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Evolution of Flower Structures and Pollination in Neotropical *Cassiinae (Caesalpiniaceae)* Species *)

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With 9 Figures

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Summary

GOTTSBERGER G. & SILBERBAUER-GOTTSBERGER I. 1988. Evolution of flower structures and pollination in neotropical *Cassiinae (Caesalpiniaceae)* species. – Phyton (Austria) 28 (2): 293–320, 9 figures. – English with German summary.

Poricidal anther dehiscence occurs in the majority of the species of the subtribe *Cassiinae (Caesalpiniaceae);* it implies a constraint for pollination through pollen-collecting female bees able to vibrate flowers. In open pollen-flowers, poricidal anthers also provide protection against pollen depletion by rainfall, as well as provide a means for more efficient and more economic pollination. The ovaries of the *Cassiinae* as also in the majority of the *Fabales* are elongated. It is shown that the longer the ovaries the more ovules they contain. The trend in the *Cassiinae* to approximate the position of the pollen releasing anther openings and the stigma is realized in different ways. In *Cassia* and many *Senna* species, at least some of the stamens are so long that the anther openings reach about the same level as the stigma. But there are also species, which bear flowers with all stamens much shorter than the gynoecium. In *S. obtusifolia,* for instance, the gynoecium is bent down to the anther openings. In several *Chamaecrista* species with short stamens only, a modified tube-like petal is formed, which functions as a prolongation of the stamens. Concomitantly, in all three genera there is a trend towards heteranthery and increasing zygomorphy of the flowers. In some cases these morphological constraints are accom-

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*) Dedicated to Univ.-Prof. Dr. Friedrich EHRENDORFER on the occasion of his 60th birthday.

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panied by a trend for pollination by smaller bees towards a more effective pollination by larger bees, especially notable in the small-flowered *Chamaecrista* species with the tube-like petal. Structures for pollen protection and pollen economy were developed also by the *Fabaceae*. However, these parallel trends in evolution in *Cassiinae* and *Fabaceae* were attained on different morphological grounds.

Zusammenfassung

GOTTSBERGER G. & SILBERBAUER-GOTTSBERGER I. 1988. Blütenevolution und Bestäubungsmechanismen bei neotropischen *Cassiinae*-Arten *(Caesalpiniaceae)*. – Phyton (Austria) 28 (2): 293–320, 9 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Das Öffnen der Antheren durch apikale Poren oder Schlitze ist ein Merkmal der meisten Arten der Subtribus *Cassiinae (Caesalpiniaceae)*. Durch diese porizide Dehiszenz der Antheren können die Blüten nur durch Pollen-sammelnde weibliche Bienen bestäubt werden, die fähig sind, die Blüten zu vibrieren. In offenen Pollenblumen sind porizide Antheren auch ein Schutz gegen das Ausschwemmen des Pollens durch Regen. Die eingeschränkte Antherenöffnung führt aber außerdem zu einer effizienteren und ökonomischeren Bestäubung. So wie viele Vertreter der *Fabales*, besitzt auch ein überwiegender Teil der *Cassiinae* in die Länge gestreckte Fruchtknoten. Je länger diese sind, desto mehr Samenanlagen sind ausgebildet. Es zeigt sich auch die Tendenz, Antherenöffnungen und Narbe innerhalb einer Blüte einander zu nähern. Das wird einmal dadurch erreicht, daß in *Cassia*- und vielen *Senna*-Arten mindestens 2 oder 3 Staubgefäße ungefähr so lang wie das Gynözeum sind. Aber auch bei Arten mit untereinander gleich langen, aber kürzeren Stamina als das Gynözeum, wie beispielsweise bei *S. obtusifolia*, erfolgt eine Annäherung von Antherenöffnungen und Stigma durch ein eingekrümmtes Gynözeum. Bei den *Chamaecrista*-Arten mit kurzen Staubgefäßen dagegen ist das innerste Kronblatt zu einer Tüte umgebildet, die die Antheren und den Basalteil des Gynözeums mehr oder weniger umhüllt und als eine Verlängerung des Andrözeums funktioniert. In allen drei Gattungen ist die Stamendifferenzierung mit einer zunehmenden Zygomorphie der Blüte verbunden, was bei einigen Arten zu einer effektiveren Bestäubung durch größere Bienen führt. Am auffallendsten zeigt sich das bei den *Chamaecrista*-Arten mit dem tütenförmigen Kronblatt, die trotz ihrer kleinen Blüten nur von größeren Bienen bestäubt werden können. Morphologische Umgestaltungen, die Pollenschutz, Pollenökonomie und eine gezieltere Bestäubung ermöglichen, weisen auch die verwandten Fabaceen auf. Allerdings basieren diese parallelen Trends in der Evolution der *Cassiinae* und *Fabaceae* auf unterschiedlicher morphologischer Grundlage.

