Pollen and reproductive morphology of *Rhigiophyllum* and *Siphocodon* (Campanulaceae): two unique genera of the fynbos vegetation of South Africa

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ABSTRACT

Pollen grains of *Rhigiophyllum squarrosum* Hochst., *Siphocodon spartioides* Turcz. and *S. debilis* Schltr., are flattened and triangular with pores at the angles. This morphology is radically different from known pollen of the Campanulaceae *s.str.*: the Campanulaceae are treated here as a family separate from the Lobeliaceae, Cyphiaceae, Nemacladaceae, Pentaphragmataceae and Sphenocleaceae (Lammers 1992). As traditionally conceived, the Campanulaceae is very heterogeneous and, in many classifications, these families were treated as subfamilies of a much-enlarged Campanulaceae. The consistently different floral morphology, biochemistry and pollen structure of the Lobeliaceae favours the recognition of this predominantly tropical group as a separate family.

The pollen grains of these species are described in comparison with other members of the Campanulaceae. Based on surface characteristics of their pollen grains, we conclude that they represent an early offshoot of the wahlenbergioid lineage in southern Africa. We suggest that this unique pollen may also be the result of a highly selective regime in the fynbos, associated with specialized pollinators, and base-poor soils, in addition to possible adaptations for ant dispersal and fire. *Rhigiophyllum* Hochst. and *Siphocodon* Turcz. are also unique in having free carpel-like structures within the ovary. These shrink to form seed pockets around the seeds and disperse as units when the capsule matures. Data from molecular studies support the contention that these taxa form a sister group to all other wahlenbergioids and that this should be formally recognized in a classification system. We treat *Rhigiophyllum* and *Siphocodon* within the Campanulaceae: Wahlenbergioideae, as a separate tribe, the **Rhigiophylleae** *tribus nov.*, the species of which are distinguishable from other wahlenbergioids by unique angulaperturate pollen, epipetalous stamens, free carpel-like structures and seed pockets.

INTRODUCTION

During the course of a palynological re-investigation of the Campanulaceae[1] *s.str.*, a number of pollen samples were obtained from material in the herbarium of the Royal Botanic Garden Edinburgh and sent to the third author for scanning electron micrograph imaging (SEM). Subsequently, samples representing *Rhigiophyllum squarrosum* Hochst. and *Siphocodon spartioides* Turcz., were found to have flattened, angular (triangular) pollen grains with pores at the angles. This morphology is radically different from all known pollen of the Campanulaceae, although it was reported for both genera in the landmark paper (in Russian) by Avetisian in 1967, which we had inadvertently overlooked. Initially, we suspected that the samples were contaminated, possibly due to alien pollen on the stigmas of the herbarium material. However, an examination of material at the Compton Herbarium at Kirstenbosch by the second author using light microscopy, confirmed that both of these species indeed had radically different pollen morphology. A third species, *S. debilis* Schltr., was also examined by the second author and found to have pollen similar to its congener but was not included in the SEM analyses.

This report describes the pollen shape and surface features of the exine of the two principal species and genera involved. We also discuss other features of these two genera such as floral morphology and the unique seed pockets, particularly with respect to their possible ecological significance. Finally, we discuss the systematic usefulness of these findings for a revised classification of the wahlenbergioid genera and describe a new tribe, the Rhigiophylleae, to accommodate *Rhigiophyllum* and *Siphocodon*.

MATERIALS AND METHODS

Pollen (Table 1) was examined with a JEOL model 880 scanning electron microscope after cleaning with acetolysis (Erdtman 1960) and made electrically conductive with gold/palladium (Chissoe & Skvarla 1996). For the light microscope (LM) examination, pollen of the respective species was removed from alcohol-preserved flowers. The pollen was placed on a microscope slide in a drop of water and examined. The gynoecium of *Rhigiophyllum* was exposed by a longitudinal free-hand section through the hypanthium wall and the removal of tissue with forceps.

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[1] The Campanulaceae is treated here as a family separate from the Lobeliaceae, Cyphiaceae, Nemacladaceae, Pentaphragmataceae and Sphenocleaceae (Lammers 1992). As traditionally conceived, the Campanulaceae is very heterogeneous and, in many classifications, these families were treated as subfamilies of a much-enlarged Campanulaceae. The consistently different floral morphology, biochemistry and pollen structure of the Lobeliaceae favours the recognition of this predominantly tropical group as a separate family. Welman (2000) treats the Campanulaceae separately from Lobeliaceae, within which she included the genus *Cyphia* P.J.Bergius.

TABLE 1.—Species of Campanulaceae and Lobeliaceae for which pollen samples were examined in this study

Species	Collector/No.	Herbarium
Burmeistera vulgaris E.Wimm.	*R. Lent 526*	Bebb
Campanumoea javanica Blume	*A. Henry 9634*	RBGE
Codonopsis convolvulacea Kurz	*Chungtien-Liang-Dali Expedition 648*	RBGE
Craterocapsa montana (A.DC.) Hilliard & B.L.Burtt	*O.Hilliard & B.L. Burtt 13221*	RBGE
Cyclocodon lancifolius (Roxb.) Kurz	*Collector unknown 1563*	RBGE
Jasione montana L.	*F.J. Hermann 4405*	Bebb
Leptocodon gracilis (Hook.f.) Lem.	*Sinclair & Long 4980*	RBGE
Merciera brevifolia A.DC.	*Schlechter 7211*	RBGE
Microcodon hispidulus (L.f.) Sond.	*Collector unknown 1993*	RBGE
Prismatocarpus fruticosus (L.) L'Hér.	*C.M. van Wyk 3420*	RBGE
Rhigiophyllum squarrosum Hochst.	*Schlechter 9616*	RBGE
Roella prostrata E.Mey. ex A.DC.	*R. Dümmer 938*	RBGE
Siphocodon spartioides Turcz.	*E. Esterhuysen 35770*	RBGE
Wahlenbergia marginata (Thunb. ex Murray) A.DC.	*J. & C. Taylor 16613*	Bebb

RBGE, Royal Botanic Garden, Edinburgh.

Brief history of original description of Rhigiophyllum and Siphocodon

Hochstetter (1842) established the genus *Rhigiophyllum* for the sole species *R. squarrosum*, which was first collected near Elim, Bredasdorp. *Siphocodon* was established a decade later by Turczaninow (1852) for *S. spartioides*, based on collections from Klein Houwhoek, east of Grabouw, and from Swartberg, Caledon. Forty-five years later, Schlechter (1897) described a second species, *Siphocodon debilis* from Elim.

Ecology, distribution and morphology

Rhigiophyllum squarrosum and both species of *Siphocodon* occur on nutrient-poor soils associated with sandstone slopes of the southwestern Cape and are typical, but highly localized, fynbos plants. *Rhigiophyllum* occurs from Akkedisberg, northeast of Stanford to Napier and Bredasdorp, whereas *S. spartioides* occurs from Sir Lowry's Pass near Somerset West to the Langeberg in Riversdale and *S. debilis* occurs from the Hottentots Holland Mountains near Stellenbosch to Bredasdorp and inland to Riviersonderend (Figure 1).

Rhigiophyllum squarrosum is a rigid, sparsely branched subshrub, ± 0.30–0.45 m tall with the habit of species of *Roella* L. Its broadly ovate, coriaceous leaves are imbricate, squarrose, entire and in four ranks. Lanceolate bract-like leaves subtend the azure-violet flowers, which are aggregated in a terminal head. The corolla is elongated and consists of a long narrow tube terminated by five spreading obtuse lobes. The style is filiform, exserted, and terminates into three short stigmatic lobes (Figure 2A, B).

The two species of *Siphocodon* are radically different in appearance from *Rhigiophyllum*. They are glabrous, wiry subshrubs (*S. spartioides* is 0.3–0.6 m tall, *S. debilis* somewhat smaller) with sparse, minute, scale-like, appressed leaves. The flowers are solitary, terminal and axillary, mostly towards the apices of the stems in a loose, few-flowered inflorescence. The flowers of *Siphocodon spartioides* are bluish purple, whereas those of *S. debilis* are violet or whitish with pinkish brown honey-guides on the corolla tube. The corolla is narrowly tubular-campanulate with five spreading obtuse lobes incised to about one-third the length of the tube. The style is filiform, included and terminates into three short stigmatic lobes in *S. spartioides*, whereas in *S. debilis* the stigma is capitate (Figure 2C–E).

On closer inspection of the corolla and capsule of both genera, a number of common features are found. For example, both have rather long, tubular corollas with the stamens adnate via the filaments to the corolla tube, the latter feature being unique among the Campanulaceae. The stamens of *Rhigiophyllum squarrosum*, which are almost exserted, are attached below the apex of the corolla tube but the filaments are decurrent nearly to the base. In *Siphocodon debilis*, the stamens are included and are attached at the middle of the corolla tube, whereas in *S. spartioides*, they are attached in the upper part of the tube.

