A SURVEY OF ANther GLANDS IN THE MIMOSoid LEGUME TReBS PARKitEAe AND MImoseAE

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In a broad survey of anther glands in the mimosoid legume tribes Parkieae and Parkieae, representatives from 30 genera with anther glands were studied using scanning electron microscopy. Four kinds of anther glands could be distinguished. The Piptadenia-type gland, found in all but four of the genera surveyed, is usually spherical to ellipsoid in shape and often borne on a stipe. The cells making up the gland vary in size among species and are often sculptured. Six different kinds of sculpturing can be recognized: smooth, reticulate, striate, rugulate, scabrate, and papillate. The Gagnebina-type gland is the least specialized, consisting of a simple extension of the connective with irregularly projecting cells. The Prosopis africana-type gland is borne ventrally between the thecae, the connective extending hump-like over the apex of the anther. The Pentaclethra-type gland, found only in the genus Pentaclethra, is distinguished by a median dorsal furrow and a ventral conical structure similar to a food body or osmophore. Anatomical sections revealed two different subtypes within the Piptadenia-type gland. Some glands are composed of a homogeneous matrix of isodiametric cells, whereas others have two layers: a peripheral layer of large radially elongated cells, and a central sphere of smaller isodiametric cells and large air spaces. Some characters of anther glands have clear taxonomic significance, and more detailed surveys within genera will undoubtedly provide additional taxonomic markers.

Key words: anther glands; anther appendages; anther morphology; Fabaceae; Mimosoideae; Mimosae; Parkieae.

Anther glands in the Mimosoideae are extensions of the anther connective that have a secretory function (Chaudhry and Vijayaraghavan, 1992; Endress, 1994). Although connective protrusions are relatively common in angiosperms (Endress and Stumpf, 1991), it is less common that these protrusions are differentiated as secretory organs. Among the lower Rosidae, Endress and Stumpf (1991) reported anther glands from Crassulaceae, Cephalotaceae, some Mimosoideae, and some Sapindaceae and Rutaceae. Tucker (1996) noted anther appendages among some papilionoid and caesalpinoid legumes as well as in the mimosoids. They have also been reported from the Myrtaceae (Beardsell, Williams, and Knox, 1989; Landrum and Bonilla, 1996), Violaceae (Fahn, 1979) and Solanaceae (Sazima et al., 1993).

Until recently, anther glands have figured prominently in the taxonomy of the subfamily Mimosoideae. In 1842, Bentham recognized two subtribes in the tribe Eumimo- seae based on the presence (Adenantherae) or absence (Gymnantherae) of anther glands. Although he was beginning to question the reliability of this character by 1875 when his comprehensive treatment of the Mimosoideae appeared, Bentham nonetheless recognized the tribe Adenantherae ("usually glanduliferous") as distinct from the tribe Eumimo- seae ("usually without glands"). This classification persisted in one form or another until 1981, when Elias combined the two tribes as the Mimo- seae, noting that floral and pollen characters indicated they did not form natural groups.

It is surprising, then, that anther glands in the Mimosoideae have been so little studied. Tucker (1988) in her work on the floral development of Neptunia pubescens noted varying expression of anther glands between different sexual morphs. In male flowers, the glands were dactyloid and proportionately larger than in perfect flowers, and in sterile flowers, the staminodia occasionally bear only an apical gland. Tucker hypothesized that the glands might serve an elater-like function in addition to acting as attractants.

Anther glands are usually reported to function in pollination (Chaudhry and Vijayaraghavan, 1992; Endress, 1994), but there is scant evidence to support this assertion. Chaudhry and Vijayaraghavan (1992) studied the development of anther glands in Prosopis juliflora and found that they are made up of secretory cells that produce a protein/carbohydrate exudate. The cells lyse, and the exudate is passed through cuticular openings to the exterior of the gland. Chaudhry and Vijayaraghavan also noted that anther glands function in pollination by providing a food source to attract pollinators.

To date there has been no broad comparative study of the structure of anther glands in the Mimosoideae. The objectives of the present study were to: (1) survey the structure of anther glands in the mimosoid tribes Parkieae and Mimosae (here referred to as the basal mimosoids)
using scanning electron microscopy (SEM); (2) examine the internal structure and chemistry of the glands using light microscopy and histochemistry; and (3) to gather data on mimosoid taxa and a suitable Caesalpinoid outgroup (*Burkea*), which later can be placed in a phylogenetic context.

**MATERIALS AND METHODS**

The SEM study included samples from most genera in the Mimosaceae and Parkiaceae from which anther glands have been reported, and one genus from the Caesalpinioideae (see Table 1, vouchers in Appendix 1). The only genera not examined were *Leucaena* (currently being studied by C. Hughes, Oxford Forestry Institute), and the recently described *Lemurodendron* (Villiers and Guinet, 1989) from Madagascar. *Calliandra* is reported by Hernández and Guinet (1990) as occasionally having an anther appendage, as was also omitted as none of the specimens we examined had appendages. Two or more species were examined in 11 of the genera, in order to provide a rough assessment of variation within genera. Samples of ten species were studied from both material in liquid and reconstituted dried material to evaluate differences caused by preservation. It was found that dried material did not differ significantly from material in liquid in most characters. An exception was surface sculpturing of the cells of the anther connective and the anther gland, which was somewhat smoother and less distinct in the reconstituted material. In general, it was possible to score herbarium material for cell sculpturing with some degree of confidence, in spite of minor differences due to preservation.

