Review

Elaiophores: their taxonomic distribution, morphology and functions

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ABSTRACT

Elaiophores are floral glands that secrete non-volatile oils as a reward for their pollinators. Their secretions mediate a specialized interaction between oil-producing plants and a few species of oil-collecting bees - Apidae and Melittidae. The present review focuses on the morphological and functional aspects of these secretory structures. We also provide information on their chemistry and pollination ecology. Our survey is organized taxonomically among the plant families for which elaiophore occurrence has been confirmed -for the monocots, Iridaceae and Orchidaceae, and for the eudicots, Calceolariaceae, Cucurbitaceae, Krameriaceae, Malpighiaceae, Plantaginaceae, Primulaceae, Scrophulariaceae, Solanaceae and Stilbaceae. Most oil flowers are zygomorphic, bisexual, nectarless and present their elaiophores on the protective whorls or on the androecium. Trichomal elaiophores are reported in all of these families except Krameriaceae and Malpighiaceae, and they vary in the density and morphology of the trichomes. Epithelial elaiophores occur in some monocot representatives and in Krameriaceae and Malpighiaceae, and are similar among species. An intermediate type of elaiophore is reported in some species of Orchidaceae. Regardless of elaiophore type, these glands have similar subcellular features and secretion-release mechanisms. Finally, we note the dearth of information on elaiophore ultrastructure and functioning for several plant families.

Keywords: Asparagales, bees, Cucurbitales, Ericales, Lamiales, Malpighiales, oil flowers, Solanales, Zygophyllales

Introduction

Elaiophores are a type of floral secretory structure whose secretions act as the primary attractant in a mutual relationship between oil-producing flowers and oil-collecting bees –thus their potential pollinators.

This specialized pollination system was first reported in *Angelonia* and *Calceolaria* species by Vogel (1969; 1971; 1974). His discovery opened up a new area of research that

has since been explored by many authors. In addition to Vogel's early publications and those of others presented here, general and more recent information on oil-producing flowers and/or on oil-collecting bees can be found in Simpson & Neff (1981), Buchmann (1987), Rasmussen & Olesen (2000), Machado (2004), Alves-dos-Santos *et al*. (2007) and Renner & Schaefer (2010).

In his first full publication (1974) on the subject Ölblumen und ölsammelnde Bienen (*Oil flowers and oil collecting*

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bees) Vogel provided information on the morphology, chemical nature of secretions and ecological functions of elaiophores in some species of the Iridaceae, Krameriaceae, Malpighiaceae, Orchidaceae and Scrophulariaceae. Some Scrophulariaceae species are now included in the Calceolariaceae, Plantaginaceae and Stilbaceae (*sensu* APG IV 2016). Since then, other families have been added to the list including the Cucurbitaceae (Vogel 1976b *apud* Simpson & Neff 1981), Fabaceae (Vogel 1988), Gesneriaceae (Steiner 1985b), Melastomataceae (Buchmann & Buchmann 1981), Primulaceae (Vogel 1976a) and Solanaceae (Simpson & Neff 1981). These now total 14 families with known or suspected oil-producing species (see Tab. 1). For the Fabaceae, Gesneriaceae and Melastomataceae there is not yet sufficient evidence to confirm that the oil-producing structures are actually true elaiophores (*sensu* Vogel), so they are not included in the list of plant families that offer oil as a reward to their pollinators.

The wide distribution of the elaiophores among unrelated families of monocots and eudicots (Tabs. 1, 2) indicates a polyphyletic evolution for this character (Vogel 1974; Buchmann 1987; Renner & Schaefer 2010). According to Renner & Schaefer (2010) oil flowers evolved at least 28 times after the K-T boundary and they have also been lost 36-40 times.

According to Vogel (1974) the oil can be produced by elaiophores constituted by a set of secretory trichomes or by a secretory epithelium recovered by a single cuticle under which the secretion is stored.

In general, elaiophore secretions consist mainly of fatty acids and/or glycerides (see Vogel 1974; Simpson *et al*. 1977; Seigler *et al*. 1978; Simpson *et al*. 1979; Simpson & Neff 1981; Buchmann 1987; Cocucci 1991; Vinson *et al*. 1997; Reis *et al*. 2000; Reis *et al*. 2003; Seipold *et al*. 2004; Reis *et al*. 2006; Reis *et al*. 2007; Dumri *et al*. 2008; Vogel 2009). However, other constituents have also been reported as minor constituents including: aldehydes, amino acids, carbohydrates, carotenoids, hydrocarbons, isoprenoid compounds, ketones, phenolic compounds, saponins, and terpenes (see Vogel 1974; Simpson & Neff 1981; Cane *et al*. 1983; Buchmann 1987; Lobreau-Callen 1989; Reis *et al*. 2006).

The floral oil is gathered by female solitary bees belonging to a number of genera of the Melittidae (Melittinae subfamily) and Apidae (Centridini, Ctenoplectrini, Tapinotaspidini and Tetrapediini tribes) (*sensu* Michener 2007; Tab. 1). The abdomen (Ctenoplectrini bees) or the front and/or middle legs of these bees generally have specialized oil-collecting structures, such as pads or combs of branched or simple setae (see Vogel 1974; Neff & Simpson 1981; Cocucci *et al*. 2000; Machado 2004; Alves-dos-Santos *et al*. 2007; Michener 2007). According to Vogel (1974) and Neff & Simpson (1981) the features of the oil-collecting organs can be correlated with the type of elaiophore (i.e. epithelial or trichomal). That is, bees that visit trichomal elaiophores generally have pads of setae, while bees visiting epithelial elaiophores have brush-like combs of modified setae or combs of spatulate setae.

The bees use the oil, sometimes mixed with pollen, for larval food provisioning (see Vogel 1974; Simpson *et al*.1977; Vinson *et al*.1996; Vinson *et al*.1997; Alves-dos-Santos *et al*. 2002; Michener 2007; Reis *et al*. 2007; Vogel 2009; Schäffler & Dötterl 2011); for nest waterproofing (see Neff & Simpson 1981; Simpson & Neff 1981; Cane *et al*.1983; Buchmann 1987; Alves-dos-Santos *et al*. 2002; Michener 2007; Vogel 2009; Schäffler & Dötterl 2011) or for nest construction (see Vinson *et al*. 1996; Alves-dos-Santos *et al*. 2002). Since the oil flowers are generally without nectar and considering that there is no clear evidence the adult bees consume the floral oil, the bees are also likely to be dependent on nectar from other flowers (Michener 2007).

After more than 40 years since the discovery of this specialized pollination system, information on the distribution of elaiophores among the angiosperms remains imprecise and incomplete. This compilation focuses mainly on the taxonomic distribution and the morphological features of elaiophores but also provides information on oil chemistry and pollination ecology. Our intent is to contribute to a better understanding of the distribution, diversity and functional aspects of elaiophores among angiosperms, with the hope of stimulating new study in this interesting field. Our findings are organized on the basis of the plant taxonomic groups in which elaiophores are known to occur.

Asparagales

Iridaceae

Iridaceae is an almost cosmopolitan family of some 2115 species in 66 genera (Stevens 2001). This family is particularly diverse in Africa and shows considerable floral diversification and a wide range of pollination syndromes (Rudall *et al*. 2003; Goldblatt & Manning 2006). The flowers offer pollen, nectar and sometimes oil for the pollinators, which include bees, beetles, flies, butterflies, moths and birds (Rudall *et al*. 2003; Goldblatt & Manning 2006).

Oil-secreting trichomes are recorded on several New World genera of the Sisyrinchieae, Tigridieae and Trimezieae (Iridoideae) (Rudall *et al*. 2003; Chaveau *et al*. 2012; see Tab.1). According to Chaveau *et al*. (2012) the trichomal elaiophores have evolved independently multiple times in the tribes of Iridoideae, corroborating the findings of Renner & Schaefer (2010).

The trichomes can be concentrated on the base of the staminal column, on the base of the inner surface of the tepals or along the middle vein of each tepal (Vogel 1974; Goldblatt *et al*.1998; Cocucci & Vogel 2001; Chaveau *et al*. 2011; 2012; Silvério *et al*. 2012; see Tab.2). In the Sisyrinchieae, trichomes can occur on both the column

Table 1. Taxa with known or suspected oil-producing flowers and their related oil-collecting bees.

Taxonomic classification*				Taxa with oil-offering flowers in at least one species (total of species in the genus)**	Genus of oil-collecting bees	References
Asparagales	Iridaceae	Iridoideae		Crocoideae	*Tritoniopsis* (20)	*Rediviva*	Manning & Goldblatt 2002
				Sisyrinchieae	*Sisyrinchium* (85)	*Chalepogenus, Lanthanomelissa, Tapinotaspis*	Vogel 1974; Buchmann 1987; Goldblatt *et al.* 1998; Cocucci & Vogel 2001; Chaveau *et al.* 2011; Chaveau *et al.* 2012; Silvério *et al.* 2012
				Tigridieae	*Alophia* (5), *Calydorea* (8), *Cardenanthus* (8), *Cipura* (6), *Cypella* (20), *Ennealophus* (5), *Herbertia* (5), *Kelissa* (1), *Mastigostyla* (16), *Onira* (1), *Tigridia* (30)	*Centris, Chalepogenus, Paratetrapedia*	Vogel 1974; 1988; Buchmann 1987; Goldblatt *et al.* 1998; Chaveau *et al.* 2011; Chaveau *et al.* 2012
				Trimezieae	*Trimezia* (20)	-	Simpson & Neff 1981; Buchmann 1987; Chaveau *et al.* 2012
	Orchidaceae (*sensu* Chase *et al.* 2015)	Epidendroideae	Cymbidieae	Catasetinae	*Grobya* (5)	*Paratetrapedia*	Mickeliunas *et al.* 2006; Pansarin *et al.* 2009
				Maxillariinae	*Rudolfiella* (6)	-	Davies & Stpiczyńska 2009
				Oncidiinae	*Chytroglossa* (3), *Cyrtochilum* (137), *Gomesa* (119), *Hintonella* (1), *Lockhartia* (28), *Oncidium* (311), *Ornithocephalus* (55), *Phymatidium* (10), *Platyrhiza* (1), *Trichocentrum* (70), *Vitekorchis* (4), *Zygostates* (22)	*Centris, Lophopedia, Tetrapedia*	Vogel 1974; Singer & Cocucci 1999; Alves-dos-Santos *et al.* 2002; Reis *et al.* 2003; Reis *et al.* 2006; Pacek & Stpiczyńska 2007; Stpiczyńska *et al.* 2007; Aliscioni *et al.* 2009; Pansarin & Pansarin 2011; Torretta *et al.* 2011; Neubig *et al.* 2012; Pacek *et al.* 2012; Blanco *et al.* 2013
		Orchidoideae	Cranichideae	Cranichidinae	*Ponthieva* (66)	-	Dressler 1993 *apud* Salazar *et al.* 2009
			Orchideae	Brownleeinae	*Disperis* (78)	*Rediviva*	Buchmann 1987; Manning & Linder 1992; Pauw 2006; Whitehead *et al.* 2008; Waterman *et al.* 2009
				Coryciinae	*Ceratandra* (6), *Corycium* (15), *Evotella* (1), *Pterygodium* (19)	*Rediviva*	Buchmann 1987; Whitehead & Steiner 1992; 1993; Linder & Kurzweil 1994; Steiner 1998; Pauw 2006; Waterman *et al.* 2009; Steiner *et al.* 2011
				Disinae	*Huttonaea* (5)	*Rediviva*	Buchmann 1987; Whitehead *et al.* 2008; Steiner 2010
				Orchidinae	*Satyrium* (86)	-	Buchmann 1987
Cucurbitales	Cucurbitaceae	Cucurbitoideae Joliffieae grade (sensu Kocyan *et al.* 2007)			*Baijiania* (1), *Indofevillea* (2), *Momordica* (47), *Siraitia* (4), *Telfairia* (3), *Thladiantha* (25)	*Ctenoplectra*	Vogel 1981; 1988; Schaefer & Renner 2008; 2011; Sung *et al.* 2009; Renner & Schaefer 2010; Schaefer *et al.* 2012

Table 1. Cont.

