

Elaiophore Structure and Oil Secretion in Flowers of *Oncidium trulliferum* Lindl. and *Ornithophora radicans* (Rchb.f.) Garay & Pabst (Oncidiinae: Orchidaceae)

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- **Background and Aims** Many orchid flowers have glands called elaiophores and these reward pollinating insects with oil. In contrast to other reward-producing structures such as nectaries, the anatomy of the elaiophore and the process of oil secretion have not been extensively studied. In this paper, elaiophore structure is described for two members of Oncidiinae, *Oncidium trulliferum* Lindl. and *Ornithophora radicans* (Rchb.f.) Garay & Pabst.
- **Methods** Elaiophores of both species were examined using light microscopy, scanning electron microscopy and transmission electron microscopy.
- **Key Results and Conclusions** In flowers of *Oncidium trulliferum* and *Ornithophora radicans*, oil is secreted by morphologically distinct elaiophores associated with the labellar callus. However, in *O. trulliferum*, elaiophores also occur on the lateral lobes of the labellum. In both these species, the epithelial elaiophores are composed of a single layer of palisade-like epidermal cells and a distinct subepithelial layer. Secretory elaiophore cells may contain numerous, starchless plastids, mitochondria and smooth endoplasmic reticulum profiles. In *O. trulliferum*, the cytoplasm contains myelin-like figures but these are absent from *O. radicans*. In the former species, cavities occur in the cell wall and these presumably facilitate the passage of oil onto the elaiophore surface. In *O. radicans*, the accumulation of oil between the outer tangential wall and the cuticle causes the latter to become distended. Since it is probable that the full discharge of oil from the elaiophores of *O. radicans* occurs only when the cuticle is ruptured by a visiting insect, this may contribute towards pollinator specificity. The structure of the elaiophore in these species resembles both that found in previously investigated species of Oncidiinae and that of certain members of the Malpighiaceae.

Key words: Elaiophore, *Oncidium trulliferum*, *Ornithophora radicans*, Orchidaceae, oil secretion, pollination.

INTRODUCTION

In Orchidaceae, floral rewards including nectar, fragrances, oils and a number of other compounds, such as resin-like substances and waxes, all play an important role in pollination (van der Pijl and Dodson, 1969; Proctor and Yeo, 1975; Dressler, 1990; Proctor *et al.*, 1996). In contrast to many of these, nectar and oil belong to a class of rewards characterized by their great nutritional value.

In many orchids, oil is produced in specialized, secretory, floral glands called elaiophores. Floral oils are known to be secreted by certain African and Neotropical orchids and many of these species share a number of floral features such as yellow-green or yellow and pink colouration, often with brown markings and either the complete absence of fragrance or the presence of a sharp, pungent scent. Oils secreted by New World orchids are usually gathered by bees of the genera *Tetrapedia*, *Paratetrapedia* and *Centris* (Buchmann, 1987; Singer and Cocucci, 1999), whereas African oil-producing orchids are mainly visited by *Rediviva* spp. (Steiner and Whitehead, 1991; Steiner, 1989, 1993, 1998; Pauw, 2006). Once gathered, floral oil is either mixed with pollen and fed to developing larvae (Michener, 2000) or used in the nest to seal and waterproof cells (Cane *et al.*, 1983; Endress, 1994; Silvera, 2002, and

references therein; Singer *et al.*, 2006). In orchids, floral elaiophores are located upon the petals (e.g. *Ornithocephalinae*; Toscano de Brito, 2001), on the labellar callus (e.g. *Oncidium* Sw; Buchmann, 1987; Toscano de Brito, 2001; Stpiczyńska *et al.*, 2007), the lip-appendage (e.g. *Pterygodium* Sw; Pauw, 2006) or the column (e.g. *Grobysa amherstiae* Lindl; Mickeliunas *et al.*, 2006).

Elaiophores are of two types; trichomal and epithelial elaiophores (Vogel, 1974). Trichomal elaiophores occur in *Disperis* Sw. (Buchmann, 1987), certain species of *Ornithocephalus* Hook. (Toscano de Brito, 2001), *Grobysa amherstiae* (Mickeliunas *et al.*, 2006), *Zygostates* Lindl. (Toscano de Brito, 2001) and *Phymatidium delicatulum* Lindl. (Reis *et al.*, 2006). In trichomal elaiophores, oil is secreted by specialized hairs and in some orchids, such as *Phymatidium falcifolium* Lindl., these trichomes are capitate. Epithelial elaiophores are more common and occur in many species of *Oncidium*, where their resemblance to those of Malpighiaceae is thought to be due to convergence (Singer and Cocucci, 1999; van der Cingel, 2001; Singer *et al.*, 2006; Stpiczyńska *et al.*, 2007; Davies and Stpiczyńska, 2008).

The chemical composition of the oily secretion is well known for some species (Reis *et al.*, 2000, 2003, 2006). For example, analysis of oil derived from flowers of certain orchids belonging to the '*Gomesa* R. Br. clade',

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a monophyletic Oncidiinae group restricted to eastern Brazil and north-eastern Argentina (Reis *et al.*, 2000; Singer *et al.*, 2006), which includes both *Oncidium trulliferum* Lindl. and *Ornithophora radicans* (Rchb.f.) Garay & Pabst, revealed the presence of diacylglycerols. Moreover, similar compounds occur in species formerly assigned to Ornithocephalinae, such as *Phymatidium tillandsioides* Barb. Rodr. (syn. *Phymatidium falcifolium*) and *Zygotates lunata* Lindl. (Reis *et al.*, 2000, 2003). The major component of the floral oil of *Ornithophora radicans*, oncidinol, has been identified as (2S,3'R,7'R)-1-acetyl-2-(3',7'-diacetoxy-eicosanoyl)-glycerol (Reis *et al.*, 2003). Similarly, in *Oncidium loefgrenii* Cogn. and *Gomesa*, also members of the 'Gomesa clade', the secreted oil is thought to contain acyl glycerols (R. B. Singer, pers. comm.). Yet, despite rigorous analyses of orchid elaiophore secretions, the anatomy of the elaiophore itself, with few exceptions (Singer and Cocucci, 1999; Stpiczyńska *et al.*, 2007; Davies and Stpiczyńska, 2008), has been largely neglected. Indeed, detailed ultrastructural studies of the orchid elaiophore are known for only three species, namely *Trichocentrum cavendishianum* (Bateman) M. W. Chase & N. H. Williams, *Gomesa recurva* R. Br. and *Oncidium loefgrenii* (now transferred to *Menezesiella* Chiron & V. P. Castro; Chiron and Castro Neto, 2006).

