

Morphology of Floral Papillae in *Maxillaria* Ruiz & Pav. (Orchidaceae)

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• **Background and Aims** The labellar papillae and trichomes of *Maxillaria* Ruiz & Pav. show great diversity. Although papillae also occur upon other parts of the flower (e.g. column and anther cap), these have not yet been studied. Labellar trichomes of *Maxillaria* are useful in taxonomy, but hitherto the taxonomic value of floral papillae has not been assessed. The aim of this paper is to describe the range of floral papillae found in *Maxillaria* and to determine whether papillae are useful as taxonomic characters.

• **Methods** Light microscopy, histochemistry, low-vacuum scanning and transmission electron microscopy.

• **Key Results** A total of 75 taxa were studied. Conical papillae with rounded or pointed tips were the most common. The column and anther cap usually bear conical, obpyriform or villiform papillae, whereas those around the stigmatic surface and at the base of the anther are often larger and swollen. Labellar papillae show greater diversity, and may be conical, obpyriform, villiform, fusiform or clavate. Papillae may also occur on multiseriate trichomes that perhaps function as pseudostamens. Labellar papillae contain protein but most lack lipid. The occurrence of starch, however, is more variable. Many papillae contain pigment or act as osmophores, thereby attracting insects. Rewards such as nectar or a protein-rich, wax-like, lipoidal substance may be secreted by papillae onto the labellar surface. Some papillae may have a protective role in preventing desiccation. Species of diverse vegetative morphology may have identical floral papillae, whereas others of similar vegetative morphology may not.

• **Conclusions** Generally, floral papillae in *Maxillaria* have little taxonomic value. Nevertheless, the absence of papillae from members of the *M. cucullata* alliance, the occurrence of clavate papillae with distended apices in the *M. rufescens* alliance and the presence of papillose trichomes in some species may yet prove to be useful.

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Key words: Anther, column, histochemistry, labellum, low-vacuum scanning electron microscopy, papillae, pseudopollen, pseudostamen.

INTRODUCTION

Orchids largely attract specific pollinators by means of a combination of visual and olfactory cues (e.g. van der Pijl and Dodson, 1969). However, on alighting upon the labellum, tactile stimuli and rewards often take on an equally important role. Such rewards include pollen, nectar, oils and pseudopollen (van der Pijl and Dodson, 1969; Dressler, 1993). However, it has been estimated that approx. one-third of orchid species provide no reward, merely 'empty promises' (Ackerman, 1984). Nevertheless, those species that reward pollinators often double their chances of fruiting (Neiland and Wilcock, 1998).

Pollen of epidendroid orchids is inaccessible to pollinators as it is bound into pollinia. Consequently, nectar is the most common reward amongst these orchids (Dressler, 1993). Even so, Porsch (1908) and van der Pijl and Dodson (1969) have estimated that one-third of orchid species produce little or no nectar. Indeed, until recently, it was generally believed that all members of the Neotropical genus *Maxillaria* lacked nectar. However, it is now known that this is incorrect since, lately, nectar has been demonstrated for a number of species including *M. coccinea* (Jacq.) L. O. Williams ex Hodge (Stpiczyńska *et al.*, 2004),

M. jenischiana (Rchb.f.) C. Schweinf., *M. imbricata* Barb. Rodr., *M. sophronitis* (Rchb.f.) Garay (Davies *et al.*, 2003a, b), *M. parviflora* (Poepp. & Endl.) Garay (Singer, 2003; Singer and Koehler, 2003; Stpiczyńska *et al.*, 2004), *M. pendens* Pabst and *M. rigida* Barb. Rodr. (Singer and Koehler, 2003). Similarly, pseudopollen has been reported from *Maxillaria* (Janse, 1886; Porsch, 1905; van der Pijl and Dodson, 1969; Davies and Winters, 1998; Davies *et al.*, 2000; Davies *et al.*, 2003b) and occurs in the *M. grandiflora* and *M. discolor* alliances as well as in *M. longissima* Lindl. In each case, pseudopollen is formed by the fragmentation of uniseriate, moniliform hairs into individual component cells or short chains of cells rich in protein (Davies *et al.*, 2000, 2003b). Members of the *M. splendens* alliance are also thought, solely on morphological grounds, to possess pseudopollen-forming labellar hairs (Davies and Winters, 1998; Davies *et al.*, 2000, 2003a, b) which differ from the above in that they are few-celled and the component cells are elongate rather than elliptical or lemon-shaped as in the *M. grandiflora* alliance or fusiform as in *M. longissima*. So far, however, labellar hairs from the *M. splendens* alliance have not been tested for food substances. Other species of *Maxillaria*, such as members of the *M. acuminata* and *M. discolor* alliances, produce a wax-like material upon their labella and this is thought to be collected by bees for

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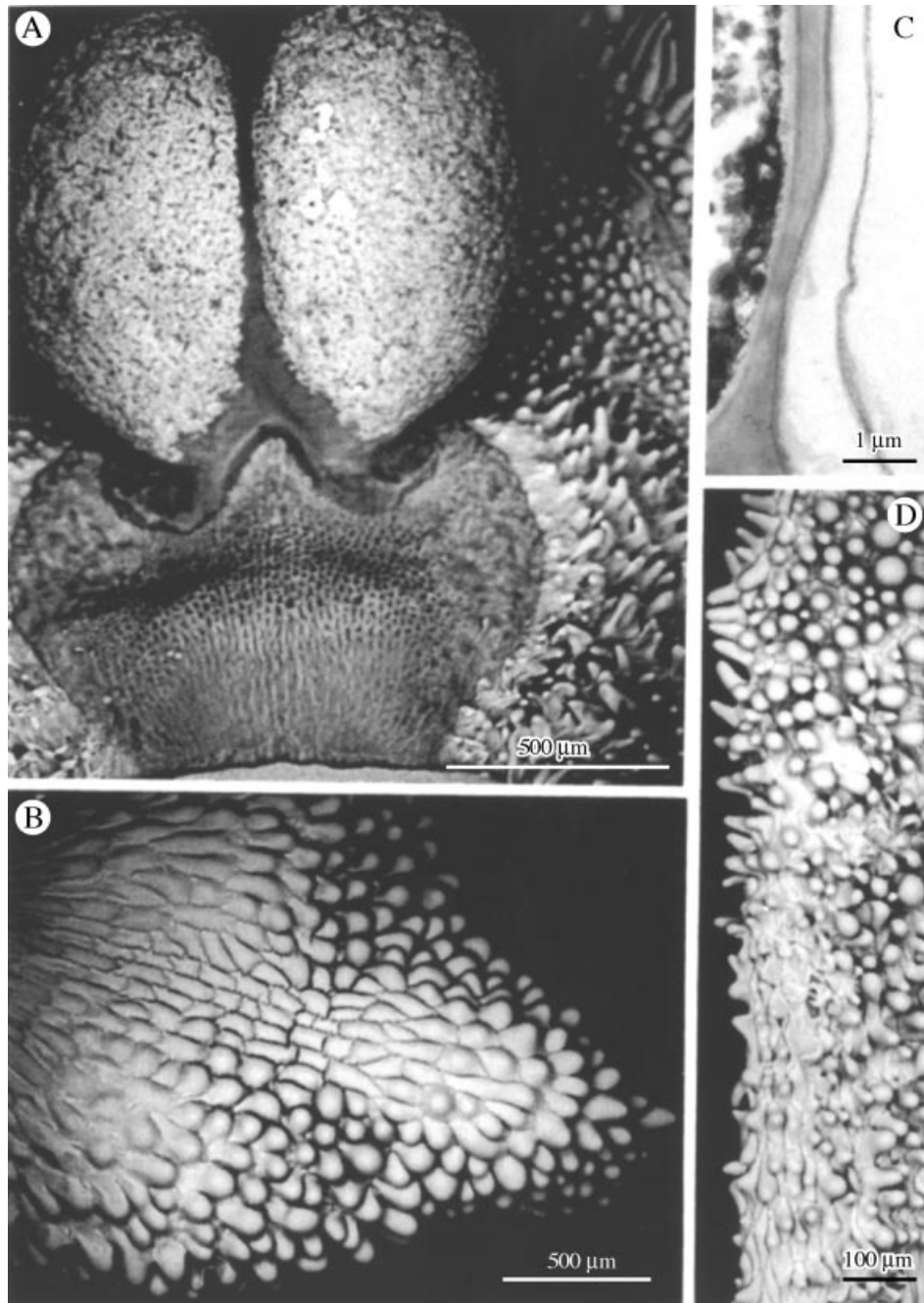


