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Authors

JEFFREY, DAVID C
ARDITTI, JOSEPH
KOOPOWITZ, HAROLD

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SUGAR CONTENT IN FLORAL AND EXTRAFLORAL EXUDATES OF ORCHIDS: POLLINATION, MYRMECOLOGY AND CHEMOTAXONOMY IMPLICATION

By DAVID C. JEFFREY, JOSEPH ARDITTI and HAROLD KOOPOWITZ

Department of Organismic Biology, University of California, Irvine, California 92664

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Summary

Sugars present in the floral and extrafloral exudates from a number of orchid species have been analysed. All contain fructose, glucose and sucrose. Raffinose is the next most common sugar and stachyose occurs less frequently. Cellobiose, gentiobiose, lactose, maltose, melibiose, melezitose and a few large oligosaccharides may also be present. The distribution of these sugars in orchids may have some chemotaxonomic implications. There appears to be no correlation between the sugar content of exudates and orchid pollinators. This would seem to suggest that scent, form and colour are the major attractants to pollinators in orchids. Floral and extrafloral exudates in orchids may also function as attractants for ants which probably feed on them and repel grazers.

Introduction

Many orchids, both in their native habitat and under cultivation, secrete copious amounts of floral and extrafloral exudates or nectar (Darwin, 1904). Secretion occurs from organs of great diversity of position and structure (Darwin, 1904; Van der Pijl and Dodson, 1966; Thien, 1969). They were apparently first described as small droplets on the buds of *Cattleya mendelii* and called honey (Burbidge, 1885). A more specific description of the exudates was given by a 'Mr. Rogers, of Sevenoakes' who informed Darwin that he had removed 'crystals of sugar of considerable size from the nectary of *Aerides cornutum*' (Darwin, 1904).

Qualitative analyses of orchid exudates or nectars have been attempted relatively recently (Table 1). Various orchid nectars were found to give positive results with Fehling's reagent, indicating the presence of reducing sugars (Daumann, 1941; Sunding, 1963). Fructose, glucose, sucrose, and in some instances, more complex sugars have been found in orchid nectars (Baskin and Bliss, 1969; Daumann, 1941; Frey-Wyssling and Häusermann, 1960; Payne, 1965; Percival, 1961). Yet, despite one notable study (Baskin and Bliss, 1969), information on the sugar content of orchid exudates is available for relatively few species only.

The occurrence of various sugars, like other substances, whether present in the plant as a whole, or in special organs or exudates is potentially useful in chemotaxonomy or a means for explaining pollinator preferences, and attraction for other symbionts. Since an evaluation of these factors requires information regarding a larger number of species

than currently available (Baskin and Bliss, 1969), we have examined a number of additional taxa.

MATERIALS AND METHODS

Exudate samples were collected from sepals, petals, ovaries, nectaries, peduncles and pedicels of orchid flowers with micropipets (Drummond Scientific Company, Broomall, Pennsylvania, USA), stored in vials and frozen until used.

Immediately prior to spotting the chromatograms, each sample was diluted with 0.5 ml of distilled water or 70% ethanol. The solution was spotted on borate-impregnated silica gel G plates, developed twice in the same dimension, and the sugars resolved according to a previously described method (Jeffrey, Arditti and Ernst, 1969).

RESULTS AND DISCUSSION

All exudates so far analysed contained fructose, glucose and sucrose (Table 1). In addition, some contained a variety of more complex sugars. Among these, raffinose was common. Maltose, gentiobiose, stachyose, melibiose, lactose, melezitose and a number of unidentified oligosaccharides can also be found in several exudates.

The methods employed by us and others (Baskin and Bliss, 1969; Jeffrey and Arditti, 1968, 1969; Jeffrey *et al.*, 1969) are sensitive enough to allow for the qualitative detection of saccharides in quantities as low as 0.1 μg. It is unlikely, therefore, that important sugar components of orchid exudates may have escaped detection.

