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## Floral-oil-producing Plantaginaceae species: geographical distribution, pollinator rewards and interactions with oil-collecting bees

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MARTINS, A.C. & ALVES-DOS-SANTOS, I. **Floral-oil-producing Plantaginaceae species: geographical distribution, pollinator rewards and interactions with oil-collecting bees.** *Biota Neotrop.* 13(4): <http://www.biotaneotropica.org.br/v13n4/en/abstract?article+bn01313042013>

**Abstract:** Floral oils as reward to pollinators occur in eleven plant families and appeared at least 28 times in the evolutionary history of flowering plants. They are produced in epithelial or tricomatic glands and collected by oil bee visitors. The present paper focuses on floral-oil-producing species of Plantaginaceae, a Neotropical group namely *Angelonia* clade. This group comprises around 40 described species in the genera *Angelonia*, *Basistemon*, *Monttea*, *Monopera* and the oil-less *Melosperma*. We present a revision of all species of the *Angelonia* clade, their geographical distribution, resources offered to pollinators and records of flower visitors, especially oil-collecting bees. These plants rely only on oil-collecting species in the tribe Centridini and Tapinotaspidini for a successful pollination, being the interaction between both partners an especial case of bee/flower adaptation in Neotropical region. Some bee species depend only on the oil of Plantaginaceae flowers to survive, while others can collect on several floral oil sources. The pollinating bees explore the oil glands located in sacs using specialized hairs in the forelegs. With this study, we hope to inspire further research relating to this fascinating group of plants, in which most species are rare and occur in highly endangered habitats in South American open vegetation biomes. **keywords:** *plant-insect interactions, oil-collecting bees, oil-flowers, Plantaginaceae, Apidae.*

MARTINS, A.C. & ALVES-DOS-SANTOS, I. **As espécies produtoras de óleo floral da família Plantaginaceae: distribuição geográfica, recursos oferecidos e interações com abelhas coletoras de óleo.** *Biota Neotrop.* 13(4): <http://www.biotaneotropica.org.br/v13n4/pt/abstract?article+bn01313042013>

**Resumo:** Os óleos florais como recompensa a polinizadores estão presentes em onze famílias e surgiram ao menos 28 vezes na história evolutiva das plantas floríferas. Estes são produzidos em glândulas tricômáticas ou epiteliais e coletados por abelhas coletoras de óleo. O presente trabalho foi focado nas espécies produtoras de óleo floral de Plantaginaceae, um grupo neotropical conhecido como clado *Angelonia*. Este grupo compreende cerca de 40 espécies nos gêneros *Angelonia*, *Basistemon*, *Monttea*, *Monopera* e *Melosperma*, que não produz óleo floral. Nós apresentamos uma revisão de todas as espécies no clado *Angelonia*, sua distribuição geográfica, recursos oferecidos e registros de visitantes florais, especialmente abelhas coletoras de óleo. Estas plantas dependem das abelhas coletoras de óleo das tribos Centridini e Tapinotaspidini para uma polinização bem-sucedida, sendo a interação entre ambos os parceiros um caso especial de adaptação abelha/planta na Região Neotropical. Algumas espécies dependem somente do óleo coletado em espécies do clado *Angelonia*, enquanto outras também podem coletar em várias fontes de óleos florais. Essas abelhas exploram as glândulas de óleo localizadas em bolsas utilizando pelos especializados nas pernas anteriores. Com o presente trabalho esperamos inspirar estudos futuros com este fascinante grupo de plantas, que são em sua maioria espécies raras e que ocorrem nos altamente ameaçados biomas de vegetação aberta da América do Sul.

**Palavras-chave:** *interações inseto-planta, abelhas coletoras de óleo, flores de óleo, Plantaginaceae, Apidae*

## Introduction

The origin of floral oil production in angiosperms is polyphyletic as well as the oil-collecting behavior in bees (Renner & Schaefer 2010). Specifically floral oil production evolved at least 28 times and was lost 36-38 times in the evolutionary history of flowering plants (Renner & Schaefer 2010). Stefan Vogel (Univ. Vienna) first observed oil production glands on the corolla of *Angelonia* and *Calceolaria* (Vogel 1969). Further Vogel's investigations were compiled in extensive monographs, where he distinguished the oil-producing glands in two types: I. Trichomatic elaiophores - fields of hundreds to thousands of glandular trichomes (Cucurbitaceae, Iridaceae, Myrsinaceae (*Lysimachia*), part of Orchidaceae, Scrophulariaceae s.l., Solanaceae (*Nierenbergia*)); and II. Epithelial elaiophores - groupings of secretory epidermal cells recovered by a thin cuticle (Krameriaceae, Malpighiaceae and part of Orchidaceae) (Vogel 1974, 1986, 1990). Nowadays this floral reward is the third most common reward to specialized pollinators (Simpson & Neff 1981).

Neotropical oil-producing species in Plantaginaceae and Calceolariaceae were until recent years classified in the traditional and polyphyletic family Scrophulariaceae (Olmstead et al. 2001). Scrophulariaceae *sensu lato* comprised also the African floral-oil-producing genera *Anastrabe*, *Bowkeria* and *Ixianthes*, which were re-classified in Stilbaceae, and *Alonsoa*, *Colpias*, *Diascia* and *Hemimeris*, which were maintained in Scrophulariaceae *sensu stricto* (Olmstead et al. 2001, Oxelman et al. 2005). Furthermore the Neotropical Andean genus *Calceolaria*, with around 200 species, (Molau 1988), was classified in the new family Calceolariaceae (Olmstead et al. 2001) while the remaining Neotropical oil genera were re-classified in the newly expanded Plantaginaceae (Albach et al. 2005).

Plantaginaceae is a widespread family that comprises about 90 genera and 1900 species mainly distributed in temperate regions. In general, it is difficult to distinguish from Scrophulariaceae *sensu stricto* and related families, all possessing large and zygomorphic flowers (Stevens 2012). On the other hand, the oil-producing species appeared only in the tribe Angeloniae, which comprises also the oil-less *Ourisia*, sister-group to *Angelonia* clade (Albach et al. 2005). The production of floral oils as a reward to pollinators in the *Angelonia* clade seems to be an ancestral condition, with losses in *Basistemon*, and origin of nectaries in *Melosperma andicola* and *Monttea*, which offers oil and nectar. (Simpson et al. 1990, Vogel & Cocucci 1995, Sérsic & Cocucci 1999, Tadey 2011). Moreover another Plantaginaceae, *Mecardonia tenella* was reported to attract males and females of the oil-collecting bee *Lanthanomelissa betinae* (Cappellari et al. 2009), but the purpose of the visit remains unknown. However the evidence of oil-production in *M. tenella* deserves further investigation, but since this genus is included in Gratiolae, which is sister-group to Angeloniae (Albach et al. 2005), it could represent an ancestral state of oil-production in Plantaginaceae (Cappellari et al. 2009).

