



A literature review of the pollination strategies and breeding systems in Oncidiinae orchids

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ABSTRACT

Oncidiinae is an exclusively Neotropical orchid subtribe with about 1600 described species and an impressive array of vegetative and floral morphological adaptations. We present the results of a literature survey on the pollination strategies and breeding systems of this orchid subtribe. The flowers are pollinated by a wide range of insects (mostly bees) and, sometimes, hummingbirds. Several genera reward their pollinators with floral resources such as oils, nectar or perfumes. Whereas pollination by oil-gathering bees likely evolved several times within Oncidiinae, exclusive pollination by perfume-gathering male Euglossine bees is likely restricted to a set of closely-related genera. Pollination by food or sexual deception is also present within the subtribe. Up to date, the pollen-vectors of the 92 species of Oncidiinae studied so far are as follows: 84.7 % are pollinated by bees, 6.5 % by wasps, 4.3 % by hummingbirds, 3.2 % by butterflies and 3.2 % by flies. Oncidiinae orchids are preferentially self-incompatible (69.4 % of the species studied so far), some may also present protandry as a mechanism to promote cross-pollination. Fruiting success is generally low. The rate of visitation with subsequent pollination is low, in general, which contributes to the low reproductive success of this plant group.

Keywords: breeding systems, deception, elaiophores, fruiting success, nectaries, Oncidiinae, orchids, osmophores, pollination strategies

Introduction

Orchid flowers and their structures have long been studied in detail by researchers from all around the world, lured by their high potential as ornamental plants (Dressler 1961; 1974; Pijl & Dodson 1966; Cingel 2001). One of the most representative orchid subtribes is Oncidiinae (Epidendroideae: Cymbidieae), which shares with

Pleurothallidinae the largest numbers of species within the Neotropics (Chase *et al.* 2009; 2015). In its current circumscription, the subtribe holds 65 genera and about 1600 species (Chase 2009; Neubig *et al.* 2012; Chase *et al.* 2015). Givnish *et al.* (2015) dated the divergence time of the Oncidiinae to approximately 20 my. The geographical distribution of the subtribe ranges from southern United States and northern Mexico to southern Brazil and northern

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Argentina. They comprise terrestrial or epiphytic herbs, inhabiting a wide variety of environments, from well-drained hill slopes to wetlands. They normally bear sympodial growth, uninodal pseudobulbs and distichous and bifacial leaves (Chase 2009) (Fig. 1). The flowers of Oncidiinae orchids generally feature lips much bigger than the rest of the perianth, often presenting ornamentations – the so-called “callus” or “calli” (Fig. 1) – or secretions, which serve as attractors to pollinators or floral visitors. They also may present a thickened structure on the base of the column, the tabula infrastigmatica (Fig. 1). This structure is supposed to assist in the stabilization of floral visitors, which grab the tabula while foraging for floral rewards (Dressler 1981; 1993). Lastly, it is important to highlight the presence of a complex pollinarium bearing 2 or 4 indivisible pollinia. In the practice, such pollinia prompt the transfer of all the pollinic contents during a single or very few pollination events (Dressler 1993; Singer *et al.* 2006; Judd *et al.* 2009), facilitating the monitoring of pollen-flow during pollination studies.

Convergent evolution in response to functionally similar pollinators may be responsible for similar floral traits (Fig. 2) evolving within independent clades in Oncidiinae, in particular the development of oil-bee pollination in many non closely-related taxa (Papadopulos *et al.* 2013). These convergences were misinterpreted by early taxonomists, a fact that created considerable taxonomic problems in the subtribe. Until the end of the last decade, the taxonomic and phylogenetic relationships among Oncidiinae genera were not clear, because several genera were usually described based upon few morphological features that were proven not to reflect the actual parental relations between the taxa (Faria 2004). In *Genera Orchidacearum* (Chase 2009) is presented a phylogenetic framework based on DNA analyses, with a robust generic sampling, clarifying some issues and proposing recircumscriptions in several genera. Neubig *et al.* (2012) produced a phylogeny based on plastid and nuclear loci of 590 species of Oncidiinae, largely corroborating the results of the previous work (Chase 2009). *Oncidium*, the type genus of the subtribe, has always been on debate due to the inconsistent traditional boundaries assumed over the years. In its broader delimitation, it covers more than 400 species popularly known as “dancing ladies” or “golden shower orchids”, defined by the characteristic callosity observed in the lip, resembling tumors (from the greek word “onkos” = swelling or tumor). It was not a surprise when studies involving molecular characters, such as this of Chase & Palmer (1992) using plastid DNA and this of Williams *et al.* (2001a; b) using plastid and nuclear DNA sequences, proved that *Oncidium* in a broader sense is a polyphyletic grouping. With the advent of cladistic methods allied to analyses of molecular characters, *Oncidium sensu lato* was recircumscribed and several species were transferred to different genera (Chase *et al.* 2009; Chase & Whitten 2011; Neubig *et al.* 2012).

To our knowledge, the first studies of Oncidiinae regarding aspects of reproductive biology are the preliminary observations of Darwin (1885) that paid attention on column/pollinarium structure and eventually mentions fragmentary information from his correspondent (especially Johann Friedrich Fritz Muller, that was based on Santa Catarina – Southern Brazil – and made some preliminary observations on a species of *Gomesa*). Much later, Pijl & Dodson (1966) compiled numerous reports. However, as already noticed for other authors (Caballero-Villalobos *et al.* 2017) most of these observations are limited to the mere observation of bees/hummingbirds onto flowers, without really proving that these animals acted as pollen-vectors. Indeed, some of the suggestions made by Pijl & Dodson (1966), such as the existence of pollination through pseudoantagonism need to be reappraised under a new light, owing to new evidences (see below). Many years later, Cingel (2001) published a comprehensive treatise on orchid pollination, but kept many of the preliminary (and sometimes, erroneous) inferences found in Pijl & Dodson (1966). More recently, Chase (2009) compiled all the known information up to the date and discussed some of the issues of the previously mentioned works, being a more reliable and updated source of information on pollination within Oncidiinae.

In spite of the increasing interest on the pollination biology of orchids during the last decades, an overview of the Oncidiinae orchids is still lacking. The study of the pollination biology of these plants frequently poses important problems that prevent a quick increase of the available information. Many times, these plants are rare or do not form large or accessible populations. Even when the number of individuals is large enough within a small area, plants may not flourish satisfactorily in quantitative terms (not all individuals flower) or flower irregularly, therefore not drawing sufficient attention from potential pollinators.

Methods

This compilation focuses mainly on pollination strategies, but also provides information on breeding systems and fruiting successes among the species of this subtribe. We followed the circumscription of Oncidiinae as proposed by Chase (2009) and Neubig *et al.* (2012). In our bibliographic revision, we considered pollinators all the visitors that were seen or captured carrying pollinaria of a given orchid species, since an insect carrying a pollinarium is very likely to be a pollinator of the species that produced the pollinarium, according to Dressler (1976). The names of plants followed The International Plant Names Index (IPNI 2019) and The Plant List (2019) and names of animals were checked at Global Biodiversity Information Facility (GBIF 2019) and Integrated Taxonomic Information System (ITIS 2019) databases. Our aims are to elucidate (1) the



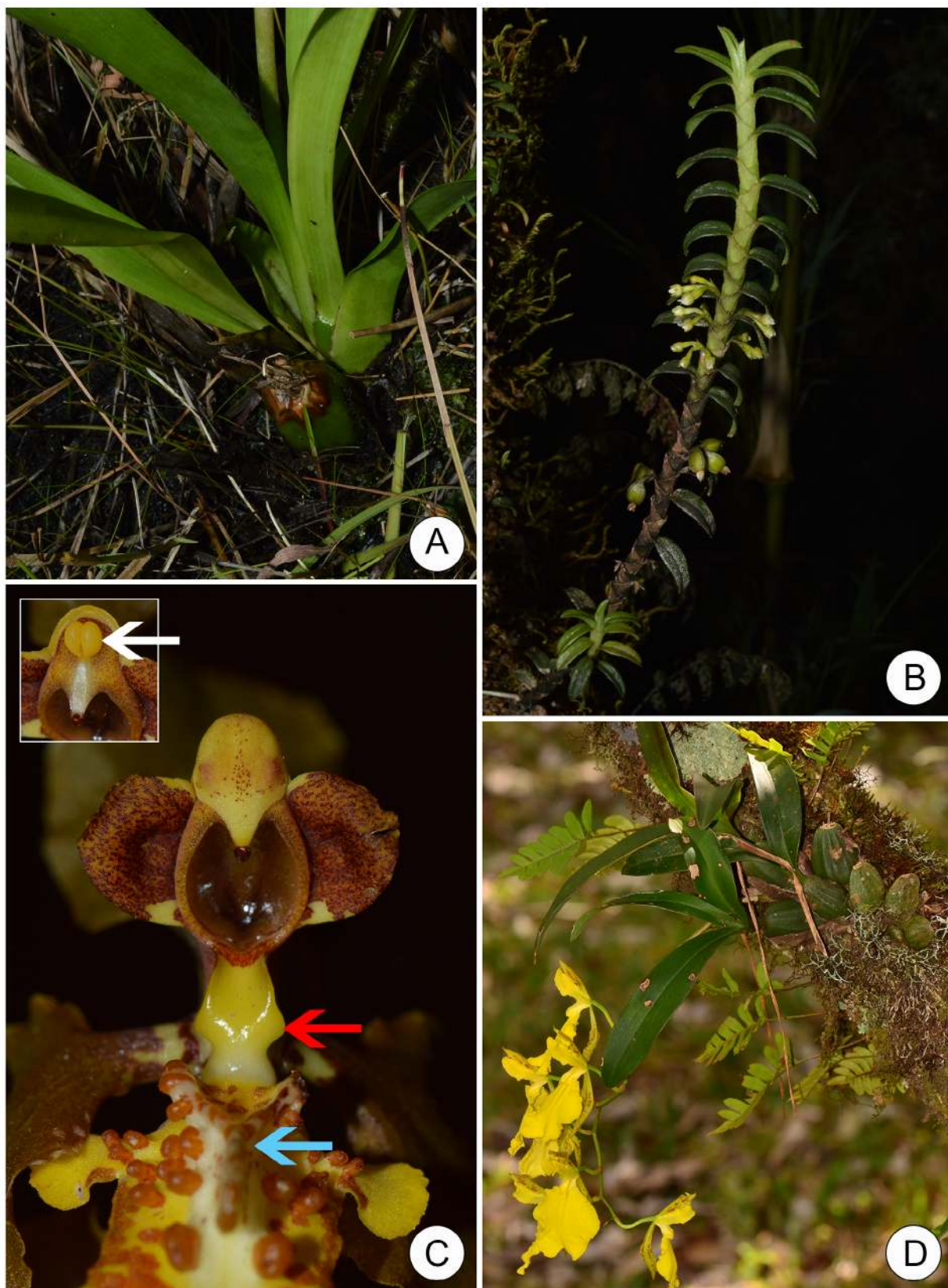


Figure 1. Habits, growth types and morphological features of the Oncidiinae. **A.** The terrestrial *Gomesa hydrophila*, adapted to wetlands; **B.** Monopodial growth and distichous leaves in an unidentified species of *Fernandezia*; **C.** Detail of pollinia (white arrow), tabula infrastigmatica (red arrow) and the callus (light blue arrow) in flower of *Gomesa imperatoris-maximiliani*; **D.** Epiphytism, uninodeal pseudobulbs and sympodial growth in the “oncidoid” orchid *Gomesa concolor*.



pollination strategies based upon the presence or absence of a given floral reward and the group of animals involved in each case; (2) the breeding systems; and (3) the fruiting success represented by the natural observed fruit set of the orchids. Results are organized based on the floral resource (or absence of it) offered by each group of orchids. At each section (strategy), we address important works regarding the subject matter; the type of resource and main chemical compounds (if applicable); the secretory structures and their locations (if applicable); the pollinators and their behaviors; studies of cases; and the group of orchids that present each strategy.

