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Reproductive biology of *Cyrtopodium polyphyllum* (Orchidaceae): a Cyrtopodiinae pollinated by deceit

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ABSTRACT

The genus *Cyrtopodium* comprises about 42 species distributed from southern Florida to northern Argentina. *Cyrtopodium polyphyllum* occurs on rocks or in sandy soils, in *restinga* vegetation along the Brazilian coast. It flowers during the wet season and its inflorescences produce a high number of resupinate yellow flowers. *Cyrtopodium polyphyllum* offers no rewards to its pollinators, but mimics the yellow, reward-producing flowers of nearby growing *Stigmaphyllon arenicola* (oil) and *Crotalaria vitellina* (nectar) individuals. Several species of bee visit flowers of *C. polyphyllum*, but only two species of *Centris* (*Centris tarsata* and *Centris labrosa*) act as pollinators. Visits to flowers of *C. polyphyllum* were scarce and, as a consequence, low-fruit set was recorded under natural conditions. Such low-fruit production contrasts with the number of fruits each plant bears after manual pollination, suggesting deficient pollen transfer among plants. *C. polyphyllum* is self-compatible and has a high-fruit set in both manual self- and cross-pollinated flowers. Furthermore, fruits (2%) are formed by self-pollination assisted by rain. This facultative self-pollination mechanism is an important strategy to provide reproductive assurance to *C. polyphyllum* as rainfall restricts the foraging activity of its pollinating bees. Fruits derived from treatments and under natural conditions had a similar high rate of potentially viable seed. Moreover, these seeds had a low polyembryony rate, which did not exceed 5%. *C. polyphyllum* acts by deceit involving optical signals and exploits other yellow-flowered species within its habitat by attracting their pollinators. The low capsule production under natural conditions was expected, but its reproductive success is assured through self-pollination by rain and high seed viability.

INTRODUCTION

The neotropical genus *Cyrtopodium* (Epidendroideae, Cymbidieae, Cyrtopodiinae) comprises about 42 species distributed from southern Florida to northern Argentina (Batista & Bianchetti 2004), and includes *Cyrtopodium polyphyllum* (Vell.) Pabst *ex* F. Barros (*i.e. Cyrtopodium paranaense* Schltr.), which occurs mainly from south to southeastern Brazil (Hoehne 1942).

Most orchid species are pollinated by Hymenoptera that exploit different rewards or are attracted by deceit (van der Pijl & Dodson 1966; Dressler 1981). Deception often arises from an insect's inability to distinguish between rewarding and non-rewarding flowers (revision in Renner 2006). About one third of all Orchidaceae are deceptive (van der Pijl & Dodson 1966; Ackerman 1986; Nilsson 1992), and, according to Dressler (1993), there are 4800 deceptive generalized 'food flower' mimics among the orchids. Non-rewarding orchids attract their pollinators in a variety of ways, including food fraud (Dafni 1984; Ackerman 1986; Nilsson 1992). Out of the rewards species present to their pollinators, nectar, is the most common and widespread among Orchidaceae (van der Pijl & Dodson 1966; Nilsson 1992), and is exploited by several groups of social and solitary bees (see van der Pijl & Dodson 1966 for a review). Other rewards in the

Orchidaceae that are collected by bees are floral fragrances, pollen, food hairs, pseudopollen and edible oils (van der Pijl & Dodson 1966; Williams 1982).

The Cyrtopodiinae *Grobya amherstiae* Lindl. is pollinated by *Paratetrapedia fervida* Smith (Anthophoridae) bees that collect floral oils produced by trichomatic and epidermal elaiophores at their lip apex and column base (Mickeliunas *et al.* 2006). The offering of floral oils as a reward was studied by Vogel (1974) for some species of subtribes Ornithocephalinae and Oncidiinae. According to more recent studies on the pollination biology of *Oncidium* species, the floral oil produced by elaiophores is collected by *Tetrapedia* bees (Anthophoridae: Tetrapediini) (Schlindwein 1995; Singer & Cocucci 1999). However, data on the floral biology and pollination mechanisms of Cyrtopodiinae are very scarce. According to Chase & Hills (1992), species of *Cyrtopodium* offer no reward to their pollinators, and thus attract Centridini and Euglossini bees by deceit. Orchid species pollinated by deceit generally have low reproductive success under natural conditions, mainly due to the low frequencies of effective pollinators (*e.g.* Montalvo & Ackerman 1987; Ackerman 1989; Zimmerman & Aide 1989). The variation in the probability of a given flower setting fruit is influenced by several factors. Phenology, inflorescence type, habitat, plant density, population size and weather variation (Kindlmann & Balounová 2001) may affect both the reproductive success and the composition of the surrounding plant community (Tremblay *et al.* 2005).