In this paper, we compiled all species of the *Angelonia* clade, their geographical distribution, morphological traits related to pollination in oil flowers and oil-collecting visitors. We discuss the gaps in the available information and in pollination studies, and the information that would be required for a better understanding of the interaction of the flowers and their bee visitors.

## How the Data was Compiled

Data on the taxonomy and geographical distribution of the plants were compiled from Barringer (1981, 1983, 1985) and Souza & Giulietti (2009). Taxonomic information for species occurring in Brazil was updated according to Souza & Giulietti (2009) synonym

proposal. Information about pollination and interactions with flower visitors was compiled from the literature using the website Web of Knowledge (<http://www.webofknowledge.com/>) and Google Scholar (<http://scholar.google.com>) by searching for the keywords: *oil-bees*, *oil-flowers*, *Plantaginaceae*, *Neotropical*, as well as the name of plant and bee genera involved in the described interactions (for example, *Angelonia* or *Centris*). The names of flower bee visitors were updated according to Moure et al. (2012). The resources offered to flower visitors were inferred through the morphological features of the flowers, as described in the literature (e.g. the presence of nectaries or elaiophores). Vegetation types for the localities where pollination studies were performed, when not described in the respective papers, were inferred by assembling the geographic coordinates of the study site with the WWF map of ecoregions (Olson & Dinerstein 2002) in DIVA-GIS (Diva-Gis, 2011).

Morphological features for the oil producing species were compiled from the literature (Barringer 1981, 1983, 1985, Souza & Giulietti 2009, Simpson et al. 1990, Sérsic & Cocucci 1999). We consider here the most important features related to flower visitors, the presence of the developed calluses and size of oil sacs (Martins et al. 2013). Here is used the term *proximal callus* (Vogel & Machado 1990), for the structure of *Angelonia* flowers named also as *anterior callus* (Vogel & Machado 1990), *horn* (Barringer 1981) or *appendix* (Souza & Giulietti 2009). The term "oil sac" was preferred to refer to the place where most of the glandular trichomes were located in the corolla of Plantaginaceae oil-flowers, instead of *giba* (Souza & Giulietti 2009), *pouch* (Vogel & Machado 1990) or *spur*, the common term used for the Scrophulariaceae s.l. flowers (Steiner & Whitehead 1990).

For illustration and comparative purposes, three species in the clade were collected in the following localities in Brazil, with the respective coordinates: *Angelonia eryostachis*, Rio Preto State Park in São Gonçalo do Rio Preto (Minas Gerais) (18° 12' S, 43° 19' W); *Angelonia integerrima*, Vila Velha State Park in Ponta Grossa (Paraná) (30° 07' S, 51° 14' W); and *Basistemon silvaticus*, Porto Murinho (Mato Grosso Sul) (21° 37' S, 57° 49' W). The collected flowers were fixed in FAA (37% formaldehyde, acetic acid and 50% ethanol, 1:1:2). Those species were selected because they are relatively unknown in terms of morphology and interactions with pollinators and represent different morphological types within the Plantaginaceae oil-producing species. The localities for collecting were chosen according to the geographical distribution of the species (Souza & Giulietti 2009), as well as accessibility.

Fresh flowers of *A. integerrima* were dissected tangentially or kept completely for photographs in different views. Several pictures of each view were captured with a camera coupled to a Leica Stereoscopic Microscope, and later assembled with Automontage Pro software. *A. eryostachis* and *B. silvaticus* flowers were dissected by cutting them tangentially, and one of each was illustrated using a camera lucida. The images were then treated in CorelDraw.

## Angelonia clade

The clade *Angelonia* comprises the five genera *Angelonia*, *Basistemon*, *Monttea*, *Monopera* and *Melosperma* (Albach et al. 2005) (Figure 1). In fact, the phylogenetic position of *Monopera* within the *Angelonia* clade (Albach et al. 2005) is inferred by morphological similarities with *Angelonia* (Barringer 1983). Although records of the environments in which they occur are incomplete, the available data show that the species of this clade are more strongly associated with open and dry vegetation areas, such as the savannas, seasonally dry tropical forest and Chaco biomes in Neotropical Region.



**Figure 1.** Floral-oil-offering species in Plantaginaceae. **a.** *Monopera perennis*, Porto Murtinho (21° 34' 21" S e 57° 48' 65" W), Brazil (Photo by Gabriel A. R. Melo); **b.** *Monttea aphylla*, Villavicencio Natural Reserve, Argentina (32° 35' 7" S, 68° 59' 2" W) (Photo by Mariana Taniguchi); **c.** *Angelonia goyazensis*, Rio Preto State Park, Brazil; **d.** *Basistemom silvaticum*, Porto Murtinho, Brazil.

The most widely distributed and diverse genus is *Angelonia* (Figure 2a), with around 30 species that occur from Mexico to Argentina (Barringer 1981, Souza & Giulietti 2009) (Table 1). These numbers are possibly inaccurate, however, as this genus needs a taxonomic revision (VC Souza, personal communication). Many *Angelonia* species are endemic to Brazil (e.g. *A. alternifolia*, *A. arguta*), while some are distributed broadly in South and Central America, as *A. angustifolia* (Table 1). *Angelonia* species are herbs or shrubs and live in humid or flooded soil near rivers (Figure 2b). On the other hand, *Monopera* contains only two herbaceous species, *M. perennis*, occurring in Brazil (Mato Grosso do Sul) and Paraguay, and *M. micrantha*, occurring in seasonally dry tropical forest in northeastern Brazil (Souza & Giulietti 2009). Records of *Monopera* are rare in both herbaria and literature: there are only 27 records in the database of Species Link (<http://www.splink.org.br/>).

*Basistemom* occurs in parts of Central Brazil and across the Andean countries Argentina, Bolivia, Colombia, Peru and Venezuela (Barringer 1985). Barringer (1985) consider eight species in this genus, however Souza & Giulietti (2009) synonymized *B. argutus*, *B. intermedius*, *B. klugii*, and *B. pulchellus* in *B. peruvianus* due to the many characters in common and slightly differences that does not justify the separation. In addition, *Basistemom* species are rarely collected, and for most of these species, with the exception of *B. silvaticum* and *B. spinosus*, we known only the type specimens.