Introduction

Dehiscence of anthers by short slits or pores is a prominent character in species of the subtribe *Cassiinae (Caesalpiniaceae)*. A recent estimation showed that there are 15,000 to 20,000 species out of 544 genera and 72 families that share this special morphological character of anther dehiscence (BUCHMANN 1983). As flowers with poricidal anthers usually do not secrete nectar, successful pollination can only come about through actively pollen-collecting female bees able to vibrate flowers. A thorough revision

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concerning exploration of poricidal anthers by bees was done by BUCHMANN 1983.

Many bees are able to make their bodies vibrate. During their visits to flowers such behavior induces vibration of stamens and other flower parts. In poricidal anthers such vibrations cause a rapid expulsion of pollen through the pores. The pollen sticks to the bees' body and can be transmitted to the stigma while the bee vibrates another flower. This unique form of pollination, because of the buzzing sound produced by the bees, was termed "buzz pollination" (BUCHMANN 1974). Even a biophysical model of the functioning of this buzzing was elaborated (BUCHMANN & HURLEY 1978). BUCHMANN 1983 gave a complete list of papers of anthecological work on *Cassia* species. Only a few case histories are not yet mentioned in BUCHMANN's revision. For example, JANZEN 1983 did some observations on *Cassia biflora* in Costa Rica, DELGADO SALINAS & SOUSA SÁNCHEZ 1977 worked on the floral biology of several of the *Cassia* species in Mexico, and NUNEZ VIDAL & al. 1983 on *Cassia laevigata* in Brazil. CAMARGO & al. 1984 and CAMARGO & MAZUCATO 1984 reported on several bee species visiting Cassias in São Paulo State, and DULBERGER 1981 studied the ornamentals *Cassia didymobotrya* and *C. auriculata* in Israel; in this last paper it was tried to interpret the functioning of various morphological characters of the *Cassia* flowers during pollination.

The genus *Cassia* is today considered to be in the subtribe *Cassiinae*, including three morphologically distinct genera *Cassia, Senna* and *Chamaecrista* (IRWIN & BARNEBY 1981).

The present paper is intended to comment on flower adaptation and evolution of the *Cassiinae* in relation to pollination events (see GOTTSBERGER 1987).

Material and Methods

During numerous field excursions, mainly in the Central Brazilian savanna-like vegetation called "cerrado" or "campo cerrado", phenology, flower duration, floral mechanisms as well as pollination events of sixteen *Cassiinae* species were observed and documented. We worked principally in two places, viz., in the region of Botucatu: in the surroundings of the city, at Fazenda Treze de Maio and in Pardinho (22° 45′ S, 48° 25′ W), state of São Paulo, from the years 1973 to 1981, and second at Fazenda Bela Tanda in the region of Indianópolis (19° 3′ S, 47° 57′ W), state of Minas Gerais, in 1983 and 1986. One *Chamaecrista* species was observed at the dunes in São Luís (2° 30′ S, 44° 17′ W), state of Maranhão, in 1982.

Measurements of floral parts as well as the localization of pollen grains on the flower-visiting bees were done with the aid of a binocular microscope. The medium values ($\bar{x}$) of measurements of three flowers of each species were used for comparison.

Herbarium specimens of the studied *Cassiinae* species are deposited in the herbaria BOTU, UB, NY, U and GI.

