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Taxonomic significance of pollen types in the Guyana Highland-centred composite genera of Mutisioideae (Asteraceae)

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The Guyana Highland-centred genera, or *Stenopadus* group, are a complex of species that belong to the tribes Mutisieae and Stifftieae of Asteraceae. The pollen morphologies of 29 species, from 12 of 13 genera of this complex, are described and illustrated using light and scanning electron microscopy. The exine sculpture and structure are highly significant. Four exine types, previously characterized, were distinguished: *Gongylolepis*, *Wunderlichia*, *Mutisia*, and *Stenopadus*. The characterization of the *Stenopadus* exine type is enlarged here. These exine types led to the recognition of four well-defined pollen types, whereas the spine length and exine thickness characterized six subtypes. Pollen types circumscribe genera or groups of genera, and some subtypes distinguish species. The pollen morphology within the complex is discussed in relation to the rest of Mutisioideae and other palynologically allied tribes of Cichorioideae. There is little correlation between pollen types and tribes; only the *Stenopadus* exine type is exclusive to the Stifftieae tribe. The remaining types are shared by the two tribes of the complex. Pollen morphology supports the hypothesis that this group of genera is close to the *Gochnatia* complex and the Cardueae tribe. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **156**, 327–340.

ADDITIONAL KEYWORDS: Cardueae – exine – *Gochnatia* complex – Guyana complex – Mutisieae.

INTRODUCTION

As part of the study of the Mutisioideae subfamily (Katinas *et al*., in press), pollen morphology was included in the morphological characterization of a large number of genera. An important pollen diversity became apparent, but, as the coverage of the study was broad, a further discussion of pollen features within the different taxa is necessary. In particular, the pollen of the Guyana Highland-centred genera attracted our attention because of its morphological variation. This complex of genera, also known as the *Stenopadus* group (Bremer, 1993, 1994), inhabits the Guyana Highlands of northern Brazil, Colombia, Guyana, and Venezuela, but also extends to the Andes of Colombia, Ecuador, and Peru, and eastern Brazil (Katinas *et al*., in press), and has been detected recently in the Dominican Republic (Jiménez Rodríguez *et al*., 2004). Most species of the Guyana Highland-centred genera grow in small populations in tepui summits, and most are endangered because of the active erosion suffered by these geological formations (Maguire, 1956). The genera of this complex belong to two tribes of Mutisioideae: tribe Mutisieae, with the genera *Achnopogon*, *Duidaea*, *Eurydochus*, *Glossarion*, *Gongylolepis*, *Neblinaea*, and *Salcedoa*; and tribe Stifftieae, with the genera *Chimantaea*, *Quelchia*, *Stenopadus*, *Stifftia*, *Stomatochaeta*, and *Wunderlichia* (Pruski, 1989a, b, 1991; Jiménez Rodríguez *et al*., 2004). Some authors consider that this complex, which possesses a high degree of endemism and biogeographical isolation, is of great

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interest with regard to the origin of the Mutisieae. Carlquist (1957) considered that this complex was enigmatic within the Asteraceae because of its primitive morphological features. Pruski (1991) suggested that the Guyana Highland-centred genera could represent the most primitive group within the tribe Mutisieae. Bremer (1993, 1994) considered the *Stenopadus* group as one of the possible ancestors of Asteraceae. Recent phylogenetic studies have placed this group near to basal clades, probably originating in South America (Panero & Funk, 2002; Funk *et al*., 2005). Because of its basal position within Asteraceae, this tribe possesses great importance in the taxonomic relations within the family.

Palynological studies in this group are scarce. Wodehouse (1929) referred to pollen of *Wunderlichia*. Carlquist (1957) examined and illustrated unacetolysed pollen from some species of *Achnopogon*, *Chimantaea*, *Duidaea*, *Gongylolepis*, *Neblinaea*, *Stifftia*, and *Stenopadus*, as part of an anatomical study of the Guyana group. Barroso & Maguire (1973), in an anatomical study of the genus *Wunderlichia*, included pollen description and micrographs of *W. mirabilis* and *W. senaeii.* Jiménez Rodríguez *et al*. (2004) included pollen features in the morphological description of the genus *Salcedoa*, which contributed to the inclusion of this genus in the Guyana group. Katinas *et al*. (in press) characterizes the pollen of 16 species from 12 of 13 genera of the complex.

The main aims of this study were as follows: (1) to describe the pollen morphology of the Guyana Highland-centred genera using light microscopy (LM) and scanning electron microscopy (SEM) in order to clarify details of variations in pollen morphology; (2) to define the pollen types in these species; and (3) to contribute to the understanding of relationships within the tribe Mutisieae and family Asteraceae, based on pollen types.

MATERIAL AND METHODS

Pollen grains were obtained from herbarium specimens deposited at FM, LP, MO, and US (Holmgren *et al*., 1990) (Table 1). One conspicuous problem was the small number of herbarium specimens available. Moreover, some of these specimens lacked pollen, limiting the number of samples available for study; for this reason, in most species, only one specimen was examined. Material of *Achnopogon* was not available for this study. Pollen of 29 species, from 12 of 13 genera of the complex, was acetolysed and chlorinated in the standard manner (Erdtman, 1960). For LM, slides were prepared by mounting the pollen in glycerol jelly and sealed with paraffin. Pollen grain diameter measurements are based on 25 grains, when applicable, for each specimen. Exine thickness and spine length measurements were obtained from 15 grains. The diameter of echinate types excludes the spines. The pollen size classification follows Erdtman (1969). Light micrographs were taken using Axiophot (Zeiss) equipment. For SEM, acetolysed grains were suspended in 90% ethanol, mounted on stubs, and sputter-coated with gold–palladium. Some pollen grains were fractured with glass rods. Scanning electron micrographs were obtained using digital imaging on a JEOL JSM 5800 scanning electron microscope. The terminology in general follows Punt *et al*. (2007). The exine structural types were taken from Stix (1960), Tellería, Urtubey & Katinas (2003), and Katinas *et al*. (in press). Pollen types were established following Punt (1971), according to the principle: 'Pollen type is a term which indicates that pollen grains can be distinguished from other pollen grains either by one distinct character or by a combination of characters making the pollen grains distinct from other pollen grains'.

RESULTS

The 29 species examined show considerable variation in pollen morphology. A general description is provided, and then each pollen type recognized in the group is characterized. Measurements of pollen types are shown in Table 1. Finally, a key to identify the pollen types and subtypes is presented. Features in SEM are also mentioned where appropriate.