Taxonomic classification*			Taxa with oil–offering flowers in at least one species (total of species in the genus)**	Genus of oil-collecting bees	References
Ericales	Primulaceae	Myrsinoideae	*Lysimachia* (180)	*Macropis*	Vogel 1976a; 1986; 1988; Simpson *et al.*1983; Cane *et al.*1983; Anderberg *et al.* 2007; Dötterl & Schäffler 2007; Schäffler & Dötterl 2011; Schäffler *et al.* 2012
Fabales	Fabaceae	Caesalpinioideae	*Caesalpinia* spp.*** *Hoffmannseggia* spp.***	*Centris* ???	Vogel 1988
Lamiales	Plantaginaceae(Olmstead *et al.* 2001; Albach *et al.* 2005)	**Calceolariaceae**	*Calceolaria* (245)	*Centris, Chalepogenus, Tapinotaspis*	Vogel 1974; 1988; Molau 1988; Rasmussen & Olesen 2000; Sérsic 2004; Cosacov *et al.* 2012; Cosacov *et al.* 2014; Murúa *et al.* 2014
		Gesneriaceae	*Drymoniaserrulata***	-	Steiner 1985b
		Angelonieae	*Angelonia* (26), *Basistemon* (8), *Monopera* (2), *Monttea* (3)	*Arhysoceble, Caenomanda, Centris, Chalepogenus, Lophopedia, Paratetrapedia, Tapinotaspis, Tetrapedia*	Vogel 1974; 1988; Simpson *et al.* 1990; Vogel & Machado 1991; Sérsic & Cocucci 1999; Machado *et al.* 2002; Aguiar & Melo 2009; Tadey 2011; Martins & Alves-dos-Santos 2013; Martins *et al.* 2013; Martins *et al.* 2014; Ferreiro *et al.* 2015
		Gratioleae	*Mecardonia* (10)	*Chalepogenus*	Cappellari*et al.* 2009
	Scrophulariaceae	Hemimerideae	*Alonsoa* (11), *Colpias* (1), *Diascia* (50), *Hemimeris* (4)	*Rediviva*	Vogel 1974; 1984; Steiner 1989; 1990; 1996; 1999; 2009; Simpson *et al.* 1990; Steiner & Whitehead 1990; 1991; 2002; Whitehead & Steiner 1992; Kampny 1995; Olmstead *et al.* 2001; Fischer 2004; Pauw 2005; Dumri *et al.* 2008; Whitehead *et al.* 2008; Kuhlmann & Hollens 2015
	Stilbaceae	Bowkerieae (Oxelman *et al.* 2005; Tank *et al.* 2006)	*Anastrabe* (1), *Bowkeria* (5), *Ixianthes* (1)	*Rediviva*	Vogel 1974; Steiner & Whitehead 1990; 1991; 1996;Whitehead & Steiner 1992; Steiner 1993

Table 1. Cont.

Taxonomic classification*		Taxa with oil–offering flowers in at least one species (total of species in the genus)**	Genus of oil-collecting bees	References
Malpighiales	Malpighiaceae	Most of the neotropical genera (≈1100 spp.: *e.g. Acmanthera, Aspicarpa, Banisteriopsis, Barnebya, Blepharanda, Bunchosia, Burdachia, Byrsonima, Callaeum, Camarea, Clonodia, Cordobia, Diacidia, Dicella, Dinemagonum, Dinemandra, Diplopterys, Galphimia, Gaudichaudia, Glandonia, Heladena, Henleophytum, Heteropterys, Hiraea, Janusia, Lophanthera, Lophopterys, Lubelina, Malpighia, Mascagnia, Mcvaughia, Mezia, Peixotoa, Peregrina, Pterandra, Spachea, Stigmaphyllon, Tetrapterys, Tricomaria, Triopterys, Verrucularia*)	*Centris, Epicharis, Monoeca, Paratetrapedia, Tetrapedia*	Vogel 1974; Lorenzo 1981; Steiner 1985a; Buchmann 1987; Lobreau-Callen 1989; Sazima & Sazima 1989; Simpson 1989; Anderson 1990; Barros 1992; Mamede 1993; Cocucci *et al.* 1996; Vinson *et al.* 1997; Teixeira & Machado 2000; Castro *et al.* 2001; Seipold *et al.* 2004; Sigrist & Sazima 2004; Carvalho *et al.* 2005; Benezar & Pessoni 2006; Costa *et al.* 2006; Oliveira *et al.* 2007; Reis *et al.* 2007; Vilhena & Augusto 2007; Ribeiro *et al.* 2008; Bezerra *et al.* 2009; Dunley *et al.* 2009; Amorim & Marco 2011; Cappellari *et al.* 2011; Mendes *et al.* 2011; Possobom 2013; Sazan *et al.* 2013; Possobom *et al.* 2015
Myrtales	Melastomataceae	Olisbeoideae (*sensu* Stone 2006) · *Mouriri myrtilloides* subsp. *parvifolia****	*Paratetrapedia*	Buchmann & Buchmann 1981
Solanales	Solanaceae	Petunioideae · *Nierembergia* (21)	*Centris, Chalepogenus, Lanthanomelissa, Paratetrapedia, Tapinotaspis*	Simpson & Neff 1981; Cocucci 1991; Cosacov *et al.* 2008; Tate *et al.* 2009; Nattero *et al.* 2010
Zygophyllales		**Krameriaceae** · *Krameria* (18)	*Centris*	Vogel 1974; Simpson *et al.*1977; Seigler *et al.* 1978; Simpson & Neff 1981; Simpson 1982; 2007; Simpson & Saliwon 1999; Simpson *et al.* 2004; Gimenes & Lobâo 2006; Carneiro *et al.* 2015

* Except in cases where the source is specified between parentheses, the taxonomic classification is based on Stevens (2001).

**The presence of oil secretion is based on studies on morphology, chemistry and/or pollination ecology. The number of species of each genus is based on The Plant List (2013), Chase *et al.* (2015, for Orchidaceae) or on the cited references.

***There is not enough information to assume that the oil-secreting structures really act as elaiophores in these species.

Table 2. Location and morphology of the oil-secreting structures in the plant taxa for which we were able to find published information.

Taxa		Gland morphology and location	Reference
Asparagales Iridaceae	*Alophia tigridioides*	UT - adaxial surface of the inner tepals	Vogel 1974
	Cypella herbertii		
	Ennealophus euryandrus (=*Sphenostigma euryandra*)		
	Sisyrinchium spp.	UT - adaxial surface of the inner tepals or along stamen column	Vogel 1974; Rudall *et al.* 2003; Cocucci & Vogel 2001; Chaveau *et al.* 2011; Silvério *et al.* 2012
	Tigridia meleagris	UT - adaxial surface of the inner tepals	Rudall *et al.* 2003
Asparagales Orchidaceae	*Ceratandra* spp.	E - Callus	Steiner 1998
	Cyrtochilum meirax	CE - not clear	Davies *et al.* 2014
	Gomesa bifolia	CE - Callus	Aliscioni *et al.* 2009
	Gomesa echinata	PE - Callus	Stpiczyńska *et al.* 2013
	Gomesa flexuosa	CE/UT - Callus	Gomiz *et al.* 2013
	Gomesa loefgrenii (as *Oncidium loefgrenii*)	PE - Callus	Stpiczyńska *et al.* 2007
	Gomesa longipes	CE/UT - Callus	Davies *et al.* 2014
	Gomesa paranensoides (as *Oncidium paranaense*)	CE - lateral lobes of the labellum	Singer & Cocucci 1999
	Gomesa radicans (as *Ornithophora radicans*)	PE - Labellum/callus complex	Stpiczyńska & Davies 2008
	Gomesa ranifera	PE - Callus	Stpiczyńska *et al.* 2013
	Gomesa recurva	E - Labellum	Stpiczyńska *et al.* 2007
	Gomesa riograndensis	PE - Callus	Gomiz *et al.* 2013
	Gomesa varicosa	CE - Callus	Gomiz *et al.* 2013
	Gomesa venusta (as *Oncidium trulliferum*)	PE - lateral lobes of the labellum and callus	Stpiczyńska & Davies 2008
	Grobya amherstiae	PE/UT - apex of the labellum, UT - base of the column, E - abaxial surface of the labellum (oil guide)	Pansarin *et al.* 2009
	Lockhartia spp.	UT - Callus	Blanco *et al.* 2013
	Oncidium amazonicum	PE - Callus	Stpiczyńska *et al.* 2013
	Oncidium bicallosoides (as *Sigmatostalix bicallosa*)	PE- Callus	Vogel 1974
	Oncidium cheirophorum	CE - lateral lobes of the labellum	Pacek & Stpiczyńska 2007
	Oncidium heteranthum	CE/UT - Callus	Davies *et al.* 2014
	Oncidium ornithorhynchum	PE - lateral lobes of the labellum	Vogel 1974; Davies & Stpiczyńska 2009
	Oncidium oxyceras	PE - Callus	Stpiczyńska *et al.* 2013
	Oncidium sect.Cyrtochilum	PE - Labellum	Vogel 1974
	Ornithocephalus ciliatus (as *Ornithocephalus kruegeri*)	UT - Callus	Pacek & Stpiczyńska 2007
	Ornithocephalus gladiatus	CE/UT - lateral lobes of the labellum	Pacek *et al.* 2012
	Phymatidium falcifolium	UT - Callus	Pacek *et al.* 2012
	Rudolfiella picta	PE - Callus	Davies & Stpiczyńska 2009
	Trichocentrum cavendishianum	PE - lateral lobes of the labellum	Stpiczyńska *et al.* 2007
	Trichocentrum pumilum	UT - lateral lobes of the labellum	Pansarin & Pansarin 2011
	Vitekorchis excavata	CE/UT -Callus	Davies *et al.* 2014
	Zygostates alleniana	UT - central and lateral lobes of the labellum	Gomiz *et al.* 2014
	Zygostates grandiflora	UT - Callus	Pacek *et al.* 2012
	Zygostates lunata	UT - Callus	Pacek *et al.* 2012
	Zygostates pustulata	UT - Callus	Vogel 1974
Cucurbitales Cucurbitaceae	*Indofevillea jiroi*	T - base of the inner surface of the five petals	Schaefer *et al.* 2012
	Momordica spp.	T - base of the inner surface of one or three petals	Vogel 1988
	Thladiantha spp.	T - base of the inner surface of the five petals	

Table 2. Cont.

