

Secretory structures of leaves of *Ophryosporus* Meyen (Asteraceae, Eupatorieae), a genus with medicinal properties¹

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ANABELA PLOS^{*}; GISELA SANCHO AND LAURA IHARLEGUI (División Plantas Vasculares, Museo de La Plata, Facultad de Ciencias Naturales y Museo, UNLP. Paseo del Bosque s.n., La Plata, 1900, Buenos Aires, Argentina.) J. Torrey Bot. Soc. 138: 391–399. 2011—*Ophryosporus* includes ca. 40 species restricted to the Andes of Ecuador to Argentina, with a few species inhabiting Brazil. Some of its species have multiple medicinal uses such as analgesic, antisyphilitic, anti-inflammatory and antiprotozoal activity, expectorant, relief of migraine, wound healing, antiseptic and antimicrobial activities. Despite of the number of chemical studies on this genus, its secretory structures are scarcely studied. An anatomical survey of leaves shows that two types of secretory structures coexist: 1) secretory reservoirs and 2) glandular trichomes. The secretory reservoirs are schizogenous and have an uniseriate epithelium. The glandular trichomes are biseriate vesicular represented by subtypes α and β . The profuse development of secretory reservoirs in leaves of *Ophryosporus* could affect foraging by folivorous insect and may be the primary source of secondary metabolites with potential medicinal uses.

Key words: anatomy, Asteraceae, morphology, trichomes.

Introduction. Many of the important natural chemicals, which have been used by man through the ages, are produced by secretory tissues of vascular plants. These tissues differ in structure, topographic position and materials secreted. The secreted material is usually eliminated from the secretory cells to the outside of the plant or into specialized intercellular spaces. The secretory tissues may consist of single cells or small to very large groups of cells. Tissues secreting lipophilic substances may be present either on the plant surface, mostly in the form of trichomes, or inside the plant body. In the latter case, they may be represented by single specialized cells, by rows of cells, or by structures consisting of an epithelium surrounding an intercellular space. The latter structure, if it is more or less isodiametric in shape is termed secretory cavity and when elongated it is called secretory duct (Fahn 1988).

In Asteraceae, secretory anatomical structures usually are present in roots, rhizomes,

and aerial parts (e.g. Thouvenin 1884, Col 1903, Tetley 1925, Metcalfe & Chalk 1950, Curtis & Lersten 1986, Jeffrey 2007, Göpfert *et al.* 2009). Indeed, the anatomical secretory structures described for Asteraceae are cavities, ducts and glandular trichomes (Col 1903, Tetley 1925, Metcalfe & Chalk 1950, Ramayya 1962, Fahn 1988, Lersten & Curtis 1988, Simon *et al.* 2002, Milan *et al.* 2006, Andreucci *et al.* 2008).

As well as in the rest of the family, in the tribe Eupatorieae the chemical compounds are mainly secreted by glandular trichomes of leaves (Taleb-Contini *et al.* 2007) and secretory cavities and ducts of the mesophyll. These structures in leaves of some Eupatorieae as *Bahianthus* R.M. King & H. Rob. were described as “resiniferous pockets” (King *et al.* 1979), “pellucid dots” in *Critonia* P. Browne (King & Robinson 1971), “secretory cavities” in *Liatris* Gaertn. ex Schreb. (Metcalfe & Chalk 1950), and “bicellular cavities” and “tubular cavities” in *Eupatorium* L. (Curtis & Lersten 1986, Lersten & Curtis 1986). Many of these cavities have a typically schizogenous origin and they are lined with an epithelium (Curtis & Lersten 1986, Lersten & Curtis 1986, Ragonese 1988, Simon *et al.* 2002, Milan *et al.* 2006).

Ophryosporus Meyen (Eupatorieae, Cironiinae) includes ca. 40 species (King & Robinson 1987, Bremer 1994, Hind & Robinson 2007, Sagástegui Alva & Rodríguez Rodríguez 2008) restricted to the Andes of

¹ Research for this article was supported by Agencia Nacional de Promoción Científica y Tecnológica, SECYT, Argentina and Comisión Nacional de Investigaciones Científicas y Tecnológicas, CONICET.

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² We would like to thank the curators of F, GH, LP, LPB, NY, RB, SGO, and US who provided material for study. We acknowledge Liliana Katinas and the reviewers for useful comments on the manuscript.