Pollination strategies

Floral oils

Elaiophores (oil-secreting glands) are present in a number of Angiosperm families (reviewed in Renner & Schaefer 2010 and Possobom & Machado 2017), mainly from the Americas, but also from Southern Africa. So far, this pollination strategy is known to occur within the families Calceolariaceae, Cucurbitaceae, Iridaceae, Krameriaceae, Malpighiaceae, Orchidaceae, Plantaginaceae, Primulaceae, Scrophulariaceae, Solanaceae and Stillbaceae

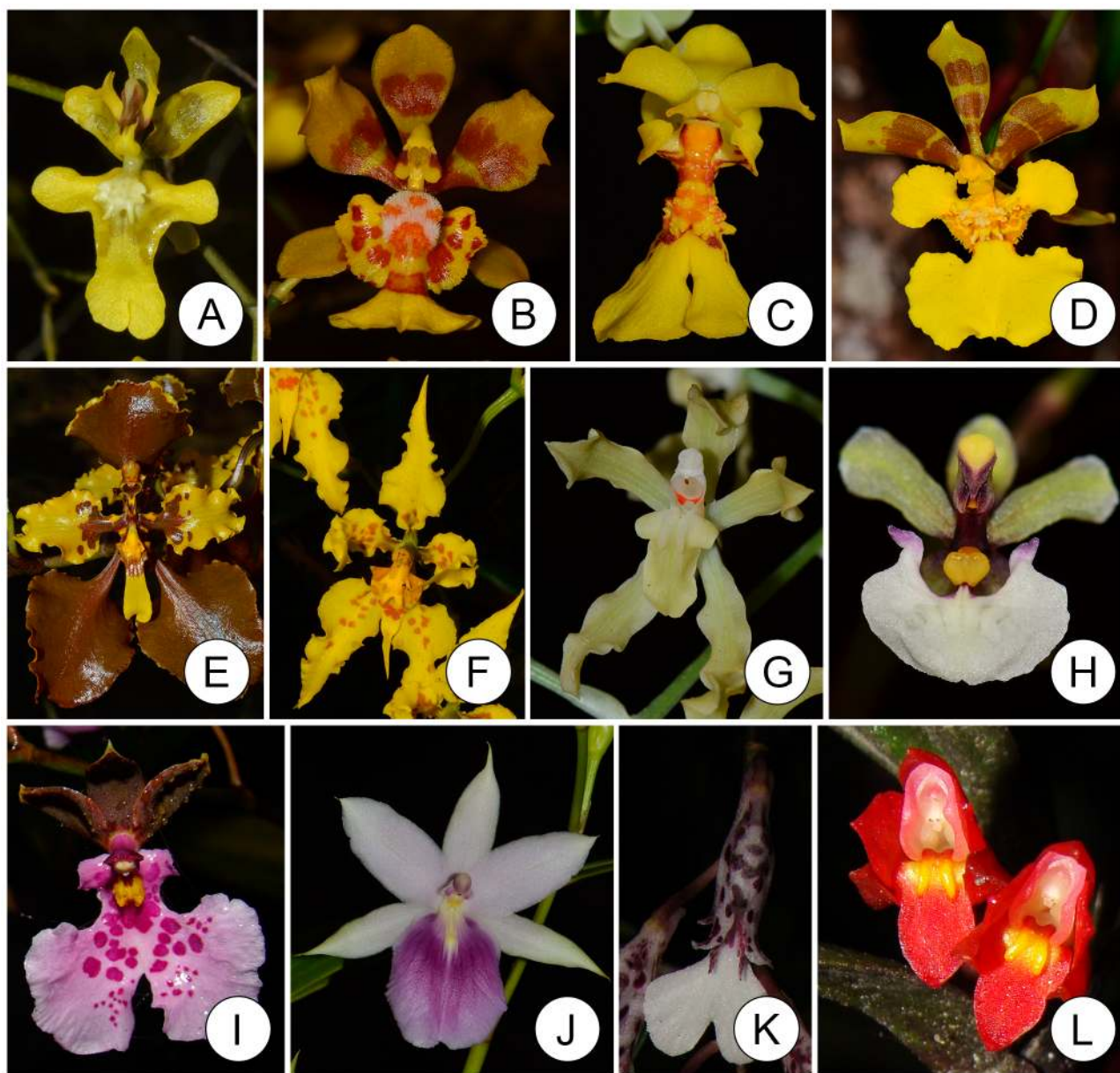


Figure 2. Diversity of flowers within Oncidiinae. Note the representativeness of yellow/brown flowers (A-F), corresponding to the “oncidioid” orchids. **A.** *Oncidium ornithorrhynchum*; **B.** *Grandiphyllum divaricatum*; **C.** *Lockhartia lunifera*; **D.** *Gomesa longipes*; **E.** *Cyrtorchilum tetracopis*; **F.** *Cyrtorchilum auropurpureum*; **G.** *Gomesa crispa*; **H.** *Gomesa radicans*; **I.** *Caucaea* sp.; **J.** *Miltonia regnellii*; **K.** *Rodriguezia decora*; **L.** *Fernandezia* sp.

(Renner & Schaefer 2010; Possobom & Machado 2017). Solitary bees of different Apidae tribes (Renner & Schaefer 2010; Possobom & Machado 2017) gather these oils and mix them with pollen, in order to nurture their larvae. From a chemical point of view, these oils are mainly acyl-glycerols and hydrocarbons (Reis *et al.* 2000; 2006; 2007; Reis 2005; Singer *et al.* 2006). Vogel (1969; 1974) was the first researcher to demonstrate the existence of elaiophores in Orchidaceae and other families of plants. The locations and features of these glands have been elucidated in anatomical (Singer & Cocucci 1999a; Alcántara *et al.* 2006; Pácek & Stpiczynska 2007; Stpiczynska *et al.* 2007;

2013; Stpiczynska & Davies 2008; Davies & Stpiczynska 2009; Aliscioni *et al.* 2009; Pácek *et al.* 2012; Blanco *et al.* 2013; Gomiz *et al.* 2013; 2014; 2017; Davies *et al.* 2014) and chemical (Reis *et al.* 2000; 2007; Silvera 2002) studies. These works described the morphological structure of the elaiophores and characterized their secretions, supporting the possibility that oil-collecting bees perform their pollination, as a result of deliberate gathering behavior (Singer *et al.* 2006; Torretta *et al.* 2011). In fact, some species produce sufficient quantity of floral oils (mainly acyl-glycerols) and offer them as a reward to pollinators (Tab. 1).

Table 1. Pollinators, floral resources and pollination strategies in Oncidiinae orchids. Reward uncertain/Strategy uncertain = We make this assumption for the studies that do not clearly indicate the gathering of a floral reward by the pollinators, and we may make inferences on the possible pollination strategy based upon floral features and closely related taxa. * = Misidentification.

Oncidiinae species and synonyms in literature	Pollination features (1) Pollinator group; (2) Floral resource aimed; (3) Pollination strategy	Pollinator species	References for pollinators and floral resources
<i>Aspasia principissa</i> Rchb.f.	(1) Euglossini bees (2) Nectar, absent (3) Deception of nectar	<i>Eulaema bombiformis</i> (Packard, 1869); <i>Eulaema cingulata</i> (Fabricius, 1804); <i>Eulaema meriana</i> (Olivier, 1789); <i>Eulaema nigrita</i> Lepeletier, 1841; <i>Exaerete frontalis</i> (Guérin-Méneville, 1845); <i>Exaerete smaragdina</i> (Guérin-Méneville, 1845)	Williams (1974; 1982); Ackerman (1983); Roubik & Ackerman (1987); Zimmerman & Aide (1989)
<i>Aspasia psittacina</i> (Rchb.f.) Rchb.f. * <i>Aspasia epidendroides</i> Lindl.	(1) Euglossini bees (2) Nectar, absent (3) Deception of nectar	<i>Eulaema cingulata</i> (Fabricius, 1804); <i>Eulaema polychroma</i> (Mocsáry, 1899) - mistakenly identified as <i>Eulaema tropica</i> L.	Dodson & Frymire (1961b); Pijl & Dodson (1966); Williams (1974; 1982)
<i>Brassia antherotes</i> Rchb.f.	(1) Wasps (2) Nectar, absent (3) Deception of nectar	Unidentified Vespidae	Ospina-Calderón <i>et al.</i> (2007)
<i>Brassia</i> aff. <i>arcuigera</i> Rchb.f. * <i>Brassia</i> aff. <i>antherotes</i> Rchb.f.	(1) Wasps (2) Reward uncertain (3) Strategy uncertain, pseudoantagonism (misinterpretation)	<i>Campsomeris columba</i> (Saussure, 1858)	Pijl & Dodson (1966); Dodson (1990)
<i>Brassia ochroleuca</i> Barb.Rodr.	(1) Wasps (2) Reward uncertain (3) Strategy uncertain, pseudoantagonism (misinterpretation)	<i>Pepsis</i> sp. (<i>Pepsis gloriosa</i> ?)	Pijl & Dodson (1966); Dodson (1990)
<i>Capanemia thereziae</i> Barb.Rodr.	(1) Wasps (2) Nectar (3) Supply of nectar	<i>Polybia fastidiosuscula</i> de Saussure, 1854	Singer & Cocucci (1999a); Buzatto <i>et al.</i> (2012)
<i>Cischweinfia dasyandra</i> (Rchb.f.) Dressler & N.H.Williams	(1) Euglossini bees (2) Nectar, absent (3) Deception of nectar	Unidentified Euglossini bees	Williams (1982); Chase (2009)
<i>Comparettia coccinea</i> Lindl.	(1) Butterflies (2) Nectar (3) Supply of nectar	<i>Heliconius erato phyllis</i> Fabricius, 1775; <i>Heliconius ethilla narcaea</i> Godart, 1819	Pansarin <i>et al.</i> (2015)
<i>Comparettia falcata</i> Poepp. & Endl.	(1) Hummingbirds (2) Nectar (3) Supply of nectar	<i>Amazilia tzacatl</i> (De la Llave, 1833); <i>Chlorostilbon maugaeus</i> (Audebert & Vieillot, 1801)	Dodson (1965); Pijl & Dodson (1966); Vogel (1969); Rodríguez-Robles <i>et al.</i> (1992); Ackerman <i>et al.</i> (1994); Meléndez-Ackerman <i>et al.</i> (1997)



Table 1. Cont.

Oncidiinae species and synonyms in literature	Pollination features (1) Pollinator group; (2) Floral resource aimed; (3) Pollination strategy	Pollinator species	References for pollinators and floral resources
<i>Cyrtochiloides ochmatochila</i> (Rchb.f.) N.H.Williams & M.W.Chase = <i>Oncidium ochmatochilum</i> Rchb.f.	(1) Oil-collecting bees (2) Reward uncertain (3) Strategy uncertain	<i>Centris</i> sp.	Dodson (1965); Pijl & Dodson (1966)
<i>Cyrtochilum macranthum</i> (Lindl.) Kraenzl. = <i>Oncidium macranthum</i> Lindl.	(1) Oil-collecting bees and Bombini bees (2) Reward uncertain (3) Strategy uncertain	<i>Bombus hortulanus</i> Smith, 1904; <i>Centris</i> sp.	Dodson (1962; 1965); Pijl & Dodson (1966)
cf. <i>Gomesa</i> sp, = <i>Oncidium</i> sp.	(1) Oil-collecting bees (2) Reward uncertain (3) Probably supply of floral oils	<i>Tetrapedia rugulosa</i> Friese, 1899	Schlindwein (1995; 1998)
<i>Gomesa bifolia</i> (Sims) M.W.Chase & N.H.Williams	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Centris trigonoides</i> Lepeletier, 1841	Aliscioni <i>et al.</i> (2009); Torretta <i>et al.</i> (2011)
<i>Gomesa</i> cf. <i>blanchetii</i> (Rchb.f.) M.W.Chase & N.H.Williams * <i>Gomesa montana</i> (Barb.Rodr.) M.W.Chase & N.H.Williams	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Centris analis</i> (Fabricius, 1804)	Pansarin <i>et al.</i> (2016)
<i>Gomesa cornigera</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Baptistonia cornigera</i> (Lindl.) Chiron & V.P.Castro = <i>Baptistonia fimbriata</i> (Lindl.) Chiron & V.P.Castro = <i>Oncidium cornigerum</i> Lindl. = <i>Oncidium fimbriatum</i> Lindl.	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Paratetrapedia fervida</i> (Smith, 1879); <i>Tetrapedia diversipes</i> Klug, 1810	Singer (2003); Reis <i>et al.</i> (2003; 2007); Faria (2004); Reis (2005); Singer <i>et al.</i> (2006); Chiron (2008; 2010); Chiron <i>et al.</i> (2009); Pansarin & Pansarin (2010; 2011); Gomiz <i>et al.</i> (2017)
<i>Gomesa paranensisoides</i> M.W.Chase & N.H.Williams = <i>Oncidium paranense</i> Kraenzl.	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Tetrapedia diversipes</i> Klug, 1810	Singer & Cocucci (1999a); Singer (2004); Singer <i>et al.</i> (2006)
<i>Gomesa pubes</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Baptistonia pubes</i> (Lindl.) Chiron & V.P.Castro = <i>Oncidium pubes</i> Lindl.	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Tetrapedia</i> sp.; <i>Tetrapedia diversipes</i> Klug, 1810	Reis <i>et al.</i> (2000; 2003); Singer (2003; 2004); Faria (2004); Reis (2005); Singer <i>et al.</i> (2006); Reis <i>et al.</i> (2007); Chiron (2008; 2010); Chiron <i>et al.</i> (2009); Pansarin & Pansarin (2010)
<i>Gomesa varicosa</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium varicosum</i> Lindl.	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Centris</i> sp.; <i>Epicharis flava</i> (Friese, 1900)	Reis (2005); Gomiz <i>et al.</i> (2013); Pansarin <i>et al.</i> (2016)
<i>Ionopsis</i> sp.	(1) Meliponini bees (2) Nectar, absent (3) Deception of nectar	<i>Trigona fulviventris</i> Guérin-Méneville, 1845	Roubik (2000)
<i>Ionopsis utricularioides</i> (Sw.) Lindl.	(1) Oil-collecting bees, Ceratinini bees, Meliponini bees and Halictidae bees (2) Nectar, absent (3) Deception of nectar	<i>Augochlora</i> sp.; <i>Ceratina</i> sp.; <i>Nannotrigona</i> <i>testaceicornis</i> (Lepeletier, 1836); <i>Paratetrapedia flaveola</i> Aguiar & Melo, 2011; <i>Paratrigona lineata</i> (Lepeletier, 1836)	Montalvo & Ackerman (1987); Pansarin & Pansarin (2010); Aguiar (2014); Aguiar & Pansarin (2019)
<i>Leochilus</i> sp.	(1) Wasps (2) Reward uncertain (3) Probably supply of nectar	<i>Pachodynerus nassidens</i> (Latreille, 1812)	Pijl & Dodson (1966)