Material preserved in FAA (formalin-acetic acid-alcohol) was put through an ethanol dehydration series and critical-point dried using a Toumimi critical-point dryer. Samples were then sputter-coated using a BAL-TEC sputter-coater, and observed on a Hitachi 4500-S SEM. Dried material from herbarium specimens was rehydrated in a 5% solution of 286 **[Vol. 84A MERICAN J OURNAL OF B OTANY**

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### Table 1. Distribution of anther glands in genera of the Parkiaceae and Mimosaceae

<table>
<thead>
<tr>
<th>Genus</th>
<th>Total no. species</th>
<th>No. species with glands</th>
<th>No. species sampled/SEM</th>
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</thead>
<tbody>
<tr>
<td>Parkiaceae</td>
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<tr>
<td><em>Parapiptadenia</em></td>
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<tr>
<td><em>Parkia</em></td>
<td>8</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td><em>Pentaclethra</em></td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Mimosaceae</td>
<td></td>
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<tr>
<td><em>Adenanthera</em></td>
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<td>12</td>
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</tr>
<tr>
<td><em>Alantisolodendron</em></td>
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<tr>
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<tr>
<td><em>Calpocalyx</em></td>
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<tr>
<td><em>Cyclodiscus</em></td>
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<td><em>Desmanthus</em></td>
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<td>24</td>
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<tr>
<td><em>Dichrostaechys</em></td>
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<tr>
<td><em>Elephantorrhiza</em></td>
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<tr>
<td><em>Goldmania</em></td>
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<td></td>
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<tr>
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<tr>
<td><em>Newtonia</em></td>
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<td><em>Parapiptadenia</em></td>
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<td>6</td>
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<td><em>Pitaxylocarpa</em></td>
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<td>2</td>
<td></td>
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<tr>
<td><em>Prosopis</em></td>
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<td>4</td>
<td></td>
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<td><em>Schleinitzia</em></td>
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<td>4</td>
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<td><em>Stryphnodendron</em></td>
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<td>21</td>
<td></td>
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<tr>
<td><em>Tetrapleura</em></td>
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<td>2</td>
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</tr>
<tr>
<td><em>Xylia</em></td>
<td>8</td>
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<td></td>
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### RESULTS

**Variation in the presence of anther glands**—Anther glands are present in the majority of genera in the basal tribes of mimosoids, having been recorded from 33 of 38 genera (Table 1). Only five genera are reported always to lack some sort of extension of the anther connective: *Abrevillea, Amblygonocarpus, Kanaloa,* and *Mimos* in the tribe Mimosae; and *Mimozyganthus* in the tribe Mimozyganeae. All of these are either mono- or ditypic except *Mimosa, Leucaena,* although frequently reported to lack anther glands, in fact includes five species with connective appendages (C. Hughes, Oxford Forestry Institute, personal communication), and *Desmanthus* has one recently described species with anther glands (Contreras, 1986; Luckow, 1993). In addition to the latter two genera, nine others are polymorphic for the presence of anther glands: *Alantisolodendron, Anadenanthera, Dichrostaechys, Entada, Neptunia, Newtonia, Parkia, Prospis,* and *Xylia* (Table 1). *Calliandra,* a monotypic genus from Mexico, is reported to have anther glands only rarely and is thus polymorphic within one species (Hernández and Guinet, 1990).

Lewis and Elias (1981) noted that species of *Entada, Dichrostaechys,* and *Gagnebina* from Madagascar tend to lack anther glands, and interpreted this as local specialization. Although this generalization is true for *Entada* and *Dichrostaechys,* there are notable exceptions. For example, the Madagascan species of *Xyloclécarpa* lacks glands. Species of the Madagascan gen-
era Gagnebina and Alantsilodendron do not lack glands per se but have a unique kind of appendage (see below), and Alantsilodendron is polymorphic for appendages within Madagascar. The species of Newtonia lacking anther glands are found throughout the range of the genus in Africa. Only Australian species of Neptunia lack anther glands, except for the widespread aquatic species, *N. oleracea*. Desmanthus and Anadenanthera are the only exclusively New World taxa that are polymorphic for the presence of anther glands. In the few polymorphic genera that have been analyzed cladistically, absence of anther glands represents a secondary loss rather than the primitive condition (Luckow, 1993; Luckow and Hopkins, 1995). For example, almost all Old World species of Parkia have lost anther glands, but there are several independent losses among the New World species as well (Luckow and Hopkins, 1995).