Due to the nature of the exudate it was not practical to collect samples which could provide comparable quantitative data on the sugar content of each nectar. The ratios between the sugars present can be determined in each exudate (Baskin and Bliss, 1969), but trends are difficult to establish in such comparisons. Also, no essential differences can be noted between exudates from intrafloral and extrafloral sources (Baskin and Bliss, 1969; Percival, 1961).

Trends do become discernible when comparisons are made within or between genera. Raffinose appears to be generally absent from *Epidendrum* and *Cattleya* exudates, but is more common in *Laelia*. It is universally present in the genera *Oncidium* and *Angraecum* and in almost all *Laeliocattleya*, so far studied and also in a number of species belonging to unrelated genera. Melibiose where present, was found only in very small quantities and its distribution is across tribal lines. The exudates of *Sobralia* (Polychondroideae) *Laelia tenebrosa*, *Cattleyopsis lindenii* and the hybrid genus *Brassocattleya* (the last three, Kerosphaeroideae) all contain melibiose.

The tetrasaccharide stachyose is present in some *Cymbidium* species and hybrids as well as in the unrelated *Mormodes ignea*. No pattern can be discerned from the available information regarding the distribution of gentiobiose, maltose, cellobiose and lactose. Notably, melezitose has been found only in *Oncidium*.

When genera are examined for uniformity of sugar content rather than for distribution of sugars, *Oncidium* appears to be outstanding. All species analysed, uniformly contain raffinose in their exudates, and *Oncidium* is the only genus to contain melezitose. Exudates from *Cymbidium*, on the other hand, show a tendency to contain stachyose.

The role of sugar content of exudates in the physiology or life cycle of the orchids must be considered. In some instances, it undoubtedly serves to attract and feed pollinators (Van der Pijl and Dodson, 1966; Thien, 1969). However, some orchid species

do not produce nectar and depend on other means for attracting pollinators (Baskin and Bliss, 1969; Darwin, 1904; Van der Pijl and Dodson, 1966). Furthermore, there are orchids which produce sugar containing exudates at times (Adams, 1959) or in places which may be of little value in the process of pollination even when they may attract potential pollinators. Fructose, glucose and sucrose are highly attractive to honey bees and appear to act as attractants for these pollinators in other plants (Wykes, 1952a, b) However, in orchids the presence of these sugars does not appear to attract bees in particular, nor is there any reason to expect that New World bees will be attracted by the same sugars as honey bees (Old World). Some species which contain fructose, glucose and sucrose are pollinated by a variety of bees (Table 1) whereas others, with similar sugar content, depend on moths, wasps, birds, butterflies and flies. Raffinose, a sugar not attractive to honey bees (Wykes, 1952a), is found in some bee-pollinated Old and New World orchid species. It is also found in the moth-pollinated Madagascar species *Angraecum sesquipedale* (Table 1).

It appears necessary to conclude that production of sugar-containing exudates may be connected with, but is not necessarily always an important factor in, the attraction of pollinators. Flower fragrances, 'scent-coding', morphology and colouration as recently implicated are undoubtedly the key pollinator attractants in orchids (Dodson and Frymire, 1961; Dodson and Hills, 1966; Hills, Williams and Dodson, 1968; Van der Pijl and Dodson, 1966). On the other hand, it is very possible that exudates and nectars may serve to attract and maintain 'protectors' like ants (Janzen, personal communication) or wasps (Arditti, unpublished). Such exudates do not have to be present at times or locations related to pollination and this indeed is the case in some orchids (Adams, 1959).

