

## POLLINATION ECOLOGY STUDIES IN *CRATYLIA* MART. EX BENTH. (LEGUMINOSAE: PAPILIONOIDEAE) AND ITS TAXONOMIC AND EVOLUTIONARY IMPLICATIONS

Luciano Paganucci de Queiroz<sup>1</sup>

**ABSTRACT:** (Pollination ecological studies in *Cratylia* Mart. ex Benth. (*Leguminosae: Papilionoideae*) and its taxonomic and evolutionary implications) - Pollination ecology studies of *Cratylia hypargyrea* and *C. mollis* have shown that these are melittophilous species pollinated by large bees of the genera *Xylocopa* and *Centris*. Both species show floral adaptations, such as large flowers and a fleshy calyx, which restrict pollination activity to these large bees, limiting access to nectar by other visitors. The phenological strategy of mass flowering adopted by these plants seems to be an adjustment to the foraging pattern of these large bees. Pollination data helps to elucidate the evolution of floral features in *Cratylia* and related groups, such as *Galactia*, *Camptosema* and *Dioclea* sect. *Macrocarpon*. Melittophilous ancestors, probably pollinated by different kinds of bees, may have given rise to two evolutionary paths each of which resulted in floral specializations restricting floral visits to large bees. One path, characterized by a sharply bent keel and somewhat callose standard led to *Dioclea* sect. *Macrocarpon*. The other, characterized by flower enlargement and a fleshy calyx led to the *Cratylia* flower type. Ornithophily may have subsequently appeared in *Camptosema*, derived from such a floral structure, through a colour change to red and loss of reflectivity of the standard.

**Key words:** *Cratylia*; Pollination; Evolution

**RESUMO:** (Estudos de ecologia de polinização em *Cratylia* Mart. ex Benth. (*Leguminosae: Papilionoideae*) e suas implicações taxonômicas e evolutivas) - Estudos de ecologia da polinização de *Cratylia hypargyrea* e *C. mollis* demonstraram que estas espécies são melitófilas, polinizadas por abelhas de grande porte dos gêneros *Xylocopa* e *Centris*. Estas duas espécies de *Cratylia* apresentam adaptações na estrutura floral, como flores grandes e cálice carnososo, que restringem a atividade de polinização a estas grandes abelhas, limitando o acesso de outros visitantes ao néctar. A estratégia fenológica de floração maciça apresentada por estas plantas pode representar um ajuste ao padrão de forrageamento destas grandes abelhas. Os dados oriundos do estudo da polinização ajudam a compreender a evolução dos caracteres florais em *Cratylia* e em grupos mais próximos, como *Galactia*, *Camptosema* e *Dioclea* sec. *Macrocarpon*. A partir de ancestrais melitófilos provavelmente polinizados por diferentes grupos de

<sup>1</sup> Universidade Estadual de Feira de Santana, Departamento de Ciências Biológicas. Km 03 - BR 116, Campus Universitário. 44031-460, Feira de Santana, BA

abelhas, duas tendências evolutivas poderiam ter-se estabelecido, as quais resultaram em especializações florais às grandes abelhas como visitantes. Uma destas tendências, marcada pela acentuada curvatura da carena e estandarte caloso, caracteriza *Dioclea* sec. *Macrocarpon*. A outra, marcada pelo aumento do tamanho da flor e cálice carnosos levou à flor tipo *Cratylia* e; a partir de tal estrutura floral, a ornitofilia pode ter-se desenvolvido em *Camptosema* através da mudança de coloração para o vermelho e perda da capacidade de reflexão do estandarte.

**Palavras-chave:** *Cratylia*; Polinização; Evolução

## Introduction

Pollination ecology and systematics have largely developed independently. Examples of information being shared between these two fields are rare, although each relies heavily upon flower morphology. Taxonomy may thus provide pollination studies with a general vision of the studied group, making possible the formulation of working hypotheses. Information about pollination can, conversely, help taxonomists clarify evolutionary pathways.

