Stigma morphology in the *Leguminosae*: The wet, papillate (WP) stigma in *Caesalpinioideae*

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Summary. The stigmas of 65 species from 32 genera representing all tribes in the subfamily *Caesalpinioideae* have been studied using light and electron microscopy. Stigmas differ greatly in size but all are papillate. The number, size, and morphology of papillae is variable both between genera and species. Two types of stigma have now been recorded in *Caesalpinioideae*, wet papillate and wet, non-papillate, and these morphological characters may help in classification.

All stigmas examined from freshly collected and unfixed flowers were wet, the secretion accumulating in the interstices between papillae and sometimes flooding the stigma surface. The secretion is heterogeneous containing protein, lipid and carbohydrate.

INTRODUCTION

This paper describes the stigma morphology and anatomy of receptive stigmas from 65 species (and two unnamed species) of 32 genera classified in the subfamily *Caesalpinioideae* (*Leguminosae*). Genera from all tribes in the *Caesalpinioideae* are represented.

Two forms of stigma, WN (wet, non-papillate) and WP (wet, papillate; Heslop-Harrison & Shivanna 1977, Heslop-Harrison 1992), have been reported in *Caesalpinioideae* (Owens 1985, 1989). The WN form is found in only two tribes, *Caesalpinieae* (Owens 1990) and Cassieae (Owens & Lewis 1989, Dulberger *et al.* 1994), but the distribution and variability of the WP form is less well documented. Stigmas of the WP form are commonly found in the subfamily *Papilionoideae* (Shivanna & Owens 1989).

The results are discussed in relation to pollinator, breeding system, the pollen-stigma interaction and to the taxonomy and evolution of the subfamily.

MATERIAL & METHODS

The genera and species examined in this paper are listed in Appendix 1 together with their Kew accession number (if cultivated now or in the past) or their collector identification number (for other collections), their country of origin and their stigmatic type. The number of flowers examined for each species depended on availability but was not less than three taken at random from inflorescences.

Flowers and/or inflorescences were collected in a mixture of 5 parts glacial acetic

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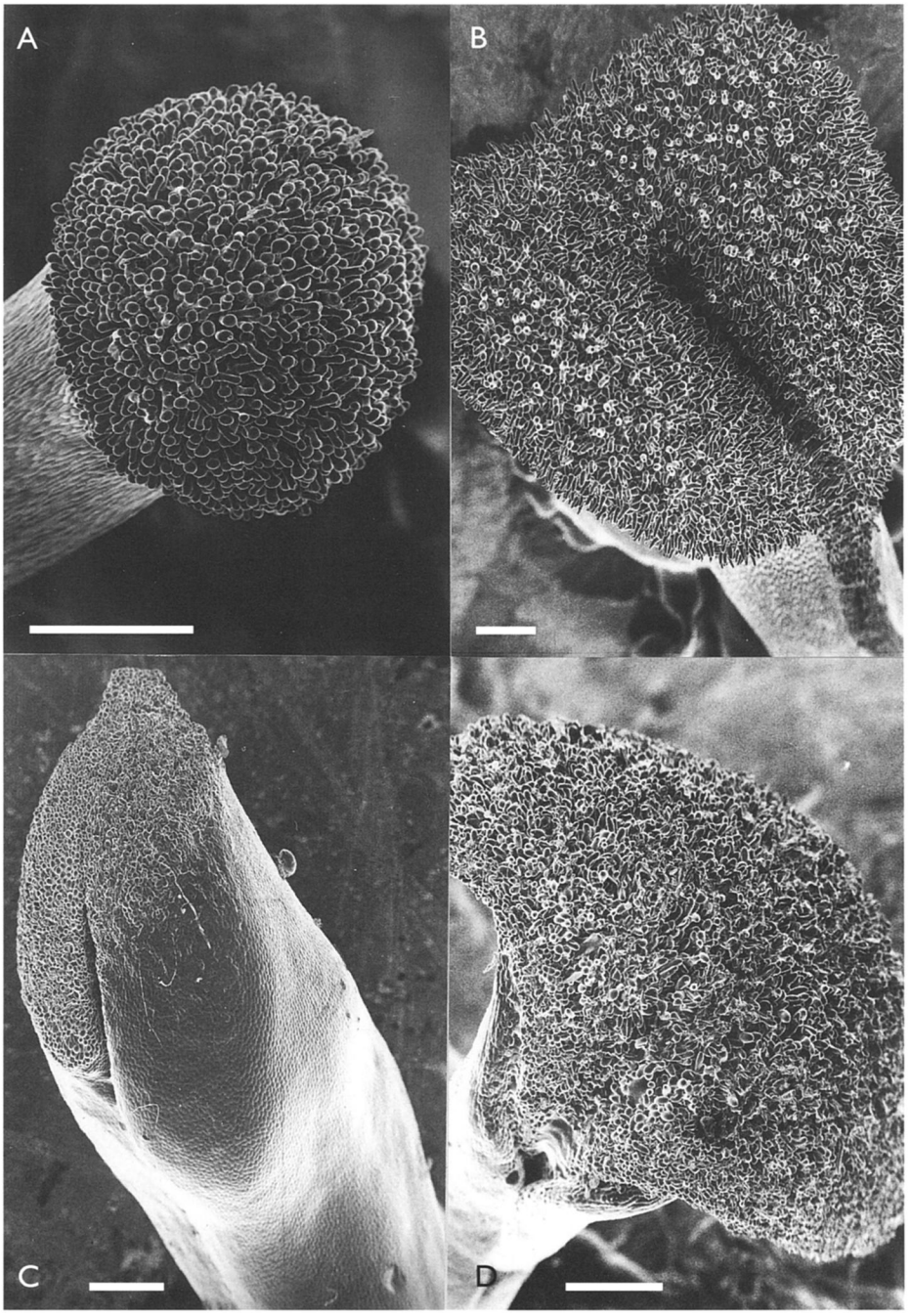