FIG. 1. A, Pollinia of *Maxillaria* cf. *notylioglossa* with associated conical and villiform papillae. B, Anther cap of *M. seidelii* with conical and obpyriform papillae. C, TEM of cell wall of labellar papilla of *M. vernicosa* showing relatively thick cuticle. D, Column of *M. seidelii* with conical and obpyriform papillae. Scale bars = 500 μm (A and B), 100 μm (D) and 1 μm (C).

nest-building (van der Pijl and Dodson, 1969), although, in that it contains lipids and aromatic amino acids, it clearly also has nutritional value (Davies *et al.*, 2003a, b). Pheromone-like compounds have been demonstrated for some *Maxillaria* spp. (Roubik, 2000), but hitherto, pseudocopulation is not known to occur in *Maxillaria sensu stricto*. However, this phenomenon has been demonstrated for *Trigonidium obtusum* Lindl., which molecular evidence suggests is 'nested' within *Maxillaria* (Singer, 2002).

Although many *Maxillaria* spp. offer rewards, the vast majority seemingly do not, and these are thought to attract insects by 'deceit' using a combination of features such as colour, fragrance and pilosity. The labella of such flowers generally lack trichomes but are clothed with abundant epidermal papillae. These papillae show great morphological diversity (Davies and Winters, 1998; Davies *et al.*, 2003a) but the reasons for such differences are not clear. It is possible that some may function as osmophores. For

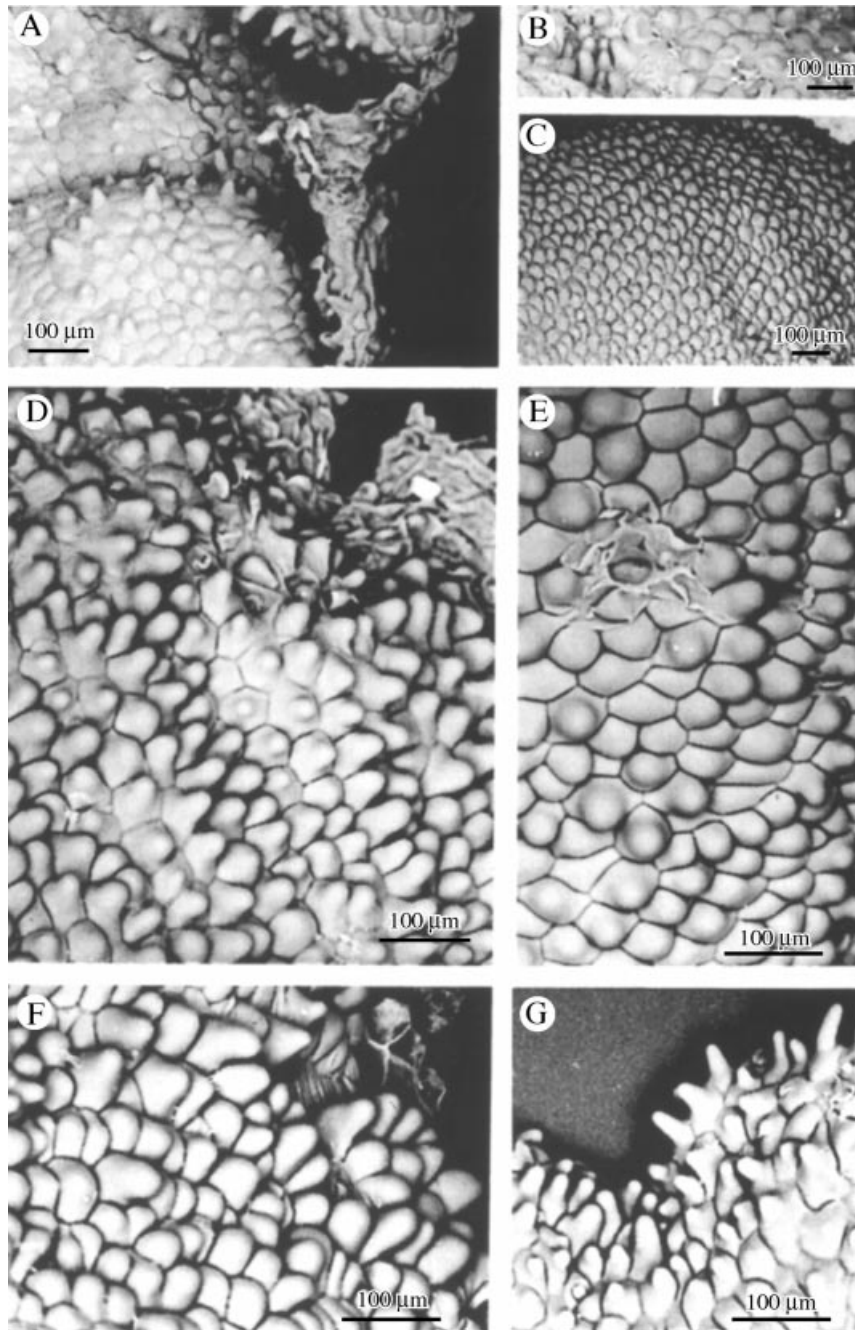


FIG. 2. Conical labellar papillae with broad points of insertion and rounded apices of *M. mosenii* (A), *M. cogniauxiana* (B), *M. vernicosa* (C), *M. minuta* (D) and *M. seidelii* (E). F and G, *M. cf. minuta* showing typical and marginal labellar papillae, respectively. Scale bar = 100 µm.

example, the flower of *M. picta* Hook. has a strong honey-like fragrance but lacks nectar or any other reward (Singer and Cocucci, 1999). However, its labellum, whilst lacking trichomes, is heavily clothed with villiform papillae (Davies and Winters, 1998). Singer and Cocucci (1999) report that *M. picta* is pollinated by the stingless bee *Trigona spinipes*, which, on backing out of the flower, appears somewhat drowsy. It may be that the papillae produce an intoxicating fragrance which, by partially anaesthetizing the insect, facilitates pollination. Indeed, van der Pijl and Dodson