It is thought that the structure of the elaiophore and the chemical composition of its secretion, like that of the nectary (Smets, 1986; Smets *et al.*, 2000; Rudall, 2002), may have taxonomic significance (Toscano de Brito, 2001; Singer *et al.*, 2006, and references therein). The aim of this study is to compare the structure of elaiophores in two contrasting species of the 'Gomesa clade' of Oncidiinae, namely, *Ornithophora radicans* and *Oncidium trulliferum*.

MATERIALS AND METHODS

Fresh flowers of *Oncidium trulliferum* Lindl. (Accession No. S20060407) and *Ornithophora radicans* (Rchb.f.) Garay & Pabst (Accession No. S19960344) were obtained from the Swansea Botanical Complex, Swansea, UK. Both are Brazilian species and belong to the 'Gomesa clade' of Oncidiinae.

The flower of *O. trulliferum* is greenish-yellow or golden with chestnut markings. The labellum is 3-lobed. The lower edge of each of the golden, lateral lobes of the labellum is thickened and marked chestnut and this coloration continues onto the mid-lobe resulting in the formation of a V-shaped, chestnut band. The rounded mid-lobe of the labellum is itself 3-lobed. The callus is complex, butterfly-shaped, lobed and spotted chestnut. The column is yellow with a prominent tabula infrastigmatica.

Ornithophora Barb. Rodr. is a monotypic genus. Flowers of *O. radicans* have greenish-yellow or whitish-green tepals. The labellum is 3-lobed, has a slender claw and the white lamina is transversely lunate or sagittate to semi-rotund with a pair of acute, backwardly pointing auricles. The yellow callus, borne on the claw, comprises fleshy lobules, whereas the disc is 2–6-cristate at its base. The column is purple and, like that of *O. trulliferum*, bears a tabula infrastigmatica.

The position of the elaiophore in fresh, intact flowers of *Oncidium trulliferum* and *Ornithophora radicans* was determined using an Olympus SZX12 stereo-microscope. Hand-cut sections through fresh elaiophore tissue were tested for starch and lipids using IKI and a saturated alcoholic solution of Sudan III or 0.3 % ethanolic Sudan Black, respectively. Pieces of elaiophore tissue (approx. 1 mm thick) were fixed in 2.5 % glutaraldehyde/4 % formaldehyde in phosphate buffer (pH 7.4; 0.1 M) for 4 h at 4 °C, washed in phosphate buffer and post-fixed in 1 % osmium tetroxide at 0 °C for 1.5 h. The fixed material was then dehydrated using a graded ethanol series and infiltrated and embedded in Spurr's resin. Semi-thin sections (0.7–1 µm thick) were stained for general histology using 0.25 % toluidine blue O in 0.25 % (w/v) aqueous sodium tetraborate solution (TBO). Micrometry and photomicrography of the elaiophores were undertaken using a Nikon Eclipse 600 microscope with screen measurement version 4.21 software. Transmission electron microscopy (TEM) sections were cut at 60 nm using a Reichert Om U-3 ultramicrotome and a glass knife. Sections were stained with uranyl acetate (40 min) and lead citrate (10 min) (Reynolds, 1963) and examined using a TESLA BS-340 transmission electron microscope at an accelerating voltage of 60 kV. For SEM, fixed pieces of labellum were dehydrated and subjected to critical-point drying using liquid CO₂. They were then sputter-coated with gold and examined by means of a TESLA BS-300 at an accelerating voltage of 25 kV.

RESULTS

Oncidium trulliferum

The elaiophores of *Oncidium trulliferum* are located symmetrically on the lower margins of the lateral lobes of the labellum and also on the callus (Fig. 1). Elaiophore activity commences at the beginning of anthesis and continues throughout the whole lifespan of the flower, by which time the labellum is completely covered with secretion. Small droplets of secretion occur on the callus and between the callus and the elaiophores at the base of the lateral lobes of the labellum, where they sometimes take on a stringy appearance (Fig. 1A and C). The whole of that area, including callus, as well as the pollinaria and the margins of tepals, stain with Sudan III and Sudan Black. Oily droplets within the elaiophore cells stain intensely with Sudan III (Fig. 2A).

Elaiophores on both the callus and lateral lobes of the labellum consist of a single layer of secretory epithelium beneath which occurs a single layer of small, subepithelial cells (Fig. 2B–D). Epithelial cells from both types of elaiophore have mean dimensions of 51.44 µm × 27.78 µm and a palisade-like arrangement, whereas the subepithelial layer has a mean thickness of 26.72 µm.

The secretory tissue of the lateral lobe elaiophore has a vascular supply (Fig. 2B) but only the glandular epidermis covering the callus bears stomata (Fig. 1D). The outer tangential walls of secretory epidermal cells have a mean thickness of 2.41 µm, whereas radial walls are thinner