The present study reports on the pollination mechanism and reproductive biology of *C. polyphyllum* occurring in the *restinga* vegetation of the Atlantic rain forest in southeastern Brazil. The purpose of the study is twofold: (i) to describe pollination by deceit and the association with co-blooming species with similar visual signals and (ii) to present and discuss its reproductive success in relation to this type of pollination mechanism.

MATERIAL AND METHODS

Study sites

The floral and reproductive biology of *Cyrtopodium polyphyllum* was studied at two different sites in Ubatuba (approx. 23°22′ S, 44°50′ W; 0–50 m a.s.l.) in the State of São Paulo, southeastern Brazil. Observations were made in the Natural Reserve of Picinguaba and at Praia da Fortaleza, two areas mainly composed by Atlantic rain forest. Climate is tropical humid (‘Af.’; see Köppen 1948), with an annual rainfall of up to 2600 mm, an average annual temperature of 21 °C and no well-defined dry cold season, even during the so-called dry months (from May to September); the wet season occurs from October to March (data source: Instituto Agronômico de Campinas, Campinas, Brazil). Both studied populations occur in *restinga* vegetation and grow on rocks or in sandy soils. At the Picinguaba study site, model plants of nectar-producing *Crotalaria vitellina* L. (Fabaceae) predominate, together with *C. polyphyllum*, whereas at the Praia da Fortaleza site, the model oil-producing plants *Stigmaphyllon arenicola* C.E. Anderson (Malpighiaceae) are more abundant. Five widely scattered individuals of *C. polyphyllum* (seven inflorescences) without model plants nearby were studied in forest margins.

Plant and flower features

Fieldwork was carried out during three *Cyrtopodium polyphyllum* flowering seasons, from August 2004 to December 2006. Data on phenology, the production of pseudobulbs, leaves and inflorescences, as well as features of flower anthesis, pollinators and fruit dehiscence were recorded.

Morphological features of fresh and FAA (formalin–acetic acid–alcohol) preserved flowers collected in the field (n = 30) were recorded and drawn under a binocular stereomicroscope equipped with a ‘camera lucida’. Measurements were made from drawings and directly from floral structures using a caliper rule. Fresh flowers were immersed in neutral red to localise osmophores (Dafni 1992). Flowers were preserved in buffered neutral formalin (Clark 1981) and stored in 70% ethanol. Microtome longitudinal sections of the labellum were tested for lipids using Sudan black B solution (Pearse 1968). Plant voucher for *C. polyphyllum* – Ubatuba, XI.2005, *L. Mickeliunas and E.R. Pansarin 48* was deposited at the Herbarium of the Universidade Estadual de Campinas (UEC).

Pollination mechanism and pollinators

Detailed observations of the pollination process, visitation frequencies, visitors and capture of pollinators on flowers of *Cyrtopodium polyphyllum* were carried out from 26 to 29 November 2004, from 15 to 16 November, 28 November to 1 December, 8 to 9 and 12 to 14 December 2005, and from 23 to 24 November, 6 and 13 to 15 December 2006, totalling 106 h. The daily observation period was from 08:00 to 14:00 h. Immediately after this period, flowers were bagged to exclude any possible visits after the observation period and nocturnal pollination. Additional observations were made on the three individuals located in forest margins from 13 to 14 December 2005, from 23 to 24 November and from 15 to 16 December 2006, totalling 13 h of observations. Insects were collected, identified and vouchers are deposited at the Museu de História Natural of the Universidade Estadual de Campinas (ZUEC).