FIG. 1. Scanning electron micrographs. **A** The capitate stigma of *Brownea* × *crawfordii* showing the densely-packed obpyriform stigmatic papillae (fresh material). Scale bar 200μm. **B** The bilobed stigma of *Bauhinia tomentosa* (fresh material). Scale bar 200μm. **C** The clavate stigma of *Bauhinia pentandra* showing a marked groove (fresh material). Scale bar 200μm. **D** The peltate stigma of *Gleditsia caspica* (fresh material). Scale bar 200μm.

acid, 10 parts formalin, 85 parts 70% ethanol or directly into 50% ethanol in the field, at the Fairchild Tropical Garden or the U.S.D.A. Plant Introduction Centre, Miami, Florida, U.S.A., or from the Living Collections Department, Royal Botanic Gardens, Kew. They were kept in fixative or ethanol or transferred to Kew spirit (53% industrial spirit, 37% water, 5% glycerol, 5% formalin).

Stigmas and styles were dissected from flowers and examined under a dissecting microscope and a microscope fitted with epi-objectives where possible. They were then dehydrated in ethanol, critically point-dried and palladium-coated using conventional techniques (Gale & Owens 1983). Specimens were observed and photographed in a Cambridge S240 SEM. Stigmas were classified according to Heslop-Harrison & Shivanna (1977).

RESULTS

Stigma morphology

In the majority of species, stigmas were positioned more or less at the apex of the style appearing morphologically symmetrical (Appendix 1). The stigmas of *Brownea* and the bilobed stigmas in *Bauhinia* were particularly good examples of such symmetry (Figs. 1A, B). Exceptions were the clavate and capitate stigmas of *Bauhinia pentandra* and *Bauhinia rufa* respectively which, while positioned at the apex of the style, are morphologically asymmetrical (Fig. 1C). However, considerable variation was found in the stigmatic form, from capitate (Fig. 1A) to bilobed (Fig. 1B) to peltate (Fig. 1D).

Stigma size was variable between species and genera. In the largest flowers, the approximate stigmatic diameter was 2 mm in *Baikiaea insignis* (Fig. 2A), and 1 mm in *Brownea* × *crawfordii* (Fig. 1A). In smaller flowers, the approximate stigma diameter is 0.7-0.8 mm in *Cercis chinensis*, and 0.3 mm at the widest point in *Bauhinia jenningsii*.

Papillar anatomy and morphology

Stigmatic papillae are unicellular or rarely bicellular (*Bauhinia tomentosa* and *Gleditsia caspica*), are covered by a stigmatic cuticle, and have a large vacuole and peripheral cytoplasm in all species examined (Fig. 2B). In the genera *Cercis* and *Gleditsia*, the length of the peripheral papillae of the stigma are sometimes longer than those towards the centre and in *B. jenningsii* hairs similar to those on the surface of the stylar epidermis may be found among the outer stigmatic papillae. Stigmatic papillae may be cylindrical (Fig. 1D; *Gleditsia*, *Cercis*), cylindrical with swollen or bulbous tips (Figs. 1A; 2C, D; *Poeppigia*, *Schotia*, *Daniellia*, *Afzelia*, *Hymenaea*, *Elizabetha*, *Brownea*, *Berlinia*, *Macrolobium*) or obpyriform (Figs. 3A, B; *Tamarindus*, *Berlinia*). In *Intsia bijuga* and *Brodriguesia santosii*, papillae are short, have a swollen base and a nipple-like tip, and are relatively sparse. Sparse papillae are also found in *Afzelia* (Fig. 2C). While in most species stigmatic papillae are attached to unspecialised cortical cells at their bases, in some *Bauhinia* species papillae are attached to a larger cortical cell or a group of cortical cells (*B. tomentosa*) at their base.