*Cratylia* is a small Neotropical genus, with five species distributed mainly in eastern Brazil (QUEIROZ, 1991), belonging to the tribe Phaseoleae subtribe Diocleinae. In this subtribe the flower structure provides important characters for generic delimitation but, even so, the generic boundaries are confused and unstable, this fact being first recognized by BENTHAM (1859) who underlined that *Cratylia* is apparently intermediate between *Dioclea* and *Camptosema*. Traditional taxonomic methods for clarifying these boundaries have been subjective, and the classification does not, as a result, reflect an evolutionary analysis of the groups involved. On the other hand, these genera present variations in floral morphology which indicate adaptation to different pollination agents (ARROYO, 1981).

This work is the first of a series focusing the evolutionary relationships into this generic complex, aiming to investigate the possible relation between flower structure and evolutionary divergence as a result of changes in pollen vector, and its impact on the taxonomy of the group.

Pollination of species of *Cratylia* are described here for the first time and the relationship between floral morphology, mass flowering and visitor behaviour discussed. Also outlined are possible evolutionary relationships between the genera *Dioclea*, *Camptosema* and *Galactia* with *Cratylia* based upon floral morphology and pollination data.

## Material and methods

*Cratylia hypargyrea* Mart. ex Benth. was studied in the Atlantic forest reserve of the Companhia Vale do Rio Doce (Linhares, ES, ca. 19° 24' S, 40° 28' W) from 23 - 27 April 1990, for a total of 50 hours of observation. *Cratylia mollis* Mart. ex Benth. was studied in open shrubby caatinga within the reserve of the Centro de Pesquisas do Trópico Semi-Árido (CPATSA/EMBRAPA) in Petrolina, PE (ca. 09° 04' S, 40° 18' W) from 03 - 05 May 1990 (32 hours). Botanical vouchers (L.P.de Queiroz 2480 for *C. hypargyrea* and J.L.Lima 450 for *C. mollis*) are housed in the HUEFS herbarium, while collected insects, investigated for presence and distribution of pollen, are housed in the collection of Entomology laboratory of the Universidade Estadual de Feira de Santana.

## Results and discussion

### Pollination ecology

*C. hypargyrea* is a liana of the forest edge in Mata Atlântica, while *C. mollis* is a shrub of caatinga. Both species have papilionoid flowers. This floral architecture (Fig. 1) is an adaptation to pollination by bees (LEPPIK, 1966; FAEGRI & van der PIJL, 1979) and shows little variation among species of *Cratylia* (1). The calyx is fleshy, tubular and overlaps the petals claws. The standard is membranaceous and lacks a callus. The wings have lunate-lamellate sculptured areas in their basal region (in Stirton's terminology; STIRTON, 1981), which makes the epidermis rough in this region. The wings are loosely connected to the keel by longitudinal folds. The keel is open in its upper margin and has no beak at its apex. The androecium and the gynoecium are both held within the keel. The staminal sheath has two openings at its base (Fig. 1B) through which insects may access to nectar. The gynoecium is stipitate and the stigma is at the same level as the anthers. The nectary surrounds the base of the stipe (Fig. 1C), and is overlapped by the staminal sheath, the base of which plays a role as a nectariferous chamber.

The flowers are pinkish in *C. hypargyrea* and magenta in *C. mollis*. Both standards have a yellowish cream target that probably act as a nectar guide. Anthesis occurs from 07:00 to 09:30 h in both species,

and is characterized by the unfolding and bending backwards of the standard. At the same time the flowers release a lightly sweet odour, the nectar becomes available, the anthers open and the stigma receptive. The flowers last one day. The day following anthesis, the petals change colour, becoming whitish, and the standard bends onto the wings.

The floral architecture found in these melittophilous species, in which the nectar is concealed by the tubular fleshy calyx, petals claws and staminal sheath may represent a specialization to restrict visits to bees which are strong enough to work the flower mechanism and access the nectar legitimately, as is the case with large polylectic Anthophoridae bees (van der PIJL, 1954). The pollinators of *C. hypargyrea* and *C. mollis* are large species of genera *Xylocopa* and *Centris*, which match the size of the flower (Table 1).

