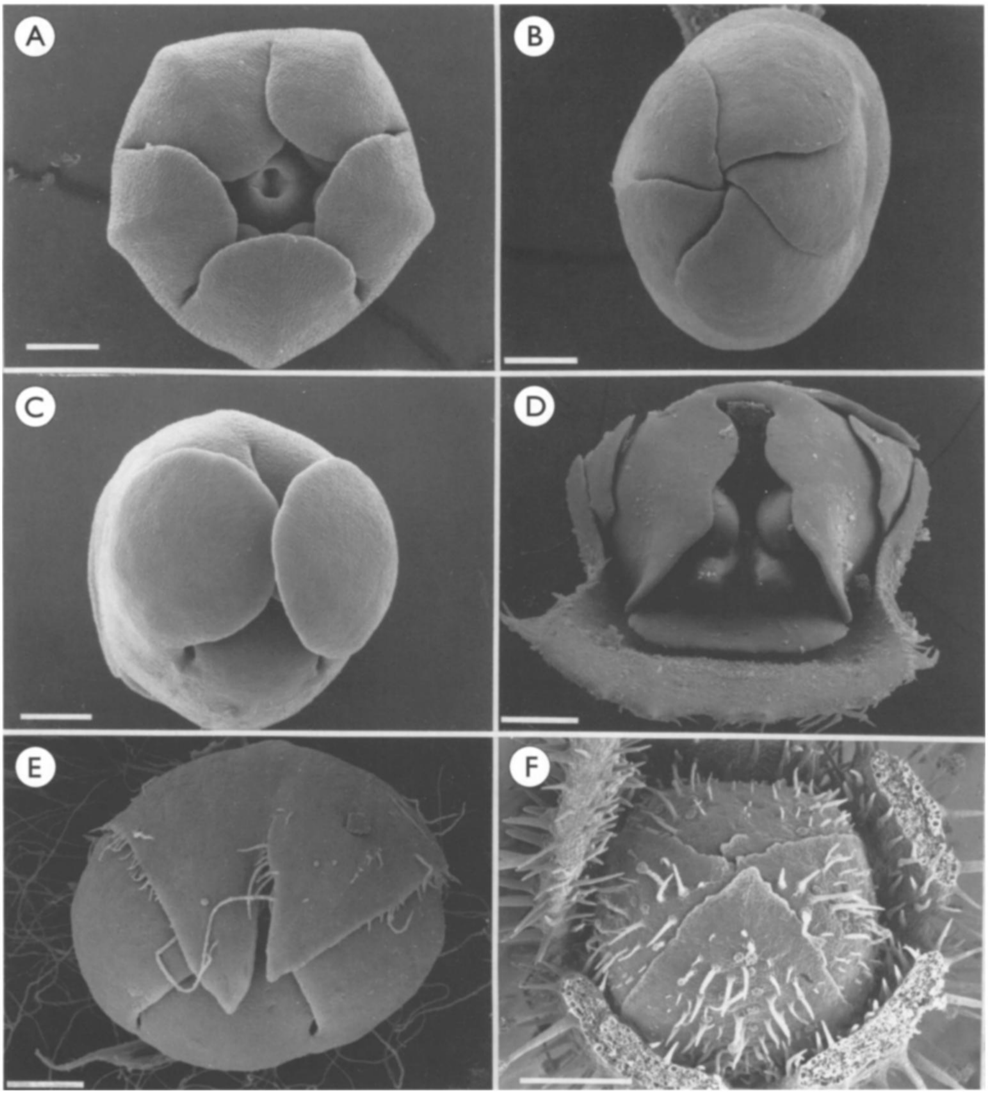


Fig. 4. Corolla aestivation, details as in Scotland *et al.* (1994) & Scotland *et al.* (in prep.). **A** *Odontonema schomburgkianum*, ascending-cochlear; **B** *Eranthemum pulchellum*, left-contort; **C** *Crabbea velutina*, quincuncial; **D** *Acanthus spinosus*, open; **E** *Nelsonia canescens*, descending-cochlear; **F** *Andrographis paniculata*, ascending-cochlear. Scale bars = 128.5, 128.5, 128.5, 450, 300 and 250 µm respectively.

aestivation patterns. Quincuncial aestivation is also found in *Borneacanthus* and *Hulemacanathus* (Bremekamp 1960: 154), *Barleriola, Boutonia, Chroesthes, Lepidagathis* and *Lophostachys,* (Lindau 1893, 1895; Benoist 1967; Daniel 1993; Scotland *et al.* 1994). Bremekamp (1960) claimed that *Calacanthus* also has quincuncial aestivation although Lindau (1895) and Clarke (1885) describe it as left-contort and the genus may simply have been associated with taxa with quincuncial aestivation because *C. dalzelliana* T. Anderson has been described as *Lepidagathis grandiflora* Dalzell. Unpublished pollen data of the first author demonstrates that *C. dalzelliana,* although biporate, has pseudocolpi with two distinct bands of sexine surrounding the aperture, typical of many genera with left-contort aestivation.

Corolla aestivation is highly conserved across many genera of *Acanthaceae* although polymorphic within a few. In some situations, for example *Acanthus spinosus* documented as open by Scotland *et al.* (1994), mature flowers show a characteristic ascending cochlear pattern with the ventral (abaxial) petal outermost.

TABLE 1. Taxonomic distribution of aestivation patterns in *Acanthaceae.*

Descending-cochlear
Nelsonioideae sensu Lindau

Ascending-cochlear
Justicieae sensu Bremekamp
Andrographideae sensu Lindau
Acanthoideae sensu Bremekamp [not *Acanthus spinosus*]
Thunbergia crispa and *T. erecta*

Quincuncial
Barlerieae sensu Lindau [not determined for *Neuracanthus*]
Borneacanthus
Chroesthes

Left-contort
Contortae sensu Lindau less *Barlerieae*
Anomacanthus R. D. Good
Mendoncia Vell. ex Vand.
Meyenia Nees
Thunbergia Retz.
Pseudocalyx Radlk.

Open
Acanthus spinosus L.

POLLEN MORPHOLOGY

Due to the enormous range of pollen variation within *Acanthaceae* (Radlkofer 1883; Lindau 1893, 1895; Raj 1961, 1973; Bremekamp 1944, 1965; Furness 1985, 1989, 1990a, 1990b, 1992, 1993, 1994, 1995a, 1995b, 1996, 1997, 1998; Balkwill & Getliffe Norris 1988; Scotland 1990, 1991, 1992a, 1992b, 1993; Daniel 1998; Carine & Scotland 1999) both Lindau (1895) and Bremekamp (1965) emphasized pollen characters particularly at the tribal and subtribal levels. The tribes and subtribes recognized by Bremekamp (1965) did not account for all genera and were often based exclusively on pollen morphology. For example, genera with highly distinct pollen, *Whitfieldia* (Fig. 8), *Blechum* (Fig. 9C & D) and *Louteridium* (Fig. 7D), were placed in their own subtribe and tribes. Other tribes and subtribes, such as *Trichanthereae* (Fig. 7A – C) (*Sanchezia, Bravaisia, Trichanthera, Suessenguthia, Trichosanchezia*) and *Hygrophileae* (Fig. 9A & B) (*Hygrophila* and *Brillantaisia*) included few genera on the basis of shared diagnostic pollen characters but are supported by other gross morphological characters (Daniel 1988a; Sidwell 1998). Other tribes, such as *Ruellinae* were diagnosed by a loose combination of pollen characters and the relationship between group membership and pollen data remains unclear. A problem with a tribal and subtribal classification based almost exclusively on pollen data is that of homoplasy. Carine & Scotland (in press) demonstrated, that within a single genus (*Strobilanthes*), very distinct pollen morphologies can be highly homoplastic; data sets partitioned into pollen and all other gross morphological characters yielded trees that are totally incongruent. This means that pollen data should be used with caution and not in isolation from other gross morphological characters. Carine and Scotland (in press) demonstrated that individual pollen characters, within *Strobilanthes*, indicate relationships but only at low taxonomic levels.

Below we describe and illustrate a representative sample of pollen variation in the context of discussing the tribal and sub-tribal classification of Bremekamp (1965) (Appendix 2) and tribal classification of Lindau (1895) (Appendix 1). Our aim is to discuss a range of pollen morphological variation for the family and provide a consolidated set of illustrations of the major pollen types within *Acanthaceae sensu* Bremekamp (1965). All details regarding pollen preparation and microscopy are as Scotland (1993) and the few images from unvouchered material have been double checked against vouchered material to check that the pollen is as stated. Material without a known collector is marked "*s.c.*"

Acanthoideae sensu Bremekamp (1965)

Bremekamp's *Acanthoideae* equals Lindau's (1895) tribes *Acantheae* and *Aphelandreae.* This group was diagnosed by van Tieghem (1908) for genera that possessed retinaculate fruits but lacked cystoliths. These genera are further characterized by 4 monothecate anthers and colpate pollen (Bremekamp 1965). A selection of the pollen of some representative genera from this group is shown in Fig. 5 and Fig. 6A & B. The presence of tricolpate pollen (i.e., simple rather than compound apertures) is a constant feature of all genera within this group and is diagnostic of this group within *Acanthaceae,* although there are reports of some species or specific collections of some species having irregular numbers of colpi (Furness 1993; Daniel 1998). Illustrations and discussion of pollen variation within this group can be found in Raj (1961, 1973), Wasshausen (1975, 1990); Balkwill & Getliffe Norris (1988); McDade (1984, 1988); Furness (1990a, 1990b, 1993, 1996, 1997); Daniel (1983, 1988b, 1997, 1998).

Within his *Acanthoideae,* Bremekamp (1965) recognized 5 distinct tribes (Appendix 2). Three of the tribes (*Haselhoffieae, Rhombochlamydeae, Stenandriopsideae*) each contained one genus (*Haselhoffia* Lindau = *Physacanthus* Benth. ex C. B. Clarke, *Rhombochlamys* Lindau and *Stenandriopsis* S. Moore) respectively. *Stenandriopsis* is synonymous with *Stenandrium* Nees (Vollesen 1992) and *Physacanthus* has left-contort corolla aestivation (Bentham 1876; Burkill & Clarke 1899 – 1900), compound pollen apertures and pseudocolpi (Fig. 6C & D) and is here provisionally classified with other genera that possess left-contort corolla aestivation.

Trichanthereae sensu Bremekamp (1965)

Figs 7A – C illustrate two of the five genera from the *Trichanthereae.* All five genera have highly diagnostic bi-aperturate pseudocolpate pollen (Lindau 1895; Raj 1961, 1973; Vasanthy & Pocock 1986; Daniel 1988a, 1998; Scotland 1993). There is little doubt, on the basis of pollen and other gross morphological features (Lindau 1895; Bremekamp 1965; Daniel 1988a), that the following five genera belong here: *Bravaisia, Sanchezia, Suessenguthia, Trichanthera* and *Trichosanchezia.*

Louterideae sensu Bremekamp (1965)

Bremekamp (1965) followed Lindau's (1895) classification of *Louteridium* as a monogeneric tribe based on pollen morphology. The pollen is very large (100 – 140 µm), pantoporate and highly diagnostic for the genus (Fig. 7D and Lindau 1895; Raj 1961; Scotland 1993; Daniel 1998).

Whitfieldieae sensu Bremekamp (1965)

Fig. 8 illustrates a representative sample of *Whitfieldia* pollen which varies considerably in aperture number, shape and the presence or absence of spinules on the tectum (Raj 1961, 1973; Furness & Vollesen 1991; Scotland 1993) sometimes even within the same species (Fig. 8A & B). This pollen type is unique to this genus which is placed in its own tribe [*Whitfieldieae*] by Bremekamp (1965). Bremekamp (1965) suggested that *Chlamydacanthus* may also belong here although Lindau (1895) placed this genus in a very different part of *Acanthaceae.* Lindau (1895) classified *Whitfieldia* within his *Ruellieae,* due to the presence of left-contort corolla aestivation, although Manktelow (2000) has shown that *Whitfieldia* lacks the staminal filament curtain typical of other genera with left-contort corolla aestivation.

Ruellieae sensu Bremekamp (1965)

Ruellieae sensu Bremekamp (1965) comprises *Hygrophileae, Petalideae, Strobilantheae, Ruellieae* and *Barlerieae sensu* Lindau (1895). Bremekamp (1965) further divided *Ruellieae* into 6 subtribes, once again, with high emphasis on distinct pollen morphologies. These are discussed in turn below.

Hygrophilinae sensu Bremekamp (1965)

Hygrophilinae sensu Bremekamp (1965) is Lindau's *Hygrophileae* with the exclusion of *Eremomastax* and *Mellera* which Bremekamp (1965) placed in *Petalideae.* The two included genera, *Hygrophila* and *Brillantaisia,* have four-aperturate (Fig. 9A & B), pseudocolpate pollen (Raj 1961, 1973; Scotland 1993; Furness 1994; Daniel 1998; Sidwell 1998) and a close relationship between these two genera is widely acknowledged (Lindau 1895; Bremekamp 1965; Sidwell 1998).

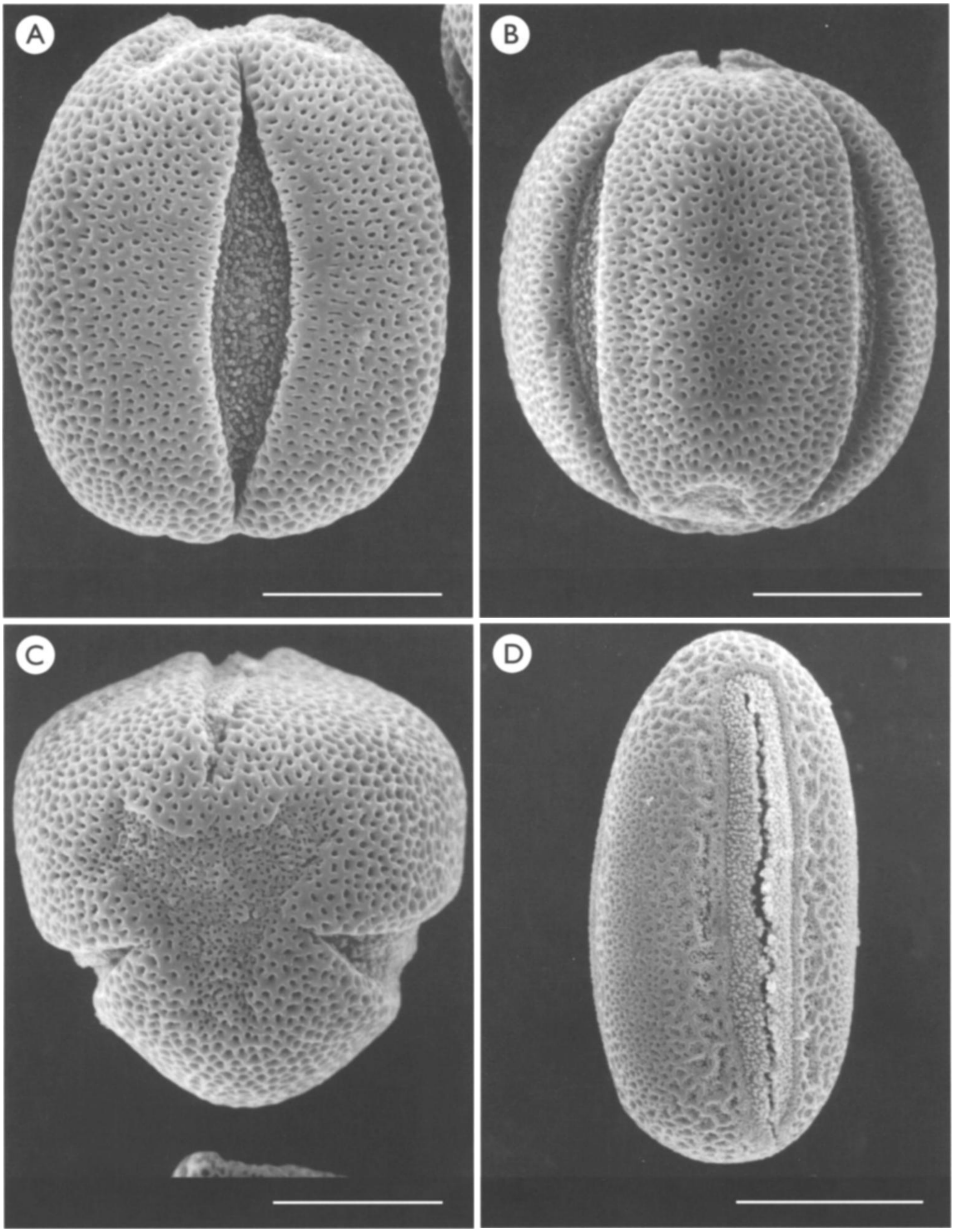


FIG. 5. Pollen of *Sclerochiton* and *Acanthopsis*. **A – C** *S. ilicifolius*. **A** apertural view of colpus; **B** mesocolpial view; **C** polar view showing three apertures and trilete polar depression. From *Meeuse* 9657 (BM); **D** *A. hoffmannseggiana*, apertural view of colpus. From *Schlieben* 8767 (BM). Scale bars = 10, 10, 10 and 20 µm respectively.

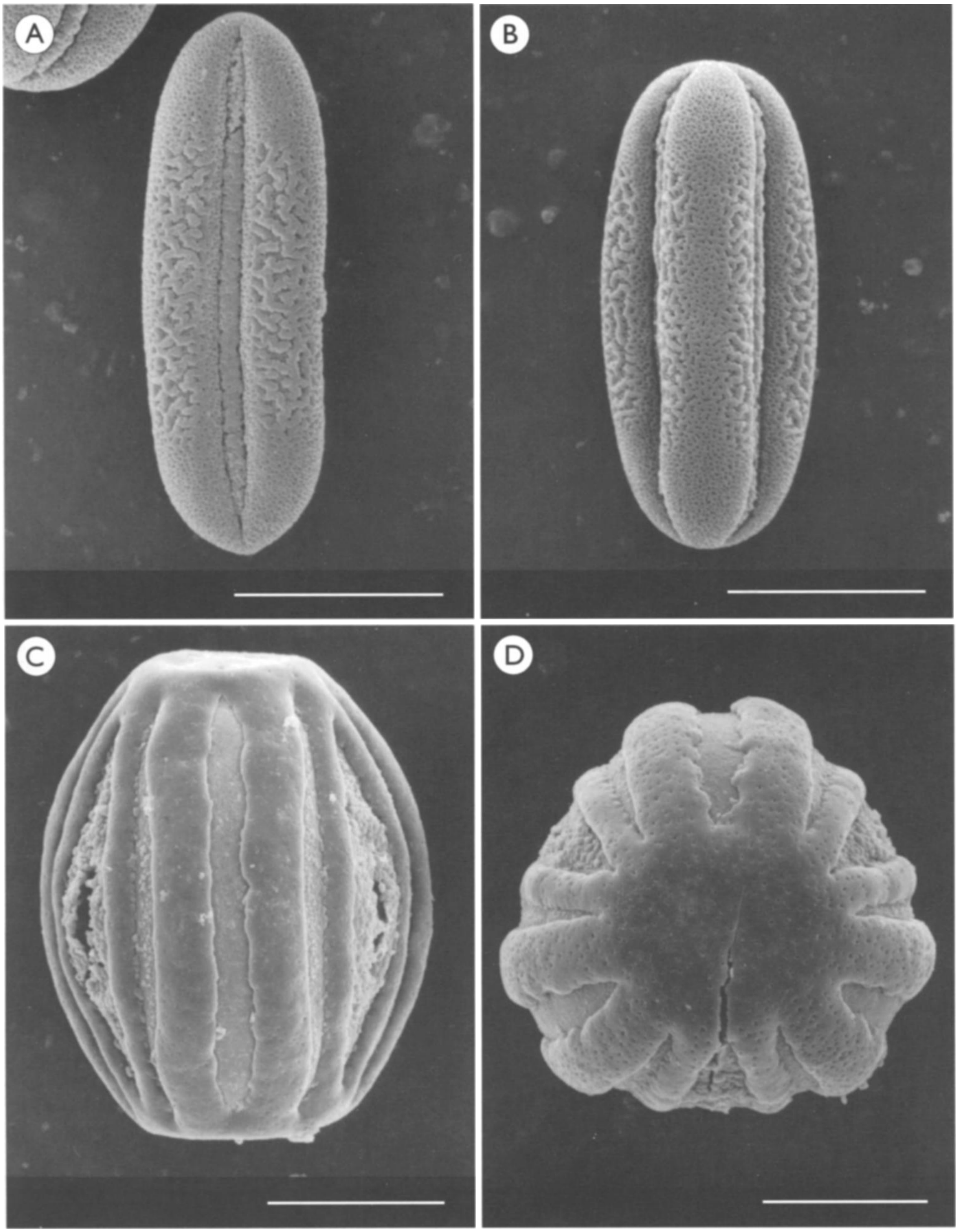


FIG. 6. Pollen of *Aphelandra* and *Physacanthus*. **A** & **B** *A. scabra*. **A** apertural view of colpus; **B** mesocolpial view. From *Cham. & Schlecht.* 2834 (BM); **C** & **D** *P. batanganus*. **C** mesocolpial view showing compound apertures, pseudocolpi and longitudinal ribs; **D** polar view showing twelve longitudinal ribs. From *Le Testu* 5072 (BM). Scale bars = 20, 20, 17.6 and 15 μm respectively.

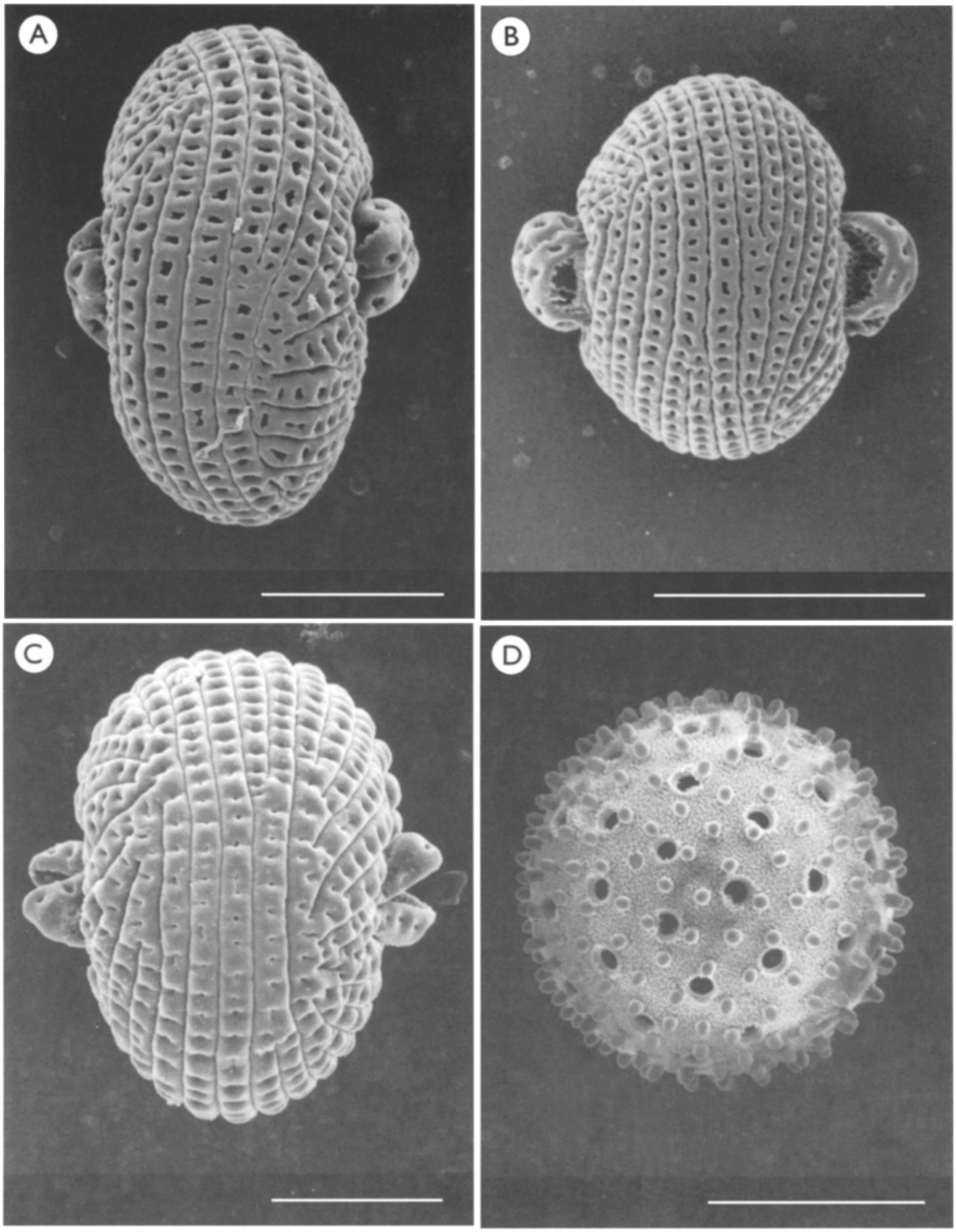


FIG. 7. Pollen of *Sanchezia*, *Bravaisia* and *Louteridium*. **A** *S. speciosa* showing two apertures. From *Rosas* 960 (BM); **B** *S. nobilis* showing extended areas of exine surrounding the apertures. From *Ahmed* 8 (BM); **C** *B. berlandieriana*, bi-aperturate. From *Cabrera* 1149 (BM); **D** *L. donnell-smithii*, panto-porate with prominent spines. From *Contreras* 5510 (BM). Scale bars = 30, 60, 20 and 60 µm respectively.

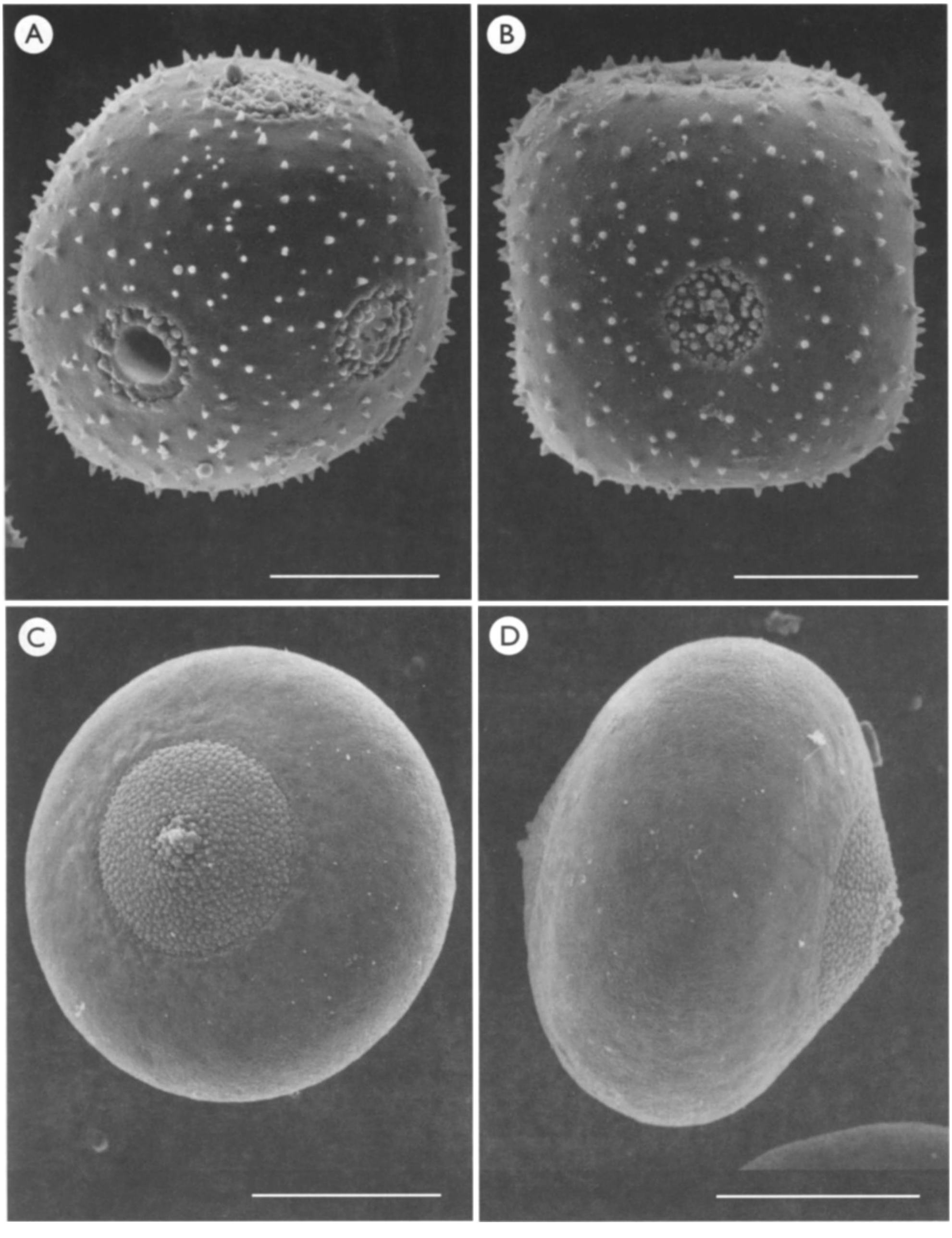


FIG. 8. Pollen of *Whitfieldia*. **A** *W. elongata*, spherical, panto-porate and spinulose. From *Lieuker & Fraud* 69 (BM); **B** *W. elongata*, square, spinulose, with an aperture on each face. From *Richards* 3012 (BM); **C** *W. preussii*, apertural view, bi-aperturate. From *s.c.* 516 (BM); **D** *W. lateritia*, bi-lateral symmetry. From *Elliot* 4933 (BM). Scale bars = 20, 20, 20 and 20 µm respectively.