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<i>Leochilus labiatus</i> (Sw.) Kuntze	(1) Halictidae bees (2) Nectar (3) Supply of nectar	<i>Lasioglossum (Dialictus)</i> sp.	Chase (1986)
<i>Leochilus scriptus</i> (Scheidw.) Rchb.f.	(1) Wasps (2) Nectar (3) Supply of nectar	<i>Stelopolybia areata</i> (Say); <i>Stelopolybia hamiltoni</i> Richards, 1978	Chase (1986)
<i>Macradenia brassavolae</i> Rchb.f.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa hemichlora</i> Cockerell, 1917; <i>Euglossa villosiventris</i> Moure, 1968	Williams (1982); Singer <i>et al.</i> (2006)
<i>Macradenia paraensis</i> Barb.Rodr. * <i>Macradenia multiflora</i> (Kraenzl.) Cogn.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Eufriesea violacea</i> (Blanchard, 1840); <i>Euglossa</i> sp.	Essinger (2005); Koch (2016)
<i>Macroclinium lineare</i> (Ames & C.Schweinf) Dodson = <i>Notylia linearis</i> Ames & C.Schweinf.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa cybelia</i> Moure, 1968; <i>Euglossa deceptrix</i> Moure, 1968; <i>Euglossa dodsoni</i> Moure, 1965; <i>Euglossa dressleri</i> Moure, 1968	Roubik & Ackerman (1987)
<i>Macroclinium wulschlaegelianum</i> (H.Focke) Dodson = <i>Notylia wulschlaegeliana</i> H.Focke	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Eufriesea surinamensis</i> (Linnaeus, 1758) = <i>Euplusia surinamensis</i> (Linnaeus, 1758);	Pijl & Dodson (1966); Dodson (1967); Williams (1982);
<i>Macroclinium xiphophorus</i> (Rchb.f.) Dodson = <i>Notylia xiphophorus</i> Rchb.f.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Eufriesea surinamensis</i> (Linnaeus, 1758) = <i>Euplusia surinamensis</i> (Linnaeus, 1758);	Dodson & Frymire (1961b); Pijl & Dodson (1966); Dodson (1967); Williams (1982)
<i>Miltoniopsis warszewiczii</i> (Rchb.f.) Garay & Dunst. = <i>Miltonia endresii</i> G.Nicholson	(1) Colletidae bees (2) Reward uncertain (3) Strategy uncertain	<i>Ptiloglossa ducalis</i> Smith, 1853	Dodson (1965); Pijl & Dodson (1966)
<i>Notylia</i> sp. 1	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa dodsoni</i> Moure, 1965; <i>Euglossa tridentata</i> Moure, 1970	Dressler (1968)
<i>Notylia</i> sp. 2	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa championi</i> Cheesman, 1929; <i>Euglossa mixta</i> Friese 1899; <i>Euglossa tridentata</i> Moure, 1970	Roubik & Ackerman (1987)
<i>Notylia</i> sp. 3	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa chalybeata iopocila</i> Dressler; <i>Euglossa sapphirina</i> Moure, 1968	Singer <i>et al.</i> (2006)
<i>Notylia albida</i> Klotzsch	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa hemichlora</i> Cockerell, 1917	Ackerman (1983); Roubik & Ackerman (1987)
<i>Notylia barkeri</i> Lindl.	(1) Euglossini bees (2) Perfumes (3) Supply of perfumes	<i>Euglossa dissimula</i> Dressler, 1978; <i>Euglossa tridentata</i> Moure, 1970; <i>Euglossa variabilis</i> Friese, 1899; <i>Euglossa viridissima</i> Friese, 1899	Ackerman (1983); Roubik & Ackerman (1987); Gerlach & Schill (1991); Warford (1992); Damon & Salas-Roblero (2007);



Table 1. Cont.

Oncidiinae species and synonyms in literature	Pollination features (1) Pollinator group; (2) Floral resource aimed; (3) Pollination strategy	Pollinator species	References for pollinators and floral resources
<i>Notylia</i> aff. <i>barkeri</i> Lindl.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa</i> sp.; <i>Euglossa hansonii</i> Moure, 1965; <i>Euglossa ignita</i> Smith, 1874; <i>Euglossa tridentata</i> Moure, 1970	Pijl & Dodson (1966); Dodson (1967); Dressler (1968); Williams (1982)
<i>Notylia</i> cf. <i>barkeri</i> Lindl.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa</i> sp.; <i>Euglossa erythrochlora</i> Moure, 1968;	Pijl & Dodson (1966); Dodson (1967); Dressler (1968); Williams (1982)
<i>Notylia buchtienii</i> Schltr.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa augaspis</i> Dressler, 1982	Dodson (1965; 1967); Pijl & Dodson (1966); Williams (1982); Gerlach & Schill (1991)
<i>Notylia</i> cf. <i>buchtienii</i> Schltr.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa ignita</i> Smith, 1874	Dodson (1965; 1967); Pijl & Dodson (1966); Williams (1982)
<i>Notylia</i> cf. <i>durandiana</i> Cogn.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa</i> sp.; <i>Eulaema nigrita</i> Lepeletier, 1841	Singer & Koehler (2003)
<i>Notylia</i> cf. <i>longispicata</i> Hoehne & Schltr.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa chalybeata iopocila</i> Dressler; <i>Euglossa sapphirina</i> Moure, 1968	Singer & Koehler (2003)
<i>Notylia nemorosa</i> Barb.Rodr.	(1) Euglossini bees (2) Perfumes (3) Supply of perfumes	<i>Eulaema nigrita</i> Lepeletier, 1841; <i>Euglossa melanotricha</i> Moure, 1967	Singer & Koehler (2003); Singer (2004); Singer <i>et al.</i> (2006)
<i>Notylia orbicularis</i> A.Rich & Galeotti = <i>Notylia tridachne</i> Lindl. & Paxton	(1) Euglossini bees (2) Perfumes (3) Supply of perfumes	<i>Euglossa viridissima</i> Friese, 1899	Warford (1992)
<i>Notylia panamensis</i> Ames	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa hemichlora</i> Cockerell, 1917	Pijl & Dodson (1966); Dodson (1967); Dressler (1968); Williams (1982)
<i>Notylia pentachne</i> Rchb.f.	(1) Euglossini bees (2) Perfumes (3) Supply of perfumes	<i>Euglossa cognata</i> Moure, 1970; <i>Eulaema bombiformis</i> (Packard, 1869); <i>Eulaema cingulata</i> (Fabricius, 1804); <i>Eulaema meriana</i> (Olivier, 1789); <i>Exaerete frontalis</i> (Guérin-Méneville, 1845)	Pijl & Dodson (1966); Dodson (1967); Dressler (1968); Williams (1982); Ackerman (1983); Roubik & Ackerman (1987)
<i>Notylia trisepala</i> Lindl. & Paxton	(1) Euglossini bees (2) Perfumes (3) Supply of perfumes	<i>Euglossa viridissima</i> Friese, 1899	Warford (1992)
<i>Notylia</i> cf. <i>trisepala</i> Lindl. & Paxton = <i>Notylia</i> cf. <i>turalbae</i> Schltr.	(1) Euglossini bees (2) Perfumes (3) Supply of perfumes	<i>Euglossa hansonii</i> Moure, 1965; <i>Euglossa tridentata</i> Moure, 1970	Dressler (1968)
<i>Oncidium hyphaematicum</i> Rchb.f.	(1) Oil-collecting bees (2) Reward uncertain (3) Strategy uncertain, pseudoantagonism (misinterpretation)	<i>Centris buchwaldi</i> Friese, 1901	Dodson & Frymire (1961a); Pijl & Dodson (1966)



Table 1. Cont.

Oncidiinae species and synonyms in literature	Pollination features (1) Pollinator group; (2) Floral resource aimed; (3) Pollination strategy	Pollinator species	References for pollinators and floral resources
<i>Oncidium kegeljani</i> (E.Morren) M.W.Chase & N.H.Williams = <i>Odontoglossum kegeljani</i> E.Morren	(1) Bombini bees (2) Nectar, absent (3) Deception of nectar	<i>Bombus hortulanus</i> Smith, 1904	Dodson (1962); Pijl & Dodson (1966)
<i>Oncidium planilabre</i> Lindl.	(1) Oil-collecting bees (2) Reward uncertain (3) Strategy uncertain, pseudoantagonism (misinterpretation)	<i>Centris geminata</i> Cockerell, 1914	Dodson & Frymire (1961a); Pijl & Dodson (1966)
<i>Oncidium roseum</i> (Lindl.) Beer = <i>Cochlioda rosea</i> (Lindl.) Benth.	(1) Hummingbirds (2) Nectar (3) Supply of nectar	Unknown hummingbirds	Dodson (1965); Pijl & Dodson (1966)
<i>Oncidium sphacelatum</i> Lindl.	(1) Oil-collecting bees (2) Floral oils, absent (3) Deception of floral oils	<i>Centris mexicana</i> Smith, 1854; <i>Centris nitida</i> Smith, 1874	Damon & Cruz-López (2006); Damon & Salas-Roblero (2007); Pemberton (2008)
<i>Oncidium vulcanicum</i> (Rchb.f.) M.W.Chase & N.H.Williams = <i>Cochlioda vulcanica</i> (Rchb.f.) Benth. & Hook.f. ex Rolfe	(1) Hummingbirds (2) Nectar (3) Supply of nectar	Unknown hummingbirds	Dodson (1965); Pijl & Dodson (1966)
<i>Ornithocephalus</i> sp.	(1) Euglossini bees (2) Reward uncertain, possibly seeking for nectar (3) Strategy uncertain	<i>Euglossa cybelia</i> Moure, 1968	Cingel (2001)
<i>Ornithocephalus bicornis</i> Lindl.	(1) Oil-collecting bees (2) Reward uncertain (3) Probably supply of floral oils	<i>Paratetrapedia calcarata</i> (Cresson, 1878)	Pijl & Dodson (1966); Brito (2001); Silvera (2002)
<i>Ornithocephalus ciliatus</i> Lindl. = <i>Ornithocephalus avicula</i> Rchb.f. = <i>Ornithocephalus kruegeri</i> Rchb.f.	(1) Oil-collecting bees (2) Reward uncertain (3) Probably supply of floral oils	<i>Paratetrapedia testacea</i> (Smith, 1854)	Dodson (1965); Pijl & Dodson (1966); Brito (2001); Pácek & Stpiczynska (2007)
<i>Ornithocephalus cochleariformis</i> C.Schweinf.	(1) Oil-collecting bees (2) Reward uncertain (3) Probably supply of floral oils	<i>Paratetrapedia</i> sp.	Brito (2001); Silvera (2002)
<i>Ornithocephalus</i> cf. <i>patentilobus</i> C.Schweinf.	(1) Oil-collecting bees (2) Reward uncertain (3) Probably supply of floral oils	<i>Paratetrapedia testacea</i> (Smith, 1854)	Dodson (1965); Pijl & Dodson (1966); Brito (2001)
<i>Ornithocephalus powellii</i> Schltr.	(1) Oil-collecting bees (2) Reward uncertain (3) Probably supply of floral oils	<i>Paratetrapedia calcarata</i> (Cresson, 1878)	Pijl & Dodson (1966); Brito (2001)
<i>Phymatidium delicatulum</i> Lindl.	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Tetrapedia amplatarsis</i> Friese 1989; <i>Trigonopedia</i> sp.	Brito (2001); Reis <i>et al.</i> (2006); Singer <i>et al.</i> (2006); Pácek <i>et al.</i> (2012); Cabral (2014)
<i>Rodriguezia bahiensis</i> Rchb.f.	(1) Xylocopini bees and flies (2) Nectar (3) Supply of nectar	<i>Philopota</i> sp.; <i>Xylocopa suspecta</i> Moure & Camargo, 1988	Carvalho & Machado (2006)



Table 1. Cont.