**Variation in morphology**—Morphological variation of anther glands and anthers among the 30 genera surveyed is summarized in Tables 2 and 3. A complete set of photographs is available on the World Wide Web at [http://www.bio.cornell.edu/hortorium/luckow/](http://www.bio.cornell.edu/hortorium/luckow/). As noted by Endress and Stumpf (1991), mimosoid anthers are, with several notable exceptions, introrse and dorsifixed (Table 2, Figs. 3–8). The anthers of bat-pollinated species of Parkia are nearly basifixed, with the filament greatly thickened and tucked into a basal fold (Fig. 5). *Burkea*, our sample of Caesalpinioideae, was the only species in the survey to have latrorse anthers (Figs. 1, 2),

### Table 2. Characteristics of anthers from SEM survey. Abbreviations are as follows: AG = anther gland, conn = connective, n. = nearly, int/lat = introrse but with the central part of the connective showing through on the ventral side.

<table>
<thead>
<tr>
<th>Species</th>
<th>Position of stomia</th>
<th>Filament attachment</th>
<th>Dorsal furrow (μm)</th>
<th>Anther size (μm)</th>
<th>Length ratio (AG/Anther)</th>
<th>Conn. cell sculpture</th>
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</thead>
<tbody>
<tr>
<td><em>Burkea africana</em></td>
<td>latrorse</td>
<td>n. basifixed</td>
<td>1/central</td>
<td>1800</td>
<td>1:11</td>
<td>smooth</td>
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<tr>
<td><em>Parkia multijuga</em></td>
<td>introrse</td>
<td>dorsifixed</td>
<td>2/thecae</td>
<td>1287</td>
<td>1:6</td>
<td>striate</td>
</tr>
<tr>
<td><em>Parkia velutina</em></td>
<td>introrse</td>
<td>dorsifixed</td>
<td>2/thecae</td>
<td>832</td>
<td>1:5</td>
<td>striate</td>
</tr>
<tr>
<td><em>Pentaclethra macroloba</em></td>
<td>introrse</td>
<td>dorsifixed</td>
<td>1/central</td>
<td>1500</td>
<td>1:3</td>
<td>smooth</td>
</tr>
</tbody>
</table>

*Caesalpinioideae*  
*Burkea africana*  
*Parkieae*  
*Pentaclethra macroloba*  
*Mimoseae*  
*Adenanthera microsperma*  
*Adenanthera pavonina*  
*Alantsilodendron alauudianum*  
*Anadenanthera macrocarpa*  
*Calpocalyx brevibracteatus*  
*Calpocalyx dinklagei*  
*Clycodiscus gabunensis*  
*Desmanthus balsensis*  
*Dichrostachys cinerea*  
*Dichrostachys spicata*  
*Elephantorrhiza elephantina*  
*Elephantorrhiza goetzii*  
*Entada manii*  
*Entada polystachya*  
*Entada wahlbergii*  
*Filaeeopsis discophora*  
*Gagnebina commersoniana*  
*Gagnebina pervilleana*  
*Indopiptadenia oudhensis*  
*Microlobius foetidus*  
*Neptunia pubescens*  
*Newtonia suseolens*  
*Parapiptadenia rigida*  
*Piptadenia adiantoides*  
*Piptadenia viridiflora*  
*Piptadeniastrum africanum*  
*Plathymentia reticulata*  
*Prosopis juliflora*  
*Prosopis fasifera*  
*Pseudopiptadenia leptostachya*  
*Pseudoprosopis claessensi*  
*Schleinitzia insularum*  
*Strypnodendron pulcherrimum*  
*Strypnodendron sp.*  
*Tetrapleura tetraptera*  
*Xerocladia viridiramis*  
*Xylica torreana*  

March 1997 | LUCKOW AND GRIMES—ANTHER GLANDS IN MIMOSOID LEGUMES | 287
Figs. 1–9.  1–2. Burkea africana (Caesalpinioideae). 1. Anther with latrorse dehiscence. Bar = 600 μm. 2. Connective extension. Bar = 150 μm. 3. Ventral view of an anther of Piptadeniastrum africanum. The gland is relatively large as compared to the size of the anther. Bar = 150 μm. 4. Ventral view of an anther of Indopiptadenia oudhensis having nearly latrorse dehiscence. The gland is relatively small as compared to the size of the anther. Bar = 375 μm. 5. Dorsal view of anther of Parkia platycephala. Note the lateral furrows between the thecae and the connective. Bar = 429 μm. 6. Dorsal view of an anther of Piptadenia viridiflora. There is a U-shaped furrow between the thecae and the connective, and
although anthers of the mimosoid Indopiptadenia (Fig. 4) are nearly latrorse. Dichrostachys and Alantisildendron often have the anther sacs displaced laterally, such that the connective is visible on the ventral side between the thecae (Fig. 8), and the stoma are thus somewhat lateral. In several genera, there are two distinct furrows on the dorsal surface of the anther where the thecae meet the connective (Fig. 5); in Piptadenia viridiflora, these furrows are continuous and form a U-shaped structure (Fig. 6). A single median dorsal furrow, common in the Caesalpinioideae (see Endress and Stumpf, 1991), was seen among the mimosoids only in Pentaclethra (see Fig. 30).
Four distinct kinds of anther glands can be recognized in the lower mimosoids (Table 3), which we have called the Piptadenia type, the Gagnebina type, the Prosopis africana type, and the Pentaclethra type of glands.