Taxa		Gland morphology and location	Reference
Ericales Primulaceae	*Lysimachia* spp.	MT - base of the inner surface of the petals and of the anther filaments	Simpson *et al.* 1983; Vogel 1986 (*apud* Buchmann 1987)
Lamiales Calceolariaceae	*Calceolaria* spp.	MT - inside the saccate lower lip	Vogel 1974; Sérsic 2004
Lamiales Plantaginaceae	*Angelonia* spp.	MT - inside the two sacs of the lower lip	Vogel 1974; Vogel & Machado 1991; Simpson *et al.* 1990; Sérsic & Cocucci 1999
	Monttea spp.	MT - in the two depressions of the lower lip	
Lamiales Scrophulariaceae	*Alonsoa unilabiata*	MT - on the two shallow sacs on the base of the lateral lobes (upper side of the corolla)	Steiner 1989
	Colpias mollis	MT - on the paired sacs on the base of the corolla lobes at the lower side of the tube.	Vogel 1974; Steiner & Whitehead 2002
	Diascia spp.	MT - inside paired spurs of different lengths at the lower side of the corolla	Vogel 1974; 1984
	Hemimeris racemosa	MT - around the entrance of two shallow sacs at the base of the dorsal corolla lobe.	Pauw 2005
Lamiales Stilbaceae	*Bowkeria verticillata*	MT - inside the saccate lower lip	Vogel 1974
Malpighiales Malpighiaceae	*Banisteriopsis* spp.	PE - in pairs on the abaxial surface of four or five sepals	Araújo & Meira 2016; Possobom 2013
	Byrsonima coccolobifolia		Possobom 2013
	Camarea affinis		Mamede 1993
	Dinemandra ericoides		Cocucci *et al.* 1996
	Diplopterys pubipetala		Possobom *et al.* 2015
	Galphimia brasiliensis		Castro *et al.* 2001
	Heteropterys chrysophylla		Vogel 1974
	Hiptage sericea		Subramanian *et al.* 1990
	Janusia guaranitica		Lorenzo 1981
	Malpighia spp.		Vogel 1974; Laskowsky & Bautista 1999
	Peixotoa reticulata		Possobom 2013
	Stigmaphyllon littorale		Vogel 1974
Solanales Solanaceae	*Nierembergia* spp.	MT - inside corolla tube and on the base of the anther filaments	Cocucci 1991
Zygophyllales Krameriaceae	*Krameria* spp.	PE - on the two modified petals	Vogel 1974; Simpson 1982

T = trichomal elaiophore; E = epithelial elaiophore (no differentiation was made by the author); UT = unicellular trichomes; MT = multicellular trichomes; CE = cuboid epithelial cells; PE = palisade-like epithelial cells.

and the tepals, while in the other two tribes they occur only on the tepals, generally on the inner ones (Goldblatt *et al.* 1998; Chaveau *et al.* 2011; 2012; Silvério *et al.* 2012; Fig. 1A). Trichomes on both inner and outer tepals occur in *Herbertia* species (Tigridieae) (Chaveau *et al.* 2012). Although most of these Iridoideae members have oil-producing trichomes, they are absent or are nectar-producing in some species (Chaveau *et al.* 2012).

Only one Old World representative of the Crocoideae subfamily seems to produce floral oil (Manning & Goldblatt 2002; see Tabs. 1, 2). Unlike the Iridoideae members, *Tritoniopsis parviflora* flowers are bilaterally symmetrical and, in addition to the septal nectary, have epithelial elaiophores located over the proximal parts of the perianth (Manning & Goldblatt 2002).

The first morphological description of the elaiophores in Iridaceae was made by Vogel (1974) in some *Cypella*, *Alophia*, *Ennealophus* (as *Sphenostigma*) and *Sisyrinchium* species (Tab. 2). In addition to that study, data on these

glands is restricted to other *Sisyrinchium* species (Cocucci & Vogel 2001; Chaveau *et al.* 2011; 2012; Silvério *et al.* 2012), *Tritoniopsis parviflora* (Manning & Goldblatt 2002) and very few species of the Trimezieae and Tigridieae (Chaveau *et al.* 2012) (Tab. 2). Most of these authors carried out superficial analyses using light microscopy and/or histochemical tests. Vogel (1974), Cocucci & Vogel (2001) and Manning & Goldblatt (2002) also provided data on pollination ecology.

The trichomes are unicellular, elongated and with a wide (capitate) apex (see Vogel 1974; Cocucci & Vogel 2001; Silvério *et al.* 2012). In most species a subcuticular space is formed at the apex of the trichome where the oil is accumulated before its release by cuticular rupture. When this space is absent, the oil apparently permeates the intact cuticle (see Vogel 1974; Cocucci & Vogel 2001). Among the taxa, differences seem to occur in the length, shape and curvature of the trichomes, as well as in the thickness of the cell walls and cuticle (see Vogel 1974; Cocucci & Vogel 2001; Chaveau *et al.* 2011; Silvério *et al.* 2012).
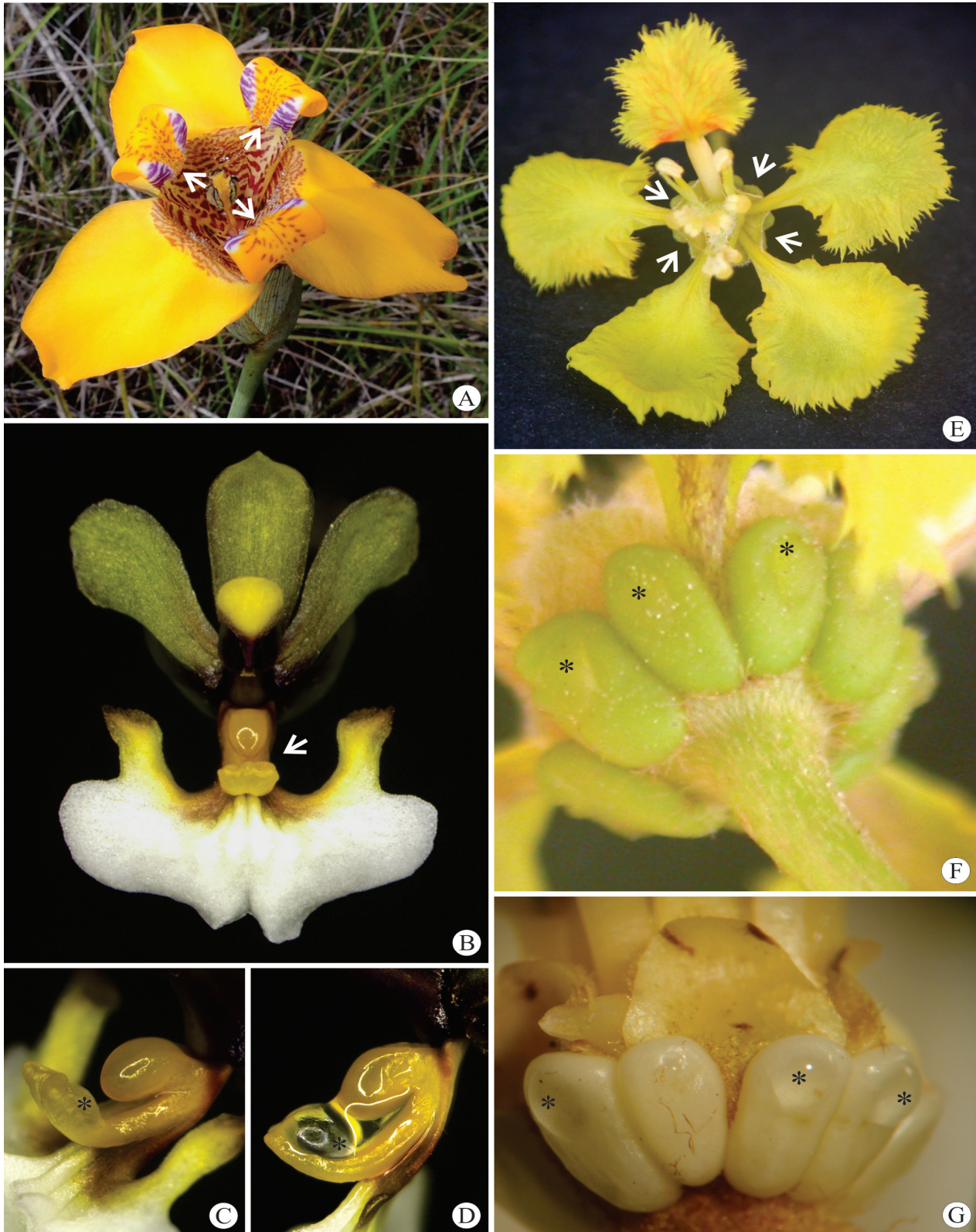
Figure 1. Location of the oil-secreting structures in flowers of the Iridaceae, Orchidaceae and Malpighiaceae species. **A**. *Trimezia* sp. (Iridaceae). Note the three inner tepals where the supposed oil-secreting trichomes occur (arrows). **B –D**. *Gomesa radicans* (syn. *Ornithophora radicans,* Orchidaceae). **B**. Note the conspicuous epithelial elaiophore on the callus (arrows). **C**. Prominent subcuticular space where the oil accumulates (*). **D**. Abundant secretion on elaiophores. **E-F**. *Diplopterys pubipetala* (Malpighiaceae). Note the paired epithelial elaiophores on the calyx (arrows). **G**. Epithelial elaiophores on the calyx of *Byrsonima coccolobifolia.* (*) indicates the hyaline secretion on the distal region of the glands. Photos (B-D): Sérgio Akira Adachi.

The epithelial elaiophores have not yet been investigated comprehensively. Manning & Goldblatt (2002) suggested the lipidic secretion covers the outer surface of the perianth tube and the basal part of the claws of all tepals. They also supposed the presence of epithelial elaiophores, since they did not observe trichomes in these flowers.

No data on cellular ultrastructure is available for elaiophores of the Iridaceae species.

Some information on the chemical nature of the oil from Iridaceae species was provided by Vogel (1974) and Simpson & Neff (1981). Free fatty acids and acylglycerols seem to be the main components of the oil.

Centridini (*Centris*) and Tapinotaspidini (*Chalepogenus, Lanthanomelissa, Paratetrapedia* and *Tapinotaspis*) bees seem to be the most frequent visitors of the New World Iridaceae (see Vogel 1974; Buchmann 1987; Cocucci & Vogel 2001; Alves-dos-Santos *et al.* 2007).These bees land on the perianth or on the column and flex to collect the oil from the trichomes, generally with their front legs, while they contact the reproductive parts with the ventral (sternotribic pollination) or dorsal (nototribic pollination) surfaces of their heads, thoraxes or abdomens (see Vogel 1974; Cocucci & Vogel 2001). The oil-collecting bee *Rediviva gigas* (Melittidae) has been observed visiting flowers of the African *T. parviflora* (Manning & Goldblatt 2002) but the authors do not provide any further detail about its behavior in relation to elaiophores.