Oncidiinae species and synonyms in literature	Pollination features (1) Pollinator group; (2) Floral resource aimed; (3) Pollination strategy	Pollinator species	References for pollinators and floral resources
<i>Rodriguezia decora</i> (Lem.) Rchb.f.	(1) Butterflies (2) Nectar (3) Supply of nectar	<i>Ascia monuste</i> (Linnaeus, 1764); <i>Astraptus fulgurator</i> Walch, 1775; <i>Dryas iulia</i> Fabricius, 1775; <i>Urbanus dorantes</i> Stoll, 1790	Pansarin <i>et al.</i> (2018)
<i>Rodriguezia granadensis</i> (Lindl.) Rchb.f.	(1) Euglossini bees (2) Nectar (3) Supply of nectar	<i>Eulaema cingulata</i> (Fabricius, 1804); <i>Eulaema meriana</i> (Olivier, 1789); <i>Exaerete smaragdina</i> (Guérin-Méneville, 1845)	Ospina-Calderón <i>et al.</i> (2015)
<i>Rodriguezia lanceolata</i> Ruiz & Pav. = <i>Rodriguezia secunda</i> Kunth	(1) Hummingbirds and butterflies (2) Nectar (3) Supply of nectar	<i>Amazilia fimbriata</i> (Gmelin, 1788); <i>Amazilia versicolor</i> (Vieillot, 1818); <i>Heliconius hermathena</i> Hewitson, 1854	Dodson (1965); Braga (1977); Pansarin <i>et al.</i> (2018)
<i>Rodriguezia leeana</i> Rchb.f.	(1) Euglossini bees (2) Reward uncertain, (3) Probably supply of nectar	<i>Euglossa nigropilosa</i> Moure, 1965	Dodson (1965); Pijl & Dodson (1966); Williams (1982)
<i>Rosioglossum grande</i> (Lindl.) Garay & G.C.Kenn = <i>Odontoglossum grande</i> Lindl.	(1) Oil-collecting bees (2) Reward uncertain (3) Strategy uncertain	<i>Centris</i> sp.	Dodson (1965); Pijl & Dodson (1966)
<i>Telipogon peruvianus</i> T.Hashim	(1) Tachinid flies (2) Mates (3) Pseudocopulation	<i>Eudejeania</i> aff. <i>browni</i> Curran, 1941	Martel <i>et al.</i> (2016)
<i>Tolumnia bahamense</i> (Nash) Braem = <i>Oncidium bahamense</i> Nash	(1) Oil-collecting bees (2) Reward uncertain (3) Strategy uncertain, pseudoantagonism (misinterpretation)	<i>Centris versicolor</i> Fabricius, 1775	Nierenberg (1972)
<i>Tolumnia guibertiana</i> (A.Rich.) Braem	(1) Oil-collecting bees (2) Floral oils, absent (3) Deception of floral oils	<i>Centris poecila</i> Lepeletier, 1841	Vale <i>et al.</i> (2011)
<i>Tolumnia henekenii</i> (M.R.Schomb. ex Lindl.) Nir = <i>Oncidium henekenii</i> M.R.Schomb. ex Lindl.	(1) Oil-collecting bees (2) Mates (3) Pseudocopulation	<i>Centris</i> aff. <i>versicolor</i> Fabricius, 1775 – Probably male of <i>Centris insularis</i> Smith, 1874	Dod (1976); Cingel (2001)
<i>Tolumnia lucayana</i> (Nash) Braem = <i>Oncidium lucayanum</i> Nash	(1) Oil-collecting bees (2) Floral oils, absent (3) Deception of floral oils	<i>Centris versicolor</i> Fabricius, 1775	Nierenberg (1972); Dodson (1975); Ackerman (1986)
<i>Tolumnia quadriloba</i> (C.Schweinf.) Braem = <i>Oncidium quadrilobum</i> C.Schweinf	(1) Oil-collecting bees (2) Reward uncertain (3) Probably deception of floral oils	<i>Centris</i> sp.	Nierenberg (1972)
<i>Tolumnia variegata</i> (Sw.) Braem = <i>Oncidium variegatum</i> (Sw.) Sw.	(1) Oil-collecting bees (2) Floral oils, absent (3) Deception of floral oils	<i>Centris versicolor</i> Fabricius, 1775	Nierenberg (1972); Ackerman & Montero-Oliver (1985); Ackerman (1986); Ackerman <i>et al.</i> (1997)
<i>Trichocentrum andrewsiae</i> (R.Jiménez & Carnevali) R.Jiménez & Carnevali = <i>Lophiaris andrewsiae</i> R.Jiménez & Carnevali	(1) Oil-collecting bees (2) Reward uncertain (3) Probably deception of floral oils	<i>Centris</i> sp.	Cen (2016)



Table 1. Cont.

Oncidiinae species and synonyms in literature	Pollination features (1) Pollinator group; (2) Floral resource aimed; (3) Pollination strategy	Pollinator species	References for pollinators and floral resources
<i>Trichocentrum ascendens</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium ascendens</i> Lindl.	(1) Meliponini bees (2) Resin (3) Supply of resin	<i>Frieseomelitta nigra</i> (Cresson, 1878) = <i>Trigona nigra</i> Cresson	Parra-Tabla & Magaña-Rueda (2000); Parra-Tabla <i>et al.</i> (2000); Silvera (2002)
<i>Trichocentrum capistratum</i> Linden & Rchb.f. = <i>Trichocentrum panamense</i> Rolfe	(1) Euglossini bees (2) Reward uncertain, (3) Probably deception of nectar	<i>Euglossa allosticta</i> Moure, 1969; <i>Euglossa bursigera</i> Moure, 1970; <i>Euglossa cordata</i> (Linnaeus, 1758); <i>Euglossa crassipunctata</i> Moure, 1968; <i>Euglossa deceptrix</i> Moure, 1968; <i>Euglossa gorgonensis</i> Cheesman, 1929; <i>Euglossa tridentata</i> Moure, 1970; <i>Euglossa variabilis</i> Friese, 1899	Pijl & Dodson (1966); Williams (1982); Ackerman (1983); Roubik & Ackerman (1987)
<i>Trichocentrum carthagense</i> (Jacq.) M.W.Chase & N.H.Williams = <i>Trichocentrum oerstedii</i> (Rchb.f.) R.Jiménez & Carnevali	(1) Oil-collecting bees (2) Reward uncertain, possibly seeking for floral oils (3) Strategy uncertain	<i>Centris</i> sp.	Cen (2016)
<i>Trichocentrum jonesianum</i> (Rchb.f.) M.W.Chase & N.H.Williams = <i>Oncidium jonesianum</i> Rchb.f.	(1) Oil-collecting bees (2) Reward uncertain, possibly seeking for floral oils (3) Strategy uncertain	<i>Epicharis</i> sp.	Singer (2004); Gomiz <i>et al.</i> (2017)
<i>Trichocentrum lanceanum</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium lanceanum</i> Lindl.	(1) Oil-collecting bees (2) Reward uncertain, possibly seeking for floral oils (3) Strategy uncertain	<i>Centris</i> sp.	Dodson (1965); Pijl & Dodson (1966)
<i>Trichocentrum luridum</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium cosympheporum</i> C.Morren	(1) Oil-collecting bees (2) Floral oils, absent (3) Deception of floral oils	<i>Centris ruthannae</i> Snelling, 1966	Carmona-Díaz & García-Franco (2009)
<i>Trichocentrum pumilum</i> (Lindl.) M.W.Chase & N.H.Williams	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Lophopedia nigrispinis</i> (Vachal, 1909); <i>Tetrapedia diversipes</i> Klug, 1810	Pansarin & Pansarin (2011)
<i>Trichocentrum stipitatum</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium stipitatum</i> Lindl.	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils, pseudoantagonism (misinterpretation)	<i>Centris</i> sp.; Possibly <i>Centris inermis</i> Friese, 1899	Dodson (1965); Pijl & Dodson (1966); Silvera (2002)
<i>Trichocentrum tigrinum</i> Linden & Rchb.f.	(1) Euglossini bees (2) Reward uncertain, possibly seeking for nectar (3) Probably deception of nectar	<i>Eulaema cingulata</i> (Fabricius, 1804)	Dodson (1962); Pijl & Dodson (1966); Williams (1982);
<i>Trichoceros antennifer</i> (Humb. & Bonpl.) Kunth = <i>Trichoceros parviflorus</i> Kunth	(1) Tachinid flies (2) Mates (3) Pseudocopulation	<i>Paragymnomma</i> sp.	Dodson (1962); Pijl & Dodson (1966)
<i>Trichopilia</i> sp.	(1) Euglossini bees (2) Reward uncertain, possibly seeking for nectar (3) Strategy uncertain	<i>Euglossa cybelia</i> Moure, 1968	Roubik & Ackerman (1987)
<i>Trichopilia</i> cf. <i>leucoxantha</i> L.O.Williams	(1) Euglossini bees (2) Reward uncertain, possibly seeking for nectar (3) Strategy uncertain	<i>Euglossa heterosticta</i> Moure, 1968	Williams (1982)



Table 1. Cont.

Oncidiinae species and synonyms in literature	Pollination features (1) Pollinator group; (2) Floral resource aimed; (3) Pollination strategy	Pollinator species	References for pollinators and floral resources
<i>Trichopilia maculata</i> Rchb.f.	(1) Euglossini bees (2) Reward uncertain, possibly seeking for nectar (3) Strategy uncertain	<i>Euglossa bursigera</i> Moure, 1970; <i>Euglossa dissimula</i> Dressler, 1978; <i>Euglossa imperialis</i> Cockerell, 1922; <i>Euglossa tridentata</i> Moure, 1970	Ackerman (1983); Roubik & Ackerman (1987)
<i>Trichopilia rostrata</i> Rchb.f.	(1) Euglossini bees (2) Reward uncertain, possibly seeking for nectar (3) Strategy uncertain	<i>Euglossa hemichlora</i> Cockerell, 1917	Dodson (1962); Pijl & Dodson (1966); Williams (1982)
<i>Trichopilia subulata</i> (Sw.) Rchb.f.	(1) Euglossini bees (2) Reward uncertain, possibly seeking for nectar (3) Strategy uncertain	<i>Eufriesea mussitans</i> (Fabricius, 1787); <i>Euglossa dressleri</i> Moure, 1968; Unidentified <i>Euglossa</i> spp.	Williams (1982); Ackerman (1983); Roubik & Ackerman (1987)
<i>Trizeuxis falcata</i> Lindl.	(1) Meliponini bees (2) Reward uncertain (3) Strategy uncertain	Unknown Meliponini bees	Dodson & Dodson (1980)
<i>Warmingia eugenii</i> Rchb.f.	(1) Euglossini bees (2) Reward uncertain (3) Probably supply of perfumes	<i>Euglossa iophyrra</i> Dressler, 1982	Singer & Gerlach (2002); Singer (2004); Singer <i>et al.</i> (2006)
<i>Zelenkoa onusta</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium onustum</i> Lindl.	(1) Xylocopini bees (2) Reward uncertain (3) Strategy uncertain	<i>Xylocopa cf. transitoria</i> Pérez, 1901	Dodson & Frymire (1961a); Pijl & Dodson (1966)
<i>Zygostates alleniana</i> Kraenzl.	(1) Oil-collecting bees (2) Floral oils (3) Supply of floral oils	<i>Lophopedia nigrispinis</i> (Vachal, 1909)	Gomiz <i>et al.</i> (2014)

Vogel (1974) classified the elaiophores in two distinct types: epithelial, when the oils are secreted by layers of the epidermal tissue (Fig. 3A), and trichomal, when the secretory tissue is composed by uni- or multicellular trichomes (Fig. 3B). In the Oncidiinae, the genera *Lockhartia*, *Ornithocephalus*, *Phymatidium* and *Zygostates* have trichomal elaiophores (Reis 2005; Blanco *et al.* 2013). However, most species of oil-secreting Oncidiinae orchids present epithelial elaiophores (Blanco *et al.* 2013; Gomiz *et al.* 2014) and secrete the oils directly onto an epidermis. Then, bees gather the oils through scratching movements over the lip, during which the oils adhere to their legs by capillarity (Stpiczyńska *et al.* 2007; Stpiczyńska & Davies 2008; Torretta *et al.* 2011). Conversely, sometimes the oil may accumulate under a thick layer of cuticle, forcing the visitor to “squeeze” and break the cuticle in order to achieve the content (Singer & Cocucci 1999a; Stpiczyńska *et al.* 2007). Also, some species may produce and retain oils inside their flowers but no apparent structure is involved in its secretion, therefore they are functionally rewardless flowers because the resources are not externalized (Reis 2005; Stpiczyńska *et al.* 2007). In several Oncidiinae species the elaiophores are most present

in the callus and parts of the lateral lobes (Stpiczyńska *et al.* 2007; Stpiczyńska & Davies 2008). In a few cases, the elaiophores occur solely on the lateral lobes (Singer & Cocucci 1999b; Stpiczyńska *et al.* 2007; Stpiczyńska & Davies 2008; Pansarin *et al.* 2016).

The presence of a tabula infrastigmatica in an Oncidiinae orchid flower is an indication that oil-collecting bees may be acting. Dressler (1981; 1993) suggested that those bees hold the tabula infrastigmatica using their mandibles to stabilize themselves in the flowers, making possible the extraction of floral oils. In fact, several oil-collecting bees have been already reported pollinating species of Oncidiinae (Tab. 1), but the use of the tabula infrastigmatica is yet to be demonstrated. Oil-secreting flowers are pollinated by bees belonging to Melittidae, Ctenoplectridae and Apidae, though only the latter has representatives in the Neotropics (Buchmann 1987; Vinson *et al.* 1996; Singer & Cocucci 1999a; Cingel 2001; Torretta *et al.* 2011; Neubig *et al.* 2012). Among these, the pollinators of Oncidiinae species are distributed in the genera *Centris* (Centridini), *Epicharis* (Epicharitini), *Lophopedia* and *Paratetrapedia* (Tapinotaspidiini), and *Tetrapedia* (Tetrapedini) (Tab. 1).