The capsule dehiscence is by means of a plug in *Rhigiophyllum* (Figure 3C) or circumscissile by means of an operculum in *Siphocodon* (Figure 3E). In both genera, these structures comprise the upper part of the ovary and the style, surrounded by the persistent corolla. In *Rhigiophyllum*, the line of dehiscence is above the calyx lobes and the seeds (within seed pockets) are dispersed through a narrow hole, whereas in *Siphocodon* it is below, so that, when the operculum detaches, the remaining lower
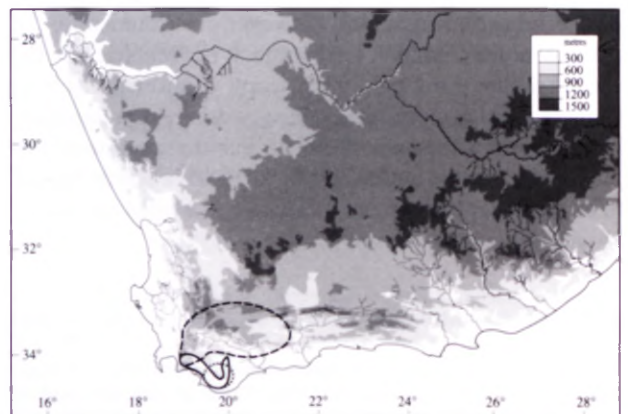

FIGURE 1.—Known distribution of *Rhigiophyllum squarrosum* (dotted line); *Siphocodon spartioides* (solid line) and *S. debilis* (dashed line).
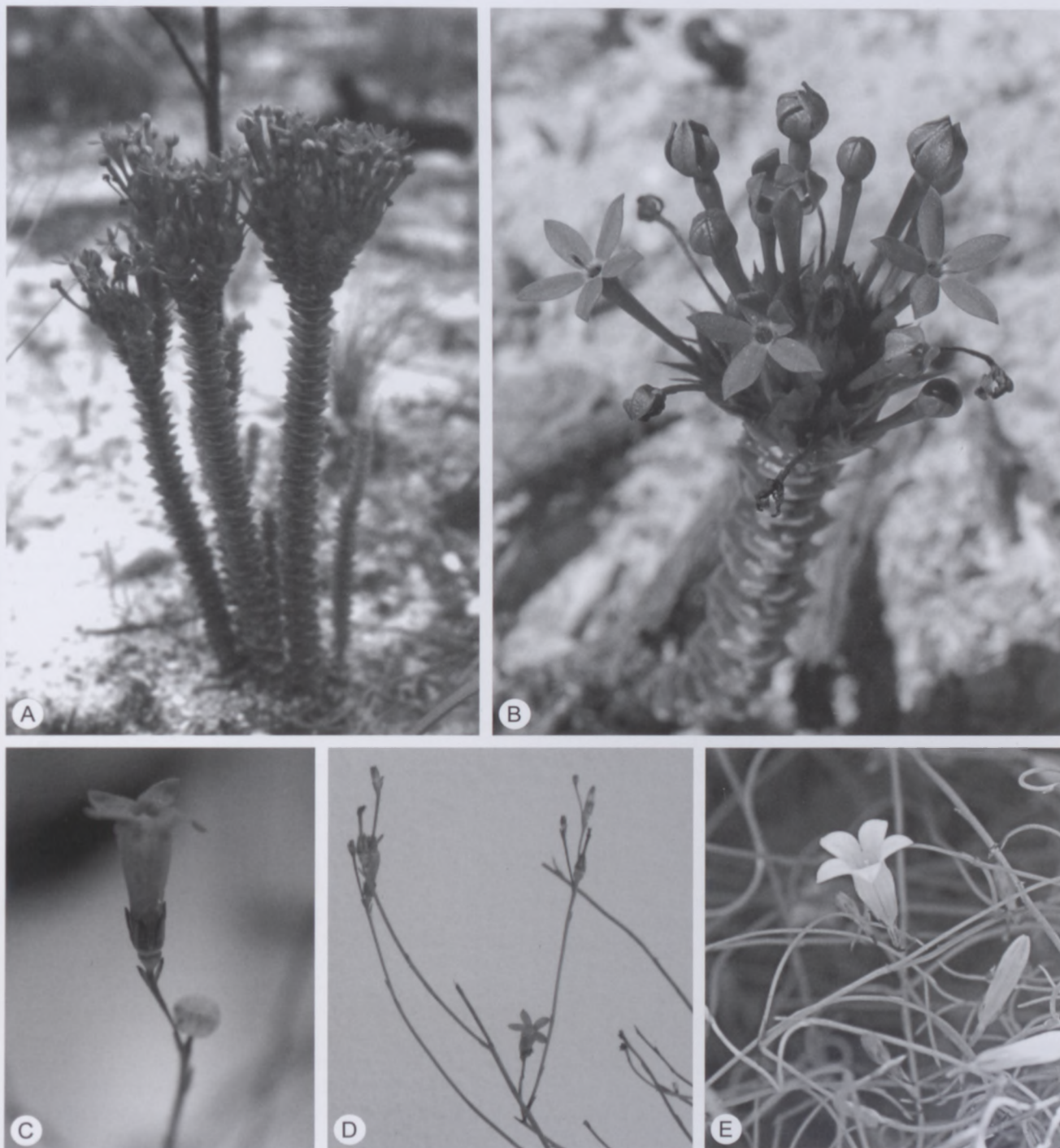
FIGURE 2.—A, B, *Rhigiophyllum squarrosum*: A, habit; B, details of inflorescence. C, D, *Siphocodon spartioides*: C, details of flower and remains of capsule; D, slender wiry stems. *S. debilis*: E, details of flower showing honey-guides and the twisted, entwined stems. Photographs: A, W.M.M. Eddie; B–E, C.N. Cupido.

part of the capsule is a neat, open, cup-like structure. In *Rhigiophyllum*, the remainder of the capsule easily detaches from the pedicel and disperses, probably with some seeds remaining inside. Since the line of dehiscence in the capsule of *Rhigiophyllum* is above the calyx lobes, it resembles that of *Roella* and therefore differs in positional homology from the mechanism in *Siphocodon*.

Unlike other wahlenbergioids, these two genera have (2)3 free carpel-like structures within the inferior ovary, each of which has two to several pendulous ovules attached near the top (Figure 4B7). It is difficult to decide if the seed pockets separate from the wall of the infe-

rior ovary of adult flowers or if they are formations *sui generis* (proliferations of the placentae) (Erbar & Leins pers. comm.)*. Some ovules appear to abort before maturity leaving just one or two seeds per structure (Figure

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* Profs Claudia Erbar and Peter Leins conducted a preliminary investigation of the ovary of *Rhigiophyllum* from material supplied by the second author. They report that the inferior ovary develops as in all other cases [of Campanulaceae] due to an intercalary growth in the floral axis and that the seed pocket is a special form of an endocarp. The epidermis (and eventually a few cells of deeper layers) of the ovary locules separates from the wall of the inferior ovary to form the seed pockets. A complete ontogenetical study (including histology and SEM-investigation) is planned and the results will be published in due course.
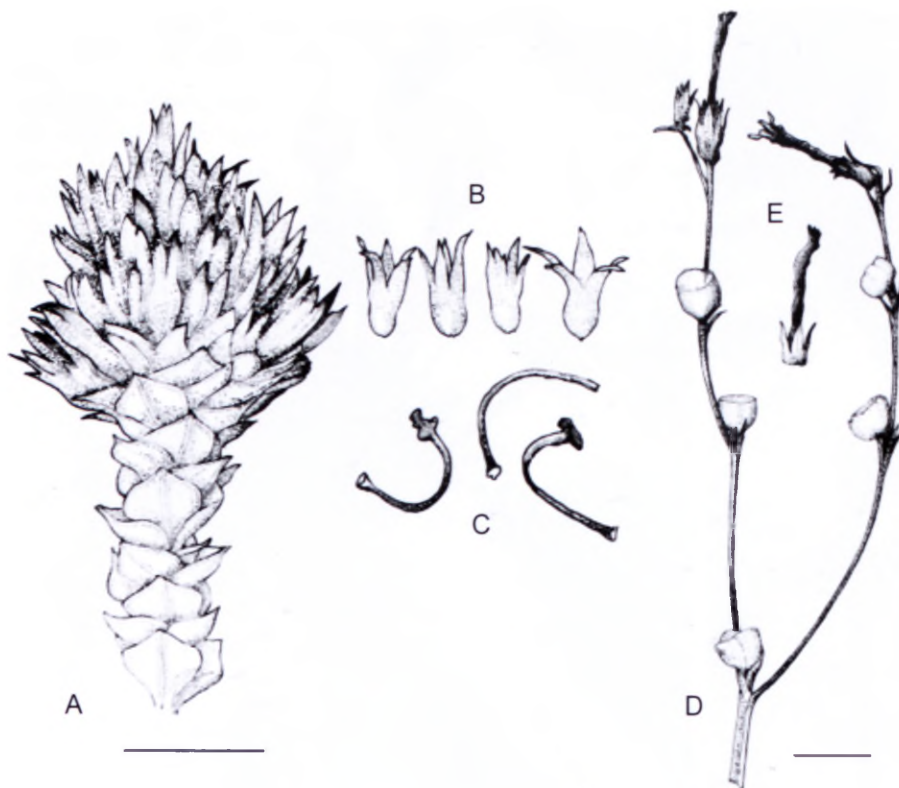
FIGURE 3.—A–C, *Rhigiophyllum squarrosum*, *Cupido s.n.*: A, fruiting head showing aggregation of mature capsules; B, individual mature capsules removed from head and showing spreading calyx lobes; C, withered corollas enclosing styles with attached plug (ovary top). D, E, *Siphocodon spartioides*, *Eddie 1017*: D, branched stem showing remains of dehisced capsules; E, corolla enclosing style and attached to upper calyx and calyx lobes (circumscissile lid or operculum). Scale bars: A–C, 10 mm; D, E, 10 mm. Artist: W.M.M. Eddie.

4E11). The walls of these carpel-like structures shrink to enclose the seed at maturity, forming a carunculated pocket (Figure 4D10), which is released entire from the mature capsule. This structure was apparently overlooked by Botting Hemsley in *Hooker's Icones plantarum* (1897) where he described the ovary simply as: '*Ovarium 3-loculare, loculis pluriovulatis, ovulis pendulis*'. In Sonder (1865: 596), this seed pocket is apparently misidentified as a 'very loose, rugose testa'. The protuberances on the surface of the seed pocket are similar in both genera although in *Siphocodon* they are more round and regular. There are also slight differences in seed shape. *Siphocodon* seeds are slightly diamond-shaped in comparison with the oval seeds of *Rhigiophyllum*. In both genera the seeds have a strong electrostatic charge and 'jump' to about 0.1 m when manually extracted from the pockets. The function of the seed pocket is unknown, but it may perform a role in dispersal, for example by ants. The seeds of these three taxa are large and few in number and this may be correlated with the establishment of the seedling in nutrient-poor environments (Eddie & Cupido 2001). The shiny testa of the seed would suggest that dormancy and nutrient release by fire may be important components in their ecology. Shiny testae are a feature of many annual species of the Campanulaceae where seed dormancy is the norm (Eddie 1997).