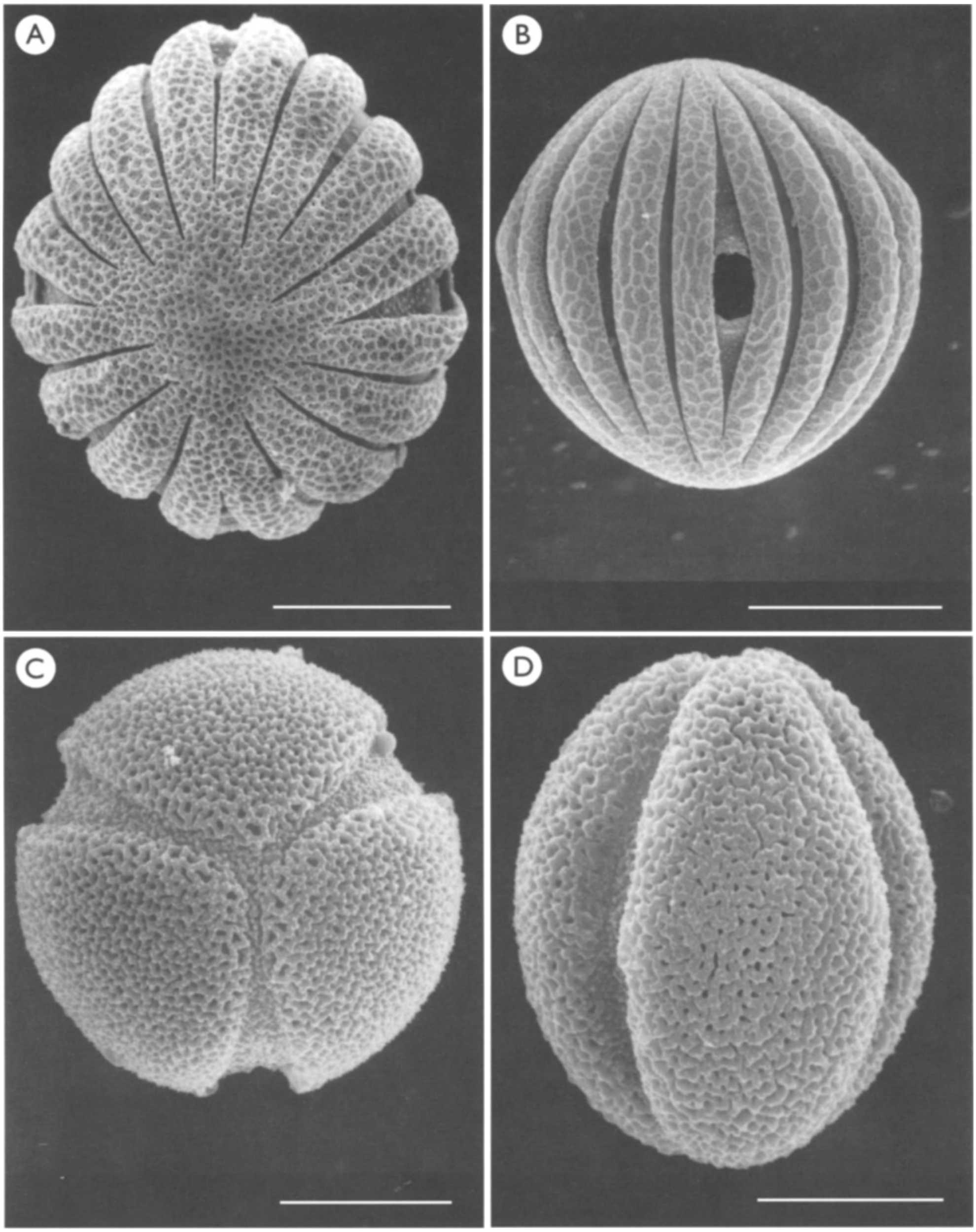


FIG. 9. Pollen of *Hygrophila* and *Blechum*. **A** *H. angustifolia*, polar view, pseudocolpate, 4-aperturate. From *s.c.* 481b (BM); **B** *H. auriculata* apertural view showing compound colporate aperture. From *Siddigi* 4274 (BM); **C** & **D** *B. pyramidatum*. **C** polar view, tri-aperturate with apertures joined at the poles (syncolpate); **D** mesocolpial view. From *Stearn* 289 (BM). Scale bars = 15, 20, 15 and 15 µm respectively.

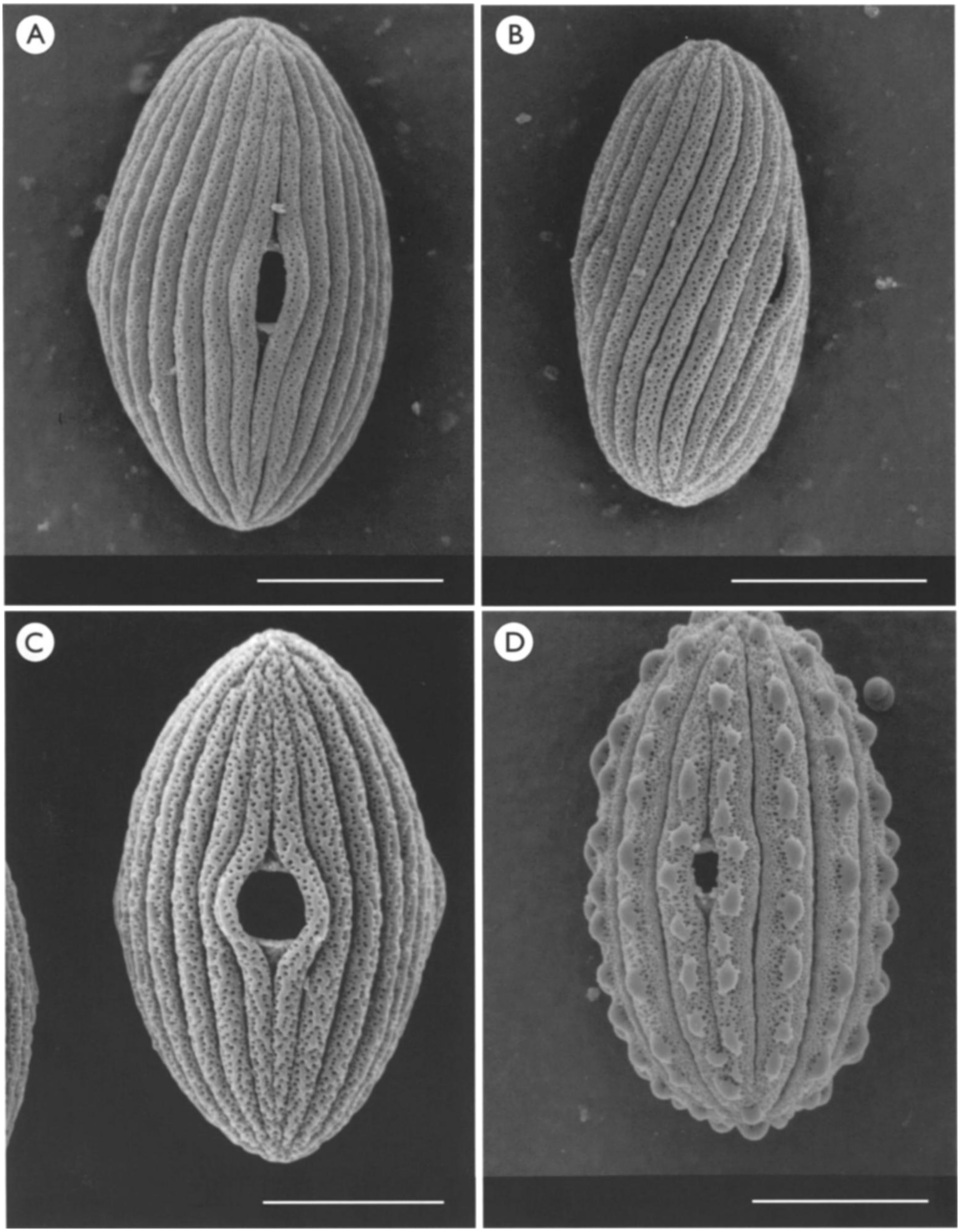


FIG. 10. Pollen of *Strobilanthes*. **A** *S. kunthiana*, tectum punctate, pseudocolpate, tri-colporate. From *Gamble* 17859 (BM); **B** *S. consanguinea*, tectum punctate, pseudocolpate, tri-colporate with longitudinal ribs in spirals. From *Beddome* 132 (BM); **C** *S. sp. nov.*, tectum punctate, pseudocolpate, showing compound aperture. From *Scotland* 93 (FHO); **D** *S. urceolaris*, pseudocolpate with aggregates of exine on each longitudinal rib. From *Schmid* s.n. (BM). Scale bars = 20, 25, 15 and 15 μm respectively.

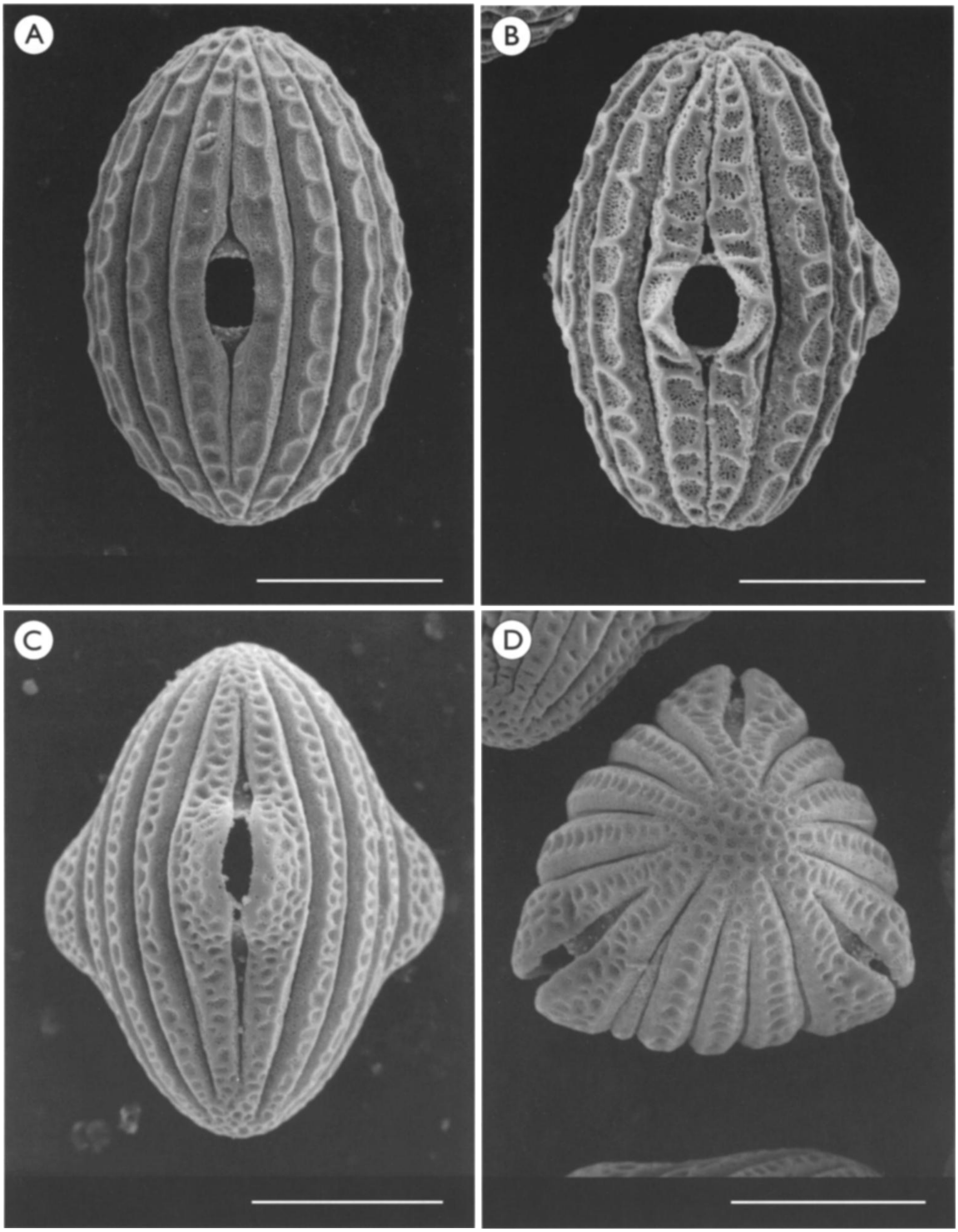


FIG. 11. Pollen of *Strobilanthes*. **A** *S. chaffonjonii*, pseudocolpate, bi-reticulate. From *Farges* 1090 (BM); **B** *S. flexicaulis*, pseudocolpate, bi-reticulate, exine priminent surrounding apertures. From *Faurie* 1473 (BM); **C** & **D** *S. lancifolia*. **C** pseudocolpate, bi-reticulate, apertural view; **D** polar view. From *Beddome* 233 (BM). Scale bars = 25, 25, 20 and 20 µm respectively.

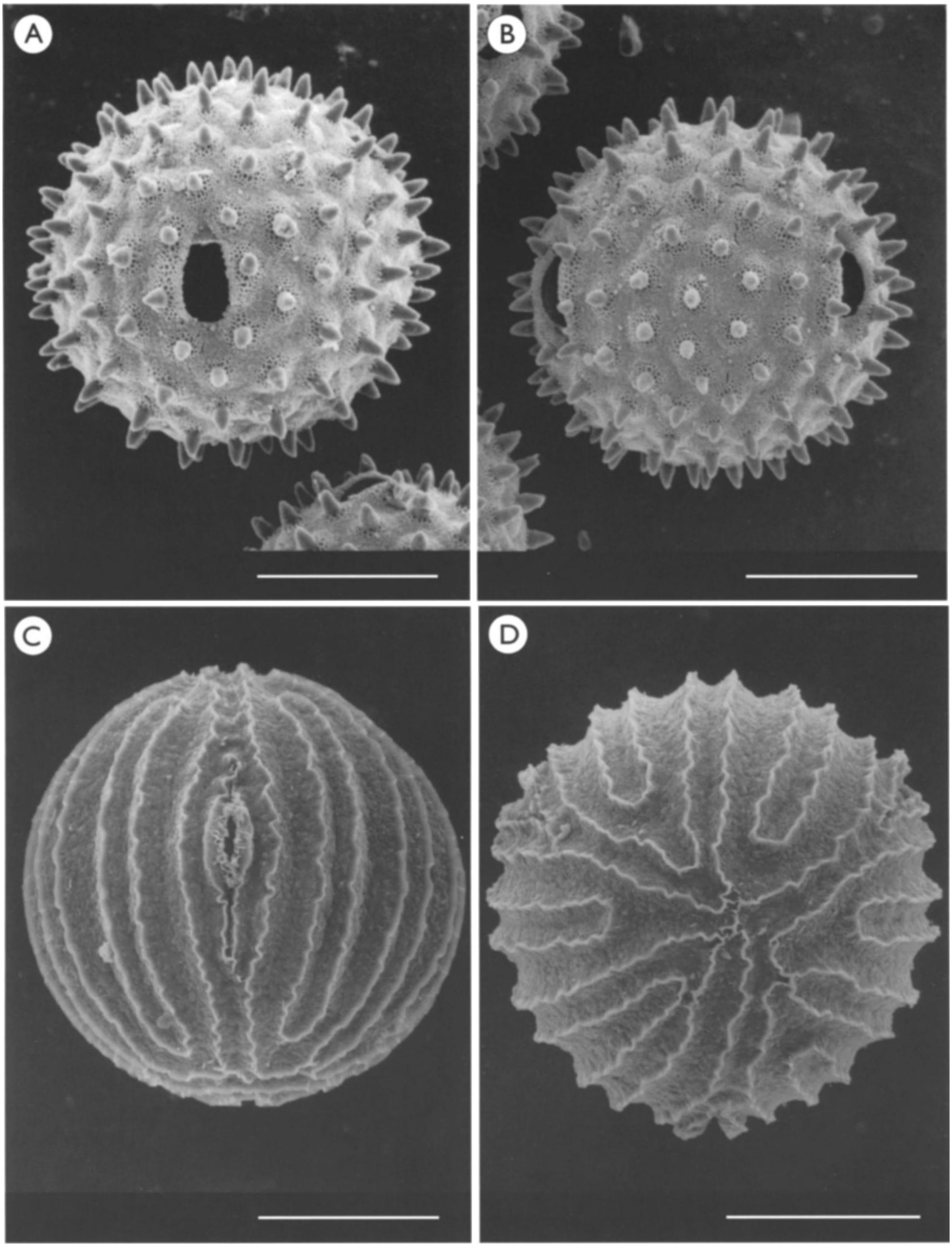


FIG. 12. Pollen of *Strobilanthes*. **A** & **B** *S. rhamnifolia*. **A** apertural view, spherical with spines; **B** meso-apertural view showing two of three brevi-colporate apertures. From *Thwaites C.P.* 2007 (BM); **C** & **D** *S. maculata*. **C** apertural view showing raised areas of tectum forming discrete longitudinal lines; **D** polar view. From *Kew Cult.*, unvouchered. Scale bars = 30, 30, 20 and 20 μm respectively

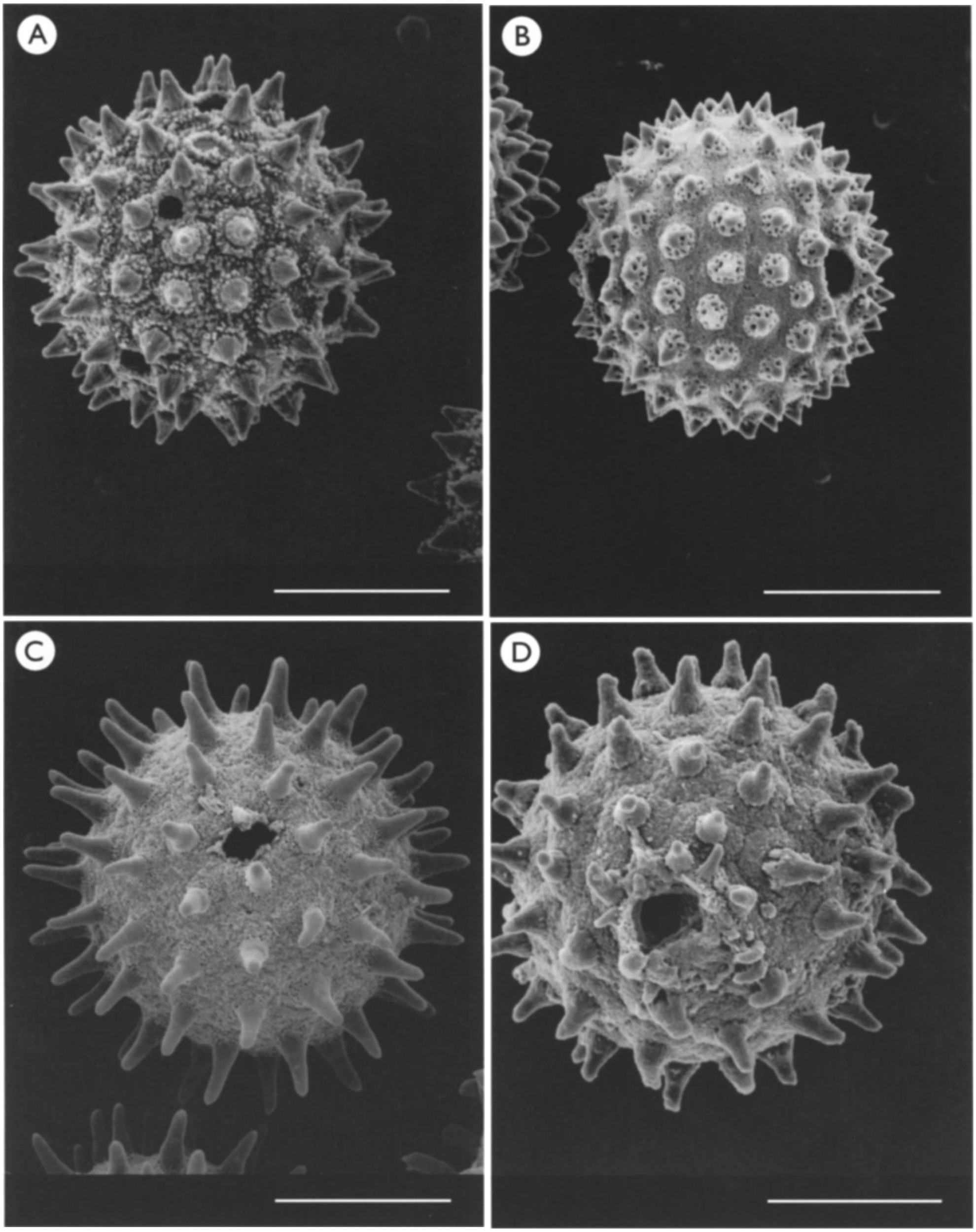


FIG. 13. Pollen of *Strobilanthes*. **A** *S. calycina*, spherical, panto-porate with spines. From *Sohmer et al.* 8532 (BM); **B** *S. walkeri*, tri-brevicolporate with spines. From *Mathew et al.* 28825 (K); **C** *S. lurida*, tri-porate with spines. From *Beddome* 175 (BM); **D** *S. hookeri*, apertural view, panto-porate with spines. From *Sohmer & Sumithraarachchi* 9997 (K). Scale bars = 25, 25, 30 and 25 μm respectively.

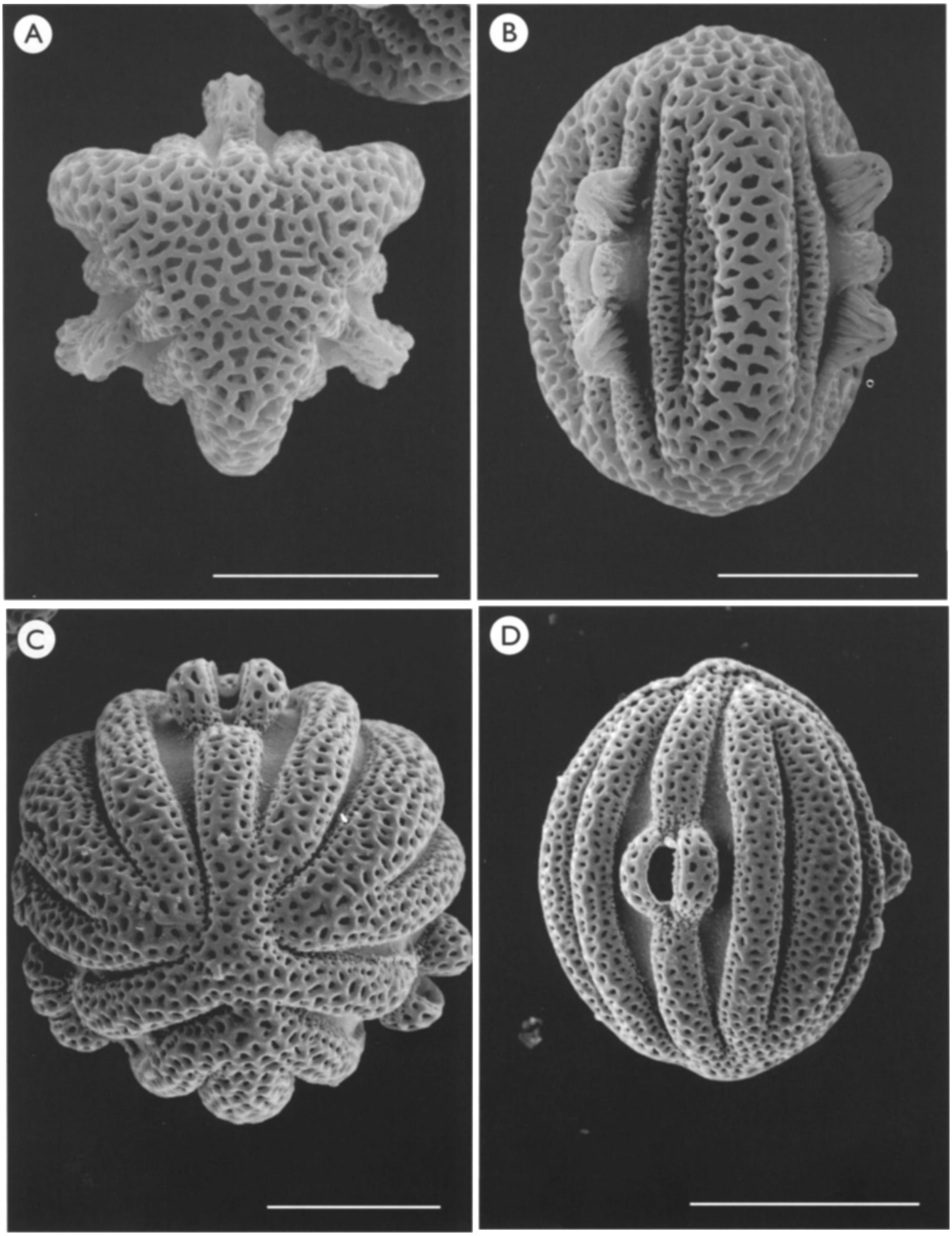


FIG. 14. Pollen of *Petalidium* & *Mellera*. **A** & **B** *P. glandulosum*. **A** polar view showing raised tectum surrounding the apertures; **B** mesocolpial view, pseudocolpate, four raised areas of tectum surrounding each aperture. From *Exell et al.* 2266 (BM); **C** & **D** *M. lobulata*. **C** polar view showing twelve longitudinal ribs and pseudocolpi; **D** apertural view showing two raised areas of tectum associated with each aperture. From *Taylor* 3296 (BM). Scale bars = 30, 30, 17.6 and 30 µm respectively.

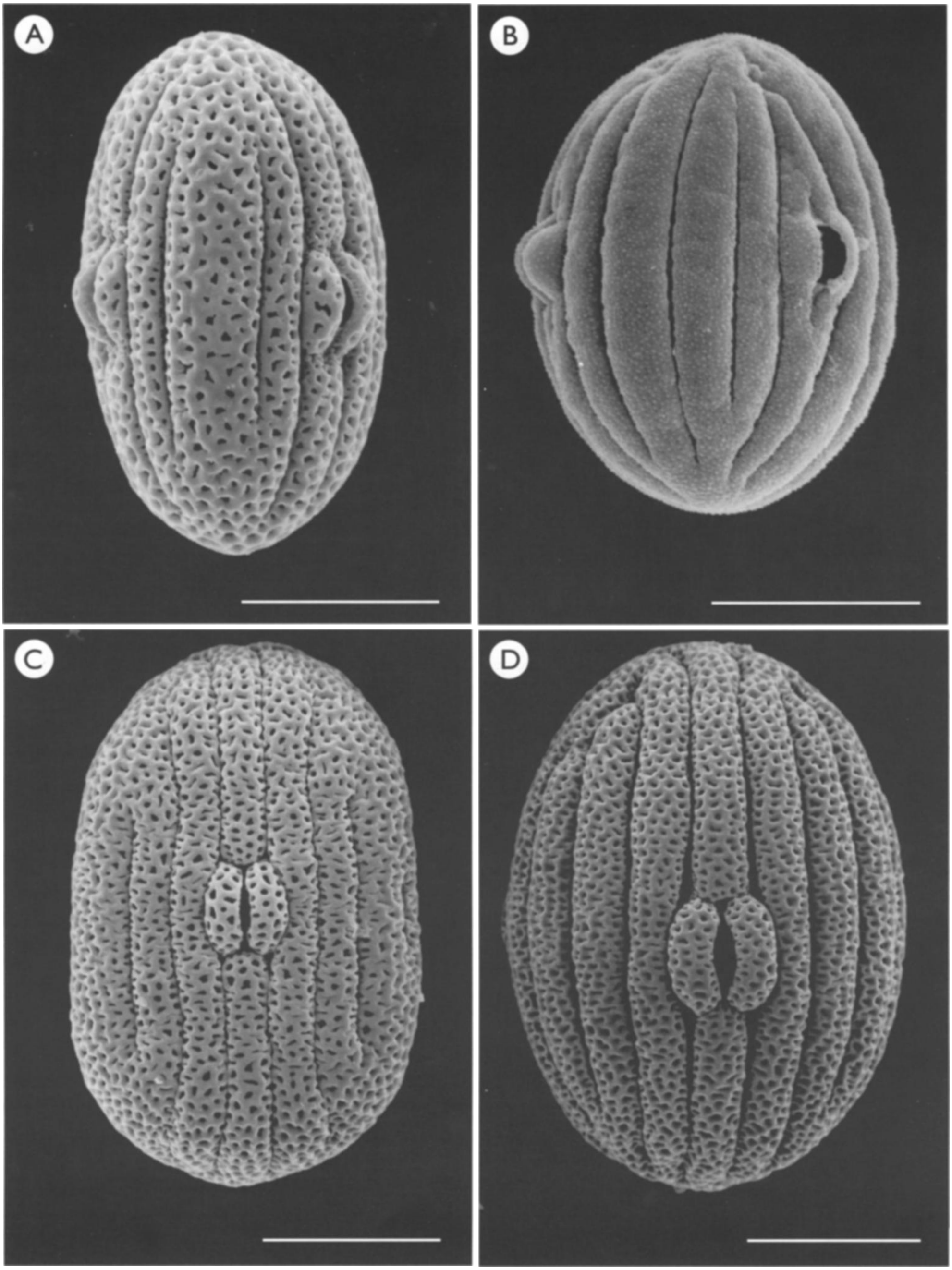


FIG. 15. Pollen of *Phaulopsis*, *Dyschoriste*, *Mimulopsis* & *Epiclastopelma* showing two raised areas of tectum associated with each aperture **A** *P. imbricata*. From *Schlecter* 2927 (BM); **B** *D. vagans*. From *s.c.* 52 (BM); **C** *M. solmsii*. From *Curb* 141 (BM); **D** *E. macranthum*. From *Schlieben* 2839 (BM). Scale bars = 15, 20, 20 and 25 μm respectively.