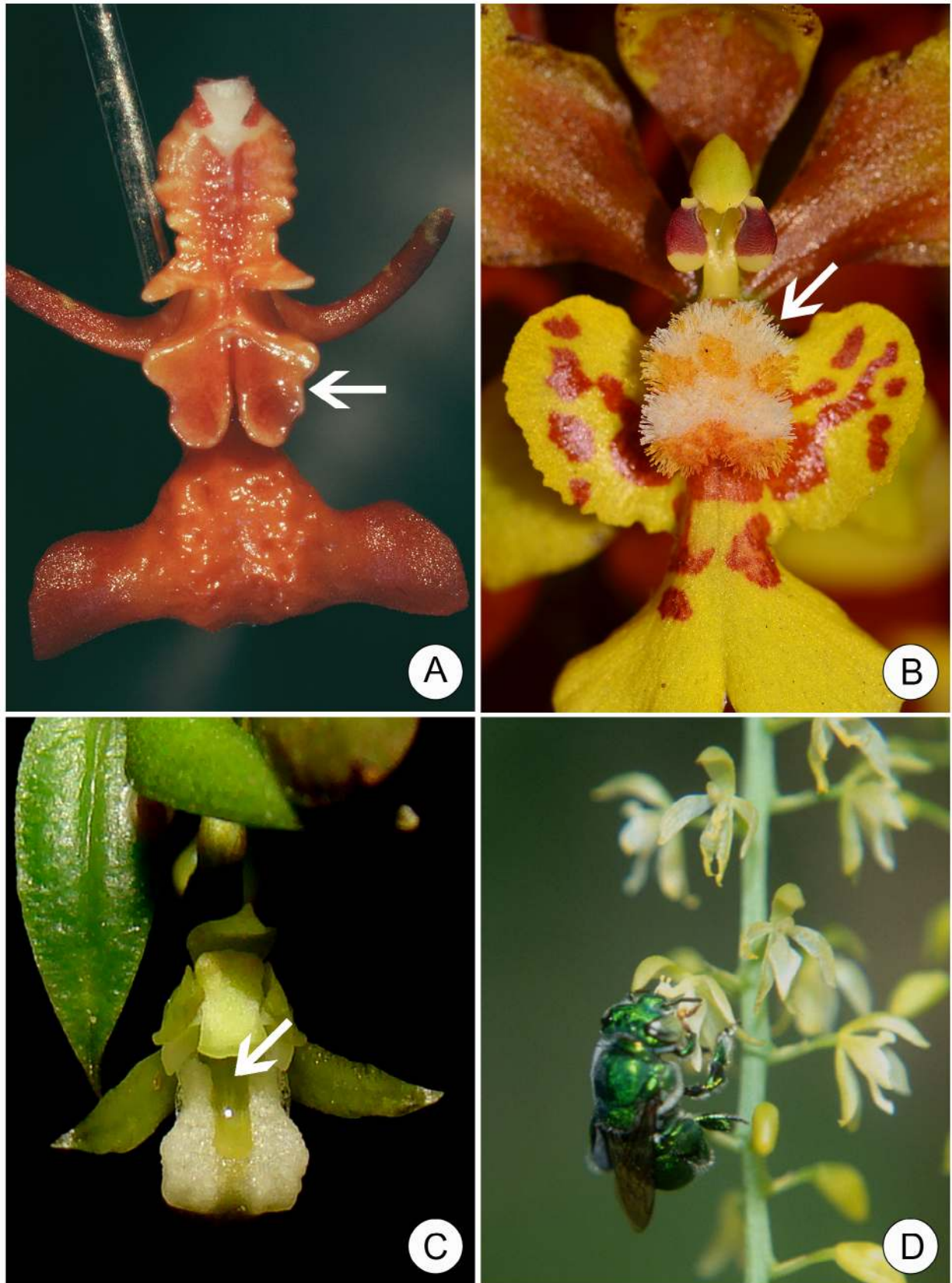


Figure 3. Floral structures and supply of resources in Oncidiinae orchids. **A.** Epithelial elaiophores (arrow) of *Gomesa pubes*; **B.** Trichomal elaiophores (arrow) of *Grandiphylum divaricatum*; **C.** Flower with nectaries (arrow) of *Capanemia thereziae*; **D.** Fragrant flower of *Notylia* sp. visited by an euglossine bee.

These insects deliberately collect the contents from the elaiophores by grasping them and during this process promote the pollination while carrying pollinaria attached to different parts of their body. A similar grasping behavior is performed by *Centris* bees while pollinating some Malpighiaceae species, which grasp the constrictions at the base of the petals while using their forelimbs for the gathering (Vogel 1974; 1990).

Some authors believe that the flowers of many *Oncidiinae* orchids mimic the oil-secreting flowers of several Malpighiaceae (Chase *et al.* 2009; Neubig *et al.* 2012). Just as several *Oncidiinae* orchids, American malpighiaceae plants bear floral oils, and both taxa exhibit similar coloration, morphology and light absorption spectra (Silvera 2002; Chase *et al.* 2009; Neubig *et al.* 2012). The resemblance between flowers of some *Oncidiinae* and Malpighiaceae species may be due to convergence due to the sharing of pollinators (Singer & Cocucci 1999b; Cingel 2001; Singer *et al.* 2006; Stpiczyńska *et al.* 2007; Davies & Stpiczyńska 2008; Papadopulos *et al.* 2013). Stpiczyńska *et al.* (2007) and Stpiczyńska & Davies (2008) indicate anatomic and structural features shared between the elaiophores of *Oncidiinae* species investigated thus far and those of Malpighiaceae. The similarities extend to the chemical level, as demonstrated by the presence of both oncidinol and byrsonic acid produced in these two unrelated taxa (Reis *et al.* 2007). In addition, Powell (2008) and Papadopulos *et al.* (2013) established that many *Oncidiinae* with yellow flowers closely match yellow Malpighiaceae species also in terms of spectral reflectance. Then, anatomical and chemical features may be responsible for the successful sharing of pollinators between *Oncidiinae* and Malpighiaceae, even though these bees may have evolved to pollinate the latter at a first moment (Stpiczyńska & Davies 2008).

In a recent study, Pansarin *et al.* (2016) described the pollination mechanisms and pollinators of *Gomesa varicosa* and *G. cf. blanchetii* – misidentified as *G. montana*. They mentioned several species of bees attracted by these two orchids, belonging to Bombini (*Bombus*), Centridini (*Centris*), Epicharitini (*Epicharis*), Tapinotaspidiini (*Lophopedia*), Tetrapedini (*Tetrapedia*) and Xylocopini (*Xylocopa*). However, only *Centris* and *Epicharis* bees were able to pollinate them. The authors indicate that the elaiophores are present only in the lateral lobes of the lip, but the callus deceives the bees due to resemblance to stamens of some Malpighiaceae species, where Centridini bees collect pollen (Sigríst & Sazima 2004; Pansarin *et al.* 2016).

Elaiphores in *Oncidiinae* species have arisen at least seven times (Renner & Schaefer 2010), being considered as a parallelism found in different groups of the subtribe. Buchmann (1987) mentions that 50 species out of 350 of the former *Oncidium s.l.* bear elaiophores, many of these species currently placed within the genus *Gomesa*. Within *Oncidiinae*, pollination by oil-collecting bees while gathering floral oils was already reported to species of *Gomesa*,

Ornithocephalus, *Phymatidium*, *Trichocentrum* and *Zygostates* (see Tab. 1 for complete list of species).

Nectar

Nectar is essentially constituted by water and diluted sugars. The production of nectar in a flower increases its visitation frequency, and it constitutes a resource aimed by most groups of pollinators (Pijl & Dodson 1966; Calvo 1990; Neiland & Wilcock 1998). The structures and locations of the nectaries (nectar-secreting glands) in *Oncidiinae* may differ from one species to another. In *Rodriguezia bahiensis*, *R. venusta* and *Comparettia coccinea*, the lateral sepals are connate to form the nectariferous spur (Carvalho & Machado 2006; Leitão *et al.* 2014; Pansarin *et al.* 2015). In *Oncidium strictum* – as *Symphyglossum sanguineum* – the nectaries are located at the auricles of the lip (Stpiczyńska & Davies 2006). The secretory tissue may be formed by a single-layered epidermis with the presence of some stomata, followed by a couple of layers of subepidermal cells (Stpiczyńska & Davies 2006; Buzatto *et al.* 2012). In other cases, a tongue-like, trichomed nectar gland composes the secretory tissue (Leitão *et al.* 2014; Pansarin *et al.* 2015). The animals drink the nectar from the nectaries and, while doing so, remove the pollinarium, which adheres to their body (Singer & Cocucci 1999a). Pollinator behavior considerably varies, depending on the specific group of animal pollen-vectors.

Hummingbirds are one of the animal groups that pollinate *Oncidiinae* orchids while seeking for nectar (Dodson 1965; Pijl & Dodson 1966; Rodríguez-Robles *et al.* 1992; Meléndez-Ackerman *et al.* 1997; Siegel 2011). Due to their fast movements, they demand high levels of energy, so they visit orchid flowers looking after food sources. Although these birds also feed on insects and spiders they find in flowers, much of the energy needed comes from feeding on nectar (Pijl & Dodson 1966; Siegel 2011). These birds are very efficient to access the nectaries and remove their liquid content while hovering in front of the flowers (Rodríguez-Robles *et al.* 1992; Siegel 2011). Bird-pollinated orchids generally show some degree of guidance of the bill, by the shape and form of some parts of the perianth (Dodson 1965; Pijl & Dodson 1966). The curvature of some flowers matches the curvature of the beaks to enhance feeding. To reach a position favoring nectar withdrawal, birds need to force their beaks against the column and thus contact the orchid pollinarium. Ornithophilous orchids usually have a callus that partially closes the floral tube at the level of the anther and stigma (Pijl & Dodson 1966). In *Comparettia falcata*, for example, the nectary spur is formed by the fusion of the lateral sepals. The position and orientation of the column guarantees that visitors that are able to reach the nectar end up dislodging the pollinarium and/or pollinating the flower (Rodríguez-Robles *et al.* 1992). Hummingbird-pollinated orchids generally present vivid coloration, as bright red, pink, purple, orange and yellow.



According to Buchmann & Nabhan (1996), several insects cannot perceive the red end of the light spectrum and, consequently, do not visit these flowers in search of nectar, which are left alone for the hummingbirds. Furthermore, these birds pollinate orchids that usually lack odors. It is also noteworthy the development of dark (blue, gray or brown) and cryptic pollinia in these orchids, because bright yellow pollinia would contrast with the dark beaks and bring the attention of the birds, which could try to get rid of it (Dressler 1981; Siegel 2011). The genera of hummingbird pollinators identified so far are *Amazilia* and *Chlorostilbon*. Pollination by hummingbirds in Oncidiinae was already reported for *Comparettia*, *Oncidium* and *Rodriguezia* (see Tab. 1 for complete list of species).

Butterflies may also be pollinators of some nectariferous Oncidiinae orchid species. Braga (1977) described the process in which individuals of *Heliconius hermathena* collect nectar in flowers of *Rodriguezia lanceolata* (as *R. secunda*) and adhere the pollinaria on the head, close to the proboscis, promoting pollination. Pansarin *et al.* (2015) reported the pollination of *Comparettia coccinea* by two species, *Heliconius ethilla narcaea* and *H. erato phyllis*. After landing on the flowers, the butterflies inserted their proboscis into the nectariferous spur guided by the horn-shaped lip callus. The pollinaria adhere to one of the eyes of the insects, depending on which nectariferous entrance they choose. Sometimes, these Nymphalidae butterflies were observed carrying pollinaria on both eyes. So far, *Ascia*, *Astraptes*, *Dryas*, *Heliconius* and *Urbanus* are the genera of butterflies that have been observed pollinating Oncidiinae orchids. These insects pollinate species of *Comparettia* and *Rodriguezia* (see Tab. 1 for complete list of species).

Other insects reported to search for nectar in Oncidiinae orchids are wasps. According to Pijl & Dodson (1966) wasps are not particularly efficient pollinators. In the nectariferous orchid *Capanemia thereziae* Barb.Rodr., for example, they are much bigger than the flowers and use a substantial part or the whole inflorescence as a landing platform (Singer & Cocucci 1999a). They hover in front of the flowers until locate somewhere to land, or walk on the tree until reach the inflorescence which is pendulous and sometimes lie on the surface of the tree. Then, they search for the nectar stored at the base of the lip (Fig. 3C) and end up removing the pollinarium eventually, which attaches to the clipeum of the insect. Each wasp may transport several pollinaria at the same time, and thus have the potential to pollinate more than one flower. However, many pollinaria may disturb these wasps and make them to try to clean their heads, what may lead to the loss of pollinaria (Singer & Cocucci 1999a). The pollination takes place when one of these pollinia is arrested on the concave stigmatic surface of a flower, which easily retains it. Remarkably, *C. thereziae* presents different features in relation to the other species of the genus. It bears greenish, scentless, nectar-bearing flowers (vs. white, fragrant, nectarless flowers), which agree with the wasp-

pollinated syndrome according to Pijl & Dodson (1966). The wasp genera of pollinators recorded so far for Oncidiinae are *Campsomeris*, *Pachodynerus*, *Pepsis*, *Polybia* and *Stelopolybia*. So far, pollination by wasps collecting nectar in Oncidiinae orchids has been reported to *Capanemia* and *Leochilus* (see Tab. 1 for complete list of species).