Description of pollen grains of Rhigiophyllum squarrosum *and* Siphocodon spartioides

Figures 5 and 6 show the radical differences in pollen morphology between *Rhigiophyllum squarrosum* and *Siphocodon spartioides* and other wahlenbergioid genera such as *Wahlenbergia* Schrad. ex Roth, *Craterocapsa* Hilliard & B.L.Burtt, *Prismatocarpus* L'Hér., *Roella*, *Merciera* A.DC. and *Microcodon* A.DC. and between platycodonoid genera such as *Leptocodon* (Hook.f.) Lem.,

Campanumoea Blume, *Cyclocodon* Griff. ex Hook.f. & Thomson and *Codonopsis* subgen. *Pseudocodonopsis* Kom.

Pollen grains disperse as monads and they are superficially like *Alnus* Miller/*Betula* L./*Corylus* L. (Betulaceae) or *Rhamnus* L. (Rhamnaceae), but very unlike the pollen of *Pentaphragma* Wall. ex G.Don (Pentaphragmataceae), which was formerly considered to be close to the Campanulaceae, and which has trilobate pollen with the pores between the lobes (Dunbar 1978, 1979, 1981). Their shape in polar view is reminiscent of species of *Acarpha* Grieb. (Calyceraceae) (De Vore *et al.* 2007) or species of *Lopezia* Cav. (Onagraceae) (third author). They are angular (triangular and obtuse or straight to slightly convex) in polar view; non-angular (elliptic and obtuse) in equatorial view; trizonoporate (rarely tetrazonoporate) (stephanoporate of Faegri & Iversen 1975) in equatorial zone; pori circular, situated at the angles (angulaperturate) and non-vestibulate; large, ± 50 µm diameter (*R. squarrosum*, Figure 5A) or ± 40 µm diameter (*Siphocodon spartioides*, Figure 5B); sculpturing is verrucate in *S. spartioides*, or psilate in *R. squarrosum*.

Palynological investigations of the Campanulaceae

Studies of the pollen of the Campanulaceae are extensive and the family is comparatively well known palynologically, but there are gaps in our knowledge of the wahlenbergioid taxa of the southern hemisphere, and of many endemic campanuloid taxa of central Asia. A brief, if diverse, survey of Campanulaceae pollen was provided by Erdtman (1952), followed by a similar survey of 21 genera by Chapman (1967). Avetisian (1967) provided a firm foundation for a systematic re-appraisal of the family using palynological characters, but the most thorough examination of the family using scanning electron microscopy was conducted by Dunbar (1973a–c,
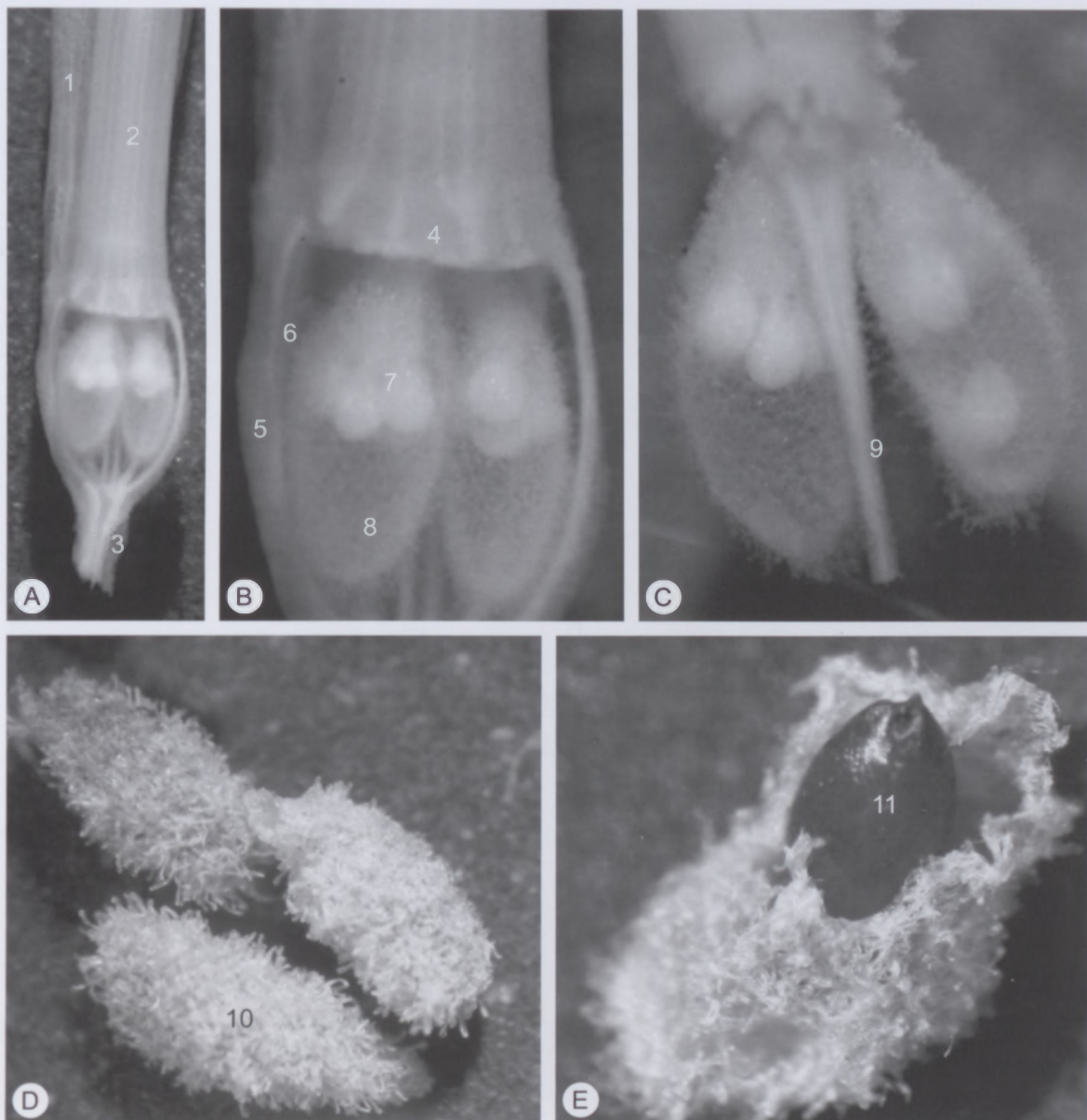
FIGURE 4.—LM photographs of *Rhigiophyllum squarrosum*. A, gynoecium and corolla showing: A1, calyx lobes; A2, corolla; A3, peduncle. B, detail of gynoecium showing: B4, corolla; B5, calyx lobe; B6, ovary wall; B8, separate carpel-like structures; enclosing B7, pendulous ovules. C9, central veins of ovary; D10, carunculated seed pockets formed by shrinking carpel-like structures; E11, seed pocket showing a mature seed. Photographer: C.N.Cupido.

1975a, b, 1978, 1979, 1981, 1984), who also studied ontogeny, and by Dunbar & Wallentinus (1976) using phenetic methods. The pollen of the Campanulaceae can be divided into two broad groups as follows:

1. The platycodonoid taxa of Asia and Africa (e.g. *Platycodon* A.DC., *Cyananthus* Wall. ex Benth., *Codonopsis* Wall., *Cyclocodon*, *Campanumoea*, and *Canarina* L.) have pollen that is either 6–10-colpate, 3-colporate, or 5- or 6-colporate (Figure 6). They have in common an oblate-spheroidal shape, a relatively high number of colpi and an exine sculpturing that consists of spinules, verruca-like spinules, or verrucae, between which are small pits of uniform diameter, or a reticulum in low relief with very small lumina. The ektexine structure consists of a tectum perforated by mostly narrow channels, medium to high bacula that are closely adpressed in some species, and a reduced or absent foot layer. The endexine is almost undivided.