Visits by *Xylocopa frontalis* to flowers of *C. hypargyrea* and by *X. grisescens*, *X. cf. grisescens*, *X. carbonaria* and *X. cearensis* to flowers of *C. mollis* are similar. In all *Xylocopa* species, the visit starts with the bee flying over the inflorescences before selecting one flower. The bee alights on the flower and grasps the sculptured region of the wings with its claws (Fig. 3). It positions its head against the target of the standard and pushes it back while pushing down the wings and keel. The bee then sticks its tongue between the standard and the staminal sheath and through the openings in the base of the staminal sheath to gather the nectar. When the keel is lowered, the anthers and the stigma are exposed and touch the ventral region of the abdomen. When the bee leaves the flower, the petals return to their original position. A visit to one flower last from two to five seconds. Due to their larger size, *X. frontalis*, *X. grisescens*, and *X. cf. grisescens* receive pollen in the middle of their abdominal region and thus act as true pollinators. The smaller *X. carbonaria* and *X. cearensis* bees, on the other hand, receive pollen in the terminal region of their abdomen, many times visit to take nectar without having exposed the reproductive organs. They are thus considered occasional pollinators.

*Centris longimana* makes very fast flights over *C. hypargyrea* plants, suddenly changing direction, before going to a flower. Its visiting behaviour is similar to that described for the *Xylocopa* species. Due to its

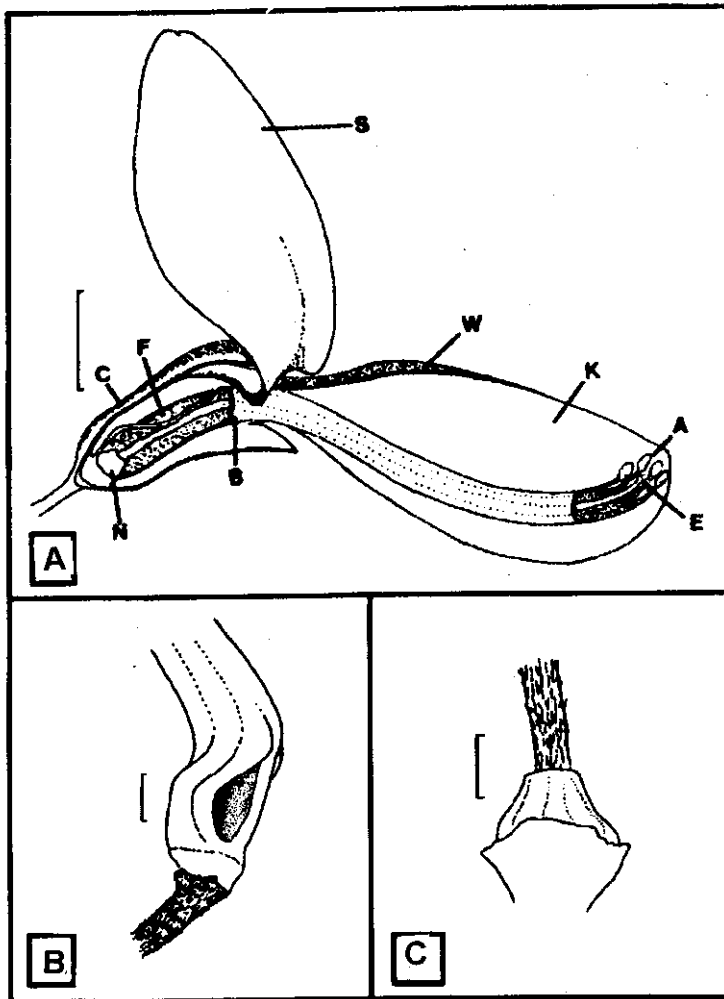


Figure 1: A: Schematic longitudinal section of a generalized *Cratylia* flower, highlighting the structures related to pollination (scale bar = 5 mm); B: Base of the staminal sheath showing the opening by which insects can take nectar (scale bar = 2 mm); C: Floral nectary at base of the stipe (scale bar = 1 mm). Legend: a: anthers; b: staminal sheath; c: calyx; e: stigma; f: opening of the base of staminal sheath; k: keel petal; n: nectary; s: standard petal; w: wing petal.

size, this bee receives pollen in the distal region of its abdomen (Fig. 3). The visit last about three seconds.