Ants have been found in the hollow pseudobulbs of *Caulathron* (*Diacrium*) *bicornutum*, (Plate 1,a), and in those of *C.* (*D.*) *bilamellatum*, *Epidendrum imatophyllum* (Bequaert, 1922; Rodway, 1895). *Schomburgkia tibicinis* from Vera Cruz, Mexico, harbours in a small opening at the base of its pseudobulbs the ant *Neoponera* (*Pachycondyla*) *villosa* Fabr. whose bite is reported as being very painful (Mayr, 1862). This orchid is a true myrmecophyte and has 'voluminous, elongated pseudobulbs, which are hollow with a smooth inner lining and usually inhabited by ants; these come and go through a small opening pierced at the base of the pseudobulb . . .' (Bequaert, 1922, this paper contains a short review of Orchidaceae and ants). An 'oval ball' formed by the roots of *Coryantes* serves as a 'perfectly safe habitation and barracks' for ants who 'can easily take up the abode and fill in the lattice-like spaces' (Rodway, 1895). *Gongora*, *Grammatophyllum*, *Vanda*, *Cattleya*, *Dendrobium*, *Coelogyne*, *Vandopsis*, *Vanilla*, *Arundina*, *Oncidium* and *Spathoglottis* are all orchid genera with species which may be inhabited by ants (Arditti, unpublished; Bequaert, 1922; Rodway, 1895; Soysa, 1940; Wheeler, 1942). Probably the ants are attracted to orchids, as they are to acacias (Janzen, 1966, 1967, personal communication) due to the presence of sugar-containing exudates (Brown, 1960). This assumption is supported by recent observation of the orchid *Encyclia cordigera* (D. H. Janzen, personal communication) in Costa Rica. During one morning *Pseudomyrmex*, *Crematogaster*, *Azteca*, *Camponotus*, two species of small Solenopsini and unidentified dolichoderine visited the orchids. Occupational density ranged between 75 and 672 ant-minutes (one ant on one inflorescence during 1 minute is an 'ant-minute') per hour during a morning. All of these ants are known to prey on insects. At least one ant was present on the stem surface 24.1% of the time and the longest period without the presence of an ant was 9 minutes.

Having the ants crawling over the entire plants as in *Cattleya violaceae* (Arditti, unpublished), *Encyclia cordigera* (Plate 1, b; Janzen, personal communication) and *Oncidium altissumum* (Rodway, 1895), nestled in the roots as in *Coryanthes* (Rodway, 1895) or generally living in close association with the plant is of distinct advantage to the orchid (Soysa, 1940). The ants serve to protect orchids from grazers, other ants, a variety of 'sucking, biting insects' (Soysa, 1940), 'cockroaches and other pests' (Rodway, 1895). In *Encyclia cordigera*, a black formicine ant, residing within the pseudobulb repulsed visiting *Pseudomyrmex gracilis* workers who attempted to enter the stem through a 2 mm diameter hole (Janzen, personal communication). Most of the insects which might graze on this orchid are too large for the ants to capture or kill, but, they are undoubtedly driven off by the ants' attacks. Hence 'the ants are in effect scarecrows' (Janzen, personal communication).

A direct relationship exists between ant visits and lack of grazing in *Encyclia cordigera*. The lowest bud on a stem was visited most frequently and was also the only one with no bites on it (Janzen, personal communication). Very painful experiences of unwary orchid collectors (Arditti, unpublished; Rodway, 1895) leave no doubt of the protection afforded orchids by ants. Ants derive shelter and perhaps nourishment from their orchid hosts. They can be often seen crawling on the flowering stems, pedicels, ovaries or flowers (Plate 1) where exudates are generally found. We have not observed actual nectar feeding or collection by ants. However, in *E. cordigera* ants pause briefly at the bases of buds and brush their mouth parts over areas which produce nectar (Janzen, personal communication). This would suggest that like in *Acacia* (Brown, 1960; Janzen, 1966, 1967) the ant–orchid association is clearly mutualistic. The orchids derive protection whereas the ants obtain food and shelter.

Three conclusions can be drawn from the presently available information on sugar content of orchid exudates (Table 1).

(1) Secretion of sugar containing exudates by orchids (or the lack of it) as well as the saccharides present in these nectars, can in some cases, if carefully applied, be of some, although at present slight, chemotaxonomic value.

(2) There appears to be no relation between sugar content of orchid exudates in the species examined and their pollinators.

(3) Sugar containing exudates in orchids may serve to maintain 'protector' ants or wasps.