*Monttea* and *Melosperma* are sister-groups (Albach et al. 2005). *Monttea* present three species occurring in Argentina and Chile: *M.*

*aphylla*, *M. chilensis* and *M. schickendantzii*, while *Melosperma* comprises only one species, *M. andicola*. The *Monttea* and *Melosperma* species occur only in arid regions of temperate South America, being the last one restricted to Andean regions (Sérsic & Cocucci 1999).

### Morphology of Plantaginaceae Oil-Rewarding Flowers

The floral-oil-producing Plantaginaceae vary in terms of habit and morphology, although some traits are common to all species, such as purple or white flowers, two pairs of stamens and trichomatic elaiophores located in one or two sacs (Table 2). The flowers are gamopetalous, forming a not-very-well-defined tube, which, in the majority of *Angelonia* species, possess five lobes and is similar to an open mouth (Figure 1c). The pair of oil sacs varies between species in size and shape, and holds the trichomatic elaiophores (Figure 3a,b) (Table 2), which bees explore with their forelegs (Vogel 1974). In *Angelonia* clade, both male and female reproductive organs are located in the superior part of the corolla entrance (Figures 4 and 5), and at least in *Angelonia* and *Basistemom* the development is protandrous, a mechanism to avoid self-pollination. The flowers of *M. aphylla*, is weakly self-compatible and minimally autogamous, as well as most of species studied by Vogel & Machado (1991). The literature present data on the pollination biology of six species of *Angelonia*: *A. salicariifolia* (cited as *A. hirta*), *A. campestris* (cited as two species, *A. bisaccata* and *A. hookeriana*), *A. pubescens*,

**Table 1.** Geographical distribution, flower resources offered, and flower visitors of oil-producing Plantaginaceae species (*Angelonia* clade), *Angelonia*, *Basistemon*, *Melosperma*, *Monopera* and *Monttea* (according to Albach et al. 2005, with inclusion of the *Monopera* genus). Offered resource: O: oil, P: pollen and N: nectar. Species names are cited as well as the pollination studies conducted on their flowers, and the synonyms correspond to the Souza & Giulietti (2009) proposal for Brazilian species. Information on geographical distribution was compiled from Barringer (1981, 1983, 1985), with the addition of data from Souza & Giulietti (2009) for *Angelonia*, *Monopera* and *Basistemon*, and from Simpson et al. (1990) and Sersic & Cocucci (1999) for *Monttea* and *Melosperma*. 3. The vegetation type used was that mentioned in the original work on the pollination ecology of each species, except for cases where the vegetation was not described, and, in this case ecoregions from the world system were used instead (Olson & Dinerstein 2002). For bee's author's names see Moure et al. 2012.

Species <sup>1</sup>	Synonym	Geographical distribution <sup>2</sup>	Offered resource	Flower visiting species and resources they collect	Localities and vegetation type <sup>3</sup> where pollination studies were conducted
<i>Angelonia</i>					
<i>A. acuminatissima</i>	-	Bolivia (Santa Cruz) and Paraguay (Concepción)	O, P	-	-
<i>A. alternifolia</i> V.C. Souza	-	Brazil (Goiás)	O, P	-	-
<i>A. minor</i> Fisch. & C.A. Mey	<i>A. angustifolia</i>	Brazil (Acre, Alagoas, Amapá, Amazonas, Bahia, Mato Grosso, Pará), <i>Costa Rica</i> , <i>Cuba</i> , <i>Jamaica</i> and <i>Mexico</i> .	O, P	-	-
<i>A. arguta</i> Benth	<i>A. serrata</i>	Brazil (Bahia, Ceará, Espírito Santo, Minas Gerais, Pernambuco, Piauí)	O, P	-	-
<i>A. biflora</i> Benth	<i>A. grandiflora</i>	Brazil (Ceará, Pernambuco, Paraíba, Piauí, Rio Grande do Norte)	O, P	<b>Oil:</b> <i>Centris (Hemisiella) triginoides</i> , <i>Centris (Trachina) fuscata</i> (Vogel 1974)	- Tropical rainforest/Macapá (AP)
<i>A. blanchetii</i> Benth	-	Brazil (Bahia, Minas Gerais)	O, P	-	-
<i>A. campestris</i>	<i>A. bisacata</i> , <i>A. hookeriana</i> , <i>A. ciliolata</i>	Brazil (Bahia, Ceará, Minas Gerais, Paraíba, Pernambuco, Piauí)	O, P	<b>Oil:</b> <i>Centris (Paracentris) xanthomelaena</i> , <i>Tetrapedia</i> cf. <i>rugulosa</i> - <b>Pollen:</b> <i>Plebeia mosquito</i> , <i>Trigona spinipes</i> (Vogel & Machado 1991)	Caatinga (Seasonally dry tropical forest)/ Alagoinhas (PE)
<i>A. ciliaris</i> B.L. Rob	-	Belize (Belize, El Cayo, Orange Walk), <i>Guatemala</i> (Petén) and <i>Mexico</i> (Tabasco)	O, P	-	-
<i>A. chiquitensis</i> Herzog	-	Bolivia (only known holotype of Santa Ana de Chiquitos, Santa Cruz)	O, P	-	-
<i>A. cornigera</i> Hook	<i>Psidium cornigerum</i>	Brazil (Bahia, Espírito Santo, Maranhão, Pernambuco, Paraíba, Piauí, Sergipe)	O, P	<b>Oil:</b> <i>Caenonomada unicalcarata</i> , <i>Centris hypitidis</i> , <i>Tapinotaspis nordestina</i> ; <b>oil and pollen:</b> <i>Chalepogonus</i> sp. (Aguilar & Melo 2009, Machado et al. 2002, Martins et al. 2013)	Caatinga (Seasonally dry tropical forest)/Buique (PE) and São Miguel do Tapuio (PI)
<i>A. crassifolia</i> Benth	-	Brazil (Distrito Federal, Goiás, Minas Gerais)	O, P	-	-
<i>A. eriostachys</i> Benth.	<i>A. spectabilis</i>	Brazil (Minas Gerais)	O, P	<b>Oil:</b> <i>Centris (Paracentris) burgdorfi</i> ; <i>Centris (Xanthemisia) bicolor</i> ; <i>Tetrapedia</i> cf. <i>peckolti</i> , Martins et al 2013.	Cerrado (São Gonçalo do Rio Preto, MG)

Table 1. Continued...