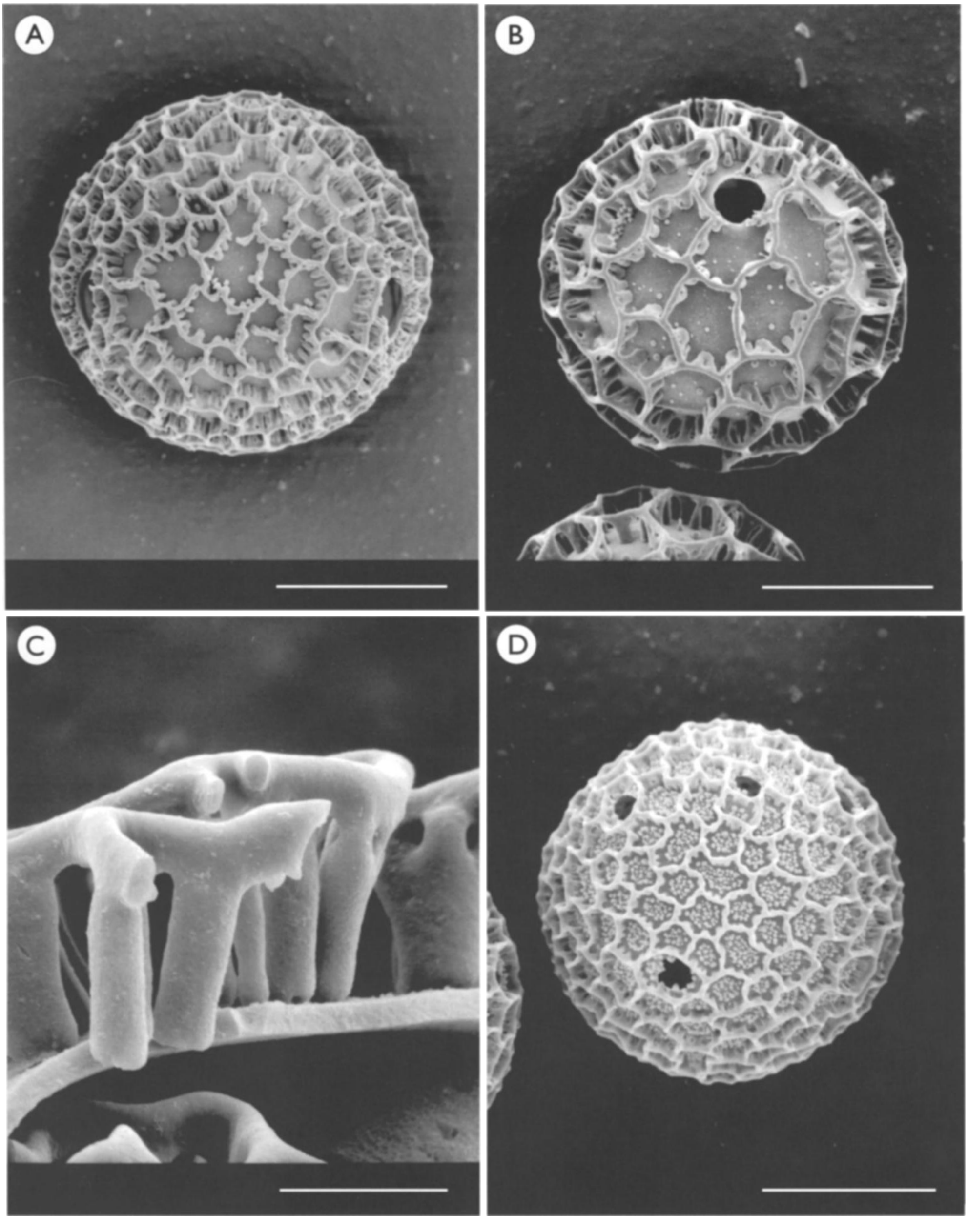


FIG. 16. Pollen of *Ruellia*. **A – C** *R. grandiflora*. **A** open reticulate tectum, tri-porate. From *Popov* 7/7 (BM); **B** open reticulate tectum with occasional small granules of exine in the lumina. From *Popov* 6/1 (BM); **C** section of wall. From *Popov* 7/7 (BM); **D** *R. patula*, panto-porate, with many small granules of exine in each lumen. From *Popov* 71/327 (BM). Scale bars = 43, 43, 6 and 25 µm respectively.

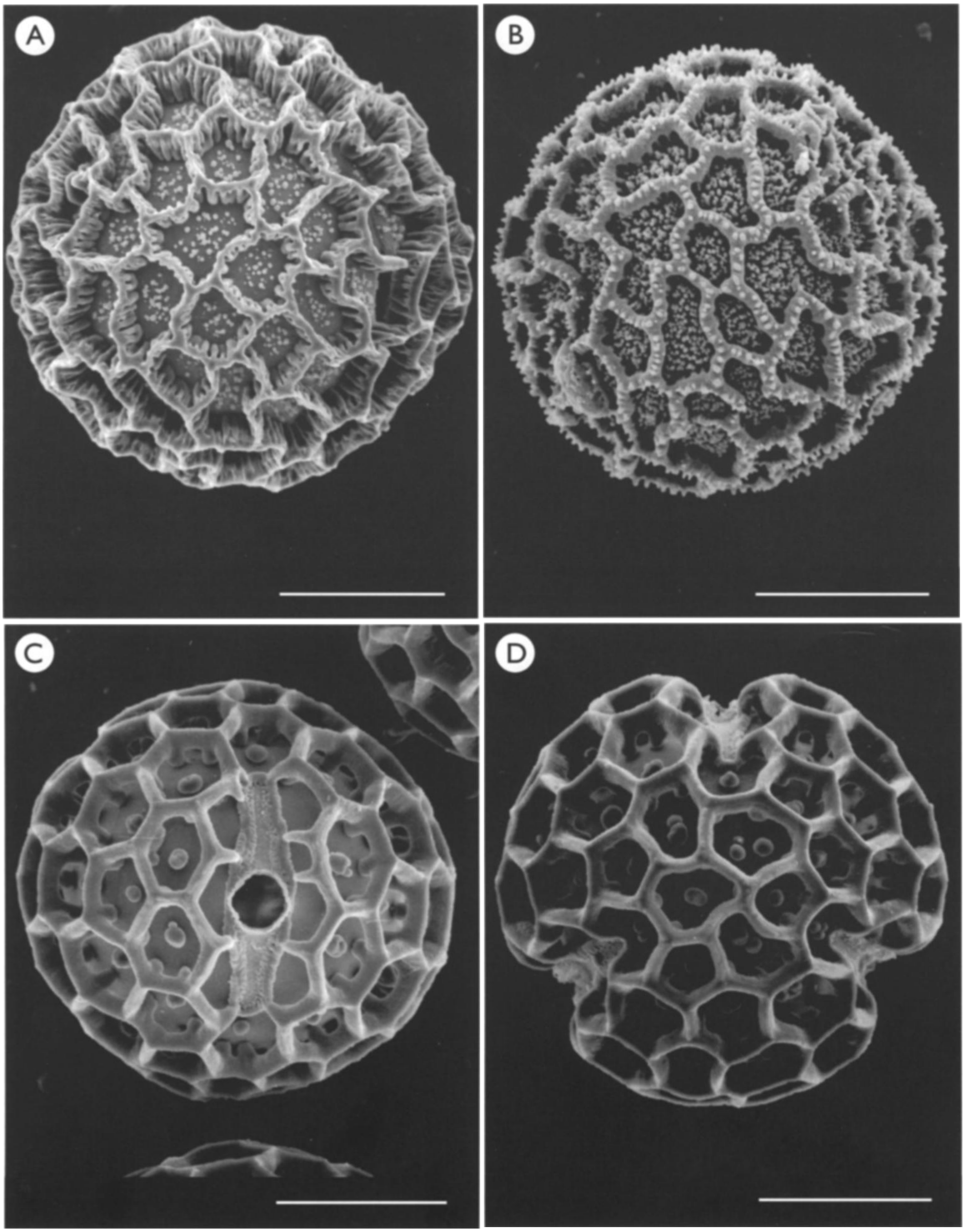


FIG. 17. Pollen of *Ruellia* & *Eranthemum*. **A** *R. albiflora*, open reticulate tectum, tri-porate. From *Palmer* 1274 (BM); **B** *R. venusta*, open reticulate tectum with spinules on tectum and in each lumen. From *Hance* 13767 (BM); **C** & **D** *E. nervosum*. **C** apertural view, open reticulate tectum, tri-colporate, granules of exine in lumina; **D** polar view. From *Stainton* 6413 (BM). Scale bars = 27, 25, 25 and 25 µm respectively.

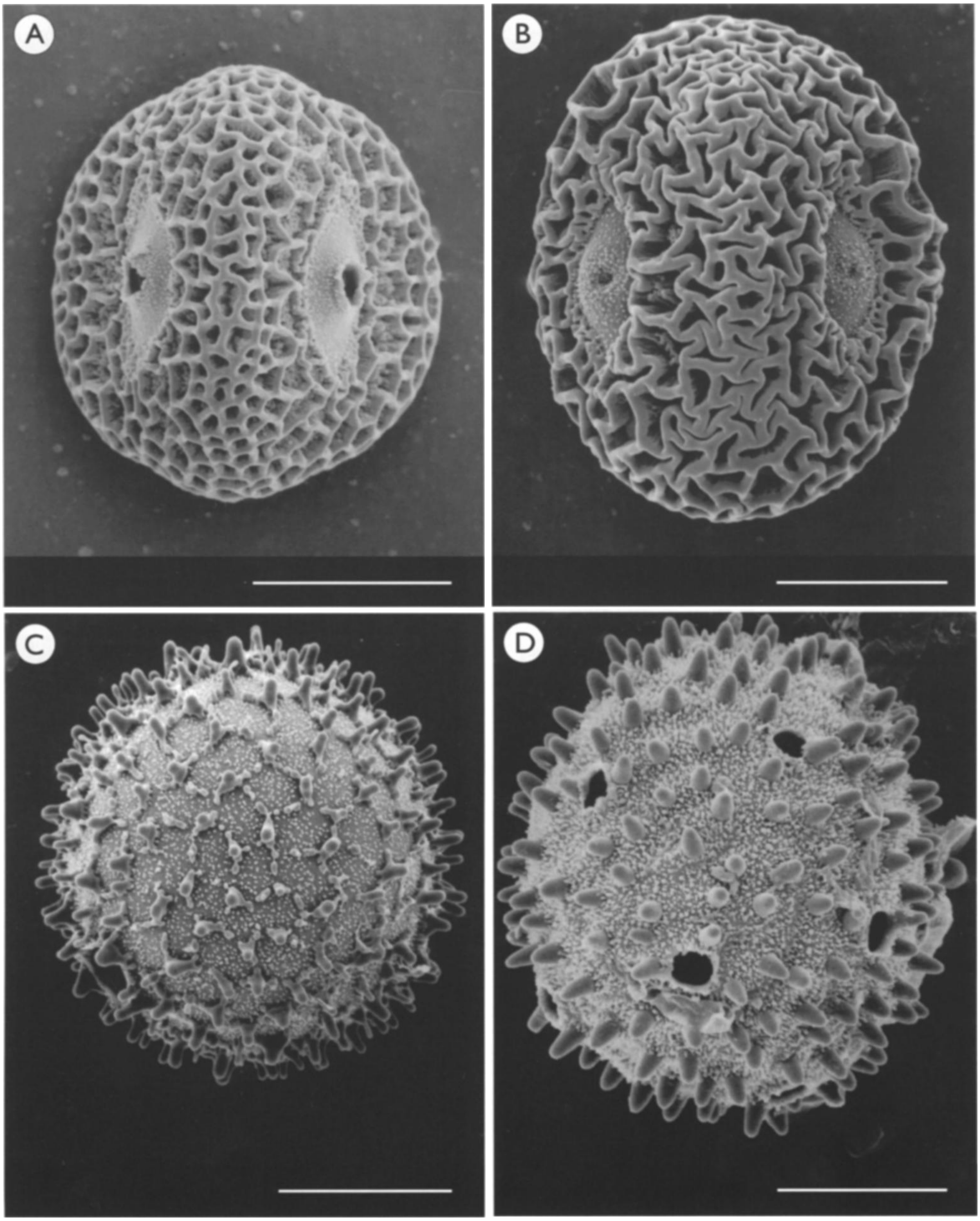


FIG. 18. Pollen of *Lankesteria, Dischistocalyx* & *Acanthopale.* **A** *L. elegans,* tri-pororate, open reticulate tectum with small granules of exine in lumina. From *Taylor* 3294 (BM); **B** *L. barteri,* reticulate tectum less open in mesocolpial area. From *Talbot* 1531 (BM); **C** *D. hirsutus,* tectum reduced to rounded spines with small granules of random exine, tri-porate. From *Gossweiler* 7998 (BM); **D** *A. confertiflora,* panto-porate, exine reduced to rounded spines with scattered small granules of exine. From *Osmaston* 2197 (BM). Scale bars = 43, 27, 30 and 25 µm respectively.

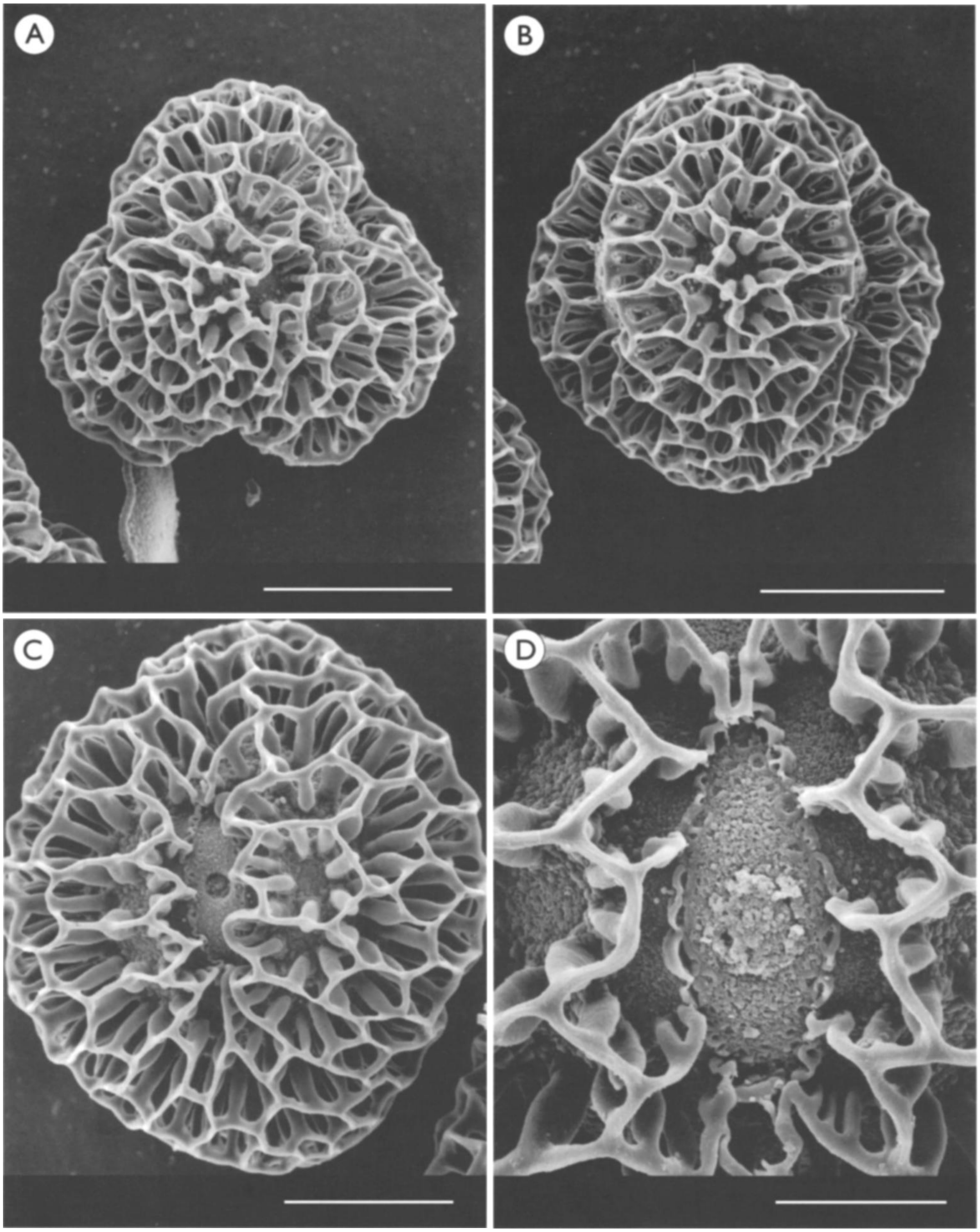


FIG. 19. Pollen of *Barleria*. **A – D** *Barleria micans*. **A** polar view, open reticulate tectum, tri-brevicolporate; **B** mesocolpial view; **C** apertural view; **D** detail of brevi-colporus. From Kew Cult. Scale bars = 43, 43, 30 and 15 µm respectively.

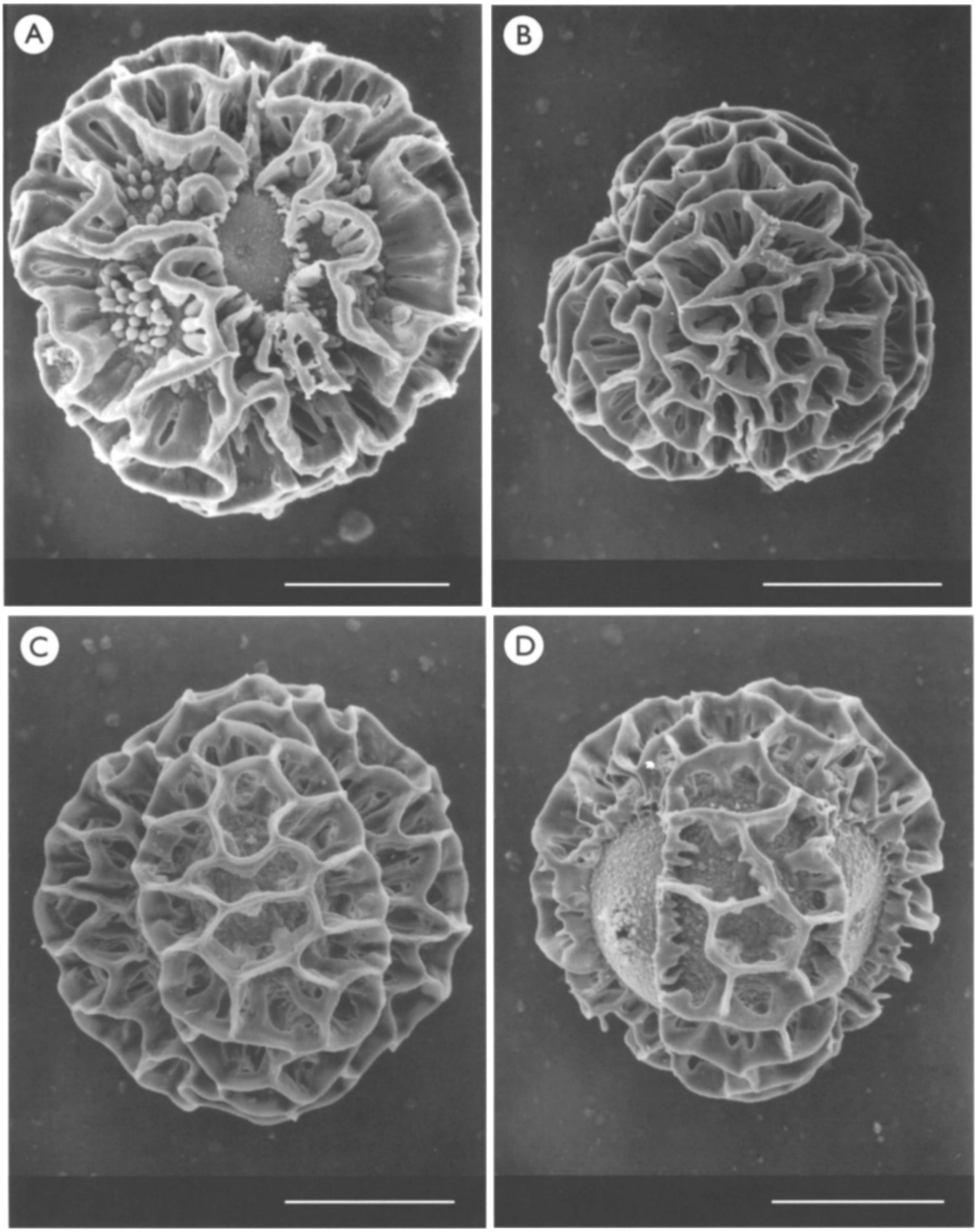


FIG. 20. Pollen of *Barleria*. **A** & **B** *B. prionitis*. **A** tri-brevicolporate, open reticulate tectum with granules of exine in lumina; **B** polar view. From Kew Cult.; **C** & **D** *Barleria hochstetteri*. **C** tri-colporate, mesocolpial view; **D** mesocolpial view showing two granular colpori. From *Popov* 69/69 (BM). Scale bars = 20, 30, 30 and 30 μm respectively.

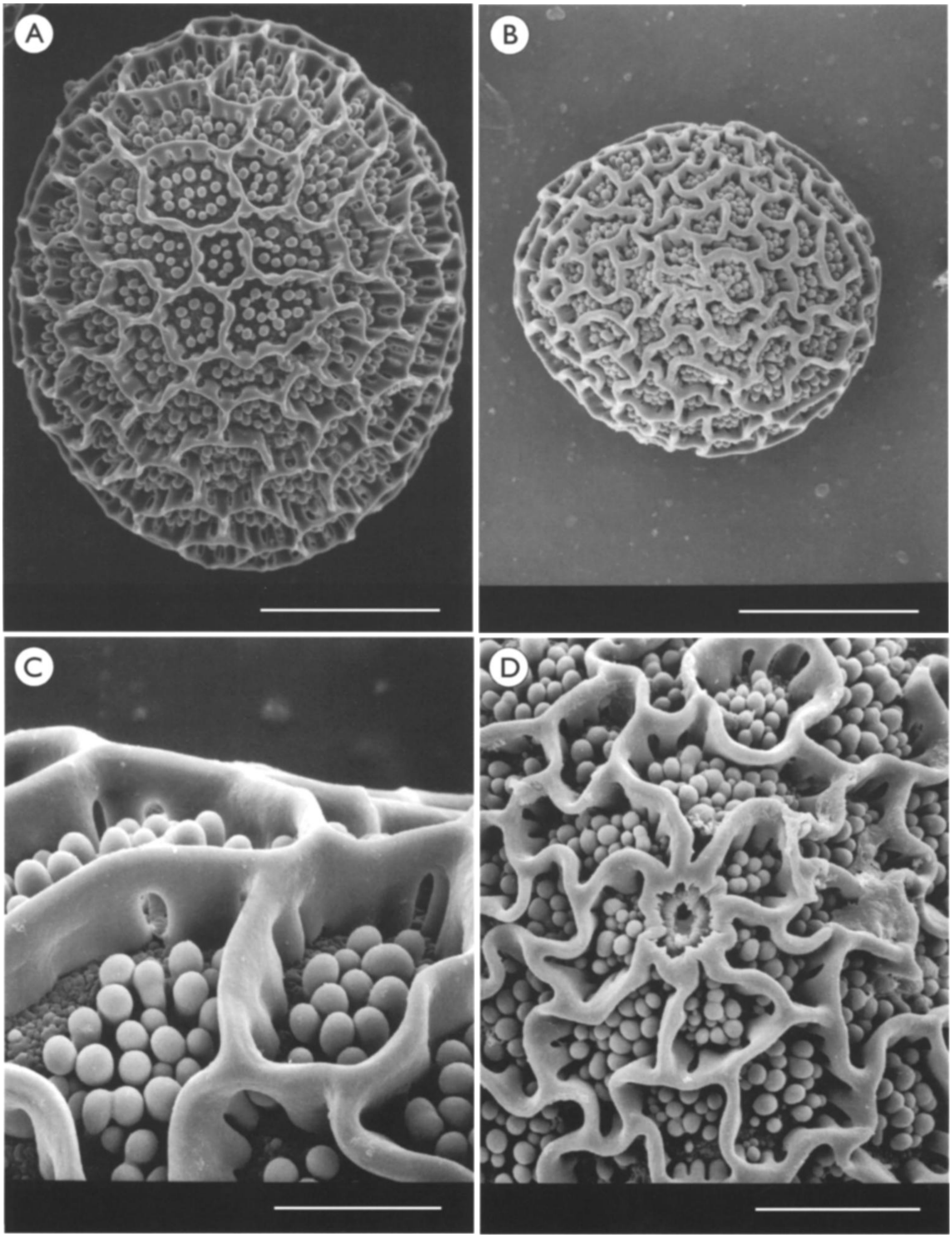


FIG. 21. Pollen of *Crabbea* and *Boutonia*. **A** *C. velutina*, sub-spherical, tri-porate, open reticulate tectum with scattered granules of exine in lumina. From *Robson* 915 (BM); **B – D** *B. cuspidata*. **B** sub-spherical shape, tri-porate, open reticulate tectum with scattered granules in lumina; **C** detail of scattered granules in lumina; **D** close up of aperture. From *s.c.* s.n. Madagascar (BM). Scale bars = 30, 43, 7.5 and 13.6 μm respectively.

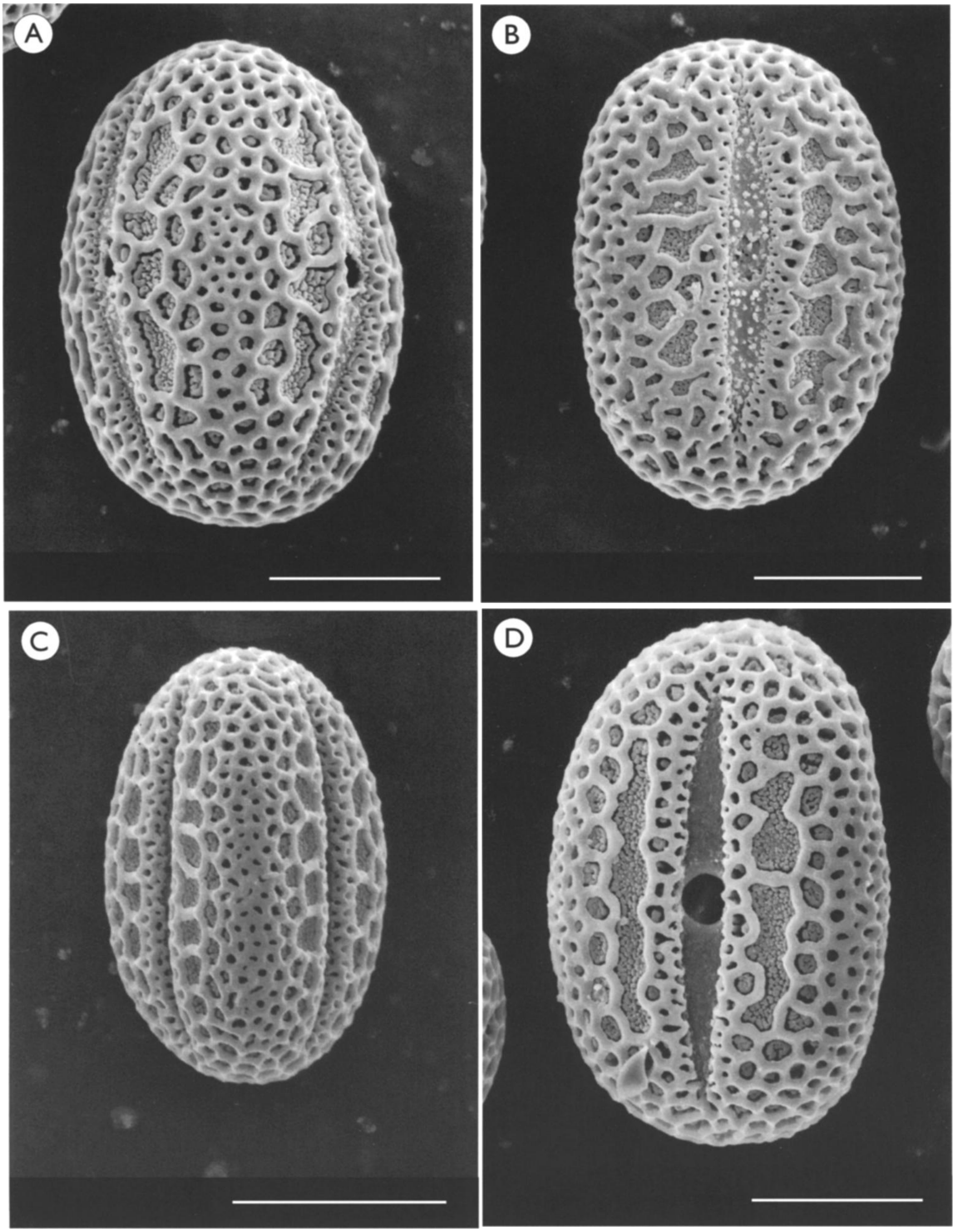


FIG. 22. Pollen of *Chroesthes* and *Lepidagathis*. **A** & **B** *C. lanceolata*. **A** tricolporate, dense aggregated granules in the lumina, reticulate tectum more open in area adjacent to apertures; **B** detail of granulated colpus. From *Garret* 221 (BM); **C** & **D** *L. hyalina*. **C** mesocolpial view, tri-colporate, reticulate tectum more open in area adjacent to apertures; **D** apertural view. From *Shaan* 16683 (BM). Scale bars = 17.6, 15, 20 and 12 µm respectively.

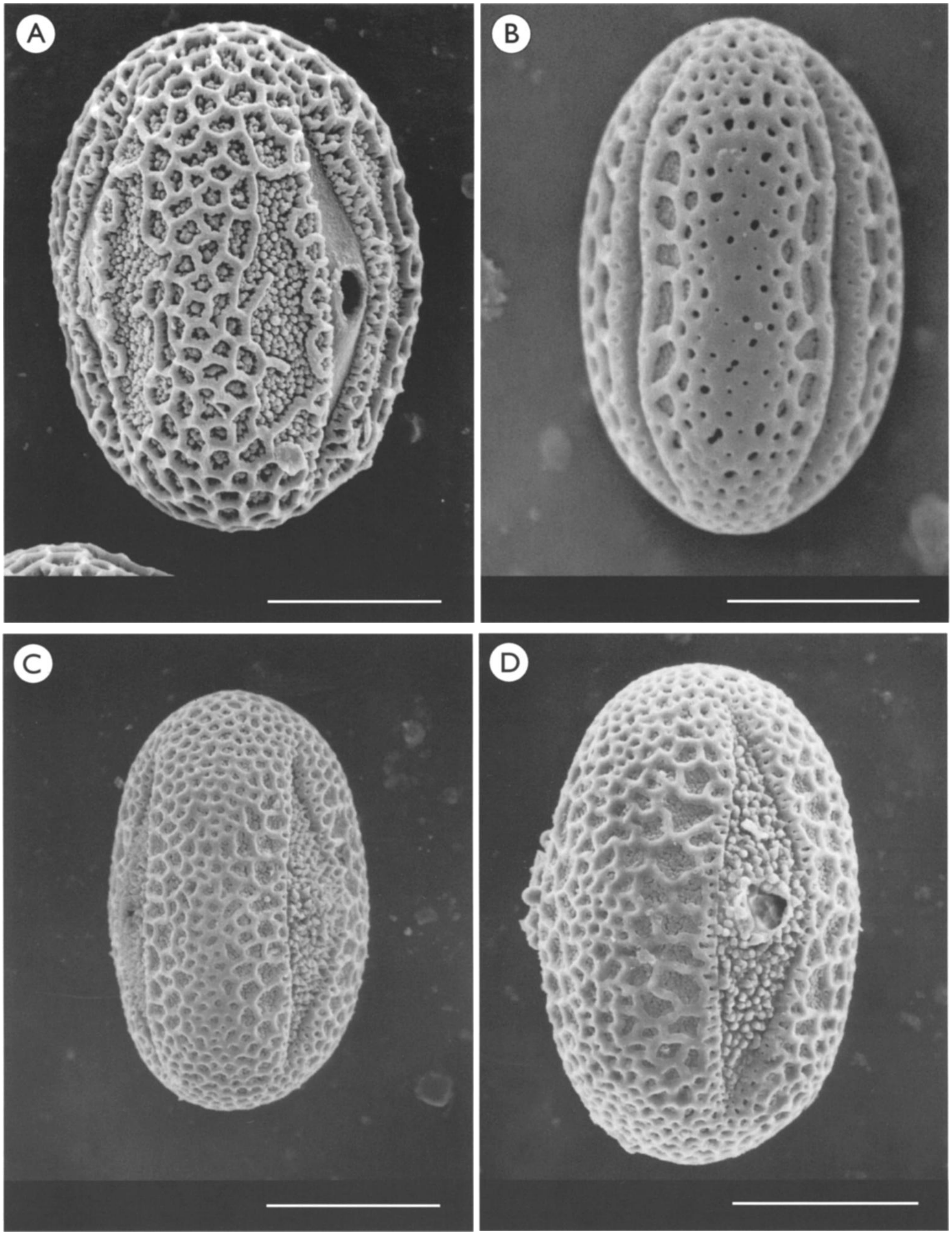


FIG. 23. Pollen of *Lepidagathis & Hulemacanthus*. **A** *L. scariosa*, mesocolpial view, tricolporate, open reticulate tectum with scattered granules in lumina. From *Young et al.* 14886 (BM); **B** *L. alopecurioidea*, mesocolpial view, tri-colporate, area bordering aperture with open reticulate tectum becoming less open in mesocoplial area. From *Proctor* 18843 (BM); **C** & **D** *H. novoguineensis*. **C** mesocolpial view, tri-colporate; **D** apertural view showing granulated colpus. From *Carr* 12309 (BM). Scale bars = 20, 10, 23.1 and 20 μm respectively.

