NECTARY STRUCTURE OF *Ornithidium sophronitis* RCHB.F. (ORCHIDACEAE: MAXILLARIINAE)

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Abstract

Most orchids do not produce floral food-rewards. Instead, they attract pollinators by mimicry or deceit. When present, the most common floral food-reward is nectar. To date, nectary structure has been described for only two species of *Maxillaria sensu lato*, namely *Maxillariella anceps* and *Ornithidium coccineum* (formerly *Maxillaria anceps* and *M. coccinea*, respectively). Here, we describe that of a third species, *Ornithidium sophronitis* (formerly *Maxillaria sophronitis*). This species possesses floral characters concomitant with ornithophily. A 'faucet and sink' arrangement is present, with nectar secreted by a protuberance on the ventral surface of the column, collecting between column and tepal bases.

The nectary of *O. sophronitis* shares many features with that of *O. coccineum*. It has a single-layered epidermis and 3-5 layers of small, subepidermal, collenchymatous, secretory cells. Beneath these occur 2-3 layers of larger, subsecretory, parenchymatous cells supplied by phloem. Nectary cell vacuoles contain osmiophilic material and proteinaceous intravacuolar bodies. Moreover, distension of the nectary cuticle occurs as nectar accumulates between it and the secretory epidermis. Subsecretory cells, however, have thinner walls and contain flocculent, intravacuolar precipitates that may be related to the presence of flavonoids.

Since the floral and nectary structure of *O. sophronitis* is very similar to that of closely related *Ornithidium coccineum*, it may have evolved in like manner in response to similar pollinator pressures.

Key words: labellum; nectary; cuticle; nectar; ornithophily; *Maxillaria*; *Ornithidium*

INTRODUCTION

Although many angiosperm families produce floral food-rewards, these are often absent from orchid flowers and here, pollinator attraction by mimicry and deceit tend to predominate (van der Pijl and Dodson, 1969; Ackerman, 1984; van der Cingel, 2001). However, rewards, when present in a flower, not only serve to attract potential pollinators, but also maintain a high incidence of pollinator visits and generally confer evolutionary advantage, in that they can double its chances of developing fruit and seed (Neiland and Wilcock, 1998). The most common food-reward in Orchidaceae is nectar (van der Pijl and Dodson, 1969), and its presence significantly enhances the efficiency of pollination, as compared with other types of floral-food rewards or deceit alone (Dafni and Ivri, 1979; Johnson and Bond, 1997; Neiland and Wilcock, 1998; Johnson and Nilsson, 1999; Neiland and Wilcock, 2000). However, the cost of nectar production and subsequent fruit and seed maturation can be great in terms of material and energy expenditure, and this may outweigh the benefits (Ackerman, Rodriguez-Robles and Meléndez, 1994; Meléndez-Ackerman, Ackerman and Rodriguez-Robles, 2000, and references therein).

The Neotropical genus *Maxillaria* Ruiz and Pav., as traditionally defined, is thought to contain some 580 species and has long been considered to be an assemblage of morphologically disparate taxa (Whitten et al. 2007). Recent phylogenetic analyses indicate that *Maxillaria* is indeed grossly polyphyletic (Blanco et al. 2007, and references therein). As a result, Blanco et al. (2007) have proposed a new classification of core Maxillariinae that recognizes 17 genera (including *Ornithidium* Salisb. ex R. Br., *Camaridium* Lindl. and *Maxillariella* M.A. Blanco & Carnevali). However, the proportion of *Maxillaria* (as previously circumscribed) that produces nectar is thought to be small and

Davies, Stpiczyńska and Gregg (2005) estimate it to be as little as 8%. To date, our knowledge of nectary structure for *Maxillaria* is confined to just two species; *Ornithidium coccineum* (Jacq.) Salisb. ex R. Br. [formerly *Maxillaria coccinea* (Jacq.) L. O. Williams ex Hodge] and *Maxillariella anceps* (Ames & C. Schweinf.) M. A. Blanco & Carneval [formerly *Maxillaria anceps* Ames & C. Schweinf.]. In the first, a 'faucet and sink' arrangement is found, with nectar secreted by a protuberance on the ventral surface of the column collecting in a 'sink' formed by the proximal part of the labellum, the bases of the other tepals and the base of the column (Stpiczyńska, Davies and Gregg, 2004). In *M. anceps*, however, nectar produced by the callus is secreted onto the adaxial surface of the labellum by means of stomata (Davies, Stpiczyńska and Gregg, 2005).