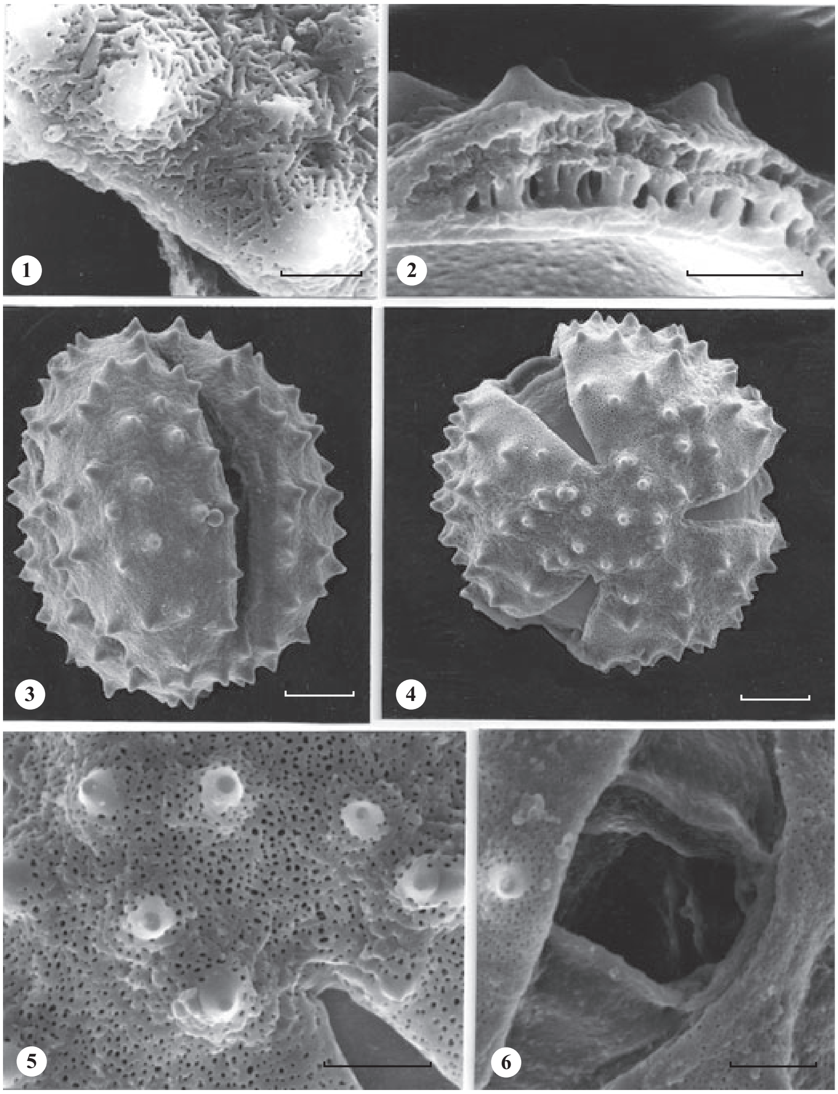
GENERAL DESCRIPTION OF POLLEN OF GUYANA HIGHLAND-CENTRED GENERA

Pollen radially symmetrical; spheroidal-subprolate to prolate; generally with large size. The range of the polar axis (*P*) varies from 45 to 113 μm, and the equatorial diameter varies from 35 to 88 μm. Tricolporate, with or without mesoaperture, colpi long or short, endoaperture lalongate, constricted or not, with horns (for example, Fig. 42), H-shaped (Fig. 44), or united in equatorial endocingulum, apertural membrane psilate (for example, Figs 6, 20) or scabrate (Fig. 30); with or without free endocolpus in the mesocolpia (Fig. 33). Exine from 3 to 17 μm thick at the equator, microechinate, slightly microechinate, microechinate-microgranulate, or echinate. Sexine about two or three times as thick as nexine, sometimes thickened at polar areas (Fig. 43) or at both polar and equatorial areas (Fig. 36); consisting of two layers: ectosexine and endosexine, with ramified (for example, Fig. 2) or, apparently, unramified (for example, Figs 52, 54) columellae, the layers separated by an internal tectum. Nexine thickened forming costae. The four main exine types reported previously were recognized and, for convenience to the reader, they are presented below.

Table 1. List of species studied arranged by pollen type [number of species by genus (in parentheses), followed by number of species examined], with collecting data, shape of pollen (*P*/*E*), size (measurements are minimum and maximum), exine thickness, and spine length

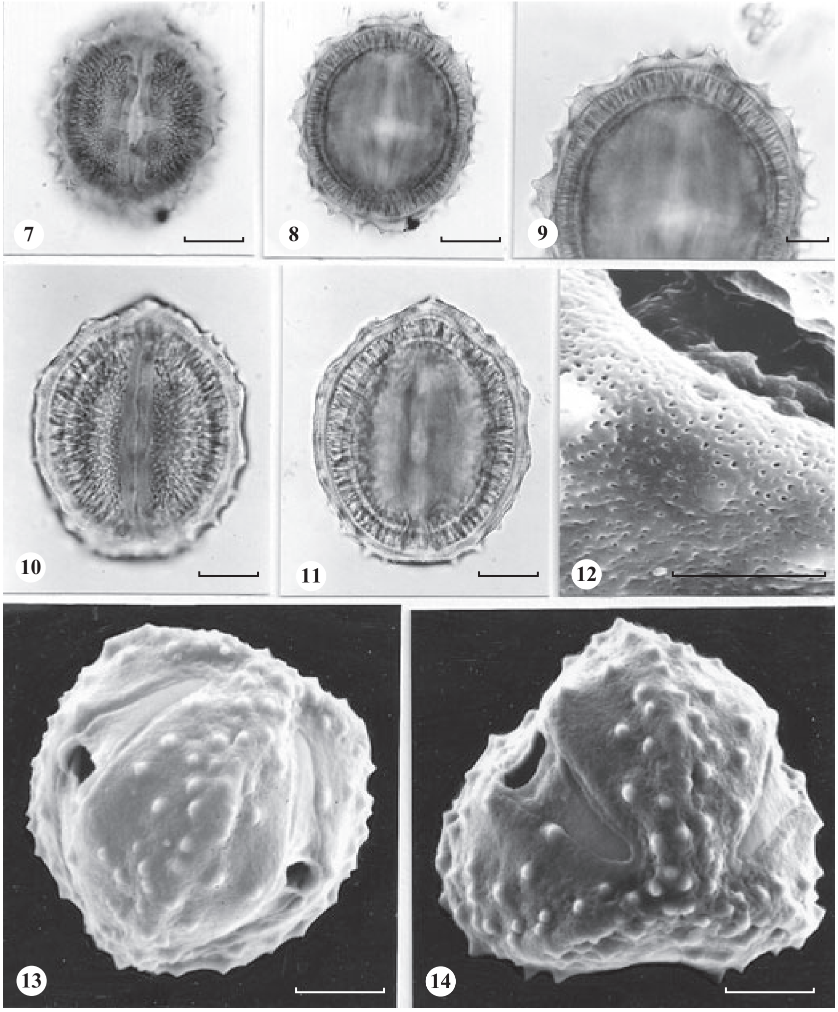
Types and taxa	Collection	Shape *P*/*E*	Polar diameter (μm)	Equatorial diameter (μm)	Exine thickness (μm)	Spine length (μm)
Type 1, subtype 1A						
Gongylolepis R. H. Schomb. (14) 6						
G. benthamiana R. H. Schomb	Steyermark & Liesner 127536 (MO)	Subprolate	72–94	61–78	10–11	2.5–4
G. bracteata Maguire	Maguire 27903 (US)	Subprolate	79–92	64–78	9–13	5–7
G. colombiana (Cuatrec.) Cuatrec.	Jahn 91 (US)	Subprolate	90–113	78–88	10–14	4–5
G. huachamacari Maguire	Maguire *et al*. 30080, 30136 (US)	Spheroidal-subprolate	74–88	70–80	14–17	5–6
G. paniculata Maguire & K. D. Phelps	Maguire 35392 (FM)	Spheroidal	88–99	73–78	11–17	5–7
G. pedunculata Maguire	Huber 12985 (US)	Spheroidal	81–87	75–86	12–13	5
Type 1, subtype 1B						
Duidaea S. F. Blake (4) 1						
Duidaea marahuacensis Steyerm.	Liesner 24644 (US)	Spheroidal-subprolate	62–72	52–64	11–14	2.5
Glossarion Maguire & Wurdack (1) 1						
Glossarion rhodanthum Maguire & Wurdack	Maguire *et al*. 37149 (US)	Prolate	74–80	56–60	12–16	2.5
Quelchia N. E. Br. (5) 1						
Quelchia bracteata Maguire, Steyerm. & Wurdack	Pipoly *et al*. 7217 (US)	Subprolate	55–62	45–48	7–10	2.5
Type 2, subtype 2A						
Eurydochus Maguire & Wurdack (1) 1						
Eurydochus bracteatus Maguire & Wurdack	Maguire *et al*. 42238 (US)	Prolate	72–80	54–60	8–10	2.5–3
Salcedoa F. Jiménez R. & Katinas (1) 1						
Salcedoa mirabalarium F. Jiménez R. & Katinas	Veloz *et al*. 2383 (LP)	Prolate	45–56	66–83	7–9	1–2
Wunderlichia Riedel ex Benth. (6) 3						
Wunderlichia azulensis Maguire & G. M. Barroso	Harleg *et al*. 25209 (MO)	Prolate	71–83	48–58	8–10	2–3
W. mirabilis Riedel ex Baker	Ratter *et al*. 2621 (MO)	Prolate	83–88	59–64	12–14	1–2.5
Type 2, subtype 2B						
W. crulsiana Taubert	Ratter *et al*. 2615 (MO)	Prolate	68–75	50–58	10–12	4–5
Type 3, subtype 3A						
Chimantaea Maguire, Steyerm. & Wurdack (9) 2						
Chimantaea cinerea (Gleason & S. F. Blake) Maguire	Steyermark 116028 (MO)	Subprolate	64–68	50–54	5–8	
C. huberi Steyerm.	Huber 12034 (LP)	Subprolate	48–57	37–42	6	
Neblinaea Maguire & Wurdack (3) 1						
Neblinaea promontorium Maguire & Wurdack	Silva & Brazão 60895 (US)	Subprolate	62–70	50–55	7	
Stifftia J. C. Mikan (7) 3						
Stifftia parviflora (Leandro) D. Don	Hering 7680 (LP)	Subprolate	46–52	35–42	5–9	*c*. 1–2
St. uniflora Ducke	Ducke s/n° (LP)	Spheroidal	48–60	42–54	6–6.5	
Stenopadus S. F. Blake 15 8						
Stenopadus campestris Maguire & Wurdack	Barriga 20878 (US)	Subprolate	59	41	7–8	
S. colveii (Steyerm.) Pruski	García Barriga 20878/US), Boom 9427 (US)	Prolate	81–96	59–67	6–10	
S. huachamacari Maguire	Maguire *et al*. 30116 (MO)	Prolate	52–64	36–43	4–6	
Type 3, subtype 3B						
Stifftia chrysantha J. C. Mikan	Cabrera 12242 (LP)	Spheroidal	65–72	58–65	*P*: 11–16 *E*: 8–14	
Type 4						
Stenopadus chimantensis Maguire, Steyerm. & Wurdack	Pipoly *et al*. 7142 (MO)	Prolate	62–72	36–52	*P*: 7–9 *E*: 3–6	
S. connelli (N. R. Br.) S. F. Blake	Liesner 23109 (MO)	Prolate	67–75	42–50	5–6	
S. jauensis Aristeg.	Steyemark 109629 (US)	Prolate	85–105	51–62	6–9	
S. sericeus Maguire & Aristeg.	Tillet 45103 (US)	Prolate	66–84	38–50	*P*: 4–10 *E*: 5–6	
S. talaumifolius	Liesner 18346 (MO)	Prolate	81–90	50–61	6–8	
Stomatochaeta (S. F. Blake) Maguire & Wurdack (5) 1						
Stomatochaeta condensata (Baker) Maguire & Wurdack	Liesner 19415 (MO)	Subprolate	52–55	40–45	5–86	