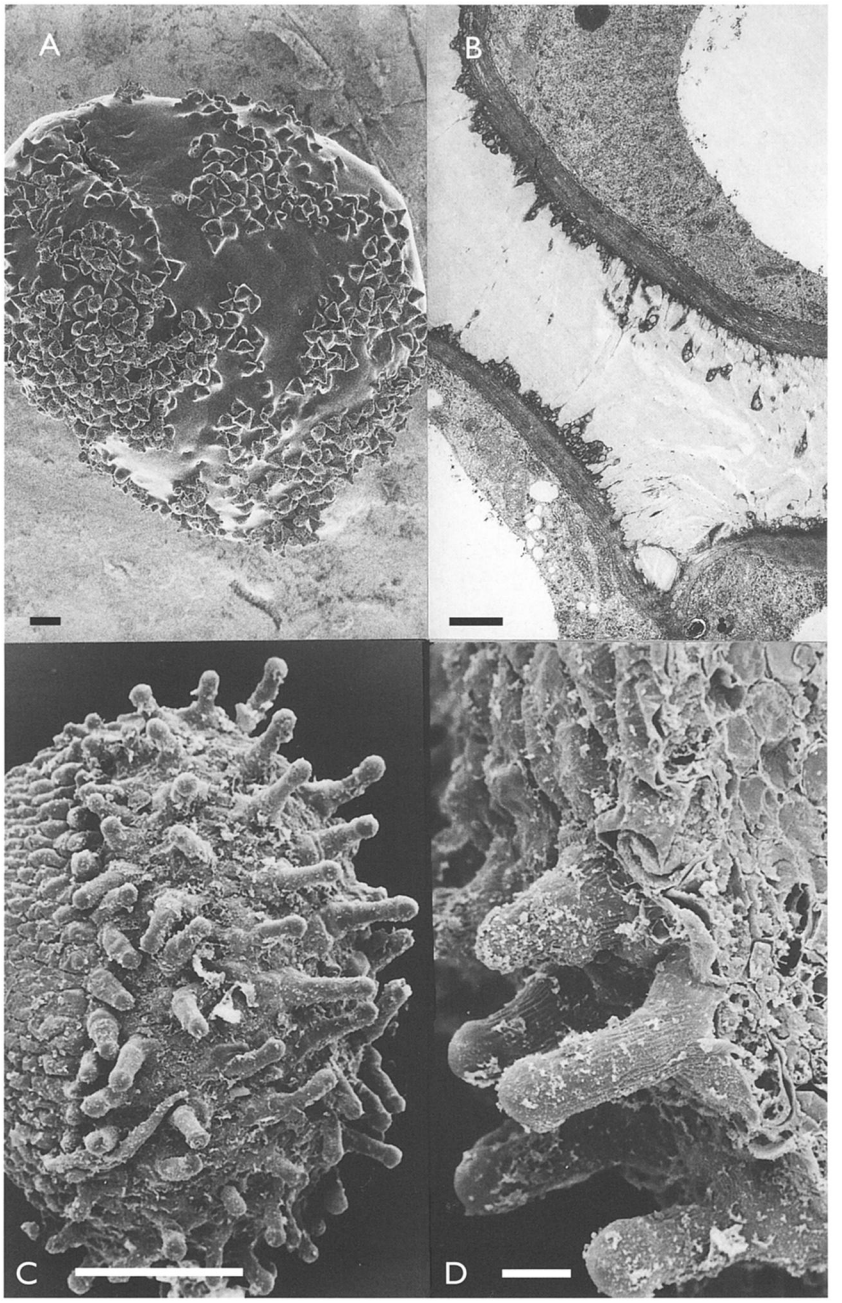

FIG. 2. **A** Scanning electron micrograph of the capitate stigma of *Baikiaea insignis*. Pollinated stigma showing stigma surface inundated with secretion. Scale bar 100μm. **B** Transmission electron micrograph of the secretion in the interstices of three stigmatic papillae in *Cercis chinensis* (transverse section). Scale bar 1μm. **C** Scanning electron micrograph of the stigma of *Afzelia quanzensis* showing the sparse stigmatic papillae. Scale bar 100μm. **D** Higher magnification of the stigmatic papillae of *Afzelia quanzensis*. Scale bar 10μm.