1) The Piptadenia type is the most common, being found in all but four of the genera surveyed. The anther glands are most often spherical in shape (Figs. 3, 4–8), but may also be ellipsoid (Fig. 9), clavate (Fig. 10), or dolabiform (Fig. 11). They are usually borne on a stalk (Figs. 6, 8–12), which varies in length among and within genera. The longest stipe occurs in Dichrostachys (Fig. 8); occasionally the gland may be completely sessile (Fig. 7). The stipe also varies in degree of differentiation from the main body of the gland. In Dichrostachys (Fig. 8), the cells of the stipe are greatly elongated, whereas in Pseudoprosopis (Fig. 9) they are smaller than the gland cells and rectangular in outline. In other species, the stalk gradually tapers distally to form the tine, which is only poorly differentiated from it (Fig. 10). In many species, anther glands are caducous, and the structure of the stipe is probably intimately related to the degree of persistence of the gland on the anther.

The Piptadenia-type anther gland ranges in size from 75 to 227 μm, most species falling within the range of 100–200 μm (Table 3). Although this range is relatively narrow, the size of the anthers varies among genera, and thus the relative proportions of these structures, expressed here as a ratio of anther gland/anther length (Table 2). For example, the anther glands of Piptadeniastrum (Fig. 3) and Indopiptadenia (Fig. 4) do not differ greatly in absolute size (122 and 96 μm, respectively), but the relative proportions are quite different. In Piptadeniastrum, the glands are nearly as conspicuous as the anthers (1:2 length ratio), but in Indopiptadenia the glands are quite small relative to the anther (1:10 length ratio).

Among species, cells of the anther gland also vary in size (and thus the number of cells making up the gland) and surface characteristics. Exceptionally large cells are found in a group of Old World genera, including Adenanthera (Figs. 12, 15), Calpocalyx, and Tetrapleura. At the other end of the spectrum is Prosopis mesicano, with very many small cells making up the gland epidermis (Fig. 13).

Five kinds of sculpturing of the cell surfaces can be distinguished in the Piptadenia-type gland (Table 3): reticulate (Fig. 14), scabrate (Fig. 15), smooth (Fig. 16), striate (Fig. 17), and rugulate (Fig. 18). Reticulate sculpturing is rare, found only in the genus Parapiptadenia. Completely smooth surfaces are also rare, and are for the most part confined to the putatively basal lineages of mimosoids, e.g. Parkia and Pentaclethra. The surfaces of the cells of most species are striate. The striations may be nearly parallel to one another and continuous (scored as striate) or broken up and at angles (scored as rugulate). These tend to grade into one another, and may vary within a single individual. The results in Table 3 refer to the state in the majority of the cells within a sample or group of samples. In a few species, the rugulae are very smooth and are scored as scabrate (Fig. 15).

In many genera, the edges of the cells are smooth, and sculpturing is confined to the central part of the cell (Figs. 19, 20), whereas in others the entire cell surface is sculptured (Figs. 17, 18). The proportion of the cell that is smooth varies continuously among genera. It was thought that this character might reflect different developmental stages, but an examination of anther glands from young buds to mature flowers demonstrated that such is not the case (Figs. 19, 20).

2) The Gagnebina type. In contrast to the “stalked-sphere” morphology of the Piptadenia type of gland, the Malagasy endemics Gagnebina and Alantsiloendron have an elongate conical appendage formed by the extension of the connective (Figs. 21–23). The cells of the appendage grow outward in several planes, forming unique finger-like projections (Figs. 17, 22). This is unlike typical anther gland cells, which project uniformly from the surface (e.g., Fig. 12). The cells of anther glands of Xylia (Fig. 24) may also project outward in several planes, similar to those of the Gagnebina type. The cells of the Gagnebina-type appendage are usually striate throughout, lacking the smooth borders seen on many Piptadenia-type glands, but may be smooth toward the apex of the appendage (Fig. 22). Burkea (Caesalpinioideae) has a connective extension similar to that in Gagnebina, but the cells do not project from the surface and are smooth throughout (Figs. 1, 2).

