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Occurrence of secretory structures in underground systems of seven Asteraceae species

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In contrast with the abundance of anatomical studies of secretory structures on aerial vegetative organs of Asteraceae species, the information about secretory structures on thickened subterranean organs is sparse. The aim of this study was to investigate the occurrence of secretory structures on thickened and nonthickened subterranean organs of seven Asteraceae species from three tribes: Eupatorieae (*Chromolaena squalida* and *Gyptis lanigera*), Vernonieae (*Chresta sphaerocephala*, *Lessingianthus bardanoides*, *L. glabratus* and *Orthopappus angustifolius*), and Plucheeae (*Pterocaulon angustifolium*). The specimens were collected in areas of *cerrado* from the State of São Paulo, Brazil. All species of the tribe Vernonieae studied exhibited endodermic cells, other than the epithelial cells of the canal, with secretory activity in the roots. In *C. sphaerocephala* roots, two types of endodermic cell were found, but only one had secretory activity. Secretory canals were found in the tuberous and nontuberous roots of all studied species. These data agree with the results from the literature for Asteraceae species. Here, we describe for the first time in Asteraceae the presence of secretory idioblasts in *C. sphaerocephala*. Secretory trichomes are present in the *Orthopappus angustifolius* rhizophore. Histochemical tests have shown that all types of secretory structure possess substances containing lipids. *Botanical Journal of the Linnean Society*, 2008, **157**, 789–796.

ADDITIONAL KEYWORDS: canals – Compositae – idioblasts – light microscopy – lipid substances – roots – secretion – secretory endoderm – trichomes – xylopodium.

INTRODUCTION

The secretory structures on aerial vegetative organs of Asteraceae species have been studied intensively with useful results for taxonomic studies (amongst others: Solereder, 1908; Carlquist, 1958; Werker & Fahn, 1982; Ascensão & Pais, 1987; Werker *et al.*, 1994; Castro, Leitão-Filho & Monteiro, 1997; Monteiro *et al.*, 2001; Milan, Hayashi & Appezzato-da-Glória, 2006). However, secretory structures on thickened subterranean organs have attracted little attention and there are only a few published studies on this subject (Hoehne, Grotta & Scavone, 1952; Panizza & Grotta, 1965; Ragonese, 1988; Curtis & Lersten, 1990; Łotocka & Geszprych, 2004; Machado *et al.*, 2004; Hayashi & Appezzato-da-Glória, 2005; Vilhalva & Appezzato-da-Glória, 2006). Except for the studies on the secretory trichomes in two species of *Chrysolaena* (as *Vernonia*) (Hayashi & Appezzato-da-Glória, 2005), these publications describe the presence of lipid canals, lipid cavities, or oil reservoirs on rhizomes, rhizophores, and xylopodia from species belonging to different tribes, such as the Astereae, Cardueae, Eupatorieae, Heliantheae, and Vernonieae.

Tetley (1925) described two types of secretory canal in Asteraceae roots: endodermic and non-endodermic.

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Melo-de-Pinna & Menezes (2003) studied 11 species of *Richterago* and listed another 42 Asteraceae with secretory canals from different tribes. The position of these secretory canals can vary amongst the species. In general, they are present on the inner cortex and phloem, but may also occur associated with the pericycle (Melo-de-Pinna & Menezes, 2003). In addition to the canals associated with the pericycle, new secretory canals are observed in the secondary phloem parenchyma in *Blainvillea acmella* (L.) Philipson [as *Spilanthes acmella* (L.) Murray] as the root grows (Grotta, 1944).

As there are few studies of secretory structures on subterranean organs and they may be useful for taxonomic investigations, as suggested by Tetley (1925), the aim of this article was to investigate the occurrence of secretory structures in thickened and non-thickened subterranean organs of seven Asteraceae species from the tribes Eupatorieae (two), Vernonieae (four), and Plucheeae (one), extending the knowledge on this subject.

MATERIAL AND METHODS

Adult plant material of seven Asteraceae species was collected from natural populations in areas of *cerrado* in the State of São Paulo, Brazil (Table 1) situated in the following localities: Botucatu (22°53′S, 48°29′W), Itirapina (22°13′S, 47°54′W), and Mogi Guaçu (22°18′S, 47°11′W).