The aim of the present paper is to describe the structure of the floral nectary of a third species formerly assigned to *Maxillaria*, namely *Ornithidium sophronitis,* and to compare it with that of closely related taxa.

MATERIALS AND METHODS

Nectary tissue of *Ornithidium sophronitis* Rchb.f. flowers was prepared and examined using light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM), as previously described (Davies and Stpiczyńska, 2009). Also, as before, semi-thin sections were stained with toluidine blue O (TBO), and hand-cut sections of fresh material were tested for starch, as well as acidic polysaccharides and mucilage, using IKI and ruthenium red (Jensen, 1962), respectively.

Nectar-sugar concentration of fresh flowers was determined using refractometry and nectar tested for glucose using glucose-sensitive test sticks (Clinistix).

RESULTS

Flowers of *O. sophronitis* are weakly zygomorphic and diurnal. They lack fragrance and honey guides, but the yellow column and central area of the labellum contrast markedly with the other tepals, which are bright red in colour (Figs 1A-B). Cryptic, cream-coloured anther caps are present (Fig. 1B). The labellum is strongly folded (Fig. 1B) and copious floral nectar is produced.

Tepals of *O. sophronitis* are papillose and glisten (Fig. 1A). In section, these papillae are dome-shaped, with a smooth, convex, outer tangential wall, lacking striations.

A small protuberance, some half way along the length of the ventral surface of the column, secretes nectar, and this collects between the column, the other tepals and the almost vertical, concave, proximal part of the relatively immobile labellum (Fig. 1B). Such is the volume of nectar produced, that it also often flows forward onto the mid-lobe of the labellum.

Refractometry of *O. sophronitis* nectar gave a value of 64% (w/w) sugar. Nectar was present in unopened buds of *O. sophronitis* and this, together with nectar tested 2-3 d into anthesis and again at late anthesis (close to senescence), was shown to contain glucose. Nectar was often produced in abundance, but at other times, none could be found.

The outer, tangential epidermal wall of the nectary has a thin, reticulate cuticle. SEM and TEM observations did not reveal ectodesmata, pores or cracks through which nectar could exude. However, characteristic, cuticular swellings (8-10 μm high) are present, and these usually occur at points coinciding with the middle lamella of radial walls between adjoining epidermal cells (Fig. 2A). These swellings occur exclusively on the surface of the nectary protuberance, being absent from neighbouring column cells (Fig. 2B).

The nectary consists of a single-layered epidermis and 3-5 layers of subepidermal, secretory cells (Figs 3A-C), beneath which occur 2-3 layers of subsecretory parenchymatous cells. Secretory cells are small (17.5 – 22.0 μm diameter), whereas subsecretory parenchyma cells are larger (40.9 μm mean diameter). Both secretory and subsecretory cells are compactly arranged. The nectary is supplied by phloem strands embedded in ground parenchyma directly beneath the subsecretory tissue (Fig. 3D). Staining with TBO revealed that the walls of secretory cells are cellulosic, whereas staining with ruthenium red revealed the presence of acidic polysaccharides in the middle lamella. A characteristic feature of these nectary cells is the presence of irregular, intravacuolar, protein bodies of variable size (Figs 3A, C, E). Starch was not detected in the plastids of nectary cells on treatment with IKI (Fig. 3B).

The secretory cells are collenchymatous (Figs 3A-E), with relatively thick walls (mean 2.5 μm) containing numerous pits (Fig. 4C) and plasmodesmata (Fig. 4D). Nuclei were visible in the densely granular, parietal cytoplasm. The latter also contained numerous mitochondria, endoplasmic reticulum (ER) profiles, dictyosomes (Figs 4A-D) and darkly-stained, osmiophilic material (Figs 4A, C). Numerous, dilated vesicles frequently occurred in close proximity to the cell wall (Figs 4B-C). Plastids contained numerous, small plastoglobuli, but few lamellae. A granular, proteinaceous, intravacuolar body may be present (Fig. 3E) and this usually contains several globoids.

Subsecretory parenchyma cells (Figs 3A, C-D) have distinctly thinner walls (mean 0.5 μm) with abundant plasmodesmata. Few mitochondria are present

and the cytoplasm contains starchless plastids, ER, and dictyosomes. Flocculent, intravacuolar precipitates may also be present (Fig. 3C), and these may be related to the presence of flavonoids.