3) The Prosopis africana type. In contrast to other species of Prosopis that display the typical Piptadenia-type stalked-sphere morphology (Fig. 28), Prosopis africana has very unusual morphology of the anthers and anther gland (Figs. 25–27). The anther is V-shaped, in contrast to the typical mimosoid anther in which the thecae are borne more or less parallel to one another (Figs. 3, 4). The stomia do not extend above the shoulder as in most species (e.g., Fig. 4), but are short and form small pockets on the ventral surface (Fig. 25). The connective extends hump-like over the apex of the anther and the sessile anther gland is borne ventrally between the thecae (Figs. 25, 26). In all other species of mimosoids examined, the gland was either apical or dorsal (e.g., Figs. 3–8). The gland is a triangular-shaped flap in rehydrated material, although it is likely to be different in fresh or preserved flowers. A drawing in Flora of Tropical East Africa (Brenan, 1959, p. 34) depicts the connective as forming a triangular hood over an inflated bulbous gland, and it may be that the this triangular flap is inflated in fresh material. However, the drawing is not consistent with our observations of the shape of the connective, and the depiction of the dorsal view of the anther also disagrees with our observations. Prosopis africana is the only species in which the sculpturing on the cells of the anther gland were found to be papillate (Fig. 27).

4) The Pentaclethra type. Pentaclethra macroloba has exceptionally large anthers and glands, nearly twice as large as any other species examined (Figs. 29–32, Tables 2, 3). The dorsal side of both the anther and the gland has a median furrow (Fig. 30). Median dorsal furrows are characteristic of the Caesalpinioideae, and they were not observed in any other mimosoids in this study. The gland is sessile, and the cell surfaces are completely smooth. The most striking feature is a specialized conical structure similar to a food body or osmophore borne on the ventral surface of the gland just above the anther sacs (Figs. 31, 32). Such a structure was not seen elsewhere in the Mimosioideae.

Changes in the cells of anther glands at different de-
Figs. 19–27. 19–20. Cells of the anther gland of *Dichrostachys cinerea* prior to anthesis (19) and postanthesis (20). Notice the perforations in the cells in the postanthesis gland. Bars = 15 μm. 21. Ventral view of an anther of *Alantsilodendron alluaudianum*. The connective is visible between the thecae, and there is a small connective extension. Bar = 275 μm. 22–23. Connective extension of *Gagnebina pervilleana*. The cells of the appendage grow outward in several planes. Bars = 50 and 20 μm, respectively. 24. Anther gland of *Xylia torreana* in which the cells are also nonplanar. The cells of the stalk are smaller and more regularly arranged than those of the anther gland. Bar = 100 μm. 25–27. Anther and gland of *Prosopis africana*. 25. Ventral view of V-shaped anther showing pocket-like stomia. Bar = 200 μm. 26. Triangular anther gland borne
velopmental stages were observed in *Dichrostachys cinerea* and *Schleinitzia insularum*. The cells of *D. cinerea* lose turgor as they mature (Figs. 19, 20), and cracks appear in the smooth areas of the cells at anthesis (Fig. 20). Anther gland cells of *S. insularum* also lose turgor as they mature (Figs. 33, 34), but the cells collapse at anthesis (Fig. 35). Although this collapse may appear somewhat similar to the finger-like projections in the *Gagnebina* type of gland (Figs. 21–23), the cells of the latter actually grow outward in several planes, even in young buds.

Variation in anatomy and histochemistry—Light microscopy revealed two anatomical subtypes within the *Piptadenia* type of gland. The *Piptadenia* subtype, observed in *Dichrostachys, Elephantorrhiza, Piptadenia, Prosopis, Schleinitzia*, and *Styrphnodendron*, has cells that are isodiametric and of nearly equal size throughout (Figs. 36–38). The epidermal cells are not well differentiated from those at the center of the gland, nor are there any large intercellular spaces. Most cells contain areas that stain red in safranin/fast green (Fig. 38), and these are largest in the peripheral cells. These areas are presumed to be vacuoles, as a red-staining nucleus is also visible in some cells.

The *Adenanthera* subtype, found in *Adenanthera* and *Calpocalyx*, consists of two well differentiated layers of cells (Figs. 39, 40). The cells of the epidermal layer are relatively large (= 50 × 20 μm) and radially elongated. They also contain red-staining inclusions. The center of the gland consists of smaller isodiametric cells with large intercellular spaces (Fig. 40). It is unlikely that the air spaces are artifacts, as the overall structure of these glands is very similar to that observed in the Myrtaceae by Beardsell, Williams, and Knox (1989). In none of the species examined with light microscopy was any well-developed vascular tissue observed in the anther gland or stalk.

The anatomy of the *Gagnebina* type of anther gland is most similar to the *Piptadenia*-type, consisting of a homogenous matrix of cells (Figs. 41, 42). The cells of the appendage of *Alantsilodendron alluaudianum* stain heavily, as do the connective cells, indicating that they probably contain significant amounts of tannins (Fig. 41).

Additional histochemical tests for polyphenols (Ferric Chloride), lipids (Nile blue, Sudan IV), and proteins (Coomassie Blue) showed no reaction with the vacuolar contents (Table 4). The cell walls of both the connective and the anther glands showed a positive reaction with ferric chloride in three species, indicating that they probably contain tannins. In most cases, the reactions of the cell walls of the anther glands paralleled those of the connective, and a positive reaction probably indicates their derivation from the tissue of the connective rather than having any functional significance. Given the overall negative reactions to the histochemical tests in Table 4, it seems likely that the vacuoles contain either carbohydrates or perhaps terpenoids. Gas chromatographic studies are currently underway to more precisely characterize the chemistry of the anther glands.