2. The campanuloid and wahlenbergioid taxa have pollen that is 3- or 4-porate, 6-porate, or 12-porate (Figure 5). The porate taxa are mostly zonotreme or rarely pantoporate. The pantoporate condition is approached in those species that have an increased number of pores and where the position of the pores becomes irregular and not strictly zonotreme. The shape of the pollen is spheroidal or oblate-spheroidal, rarely suboblate or prolate-spheroidal. The exine sculpture consists of spinules of different number, shape and size. Between the spinules there are ridges, protrusions or a low-relief reticulum, finger-like structures, or ridges with the top end bent upwards (Dunbar 1975a). The ektexine structure (and sculpture) varies from simple to complex. Complex ektexine consists of a surface covered by spinules, distinctly divided basally, short ridges/protrusions between spinules, a sponge-like tectum, stubble-like bacula continuous with an undivided foot layer, and connections to the tectum may be thin. Less complex ektexine con-
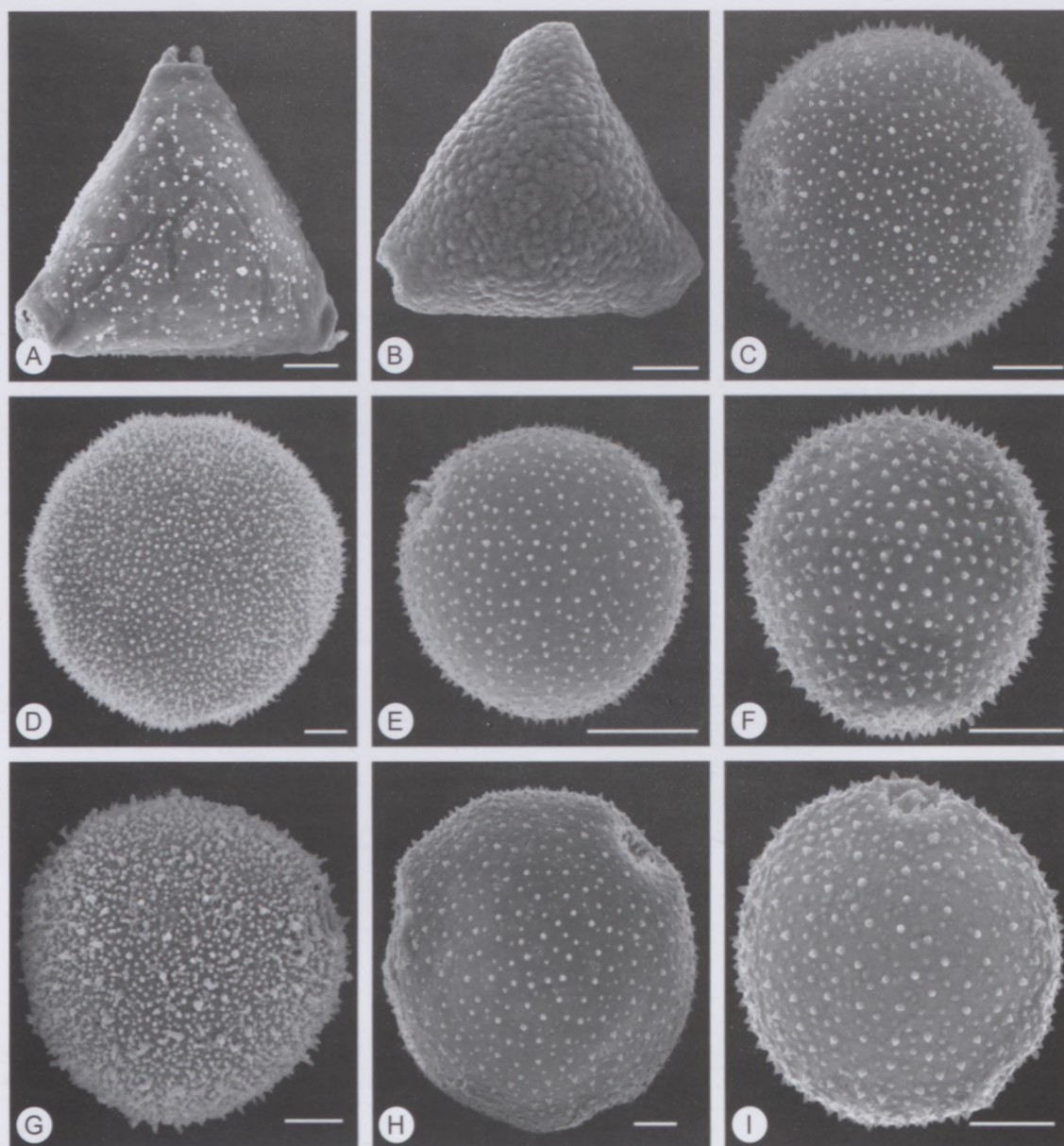
FIGURE 5.—SEM micrographs of pollen of wahlenbergioid genera of Campanulaceae plus *Jasione* (all polar view except C). A, *Rhigiophyllum squarrosum* Hochst.; B, *Siphocodon spartioides* Turcz.; C, *Prismatocarpus fruticosus* (L.) L'Hér. (equatorial view); D, *Wahlenbergia marginata* (Thunb. ex Murray) A.DC.; E, *Craterocapsa montana* (A.DC.) Hilliard & B.L.Burtt; F, *Microcodon hispidulus* (L.f.) Sond.; G. *Roella prostrata* E.Mey. ex A.DC.; H, *Merciera brevifolia* A.DC.; I, *Jasione montana* L. Scale bars: A–C, E–G, 10 µm; D, H, I, 5 µm. SEM micrographs by J.J. Skvarla.

sists of a surface covered by spinules, which, in some species, divide basally, together with protrusions, low-relief reticula, a thin, distinctly outlined tectum perforated by channels, high bacula that are continuous with the tectum and an undivided foot layer. Simple ektexine consists of a surface covered by discrete spinules, less distinctly divided than the complex type, and low protrusions. The uniformly outlined tectum is perforated by narrow channels and has the same thickness as the undivided foot layer. The bacula are medium/high, and are continuous with the tectum and foot layer. The endexine, which varies in thickness, is lamellated, except in the simple ektexine type.

Knowledge of pollen morphology in the wahlenbergioid genera is patchy and mostly concentrated on the genus *Wahlenbergia* (Thulin 1974; Dunbar 1975a, b), although a detailed study of the pollen of *Hetero-*

chaenia A.DC. was undertaken by Badré *et al.* (1972), and by Straka & Simon (1969). Wahlenbergioid genera such as *Prismatocarpus*, *Roella*, and *Wahlenbergia* are all in Dunbar's Group 1, i.e. pollen grains that are mostly radially symmetrical, isopolar, zonotreme, 3–5-porate, spheroidal and tectate. Spinules are evenly distributed over the non-apertural surface of the pollen grains. These three genera did not show any particular clustering with each other with respect to the other taxa (Dunbar 1975a, b). Apparently Von Brehmer (1915) considered the pollen morphology to be of no value as a taxonomic character in *Wahlenbergia*. However, Erdtman (1952) placed *Wahlenbergia*, *Roella* and *Prismatocarpus* in a group of genera with (2)3–(5)-porate, suboblate to oblate spheroidal pollen with spinuliferous sexine, which is thinner than the nexine. Avetisian (1967) studied five species of *Wahlenbergia* (including *W. hederacea* (L.) Rchb.), seven species of *Lightfoo-*
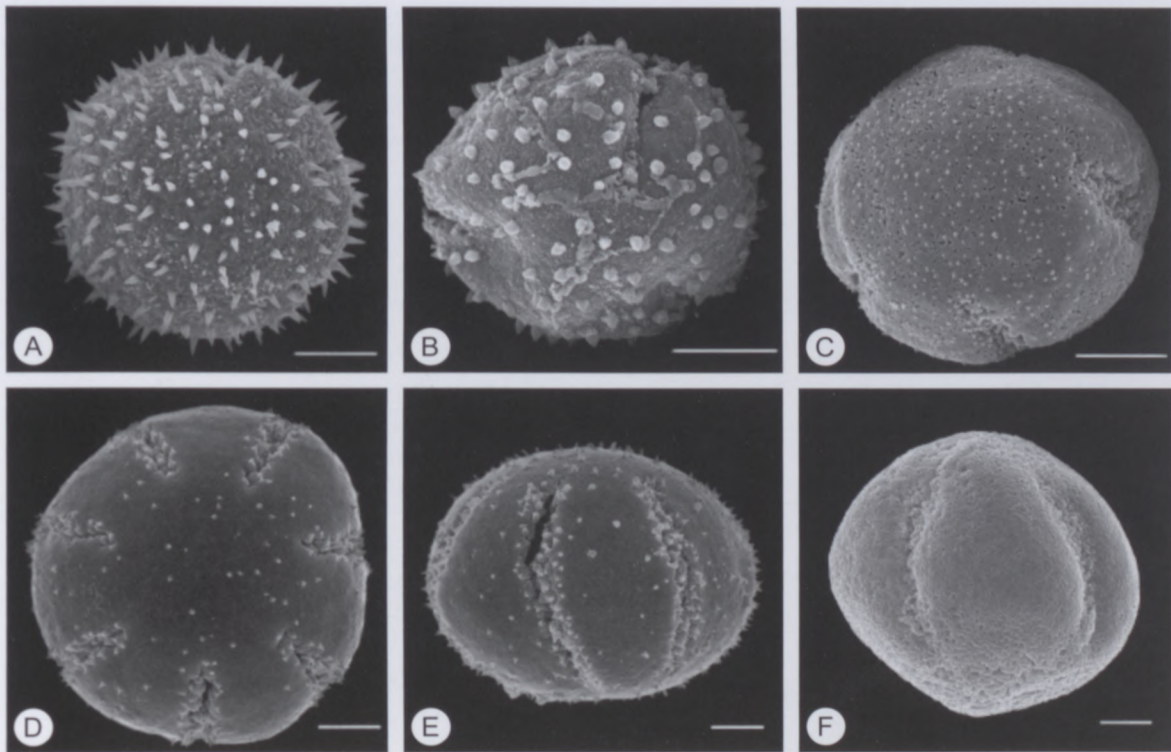
FIGURE 6.—A–F, SEM micrographs of pollen of platycodonoid genera of Campanulaceae and Lobeliaceae (all polar view except E and F): A, *Codonopsis* (subgen. *Pseudocodonopsis* Kom.) *convolvulacea* Kurz.; B, *Cyclocodon lancifolius* (Roxb.) Kurz; C, *Campanumoea javanica* Blume; D, E, *Leptocodon gracilis* (Hook.f.) Lem.; F, *Burmeistera vulgaris* E.Wimm. (Lobeliaceae). Scale bars: A–C, 10 μm; D–F, 5 μm. SEM micrographs by J.J. Skvarla.

tia L'Hér. *nom. illeg.* and *Cephalostigma* A.DC., and claimed to be able to differentiate between these three taxa. Straka & Simon (1969) distinguished two types of wahlenbergioid pollen in the Madagascan flora. The *Cephalostigma*-type is characteristic of *C. hirsutum* Edgew. and is 4–6-pantoporate, whereas the *Wahlenbergia*-type, which is 3-zonoporate is characteristic of *W. perrieri* Thulin and *W. madagascariensis* A.DC., in addition to the Mascarene endemic genera *Berenice* Tul. and *Heterochaenia* (Thulin 1975).