Breeding system, natural fruit set and seed viability

The experimental treatments to investigate the breeding system of *Cyrtopodium polyphyllum* were performed in the natural habitat, and included manual self- and cross-pollinations and emasculations. They involved 30 flowers (three inflorescences) per treatment in Picinguaba and 30 flowers (three inflorescences) in Praia da Fortaleza. Treatments were randomly applied to each inflorescence, using flowers on their first day of anthesis. Eighty-seven flowers (one inflorescence) and 1359 flowers (30 inflorescences) were used to check self-pollination by rain in Picinguaba and at Praia da Fortaleza, respectively. The fruit set under natural conditions for 2380 flowers (30 inflorescences) in Picinguaba and 2028 flowers (30 inflorescences) at Praia da Fortaleza was recorded when fruits were dehiscent.

A test for potentially viable seeds was performed on fruits obtained through manual pollinations, self-pollination by rain and on 60 fruits that developed under natural conditions (30 fruits from each study site). Fresh seeds were placed in a 1% solution of 2,3,5-triphenyltetrazolium chloride, and all well-developed embryos stained red, indicating viable seeds, while none of the rudimentary embryos were stained. Given these results, samples of 200 seeds per fruit were scored for viability and seeds with well-developed embryos were considered viable, whereas those with rudimentary or no embryos were considered nonviable. During seed examination, the occurrence of polyembryony was recorded.

RESULTS

Plant and flower features

Cyrtopodium polyphyllum (Fig. 1A,B) occurs singly or in small patches and grows intermingled with or near to patches of the mass-flowering individuals of *Stigmaphyl-*

Fig. 1. A: Flower of *Cyrtopodium polyphyllum,* a rewardless orchid. B: *Cyrtopodium polyphyllum* (Cp) co-occurring with *Stigmaphyllon arenicola* (St). C: Flower of *Crotalaria vitellina* that offers nectar as a reward. D: Flower of *Stigmaphyllon arenicola* that offers floral oil as a reward. E: Seed of *Cyrtopodium polyphyllum* with a well-developed embryo and seed with a rudimentary embryo (arrow). F: Seed of *C. polyphyllum* with two embryos.

lon arenicola (Fig. 1B,D) and of *Crotalaria vitellina* (Fig. 1C). In October, each plant of *C. polyphyllum* develops a new fusiform pseudobulb and, sometimes, simultaneously develops a lateral and paniculate, mostly erect, inflorescence that produces an average of 130 resupinate flowers. The main flowering period occurs in November, but several flowering plants were recorded until January. However, the blooming, which coincides with long periods of rainfall, of *C. polyphyllum* begins after and ends before that of its model plants, *S. arenicola* and *C. vitellina* (M.C.H. Mamede, unpublished results; A.M.G. de Azevedo Tozzi, unpublished results; Romera 1999). The model species have showy yellow flowers like those of *C. polyphyllum*, and are similar in size. *Cyrtopodium polyphyllum* flowers have ovate–lanceolate sepals with undulate margins and obovate petals. The three-lobed and (14-mm long) yellow lip presents a central callus similar to an elaiophore. The arched column (Fig. 2D) is green to yellowish and presents a concave and transversally disposed oval stigmatic cavity (Fig. 2C). The pollinarium presents two oval, yellow and waxy pollinia (Fig. 2B), and the viscidium is cordiform and white hyaline. A thick rostellum separates the pollinarium from the stigmatic surface. Composed of multicellular protrusions (Fig. 3A), the osmophores, which occur on the adaxial surface of the lip and secrete lipophilous substances (fragrance compounds) (Fig. 3B), are more evident on the callus. Flowers open in the morning hours and their odour and weak fragrance is perceptible at short distances mainly during the hottest hours of the day (11:00–14:00 h). Untouched flowers last about 21 days, while pollinated flowers fade quickly. Fruits are ripe from July to September.