Ecuador to Argentina, with a few species inhabiting Brazil (King & Robinson 1987). Some of the species of *Ophryosporus* have multiple medicinal uses as analgesic, antisyphilitic (De Lampasona *et al.* 1997, Barboza *et al.* 2006), anti-inflammatory activity (Favier *et al.* 1998), antiprotozoal activity, expectorant, relief of migraine (Fournet *et al.* 1994), wound healing, antiseptic and antimicrobial activities (Rojas *et al.* 2003).

In *Ophryosporus*, although some chemical compounds have been fairly well studied (Bohlmann & Zdero 1979, Bohlmann *et al.* 1984, Zardini 1984, Ferracini *et al.* 1989, Sigstad *et al.* 1992 and 1993, Fournet *et al.* 1994, Rojas de Arias *et al.* 1994, Sigstad *et al.* 1996, De Lampasona *et al.* 1997, Favier *et al.* 1997 and 1998, Kim *et al.* 2001, Oliva *et al.* 2002, Herz 2004, Lopez Arze *et al.* 2004, Barboza *et al.* 2006, Barrero *et al.* 2006, Bascope & Sterner 2007), their association to secretory anatomical structures still has not been explored.

Due to the chemical and medicinal importance of *Ophryosporus*, the aim of this survey is to study the leaf secretory structures of *Ophryosporus* in order to find their association to the presence of medicinal chemical compounds.

Materials and Methods. Thirty one of the ca. 40 species of *Ophryosporus* were analyzed. Data were derived from the study of the herbarium specimens from F, GH, LP, LPB, NY, RB, SGO, US (abbreviated according to Holmgren *et al.* <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>). A total of 55 specimens were studied (Appendix 1).

For light microscopy examination, leaves of selected specimens were rehydrated. Transverse sections of leaves were cut by free hand and stained in 2% safranin as generic stain (Johansen 1940), blue Nile for total lipids (Cain 1947) and Sudan III for essential oils (Johansen 1940). For the study of paradermal view, leaves were analyzed with a Nikon SMZ 1000 stereoscopic microscope equipped with a camera lucida and a digital camera. In some cases, small rectangular areas of epidermis were removed from the middle portion of the leaf blade, decolorized with 50% sodium hypochlorite and stained with safranin for light microscope observations. In some species we use the Payne's method (1969). Selected material was also fixed in formalin-acetic acid-

alcohol and processed by the usual technique of paraffin infiltration (Johansen 1940). Transverse serial sections were cut 10–15 μm thick and stained with safranin and Astra Blue (Gerlach 1969). Light microscope observations and photographs were taken on a Nikon Eclipse E 200 microscope equipped with a camera lucida and a digital camera. To establish the relative diameter of secretory structures, length and width of lumens were measured in 10–30 structures for each species.

Terminology of trichomes follows Ramayya (1962). Relative amount of leaf secretory reservoirs was arbitrary established in an increasing rank of one to five (indicated with asterisks, “*”, in Table 1).

Results. Two kinds of secretory structures, glandular trichomes and secretory reservoirs, were found in the studied species of *Ophryosporus*.

GLANDULAR TRICHOMES. Glandular trichomes have been found in 16 of the 31 studied species (Table 1, Appendix 1), on both leaf surfaces (13 species), on the adaxial surface (one species), or on the abaxial surface (two species). In most species of *Ophryosporus*, glandular trichomes are scattered on the veins and usually absent on the blade. Exceptionally, *O. angustifolius* has its leaf surfaces covered with glandular trichomes.

Glandular trichomes of *Ophryosporus* are biserial vesicular represented by two subtypes (α and β). Trichomes of subtype α in *Ophryosporus* have a compound foot and a body differentiated into stalk and head. The stalk has two rows of 3 to 6 thin and smooth walled cells that vary in length (Fig. 1 A, B). The head has two rows of 3 to 5 cells much smaller than those of the stalk. Apical cuticle vesicle was not observed in this subtype of trichome although the content of head cells is denser than in the stalk cells.