Species <sup>1</sup>	Synonym	Geographical distribution <sup>2</sup>	Offered resource	Flower visiting species and resources they collect	Localities and vegetation type <sup>3</sup> where pollination studies were conducted
<i>A. goyazensis</i> Benth.	-	Brazil (Bahia, Distrito Federal, Minas Gerais)	O, P	<b>Oil:</b> <i>Centris (Centris) aenea</i> ; <i>Centris (Paracentris) burgdorfi</i> ; <i>Centris (Paracentris) klugii</i> , <i>Paratetrapedia punctata</i> ; <b>Oil and pollen:</b> <i>Arhysoceble</i> sp (Martins et al 2013)	Cerrado (São Gonçalo do Rio Preto, MG)
<i>A. haslerana</i> Chodat.	-	Paraguay (Caaguazu, Central, La Cordillera, Paraguari, San Pedro)	O, P	-	-
<i>A. incurvata</i> Barringer	-	Argentina (Chaco, Corrientes, Formosa, Misiones), Paraguay (Boquerón, Central, Concepción, Itapua, La Cordillera, Olimpo, Paraguari, Presidente Hayes)	O, P	-	-
<i>A. integerrima</i> Spreng.	-	Argentina (Chaco, Corrientes, Entre Rios, Formosa, Misiones, Santa Fé); Brazil (Mato Grosso do Sul, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), Paraguay (Misiones, Paraguari, San Pedro) and Uruguay (Rio Negro, Rivera).	O, P	<b>Oil:</b> <i>Arhysoceble</i> sp, <i>Centris (H.) trigonoides</i> , <i>Centris (Hemisiella) vulpecula</i> , <i>Centris (T.) fuscata</i> ; <b>oil and pollen:</b> <i>Arhysoceble</i> aff. <i>huberi</i> , <i>Chalepogonus</i> aff. <i>luciane</i> , <i>Tetrapedia</i> spp. <b>Pollen:</b> <i>Dialictus</i> sp, <i>Mourella caerulea</i> , <i>Trigona spinipes</i> , <i>Plebeia droryana</i> , <i>Plebeia emerina</i> (Gonçalves & Melo 2005, Martins et al. 2013, Pinheiro et al. 2008, Vogel 1974)	Cerrado/ Pirassumunga (SP) Campos sulinos/ Ponta Grossa (PR), Porto Alegre and Viamão (RS)
<i>A. jamaicensis</i> Barringer	-	Jamaica	O, P	-	-
<i>A. linarioides</i> Taub.	-	Brazil (Bahia, Goiás, Minas Gerais)	O, P	-	-
<i>A. parviflora</i> Barringer	-	Mexico (Yucatán)	O, P	-	-
<i>A. pilosella</i> J. Kickx f.	-	Cuba (Camaguary, Isla de Pinos, Las Villas, Oriente, Pinar del Rio)	O, P	-	-
<i>A. pratensis</i> Gardner	-	Brazil (Bahia, Ceará, Goiás, Minas Gerais, Piauí)	O, P	-	-
<i>A. procumbens</i> Nees & Mart.	<i>A. cofreana</i> , <i>A. veronicoides</i>	Brazil (Bahia, Minas Gerais)	O, P	-	-
	<i>Physidium prucumbens</i> , <i>Schelveria argutta</i> ,				

Table 1. Continued...

Species <sup>1</sup>	Synonym	Geographical distribution <sup>2</sup>	Offered resource	Flower visiting species and resources they collect	Localities and vegetation type <sup>3</sup> where pollination studies were conducted
<i>A. pubescens</i> Benth.		Brazil (Alagoas, Bahia, Ceará, Goiás, Maranhão, Pará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte)	O, P	<b>Oil:</b> <i>Centris thelyopsis</i> , <i>Tetrapedia cf rugulosa</i> <b>Oil and Pollen:</b> <i>Centris hypitidis</i> , <i>Arhysoceble huberi</i> (Martins et al. 2013, Vivallo & Melo 2009, Vogel & Machado 1991)	Caatinga (Seasonally dry tropical forest) Alagoinhas (PE) Teresina de Goiás (Caatinga)
<i>A. salicariifolia</i> Humb. & Bompl.	<i>A. evitae</i> <i>A. hirta</i> , <i>A. gardneri</i> , <i>A. leandrii</i> , <i>Physidium gardneri</i>	Brazil (Alagoas, Bahia, Espírito Santo, Mato Grosso do Sul, Paraíba, Pernambuco, Rio de Janeiro, Sergipe), <i>Argentina</i> (Corrientes, Formosa, Misiones), <i>Colombia</i> , <i>Cuba</i> , <i>Guiana</i> , <i>Paraguay</i> , <i>Puerto Rico</i> , <i>Trinidad e Tobago</i> and <i>Venezuela</i>	O, P	<b>Oil:</b> <i>Centris (T.) fuscata</i> , <i>C. (Centris) aenea</i> , <i>C. (H.) trigonoides</i> , <i>C. (Hemisiella) tarsata</i> , <i>C. (P.) xanthomelaena</i> , <i>Centris (Melacentris) obsoleta</i> (Machado et al. 2002; Vogel & Machado 1991), <i>Centris (H.) analis</i> , <i>Caenonomada bruneri</i> ; <b>oil and pollen:</b> <i>Tetrapedia</i> sp.; <b>pollen:</b> <i>Dialictus</i> sp (Aguar & Melo 2009, Martins et al. 2013).	Chaco/Porto Murtinho (MS) Caatinga (Seasonally dry tropical forest)/Alagoinhas (PE)
<i>A. tomentosa</i> Moricand ex Benth	-	Brazil (Bahia, Goiás, Minas Gerais)	O, P	-	-
<i>A. verticillata</i> Philcox	-	Brazil (Bahia)	O, P	-	-
<b>Basistemom</b>					
<i>B. bogotensis</i> Turcz	-	Colombia (Cundinamarca) and Venezuela (Falcon)	P (?)	-	-
<i>B. peruvianus</i> Benth ex. B.D. Jacks	<i>B. pulchellus</i> , <i>B. klugii</i> , <i>B. argutus</i> , <i>B. intermedius</i> Edwin	Peru (Huanuco) Bolivia (El Beni), Brazil (Rio de Janeiro, Mato Grosso), Peru (San Martin)	P (?) O (?), P (?)	-	-
<i>B. silvaticus</i> (Herzog) Baezmi & J.F. Macbr.	<i>Saccanthus silvaticus</i>	Bolivia (Chquisaca) and Brazil (Mato Grosso do Sul)	O, P	<b>Oil:</b> <i>Centris hypitoides</i> , <i>Arhysoceble aff. huberi</i> , <i>Caenonomada bruneri</i> , <i>C. aff. unicalcarata</i> ; <b>oil and pollen:</b> <i>Tetrapedia cf. peckolii</i> ; <b>pollen:</b> <i>Dialictus</i> sp. (Martins et al. 2013). <b>Oil:</b> <i>Arhysoceble aff. huberi</i> (cited as <i>Paratetrapedia</i> sp.) (Vogel & Cocucci 1995)	Chaco/ Yaquiásmé (Salta)
<i>B. spinosus</i> (Moldenke)	<i>Saccanthus violaceus</i>	Argentina (Salta, Jujuy, Formosa, Tucuman), Bolivia (Chuquisaca, Santa Cruz) and Paraguay (Chaco, Concepción)	O, P	-	-
<b>Melosperma</b>					
<i>M. andicola</i> Benth	-	Argentina and Chile	N, P	-	Andean/Parque Nacional Aconcagua (Mendoza)

## Floral-oil-producing Plantaginaceae

Table 1. Continued...