DISCUSSION

It has long been speculated that *O. sophronitis* is ornithophilous. Unfortunately, direct evidence to support this has not been forthcoming. Recently, however, Whitten and co-workers (2007) have again asserted that the most brightly coloured *Ornithidium* species are probably hummingbird-pollinated, whereas those with more open, greenish flowers are probably bee- or wasp-pollinated.

Ornithophily has evolved many times (Specht, 2006; Cronk and Ojeda, 2008), usually from entomophily. Bird-pollinated flowers are often red, pink, orange, yellow or white; less frequently, reddish-violet and blue (Proctor and Yeo, 1973; Ortega-Olivencia et al. 2005; Micheneau, Fournel and Pailler, 2006). They exhibit diurnal anthesis, are weakly zygomorphic with a backwardly curved labellum that is strongly folded or has a substantial callus, thereby partially closing the floral tube at the level of the anther and stigma. They produce abundant nectar, but no fragrance, and they lack nectar guides. Floral tissues are often tough due to the presence of collenchyma (Stpiczyńska, Davies and Gregg, 2004, 2005; Stpiczyńska and Davies, 2006) and can withstand contact with a hard beak (van der Pijl and Dodson, 1969; van der Cingel, 2001). The presence of anther caps and pollinaria on beaks of birds usually evokes a bill-cleaning response and consequently, many pollinaria are either lost or destroyed. It is thus, perhaps, significant that some 50% of hummingbird-pollinated orchids have blue, grey, brown, cream or greyish-white, cryptic anther caps. These are thought to illicit a lesser response than more conspicuous, yellow anther caps and thereby facilitate pollination (Dressler, 1971). Flowers of *O. sophronitis* possess all these characters and are therefore, probably, bird-pollinated. Moreover, papillae on the adaxial tepal surface are smooth and convex, and the outer tangential wall lacks striations. The optical geometry of such cells is conducive to moderate surface reflection (Kay, Daoud and Stirton, 1981) and may account for the glistening appearance of the flowers. This, in turn, possibly helps to attract pollinators.

Orchid nectaries are generally thought to have perigonal origins (Smets et al. 2000; Rudall, 2002; Rudall and Bateman, 2002) and are usually formed from the proximal part of labellum, or less frequently, from sepals (Dressler, 1993). Howev-

er, in *O. sophronitis,* the nectary, like that of *O. coccineum*, is a small protuberance located on the column (Stpiczyńska et al. 2004) and thus, cannot be considered perigonal. In such 'faucet and sink' arrangements, nectar collects in a cavity formed by the proximal part of the labellum, the base of the column and the bases of the other tepals. Although not yet fully investigated, similar protuberances have been reported (Stpiczyńska et al. 2004) to occur in *Maxillaria aggregata* (H.B.K.) Lindl. (syn. *Ornithidium aggregatum* Rchb.f.), *M. fulgens* (Rchb.f.) L. O. Williams, *M. nubigena* (Rchb.f.) C. Schweinf. (syn. *Ornithidium nubigenum* Rchb.f.) and *M. ruberrima* (Lindl.) Garay (syn. *Ornithidium ruberrimum* (Lindl.) Rchb.f.). Rodrigo B. Singer (pers. comm., 2003) has also observed them in *M. brevilabia* Ames & Correll (syn. *Camaridium brevilabium* (Ames & Correll) M. A. Blanco), *M. concavilabia* Ames & Correll and *M. horichii* Senghas (syn. *Camaridium horichii* (Senghas) M. A. Blanco). Remarkably, all these species have red, orange, pink or white flowers, or translucent flowers suffused with pink. However, Singer also reports a similar protuberance in *M. parviflora* (Poepp. & Endl.) Garay. In this species, stingless bees (Meliponini), the typical pollinators of *Maxillaria sensu lato,* were observed feeding upon droplets of nectar that had collected in a 'conch-like cavity of the lip.' This is interesting, since the nectar-sugar concentrations of entomophilous *Maxillariella anceps* (Davies et al. 2005) and presumed ornithophilous *O. sophronitis* are very similar (66.5% and 64% (w/w) sugar, respectively). Moreover, observation of cultivated *O. sophronitis* showed that, at intervals, nectar was produced in abundance, but that these episodes alternated with periods when no nectar could be found. This strongly indicates that floral nectar can be re-absorbed, as has also been recorded for a number of other orchid species (Stpiczyńska, 2003; Davies and Stpiczyńska, 2008, and references therein).