Pollination process and pollinators

Flowers of *Stigmaphyllon arenicola* and *Crotalaria vitellina* were frequently visited by Centridini bees, which collected floral oil and nectar, respectively. Visits to flowers of *Cyrtopodium polyphyllum* were fairly rare, one to four per day, and occurred at irregular intervals, but mainly between 10:00–14:00 h and only on sunny days, as rainfall and cloud cover restrict the bee foraging activity. During visits, the bees landed directly on the central callus of the lip and probed for reward (Fig. 2A) but, as there was none, visits were very quick, lasting about 1–2 s. While landing, or when the bees abandoned the flower, the viscidium contacted the bee head where the pollinarium was deposited (Fig. 2E–F). Pollinaria were removed alone or, sometimes, with the anther cap. Only two species of *Centris* (*C. tarsata* and *C. labrosa*, Table 1) did succeed in removing the pollinarium because their size matches fairly well the flower morphology and size (Fig. 2A). The other *Centris* species, as well as *Epicharis schrottkyi*, were too big (Table 1) to remove pollinaria. During some visits, *E. schrottkyi* were clearly observed scratching the labellum for oil, but soon after switched their behaviour to pollen harvesting by buzzing. Additionally, some other species, like *Xylocopa brasilianorum* and *Bombus morio*, approached the inflorescences, but most did not land on a flower. When they did land, they looked disoriented and soon abandoned flowers without removing any pollinaria. Flowers of *C. polyphyllum* attracted a wide range of solitary native bees, with the exception of euglossines (Table 1).

Flowers of one of the widely scattered individuals of *C. polyphyllum* were visited by *X. brasilianorum* once. The bee approached a flower by hovering in front of it but, in most observations, did not land on it. In five observations, the bee actually landed on the flower but looked disoriented, although in some flowers it tried to probe for nectar at the column base. No pollinia were removed or deposited. One individual of *Bombus morio* approached the inflorescence once but did not visit it. No other visitors were recorded on these individuals that developed only two fruits after self-pollination by rain. This type of pollination was recorded on 31 individuals of *C. polyphyllum* and occurred only on rainy days when water accumulated in the stigma cavity and dissolved its adhesive substance forming a viscous drop, which contacted the pollinarium causing it to swell. Through evaporation the drop shrank and moved the swollen pollinarium with the anther onto the stigmatic surface thus promoting self-pollination, and the flower actually developed fruits with viable seeds at both study sites (Table 2) (L.M. Pansarin *et al.*, unpublished results).

Breeding systems, natural fruit set and seed viability

Cyrtopodium polyphyllum is self-compatible. Fruit set in self-pollinated flowers was 17% and 63%, and in cross-pollinated flowers it was 63% and 77%, in Picinguaba and Praia da Fortaleza, respectively. No fruits developed after emasculation. Flowers self-pollinated by rain yielded 2% dehiscent fruits in Picinguaba and 2% at Praia da Fortaleza. Under natural conditions, fruit set was low, with 1% and 2%, in Picinguaba and Praia da Fortaleza, respectively. It is worth mentioning that the highest fruit set (2%) occurred at the site where *Stigmaphyllon arenicola* was the most abundant model plant. No biotic pollinations occurred to *C. polyphyllum* individuals from the forest margins. The results of fruit set are summarised in Table 2.

Fruits obtained in treatments and under natural conditions presented a high percentage of viable seeds, over 90% on average (Table 2). There was little difference in seed viability among fruits obtained from treatments or those developed under natural conditions. Most seeds had well-developed embryos: less than 10% had rudimentary embryos (Fig. 1E). Seeds with polyembryony (two embryos; Fig. 1F) were recorded in fruits from treatments as well as in those developed in natural conditions. These embryos were similar in size to those of seeds with one embryo. Moreover, these seeds showed a low rate of polyembryony, which did not exceed 5% (Table 2).