Orchidaceae

Orchidaceae, one of the largest families of the angiosperms, is cosmopolitan and has 880 genera and 27800 species (Stevens 2001). The flowers can be deceptive or they can offer different resources for their pollinators such as nectar, fragrances, and oils (see Singer 2003). Pollinators include bees, wasps, hummingbirds, moths and flies (see Singer 2003).

According to Renner & Schaefer (2010) the family shows many more than 12 independent origins for oil flowers, most represent the youngest lineages to produce oil as a floral reward.

Oil-producing species seem to be restricted to a few subtribes of the Epidendroideae and the Orchidoideae (*sensu* Chase *et al.* 2015), including New World and African species (see Tab. 1). In such taxa, the oil glands occupy different positions on the flowers and they have no simple morphological pattern being of the epithelial and/or trichomal types (Tab. 2).

Most species bearing elaiophores, belong to the neotropical Oncidiinae, which includes 61 genera and 1600 species and a great diversity of pollination systems (Neubig *et al.* 2012; Tab. 1). The flowers of several species can either reward their pollinator with oil or mimic the Malpighiaceae oil flowers and perhaps also the Calceolariaceae ones (see Neubig *et al.* 2012). In this subtribe, the oil-secreting organs most often occur on the two lateral lobes of the labellum or on the callus (Neubig *et al.* 2012, Tab.2, Fig.1). In the South African Coryciinae, the oil is generally secreted from the tip of the labellum appendage (Waterman *et al.* 2009), while in *Huttonaea* (Disinae) there are generally multicellular verrucae in each of the two petal sacs which secrete oil (Steiner 2010). For other subtribes with oil-producing flowers there is little information or such as there it is restricted to just a few species (e.g. Brownleeinae, Catasetinae, Cranichidinae, Maxillariinae, Orchidinae; Tab.1).

Structural aspects of the elaiophores were first described by Vogel (1974) in *Zygostates* and *Oncidium* (including one *Sigmatostalix*) species (Tab. 2). Since then, about 50 species, almost all Oncidiinae members, have been studied in relation to the morphology, histochemistry and ultrastructure of their elaiophores (see Tab.2).

Trichomal elaiophores are generally constituted by a set of unicellular hairs which may occupy one or two distinct areas (Vogel 1974; Pacek & Stpiczyńska 2007; Pansarin *et al.* 2009; Pacek *et al.* 2012; Blanco *et al.* 2013; Gomiz *et al.* 2014). The trichomes can be either short (Pansarin *et al.* 2009; Pacek *et al.* 2012; Blanco *et al.* 2013) or elongated (Vogel 1974; Pacek & Stpiczyńska 2007; Pansarin *et al.* 2009; Pansarin & Pansarin 2011; Pacek *et al.*2012; Blanco *et al.* 2013; Gomiz *et al.* 2014). These unicellular trichomes have uniform width in most species but are capitate in *Phymatidium falcifolium* (Pacek *et al.* 2012). In *Lochartia* species they can be capitate, bifid or branched at the apex (Blanco *et al.* 2013).

The epithelial elaiophores are generally constituted by one layer of cuboid (Singer & Cocucci 1999; Pacek & Stpiczyńska 2007; Pacek *et al.* 2012; Gomiz *et al.* 2013; Davies *et al.* 2014) or palisade-like (Stpiczyńska *et al.* 2007, Stpiczyńska & Davies 2008; Davies & Stpiczyńska 2009; Gomiz *et al.* 2013; Stpiczyńska *et al.* 2013) epithelial cells which are covered by a cuticle. Sometimes the elaiophore presents a wrinkled surface as in *Oncidium cheirophorum* (Pacek & Stpiczyńska 2007). Below the secretory epithelium can have a few layers (1-3) of subepithelial parenchyma (Pacek & Stpiczyńska 2007; Stpiczyńska *et al.* 2007; Stpiczyńska & Davies 2008; Aliscioni *et al.* 2009; Davies & Stpiczyńska 2009; Pacek *et al.* 2012; Gomiz *et al.* 2013; Stpiczyńska *et al.* 2013) and also a ground vascularized parenchyma (Pacek & Stpiczyńska 2007; Aliscioni *et al.* 2009; Davies & Stpiczyńska 2009; Pacek *et al.* 2012; Stpiczyńska *et al.* 2013). In *Oncidium ornithorhynchum* the subepithelial parenchyma is unusual, since it shows well-developed intercellular spaces, where a flocculent material accumulates in the pre-secretory stage (Davies & Stpiczyńska 2009).

Most of species have well-defined epithelial elaiophores (Pacek & Stpiczyńska 2007; Stpiczyńska *et al.* 2007; Stpiczyńska & Davies 2008; Aliscioni *et al.* 2009; Davies & Stpiczyńska 2009; Pacek *et al.* 2012; Gomiz *et al.* 2013; Stpiczyńska *et al.* 2013) but some, such as *Gomesa recurva*

(Stpiczyńska *et al.* 2007) and *Cyrtochilum meirax* (Davies *et al.* 2014) have morphologically undifferentiated, constituted by oval or cuboid epithelial cells, lacking secretory features such as a dense and abundant cytoplasm.

Flowers of *Grobya amherstiae* represent an interesting example, since they have three types of oil-secreting structures, classified as elaiophores by researchers (Pansarin *et al.* 2009). According to these authors, the elaiophores are trichomal on the column base, epithelial but poorly differentiated on the internal surface of the labellum, and both epithelial and trichomal at the apex of the labellum. Considering that the secretion of the internal portion of the labellum is not collected by the pollinator *Paratetrapedia fervida* (Mickeliunas *et al.* 2006), the authors suggest such elaiophores act as a guide to the bees (Pansarin *et al.* 2009). It is important to emphasize that it is not possible to classify this structure as a true elaiophore, since the meaning of the term is not restricted just to secretion of oil but also to reward to pollinators.

As in *G. amherstiae* (Pansarin *et al.* 2009), other Orchidaceae species have oil-secreting areas on the labellum that are constituted by a glabrous epithelium besides papillose and/or elongated (trichome-like) cells. Such structures were interpreted as intermediate elaiophores and have been described in *Ornithocephalus gladiatus* (Pacek *et al.* 2012), *Gomesa flexuosa* (Gomiz *et al.* 2013), *Gomesa longipes*, *Vitekorchis excavata* and *Oncidium heteranthum* var. *album* (Davies *et al.* 2014).

Davies *et al.* (2014) characterized the appearance of the secretions of some species as "wax-like heterogeneous" (*G. longipes*), "wax-like" (*V. excavata*), "oil-like" (*O. heteranthum* var. *album*) and "oil-like, but more volatile" (*Cyrtochilum meirax*). These features associated with the absence of information about the visitor behavior, raise the question whether all of the oil-secreting structures they describe are truly elaiophores.

In most plant species the lipidic secretion accumulates beneath the cuticle before its release (Singer & Cocucci 1999; Pacek & Stpiczyńska 2007; Stpiczyńska *et al.* 2007; Stpiczyńska & Davies 2008; Pacek *et al.* 2012; Stpiczyńska *et al.* 2013). Generally the secretions are released after cuticle rupture, sometimes triggered only by floral visitors (Stpiczyńska *et al.* 2007; Stpiczyńska & Davies 2008; Pacek *et al.* 2012; Stpiczyńska *et al.* 2013). However, in some species the authors did not observe the detachment or disruption of the cuticle, suggesting that the secretion passes through the cell wall and cuticle (Aliscioni *et al.* 2009; Pansarin & Pansarin 2011; Davies *et al.* 2014).

The ultrastructural features of the secretory cells are very similar among species (Stpiczyńska *et al.* 2007; Stpiczyńska & Davies 2008; Aliscioni *et al.* 2009; Davies & Stpiczyńska 2009; Pacek *et al.* 2012; Blanco *et al.* 2013; Davies *et al.* 2014). In general, the secretory cells have central nuclei and dense cytoplasms with a predominance of endoplasmic reticulum, numerous mitochondria, plastids with plastoglobuli and lipid droplets. Vacuoles with myelin-like figures, plastids

with starch grains, dyctiosomes and vesicles near or in fusion with the plasmalena are also commonly described in the elaiophores of Orchidaceae species. In some species there are secretion-filled cavities on the outer periclinal cell wall which is covered by a lamellate and/or reticulate cuticle. In epithelial elaiophores, a dissolution of the middle lamella sometimes occurs between adjacent cells, and here the secreted material accumulates.

Information on floral oil composition is available for the following species: *Oncidium pubes* (Reis *et al.* 2000), *Gomesa radicans* (as *Ornithophora radicans*; Reis *et al.* 2003), *Phymatidium tillandsioides* and *P. delicatulum* (Reis *et al.* 2006). Acylglycerols, diacylglycerols or triacylglycerols predominate in the floral oil of several of these species.

The South American oil-producing orchids seem to be pollinated mainly by Centridini (*Centris*), Tapinotaspidini (*Lophopedia*, *Paratetrapedia*) and Tetrapediini (*Tetrapedia*) bees (Vogel 1974; Singer & Cocucci 1999; Mickeliunas *et al.* 2006; Pansarin & Pansarin 2011; Torretta *et al.* 2011; Tab. 1). Pacek *et al.* (2012) hypothesized that trichomal elaiophores may best suit smaller bees, such as the *Paratetrapedia* species, which collect the secretion with delicate movements, whereas the epithelial elaiophores may best suit larger bees, such as *Centris* species, which hold the tabula infrastigmatica with their mandibles while collecting the oil with their front or middle legs. During an oil-collection visit, the pollinarium can attach to the heads of *Centris* (Torreta *et al.* 2011) or Tetrapedia (Singer & Cocucci 1999) bees or to the dorsal surface of the thoraxes (scutellum) of *Paratetrapedia* bees (Mickeliunas *et al.* 2006).

The South African oil-producing species are pollinated by *Rediviva* (Melittidae) bees, which use their front legs to collect the oil from trichomal or epithelial elaiophores on the labellum appendages or from the verrucae on the petal sacs (Manning & Linder 1992; Whitehead & Steiner 1992; 1993; Pauw 2006; Whitehead *et al.* 2008; Steiner 2010; Tab. 1). The pollinarium of some of these Orchidaceae species can attach to the ventral surface of the abdomen, thorax or to several sites on the front, middle or hind legs of the *Rediviva* bees (Manning & Linder 1992; Pauw 2006; Steiner 2010).

Although studies of oil flowers in orchids remain scarce, data show in general that the elaiophores exhibit great diversity in terms of location, morphology and release mechanisms. Based on this diversity, Davies & Stpiczyńska (2009) postulated that the elaiophores probably evolved in response to pollinator pressures.

Cucurbitales

Cucurbitaceae

Cucurbitaceae is a tropical and subtropical family with 98 genera and 1000 species (Stevens 2001). The flowers are actinomorphic and generally unisexual and the species are monoecious or dioecious (Schaefer & Renner 2010; 2011).