The species studied by Thulin (1975) and formerly placed in *Cephalostigma* included: *Wahlenbergia erecta* (Roth ex Schult.) Tuyn; *W. flexuosa* (Hook.f. & Thomson) Thulin; *W. hirsuta* (Edgew.) Tuyn; *W. hookeri* (C.B.Clarke) Tuyn; *W. ramosissima* (Hemsl.) Thulin; and *W. perrottettii* (A.DC.) Thulin. He concluded that *Wahlenbergia*, *Cephalostigma* and *Lightfootia* could not be distinguished on pollen characters, although *W. hirsuta* has an increased numbers of pores that could be of taxonomic value. According to Thulin, with increasing number of pores, the position of the pores becomes irregular and not strictly zonotreme. Several differences in spinule size and density exist between different groups of the genus *Wahlenbergia*. For example, the *W. undulata* (L.f.) A.DC. group has longer spinules than other groups, and the area of the exine between the spinules in the *W. undulata* and *W. madagascariensis* groups is distinctly granular or with short ridges. Thulin (1974) also reported that the pollen of *Namacodon* Thulin disperses in tetrads, unlike the pollen grains of all other taxa in the family, which disperse as monads—tetrads have been recorded in *Legousia falcata* (Ten.) Fritsch ex Janch. (first author, unpublished data).

Molecular studies

Recent molecular studies using *trn*L-F and ITS gene sequences (Cupido 2008) and combined chloroplast DNA datasets (*rbc*L, *atp*B and *mat*K) (Haberle *et al.* 2009) have shown quite conclusively that the strongest molecular affinities of *Rhigiophyllum* are with the two species of *Siphocodon* (Figures 7; 8). *Merciera*, *Roella* and *Prismatocarpus* form a well-supported clade, but the relationships within this clade are largely unresolved. *Merciera* however, forms a weakly supported subclade. *Roella*, *Prismatocarpus* and *Wahlenbergia* were also found to be paraphyletic, the latter massively so. *Theilera* E.Phillips was found to be closest to several species of *Wahlenbergia*, all of which were formerly treated as *Lightfootia*, and in a clade comprising *Craterocapsa* and *Wahlenbergia procumbens* (L.f.) A.DC., *W. huttonii* (Sond.) Thulin, and *W. stellarioides* Cham.

Another surprising result of the molecular studies has shown that *Rhigiophyllum* and *Siphocodon* form a sister group to all the other southern hemisphere wahlenbergioids, including taxa from the Mascarene Islands and St Helena (Haberle *et al.* 2009). This has profound implications, for it suggests that this split in lineages was a very ancient one. Previous molecular studies (Eddie *et al.* 2003) using ITS nrDNA found a clear dichotomy between the colpate/colporate platycodonoid taxa and the porate wahlenbergioid and campanuloid taxa. This major split in the Campanulaceae is hypothesized to be a consequence of the isolation engendered by tectonic activity in a fragmenting Early Tertiary Gondwana (Eddie *et al.* 2003). Subsequent evolution of these two lineages was independent, with the bulk of the platyco-

B2a

B2

B2b

B

B1a

B1

B1b

A

61
61
54
93 63
85
50
80
52
56 52
98
72
97
92
81
71
64 61
100
82
66
97
99

Wahlenbergia axillaris
Wahlenbergia cinerea
Wahlenbergia neorigida
Theilera guthriei
Theilera robusta
Wahlenbergia sp. 1 Genadendal
Wahlenbergia sp. Cup. 264
Craterocapsa montana
Craterocapsa congesta
Craterocapsa tarsodes
Wahlenbergia tenella
Wahlenbergia tenerrima
Wahlenbergia fruticosa
Wahlenbergia desmantha
Wahlenbergia parvifolia
Wahlenbergia thunbergii
Wahlenbergia procumbens
Wahlenbergia ecklonii
Wahlenbergia adpressa
Wahlenbergia exilis
Wahlenbergia oxyphylla
Wahlenbergia sp. Cup. 261
Wahlenbergia pilosa
Wahlenbergia acaulis
Wahlenbergia sp. Cup. 253
Wahlenbergia subulata
Wahlenbergia longifolia
Wahlenbergia sp. Chatsworth
Wahlenbergia polyantha
Wahlenbergia thunbergiana
Microcodon glomeratus
Microcodon sparsiflorus
Malmesbury plant
Treichelia longibracteata
Wahlenbergia psammophila
Wahlenbergia sp. BK
Wahlenbergia depressa
Wahlenbergia capillacea
Wahlenbergia undulata
Wahlenbergia cuspidata
Wahlenbergia virgata
Prismatocarpus crispus
Wahlenbergia capensis
Wahlenbergia cernua
Wahlenbergia krebsii
Prismatocarpus sessilis
Roella prostrata
Prismatocarpus fruticosus
Prismatocarpus diffusus
Prismatocarpus campanuloides
Prismatocarpus nitidus
Roella muscosa
Roella squarrosa
Roella amplexicaulis
Prismatocarpus schlechteri
Prismatocarpus pedunculatus
Prismatocarpus brevilobus
Merciera azurea
Merciera leptoloba
Merciera eckloniana
Merciera brevifolia
Roella psammophila
Roella cuspidata
Roella arenaria
Roella secunda
Roella sp. Genadendal
Roella incurva
Roella ciliata
Wahlenbergia androsacea
Wahlenbergia paniculata
Wahlenbergia annularis
Wahlenbergia huttonii
Rhigiophyllum squarrosum
Siphocodon spartioides
Siphocodon debilis
Lobelia jasionoides
Lobelia comosa
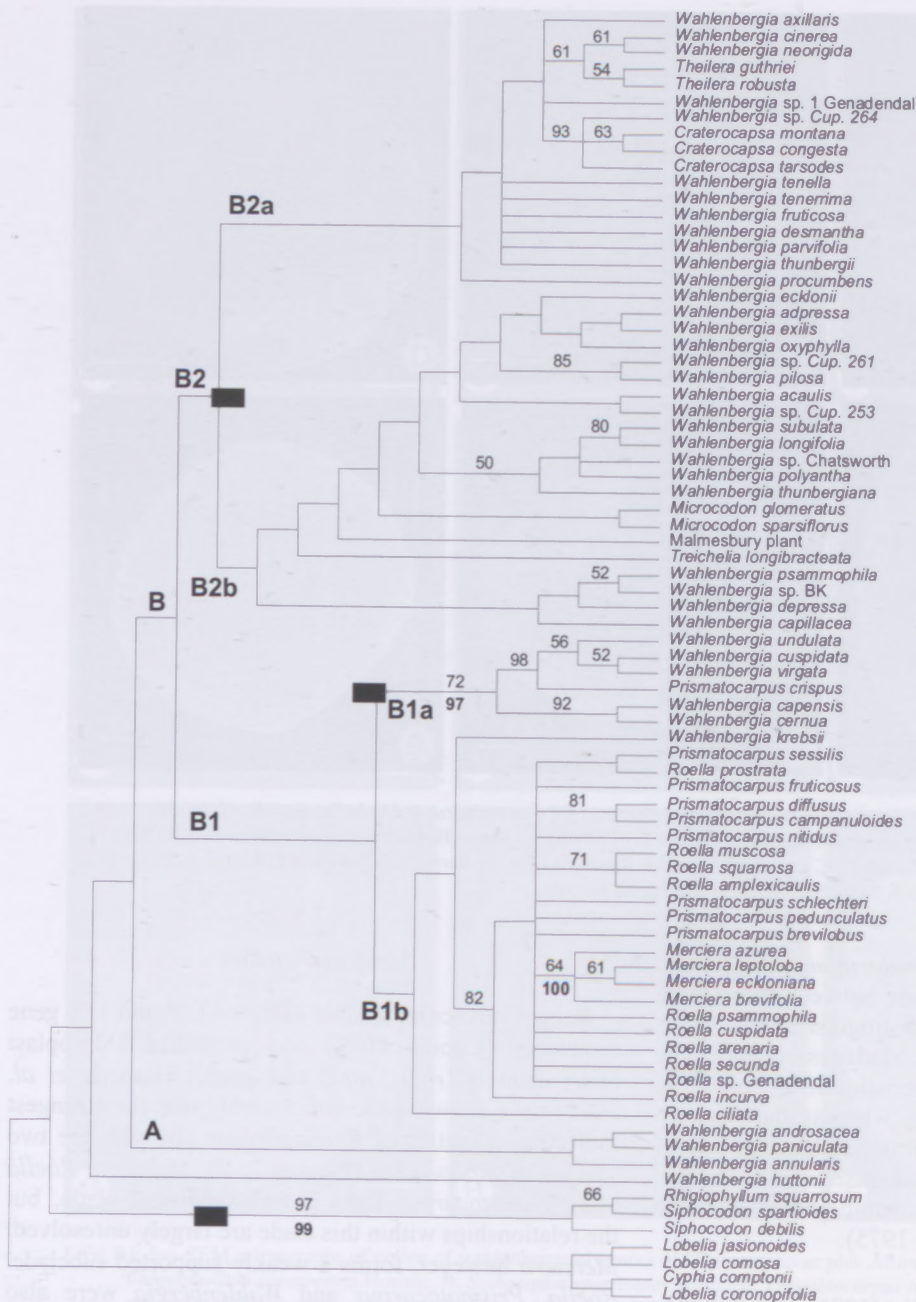Cyphia comptonii
Lobelia coronopifolia

FIGURE 7.—Strict consensus of 165 equally parsimonious trees (length = 859, CI = 0.511, RI = 0.739) found after heuristic search of the ITS data set for 75 taxa of the South African Campanulaceae and four Lobeliaceae/Cyphiaceae (outgroup). Bootstrap values ≥ 50 % indicated above branches. Numbers below branches indicate posterior probability values expressed as percentages (from Cupido 2008). ■, clades common to all analyses.

donoids in eastern Asia, the wahlenbergioids in Africa, and the campanuloids differentiating primarily in northern Africa and the evolving Mediterranean region.