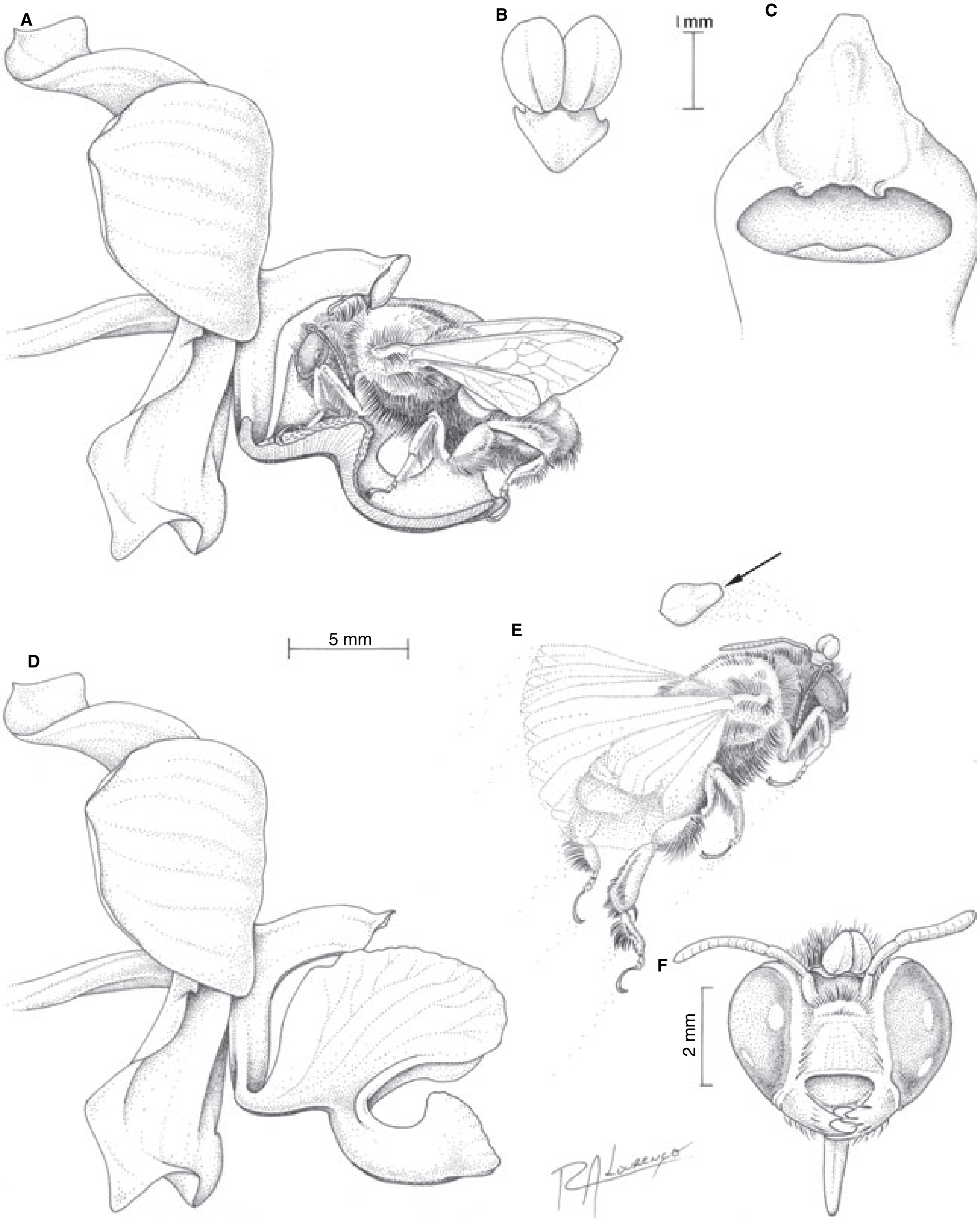

Fig. 2. Floral features and pollination mechanism of *Cyrtopodium polyphyllum*. A: Longitudinal section of a flower of *C. polyphyllum* with *Centris labrosa* landed on the lip central callus. Note that the bee size matches well the flower morphology and size. B: Detached pollinarium. C: Detail of the column showing anther and stigmatic cavity. D: Flower in lateral view. Compared with (A), almost no position changes of the labellum can be noticed during visits. E: *Centris labrosa* with a pollinarium on its head. Note the removed anther cap (arrow). F: Detail in front view of the head of *Centris labrosa* with an attached pollinarium.

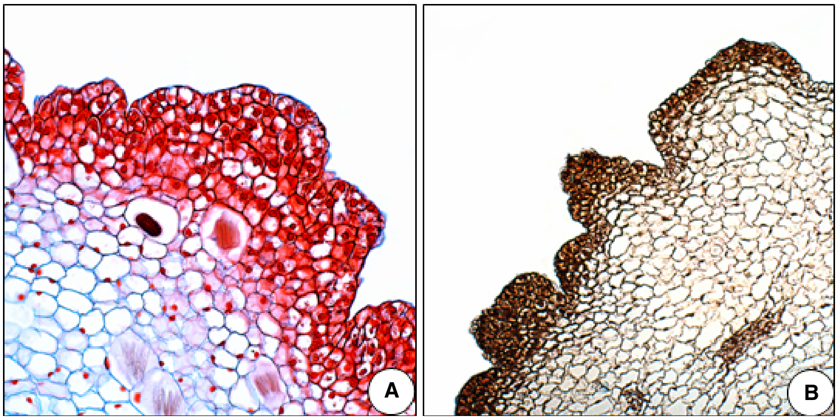

Fig. 3. Longitudinal sections of *Cyrtopodium polyphyllum* labellum. A: Osmophores composed of multicellular protrusions. B: Secretion of lipophilous substances (fragrance compounds), evidenced by Sudan Black B test. A = ×40; B = ×20.