The nectary tissue of *O. sophronitis* shares a number of unusual features with other presumed ornithophilous species, such as *O. coccinea* and *Hexisea imbricata* (Lindl.) Rchb.f. (Stpiczyńska et al. 2004, 2005), in particular, the presence of collenchyma. It is thought that the thickened cell walls of this tissue probably provide an apoplastic route for nectar movement within the nectary, especially in the absence of cutinized layers and other barriers that could impede nectar flow, whilst simultaneously preventing damage caused by the beaks of visiting birds. However, the numerous plasmodesmata might indicate an additional symplastic route in this species, as has already been recorded for other taxa (Fahn, 2000; Stpiczyńska et al. 2004; Nepi, 2007). A second character shared with *O. coccinea* and *H. imbricata* is the presence of
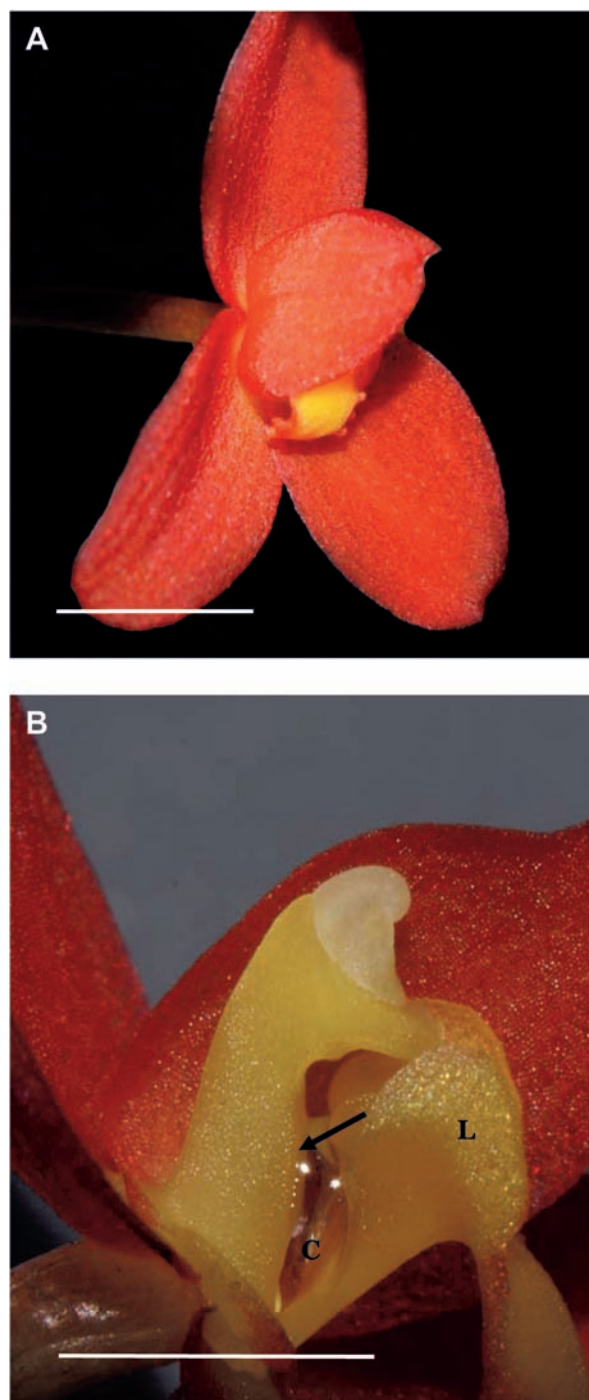