For anatomical study, three underground systems of adult plants were fixed in formalin–acetic acid–alcohol 50 (FAA 50) (Johansen, 1940), dehydrated in a graded ethanol series, and embedded in plastic resin (Leica Historesin). Serial sections (5–7 μm thick) were cut on a rotary microtome and stained with toluidine blue O (Sakai, 1973). Freehand cross-sections were also cut and stained with Astra blue and basic fuchsin, and then dehydrated in a graded ethanol series, and 50 and 100% butyl acetate, respectively. Permanent slides were mounted in synthetic resin.

For scanning electron microscopic analyses, samples of *Orthopappus angustifolius* rhizophore were fixed in FAA 70 solution (Johansen, 1940), dehydrated in a graded ethanol series, and critical point dried with CO_2 (Horridge & Tamm, 1969). Samples were attached to aluminium stubs and coated with gold (30–40 nm). The samples were then examined under a Zeiss DSM940A scanning electron microscope at 10 kV.

The main classes of metabolite in the secreted material were investigated in sections from fresh or plastic resin-embedded samples using the following histochemical tests: Sudan black B (Jensen, 1962) for total lipids; Nile blue A (Jensen, 1962) for neutral and acidic lipids; Nadi reagent (David & Carde, 1964) for terpenoids; ruthenium red (Johansen, 1940) for pectins; and ferric trichloride (Johansen, 1940) for phenolic compounds.

Images were captured digitally with a Leica DM LB microscope using a video camera attached to a PC, employing IM50 image analysis software.

RESULTS AND DISCUSSION

Many perennial species in the herbaceous stratum of the *cerrado* (Filgueiras, 2002), such as the seven Asteraceae studied here (Table 2), possess thickened subterranean organs, such as tuberous roots, rhizophores (for definition of the term, see Hayashi & Appezzato-da-Glória, 2005), or a xylopodium (for definition of the term, see Lindman, 1900), which avoid damage from fire. Other species develop their entire system of trunks and branches subterraneously, with only the small vegetative branches or yearly reproductive sprouts protruding above the soil. Rizzini & Heringer (1966) named these systems 'diffuse subterranean systems', which have branches of caulinar structure (soboles) or radicular structure (gemmiferous roots). This example of cryptophytism can be found in *Chresta sphaerocephala*. Therefore, all studied Asteraceae species present secretory struc-

Table 1. Species studied, tribe, locality, and date of collection and accession number in UEC and ESA herbaria, Brazil

Species	Tribe	Locality of collection	Date of collection	Accession number
Chromolaena squalida (DC.) R.M.King & H.Rob.	Eupatorieae	Mogi Guaçu	01/03/2001	UEC 118440
Gyptis lanigera (Hook. & Arn.) R.M.King & H.Rob.	Eupatorieae	Botucatu	18/03/2005	ESA 94509
Pterocaulon angustifolium DC.	Plucheeae	Botucatu	26/01/2005	ESA 88783
Chresta sphaerocephala DC.	Vernonieae	Botucatu	11/05/2005	ESA 94508
Lessingianthus bardanoides (Less.) H.Rob.	Vernonieae	Itirapina	29/01/2003	ESA 84369
Lessingianthus glabratus (Less.) H.Rob.	Vernonieae	Itirapina	24/01/2003	ESA 84368
Orthopappus angustifolius (Sw.) Gleason	Vernonieae	Botucatu	20/12/2004	ESA 88780
		Itirapina	24/01/2005	ESA 88782

Table 2. Types of secretory structure in subterranean systems of seven species of Asteraceae from the Brazilian *cerrado*

Species	Subterranean system type	Secretory structure
Chromolaena squalida	Xylopodium with adventitious roots	Canals in roots
Gyptis lanigera	Moniliform tuberous root	Canals
Pterocaulon angustifolium	Xylopodium with adventitious roots	Canals in both
Chresta sphaerocephala	Gemmiferous root	Idioblasts and canals
Lessingianthus bardanoides	Xylopodium with adventitious roots	Canals in roots
Lessingianthus glabratus	Xylopodium with adventitious roots	Canals in roots
Orthopappus angustifolius	Rhizophore with adventitious roots	Canals in roots and glandular trichomes in rhizophore