(1969) report that vanillin production in *M. rufescens* Lindl. is confined to those parts of the labellum around the 'hair'. Another possibility is that even in apparently rewardless species, food substances may indeed be present but these are located within papillae and are only accessible to gnawing insects. Direct evidence for this is lacking. Nevertheless, this may be the case in *M. rufescens*, where, according to Porsch (1905) the unicellular 'hairs' have delicate walls and contain aleurone and oil droplets. In most cases, however, regardless of whether rewards are present or not, it is

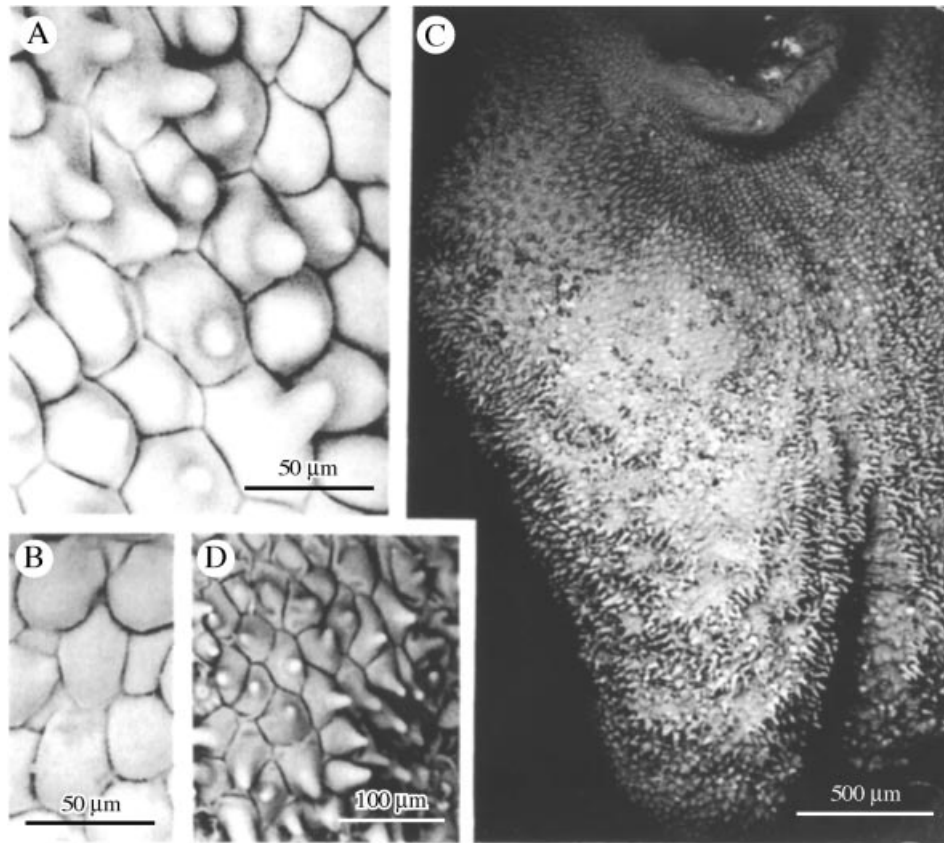


FIG. 3. A, Conical labellar papillae of *M. meleagris*. B, Some parts of the labellum of *M. meleagris* may lack papillae. C, Papillose labellum of *M. densa*. D, Conical labellar papillae of *M. densa* with pointed apices. Scale bars = 500 µm (C), 100 µm (D) and 50 µm (A and B).

probable that labellar papillae play an important role in both attracting and guiding visiting insects deeper into the flower, thus facilitating pollination. This is accomplished by means of olfactory and tactile stimuli and, since many papillae are highly pigmented, visual cues. The main pollinators of *Maxillaria* are stingless bees (Meliponini) (Singer and Cocucci, 1999; Roubik, 2000), although euglossine bees (van der Pijl and Dodson, 1969), Ponerinae ants (Singer, 2003) and hummingbirds (Dodson, 1965—cited in van der Pijl and Dodson, 1969) have also been observed visiting these flowers. To date, however, there is no concrete evidence that hummingbirds pollinate *Maxillaria* spp.

Davies and Winters (1998) proposed that labellar features could provide useful taxonomic characters for determining infrageneric relations within *Maxillaria*. Subsequent work has proven this to be the case in that pseudopollen appears to be restricted to a handful of infrageneric alliances, and that these can be distinguished, to a degree, on the basis of this feature (Davies *et al.*, 2000, 2003b). By contrast, the taxonomic value of papillae has, hitherto, not been assessed.

The present paper examines the morphological diversity of floral papillae in *Maxillaria*; those occurring on the lip as well as those on the column and anther cap. Moreover, it

discusses their possible functions and their value as taxonomic characters.

MATERIALS AND METHODS

A total of 75 taxa were examined for floral papillae and/or trichomes using light microscopy and/or low-vacuum scanning electron microscopy. Wherever possible, the column, anther cap and labellum were examined. The labellum of one specimen of *M. vermicosa* Barb. Rodr. was also examined using transmission electron microscopy (TEM) and a number of species, having different types of labellar papillae, were selected for histochemistry. Authorities for plant names follow Brummitt and Powell (1992). Plants with accession numbers prefixed 'KLD' were obtained from the first author's collection, whereas those prefixed 'S' were grown at Swansea Botanical Complex, Swansea, UK. Those prefixed 'MM' were obtained from Dr M. McIlmurray at the National Collection of Maxillarias, Shirley, Croydon, UK and those prefixed 'BSNS', 'XX', 'G' or 'GXX' from the National Botanic Garden, Glasnevin, Eire. Further plants were obtained from The Royal Botanic Garden Edinburgh, UK and from Dr E. D. L. Schmidt, Wageningen, The Netherlands and these are prefixed 'E'

