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Nectary Structure and Nectar Secretion in *Maxillaria coccinea* (Jacq.) L.O. Williams ex Hodge (Orchidaceae)

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• *Background and Aims* It had previously been assumed that *Maxillaria* spp. produce no nectar. However, nectar has recently been observed in *Maxillaria coccinea* (Jacq.) L.O. Williams ex Hodge amongst other species. Furthermore, it is speculated that *M. coccinea* may be pollinated by hummingbirds. The aim of this paper is to investigate these claims further.
• *Methods* Light microscopy, histochemistry, scanning and transmission electron microscopy.
• *Key Results* This is the first detailed account of nectar secretion in *Maxillaria* Ruiz & Pav. A 'faucet and sink' arrangement occurs in *M. coccinea*. Here, the nectary is represented by a small protuberance upon the ventral surface of the column and nectar collects in a semi-saccate reservoir formed by the fusion of the labellum and the base of the column-foot. The nectary comprises a single-layered epidermis and three or four layers of small subepidermal cells. Beneath these occur several layers of larger parenchyma cells. Epidermal cells lack ectodesmata and have a thin, permeable, reticulate cuticle with associated swellings that coincide with the middle lamella between adjoining epidermal cells. Nectar is thought to pass both along the apoplast and symplast and eventually through the stretched and distended cuticle. The secretory cells are collenchymatous, nucleated and have numerous pits with plasmodesmata, mitochondria, rough ER and plastids with many plastoglobuli but few lamellae. Subsecretory cells have fewer plastids than secretory cells. Nectary cells also contain large intravacuolar protein bodies. The floral morphology of *M. coccinea* is considered in relation to ornithophily and its nectary compared with a similar protuberance found in the entomophilous species *M. parviflora* (Poepp. & Endl.) Garay.
• *Conclusions* Flowers of *M. coccinea* produce copious amounts of nectar and, despite the absence of field data, their morphology and the exact configuration of their parts argue strongly in favour of ornithophily.

Key words: Hummingbird pollination, *Maxillaria coccinea*, nectary ultrastructure, Orchidaceae, scanning electron microscopy, transmission electron microscopy.

INTRODUCTION

Rewards often play an important role in the pollination of orchids. Indeed, it has been demonstrated that orchid species that reward potential pollinators may increase their chances of producing fruit by almost two-fold (Neiland and Wilcock, 1998). Such rewards include pollen, nectar, oils and pseudopollen (van der Pijl and Dodson, 1969). Pollen, however, cannot serve as a reward in epidendroid orchids since it occurs in discrete masses within pollinia and is generally inaccessible to foraging insects. Consequently, in these species potential pollinators are usually rewarded with nectar (van der Pijl and Dodson, 1969; Arditti, 1992; Dressler, 1993). However, although nectar is the most common reward amongst these orchids, it has been estimated that as many as one-third of orchid species produce little or no nectar (Porsch, 1908) and a similar number produce no reward whatsoever (van der Pijl and Dodson, 1969; Ackerman, 1984).

The neotropical genus *Maxillaria* Ruiz & Pav. is represented throughout the American tropics and subtropics (Bechtel *et al*., 1981) and some of its members have evolved a number of strategies for rewarding potential pollinators. These rewards include the production of pseudopollen (Davies and Winters, 1998; Davies *et al*., 2000, 2002, 2003*b*) and a wax-like material secreted by the labellum (van der Pijl and Dodson, 1969; Davies *et al*., 2003*a*). Pseudopollen is formed in the *M. grandiflora* and *M. discolor* alliances as well as in *M. longissima* Lindl. by the fragmentation of multicellular hairs into individual cells rich in protein and starch (Davies and Winters, 1998; Davies *et al*, 2000, 2002, 2003*b*) and is collected by Meliponini (stingless bees: R. B. Singer, pers. comm., 2003) or euglossine bees (Dodson and Frymire, 1961; Dodson, 1962). Similarly, the wax-like secretion produced by the labella of members of the *M. acuminata* alliance is rich in lipids and aromatic amino acids (Davies *et al*., 2003*a*) and is said to be collected by bees for nest building (van der Pijl and Dodson, 1969), although it clearly has a nutritive function too. Remarkably, those species of *Maxillaria* that produce pseudopollen and lipoidal labellar secretions tend not to produce nectar (van der Pijl and Dodson, 1969; Davies *et al*., 2000, 2003*a*). Indeed, it was once generally thought that *Maxillaria* spp. did not produce nectar. Recently, however, nectar has been reported in a number

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of species, including *M. coccinea* (Jacq.) L.O. Williams ex Hodge, *M. jenischiana* (Rchb.f.) C. Schweinf., *M. imbricata* Barb. Rodr., *M. sophronitis* (Rchb.f.) Garay (Davies *et al*, 2003*a*, *b*), *M. parviflora* (Poepp. & Endl.) Garay, *M. rigida* Barb. Rodr. and *M. pendens* Pabst (Singer, 2003; Singer and Koehler, 2003).