Nectar, pollen and occasionally oil are the rewards for floral visitors (Nepi & Paccini 1994; Vogel 2009) which are mainly bees, but also bats, hawkmoths, flies and butterflies (see Schaefer & Renner 2011 and references therein).

Renner & Schaefer (2010) show that the floral oil evolved only once (57-42 myr) but was lost at least six times in this family. So far, oil flowers are known or suspected in six genera belonging to the Joliffieae grade (*sensu* Kocyan *et al*. 2007; Tab. 1) whose species predominate in the Old World: *Momordica*, *Thladiantha* (Vogel 1976b; 1981; 1988; 2009; Schaefer & Renner 2011), *Baijiania*, *Siraitia*, *Telfairia* (see Renner & Schaefer 2010; Schaefer & Renner 2011; Schaefer *et al*. 2012) and *Indofevillea* (Schaefer *et al*. 2012).

According to Vogel (1988) the male flowers of *Momordica* and *Thladiantha* produce nectar and oil, while the female flowers produce only oil, and in lower amounts than the male flowers (Vogel 1988). The oil-secreting trichomes form dense covers on the base of all five petals (*Thladiantha* and *Indofevillea*) or of 1-3 petals (*Momordica*) (Vogel 1988; Schaefer *et al*. 2012, Tab. 2).

In our survey we were unable to find detailed information on glandular trichome morphology, secretory processes and/or chemical analyses of the secretions. Some detailed information about elaiophore morphology of *Momordica* and *Thladiantha* species is likely provided by Vogel (1976b; 1990b) but we were unable to access these publications.

Ctenoplectra (Ctenoplectrini) bees are the main visitors of the oil-producing Cucurbitaceae species (Vogel 1981; 1988; Schaefer & Renner 2008; Sung *et al*. 2009, Tab.1). To collect the oil, these bees mop the surface of the elaiophore with their abdominal (metasomal) brushes (Vogel 1981; 1988). While they collect the oil from the male flowers, the pollen grains can stick to the dorsal surfaces of their bodies.

Ericales

Primulaceae

The Primulaceae is a cosmopolitan family with 58 genera and 2590 species (Stevens 2001). The flowers are actinomorphic, pollinated by bees or flies and they have nectar and pollen as the main rewards (Anderberg 2004; Stahl & Anderberg 2004).

Oil flowers also occur but are restricted to the *Lysimachia* (Tabs. 1, 2), a genus that includes approximately 180 morphologically diverse and widespread species most of which occur throughout the temperate and subtropical regions of the Northern Hemisphere (see Hao *et al*. 2004; Anderberg *et al*. 2007).

Since 1976 (Vogel 1976a) it is known that some *Lysimachia* species have glandular trichomes whose secretions are collected by bee species of the Holartic genus *Macropis* (Melittidae). Simpson *et al*. (1983) provided some data on the glandular trichomes of *Lysimachia* species, especially in the *L. ciliata*. In 1986, Vogel provided detailed structural and ultrastructural characterization of the secretory trichomes of

several *Lysimachia* species, as well as microchemical analyses of their secretions (see Buchmann 1987; Anderberg *et al*. 2007). He found oil-producing trichomes in 78 *Lysimachia* species (see Buchmann 1987).

The oil-producing trichomes are multicellular, capitate and located on the basal part of the petals or of the anther filaments (Vogel 1976a; Simpson *et al*. 1983, Tab.2). They comprise a stalk with one to three cells and a head with 8 or 16 cells (Simpson *et al*. 1983). The secretion is accumulated in the subcuticular space formed by the detachment of the cuticle from the outer periclinal cell wall (Simpson *et al*. 1983).

Among other components, fatty acids and diglycerides have already been detected in the floral oil from *Lysimachia* species (Simpson & Neff 1981; Cane *et al*. 1983; Simpson *et al*. 1983; Buchmann 1987).

Females of the oil-collecting *Macropis* (Melittidae) bees are the pollinators of the oil flowers of *Lysimachia* (Vogel 1976a, Tab. 1). Cane *et al*. (1983) provided the first evidence of the use of the floral oil of *L. ciliata* by *Macropis nuda* bees as a brood-cell lining, in addition to its role as larval provision. These bees landed on the androecium, curled around the anthers and mopped the glandular trichomes with their front and middle legs to collect the oil (Cane *et al*. 1983; Vogel 1986 *apud* Buchmann 1987; Vogel 1988). Pollen grains are collected sternotribically (Cane *et al*. 1983).

To understand how the *Macropis* bees find the *Lysimachia* plants, Dötterl & Schäffler (2007) analyzed the scents emitted by the green parts, flowers, and pure oil of *L. punctata*. These authors found evidence that the aromatic compounds detected in the oil and in the flowers may be responsible for the attraction of the oil-collecting bee *M. fulvipes*. Schäffler *et al*. (2012) showed that the floral scents of *Lysimachia* oil-producing species has lower variability than the non-oil species and they also found a correlation between the yellow flowers (bee-green) and oil secretion. Thus, such authors also provide evidence that floral scents and colors of *Lysimachia* species are under selection by *Macropis* bees.

Lamiales

Calceolariaceae

Calceolariaceae comprises two genera, *Calceolaria* and *Jovellana*, and 260 species (Stevens 2001). *Calceolaria* species are restricted to the Andes region while *Jovellana* species (six spp.) occur in Chile and New Zealand (Andersson 2006). In this family, the melittophily is predominant, with pollen or oil as floral rewards (Molau 1988; Sérsic 2004).

Oil is restricted to *Calceolaria* (see Tabs. 1, 2) which, according to Renner & Schaefer (2010), is one of the youngest lineages to offer this floral resource with at least six independent losses of this character. The flowers of the *Calceolaria* species have a bilabiate and generally yellow

corolla, most of them with a set of oil-producing trichomes on the edge of the abaxial surface, facing the inside of the saccate lower lip (Vogel 1974; Molau 1988; Andersson 2006; Mayr & Weber 2006; Cosacov *et al*. 2009). According to Sérsic (2004) approximately 18 % (≈ 49 spp.) of the *Calceolaria* species lack oil glands.

The most comprehensive study of the floral biology and pollination of the *Calceolaria* species was carried out by Sérsic (2004). Information on the structure, ultrastructure, and chemical compositions of the secretions and on the elaiophores visitors of the *Calceolaria* species was also provided by Vogel (1974), in addition to Sérsic (2004).

The elaiophores may vary in terms of location, size, shape, trichome density and cell number (Vogel 1974; Sérsic 2004). In general, the trichomes are multicellular and comprise a stalk and a glandular head. The stalk is uniseriate and has from one to eight highly-vacuolated cells with chloroplasts. The apical cell of the stalk, the neck cell, has a cutinized cell wall. The head is formed by four to 35 radially-distributed cells with small vacuoles and dense and abundant cytoplasms (Vogel 1974; Sérsic 2004). The secretion accumulates beneath the cuticle, where generally no pores are visible (Sérsic 2004).

According to Schnepf (1969), the secretory cells have dense cytoplasm with numerous poorly differentiated leucoplasts generally enveloped by cisternae of the endoplasmic reticulum, in addition to dictyosomes that predominate in younger stages.

Vogel (1974) found diacylglycerol of acetic acid and β-acetoxy palmitic acid as the main compounds of the oil of *Calceolaria pavonii*, besides non-volatile isoprenoid compounds and some trisaccharides. Using thin-layer chromatography, Sérsic (2004) and Cosacov *et al*. (2012) show that the floral oils are mixtures of different lipid fractions, but the compounds were not identified.

Centridini (*Centris*) and Tapinotaspidini (*Chalepogenus*, *Tapinotaspis*) bees are the main visitors of the *Calceolaria* species (Vogel 1974; Rasmussen & Olesen 2000; Sérsic 2004; Cosacov *et al*. 2012; 2014; Murúa *et al*. 2014, Tab 1). The oil is generally collected with the front legs and it is transferred to the hind legs during flight (Sérsic 2004).

There are different flower morphotypes according to the visitor for *Chalepogenus* (Tapinotaspidini) or *Centris* (Centridini) bees (Molau 1988; Sérsic 2004). A Tapinotaspidini flower normally has a small hooded upper lip, short stamens and a flattened lower lip that functions as a landing surface for the small *Chalepogenus* bees (Molau 1988; Sérsic 2004). The opening of this flower is small, the elaiophores are easily accessible and the pollination is always nototribic (Molau 1988; Sérsic 2004). The Centridini flowers can be open (wide opening) or closed and they generally have an inflated and non-flattened lower lip. The pollination is nototribic in open flowers and can be nototribic or sternotribic in closed flowers (Molau 1988; Sérsic 2004).

Plantaginaceae

The Plantaginaceae is a cosmopolitan family predominant in temperate regions with approximately 90 genera and 1900 species (Stevens 2001). The flowers are zygomorphic, morphologically diverse and can be pollinated by abiotic (wind, water) or biotic vectors (bees, flies or birds) which are attracted mainly to nectar or, sometimes, to oil (Kampny 1995; Stevens 2001; Albach *et al*. 2005).

Oil as reward is almost restricted to the neotropical Angelonieae tribe (Tab. 1), which comprises four genera with oil flowers (*Angelonia*, *Basistemon*, *Monopera* and *Monttea*) and two genera that lack that reward (*Melosperma* and *Ourisia*) (see Martins & Alves-dos-Santos 2013; Martins *et al*. 2014). The flowers of the *Monttea* species also have nectar-secreting tissue at the base of the ovary (Sérsic & Cocucci 1999), sometimes with no detectable nectar (Simpson *et al*. 1990; Tadey 2011). In addition, oil-producing flowers are also recorded in one Gratioleae species, *Mecardonia tenella*, but no information is available regarding interaction with oil-collecting bees (Cappellari *et al*. 2009, Tab. 1).

In contrast with the findings of Renner & Schaefer (2010) that point out one independent origin of oil flowers in Plantaginaceae, Martins *et al*. (2014) found that the oil-producing condition evolved four or five times within the Angelonieae.

Martins & Alves-dos-Santos (2013) present a consistent review containing information on geographical distribution, flower morphology and oil-collecting bees of oil-producing Angelonieae species. In general, the oil flowers are purple or white, gamopetalous and have a set of oil-secreting trichomes located on the inner side of one (*Monopera*) or two (*Angelonia*, *Monttea* and *Basistemon*) more-or-less defined corolla sacs (see Martins & Alves-dos-Santos 2013).

Vogel (1974) provided the first record of the morphology of the secretory trichomes in *Angelonia* species, especially in *A. angustifolia* (Tab. 2). After this, some superficial information has appeared in the work of Simpson *et al*. (1990), Vogel & Machado (1991) and Sérsic & Cocucci (1999) (Tab. 2). In general the secretory trichomes are constituted by a multicellular stalk and a digitate or capitate multicellular head. They vary in relation to the morphology, head and stalk cell number, positioning and density.

Information on subcellular features of these secretory trichomes could not be found.

Based on thin-layer chromatography, Vogel &Machado (1991) concluded that the oil from four *Angelonia* species consists of mono and/or diglycerides of monohydroxy fatty acids similar to that observed by Vogel (1974).