Species <sup>1</sup>	Synonym	Geographical distribution <sup>2</sup>	Offered resource	Flower visiting species and resources they collect	Localities and vegetation type <sup>3</sup> where pollination studies were conducted
<b>Monopera</b>					
<i>M. micrantha</i> (Benth.) Barringer	<i>A. micrantha</i>	Brazil (Bahia, Pernambuco, Piauí)	O (?), P (?)	-	
<i>M. perennis</i> (Hassl.) Barringer	<i>A. micrantha</i> var: <i>perennis</i>	Brazil (Mato Grosso, Mato Grosso do Sul, Cuiabá, Goiás) and <i>Paraguay</i> (Central, Concepción)	O, P (?)	<b>Oil:</b> <i>Caenomada bruneri</i> (Aguiar & Melo 2009)	Chaco/Porto Murtinho (MS)
<b>Monttea</b>					
<i>M. aphylla</i> (Miers) Benth. & Hook.		Argentina (Mendoza, San Luis, La Rioja) and <i>Chile</i>	O, Pe N	<b>Oil:</b> <i>Centris</i> ( <i>Penthemisia</i> ) <i>brethesi</i> , <i>Centris</i> ( <i>Wagenknechtia</i> ) <i>varchorum</i> , <i>Centris</i> ( <i>Paracentris</i> ) <i>tricolor</i> (Simpson et al 1990, Tadey, 2011). <b>Nectar:</b> <i>Centris</i> ( <i>Wagenknechtia</i> ) <i>rhodophthalma</i> (males), <i>Bombus opifex</i> , <i>Xylocopa</i> sp (Sérsic & Cocucci 1999, Simpson et al. 1990), <i>Mesonychium jensenii</i> (probably nectar) (Tadey, 2011).	Monte/Potrillos (Mendoza); Las Quijadas (San Luis); Piedra Pintada (La Rioja), between Arroyito and El Chacón (Tadey 2011)
<i>M. chilensis</i> Gay		<i>Chile</i> (IV Región)	O, Pe N	<b>Oil:</b> <i>C. (Paracentris)</i> <i>nigerrima</i> , <i>Centris</i> ( <i>Penthemisia</i> ) <i>chilensis</i> (females) - <b>Nectar:</b> males (Sérsic & Cocucci 1999)	<i>Chilean Matorral</i> / Coquimbo (IV Región)
<i>M. schickendantzii</i> Griseb.		Argentina (Córdoba) and <i>Chile</i>	O, Pe N	<b>Oil:</b> <i>Centris</i> ( <i>P. tricolor</i> ) <b>Nectar:</b> <i>Bombus opifex</i> (Sérsic & Cocucci 1999)	Chaco/ Depto. Pocho (Córdoba)



**Table 2.** Floral morphology of oil-offering *Angelonia* clade species, with focus on pollination related traits, compiled from Souza & Giulietti (2009) for the species occurring in Brazil and complemented with information about the non-Brazilian species present in Barringer (1981) (*Angelonia*), (1985) (*Basistemom*) (1983), (*Monopera*), Simpson et al. (1990) (*Monttea aphlla*) and Sêrsic & Cocucci (1999) (*Monttea* and *Melosperma*).

Species	Flower arrangement	Flower color	Proximal callus	Oil sacs
<b>Angelonia</b>				
<i>A. acuminatissima</i>	terminal raceme	violet	bifid	prominent
<i>A. alternifolia</i>	terminal raceme	purple	discrete or absent	rounded, discrete
<i>A. angustifolia</i>	solitary	purple or lilac	bifid	rounded
<i>A. arguta</i>	solitary, almost a raceme	purple	bifid	rounded
<i>A. biflora</i>	solitaria	purple or blue	bifid	rounded, discrete
<i>A. blanchetii</i>	solitary, almost a raceme	pink or purple	bifid	rounded
<i>A. campestris</i>	solitary	violet or purple	discrete or absent	prominent
<i>A. ciliaris</i>	terminal raceme	blue with purple dots	bifid	?
<i>A. chiquitensis</i>	terminal raceme	violet or blue	bifid	?
<i>A. cornigera</i>	solitary	purple or white	bituberculate	prominent and laterally expanded
<i>A. crassifolia</i>	solitary	violet or purple	bifid	rounded
<i>A. eriostachys</i>	terminal raceme	lilac or purple, with dark spots	discrete or absent	rounded, discrete
<i>A. goyazensis</i>	terminal raceme	purple, lilac or white	bifid	prominent
<i>A. haslerana</i>	1-2 axils of upper leaves	violet or rose	discrete or absent	discrete
<i>A. hirta</i>	terminal raceme	violet and white, with brown spots	bifid	prominent
<i>A. incurata</i>	terminal raceme	violet	bifid	?
<i>A. integerrima</i>	thyrses	lilac or blue, with purple spots	discrete or absent	prominent
<i>A. jamaicensis</i>	raceme	violet	?	?
<i>A. linarioides</i>	solitary	purple, lilac or white	bifid	prominent, but almost unisaccate
<i>A. parviflora</i>	raceme	purple	bifid	?
<i>A. pilosella</i>	raceme	purple	bifid	?
<i>A. pratensis</i>	solitary	purple	bifid	prominent
<i>A. procumbens</i>	solitary	rose, white or pale blue with spots lilac or brown	long and linear	discrete
<i>A. pubescens</i>	solitary	purple	linear with globular apex	prominent and laterally expanded
<i>A. salicariifolia</i>	terminal raceme	purple, blue, rose, lilac and white	bifid	prominent
<i>A. tomentosa</i>	terminal raceme	purple or blue	discrete or absent	rounded, discrete
<i>A. verticillata</i>	terminal raceme	purple	discrete or absent	rounded, discrete
<b>Basistemom</b>				
<i>B. bogotensis</i>	axillary and solitary	white	absent	discrete, glabrous
<i>B. peruvianus</i>	axillary clusters	white	absent	discrete, slightly glandular pubescent
<i>B. silvaticus</i>	solitary and axillary	purple or white	absent	discrete, glandular pubescent
<i>B. spinosus</i>	solitary, in the axils of leaves	reddish purple	absent	discrete, densely glandular pubescent
<b>Monopera</b>				
<i>M. micrantha</i>	solitary	lilac	absent	unisaccate
<i>M. perennis</i> Barringer	solitary	lilac	absent	unisaccate
<b>Monttea</b>				
<i>M. aphylla</i>	axillary	white to lilac	absent	Discrete, densely glandular
<i>M. chilensis</i>	axillary	white to lilac	absent	Discrete, densely glandular
<i>M. schickendantzii</i>	axillary	white to lilac	absent	Discrete, densely glandular



**Figure 2.** *Angelonia salicariifolia*, Porto Murinho, Brazil: **a.** Habit: herbaceous plant growing in islands of humid soil among the flooded areas; **b.** Opened flowers show the open-mouth trait, common to most species of *Angelonia*.