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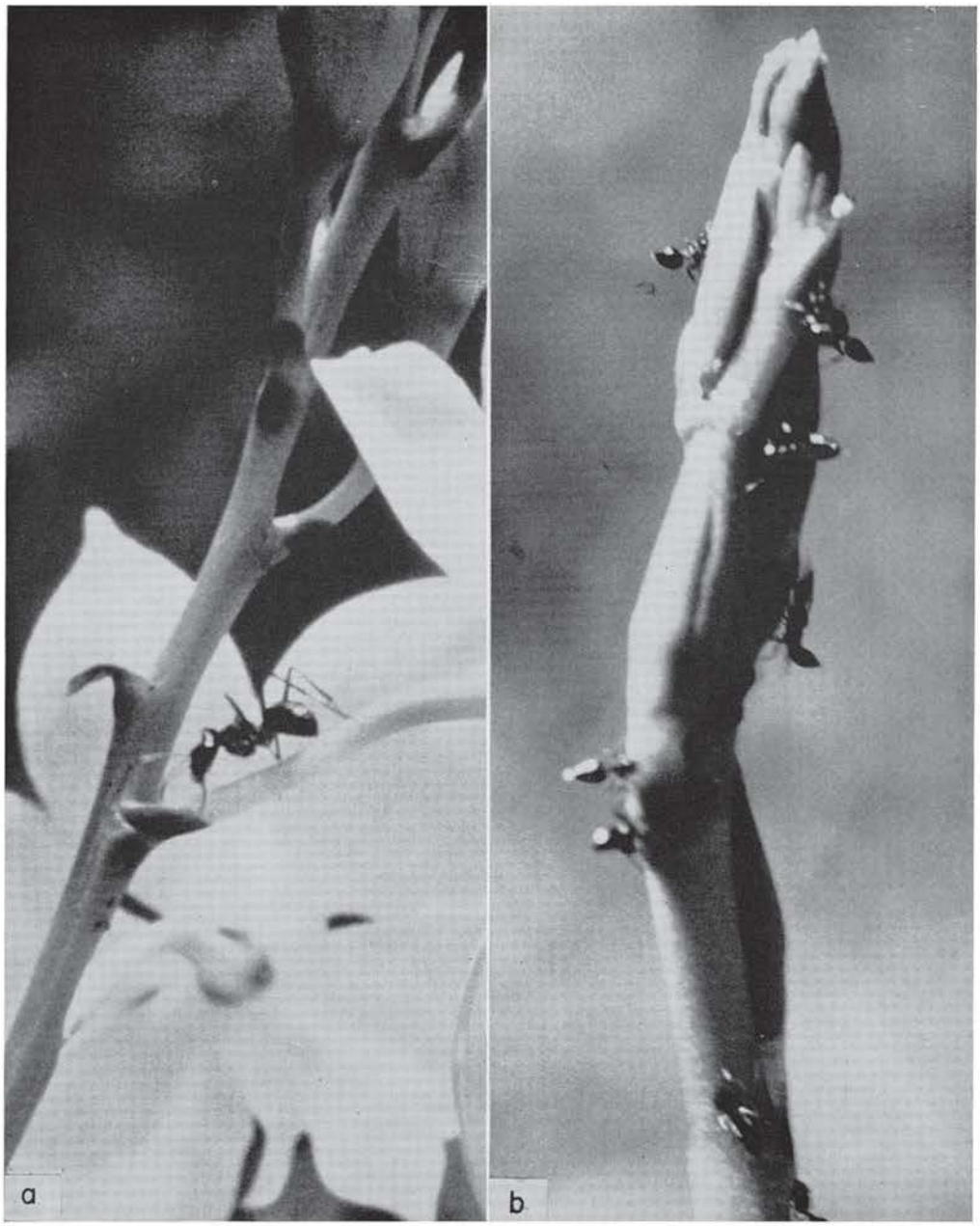

(a) Unidentified ant on *Caulathron* (*Diacrium*) *bicornutum* in Venezuela. It is not clear whether this is the pseudobulb-inhabiting species or a visitor. The ant appears to be foraging in an area which may produce exudates. (Courtesy G. C. K. Dunsterville.) (b) *Crematogaster* on *Encyclia cordigera* in Costa Rica. (Courtesy D. H. Janzen.)