**DISCUSSION**

**Phylogenetic implications**—The anther appendage of *Burkea* (Caesalpinioideae) is relatively simple when compared to those in the Mimosoideae, consisting of an extension of the connective, the cells not well differentiated relative to the rest of the anther (Figs. 1, 2). In contrast to most mimosoids, the anthers are latrorse and there is no surface sculpture on the cells of either the connective or anther appendage. It is not clear that any secretory function is associated with the connective extension.

It is tempting to consider the *Gagnebina*-type gland as “primitive” within the mimosoids, and possibly transitional between *Burkea* and the rest of the mimosoids, because of its simple appendage-like structure. However, there are notable differences, such as the projection of the cells in different planes and surface sculpturing on the cells in the mimosoid genera. Furthermore, based on recent phylogenetic analyses (Luckow, 1995), the *Gagnebina*-type gland could be viewed as a modification of the *Piptadenia*-type gland, a hypothesis strengthened by the anatomical similarities between the two types. Thus, it seems unlikely that appendages in *Burkea* are homologous with those in the Mimosoideae.

*Pentaclethra* is usually considered to be basal among the mimosoids, linking them to the Caesalpinoid genus *Dimorphandra*. Both the anther and the gland of *Pentaclethra* share features suggestive of the Caesalpinioideae, including relatively large size of the anther and a median dorsal furrow. Using *Burkea* as an outgroup, it is also likely that smooth surfaces on the anther connective and gland cells are “primitive” features.

Nevertheless, the gland of *Pentaclethra* has many unique characters not seen in any other genera, such as the bizarre conical structure on the ventral surface. The function of this structure is unknown. *Pentaclethra macroloba* is reported to be beetle-pollinated (Kress and Beach, 1994), and it may be that the gland functions in scent production and emission. Alternatively, ant associations have been reported for this species (Bennett and Breed, 1985), and the conical structure may be some sort of food body. Studies are currently underway to investigate these hypotheses.

Our work provides further evidence that the tribe Parkeae (*Pentaclethra* + *Parkia*) is not a natural group. The only feature of the anther gland that the two genera share is smooth surfaces on the cells making up the gland. The *Piptadenia*-type gland of *Parkia* is typical of the tribe Mimosoideae. Furthermore, one of the more unusual features of the anther glands of *Parkia*, lateral dorsal furrows at the junction of the connective with the theca, is not seen in *Pentaclethra*, but is found in other genera in the tribe Mimosoideae.

Among some genera of the Mimosoideae, characters of the anther glands demonstrate close correspondence to previously proposed phylogenetic hypotheses. For example, anther glands of *Adenanthera*, *Pseudoprosopis*, and *Tetrapleura* are composed of exceptionally large...
Figs. 28–35. 28. Anther of *Prosopis juliflora*. Note the typical stipitate *Piptadenia*-type morphology. Bar = 231 μm. 29–32. Anther and gland of *Pentaclethra macroloba*. 29. Ventral view of the anther and gland. Bar = 500 μm. 30. Dorsal view showing dorsal furrow on both anther and gland. Bar = 500 μm. 31. Anther gland with unique conical structure. Bar = 200 μm. 32. Closer view of the conical structure on the ventral surface of the gland. Bar = 75 μm. 33–35. Anther gland of *Schleinitzia insularum* before (33) and after (34, 35) anthesis. The cells collapse at maturity. Bars = 50 μm in Figs. 33 and 34 and 15 μm in Fig. 35.
Figs. 36–42. 36–37. Paraffin sections of an anther (36) and anther gland (37) of *Piptadenia viridiflora*. The anther gland is homogeneous throughout, with many small isodiametric cells. Bars = 1 mm in Fig. 36, 60 μm in Fig. 37. 38. Anther gland of *Prosopis pubescens* which also consists of a homogeneous layer of cells. Note the red-staining inclusions in the cells. Bar = 30 μm. 39–40. Anther glands of *Calpocalyx dinklagei*. There are two layers of cells: a peripheral layer of large radially elongated cells with red inclusions and an internal sphere of smaller isodiametric cells with large air spaces between them. Bars = 2 mm in Fig. 39 and 60 μm in Fig. 40. 41. Anther glands of *Alantsilodendron alluaudianum*. The projecting, finger-like cells of the anther glands stain very dark in safranin/fast green. Bar = 90 μm. 42. The anther gland of *Gagnebina pervilleana* is composed of a homogeneous layer of cells. Note the septae between the pollen grains. Bar = 100 μm.
cells with scabrate sculpturing (Table 3, Figs. 9, 12, 15). These genera, along with the genus *Amblygonocarpus* (which lacks anther glands), were united as the *Adenanthera* group by Lewis and Elias (1981).