Trichomes of subtype β have a simple foot and a body not differentiated into stalk and head. The body has two rows of 5 to 7 thin-walled cells (Fig. 1 C). The cells of the secretory head have a thin cuticle which lifts to form a large subcuticular chamber for the secretory material which is produced by the apical cells (Ramayya 1962). No pore or crack was found on the chamber cuticle, then we assume that the secretory material is released when the cuticle breaks either due to mechan-

Table 1. Secretory structures in *Ophryosporus*. B = blade; G = bisetate vesicular glandular trichome; M = mesophyll; V = veins; α : glandular trichome subtype α ; β : glandular trichome subtype β ; number of asterisks (*) refer to increasing relative amount of secretory cavities. References: A, Barboza *et al.* (2006); B, Barroero *et al.* (2006); C, Bascope & Sterner (2007); D, Bohlman *et al.* (1984); E, Bohlmann & Zdero (1979); F, De Lampasona *et al.* (1997); G, Favier *et al.* (1997); H, Favier *et al.* (1998); I, Ferracini *et al.* (1989); J, Fournet *et al.* (1994); K, Herz (2004); L, Kim *et al.* (2001); M, Lopez Arze *et al.* (2004); N, Oliva *et al.* (2002); O, Rojas de Arias *et al.* (1994); P, Rojas *et al.* (2003); Q, Sigstad *et al.* (1992); R, Sigstad *et al.* (1993); S, Sigstad *et al.* (1996); T, Zardini (1984); U, Zdero *et al.* (1990).

	Trichomes				Secretory Cavities			References		
	Abaxial		Adaxial		Arrangement	Relative diameter [length /width (in μ m)]		Relative amount	Medicinal uses	Active principles isolated
	Abaxial	Adaxial	Primary midveins	Mesophyll						
<i>O. angustifolius</i>	G β (V+B)	G β (V+B)	paired (M)	single (M + V)	11,4–19 \times 16,15–26,6	11,4–16,15 \times 13,3–19,95	**	–	E, K	
<i>O. apricus</i>	G α β (V)	G α β (V)	paired (M + V)	single (V)	12–18 \times 18–24	28–30 \times 32–42	****	–	–	
<i>O. axilliflorus</i>	absent	absent	single (M + V)	single (M + V)	10–18 \times 16–22	26–36 \times 40–54	****	A, B, H, N	A, B, H, K, N	
<i>O. bipinnatifidus</i>	G β (V)	G β (V)	single (M + V)	single (M + V)	6 \times 10	10 \times 22	**	–	–	
<i>O. burkartii</i>	absent	absent	single (M + V)	single (M + V)	6–8 \times 18–24	8–14 \times 14–22	****	–	–	
<i>O. carchiensis</i>	G α (V)	G α (V)	paired (M + V)	single (V)	4–16 \times 6–20	14–50 \times 38–50	****	–	–	
<i>O. charua</i>	absent	absent	single (M + V)	single (M + V)	6–8 \times 8–16	20–30 \times 80–86	***	A, C, F, G, T	C, F, G, K, L	
<i>O. chilca</i>	G β (V+B)	G β (V+B)	single (V)	single (V)	12–16 \times 20–24	absent	**	–	D, K	
<i>O. cumingi</i>	G α (V)	G α (V)	single (M + V)	single (M + V)	14–20 \times 20–40	25,65–38 \times 28,5–39,9	***	–	–	
<i>O. eleutherantherus</i>	G β (V+B)	G β (V+B)	single (M + V)	single (M + V)	6–10 \times 8–30	16–22 \times 40–60	**	–	–	
<i>O. ferreyrii</i>	G β (V+B)	G β (V+B)	single (M + V)	single (M + V)	12–14 \times 18–26	26 \times 46	**	–	–	
<i>O. foliolosus</i>	absent	absent	single (M + V)	single (M + V)	18–20 \times 18–26	16–26 \times 30	****	–	–	
<i>O. floribundus</i>	G β (V+B)	G β (V+B)	paired (M)	single (M + V)	14–22 \times 18–42	24–40 \times 28–42	****	–	G, Q, K, U	
<i>O. freyreysi</i>	absent	absent	paired (M)	single (M + V)	20 \times 24–26	14–46 \times 24–72	*****	–	–	
<i>O. galtoedes</i>	absent	absent	single (M + V)	single (M + V)	10–20 \times 14–22	16–30 \times 30–42	**	–	–	
<i>O. heptanthus</i>	G β (V+B)	G β (B)	paired (M)	single (M + V)	16–24 \times 18–26	8–22 \times 14–28	**	B	B, G, I, Q, K, M	
<i>O. johnstonii</i>	G β (V+B)	G β (V+B)	paired (M)	single (M + V)	20 \times 52	8–20 \times 20–50	**	–	–	
<i>O. laxiflorus</i>	absent	absent	paired (M)	single (M + V)	20–22 \times 24–46	24–26 \times 30–36	****	–	–	
<i>O. lorentzii</i>	absent	G β (B)	paired (M)	single (M)	absent	10–20 \times 24–44	**	S	K, L	
<i>O. macrodon</i>	absent	absent	single (M + V)	single (M + V)	8–12 \times 14–26	34–40 \times 40–44	****	–	K, R	
<i>O. organensis</i>	absent	absent	paired (M)	single (M + V)	10–22 \times 16–38	12–22 \times 14–42	****	–	–	
<i>O. paradosus</i>	absent	absent	single (M + V)	single (M + V)	6–12 \times 10–22	14–22 \times 24–48	**	–	–	
<i>O. peruvianus</i>	absent	absent	paired (M)	single (M + V)	26–32 \times 34–36	24–28 \times 34–64	****	–	–	
<i>O. pinifolius</i>	G β (V+B)	absent	paired (M)	single (M+V)	24–26 \times 32–46	18–42 \times 40–100	****	P	D, P, K	
<i>O. piqueroioides</i>	absent	absent	single (M + V)	single (M + V)	6–8 \times 8–20	8–10 \times 14–24	**	J, O	K, O, Q	
<i>O. regnelli</i>	absent	absent	paired (M)	single (M+V)	10–26 \times 22–46	14–34 \times 44–60	*****	–	–	
<i>O. sagastegui</i>	G β (V+B)	G β (V+B)	single (M + V)	single (M + V)	6–12 \times 24–48	8–10 \times 26–28	**	–	–	
<i>O. sodiroi</i>	absent	absent	single (M)	single (M)	absent	14–26 \times 32–100	****	–	–	
<i>O. steinbachii</i>	G α (V)	G β (V)	single (M + V)	single (M + V)	20 \times 32	22–34 \times 32–40	****	–	–	
<i>O. triangularis</i>	absent	absent	single (M + V)	single (M + V)	4–8 \times 14–24	6–10 \times 20–50	**	–	K	
<i>O. venosissimus</i>	G α (V)	G α (V)	paired (M)	single (M + V)	14–20 \times 22–30	18–40 \times 44–64	****	–	–	