Significant variation in stigma form and papillar shape was found in *Bauhinia*. In fresh flowers, stigmas of different species vary in colour from green to greenish-white independently of the colour of the style or the petals. Morphologically the stigmas can be separated into four categories:- bilobed (Fig. 1B), grooved and capitate (Fig. 3C; 4A, B), capitate and lacking a distinct groove, and clavate (Fig. 1C). *Bauhinia aculeata*, *B. acuminata*, *B. candicans*, and *B. forficata* are markedly bilobed. In *B. acuminata* papillae are long and slender and obpyriform while in all other species they are obpyriform but more squat in appearance and perhaps ampulliform. The stigma of *B. tomentosa* is also markedly bilobed but papillae taper from base to tip and may vary in an apparently random fashion from slender to stout. In the grooved and capitate stigma of *Bauhinia faberi*, papillae have a swollen base and elongate tip (Fig. 4A). *B. blakeana*, *B. corymbosa*, and *B. galpinii* are also in the grooved and capitate category (Appendix 1), but once again the morphology of the stigmatic papillae is variable. Short papillae with a swollen base and a nipple-like tip are found in *B. galpinii* (Fig. 3D), while elongate, obpyriform papillae are present in *B. blakeana* (Figs. 4B, C). Cylindrical papillae are found in *B. corymbosa*. Capitate forms lacking a distinct groove and with cylindrical papillae such as in *B. divaricata* and *B. jenningsii* are rare. Clavate stigmas are found in *B. monandra*, *B. pentandra*, and *B. rufa*. Papillae are short and isodiametric in *B. pentandra* (Fig. 1C).

Collapse of stigmatic papillae in freshly collected material is a characteristic of many species particularly when stigmas become inundated with stigmatic secretion as the flower ages (e.g. Fig. 1D, *Gleditsia caspica* and *Bauhinia tomentosa*). Stigmatic papillae of some bud stigmas are also collapsed.

Stigmatic secretion

All stigmas of the species included in Appendix 1, which were examined from freshly opened flowers, were of the wet, papillate type (WP; Fig. 2A). The amount of visible secretion varied from considerable, inundating the papillae (Fig. 2A) to sparse (Figs. 1A, B, D). In *Cercis* there is no evidence that the stigmatic cuticle is intact at this stage. Stigmatic secretion was recorded on stigmas from buds of *Cercis* species. Those stigmas which were available for study only as fixed material could be identified as papillate although any evidence of surface secretion was restricted to granular accretions attached to stigmatic papillae (Figs. 2C, D).

Stigmatic secretions stain for proteins (Coomassie brilliant blue), lipids (Auramine O, Sudan black B), and carbohydrates (Alcian blue, Periodic acid-Schiffs) in species of *Bauhinia*, *Brownea*, *Cercis*, and *Gleditsia*, although the intensity of stain for carbohydrates is low. The secretion appears heterogeneous and granular in both the light microscope and in the transmission electron microscope (Figs. 2B, 4D). In both *Cercis* and *Gleditsia*, lipid appears to predominate. In *Cercis* and *Gleditsia*, protein and carbohydrate are often enclosed in large discrete domains (Fig. 4D) while in addition, small vesicles accumulate in electron opaque material close to the papillar cell walls (Fig. 4D). The outer cells walls also appear to be disrupted, the fibrils becoming dispersed in the secretion and vesicles accumulating at the outer surface of the cell wall (Fig. 2A, 4D).