E, equatorial; *P*, polar.



Figures 1–6. *Gongylolepis*. Type 1, subtype 1A. Figs 1, 2. *Gongylolepis huachamacari*. Fig. 1. Details of pollen surface. Fig. 2. Wall stratification seen on broken grain. Figs 3–6. *Gongylolepis paniculata*. Fig. 3. Equatorial view. Fig. 4. Polar view. Fig. 5. Detail of exine surface. Fig. 6. Detail of psilate apertural membrane. All illustrations scanning electron microscopy. Scale bars, 5 μm.

1. Exine *Gongylolepis* type (Katinas *et al*., in press) (for example, Figs 1, 2, 9): echinate, spines up to *c*. 6 μm long with variable number of apical channels, tectum very perforate. Ectosexine thinner than endosexine, ectosexine slightly columellate, endosexine with stout and ramified columellae, the layers separated by a conspicuous internal tectum. Ratio ectosexine/endosexine between spines: 1 : 4; 1 : 5. The length of spines allows two subtypes (1 and 2) to be distinguished.
2. Exine *Wunderlichia* type (Tellería *et al*., 2003; redefined in Katinas *et al*., in press) (Figs 21, 25): echinate, spines usually less than 5 μm long with apical channel, tectum very perforate. Ectosexine equal or slightly thinner than endosexine; ectosexine with compact inner layer and thinner scarcely columellate outer layer. Ratio ectosexine/endosexine between spines: 1 : 1; 1 : 1.5. The difference in spine length allows two subtypes (1 and 2) to be recognized.
3. Exine *Mutisia* type (Stix, 1960; redefined in Katinas *et al*., in press) (for example, Figs 31, 39): scabrate, verrucate, microechinate, echinate with short spines (usually less than 2 μm), tectum imperforate or scarcely perforate. Broad range of exine thickness (4–18 μm). Ectosexine equal to, thinner, or thicker than endosexine, ectosexine slightly columellate or with compact aspect, endosexine with



Figures 7–14. *Gongylolepis paniculata*. Fig. 7. Equatorial view, high focus. Fig. 8. Equatorial view, optical section. Fig. 9. Equatorial view in optical section showing the exine structure. Type 1, subtype 1B. Figs 10–14. *Duidaea marahuacensis*. Fig. 10. Equatorial view, high focus, showing the thick columellae in transverse section. Fig. 11. Equatorial view, optical section, showing the exine structure. Fig. 12. Detail of pollen surface. Fig. 13. Equatorial view. Fig. 14. Polar view. Scale bars: Figs 7–11, 13, 14, 10 μm; Fig. 12, 5 μm.

stout and ramified columellae, the layers separated by an inconspicuous or conspicuous internal tectum. Ratio ectosexine/endosexine: 1 : 1; 1 : 2; 1 : 2.5; 1.5 : 1; 2 : 1; 2.5 : 1. The difference in exine thickness at the polar and equatorial areas allows two subtypes (1 and 2) to be distinguished.