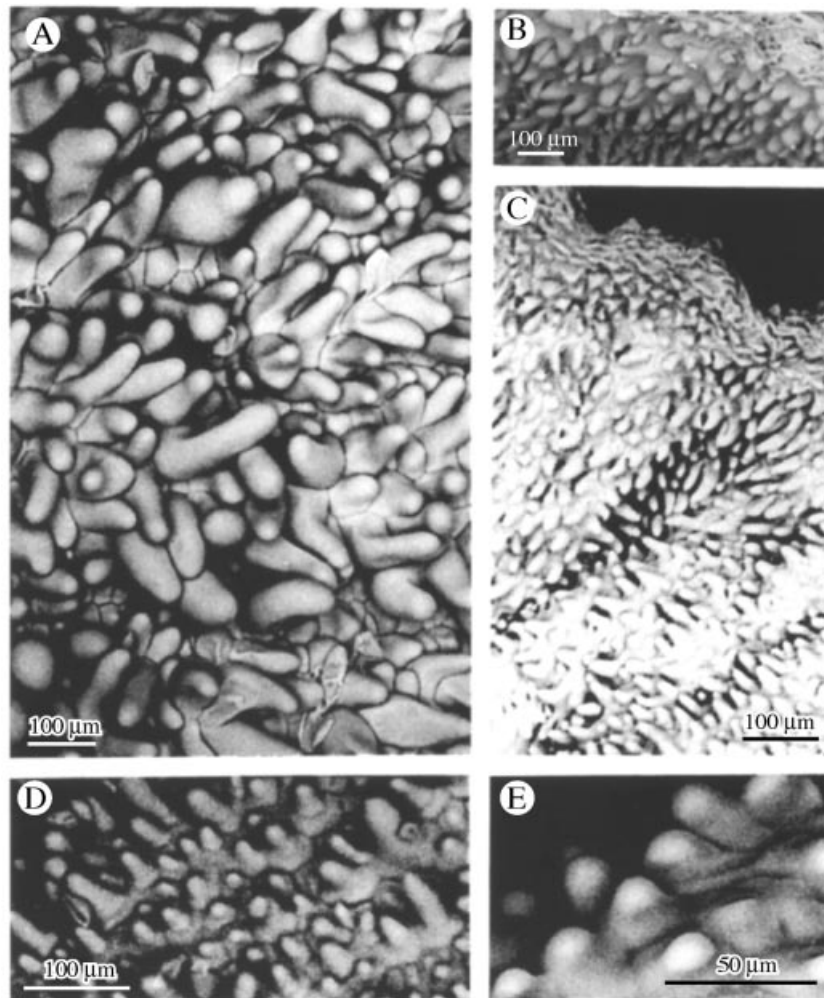


FIG. 4. A, Villiform labellar papillae of *M. pulchra*. B–E, Short conical labellar papillae of *M. elatior* (B), *M. desvauxiana* (C), *M. procurrens* (D) and *M. coccinea* (E). Scale bars = 100 µm (A–D) and 50 µm (E).

and ‘ED’, respectively. Herbarium specimens were deposited at the National Museum of Wales, Cardiff, UK.

Low-vacuum SEM

Following preliminary examination by means of light microscopy, specimens were prepared for low-vacuum SEM. Examples showing different types of papillae were dissected and immediately examined by means of back-scattered electron imaging using a JSM 5200 LV-SEM in low-vacuum mode at an accelerating voltage of 20–25 kV.

TEM

Pieces of labella of *M. vernicosa* (S20010100) were removed, prepared for TEM as described in previous papers (Davies *et al.*, 2000, 2003a) and examined using a JEOL 1201 TEM at an accelerating voltage of 80 kV.

Histochemistry

Labellar papillae were tested for starch, lipids and aromatic amino acids using IKI, saturated ethanolic Sudan III and the xanthoproteic test, respectively (Davies *et al.*, 2000, 2003a, b).

RESULTS

Morphology

The labellum, column and anther cap may be glabrous or papillose but, whereas the unicellular papillae found near the anther and on the column and anther cap are almost invariably conical, obpyriform or villiform (Fig. 1A, B and D), those occurring on the labellum show greater diversity and may be conical with rounded (Figs 2A–G and 4B–E) or pointed tips (Fig. 3A, C and D), obpyriform to clavate with greatly distended apices (Fig. 6A and B), villiform (Fig. 4A),

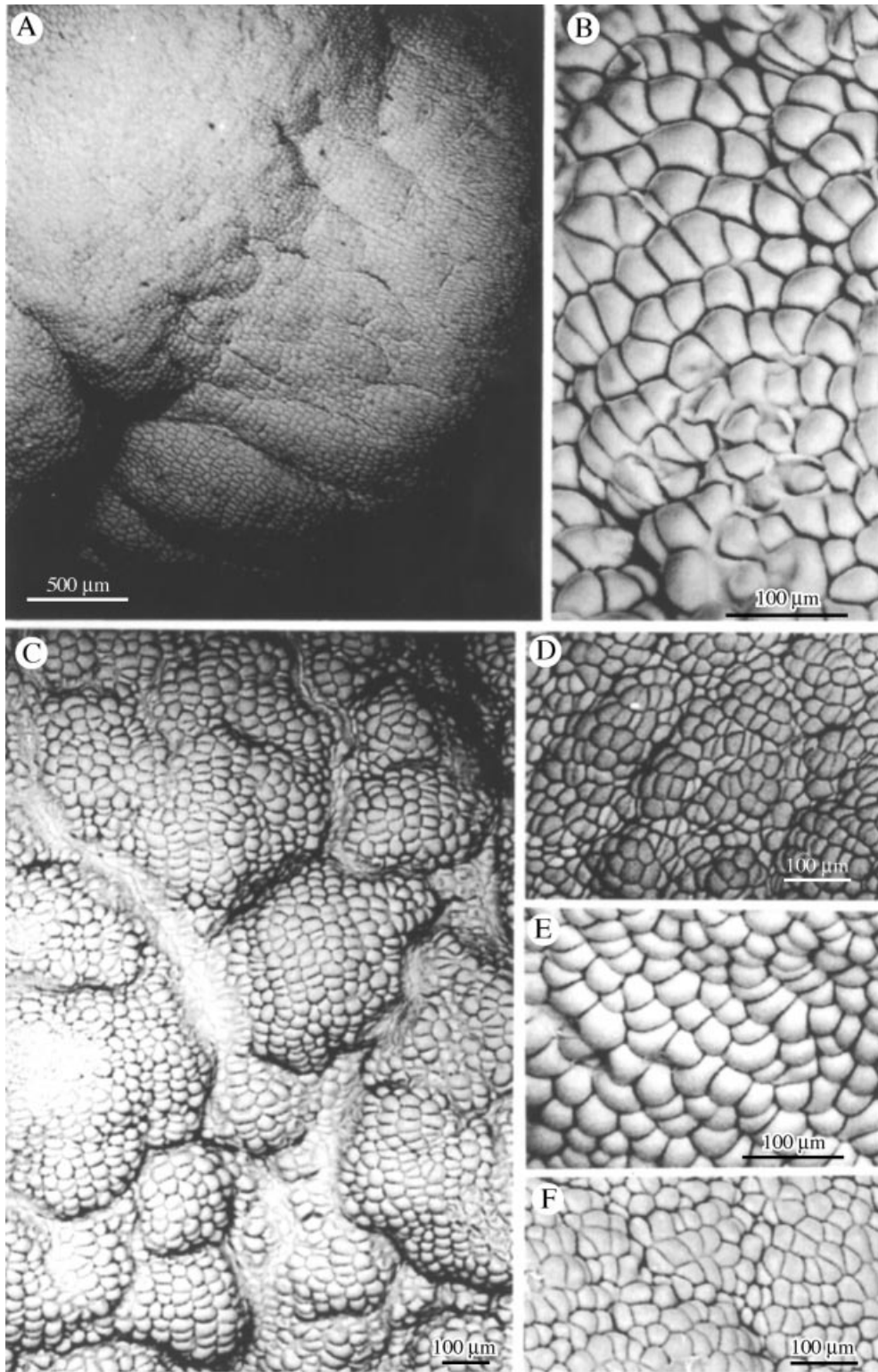


FIG. 5. Glabrous labellar surfaces of *M. cucullata* (A and B), *M. hematoglossa* with striped, dark flowers (C), striped flowers (D) and yellow, spotted flowers (E) and *M. lezarzana* (F). Scale bars = 500 μm (A) and 100 μm (B–F).

fusiform or borne upon multiseriate, labellar trichomes (Fig. 6C). In *M. lepidota* Lindl., labellar papillae, as previously described (Davies and Winters, 1998), become

modified into unicellular, spherical glands. These are more abundant on the ventral surface of the labellum than the dorsal.