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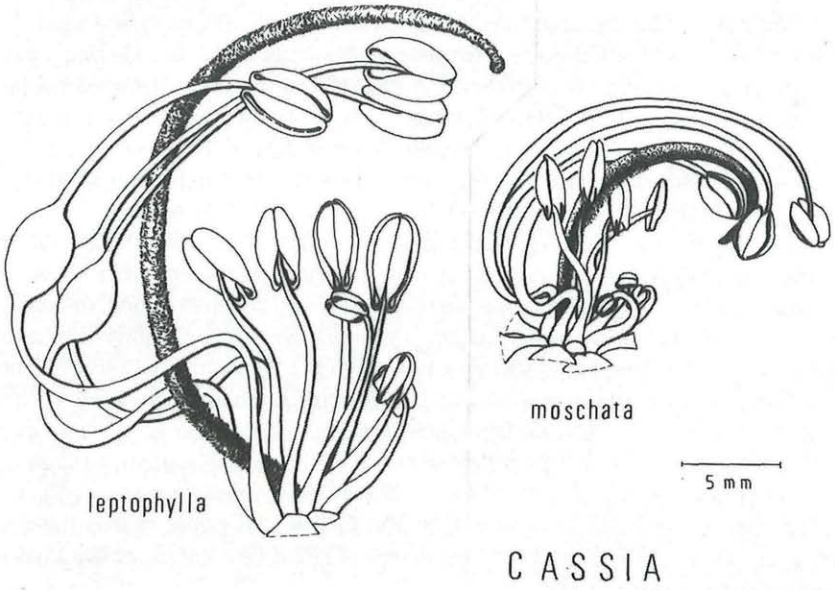

Fig. 1. Androecium and gynoecium of two *Cassia* species (redrawn from IRWIN & BARNEBY 1982).

Case Histories

Cassia Species

Cassia leptophylla VOG. and *Cassia moschata* H. B. K., just as other *Cassia* species (IRWIN & BARNEBY 1981), show strong heteranthery (Fig. 1). The filaments of all stamens are relatively long. The sigmoidally curved filaments of the three abaxial stamens are many times longer than their anthers, four or five stamens have shorter und straight filaments, and two or three adaxial stamens are reduced. The ovary and the style are similarly curved as the three abaxial stamens. The intrafloral behavior of a large Xylocopa bee was described by DELGADO SALINAS & SOUSA SÁNCHEZ 1977 for *Cassia fistula* L. While sitting on the group of stamens with shorter filaments in the center of the flower and collecting pollen actively with their mouth organs and legs from the semi-rimose openings, the bees vibrate and,

Fig. 2. Androecium and gynoecium of four *Senna* and four *Chamaecrista* species (*S. surratensis, S. pendula* and *Ch. cathartica* redrawn form IRWIN & BARNEBY 1982; *S. obtusifolia* redrawn from DELGADO SALINAS & SOUSA SÁNCHEZ 1977; *S. rugosa, Chamaecrista desvauxii* var. *parvifoliola* and *Ch. flexuosa*, originals).