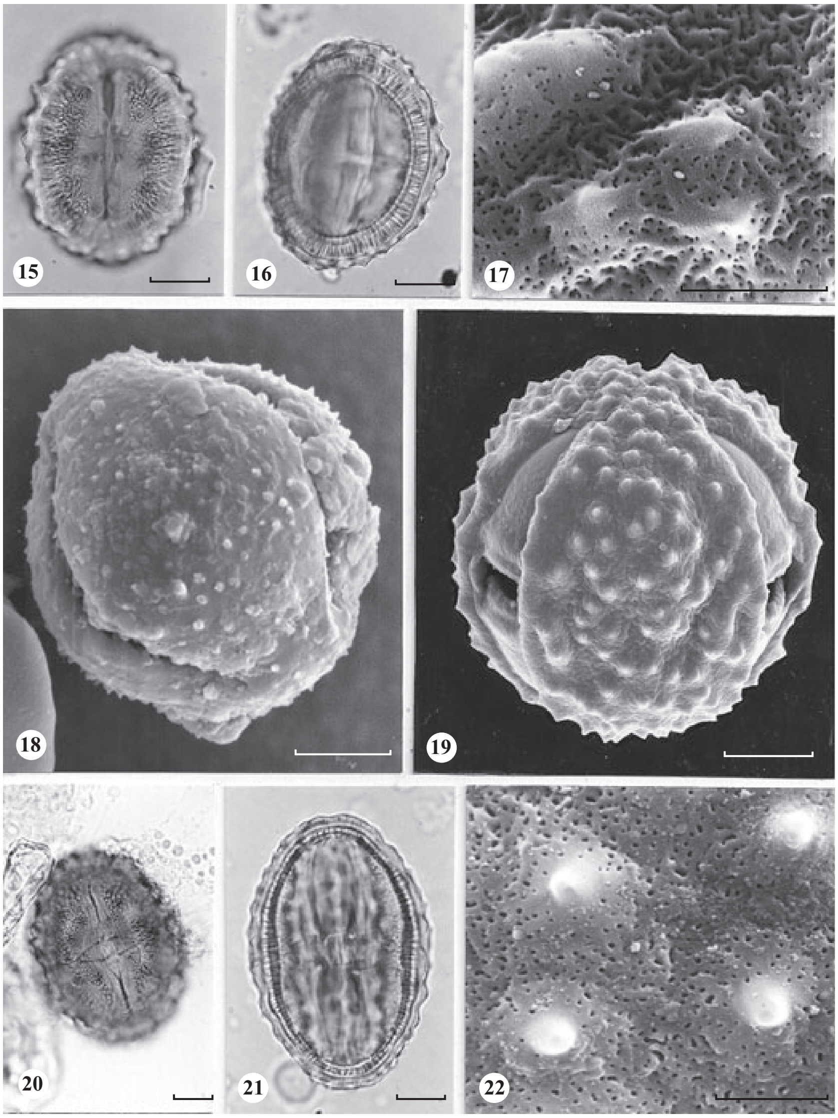
4. Exine *Stenopadus* type (Katinas *et al.*, in press; enlarged here) (for example, Figs 45, 54): psilate (with light microscope), very perforate, with scarce and inconspicuous microspines (with LM). Ectosexine equally thick as endosexine, ectosexine columellate; endosexine columellate, thin columellae, apparently unramified. The arrangement of the columellae of the ectosexine is in a concordant pattern with the columellae in the endosexine. Ratio ectosexine/endosexine: 1 : 1.

These exine types allowed four pollen types and six subtypes to be recognized on the basis of either spine length or exine thickness. For practical reasons, the pollen types and subtypes were numbered.

DESCRIPTION OF POLLEN TYPES

Type 1 (Figs 1–18)

Pollen spheroidal to subprolate, generally subprolate, spheroidal or elliptic in equatorial view, circular in polar view, large size, $P \times E = (55–113 \times 45–88)$ μm. Colpi long or short, with psilate membrane, endoaperture lalongate, sometimes constricted at colpus, mesoaperturate. Exine *Gongylolepis* type, 7–17 μm thick, sometimes slightly thickened at the poles. Nexine *c.* 2–3 μm thick. Colpi long in *Gongylolepis*



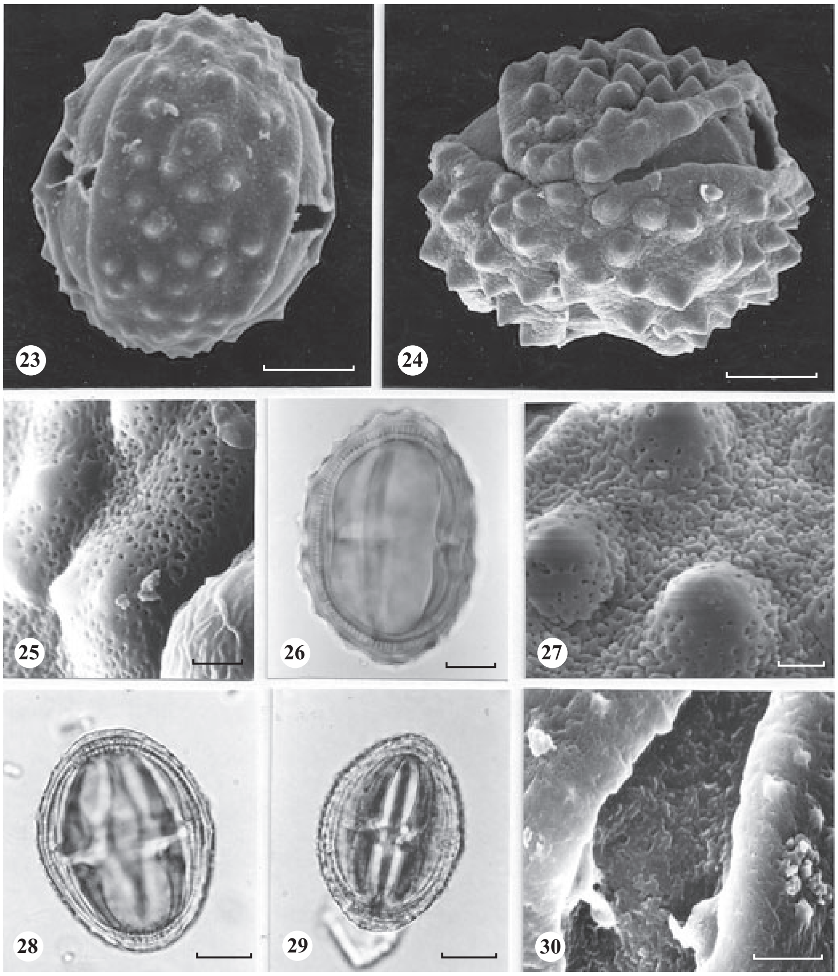
Figures 15–22. Type 1, subtype 1B (*continued*). Figs 15–17. *Quelchia bracteata*. Fig. 15. Equatorial view, high focus (light microscopy, LM). Fig. 16. Equatorial view, optical section showing the structure exine (LM). Fig. 17. Detail of exine surface (scanning electron microscopy, SEM). Fig. 18. *Glossarion rhodanthum*. Equatorial view (SEM). Type 2, subtype 2A. Fig. 19. *Eurydochus bracteatus*. Equatorial view, high focus (LM). Figs 20–22. *Salcedoa mirabalarium*. Fig. 20. Equatorial view (SEM). Fig. 21. Equatorial view in optical section showing the exine structure (LM). Fig. 22. Detail of exine surface (SEM). Scale bars: Figs 15, 16, 19–22, 10 µm; Figs 17, 18, 5 µm.

colombiana, *G. bracteata*, *G. huachamacari*, *G. paniculata*, and *G. pedunculata*, and short in *G. benthamiana* (47–70 µm in length). SEM: tectum very perforate with striate aspect in *G. huachamacari* (Fig. 1) and microreticulate aspect in *G. paniculata* (Fig. 5). On the basis of spine length, two subtypes were recognized.