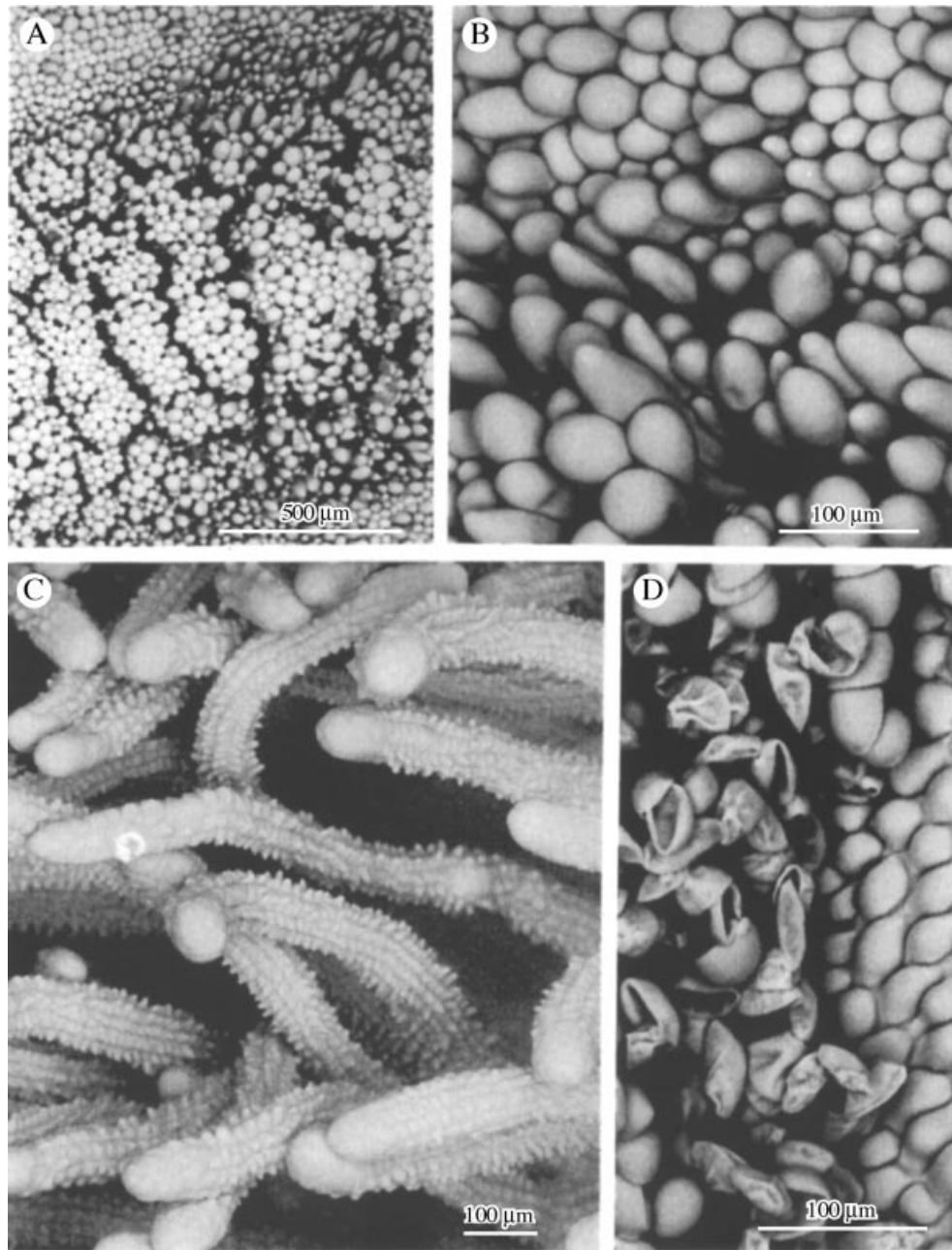


FIG. 6. A and B, Labellar surface of *M. rufescens* showing small, peripheral, obpyriform papillae and larger, central obpyriform to clavate papillae with distended apices. C, Papillose, multiserial trichomes of *M. camaridii* that may function as pseudostamens. D, Labellar papillae of *M. johniana* with associated pseudopollen. Scale bars = 500 μm (A) and 100 μm (B–D).

Around the anther and stigmatic surface, papillae may become enlarged or swollen and appear to contain a thin layer of peripheral cytoplasm and a large vacuole with watery cell sap that occupies most of the cell. Moreover, in many species (e.g. *M. lindleyana* Schltr. and *M. villosa* (Barb. Rodr.) Cogn.), many of these conical papillae are replaced by villiform papillae, some of which are curved like a scythe.

Conical papillae (Figs 1A, B and D, 2A–G, 3A, C and D and 4B–E) are the most common in *Maxillaria* and are

ubiquitous, occurring on the column, the anther cap and the labellum of a great many species, regardless of their vegetative morphology. Thus, xeromorphic species such as *M. minuta* Cogn. (Fig. 2D, F and G), *M. pumila* Hook., *M. ferdinandiana* Barb. Rodr., *M. plebeja* Rchb.f. (*M. pumila* alliance), *M. vitelliniflora* Barb. Rodr., *M. vernicosa* Barb. Rodr. (Fig. 2C), *M. seidelii* Pabst (Fig. 2E) (*M. subulata* alliance), *M. mosenii* Kraenzl. (Fig. 2A) and *M. cogniauxiana* Hoehne (Fig. 2B) (*M. madida* alliance), together with mesomorphic ascending types such as