Likewise, our results accord well with recent work on the *Xylica*, *Dichrostachys*, and *Leucaena* groups (Harris et al., 1994; Luckow, 1995). For example, the clavate shape of the anther glands of *Neptunia* and *Schleinizia* (Table 3) is consistent with general ideas of relationship between these taxa (Luckow, 1995). In this study, the Gagnebina-type gland is found only in *Alantsilodendron* and *Gagnebina*, two genera considered to be closely related based on other data. The unusual nonplanar arrangement of cells of the Gagnebina-type gland occurs also in *Xylica* (Fig. 22), recently considered an outgroup to the other two genera. The closely related genera *Dichrostachys* (Fig. 7) and *Alantsilodendron* (Fig. 19) have the unusual feature of a connective visible on the ventral side between the thecae.

*Prosopis africana* has consistently been recognized as anomalous within the genus, and has been placed in its own section (Bentham, 1875; Burkart, 1976). Unlike other species of *Prosopis*, *P. africana* lacks stipitate spines and brachyblasts, has internally glabrous petals, and pollen with costa (Guinet, 1969). Guinet (1969) considered it to be closest to *Entada* or *Newtonia*, based on characters of the pollen. Our observations confirm the uniqueness of *P. africana*. Many characters, such as the V-shaped anther, the small stoma, and the structure of the anther gland, are singular not just within *Prosopis*, but within the Mimosae as a whole.

In a few cases, characters of the anther glands suggest novel hypotheses of relationship that need to be explored further. For example, the anatomy of the anther glands of *Calpocalyx* and *Adenanthera* is similar and quite different from that of the other genera examined (Figs. 39, 40). *Calpocalyx* was considered most closely related to *Xylica* in Lewis and Elias’ scheme (1981), but these data indicate that it may be related to the *Adenanthera* group. A more exhaustive survey of the anatomy of the relevant genera is needed to demonstrate this.

*Piptadenia* and *Entada* show remarkable infrageneric variation in characters of both the anthers and glands (Tables 2, 3). The two species of *Piptadenia* examined differed in the shape of the anther, the presence of a U-shaped dorsal furrow defining the thecae, the anther glands being stipitate or sessile, and the amount of the cell surface that is sculptured. The three species of *Entada* varied in many of the same characters (anther shape, glands stipitate or sessile, and amount of sculpturing) as well as in the size of the anthers. Infrageneric variation in the structure of anther glands has also been reported for *Schleinizia* (Nevling and Niezgoda, 1978), and comprehensive studies of the anther glands in these genera may shed light on the relationships among their species.

Although a phylogenetic analysis of the basal mimosoids is needed to unequivocally assess the homology of anther glands among the genera, it seems likely that the Piptadenia-type gland represents a developmentally homologous structure. The uniqueness of the anther gland of *Pentaclethra*, as well as the overall similarity of the anthers to those of other Caesalpinioideae, suggest it may not be homologous to those of the rest of the Mimosoideae.

**Functional considerations**—At least four hypotheses for the function of anther glands in the Mimosoideae can be proposed. The hypothesis that has been advanced most often is that they act as a food reward for pollinators, i.e., that the insect pollinates the flower while eating the glands (Chaudhry and Vijayaraghavan, 1992). A second hypothesis, suggested by Endress (1994), is that anther glands exude a sticky substance that attaches pollen to the bodies of floral visitors. Another possibility is that anther glands could function to protect the developing anthers and ovariess from insect predators. The glands form a mass of tissue at the apex of the flower in bud, and the glands are often caducous at anthesis, suggesting that they might function prior to anthesis. A fourth hypothesis, recently suggested by Landrum and Bonilla (1996), is that anther glands might function to attract pollinators as well as provide a reward. This is supported by several lines of evidence from our own work. The *Adenanthera* type of anatomy is very similar to that seen in the osmophores of other plants which function in the production and emission of odor. Vogel (1990) characterized osmophores as having large papillate epidermal cells, and internal aeration via intercellular spaces, both features of the *Adenanthera* type of gland. Sazima et al. (1993) reported this anatomical structure in the elaborated anther connectives of *Cyphomandra* (Solanaceae), which produce perfume as a floral reward for euglossine bees. The unique structure of the gland of *Pentaclethra* is likewise very suggestive of an osmophore.

It is not clear from the present data exactly how anther glands function in the Mimosae, nor what the actual mode of secretion might be. Given the morphological and anatomical diversity observed, it might be that all of the above hypotheses are valid, and anther glands serve different purposes in different taxa. We are currently collecting additional chemical data as well as field observations of insect visitors in order to test these hypotheses.

**LITERATURE CITED**


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**Table 4. Results of histochemical tests on the anther glands of four genera. Rxn = reaction.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Ferric chloride</th>
<th>Nile blue</th>
<th>Sudan IV</th>
<th>Coomassie blue</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dichrostachys</em></td>
<td>Cell walls</td>
<td>Cell walls</td>
<td>Cell walls</td>
<td>Cell walls</td>
</tr>
<tr>
<td><em>Schleinizia</em></td>
<td>Cell walls</td>
<td>No. Rxn.</td>
<td>Cell walls</td>
<td></td>
</tr>
</tbody>
</table>


APPENDIX 1. List of vouchers of specimens used in the anther gland study. The herbaria in which the vouchers are deposited are in parentheses. An asterisk indicates that the specimen was pickled; unmarked samples were from dried herbarium specimens.