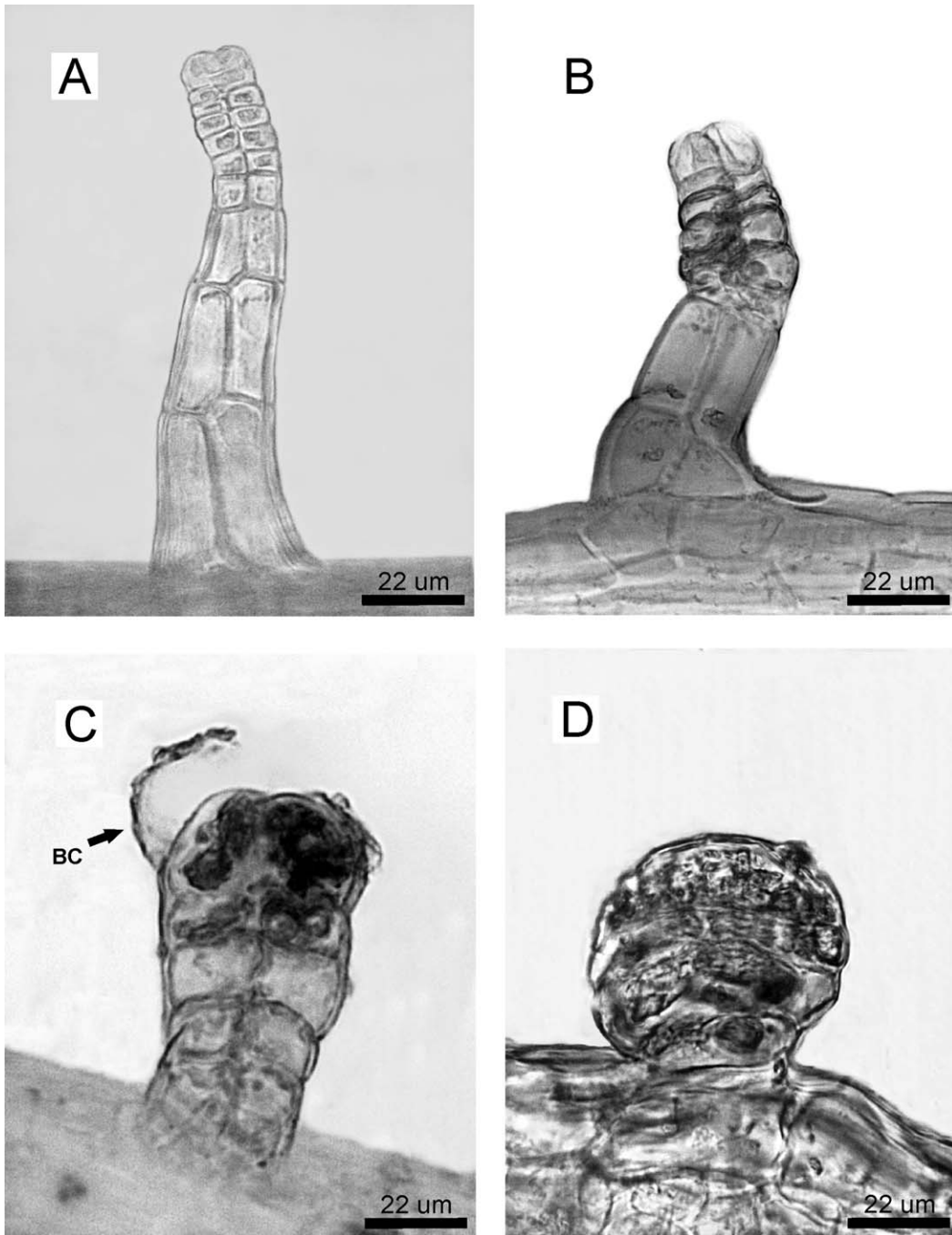


FIG. 1. Biseriate vesicular glandular trichomes. A, B, Subtype α . C, D, Subtype β . Scale bars: A, B, C, D, 22 μm . (A, *Ophryosporus venosissimus* from Lewis 37316, LPB; B, *O. steinbachii* from Steinbach 5726, F; C, *O. apricus* from Meza 212, LP; D, *O. pinifolius* from Huschel 76068, SGO). BC. Broken cuticle.

ical event or at the end of the life of the gland (Andreucci *et al.* 2008). In two species, *O. angustifolius* and *O. apricus*, glandular trichomes subtype β have cells broader than longer or isodiametrical (Fig. 1 D).

SECRETORY RESERVOIRS. Secretory reservoirs were found in all 31 studied species and they vary in arrangement, size, length and relative amount (Table 1). Secretory reservoirs were always associated to veins or in the mesophyll, near the xylem as well as the phloem (Fig. 2 A, B). The exact number of secretory reservoirs could not be compared due to leaf size variation among species. However, by simple observation, some species apparently have a relative higher number of secretory reservoirs than others (Table 1).

The secretory reservoirs are arranged individually in most of the species or less commonly they are paired (e.g., *O. cuningii*, Fig. 2 B). Leaf paradermal views and serial sections showed that secretory reservoirs of *Ophryosporus* are unconnected ducts and cavities, both of variable length. However, differences between the two shapes were not always clear. Ducts are elongated and they only were found in *O. peruvianus* (Fig. 2 C, D). Cavities are rounded (*O. steinbachii*, Fig. 2 E, F) to more commonly elliptic (e.g., *O. axilliflorus*, *O. apricus*, *O. cuningii*, *O. heptanthus*, *O. venosissimus*). Relative diameter of secretory structures (in cross section) varies from 4–50 μm long / 6–100 μm wide. Despite their differences in positions and size, the secretory structures are anatomically similar in having a lumen delimited by an uniseriate epithelium. The epithelial cells varied from 4 to 7 and have vacuolated cytoplasm in some cases or densely-staining cytoplasm in others (Fig. 2 G and H respectively). The lumen is usually filled with viscous yellowish to dark-brown (in stained cross sections) oil, rounded up into spherical droplets.

Discussion. The presence of secretory structures is very common in Asteraceae (Col 1903, Tetley 1925, Metcalfe & Chalk 1950, Fahn 1988). In *Ophryosporus* all studied species showed a well developed system of reservoirs as secretory structures; a half of the species also showed glandular trichomes. The reservoirs found in *Ophryosporus* are similar in shape, position and anatomy to other found in Asteraceae (Metcalfe & Chalk 1950, Ramayya

1962, Fahn 1988, Lersten & Curtis 1988, Simon *et al.* 2002, Milan *et al.* 2006, Andreucci *et al.* 2008), although rounded cavities as those of *O. steinbachii* appear to be uncommon in the family (Curtis & Lersten 1986). Comparing with other Eupatorieae, we found in *Ophryosporus* the typical secretory structures also present in *Eupatorium*. However, bicellular cavities as well as cavities formed by modification of bundle sheath cells of some species of *Eupatorium* (Curtis & Lersten 1986, Lersten & Curtis 1986) were not observed in *Ophryosporus*. Variation in cytoplasm of reservoir epithelial cells (i.e. vacuolated cytoplasm or densely-staining cytoplasm) could be associated with maturity of the cavity (Lersten & Curtis 1986).