TABLE 1. *Distribution and classification of papillae and trichomes*

Taxon	Accession no.	Type of papilla			Type of labellar trichome
		Column	Anther cap	Labellum	
<i>Maxillaria acuminata</i> Lindl.	MMB14			c, o	–
<i>M. acutifolia</i> Lindl.	MMB64			o, cl	–
<i>M. buchtienii</i> Schltr.	KLD199813	c	c	o	s (3–4 cells)
<i>M. camaridii</i> Rchb.f.	KLD199920	c	c	c	mu
<i>M. cerifera</i> Barb. Rodr.	ED95–70			c	–
<i>M. chartacifolia</i> Ames & C. Schweinf.	MMA18	o	o	–	–
<i>M. chlorantha</i> Lindl.	S0000079			o	s (3–4 cells)
<i>M. chrysantha</i> Barb. Rodr.	S19940012	c	c	–	–
<i>M. coccinea</i> (Jacq.) L.O. Williams ex Hodge	KLD199803, S19950015	–	c	c	–
<i>M. cogniauxiana</i> Hoehne	KLD199701			c	–
<i>M. cucullata</i> Lindl.	GXXXF012515			–	–
<i>M. dalessandroi</i> Dodson	KLD199908			o	m
<i>M. densa</i> Lindl.	S19970029	–	c	c	–
<i>M. desvauxiana</i> Rchb.f.	KLD199804			c	–
<i>M. discolor</i> (Lodd. ex Lindl.) Rchb.f.	S19990261, MMB62	c	c	c, o	m
<i>M. elatior</i> Rchb.f.	KLDX19971, KLD200005			c	–
<i>M. elegantula</i> Rolfe	S19980054	c, v		o	m
<i>M. ferdinandiana</i> Barb. Rodr.	MMC17	o, v	c, o	c, v	–
<i>M. fractiflexa</i> Rchb.f.	S19980052	c	c	c, v	s (3–4 cells)
<i>M. fucata</i> Rchb.f.	KLD199916, KLD199933			o	m
<i>M. cf. gracilis</i> Lodd.	S19980072	c	c	c, o	s (3–4 cells)
<i>M. hedwigae</i> Hamer & Dodson	BSNS089			f, v	–
<i>M. hematoglossa</i> A. Rich & Galeottii	KLD198601, KLD199811, KLD199704, S19920439, S19910275, KLD1998100, E19191019, KLD199602, S199930276, KLD1998101	c	c, o	–	–
<i>M. hillsii</i> Dodson	S19990292			o	m
<i>M. huancabambe</i> (Kraenzl.) C. Schweinf.	S20010484			c, o	–
<i>M. imbricata</i> Barb. Rodr.	MMA21	c	c, o		–
<i>M. infausta</i> Rchb.f.	MMA13	c, o	c, o, v	c	–
<i>M. irrorata</i> Rchb.f.	KLD199824	c	c, v	o	m
<i>M. jensischiana</i> (Rchb.f.) Garay & C. Schweinf.	S19980077	c, o	c, o	c	–
<i>M. jocunda</i> Lehm. & Kraenzl.	S19990297	–	c	o	m
<i>M. johniana</i> Kraenzl.	MMA41			o	m
<i>M. cf. lehmanii</i> Rchb.f.	KLD199911			o	m
<i>M. lepidota</i> Lindl.	S19950277			o with glands	s (2–3 cells)
<i>M. lezarzana</i> Soto Arenas & F. Chiang	KLD199102, KLD199706	–	c	–	–
<i>M. cf. lilliputana</i> D.E. Benn. & E.A. Christenson	S19980062	c, v	–	–	m
<i>M. lindleyana</i> Schltr.	KLD199806	c	c	o	–
<i>M. longissima</i> Lindl.	S20010485			o	m
<i>M. meleagris</i> Lindl.	KLD199603, KLD199604, KLD199919, S20000208	c	c	c	–
<i>M. minuta</i> Cogn.	S19960283	–	c	c	–
<i>M. cf. minuta</i> Cogn.	S19980011	–	c	c	–
<i>M. molitor</i> Rchb.f.	KLD199828, KLD199929			o	m
<i>M. moralesii</i> Carnevali & Atwood	BSNS number unknown	–	–	c, o, cl	–
<i>M. mosenii</i> Kraenzl.	S19970030			c	–
<i>M. mosenii</i> Kraenzl. var. <i>hatschbachii</i> (Schltr.) Hoehne	S19990245, S19980051	c	c	c	–
<i>M. notylioglossa</i> Rchb.f.	ED97-16, S20030488	o, v	o	c, o	–
<i>M. cf. notylioglossa</i> Rchb.f.	S19990147	c, v	c	c, o	–
<i>M. nutans</i> Lindl.	KLD199909			o	m
<i>M. ochroleuca</i> Lodd. ex Lindl.	KLD199714			o	s (3–4 cells)
<i>M. oreocharis</i> Schltr.	S19980012	–	c	c	–
<i>M. parviflora</i> (Poepp. & Endl.) Garay	MMC8	c	–	c	–
<i>M. picta</i> Hook.	KLD199917			v	–
<i>M. plebeja</i> Rchb.f.	KLD2000001	–	–	c	–
<i>M. ponerantha</i> Rchb.f.	MMC9		c	c, v	–
<i>M. procurrens</i> Lindl.	KLD199812	–	–	c	–
<i>M. pseudoreichenheimiana</i> Dodson	MMC16	c, v	o, v	o	s (2 cells)
<i>M. pulchra</i> (Schltr.) L.O. Williams	S19910274	c		c, v	mu
<i>M. pumila</i> Hook.	MMB60	c, o	o	c, o	–
<i>M. reichenheimiana</i> Endres & Rchb.f.	MMA50	c, v	v	o	s (2 cells)
<i>M. rufescens</i> Lindl.	BSNS532, KLDX20001, S19980055, BSNS230	c	c	o, cl	–

TABLE 1. Continued

Taxon	Accession no.	Type of papilla			Type of labellar trichome
		Column	Anther cap	Labellum	
<i>M. sanderiana</i> Rchb.f.	KLD199815, KLD199816			o	m
<i>M. schunkeana</i> Campacci & Kautsky	S19980056	–	c	c	–
<i>M. seidelii</i> Pabst	S19970500	c, o	c, o, v	c	–
<i>M. cf. setigera</i> Lindl.	S19980057	c with simple 2–3 celled trichomes	c	o	m (2–3 cells)
<i>M. sophronitis</i> (Rchb.f.) Garay	S19950281			c	–
<i>M. striata</i> Rolfe	KLD199910			v	–
<i>M. tenuibulba</i> E.A. Christenson	MMB16	o	o	c, o, cl	–
<i>M. tenuifolia</i> Lindl.	S00000282, KLDX20002, MMA48	c, v	c, v	v	–
<i>M. tenuis</i> C. Schweinf.	KLD199923				s
<i>M. cf. triloris</i> E. Morren	KLD199707			o	s (2–3 cells)
<i>M. uncata</i> Lindl.	S20000209	–	c	c	–
<i>M. variabilis</i> Bateman ex Lindl.	XX012504, XX012505, MMA28, KLD199105, KLD199714	c, v	c	c, v	–
<i>M. vernicosa</i> Barb. Rodr.	G1960002066, S20010100	c	c	c	–
<i>M. villosa</i> (Barb. Rodr.) Cogn.	S19990262	c	c,v	o	s (3–5 cells)
<i>M. violaceopunctata</i> Rchb.f.	S19990263	–	c	o	s (4–6 cells)
<i>M. vitelliniflora</i> Barb. Rodr.	MMB12	c, o	c, o	c	–

Types of papillae: c = conical; cl = clavate; f = fusiform; – = absent (i.e. glabrous); o = obpyriform; v = villiform. Types of trichome: m = moniliform; mu = multiseriate; s = simple; – = absent.

M. densa Lindl. (Fig. 3C and D), *M. jenischiana* (Rchb.f.) C. Schweinf., *M. elatior* Rchb.f. (Fig. 4B) and *M. coccinea* (Fig. 4E), caespitose types such as *M. meleagris* Lindl. (Fig. 3A) and *M. desvauxiana* Rchb.f. (Fig. 4C), and cane types such as *M. procurrens* Lindl. (Fig. 4D) all have conical labellar papillae, although even papillose labella may have some glabrous regions (Fig. 3B).