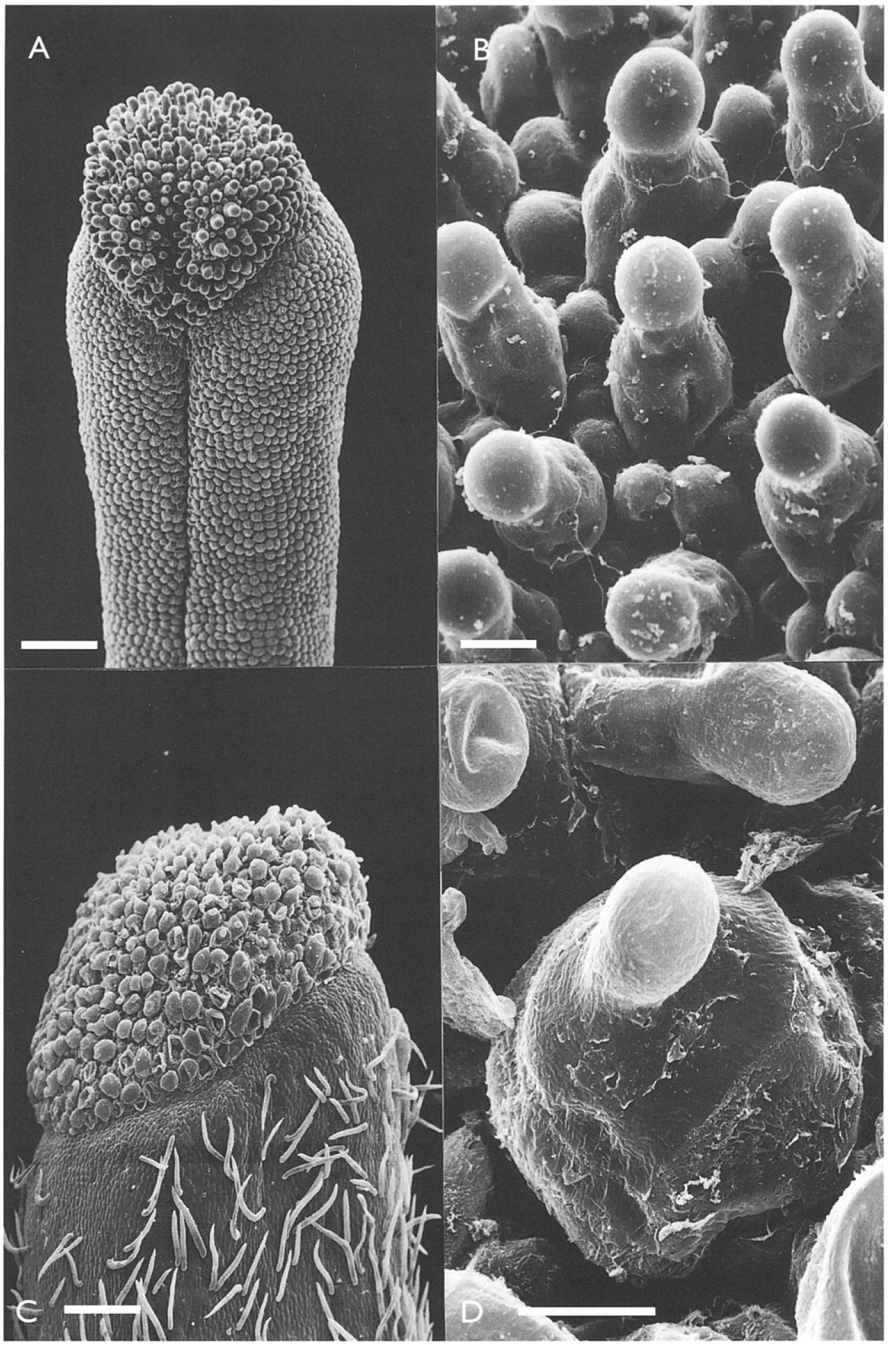

FIG. 3. Scanning electron micrographs. **A** The capitate and grooved stigma of *Tamarindus indica*. Scale bar 100μm. **B** Higher magnification of the stigmatic papillae of *Tamarindus indica*. Scale bar 10μm. **C** The capitate stigma of *Bauhinia galpinii*. Scale bar 100μm. **D** Higher magnification of the obpyriform stigmatic papillae of *Bauhinia galpinii*. Scale bar 10μm.

DISCUSSION

WP stigmas have been found in all tribes of the subfamily *Caesalpinioideae*. In *Amherstieae*, *Cercideae* and *Detarieae* all species examined in this paper have WP stigmas. In *Caesalpinieae* and *Cassieae*, species with both WN and WP stigmas are found. However, genera and species with WN stigmas are classified into different groups from those with WP stigmas. In the *Caesalpinia*, *Dimorphandra*, and *Peltophorum* groups of the tribe *Caesalpinieae*, the morphology of the WN stigma has been suggested as a useful character in the delimitatation of genera or groups of genera (Owens 1990) and in *Cassieae*, there is evidence that stigmatic morphology may be helpful in separating genera (Owens & Lewis 1989, Dulberger *et al.* 1994). The data in this paper do not allow a clear and unified hypothesis for the tribes studied although the considerable diversity found so far indicates that stigmatic morphology may be a useful feature for specific groups. In *Bauhinia*, for example, variation in stigmatic morphology separates groups of species. *B. aculeata*, *B. acuminata*, *B. candicans*, *B. forficata*, and *B. tomentosa*, which all have large, bilobed papillate stigmas, appear to form a natural group as do the clavate stigmas of *B. pentandra* and *B. rufa* but there is no taxonomic treatment which links them closely (De Wit 1956, Wunderlin *et al.* 1987). It is no surprise that the greatest diversity in stigma morphology is found in the genus *Bauhinia* since the greatest pollen diversity at the generic level is also found in this genus (Ferguson & Pearce 1986). The differences in the stigmas of differing accessions of *Bauhinia thonningii* and *Tamarindus indica* probably indicate a difference in stage of maturity and receptivity.

The consensus now is to recognise the *Detarieae* and *Amherstieae* as one tribe and these data would support such a combination.

In some cases, variability in shape and spacing of stigmatic papillae may reflect potential pollinator relationships. For example, *Brownea* × *crawfordii* and *Elizabetha speciosa* are bird-pollinated and *Bauhinia rufa* is bat-pollinated (Arroyo 1981). On the other hand there may be no link at all as with WN stigmas in *Caesalpinieae* (Owens 1990). While a relationship between pollinator and pollen morphology has been indicated in several genera in *Leguminosae* (Ferguson & Skvarla 1982, Guinet & Ferguson 1989) and in *Bauhinia* in particular (Ferguson & Pearce 1986), there is still no firm relationship with stigmatic form. The sparse stigmatic papillae of *Afzelia bella* and the discovery of tetrad pollen (Ferguson & Banks 1994) may provide an interesting correlation but the rare occurrence of tetrad pollen in just three genera and eight species of *Caesalpinioideae* does not indicate considerable significance to the subfamily as a whole. Exine morphology and stigma form do not appear to be related (Owens 1989).