Figs 1A-B. *Onithidium sophronitis* (A) has weakly zygomorphic, bright red flowers with connivent petals and a yellow area upon the labellum. Note also that the tepals are papillose and glisten. Dissected flower of *O. sophronitis* (B) showing position of protuberant nectary (arrow) on ventral surface of column. Note also the cavity, the site of nectar accumulation, formed by the bases of column, tepals and strongly folded labellum, as well as the cream-coloured anther cap. Scale bars = 5 mm, throughout.
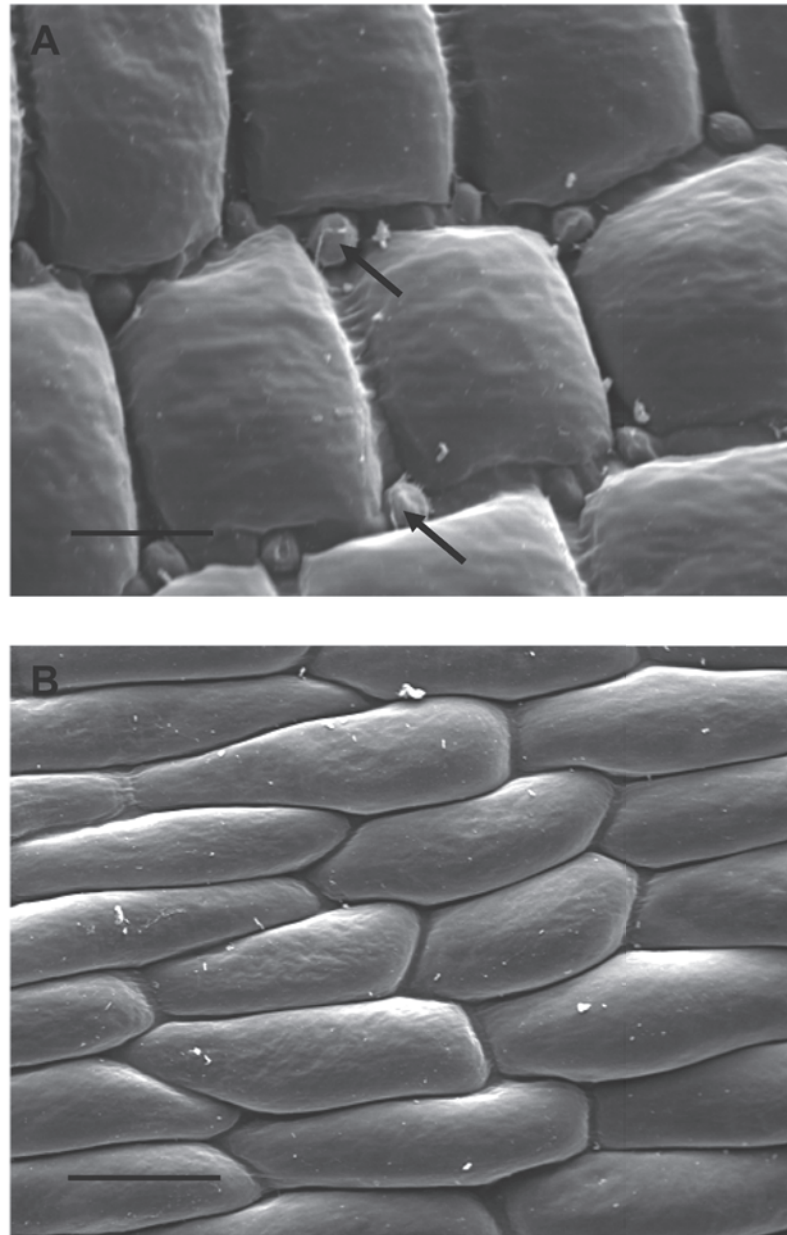
Figs 2A-B. Epidermal cells of *O. sophronitis* nectary (A) and adjacent region of column (B), respectively. Both have a thin, reticulate cuticle. However, small, spherical, cuticular swellings (arrows) occur between the epidermal cells of the nectary (A), whereas these are absent elsewhere on the column (B). Scale bars = 10, 40 μm, respectively.
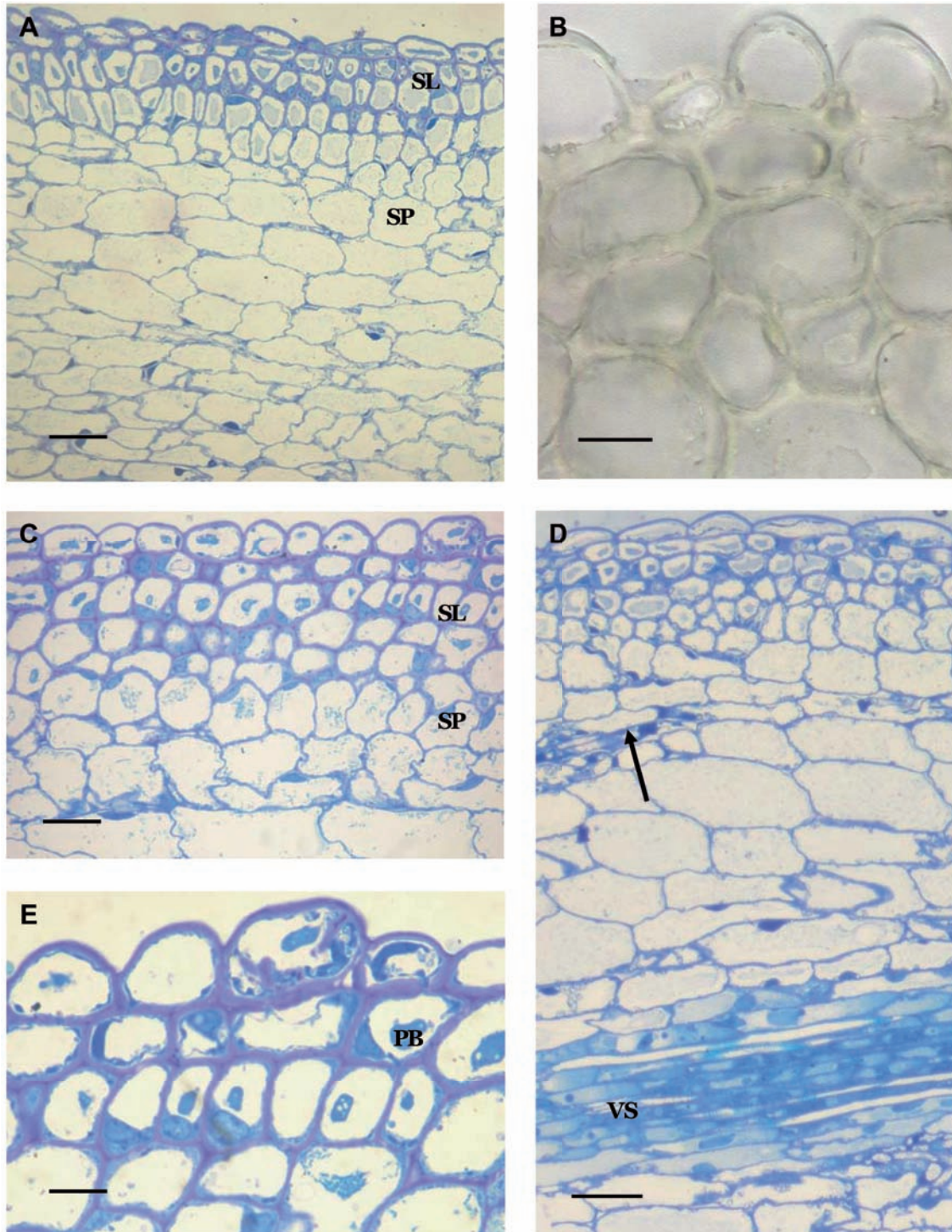
Figs 3A-E. Section (A) through nectary of *O. sophronitis* showing collenchymatous, secretory layer and subsecretory parenchyma. (B) Hand-cut section through