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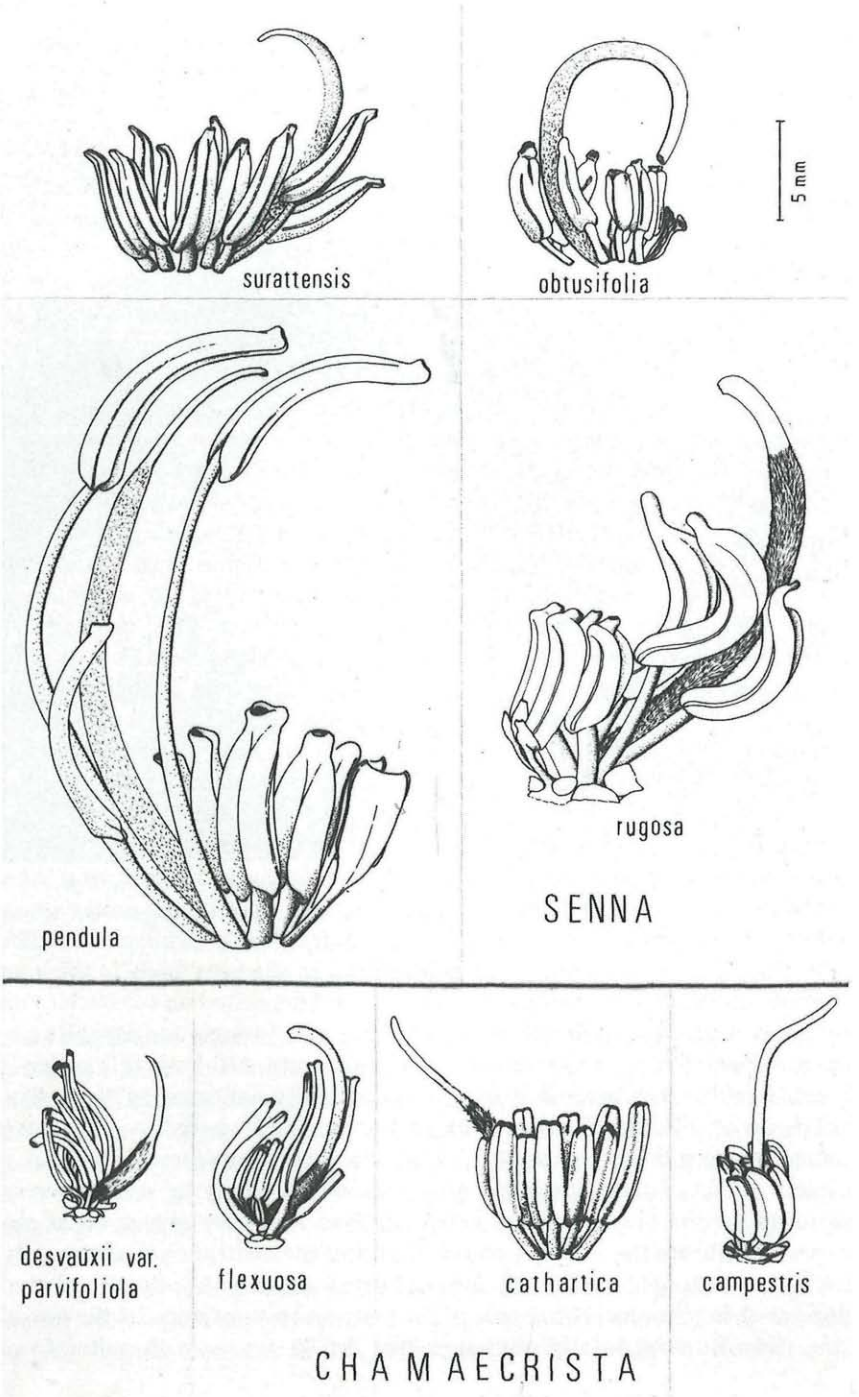

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thus, facilitate the pollen expulsion from the anthers. Vibration is transmitted to the three long elastic abaxial stamens; a part of their pollen is deposited on the dorsal side of the bees' body.

Senna Species

The Brazilian forest species, *Senna affinis* (BENTH.) IRWIN & BARNEBY (Syn. *Cassia affinis* BENTH.), was observed in Botucatu and Pardinho. The ca. 3 m tall shrubs during the flowering period were overcrowded with relatively large flowers. The small pores or slits of the anthers open or close according to ambient humidity. During rain the pores are closed and only opened again after the anthers have dried. Also early in the morning, when the plants are wet with dew, the anthers remain closed; only after the dew has evaporated in the sun do the anthers open.