The ultrastructure and the composition of stigmatic secretion revealed by the microscopic stains applied does not suggest any significant difference between the WP stigmas of the *Caesalpinioideae* and others in *Papilionoideae* (Heslop-Harrison 1992). However, such stains do not allow identification of specific compounds.

Interestingly, the speed of pollen germination on the WP stigmatic surface is generally slower than that on WN stigmas (Owens 1989). In *Cercis chinensis*, *C. siliquastrum* and *Bauhinia tomentosa*, the time to pollen germination is about one

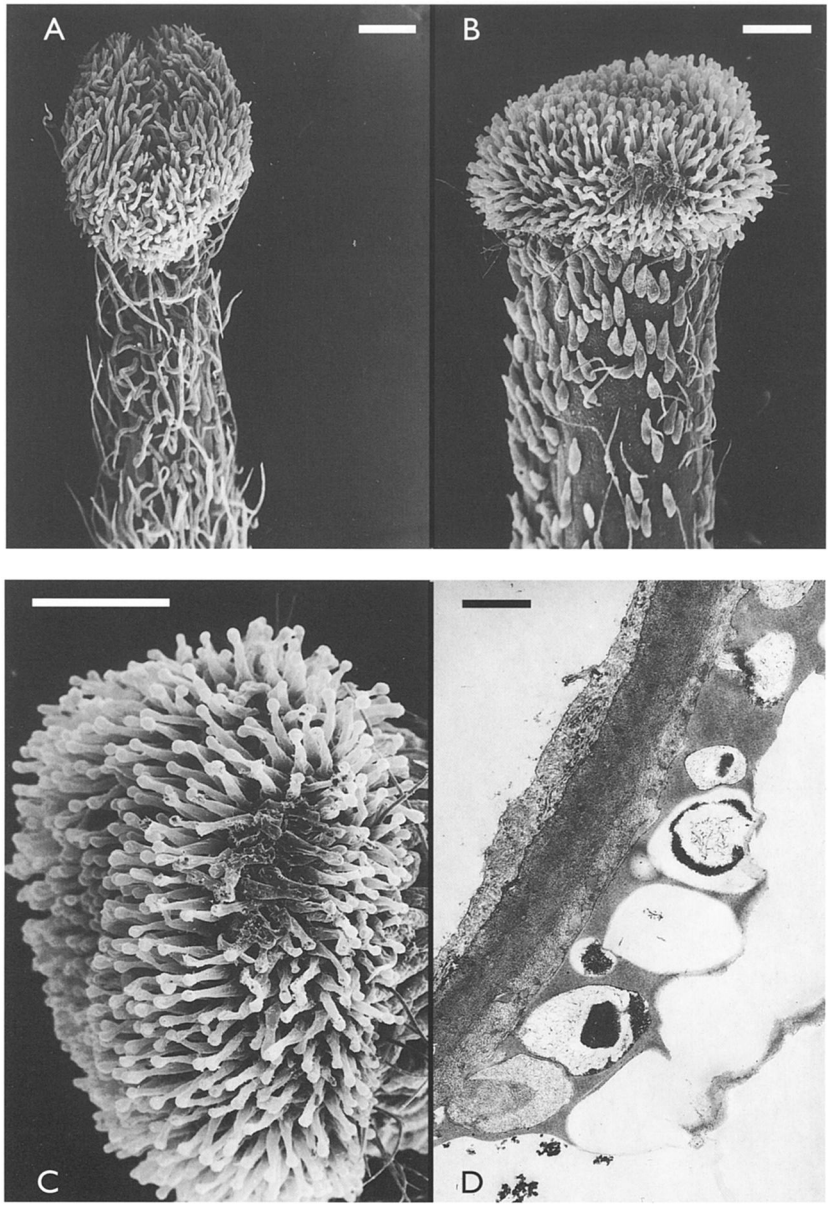

FIG. 4. Scanning electron micrographs. **A** The capitate stigma of *Bauhinia faberi* showing the dense elongate papillae. Scale bar 200μm. **B** The capitate stigma of *Bauhinia blakeana*. Scale bar 200μm. **C** Higher magnification of the elongate yet obpyriform stigmatic papillae of *Bauhinia blakeana*. Scale bar 200μm. **D** Transmission electron micrograph of secretion in the interstices of the stigmatic papillae in *Gleditsia caspica*. Loosened fibrils and vesicles are present in the outer cell wall of the stigmatic papillae. The secretion is heterogeneous containing lipid (asterisks) and carbohydrate (arrows). Protein may have been lost from the clear areas (arrow heads) embedded in the lipid. Scale bar 1μm.

hour, while in *B. pentandra* the time to germination is three hours (Owens 1989).