The glandular trichomes of *Ophryosporus* are the usual of Asteraceae (Ramayya 1962, Lersten & Curtis 1988, Simon *et al.* 2002, Milan *et al.* 2006, Andreucci *et al.* 2008). Glandular trichomes have been indicated as the primary production sites of many of the bioactive secondary metabolites (Duke 1994, Rossi Monteiro *et al.* 2001, Göpfert *et al.* 2009). However, only nearly the fifty percent of the studied species of *Ophryosporus* have glandular trichomes whereas all studied species have secretory reservoirs. Some of the species without glandular trichomes showed high development of the secretory reservoir system (e.g., *O. axilliflorus*, *O. freyreysi*, *O. regnellii*), although postulating an inverse correlation in occurrence of the two secretory structures would require more studies. Moreover, it could be the case that both glandular trichomes and reservoirs, have different ecological roles not directly related to each other. Some of the ecological roles postulated for plant secretory structures are protection against insects and plant pathogens, attraction of pollinators or other beneficial insects, allelopathic effects, and protection against extreme environmental conditions (Langenheim 1994). In some Asteraceae, glandular trichomes have been indicated as containing potent phytotoxins which are found only in the subcuticular space of the glands to avoid autotoxicity (e.g., Göpfert *et al.* 2009). Then, glandular trichomes would represent repositories of chemical that defend against insects and microbial pathogens (Duke 1994). Sesquiterpene lactones, as those found in *Ophryosporus*, are usually accumulated in glandular trichomes of leaves and are related to plant