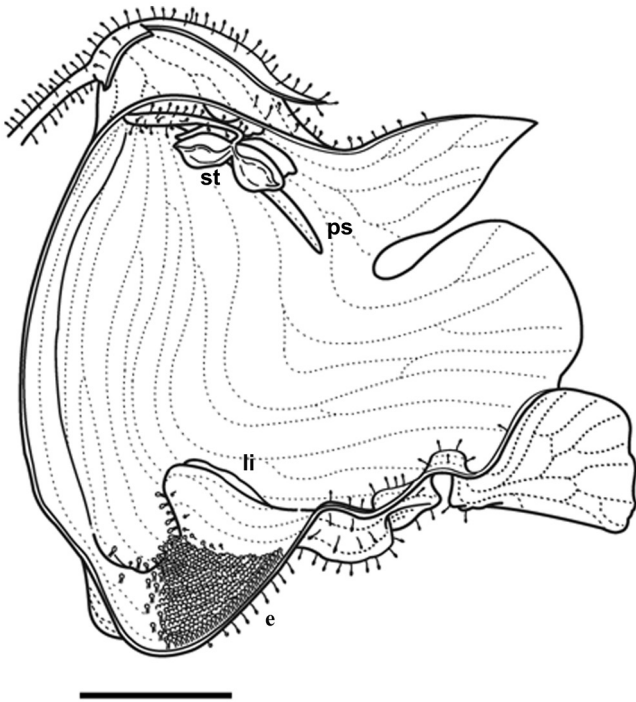
**Figure 3.** Oil sacs in the *Angelonia integerrima* flower. **a.** Frontal view of bud, showing the pair of oil sacs; **b.** The corolla is cutted lengthwise to show the interior of the right pouch, allowing observation of the green elaiophores. (Scale = 1 mm).

*A. cornigera*, *A. goyazensis* and *A. eryostachis* (Vogel & Machado 1991, Machado et al. 2002, Aguiar & Melo 2009, Martins et al. 2013).

*Angelonia* species have more specialized flowers in which two well-defined oil sacs are present in most of them (Figure 3a) (Table 2). The inner oil sac possesses fields of hundreds of oil trichomes forming a green carpet when observed laterally (Figure 3b) and they are separated by the ligulae (Figure 4). On the inside of the oil sacs there are a variable number of trichomes, depending on the species. In *A.*

*eryostachis*, for example, they comprise a dense carpet in part of the sac (Figure 4). Souza & Giulietti (2009) recognized six morphological patterns based on the Brazilian species based on leaf arrangement, inflorescence patterns, and presence of callus (or appendix) in the corolla and format of oil sacs. Notwithstanding there is no phylogenetic corroboration for this proposal of patterns between the species.

We recognized two different types of flowers in the genus *Angelonia*, short and long corolla tube, both requiring different

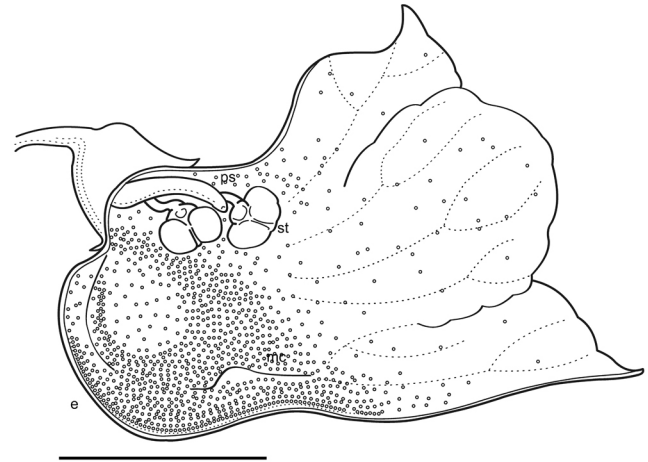


**Figure 4.** Lateral view of the *Angelonia eriostachys* flower, sectioned transversally and showing “oil sacs” and other parts of the inner corolla with trichomes. (e) elaiophores; (st) stamens; (ps) pistil; (li) ligula. (Scale = 2.5 mm).

modes of visiting behavior (Martins et al. 2013). In the short tubed corolla, the bees need to hold their bodies in the flowers and probably use the mandibles to do that. The short tubed *Angelonia* flowers also possess well-developed proximal calluses (long and bifid in most), which probably are related to force a correct position of the pollinator during visits, i.e. touching the fertile organs (Vogel & Machado 1991, Martins et al. 2013). Moreover, some species of *Angelonia* have especially deep oil sacs, *A. cornigera* and *A. pubescens*, requiring long legs to access them. In *A. cornigera* a special case of adaptation by long-legged pollinators was reported (Machado et al. 2002), resembling the interactions between the *Diascia* oil flowers and *Rediviva* bees (Steiner & Whitehead 1990). However, the relationships between deep oil sacs and long bee legs are still poorly understood for *Angelonia* species. Currently there is no available information on shape and size of corolla for most species in the literature, as well as a phylogenetic hypothesis, impeding a proper inference about the evolution of floral morphology.

Besides general similarities *Monopera*'s flowers are clearly distinguished from *Angelonia* ones in possessing only one well developed oil sac and the lack of calluses (Barringer 1983). They are supposed to be sister-groups, despite the lack of a phylogenetic hypothesis. Indeed *Monopera* could represent an ancestral state of the less-specialized flowers in relation to *Angelonia*.