Centridini (*Centris*) bees are the main visitors observed in most of the oil flowers of the Plantaginaceae species, but Tapinotaspidini (*Arhysoceble*, *Caenomanda*, *Chalepogenus*, *Lophopedia*, *Paratetrapedia*, *Tapinotaspis*) and Tetrapediini (*Tetrapedia*) bees have also been recorded (Vogel 1974; Simpson *et al*. 1990; Vogel & Machado

1991; Sérsic & Cocucci 1999; Machado *et al.* 2002; Tadey 2011; Martins *et al.* 2013; Ferreiro *et al.* 2015). In general, the bees land on the flowers and insert their front legs into the floral sacs simultaneously to gather the oil, meanwhile they contact the reproductive parts, generally with their heads or with the dorsal surfaces of their thoraxes (Vogel 1974; Simpson *et al.* 1990; Vogel & Machado 1991; Machado *et al.* 2002; Martins *et al.* 2013).

Scrophulariaceae

The Scrophulariaceae *sensu stricto* is a family with approximately 59 genera and 1880 species, which occur predominantly in the southern hemisphere, particularly in Africa (Olmstead *et al.* 2001; Stevens 2001). Bees, butterflies, hawkmoths, moths and birds can pollinate the flowers that offer nectar, pollen and sometimes oil as reward (Kampny 1995; Fischer 2004).

In this family, oil flowers are restricted to the small Hemimeridae tribe (≈170 spp.), which is constituted by one South American or South African (*Alonsoa*) and five exclusively African genera (*Colpias, Diascia, Diclis, Hemimeris, Nemesia*) (Steiner 1996; Olmstead *et al.* 2001; Oxelman *et al.* 2005; Tank *et al.* 2006). Renner & Schaefer (2010) indicated four independent origins of the oil flowers in the African Scrophulariaceae.

Flowers of some African species of *Alonsoa, Colpias, Diascia* and *Hemimeris* have oil-secreting trichomes inside and/or around the entrances of the shallow or deep sacs or spurs located at the lower or upper side of the corolla generally at the base of the lateral lobes (Vogel 1974; 1984; Steiner 1989; 1990; 1996; 1999; 2009; Simpson *et al.* 1990; Kampny 1995; Olmstead *et al.* 2001; Steiner & Whitehead 2002; Fischer 2004; Pauw 2005; Dumri *et al.* 2008; Tabs. 1, 2).

Diascia barbera was the first Scrophulariaceae s.s. species studied by Vogel (1974). Thereafter, elaiophores have been described, at least superficially, in some species of *Alonsoa* (Steiner 1989) *Colpias* (Steiner & Whitehead 2002), *Hemimeris* (Pauw 2005) and in other species of *Diascia* (Vogel 1974; 1984). There is some diversity in the density, number and distribution of the trichomes. In general, the multicellular trichomes are short-stalked (1-2 cells) and have a spherical secretory head covered by a cuticle. The secretory head may present two or three cells in *Alonsoa unilabiata* (Steiner 1989) to several cells in *Hemimeris, Colpias* and *Diascia* species (Vogel 1974; 1984; Steiner & Whitehead 2002; Pauw 2005).

Some reports indicate the release of droplets of the secretion through the cuticle or the release of the oil only after cuticle rupture (Vogel 1974; 1984; Steiner & Whitehead 2002). In addition to this, there is no detailed information on the secretory processes, nor on the ultrastructural aspects of the secretory cells.

Information on the chemical composition of the floral oils is provided by Dumri *et al.* (2008) for six *Diascia* species.

According to these authors, partially acetylated acylglycerols of (3R)-acetoxy fatty acids are the most common compounds.

Several *Diascia* species have translucent, UV-absorbing, yellow-dotted depressions at the base of the upper corolla lobe termed "windows", which show great morphological diversity among species (see Steiner 1990; Kampny 1995). Steiner (1990) described this variation in the windows of several *Diascia* and suggested their function in terms of the orientation of the pollinators.

In 1984, Vogel assumed that the oil-collecting *Rediviva* bees were the effective pollinators of the *Diascia* species. After that, other authors have reported female bees of this genus as the main visitors to *Alonsoa* (Steiner 1989; Kuhlmann & Hollens 2015), *Colpias* (Steiner & Whitehead 2002; Kuhlmann & Hollens 2015), *Hemimeris* (Steiner 1989; Pauw 2005; Kuhlmann & Hollens 2015), besides several other *Diascia* species (Vogel 1984; Steiner 1989; 1990; 2009; Steiner & Whitehead 1990; 1991; Whitehead & Steiner 1992; Whitehead *et al.* 2008; Kuhlmann & Hollens 2015) (see Tab. 1). In general, these bees place their heads at the base of the upper corolla lobe ("window") and at the same time introduce both their front legs, which have specially modified setae, into the sacs or spurs to collect oil from the elaiophores. The pollen grains are generally deposited on the ventral surface of the bee's body (sternotribic pollination) (Vogel 1984; Steiner 1989; 1990; 2009; Pauw 2005), but also on the dorsal surface of the body (nototribic pollination), on the head or thorax (Steiner & Whitehead 2002).

Some researchers observed that there is species-specific variation in the length of the front legs of the *Rediviva* bees and the spurs of the *Diascia* flowers, suggesting co-evolution between these groups (Vogel 1984; Steiner & Whitehead 1990; 1991). In addition, according to Kuhlmann & Hollens (2015) there is a relation between the type of tarsal pilosity and the availability of floral oil and elaiophore morphology, also suggesting a convergent evolution.

Stilbaceae

The Stilbaceae is a small family with 11 genera and 39 species which occurs primarily in South Africa (Stevens 2001). Its current circumscription is the result of several studies that have included taxa previously placed in other families (see Rourke 2000; Olmstead *et al.* 2001, Oxelman *et al.* 2005). There are few reports on the pollination biology of this family but it is known that *Retzia* species are bird pollinated and some species from *Anastrabe, Bowkeria* and *Ixianthus* are bee pollinated (Steiner 1993; Kampny 1995; Linder 2004). The floral rewards are pollen, nectar and/or oil (Steiner 1993; Kampny 1995; Linder 2004).

According to Renner & Schaefer (2010), the oil flowers have arisen only once in this family. Oil-secretion is known in *Anastrabe* (Whitehead & Steiner 1992), *Bowkeria* (Vogel 1974; Steiner & Whitehead 1990; 1991; Whitehead & Steiner 1992) and *Ixianthus* (Steiner 1993; Steiner &

Whitehead 1996), all belonging to the Bowkerieae tribe that was previously place in the Scrophulariaceae (see Barringer 1993; Oxelman *et al*. 2005; Tank *et al*. 2006; Tab.1). According Barringer (1993) the flowers of these genera have a campanulate to funnelform corolla with a conspicuous sac or pouch in the distal half of the tube.

The first and only record on the elaiophore morphology in this family was made by Vogel (1974) in *Bowkeria verticillata* (Tab. 2). According to him, the trichomal elaiophore occurs on the lower inner surface of the corolla sac. The multicellular trichomes are formed by a head with 18-22 cells and a one-two celled stalk. The secretions accumulate under the cuticle, but there is no information about their release.

Information on subcellular features and the chemical nature of the secretions was not able to be found.

Rediviva bees have been observed collecting oil from the elaiophores of a few species of *Anastrabe* (Whitehead & Steiner 1992), *Bowkeria* (Steiner & Whitehead 1991; Whitehead & Steiner 1992) and *Ixianthes* (Steiner & Whitehead 1996) (Tab. 1). According to Steiner & Whitehead (1996) the bees collect the oil with their front and middle legs, while they contact the reproductive parts of the flowers with the dorsal surfaces of their bodies.

Malpighiales

Malpighiaceae

The Malpighiaceae comprises 77 genera and 1300 species distributed in tropical and subtropical regions, with clear predominance (85 %) in the New World (Anderson 1990; Davis & Anderson 2010). Oil-collecting bees are the main pollinators of the Malpighiaceae flowers, but pollen-collecting bees and wasps are also recorded as floral visitors (Anderson 1979).

This family represents the oldest and the most important clade that offers floral oil as a reward (Vogel 1974; Renner & Schaefer 2010). The oil is secreted by glands located on the abaxial sides of the sepals in most neotropical Malpighiaceae species (Vogel 1974).

The flowers of the New World members are morphologically very uniform and this fact seems to be related to the attraction, orientation and reward of the specific pollinators. (Anderson 1979). In general they are bilaterally symmetrical, have a pair of glands in four or in all five sepals, five free and clawed petals with the posterior one differentiated from the others, ten stamens and a tricarpellate gynoecium (Anderson 1979; Fig. 1D-F). In turn, the flowers of the approximately 150 Old World members can display a diverse array of morphologies, generally lacking the characteristic bilateral symmetry and the sepal glands (Davis & Anderson 2010). Most of these species have actinomorphic or zygomorphic flowers but in the latter case with two posterior petals (Zhang *et al*. 2010; Davis *et al*. 2014).

Many morphological and molecular evidences indicate that this family appeared in the New World (Taylor & Crepet 1987; Anderson 1979; 1990; Davis *et al*. 2001; Davis *et al*. 2002; Davis *et al*. 2004; Davis & Anderson 2010) and reach the Old World nine times (Davis & Anderson 2010). Davis & Anderson (2010) show that the Old World clades are more closely related to New World ones, than to one another. Based on this and other evidences, several authors have suggested the floral conservatism is result of the stabilizing selection imposed by the specialized oil bees, which are neotropical endemics (Anderson 1979; Davis & Anderson 2010; Davis *et al*. 2014).

Despite the large numbers of representatives with oil flowers (Tab. 1) and the importance of the oil in the evolutionary process of this plant group, few species were studied in relation to the morphological and functional aspects of the elaiophores (Tab. 2).

Vogel (1974) was the first to demonstrate that the sepal glands are oil-secreting rather than nectar-secreting as previously believed. In this publication he provided some data on the morphology of the elaiophores of *Malpighia glabra*, *Heteropterys chrysophylla* and *Stigmaphyllon littorale*, among other neotropical species and the paleotropical species *Hiptage benghalensis* and *Acridocarpus smeathmannii* he treated more superficially.

The sepal glands are synapomorphic for the family, their absence being considered a derived feature (Vogel 1974; 1990a; Anderson 1979; 1990). They occur in 90 % of the neotropical species in which they are related with oil secretion (Vogel 1974; 1990a; Anderson 1979; 1990). In contrast, such glands are present in few paleotropical species all belonging to the genera *Hiptage*, *Tristellateia*, *Rhinopterys* and *Acridocarpus* (Vogel 1990a). In these species, the glands are smaller, intersepalics and seems to be related with extrafloral nectar secretion, the pollen being the only reward to the pollinators (Vogel 1974; 1990a). Nevertheless, there is a report suggesting lipophilic secretions by the sepal glands of a paleotropical species, *Hiptage sericea* (Subramanian *et al*. 1990).