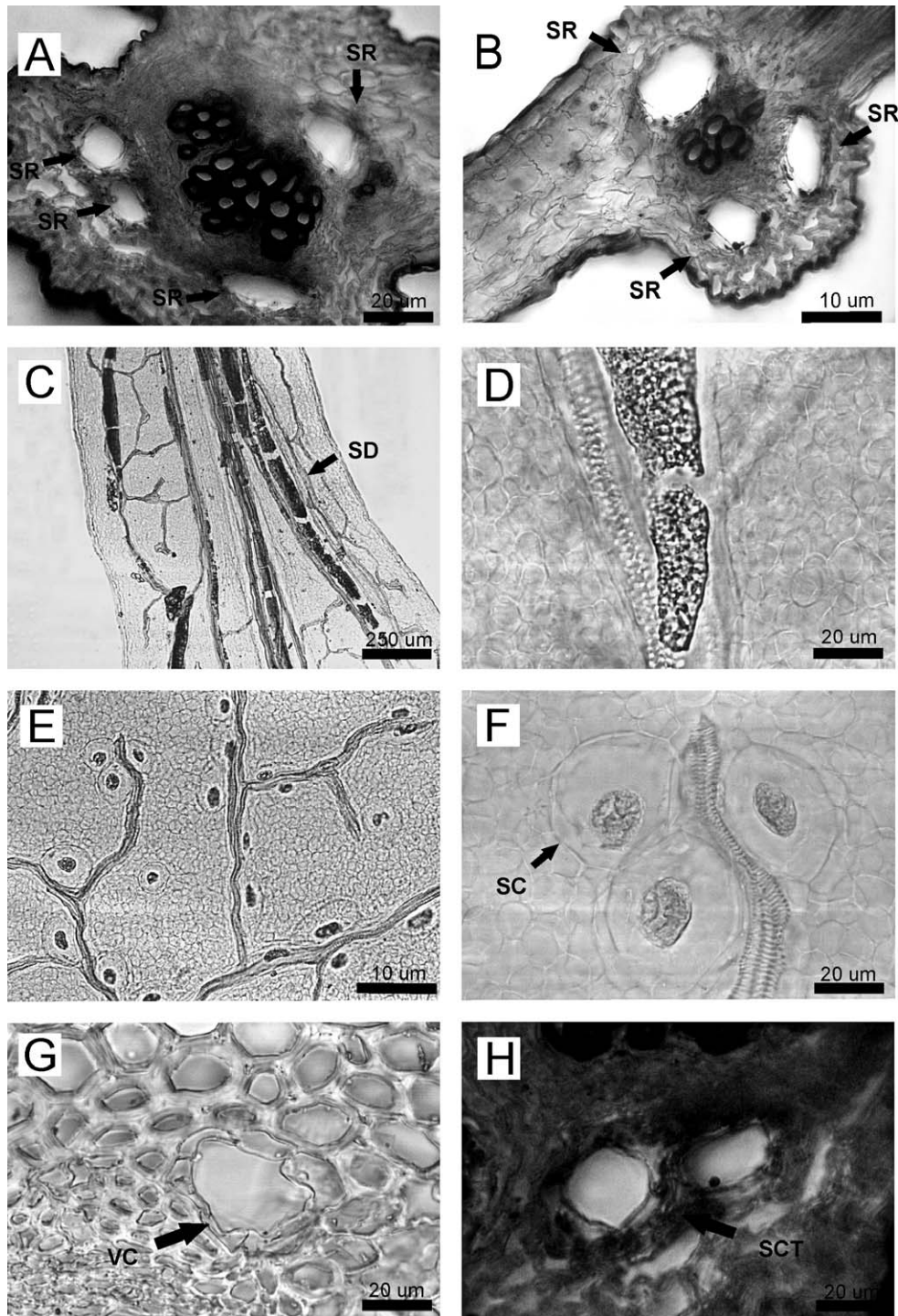


FIG. 2. Leaf secretory reservoirs. A, Midvein cross-section. B, Mesophyll cross-section. C, D, Ducts in paradermal view. E, F, Rounded cavities in paradermal view. G, H, Uniseriate epithelium. G, Epithelial cells with vacuolated cytoplasm. H, Epithelial cells with densely staining cytoplasm. Scale bars: A, D, F, G, H, 20 μ m; B, C, 250 μ m; E, 10 μ m. (A, B, *O. cumingii* from Herzog 2219 LP; C, D, *O. peruvianus* from Fosberg 27691 NY; E, F, *O. steinbachii* from Steinbach 5726, F; G, *O. venosissimus* from Jimenez 46, LP; H, *O. axilliflorus* from Kiesling *et al.* 705, LP). SC. Secretory cavity. SCT. Staining cytoplasm. SD. Secretory duct. SR. Secretory reservoir. VC. Vacuolated cytoplasm.

defence against predators (Wagner 1991, Duke 1994, Werker 2000). However, glandular trichomes are not particularly dense in most of the studied species of *Ophryosporus*, and they are usually restricted to the main veins. Thus, in the case of *Ophryosporus*, secretory reservoirs appear to be the ideal structures suited to defend against herbivores (Dussourd & Denno 1991).

The activity of medicinal plants can be attributed to their secondary metabolites that are primary synthesized, secreted and stored by secretory (Combrinck *et al.* 2007). The present study shows that only five of the eleven species of *Ophryosporus* with medicinal properties or with isolated active principles, have trichomes whereas the other six have only reservoirs as secretory structures. In the last years, the potent bioactivities of sesquiterpene lactones typical of Asteraceae such as anti-malarial activity of artemisinin, drew significant interests in the biochemistry of these compounds (Göpfert *et al.