Although most *Maxillaria* spp. are pollinated by stingless bees (Roubik, 2000), the floral morphology of some red-flowered species such as *M. coccinea* and *M. sophronitis* and the abundant nectar they produce would suggest that these plants may be pollinated by hummingbirds. However, published evidence for this is seemingly based solely on an observation reported by van der Pijl and Dodson (1969), where the hummingbird *Pantrope insignis* (*sic Panterpe insignis*) was seen visiting an unidentified species of *Maxillaria* with tubular pink flowers. Nevertheless, Ackerman and del Castillo Mayda (1992) too have stated that hummingbird pollination is likely to occur in *M. coccinea*, although the present authors are not aware of any direct observations that would confirm this.

By now, it is generally thought that nectar secretion in Orchidaceae may be a derived condition and that primitive orchids rewarded pollinators with pollen (Kocyan and Endress, 2001). Thus, the morphology of orchid nectaries has been widely studied (van der Pijl and Dodson, 1969), and Dressler (1993) believes that the 'lily-like ancestors of the orchids probably had shallow nectar glands between the perianth and the ovary'. In extant orchids, however, nectar is not produced in septal glands but in a relatively shallow nectary on the lip or tepals or between the column and the lip (e.g. *Bulbophyllum* Thouars, *Cirrhopetalum* Lindl., *Epipactis* Sw., *Listera* R. Br., *Pleurothallis* R. Br., *Stelis* Sw.), in glandular ring-like nectaries at the top of the receptacle or in spurs (e.g. *Angraecum* Bory) or in tubular nectaries embedded in the ovaries (cuniculus) (e.g. *Brassavola* R. Br., *Rhyncholaelia* Schltr.). Other orchids (e.g. *Cymbidium* Sw., *Grammatophyllum* Blume, *Vanda* Jones) produce nectar at the base of the outer surface of the tepals, and it has been proposed (van der Pijl and Dodson, 1969; Dressler, 1993) that the mentum may also function as a nectar spur (e.g. *Scaphyglottis* Poepp. & Endl., *Dendrobium* Sw.). However, only rarely has the column ever been observed to secrete nectar (e.g. *Stelis* Sw.; Porsch 1908, cited in van der Pijl and Dodson, 1969). Conversely, in contrast to gross morphological studies, detailed, ultrastructural studies of the orchid nectary are rare and have been largely confined to a handful of insect-pollinated terrestrial and mainly European species (e.g. Figueiredo and Pais, 1992; Pais and Figueiredo, 1994; Stpiczyñska, 1997; Stpiczyñska and Matusiewicz, 2001).

Thus, the present paper differs from previous studies in that it considers, for the first time, the ultrastructure of the nectary of a presumed hummingbird-pollinated, epiphytic orchid and presents, again for the first time, a detailed account of nectary structure and nectar secretion in the genus *Maxillaria*.

MATERIALS AND METHODS

Plants of *M. coccinea* (Jacq.) L.O. Williams ex Hodge (accession no. S19950015) were grown at Swansea Botanical Complex, UK. Herbarium specimens were prepared and deposited at the National Museum and Gallery of Wales, Cardiff, UK.

Authorities for plant names follow Brummitt and Powell (1992). Flowers were sampled well into the secretory stage (approx, day 6 of anthesis) and preliminary determination of the position of the nectary was achieved using a hand lens.

Light microscopy and histochemistry

Further detailed study of the position of the nectary in complete, fresh flowers was achieved using an Olympus SZX12 stereo-microscope. Hand-cut sections through the living nectary were tested for starch and lipids using IKI and a saturated alcoholic solution of Sudan III, respectively. Small pieces of nectary were fixed in 2·5 % glutaraldehyde/5 % sucrose in phosphate buffer (pH 6·8; 0·075 M) at 20 °C for 4 h, washed in phosphate buffer and post-fixed in 1 % osmium tetroxide at 0 °C for 2 h. The fixed material was then dehydrated using a graded ethanol series, infiltrated and embedded in Spurr resin. Semi-thin sections (1 μm) were stained for general histology (O'Brien *et al*., 1965) using 1 % (w/v) toluidine blue in 1 % (w/v) aqueous sodium tetraborate solution (Vaughn, 1987). Staining with Coomassie brilliant blue R-250 (Fisher, 1968) and ruthenium red (Jensen, 1962) revealed the presence of protein and mucilage/acidic polysaccharides, respectively. Micrometry and photomicrography of nectaries were accomplished using a Nikon Eclipse 600 microscope.

TEM and SEM

Sections (approx. 60 nm) were stained with uranyl acetate and lead citrate and examined using a TESLA BS-340 transmission electron microscope at an accelerating voltage of 60 kV. Fixed pieces of column and labellar tissue were dehydrated through a graded ethanol series and, following critical-point drying using liquid CO_2, were sputter-coated with gold and examined using a TESLA BS-300 scanning electron microscope at an accelerating voltage of 20 kV.