Subtype 1A (Figs 1–9): Spines up to *c*. 7 µm in length. Present in *Gongylolepis* (*G. benthamiana*, *G. bracteata*, *G. colombiana*, *G. huachamacari*, *G. paniculata*, and *G. pedunculata*). Remarks: there are biaperturate grains in *G. pedunculata*.

Subtype 1B (Figs 10–18): Spines less than 2.5 µm in length. Present in *Duidaea marahuacensis*, *Glossarion rhodanthum*, and *Quelchia bracteata*. Remarks: the nexine is scarcely distinguishable in pollen of *Duidaea marahuacensis*.

Type 2 (Figs 19–27)
Pollen prolate, elliptic or elliptic-subrectangular in equatorial view, circular in polar view, large size,



Figures 23–30. Type 2, subtype 2A (*continued*). Figs 23–25. *Wunderlichia mirabilis*. Fig. 23. Equatorial view (scanning electron microscopy, SEM). Fig. 24. Detail of exine surface (SEM). Fig. 25. Optical section of equatorial view showing the exine structure (light microscopy, LM). Type 2, subtype 2B. Figs 26, 27. *Wunderlichia crulsiana*. Fig. 26. Polar view (SEM). Fig. 27. Detail of exine surface (SEM). Type 3, subtype 3A. Fig. 28. *Chimantaea cinerea*. Equatorial view in optical section showing the exine structure (LM). Figs 29, 30. *Chimantaea huberi*. Fig. 29. Equatorial view in optical section (LM). Fig. 30. Detail of scabrate apertural membrane (SEM). Scale bars: Figs 23, 25, 26, 28, 29, 10 μm; Figs 24, 27, 2 μm; Fig. 30, 5 μm.

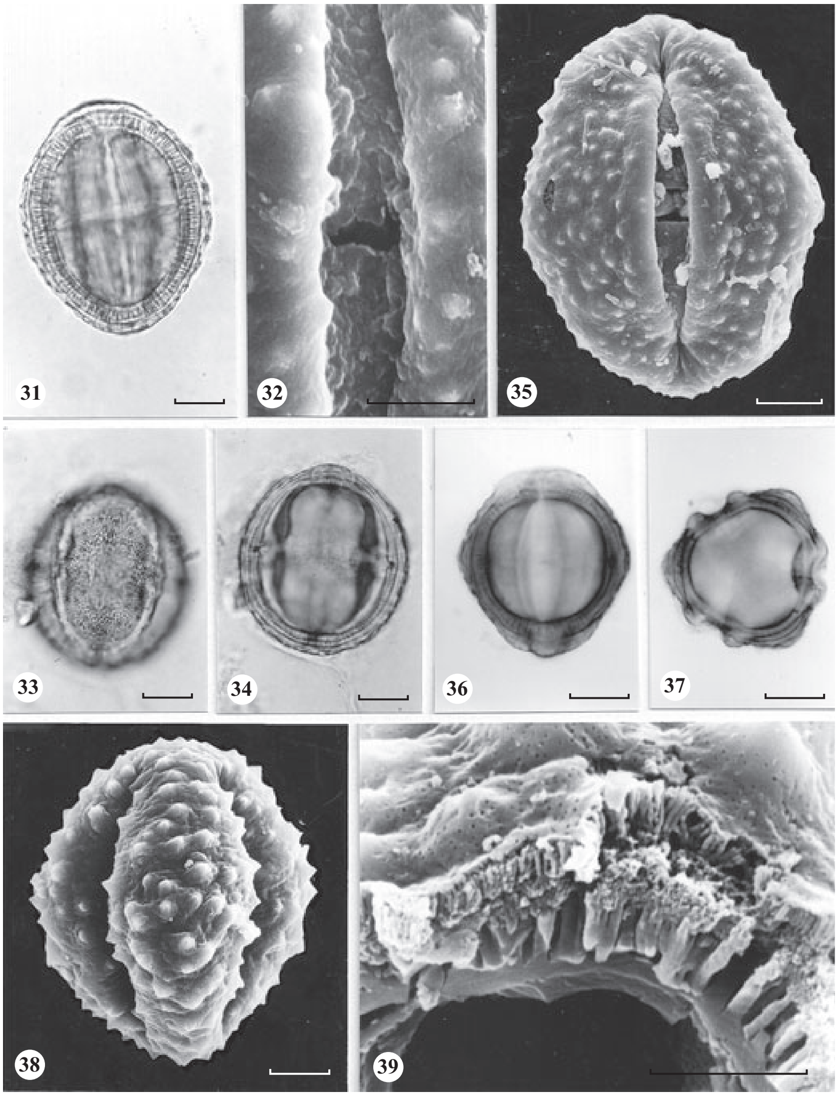
$P \times E = (45–88 \times 48–83)$ μm. Colpi long with psilate membrane, with or without endocingulus and free endocolpi, mesoaperturate. Exine *Wunderlichi*a type, 7–14 μm, equally thick in the whole grain. Nexine 1.5–2.5 μm thick. SEM: tectum very perforate, almost microreticulate. On the basis of spine length, two subtypes were recognized.

Subtype 2A (Figs 19–25): Exine with spines 1–3 μm in length. Present in *Eurydochus bracteatus*, *Salcedoa mirabalarium*, and *Wunderlichia* (*W. azulensis* and *W. mirabilis*).

Subtype 2B (Figs 26, 27): Exine with spines 4–5 μm in length. Present in *W. crulsiana*.

Type 3 (Figs 28–43)
Pollen spheroidal to subprolate, elliptic or elliptic-subrectangular in equatorial view, circular in polar view, large size, $P \times E = (46–96 \times 35–67)$ μm. Colpi long with psilate or scabrate membrane, with or without endocingulus and free endocolpi (Fig. 33). Exine *Mutisia* type, equally thick over the whole grain or conspicuously thickened towards the equator and the poles. The difference in exine thickness at the equatorial and polar level allows two subtypes to be recognized (Fig. 3A, B).

Subtype 3A (Figs 28–34, 38, 39): Exine 4–10 μm thick in the whole grain or slightly thickened at the poles. Ratio ectosexine/endosexine amongst spines: 1 : 1;