Caesalpinioideae are often considered to be the basal subfamily in *Leguminosae*. WP stigmas have been found in all species studied so far of the subfamily *Papilionoideae* (Small & Brookes 1983, Shivanna & Owens 1989) and the results in this paper would suggest a closer relationship between those genera with WP stigmas in the *Caesalpinioideae* and those in *Papilionoideae*. The evolution of species in the *Papilionoideae* from species with WP stigmas in *Caesalpinioideae* appears logical as does the evolution of species in the *Mimosoideae* from species in the *Caesalpinioideae* with WN, crateriform stigmas (Owens & Lewis 1989).

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APPENDIX 1.

The incidence and distribution of wet papillate (WP) stigmas in genera and species of the five tribes of *Caesalpinioideae*. (All stigma form classifications in bold (**WP**) were made from freshly collected flowers where secretion and papillae could be observed. The rest were from fixed material and could only be identified as papillate (P)).
LCD = Living Collections Department, Royal Botanic Gardens, Kew

Species	**Collector, Kew accession/ Collector's Number, Collection site or Country of origin**	**Stigma form**
Tribe: *Caesalpinieae*		
Gleditsia group		
Gleditsia caspica Desf.	LCD 1973 11949	**WP;** grooved, peltate
Gleditsia japonica Miq.	LCD 1973 11972	**WP;** grooved, peltate
Gleditsia koraiensis Nakai	LCD 1970 1574	**WP;** grooved, peltate
Peltophorum group		
Peltophorum pterocarpum (DC.) K. Heyne	Owens 77 446, Fairchild Tropical Garden, Miami, Florida, U.S.A.	**WP;** grooved, peltate
Jacqueshuberia amplifolia Cowan	Zarucchi 2137, Colombia	P; bilobed
Poeppigia group		
Poeppigia procera Presl	Lewis *et al.* 1125, Brazil	P; capitate
Tribe: *Cassieae*		
subtribe *Dialiinae*		
Dialium orientale Baker f.	Greenway 10452, Kenya	P; capitate
Mendoravia dumaziana Capuron	McWhirter 212, Madagascar	P; grooved, peltate
subtribe *Duparquetiinae*		

Duparquetia orchidacea Baill.	Coombe 177, Nigeria	P; grooved
Duparquetia orchidacea Baill.	Polhill *et al.* 5217, Cameroon	P; grooved
Tribe: *Cercideae*		
subtribe *Cercidinae*		
Cercis chinensis Bunge	LCD 1933 31601	**WP;** grooved, capitate
Cercis griffithii Boiss.	LCD 1968 37814	**WP;** grooved, capitate
Cercis occidentalis Torr. ex A. Gray	LCD 1975 04881	**WP;** grooved, capitate
Cercis siliquastrum L.	LCD 1945 28701	**WP;** grooved, capitate
subtribe *Bauhiniinae*		
Bauhinia group		
Bauhinia aculeata L.	Owens X124B, USDA, Miami, Florida, U.S.A.	**WP;** bilobed
Bauhinia acuminata L.	Owens 83 409A Fairchild Tropical Garden, Miami, Florida, U.S.A.	**WP;** bilobed
Bauhinia binata Blanco	Owens M22268, USDA, Miami, Florida, U.S.A.	**WP;** grooved, peltate
Bauhinia blakeana Dunn	Owens 78 796A, Fairchild Tropical Garden, Miami, Florida, U.S.A.	**WP;** grooved, capitate
Bauhinia candicans Benth.	LCD 1952 7901	**P;** bilobed
Bauhinia candicans Benth.	LCD 1973 12273	**WP;** bilobed
Bauhinia c.f. commersoniana Decne.	McWhirter 205, Madagascar	P; capitate
Bauhinia corymbosa Roxb.	Owens 69 554A, Fairchild Tropical Garden, Miami, Florida, U.S.A.	**WP;** grooved, capitate
Bauhinia divaricata L.	Owens s.n., Fairchild Tropical Garden, Miami, Florida, U.S.A.	**WP;** capitate
Bauhinia faberi Oliv.	Owens 129190-9847, USDA, Miami, Florida, U.S.A.	**WP;** grooved, capitate
Bauhinia forficata Link	Owens X 16 43, Fairchild Tropical Garden, Miami, Florida, U.S.A.	**WP;** bilobed
Bauhinia galpinii N.E. Br.	Owens s.n., Fairchild Tropical Garden, Miami, Florida, U.S.A.	**WP;** grooved, capitate
Bauhinia glabra Jacq.	Plowman *et al.* 6674 Peru	P; capitate, cone-shaped
Bauhinia jenningsii P. Wilson ex Britton	LCD 1992 52	**WP;** capitate, cone-shaped
Bauhinia macrantha Oliv.	Brenan & Greenway 15672, Zimbabwe	P; grooved, peltate
Bauhinia monandra Kurze	Tanner 15670, Tanzania	P; clavate, bilobed
Bauhinia pentandra (Bong.) Steud.	LCD s.n.	**WP;** clavate, bilobed
Bauhinia rufa (Bong.) Steud.	Lewis 1407, Brazil	P; clavate
Bauhinia taitensis Taub.	Greenway & Kanier 12733, Kenya	P