RESULTS

Floral morphology

The flowers of *M. coccinea* are produced in axillary fascicles. They are globose with scarlet tepals and a scarlet and yellow labellum. The sepals are ovate-lanceolate, acuminate and +/– forwardly pointing. The dorsal sepal is 10 mm long × 5 mm broad and the lateral sepals are oblique and measure 11 mm long × 5 mm broad. Mentum absent. Petals are ovate-lanceolate, acuminate and oblique, 7 mm long × 4 mm broad and form a hood over the column. Labellum arcuate, 3-lobed and immovable, 7 mm long × 4 mm broad, the mid-lobe is 4 mm long × 3 mm broad, linguiform and strongly reflexed with a simple, hemispherical callus. Lateral lobes erect, 1·5 mm long × 1 mm broad.

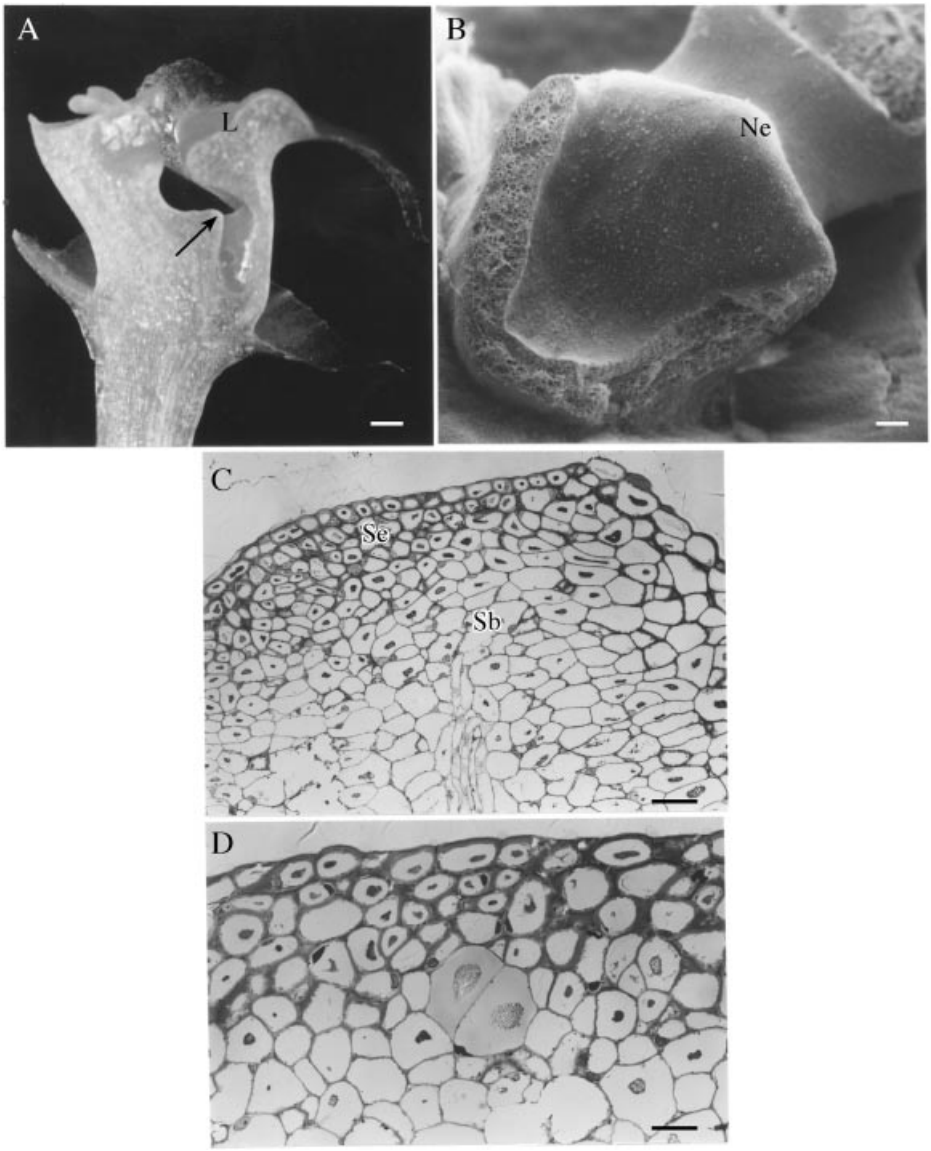

FIG. 1. A, Median longitudinal section of flower of *M. coccinea*. Nectar is secreted by the protuberance (arrow) and accumulates in the reservoir beneath the column. Scale bar = 1 mm. B, Part of column showing the nectary protuberance. Scale bar = 100 µm. C, Section through nectary protuberance showing secretory and subsecretory tissues and vascular bundle. Scale bar = 50 µm. D, Section through nectary showing secretory tissue; the subsecretory parenchyma containing two cells with raphides. Scale bar = 20 µm. Key (all figures): Ne = nectary; L = labellum; Se = secretory tissue; Sb = subsecretory tissue; N = nucleus; P = plastid; m = mitochondrion; c = cuticle; V = vacuole; Pb = protein body; Cs = cuticular swelling; CW = cell wall.