Only large, strong Anthophoridae bees can work the flower mechanism of *C. hypargyrea* and *C. mollis* to take nectar, promoting pollination of the flower. van der PIJL (1954) classified relatively large melittophilous flowers with the nectar protected and hidden at the bottom of the calyx in a separate "Xylocopa pollinated flowers' syndrome". The morphology of the *Cratylia* species matches this syndrome except that in *Cratylia* the pollination is stemotribic while van der PIJL (1954) noted a tendency to nototriby in *Xylocopa* flowers. In *Cratylia*, characteristics that may contribute to limiting pollination to xylocopid bees are flower length (more than 2 cm) and the fleshy tubular calyx. Papilionoideae species with smaller flowers generally have a greater diversity of bee pollinators, as occurs in species of *Astragalus* (GREEN & BOHART, 1975), *Lupinus* (WAINWRIGHT, 1978), *Stylosanthes* (PEREIRA-NORONHA *et al.*, 1982) and *Galactia* (QUEIROZ, unpubl. obs.<sup>1</sup>). ARROYO (1981) pointed out that flowers of some Papilionoideae diverge from the general pattern to exclude small bees, and specializing in pollination by larger bees, including *Xylocopa* and *Centris*. The tubular resistant fleshy calyx of species of *Cratylia* should also play an important role. It is well known that several species of *Xylocopa* pierce flowers to rob nectar illegitimately (van der PIJL, 1954). The shape and texture of the calyx hide nectar inside a hard-walled container forcing the bees to take nectar in a legitimate fashion, from the front, alighting on the wings and working the floral mechanism to get at the nectar, making pollination more efficient.

Nevertheless, some insects do manage to get round the nectar protection mechanisms. Three different approaches were taken by different visitors to *C. hypargyrea* and *C. mollis* flowers. (i) *Euglossa cf. cordata* and *Centris* sp.2 (*C. hypargyrea*) and *Centris nitens*, *Centris* sp.1 and *Melipona asilvai* (*C. mollis*) behave similarly to *Xylocopa* species but, because of their smaller size, do not expose the reproductive organs of the flower and thus do not pollinate the flowers; (ii) *Trigona spinipes* visits flowers of *C. mollis* for pollen and nectar in large groups cutting the

---

<sup>1</sup> Unpublished observations made on a population of *Galactia jussiaeana* at Feira de Santana, BA, shown that different groups of bees as small as *Apis mellifera* and *Euglossa cordata* and as large as *Bombus atratus* and *Centris* sp. act as pollinators.

Table 1. Flower visitors of *Cratylia hypargyrea* and *Cratylia mollis*

	<i>C. hypargyrea</i>	<i>C. mollis</i>
Hymenoptera		
Anthophoridae		
<i>Centris (Centris) nitens</i> Lepeletier, 1841		+
<i>C. (Ptilotopus) sp. 1</i>	+	
<i>C. (Trachina) longimana</i> Fabricius, 1804	*	
<i>Centris sp. 2</i>	+	
<i>Xylocopa (Megaxylocopa) frontalis</i> (Olivier, 1789)	*	
<i>X. (Neoxylocopa) carbonaria</i> Smith, 1854		*
<i>X. (Neoxylocopa) cearensis</i> Ducke, 1910		*
<i>X. (Neoxylocopa) griseescens</i> Lepeletier, 1841		*
<i>X. (Neoxylocopa) cf. griseescens</i> Lepeletier, 1841		*
Apidae		
<i>Apis mellifera</i> Linneu, 1758		+
<i>Euglossa (Euglossa) cf. cordata</i> Linneu, 1758	+	
<i>Melipona asilvai</i> Moure, 1971		+
<i>Trigona spinipes</i> (Fabricius, 1793)		-
Lepidoptera		
Hesperidae		
<i>Chioides cattilus</i> (Cramer, 1779)		+
<i>Cymaenes tripuncta theogenes</i> (Capronnier, 1874)	+	
<i>Vettius diversus</i> (Hern.-Sch., 1869)	+	

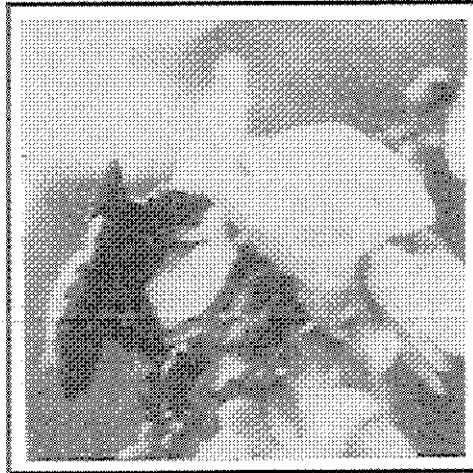
Kind of visitor: \* : pollinator; + nectar thief; - nectar and pollen thief.