DISCUSSION AND CONCLUSIONS

Pollen morphology of Rhigiophyllum and Siphocodon

The triangular pollen of *Rhigiophyllum* and *Siphocodon* is so unlike the known pollen of the Campanulaceae that it throws their relationship with that family into question. Kolakovsky (1987: 1573) excluded both genera from the Campanulaceae, yet, from molecular data (Eddie *et al.* 2002; Haberle *et al.* 2009) and their possession of porate pollen, it would appear that these genera are correctly placed close to typical wahlenbergioid, porate taxa. From a biogeographical viewpoint, one would favour a relationship with the wahlenbergioid taxa so characteristic of southern Africa, and with which they have traditionally been associated. The surface sculpturing of the

pollen is more simplified, lacks the dense spinuliferous condition, and recalls the surface features of the pollen found in the platycodonoid genera. This suggests that these two genera may represent an older lineage of the Campanulaceae in southern Africa that is somewhat intermediate between platycodonoids and wahlenbergioids, or it may be that the pollen morphology is convergent with that of the platycodonoids (perhaps the result of paedomorphosis and/or neoteny). However, some porate pollen in the Campanulaceae is simpler in structure than the dense spinuliferous type. Avetisian (1967) suggested that tropical colpate/colporate pollen is the most primitive type within the Campanulaceae, whereas porate pollen from temperate zones, including pantoporate pollen, is considered an advanced type (Van Campo 1966; Muller 1970; Punt 1976). Dunbar's (1984) results agree partially with this view with respect to complex exine. Perhaps the unique triangular pollen represents a highly specialized adaptation either to conditions pertaining to their pollinators or to some, yet unknown, biological component
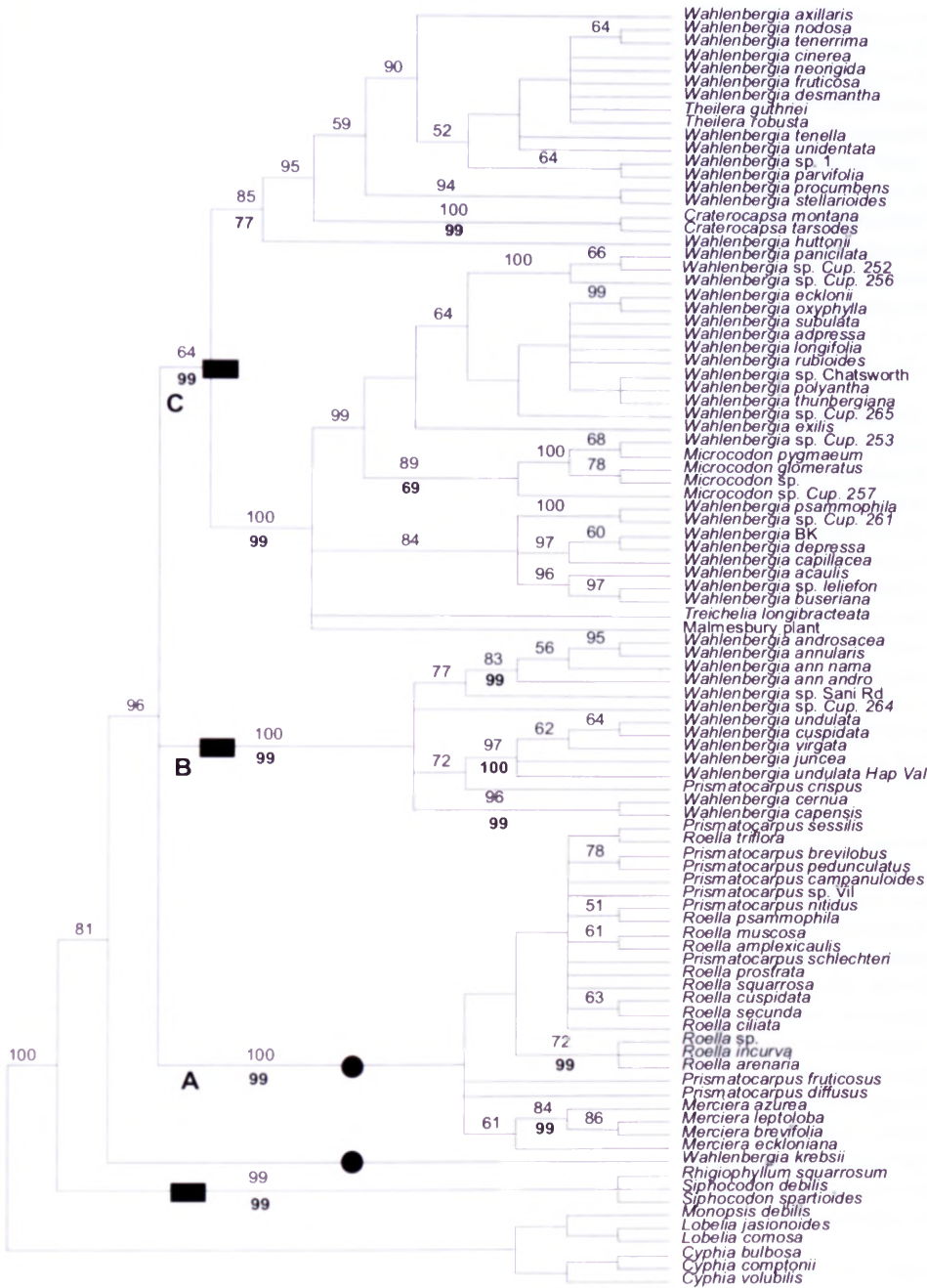
FIGURE 8.—Strict consensus of 415 equally parsimonious trees (length = 945, CI = 0.684, RI = 0.872) found after heuristic search of the *trn*L-F data set for 90 taxa of the South African Campanulaceae and six Lobeliaceae/Cyphiaceae (outgroup). Bootstrap values ≥ 50 % indicated above branches. Numbers below branches indicate posterior probability values expressed as percentages (from Cupido 2008). ■, clades common to all analyses; ●, clades common between *trn*L-F and the combined analysis.

of the fynbos vegetation. This explanation seems highly plausible, but no other members of the Campanulaceae have this type of pollen, so the functional significance of the triangular pollen remains unresolved.

General morphology and ecology of the fynbos wahlenbergioids

Rhigiophyllum and *Siphocodon* share a number of morphological features with other fynbos taxa such as *Merciera, Theilera, Roella, Prismatocarpus* and many fynbos species of the group formerly included in the illegitimate genus *Lightfootia*. They all show radical departures in a whole suite of morphological characters from the temperate Campanulaceae *bauplan*, although most can loosely be described as ericoid. All are dwarf undershrubs or shrublets, somewhat rigid or wiry, and frequently with ericoid leaves in fascicles (e.g. *Merciera* and *Theilera*), or imbricate, as in *Rhigiophyllum*.

Many of them have long tubular flowers (*Merciera, Theilera, Rhigiophyllum,* and *Siphocodon*) and indehiscent capsules (*Merciera*) or at least an unusual capsule dehiscence mechanism (*Prismatocarpus, Roella, Rhigiophyllum,* and *Siphocodon*). Several of these genera (e.g. *Merciera, Theilera,* and *Prismatocarpus,* subgen. *Afrotrachelium* Adamson) even show a remarkable, if superficial, resemblance to the Lobeliaceae and Stylidiaceae, and the flowers of *Rhigiophyllum* look similar to those of *Calycera* Cav. (Calyceraceae). The flowers are either solitary and more or less sessile (*Roella, Prismatocarpus, Theilera* and *Merciera*), in loose terminal inflorescences (*Prismatocarpus, Siphocodon*), or rarely in dense heads (*Rhigiophyllum*). These features suggest a general convergence in morphologies that may correlate with similar ecologies. However, as shown by the molecular studies, these subgroups are not part of the same phylogenetic sublineages and their similarities are probably superficial. They may be best considered as parallel ecotypes.

Rhigiophyllum is so dissimilar morphologically from both species of *Siphocodon* that, on first inspection, a close relationship between these two genera is not obvious. Furthermore, *Siphocodon spartioides* is very unlike *S. debilis*, yet, the infrageneric disparity in morphology between *Siphocodon spartioides* and *S. debilis* offers a possible clue to the evolutionary history of all three taxa, in addition to that of the fynbos wahlenbergioids in general. This disparity suggests that divergent selection pressure has been intense, driving three closely related species towards radically different morphologies. A similar situation is seen in the two species of *Musschia* Dumort. (Campanulaceae) on Madeira (Eddie *et al.* 2003).

The evolutionary divergence of *Rhigiophyllum* and *Siphocodon* probably occurred early, in concert with the progressive aridity of the Cape Region (Cupido 2008). From the similarity of their floral morphology with other fynbos plants, we can infer that these taxa have highly specialized pollination syndromes, probably with long-proboscid flies (including horse flies, tangle-wing flies and bee flies) as the principal pollen vectors (Goldblatt *et al.* 1995). However, until further studies are completed, we simply do not know what adaptive advantages, if any, are conferred by the unique pollen morphology, and ontogenetic studies are required to determine the significance of the triangular shape before and after tetrad formation.

It is clear that these three species display a highly integrated complex of adaptations to the fynbos vegetation and that nuances in ecological requirements probably account for the differences between them, but the functional aspects of these adaptations remain unclear. This argument applies also to all the other wahlenbergioid genera in the fynbos, and therefore the merging of genera such as *Theilera* and the illegitimate *Lightfootia* in *Wahlenbergia* is surely premature (Lammers 1995; Goldblatt & Manning 2000), although Lammers (2007: 382) acknowledged that some species, currently included in *Wahlenbergia*, could be given separate generic recognition. From this perspective, the recognition of *Rhigiophyllum* and *Siphocodon* should be upheld.