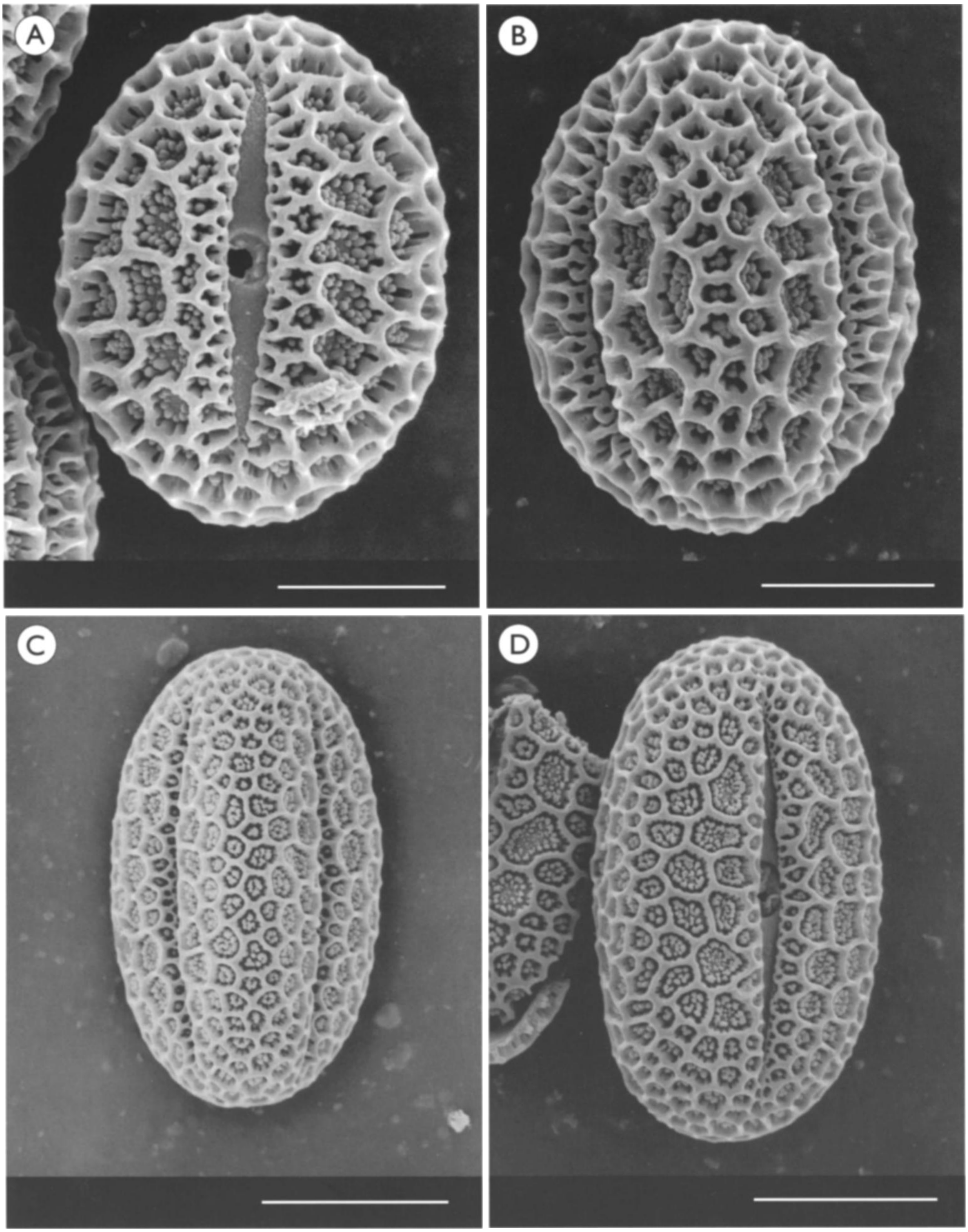


FIG. 24. Pollen of *Barleriola* & *Lophostachys*. **A** & **B** *B. solanifolia*. **A** tri-colporate, open reticulate tectum with granules in lumina; **B** mesocolpial view. From *Fuertes* 406 (BM); **C** & **D** *L. falcata*. **C** tri-colporate, open reticulate tectum with granules in lumina; **D** apertural view. From *Peulaiel* 3734 (BM). Scale bars = 13.6, 13.6, 30 and 25 µm respectively.

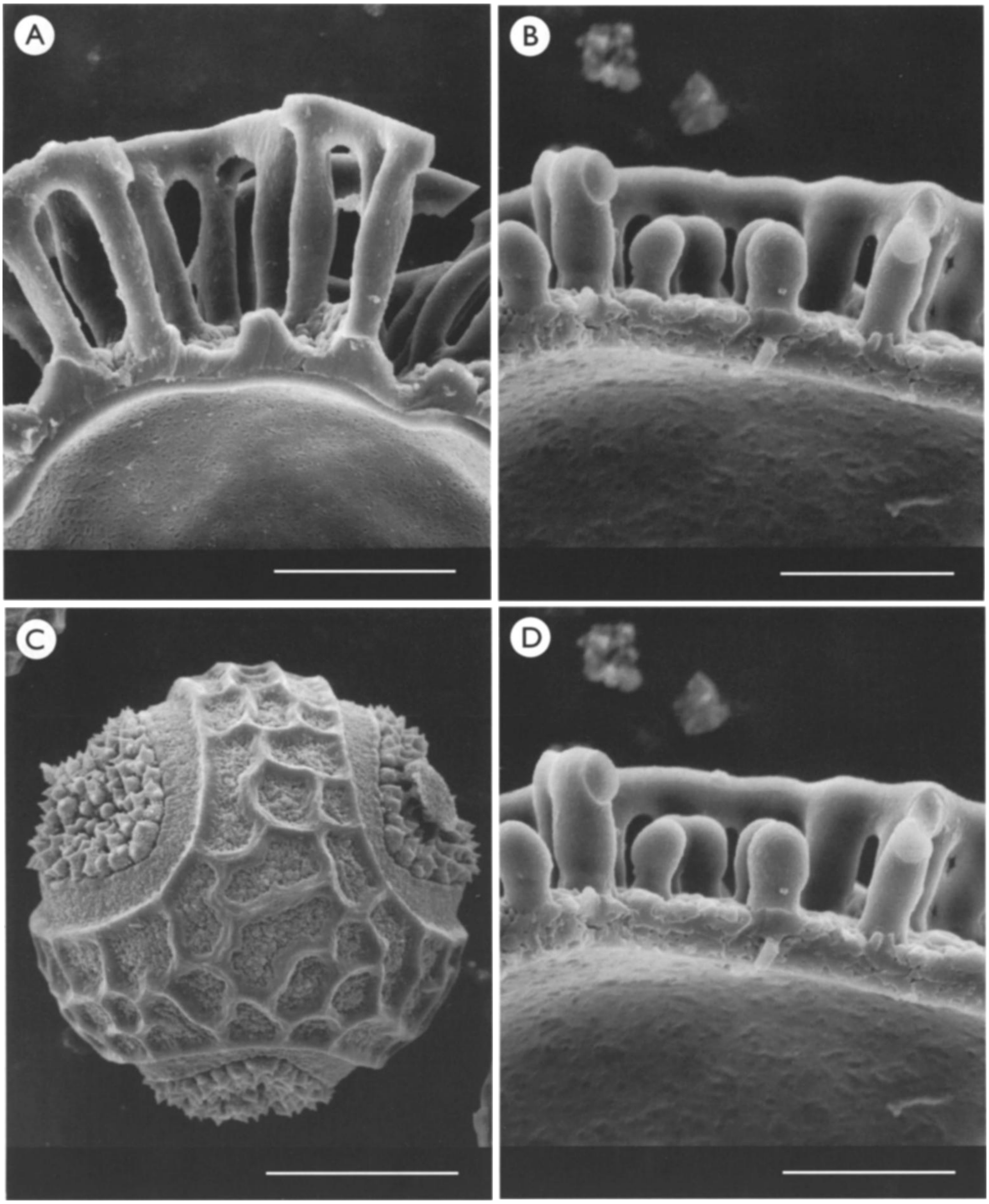


FIG. 25. Pollen of *Barleria*, *Crabbea*, *Diotacanthus* & *Cystacanthus*. **A** *B. bispinosa*, detail of wall showing depth of reticulum (see text). From *Wood* 2942 (BM); **B** *C. velutina*, detail of wall showing depth of reticulum (see text). From *Robson* 915 (BM); **C** *D. grandis*, tri-pororate with distinct aperture margins and granular aperture. From *s.c.* 435 (BM); **D** *Cystacanthus turgida*, tri-colporate with distinct aperture margin. From *Kloss* s.n. (BM). Scale bars = 12, 6, 15 and 12 µm respectively.

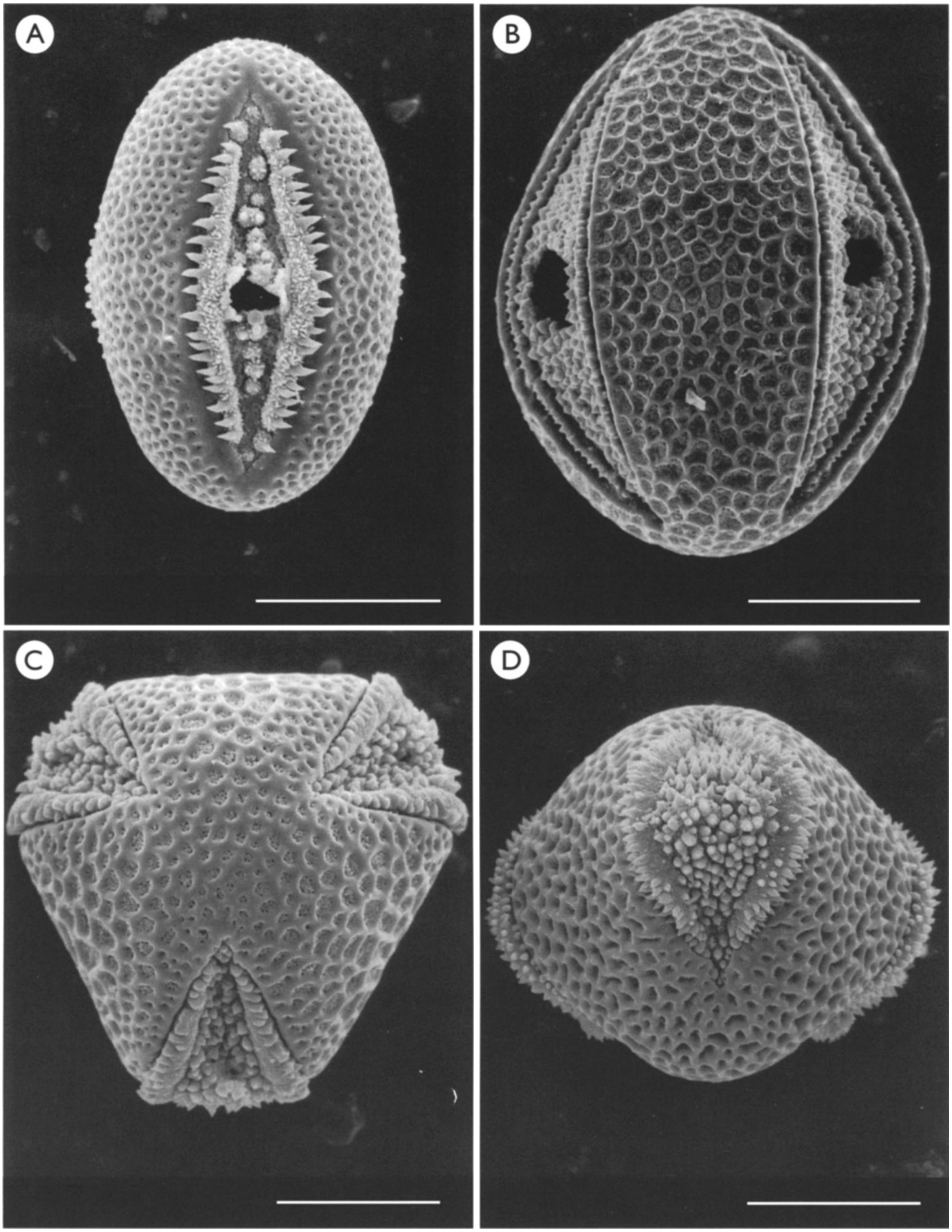


FIG. 26. Pollen of *Phlogacanthus* & *Andrographis*. **A** *P. curviflorus* tricolporate, distincte aperture margins. From *Kingdon-Ward* 20327 (BM); **B** *A. paniculata* tricolporate, distinct aperture margins. From *s.c.* 357 (BM); **C** & **D** *Haplanthodes tentaculatus*. **C** polar view showing distinct thickened aperture margins; **D** apertural view. From *s.c.* 410 (BM). Scale bars = 20, 12, 10 and 10 μm respectively.

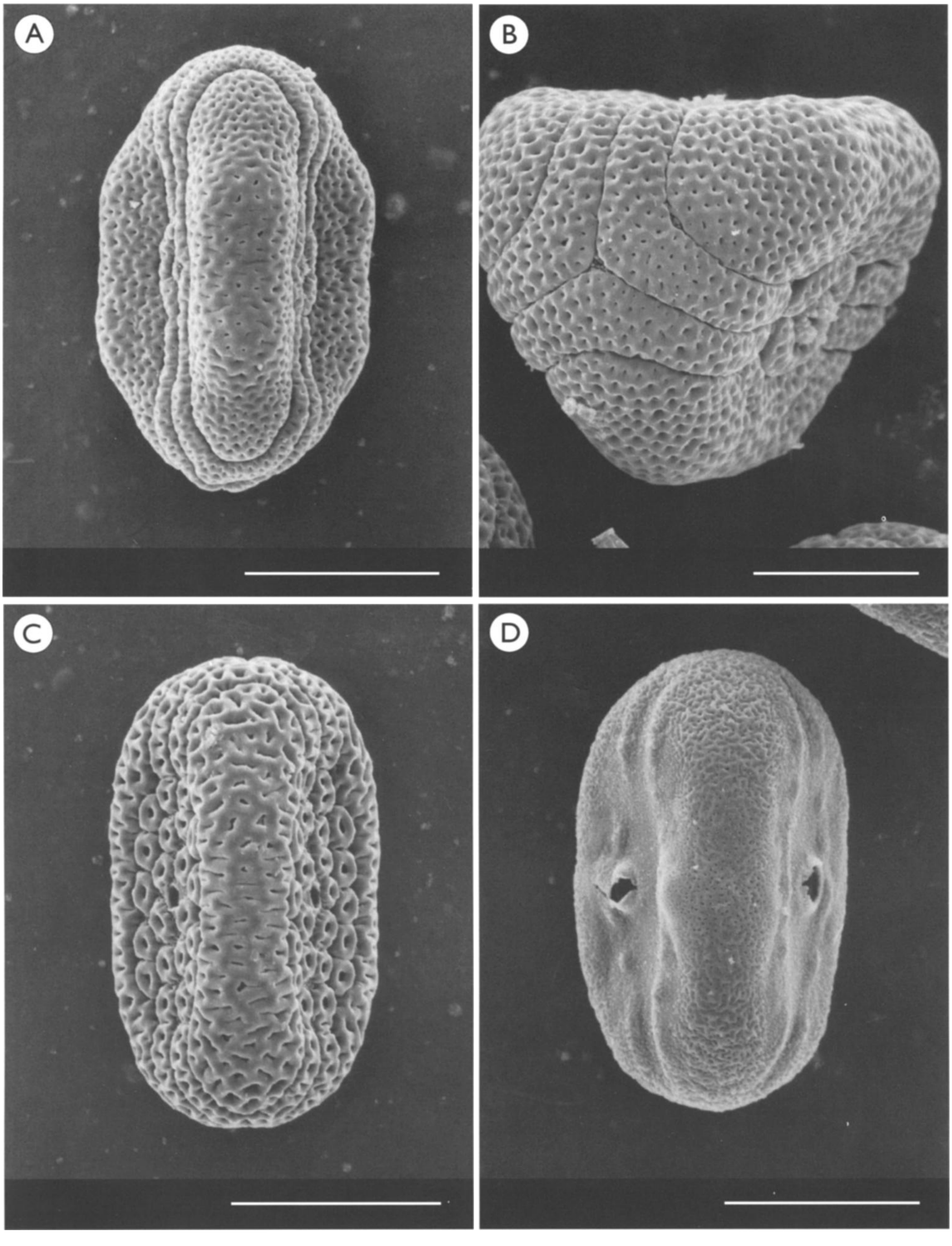


FIG. 27. Pollen of *Asystasia*. **A** & **B** *A. gangetica* **A** mesocolpial view showing broad rib not joined to others at pole; **B** polar view. From *Wyld* 183 (BM); **C** *A. guttata*, mesocolpial view showing broad rib not joined together with others at pole. From *Glover et al.* 794 (BM); **D** *A. africana*, no distinct ribs, mesocolpial area not demarcated at pole. From *Dummer* 243 (BM). Scale bars = 23.1, 12, 38 and 20 μm respectively.

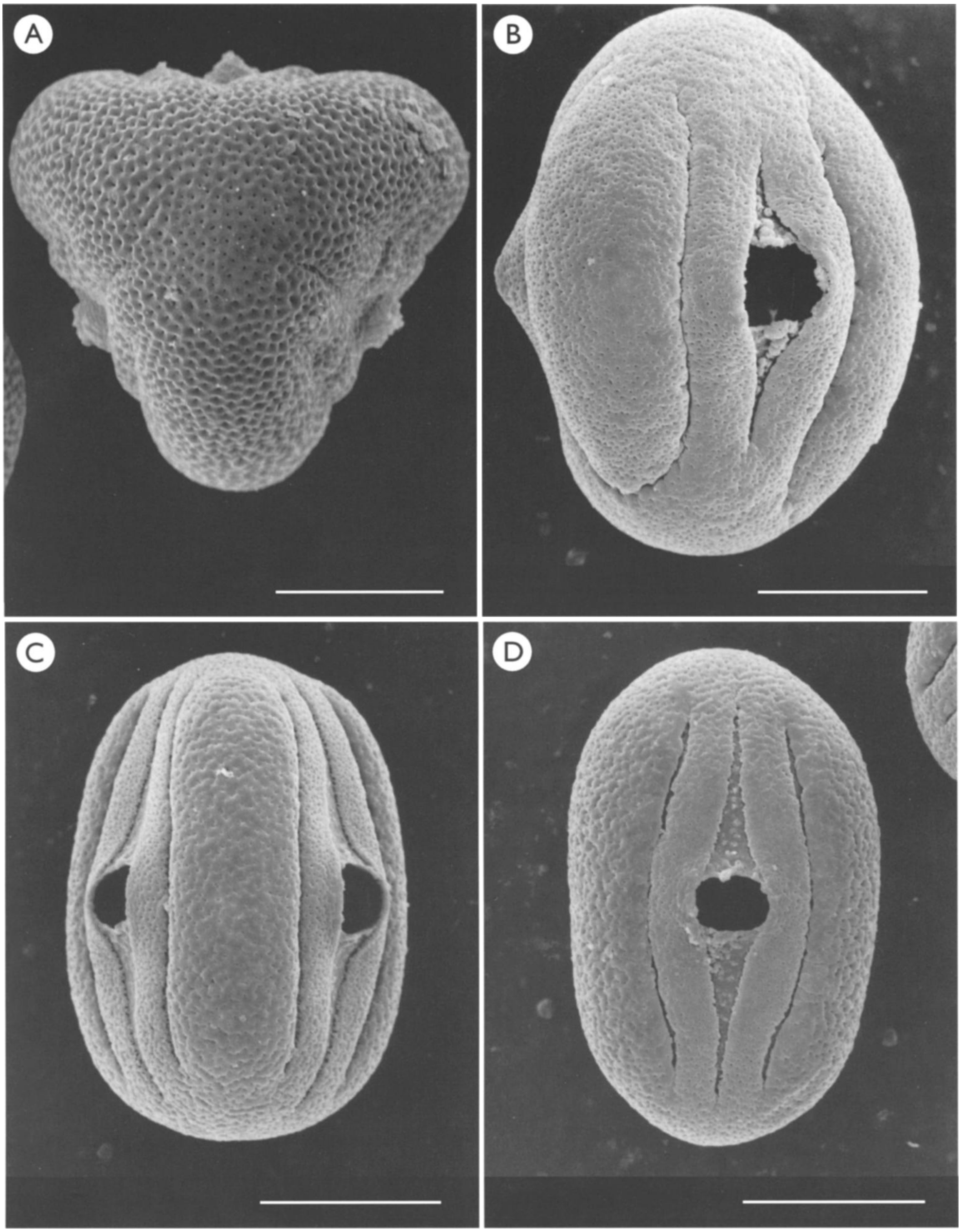


FIG. 28. Pollen of *Asystasia* & *Spathacanthus*. **A** *A. travancorica*, polar view, mesocolpial area not demarcated at pole. From Kew Cult; **B – D** *S. hoffmanni*. **B** mesocolpial rib demarcated at one pole but not at the other; **C** mesocolpial view; **D** apertural view. From *Lent* 1414 (BM). Scale bars = 12, 20, 25 and 25 µm respectively.

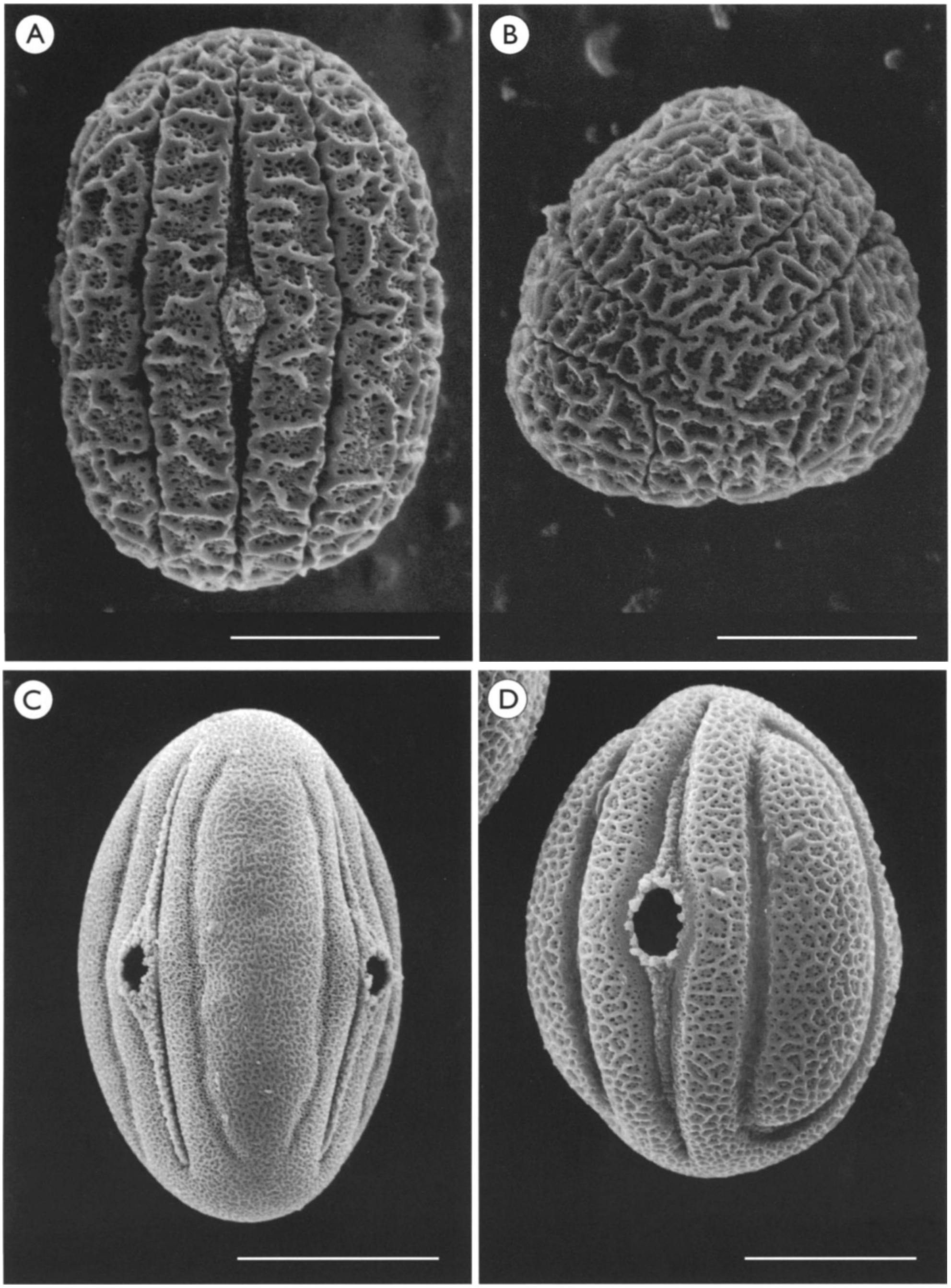


FIG. 29. Pollen of *Pachystachys*, *Anisacanthus* & *Carlowrightia*. **A** & **B** *P. lutea*. **A** apertural view showing two narrow ribs associated with aperture; **B** polar view showing three broad ribs demarcated from others at pole. From Kew Cult; **C** *A. insignis*, broad ribs not demarcated at pole. From *Pringle* 268 (BM); **D** *C. pectinata*, broad ribs demarcated at pole. From *Hinton* 2990 (BM). Scale bars = 20, 20, 30 and 12 μm respectively.

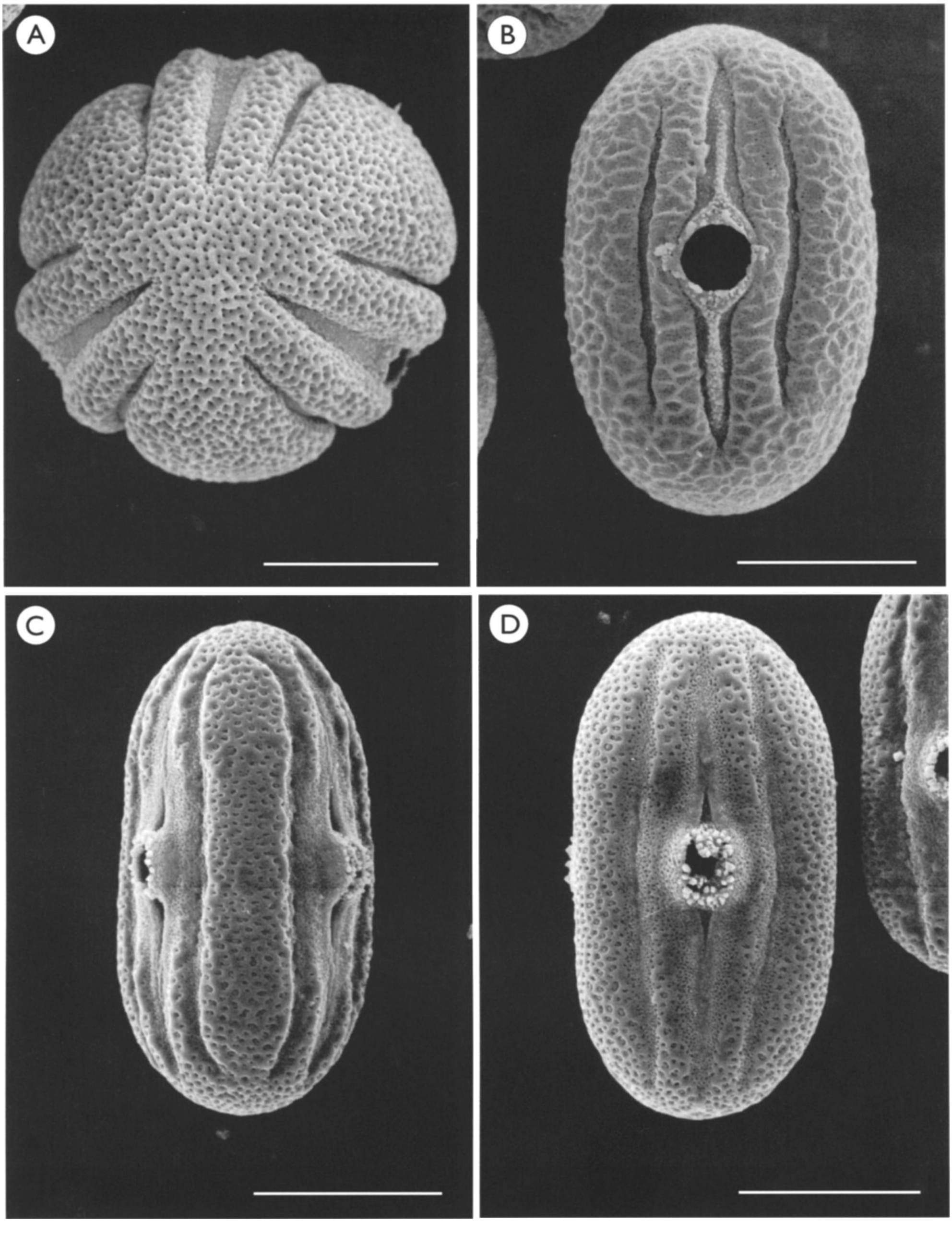


FIG. 30. Pollen of *Mackaya*, *Ancistranthus* and *Justicia*. **A** *M. bella*, polar view, tri-colporate, six pseudocolpi and two narrow ribs associated with each aperture. From *Wall* 611 (BM); **B** *A. harpochiloides*, apertural view with two narrow ribs associated with each aperture. From *Ekman* 16671 (BM); **C** & **D** *J. bentii*. **C** mesocolpial view; **D** apertural view. From *Guichard et al.* 410 (BM). Scale bars = 20, 20, 20 and 20 µm respectively.