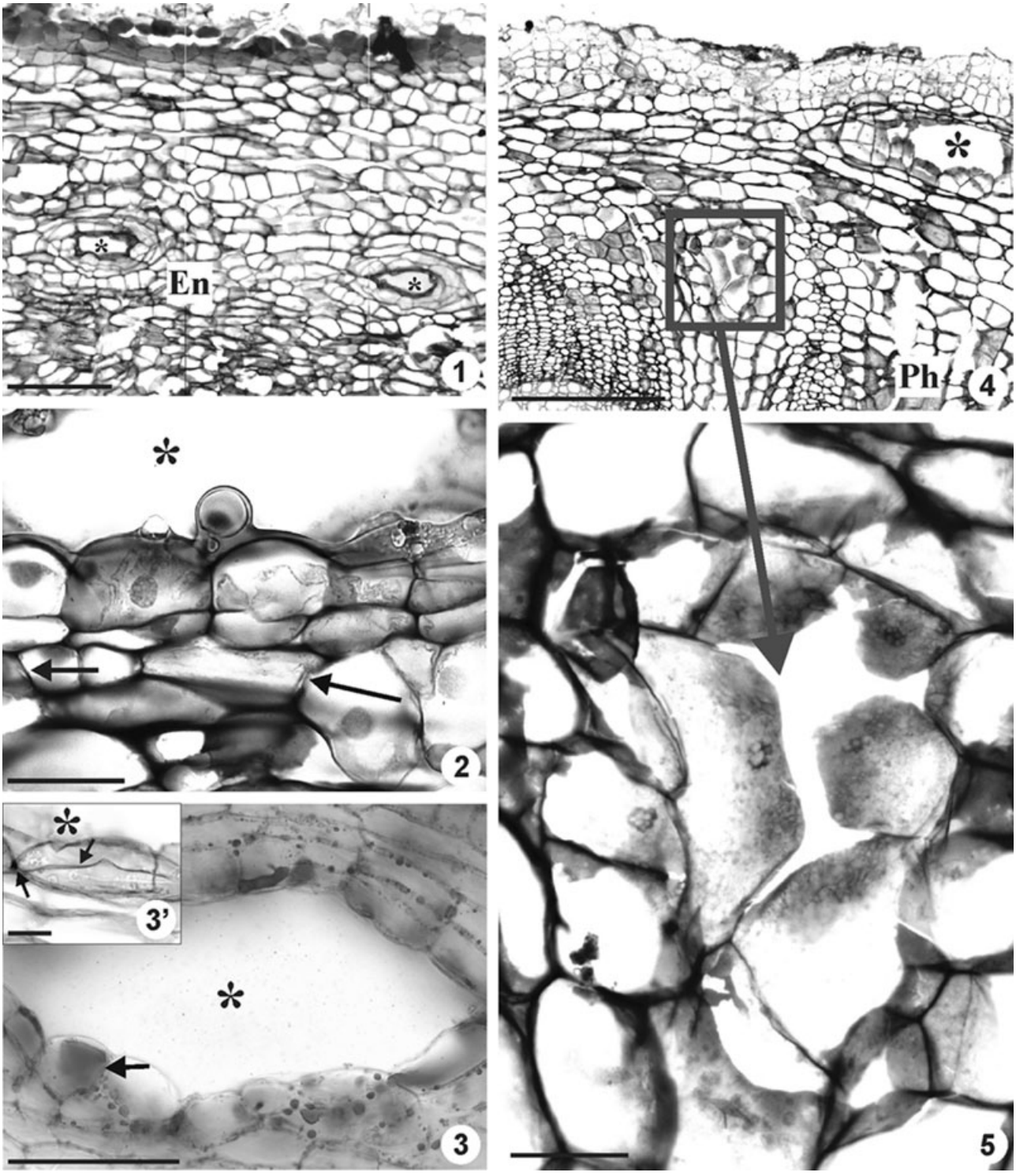
tures on the subterranean systems consisting of thickened organs and their adventitious roots (Table 2).