Mimosoideae

Anadenanthera microsperma Teyms. & Binn. G. A. Avery 819 (NY), S. C. Tucker 26451 (LSU)*

Anadenanthera pavonina L. J. Armstrong 36-85/86/Tucker 27998 (LSU)*, Lorenz 7094 (NTBG)*

Antillocodium alluaudianum (R. Vig.) Villiers Luckow 4113 (BH)*

Anadenanthera macrocarpa (Benth.) Brenan Renzoize 3502 (NY)

Calpocalyx brevibracteatus Harms J. Deaw. Sp. 353 (NY), G. Pyne 26 (K)*

Calpocalyx dinklagei Harms D. W. Thomas 4722 (NY), J. P. M. Brenan 9298 (K)*

Clycodiscus gabunensis Harms J. F. E. de Wilde 7872 (NY)

Desmanthus balsensis J. L. Contreras L. J. Contreras 1145 (TX)

Dichrostachys cinerea (L.) Wight and Arnott J. H. Ross 1934 (NY), Luckow s.n. (BH)*

Dichrostachys spicata (F. Muell.) Dom. Luckow s.n. (BH)*

Elephantorrhiza elephantina (Burch.) Skeels (received as E. bur- chellii Benth.) Drex s.n. (NY)

Elephantorrhiza goezeti (Harms) Harms Lorence 7696 (NTBG)*

Entada waltherii Harv. (received as E. flexuosa Hutch. & Dalz.) A. A. Bullock 1168 (K)*

Entada manni (Oliv.) Tisserant Onachie F. H. J. 3355 (K)*

Entada polystachya (L.) DC. A. Molina R. 12875 (NY)

Filaropsis discophora Harms Le Testu 9434 (K)

Gagnebina commersoniana (Baill.) R. Vig. Boizen 2759 (NY)

Gagnebina pervileana (Baill.) G. P. Lewis & Guinet Luckow 4221 (BH)*

Indopiptadenia oualensis (Brandis) Brenan Thompson 135 (K) HORT.

Microlobius foetidus (Jacq.) M. Sousa & G. Andrade C. E. Hughes 1719 (NY)

Neptania prostrata (Lam.) Baill. A. T. A. Ritchie 1412 (K)*

Neptania pubescens Benth. Luckow s.n. (BH)*

Newtonia suaveolens (Miq.) Brenan R. T. Pennington, E. C. Rowe, et al. 85 (K)*

Parapiptadenia rigida (Benth.) Brenan J. M. Silva 891 (NY)

Parkia multiflora Benth. A. A. Oliviera 383 (NY)

Parkia platycaphala Benth. A. M. Amorim 577 (NY)

Parkia velutina B. J. M. Pires 51584 (NY)

Pentaclethra macroloba (Willd.) Kunze Bishby 1264 (NY)

Piptadenia adiantoides (Spr.) Macbride H. C. de Lima 2953 (K)*

Piptadenia viridiflora (Kunth) Benth. G. Aymard 7759 (NY), G. Lewis 1772 (LSU)*

Piptadeniastrum africanaum (Hook. f.) Brenan Zenker 2764 (K)

Plathymeria reticulata Benth. Sidney 1191 & Onishi 412 (NY)

Prosopis africanaum Mexican (Dressler) Burkart Burkart Moran 17061 (NY)

Prosopis africana (Guill. & Perr.) Rauch. Kotschy 387 (NY)

Prosopis pubescens Benth. L. C. Higgins 14418 (NY), Tucker 28899 (LSU)*

Prosopis juliflora (Swartz) DC. Pennington & Sarakah K. 9508 (NY), Tucker 28045 (LSU)*

Pseudopiptadenia leptostachya (Benth.) Rauchert E. Pereira 7152 (NY)

Pseudoprosopis callesensii (de Wild) Gilbert & Bouquet G. Trou- pio 5414 (NY), A. Troupin 3727 (K)*

Schleiniizia insularum (Guill.) Burkart Rinehart 17441 (K), Luckow s.n. (BH)*

Styphnodendron pulcherrimum (Willd.) Hochr. J. M. Pires & N. T. Silva 1410 (NY)

Styphnodendron sp. D. Stevenson and D. Daly 5991 (LSU)*

Tetrapleura tetraptera (Schumach. & Thom.) Taub. H. C. de Lima 2660 (NY), Ero 2741 (K)

Xerocladia viridiramis (Burch.) Taub. Germischuizen 3453 (K)

Xyla torreana Brenan E. A. Banda et al. 744 (MO)

Caesalpinioideae

Burkea africana Hook. Th. C. E. Fries 1989 (NY)