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APPENDIX

Table 1. *Sugar content in floral and extrafloral exudates and pollinators of several orchid species*

Species or hybrid	Exudate		Pollination	
	Sugars present*	Reference†	Pollinator	Reference
Aerides cornutum	'Sugar'	Darwin (1904)		
A. odoratum	G, F, S, R	Percival (1961)		
Angraecum comorense	G, F, S			
A. eburneum	G, F, S, R			
A. sesquipedale	G, F, S, R Melezitose (?)		*Xanthopan morgani predicta* (Moth)	Warner (1934, 1944)
Angraecum × *Veitchii*	G, F, S, R (?)			
Ansellia africana	G, F, S	Baskin and Bliss (1969)		
Arpophyllum giganteum	G, F, S			
Ascocentrum ampulaceum	G, F, S			
Brassocattleya × *Nanipuakea*	G, F, S Gentiobiose (?) Melibiose (?)	Baskin and Bliss (1969)		
Brassolaeliocattleya × *Marchesa*	G, F, S			
Blc Sylvia Fry	G, F, S	Jeffrey and Arditti (1969)		
Blc The Baroness × *Lc* Grandee	G, F, S			
Brassavola glauca	G, F, S		A related species, *B. dygbiana*, is pollinated by a sphingid moth	
Catasetum discolor	G, F, S, R	Jeffrey and Arditti (1968)	*Eulaema cingulata* (bee)	Dodson (1965); Van der Pijl and Dodson (1966)
Cattleya sp.‡	G, F, S	Frey-Wyssling and Hauserman (1960)	All *Cattleya* species listed are bee pollinated	Dodson (1965); Van der Pijl and Dodson (1966)
C. amethystoglossa	G, F, S			
C. aurantiaca	G, F, S	Baskin and Bliss (1969)		
C. bowringiana	G, F, S and unknown oligosaccharides	Baskin and Bliss (1969)		
Cattleya × Edithae 'White Empress'	G, F, S, R			
Cattleya × Enid 'Alba'	G, F, S			
Cattleya × Estelle × *C. intermedia alba*	G, F, S and a 'more complicated' sugar	Baskin and Bliss (1969); Payne (1965)		
C. forbesii	G, F, S			
C. guatemalensis	G, F, S, R			
C. guttata alba	G, F, S	Jeffrey and Arditti (1969)		
C. intermedia	G, F, S, R (?)			
C. intermedia acquinii	G, F, S			
C. labiata	Reducing sugars	Sunding (1963)		
C. loddigesii alba	G, F, S, R	Jeffrey and Arditti (1969)		
C. maxima (Horace)	G, F, S		*Eulaema polychroma* (bee)	Dodson (1965); Van der Pijl and Dodson (1966)
C. mossia × *C. albida*	G, F, S			
C. × Nigritian	G, F, S	Jeffrey and Arditti (1969)		
C. percivaliana	G, F, S			
C. skinneri	G, F, S, R			
C. trianae 'Bill Taft'	G, F, S			
C. trianae 'President'	G, F, S			
Cattleyopsis lindenii	G, F, S, R Melibiose (?)	Baskin and Bliss (1969)	Bees	Arditti (1969)
Cattleytonia 'Rosy Jewell'	G, F, S			