To a lesser extent, studies have shown the gathering of nectar by different groups of bees that forage on Oncidiinae orchids and promote their pollination. We may cite: (1) Xylocopini: bees of *Xylocopa suspecta* were reported gathering nectar and pollinating flowers of *Rodriguezia bahiensis* (Carvalho & Machado 2006); (2) Halictid: bees of the genus *Lasioglossum* present short tongue suited to process nectaries in flowers of *Leochilus labiatus*, which in turn bear a shallow, open nectar cavity at the base of its lip (Chase 1986); and (3) Euglossini: males of *Eulaema meriana*, *El. cingulata* and *Exaerete smaradigna* pollinate *Rodriguezia granadensis* while foraging for nectar (Ospina-Calderón *et al.* 2015).

Lastly, Acroceridae flies had their first record of pollination of an Oncidiinae species performed by Carvalho & Machado (2006), who described the pollination of *Rodriguezia bahiensis* by these insects (among others such as some aforementioned bees). These flies land on the flowers frontally and spend a substantially high time on the same flower (approximately 3 minutes). They insert their mouthparts between the lip and the column and force the column with their heads or backs, easily removing the pollinaria. The viscidium glues to the apex of their back and, then, are carried to another flower. The flies of the genus *Philopota* Wiedemann, 1830 present the apical dorsal portion of the thorax well developed, which facilitates the removal and deposition of pollinaria in an orchid flower (Luz 2004; Carvalho & Machado 2006). These insects usually visit only one flower per inflorescence and, by doing so, they prevent the loss of pollinaria that often occurs involving other groups of pollinators (Carvalho & Machado 2006).

In spite of being the most offered floral resource among orchids, nectar is not easily found in members of Oncidiinae. So far, the known genera that supply this floral resource to their visitors are *Capanemia*, *Comparettia*, *Leochilus*, *Oncidium* and *Rodriguezia* (see Tab. 1 for complete list of species).

Perfumes

Odors play an important role in the attraction of some animal species. In some Oncidiinae orchids (Tab. 1), the osmophores (perfume glands) bear combinations of terpenes and aromatics (Vogel 1963a; 1966a; b; Williams 1982; Williams & Whitten 1983; Antón *et al.* 2012). These structures may be composed by a solely layer of cells or by uni- to multicellular pappillae. More informations about the chemical composition, micromorphology, ultrastructure, morphology and anatomy of some osmophores are discussed



and detailed in Stern *et al.* (1986), Vogel (1990), Gerlach & Schill (1991), Kaiser (1993), Endress (1994), Dudareva & Pichersky (2006), Cseke *et al.* (2007), Antón *et al.* (2012) and Uribe-Holguin (2016). The location of these glands in orchids may vary, between the adaxial surface of sepals, petals or parts of the lip (Dressler 1993). Male Euglossine bees are known for actively collecting perfumes from either floral or non-floral sources, that they likely use during courtship (Ramírez *et al.* 2002) (see below). Among perfume-secreting flowers, Orchidaceae accounts for 84 % of the known pollination interactions, Araceae for 6 % and the remaining 10 % by nine different families (Amaryllidaceae, Apocynaceae, Bignoniaceae, Euphorbiaceae, Gesneriaceae, Haemodoraceae, Iridaceae, Solanaceae and Theaceae) (Ramírez *et al.* 2002). Within Orchidaceae, this pollination strategy is restricted to subfamily Epidendroideae, within the subtribes Catasetinae, Stanhopeinae and part of Zygopetaliinae and Oncidiinae.

The compounds of some floral scents are gathered specially by males of Euglossini bees (Fig. 3D), an exclusive tribe of the Neotropics (Pijl & Dodson 1966; Dressler 1982; Williams 1982). Cruger (1865) was the first to describe the relationship between orchid flowers and euglossine bees, also described by Darwin (1885), but the true nature of this interaction was not fully understood until recently. At a first moment, researchers believed that several fragrances were collected by the males in order to use them as precursors for sex pheromones to attract females (Ackerman 1983; Williams 1982). Actually, Euglossini males make up a bouquet of fragrances which is indicative of their fitness for females and that can be “sprayed” near the females. Then, is the female who decides which individual to copulate with, by “measuring” its fitness (Bembé 2004; Eltz *et al.* 2005). The behavior of Euglossini bees at the flowers follows a pattern that has already been described by many authors, as Dressler (1982) and Williams (1982). After being attracted by the odor of the flowers, they hover for a moment in front of them before landing. Then, they stabilize themselves over the flowers by placing their heads between the column and the lip and grasping the flower with their midlegs. The gathering of the scents is performed by brushing the secreting tissues with their forelegs, in a similar manner to what oil-collecting bees do. These insects absorb the substances with their modified forelegs, specifically the foretarsal brushes, and transfer them to expanded, bottle-like (sponge-like inside) cavities in the hind legs (Vogel 1963b; 1966b; Kimsey 1984).

The Euglossini that collect these aromatic compounds in Oncidiinae species are divided in four genera: *Euglossa*, *Eulaema*, *Eufriesea* and *Exaerete* (Tab. 1). Interactions between Oncidiinae orchids and perfume-collecting male Euglossini bees were reported for *Notylia* Lindl. and are probably present in *Macradenia*, *Macroclinium* and *Warmingia* (see Tab. 1 for complete list of species), all phylogenetically close genera. Therefore, unlike the floral

oils, which would have appeared several times independently within Oncidiinae (Renner & Schaefer 2010), exclusive pollination by perfume-gathering male Euglossine bees is likely restricted to this set of closely-related genera. In addition, both male and female euglossine bees may forage for nectar, as any other Hymenoptera (Williams 1982).

Deceptive strategies

Floral scents are not solely employed to attract male Euglossini bees. These fragrances are equally important on mechanisms based on deception, acting as a fake signal to mislead insects looking for food or sexual partners (Aguiar 2014; Martel *et al.* 2016). In some cases, these compounds are unnoticeable to the human nose. *Ionopsis utricularioides*, for example, presents 22 chemical compounds that were not studied until recently (Aguiar 2014). However, deceptive strategies are not only based upon perception of fragrances, sometimes they may also take place through some degree of mimicry. In Oncidiinae, deception mechanisms are divided basically in generalized food-deception (plants known as food-frauds) and sexual deception (by pseudocopulation or pre-copulatory behavior).

Food-frauds (deception of resources)

Some orchids developed mechanisms to mislead their potential pollinators, by presenting features that resemble secretory tissues/structures or imitating the general appearances of rewarding species (Caballero-Villalobos *et al.* 2017). Generally, flowers of rewardless species are fragrant and their volatiles consist of monoterpenoids and sesquiterpenoids (Flach *et al.* 2004; Singer *et al.* 2006; Davies & Stpiczyńska 2012). According to Tremblay *et al.* (2005), about a third of the known orchids deceive pollinators. For example, *Oncidium kegeljani* (as *Odontoglossum kegeljani*), is pollinated by male bees of *Bombus robustus* var. *hortulans* (Bombini) in Ecuador (Pijl & Dodson 1966). The insects come to the flowers and attempt to reach false nectaries, which are actually empty. The callus impedes the advance of the visitor into the flower and, by forcing the passage, they detach the viscidium of the pollinarium with their heads. The position of the stipe is reset by curving downwards, making the pollinia to assume a position in front of the head of the animal (Pijl & Dodson 1966) (Fig. 4A). This arrangement facilitates pollination when the individual visits subsequent flowers. Williams (1982), in turn, reported both male and female Euglossini bees pollinating *Cischweinfia dasyandra*, in search for nectar. However, Chase (2009) dissected five species of the genus and no nectar was detected.

Silvera (2002) concluded that some Oncidiinae species may present Batesian mimicry, because despite producing no reward, they attract the pollinators of Malpighiaceae species which serve as vectors for their pollination processes. Ackerman & Montero-Oliver (1985) and Montalvo &



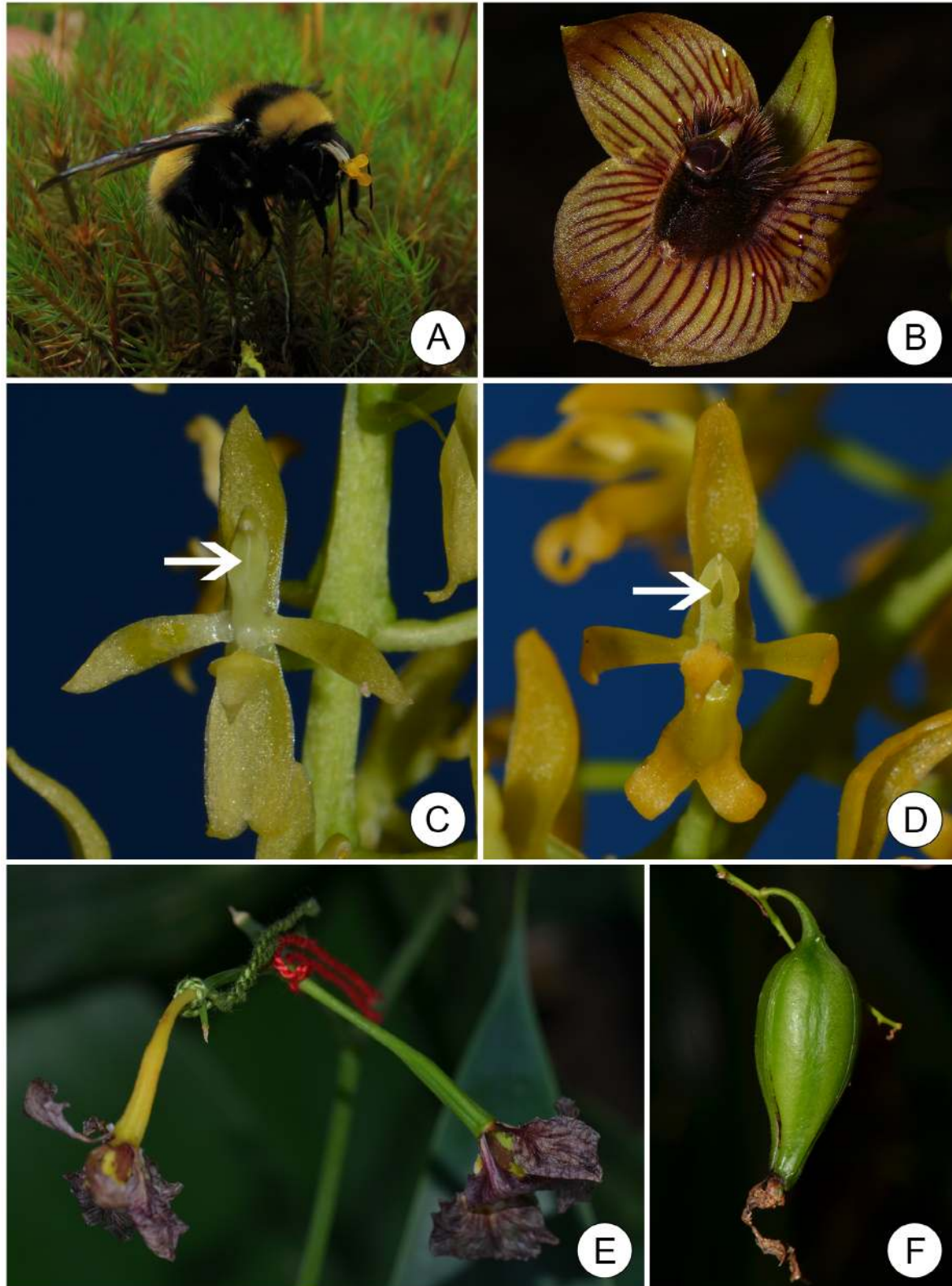


Figure 4. Deceptive pollination strategies and aspects of the breeding systems in Oncidiinae orchids. **A.** Pollinaria of an unidentified species of *Oncidium* attached to *Bombus rubicundus*, a putative case of deception of resources; **B.** Flower of *Telipogon ortizii*, a putative case of sexually deceptive species; **C-D.** Protandry in *Notylia* cf. *hemitricha*; **C.** Male function, when the stigmatic cavity is closed (arrow) and unable to receive pollen loads; **D.** Female function, when the column walls open and expose the stigmatic cavity (arrow), allowing its pollination; **E.** Development of fruits by self-pollination (green mark) and cross-pollination (red mark) in *Gomesa imperatoris-maximiliani*. Note its tendency to self-incompatibility, since fruits formed by selfing are aborted; **F.** Well-developed fruit of *Gomesa flexuosa*.