Bauhinia tomentosa L.	LCD 1977 3280	**WP;** bilobed
Bauhinia tomentosa L.	Owens s.n., Fairchild Tropical Garden, Miami, U.S.A.	**WP;** bilobed
Bauhinia sp.	Leechman XIIIb, Guyana	P
Piliostigma group		
Bauhinia thonningii Schum.	Keay 37156, Nigeria	P; grooved, peltate
Bauhinia thonningii Schum.	Milne-Redhead 3808, Zimbabwe	P; grooved, capitate
Tribe: *Detarieae*		
Cynometra group		
Cynometra alexandri C.H. Wright	Styles 68, Uganda	P; grooved
Zenkerella capparidacea (Taub.) J. Léonard	Drummond & Hemsley 1756, Tanzania	P; peltate
Schotia africana (Baill.) Keay	Coombe 191, Cameroon	P; grooved, peltate
Hymenostegia group		
Hymenostegia afzelii (Oliv.) Harms	Polhill *et al.* 5218, Cameroon	P; grooved
Hymenostegia afzelii (Oliv.) Harms	Brenan 9002, Nigeria	P; grooved
Daniellia ogea (Harms) Holland	Brenan 8817, Nigeria	P; capitate
Afzelia bella Harms	McKey 122, Cameroon	P; capitate
Afzelia bipindensis Harms	Brenan 8889, Nigeria	P
Afzelia quanzensis Welw.	Kirkup 67, Kenya	P; sparse papillae, capitate
Afzelia quanzensis Welw.	Tanner 306, Tanzania	P; sparse papillae, capitate
Afzelia quanzensis Welw.	Brenan & Greenway 8049, Zimbabwe	P; sparse papillae, capitate
Intsia bijuga (Colebr.) Kuntze	Jeffrey 617, Seychelles	P; grooved, capitate
Brodriguesia santosii Cowan	Lewis *et al.* 1018, Brazil	P; capitate
Hymenaea group		
Peltogyne paniculata Benth.	Lewis 1674, Brazil	P
Hymenaea parvifolia Huber	Lewis 1421, Brazil	P; capitate
Detarium group		
Baikiaea insignis Benth.	LCD 1994 48301	**WP;** capitate
Copaifera langsdorffii	Lewis s.n., Brazil	P; capitate
Copaifera sp.	de Carvalho 2174, Brazil	P; capitate

Brownea group		
Elizabetha speciosa Ducke	Lewis *et al.* s.n., Brazil	P; sparse papillae, capitate
Phyllocarpus riedellii Tul.	Lewis 1615, Brazil	P; capitate
Brownea × *crawfordii* W. Watson	LCD 1969 12155	**WP;** sparse papillae, grooved, capitate
Tribe: *Amherstieae*		
Berlinia group		
Isoberlinia doka Craib & Stapf	Latilo & Daramola 28853, Cameroon	P; capitate
Berlinia coriacea Keay	Keay 37028, Nigeria	P; capitate
Berlinia grandiflora (Vahl) Hutch. & Dalziel	Keay & De Wit 37337, Nigeria	P
Berlinia sp. aff. B. craibiana Baker f.	Greenway 8188, Zambia	P
Berlinia sp. aff. B. exfoliatum Baker f.	Greenway 8188, Zambia	P
Macrolobium group		
Gilbertiodendron dewevrei (De Wild.) J. Léonard	Troupin 4503, Zaire	P; capitate
Paramacrolobium coeruleum (Taub.) J. Léonard	Lucas 238, Kenya	P; grooved, peltate
Macrolobium angustifolium (Benth.) Cowan	Zarucchi 2158, Colombia	P; capitate
Amherstia group		
Tamarindus indica L.	Owens 79391, Fairchild Tropical Garden, Miami, Florida, U.S.A.	**WP;** grooved
Tamarindus indica L.	Tanner 333, Tanzania	P; capitate
Tamarindus indica L.	Lewis s.n., Brazil	P; grooved
Tamarindus indica L.	Renvoize 717, Aldabra	P; grooved
Brachystegia group		
Brachystegia boehmii Taub.	Brenan 7970, Zimbabwe	P; capitate
Brachystegia eurycoma Harms	Adebusoyi 40948, Nigeria	P; peltate
Brachystegia fascifolia Harms	Brenan 7827, Zimbabwe	P; grooved
Brachystegia nigerica Hoyle & A.P.D. Jones	Prior s.n., Nigeria	P; grooved
Brachystegia spiciformis Benth.	Bullock 1055, Zambia	P; grooved
Brachystegia spiciformis Benth.	Brenan & Greenway 7828, Zambia	P
Brachystegia stipulata De Wild.	Brenan & Greenway 7979, Zambia	P