The androecium has three abaxial stamens with long filaments and long anthers, one always exceeding the others. They are so positioned that the two shorter ones are together and the longest is separated. These two more or less joined stamens are in front of the outermost dish-like petal, opposed to the gynoecium, which is accompanied by the third of the long stamens (Tab. 1, Fig. 3 c; see also *Senna rugosa* Fig. 2 and 3 b, which has a very similar flower construction). The two proximate stamens and the gynoecium alternate their position in such a way that there are flowers with the gynoecium either left or right from the mid line of the flower (enantiostyly). A group of four shorter stamens shows large anthers with short filaments positioned in the center of the flower and directed with the apertures towards an approaching flower visitor. The somewhat crooked gynoecium is nearly twice as long as the longest stamen. Thus, only large bees of the genera Xylocopa, Centris, and Epicharis (Fig. 3 c, d; Tab. 2) are successful pollinators. They vibrate the central stamens during their visits and receive the pollen on the ventral side of their bodies on the inner side of their legs and on their mouth parts (especially Xylocopa). The vibration of the central anthers is transmitted by the bees' body to the long stamens and causes the pollen to be ejected and deposited on the back or on the sides of the bees, on the thorax of the larger Xylocopa and Epicharis, and on the abdomen of the smaller Centris species. Although this pollen is brushed off by the bees, it is only with difficulty collected by them. The pollen is deposited on the bees' body just at the place where the stigma may touch or where the stigma approximates closely during vibration. In fact, a direct contact of the stigma and a bee could only rarely be seen, whereas close approximation was more common. Bombus morio was often observed to vibrate the longer stamens first and the central ones afterwards. On individuals of Bombus, by far the largest amount of pollen was found deposited only on the ventral side of the body and almost none on the dorsal side. Bombus apparently pollinates this *Senna* species with pollen from

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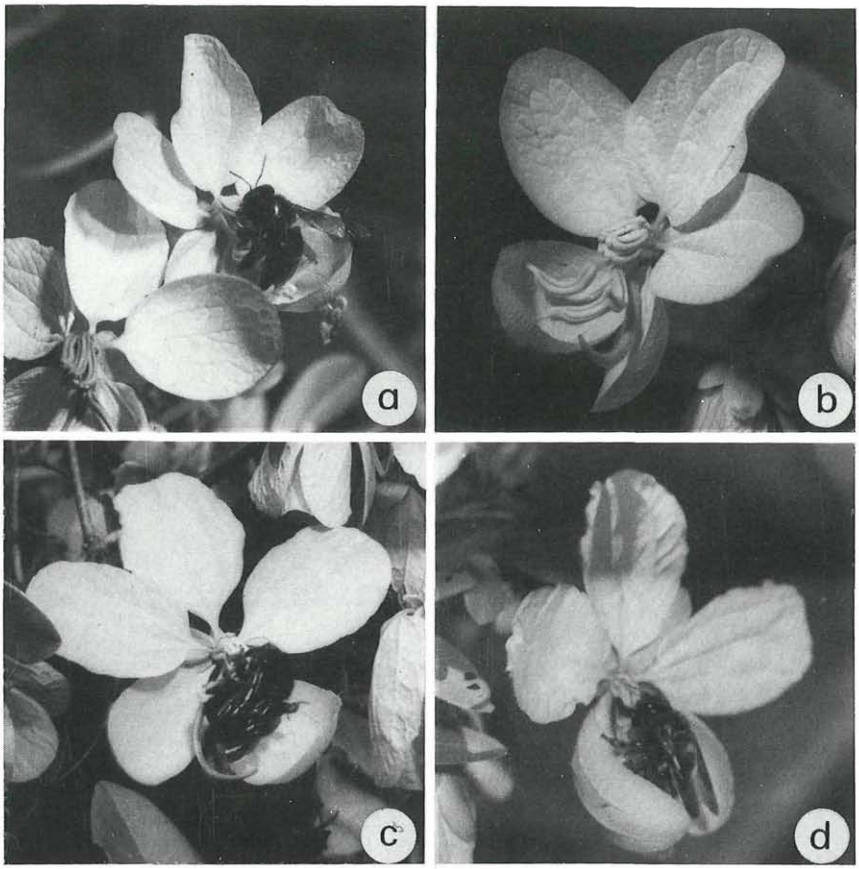

Fig. 3. a) *Senna rugosa*, flower visited by Xylocopa macrops (0.8×). – b) *S. rugosa*, flower showing the differentiated androecium (about nat. size). – c) *S. affinis*, flower visited by Bombus morio (0.9×). – d) *S. affinis*, visited by Epicharis rustica flava (0.9×).

the ventral side when entering or leaving the flower. This relatively large bee also comes close to the stigma or even touches it with its ventral body side. Often a large amount of pollen is deposited on the ventral mid line of the bees, from where it is with difficulty brushed off. Pollination through Bombus may, therefore, occur through pollen from the central anthers as well as from the three longer ones. The females of Oxaea flavescens, although visiting *Senna affinis* frequently, are too small to act as efficient pollinators.