The base of the labellum is sub-saccate due to the partial fusion of the lip to the column foot. A transverse labellar ridge separates the reflexed mid-lobe of the labellum from the steeply sloping, proximal region of the lip, thereby partially closing the floral tube directly beneath the reproductive structures. Column short, white, 4 mm long × 2 mm broad at tip and with prominent, basal protuberance. Pollinia 4, of equal size.

The nectary is represented by a pronounced protuberance at the base of the column (Fig. 1A and B). Exuded nectar accumulates beneath the column in the semi-saccate reservoir formed by the fusion of the labellum and the base of the column-foot.

Light microscopy and histochemistry

The nectary consists of a single-layered epidermis and three or four layers of subepidermal secretory cells (Fig. 1C). Beneath these are several layers of parenchyma. Secretory cells are small (approx. 16·38 µm diameter, range 14·17–18·42 µm), whereas subsecretory parenchyma cells are larger (30 µm diameter, range 26·5–38·2 µm). Some of the subsecretory parenchyma cells contain raphides. The nectary is supplied by a single vascular bundle comprising xylem and phloem (Fig. 1C). Staining with toluidine blue indicated that the walls of secretory cells consist of cellulose whereas staining with ruthenium red showed that the middle

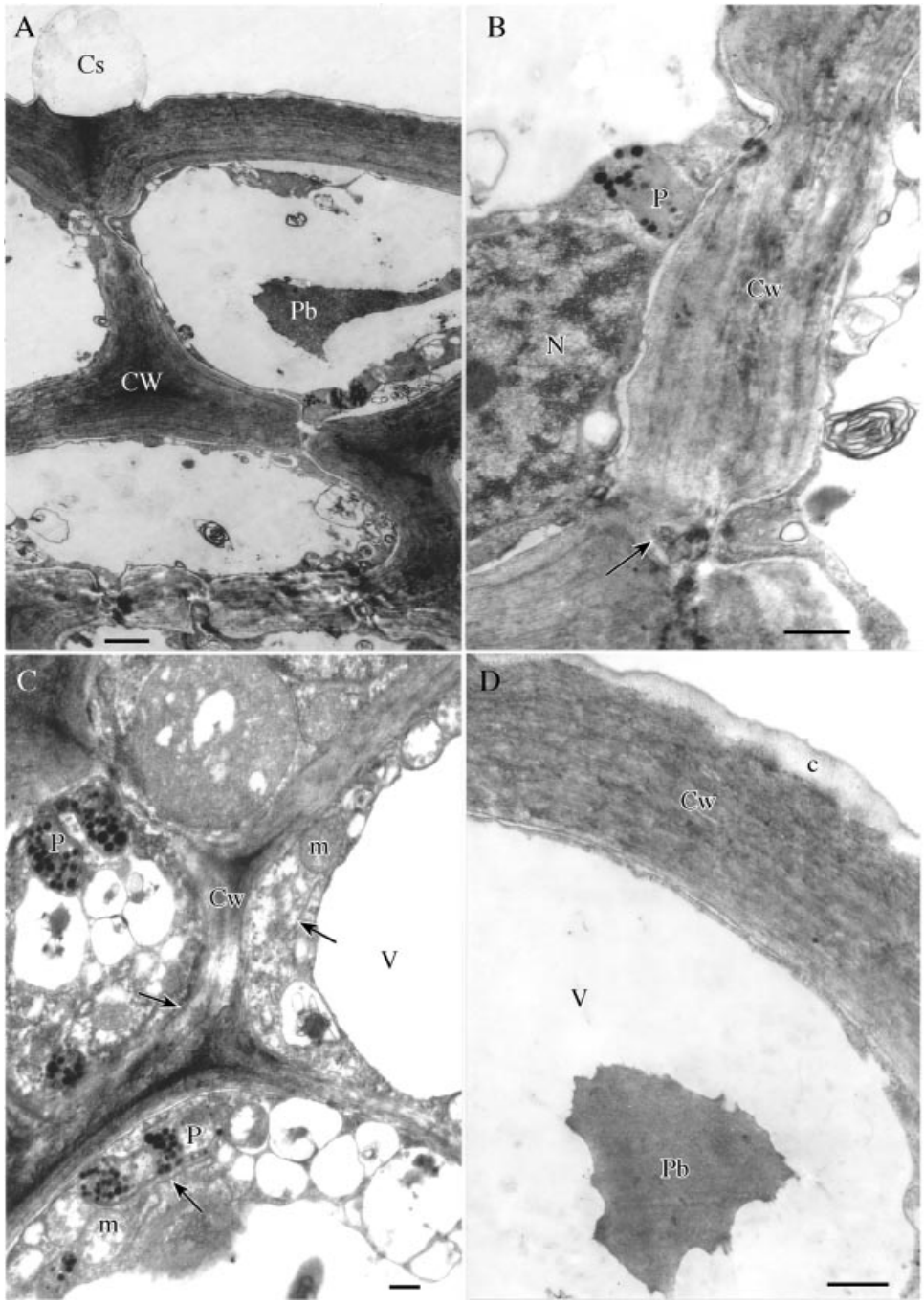

FIG. 2. A, Cell walls of secretory cells with numerous pits; the epidermal cell showing swelling of cuticle. Scale bar = 2 μm. B, Section through thick cell wall of secretory epidermis showing plasmodesma within pit (arrow). Scale bar = 1 μm. C, Cytoplasm of secretory cell with abundant mitochondria, ER (arrows) and plastids containing numerous plastoglobuli. Scale bar = 1 μm. D, Outer tangential wall of epidermis with reticulate cuticle. Note the single, finely granular, intravacuolar protein body. Scale bar = 1 μm.