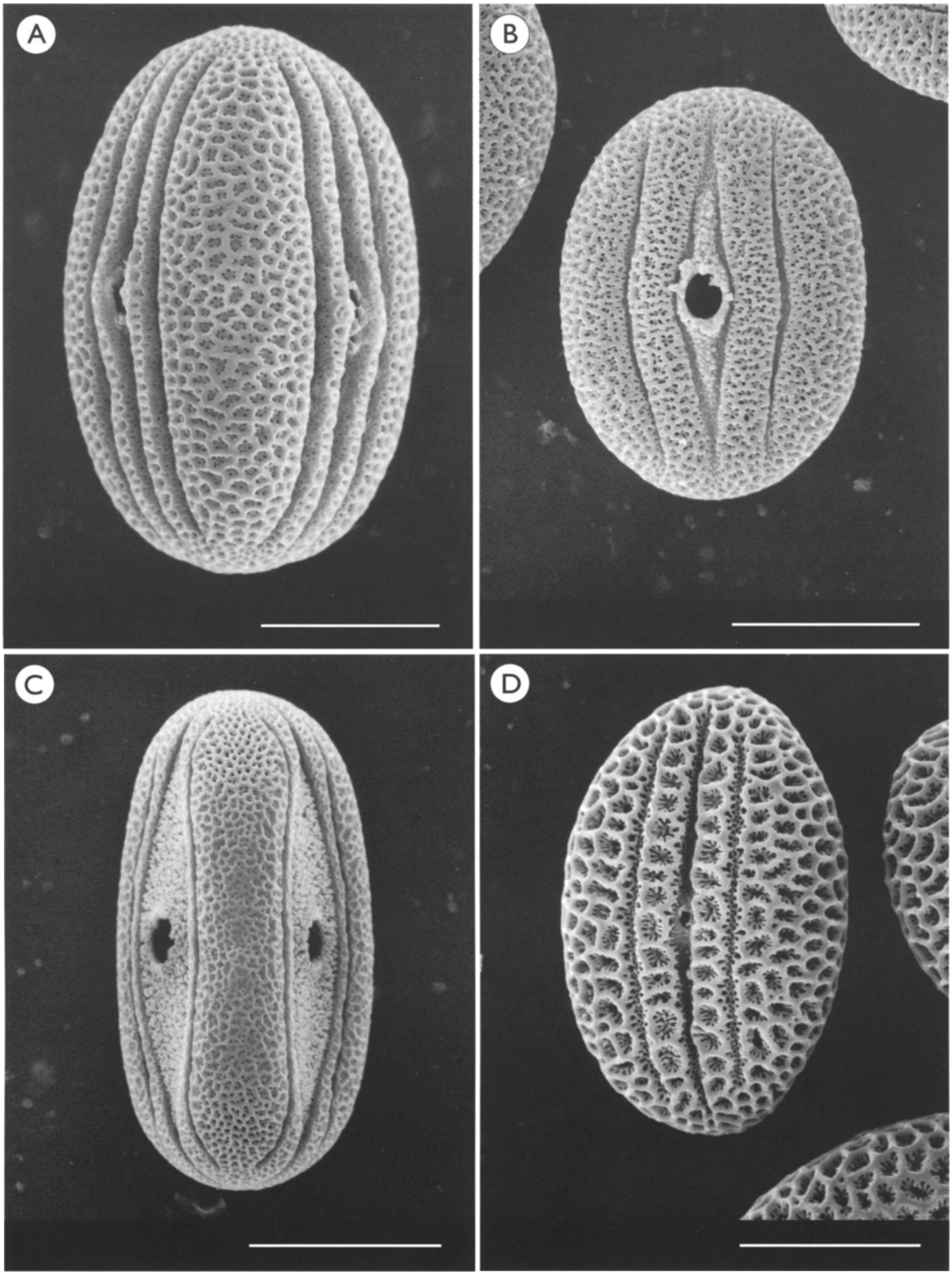


FIG. 31. Pollen of *Dicliptera*, *Schaueria*, *Henrya* and *Peristrophe*. **A** *D. melleri*, tri-colporate with six longitudinal ribs with pseudocolpi. From *Eyles* 188 (BM); **B** *S. calycotricha*, apertural view. From Kew cult., unvouchered; **C** *H. insularis*, mesoapertural view. From *Gentry* 3043 (BM); **D** *P. speciosa*, two longitudinal ribs associated with each aperture. From Kew Cult., unvouchered. Scale bars = 12, 20, 20 and 25 µm respectively.

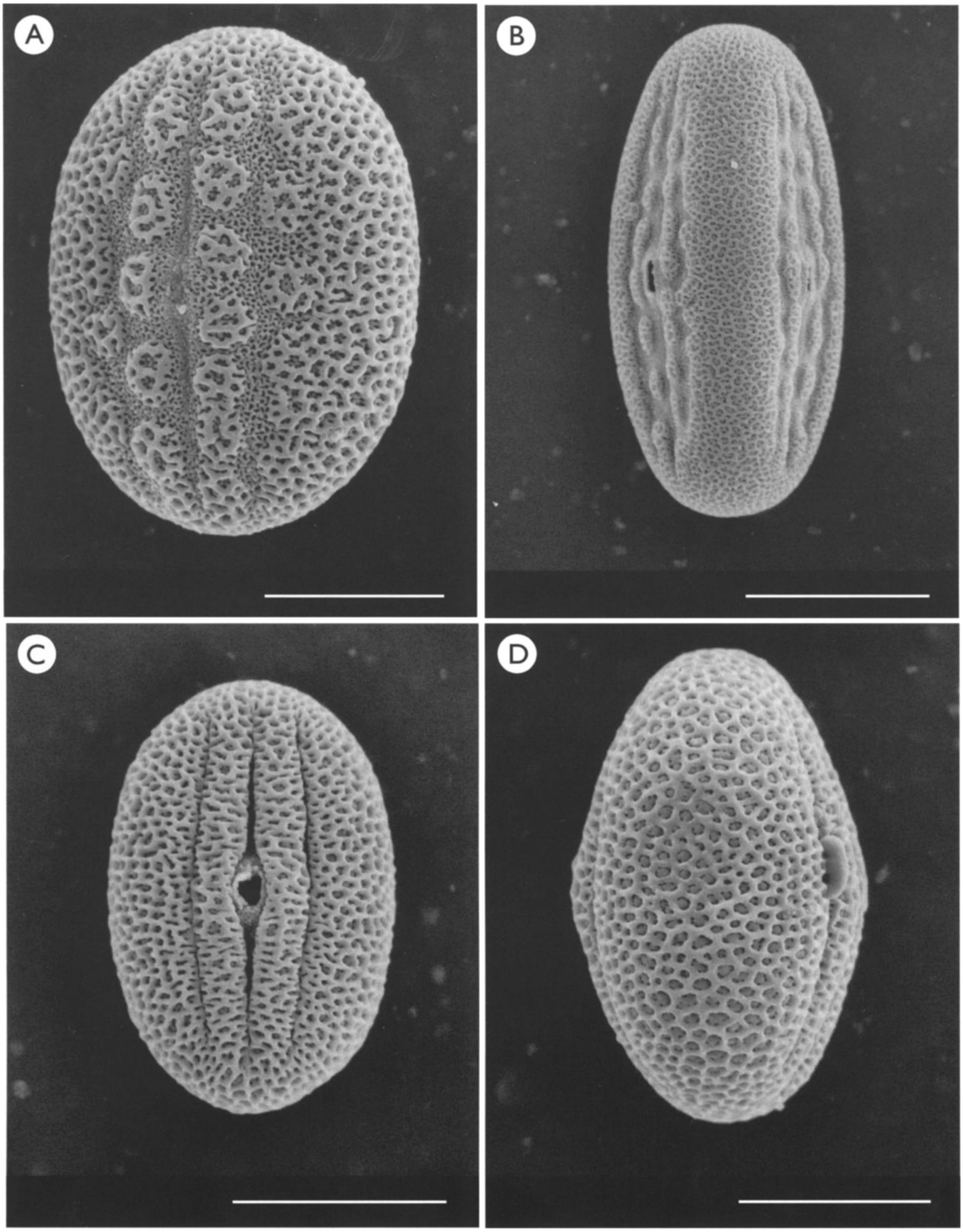


FIG. 32. Pollen of *Justicia*. **A** *J. pilosella*, bi-colporate, insulae on either side of aperture lying on trema area. From *Palmer* 9299 (BM); **B** *J. mirabiloides*, tri-colporate with insulae on either side of aperture on trema area. From *Schlieben* 4071 (BM); **C** & **D** *J. asystasioides*. **C** bi-colporate, longitudinal ribs and distinct pseudocolpi; **D** meso-apertural view. From *Schlieben* 2202 (BM). Scale bars = 15, 20, 20 and 15 µm respectively.

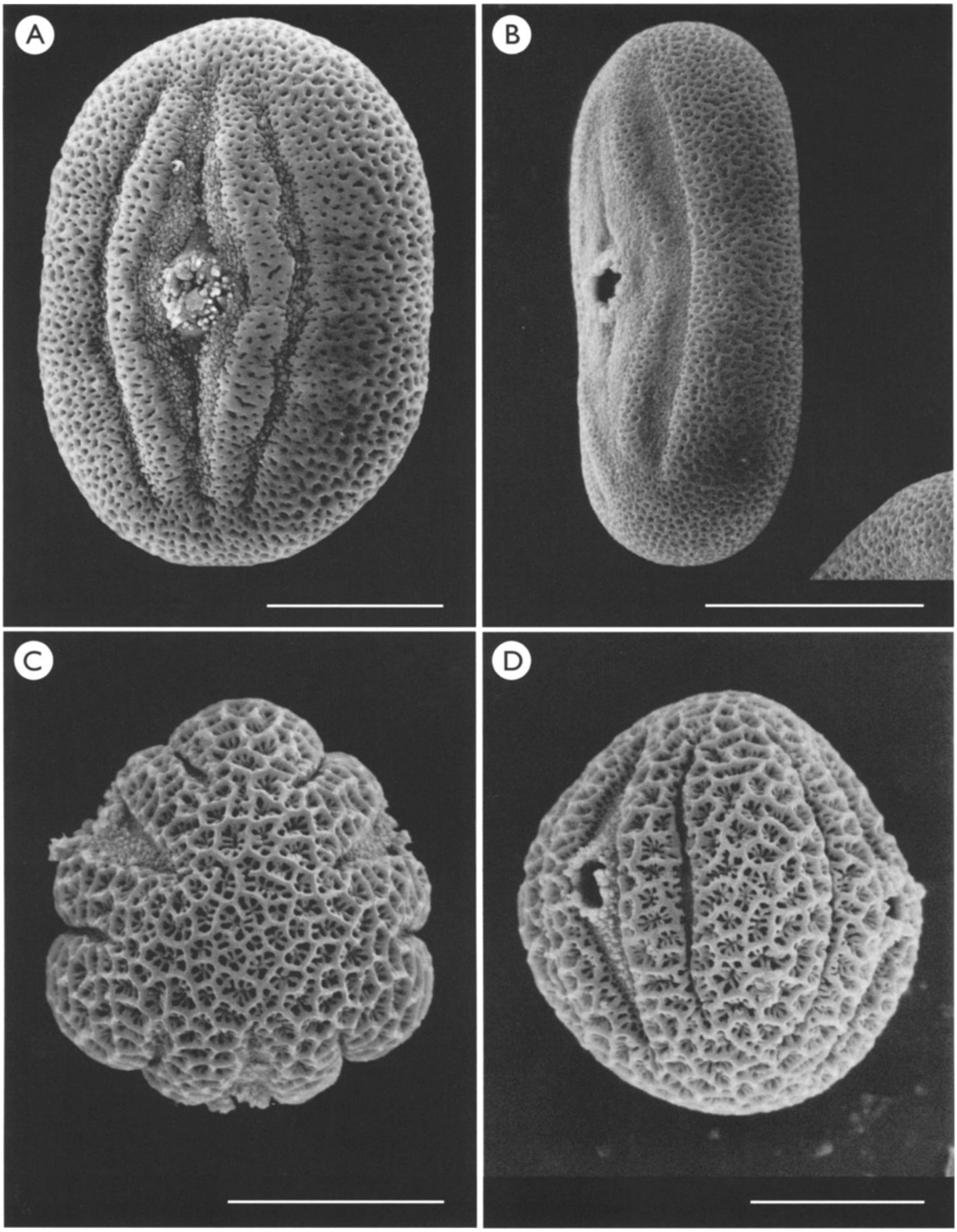


FIG. 33. Pollen of *Rungia* & *Pseuderanthemum*. **A** & **B** *R. chinensis*. **A** bi-colporate, longitudinal ribs and pseudocolpi; **B** meso-apertural view. From *Hsu* 5116 (BM); **C** & **D** *P. velutinum*. **C** polar view, tri-colporate, longitudinal ribs with pseudocolpi; **D** meso-apertural view. From Kew Cult, unvouchered. Scale bars = 10, 15, 20 and 20 µm respectively.

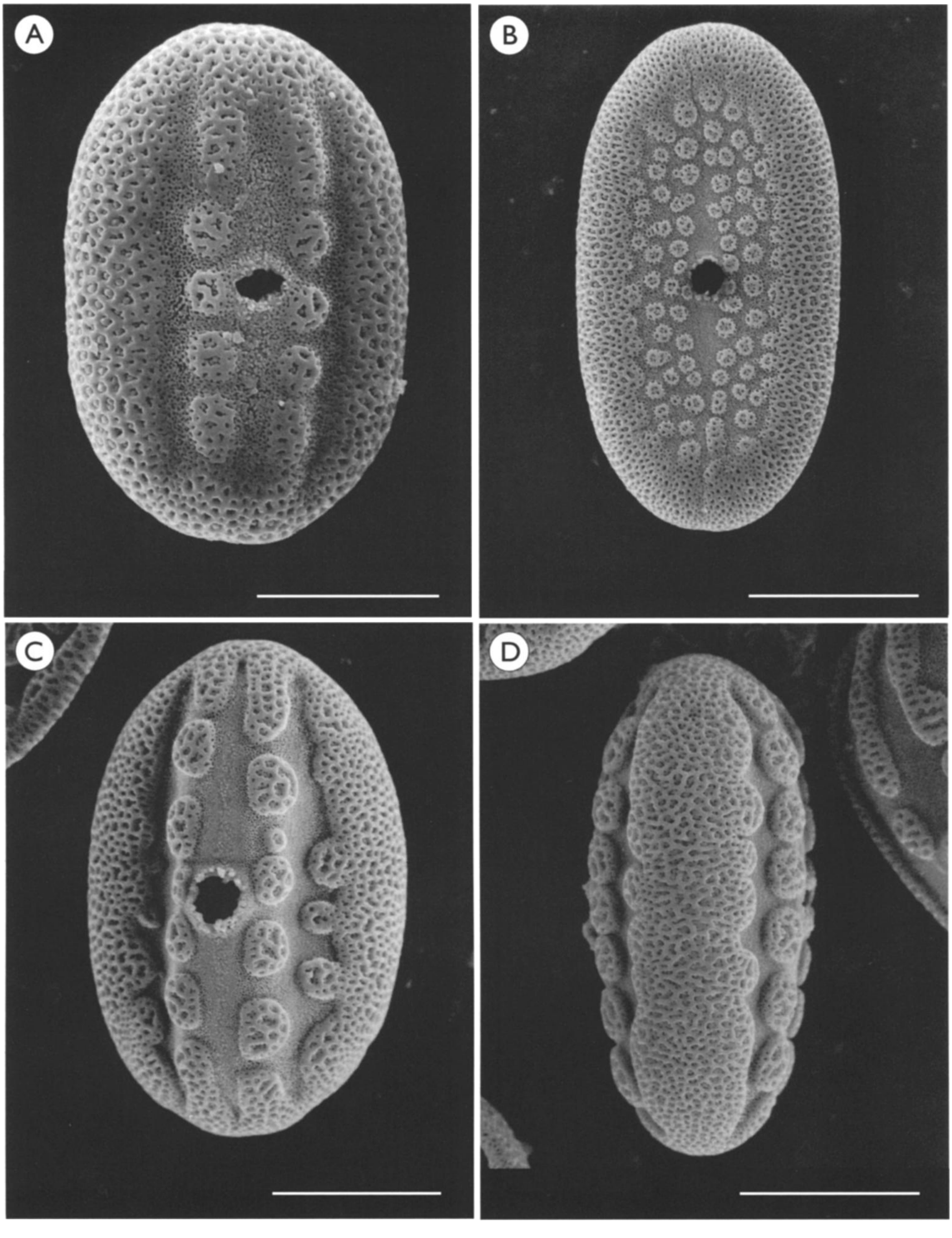


FIG. 34. Pollen of *Justicia* and *Anisotes*. **A** *J. americana*, bi-colporate, single row of insulae on trema area on each side of aperture. From *Barker* 1661 (BM); **B** *J. brasiliana*, bi-colporate, many insulae on trema area. From *Curtiss* 711 (BM); **C** & **D** *A. ukambensis*. **C** bi-colporate, insulae and trema area; **D** meso-apertural view. From *Scheffler* 181 (BM). Scale bars = 12, 20, 20 and 20 µm respectively.

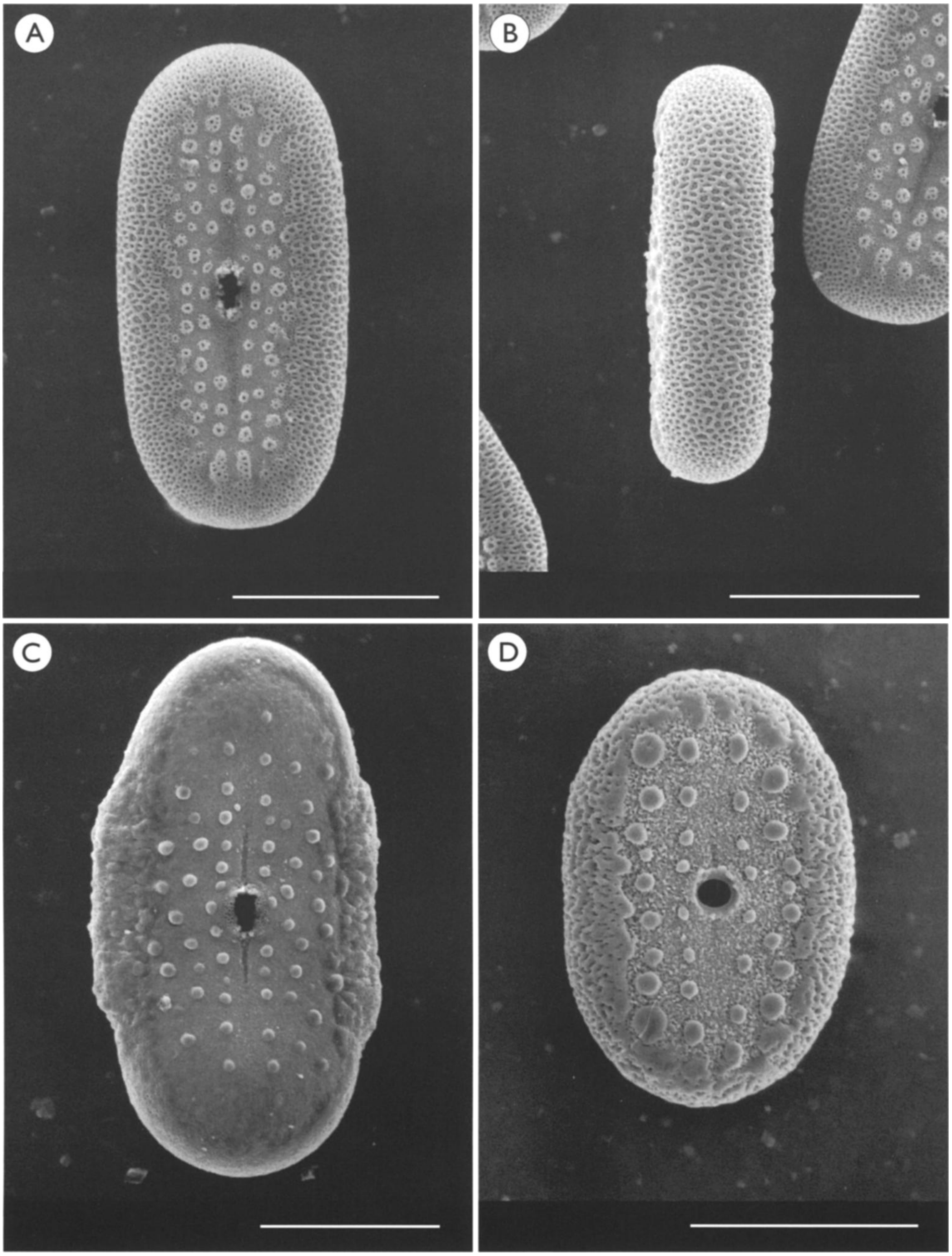


FIG. 35. Pollen of *Justicia* and *Chlamydostachya*. **A** & **B** *J. spicigera*. **A** bi-colporate, many insulae on trema area; **B** meso-apertural view. From *Ekman* 13621 (BM); **C** *J. aurea*, bi-colporate, extensive trema area with small insulae. From *Blackmore et al.* 1921 (BM); **D** *C. spectabilis*, bi-colporate, extensive trema area with insulae. From *Schlieben* 3755 (BM). Scale bars = 30, 30, 30 and 30 μm respectively.

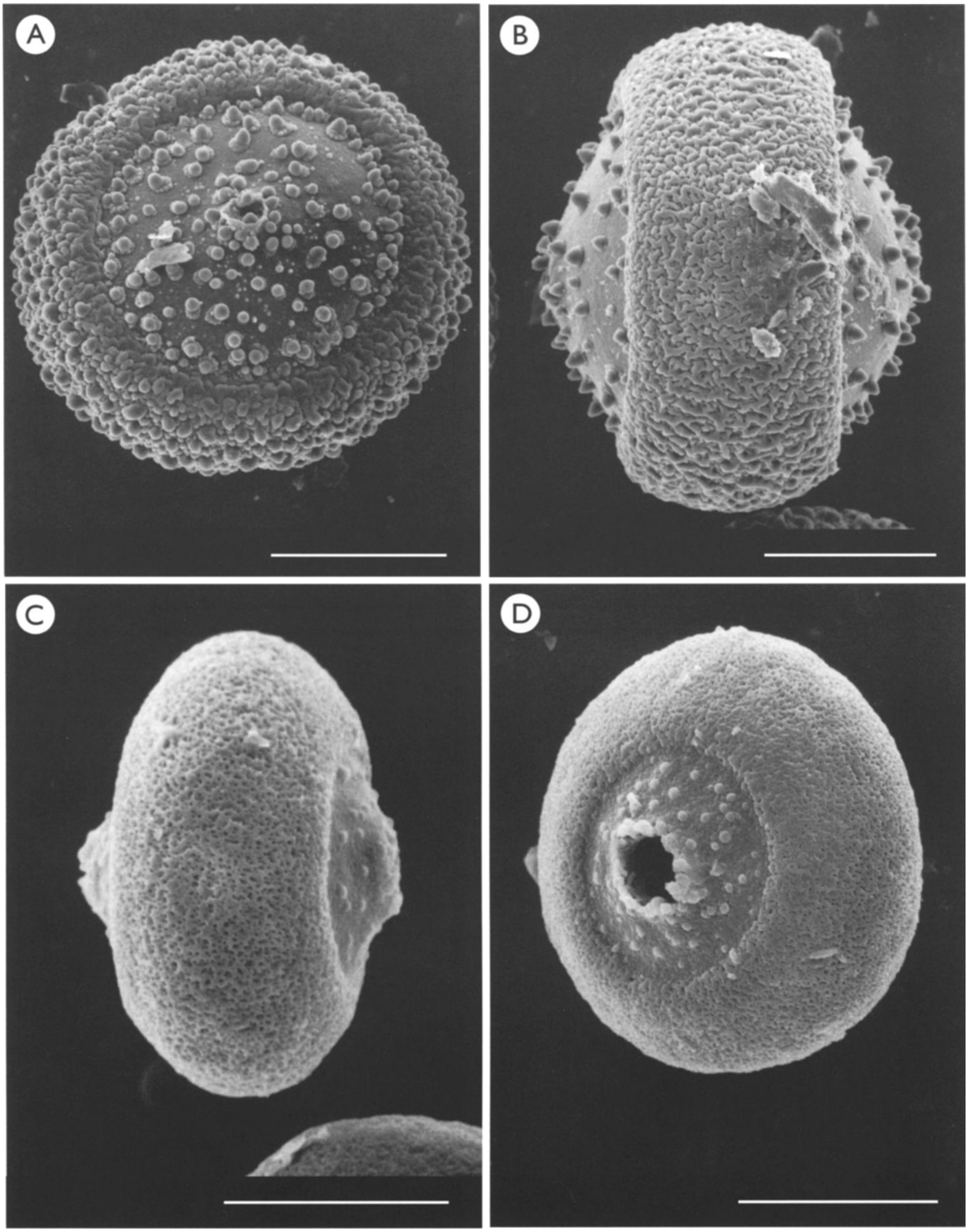


FIG. 36. Pollen of *Chlamydacanthus* & *Ptyssiglottis*. **A** & **B** *C. euphorbioides*. **A** extensive trema area with insulae; **B** bi-lateral, bi-aperturate. From *Hildebrandt* 3377 (BM); **C** & **D** *P. terminalis*. **C** bi-lateral, bi-aperturate; **D** apertural view. From *Forbes* 3821 (BM). Scale bars = 30, 25, 15 and 12 μm respectively.

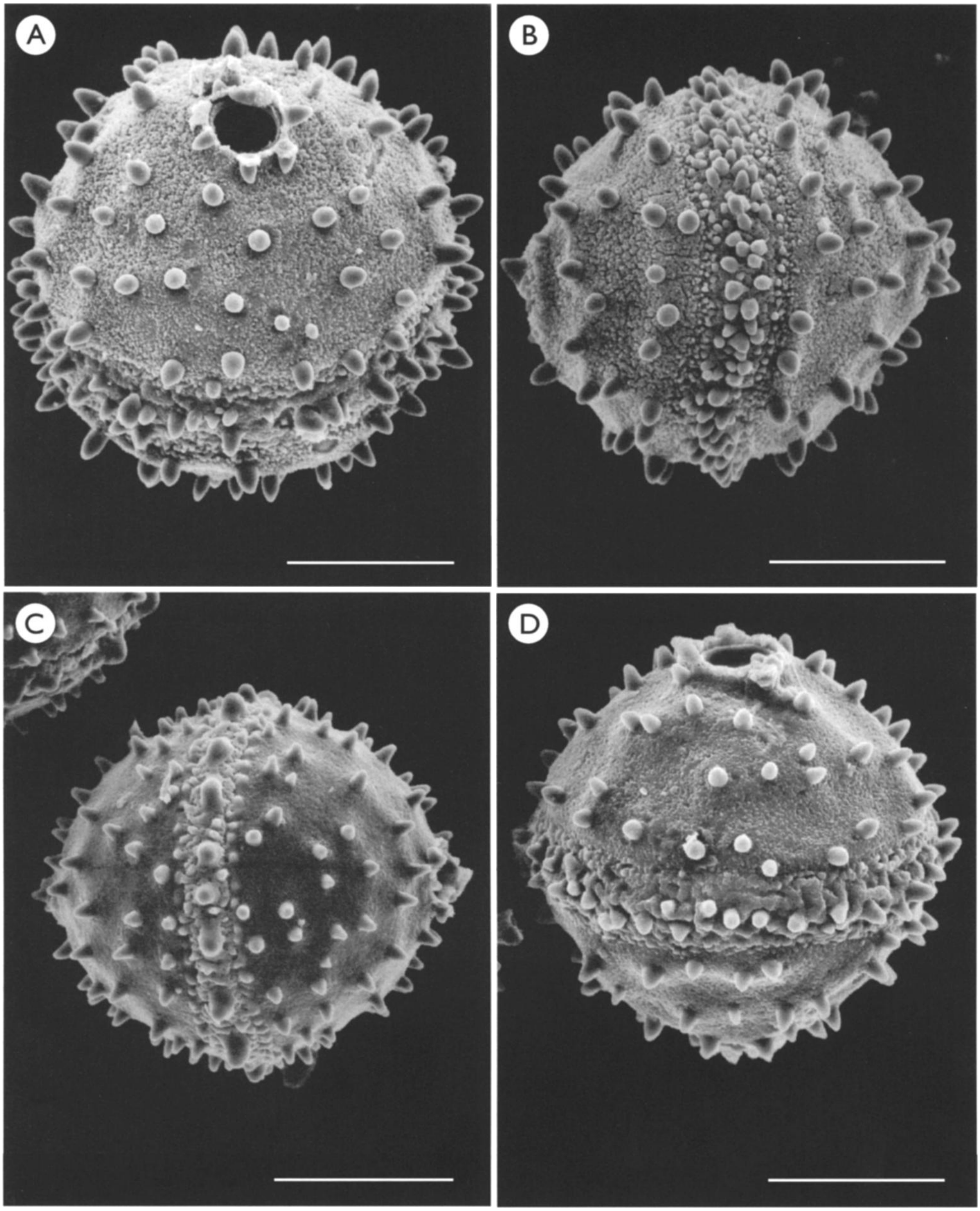


FIG. 37. Pollen of *Stenostephanus*. **A** & **B** *S. thyrsoides*. **A** bi-porate with extensive trema area and insulae; **B** mesoapertural view of sexine band encircling the grain. From *s.c.* 112 (BM); **C** *S. puberulus*, bi-porate with extensive trema area and insulae. From *Funcke et al.* 1309 (BM); **D** *S. crenulatus*, bi-porate with extensive trema area and insulae. From *Buchtein* s.n. (BM). Scale bars = 17.6, 17.6, 23.1 and 15 µm respectively.