* 2009). In eleven species of *Ophryosporus* (Table 1), sesquiterpene lactones were isolated together with other chemical compounds associated with medicinal activity as mono and sesquiterpenes (Zdero *et al.* 1990, Sigstad *et al.* 1996), diterpenes (Bohlman *et al.* 1984, Ferracini *et al.* 1989, Zdero *et al.* 1990, Favier *et al.* 1997), benzofurans and dihydrobenzofurans (Bohlman & Zdero 1979, Ferracini *et al.* 1989, Zdero *et al.* 1990, Sigstad *et al.* 1992, Sigstad *et al.* 1993, Sigstad *et al.* 1996, De Lampasona *et al.* 1997, Favier *et al.* 1998), coumarins, chromenes and aromatic compounds (Bohlman & Zdero 1979, Bohlman *et al.* 1984, Ferracini *et al.* 1989, Zdero *et al.* 1990, Sigstad *et al.* 1992, Sigstad *et al.* 1993, Sigstad *et al.* 1996, De Lampasona *et al.* 1997, Favier *et al.* 1998) and flavones, flavonones and their glycosides (Ferracini *et al.* 1989, Zdero *et al.* 1990, Favier *et al.* 1997) (Table 1). The above types of terpenes, when they occur together, are usually called “essential oils” (Langenheim 1994) and secreted by a variety of anatomical structures (e.g. epidermal cells, trichomes, ducts, etc.). This could indicate that the primary source of potentially medicinal secondary metabolites in *Ophryosporus* is the leaf system of secretory reservoirs. As observed in Table 1, some species of *Ophryosporus* apparently have a relative higher number of secretory reservoirs than others. Although development of secretory reservoirs may vary