lamella and the outer tangential walls of epidermal cells contain acidic polysaccharides. A characteristic feature of these nectary cells is the presence of a large, intravacuolar, protein body that is finely granular and irregular in shape (Fig. 1C and D) and stains with Coomassie brilliant blue R-250. Such cells, whilst lacking accumulated starch, nevertheless contain numerous lipid droplets.

TEM and SEM

The secretory cells are collenchymatous in that they possess unusually thick walls (2·5 μm, range 2·3–3·26 μm). Numerous pits with associated plasmodesmata connect the protoplasts of contiguous epidermal and secretory cells (Fig. 2A and B). The cytoplasm contains numerous mitochondria and rough ER profiles, which are associated with the plasmodesmata. The plastids contain many small

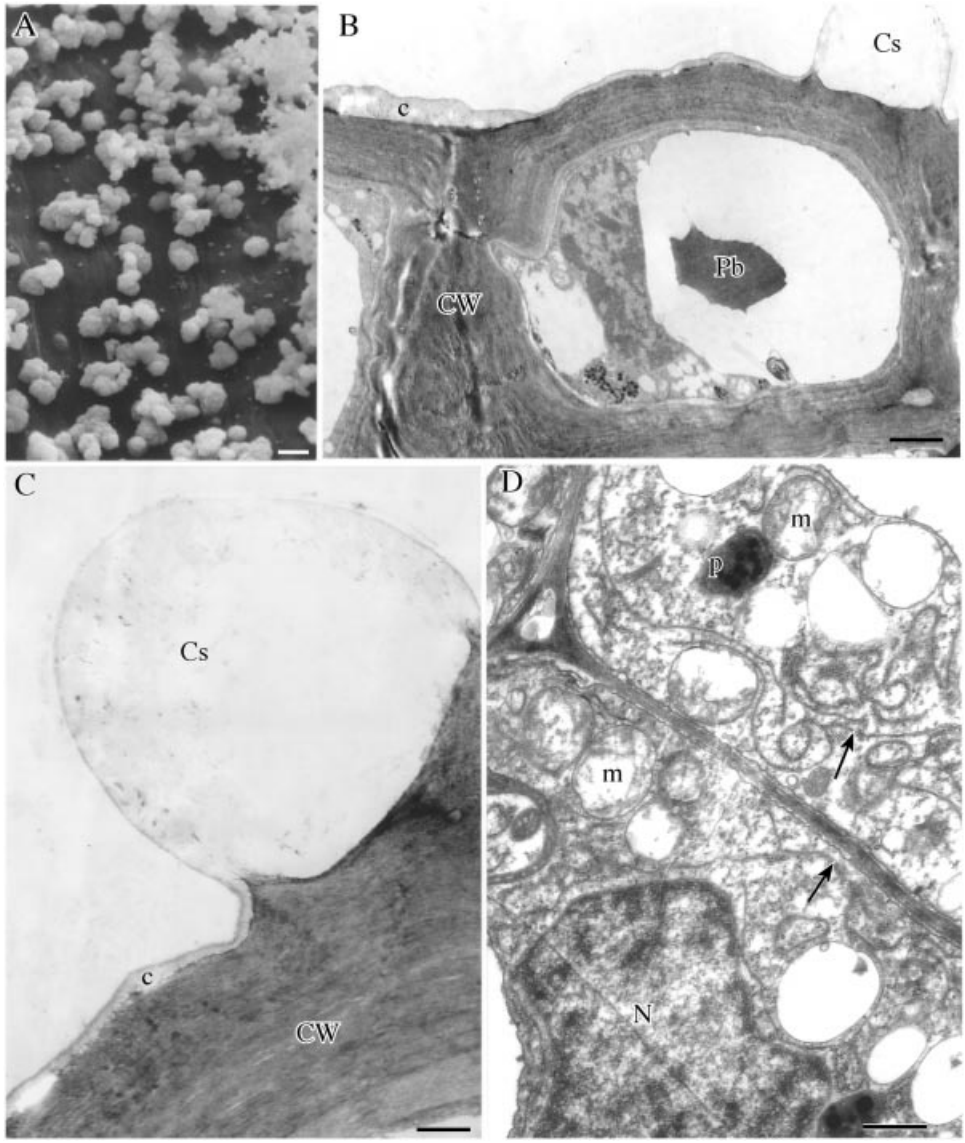

FIG. 3. A, SEM showing cuticular swellings on surface of nectary. Scale bar = 10 μm. B, Epidermal cell wall with cuticular swelling coinciding with junction between adjoining epidermal cells. Scale bar = 3 μm. C, Epidermal cell wall with cuticular swelling. Scale bar = 1 μm. D, Subsecretory parenchyma with thin cell walls and dense cytoplasm containing numerous ER profiles (arrows) and mitochondria. Scale bar = 5 μm.

plastoglobuli but few lamellae (Fig. 2C). Secretory vesicles associated with the cell wall tend to be absent.