The xylopodia of *Chromolaena squalida*, *Lessingianthus bardanoides*, and *L. glabratus* lack secretory structures, but *Pterocaulon angustifolium* has lipidic secretory canals at the inner cortex (Figs 1, 2). In *Calea verticillata* (Klatt) Pruski and *Isostigma megapotamicum* (Spreng.) Sherff, Vilhalva & Appezzato-da-Glória (2006) showed, for the first time in the xylopodium, the occurrence of secretory canals in the secondary phloem.

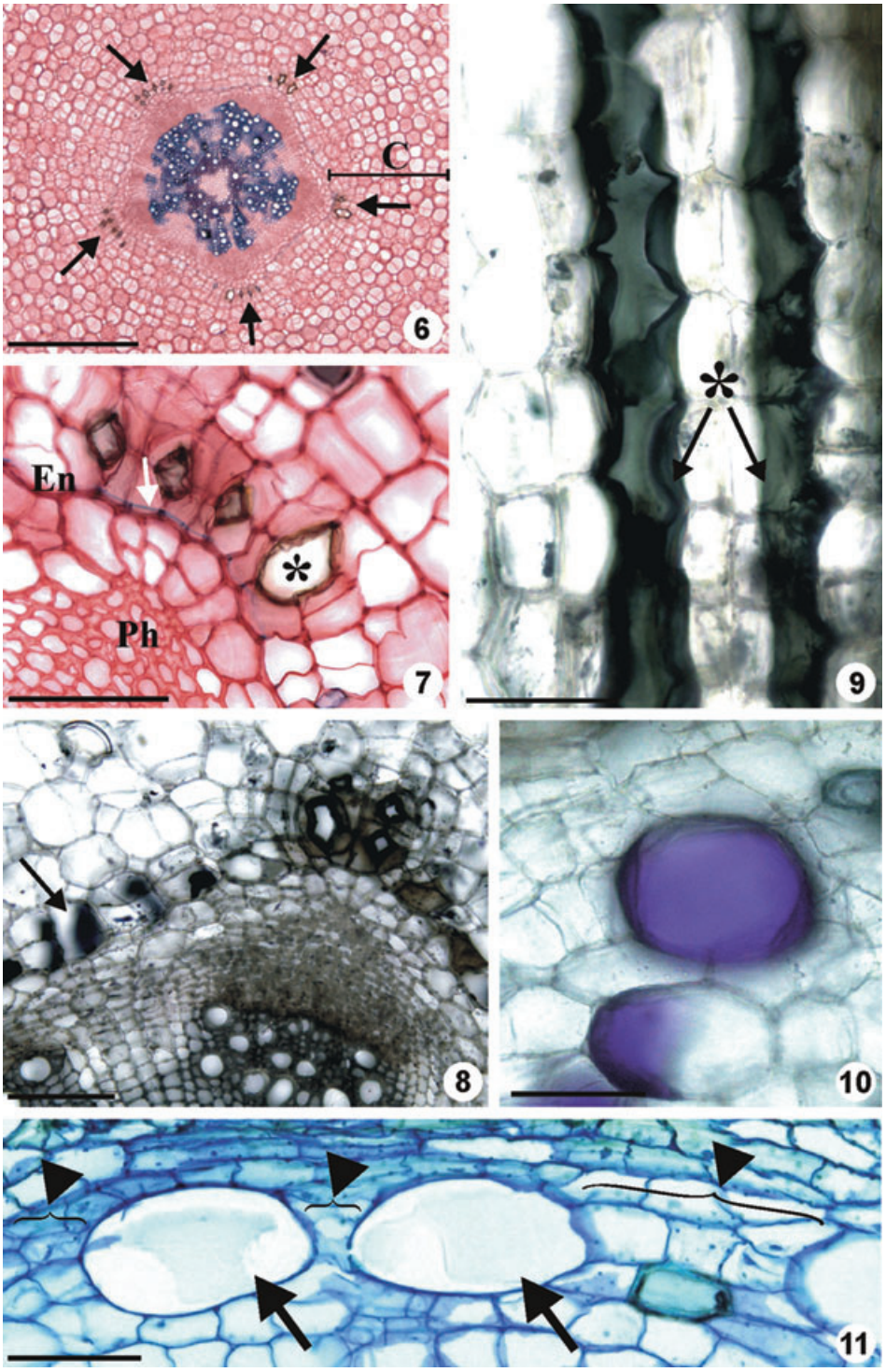
There were secretory canals in the roots (Figs 3–9) of all analysed species. These canals, unless in the root primary structure, consisted of four epithelial cells surrounding the lumen: two outer cells of the cortical parenchyma and two inner cells of the endodermis. Thus, they were endodermic canals according to Tetley (1925). In our species, they were always located in front of the primary phloem (Fig. 6), arranged in one or two layers (Figs 7, 8, respectively), and their secretion reacted positively on histochemical tests for the presence of lipid (Figs 8, 9). Panizza & Grotta (1965) also observed the relationship between the canals and the phloem in roots of *Solidago microglossa* D.C. These canals probably protect against phloem-feeding insects. Indeed, in *Santolina leucantha* Bertol. (Anthemideae), root canals secrete a yellow-amber oil resin composed of terpenoids and other compounds which can act as allelopathic substances with ecological importance (Pagni & Masini, 1999). Rosner & Führer (2002) also demonstrated that the resin canal system is important for defence against bark beetles in *Picea abies* (L.) Karsten (Pinaceae).