Species or hybrid	Exudate		Pollination	
	Sugars present*	Reference†	Pollinator	Reference
Chysis laevis	G, F, S	Baskin and Bliss (1969)		
Coelogyne cristata‡	G.F.S	Percival (1961)		
Coryanthes‡	'Almost pure water'	Darwin (1904)	All *Coryanthes* listed are bee pollinated	Dodson (1965); Van der Pijl and (1966)
Cycnoches chlorochilon	G, F, S	Baskin and Bliss (1969)	*Eulaema cingulata* (bee—all *Cycnoches* spp. listed are bee pollinated)	Dodson (1965); Van der Pijl and Dodson (1966)
C. chlorochilon male flower	G, F, S, R Melibiose (?) St (?)		*Eulaema cingulata* (bee)	Dodson (1965); Van der Pijl and Dodson (1966)
Cymbidium sp.	G, F, S	Frey-Wyssling and Hauserman (1960)		
Cymbidium aloifolium	G, F, S	Baskin and Bliss (1969)	*Xyloxopa* sp. (bee) *Vespa cincta* (wasp)	Van der Pijl and Dodson (1966)
C. canaliculatum	G, F, S	Baskin and Bliss (1969)		
C. canaliculatum 'Canadian'	G, F, S, R (?)			
C. devonianum	G, F, S, R			
Cymbidium × Evening star	G, F, S, R, St (?)			
Cymbidium × Fairy Wand	G, F, S			
Cymbidium × King Arthur	G, D, S			
Cymbidium × Lillian Stewart	G, F, S, T, St (?)			
Cymbidium × Oriental legend 'Temple Bell'	G, F, S			
Cymbidium × Pauwelsii 'The King' × *C.* × Ophir	G, F, S 'Unknown'	Percival (1961)		
Cymbidium × Peter Pan 'Green sleeves'	G, F, S, R, St			
Cymbidium × Samarkand	G, F, S, (very high F conc.)			
Cymbidium × San Francisco	G, F, S			
Cymbidium × Showgirl	G, F, S	Percival (1961)		
Cymbidium sp.	G, F, S 'Unknown'			
Cymbidium Tiger Tail	G, F, S	Baskin and Bliss (1969)		
Cyrtopodium punctatum	G, F, S Melibiose (?)	Baskin and Bliss (1969)	*Euglossa hemichlora*	Van der Pijl and Dodson (1966)
Dendrobium‡ *crysotoxum*	G, F, S	Jeffrey and Arditti (1968)		
D. undulatum 'Bloomfeldii'	G, F, S			
Diabroughtonia × 'Alice Hart'	G, F, S			
Diacrium bicornutum‡ (*Caulathron bicornutum*)	G, F, S	Baskin and Bliss (1969)		
Epicattleya hybrid	G, F, S	Jeffrey and Arditti (1969)		
Epidendrum‡ × Anza	G, F, S, R Maltose (?)	Baskin and Bliss (1969)	*Epidendrum* listed are pollinated by bees, birds, butterflies, flies and moths	Dodson (1965); Van der Pijl and Dodson (1966)
E. atropurpureum	G, F, S, R	Baskin and Bliss (1969)		
E. cochleatum	G, F, S			
E. ('Hawkes')	G, F, S			
E. × *Obrienianum*	G, F, S			
E. stamfordianum	G, F, S			
E. stellatum	G, F, S	Baskin and Bliss (1969)		
Epidendrum (unidentified Venezuelan species)	G, F, S	Jeffrey and Arditti (1969)		