The three most adaxially positioned stamens are reduced to pollenless staminodes, which nevertheless can be important in the pollination process as well. During vibration the bees may slip off from the flower. However, by

Table 1. Length of flower parts in centimeters (three flowers per species and medium values $\bar{x}$), number of ovules, and relation values of some *Senna* and *Chamaecrista* species.

Species		Petal C	Stamen A	Ovary O	Style S	Gynoec G	Gynoph Gy	Nr.Ovul. Ov	C:O	C:G	O:S	G:A	G-A	Ov:O
Senna affinis		3.20	1.60	2.68	0.30	3.40	0.21	168						
		2.40	1.54	2.19	0.36	2.75	0.20	168						
		3.00	1.63	2.02	0.36	2.55	0.17	166						
	$\bar{x}$	**2.78**	**1.59**	**2.01**	**0.34**	**2.90**	**0.19**	**167.33**	**0.02**	**1.00**	**5.91**	**1.82**	**1.31**	**83.25**
S. multijuga		2.20	1.64	1.20	0.16	1.56	0.20	43						
		2.18	1.60	1.33	0.10	1.63	0.20	40						
		2.35	1.75	1.53	0.12	1.80	0.15	38						
	$\bar{x}$	**2.24**	**1.66**	**1.35**	**0.13**	**1.66**	**0.18**	**40.33**	**1.80**	**1.35**	**10.38**	**1.00**	**0.00**	**29.87**
S. pendula var. *glabrata*		1.95	3.40	2.72	0.64	3.16	0.24	80						
		2.28	3.39	1.90	0.58	2.72	0.24	65						
		2.60	3.08	1.93	0.66	2.79	0.20	76						
	$\bar{x}$	**2.28**	**3.29**	**2.18**	**0.63**	**2.89**	**0.23**	**73.67**	**1.05**	**0.79**	**3.46**	**0.88**	**-0.40**	**33.79**
S. rugosa		2.63	1.73	1.81	0.47	2.49	0.21	82						
		2.50	1.58	1.77	0.37	2.40	0.26	90						
		2.47	1.64	1.46	0.47	2.27	0.34	75						
	$\bar{x}$	**2.53**	**1.65**	**1.68**	**0.44**	**2.39**	**0.27**	**82.33**	**1.51**	**1.06**	**3.81**	**1.45**	**0.74**	**49.01**
Chamaecrista flexuosa		1.42	1.03	0.50	0.70	1.20	----	13						
		1.47	0.94	0.50	0.75	1.25	----	13						
		1.42	0.92	0.48	0.70	1.18	----	15						
	$\bar{x}$	**1.44**	**0.96**	**0.49**	**0.72**	**1.21**	**----**	**13.67**	**2.94**	**1.19**	**0.68**	**1.26**	**0.25**	**27.90**
Ch. desvauxii var. *parvifoliola*		1.55	0.95	0.44	0.52	0.96	----	10						
		1.85	0.90	0.50	0.66	1.16	----	10						
		1.58	1.07	0.44	0.54	0.98	----	12						
	$\bar{x}$	**1.66**	**0.97**	**0.46**	**0.57**	**1.03**	**----**	**10.67**	**3.61**	**1.61**	**0.85**	**1.06**	**0.06**	**23.20**
Ch. desvauxii var. *glauca*		2.28	1.17	0.94	0.74	1.68	----	20						
		2.30	1.40	1.00	0.85	1.85	----	21						
		2.12	1.25	1.00	0.83	1.83	----	23						
	$\bar{x}$	**2.23**	**1.27**	**0.98**	**0.81**	**1.79**	**----**	**21.33**	**2.28**	**1.25**	**1.21**	**1.41**	**0.52**	**21.77**
Ch. campestris		1.50	0.64	0.45	1.08	1.53	----	9						
		1.52	0.64	0.41	1.16	1.57	----	9						
		1.50	0.60	0.40	1.09	1.49	----	8						
	$\bar{x}$	**1.51**	**0.63**	**0.42**	**1.11**	**1.53**	**----**	**8.67**	**3.60**	**0.99**	**0.38**	**2.43**	**0.90**	**20.64**
Ch. hispidula		1.95	0.65	0.32	1.10	1.42	----	9						
		1.90	0.74	0.40	1.10	1.50	----	13						
		1.50	0.75	0.50	1.20	1.70	----	11						
	$\bar{x}$	**1.78**	**0.71**	**0.41**	**1.13**	**1.54**	**----**	**11.00**	**4.34**	**1.16**	**0.58**	**2.05**	**0.83**	**26.83**
Ch. labouriaeae		0.92	0.33	0.30	0.35	0.65	----	7						
		0.80	0.38	0.35	0.25	0.60	----	7						
		0.78	0.36	0.35	0.25	0.60	----	8						
	$\bar{x}$	**0.83**	**0.36**	**0.33**	**0.28**	**0.62**	**---**	**7.33**	**2.52**	**1.34**	**1.18**	**1.72**	**0.26**	**22.21**