flower bud petals to gather pollen and the base of the calyx of the flowers in anthesis to take nectar. *Apis mellifera* can also use these holes to take nectar. The foraging behaviour of *T. spinipes* have a negative effect on the reproductive capacity of *C. mollis*. Besides physical mutilation of flowers, this bee has an aggressive behavior, attacking other bee species that come near the flowers; (iii) Species of Hesperidae (Lepidoptera)

were seen visiting flowers of both *Cratylia* species, landing on the wings, from which they stick the proboscis to take nectar. Because of their long, thin tongues these butterflies can access nectar through the narrow space between the petal claws without working the floral mechanism and do not make contact with the reproductive organs of the flowers.

The inflorescence structure appears to play an important role in the pollination strategy of species of *Cratylia*. In both species the flowers are clustered in long pseudoracemes and display mass flowering. There are 8 to 10 pseudoracemes per branch and each individual inflorescence has many brachyblasts (contracted floral shoots) along its length (20 - 24 brachyblasts per inflorescence in *C. mollis* and 31 - 39 in *C. hypargyrea*). Each brachyblast has 6 to 9 flowers in different development states and in sequential anthesis. The presence of many inflorescences per plant and of many brachyblasts per inflorescence ensures the occurrence of many flowers simultaneously in anthesis, while the occurrence of flower buds of different ages in each brachyblast ensures a more or less constant number of flowers opening each day, new flowers replacing the aged flowers at almost the same position without any increase in the inflorescence size. This mass flowering over a relatively long period (more than three weeks) was described by GENTRY (1974) as the "cornucopia" flowering phenological pattern, into which *Cratylia* species may fit. This flowering strategy may represent, in *Cratylia*, an adjustment to the foraging routes (traplines; JANZEN, 1971) of the large xylocopid bees. The mass flowering, although energetically expensive is a strategy used by many plants to attract more visitors in situations when there is competition for pollinators despite the disadvantage that it favours territoriality among them and thus increases the rate of geitonogamic crosses (ARROYO, 1976; FRANKIE *et al.*, 1976). Although territoriality has been very well documented for species of *Centris* (FRANKIE *et al.*, 1976; FISCHER & GORDO, 1993) and *Xylocopa* (VELTHIUS & CAMARGO, 1975; GOTTSBERGER *et al.*, 1988), no territorial behaviour had been observed between pollinators of *Cratylia* species since bees remain at the plant only during the flower visit. Even so it is possible to infer that the rate of self crosses must be relatively high compared to outcrosses since the bees tend to visit various flowers in the same inflorescence (3 to 8) before moving to another plant or inflorescence. Nevertheless, even with a low rate of interplant movements in relation to the within inflorescence movements seems to maintain a desirable level of outcrossing as described by FRANKIE *et al.* (1976) for *Andira inermis*, another tropical legume. Many species of large solitary bees have some





2



3

Figure 2 *Xylocopa frontalis* in visit to a flower of *Cratylia hypargyrea*.; Figure 3. Visit of *Centris longimana* to a flower of *Cratylia hypargyrea*, showing the contact of the reproductive floral organs to the distal abdomen of the bee.

capacity to learn and memorize and there is evidence that they establish more or less fixed daily traplines. In this context, the presentation of new flowers each day in the same position encourages fidelity by pollinators and may help to include and maintain that individual plant within a pollinator's trapline (GENTRY, 1974), thereby ensuring some outcrossing.

### Evolutionary relationships

*Cratylia* is taxonomically related to *Camptosema*, *Dioclea* sect. *Macrocarpon* and *Galactia* but there is instability in the intergeneric limits with species being moved between genera by different authors. It has also been proposed to merge *Cratylia* e *Dioclea* in a single genus (examples of such instability may be found in MACBRIDE, 1943; BURKART, 1970; MAXWELL, 1978; FORTUNATO, 1994). Such proposals result from giving more weight to vegetative, fruit or seeds characters than to floral characters.