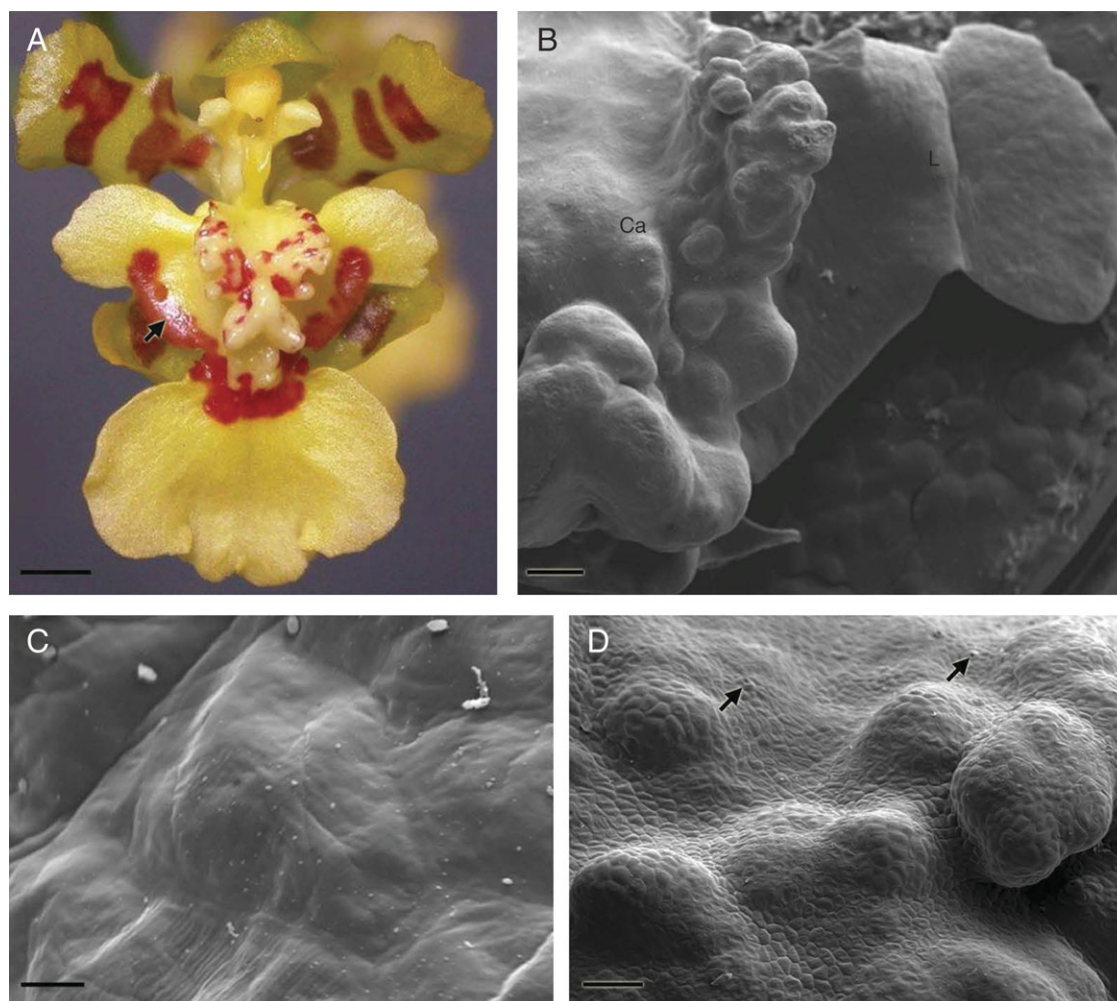


FIG. 1. Flower and elaiophore surface (SEM) of *Oncidium trulliferum*. (A) Flower with surface of elaiophore on lateral lobe of labellum covered with oil (arrow). Scale bar = 1.6 mm. (B) Part of callus (Ca) and lateral lobe of labellum (L) – the sites of floral oil secretion in this species. Scale bar = 1.0 mm. (C) Folds of cuticle covering epithelial cells of lateral lobe elaiophore. Notice the absence of pores or breaks in the cuticle. Scale bar = 10 μm . (D) Labellar callus showing position of stomata (arrows). Scale bar = 200 μm .

and have a mean thickness of 0.68 μm . Staining with TBO showed that the walls mainly consist of cellulose, and TEM observations revealed that cellulose microfibrils in the outer tangential wall are loosely arranged. The matrix thus formed contains cavities of irregular shape (Fig. 3A). These cavities vary in size from 0.68 μm to 2.29 μm . The cuticle does not become detached from the cell wall as secreted oil accumulates between it and the secretory epithelium (Figs 1C, D, 2B–D and 3A).

Cellulose microfibrils within the distal part of radial walls are also loosely arranged but here, in contrast to the outer tangential wall, cavities are absent. Epithelial cells possess a prominent, centrally placed nucleus (Figs 2C and 3B) and electron-dense, highly granular cytoplasm with numerous mitochondria and plastids. Plastids are irregularly shaped and contain unevenly distributed osmiophilic material (Fig. 3C, D). Myelin-like, membranous configurations occur both in the cytoplasm and in vacuoles, especially in the parietal cytoplasm, the basal part of the cell and in the periplasmic space (Figs 2C, D and 3D, E).

These membranous figures enclose small osmiophilic globules. Myelin-like structures also occur within larger vacuoles of subepithelial cells (Figs 2C and 3F) and these cells also contain large lipid droplets (Fig. 3F).

Ornithophora radicans

In *Ornithophora radicans*, the floral elaiophore is located on the complex labellar callus, just behind the labellar crest (Fig. 4A–D). The white lamina of the labellum stained with Sudan III and Sudan Black but the parts that stained most intensely were the auricles and the spherical lobule and associated callus structures just above the ‘waist’ of the labellum. As in the previous species, the callus functions as an epithelial elaiophore and the secretory epithelium is composed of a single layer of cells (mean cellular dimensions 47.34 μm \times 15.39 μm) in palisade arrangement (Fig. 5A–C). Secretory epithelial cells cover the whole surface of the callus outgrowths. The cuticle covering the outer tangential wall becomes detached as secreted oil