temporarily under stress pressures (extreme environmental conditions, e.g. Harborne 1994; herbivory, e.g. Dussourd & Denno 1991) the presence of a high relative amount of them also may be due to a permanent high secondary metabolite biosynthesis. From this last point of view, species with a well developed system of secretory reservoirs as *O. freyreysii*, *O. laxiflorus*, *O. organensis*, *O. regnelli*, *O. steinbachii*, and *O. venosissimus* could represent a potential new source of medicinal secondary metabolites.

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Appendix 1.

Selected specimens studied: *O. angustifolius* B. L. Rob. (*Angulo 905*, LP; *King & Bishop 7638*, US); *O. apricus* B. L. Rob. (*Meza 212*, LP; *Vásquez et al. 25499*, US); *O. axilliflorus* (Griseb.) Hieron. (*Cabrera & Kiesling 25129*, LP; *Kiesling et al. 705*, LP); *O. bipinnatifidus* B. L. Rob. (*Vargas 12630*, LP; *Rose & Rose 18805*, US); *O. burkartii* Cabrera (*Fabris & Crisci 6914*, LP; *Kiesling et al. 455*, LP); *O. carchiensis* H. Rob. (*Palacio & Tipaz 10524*, US); *O. charua* (Griseb.) Hieron. (*Castellanos 291480*, LP; *Burkart 7520*, LP); *O. chilca* (Kunth.) Hieron. (*Sagástegui et al. 11651*, NY; *Mostacero et al. 1376*, NY); *O. cumingii* Benth. ex Baker (*Herzog 2219*, LP; *Adolfo 104 c*, LP); *O. eleutherantherus* (Rusby) B. L. Rob. (*Buchtien 541*, NY); *O. ferreyrii* H. Rob. (*Edwin & Schunke 3796*, F; *Granda 597*, US); *O. foliolosus* (DC.) Reiche (*Geisse 95*, NY; *Hastings 594*, NY); *O. floribundus* (DC.) R. M. King & H. Rob. (*Pinto s.n.*, SGO); *O. freyreisii* (Thunb.) Baker (*Harley et al. 25330*, NY); *O. galiodes* (DC.) R. M. King & H. Rob. (*Sagástegui et al. 9790*, F; *Sánchez et al. 3025*, F); *O. heptanthus* (Sch. Bip. ex Wedd.) R. M. King & H. Rob. (*Nee & Atha 49979*, NY; *Solomon 7453*, NY); *O. johnstonii* B. L. Rob. (*Ricardi 3849*, LP; *Johnston 5259*, GH); *O. laxiflorus* Baker (*Hatschbach 51977*, US; *Regnell III 709*, US); *O. lorentzii* Hieron. (*Lognomo 8602 c.*, LP; *Venturi 4115*, LP); *O. macrodon* Griseb. (*Cabrera et al. 21284*, LP; *Hunziker 7144*, LP); *O. organensis* Cabrera (*Occhioni 1029*, LP); *O. paradoxus* (Hook. & Arn.) Benth. & Hook. ex B. D. Jacks. (*Crisci 360*, LP; *Boelcke 3858*, LP); *O. peruvianus* (J. G. Gmel.) R. M. King & H. Rob. (*Fosberg 27691*, NY; *Madsen 75039*, NY); *O. pinifolius* (Phil.) R. M. King & H. Rob. (*Gardner & Knees 6512*, SGO; *Huschel 76068*, SGO); *O. piquerioides* (DC.) Benth. ex Baker (*Krapovickas et al. 19074*, LP; *Cabrera & Fabris 22694*, LP); *O. regnelli* Baker (*Riedel & Lund 2360*, NY; *Oliveira 942*, LP; *Esteves 2154*, RB); *O. sagasteguii* H. Rob. (*Sagástegui 9975*, US); *O. sodiroi* Hieron. (*Barford 60090*, NY); *O. steinbachii* B. L. Rob. (*Steinbach 5726*, F); *O. triangularis* Meyen (*Cabrera 11416*, LP; *Martcorena 1845*, LP); *O. venosissimus* (Rusby) B. L. Rob. (*Jiménez 46*, LP; *Lewis 37316*, LPB).