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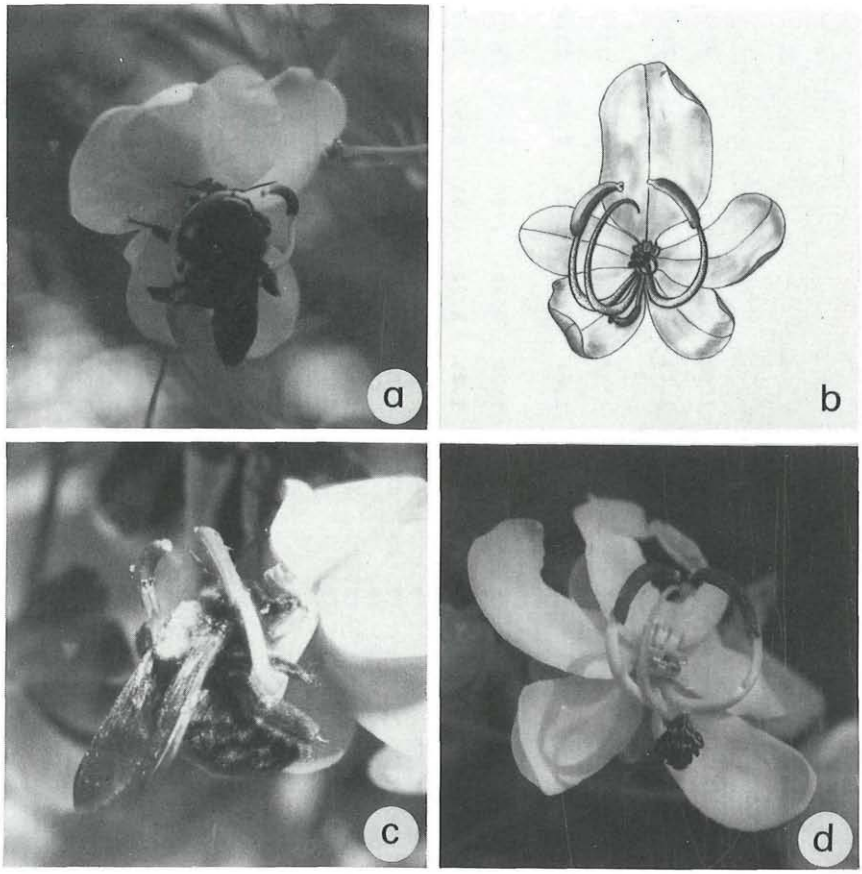

Fig. 4. *Senna pendula* var. *pendula*. – a) Stamens vibrated by Bombus morio (0.9×). – b) Flower showing the two "gateway" stamens, one of them accompanied by the gynoecium (0.9×). – c) Centris dorsata, vibrating the stamens; pollen on the thorax from previous flower visits (0.9×). – d) Trigona spinipes, biting holes into the anthers to obtain pollen (about nat. size).

biting these staminodes or also the large central anthers, the bees steady themselves and cling to the flowers. Small bees of the genus Pseudaugochloropsis vibrate the anthers of nearly all stamens one by one; as they rarely touch the stigmata they are, at most, occasional pollinators.