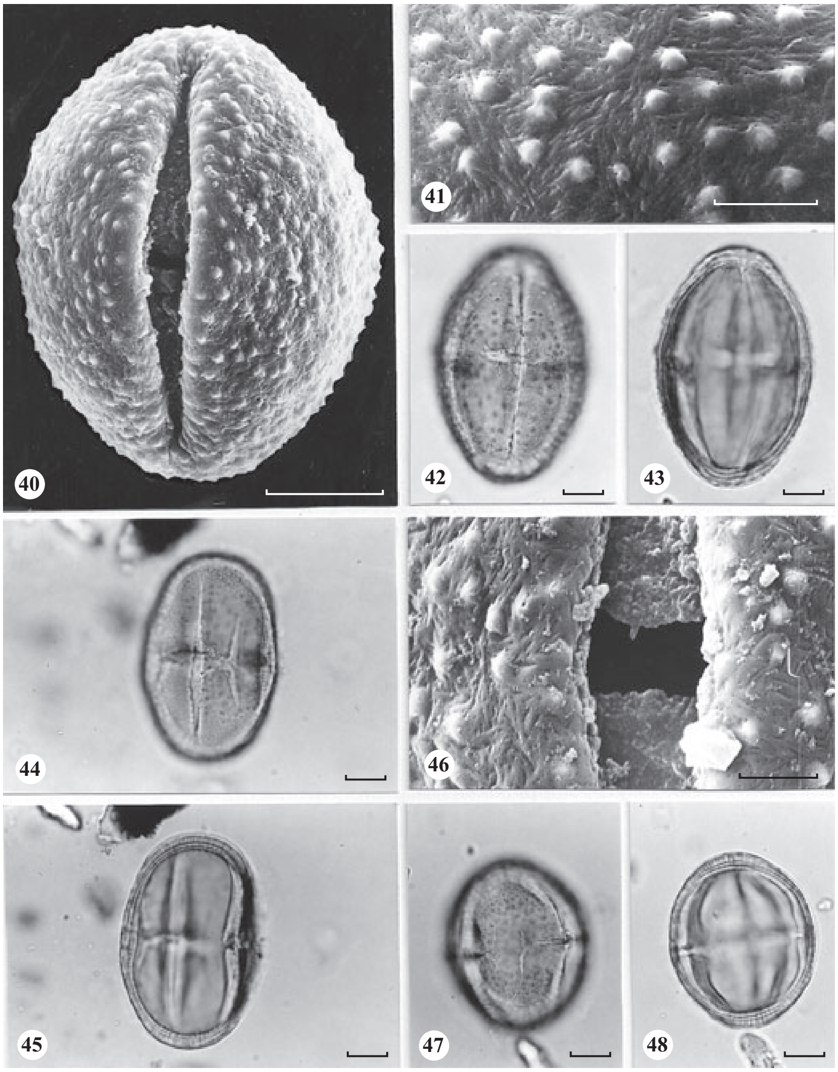
Figures 31–39. Type 3, subtype 3A (*continued*). Figs 31, 32. *Neblinaea promontorium*. Fig. 31. Equatorial view in optical section showing the exine structure (light microscopy, LM). Fig. 32. Detail of apertural membrane; note the scabrate surface and the reduced endoaperture (scanning electron microscopy, SEM). Figs 33, 34. *Stifftia uniflora*. Fig. 33. Equatorial view; note a free endocolpus (arrow) (LM). Fig. 34. Equatorial view in optical section (LM). Type 3, subtype 3B. Figs 35–37. *Stiftia chrysantha*. Fig. 35. Equatorial view (SEM). Fig. 36. Equatorial view in high focus (LM). Fig. 37. Polar view (LM). Type 3, subtype 3A (*continued*). Figs 38, 39. *Stifftia parviflora*. Fig. 38. Equatorial view (SEM). Fig. 39. Detail of exine structure in broken grain (SEM). Scale bars: Figs 31–38, 10 µm; Figs 32, 39, 5 µm.

1.5 : 1; 1 : 1.5. Nexine *c*. 1.5–2 µm thick. Present in *Chimantaea* (*C. huberi* and *C. cinerea*), *Neblinaea promontorium*, *Stifftia* (*St. uniflora*), and *Stenopadus* (*S. campestris*, *S. colveii*, and *S. huachamacari*). SEM: endoaperture very constricted in *C. huberi* and *N. promontorium* (Fig. 32), and apertural membrane entirely scabrate in *C. huberi* (Fig. 30).

Subtype 3B (Figs 35–37): Exine 11–16 µm thick at the poles, 8–14 µm thick at the equator. Present in *St. chrysantha*. Nexine very thickened at colpus (Fig. 37).

Type 4 (Figs 49–58)

Pollen subprolate-prolate, generally prolate, elliptic to rectangular in equatorial view, circular-subcircular in polar view, large size $P \times E = (52–105 \times 36–62)$ µm. Colpi long or short, with psilate or scabrate-microgranulate membrane, with or without endocingulus and free endocolpi, endoaperture lalongate with horns, or H-shaped (for example, Figs 44, 47), with or without diffuse mesoaperture. Exine *Stenopadus* type, 5–10 µm, equally thick over the whole grain or slightly thickened at the poles. Present in *Stomatochaeta condensata* and *Stenopadus* (*S. chimanten-*



Figures 40–48. Type 3, subtype 3A (*continued*). Figs 40–43. *Stenopadus huachamacari*. Fig. 40. Equatorial view (scanning electron microscopy, SEM). Fig. 41. Detail of exine surface (SEM). Fig. 42. Equatorial view in high focus showing endoaperture with horns (arrow) (light microscopy, LM). Fig. 43. Equatorial view in optical section (LM). Type 4. Figs 44, 45. *Stenopadus sericeus*. Fig. 44. Equatorial view in high focus showing the H-endoaperture (LM). Fig. 45. Equatorial view in optical section (LM). Figs 46–48. *Stomatochaeta condensata*. Fig. 46. Detail of exine surface (SEM). Fig. 47. Equatorial view in high focus showing the H-endoaperture (LM). Fig. 48. Equatorial view in optical section (LM). Scale bars: Figs 40, 42–45, 47, 48, 10 µm; Figs 41, 46, 5 µm.

sis, *S. sericeus*, *S. connelli*, *S. cucullatus, S. jauensis*, and *S. talaumifolius*). SEM: tectum very perforate with small perforations, with a striate aspect among microspines. Remarks: in the collapsed, or aborted, grains, the polar thickness is more conspicuous than that in the 'regular' grains.

Stenopadus connelli: some grains have a pyramidal or quadrangular shape, with more than three apertures (Fig. 50). These features could belong to polyploid specimens.

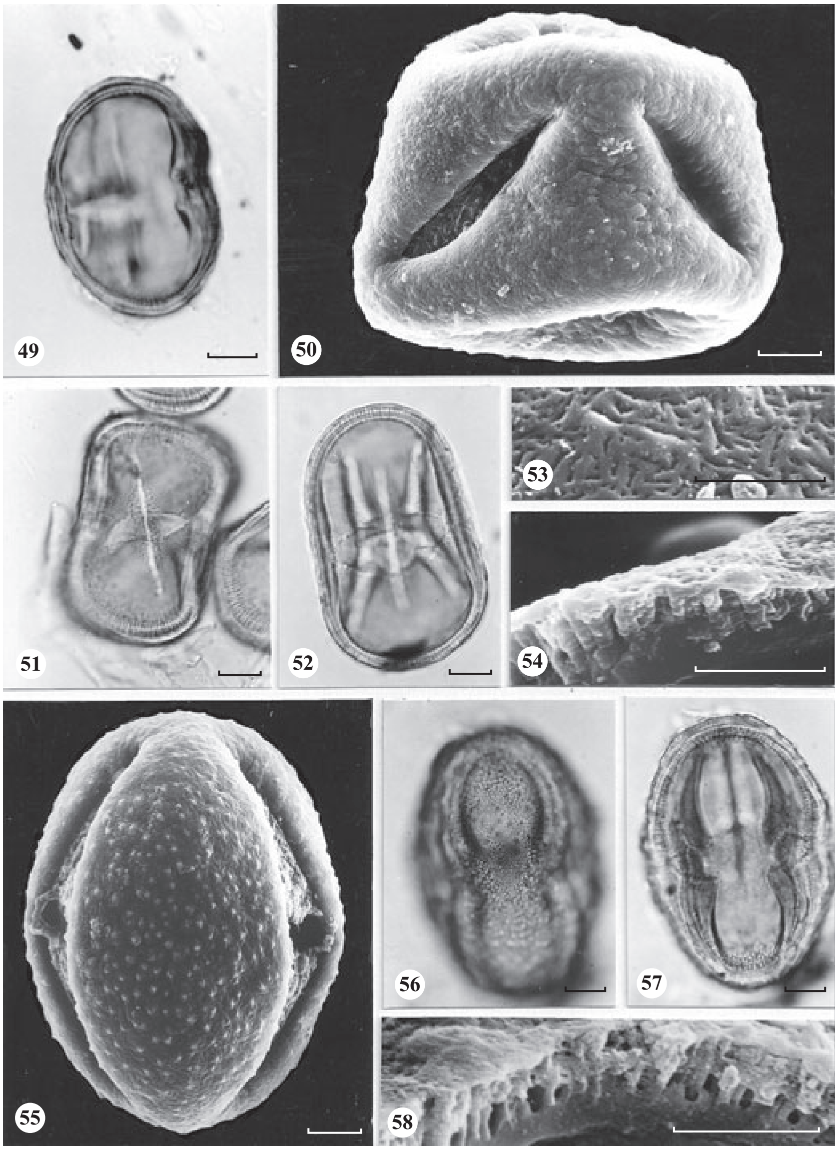
Stenopadus chimantensis: colpi 45–50 µm in length with membrane densely microgranulate only around the endoaperture. SEM: tectum psilate at the poles and very perforate with striate aspect at the equator.