The secretory epidermis possesses few stomata. The outer tangential wall lacks ectodesmata and is covered with a thin reticulate cuticle (Fig. 2D). SEM observations did not reveal pores or cracks through which nectar could exude. However, the cuticle has characteristic swellings 2–7 μm high (Fig. 3A) and these are usually found at points coinciding with the middle lamella between adjoining epidermal cells (Figs 2A and 3B and C). The swellings occur exclusively on the surface of the nectary protuberance and are absent from the epidermal cells of the nectar reservoir.

Subsecretory parenchyma cells have distinctly thinner cell walls (0·5 μm, range 0·47–0·52 μm) with abundant plasmodesmata. Their cytoplasm contains numerous mitochondria, rough ER, dictyosomes and vesicles (Fig. 3D) but fewer plastids than secretory cells.

DISCUSSION

Floral morphology and ornithophily in orchids

The flowers of *M. coccinea* fulfil many of the criteria that characterize ornithophilous flowers, namely they show diurnal anthesis, they are weakly zygomorphic, possess a backwardly curved labellum, have scarlet flowers, produce abundant nectar and lack nectar guides. Furthermore, the tissues are tough and can thus withstand contact with a hard beak. Finally, a strong fold in the labellum partially closes

the floral tube at the level of the anther and stigma and this would perhaps tend to force the bird to push its beak against the column to gain entry (van der Pijl and Dodson, 1969). However, *M. coccinea* differs from many bird-pollinated orchids in that, whereas ornithophilous flowers tend to lack odour, a sweet honey-like scent was occasionally detected in this species.

Over the years, a large number of orchid species have been presumed to be pollinated by hummingbirds solely on the basis of flower colour, presence of abundant nectar or absence of odour, but, although hummingbirds have on occasion been observed visiting such flowers, unequivocal evidence of hummingbird pollination (i.e. the transfer of pollinia) is rare. Many orchids presumed to be pollinated by hummingbirds have flowers that are various shades of red, orange or pink [e.g. *Cochlioda rosea* (Lindl.) Benth., *C. vulcanica* (Rchb.f.) Benth., *Comparettia falcata* Poepp. & Endl., *Cyrtochilum mystacinum* Lindl., *C. retusum* (Lindl.) Kraenzl., *Elleanthus aurantiacus* (Lindl.) Rchb.f., *Epidendrum ibaguense* H.B.K., *E. pseudepidendrum* Rchb.f., *Isochilus linearis* (Jacq.) R.Br. var. *carnosiflorus* (Lindl.) Correll, *Laelia milleri* Blumensch., *Masdevallia rosea* Lindl., *Rodriguezia secunda* H.B.K.], whereas others are rose-purple to purple [e.g. *Elleanthus capitatus* (Poepp. & Endl.) Rchb.f., *Epidendrum cnemidophorum* Lindl., *E. pfavii* Rolfe, *E. secundum* Jacq., *Sobralia amabilis* (Rchb.f.) L.O. Williams] or even yellow [e.g. *Elleanthus aureus* (Poepp. & Endl.) Rchb.f.]. Observations by C. H. Dodson and G. P. Frymire (all cited in van der Pijl and Dodson, 1969) of hummingbirds visiting *Elleanthus arpophyllostachys* (Rchb.f.) Rchb.f., *E. hallii* (Rchb.f.) Rchb.f., *E. hymenophorus* Rchb.f., *E. rosea* Schltr., *Epidendrum ardens* Kraenzl. and *E. scabrum* Ruiz & Pav., do not in themselves prove that these orchids are pollinated by hummingbirds. More recently, however, Singer and Sazima (2000) have reported hummingbirds both visiting and pollinating *Stenorrhynchos lanceolatus* (Aubl.) L.C. Rich. Of the above species, *Comparettia falcata*, *Elleanthus hymenophorus*, *Epidendrum cnemidophorum, E. pfavii* and *Isochilus linearis* var. *carnosiflorus* were visited by the rufous-tailed hummingbird (*Amazilia tzacatl*), *Epidendrum secundum* by an unidentified species of hummingbird (*Amazilia* sp.), *Elleanthus arpophyllostachys* by the booted racquet-tail (*Ocreatus underwoodii*), and *Sobralia amabilis* and an unidentified species of *Maxillaria* with pink tubular flowers by the fiery-throated hummingbird (*Panterpe insignis*). Singer (2003) has also reported the pollination of *Elleanthus brasiliensis* Rchb.f. by the hermit (*Phaethornis petrei*). A number of other species are also possible candidates for hummingbird pollination, but whether they are actually pollinated by hummingbirds cannot at present be corroborated due to a lack of field data.

