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.


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, Stiffia, 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 phylogeographic 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.


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 Axioskop (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; sphaeroidal-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 unitined 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 costa. 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

<table>
<thead>
<tr>
<th>Types and taxa</th>
<th>Collection</th>
<th>Shape P/E</th>
<th>Polar diameter (µm)</th>
<th>Equatorial diameter (µm)</th>
<th>Exine thickness (µm)</th>
<th>Spine length (µm)</th>
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<tbody>
<tr>
<td>Type 1, subtype 1A</td>
<td></td>
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<tr>
<td>Gongylolepis R. H. Schomb. (14) 6</td>
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<tr>
<td>G. benthamiana R. H. Schomb</td>
<td>Steyermark &amp; Liesner 127536 (MO)</td>
<td>Subprolate</td>
<td>72–94</td>
<td>61–78</td>
<td>10–11</td>
<td>2.5–4</td>
</tr>
<tr>
<td>G. bracteata Maguire</td>
<td>Maguire 27903 (US)</td>
<td>Subprolate</td>
<td>79–92</td>
<td>64–78</td>
<td>9–13</td>
<td>5–7</td>
</tr>
<tr>
<td>G. colombiana (Cuatrec.) Cuatrec.</td>
<td>Maguire et al. 30080, 30136 (US)</td>
<td>Subprolate</td>
<td>90–113</td>
<td>78–88</td>
<td>10–14</td>
<td>4–5</td>
</tr>
<tr>
<td>G. huachamacari Maguire</td>
<td>Huber 12985 (US)</td>
<td>Subprolate</td>
<td>81–87</td>
<td>75–86</td>
<td>12–13</td>
<td>5</td>
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<tr>
<td>G. pedunculata Maguire</td>
<td>Maguire 35392 (FM)</td>
<td>Spheroidal</td>
<td>82–87</td>
<td>75–86</td>
<td>12–13</td>
<td>5</td>
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<tr>
<td>Type 1, subtype 1B</td>
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<tr>
<td>Duidaea marahuacensis Steyermark</td>
<td>Liesner 24644 (US)</td>
<td>Spheroidal</td>
<td>62–72</td>
<td>52–64</td>
<td>11–14</td>
<td>2.5</td>
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<tr>
<td>Glossarion Maguire &amp; Wurdack (1) 1</td>
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<tr>
<td>Glossarion rhodanthum Maguire &amp; Wurdack</td>
<td>Maguire et al. 37149 (US)</td>
<td>Prolate</td>
<td>74–80</td>
<td>56–60</td>
<td>12–16</td>
<td>2.5</td>
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<td>Quelchia N. E. Br. (5) 1</td>
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<tr>
<td>Quelchia bracteata Steyermark, Steyerm. &amp; Wurdack</td>
<td>Pipoly et al. 7217 (US)</td>
<td>Subprolate</td>
<td>55–62</td>
<td>45–48</td>
<td>7–10</td>
<td>2.5</td>
</tr>
<tr>
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<td>Eurydochus bracteatus Maguire &amp; Wurdack</td>
<td>Maguire et al. 42238 (US)</td>
<td>Prolate</td>
<td>72–80</td>
<td>54–60</td>
<td>8–10</td>
<td>2.5–3</td>
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<td>Salcedoa F. Jiménez R. &amp; Katinas (1) 1</td>
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<td>Salcedoa mirabolarium F. Jiménez R. &amp; Katinas</td>
<td>Veloz et al. 2383 (LP)</td>
<td>Prolate</td>
<td>45–56</td>
<td>66–83</td>
<td>7–9</td>
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<tr>
<td>W. crusiana Taubert</td>
<td>Ratter et al. 2615 (MO)</td>
<td>Prolate</td>
<td>68–75</td>
<td>50–58</td>
<td>10–12</td>
<td>4–5</td>
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<tr>
<td>Type 3, subtype 3A</td>
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<td>Chimantaea Maguire, Steyerm. &amp; Wurdack (9) 2</td>
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<tr>
<td>Chimantaea cinerea (Gleason &amp; S. F. Blake) Maguire</td>
<td>Steyermark 116028 (MO)</td>
<td>Subprolate</td>
<td>64–68</td>
<td>50–54</td>
<td>5–8</td>
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<tr>
<td>C. huberi Steyerm.</td>
<td>Huber 12034 (LP)</td>
<td>Subprolate</td>
<td>48–57</td>
<td>37–42</td>
<td>6</td>
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<td>Neblinaea Maguire &amp; Wurdack (3) 1</td>
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<tr>
<td>Neblinaea promontorium Maguire &amp; Wurdack</td>
<td>Silva &amp; Brazão 60895 (US)</td>
<td>Subprolate</td>
<td>62–70</td>
<td>50–55</td>
<td>7</td>
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<tr>
<td>Stiffia J. C. Mikan (7) 3</td>
<td></td>
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<tr>
<td>Stiffia parviflora (Leandro) D. Don St. unifora Ducke</td>
<td>Hering 7680 (LP)</td>
<td>Subprolate</td>
<td>46–52</td>
<td>35–42</td>
<td>5–9</td>
<td>c. 1–2</td>
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<tr>
<td>Stenopadus S. F. Blake 15 8</td>
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<tr>
<td>Stenopadus campestris Maguire &amp; Wurdack</td>
<td>Barriga 20878 (US)</td>
<td>Subprolate</td>
<td>59</td>
<td>41</td>
<td>7–8</td>
<td></td>
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<tr>
<td>S. colveii (Steyerm.) Pruski</td>
<td>García Barriga 20878 (US), Boom 9427 (US)</td>
<td>Prolate</td>
<td>81–96</td>
<td>59–67</td>
<td>6–10</td>
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<tr>
<td>S. huachamacari Maguire</td>
<td>Maguire et al. 30116 (MO)</td>
<td>Prolate</td>
<td>52–64</td>
<td>36–43</td>
<td>4–6</td>
<td></td>
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<tr>
<td>Type 3, subtype 3B</td>
<td></td>
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<tr>
<td>Stiffia chrysantha J. C. Mikan</td>
<td>Cabrera 12242 (LP)</td>
<td>Spheroidal</td>
<td>65–72</td>
<td>58–65</td>
<td>P: 11–16</td>
<td>E: 8–14</td>
</tr>
<tr>
<td>Type 4</td>
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<tr>
<td>Stomatochaeta (S. F. Blake) Maguire &amp; Wurdack (5) 1</td>
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<tr>
<td>Stoma tochaeta condensata (Baker) Maguire &amp; Wurdack</td>
<td>Liesner 18346 (MO)</td>
<td>Prolate</td>
<td>81–90</td>
<td>50–61</td>
<td>6–8</td>
<td></td>
</tr>
</tbody>
</table>