Ackerman (1987) classified, respectively, *Tolumnia variegata* – as *Oncidium variegatum* – and *Ionopsis utricularioides* as species that use this strategy and deceive the visitors that are searching for rewards. In a recent study, Aguiar & Pansarin (2019) described a deceptive mechanism of pollination to *I. utricularioides*. They did not identify any kind of secretion in the spur of their flowers, so the species, in fact, does not produce nectar or any other reward to their visitors. These rewardless flowers present similar colors to several of the neighboring plants and make part of a guild mimicry, attracting many generalist bee species. The bees land on the lips of the flowers and try to reach the lip base by following the nectar guides. By inserting their heads between the lip and the column, they remove the pollinarium, which attaches to their proboscis (Aguiar & Pansarin 2019). The pollinators identified were members of oil-collecting bees (Tapinotaspidini), Halictidae, Ceratinini and Meliponini. Roubik (2000) also mentioned a Meliponini bee, *Trigona fulviventris*, carrying pollinaria of an unidentified species of *Ionopsis*. The pollinaria were placed on the scutellum of the stingless bee. Also, Parra-Tabla *et al.* (2000) indicated the gathering of resins by Meliponini bees (Tab. 1) in flowers of *Trichocentrum ascendens* (as *Oncidium ascendens*), which they employ in nest-building practices. Regarding food frauds, besides the already mentioned genera *Cischweinfia*, *Ionopsis*, *Oncidium*, and *Tolumnia*, deception of floral resources was also reported to *Aspasia*, *Brassia* and *Trichocentrum* (see Tab. 1 for complete list of species).

Pseudocopulation (sexual deception)

Sometimes, rewardless flowers mimic female individuals of some animal species, luring the males that pollinate them while searching for females to mate. The latter phenomenon is known as pollination by sexual deceit or pseudocopulation (Pijl & Dodson 1966; Dressler 1993; Ayasse 2006; Martel *et al.* 2016). This pollination strategy is known to occur within a few genera of the families Asteraceae, Iridaceae, but it is more important in Orchidaceae (reviewed by Vereecken *et al.* 2012). Within Orchidaceae, this pollination strategy is restricted to the clade composed by subfamilies Orchidoideae and Epidendroideae. Within Orchidoideae, this pollination strategy is very well-documented in the genera *Ophrys* and *Serapias* (Vereecken *et al.* 2012) as well as in several Australian terrestrial orchids of Diuridae and Pterostylidinae (reviewed by Phillips *et al.* 2013). Within Epidendroideae orchids, sexual mimicry has been documented in species of *Lepanthes* (Pleurothallidinae; Blanco & Barboza 2005), *Trigonidium* (Maxillariinae; Singer 2002), *Mormolyca* (Maxillariinae; Singer *et al.* 2004), *Telipogon*, *Tolumnia* and *Trichoceros* (Oncidiinae; Chase 2009; Martel *et al.* 2016).

A remarkable case involving Oncidiinae orchids is that of *Trichoceros antennifer* – as *T. parviflorus* (Dodson 1962; Pijl & Dodson 1966). Their flowers imitate the female tachinid flies of *Paragymnomma* in a high degree, presenting similar

coloration, general morphology of both column and base of the lip and lateral extensions simulating the wings of a sitting fly. The stigma of the flower reflects sunlight much as the female fly genitalia, stimulating the male flies that thereby attempt copulation with it (Dodson 1962; Pijl & Dodson 1966). The viscidium, in contact to the body of the insect, detaches and connects to the basal portion of the abdomen of the fly. The long stipe of the pollinarium reconfigures and bends down, ensuring its positioning into the stigma when the fly visits a succeeding flower (Dodson 1962; Pijl & Dodson 1966). Pseudocopulation was also suggested to occur in *Tolumnia henekenii* – as *Oncidium henekenii* – by Dod (1976). Observations involved males of *Centris* aff. *versicolor*, although Cingel (2001) suggests these insects may be the unknown male of *C. insularis*. Whereas the flowers of *T. henekenii* are very insect-like in appearance, these observations (Dod 1976) are very preliminary.

Martel *et al.* (2016) recently described a sexually deceptive pollination system in *Telipogon peruvianus*, although Dressler (1981) was the first to suggest this pollination strategy for this orchid genus. Most species of the genus imitate the appearance of an insect sitting on a flower and their columns present spiny calli and hairs (Fig. 2B). Species of *Telipogon* are known to produce volatiles but have been recorded as scentless, at least to the human perceptions (Martel *et al.* 2016). By chemical analyses, Martel *et al.* (2016) evaluated the presence of scents and the compounds present in the odor bouquet of *T. peruvianus*, predominantly composed of saturated and unsaturated hydrocarbons, which attract the orchid visitors. In spite of four Tachinid species approaching the flowers of *T. peruvianus*, only male flies of *Eudejeania* aff. *browni* (an undescribed *Eudejeania* species) were seen carrying pollinaria, attached to their legs (Martel *et al.* 2016). The behavioral responses of the male flies were similar in the presence of both *T. peruvianus* flowers and female dummies carrying chemical baits. However, in contrast to what has been described for other sexually deceptive orchids, the flies do not demonstrate pseudocopulatory behavior on *T. peruvianus* flowers. Instead, their behavior match pre-copulatory movements (touching and grasping) observed in a couple other species of Tachinid flies (Reitz & Adler 1991; Martel *et al.* 2016).

Based upon the three mentioned genera, pollination by pseudocopulation would have evolved twice within Oncidiinae: to the clade formed by *Telipogon-Trichoceros* and inside *Tolumnia* (see Tab. 1 for complete list of species).

Pseudoantagonism

Pijl & Dodson (1966) proposed the term pseudoantagonism while observing, in their words, male bees attacking flowers, which were mistaken as enemies. Indeed, the male insects of some bee species are extremely territorial, surveying their areas while resting upon near twigs or leaves, while expecting for coespecific females and



attacking any other males or flying insects that enter the territory (Pijl & Dodson 1966). According to Pijl & Dodson (1966), by mistaking flowers as enemies, the bees strike them hard several times. In the process, the viscidium supposedly attaches to the frons of the bee and the stipe bends down, assuming a frontal position in the head of the animal, between the compound eyes. Dodson & Frymire (1961b) and Pijl & Dodson (1966) reported *Centris* bees attacking the flowers of *Oncidium hyphaematicum* and *O. planilabre* in the coastal zone of Ecuador. These authors also attribute pseudoantagonism to the orchid genus *Brassia*, which is visited and pollinated by females of the wasp genera *Pepsis* and *Campsomeris* (Pijl & Dodson 1966) (Tab. 1). These insects hunt spiders and sting them, feeding the paralyzed preys to their larvae. Wasps supposedly mistake *Brassia* flowers for spiders and sting their lips. In the process, pollinia would be attached to their heads (Pijl & Dodson 1966; Dodson 1990). Pseudoantagonism was also inferred to *Tolumnia bahamense* (as *Oncidium bahamense*) and *Trichocentrum stipitatum* (as *Oncidium stipitatum*), by Dodson (1965), Nierenberg (1972) and Pijl & Dodson (1966) (Tab. 1).

However, by our observations in the field while working with pollination of *Gomesa* spp., we agree with Chase (2009) by doubting of the existence of this mechanism. It is extremely unlikely that insects remove pollinaria and even more pollinate any flower by striking them in a rapid movement. The visitors generally need to assume a given positioning over the flowers and manipulate them in a certain way in order to remove the pollinarium and promote pollination. Also, some species proposed to be pseudoantagonists actually present floral oils, as for example *Trichocentrum stipitatum* (as *Oncidium stipitatum*; Silvera 2002). So, we believe that these authors may be misinterpreting the real behavior of insects that would be only defending the inflorescences while waiting for females. In sum, we believe that Pijl & Dodson (1966) may have seen both females pollinating the flowers and male bees defending the territory while waiting for the arrival of females, and confused their genders and behaviors.

Spontaneous self-pollination

Some cases of spontaneous self-pollination/autogamy, were reported in Oncidiinae species (Pijl & Dodson 1966; Catling 1990; Brito 2001; Cingel 2001; Chase 2009). In *Erycina glossomystax* (as *Oncidium glossomystax*), the stipe may naturally bend and curl downward, forcing the pollinia into the stigma. Brito (2001) reported spontaneous self-pollination to *Hofmeisterella eumicroscopica*, but he cited another flower in which the stigma was filled with two pollinaria, therefore insect pollination takes place as well. According to Catling (1990), Cingel (2001) and Chase (2009), other species that may also be autogamous are *Erycina pumilio* (as *Psygmorchis gnomus*), *E. zamorensis* (as

P. zamorensis), *Oncidium iricolor* (as *Oncidium pollardii*), *Trichocentrum oestlundianum* (as *Oncidium oestlundianum*) and *Trichopilia fragrans*.

Breeding systems

Pollinators may dislodge the pollinarium and leave the pollinia on the stigma of the same flower or from another flower from the same individual, promoting self-pollination. Self-pollination causes the loss of genetic diversity in populations and several species developed mechanisms to avoid it (Dressler 1993). There are species of plants that do not develop fruits resulting from their own pollen or abort them at some point of the process. So, we can coarsely classify the orchids into self-compatible or self-incompatible species. Self-compatible species are able to set fruit and viable seed following self-pollination. Self-incompatible plants are the opposite, this is, unable to set fruit and viable seed after self-pollination. Many Oncidiinae fall inside the latter (Tab. 2), although intermediate cases may occur (Dressler 1993; Singer & Koehler 2003; Singer *et al.* 2004; Tremblay *et al.* 2005; Singer *et al.* 2006). Tremblay *et al.* (2005) provided a list of self-incompatible species of orchids and the references to each study, in which are included species of the Oncidiinae genera *Cyrtochilum*, *Gomesa*, *Grandiphyllum*, *Oncidium*, *Tolumnia* and *Trichocentrum*. Self-incompatibility was demonstrated for most of the Oncidiinae species studied so far (East 1940; Ackerman & Montero-Oliver 1985; Warford 1992; Ackerman 1995; Ackerman *et al.* 1997; Parra-Tabla *et al.* 2000; Cingel 2001; Torretta *et al.* 2011; Singer & Koehler 2003; Carvalho & Machado 2006; Damon & Cruz-López 2006; Pemberton 2008; Vale *et al.* 2011; Ospina-Calderón *et al.* 2015; Pansarin *et al.* 2016; 2018) (Tab. 2).

In self-incompatible orchids, the self-pollinated flowers turn yellow and fall (abort) generally after three to five days (Warford 1992) (Fig. 4E). It is important to emphasize that self-incompatibility affects the whole individual. In self-incompatible species, pollen-flow among flowers of the same individual will promote abortions as well. Rodríguez-Robles *et al.* (1992) cited *Comparettia falcata* as self-compatible but not autogamous, although the values of fructification were lower in comparison to cross-pollinated flowers in 1989 and 1990 (53.8 % and 64.3 % against 86.4 % and 86.7 %, respectively). This difference in data, despite not statistically significant, suggests that the species may be partially self-incompatible or suffer from inbreeding depression when self-pollinated (Rodríguez-Robles *et al.* 1992). Pansarin *et al.* (2016) classified *Gomesa varicosa* as partially self-incompatible, because the species presented 54 % and 87 % of fruit set for self-pollination and cross-pollination treatments, respectively. Self-compatibility was also reported to *Aspasia*, *Erycina*, *Ionopsis*, *Leochilus*, *Phymatidium*, *Telipogon* and *Warmingia* (Chase 1986; Montalvo & Ackerman 1987; Zimmerman & Aide 1989;



Table 2. Self-compatibility and natural fruit set in the Oncidiinae. ND = No data. * = Misidentification.