Wherever pseudopollen-forming trichomes occur, labellar papillae tend to be obpyriform (Fig. 6D). However, this type of papilla may occur in the absence of pseudopollen hairs as in *M. rufescens* Lindl. (Fig. 6A and B), *M. acutifolia* Lindl., *M. tenuibulba* E.A. Christenson and *M. moralesii* Carnevali & Atwood; all members of the *M. rufescens* alliance. Here, however, the apices of the papillae, in particular the larger, central papillae, are greatly distended and the papilla assumes a clavate profile. The exception is *M. hedwigae* Hamer & Dodson, where the papillae tend to be somewhat fusiform or villiform.

Glabrous labella completely devoid of papillae were found only in *M. cucullata* Lindl. (Fig. 5A and B), *M. hematoglossa* A. Rich & Galeottii (Fig. 5C–E) and *M. lezarzana* Soto Arenas & F. Chiang (Fig. 5F); all members of the *M. cucullata* alliance. Members of this group are often misidentified and since *M. hematoglossa* is such a variable species, forms with dark, light, striped and spotted flowers were examined with identical results. However, in *M. meleagris* (Fig. 3A and B), a species thought to be closely related to members of the *M. cucullata* alliance, the labellum is papillose and the conical papillae which have pointed tips resemble those of *M. densa* (Fig. 3C and D).

Thus, papillae not only vary greatly within a particular species but also according to their position upon a given organ. For example, conical papillae on the column often

become villiform around the anther (Fig. 1A) and stigmatic surface. Similarly, conical papillae on the lip surface form a fringe of longer, often villiform papillae, around the labellar margin (Fig. 2G). Detailed data for individual species are shown in Table 1.

TEM

TEM sections through the labellar epidermis of *M. vernicosa* revealed the presence of a relatively thick cuticle upon its surface (Fig. 1C).

Histochemistry

The labella of a number of species selected to show a wide range of papillar morphology were tested for food substances. Without exception, all types of papillae contained protein and most contained very little or no lipid. Starch, however was more variable, occurring in several species such as *M. jenischiana*, *M. jocunda* Lehm. & Kraenzl. and *M. buchtienii* Schltr. Some species (e.g. *M. rufescens*, *M. acutifolia* and *M. tenuibulba*) have obpyriform papillae containing all three food substances, protein, starch and lipid; those papillae at the centre of the lip often containing more starch than the others. Moreover, the labella of *M. acutifolia* and *M. tenuibulba* produce a lipoidal secretion much like that found in the *M. acuminata* alliance and some members of the *M. discolor* alliance (Davies *et al.*, 2003a, b). Simple, bicellular trichomes, whose walls stain selectively with Sudan III, occur on the labella of *M. reichenheimiana* Endres & Rchb.f. and *M. pseudoreichenheimiana* Dodson. Morphologically, these resemble the food hairs described by Davies *et al.*

TABLE 2. Histochemical analysis of labellar papillae

Taxon	Accession no.	Type of papilla	Foods present in papillae		
			Protein	Starch	Lipid
<i>M. acutifolia</i> Lindl.	MMB64	o, cl	+	+ ce	+ s
<i>M. buchtienii</i> Schltr.	KLD199813	o	+	+	–
<i>M. camaridii</i> Rchb.f.	KLD199920	c	+	–	–
<i>M. chrysantha</i> Barb. Rodr.	S19940012	a	+	–	–
<i>M. jenischiana</i> (Rchb.f.) Garay & C. Schweinf.	S19980077	c	+	+	–
<i>M. jocunda</i> Lehm. & Kraenzl.	S19990297	o	+	+	–
<i>M. lexarzana</i> Soto Arenas & F. Chiang	KLD199706	a	+	–	–
<i>M. mosenii</i> Kraenzl. var. <i>hatschbachii</i> (Schltr.) Hoehne	S19980051	c	+	–	–
<i>M. pseudoreichenheimiana</i> Dodson	MMC16	o	+	–	–
<i>M. reichenheimiana</i> Endres & Rchb.f.	MMA50	o	+	–	–
<i>M. rufescens</i> Lindl.	S19980055	o, cl	+	+	+
<i>M. cf. setigera</i> Lindl.	S19980057	o	+	+	–
<i>M. tenuibulba</i> E.A. Christenson	MMB16	c, o, cl	+	+ ce	+ s
<i>M. tenuifolia</i> Lindl.	S00000282	v	+	–	–

Types of papillae: c = conical; cl = clavate; o = obpyriform; v = villiform; a = absent.

+ and – indicate presence and absence, respectively, of food substance, whereas ce indicates that the food substance is largely concentrated in the central papillae of the labellum and s that the substance is secreted onto the labellar surface.

TABLE 3. Histochemical analysis of labellar trichomes

Taxon	Accession no.	Type of trichome	Type of labellar trichome		
			Protein	Starch	Lipid
<i>M. buchtienii</i> Schltr.	KLD199813	s (3–4 cells)	–	–	–
<i>M. jocunda</i> Lehm. & Kraenzl.	S19990297	m	+	+	–
<i>M. johniana</i> Kraenzl.	MMA41	m	+	+	–
<i>M. lilliputana</i> D.E. Benn. & E.A. Christenson	S19980062	m	+	+	–
<i>M. longissima</i> Lindl.	S20010485	m	+	–	+
<i>M. pseudoreichenheimiana</i> Dodson	MMC16	s (2 cells)	+	–	*
<i>M. reichenheimiana</i> Endres & Rchb.f.	MMA50	s (2 cells)	+	–	*
<i>M. cf. setigera</i> Lindl.	S19980057	m (2–3 cells)	+	+	–
<i>M. tenuis</i> C. Schweinf.	KLD199923	s	+	+	–

Types of trichome: m = moniliform; s = simple.

+ and – indicate presence and absence, respectively, of food substance, whereas * indicates that the cell wall only selectively stained for this substance.

(2002) for certain species of *Polystachya*. The histochemical results obtained for papillae and trichomes are presented in Tables 2 and 3, respectively.

DISCUSSION

As in other angiosperms (Kay *et al.*, 1981), the conical papilla is the most common type of papilla found in *Maxillaria*. Conical papillae occur on the labellum, the column and the anther cap and their persistence on the last two structures, even when the labellar papillae show modification, would indicate that this is a conservative character and that conical papillae are probably less derived than other papillae or indeed the glabrous condition. It is presumed that morphological modifications of papillae reflect underlying changes in their physiology, although, in many cases, identical papillae clearly perform different roles. For example, both *M. jenischiana* and *M. coccinea* have conical papillae but they cannot serve exactly the same purpose since the first species is probably insect-pollinated,

whereas the second is thought to be ornithophilous (Roubik, 2000; Stpicyńska *et al.*, 2004). Conversely, different types of papillae may have the same function and therefore determining the specific role of a particular type of papilla can be problematical. Nevertheless, much can be achieved by means of histochemistry used in conjunction with comparative morphology. Using this dual approach, we have been able to relate structure to function, although it must be remembered that the function of a particular type of papilla may vary from species to species, organ to organ and even according to its position upon that organ. Papillae may be involved in:

Attraction

In most *Maxillaria* spp., labellar papillae may become modified towards the centre and margin of the lip. Thus, in a species whose labellar papillae are largely conical, there would generally be a tendency for marginal papillae to become villiform, whereas the central ones would tend to be

more or less obpyriform. In this way, from the moment it alights upon the lip, the visiting insect is guided by means of tactile cues towards and along the median axis of the labellum. Many papillae are pigmented and act as nectar guides, drawing the insect further into the flower. Moreover, preliminary data obtained by the *in vivo* staining of flowers with a dilute aqueous solution of neutral red (Stern *et al.*, 1986) would indicate that some papillae, especially those at the margins of the tepals and labellum, may perhaps function as osmophores and provide olfactory cues (K.L. Davies, unpublished data). Similar osmophores have been observed in *Cymbidium tracyanum* L. Castle and *Gymnadenia conopsea* (L.) R. Br. (Stpiczyńska 1993, 2001). Perhaps the most remarkable papillae are to be found in *M. camaridii* Rchb.f and are seemingly involved in mimicry. These conical papillae are not unusual in themselves but are noteworthy in that they occur on the surface of multiseriate, labellar trichomes, which, in terms of size, position and colour, resemble a tuft of stamens. These hairs may thus perhaps function as pseudostamens but direct evidence for this is lacking. Such structures also occur in a similar position in *M. pulchra* (Schltr.) L.O. Williams, but here hairs tend to be glabrous. Nevertheless, the floral morphology of both species would perhaps suggest that they attract insects by deceit.

Rewards

The intensity of staining following the xanthoproteic test would indicate that the papillae of all species tested contain relatively high concentrations of aromatic amino acids. In contrast, most contain no lipid but the occurrence of starch is more variable. Protein, then, appears to be the most common food substance found within the floral papillae of *Maxillaria* and the results presented here closely resemble those obtained for pseudopollen (Davies *et al.*, 2000, 2003b). Usually, pseudopollen-forming hairs and papillae are inextricably associated and it is noteworthy that *M. johniiana* Kraenzl., *M. jocunda* and *M. lilliputana* D.E. Benn. & E.A. Christenson produce pseudopollen identical to those other members of the *M. grandiflora* alliance that have already been studied (Davies *et al.*, 2000). Furthermore, these species, together with *M. cf. setigera* Lindl., resemble the latter in that their pseudopollen and labellar papillae stain for protein and starch but not for lipid.

Members of the *M. splendens* alliance such as *M. buchtienii*, *M. chlorantha* Lindl. and *M. ochroleuca* Lodd. ex Lindl. have labella with uniseriate, relatively few-celled hairs as well as obpyriform papillae, and it has been speculated, solely on morphological grounds, that these hairs may become detached or fragment to form pseudopollen (Davies *et al.*, 2000, 2003a, b). However, histochemistry failed to demonstrate the presence of protein, starch or lipid within such hairs in *M. buchtienii*. Nevertheless, identical hairs occur in *M. ochroleuca* (Davies *et al.*, 2000) and Singer has observed *Trigona* bees (workers only) collecting these from the tip of the labellum (R. B. Singer, pers. comm.). Moreover, Singer reports that these long, yellowish hairs were chewed and stored in a paste-like form on the corbiculae. It may be that the bees actually collected

papillae rather than hairs, especially since the labellar papillae of the closely related *M. buchtienii* are known to contain numerous starch grains. Similarly, abundant starch occurs in the papillae of *M. jenischiana* and, since this species produces copious nectar, the starch is probably hydrolysed to form sugars during nectar production (Durkee, 1983). Again, starch is found in the labellar papillae of *M. rufescens* as well as in other members of that alliance.

In yet other species, such as members of the *M. acuminata* and *M. discolor* alliances, histochemistry indicated that the labellar papillae are involved in the secretion of a viscid, wax-like material rich in lipids and protein and this is gathered by visiting bees (Davies *et al.*, 2003a, b). A similar secretion also occurs in *M. acutifolia* and *M. tenuibulba*.

Protection

The exact function of the spherical glands on the ventral surface of the labellum of *M. lepidota* is still not known. Although they seemed to contain aromatic amino acids, histochemical analysis was frustrated by the intense pigmentation of the labellum. However, their position on the ventral surface of the lip would suggest that these glands are not involved in the attraction of pollinators. Instead, it may be that by secreting sugars (much like the sugary droplets found at the tips of tepals), they attract ants and these defend the plant from herbivory (Dressler, 1993; Davies *et al.*, 2003b). However, evidence for this is lacking.

The labellar epidermis of *M. chrysantha* Barb. Rodr. produces wax upon its surface and this protects the plant from desiccation. Similarly, in some xeromorphic species with somewhat dull-coloured flowers, such as those assigned to the *M. pumila*, *M. subulata* and *M. madida* alliances (Pabst and Dungs, 1977), the labellar papillae have a relatively thick cuticle. This serves not only to protect the flower from desiccation but also gives it a glossy appearance. Although it has been suggested that the glossy surface of the labellum may mimic water (Warren, 1999), or a shallow nectary, thereby attracting insects, it is perhaps more likely that insects are attracted simply because of its reflective nature.

The modified papillae associated with the stigmatic surface, anther and anther cap contain a little peripheral cytoplasm and a large vacuole with watery cell sap. They thus, in many ways, resemble water-storing or 'aqueous' tissue. These papillae tend to be larger and more swollen than those found elsewhere and may function like the paraphyses of mosses, trapping a layer of moist air. In this way, they prevent desiccation of the delicate reproductive structures.

Taxonomy

The occurrence of conical papillae on the column, anther cap and labellum of a wide range of species that differ in their vegetative morphology would indicate that this feature has little value as a taxonomic character. Moreover, obpyriform and villiform papillae are also found in species

that are clearly unrelated on morphological grounds and these may have evolved in response to similar pollinator pressures. Nevertheless, labellar papillae, or the lack thereof, could prove useful as a taxonomic character in exceptional cases and these cases deserve mention.

Glabrous labella are not common in *Maxillaria* and tend to occur largely in species assigned to the *M. cucullata* alliance. However, in *M. chartacifolia* Ames & C. Schweinf., the upper surface of the labellum is glabrous, whereas the lower is papillose with obpyriform papillae. A distinctive type of labellar papilla is also found in members of the *M. rufescens* alliance. Here, the labellar surface is clothed with obpyriform papillae, whereas those towards the centre of the lip are clavate and much larger with distended apices. Remarkably, some papillae occur upon multiseriate trichomes. Since, to date, multiseriate trichomes have been found in only two species of *Maxillaria*, namely, *M. camaridii* and *M. pulchra*, these hairs are probably far more important as taxonomic characters than the papillae they may bear.

Finally, the papillae of *Maxillaria* are highly adaptable and fulfil a variety of roles. They attract and guide visiting insects along the flower using a combination of visual, olfactory and tactile cues. They are rich in aromatic amino acids and provide rewards in the form of nectar or a viscid wax-like material containing protein and lipids, and may even offer protection from desiccation and herbivorous insects. Of course the exact function of papillae in a particular species can only be established for certain by observing how pollinators respond to them in the field. Until such data are forthcoming, morphological studies such as this can only provide half the story. Even so, of all the cell types to be found in *Maxillaria*, floral papillae must surely rank amongst the most intriguing.

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