E, equatorial; P, polar.

1. Exine *Gongylolepis* type (Katinas *et al.*, in press) (for example, 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.

2. Exine *Wunderlichia* type (Tellería *et al.*, 2003; redefined in Katinas *et al.*, in press) (Figs 21, 25). Echinulate, 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 distinguished.

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
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, $P \times E = (55–113 \times 45–88) \mu m$. Colpi long or short, with psilate membrane, endoaperture lalongate, sometimes constricted at colpus, mesoaperturate. Exine Gongylolepis type, 7–17 \mu m thick, sometimes slightly thickened at the poles. Nexine c. 2–3 \mu m thick. Colpi long in Gongylolepis

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 \mu m; Fig. 12, 5 \mu m.
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 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,
Colpi long with psilate or scabrate membrane, with or without endocingulus and free endocolpi, mesoaperturate. Exine Wunderlichia 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 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 × E = (46–96 × 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;
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 endocinclus 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-
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...
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,
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 (Telléria et al., 2003). A gap is presented in the Stenopadus type as the combination of an anthomoid 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 Chimantaeae (*C. cinerea* and *C. huberi*), Nebilianeae (*N. promontorium*), Stifftia (*St. uniflora* and *St. chrysanthra*), and some species of Stenopadus (*S. campestris*, *S. colueii*, and *S. huachamacari*). Pollen of *St. chrysanthra* 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 have 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, Lockerman & 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. chinonensis*, *S. sericeus*, *S. connelli*, *S. jaunensis*, 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 & Martícorena, 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 (Asteroideae tribe, subfamily Asteroideae) (Wodehouse, 1926; Skvarla et al., 1977; Rowley, Claugh & 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 eca- veate and microechinate pollen (Wagenitz, 1955; Parra, 1969; Dimon, 1971; Nordenstam & El-Ghazaly, 1977; Blackmore, van Helvoort & Punt, 1984; Pehli-van, 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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