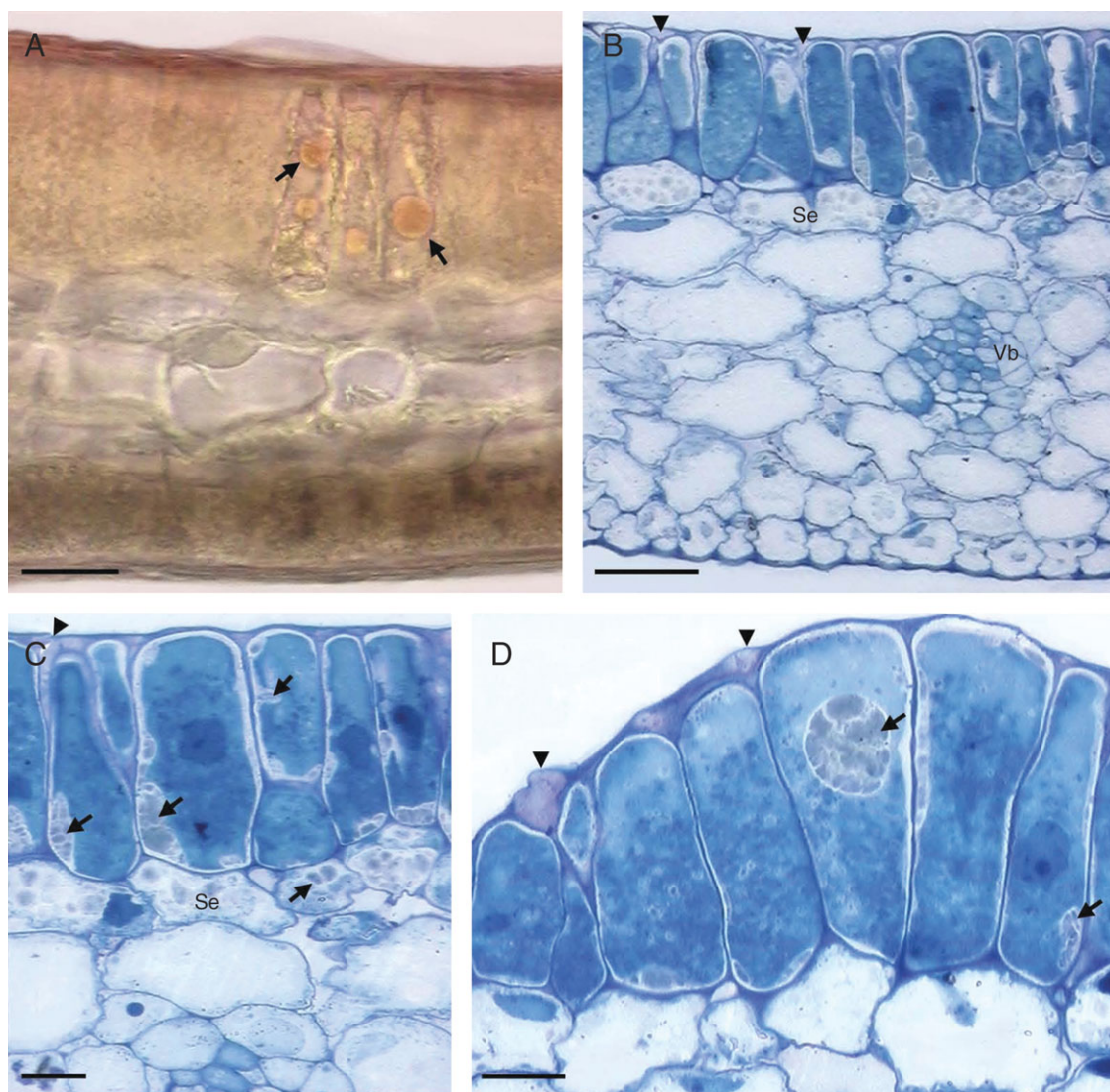


FIG. 2. Sections through elaiophores (A–C, lateral lobe elaiophore; D, callus elaiophore) of *Oncidium trulliferum* (LM). (A) Fresh, hand-sectioned elaiophore tissue showing palisade-like secretory cells containing lipid droplets (arrows) stained with Sudan III. Scale bar = 20 μm . (B) Section of elaiophore tissue showing secretory epithelium and subepithelial layer (Se). Note the position of cavities in the cell wall (arrow heads) and the vascular bundle (Vb). Scale bar = 50 μm . (C) Detail of secretory epithelium and subepithelial cells (Se) of elaiophore tissue showing position of myelin-like figures (arrows). The position of the cavity in the cell wall is indicated by an arrowhead. Scale bar = 20 μm . (D) Detail of secretory epithelium showing myelin-like figures (arrows) and cell wall cavities (arrow heads). Scale bar = 20 μm .

accumulates beneath its surface (Fig. 5A). Under the secretory epithelium occur two or three layers of cells with large amyloplasts (Fig. 5B, C). The underlying cells of the ground parenchyma also contain amyloplasts but in smaller numbers. Idioblasts with raphides occur amongst the innermost parenchyma cells. The secretory tissue has a vascular supply consisting of both xylem and phloem (Fig. 5B). Epithelial cells have relatively thin, outer tangential and radial walls (mean thickness, 0.75 μm and 0.5 μm , respectively) and thick cuticle (Figs 5C and 6A). Cavities are absent from the outer tangential cell wall. Dissolution of the middle lamella of radial walls results in the formation of intercellular spaces and frequently these contain darkly stained, osmiophilic material (Figs 5C and 6B–E). The centrally located nucleus is surrounded by numerous,

small, starchless plastids with poorly developed lamellae and sparse plastoglobuli (Fig. 6D–F). Smooth endoplasmic reticulum and mitochondria predominate in the densely stained, granular cytoplasm (Fig. 6B–F) and, in contrast to *O. trulliferum*, no myelin-like structures were observed.

DISCUSSION

Elaiophores of *O. trulliferum* and *O. radicans* are structurally well defined. In *O. radicans*, this gland is particularly elaborate and obvious. Elaiophores of certain other oil-producing orchids such as *Gomesa recurva* show no obvious morphological differentiation, even though oil is copiously produced (Stpiczyńska *et al.*, 2007). In both *O. radicans* and *O. trulliferum*, elaiophores are located on