Oncidiinae species and synonyms in literature	Self-compatibility	Natural fruit set (%)	Reference
<i>Aspasia principissa</i> Rchb.f.	Self-compatible	9.5	Zimmerman & Aide (1989); Chase (2009)
<i>Brassia antherotes</i> Rchb.f.	ND	3.38	Ospina-Calderón <i>et al.</i> (2007)
<i>Brassia verrucosa</i> Lindl.	ND	0	Damon & Salas-Roblero (2007)
<i>Comparettia coccinea</i> Lindl.	Self-compatible	ND	Pansarin <i>et al.</i> (2015)
<i>Comparettia falcata</i> Poepp. & Endl.	Self-compatible	16.9 - 19.4	Rodriguez-Robles <i>et al.</i> (1992)
<i>Cyrtochilum cimiciferum</i> (Rchb.f.) Dalström = <i>Oncidium cimiciferum</i> Rchb.f. ex Linden	Self-incompatible	ND	East (1940); Tremblay <i>et al.</i> (2005)
<i>Erycina crista-galli</i> (Rchb.f.) N.H.Williams & M.W.Chase	ND	0	Damon & Salas-Roblero (2007)
<i>Erycina glossomystax</i> (Rchb.f.) N.H.Williams & M.W.Chase	Self-compatible and self-incompatible populations	ND	Cingel (2001)
<i>Erycina pusilla</i> (L.) N.H.Williams & M.W.Chase	ND	0	Damon & Salas-Roblero (2007)
<i>Gomesa bifolia</i> (Sims) M.W.Chase & N.H.Williams	Predominantly self-incompatible	ND	Torretta <i>et al.</i> (2011)
<i>Gomesa cf. blanchetii</i> (Rchb.f.) M.W.Chase & N.H.Williams = <i>Gomesa montana</i> (Barb.Rodr.) M.W.Chase & N.H.Williams*	Self-incompatible	ND	Pansarin <i>et al.</i> (2016)
<i>Gomesa imperatoris-maximiliani</i> (Rchb.f.) M.W.Chase & N.H.Williams = <i>Oncidium crispum</i> Lodd. ex Lindl.	Self-incompatible	ND	East (1940); Tremblay <i>et al.</i> (2005)
<i>Gomesa longicornu</i> (Mutel) M.W.Chase & N.H.Williams = <i>Oncidium unicolorne</i> Lindl.	Self-incompatible	ND	East (1940); Tremblay <i>et al.</i> (2005)
<i>Gomesa varicosa</i> (Lindl.) M.W.Chase & N.H.Williams	Self-compatible and self-incompatible populations	ND	Pansarin <i>et al.</i> (2016)
<i>Grandiphyllum divaricatum</i> (Lindl.) Docha Neto = <i>Oncidium divaricatum</i> Lindl.	Self-incompatible	ND	East (1940); Tremblay <i>et al.</i> (2005)
<i>Ionopsis utricularioides</i> (Sw.) Lindl.	Self-compatible (Puerto Rico) and self-incompatible (Brazil) populations	6.1; 0.58-5.35; 5.25-7.20	Montalvo & Ackerman (1987); Pansarin <i>et al.</i> (2016); Aguiar (2014); Aguiar & Pansarin (2019)
<i>Leochilus labiatus</i> (Sw.) Kuntze	Self-compatible	0 - 12	Chase (1986); Cingel (2001); Damon & Salas-Roblero (2007)
<i>Leochilus oncidoides</i> Knowles & Westc.	ND	0 - 15	Damon & Salas-Roblero (2007)
<i>Leochilus scriptus</i> (Scheidw.) Rchb.f.	Self-compatible	60; 0 - 6	Chase (1986); Cingel (2001); Damon & Salas-Roblero (2007)
<i>Lockhartia oerstedii</i> Rchb.f.	ND	0	Damon & Salas-Roblero (2007)
<i>Notylia barkeri</i> Lindl.	Self-incompatible	0.7; 0-3	Warford (1992); Damon & Salas-Roblero (2007)
<i>Notylia longispicata</i> Hoehne & Schltr.	Predominantly self-incompatible	ND	Singer & Koehler (2003)
<i>Notylia nemorosa</i> Barb.Rodr.	Predominantly self-incompatible	12.86	Singer & Koehler (2003)
<i>Notylia orbicularis</i> A.Rich & Galeotti = <i>Notylia tridachne</i> Lindl. & Paxton	Self-incompatible	ND	Warford (1992)
<i>Notylia trisejala</i> Lindl. & Paxton	Self-incompatible	ND	Warford (1992)



Table 2. Cont.

Oncidiinae species and synonyms in literature	Self-compatibility	Natural fruit set (%)	Reference
<i>Oncidium altissimum</i> (Jacq.) Sw.	Self-incompatible	2	Ackerman (1995)
<i>Oncidium laeve</i> (Lindl.) Beer	ND	0	Damon & Salas-Roblero (2007)
<i>Oncidium ornithorrhynchum</i> Kunth	ND	0	Damon & Salas-Roblero (2007)
<i>Oncidium sphacelatum</i> Lindl.	Self-incompatible	0 - 0.25; 0.4; 1.49	East (1940); Tremblay <i>et al.</i> (2005); Damon & Cruz-López (2006); Damon & Salas-Roblero (2007); Pemberton (2008)
<i>Ornithocephalus tripterus</i> Schltr.	ND	0	Damon & Salas-Roblero (2007)
<i>Phymatidium delicatulum</i> Lindl.	Self-compatible	10.7	Cabral (2014)
<i>Rodriguezia bahiensis</i> Rchb.f.	Self-incompatible	6.57	Carvalho & Machado (2006)
<i>Rodriguezia decora</i> (Lem.) Rchb.f.	Self-incompatible	ND	Pansarin <i>et al.</i> (2018)
<i>Rodriguezia granadensis</i> (Lindl.) Rchb.f.	Self-incompatible	11.3	Ospina-Calderón <i>et al.</i> (2015)
<i>Rodriguezia lanceolata</i> Ruiz & Pav.	Self-incompatible	ND	Pansarin <i>et al.</i> (2018)
<i>Telipogon peruvianus</i> T.Hashim	Self-compatible	ND	Martel <i>et al.</i> (2016)
<i>Tolumnia guianensis</i> (Aubl.) Braem = <i>Oncidium lemonianum</i> Lindl.	Self-incompatible	ND	East (1940); Tremblay <i>et al.</i> (2005)
<i>Tolumnia guibertiana</i> (A. Rich.) Braem	Self-incompatible	15	Vale <i>et al.</i> (2011)
<i>Tolumnia variegata</i> (Sw.) Braem	Self-incompatible	1.2 - 2.6; 0.13 - 10.05	Ackerman & Montero-Oliver (1985); Ackerman <i>et al.</i> (1997); Cingel (2001); Tremblay <i>et al.</i> (2005)
<i>Trichocentrum ascendens</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Cohniella ascendens</i> (Lindl.) Christenson = <i>Oncidium ascendens</i> Lindl.	Self-incompatible	3.1 - 6.8; 0 - 3	Parra-Tabla <i>et al.</i> (2000); Tremblay <i>et al.</i> (2005); Damon & Salas-Roblero (2007)
<i>Trichocentrum candidum</i> Lindl.	ND	0	Damon & Salas-Roblero (2007)
<i>Trichocentrum carthagenense</i> (Jacq.) M.W.Chase & N.H.Williams = <i>Trichocentrum oerstedii</i> (Rchb.f.) R.Jiménez & Carnevali <i>Trichocentrum cavendishianum</i> (Bateman) M.W.Chase & N.H.Williams = <i>Oncidium cavendishianum</i> Bateman	ND	0	Damon & Salas-Roblero (2007)
<i>Trichocentrum luridum</i> (Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium cosymbephorum</i> C.Morren	Self-incompatible	ND	East (1940); Tremblay <i>et al.</i> (2005)
<i>Trichocentrum microchilum</i> (Bateman ex Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium microchilum</i> Bateman ex Lindl.	Self-incompatible	ND	Carmona-Díaz & García-Franco (2009); Cen (2016)
<i>Trichocentrum microchilum</i> (Bateman ex Lindl.) M.W.Chase & N.H.Williams = <i>Oncidium microchilum</i> Bateman ex Lindl.	Self-incompatible	0	East (1940); Tremblay <i>et al.</i> (2005); Damon & Salas-Roblero (2007)
<i>Trichocentrum pumilum</i> (Lindl.) M.W.Chase & N.H.Williams	Self-incompatible	9	Pansarin & Pansarin (2011)
<i>Trichocentrum stipitatum</i> (Lindl.) M.W.Chase & N.H.Williams	ND	1.8	Tremblay <i>et al.</i> (2005)
<i>Trichopilia tortilis</i> Lindl.	ND	0 - 5	Damon & Salas-Roblero (2007)
<i>Warmingia eugenii</i> Rchb.f.	Self-compatible	ND	Singer <i>et al.</i> (2006)



Cingel 2001; Singer *et al.* 2006; Aguiar 2014; Cabral 2014; Martel *et al.* 2016; Aguiar & Pansarin 2019) (Tab. 2), but represents a rare condition in Oncidiinae orchids as a whole (Montalvo & Ackerman 1987; Dressler 1993; Pansarin *et al.* 2016).

Mechanism to promote cross-pollination: protandry

As previously mentioned, several Oncidiinae species are self-incompatible. Yet, there are intrinsic mechanisms that eventually favour cross-pollination. In some cases, the just-removed pollinarium needs to modify its conformation and bends down the stipe before being properly inserted into the stigmatic cavity (Chase 2009). Some species present protandry as a mechanism to increase the chances for cross-pollination to take place. The protandrous plants present two fertile stages. In the first stage, the stigmatic cavity does not work as a receiver of pollen, by physical/chemical/conformation blocking, ensuring that the flowers function only as pollen donors (Fig. 4C). Then, in the second stage, the flowers change their features/configuration and become pollen receivers (Warford 1992; Singer & Koehler 2003; Singer *et al.* 2006) (Fig. 4D). In *Notylia* spp., for example, the flowers expand their stigmatic cavity at the female phase (Fig. 4D), without changing the angle between the column and the lip, making possible the placement of the pollinarium in the stigma. (Warford 1992; Singer *et al.* 2006). Indeed, older flowers at female phase and younger flowers at male phase may still coexist, allowing the occurrence of few geitonogamous pollinations (self-pollinations among flowers of the same individual) (Singer & Koehler 2003). So far, protandry was demonstrated in the Oncidiinae genera *Macradenia* and *Notylia* (Warford 1992; Singer & Koehler 2003; Singer *et al.* 2006).

Fruiting success

The fruits in Orchidaceae consist of capsules with abundant dust-like seeds (Dressler 1993; Neiland & Wilcock 1998) (Fig. 4F). Specialized literature points out that orchids as a whole often have infrequent pollinator visits and, by consequence, low natural fruit set (Darwin 1885; Dressler 1968; Montalvo & Ackerman 1987; Tremblay *et al.* 2005) (see Tab. 2 for values of fruiting within Oncidiinae). Factors such as phenology, microhabitat, inflorescence size, population size and synchronicity between plants and pollinators have been advocated as affecting fruit set in Orchidaceae (Fritz & Nilsson 1994; Donaldson *et al.* 2002; Tremblay *et al.* 2005). It is clear, however, that presence/absence of floral rewards are of importance. Silvera (2002) and Tremblay *et al.* (2005) found that the presence of floral rewards positively correlates with fruit production (sometimes almost doubling the chances of fruiting).

Alternative explanations for the observed low fruit set may rely in a combination of factors involving pollinator

behavior, presence/absence of floral rewards and breeding systems, not necessarily acting all together: (1) low pollinator abundance, so that many flowers are never visited; (2) loss of pollinaria, through deliberate removal by insects, because they may feel disturbed by the structures adhered to their bodies (JB Castro unpubl. res.); (3) rewardless flowers, whose pollinators tend to visit few flowers before leaving the plant (Dafni 1987); (4) passive pollinators that visit several flowers/inflorescences of the same individual/plant; and (5) presence of self-incompatibility (this is, in these plants all self-pollinated flowers will abort) (Singer & Koehler 2003). Rewardless orchids will tend to be unfrequently visited and, consequently, their fruit sets may be low. If pollinators are rare, this phenomenon will be accentuated. On the other hand, plant species with rewarding flowers may also display low fruit set if their pollinators are passive (visiting several flowers of the same plant/individual) and the plants are self-incompatible. Passive pollinators of rewarding flowers may tend to maximize their collecting efforts, promoting some degree of abortions, through self-pollinations (Singer & Koehler 2003).

Final considerations

The present review of the literature supports that, as a whole, Oncidiinae orchids are predominantly pollinator-dependent (unable to set fruit and viable seed in absence of pollinators). Within the so-far studied Oncidiinae orchids, floral oils prevail as the main floral reward. In a general summary of the plant resource-pollinator relationships among Oncidiinae orchids, we may cite: (1) floral oils and females of oil-collecting bees; (2) perfumes – or aromatic compounds – and males of Euglossini bees; and (3) nectar and several animal families (wasps, hummingbirds, butterflies and bees of the Halictidae, Xylocopini and Euglossini). Within Oncidiinae, the percentages of pollinators from a total of 92 orchid species surveyed (Tab. 1) are as follows: bees 84.7 % (found in 78 out of 92 species) – Euglossini 39.1 % (36/92); oil-collecting 36.9 % (34/92); Meliponini 4.3 % (4/92); Halictidae, Xylocopini and Bombini 2.1 % (2/92) each; Colletidae and Ceratinini 1.1 % (1/92) each –, wasps 6.5 % (6/92), hummingbirds 4.3 % (4/92), butterflies 3.2 % (3/92) and flies 3.2 % (3/92). Most of the Oncidiinae orchids studied so far are self-incompatible. Out of 36 research papers involving detailed reproductive biology studies, 69.4 % (25/36) of the species were self-incompatible, 22.2 % (8/36) were self-compatible and 8.3 % (3/36) had both self-incompatible and self-compatible populations (Tab. 2).

Still, there are many gaps in the knowledge of pollination of some important taxa within Oncidiinae. Most studies described the pollination of orchids from southern and southeastern Brazil. However, many species-rich genera occurring in the Andean region are poorly known, as *Brassia* (35 spp.), *Cyrtorchilum* (120 spp.), *Lockhartia*



(30 spp.), *Pachyphyllum* (40 spp.) and *Telipogon* (170 spp.). Even *Oncidium sensu stricto* presents studies out of date and not representatives of its total diversity (only 6 species out of 520 studied so far). In addition, the study of genera with few species (for example, *Seegeriella*) may reveal unique pollination strategies. As a long-term perspective, we hope that the topics discussed here – presence or absence of secretory structures, floral resources, pollinator group and behavior, mechanisms favoring cross-pollination, self-compatibility/self-incompatibility, etc. – may be plotted on more complete and dense molecular phylogenies of the clade (such as Chase *et al.* 2009 and Neubig *et al.* 2012), helping to elucidate well-supported evolutionary scenarios for the arising of pollination strategies and breeding systems in Oncidiinae orchids.

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