Table 1. Bee species and their respective number of visits to flowers of *Cyrtopodium polyphyllum* recorded at Picinguaba and Praia da Fortaleza (Ubatuba – SP).

bee species	body length (mm)	visitation number
Centris (*Hemisiella*) *tarsata* Smith, 1874	12.1	11
Centris (*Heterocentris*) *labrosa* Friese 1899	12.45	6
Centris (*Ptilotopus*) *scopipes* Friese, 1899	25.95	9
Centris (*Melacentris*) cf. *mocsaryi* Friese, 1899	21.36	4
Centris (*Centris*) *leprieuri* (Spinola, 1841)	17.02	11
Epicharis (*Triepicharis*) *schrottkyi* Friese, 1899	20.55	12
Xylocopa (*Neoxylocopa*) *brasilianorum* (Linnaeus, 1767)	24.27	2
Bombus (*Fervidobombus*) *morio* Swederus 1787	13.28	1
Oxaea (*Oxaea*) *flavescens* Klug 1807	17.95	4
Augochloropsis sp.	10.47	4

DISCUSSION

Plant and flower features

Although the centre of diversity of the genus is the Brazilian *cerrado* (Batista & Bianchetti 2004), a few species, such as reported here for *Cyrtopodium polyphyllum*, occur in sandy soils or on rocks along the Brazilian coast (Hoehne 1942), a habitat that differs drastically from that of the *cerrado* in terms of climatic features. Flowering during the wet season thus appears to be an important reproductive strategy of *C. polyphyllum*, which presents facultative self-pollination by rain (L.M. Pansarin *et al.* unpublished results). The concurrent flowering of *C. polyphyllum* with its model plants, as well as the fact that it begins after and ends before their flowering, are constraints that show the dependence of the mimic on its models, as already reported by Dafni (1987) for *Thelymitra antennifera* (Orchidaceae) and its models.

Anatomical studies of the lip of *C. polyphyllum* revealed that, although the central callus is similar to the elaiophore of *Grobya amherstiae* Lindl. (Mickeliunas *et al.* 2006), and species of Ornithocephalinae (Vogel 1974) and Oncidiinae (Vogel 1974; Schlindwein 1995; Singer & Cocucci 1999), its multicellular osmophores are more similar to those of some *Stanhopea* species (Pansarin 2000). The fragrance of *C. polyphyllum* seems not to be a collectible resource and no euglossine bees were recorded as flower visitors. It is most probable that the genus *Cyrtopodium* includes more species without rewards, in addition to oil-producing and perfume-producing species pollinated by

Table 2. Percentage of fruit set, viable seeds and polyembryony of *Cyrtopodium polyphyllum* among treatments and under natural conditions in Picinguaba and Praia da Fortaleza, Ubatuba – SP.

treatments	fruit set	seeds	polyembryony
self-pollination	17% (5/30)[a]	92% (918/1000)[a]	3% (31/1000)[a]
	63% (19/30)[b]	97% (3673/3800)[b]	1% (52/3800)[b]
cross-pollination	63% (19/30)[a]	95% (3595/3800)[a]	5% (177/3800)[a]
	77% (23/30)[b]	97% (4444/4600)[b]	2% (110/4600)[b]
emasculation	0 (0/30)[a,b]	–	–
rain-assisted self-pollination	2% (2/87)[a]	93% (373/400)[a]	2% (9/400)[a]
	2% (30/1359)[b]	92% (5526/6000)[b]	4% (238/6000)[b]
natural conditions	1% (32/2380)[a]	94% (5653/6000)[a]	4% (229/6000)[a]
	2% (49/2028)[b]	93% (5592/6000)[b]	4% (246/6000)[b]

Figures in brackets indicate the number of fruits/flowers, viable seeds/seeds and seeds with two embryos/seed.