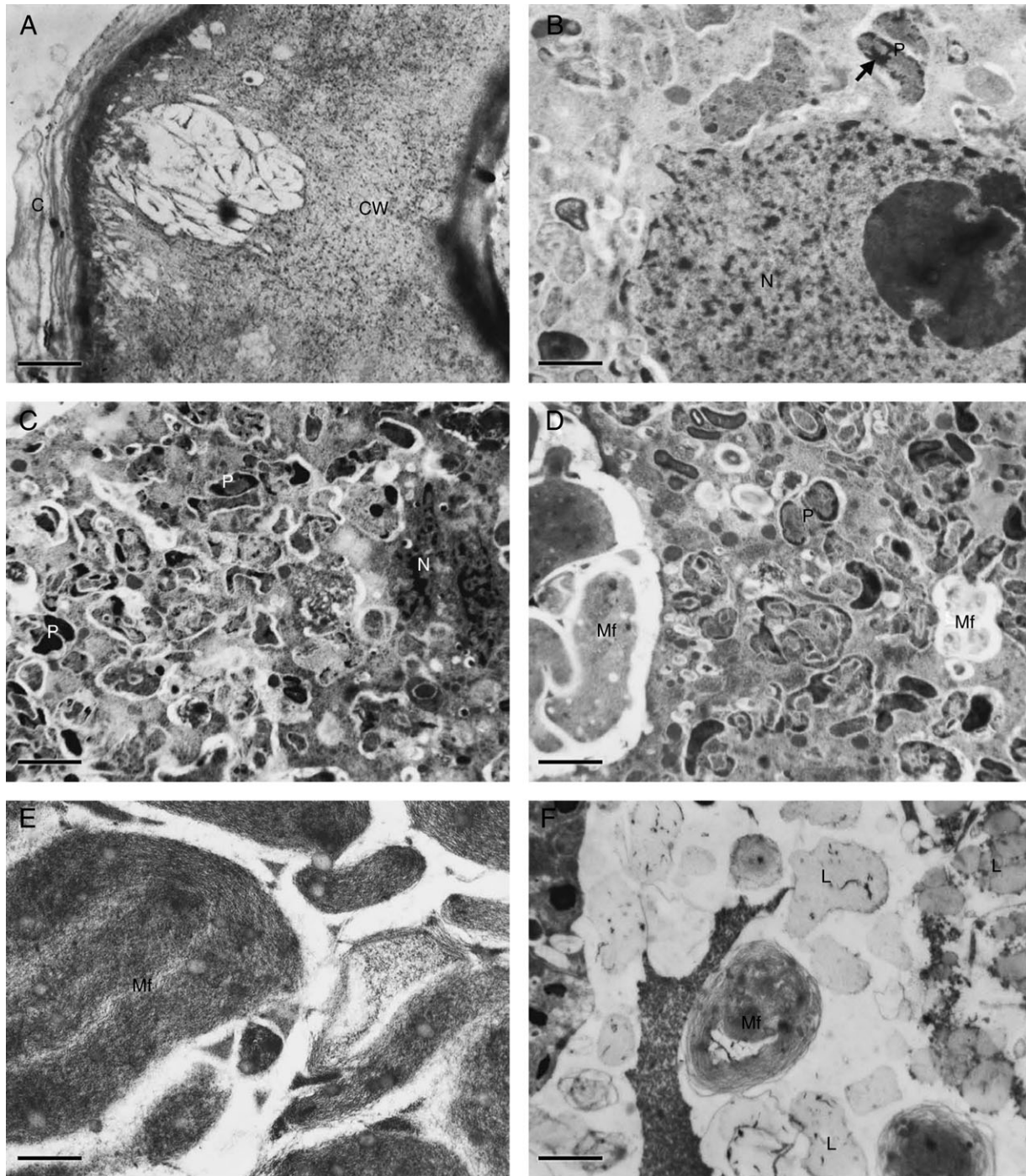


FIG. 3. Elaiophore cells (A, D–F, lateral lobe elaiophore; B and C, callus elaiophore) of *Oncidium trulliferum* (TEM). (A) Outer tangential cell wall (CW) with reticulum of cellulose microfibrils and associated cavity. Note also the lamellate cuticle (C) on cell wall surface. Scale bar = 1 μm . (B) Epithelial cell with nucleus (N) and perinuclear plastids (P) containing darkly stained material (arrow). Scale bar = 1 μm . (C) Nucleus (N) surrounded by numerous plastids (P) containing irregularly distributed, darkly stained material. Scale bar = 1 μm . (D) Epithelial cell showing plastids (P) and myelin-like figures (Mf). Scale bar = 1 μm . (E) Detail of myelin-like figures (Mf) containing osmiophilic globules. Scale bar = 0.5 μm . (F) Subepithelial cell containing lipid droplets (L) and myelin-like figures (Mf). Scale bar = 2.5 μm .

the labellar callus although, in the latter species, they also occur on the lateral lobes of the labellum. The callus is also responsible for oil secretion in *G. recurva* and *O. loefgrenii*, but not in *O. paranaense* Kraenzl. and

T. cavendishianum, where the elaiophores occur solely on the lateral lobes (Singer and Cocucci, 1999; Stpiczyńska *et al.*, 2007). That the callus is involved in oil secretion in *O. trulliferum*, *O. loefgrenii*, *G. recurva* and