As the root thickens in *Gyptis lanigera*, the number of epithelial cells that surround the endodermic canal increases by the division of the endodermic cells (Figs 4, 5) and of the cortical parenchyma. This is also observed in the canals of *Pterocaulon angustifolium* xylopodium (Figs 1, 2) and *Chromolaena squalida* roots. According to Melo-de-Pinna & Menezes (2002), secretory canals originating from the meristematic endodermis are adjacent to primary phloem in roots of *Ianthopappus corymbosus* Roque & Hind. Some authors (Melo-de-Pinna & Menezes, 2003; Łotocka & Geszprych, 2004; Luque-Arias & Sánchez, 2004; Machado *et al.*, 2004) have also observed the meristematic activity of the root endodermis in other members of Asteraceae. In the survey of Asteraceae species with secretory canals in roots, Melo-de-Pinna & Menezes (2003) observed that these canals are found in the inner cortex, pericycle, and phloem. In the moniliform tuberous root of *Gyptis lanigera*, in addition to the endodermic secretory canals, as previously mentioned, new secretory canals originate from the vascular rays during the secondary growth of the root (Figs 4, 5), as observed in the secondary phloem parenchyma in *Blainvillea acmella* by Grotta (1944). The lumen of these secondary canals is schizogenous in origin (Fig. 5), as mentioned by Solereder (1908) for other Asteraceae species.