secretory layer after treatment with IKI. Note absence of starch. (C) Section showing detail of subsecretory parenchyma with intravacuolar, flocculent material. A similar section (D) showing vascular supply to nectary and phloem strands (arrow) directly beneath the subsecretory parenchyma. (E) Detail of collenchymatous, secretory layer showing thick walls and intravacuolar protein bodies. Scale bars = 50, 20, 40, 50, 25 μm, respectively.
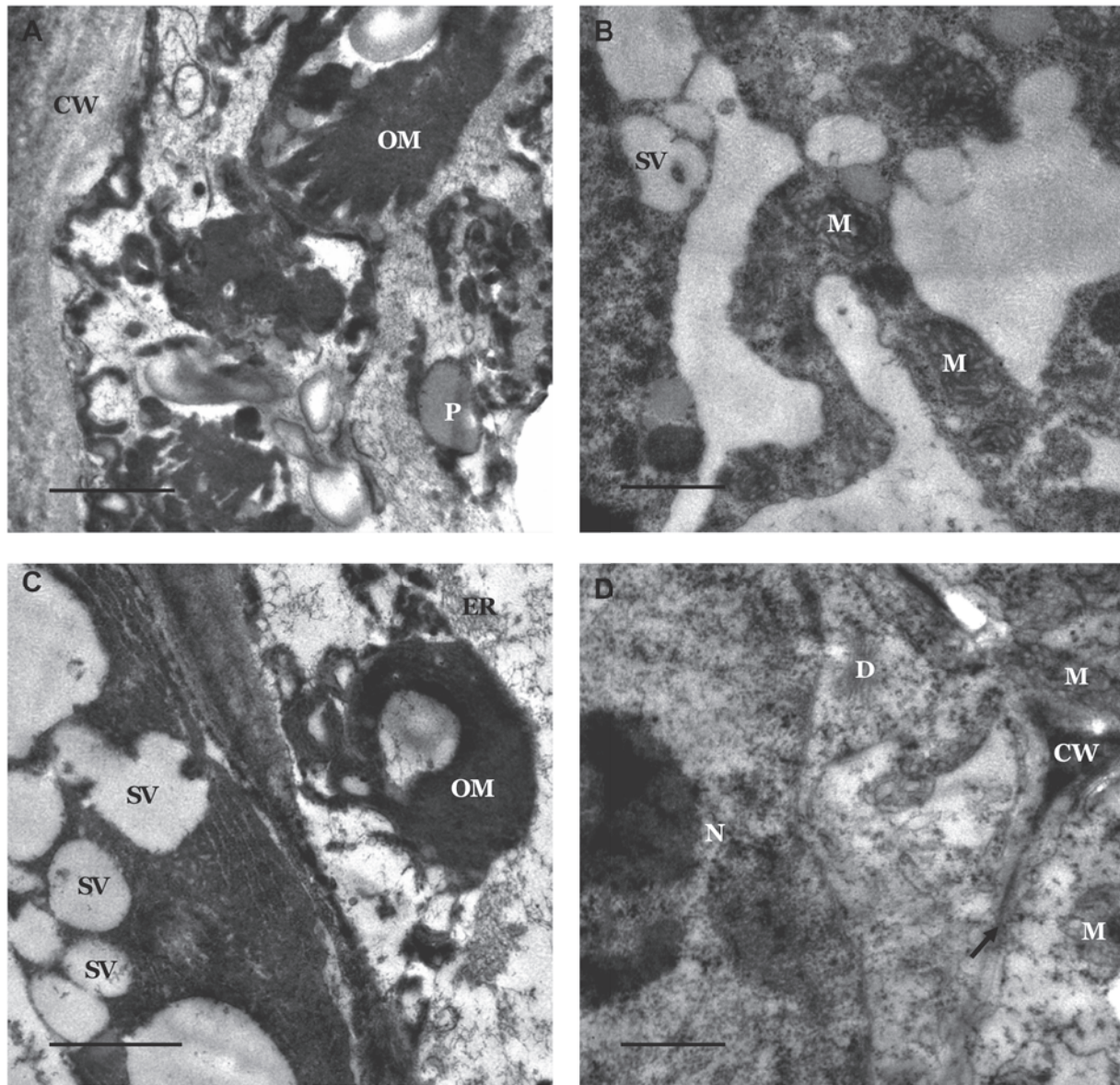
Figs 4A-D. TEM studies of *O. sophronitis*. (A) Section showing outer cell wall and dense cytoplasm containing darkly stained osmiophilic material. (B) Cytoplasm containing mitochondria and secretory vesicles. (C) A similar section to (A) with osmiophilic material, endoplasmic reticulum profiles and pit in cell wall. Note that secretory vesicles aggregate close to cell wall. (D) Section showing nucleus, mitochondria and dictyosomes, as well as plasmodesmata (arrow) in cell wall. Scale bars = 1 μm, throughout.