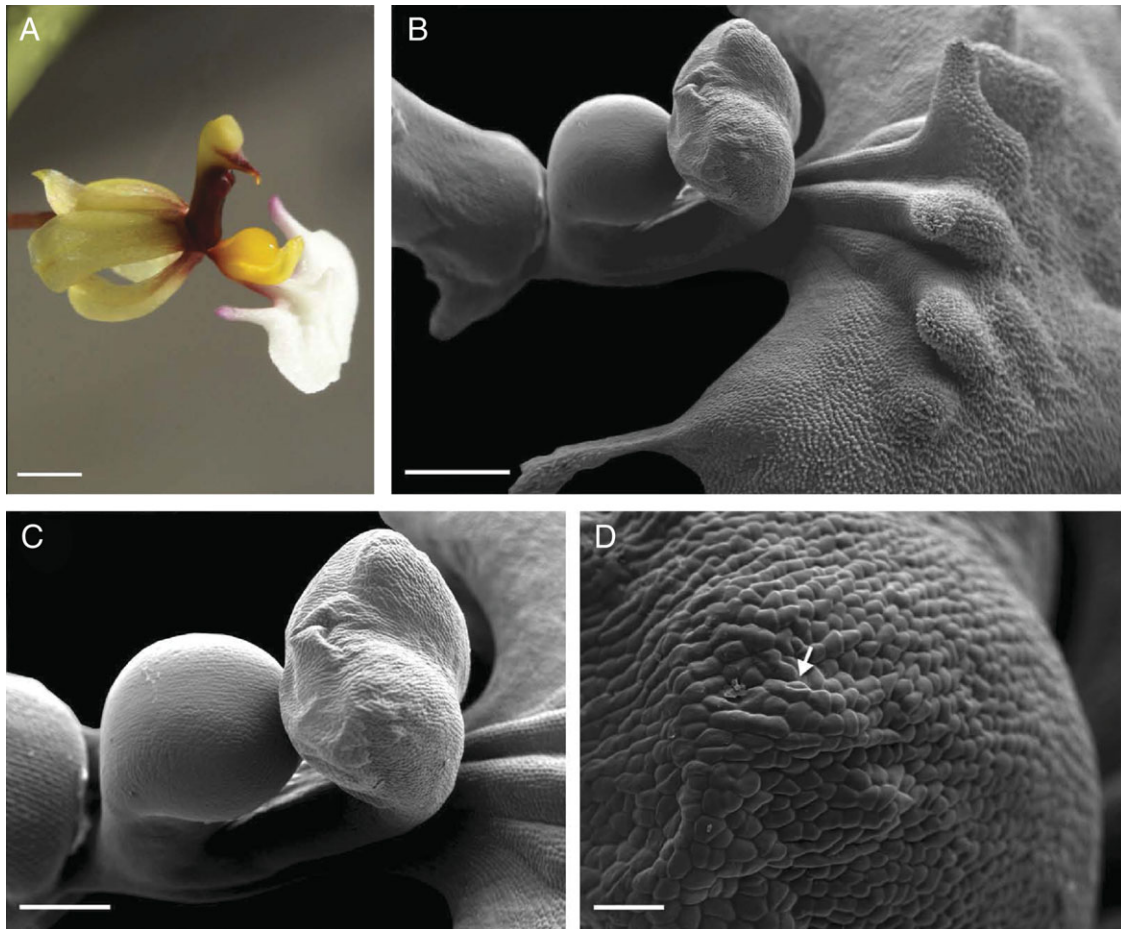


FIG. 4. Flower and elaiophore surface (SEM) of *Ornithophora radicans*. (A) Flower with yellow callus, the site of the labellar elaiophore. Scale bar = 1.7 mm. (B) Labellum showing labellar crest and callus outgrowths bearing elaiophore tissue. Scale bar = 900 μm . (C) Lobed, labellar elaiophore showing wrinkled surface. Scale bar = 500 μm . (D) Detail of elaiophore surface showing distended cuticle (arrow). Scale bar = 50 μm .

O. radicans is noteworthy since these four taxa, unlike *T. cavendishianum*, belong to the 'Gomesa clade'. Even so, the diverse degree of callus complexity found in this group would suggest that, even within the clade, the callus-elaiophore may have evolved along a number of lines in response to pollinator selection. Moreover, the likelihood that these plants are pollinated by different insect species is further supported by the presence of a tabula infrastigmatica in some, such as *O. trulliferum* and *O. radicans*, but not others. Another member of this clade, *Oncidium pubes* Lindl., was reported to be pollinated by female *Tetrapedia* spp. (cited in Singer *et al.*, 2006). Although R. B. Singer (pers comm.) observed *Trigona* spp. visiting flowers of *G. recurva*, he nevertheless doubts that they are responsible for pollinating this orchid as they are too small to dislodge its pollinaria. Instead, he proposes that *G. recurva* and *O. loefgrenii* are pollinated by species of *Monoeca* and *Tetrapedia*, respectively. Although there is currently no concrete evidence, it is thought that *O. radicans* may also be pollinated by a species of *Tetrapedia* (R. B. Singer, pers comm.).

In *O. trulliferum* and *O. radicans*, the elaiophore is of the epithelial type and possesses a single layer of palisade-like

secretory cells. The single-layered subepithelium of *O. trulliferum* contains lipid bodies and this perhaps indicates that it too is involved in elaiophore activity. Similar anatomical organization is found in *T. cavendishianum* and *O. loefgrenii* but here, the subepithelial layer is less distinct (Stpiczyńska *et al.*, 2007). Conversely, a prominent subepithelial layer occurs in the elaiophores of some malpighiaceae taxa such as *Hiptage sericea* Hook. (Arumugasamy *et al.*, 1993) and *Banisteriopsis variabilis* B. Gates (Attala and Machado, 2003).

The elaiophore cuticle of *O. radicans* becomes distended as secreted oil accumulates beneath its surface. It is probable that, in this species, full discharge of oil is not achieved until the cuticle is ruptured by a visiting insect and this may contribute towards pollinator specificity. Distension of the cuticle is also known to occur in *T. cavendishianum* (Stpiczyńska *et al.*, 2007; Davies and Stpiczyńska, 2008) and *Dinemandra ericoides* A. Juss. (Malpighiaceae), which is pollinated by species of *Centris* (Cocucci *et al.*, 1996). On the other hand, the cuticle of *O. trulliferum*, *O. loefgrenii* and *Gomesa*, which is smooth, shows no evidence of distension in response to oil accumulation (Stpiczyńska *et al.*, 2007).