From the pollen studies, and the work of Dunbar, it would appear that there are more similarities between the pollen of the Campanulaceae and the Cyphiaceae *s.lat.* than the Lobeliaceae. The unique stylar morphology of the Cyphiaceae suggests that this family may be the most ancient lineage of Campanulales in Africa and possibly derived from ancestors, which, themselves, eventually diversified in Australia as the Goodeniaceae and Stylidiaceae. This hypothesis requires further investigation. The Cyphiaceae have unicellular stylar hairs, which resemble those of the Campanulaceae more than those of Lobeliaceae (Leins & Erbar 2005), and it would be interesting to survey this character as well as secondary pollen presentation mechanisms in all South African genera of the Campanulales.

The major dichotomy between the pollen of the platycodonoids (represented in Africa and the Canary Islands by the relict *Canarina*) and the wahlenbergioids/campanuloids, suggests that this split is an ancient one (Eddie *et al.* 2003) dating from the early Tertiary. Yet, we do not know what the ancestral morphology of these ancient African progenitors was like, but from them the wahlenbergioids diversified into several morphological types such as herbs or shrubs. Perhaps the Mascarene genera such as *Nesocodon* Thulin and *Heterochaenia*, both of which recall the platycodonoids in their floral morphology, most resemble the ancient forms. In southern Africa, the onset of aridity, beginning in the Oligocene, probably is the ultimate cause of evolutionary diversification within the wahlenbergioids, with additional factors such as geographic and ecological isolation (especially soil types and pollinators). Shrubby types such as *Roella* are particularly associated with the Mediterranean climate of the Cape region, whereas herbaceous, rosette types such as *Craterocapsa* would appear to be restricted to areas with a greater moisture regime. The relictual disjunct distribution of *Craterocapsa* from eastern South Africa to the Chimanimani Mountains of Zimbabwe may be highly significant.

Taxonomic implications

One can of course attempt to analyse it, to fit it into this system of thought or that, but by its very nature it is bound to cause a diversion in the neatly-fitted jigsaw. In the end the diversion becomes the deviation that wrecks the system. No wonder those who create systems fear it like the devil.

Neil Gunn 1956 (*The Atom of Delight*)

Since their original discovery and description, *Rhigiophyllum* and *Siphocodon* were classified by all southern African workers as being close to other wahlenbergioid genera. We now know that the two genera are more divergent from all other wahlenbergioid taxa than was previously thought, yet, from molecular analyses, they are obviously still part of that nexus of southern African Campanulaceae. However, they represent a sister lineage separate from other South African taxa, which suggests that they are an old, albeit highly adapted group ($\geq$ 28 million years, Cupido 2008). The current classification of South African wahlenbergioids is not adequate for the recognition of these taxa and should therefore be modified accordingly.

Kolakovsky (1987, 1994) recognized four subfamilies within the Campanulaceae based largely on the nature of carpel dehiscence and the presence or absence of an axicorn: Prismatocarpoideae Kolak.; Canarinoideae Kolak.; Wahlenbergioideae (Endl.) Kolak.; and Campanuloideae. In this treatment, the South African genera were divided between his Prismatocarpoideae (*Craterocapsa, Namacodon, Prismatocarpus, Roella* and *Treichelia* Vatke) and his Wahlenbergioideae (*Heterochaenia, Microcodon, Theilera* and *Wahlenbergia*, plus a number of typically platycodonoid and campanuloid genera).

Takhtajan (1997) also divided the Campanulaceae into four subfamilies: (Cyananthoideae *nom. inval.?* ; Ostrowskioideae (Fed.) Takht.; Canarinoideae Kolak.; and Campanuloideae, giving great weight to the type of pollen grains. He subdivided the Campanuloideae into about thirteen tribes, including four South African tribes: the Wahlenbergieae (*Wahlenbergia, Berenice, Theilera, Gunillaea* Thulin, *Nesocodon, Heterochaenia,* and *Microcodon*); Prismatocarpeae (*Prismatocarpus, Namacodon, Roella, Craterocapsa,* and *Treichelia*); Siphocodoneae (*Siphocodon* and *Rhigiophyllum*); and Merciereae (*Merciera*). The

problem with both of these systems is that there are too many tribes, that each tribe is almost the equivalent of a genus, and that it is difficult to get a perspective of the major lineages within the subfamilies. Kolakovsky's system places far too much emphasis on the axicorn, which is probably more useful in delimiting campanuloid taxa. Takhtajan's treatment of the South African genera comes closest to our thinking but the number and boundaries of his tribes may have to be revised.

Sonder (1865) included the four tribes Lobelieae, Campanuleae, Cyphieae and Goodenovieae in the Campanulaceae. He subsequently divided the Campanuleae into three subtribes: Wahlenbergieae (capsule opening at the apex; ovules many); Merciereae (stamens free; ovary one-celled, with an incomplete septum; 4 basal ovules); and Siphocodeae (stamens epipetalous; ovary 3-celled, each cell with 2 ovules). Note that Sonder used the same suffix '-eae' for his subtribal names instead of '-inae'. He considered *Rhigiophyllum* to be a 'doubtful genus' and we think he simply tagged it on at the end of his account of the Campanuleae immediately after *Siphocodon*. He probably never intended to include it in his 'Siphocodeae' but there is some ambiguity to his account (p. 597) and it would have been clearer if he had placed it sequentially after *Roella*. *Rhigiophyllum* is certainly very distinct from *Siphocodon* and, if he had meant to include it in his Siphocodeae, he would surely not have considered it to be of doubtful status. Takhtajan (1997) placed these two genera in his tribe Siphocodoneae Takht., which he recognized along with 12 other tribes in his subfamily Campanuloideae. As far as we can determine, Takhtajan's Siphocodoneae was not formally validated. Was Takhtajan swayed by Sonder's rather ambiguous account? Lammers (2007: 671) lists the Siphocodoninae Sond. as a subtribe of the Wahlenbergieae Endl.

It would be tempting, given the highly divergent pollen morphology, to give subfamily status to *Rhigiophyllum* and *Siphocodon*. However, there are a number of other taxa that are also somewhat anomalous and do not fit comfortably into either the Wahlenbergioideae or the Campanuloideae, e.g. *Wahlenbergia hederacea*, *Feeria* Buser, *Jasione* L., *Musschia* and *Campanula* L. sect. *Pterophyllum* Damboldt. *Wahlenbergia hederacea*, which is a unique component of western European Atlantic regions, is remote from all other wahlenbergioids. *Feeria* is closer in its morphology to the wahlenbergioids, whereas *Jasione* is closer to the campanuloids (Eddie *et al.* 2003; Eddie unpubl.). Molecular studies also support the closer association between *Jasione* and the campanuloids (Cosner *et al.* 2004). These taxa probably stem from ancestral taxa common to both groups, what Eddie *et al.* (2003) referred to as 'transitional groups'. In the world of classification, there are always taxa that do not fit neatly into man-made schemes. Given the uniqueness of *Rhigiophyllum* and *Siphocodon*, we hereby include them in a new tribe of the Campanulaceae as follows:

Rhigiophylleae *Eddie & Cupido*, tribus nov. Type: *Rhigiophyllum* Hochst.

Siphocodoninae Sond. in Harv. & Sond., Flora capensis 3: 531 (1865) (as '*Siphocodeae*'). *Siphocodoneae* Takht.: 409 (1997).

Fruticuli habitu et affinitate *Roellae* vel *Prismatocarpi*, a quibus praecipue pollinis granis applanatis et triangularibus, uno poro in quoque angulo praeditis, differunt; corolla longe tubulosa, staminibus inclusis, ad tubi medium vel infra corollae orem insertis; structuris membranaceis liberis intra ovarium carpella simulantibus, in tempore maturitatis se contrahentibus, seminum marsupia rugosa vel carunculata formantibus et semina continentibus dispersis; capsula dehiscente aut obturamento supra calycis lobos amoto (*Rhigiophyllum*) aut operculo infra calycis lobos circumscissili (*Siphocodon*).

Shrublets with the appearance of, and affinity with, *Roella* or *Prismatocarpus*, principally differing from them by pollen grains that are flattened horizontally and triangular, with one pore at each angle; with corolla long-tubular, with stamens included and inserted at the middle of the tube or below the mouth of the corolla; with free membranous structures within the ovary resembling carpels, shrinking at maturity, forming rugose or carunculated seed pockets and dispersed containing the seeds; with the capsule dehiscing either by removal of a plug above the calyx lobes (*Rhigiophyllum*) or by a circumscissile operculum below the calyx lobes (*Siphocodon*).

This also necessitates that we clarify the placement of this new tribe within a suggested overall classification system of the Campanulaceae. To date, the reclassification of the Campanulaceae is still fluid and a presentation of a new system is inappropriate in this paper. However, we recommend the recognition of three subfamilies within the Campanulaceae to embrace the platycodonoids, wahlenbergioids and campanuloids, based principally on pollen morphology, but also supported by biogeography. Thus, the tribe Rhigiophylleae would be included in subfamily Wahlenbergioideae Kolak. (1987)—including Prismatocarpoideae Kolak. (1987), comprising *Wahlenbergia*, *Prismatocarpus* and allied genera possessing spherical or triangular, porate pollen and capsule dehiscence that is predominantly apical by valves. Their distribution primarily in the southern hemisphere, extending marginally into the northern hemisphere in Eurasia but poorly represented in South America.