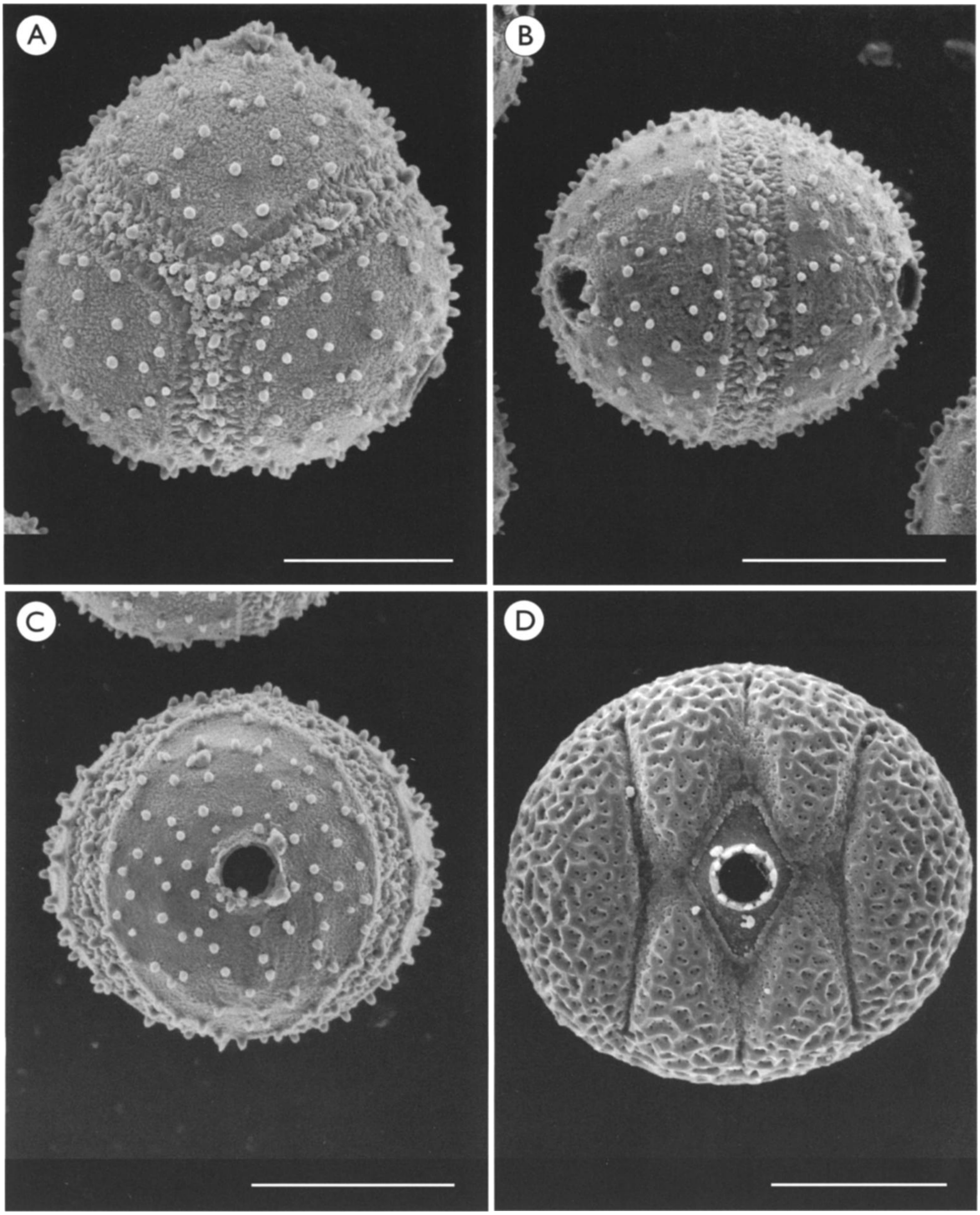


FIG. 38. Pollen of *Brachystephanus & Glossochilus*. **A – C** *B. africanus*. **A** tri-aperturate with extensive trema area surrounding each pore; **B** meso-apertural view; **C** apertural view. From *Schlieben* 3041 (BM); **D** *G. burchellii*, bilateral, bi-colporate with two pseudocolpi associated with each aperture. From *Merxmuller* 713 (BM). Scale bars = 20, 30, 30 and 15 µm respectively.

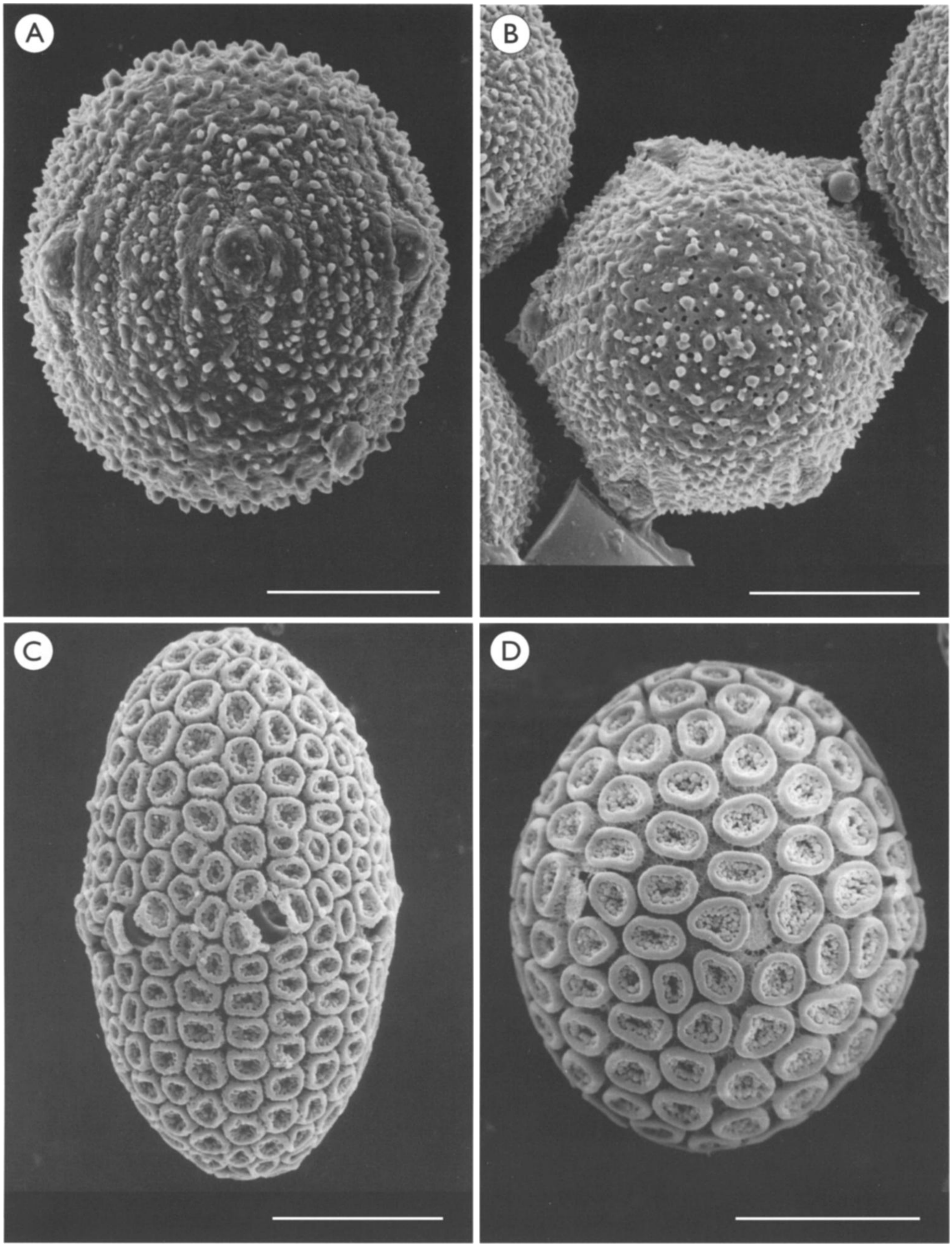


FIG. 39. Pollen of *Chlamydocardia, Poikilacanthus & Megaskepasma*. **A – B** *C. buttneri*. **A** apertural view, 6-colporate with a faint pseudocolpus area on either side of each aperture; **B** polar view, hexagonal showing six apertures. From *Taylor* 3312 (BM); **C** *P. tweedianus*, exine aggregated into insulae and covering whole grain, 6-porate. From *Lorentz* 914 (BM); **D** *M. erythrochlamys*, 6-porate. From *Broadway* s.n. (BM). Scale bars = 20, 25, 20 and 25 µm respectively.

Strobilanthinae sensu Bremekamp (1965)

Strobilanthinae sensu Bremekamp (1944) comprises *Strobilanthes* and close relatives *Aechmanthera, Stenosiphonium, Clarkeasia* and *Hemigraphis.* This group includes a high level of pollen diversity (Lindau 1895; Bremekamp 1944; Raj 1961, 1973; Scotland 1993; Carine & Scotland 1999). A small sample of the variation is shown (Figs 10 – 13). The pollen of *Strobilanthes* is very diverse compared to other genera of *Acanthaceae.*

Petalidiinae sensu Bremekamp (1965)

The *Petalidiinae sensu* Bremekamp included *Petalidium, Dyschoriste, Eremomastax* and *Mellera* and "*a considerable part of the genera included by him* [Lindau 1895] *in his Strobilantheae, have to be inserted here*" (Bremekamp 1965: 28). This would include *Mimulopsis, Echinacanthus, Phaulopsis, Sautiera, Strobilanthopsis* and *Heteradelphia* (see Scotland 1993). A selection of pollen from these genera, illustrated in Figs 14 – 15, is characterized by the raised areas of sexine surrounding the apertures (Lindau 1895; Raj 1961, 1973; Scotland 1993; Furness 1995b; Manktelow 1996; Daniel 1998).

Ruellinae sensu Bremekamp (1965)

This subtribe is equivalent to Lindau's (1895) *Ruellieae* with the exclusion of *Whitfieldia* and *Physacanthus* (Bremekamp 1965: 27). The tribe therefore includes *Ruellia* (Figs 16 – 17A & B), *Lankesteria* (Fig. 18A & B), *Eranthemum* (17C & D), *Tacoanthus, Camarotea, Spirostigma, Dischistocalyx* (Fig. 18C), and *Satanocrater.* The subtribe is characterized by *Wabbenpollen* (open-reticulate pollen) *sensu* Lindau (1895) and contorted corolla aestivation. The pollen is characteristically globose and open-reticulate (Figs 16 – 18A & B), occasionally spinulate (Fig. 18C & D), occasionally clavate (Furness & Grant 1996). Aperture number ranges from three (Fig. 17A) to many (Fig. 16D) (Lindau 1895; Raj 1961, 1973; Balkwill & Getliffe Norris 1988; Ezcurra 1993; Scotland 1993; Furness & Grant 1996; Daniel 1997, 1998). Apertures are usually porate although a few species have been shown to be colporate (Furness & Grant 1996).

Blechinae sensu Bremekamp (1965)

This sub-tribe was recognized by Bremekamp (1965: 27) and contains the genus *Blechum* on the basis of a unique syncolpate pollen morphology (Fig. 9C & D and Scotland 1993; Daniel 1995, 1998).

Barleriinae and Lepidagathidae sensu Bremekamp (1965)

Lindau's (1895) *Barlerieae* comprised taxa with quincuncial corolla aestivation including the two large genera *Barleria* and *Lepidagathis.* Lindau (1895) classified *Barlerieae* within a group comprising genera that have left-contort corolla aestivation (Appendix 1). Lindau (1895) considered pollen of *Barlerieae,* and particularly *Barleria* (Figs 19 – 20), as similar to that of *Ruellia* (Fig. 16 – 17A & B) and some other genera with left-contort aestivation. Bremekamp (1965) argued that the pollen of *Barlerieae sensu* Lindau (1895) was heterogeneous and that only *Barleria* and *Crabbea* shared pollen similarity with *Ruellia.* Bremekamp (1965: 27 – 28) separated "*Lepidagathis and near allies*" from *Barleriinae* primarily on pollen differences (Appendix 2). The *Lepidagathideae* of Bremekamp (1965) represented a tribe, whereas *Barleriinae* was classified as a subtribe of *Ruellieae* of Bremekamp (1965) reflecting the close relationship between *Barleria* (Figs 19 – 20), *Crabbea* (Fig. 21A) and *Ruellia* (Figs 16 – 17A – B) on the basis of pollen morphology. Bremekamp (1960: 155) stated *"Lindau thought that* Lepidagathis *and its allies resembled* Barleria *also in the structure of the pollen grains, but this is certainly a mistake. The pollen grains of* Barleria *are always large and globose sometimes more or less distinctly 3-lobed, but this is a deviation of minor importance, 3-porous and very distinctly reticulate, the meshes being of considerable depth; that of* Lepidagathis *and its allies, on the other hand, is rather small, ellipsoidal, 3-colporate, and if reticulate, then only superficially so".* Figs 19 – 25 show representative pollen of *Barleria, Barleriola, Boutonia, Crabbea, Chroesthes, Hulemacanthus, Lophostachys* and *Lepidagathis.* Bremekamp (1960) was mistaken, as *Barleria* pollen can be colporate (Figs 19D & 20D). Furthermore, the depth of the reticulation emphasized by Bremekamp (1960) seems to be highly variable between *Barleria* (Fig. 25A) and *Crabbea* (Fig. 25B). Raj (1973) argued that *Ruellia* and *Barleria* pollen differ very much in their sporoderm stratification whilst Furness & Grant (1996) discussed several similarities between the pollen. The question of whether the shared possession of open reticulate pollen by *Barleria, Crabbea* and *Ruellia* represents evidence for a close relationship between these taxa has been addressed explicitly by recent molecular studies (Scotland *et al.* 1995; McDade & Moody 1999). Scotland *et al.* (1995) showed that *Ruellia* and *Eranthemum,* both of which have open reticulate pollen (Fig. 17), are in a clade with other genera with left-contort aestivation. In contrast, *Barleria* and *Crabbea* are in a distinct clade characterized by quincuncial aestivation. McDade & Moody (1999) placed *Lepidagathis* as sister taxon to *Barleria.* Scotland *et al.* (in prep.) demonstrated that *ndh*F sequence data place *Barleria, Crabbea* and *Lepidagathis* in a group diagnosed by quincuncial aestivation distinct from genera with left contort corolla aestivation (Fig. 4).

Andrographideae sensu Bremekamp 1965

This group of eight genera has been recognized as a group on the basis of ovule number (usually six or more) and distinct pollen aperture margins (Lindau 1895; Raj 1961, 1973; Scotland 1992a). Figs (25C & D – 26) show a representative sample of pollen from these genera.

Justicieae sensu Bremekamp (1965)

This group represents a substantial part of the *Acanthaceae,* not only because it includes *Justicia* with c. 600 species (Graham 1988) but also because of the large number of genera included in it. Bremekamp did not list the genera that he included. The group has four or fewer ovules and ascending-cochlear corolla aestivation (Lindau 1895; Bremekamp 1965; Scotland *et al.* 1994). It is equivalent to Lindau's *Imbricatae* excluding *Acantheae, Aphelandreae* and *Andrographideae.* Lindau placed these taxa in nine tribes, giving high importance to the presence of different pollen types and the extreme range of pollen variation (Lindau 1895; Raj 1961, 1973; Daniel 1981, 1990, 1991, 1997, 1998, 1999a, 1999b; Balkwill & Getliffe Norris 1988; Graham 1988; Furness 1989). Several of Lindau's tribes were diagnosed on pollen types, such as *Spangenpollen* (Figs 27D, 28C & D, 29C, 30A & B) and *Rahmenpollen* (Figs 27A – C, 29B, 29D), described as follows (Lindau 1895: 281):

> *Spangenpollen: "Die Längsrippen sind bis auf 9 verringert, von denen 3 breiter sind, zwischen je 2 schalen Rippen finden sich im äquator die 3 Poren".*
>
> (Buckle (or strap) pollen: The longitudinal ribs reduced to nine with three broader than the other six and three pores at the equator with each pore between two narrow ridges. (Figs 27D, 28C & D, 29C, 30A & B))
>
> *Rahmenpollen: "Die 3 breiten Rippen des Spangenpollens hängen in den Polen nicht mehr mit den übrigen zusammen, sondern sind wie in einen Rahmen von ihnen einefasst".*
>
> (Framework pollen: The three broad ribs of the Spangenpollen type are no longer joined to the others at the pole. (Figs 27A – C, 29B, 29D)).

Tribes *Asystasieae* (four stamens) and *Graptophylleae* (two stamens) were diagnosed as having *Rahmnenpollen.* In contrast, *Pseuderanthemeae* (two stamens) was diagnosed as having *Spangenpollen. Spangenpollen* was further described by Lindau (1895) for *Odontonemeae. Asystasia gangetica* and *A. guttata* have *Rhamenpollen* (Fig. 27A – C). In contrast, *A. travancorica* and *A. africana* have *Spangenpollen* (Fig. 27D & 28A). *Spathacanthus hoffmannii,* included in Lindau's (1895) *Asystasieae,* has polymorphic pollen and demonstrates that the distinction between *Rhamenpollen* and *Spangenpollen* can be found in a single pollen grain (Fig. 28B). Figure 29 shows the pollen of *Carlowrightia, Pachystachys* and *Anisacanthus* that were included in Lindau's (1895) *Graptophylleae. Carlowrightia pectinata* (Fig. 29D) has *Rhamenpollen* whereas *Pachystachys lutea* (Fig. 29B) and *Anisacanthus insignis* (Fig. 29C) have *Spangenpollen.* Figs 27 – 31 show a range of genera that share pollen of the *Rahmenpollen/Spangenpollen* type, illustrating the wide range of taxa with this type of pollen. The large number of genera that share pollen of the *Rahmenpollen/Spangenpollen* type becomes an important feature when trying to understand another of Lindau's pollen types that characterized his *Justicieae.* Lindau (1895: 281 – 282) characterized *Knötchenpollen* as follows:

> *Knötchenpollen: "An Stelle der 6 schmalen Rippen treten in 1 – 3 Längsreihen liegende Knötchen auf. Die breiten Rippen hangen in den Polen zusammen. Die Zahl der Poren kann 3 betragen oder nur 2, entsprechend sind dann nur 2 breite Rippen und 4 Systeme von Knötchenreihen vohanden".*
>
> (Nodule or (little lump) pollen: In the place of each of the six narrow ridges there are one to three longitudinal rows of little lumps . The broad ridges join at the poles, pores two or three. If two pores, the consequences of this are that there are two broad ridges and four longitudinal rows of little lumps).

Figs 32 – 35 show a range of pollen from *Justicieae* of the *Knötchenpollen* type. Fig. 32A shows the 'little lumps' (insulae) and the associated region on which they lie (trema or apertural area). Fig. 32A shows pollen of *Justicia* (*Siphonoglossa*) and Fig. 33A & B, *Rungia,* both of which were classified in Lindau's (1895) *Odontonemeae.* Figs 34A & B, 35A – C demonstrate that within *Justicia* there are two-three aperturate pollen and that the ribs can be that of the *Spangen/Rhamenpollen* type (see Graham 1988). There are also examples of four-aperturate pollen (Daniel 1998). Clearly, *Rhamenpollen, Spangenpollen* and *Knötchenpollen* are variations on a common theme, rather than discrete categories as conceptualized by Lindau (1895).

A further pollen type of Lindau (1895) is pertinent here. Lindau (1895: 282) categorized *Gürtelpollen* as follows:

> "*Meist linsenförmig oder ellipsoidisch, mit 2 Poren an den Breitseiten und einem bestachelten Gürtel auf der Kante*".
>
> (Girdled pollen: Usually lens-shaped or ellipsoidal, with two pores on broad sides (one on each) with a spiny belt on the edge.)

Lindau's (1895) *Isoglosseae* contained several genera that share typical *Gürtelpollen* (Figs. 37 & 38). The genus *Brachystephanus* was also included here, although it differs from *Stenostephanus* in having three apertures (Fig. 38). Although *Gürtelpollen* seems very distinct from *Rahmen, Spangen* and *Knötchenpollen* the homology is straightforward. The area surrounding the pore of *Gürtelpollen* (Fig. 37) is equivalent to the trema area of *Knötchenpollen.* The distinct band of sexine that circles the grain of *Gürtelpollen* (Fig. 37D) is topographically equivalent to the areas surrounding the trema area of *Knötchenpollen* (Fig. 35). A main difference between *Gürtel* and *Knötchenpollen* simply corresponds to the difference in shape — spheroidal or ellipsoidal. Other extreme variations of the *Knötchenpollen* theme occur in 5 – 6-porate pollen found in *Poikilacanthus* (Fig. 39C) and *Megaskepasma* (Fig. 39D) in which discrete insulae cover the entire grain (Daniel 1991, 1998). Lindau's (1895) *Isoglossineae* also contained genera such as *Chlamydacanthus* and *Isoglossa,* (Fig. 36) illustrating the diversity of pollen types contained within it.

Bremekamp (1965: 29) delimited his *Justicieae* as follows: "*For the time being the best solution seems to be to unite the typical representatives of Lindau's Asystasieae, Graptophylleae, Pseuderanthemeae and Odontonemeae in a single subtribe for which I propose the name Odontoneminae, to retain Isoglosseae Isoglossinae as a subtribe Rhytiglossinae, the name Isoglossa being a younger synonym of Rhytiglossa, and his Justicieae as a subtribe Justiciinae*". Bremekamp (1965) made no attempt to provide a list of genera for each subtribe. McDade & Moody (1999) analysed 14 genera from *Justicieae sensu* Bremekamp (1965). The analysis shows that *Odontoneminae sensu* Bremekamp (1965) is polyphyletic, highlighting the paucity of character support offered for this taxon by Bremekamp (1965), except for the lack of a rugula.

Clearly, the subdivision *Justicieae sensu* Bremekamp (1965), is problematic. Figs 27 – 38 show a representative sample of pollen morphologies that illustrate the very distinct pollen types that form the extremes of the variation. However, throughout the whole group there is a continuous series of small gradations that shows that the variation can be regarded as virtually continuous. *Justicieae sensu* Bremekamp (1965) is a group in the analysis of McDade & Moody (1999) and this group has a combination of ascending-cochlear aestivation and pollen morphology that, although highly variable, is based on the same common plan, encompassing *Rhamen, Spangen, Knötchen* and *Gürtelpollen sensu* Lindau (1895).

Discussion

The extreme diversity of pollen types within *Acanthaceae* means that pollen variation has the potential to provide useful evidence for the discovery of taxa. However, it remains unclear how best to treat pollen variation in any analysis encompassing the whole family; decisions concerning characters and character states (transformational homology) are problematic. As in the study of Carine & Scotland (in press) it may be that pollen morphology is most accurately utilized and informative at fairly low taxonomic levels, and best used in studies of individual genera and relationships between small groups of genera. Certainly the whole complex variation documented above that surrounds *Justicia* (*Rahmen, Spangen, Gürtel* and *Knötchen* pollen) will only be assessed and understood properly in the context of other data. At other taxonomic levels, for example within those genera with left-contort aestivation and retinacula, small clusters of genera seem to have highly diagnostic and similar pollen. This situation is found in *Hygrophylinae* (*Hygrophila* and *Brillantaisia*) and *Trichanthereae* (*Bravaisia, Sanchezia, Suessenguthia, Trichosanchezia, Trichanthera*). Other taxa such as *Louteridium* and *Blechum,* have autapomorphic pollen morphology which is uninformative about generic relationships, although Bremekamp (1965) used pollen to recognize these genera at tribal and sub-tribal levels. In the classifications of Lindau (1895) and Bremekamp (1965), pollen variation has probably been over-emphasized for the delimitation of higher- level taxa within the family *Acanthaceae.*

TAXIC HOMOLOGUES WITHIN ACANTHACEAE

Introduction

There remain several reasons why a full generic cladistic analysis of morphological data is not possible at this time. (1): The monophyly of many genera is questionable. For example, several genera (*Aechmanthera, Clarkeasia, Hemigraphis, Stenosiphonium*) are nested within a non-monophyletic *Strobilanthes.* Other large genera such as *Justicia* and *Ruellia* are similar. (2): *Strobilanthes sensu lato, Justicia* and *Ruellia* constitute approximately 50% of the species-level diversity within *Acanthaceae* and are extremely heterogeneous for many characters, making any exemplar taxon approach problematic. (3): Many genera are insufficiently known, due to lack of material. For example, 21 genera are not represented in the Kew herbarium. (4): There is a lack of critical comparative anatomical studies across a broad enough range of genera within *Acanthaceae.* (5): Character coding of complex morphological variation, such as pollen morphology in *Acanthaceae,* is difficult from a transformational perspective as there are many distinct ways to code morphological variation (Hawkins 2000).

In the absence of a phylogeny estimate based on morphology, morphological data could be discussed in narrative form relative to an accepted phylogeny based on molecular data (McDade & Moody 1999; McDade *et al.* 2000). Such an approach suffers from the lack of a corroborated accurate phylogeny even in the presence of high bootstrap values and reduces morphology to a subsidiary role in classification. The approach of interpreting incongruent morphological characters relative to a simple model of character evolution — plesiomorphy, synapomorphy and convergence — and a molecular phylogeny is a far cry from the idea that cladistic analysis is a discovery procedure. Other approaches such as combined analysis of morphological and molecular data remain controversial (Kluge & Wolfe 1993; Miyamoto & Fitch 1995; Nixon & Carpenter 1996) and are cautioned against here because of a lack of critical detail on anatomy. Poorly circumscribed morphological characters combined with molecular data are unlikely to provide a clearer understanding of phylogeny. Recently, there have been several critical studies of particular morphological structures that have increased our understanding of phylogenetic issues (Scotland *et al.* 1994; Schönenberger & Endress 1998; Manktelow 2000).

Here we briefly discuss and evaluate taxic homologues that have been offered as evidence for tribal and subfamilial taxa within *Acanthaceae*.

Retinacula. The hardened outgrowth of the funiculus (retinaculum) has been the diagnostic feature and taxic homologue for *Acanthaceae sensu stricto* excluding *Anisosepalum, Elytraria, Gynocraterium, Nelsonia, Ophiorrhiziphyllon, Saintpauliopsis, Staurogyne, Anomacanthus, Mendoncia, Meyenia, Pseudocalyx* and *Thunbergia.* Homologue 1, Table 3.

Explosive fruits. The exploding capsules of *Acanthaceae* have an exactly congruent distribution to that of retinacula and are therefore absent for those genera listed above. Homologue 2, Table 3.

Cystoliths. Cystoliths are outgrowths of the epidermal cell wall. They are impregnated with calcium carbonate and are present in the leaves, stems, petioles, bracts and wood of many genera of *Acanthaceae* (Hobein 1884; van Tieghem 1908). Cystoliths are absent from other families of *Lamiales*, although occasional cystolith-like structures have been described in *Scrophulariaceae* and *Verbenaceae* (Metcalfe & Chalk 1950). Cystoliths have been described in distantly related families e.g. *Cannabaceae, Urticaceae* and *Moraceae.* Hobein (1884) recognized several taxon-specific types of cystolith within *Acanthaceae.* Cystoliths are usually clearly visible in dried herbarium material, particularly on the abaxial leaf surface, as short white streaks. The taxonomic distribution of cystoliths is restricted to those taxa with retinacula but are absent from Bremekamp's (1965) *Acanthoideae* which is equivalent to the *Acantheae* and *Aphelandreae* of Lindau (1895). Homologue 3, Table 3.

Articulated stems. This character (Bremekamp 1953, 1955, 1965) refers to the nodes of each stem, which are often swollen and have a prominent transverse ridge on the stem between the opposite leaves. Bremekamp (1953, 1955, 1965) was not more specific concerning the anatomy of this feature, and interpretation therefore remains problematic because the character is widespread within *Lamiales, Thunbergia, Mendoncia* and *Nelsonioideae.* Furthermore, Bremekamp's (1965: 25) assertion that "in the *Acanthoideae* the shoots are never articulated" is mistaken as many of these genera have a transverse ridge on the stem. Therefore, we view this character, cited as evidence for *Ruellioideae* (Bremekamp 1965; McDade & Moody 1999; McDade *et al.* 2000) as not being compatible with patterns of variation within *Acanthaceae.* Excluded.

Exalbuminous seeds. Bremekamp (1965) cited a lack of endosperm as a homologue at the level of *Acanthaceae sensu stricto.* We find no compelling reason to accept this assertion as the distribution or lack of endosperm is so poorly known for *Acanthaceae.* Excluded.

Porate pollen. The presence and absence of porate pollen was cited by Bremekamp (1965) as a distinguishing feature between *Acanthoideae* and *Ruellioideae.* This has been interpreted as a synapomorphy for *Ruellioideae* (McDade & Moody 1999; McDade *et al.* 2000) within the context of phylogeny. Porate pollen (*sensu* Bremekamp 1965) presumably refers to the presence of endoapertures. However, porate endoapertures are widespread in *Lamiales,* widespread in *Nelsonioideae,* and are also found in *Mendoncia* and most *Acanthaceae* excluding *Acanthoideae* of Bremekamp (1965). We therefore interpret this character as a general feature of little taxonomic significance at this hierarchical level within *Acanthaceae.* Excluded.

Colpate Pollen. This character is the complement of Bremekamp's (1965) porate pollen. In *Acanthoideae sensu* Bremekamp (1965) all taxa have simple (Figs 5, 6A & B) rather than compound apertures. These simple apertures are colpate which we interpret as restricted in distribution within *Acanthaceae* to *Acanthoideae sensu* Bremekamp (1965). Homologue 4, Table 3.

Four monothecate anthers. Monothecate anthers have a widespread distribution in *Acanthaceae* and are present in species of *Lepidagathis, Monothecium* and *Hulemacanthus,* etc. However, the occurrence of four monothecate anthers is restricted to *Acanthoideae sensu* Bremekamp (1965) i.e. those genera with colpate pollen and retinacula, but lacking cystoliths. Homologue 5, Table 3.

Depth of reticulation in pollen. Similarity of pollen shared between *Barleria* (Figs 19 – 20) and *Ruellia* (Figs 16 –17) has been emphasized by Lindau (1895) and Bremekamp (1965). Bremekamp (1960) specifically emphasized the depth of the reticulum as a feature indicating a close relationship between *Ruellia* and *Barleria* but excluding *Lepidagathis* and other genera with quincuncial aestivation. This character is problematic for a number of reasons. First, there seems to be a continuous distribution of depth of reticulation in pollen of those taxa with quincuncial aestivation (Figs 19, 20, 21, 22, 23, 24 & 25A, B) and in *Ruellia* pollen (Figs 16 – 17A & B) and (Furness & Grant 1996). Second *Ruellia* contains species in which the pollen is not of the standard type described by Bremekamp (1965) e.g., *Ruellia togoensis* (Furness & Grant 1996). Third, even if the depth of the reticulation could be shown to be discrete it remains unclear which genera would be included in any homology proposition. The fact remains that although Lindau (1895) and Bremekamp (1965) emphazised the similarity between *Barleria* and *Ruellia* pollen, neither author argued for (what would now be considered as) a sister group relationship between these two genera. We therefore remain unconvinced that the pollen similarity between *Ruellia* and *Barleria* has been accurately characterized or determined relative to *Ruellia, Barleria* and related genera. Excluded.