[a] Picinguaba.

[b] Praia da Fortaleza.

euglossine bees, as already suggested by Chase & Hills (1992).

As reported for other species of the genus (Chase & Hills 1992), it was expected that flowers of *C. polyphyllum* would produce no reward to their pollinators, and would therefore be pollinated by deceit. The pollination process of this orchid includes plant species of different families as model plants and different rewards, but nutritive deception, which has been documented for about 30 species (Dafni 1984), is the most common of these deceptive mechanisms. The similarity in size and colour between the flowers of *C. polyphyllum* and those of the co-occurring reward-producing species *Stigmaphyllon arenicola* and *Crotalaria vitellina* shows evidence of mimicry, as is the case of several other orchid species, as reported by Bierzychudek (1981a), Dafni (1984), Ackerman (1986) and Nilsson (1992). The similarity between orchid flowers and oil-producing Malpighiaceae flowers had already been recorded by Nieremberg (1972), and that between orchid flowers and other reward-producing flowers of a set of families were reported by Dafni (1987) and Nilsson (1992).

Pollination process and pollinators

The results presented here show that the pollinators of *Cyrtopodium polyphyllum* and those of the co-occurring model plants follow a behavioural pattern similar to that of the cases of mimicry reported by Nilsson (1983) and Dafni (1987). The pollination rates under natural conditions observed at different sites (Table 2) lead to the conclusion that this orchid species imitates a general search image of yellow flowers, namely those of *Stigmaphyllon arenicola* and *Crotalaria vitellina*. This can be corroborated by the evidence that no pollinators (*i.e. Centris* species) were observed visiting flowers of scattered individuals of *C. polyphyllum* located at forest margins. According to Johnson *et al.* (2003), the visitation rates in rewardless orchids depend both on the relative and absolute abundances of deceptive and reward-producing flowers, which, in turn, affect pollinator density in a patch and their movement patterns between patches. Furthermore, according to Renner (2006), the flower colour is the most relevant factor influencing visitation of naive bees in food-deceptive orchids, while size, shape and smell are less relevant. Therefore, the best strategy for a rewardless flower growing together with potential models would be to have a common flower colour (see Renner 2006 for a review).

Centridini bees behave in a similar way on *C. polyphyllum* flowers and on the elaiophore-bearing *Grobya amherstiae* Lindl. (Mickeliunas *et al.* 2006), species of Ornithocephalinae (Vogel 1974) and Oncidiinae (Vogel 1974; Schlindwein 1995; Singer & Cocucci 1999), but the switching behaviour of *Epicharis schrottkyi* individuals trying to collect oil then pollen by buzzing, has only been reported to date for *Epicharis* species on eglandular flowers of Malpighiaceae (Sazima & Sazima 1989).

Although deception may be achieved through the flower resemblance to larval food or to the nectariferous flowers of other families, or even to female individuals of the pollinator, food deception is more frequent in Orchidaceae (see Dafni 1984; Ackerman 1986; Nilsson 1992 for reviews). Among orchids, several model mimics have been proposed (see Ackerman 1986 for a review). A model similar to that recorded here for *C. polyphyllum* has already been reported between *Oncidium lucayanum* Nash *ex* Britton & Millsp. and flowers of Malpighiaceae species in the Bahamas, to deceive oil-collecting females of *Centris* (Nieremberg 1972). If we consider fruit set at both study sites, the deception model involving *C. polyphyllum* and *S. arenicola* is more effective than that involving *Crotalaria vitellina*.

Scarcity of bee visits, as reported here for *C. polyphyllum*, is common in non-rewarding flowers pollinated by deceit (see Ackerman 1986, 1989; Montalvo & Ackerman 1987; Zimmerman & Aide 1989). Besides, climatic factors such as cloud cover and rainfall, wind speed, air temperature, solar radiation and humidity exert a strong influence on bee activity (including on the Centridini bees in neotropical regions), and consequently on their foraging behaviour and visits to flowers (see Roubik 1992 for a review). Some rewardless species can cause reduced visitation and consequently a low reproductive success in relation to reward-producing orchids (*e.g.* Ackerman 1981, 1986; Dafni 1984; Johnson & Nilsson 1999; Salguero-Faría & Ackerman 1999; Johnson 2000; Smithson 2002).