DISCUSSION

POLLEN MORPHOLOGY

The pollen of Guyana Highland-centred genera shows a considerable morphological variability in size, shape in equatorial view (Table 1), aperture features, and exine types.

The size is generally large and the shape ranges from subspheroidal to prolate; the aperture is always



Figures 49–58. Type 4 (*continued*). Fig. 49. *Stenopadus talaumifolius*. Equatorial view in optical section (light microscopy, LM). Figs 50–54. *Stenopadus connelli.* Fig. 50. General view of irregular grain (scanning electron microscopy, SEM). Fig. 51. Equatorial view in high surface showing an irregular aperture (LM). Fig. 52. Equatorial view in optical section showing the exine structure (LM). Fig. 53. Detail of exine surface (SEM). Fig. 54. Detail of exine structure in broken grain; note the unramified columellae (SEM). Figs 55, 56. *Stenopadus cucullatus*. Fig. 55. Equatorial view (SEM). Fig. 56. Detail of exine structure; note the unramified columellae and the concordant pattern of columellae (SEM). Figs 57, 58. *Stenopadus jauensis*. Fig. 57. Equatorial view in high focus (LM). Fig. 58. Optical section of equatorial view (LM). Scale bars: Figs 49–52, 55–57, 10 μm; Figs 53, 54, 58, 5 μm.

tricolporate and the endoaperture is commonly lalongate with a variable shape. Free endocolpi are present in pollen with the *Wunderlichia*, *Mutisia*, and *Stenopadus* exine types, but are absent in pollen with the *Gongylolepis* exine type. The four exine types belong to the anthemoid pattern, characterized by the lack of cavea (Skvarla *et al*., 1977). From the exine types, a morphological series of intergrading forms, within which the extremes are dissimilar, can be hypothesized (Fig. 59). This series does not imply evolutionary trends, because there is a lack of phylogenetic studies within the genera of the complex. The *Gongylolepis* and *Stenopadus* exine types may occupy such extremes. The former exine type has long spines with apical channels, and the endosexine has stout and ramified columellae; this exine type is thick over the whole grain (for example, Fig. 9). By contrast, the *Stenopadus* exine type has very small, or vestigial,

Key to pollen types and subtypes in Guyana Highland-centred genera

1. Exine echinate, spines conspicuous, with apical channel
  2. Ratio ectosexine/endosexine: 1 : 4; 1 : 5 ……………… Type 1
    3. Spines *c.* 4–7 μm in length……………… Subtype 1a (*Gongylolepis*)
    3′. Spines *c.* 2.5 μm in length……………… Subtype 1b (*Duidaea*, *Glossarion*, and *Quelchia*)
  2′. Ratio ectosexine/endosexine: 1 : 1; 1 : 1.5 ……………… Type 2
    4. Spines *c.* 2.5–3 μm in length……………… Subtype 2a (*Eurydochus*, *Salcedoa*, *Wunderlichia*, *W. azulensis*, and *W. mirabilis*)
    4′. Spines *c.* 4–5 μm in length……………… Subtype 2b (*W. crulsiana*)
1′. Exine microechinate or almost psilate (with LM)
  5. Ectosexine with compact aspect, endosexine with stout columellae clearly ramified ……………… Type 3
    6. Exine equally thickened in the whole grain……………… Subtype 3a (*Chimantaea*, *Neblinaea*, *St. uniflora*, and *Stenopadus campestris*, *S. colveii*, and *S. huachamacari*)
    6′. Exine conspicuously thickened at the poles and the equator……………… Subtype 3b (*St. chrysantha*)
  5′. Ectosexine and endosexine clearly columellate, both layers with thin and apparently unramified columellae in concordant pattern……………… Type 4 (*Stomatochaeta*, *Stenopadus chimantensis*, *S. connelli*, *S. jauensis*, *S. sericeus*, and *S. talaumifolius*)

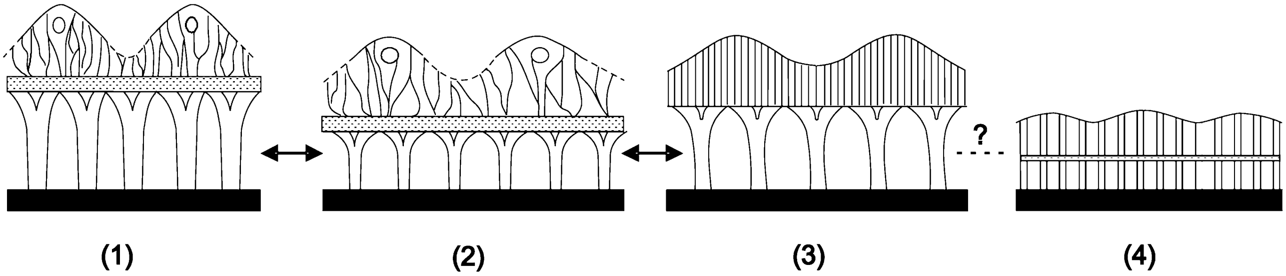


Figure 59. Scheme of hypothetical morphological series of the exine types recognized in the Guyana Highland-centred genera: (1) *Gongylolepis* type; (2) *Wunderlichia* type; (3) *Mutisia* type; and (4) *Stenopadus* type. The broken line indicates uncertain relationships of the *Stenopadus* exine type with the rest of the series.

microspines and the columellae of both the ecto- and endosexine are delicate, apparently unramified, and arranged in a concordant pattern; this exine type is thin, but sometimes thickened at the poles (for example, Fig. 52). In this series, *Gongylolepis*, *Wunderlichia*, and *Mutisia* exine types can be viewed as morphologically closely related. Both *Wunderlichia* and *Gongylolepis* types share a tectal surface which is microreticulate and has well-developed spines, although those of *Wunderlichia* pollen are shorter. They clearly differ in the ectosexine/endosexine ratio, the *Gongylolepis* type having an endosexine remarkably thicker than that of the *Wunderlichia* type. Within the broad *Mutisia* exine type, the exines with longer spines and not very compact ectosexine appear to be close to the *Wunderlichia* type (Tellería *et al.*, 2003). A gap is presented in the *Stenopadus* type as the combination of an anthemoid pattern and concordant pattern of columellae is unusual within Asteraceae. By comparison with transmission electron micrographs of pollen of Asteraceae (Skvarla *et al.*, 1977), the exine structure of the *Stenopadus* type only appears similar to that of *Tarchonanthus.* A further ultrastructural transmission electron microscopy (TEM) examination in a larger number of species of *Stenopadus*, and the study of other morphological features, are necessary to elucidate the significance of this unusual exine type.