Staminal filament curtains. Manktelow (1996, 2000) discussed the distribution of filament "curtains" within those genera with retinacula, cystoliths and left-contort aestivation. In these genera which have predominantly four stamens "the filaments are united two by two to the corolla tube and together form two folds which extend to the corolla base" (Manktelow 1996: 34). This character is restricted within *Acanthaceae* to those genera with left-contort aestivation, retinacula and cystoliths but excluding *Whitfieldia* and *Lankesteria* (Manktelow 2000). Homologue 6, Table 3.

Unicellular bristles on anthers. This character was documented by Schönenberger & Endress (1998) and argued to be synapomorphic for *Mendoncia, Thunbergia* and *Pseudocalyx,* as it is restricted within *Acanthaceae* to these genera, but taken here to include *Anomacanthus* and *Meyenia.* The presence of bristles on anthers is also found in other genera (e.g., *Dyschoriste* and *Mellera*) although the detailed anatomy and primary homology of these structures is as yet to be determined. Homologue 7, Table 3.

Poricidal thecae. This character was documented by Schönenberger & Endress (1998) and argued to be synapomorphic for *Mendoncia, Thunbergia* and *Pseudocalyx* as it is restricted within *Acanthaceae* to these genera, but taken here to include *Anomacanthus* and *Meyenia.* Homologue 8, Table 3.

Corolla aestivation. As discussed above corolla aestivation is conserved across many genera, but the same corolla patterns are also found in different groups (Table 1). Interpretation of the generality and applicability of corolla aestivation patterns is therefore complex and perhaps not amenable to interpretation at this time outside a formal full-scale phylogenetic analysis of all data. Descending-cochlear is present in *Nelsonioideae sensu* Lindau (1895), left-contort is present in *Thunbergia, Mendoncia* and *Ruellieae sensu* Bremekamp (1965) (excluding *Barleriinae*) whilst ascending-cochlear is present in *Acanthoideae, Andrographideae* and *Justicieae sensu* Bremekamp (1965). Only quincuncial aestivation is restricted to one putative taxon. Here we adopt a very conservative approach in scoring only quincuncial aestivation as a taxic homologue at the level of those taxa with cystoliths, retinacula and quincuncial aestivation i.e. *Barlerieae* of Lindau (1895). Homologue 9, Table 3.

Daubenpollen with thickened aperture margins. This pollen type is restricted to *Andrographideae sensu* Lindau (1895) and is a constant feature for all eight genera (Figs 24A & B – 25). Homologue 10, Table 3.

Rahmen-Spangen-Knötchen-Gürtelpollen. These pollen types of Lindau (1895) can be interpreted as forming a continuuum (see discussion above) and are widespread within *Justicieae sensu* Bremekamp (1965). Homologue 11, Table 3.

The classifications of Lindau (1895) and Bremekamp (1965) emphasized the presence of retinacula, cystoliths, corolla aestivation and pollen morphology to distinguish major subdivisions within *Acanthaceae.* Although both authors utilized the same homologues, they were applied in relatively different ways in constructing the classification. For example, within those taxa with retinacula, Lindau emphasized corolla aestivation (Fig. 1A) whereas Bremekamp (1965) emphasized presence or absence of cystoliths (Fig. 1B). In both classifications the similarity between *Barleria* and *Ruellia* pollen was emphasized.

Table 2 lists taxa that can be distinguished on the basis of unique combinations of corolla aestivation, cystoliths, retinacula and pollen at the level of *Acanthaceae.* Table 3 lists the 11 homologues discussed above that have been offered as taxic homologues at the very highest level within *Acanthaceae.*

Table 4 shows these 11 homologues in the context of a data matrix that includes a number of genera from each taxon from Table 2, treating each homologue (coded 1) as a hypothesis of a group. The genera chosen to represent the taxa from Table 2 are essentially chosen at random because all genera from these taxa score the same for the 11 homologues.

Three-item statement analysis

The genera from Table 4 are representative of the taxa recognized in Table 2 which can be delimited using a unique combination of characters (homologues). Of interest is whether each combination of homologues analysed together offers support for the taxa listed in Table 2. Three-item statement analysis (Nelson & Platnick 1991; Scotland in press, 2000; Williams & Siebert 2000) offers a method that seeks to explore whether hypotheses of homology in the form of their smallest constituent units (three-item statements) support a particular hierarchy [minimal tree]. Three-item analysis seeks only to explore whether a given set of taxic homologues are congruent relative to a tree. Discussion, implementation, and exploration of three-item analysis can be found in Nelson & Platnick (1991), Williams & Siebert (2000) & Scotland (in press).

The analysis of taxic homologues in the context of three-item analysis is a distinct form of analysis from standard cladistic analysis (*sca*). *Sca* seeks to explain all data from all terminal taxa relative to a simple model of character evolution treating all character states from a transformational perspective.

The three-item statement matrix [not shown] was generated using MATRIX version 2.1 (Nelson & Ladiges 1993) and TAX version 3.3 (Nelson & Ladiges 1994) and analyzed using PAUP (Swofford 1999). The analysis used homologues 1 – 11 from Table 3 to generate three-item statements. The analysis included a total of 5904 three-item statements and was conducted with all three-item statements equally weighted.

Results

The analysis resulted in a single minimal tree (Fig. 40). The analysis accommodated 5904 three-item statements. This tree, although lacking resolution, is broadly congruent with the discussion in the introduction to this paper and recent molecular studies with the following exceptions. Manktelow (2000) was

TABLE 2. Higher level taxa *sensu* Lindau (1895) and Bremekamp (1965) that can be distinguished using a combination of retinacula, cystoliths, corolla aestivation and pollen characters.

	Retinacula	**Cystoliths**	**Aestivation**	**Pollen**
1. *Nelsonioideae sensu* Lindau	Absent	Absent	Descending-cochlear	—
2. *Thunbergioideae* (plus *Mendoncioideae sensu* Lindau)	Absent	Absent	Left-contort (polymorphic in *Thunbergia*, see text)	—
3. *Acanthoideae sensu* Lindau	Present	Present	Several patterns	—
4. *Acanthoideae sensu* Bremekamp	Present	Absent	Ascending-cochlear/Open	—
5. *Ruellioideae sensu* Bremekamp	Present	Present	Several patterns	—
6. *Andrographideae sensu* Lindau	Present	Present	Ascending-cochlear	*Daubenpollen*
7. *Barlerieae sensu* Lindau	Present	Present	Quincuncial	—
8. *Contortae* (excluding *Barlerieae sensu* Lindau)	Present	Present	Left-contort	—
9. *Justicieae sensu* Bremekamp	Present	Present	Ascending Cochlear	*Rhamen/Spangen/ Knötchen/Gürtel*

TABLE 3. Taxic homologues at the level of *Acanthaceae.*

1. Retinacula
2. Explosive Fruits
3. Cystoliths
4. Colpate pollen
5. Four monothecate anthers
6. Staminal filament curtains
7. Unicellular bristled anthers
8. Poricidal thecae
9. Quincuncial corolla aestivation
10. *Daubenpollen,* thickened aperture margins
11. *Rahmen/Spangen/Knötchen/Gürtelpollen*

correct in excluding *Whitfieldia* and *Lankesteria* from other genera with left-contort corolla aestivation on the basis that these taxa lack a filament curtain. The homologues analyzed here provide no unambiguous morphological support for *Nelsonioideae* although this group has been universally accepted (Lindau 1895; Bremekamp 1965; Hossain 1971; Scotland *et al.* in prep.). Otherwise the combination of homologues from Table 3 support those taxa listed in Table 2.

Discussion

The result of the three-item analysis incorporates and accommodates all three-item statements on the minimal tree (Fig. 40). This result demonstrates that a combination of homologues used by Lindau (1895) and Bremekamp (1965) support the same tree. The disagreement between those authors, in part, represents *a priori* character weighting of selected homologues at different hierarchical levels. The paucity of homologues used here and level of agreement between these data demand some further comment regarding the analysis of morphological data. Selection of homologues (characters/character states) is an important part of any systematic study. We have attempted here to employ only those homologues that are discrete and can be scored for a number of genera with a high degree of confidence based on direct observation. Our aim was to construct a higher level hypothesis of major taxa in the *Acanthaceae* rather than attempt to estimate a generic level phylogeny. The approach adopted here of analysing relatively few, well understood high-burden homologues (Riedl 1979) is at odds with recent studies of morphological data in which the character-taxon ratio is much greater than in the present study. There is a tendency in morphological studies to assume that more characters are better. Justification for this is usually discussed relative to simulation studies (Hillis 1996; Graybeal 1998) that show phylogenetic accuracy can be improved by increasing the number of

TABLE 4. Data matrix of taxic homologues from Table 3 scored for representative genera from the taxa in Table 2.

Elytraria	00000000000
Nelsonia	00000000000
Staurogyne	00000000000
Thunbergia	00000011000
Mendoncia	00000011000
Meyenia	00000011000
Aphelandra	11011000000
Sclerochiton	11011000000
Acanthopsis	11011000000
Diotacanthus	11100000010
Phlogacanthus	11100000010
Andrographis	11100000010
Barleria	11100000100
Crabbea	11100000100
Lepidagathis	11100000100
Blechum	11100100000
Dyschoriste	11100100000
Eranthemum	11100100000
Ruellia	11100100000
Strobilanthes	11100100000
Sanchezia	11100100000
Whitfieldia	11100000000
Lankesteria	11100000000
Justicia	11100000001
Mackaya	11100000001
Dicliptera	11100000001
Pseuderanthemum	11100000001
Asystasia	11100000001
Henrya	11100000001

characters for a given problem. Second, high bootstrap values also have a direct relationship to an increased character/taxon ratio. For both these reasons many morphological studies attempt to include as many characters as possible. However, including poorly understood or badly circumscribed homologues in an analysis will add little if anything to the resulting topology (Patterson & Johnson 1997). Furthermore the character/taxon ratio of morphological studies is seldom of the magnitude that high bootstrap values can be expected (Bremer *et al.* 1999). The approach adopted here is based on three premises: first, that morphological and molecular data serve as a focal point for reciprocal illumination, one of the other. Second, that taxonomic congruence between

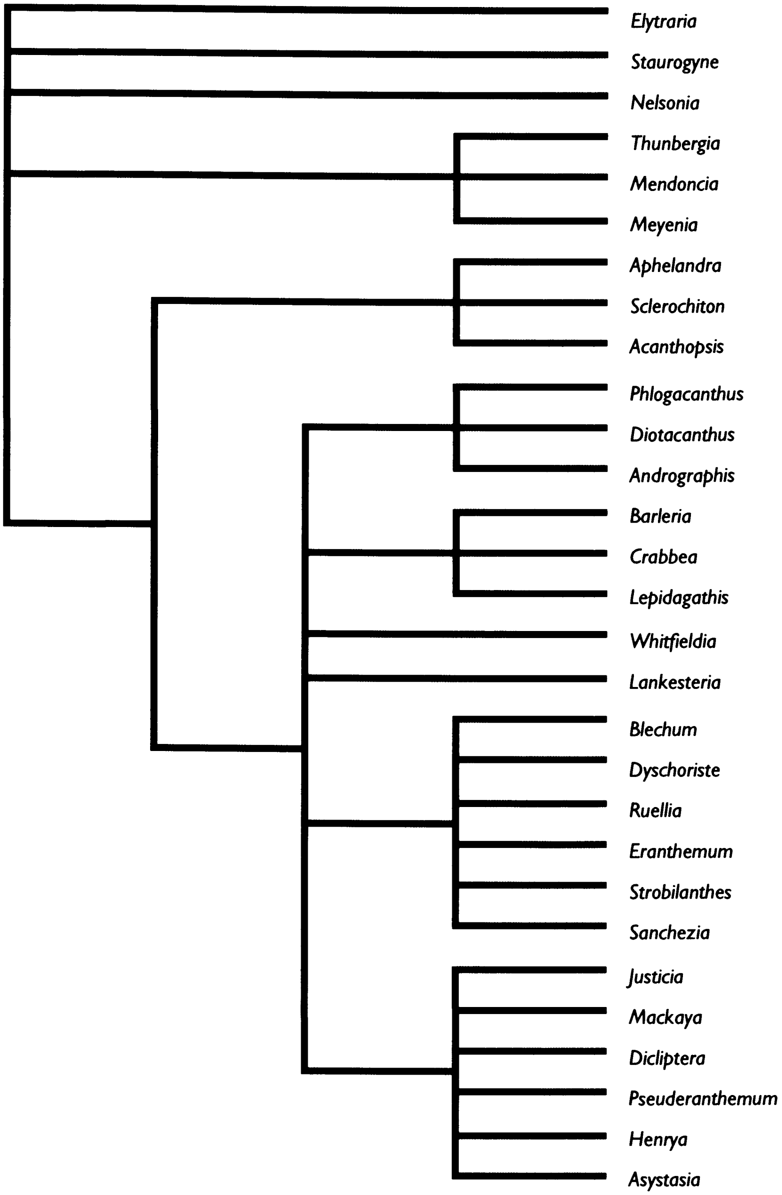


FIG. 40. Minimal three-item statement tree (see text for details).

independent data sets provides a level of corroboration not afforded by other approaches (Hillis 1995; Miyamoto & Fitch 1995). Third, that morphological data is best suited to estimating a taxic hierarchy of homology (Patterson 1982; Rieppel 1988; Scotland in press) rather than a phylogeny.

THE CLASSIFICATION

A new classification of *Acanthaceae* is presented in Appendix 3. Taxa recognized are based on combinations of morphological diagnostic features (Tables 2 and 3), the three-item analysis of morphological data (Fig. 40) and published molecular sequence analysis (Figs 2 – 4). Those genera insufficiently known, or where some doubt remains about the anatomy of a feature, are listed as unplaced within *Acanthoideae.* The genus *Thomandersia* is excluded as preliminary research indicates that this genus has been misplaced within *Acanthaceae.* Preliminary sequence analysis from several sources indicating that the genus *Avicennia* should be included within *Acanthaceae* is not dealt with here. A list of generic synonymy is presented in Appendix 4.

DISCUSSION AND CONCLUSIONS

The classification presented here represents a synthesis of morphological and molecular data from 221 accepted genera of *Acanthaceae.* Twenty of those genera remain unplaced within *Acanthoideae,* and the status of some of these genera e.g. *Acanthura* Lindau is doubtful. All of these genera contain few species, and for several described by Benoist (e.g., *Dolichostachys, Leandriella, Pericalypta, Sphacanthus, Vavara* and *Vindasia*) little material is available, highlighting the need for more field studies of *Acanthaceae* from Madagascar. *Glossochilus* is here provisionally placed with *Justiciinae* based on present knowledge, similarity to *Asystasia* and the presence of two pseudocolpi on either side of the aperture, although Manktelow (2000) suggests that this genus may have filament curtains. Other unplaced genera e.g. *Whitfieldia* and *Lankesteria* are already the subject of increased focus (Mantktelow 2000; Manktelow *et al.* submitted). *Neuracanthus* also remains unplaced due to a lack of information on corolla aestivation. Within the subtribe *Justiciinae* there are 103 genera, compared with 118 in the rest of the family. How much of this generic diversity is real, or simply representative of the current lack of agreement on the limits of *Justicia,* remains to be determined. The subtribe *Ruelliinae,* although smaller than *Justiciinae* in terms of the number of genera, contains both *Strobilanthes* and *Ruellia* with c. 450 and c. 250 species respectively.

We hope that the classification presented here will serve as a focus for future research within *Acanthaceae.*

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Appendix 1

Lindau 1895

- **Nelsonioideae**
- **Thunbergioideae**
- **Mendoncioideae**
- **Acanthoideae**
- **Contortae**
  - *Trichanthereae*
  - *Louteridieae*
  - *Hygrophileae*
  - *Petalideae*
  - *Strobilantheae*
  - *Ruellieae*
  - *Barlerieae*
- **Imbricatae**
  - *Acantheae*
  - *Aphelandreae*
  - *Andrographideae*
  - *Asystasieae*
  - *Graptophylleae*
  - *Pseuderanthemeae*
  - *Diclipterineae*
  - *Odontonemineae*
  - *Monothecineae*
  - *Porphyrocomineae*
  - *Isoglossineae*
  - *Justicieae*

Appendix 2

Bremekamp 1965

- **Acanthoideae**
  - *Haselhoffieae*
  - *Rhombochlamydeae*
  - *Stenandriopsideae*
  - *Aphelandreae*
  - *Acantheae*
- **Ruellioideae**
  - **Trichanthereae**
  - **Whitfieldieae**
  - **Louteridieae**
  - **Ruellieae**
    - *Blechinae*
    - *Ruelliinae*
    - *Barleriinae*
    - *Strobilanthidinae*
    - *Petalidiinae*
    - *Hygrophylinae*
  - **Lepidagathideae**
    - *Lepidagathinae*
    - *Chroesthidinae*
    - *Borneacanthinae*
  - **Andrographideae**
  - **Justicieae**
    - *Odonteminae*
    - *Rhytiglossininae*
    - *Justiciinae*

APPENDIX 3. CLASSIFICATION OF ACANTHACEAE

Acanthaceae Juss.
  Nelsonioideae Pfeiff.
  Thunbergioideae Kostel.
  Acanthoideae Link
    Acantheae Dumort.
    Ruellieae Dumort.
      Ruelliinae Nees
      Justiciinae Nees
      Andrographiinae Nees
      Barleriinae Nees

Nelsonioideae [retinacula absent, cystsoliths absent, descending cochlear aestivation]

Anisosepalum E. Hossain
Elytraria Michx.
Gynocraterium Bremek.
Nelsonia R. Br.
Ophiorrhiziphyllon Kurz
Saintpauliopsis Staner
Staurogyne Wall.

Thunbergioideae (including *Mendoncia*) [Primarily lianes, bristled anthers, poricidal opening of thecae, capsules or drupes]

Anomacanthus R. D. Good
Mendoncia Vell. ex Vand.
Meyenia Nees
Pseudocalyx Radlk.
Thunbergia Retz.

Acanthoideae [retinacula and explosive capsules]

Acantheae [Cystoliths absent, colpate pollen, 4 monothecate anthers]

Acanthopsis Harv.
Acanthus L.
Achyrocalyx Benoist
Aphelandra R. Br.
Blepharis Juss.
Crossandra Salisb.
Crossandrella C. B. Clarke
Cynarospermum Vollesen
Cyphacanthus Leonard
Encephalosphaera Lindau
Geissomeria Lindl.
Holographis Nees
Neriacanthus Benth.
Orophochilus Lindau
Rhombochlamys Lindau
Salpixantha Hook.
Sclerochiton Harv.
Stenandrium Nees
Streptosiphon Mildbr.
Strobilacanthus Griseb.
Xantheranthemum Lindau

Ruellieae [Cystoliths]

Ruelliinae [Left-contort aestivation and filament curtain]

Acanthopale C. B. Clarke
Aechmanthera Nees
Apassalus Kobuski
Benoicanthus Heine & A. Raynal
Blechum P. Brown
Bravaisia DC.
Brillantaisia P. Beauv.
Brunoniella Bremek.
Calacanthus T. Anderson ex Benth.
Clarkeasia J. R. I. Wood
Dischistocalyx T. Anderson ex Benth.
Duosperma Dayton
Dyschoriste Nees
Echinacanthus Nees
Epiclastopelma Lindau
Eranthemum L.
Eremomastax Lindau
Eusiphon Benoist
Hemigraphis Nees
Heteradelphia Lindau
Hygrophila R. Br.
Ionacanthus Benoist
Kosmosiphon Lindau
Leptosiphonium F. Muell.
Louteridium S. Watson
Lychniothyrsus Lindau
Mellera S. Moore
Mimulopsis Schweinf.
Pararuellia Bremek.
Petalidium Nees
Phaulopsis Willd.
Physacanthus Benth.
Polylychnis Bremek.
Pseudoruellia Benoist
Ruellia L.
Ruelliospis C. B. Clarke

Sanchezia Ruiz & Pav.
Satanocrater Schweinf.
Sautiera Decne.
Spirostigma Nees
Stenosiphonium Nees
Stenothyrsus C. B. Clarke
Strobilanthes Blume
Strobilanthopsis S. Moore
Suessenguthia Merm.
Trichanthera Kunth
Trichosanchezia Mildbr.
Zygoruellia Baill.

Andrographinae [Daubenpollen, Ascending cochlear aestivation, usually many ovules]

Andrographis Wall.ex Nees
Cystacanthus T. Anderson
Diotacanthus Benth.
Graphandra J. B. Imlay
Gymnostachyum Nees
Haplanthodes Kuntze
Indoneesiella Sreem.
Phlogacanthus Nees

Justiciinae [Ascending cochlear aestivation, 2 – 4 ovules, *Rhamen/Spangen/Knötchen/Gürtel* pollen]

Afrofittonia Lindau
Ambongia Benoist
Ancistranthus Lindau
Angkalanthus Balf. f.
Anisacanthus Nees
Anisotes Nees
Anthacanthus Nees
Aphanosperma T. F. Daniel
Ascotheca Heine
Asystasia Blume
Ballochia Balf. f.
Brachystephanus Nees
Calycacanthus K. Schum.
Carlowrightia A. Gray
Celerina Benoist
Centrilla Lindau
Cephalacanthus Lindau
Chalarothyrsus Lindau
Chamaeranthemum Nees
Chileranthemum Oerst.
Chlamydocardia Lindau
Chlamydostachya Mildbr.
Chorisochora Vollesen
Clinacanthus Nees
Clistax Mart.
Codonacanthus Nees
Conocalyx Benoist
Cosmianthemum Bremek.
Cyclacanthus S. Moore
Cylindrosolenium Lindau
Danguya Beniost
Dasytropis Urb.
Dichazothece Lindau
Dicladanthera F. Muell.
Dicliptera Juss.
Ecbolium Kurz
Filetia Miq.
Fittonia Coem.
Forcipella Baill.
Glossochilus Nees
Graptophyllum Nees
Gypsacanthus Lott, Jaramillo & Rzed.
Harpochilus Nees
Henrya Nees
Herpetacanthus Nees
Hoverdenia Nees
Hypoestes Sol. ex R. Br.
Ichtyostoma Hedrén & Vollesen
Isoglossa Oerst.
Isotheca Turrill
Jadunia Lindau
Juruasia Lindau
Justicia L.
Kalbreyeriella Lindau
Linariantha B. L. Burtt & R. M. Sm.
Mackaya Harv.
Marcania J. B. Imlay
Megalochlamys Lindau
Megalostoma Leonard
Megaskepasma Lindau
Mellitacanthus S. Moore
Metarungia Baden
Mexacanthus T. F. Daniel
Mirandea Rzed.
Monechma Hochst.
Monothecium Hochst.
Odontonema Nees
Oplonia Raf.
Oreacanthus Benth.
Pachystachys Nees
Pelecostemon Leonard
Peristrophe Nees
Phialacanthus Benth.
Podorungia Baill.
Poikilacanthus Lindau
Populina Baill.
Pranceacanthus Wassh.
Pseuderanthemum Radlk.
Pseudodicliptera Benoist
Psilanthele Lindau
Ptyssiglottis T. Anderson

Pulchranthus V. M. Baum, Reveal & Nowicke
Razisea Oerst.
Rhinacanthus Nees
Ritonia Benoist
Rungia Nees
Ruspolia Lindau
Ruttya Harv.
Samuelssonia Urb. & Ekman
Sapphoa Urb.
Schaueria Nees
Sebastiano-Schaueria Nees
Spathacanthus Baill.
Sphinctacanthus Benth.
Stenostephanus Nees
Streblacanthus Kuntze
Tessmanniacanthus Mildbr.
Tetramerium Nees
Thysanostigma J. B. Imlay
Trichaulax Vollesen
Trichocalyx Balf. f.
Xerothamnella C. T. White
Yeatesia Small

Barleriinae [Quincuncial aestivation]

Barleria L.
Barleriola Oerst.
Borneacanthus Bremek.
Boutonia DC.
Chroesthes Benoist
Crabbea Harv.
Hulemacanthus S. Moore
Lepidagathis Willd.
Lophostachys Pohl

Unplaced within Acanthoideae

Acanthostelma Bidgood & Brummitt
Acanthura Lindau
Aphelandrella Mildbr.
Camarotea Scott Elliot
Chlamydacanthus Lindau
Dolichostachys Benoist
Golaea Chiov.
Idiacanthus Leonard
Kudoacanthus Hosok.
Lankesteria Lindl.
Lasiocladus Bojer ex Nees
Leandriella Benoist
Morsacanthus Rizzini
Neuracanthus Nees
Perenideboles Ram. Goyena
Pericalypta Benoist
Sphacanthus Benoist
Vavara Benoist
Vindasia Benoist
Whitfieldia Hook.

Excluded genera

Thomandersia Baill.

APPENDIX 4. GENERIC SYNONYMY, ACCEPTED GENERA IN BOLD

Acanthodium Delile (= **Blepharis** Juss.)
Acanthopale C. B. Clarke
Acanthopsis Harv.
Acanthostelma Bidgood & Brummitt
Acanthura Lindau
Acanthus L.
    Cheilopsis Moq.
Acelica Rizzini (= **Justicia** L.)
Achyrocalyx Benoist
Adelaster Lindl. ex Veitch (= **Fittonia** Coem.)
Adenacanthus Nees (= **Strobilanthes** Blume)
Adenostachya Bremek. (= **Strobilanthes** Blume)
Adhatoda Mill. (= **Justicia** L.)
Aechmanthera Nees
Afrofittonia Lindau
    Talbotia S. Moore
Afromendoncia Gilg ex Lindau (= **Mendoncia** Vell. ex Vand.)
Amathea Raf. (= **Aphelandra** R. Br.)
Ambongia Benoist
Amphiestes S. Moore (= **Hypoestes** Sol. ex R. Br.)
Amphiscopia Nees (= **Justicia** L.)
Ancalanthus Balf. f. (= **Angkalanthus** Balf. f.)
Ancistranthus Lindau
Ancistrostylis T. Yamaz. (= **Staurogyne** Wall.)
Ancylacanthus Lindau (= **Ptyssiglottis** T. Anderson)
Androcentrum Lem. (= **Bravaisia** DC.)
Andrographis Wall. ex Nees
    Haplanthoides H. W. Li
    Haplanthus Nees
Angkalanthus Balf. f.
    Ancalanthus Balf. f.
Anisacanthus Nees
Anisosepalum E. Hossain
Anisostachya Nees (= **Justicia** L.)
Anisotes Nees
    Himantochilus T. Anderson ex Benth.
    Symplectochilus Lindau
Anomacanthus R. D. Good
    Gilletiella De Wild. & T. Durand
Anthacanthus Nees
Antheliacanthus Ridl. (= **Pseuderanthemum** Radlk.)
Apassalus Kobuski
Aphanandrium Lindau (= **Neriacanthus** Benth.)
Aphanosperma T. F. Daniel
Aphelandra R. Br.
    Amathea Raf.
    Hemisandra Scheidw.
    Hydromestus Scheidw.
    Lagochilium Nees
    Lepidacanthus C. Presl
    Sreemadhavana Rauschert
    Odontophyllum Sreem.
    Strobilorhachis Klotzsch
    Synandra Schrad.
Aphelandrella Mildbr.
Aphragmia Nees (= **Ruellia** L.)
Apolepsis (Blume) Hassk. (= **Lepidagathis** Willd.)
Arrhostoxylum Nees (= **Ruellia** L.)
Ascotheca Heine
Asteracantha Nees (= **Hygrophila** R.Br.)
Asystasia Blume
    Asystasiella Lindau
    Dicentranthera T. Anderson
    Isochoriste Miq.
    Parasystasia Baill.
    Salpinctium T. J .Edwards
    Styasasia S. Moore
Asystasiella Lindau (= **Asystasia** Blume)
Aulojusticia Lindau (= **Justicia** L.)
Averia Leonard (= **Tetramerium** Nees)
Ballochia Balf. f.
Baphicacanthus Bremek. (= **Strobilanthes** Blume)
Barleria L.
    Barleriacanthus Oerst.
    Barlerianthus Oerst.
    Barleriosiphon Oerst.
    Barlerites Oerst.
    Dicranacanthus Oerst.
    Isaloa Humbert
    Parabarleria Baill.
    Prionitis Oerst.
    Pseudo-Barleria Oerst.
Barleriacanthus Oerst. (= **Barleria** L.)
Barlerianthus Oerst. (= **Barleria** L.)
Barleriola Oerst.
Barleriosiphon Oerst.(= **Barleria** L.)
Barlerites Oerst. (= **Barleria** L.)
Belantheria Nees (= **Brillantaisia** P.Beauv.)
Beloperone Nees (= **Justicia** L.)
Benoicanthus Heine & A. Raynal
Bentia Rolfe (= **Justicia** L.)
Berginia Harv. (= **Holographis** Nees)
Blechum P. Browne
Blepharacanthus Nees ex Lindl. (= **Blepharis** Juss.)
Blepharis Juss.
    Acanthodium Delile
    Blepharacanthus Nees ex Lindl.
    Trichacanthus Zoll. & Moritzi
Borneacanthus Bremek.
Boutonia DC.
    Periblema DC.
Brachystephanus Nees
Bravaisia DC.