In neotropical Malpighiaceae the presence and number of elaiophores per flower can vary among genera, species, populations, individuals or even flowers. These glands are completely absent in all the species of the *Coleostachys*, *Echinopterys*, *Lasiocarpus*, *Ptilochaeta* and *Thryallis* (Anderson 1979), but may also be absent in some species of the *Banisteriopsis*, *Galphimia*, *Heteropterys* and *Tetrapterys* (Buchmann 1987). Most of the *Byrsonima* species have ten glands per flower but there are species totally eglandular (Anderson 1981; 2001) or with both glandular or eglandular flowers in different individuals (Teixeira & Machado 2000). In other genera, for example in the *Banisteriopsis* (Gates 1982) and *Peixotoa* (Anderson 1982), the species have typically eight glands per flower. *Banisteriopsis muricata* (Gates 1982; Sazima & Sazima 1989), *Heteropterys aceroides* (Sazima & Sazima 1989) and *Pterandra pyroidea* (Cappellari

et al. 2011) have individuals with glandular and eglandular flowers in the same or in different populations. *Banisteriopsis variabilis* (Possobom 2013) *Diplopterys pubipetala* (Possobom *et al.* 2015), *Galphimia brasiliensis* (Castro *et al.* 2001), *Heteropterys alternifolia* (Costa *et al.* 2006) and *Stigmaphyllon paralias* (Carvalho *et al.* 2005; Costa *et al.* 2006) have different numbers of elaiophores per flower in the same individuals.

Vogel (1990a) hypothesized that the absence or reduction of the number of glands in some species may represent a way of saving energy resources. Carvalho *et al.* (2005), in turn, verified that there is a compensation in the use of energy resources and not economy, since the production of oil in *Stigmaphyllon paralias* is similar in flowers with eight or ten glands.

Externally, the sepal glands are morphologically very similar among most species, being oval and sessile or short-stalked (see Vogel 1974; Subramanian *et al.* 1990; Mamede 1993; Laskowski & Bautista 1999; Castro *et al.* 2001; Possobom 2013; Possobom *et al.* 2015; Araújo & Meira 2016). Long-stalked elaiophores occur only in *Dinemagonum*, *Dinemandra*, *Heladena* and *Henleophytum* species (Simpson 1989; Cocucci *et al.* 1996).

The elaiophores of the neotropical Malpighiaceae species are of the epithelial type, since they are constituted by one layer of secretory palisade-like epithelial cells covered by a generally thick cuticle and subtended by a parenchyma with vascular bundles, which gradually merges with the sepal parenchyma (see Vogel 1974; Lorenzo 1981; Mamede 1993; Laskowski & Bautista 1999; Castro *et al.* 2001; Cocucci *et al.* 1996; Castro *et al.* 2001; Possobom 2013; Possobom *et al.* 2015; Araújo & Meira 2016; Tab. 2, Fig. 2A-D). The paleotropical *Hiptage sericea* has morphologically similar sepal glands (Subramanian *et al.* 1990). They vary mainly in relation to the epithelium, which can be flat (see Vogel 1974; Lorenzo 1981; Mamede 1993; Cocucci *et al.* 1996; Laskowski & Bautista 1999; Castro *et al.* 2001; Possobom 2013; Possobom *et al.* 2015; Fig. 2B, C) or convoluted (Vogel 1974; Subramanian *et al.* 1990; Possobom 2013; Araújo & Meira 2016; Fig. 2D). The epithelial cells can be more or less elongated and they can remain or not juxtaposed at maturity (Possobom 2013; Fig. 2B-D). Vogel (1974) postulated that the presence of a convoluted epithelium could increase the secretory surface and consequently the amount of secretion.

Another common feature is the accumulation of the secretion inside the subcuticular space (Fig. 1E-G, 2A) before anthesis and the subsequently release through the rupture of the cuticle (Vogel 1974; Subramanian *et al.* 1990; Cocucci *et al.* 1996; Castro *et al.* 2001; Possobom 2013; Possobom *et al.* 2015) which can be natural through predetermined regions ("pores") or due to the mechanical action exerted mainly by the visitors.

Ultrastructural aspects of these glands were provided by Castro *et al.* (2001), Possobom (2013) and Possobom *et al.* (2015). The epithelial secretory cells generally have conspicuous nuclei, dense cytoplasms with extensive endoplasmic reticula, numerous plastids with lipidic inclusions, mitochondria and lipid droplets (Fig. 2E-I). In addition, the presence of dictyosomes, membranous structures within the vacuole or in the periplasmic spaces and vesicles near or incorporated within the plasma membrane are also common ultrastructural features.

Information on the chemical nature of the secretions can be found in Vogel (1974), Simpson & Neff (1981), Simpson (1989), Lobreau-Callen (1989), Subramanian *et al.* (1990), Vinson *et al.* (1997), Seipold *et al.* (2004), Reis *et al.* (2007) and Cappellari *et al.* (2011). Fatty acids are the main components of the oil, but mono-, di- or triglycerides are also common (Simpson 1989; Vinson *et al.* 1997; Seipold *et al.* 2004; Reis *et al.* 2007; Cappellari *et al.* 2011). In some neotropical species, the floral oils also contain traces of carbohydrates (Lobreau-Callen 1989; Vinson *et al.* 1997; Castro *et al.* 2001; Possobom 2013.) characterizing a mixed secretion, which contains lipophilic and hydrophilic compounds. In the few paleotropical species studied, the secretions of the sepal glands can contain carbohydrates (Vogel 1974; Lobreau-Callen 1989) and also fatty acids, sitosterols and triglycerides (triolein) (Subramanian *et al.* 1990).

In their study on the chemical nature of the *Malpighia coccigera*, Seipold *et al.* (2004) hypothesized the origin of the floral oils from the modification of the route or of the enzymes involved in the biosynthesis of epicuticular waxes. According to these authors, such modifications could have produced substances suited to transfer through the plasma membrane and cell wall, but which would likely be deposited under the cuticle. They thus infer that convergence in the evolution of oil-producing flowers in several families may have been driven not only by pollinators but also by biochemical factors.

Centridini (*Centris*, *Epicharis*) bees are the most frequent oil-collecting visitors of the neotropical Malpighiaceae species, but Tetrapediini (*Tetrapedia*) and Tapinotaspidini (*Monoeca*, *Paratetrapedia*) are also very common (Vogel 1974; Steiner 1985a; Sazima & Sazima 1989; Simpson 1989; Barros 1992; Teixeira & Machado 2000; Sigrist & Sazima 2004; Carvalho *et al.* 2005; Benezar & Pessoni 2006; Costa *et al.* 2006; Oliveira *et al.* 2007; Vilhena & Augusto 2007; Ribeiro *et al.* 2008; Bezerra *et al.* 2009; Dunley *et al.* 2009; Amorim & Marco 2011; Mendes *et al.* 2011; Possobom 2013; Sazan *et al.* 2013; Possobom *et al.* 2015).

In general, the effective pollinators of the neotropical species often hold the claw of the posterior petal with their mandibles and insert their front and middle legs between the petal claws to reach and gather oil from the glands on the sepals. In this way, they contact the floral reproductive organs with the ventral surfaces of their bodies. After collection, the oil is stored on the hind legs. Some *Paratetrapedia* and *Tetrapedia* species are referred as 'oil robbers' and not as effective pollinators, since they generally land directly on the calyx for oil collection (Barros 1992;
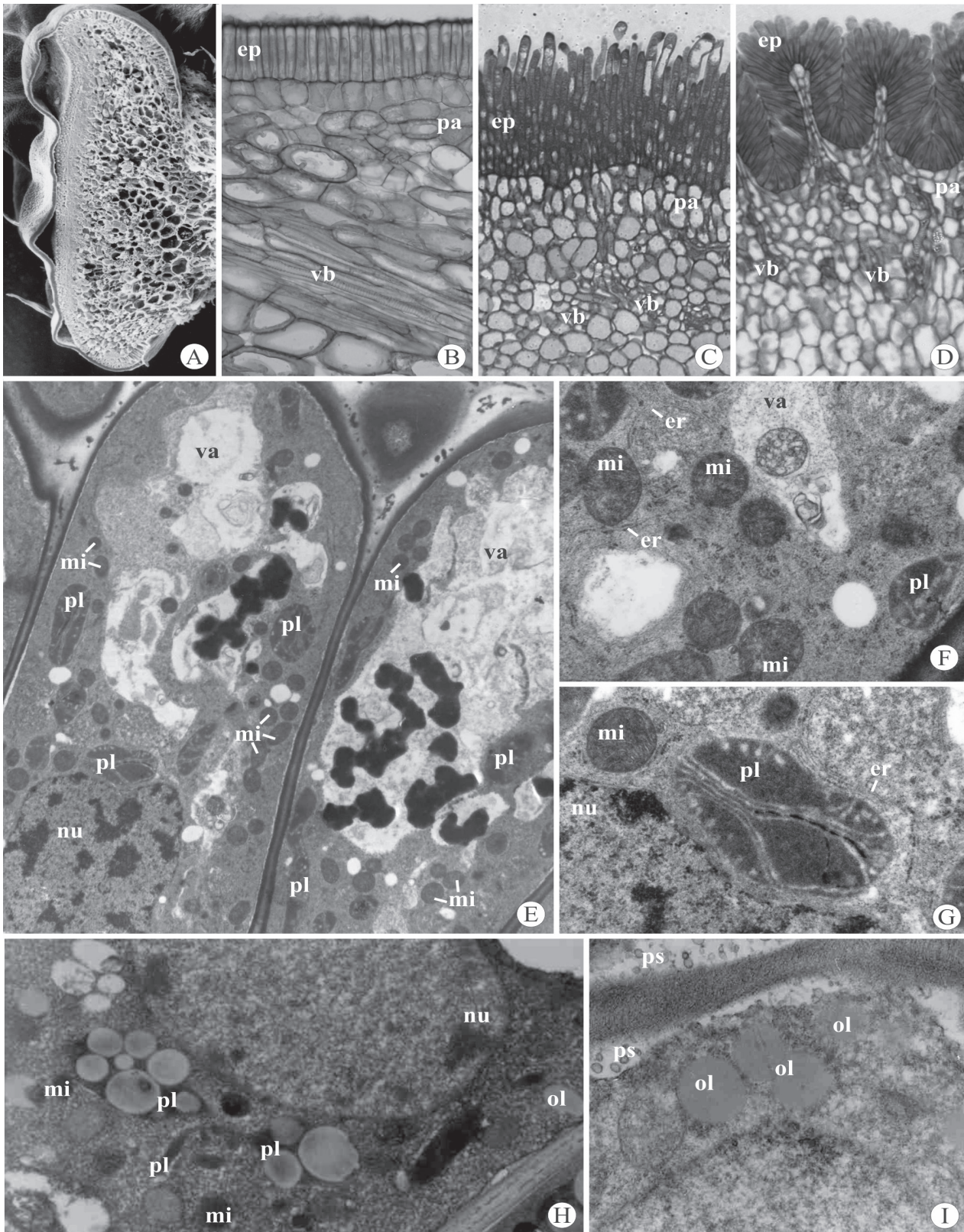
Figure 2. Structural and ultrastructural aspects of the epithelial elaiophores in Malpighiaceae species. **A**, **H**, **I**. *Byrsonima intermedia*. **B**, **E**, **F**, **G**. *Diplopterys pubipetala*. **C**. *Peixotoa reticulata*. **D**. *Banisteriopsis variabilis*. **A**. Scanning electron micrograph showing a longitudinal section. Note the wide subcuticular space. **B-D**. Light micrographs showing the structure of the elaiophores. Note central nuclei (nu), dense cytoplasm with ribossomes, vacuoles with variable content (va), plastids (pl), mitochondria (mi), endoplasmic reticulum (er), oil drops (ol) and periplasmic space (ps).