Species or hybrid	Exudate: Sugars present*	Exudate: Reference†	Pollination: Pollinator	Pollination: Reference
Epipactis atrorubens	G, F, S		*Epicatis* listed are pollinated by bees, flies and wasps	Van der Pijl and and Dodson (1966)
E. helleborine	G, F, S Melibiose	Percival (1961)		
E. palustris	G, F, S		*Apis mellifera* (bee)	Van der Pijl and Dodson (1966)
Habenaria obtusata	'Sugar'	Thien (1969)	*Aedes communis*, *A. canadensis canadensis*, *A. intrudens* (mosquito)	Arditti (1968); Raup (1930); Stoutamire (1968); Thien (1969)
Laelia flava	G, F, S, R (?)			
L. millerii	G, F, S		Undet. hummingbird	Van der Pijl and Dodson (1966)
L. pumila 'Dayana'	G, F, S			
L. rubescens	G, F, S			
L. tenebrosa	G, F, S, R Melibiose	Baskin and Bliss (1969)		
Laeliocattleya × Adolph Hecker	G, F, S, R Cellobiose	Baskin and Bliss (1969)		
Laeliocattleya × Chit Chat	G, F, S, R			
Laeliocattleya × Dorothy Fried	G, F, S, R	Jeffrey and Arditti (1969)		
Laeliocattleya × Eva	G, F, S			
Laeliocattleya × Goden Ray	G, F, S, R (?)			
Laeliocattleya × Hunter's Gold	G, F, S	Jeffrey and Arditti (1969)		
Laeliocattleya Mem Walter Armacost	G, F, S, lactose	Baskin and Bliss (1969)		
Laeliocattleya × Paradisio	G, F, S	Baskin and Bliss (1969)		
Laeliocattleya × Valantes	G, F, S	Baskin and Bliss (1969)		
Listera ovata	G, F, S	Percival (1961)	*Ophinoninae* (wasp)	Van der Pijl and Dodson (1966)
Miltonia warscewiczii	G, F, S		All *Miltonia* listed are bee pollinated	Dodson (1965); Van der Pijl and Dodson (1966)
Miltonidium × Surprise	G, F, S	Baskin and Bliss (1969)		
Mormodes igneum	G, F, S, R St (?)		*Euglossa igniventria* *E. mixta* (bee)	Van der Pijl and Dodson (1966)
Notylia	G, F, S		All *Notylia* listed are bee pollinated	Van der Pijl and Dodson (1966)
Odontoglossum cariniferum	G, F, S, R, and unknown sugar	Baskin and Bliss (1969)	All *Odontoglossum* listed are bee pollinated	Van der Pijl and Dodson (1966)
Odontoglossum 'Finest'	G, F, S	Baskin and Bliss (1969)		
Oncidium‡ *ampliatum*	G, F, S, R Melezitose (?)		All *Oncidium* listed are bee pollinated	Dodson (1965); Van der Pijl and Dodson (1966)
O. carthaginense	G, F, S, R			
O. maculatum	G, F, S			
O. nudum	G, F, S, R (?)			
O. tigrinum	G, F, S, R, Melezitose (?)			
Phaius flavus	G, F, S		All *Phaius* listed are bee pollinated	Van der Pijl and Dodson (1966)
Phalaenopsis lueddemanniana	G, F, S, R, and unknown sugar	Baskin and Bliss (1969)	All *Phalaenopsis* listed are bee pollinated	Dodson (1965); Van der Pijl and Dodson (1966)
Renanthera × Tom Thumb	G, F, S	Baskin and Bliss (1969)		
Schomburgkia‡ *undulata*	G, F, S		All *Schomburgkia* listed are bee pollinated	Dodson (1965); Van der Pijl and Dodson (1966)
Schomburgkia × Wishful Pink	G, F, S			

Species or hybrid	Exudate		Pollination	
	Sugars present*	Reference†	Pollinator	Reference
Sobralia sp.	G, F, S, Melibiose (?)	Baskin and Bliss (1969)	All *Sobralia* listed are pollinated by birds and bees	Van der Pijl and Dodson (1966)
Sophrolaeliocattleya × Estella Jewell	G, F, S	Baskin and Bliss (1969)		
Spathoglottis‡ *plicata*	G, F, S			
Trigonidum obtusum	G, F, S	Baskin and Bliss (1969)	*Trigona droryana* (bee)	Van der Pijl and Dodson (1966)
Vanda‡ × Rothschildiana	G, F, S Maltose (?)	Baskin and Bliss (1969)	All *Vanda* listed are bee pollinated	Van der Pijl and Dodson (1966)
V. suavis (*V. tricolor*)	G. F, S			
V. teres alba 'Candide'	G, F, S			
Vanilla‡ *planifollia*	G, F, S, very high R conc., Melibiose Maninotriose (?) Unknown oligo-sacharide		*Melipona beechii* (bee)	Van der Pijl and Dodson (1966)
Zygopetalum intermedium	G, F, S	Baskin and Bliss (1969)	All *Zygopetalum* listed are bee pollinated	Van der Pijl and Dodson (1966)
Z. mackyaii	G, F, S			

* F, Fructose; G, glucose; R, raffinose; S, sucrose; St, stachyose.

† No reference is given for species studied in the preparation of this paper.

‡ Association with ants observed in at least one species within the genus. Such associations have also been observed in *Encyclia cordigera* and species of *Arundina*, *Gongora*, *Grammatophyllum* and *Vandopsis*.