Pollen types and generic relationships

The pollen types described are based on the four exine types recognized: *Gongylolepis*, *Wunderlichia*, *Mutisia*, and *Stenopadus*. The spine length and exine thickness justify the distinction of six subtypes. Within each pollen type, there is some variation in size and shape in equatorial view, except for Type 2 which is uniformly prolate.

The majority of genera are characterized by one pollen type, with the exception of *Stenopadus*, which has pollen of two morphological types. The exine *Gongylolepis* type groups genera placed in separate tribes: *Duidaea* (*D. marahuacensis*), *Glossarion rhodanthum*, and *Gongylolepis* (*G. benthamiana*, *G. bracteata*, *G. colombiana*, *G. huachamacari*, *G. paniculata*, and *G. pedunculata*) in Mutisieae and

Quelchia (*Q. bracteata*) in Stifftieae. This pollen type reinforces the close relationship between *Gongylolepis*, *Duidaea*, and *Glossarion* (Pruski 1989a). However, the long spines of *Gongylolepis* pollen, which characterizes subtype 1A, support its generic delimitation. *Quelchia* was recently placed in Stifftieae (Pruski, 2004), but is the only genus of that tribe which has both tubular and bilabiate corollas, and smooth styles, as commonly occurs in the tribe Mutisieae (Jiménez Rodríguez *et al*., 2004; Katinas *et al*., in press). Pollen features provide additional evidence to place *Quelchia* in the Mutisieae tribe.

The *Wunderlichia* exine type occurs in the monospecific genera *Eurydochus* and *Salcedoa*, and in species of *Wunderlichia* (*W. azulensis*, *W. crulsiana*, and *W. mirabilis*). Within this type, pollen of *W. crulsiana* can be distinguished because its spines are longer than those observed in the pollen of the other genera. The morphological similarities between both *Wunderlichia* and *Gongylolepis* exine types support the relationship between *Gongylolepis* and *Eurydochus* (Pruski 1989a).

The *Mutisia* type characterizes *Chimantaea* (*C. cinerea* and *C. huberi*), *Neblinaea* (*N. promontorium*), *Stifftia* (*St. uniflora* and *St. chrysantha*), and some species of *Stenopadus* (*S. campestris*, *S. colveii*, and *S. huachamacari*). Pollen of *St. chrysantha* differs from that of other species because its exine is very thick at both polar and equatorial levels, and these thickened areas were a feature observed early by Carlquist (1957). Pollen types support the distinction between *Stifftia* and *Duidaea*, which have been placed in separate branches of the cladograms in molecular studies of the Asteraceae family (Kim, Loockerman & Jansen, 2002; Funk *et al*., 2005).

The remaining pollen type, with the unusual *Stenopadus* exine type, is exclusive to Stifftieae, and occurs in *Stenopadus* (*S. chimantensis*, *S. sericeus*, *S. connelli*, *S. jauensis*, and *S. talaumifolius*) and monospecific *Stomatochaeta*. This pollen type supports the close relationship between *Stenopadus* and *Stomatochaeta* (Pruski 1989a). *Stenopadus* is the only genus that presents two pollen types: *Mutisia* and *Stenopadus* types. Under the light microscope, the pollen of species of *Stenopadus* with the *Stenopadus* exine type is very distinctive. Features, such as the small microspines, rectangular or subrectangular shape, and thin exine with delicate columellae in a concordant pattern, are rare both within and outside the tribe Stifftieae.

POLLEN TYPES OF THE GUYANA COMPLEX WITHIN MUTISIOIDEAE AND ASTERACEAE

The tribes Mutisieae and Stifftieae share the closely related *Gongylolepis*, *Wunderlichia*, and *Mutisia* exine types, whereas the *Stenopadus* type is exclusive to Stifftieae.

With regard to the other genera of Mutisieae, the *Gongylolepis* type is close to the *Macroclinidium* type (Lin, Wang & Blackmore, 2005; Katinas *et al*., in press), which is exclusive to the Pertyeae group (Katinas *et al*., in press). Both types share the echinate exine, with conspicuous spines and an almost microreticulate tectal surface. However, unlike the *Gongylolepis* type, the spine structure in pollen of the *Macroclinidium* type appears to be solid (Katinas *et al*., in press); additional TEM examinations in both exine types are necessary to compare the degree of structural similarity. The *Wunderlichia* exine type characterizes at least five species of the large genus *Gochnatia* (Jiménez Rodríguez *et al*., 2004; Katinas *et al*., in press). The *Mutisia* exine type is the most common within the tribe Mutisieae (Parra & Marticorena, 1972; Tellería *et al*., 2003; Tellería & Katinas, 2004).

Within the Asteraceae family, the *Gongylolepis*, *Wunderlichia*, and *Mutisia* exine types are similar to that of Cardueae, and the *Mutisia* type is also present in the pollen of *Artemisia* (Anthemideae tribe, subfamily Asteroideae) (Wodehouse, 1926; Skvarla *et al*., 1977; Rowley, Claugher & Skvarla, 1999). Pollen with *Gongylolepis* and *Wunderlichia* exine types is similar to that of some Cardueae pollen with long and well-developed spines (for comparisons, see Tormo-Molina & Ubera-Jiménez, 1990, 1995). By contrast, the *Mutisia* exine type is similar to that of some species of *Centaurea* (Cardueae tribe), which possesses ecaveate and microechinate pollen (Wagenitz, 1955; Parra, 1969; Dimon, 1971; Nordenstam & El-Ghazaly, 1977; Blackmore, van Helvoort & Punt, 1984; Pehlivan, 1995; Villodre & García-Jacas, 2000).

CONCLUSIONS

The pollen morphology of the Guyana Highland-centred genera shows variation, mainly in exine features. The sculpture and structure have undergone extensive differentiation, allowing four pollen types and six subtypes to be recognized. If the degree of resemblance of pollen characters is viewed as affording the best indication of the degree of natural relationships, the following conclusions can be drawn.

1. There is no correspondence between pollen types and tribes, with the exception of the *Stenopadus* type, as the remaining three types are shared by the tribes Mutisieae and Stifftieae.
2. From the four pollen types circumscribed, two are exclusive to the group (*Gongylolepis* and *Stenopadus* types), whereas the *Wunderlichia* and *Mutisia* types are shared with other genera of Mutisieae.

In particular, the *Wunderlichia* type is closely related to the *Gochnatia* complex (Freire, Katinas & Sancho, 2002).

3. Pollen features of *Quelchia* provide additional evidence to place this genus in the tribe Mutisieae.
4. The pollen morphology of the Guyana Highland-centred genera, together with that of the *Gochnatia* complex (Katinas *et al*., in press), reinforces the possible relationship between the tribes Mutisieae and Cardueae (Wodehouse, 1926, 1929; Jiménez Rodríguez *et al*., 2004; Katinas *et al*., in press).
5. The exine with the anthemoid pattern, not very specialized in terms of phylogeny (Bolick, 1978; Blackmore *et al*., 1984), can be regarded as a primitive character of the group, which is in agreement with other morphological and molecular features.

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