Key: C = cavity; CW = cell wall; D = dictyosome; ER = endoplasmic reticulum; L = labellum; M = mitochondrion; N = nucleus; OM = osmiophilic material; P = plastid; PB = protein body; SL = secretory layer; SP = subsecretory parenchyma; SV = secretory vesicle; VS = vascular strand.

intravacuolar protein bodies in nectary tissue. Similar protein bodies have occasionally been recorded for both nectary cells (D u r k e e, G a l l and R e i s n e r, 1981; D u r k e e, 1983; K u o and Pate, 1985) and pseudopollen (D a v i e s, W i n t e r s and T u r n e r, 2000). In the latter, protein bodies (probably a storage product) act as a pollinator reward.

Although the nectary cuticle of certain orchids such as *Platanthera bifolia* (L.) Rich. and *P. chlorantha* Custer ex Rchb. (S t p i c z y ń s k a, 1997; 2003) is permeable to nectar, in *O. sophronitis,* the cuticle becomes distended due to the pressure formed as nectar is produced and accumulates beneath its surface, resulting in the formation of spherical swellings. These coincide in position with the middle lamella of radial (anticlinal) walls between adjoining epidermal cells. Similar cuticular swellings have also been recorded for other orchid species, such as *O. coccineum* (S t p i c z y ń s k a et al. 2004) and *Hexisea imbricata* (S t p i c z y ń s k a et al. 2005), as well as non-orchidaceous taxa, such as *Cyclanthera pedata* Schrad. (N e p i, 2007).