Floral taxonomic characters make evolutionary sense when analysed in the light of their possible role in pollination. If it were possible to reveal the evolutionary pathways which led to the different floral morphologies and pollination strategies, taxonomic hypotheses about the intergeneric limits could be rejected or supported. In the case of this group of legumes this possibility has not been explored and the observed differences in floral morphology have not been evaluated for their adaptive role.

The probable ancestors, from which those taxa may have arisen, would have had relatively small flowers (ca. 1 - 1.5 cm) with a straight, open keel, a valvular mechanism of pollen display and possibly pollination by bees of variable size. Such non-specialized floral features may still be found in groups of *Galactia* (sect. *Odonia* and *Collearia*; BURKART, 1971; QUEIROZ, unpubl. obs.). From such floral structures species of *Cratylia* and *Dioclea* sect. *Macrocarpon*, despite showing very different floral characteristics, may have acquired adaptations to prevent smaller bees from visiting flower, their pollination depending on the large xylocopid bees. In *Cratylia* this was achieved by an increase in flower size and by a narrowing of the calyx. In *Dioclea* sect. *Macrocarpon* a different floral architecture led to a similar result. In these plants the flower is smaller than in *Cratylia* and has a fleshy, wider calyx, a sharp curved keel and a somewhat callose target area on the standard making it more rigid down to the base of the claw. As a whole, the petals are

somewhat fleshier and more resistant than those of *Cratylia* flowers. In this case the major resistance offered by the flower to restrict access to the nectar is in the fleshy base of the petals, especially the standard and its callose area and not in a narrow fleshy calyx as in *Cratylia*. These adaptations, although taking a divergent path from that of *Cratylia*, also seems to have resulted in specialization to big strong bees that are able to work the floral mechanism (i.e. xylocopid bees).

*Camptosema*, as defined by BURKART (1970) possibly represents an artificial amalgamation resulting from achievement of ornithophily by parallel lineages. Some species (e.g. *C. spectabile* and *C. coriaceum* alliance) are very similar to *Cratylia*, their main divergence relying on floral characters directly related to pollination, mainly modification of colour pattern from lilac-magenta to red, and loss of reflection capacity of the standard, the anthetic flower becoming functionally tubular, reaching ornithophily. Field observations shows that species of this alliance are pollinated by hummingbirds (ARROYO, 1981; FAEGRI & van der PIJL, 1979). By another hand, other species (e.g. *C. ellipticum* and *C. scarlatinum*) seem to be more closely related to *Galactia* sect. *Collearia* but unfortunately there is no information about its pollinators.

Data from pollination biology of these groups point to future developments that may improve the taxonomy of this complex, providing working hypothesis as the possibility that ornithophily may have arisen independently in different lineages of *Galactia* beside *Cratylia*, the possible polyphyletism of *Camptosema* and *Dioclea* (also supported by pollen data, KAVANAGH & FERGUSON, 1981) and the independent acquirement of 'Xylocopa-flowers'. Unfortunately, the taxonomy in *Galactia* and *Camptosema* is in need of a complete revision, without which, the use of advanced methods, such as cladistic analyses, lack a base to be developed.

### Acknowledgments

Thanks are due to J.M.F. Camargo for bee identification; to K. Brown Jr. for butterfly identification; to R.M. de Jesus (CVRD) and J.L. de Lima (CPATSA) for help in the fieldwork; to R. Monteiro (UNESP Rio Claro) for criticism and suggestions; to Bob Allkin (RBG-Kew) for improvement of English text. This work was supported by PICD/Capes.