Structure of the nectary and nectar secretion

In *M. coccinea*, the nectary is represented by a prominent protuberance on the base of the column. The secretory tissue of the nectary has a number of unusual features. The cells here are collenchymatous in that they have thick walls. Such walls have not been described for nectaries of other plant species. In *M. coccinea*, they are probably involved, especially in the absence of cutinized layers that would impede the flow of nectar, with the movement of this substance within the nectary. Numerous plasmodesmata would perhaps indicate that, in addition to apoplastic transport, symplastic transport of nectar occurs in this species. Models for the movement of pre-nectar along the apoplast or symplast within secretory tissue and the subsequent secretion of nectar have been proposed by several researchers (e.g. Gunning and Hughes, 1976; Sawidis *et al*., 1987, 1989; Robards and Stark, 1988; Kronestedt-Robards and Robards, 1991; Sawidis, 1991, 1998; Zellnig *et al*., 1991; Fahn, 2000). Some of these studies used radiolabelling to follow the path taken by sugars within the nectary (Fahn and Rachmilevitz, 1975; Heinrich, 1975; Meyberg and Kirsten, 1981; Sawidis, 1989; Stpiczyñska, 2003). Moreover, it had been proposed that both pathways of sucrose transport may operate simultaneously even in the same plant and that this is largely dependent on the developmental stage of the organ or tissue under investigation (Bush, 1999; Delrot *et al*., 2000; Lemoine, 2000; Williams *et al*., 2000). Sucrose may be imported directly from the apoplast into sink cells either by sucrose transporters or monosaccharide transporters following hydrolysis of sucrose to glucose and fructose by cell wall invertase (β-D-fructofuranoside fructohydrolase, EC 3.2.1.26). The nectar undergoes a final modification and is eventually secreted into the space between the plasmalemma and cell wall. However, since secretory vesicles were not observed in nectary cells, even during the nectar-secretory stage, yet mitochondria were present in large numbers, then it is probable that here, as in other species (Fahn, 2000), sugars are actively transported across the plasmalemma.

Another remarkable feature is the uninterrupted layer of reticulate cuticle covering the outer tangential walls of the secretory epidermis. This, seemingly, does not impede nectar secretion. Having transversed the outer tangential wall, the nectar accumulates beneath the cuticle which, in turn, stretches and forms swellings. Usually, these swellings occur at points coinciding with the middle lamella between adjoining epidermal cells and this would perhaps indicate that within the nectary, nectar passes along the apoplast. Eventually, the nectar passes through the stretched and distended cuticle. The cuticle covering the nectary cells may be completely permeable, not only to secretory products, as in the glandular hairs of *Leonotis* (Ascensão and Pais, 1998) and *Rosmarinus* (Bottega and Corsi, 2000), but also to those substances that are resorbed, as in nectaries of *Platanthera chlorantha* (Stpiczyñska, 2003). However, in some plants, nectar may pass through a disrupted cuticle as in *Limodorum abortivum* (Pais and Figueiredo, 1994) or through cuticular pores as in the nectary hairs of *Abutilon* (Findlay and Mercer, 1971), the osmophores of *Restrepia muscifera* (Pridgeon and Stern, 1983) or the capitate hairs of *Majorana syriaca* (Werker *et al*., 1985).

The cell wall here is noteworthy in that not only does it appear to function in nectar transport but its collenchymatous nature would suggest that it may also have a supportive and/or protective function, preventing damage to the

delicate secretory tissue by the hard beaks of visiting hummingbirds.

The nectary cells of *M. coccinea* are also remarkable in that they contain intravacuolar protein bodies similar to those found in the floral and extra-floral nectaries of *Passiflora* (Durkee *et al*., 1981; Durkee, 1982), the extra-floral nectaries of *Vigna* (Kuo and Pate, 1985) and the epidermal pseudopollen-forming hairs of *Maxillaria sanderiana* (Davies *et al*., 2000). Such intravacuolar bodies are not common and, although their function in *M. sanderiana* is probably primarily storage, their role in nectary cells remains unclear and requires further investigation.

Subsecretory cells of both *M. coccinea* and those occurring in the floral or extra-floral nectaries of other species (Durkee, 1982; Stpiczyñska, 1995) often contain raphides of calcium oxalate and these, according to Elias and Gelband (1977), may be involved with phloem metabolism and the active transport of sucrose. However, Davies has reported the presence of raphides in leaf (Davies, 1999) and floral tissue (Davies *et al*., 2000) for a number of *Maxillaria* spp. and has suggested that they may simply be excretory products and may perhaps discourage herbivory by invertebrates.