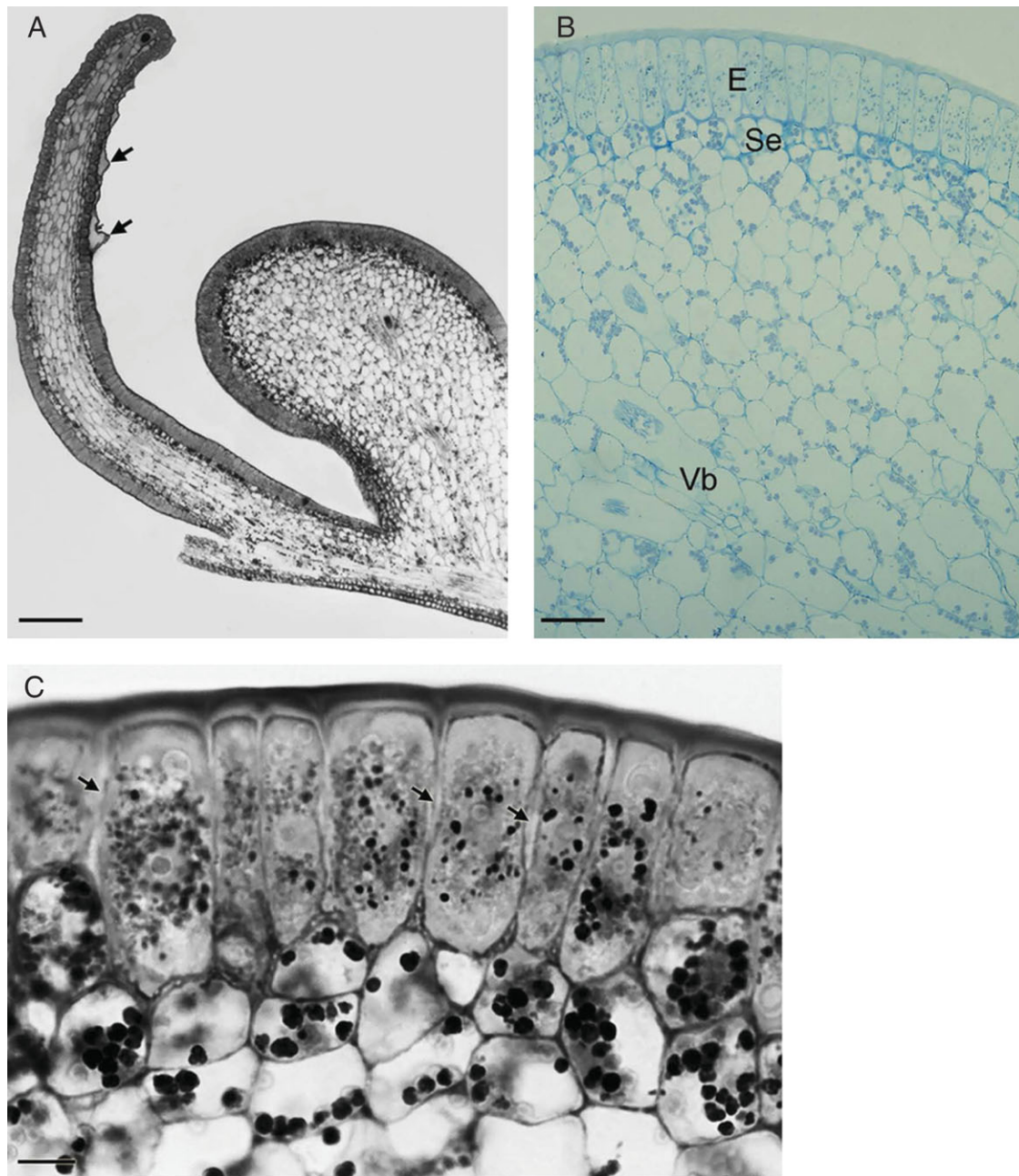


FIG. 5. Sections of elaiophore tissue of *Ormithophora radicans* (LM). (A) Section of callus outgrowths showing position of elaiophore epithelium and distended cuticle (arrows). Scale bar = 195 μm . (B) Section through callus showing palisade-like, secretory epithelium (E), subepithelial cells (Se) and vascular bundle (Vb) embedded in ground parenchyma. Scale bar = 10 μm . (C) Epithelial cells in palisade arrangement with intercellular spaces (arrows) and centrally placed nuclei surrounded by darkly stained plastids. Beneath this secretory tissue occur subepithelial cells with amyloplasts. Scale bar = 15 μm .

In *O. trulliferum*, the outer tangential cell walls contain cavities. Walls of similar structure also occur in *T. cavendishianum* and *O. loefgrenii* but not *G. recurva*. It is thought that these cavities may aid the transport of hydrophobic moieties across the hydrated cell wall, much in the same way that hydrophobic compounds are transported during the formation of cuticle (Kunst and Samuels, 2003, and references therein). Similar cavities also occur in elaiophore cell walls of the malpighiaceae

Dinemandra ericoides (Cocucci *et al.*, 1996). Intercellular spaces between the radial cell walls of *O. radicans* may also be involved in the transport or accumulation of oily secretions.

Epithelial cells of both *O. trulliferum* and *O. radicans* contain several small vacuoles and a centrally placed nucleus but, whereas smooth endoplasmic reticulum predominates in *O. radicans*, this is not the case for *O. trulliferum*. Nevertheless, numerous mitochondria and