  Androcentrum Lem.
  Onychacanthus Nees
Bremekampia Sreem. (= **Haplanthodes** Kuntze)
Brillantaisia P. Beauv.
  Belantheria Nees
  Leucoraphis Nees
  Ruelliola Baill.
Brochosiphon Nees (= **Dicliptera** Juss.)
Brunoniella Bremek.
Buceragenia Greenm. (= **Pseuderanthemum** Radlk.)
Butayea De Wild. (= **Sclerochiton** Harv.)
Buteraea Nees (= **Strobilanthes** Blume)
Calacanthus T. Anderson ex Benth.
Calliaspidia Bremek.(= **Justicia** L.)
Calophanes D. Don (= **Dyschoriste** Nees)
Calophanoides (C. B. Clarke) Ridl. (= **Justicia** L.)
Calycacanthus K. Schum.
Calymmostachya Bremek. (= **Justicia** L.)
Camarotea Scott-Elliot
Cardanthera Buch.-Ham. ex Benth. (= **Hygrophila** R. Br.)
Cardiacanthus Nees & Schauer (= **Carlowrightia** A. Gray)
Carlowrightia A. Gray
  Cardiacanthus Nees & Schauer
  Croftia Small
Carvia Bremek. (= **Strobilanthes** Blume)
Celerina Benoist
Centrilla Lindau
Cephalacanthus Lindau
Chaetacanthus Nees (= **Dyschoriste** Nees)
Chaetochlamys Lindau (= **Justicia** L.)
Chaetothylax Nees (= **Justicia** L.)
Chaetothylopsis Oerst. (= **Justicia** L.)
Chalarothyrsus Lindau
Chamaeranthemum Nees
Championella Bremek. (= **Strobilanthes** Blume)
Cheilopsis Moq. (= **Acanthus** L.)
Chileranthemum Oerst.
  Trybliocalyx Lindau
Chiloglossa Oerst. (= **Justicia** L.)
Chingiacanthus Hand.-Mazz. (= **Isoglossa** Oerst.)
Chlamydacanthus Lindau
  Theileamea Baill.
Chlamydocardia Lindau
Chlamydostachya Mildbr.
Chorisochora Vollesen
Chrestienia Montrouz. (= **Pseuderanthemum** Radlk.)
Chroesthes Benoist
Clarkeasia J. R. I. Wood
Clinacanthus Nees
Clistax Mart.
Codonacanthus Nees
Conocalyx Benoist
Copioglossa Miers (= **Ruellia** L.)
Corymbostachys Lindau (= **Justicia** L.)
Cosmianthemum Bremek.
Crabbea Harv.
Croftia Small (= **Carlowrightia** A. Gray)
Crossandra Salisb.
  Harrachia Jacq.
  Pleuroblepharis Baill.
  Polythrix Nees
Crossandrella C. B. Clarke
Cryphiacanthus Nees (= **Ruellia** L.)
Cryptophragmium Nees (= **Gymnostachyum** Nees)
Ctenopaepale Bremek. (= **Strobilanthes** Blume)
Cyclacanthus S. Moore
Cylindrosolenium Lindau
Cynarospermum Vollesen
Cyphacanthus Leonard
Cyphisia Rizzini (= **Justicia** L.)
Cyrtanthera Nees (= **Justicia** L.)
Cyrtantherella Oerst. (= **Justicia** L.)
Cystacanthus T. Anderson
Dactylostegium Nees (= **Dicliptera** Juss.)
Daedalacanthus T. Anderson (= **Eranthemum** L.)
Danguya Benoist
Dasytropis Urb.
Delphinacanthus Benoist (= **Pseudodicliptera** Benoist)
Dianthera L. (= **Justicia** L.)
Diateinacanthus Lindau (= **Odontonema** Nees)
Dicentranthera T. Anderson (= **Asystasia** Blume)
Dichazothece Lindau
Dicladanthera F. Muell.
Dicliptera Juss.
  Brochosiphon Nees
  Dactylostegium Nees
Dicranacanthus Oerst. (= **Barleria** L.)
Didyplosandra Wight ex Bremek.(= **Strobilanthes** Blume)
Diflugossa Bremek. (= **Strobilanthes** Blume)
Dimanisa Raf. (= **Justicia** L.)
Dinteracanthus C. B. Clarke ex Schinz (= **Ruellia** L.)
Diotacanthus Benth.
Dipteracanthus Nees (= **Ruellia** L.)
Dischistocalyx T. Anderson ex Benth.
  Distichocalyx Benth.
Disperma J. F. Gmel. (= **Duosperma** Dayton)
Distichocalyx Benth. (= **Dischistocalyx** T. Anderson ex Benth.)
Ditrichospermum Bremek. (= **Strobilanthes** Blume)
Dolichostachys Benoist
Dossifluga Bremek. (= **Strobilanthes** Blume)

Drejera Nees (= **Justicia** L.)
Drejerella Lindau (= **Justicia** L.)
Duosperma Dayton
  Disperma J. F. Gmel.
Duvernoia E. Mey. ex Nees (= **Justicia** L.)
Dyschoriste Nees
  Calophanes D. Don
  Chaetacanthus Nees
  Phillipsia Rolfe
Dyspemptemorion Bremek. (= **Justicia** L.)
Ebermaiera Nees (= **Staurogyne** Wall.)
Ecbolium Kurz
Echinacanthus Nees
Echinopaepale Bremek. (= **Strobilanthes** Blume)
Ecteinanthus T. Anderson (= **Isoglossa** Oerst.)
Elytraria Michx.
  Tubiflora J. F. Gmel.
Emularia Raf. (= **Justicia** L.)
Encephalosphaera Lindau
Endopogon Nees (= **Strobilanthes** Blume)
Endosiphon T. Anderson ex Benth. (= **Ruellia** L.)
Epiclastopelma Lindau
  Sooia Pocs
Eranthemum L.
  Daedalacanthus T. Anderson
Eremomastax Lindau
  Paulowilhelmia Hochst.
Eriostrobilus Bremek. (= **Strobilanthes** Blume)
Erythracanthus Nees (= **Staurogyne** Wall.)
Ethesia Raf. (= **Justicia** L.)
Eurychanes Nees (= **Ruellia** L.)
Eusiphon Benoist
Filetia Miq.
Fittonia Coem.
  Adelaster Lindl. ex Veitch
Forcipella Baill.
Forsythiopsis Baker (= **Oplonia** Raf.)
Galeottia Nees (= **Stenostephanus** Nees)
Gantelbua Bremek. (= **Hemigraphis** Nees)
Gastranthus Moritz ex Benth. & Hook. (= **Stenostephanus** Nees)
Gatesia A. Gray (= **Yeatesia** Small)
Geissomeria Lindl.
Gendarussa Nees (= **Justicia** L.)
Gerardia L. (= **Stenandrium** Nees)
Gilletiella De Wild. & T. Durand (= **Anomacanthus** R. D. Good)
Glockeria Nees (= **Stenostephanus** Nees)
Glosarithys Rizzini (= **Justicia** L.)
Glossochilus Nees
Golaea Chiov.
Goldfussia Nees (= **Strobilanthes** Blume)
Graphandra J. B. Imlay
Graptophyllum Nees
Gutzlaffia Hance (= **Strobilanthes** Blume)
Gymapsis Bremek. (= **Strobilanthes** Blume)
Gymnacanthus Oerst. (= **Ruellia** L.)
Gymnostachyum Nees
  Cryptophragmium Nees
  Odontostigma Zoll. & Moritzi
  Petracanthus Nees
Gynocraterium Bremek.
Gypsacanthus Lott, V. Jaram. & Rzed.
Habracanthus Nees (= **Stenostephanus** Nees)
Haemacanthus S. Moore (= **Satanocrater** Schweinf.)
Hallieracantha Stapf (= **Ptyssiglottis** T. Anderson)
Hansteinia Oerst. (= **Stenostephanus** Nees)
Haplanthera Hochst. (= **Ruttya** Harv.)
Haplanthodes Kuntze
  Bremekampia Sreem. (SUS)
Haplanthoides H. W. Li (= **Andrographis** Wall. ex Nees)
Haplanthus Nees (= **Andrographis** Wall. ex Nees)
Harnieria Solms (= **Justicia** L.)
Harpochilus Nees
Harrachia Jacq. (= **Crossandra** Salisb.)
Haselhoffia Lindau (= **Physacanthus** Benth.)
Heinzelia Nees (= **Justicia** L.)
Hemiadelphis Nees (= **Hygrophila** R. Br.)
Hemichoriste Nees (= **Justicia** L.)
Hemigraphis Nees
  Gantelbua Bremek.
Hemisandra Scheidw. (= Aphelandra R. Br.)
Henrya Nees
  Solenoruellia Baill.
Herpetacanthus Nees (= Standleyacanthus Leonard)
Heteradelphia Lindau
Heteraspidia Rizzini (S) (= **Justicia** L.)
Himantochilus T. Anderson ex Benth. (= **Anisotes** Nees)
Holographis Nees
  Berginia Harv.
  Lundellia Leonard
  Pringleophytum A. Gray
Hoverdenia Nees
Hulemacanthus S. Moore
Hydromestus Scheidw. (= **Aphelandra** R. Br.)
Hygrophila R. Br.
  Asteracantha Nees
  Cardanthera Buch.-Ham. ex Benth.
  Hemiadelphis Nees
  Kita A. Chev.
  Nomaphila Blume
  Plaesianthera (C. B. Clarke) Livera
  Santapaua N. P. Balakr. & Subr.
  Synnema Benth.
Hymenochlaena Bremek. (= **Strobilanthes** Blume)

- **Hypoestes** Sol. ex R. Br.
  - Amphiestes S. Moore
  - Periestes Baill.
- **Ichtyostoma** Hedrén & Vollesen
- **Idiacanthus** Leonard
- **Indoneesiella** Sreem.
- **Ionacanthus** Benoist
- Isacanthus Nees (= **Sclerochiton** Harv.)
- Isaloa Humbert (= **Barleria** L.)
- Isochoriste Miq. (= **Asystasia** Blume)
- **Isoglossa** Oerst.
  - Chingiacanthus Hand.-Mazz.
  - Ecteinanthus T. Anderson
  - Leda C. B. Clarke
  - Plagiotheca Chiov.
  - Schliebenia Mildbr.
  - Strophacanthus Lindau
- **Isotheca** Turrill
- Ixtlania M. E. Jones (= **Justicia** L.)
- Jacobinia Nees ex Moric. (= **Justicia** L.)
- **Jadunia** Lindau
- **Juruasia** Lindau
- **Justicia** L.
  - Acelica Rizzini
  - Adhatoda Mill.
  - Amphiscopia Nees
  - Anisostachya Nees
  - Aulojusticia Lindau
  - Beloperone Nees
  - Bentia Rolfe
  - Calliaspidia Bremek.
  - Calophanoides (C. B. Clarke) Ridl.
  - Calymmostachya Bremek.
  - Chaetochlamys Lindau
  - Chaetothylax Nees
  - Chaetothylopsis Oerst.
  - Chiloglossa Oerst.
  - Corymbostachys Lindau
  - Cyphisia Rizzini
  - Cyrtanthera Nees
  - Cyrtantherella Oerst.
  - Dianthera L.
  - Dimanisa Raf.
  - Drejera Nees
  - Drejerella Lindau
  - Duvernoia E. Mey. ex Nees
  - Dyspemptemorion Bremek.
  - Emularia Raf.
  - Ethesia Raf.
  - Gendarussa Nees
  - Glosarithys Rizzini
  - Harnieria Solms
  - Heinzelia Nees
  - Hemichoriste Nees
  - Heteraspidia Rizzini
  - Ixtlania M. E. Jones
  - Jacobinia Nees ex Moric.
  - Kuestera Regel
  - Libonia K. Koch
  - Linocalyx Lindau
  - Leptostachya Nees
  - Lophothecium Rizzini
  - Lustrinia Raf.
  - Mananthes Bremek.
  - Neohallia Hemsl.
  - Nicoteba Lindau
  - Orthotactus Nees
  - Parajusticia Benoist
  - Petalanthera Raf.
  - Plagiacanthus Nees
  - Plegmatolemma Bremek.
  - Porphyrocoma Scheidw. ex Hook.
  - Psacadocalymma Bremek.
  - Pupilla Rizzini
  - Rhacodiscus Lindau
  - Rhaphidospora Nees
  - Rhiphidosperma G. Don
  - Rhyticalymma Bremek.
  - Rhytiglossa Nees ex Lindl.
  - Rodatia Raf.
  - Rostellaria Nees
  - Rostellularia Rchb.
  - Saglorithys Rizzini
  - Salviacanthus Lindau
  - Sarojusticia Bremek.
  - Sarotheca Nees
  - Sericographis Nees
  - Simonisia Nees
  - Siphonoglossa Oerst.
  - Solenochasma Fenzl
  - Stethoma Raf.
  - Strobilacanthus Griseb.
  - Tabascina Baill.
  - Thalestris Rizzini
  - Thamnojusticia Mildbr.
  - Tyloglossa Hochst.
- Kalbreyeracanthus Wassh. (= **Stenostephanus** Nees)
- **Kalbreyeriella** Lindau
- Kanjarum Ramam. (= **Strobilanthes** Blume)
- Kita A. Chev. (= **Hygrophila** R. Br.)
- Kjellbergia Bremek. (= **Strobilanthes** Blume)
- Kolobochilus Lindau (= **Razisea** Oerst.)
- **Kosmosiphon** Lindau
- **Kudoacanthus** Hosok.
- Kuestera Regel (= **Justicia** L.)
- Lagochilium Nees (= **Aphelandra** R. Br.)
- Lamiacanthus Kuntze (= **Strobilanthes** Blume)
- **Lankesteria** Lindl.
- Larsenia Bremek. (= **Strobilanthes** Blume)

Lasiocladus Bojer ex Nees
  Synchoriste Baill.
Leandriella Benoist
Leda C. B. Clarke (= **Isoglossa** Oerst.)
Leiophaca Lindau (= **Whitfieldia** Hook.)
Lepidacanthus C. Presl (= **Aphelandra** R. Br.)
Lepidagathis Willd.
  Apolepsis (Blume) Hassk.
  Lindauea Rendle
  Volkensiophyton Lindau
Leptacanthus Nees (= **Strobilanthes** Blume)
Leptosiphonium F. Muell.
Leptostachya Nees (= **Justicia** L.)
Leucobarleria Lindau (= **Neuracanthus** Nees)
Leucoraphis Nees (= **Brillantaisia** P. Beauv.)
Liberatia Rizzini (= **Lophostachys** Pohl)
Libonia K. Koch (= **Justicia** L.)
Linariantha B. L. Burtt & R. M. Sm.
Lindauea Rendle (= **Lepidagathis** Willd.)
Linocalyx Lindau (= **Justicia** L.)
Lirayea Pierre (= **Mendoncia** Vell. ex Vand.)
Lissospermum Bremek. (= **Strobilanthes** Blume)
Listrobanthes Bremek. (= **Strobilanthes** Blume)
Lophostachys Pohl
  Liberatia Rizzini
Lophothecium Rizzini (= **Justicia** L.)
Louteridium S. Watson
  Neolindenia Baill.
Lundellia Leonard (= **Holographis** Nees)
Lustrinia Raf. (= **Justicia** L.)
Lychniothyrsus Lindau
Mackaya Harv.
  Odontonemella Lindau
Mackenziea Nees (= **Strobilanthes** Blume)
Macrorungia C. B. Clarke (= **Metarungia** Baden)
Mananthes Bremek. (= **Justicia** L.)
Marcania J. B. Imlay
Megalochlamys Lindau
Megalostoma Leonard
Megaskepasma Lindau
Melittacanthus S. Moore
Mellera S. Moore
  Onus Gilli
Mendoncia Vell. ex Vand.
  Afromendoncia Gilg ex Lindau
  Lirayea Pierre
  Monachochlamys Baker
Metarungia Baden
  Macrorungia C. B. Clarke
Mexacanthus T. F. Daniel
Meyenia Nees
Micranthus J. C. Wendl. (= **Phaulopsis** Willd.)
Microstrobilus Bremek. (= **Strobilanthes** Blume)
Mimulopsis Schweinf.
Mirandea Rzed.
Monachochlamys Baker (= **Mendoncia** Vell. ex Vand.)
Monechma Hochst.
  Pogonospermum Hochst.
  Schwabea Endl.
Monothecium Hochst.
Morsacanthus Rizzini
Nelsonia R. Br.
Neohallia Hemsl. (= **Justicia** L.)
Neolindenia Baill. (= **Louteridium** S. Watson)
Neozenkerina Mildbr. (= **Staurogyne** Wall.)
Neriacanthus Benth.
  Aphanandrium Lindau
Neuracanthus Nees
  Leucobarleria Lindau
Nicoteba Lindau (= **Justicia** L.)
Nilgirianthus Bremek. (= **Strobilanthes** Blume)
Nomaphila Blume (= **Hygrophila** R. Br.)
Nothoruellia Bremek. (= **Ruellia** L.)
Odontonema Nees
  Diateinacanthus Lindau
  Phidiasia Urb.
  Sciaphyllum Bremek.
  Thyrsacanthus Nees
Odontonemella Lindau (= **Mackaya** Harv.)
Odontophyllum Sreem. (= **Aphelandra** R. Br.)
Odontostigma Zoll. & Moritzi (= **Gymnostachyum** Nees)
Onus Gilli (= **Mellera** S. Moore)
Onychacanthus Nees (= **Bravaisia** DC.)
Ophiorrhiziphyllon Kurz
Oplonia Raf.
  Forsythiopsis Baker
Oreacanthus Benth.
Oreothyrsus Lindau (= **Ptyssiglottis** T. Anderson)
Orophochilus Lindau
Orthotactus Nees (= **Justicia** L.)
Pachystachys Nees
Pachystrobilus Bremek. (= **Strobilanthes** Blume)
Parabarleria Baill. (= **Barleria** L.)
Parachampionella Bremek. (= **Strobilanthes** Blume)
Paragoldfussia Bremek. (= **Strobilanthes** Blume)
Paragutzlaffia H. P. Tsui (= **Strobilanthes** Blume)
Parajusticia Benoist (= **Justicia** L.)
Pararuellia Bremek.
Parastrobilanthes Bremek. (= **Strobilanthes** Blume)
Parasympagis Bremek. (= **Strobilanthes** Blume)
Parasystasia Baill. (= **Asystasia** Blume)
Paulowilhelmia Hochst. (= **Eremomastax** Lindau)
Pelecostemon Leonard
Pentstemonacanthus Nees (= **Ruellia** L.)
Perenideboles Ram. Goyena
Periblema DC. (= **Boutonia** DC.)

Pericalypta Benoist
Periestes Baill. (= **Hypoestes** Sol. ex R. Br.)
Perilepta Bremek. (= **Strobilanthes** Blume)
Peristrophe Nees
  Psiloesthes Benoist
  Ramusia Nees
Petalanthera Raf. (= **Justicia** L.)
Petalidium Nees
  Pseudobarleria T. Anderson
Petracanthus Nees (= **Gymnostachyum** Nees)
Phaulopsis Willd.
  Micranthus J. C. Wendl.
  Phaylopsis Willd.
Phaylopsis Willd. (= **Phaulopsis** Willd.)
Phialacanthus Benth.
Phidiasia Urb. (= **Odontonema** Nees)
Phillipsia Rolfe (= **Dyschoriste** Nees)
Phlebophyllum Nees (= **Strobilanthes** Blume)
Phlogacanthus Nees
Physacanthus Benth.
  Haselhoffia Lindau
Plaesianthera (C. B. Clarke) Livera (= **Hygrophila** R. Br.)
Plagiacanthus Nees (= **Justicia** L.)
Plagiotheca Chiov. (= **Isoglossa** Oerst.)
Plegmatolemma Bremek. (= **Justicia** L.)
Pleocaulus Bremek. (= **Strobilanthes** Blume)
Pleuroblepharis Baill. (= **Crossandra** Salisb.)
Podorungia Baill.
  Warpuria Stapf
Pogonospermum Hochst. (= **Monechma** Hochst.)
Poikilacanthus Lindau
Polylychnis Bremek.
Polythrix Nees (= **Crossandra** Salisb.)
Polytrema C. B. Clarke (= **Ptyssiglottis** T. Anderson)
Populina Baill.
Porphyrocoma Scheidw. ex Hook. (= **Justicia** L.)
Pounguia Benoist (= **Whitfieldia** Hook.)
Pranceacanthus Wassh.
Pringleophytum A. Gray (= **Holographis** Nees)
Prionitis Oerst. (= **Barleria** L.)
Psacadocalymma Bremek. (= **Justicia** L.)
Psacadopaepale Bremek. (= **Strobilanthes** Blume)
Pseudacanthopale Benoist (= **Strobilanthopsis** S. Moore)
Pseudaechmanthera Bremek. (= **Strobilanthes** Blume)
Pseuderanthemum Radlk.
  Antheliacanthus Ridl.
  Chrestienia Montrouz.
Pseudo-Barleria Oerst. (= **Barleria** L.)
Pseudobarleria T. Anderson (= **Petalidium** Nees)
Pseudoblepharis Baill. (= **Sclerochiton** Harv.)
Pseudocalyx Radlk.
Pseudodicliptera Benoist
  Delphinacanthus Benoist
Pseudoruellia Benoist
Pseudostenosiphonium Lindau (= **Strobilanthes** Blume)
Psilanthele Lindau
Psiloesthes Benoist (= **Peristrophe** Nees)
Pteracanthus (Nees) Bremek. (= **Strobilanthes** Blume)
Pteroptychia Bremek. (= **Strobilanthes** Blume)
Ptyssiglottis T. Anderson
  Ancylacanthus Lindau
  Hallieracantha Stapf
  Oreothyrsus Lindau
  Polytrema C. B. Clarke
Pulchranthus V. M. Baum, Reveal & Nowicke
Pupilla Rizzini (= **Justicia** L.)
Pyrrothrix Bremek. (= **Strobilanthes** Blume)
Ramusia Nees (= **Peristrophe** Nees)
Razisea Oerst.
  Kolobochilus Lindau
Rhacodiscus Lindau (= **Justicia** L.)
Rhaphidospora Nees (= **Justicia** L.)
Rhinacanthus Nees
Rhiphidosperma G. Don (= **Justicia** L.)
Rhombochlamys Lindau
Rhyticalymma Bremek. (= **Justicia** L.)
Rhytiglossa Nees ex Lindl. (= **Justicia** L.)
Ritonia Benoist
Rodatia Raf. (= **Justicia** L.)
Rostellaria Nees (= **Justicia** L.)
Rostellularia Rchb. (= **Justicia** L.)
Ruellia L.
  Aphragmia Nees
  Arrhostoxylum Nees
  Copioglossa Miers
  Cryphiacanthus Nees
  Dinteracanthus C. B. Clarke ex Schinz
  Dipteracanthus Nees
  Endosiphon T. Anderson ex Benth.
  Eurychanes Nees
  Gymnacanthus Oerst.
  Nothoruellia Bremek.
  Pentstemonacanthus Nees
  Salpingacanthus S. Moore
  Sclerocalyx Nees
  Siphonacanthus Nees
  Stemonacanthus Nees
  Stenoschista Bremek.
  Stephanophysum Pohl
  Tacoanthus Baill.
  Tremacanthus S. Moore
  Ulleria Bremek.
Ruelliola Baill. (= **Brillantaisia** P. Beauv.)
Ruelliopsis C. B. Clarke

- **Rungia** Nees
- **Ruspolia** Lindau
- **Ruttya** Harv.
  - Haplanthera Hochst.
- Saglorithys Rizzini (= **Justicia** L.)
- **Saintpauliopsis** Staner
- Salpinctium T. J. Edwards (= **Asystasia** Blume)
- Salpingacanthus S. Moore (= **Ruellia** L.)
- Salpingantha Lem. (= **Salpixantha** Hook.)
- Salpinxantha Urb. (= **Salpixantha** Hook.)
- **Salpixantha** Hook.
  - Salpingantha Lem.
  - Salpinxantha Urb.
- Salviacanthus Lindau (= **Justicia** L.)
- **Samuelssonia** Urb. & Ekman
- **Sanchezia** Ruiz & Pav.
  - Steirosanchezia Lindau
- Santapaua N. P. Balakr. & Subr. (= **Hygrophila** R. Br.)
- **Sapphoa** Urb.
- Sarojusticia Bremek. (= **Justicia** L.)
- Sarotheca Nees (= **Justicia** L.)
- **Satanocrater** Schweinf.
  - Haemacanthus S. Moore
- **Sautiera** Decne.
- **Schaueria** Nees
- Schliebenia Mildbr. (= **Isoglossa** Oerst.)
- Schwabea Endl. (= **Monechma** Hochst.)
- Sciaphyllum Bremek. (= **Odontonema** Nees)
- Sclerocalyx Nees (= **Ruellia** L.)
- **Sclerochiton** Harv.
  - Butayea De Wild.
  - Isacanthus Nees
  - Pseudoblepharis Baill.
- **Sebastiano-Schaueria** Nees
- Semnostachya Bremek. (= **Strobilanthes** Blume)
- Semnothyrsus Bremek. (= **Strobilanthes** Blume)
- Sericocalyx Bremek. (= **Strobilanthes** Blume)
- Sericographis Nees (= **Justicia** L.)
- Simonisia Nees (= **Justicia** L.)
- Sinthroblastes Bremek. (= **Strobilanthes** Blume)
- Siphonacanthus Nees (= **Ruellia** L.)
- Siphonoglossa Oerst. (= **Justicia** L.)
- Solenochasma Fenzl (= **Justicia** L.)
- Solenoruellia Baill. (= **Henrya** Nees)
- Sooia Pocs (= **Epiclastopelma** Lindau)
- **Spathacanthus** Baill.
- **Sphacanthus** Benoist
- **Sphinctacanthus** Benth.
- **Spirostigma** Nees
- Sreemadhavana Rauschert (= **Aphelandra** R. Br.)
- Standleyacanthus Leonard (= **Herpetacanthus** Nees)
- **Staurogyne** Wall.
  - Ancistrostylis T. Yamaz.
  - Ebermaiera Nees
  - Erythracanthus Nees
  - Neozenkerina Mildbr.
  - Staurogynopsis Mangenot & Ake Assi
  - Zenkerina Engl.
- Staurogynopsis Mangenot & Ake Assi (= **Staurogyne** Wall.)
- Steirosanchezia Lindau (= **Sanchezia** Ruiz & Pav.)
- Stemonacanthus Nees (= **Ruellia** L.)
- Stenandriopsis S. Moore (= **Stenandrium** Nees)
- **Stenandrium** Nees
  - Gerardia Benth.
  - Stenandriopsis S. Moore
- Stenoschista Bremek. (= **Ruellia** L.)
- **Stenosiphonium** Nees
- **Stenostephanus** Nees
  - Galeottia Nees
  - Gastranthus Moritz ex Benth. & Hook.
  - Glockeria Nees
  - Habracanthus Nees
  - Hansteinia Oerst.
  - Kalbreyeracanthus Wassh.
  - Syringidium Lindau
- **Stenothyrsus** C. B. Clarke
- Stephanophysum Pohl (= **Ruellia** L.)
- Stethoma Raf. (= **Justicia** L.)
- **Streblacanthus** Kuntze
- **Streptosiphon** Mildbr.
- **Strobilacanthus** Griseb.
- **Strobilanthes** Blume
  - Adenacanthus Nees
  - Adenostachya Bremek.
  - Baphicacanthus Bremek.
  - Buteraea Nees
  - Carvia Bremek.
  - Championella Bremek.
  - Ctenopaepale Bremek.
  - Didyplosandra Wight ex Bremek.
  - Diflugossa Bremek.
  - Ditrichospermum Bremek.
  - Dossifluga Bremek.
  - Echinopaepale Bremek.
  - Endopogon Nees
  - Eriostrobilus Bremek.
  - Goldfussia Nees
  - Gutzlaffia Hance
  - Gymapsis Bremek.
  - Hymenochlaena Bremek.
  - Kanjarum Ramam.
  - Kjellbergia Bremek.
  - Lamiacanthus Kuntze
  - Larsenia Bremek.
  - Leptacanthus Nees
  - Lissospermum Bremek.
  - Listrobanthes Bremek.

  - Mackenziea Nees
  - Microstrobilus Bremek.
  - Nilgirianthus Bremek.
  - Pachystrobilus Bremek.
  - Parachampionella Bremek.
  - Paragoldfussia Bremek.
  - Paragutzlaffia H. P. Tsui
  - Parastrobilanthes Bremek.
  - Parasympagis Bremek.
  - Perilepta Bremek.
  - Phlebophyllum Nees
  - Pleocaulus Bremek.
  - Psacadopaepale Bremek.
  - Pseudaechmanthera Bremek.
  - Pseudostenosiphonium Lindau
  - Pteracanthus (Nees) Bremek.
  - Pteroptychia Bremek.
  - Pyrrothrix Bremek.
  - Semnostachya Bremek.
  - Semnothyrsus Bremek.
  - Sericocalyx Bremek.
  - Sinthroblastes Bremek.
  - Supushpa Suryan.
  - Sympagis (Nees) Bremek.
  - Taeniandra Bremek.
  - Tarphochlamys Bremek.
  - Tetraglochidium Bremek.
  - Tetragoga Bremek.
  - Tetragompha Bremek.
  - Thelepaepale Bremek.
  - Triaenacanthus Nees
  - Xanthostachya Bremek.
  - Xenacanthus Bremek.
- **Strobilanthopsis** S. Moore
  - Pseudacanthopale Benoist
- Strobilorhachis Klotzsch (= **Aphelandra** R. Br.)
- Strophacanthus Lindau (= **Isoglossa** Oerst.)
- Styasasia S. Moore (= **Asystasia** Blume)
- Stylarthropus Baill. (= **Whitfieldia** Hook.)
- **Suessenguthia** Merxm.
- Supushpa Suryan. (= **Strobilanthes** Blume)
- Sympagis (Nees) Bremek. (= **Strobilanthes** Blume)
- Symplectochilus Lindau (= **Anisotes** Nees)
- Synandra Schrad. (= **Aphelandra** R. Br.)
- Synchoriste Baill. (= **Lasiocladus** Bojer ex Nees)
- Synnema Benth. (= **Hygrophila** R. Br.)
- Syringidium Lindau (= **Stenostephanus** Nees)
- Tabascina Baill. (= **Justicia** L.)
- Tacoanthus Baill. (= **Ruellia** L.)
- Taeniandra Bremek. (= **Strobilanthes** Blume)
- Talbotia S. Moore (= **Afrofittonia** Lindau)
- Tarphochlamys Bremek. (= **Strobilanthes Blume**)
- Teliostachya Nees (= **Lepidagathis** Willd.)
- **Tessmanniacanthus** Mildbr.
- Tetraglochidium Bremek. (= **Strobilanthes** Blume)
- Tetragoga Bremek. (= **Strobilanthes** Blume)
- Tetragompha Bremek. (= **Strobilanthes** Blume)
- **Tetramerium** Nees
  - Averia Leonard
- Thalestris Rizzini (= **Justicia** L.)
- Thamnojusticia Mildbr. (= **Justicia** L.)
- Theileamea Baill. (= **Chlamydacanthus** Lindau)
- Thelepaepale Bremek. (= **Strobilanthes** Blume)
- **Thunbergia** Retz.
- Thyrsacanthus Nees (= **Odontonema** Nees)
- **Thysanostigma** J. B. Imlay
- Tremacanthus S. Moore (= **Ruellia** L.)
- Triaenacanthus Nees (= **Strobilanthes** Blume)
- Trichacanthus Zoll. & Moritzi (= **Blepharis** Juss.)
- **Trichanthera** Kunth
- **Trichaulax** Vollesen
- **Trichocalyx** Balf. f.
- **Trichosanchezia** Mildbr.
- Trybliocalyx Lindau (= **Chileranthemum** Oerst.)
- Tubiflora J. F. Gmel. (= **Elytraria** Michx.)
- Tyloglossa Hochst. (= **Justicia** L.)
- Ulleria Bremek. (= **Ruellia** L.)
- **Vavara** Benoist
- **Vindasia** Benoist
- Volkensiophyton Lindau (= **Lepidagathis** Willd.)
- Warpuria Stapf (= **Podorungia** Baill.)
- **Whitfieldia** Hook.
  - Leiophaca Lindau
  - Pounguia Benoist
  - Stylarthropus Baill.
- **Xantheranthemum** Lindau
- Xanthostachya Bremek. (= **Strobilanthes** Blume)
- Xenacanthus Bremek. (= **Strobilanthes** Blume)
- **Xerothamnella** C. T. White
- **Yeatesia** Small
  - Gatesia A. Gray
- Zenkerina Engl. (= **Staurogyne** Wall.)
- **Zygoruellia** Baill.