In comparison with *Angelonia*, the flowers of *Basistemom silvaticus* possess roughly defined oil sacs in which the elaiophores are widely spread, even occurring on other parts of the inner corolla (Figure 5). In addition the flowers of *Basistemom* do not possess ligulae and the trichomes are less dense and more widely distributed on the inner corolla (Figure 5) (Table 2). Moreover the flower entrance is larger, and the access to the elaiophores is easier for visitors (Figure 5). Based on herbarium material, Barringer (1985) observed that *Basistemom* species either do not present any glandular trichomes



**Figure 5.** Lateral view of the *Basistemom silvaticus* flower, sectioned and showing the widely distributed elaiophores (e), stamens (st), pistil (ps) and median callus (mc). (Scale = 2.5 mm).

in the corolla (*Basistemom bogotensis*, *B. intermedius*, *B. klugii* and *B. peruvianus*), present trichomes only at the base of the corolla (*Basistemom argutus*), or present trichomes in low (*Basistemom pulchellus*), intermediate (*Basistemom silvaticus*) or high densities (*B. spinosus*). Nonetheless, the oil production has been confirmed only in *B. spinosus* (Vogel & Cocucci 1995) and in *B. silvaticus* flowers (Martins et al. 2013).

Similarly to *Basistemom* flowers, in *Monttea* the oil sacs are roughly defined, but it is still recognized as bissacate, normally white or lilac and with similar size between species (Simpson et al. 1990, Sérsic & Cocucci 1999). *Monttea schickendantzii* and *M. chilensis* have a curvature conspicuously forming two sacs, which are separated by a structure named *ridge* by Sérsic & Cocucci (1999). The ridge is not observed in *M. aphylla*, but seems to be vestigial in *Melosperma andicola* (Sérsic & Cocucci 1999). In fact this structure is probably homologous to the proximal callus of *Angelonia* and medium callus of *Basistemom* (Martins et al. 2013). Besides four didynamous stamens, the flower of *Monttea* also possesses a staminoid (Simpson et al. 1990). The presence of nectary was detected in all *Monttea* species and *Melosperma* as a set of cells around the base of the ovary (Simpson et al. 1990, Sérsic & Cocucci 1999). Although in *Monttea* the nectar production appears only in the beginning of anthesis and in *Melosperma* they are not produced in collectable quantities (Sérsic & Cocucci 1999). The trichomatic elaiophores in *Monttea* are densely concentrated in the sacs, but also dispersed in other parts of inner corolla, while *Melosperma andicola* present some glandular trichomes in the inner corolla, but no secretion was detected (Sérsic & Cocucci 1999).

## Oil-Collecting Bees in Neotropical Region

Oil-collecting behavior in bees occur in species of Melittinae and Apinae, classified in two lineages within Apidae (one family based classification of bees, see Melo & Gonçalves 2005). In Apinae the oil-collecting behavior is polyphyletic according to morphological (Roig-Alsina & Michener 1993) and molecular phylogenies (Cardinal et al. 2010), and this behavior is present in four tribes: Centridini, Ctenoplectrini, Tapinotaspidiini and Tetrapediini.

The elaiophores' morphological types, as well as their position, size and other flower characters, are related to morphological adaptations and the bees' behavior (Vogel 1974, Neff & Simpson 1981, Buchmann 1987, Cocucci et al. 2000). The morphological features

associated with oil gathering include combs, setae and plumose hairs on the anterior and/or middle legs, or on the sternum in females and males (Neff & Simpson 1981, Cocucci et al. 2000, Aguiar & Melo 2007, Taniguchi 2010). Females use floral oils to line the surface of the nest cell wall and mix it with pollen to feed larvae (Buchmann 1987, Cane et al. 1983). The males of Tetrapediini and Tapinotaspidini also collect floral oil for still unknown purposes (Vogel & Machado 1991, Aguiar & Melo 2009, Cappellari et al. 2011).

In the Neotropical region, oil-collecting bees are represented by the genera *Centris* (230 species), *Epicharis* (31), *Tetrapedia* (28) and 13 genera within Tapinotaspidini (130 species) (Moure et al. 2012, Aguiar 2007), all of these species being solitary and wood- or ground-nesting bees (Alves-dos-Santos et al. 2007). All *Centris* bees collect floral oils, except for some species in the subgenera *Paracentris*, *Penthemisia* and *Wagenknechtia*, which presumably do not collect oils (Michener 2007). *Centris* species collect floral oils in Calceolariaceae, Iridaceae, Krameriaceae, Malpighiaceae, Orchidaceae, Plantaginaceae and Solanaceae (Vogel 1974, Simpson et al. 1977, Cocucci 1991, Simpson et al. 1990, Vogel & Machado 1991, Rasmussen 1999). Some species can exploit remarkably different flowers, for example *Centris* (*Heterocentris*) *analís*, collects floral oils in Malpighiaceae (Oliveira & Schlindwein 2009) and in the flowers of *Angelonia* (Plantaginaceae) (Martins et al. 2013). Females of *Centris* (*Paracentris*) and *C.* (*Wagenknechtia*) are more strongly associated with Plantaginaceae flowers and have some modifications in their oil-collecting apparatuses (Simpson et al. 1990).

A great diversity of morphological traits associated with oil collection is characteristic of Tapinotaspidini bees (Roig-Alsina 1997, Cocucci et al. 2000). Tapinotaspidini bees forage for oil on Malpighiaceae (Teixeira & Machado 2000), Orchidaceae (Vogel 1974, Mickelunas et al. 2006), Iridaceae (Cocucci & Vogel 2001), Solanaceae (Cocucci 1991), Melastomataceae (Buchmann & Buchmann 1981), Krameriaceae (Simpson 1989), Calceolariaceae (Rasmussen 1999) and Plantaginaceae flowers (Vogel & Machado 1991, Aguiar & Melo 2009).

Bees of the genus *Tetrapedia* (Tetrapediini) collect floral oils from Plantaginaceae (*Angelonia*) (Vogel & Machado 1991), Iridaceae (*Sysirinchium*) (Alves-dos-Santos 1999), Orchidaceae (*Oncidium*) (Singer & Cocucci 1999) and Malpighiaceae (Buchmann 1987). They make illegitimate flower visits to all of these families, and do not contact the reproductive organs while gathering the oil resource. In *Tetrapedia*, the oil-collecting apparatus consists of a comb on the external margin of the anterior basitarsus (Neff & Simpson 1981, Alves-dos-Santos et al. 2006).