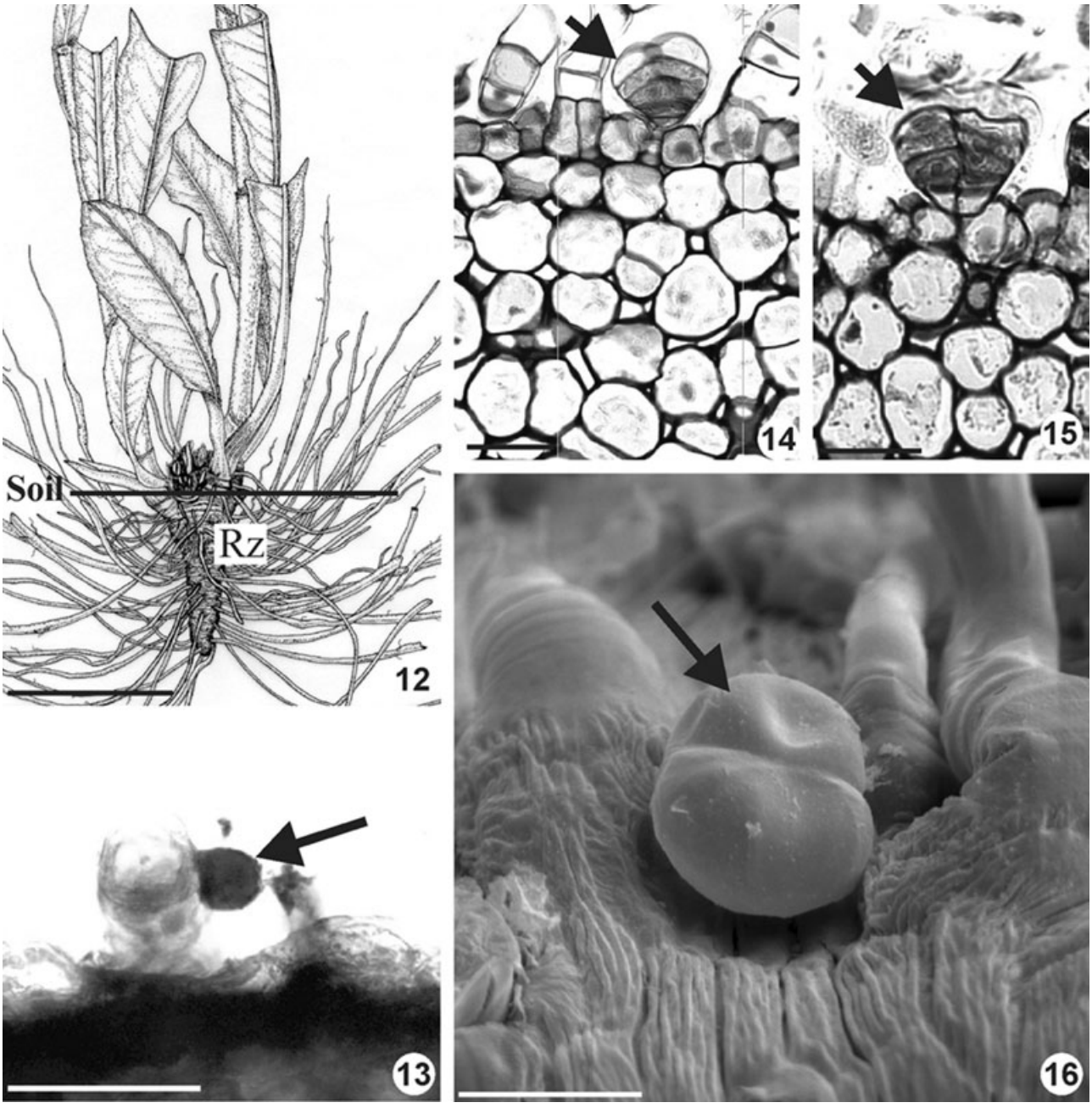
Interestingly, only in the species of the tribe Vernonieae do endodermic cells other than the epithelial cells of the canal have secretory activity (Fig. 8) in the roots, as reported in *Chrysolaena herbacea* (Vell.) H.Rob, *Ch. platensis* (Spreng.) H.Rob., *Lessingianthus grandiflorus* (Less.) H.Rob., and *L. brevifolius* (Less.) H.Rob [as *Vernonia herbacea* (Vell.) Rusby, *V. platensis* (Spreng.) Less., *V. grandiflora* Less., and *V. brevifolia* Less., respectively] by our research group (Hayashi & Appezzato-da-Glória, 2005, 2007). Amongst the functions attributed to the endodermis is the role of lipid metabolism (Van Fleet, 1961). The oxide reduction of phenols may be one of the main functions of the endodermis that determines the metabolism of lipid substances in this tissue (Van Fleet, 1961). Luque, Menezes & Semir (1997) and Luque-Arias & Sánchez (2004) agree with the secretory character of the endodermis, as they observed lipid drops inside the endodermic epithelial cells and in the canal lumen, as shown in our species (Figs 2, 3). A further intriguing trait is the presence of two types of endodermic cell in *C. sphaerocephala* root: large and small (Figs 10, 11). Both possess Casparian strips, but only the large cells react to Nadi solution with an intense violet staining of



Figures 1–5. Fig. 1. Transverse section of secretory canals (*) in the xylopodium of *Pterocaulon angustifolium*; scale bar, 300 μm. Fig. 2. Detail of the canal (*) whose lumen increases by the division of the endodermic cells (arrows) and of the cortical parenchyma; scale bar, 40 μm. Figs 3, 3′. *Chresta sphaerocephala* root. Fig. 3. Lipid drops (arrowed) inside the endodermic epithelial cells of the secretory canal; scale bar, 120 μm. Fig. 3′. Detail of the division of the endodermic cell (arrow); scale bar, 40 μm. Figs 4, 5. Endodermic secretory canals (*) and new schizogenous canals (detail) originating in the vascular rays during the secondary growth of *Gyptis lanigera* moniliform tuberous root; Fig. 4: scale bar, 400 μm. Fig. 5: scale bar, 60 μm. En, endodermic cells; Ph, phloem.