## References

- ARROYO, M.T.K. Geitonogamy in animal pollinated tropical Angiosperms - a stimulus for the evolution of Self-Incompatibility. *Taxon*, n.25, p.543-548, 1976.
- ARROYO, M.T.K. Breeding systems and pollination biology in Leguminosae. In: RM Polhill, PH Raven (ed.). *Advances in Legume Systematics* Royal Bot Gard, Kew, 1981. 2part., p. 723-769.
- BENTHAM, G. Leguminosae. In: Martius, Eichler, Urban (ed.) *Flora Brasiliensis* München, 1859. v.15, part 1.
- BURKART, A. Las Leguminosas Faseólas Argentinas de los géneros *Mucuna*, *Dioclea* y *Camptosema*. *Darwiniana* n.16, p.175 - 218, 1970.
- BURKART, A. El género *Galactia* (Legum.-Phaseoleae) en Sudamérica, con especial referencia a la Argentina y países vecinos. *Darwiniana* n.16, p.663-795, 1971.
- FAEGRI, K., van der PIJL, L. *The principles of pollination ecology*. Oxford: Pergamon Press, 1979.
- FISCHER, E, GORDO, M. *Qualea cordata*, pollination by the territorial bee *Centris tarsata* in the "campos rupestres", Brazil. *Ciência e Cultura* v.45, n.2, p.144-147, mar-apr.,1993.
- FORTUNATO, R.H. Revision del género *Collaea* (Leguminosae, Papilionoideae, Phaseoleae, Diocleinae). In: Congreso Latino-Americano de Botánica, 7.Mar del Plata. 1994. Resumos: 252. Mar del Plata. 1994. p.252
- FRANKIE, G.W., OPLER, P.A., BAWA, K. Foraging behaviour of solitary bees: implications for outcrossing of a Neotropical forest tree species. *J.Ecol.* n.64, p.1049-1057, 1976.
- GENTRY, A. Coevolutionary patterns in Central American Bignoniaceae. *Ann. Missouri Bot. Gard.* n.61, p.728-759, 1974.
- GOTTSBERGER, G., CAMARGO, J.M.F., SILBERBAUER-GOTTSBERGER, I. A bee-pollinated tropical community: The beach dune vegetation of Ilha de São Luís, Maranhão, Brazil. *Bot.Jahrb.Syst.* n.109, p.469-500, 1988.
- GREEN, T.W., BOHART, G.E. The pollination ecology of *Astragalus cibarius* and *Astragalus utahensis* (Leguminosae). *Am. J. Bot.* n.62, p. 379-386, 1975.
- JANZEN, D.H. Euglossine bees as long-distance pollinators of tropical plants. *Science* n.171, p. 203-205, 1971.

- KAVANAGH, T. A., FERGUSON, I. K. Pollen morphology and taxonomy of the subtribe Diocleinae (Leguminosae: Papilionoideae: Phaseoleae). *Rev. Palaeobot. Palynol.* n.32, p.317-367, 1981.
- LEPPIK, E.E. Floral evolution and pollination in the Leguminosae. *Ann. Bot. Fenn.* n.3, p.299-308, 1966.
- MACBRIDE, J.F. Flora of Peru, Leguminosae. *Publ. Field Mus. Nat. Hist. Chicago, Bot. Ser.* n.13, p.28-269, 1943.
- MAXWELL, R.H. Problems in the placement of *Dioclea paniculata* Killip. *Ms. Phytologia* n.40, p.243-252, 1978.
- PEREIRA-NORONHA, M.R.; SILBERBAUER-GOTTSBERGER, I., GOTTSBERGER, G. Biologia Floral de *Stylosanthes* (Fabaceae) no cerrado de Botucatu, estado de São Paulo. *Rev. brasil. Biol.* n.42, p.595-605, 1982.
- PIJL, L. van der. *Xylocopa* and flowers in the tropics. I. The bees as pollinators. *Proc. K. Ned. Akad. Wet.* n.57, p.413-423, 1954.
- QUEIROZ, L.P. de. O gênero *Cratylia* Martius ex Benth (Leguminosae: Papilionoideae: Phaseoleae): revisão taxonômica e aspectos biológicos. Dissertação (Mestrado em Biologia Vegetal). UNICAMP. 1991. Campinas.
- STIRTON, C.H. Petal sculpturing in Papilionoid Legumes. In: RM Polhill, PH Raven (ed). *Advances in Legume Systematics*. Kew: Royal Bot Gard, Part. 2, p.771-788, 1981.
- VELTHIUS, H.H., CAMARGO, J.M.F. Observations on male territories in a carpenter bee, *Xylocopa* (*Neoxylocopa*) *hirsutissima* Maidl (Hymenoptera, Anthophoridae). *Z. Tierpsychol.* n.38, p.409-418, 1975.
- WAINWRIGHT, C.M. The floral biology and pollination ecology of two desert lupines. *Bull. Torrey Bot. Club* n.105, p.24-38, 1978.