This study has shown that what at first sight appears as novel, morphological divergences are integrated with many other features of a plant's morphology, ecology and evolution, and that no single aspect can ultimately be divorced from the plant as a whole. Because these unique plants are so finely tuned to their unique environment, they are highly vulnerable to disturbance, habitat degradation and climate change. We still know very little about them but we hope that their protection is assured and that further studies of such intriguing plants will be forthcoming.

REFERENCES

AVETISIAN, E.M. 1967. Morfologiya pyl'cy sem. Campanulaceae I blizkikh k nemu semeystv (Sphenocleaceae, Lobeliaceae, Cyphiaceae) v filogenii. *Flora I rastitel 'nost' armyanskoy SSR.* Trudy botaniczeskogo institute 16. – Erevan.

BADRÉ, F., CADET, T. & MALPLANCHE, M. 1972. Étude systématique et palynologique de genre *Heterochaenia* (Campanulaceae) endémique des Mascareignes. *Adansonia* 12: 267–278.

BOSTOCK, P.D. 2009. "TRANSLAT"—*Botanical Latin translation software.* http://www.ozemail. com.au (accessed October 2009).

BOTTING HEMSLEY, W. 1897. *Rhigiophyllum squarrosum* Hochst. In W.T. Thiselton-Dyer, *Hooker's Icones plantarum* XXVI: t. 2555.

CHAPMAN, J.L. 1967 [1966]. Comparative palynology in Campanulaceae. *Transactions of the Kansas Academy of Science* 69, 3–4: 197–200.

CHISSOE, W.F. & SKVARLA, J.J. 1996. Combining sputter coating with OTOTO treatment to eliminate charging artifacts in pollen preparations. *Proceedings of the Oklahoma Academy of Science* 76: 83–85.

COSNER, M.E., RAUBESON, L.A. & JANSEN, R.K. 2004. Chloroplast DNA rearrangement in Campanulaceae: phylogenetic utility of highly rearranged genomes. *BMC Evolutionary Biology* 4: 27 (http:\www.biomedcentral.com/1471–2148/4/27).

CUPIDO, C.N. 2008. *Systematic studies of the South African Campanulaceae (Campanuloideae) with an emphasis on generic delimitations.* Ph.D. thesis, University of Cape Town.

DE VORE, M.L., ZHAO, Z., JANSEN R.K. & SKVARLA, J.J. 2007. Pollen morphology and ultrastructure of Calyceraceae. *Lundellia* 10: 32–48.

DUNBAR, A. 1973a. Pollen ontogeny in some species of Campanulaceae. A study by electron microscopy. *Botaniska Notiser* 126: 277–315.

DUNBAR, A. 1973b. A short report on the fine structure of some Campanulaceae pollen. *Grana* 13: 25–28.

DUNBAR, A. 1973c. A review of the ultrastructure and ontogeny of some angiosperm pollen. *Grana* 13: 85–92.

DUNBAR, A. 1975a. On pollen of Campanulaceae and related families with special reference to the surface ultrastructure. I. Campanulaceae Subfam. Campanuloideae. *Botaniska Notiser* 128: 73–101.

DUNBAR, A. 1975b. On pollen of Campanulaceae and related families with special reference to the surface ultrastructure. II. Campanulaceae Subfam. Cyphioideae and Subfam. Lobelioideae; Goodeniaceae; Sphenocleaceae. *Botaniska Notiser* 128: 102–118.

DUNBAR, A. 1978. Pollen morphology and taxonomic position of the genus *Pentaphragma* Wall. (Pentaphragmataceae). The use of compound fixatives. *Grana* 17: 141–147.

DUNBAR, A. 1979. On pollen of Campanulaceae and *Pentaphragma*. The use of compound fixatives. *IV International Palynolological Conference, Lucknow 1976–1977*, 1: 445–448.

DUNBAR, A. 1981. The preservation of soluble material on the surface and in cavities of the pollen wall of Campanulaceae and Pentaphragmataceae. *Micron* 12: 47–64.

DUNBAR, A. 1984. Pollen morphology in Campanulaceae IV. *Nordic Journal of Botany* 4: 1–19.

DUNBAR, A. & WALLENTINUS, H-G. 1976. On pollen of Campanulaceae. III. A numerical taxonomic investigation. *Botaniska Notiser* 129: 69–72.

EDDIE, W.M.M. 1997. *A global reassessment of the generic relationships in the bellflower family (Campanulaceae).* Ph.D. thesis, University of Edinburgh.

EDDIE, W.M.M. & CUPIDO, C.N. 2001. Abstract: Some observations on the reproductive morphology of the wahlenbergioid genera of the family Campanulaceae *s. str.* from the fynbos vegetation of South Africa. *Botany 2001, Annual Conference of the Botanical Society of America, held in Albuquerque, New Mexico on 12–16 August, 2001*: 444.

EDDIE, W.M.M., HABERLE, R.C. & JANSEN, R.K. 2002. Abstract: The phylogeny of the Campanulaceae inferred from DNA sequences of the chloroplast gene *matK*. *Botany 2002, Annual Conference of the Botanical Society of America, held in Madison, Wisconsin on 2–7 August, 2002*: 144.

EDDIE, W.M.M., SHULKINA, T., GASKIN, J., HABERLE, R.C. & JANSEN, R.K. 2003. Phylogeny of Campanulaceae *s.str.* inferred from ITS sequences of nuclear ribosomal DNA. *Annals of the Missouri Botanical Garden* 90: 554–575.

ERDTMAN, G. 1952. *Pollen morphology and plant taxonomy.* Almquist & Wiksell, Sweden.

ERDTMAN, G. 1960. The acetolysis method. A revised description. *Svensk Botanisk Tidskrift* 54: 561–564.

FAEGRI, K. & IVERSEN, J. 1975. *Textbook of pollen analysis*, edn 3. Blackwell, Oxford.

GOLDBLATT, P. & MANNING, J. 2000. Cape plants. A conspectus of the Cape flora of South Africa. *Strelitzia* 9. National Botanical Institute, Cape Town and Missouri Botanical Garden, St. Louis.

GOLDBLATT, P., MANNING J.C. & BERNHARDT, P. 1995. Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa; floral divergence and adaptation for long-tongued fly pollination. *Annals of the Missouri Botanical Garden* 82: 517–534.

HABERLE, R.C., DANG, A., LEE, T., PEÑAFLOR, C., CORTES-BURNS, H., OESTREICH, A., RAUBESON, L., CELLINESE, N., EDWARDS, E.J., KIM, S-T., EDDIE, W.M.M. & JANSEN, R.K. 2009. Taxonomic and biogeographic implications of a phylogenetic analysis of the Campanulaceae based on three chloroplast genes. *Taxon* 58: 715–734.

HOCHSTETTER, C.F.F. 1842. Nova genera plantarum Africae. *Flora* 25: 225–240.

KOLAKOVSKY, A.A. 1987. System of the Campanulaceae family from the Old World (in Russian). *Botanicheskii zhurnal* 72: 1572–1579. Moscow, Leningrad.

KOLAKOVSKY, A.A. 1994. The conspectus of the system of the Old World Campanulaceae (in Russian). *Botanicheskii zhurnal* 79: 109–124. Moscow, Leningrad.

LAMMERS, T.G. 1992. Circumscription and phylogeny of the Campanulales. *Annals of the Missouri Botanical Garden* 79: 388–413.

LAMMERS, T.G. 1995. Transfer of the southern African species of *Lightfootia*, nom. illeg., to *Wahlenbergia* (Campanulaceae: Campanuloideae). *Taxon* 44: 333–339.

LAMMERS, T.G. 2007. *World checklist and bibliography of Campanulaceae.* Royal Botanic Gardens, Kew.

LEINS, P. & ERBAR, C. 2005. Floral morphological studies in the South African *Cyphia stenopetala* Diels (Cyphiaceae). *International Journal of Plant Science* 166: 207–217.

MULLER, J. 1970. Palynological evidence on early differentiation of Angiosperms. *Biological Reviews of the Cambridge Philosophical Society* : 417–450.

PUNT, W. 1976. Evolutionary trends in the pollen grains of Dichapetalaceae. In I.K. Ferguson & J. Muller, *The evolutionary significance of the exine*: 139–146. Academic Press, London.

SCHLECHTER, F.R.R. 1897. Plantae Schlechterianae novae vel minus cognitae describuntur. I. *Botanische Jahrbücher* 24: 434–454.

SONDER, O.W. 1865. *Siphocodon* and *Rhigiophyllum*. In W.H. Harvey & O.W. Sonder, *Flora capensis* 3: 596–597. Hodges, Smith, Dublin.

STRAKA, H. & SIMON, A. 1969. Palynologia madagassica et mascarenica, Fam. 187: Campanulaceae. *Pollen et Spores* 11: 326–331.

TAKHTAJAN, A. 1997. *Diversity and classification of flowering plants.* Columbia University Press, New York.

THULIN, M. 1974. *Gunillaea* and *Namacodon.* Two new genera of Campanulaceae in Africa. *Botaniska Notiser* 127: 165–182.

THULIN, M. 1975. The genus *Wahlenbergia* in tropical Africa and Madagascar. *Symbolae Botanicae Upsaliensis* 21: 1–233.

TURCZANINOW, P.K.N.S. 1852. *Siphocodon. Bulletin de la Société Imperiale des Naturalistes de Moscou* 25: 175.

VAN CAMPO, M. 1966. Pollen et phylogénie, Les Bréviaxes. *Pollen et Spores* 8: 57–73.

VON BREHMER, W. 1915. Über die systematische Gliederung und Entwicklung der Gattung *Wahlenbergia* in Afrika. In A.Engler, Beiträge zur Flora von Afrika, XLIV. *Botanische Jahrbücher* 53: 9–71.

WELMAN, W.G. 2000. Campanulaceae. In O.A. Leistner, Seed plants of southern Africa: families and genera. *Strelitzia* 10: 200–202. National Botanical Institute, Pretoria.