Figures 6–11. Fig. 6. Transverse section of *Orthopappus angustifolius* adventitious root with secretory canals (arrows); scale bar, 800 μm. Figs 7, 8. Details of the secretory canals (*) arranged in one layer (Fig. 7) or two layers (Fig. 8). Note the endodermic cells with Casparian strips (arrow) in Fig. 7 and the positive staining of the endodermic (arrow) and epithelial cells by Sudan black B in Fig. 8; Fig. 7: scale bar, 120 μm. Fig. 8: scale bar, 100 μm. Fig. 9. Longitudinal section of the secretory canals (*) staining positively with Sudan black B; scale bar, 60 μm. Fig. 10. Secretory idioblasts of *Chresta sphaerocephala* root with intense violet staining by Nadi reaction; scale bar, 200 μm. Fig. 11. Root endodermis of *C. sphaerocephala* with larger (arrows) and smaller (arrowheads) cells; scale bar, 100 μm. C, cortex; En, endodermic cells; Ph, phloem.



Figures 12–16. *Orthopappus angustifolius*. Fig. 12. General view of the adult plant's underground system showing rhizophore (Rz) and adventitious roots; scale bar, 4 cm. Fig. 13. Intense violet staining of the trichome secretion (arrowed) by Nadi reaction; scale bar, 30 μm. Figs 14, 15. Biseriate glandular trichome in the rhizophore epidermis (arrow); scale bar, 60 μm. Fig. 16. Scanning electron micrograph of glandular trichome; scale bar, 72 μm.

the secretion (Fig. 10), indicating an oleoresin containing terpenoids. As the root thickens in *C. sphaerocephala*, other lipid secretory cells (Fig. 10), similar to the large cells of the endodermis, are observed amongst the cells of the phloematic rays. This is the first report of the presence of secretory idioblasts in Asteraceae roots.

The *O. angustifolius* rhizophore (Fig. 12) has biseriate glandular trichomes (Figs 13–16), similar to those described in *Ch. herbacea* and *Ch. platensis* (Hayashi & Appezzato-da-Glória, 2005). These trichomes exhibit a secretion (Fig. 13) that also reacts to Nadi solution with intense violet staining, indicating an oleoresin containing terpenoids. Lipids have been

reported in biseriate glandular trichomes on aerial organs of other Asteraceae species: *Chrysanthemum morifolium* cv. Dramatic (Vermeer & Peterson, 1979), *Inula crithmoides* L. and *I. graveolens* L. (Werker & Fahn, 1982), *Artemisia dracunculus* L. (Werker *et al.*, 1994), and *Stevia rebaudiana* (Bert.) Bert. (Monteiro *et al.*, 2001), whereas lipids, as well as noncellulosic polysaccharides and proteins, have been reported for *I. viscosa* (L.) Ait. (Werker & Fahn, 1981, 1982).

The trichome density on aerial organs has been related to the maintenance of water balance (Werker, 2000) and the reflection of excessive solar radiation (Levizou *et al.*, 2005). Superficial structures have been shown to act as pest deterrents which obstruct the ovipositioning and feeding habits of insects on leaf surfaces (Handley, Ekbom & Gren, 2005). Indeed, *Artemisia ludoviciana* possesses glandular and non-glandular trichomes and secondary plant substances, including sesquiterpene lactones, and thus may use physical and/or chemical defences against herbivores, except for the specialist feeder *Hypochlora alba* (Dodge) which ingests these trichomes (Smith & Kreitner, 1983). Secretory trichomes and their function are usually described on aerial organs of Asteraceae, but many questions remain about the function and presence of trichomes in below-ground organs, as verified here in *O. angustifolius* and in *Ch. herbacea* and *Ch. platensis* by Hayashi & Appezzato-da-Glória (2005).

Many representatives of Asteraceae possess some form of perennating underground organ, which often has some type of secretory structure, as shown here. As secretory structures have high taxonomic value, our study provides data for future investigations focusing on the systematics of the family.

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