Nectary cells of *M. coccinea*, in contrast to those of other plants studied, contain no amyloplasts. The absence of amyloplasts is noteworthy since these organelles usually play an important role in nectar production. Starch stored within amyloplasts at the pre-secretory stage can be utilized both as a source of energy for highly metabolic processes and as a source of sugars for nectar synthesis. During successive stages of secretory activity, plastids generally become elongated or develop an irregular profile and this is usually associated with a depletion in starch content (Durkee *et al*., 1981; Sawidis *et al*., 1989; Nepi *et al*., 1996; Sawidis, 1998). Unfortunately, since the nectaries of *M. coccinea* were studied only at the secretory stage, we were unable to ascertain whether starch accumulates during the pre-secretory stage. Nevertheless, plastids devoid of starch, similar to those present in *M. coccinea*, and containing numerous plastoglobuli but few internal lamellae, have been observed, on occasion, in the nectary cells of *Gymnadenia conopsea* (Stpiczyñska and Matusiewicz, 2001). These closely resembled leucoplasts engaged in terpenoid synthesis (Gleizes *et al*., 1983; Cheniclet and Carde, 1985; Heinrich and Schultze, 1985; Turner *et al*., 1999) and the plastids which occur within the labellar papillae of *Maxillaria* cf. *notylioglossa* (Davies *et al*., 2003*a*). Thus, in the absence of starch, it is possible that sugars secreted in the nectar of *M. coccinea* are delivered in the phloem sap and then modified in the secretory cells before finally being secreted.

Comparative morphology

A protuberance on the ventral surface of the column, not unlike that found in *M. coccinea*, also occurs in *M. parviflora* (Poepp. & Endl.) Garay. This species, however, differs from *M. coccinea* in that its flowers are much smaller (5 mm diameter), are white with a yellow mid-lobe to the labellum and the angle between the labellum and column is greater. Furthermore, the mid-lobe of the lip is horizontal, not vertical and reflexed. Such protuberances have also been noted by others (Bennett and Christenson, 1993; M. McIllmurray, pers. comm., 2003) for *M. parviflora* but Bennett and Christenson (1993) interpreted this protuberance as a tabula infrastigmatica.

The tabula infrastigmatica, is best known from several species of Oncidiinae where the labellum is well developed at the expense of the other perianth parts, and is vertical. Situated on the column, the tabula occurs as a pad or plate which is often distinctive in colour or texture from the rest of the column and affords purchase for bees (mostly *Centris*) that alight on the vertical lip. By grasping the tabula with their mandibles, these insects can freely use their legs to gather oil droplets (Dressler, 1993). Moreover, orchids possessing a tabula tend not to produce nectar, whereas nectar-producing flowers such as those of entomophilous *Maxillaria* spp. tend to have a more or less horizontal lip and lack a tabula.

Maxillaria parviflora, however, is rather peculiar in that it produces nectar, has a horizontal lip and a protuberance which can, on morphological grounds, be interpreted as either a nectary (as in *M. coccinea*) or a tabula. R. B. Singer (pers. comm., 2003) has observed droplets of nectar collecting in 'a conch-like cavity of the lip' in this species. These droplets are licked by stingless bees (Meliponini) and Ponerinae ants, the pollinarium adhering to the frons or clypeus (Singer, 2003). Singer also reports that flowers of similar morphology occur in *M. brevilabia* Ames & Correll, *M. concavilabia* Ames & Correll and *M. horichii* Senghas (R. B. Singer, pers. comm., 2003). A search through published illustrations of floral dissections revealed that identical protuberances also occur in *M. aggregata* (H.B.K.) Lindl., *M. fulgens* (Rchb.f.) L.O. Williams, *M. nubigena* (Rchb.f.) C. Schweinf., *M. ruberrima* (Lindl.) Garay and *M. sophronitis* (Rchb.f.) Garay, all formerly assigned to *Ornithidium* Salisb. (Dunsterville and Garay, 1979; Bennett and Christenson, 1993). At first glance then, it would appear that the protuberance in *M. parviflora* is also a nectary rather than a tabula and that the 'faucet and sink' type of morphology found in *M. coccinea* is not unique to ornithophilous species but is, rather, universal, occurring in entomophilous species also. However, this conclusion appears to be erroneous since despite its similar appearance to the protuberance of *M. coccinea*, our semi-thin sections through the column of *M. parviflora* failed to reveal secretory tissue, thus indicating that Singer's proposal (R. B. Singer, pers. comm., 2003) that nectar is 'secreted at the lip surface inside the cavity where it is offered to pollinators' may well be correct. As a result, the true role of the protuberance in *M. parviflora* remains a mystery and serves to remind us that morphologically similar structures may indeed differ in their functions.

Finally, despite the absence of direct evidence, it would appear that *M. coccinea*, based on the unique combination of the floral features it possesses, is ornithophilous. However, ornithophily is the exception rather than the rule amongst *Maxillaria* spp. and as such, this species is atypical for the genus as a whole. Nevertheless, to the best of our knowledge, this is the only detailed study of the nectary of

any *Maxillaria* species to date, and it thus affords a useful baseline against which other species can be compared. Given the enormity of the genus and the morphological diversity of its members, it is predicted that this diversity will also be reflected in both the position and structure of the nectary. Further studies of this kind would enable us to better understand the reproductive strategies and pollination biology of *Maxillaria*.

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