Amyloplasts were absent from the nectary cells of *O. sophronitis*. This is contrary to expectation, as these organelles are often involved in nectar production. Usually, amyloplasts, and the starch grains that they contain, are particularly abundant at the presecretory stage but, as secretory activity progresses, starch disappears and the amyloplasts display irregular profiles (N e p i, 2007). Starchless nectary plastids, similar to those present in *O. sophronitis,* have also been observed for *Gymnadenia conopsea* (L.) R. Br. (S t p i c z y ń s k a and M a t u s i e w i c z, 2001) and *O. coccinea* (S t p i c z y ń s k a et al. 2004) and here, sugars present in nectar are probably delivered in the phloem.

Nectar production is seemingly restricted to only three of the 17 clades recognized by W h i t t e n et al. (2007) as comprising *Maxillaria sensu lato*, namely *Ornithidium*, *Cryptocentrum* Benth. and *Camaridium* Lindl. However, (W h i t t e n et al. 2007) were uncertain as to whether nectar is produced by others, such as the *Pityphyllum* Schltr. and *Maxillaria desvauxiana* Rchb.f. clades. To date, nectary structure and nectar secretion are known in detail for only two species of *Ornithidium* (*O. coccinea* and *O. sophronitis*) and a single species (*Maxillaria anceps*) currently assigned to the new genus *Maxillariella* (B l a n c o et al. 2007). Nectary structure of both *Ornithidium* species was very similar and may have evolved in response to similar pollinator pressures. However, these nectaries contrasted greatly with those of *M. anceps* (nectar secreted by labellar callus) and *Cryptocentrum* (nectary spur; D a v i e s and S t p i c z y ń s k a, 2007). Given the enormity of *Maxillaria sensu lato* and the vegetative and floral diversity of its members, differences in nectar structure are to be expected. Documenting these differences should prove a worthwhile and fruitful field for future research.

Acknowledgments

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Budowa nektarników *Ornithidium sophronitis* Rchb.f. (Orchidaceae: Maxillariinae)

S t r e s z c z e n i e

U większości Orchidaceae występują kwiaty mimetyczne lub zwodnicze, które nie wytwarzają atraktantów pokarmowych. Jednak spora grupa storczyków wabi zapylacze obecnością nektaru kwiatowego. Dotychczas budowa nektarników została zbadana jedynie u dwóch gatunków *Maxillaria sensu lato*: *Maxillaria anceps i Ornithidium coccineum*. W niniejszej pracy zostały opisane nektarniki u *Ornithidium sophronitis*

(poprzednia nazwa: *Maxillaria sophronitis*). W kwiatach *O. sophronitis,* podobnie jak u wcześniej badanego *O. coccineum* występuje szereg cech związanych z ornitofilią, u obydwu gatunków istnieją również liczne analogie w budowie nektarnika. Nektarnik *O. sophronitis* ma postać zgrubienia na brzusznej stronie kolumny. Wydzielony nektar zbiera się w zbiorniczku utworzonym pomiędzy podstawą kolumny i listków okwiatu. Nektarnik zbudowany jest z epidermy i 3-5 warstw małych, subepidermalnych, kolenchymatycznych komórek sekrecyjnych. Poniżej znajdują się 2-3 warstwy większych komórek miękiszu subsekrecyjnego. W warstwie tej przebiegają pasma floemu. W wakuolach komórek wydzielniczych występuje osmofilny materiał i ciała białkowe, a kutykula pokrywająca komórki epidermy nektarnika uwypukla się pod wpływem nagromadzonego nektaru. Komórki miękiszu położonego pod warstwą sekrecyjną mają cienkie celulozowe ściany i zawierają kłaczkowate osady w wakuoli, przypuszczalnie związane z obecnością flawonoidów.

Podobieństwo budowy kwiatu i mikromorfologii nektarnika *O. sophronitis* do blisko spokrewnionego gatunku *Ornithidium coccineum* wskazuje na to, że gatunki te ewoluowały w podobny sposób ze względu na podobną presję zapylaczy.