Breeding systems, natural fruit set and seed viability

Although *Cyrtopodium polyphyllum* and *Grobya amherstiae* are self-compatible, both depend on pollen vectors for pollination. While in the latter pollen transfer occurs exclusively through biotic pollinators (Mickeliunas *et al.* 2006), in *C. polyphyllum* it occurs through both biotic (*i.e.* Cendridini bees) and abiotic (namely water from rainfall) vectors (L.M. Pansarin *et al.* unpublished results). As rainfall is high in the region of Ubatuba, and rain may persist for 1 week or more during the wet season, the occurrence of facultative self-pollination by rainfall presented by *C. polyphyllum* may be an important strategy, and so far is unique in the genus, to promote fruit set in the absence of biotic pollinators. Facultative autogamy may occur in a number of species (see Catling 1990 for review) and may be an appropriate strategy when pollination frequency is habitually low. An occasional crossing event may be sufficient to infuse enough genetic variability to diminish any effects of inbreeding depression from frequent self-pollination (see Tremblay *et al.* 2005 for a review).

In Orchidaceae, the production of fruits per inflorescence is used to determine the reproductive success (*e.g.* Montalvo & Ackerman 1987; Ackerman 1989; Zimmerman & Aide 1989; Ackerman & Montalvo 1990). The natural fruit set of *C. polyphyllum* is low when compared to hand self- and cross-pollinations. This was also found in other orchid species (*e.g.* Ackerman & Oliver 1985; Montalvo & Ackerman 1987; Zimmerman & Aide 1989; Ackerman & Montalvo 1990). The fruit set of non-obligatorily autogamous orchids, as is the case of *C. polyphyllum,* is low as a consequence of deficient pollen transfer between plants where the scarcity of efficient pollinators seems to be a limiting factor (*e.g.* Janzen *et al.* 1980; Schemske 1980; Bierzychudek 1981b; Garwood & Horvitz 1985; Ackerman & Montalvo 1990; Calvo 1990; Calvo & Horvitz 1990; Burd 1994; and references therein). However, other factors, such as phenology, inflorescence size, habitat, plant density, population size and weather variation can exert a strong influence on the reproductive success of orchid species (see Kindlmann & Balounová 2001; Tremblay *et al.* 2005 for reviews).

The occurrence of a high percentage of potentially viable seeds after manual pollinations and rain-assisted self-pollinations of *C. polyphyllum* is uncommon in Epidendroideae, whose species present a great number of seeds without embryos (Lock & Profita 1975; Stort & Martins 1980; Stort & Galdino 1984; Borba *et al.* 2001; Borba & Braga 2003). As reported here for *C. polyphyllum, G. amherstiae* (Mickeliunas *et al.* 2006) and the Maxillarieae *Xylobium squalens* (Lindl.) Lindl. (Pintaúdi *et al.* 1990) also have a high incidence of potentially viable seeds.

Polyembryony has generally been reported in Orchidaceae in association with apomixis, the embryo being formed from the inner integument. In all cases, a higher percentage of polyembryony has been recorded (Catling 1982, 1987; Catling & Catling 1991). Pintaúdi *et al.* (1990) and Borba *et al.* (2001) reported the presence of a few rare two-embryo seeds among intra-specific crosses, in which the second embryo may have originated from a division of the zygote. It is probable that the supernumerary embryos in *C. polyphyllum* may have a similar origin and, as they rarely occur, they probably do not play a relevant role.

In conclusion, *C. polyphyllum* exploits other yellow-flowered model species acting by deceit through optical signals. Although self-compatible, *C. polyphyllum* depends on pollen vectors for pollination. Low-capsule production under natural conditions is a result of deficient pollen transfer due to scarcity of efficient pollinators. Moreover, low-visitation frequencies seem to be a consequence of the non-production of floral reward, in a similar way as that reported for other non-rewarding orchids pollinated by deceit (*e.g.* Ackerman 1986, 1989; Montalvo & Ackerman 1987; Zimmerman & Aide 1989). Despite the fact that capsule production through bee pollination is low, reproductive success is guaranteed through facultative self-pollination by rain and high-seed viability.

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