Teixeira & Machado 2000; Sigrist & Sazima 2004; Vilhena & Augusto 2007; Mendes *et al*. 2011; Possobom 2013).

In our previous studies, we suggest there are, in addition to the morphological cues, other features that can be related to the attraction and orientation of pollinators (Possobom 2013; Possobom *et al*. 2015). In some Malpighiaceae species, we studied the small glands located on the petal margins, mainly on the basal portion. These glands were interpreted by us as osmophores and their location near the petal claws indicate they can play an important role in bee attraction and also in precise positioning for collecting oil from the elaiophores. Despite this record, there is no experimental information showing how the bees are attracted to Malpighiaceae oil flowers.

Reis *et al*. (2007) isolated two new fatty acid derivatives (Tetrapedic acids A and B) from the nest of *Tetrapedia diversipes* bees and a new fatty acid derivative from the floral oil of *Byrsonima intermedia* (Byrsonic acid) which resembles the Oncidinol found in the floral oil of several Oncidiinae species (Orchidaceae). As these compounds (Byrsonic acid, Oncidinol, Tetrapedic acids) share similar chemical structures, the authors suggest the bees manipulate the floral oil collected from either Malpighiaceae or Orchidaceae species and, further, that the Tetrapedic acids (A and B) may be products of biotransformation by hydrolases secreted by the female's mandibles. Thus, these authors expand our understanding of how oil-collecting bees use floral oils and they also raise the possibility of chemical mimicry between some Malpighiaceae and Orchidaceae species, in addition to the well known morphological similarities.

Solanales

Solanaceae

The Solanaceae is a cosmopolitan family that includes 102 genera and 2460 species (Stevens 2001). They exhibit great diversity in terms of floral morphology and pollinator syndromes (see Knapp 2010). Their pollinators include bats, bees, butterflies, hummingbirds and moths, which forage for pollen, nectar and sometimes for oil (see Knapp 2010).

Oil flowers occurs in most of the species of *Nierembergia* (Tab. 1), for which this feature is considered a synapomorphy (Tate *et al*. 2009). Simpson & Neff (1981) provide the first report of oil production in *Nierembergia gracilis*. Cocucci (1991) carried out morphological and chemical analyses with several species of the *Nierembergia*, including observations on pollinator behavior.

In general, the *Nierembergia* species have a set of trichomal elaiophores located inside the corolla tube, forming a ring on the surface of the limb and/or on the base of the filaments (Simpson & Neff 1981; Cocucci 1991). These oil-secreting trichomes are multicellular and they are constituted by a stalk with 1-2 cells (4 cells on the filaments) and a wider head with one cell apically compressed (Cocucci

1991). The oil accumulates under the cuticle and after its release by cuticle rupture it remains between the hairs and the papillose epithelial cells of the corolla limb (Cocucci 1991).

In this family, we could not find information on the subcellular characteristics of the elaiophores.

According to Simpson & Neff (1981) the oil from *Nierembergia* flowers is constituted mainly by β-acetoxy fatty acids but also other types of lipids and phenolic compounds.

The oil can be collected with the front or the middle legs by the oil-colleting bees of Centridini (*Centris*) and Tapinotaspidini (*Chalepogenus*, *Lanthanomelissa*, *Paratetrapedia*, *Tapinotaspis*) (Cocucci 1991; Cosacov *et al*. 2008; Nattero *et al*. 2010). Most of these bees touch the fertile parts while collecting oils and the pollination may be nototribic or sternotribic (Cocucci 1991).

Zygophyllales

Krawmeriaceae

Krameria is the only genus of this family and its 18 species can occur in warm arid and semiarid areas of America, with one of them in the West Indies (Simpson & Saliwon 1999; Stevens 2001; Simpson *et al*. 2004; Simpson 2007).

The *Krameria* flowers are zygomorphic and consist generally of five conspicuous and colored sepals and five reduced petals, the lower two modified into scale-like glands, one on either side of the ovary (Simpson & Saliwon 1999; Simpson *et al*. 2004; Simpson 2007). Since 1758, such glands have been described as nectaries (see Simpson 1982). In 1974, Vogel predicted that these structures were elaiophores.

According to Renner & Schaefer (2010), the oil-producing condition has arisen only once in Krameriaceae and apparently it is also the only family which did not lose this condition in any lineage. According to Simpson *et al*. (2004) there are two major clades within Krameriaceae, one with rugose elaiophores and the other with elaiophores restricted to the distal portion or with striate secretory surfaces.

Morphological aspects of the elaiophores from *Krameria* species were reported by Vogel (1974) and Simpson (1982). In general they are constituted by one layer of more or less elongated epithelial cells covered by a cuticle and a subtending parenchyma (Vogel 1974; Simpson 1982). The secretory epithelium may occupy the entire surface or only the distal portion of the modified petals and it may be flat or undulate depending on the species (Simpson 1982). The secretions accumulate under the cuticle and may be released by pores (Vogel 1974) or after cuticle rupture by an oil-collecting bee (Simpson *et al*. 1977; Simpson & Neff 1981; Simpson 1982).

Some ultrastructural features of the secretory cells are provided by Simpson and Johnson (see Simpson & Neff

1981). According to these authors the cells have a dense cytoplasm and contain abundant leucoplasts, endoplasmatic reticulum with formation of vesicles and lipid droplets. They did not observe large lipid accumulations within the cell, concluding that the oil is transported as soon as it is synthesized.

The chemical nature of the oil was investigated in some *Krameria* species by Simpson and collaborators (Simpson *et al*. 1977; 1979; Seigler *et al*. 1978; Simpson & Neff 1981). According to these authors, the oil is constituted mainly by β-acetate substituted free fatty acids.

Centris bees are considered the most frequent visitors of *Krameria* flowers (Simpson *et al* 1977; Simpson & Neff 1981; Gimenes & Lobão 2006; Carneiro *et al*. 2015; Tab. 1). Female bees collect the oil from the elaiophores with their pairs of front and middle legs and after they transfer it to their hind legs (Simpson *et al* 1977; Simpson & Neff 1981; Gimenes & Lobão 2006; Carneiro *et al*. 2015). While collecting the oil, these bees often contact the reproductive structures, being considered effective pollinators (Simpson *et al* 1977; Gimenes & Lobão 2006; Carneiro *et al*. 2015).

Considerations

The classification of a secretory structure as an elaiophore depends on an integrated analysis involving morphological, chemical (or histochemical) and ecological aspects. The analysis of only one of these criteria can create an inaccurate, over or underestimate of occurrence.

So far, elaiophores are reported in approximately 100 plant genera, belonging to 11 families and seven orders (Tab. 1). Together, these genera total about 3000 species but it is likely only a little more than half of them actually really bear elaiophores. A reliable number for the oil-producing species remains difficult to establish, since morphological, chemical and ecological data are scarce and often imprecise, especially for the species-rich families such as the Orchidaceae. Moreover, for many of these families, accurate taxonomic identification and sufficient phylogenetic knowledge are lacking.

Most of the oil-producing plants occur in the tropics and subtropics of South America (Calceolariaceae, Iridaceae, Krameriaceae, Malpighiaceae, Orchidaceae, Plantaginaceae and Solanaceae) and Africa (Cucurbitaceae, Iridaceae, Orchidaceae, Scrophulariaceae and Stilbaceae), but *Lysimachia* species (Primulaceae) occur in temperate and subtropical regions of the North Hemisphere.

The oil flowers are mostly zygomorphic, bisexual and nectarless, but they are actinomorphic in most of the Cucurbitaceae, Iridaceae, Primulaceae and Solanaceae species. Flowers that offer both nectar and oil occur in *T. parviflora* (Iridaceae), *Monttea* (Plantaginaceae) and in the Cucurbitaceae species. Only Cucurbitaceae has unisexual flowers. The oil-secreting structures can be located either on the dorsal portions of the flowers, outside of the sepals (as in the Malpighiaceae species) or on the ventral portions, on

the inner protective whorls or on the androecium (Tab.2).

With the exception of Krameriaceae and Malpighiaceae, trichomal elaiophores occur in all other plant families. Trichomal elaiophores predominate in the Iridaceae family, but one species *T. parviflora* has the epithelial type. Epithelial, trichomal and intermediate elaiophores are reported for Orchidaceae species, which are the most diverse in relation to the location and morphology of such secretory structures. All other families have exclusively one type of elaiophore (Tab.2).

Detailed morphological descriptions of the elaiophores and ultrastructural studies are lacking for several families. In general, the epithelial elaiophores are very similar among the taxa, being often constituted by more or less elongated epithelial cells, a subepithelial parenchyma and a subtending and vascularized parenchyma. The oil-secreting trichomes are grouped in a more or less dense arrangements and can be unicellular in the monocot members or multicellular in the remaining species (Tab. 2). These trichomes are mostly capitate and also morphologically very similar among taxa. Regardless of whether the elaiophores are trichomal or epithelial the ultrastructural features of the secretory cells are very similar among the species studied so far. These cells have typical cellular machinery of glands with lipophilic secretions and seem to share similar paths of synthesis, and manners of accumulation and secretion release.

Data on chemical composition are restricted to a few species and are lacking for some families. Although the floral oils seem to be very similar among the families, the extension of the study of their chemical nature to a greater number of species could indicate more differences among taxa and improve our understanding of the interactions between the host plants and the bees.

There is scant information on the pollination ecology of most plant species with oil-producing flowers. In general, the neotropical plant species are related with the Centridini, Tapinotaspidini and Tetrapediini bees, while the African species are related with *Rediviva* (Melittidae) or, in the case of Cucurbitaceae, with *Ctenoplectra* (Ctenoplectrini) bees. The oils from Primulaceae are collected only by the *Macropis* (Melittidae) bees. These oil-collecting bees may or may not act as effective pollinators, with both sternotribic or nototribic pollen deposition, apparently depending on the plant taxa visited. The conservative morphology of the Malpighiaceae flowers always allows pollen deposition on the ventral surfaces of the bodies of the pollinators, but in other families the floral morphology and elaiophore location can vary even in the same genus, for example in the Iridaceae, Orchidaceae and Calceolariaceae.

There are very specific plant-bee interactions as the case of *Diascia* plants and some *Rediviva* bees, but there are also generalist interactions. Some oil-collecting bee species, for example, can collect floral oils from flowers that are very different morphologically. Although some authors point out some morphological and chemical cues, in general there is little information on how bees are attracted and orientated.

In conclusion we are agreed that additional morphological, chemical and ecological information is needed to obtain a better understanding of the evolution of this specialized pollination system.

Acknowledgements

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