## Plantaginaceae Oil-Flowers and Interaction with Oil Bees

The flowers of Plantaginaceae species in the *Angelonia* clade are visited by female and/or male bees that can collect pollen, oil and/or nectar, depending on the genera. All 26 *Angelonia* species produce floral oils, and the oil-collecting visitors are known for ten species (Table 1). Some non-oil-collecting bees were also recorded (such as stingless bees), collecting pollen on the flowers (Martins et al. 2013). For the *Basistemon* species, only the visitors of *B. spinosus* and *B. silvaticus* are known and they visit the flowers to collect oil and pollen (Table 1). The only recorded oil-collecting visitor of the *Monopera* genus is *Caenonomada bruneri* (Aguiar & Melo 2009). For *Monttea*, visits by some species of *Centris* (*Paracentris*) and *Centris* (*Wagenknechtia*) (Table 1) have been recorded to collect oil, besides *Bombus opifex* and *Xylocopa* sp. to collect nectar (Simpson et al. 1990, Sérsic & Cocucci 1999). *Melosperma andicola*, which produces

only pollen and a small quantity of nectar, has no recorded visitors (Sérsic & Cocucci 1999).

The morphology of the flowers requires only the use of the anterior pair of legs for the collection of floral oils, and the contact with the fertile organs occurs on the head or mesoscutum (Martins et al. 2013). The pollen transfer in some *Angelonia*, in *Monttea chilensis*, *M. schickendantzii*, *Basistemon spinosus* and *B. silvaticus* occurs through the frons of oil-bees or mesoscutum in other *Angelonia* species (Vogel & Machado 1991, Vogel & Cocucci 1995, Sérsic & Cocucci 1999, Martins et al. 2013). In *Monttea aphylla*, the ventral position of the stamens favored a sternotribic deposition of pollen (Sérsic & Cocucci 1999).

Aside from the two well-defined “oil-sacs”, the corolla of *Angelonia* flowers possesses the calluses, which oblige pollinators to enter the flower in the correct position (Vogel 1974, Vogel & Machado 1991, Machado et al. 2002, Martins et al. 2013). In general the flowers of *Angelonia* are pollinated by bees of the genus *Centris*, although they are also visited by other oil-collecting bees, for example *Caenonomada*, *Arhysoceble* and *Paratetrapedia* (Tapinotaspidini) bees. Usually the oil-bees visiting *Angelonia* flowers are generalists in terms of their oil sources, visiting also other plants such as Malpighiaceae and Krameriaceae species. *Centris* (*Xanthemisia*) *bicolor*, for example, visits Malpighiaceae flowers, as well as *Angelonia eryostachis* flowers (Martins et al. 2013).

The most evident specialization among *Angelonia* and oil-collecting bees was observed in *A. cornigera*, whose pollinators, *Tapinotaspis nordestina* (Tapinotaspidini) and *Centris hyptidis*, possess a disproportionately long pair of legs which allows them to exploit the deep oil sacs of this species (Machado et al. 2002). Among the oil-collecting bees, this evidence of adaptation is remarkable, and it was also observed in the African genus *Rediviva* (Steiner & Whitehead 1990). However *Centris hyptidis* is also able to visit other oil sources that are very distinct from *Angelonia*, such as Krameriaceae flowers (A.J.C. Aguiar, personal communication), which do not require elongated legs to access their oil sacs. Other species of *Centris* that are closely related to *C. hyptidis* do not possess this morphological adaptation to *Angelonia* flowers, despite being visitors to *Angelonia* as well (Martins et al. 2013). The same kind of adaptation was not observed in *Caenonomada* (Tapinotaspidini), another legitimate visitor of *A. cornigera* (Aguiar & Melo 2009). Consequently, the evidence of strict adaptation to *Angelonia* observed by Machado et al. (2002) has been challenged by new evidence, and further study is required in order to understand how the co-adaptation between these partners occurred.

Flowers of *Monttea* (Figure 1b) produce floral oils that are collected by *Centris* bees of the subgenera *Wagenknechtia*, *Paracentris* and *Penthemisia* (Simpson et al. 1990, Sérsic & Cocucci 1999). *Monttea aphylla* is visited by *Centris* (*Penthemisia*) *brethesi* and *Centris* (*Wagenknechtia*) *vardyorum*, and both species use anterior legs that possess pads of specialized setae with a high capacity for oil absorption (Simpson et al. 1990, Tadey 2011). *Monttea chilensis* and *M. schickendantzii* also are visited by *Paracentris* species, which also collect with the forelegs by oil absorption (Sérsic & Cocucci 1999). In contrast with the most common four-legged pattern of oil-collecting apparatus in *Centris* (Neff & Simpson 1981) the specialized visitor of *Monttea* and some *Angelonia* species have the apparatus restricted to the anterior pair of legs, where absorptive hairs replaced the oil scrapers used to grasp the epithelial elaiophors of malpighs (Simpson et al. 1990, Machado et al. 2002). Instead of being a regular source of energy, the nectaries in *Monttea* are suggested as a stimulator by taste to stretch the proboscis and turn the head upwards and intensify the contact with anthers (Sérsic &

Cocucci 1999). All oil-collecting bees registered in *Monttea* collect also nectar (Sérsic & Cocucci 1999).

In northern Argentina *Arhysoceble* aff. *huberi* (Ducke, 1908) pollinates *B. spinosus* (Vogel & Cocucci 1995), while in a Chaco vegetation area in Brazil *Centris hyptidoides* and *Caenomada* spp perform this task (Martins et al., 2013.). The flower visitors of the non-oil-producing *Basistemon* are unknown. We assume, however, that they are pollen collectors such as Halictini and Meliponini bees, because, considering the floral morphology of these flowers, pollen is probably the only resource they offer. In *Monttea* (Simpson et al. 1990) and *Angelonia* (Vogel & Machado 1991, Machado et al. 2002) these pollen collectors make illegitimate visits and they rarely or never act as pollinators.

The only one brief study reported interactions between *M. perennis* and *Caenomada bruneri* (Tapinotaspidini), an oil-collecting bee that also visits *A. salicariifolia* (Aguiar & Melo 2009). The characteristics of the interaction, however, in terms of the efficiency of flower visitors and the collecting behavior of the bees, remain totally unknown.

## Concluding Remarks

Despite some advances over the last 20 years, knowledge of the biological aspects of oil-producing Plantaginaceae species and of interactions between these species and oil-collecting bees can still be greatly improved. Due to the rarity of most species, for many of them their basic aspects are completely unknown. Even for the best-known genus, *Angelonia*, only three papers investigating ten of the almost 30 species of the group are available in the literature. Some aspects of these interactions, such as the morphological evolution of the oil sacs, the presence of calluses in the corolla and the pollination of non-oil-producing species of the *Angelonia* clade, should be investigated in order to clarify the evolution of mutualism between oil-bees and oil-flowers. Besides, other topics, as the chemistry of the oil-production, the role of the shifts to pollen or nectar as a reward in the reproduction of those plants is still completely unknown. It is important to mention that most species of the cited genera occur in highly endangered ecosystems in South America, and it is possible that many will become extinct without any further information being collected.

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