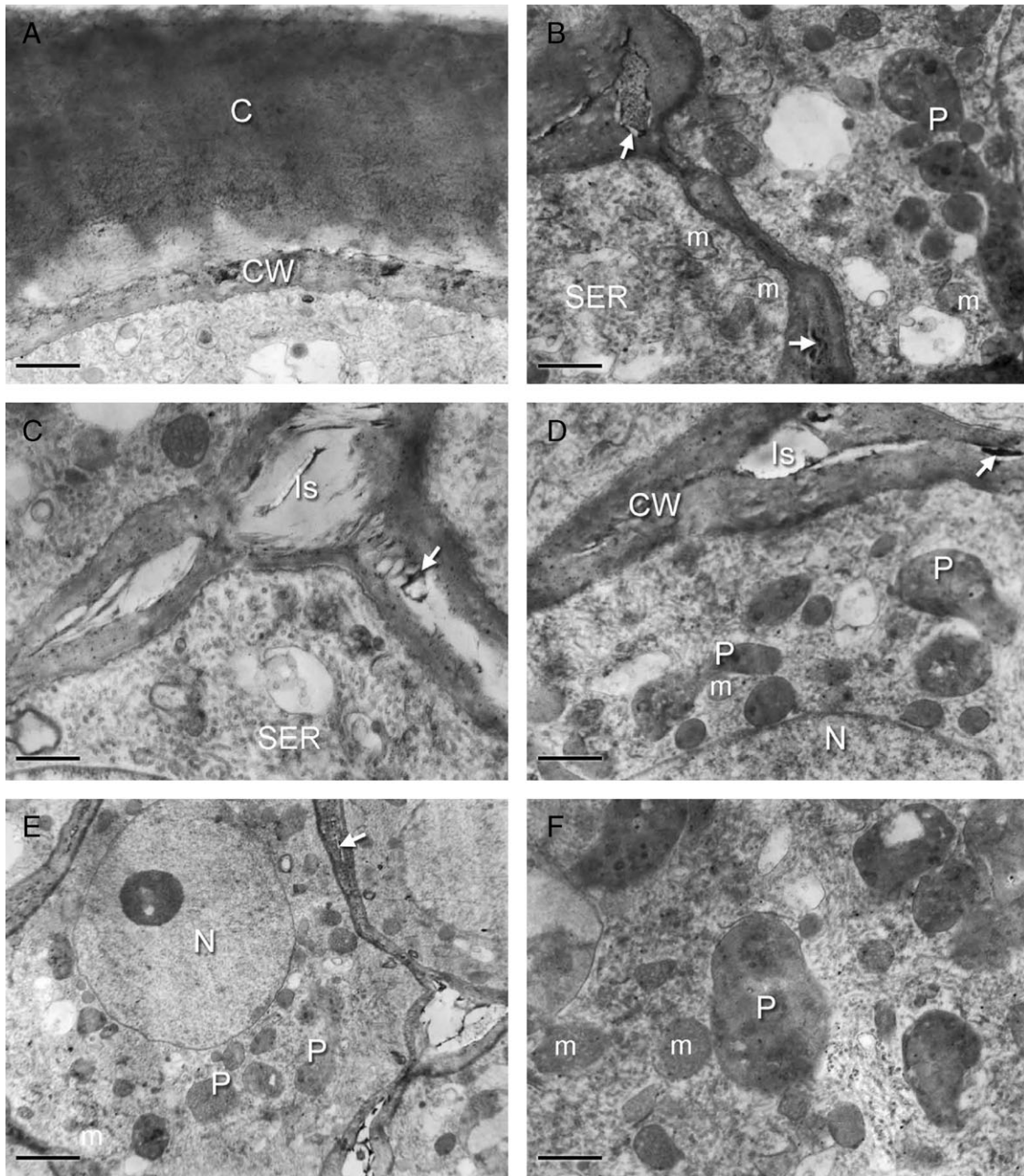


FIG. 6. Ultrastructure of elaiophore epithelial cells of *Ornithophora radicans* (TEM). (A) Outer cell wall (CW) with dark deposits covered with a thick layer of reticulate cuticle (C). Scale bar = 0.7 μm . (B) Intercellular spaces with osmiophilic content (arrows). Note that the cytoplasm mainly contains smooth endoplasmic reticulum (SER), plastids (P) and mitochondria (m). Scale bar = 0.7 μm . (C) Large intercellular spaces (Is) with dark inclusions (arrow) and cytoplasm with numerous smooth endoplasmic reticulum (SER) profiles. Scale bar = 1 μm . (D) Secretory cytoplasm with small, starchless plastids (P) and mitochondria (m) associated with the nucleus (N). Note the cell wall (CW) with dark inclusion (arrow). Scale bar = 1 μm . (E) Nucleus (N) with associated plastids (P) and mitochondria (m). Note the large intercellular spaces and the presence of dark inclusions in the cell wall (arrow). Scale bar = 3 μm . (F) Mitochondria (m) and typical, starchless plastids (P) with few plastoglobuli. Scale bar = 0.5 μm .

chromoplasts that lack starch but contain unevenly distributed osmiophilic material are present in both species. In *O. radicans*, the subsecretory parenchyma contains starch. Although no starch was observed for *O. trulliferum* during the secretory stage, this does not preclude the possibility that it may be present during the pre-secretory stage.

Osmiophilic globules occur as enclaves within myelin-like bodies of *O. trulliferum* or between the concentric membranes themselves. Similar membranous whorls were observed in epithelial cells of *T. cavendishianum* (Stpiczyńska *et al.*, 2007) and in *Hiptage sericea* (Arumugasamy *et al.*, 1993). Myelin-like structures containing dense, globular material also occur as a thylakoid

plexus in the epidermal chromoplasts of the petals of *Narcissus pseudonarcissus* (Whatley and Whatley, 1987). They are also found in the periplasmic space and in vacuoles of other types of secretory tissue, such as nectaries (Eriksson, 1977; Schnepf and Deichgräber, 1984; Wist and Davis, 2006), gum-resin ducts (Bhatt, 1987; Fahh, 2000) and leaf secretory-trichomes (Valkama *et al.*, 2003) and are frequently considered to have originated from the endoplasmic reticulum. Plastids and smooth endoplasmic reticulum membranes are known to be involved in plant lipid synthesis and this may explain their frequency in the elaiophore secretory cells of *O. radicans*, *T. cavendishianum*, *G. recurva* and *O. loefgrenii*. Smooth endoplasmic reticulum, however, does not feature prominently in elaiophore secretory cells of *O. trulliferum*. In this species, lipid droplets collect in vacuoles of subepithelial cells. Since the latter are also involved in the synthesis of oil, this may explain the absence of smooth endoplasmic reticulum from epithelial cells. Recently, Singer and co-workers (Singer *et al.*, 2006) have reported the presence of epithelial elaiophores on the labella of a number of Brazilian species of *Lockhartia* Hook. (Oncidiinae). Elaiophores probably also occur on the labella of *Rudolphiella aurantiaca* (Lindl.) Hoehne and *R. picta* (Schltr.) Hoehne (Bifrenariinae; Singer *et al.*, 2006; K. L. Davies, unpubl. res. 2006, respectively) and *Grobya galeata* Lindl. (Catasetinae *sensu* Chase *et al.*, 2003; Singer *et al.*, 2006). This indicates that elaiophores may occur more widely than previously thought. The occurrence of elaiophores of diverse form in Neotropical Oncidiinae and various other orchid subtribes suggests that they have arisen on a number of occasions and have developed along a number of evolutionary lines in response to pollinator selection.

The present study indicates that the elaiophores of Oncidiinae species investigated thus far share structural features with those of Malpighiaceae. Furthermore, Reis *et al.* (2007) have recently demonstrated similarities between oily secretions, namely oncidinol and byrsonic acid, produced by flowers of these two unrelated taxa. Thus, convergence expressed at both anatomical and molecular levels is probably largely responsible for the successful pollination of Oncidiinae by bees that have primarily evolved to pollinate Malpighiaceae.

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