A flower construction similar to *S. affinis* is shown by *Senna rugosa* (G. DON.) IRWIN & BARNEBY (Syn. *Cassia rugosa* G. DON; Fig. 2 and 3 a, b) a typical cerrado shrub. It also carries a large number of flowers, which are, however, somewhat smaller than those of *S. affinis* (Tab. 1). This species also is pollinated by relatively large bees (Tab. 2), including Bombus morio and Oxaea flavescens, which receive the pollen from the central stamens

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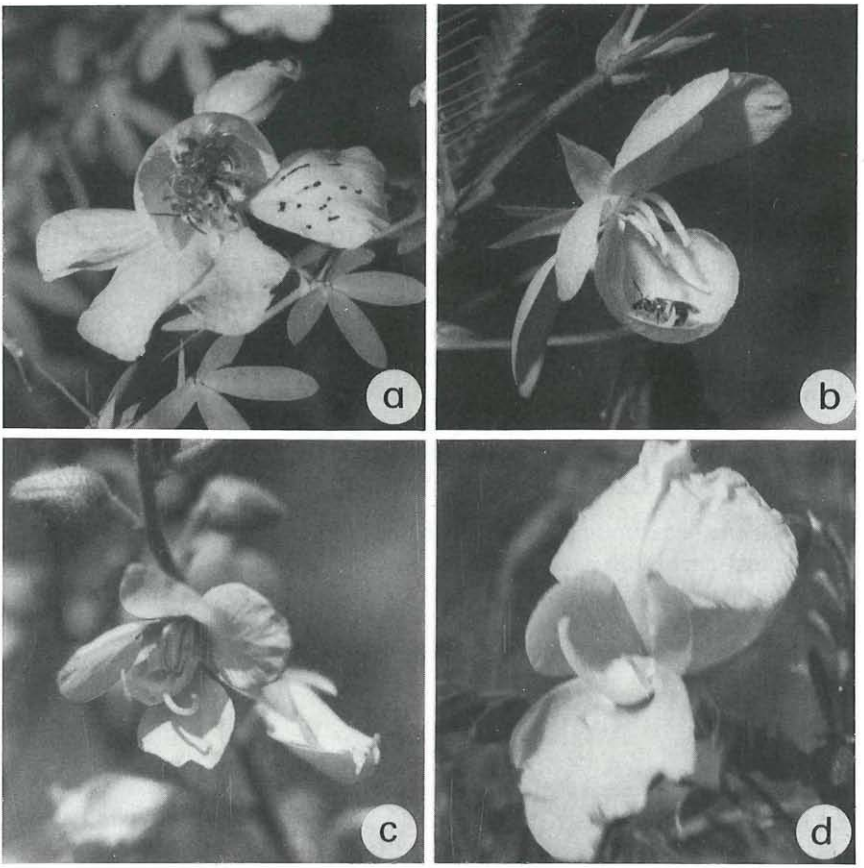

Fig. 5. a) *Chamaecrista desvauxii* var. *parvifoliola,* visited by Exomalopsis fulvofasciata (about nat. size). – b) *Ch. flexuosa* with an unidentified Augochlorini species collecting pollen fallen into the dish-like petal (1.5×). – c) *Ch. campestris* with tube-like petal; style curved in the opposite direction of the modified petal (1.4×). – d) *Ch. cathartica* var. *cathartica* with a tube-like petal and a "papilionaceous" corolla (1.4×).

on their ventral side and from the three longer stamens on their dorsal side or on the wings.

An extreme differentiation of the androecium occurs in *S. cernua* (BALB.) IRWIN & BARNEBY (Syn. *Cassia cernua* BALB., *C. sulcata* DC.) and *S. multijuga* (L. C. RICH.) IRWIN & BARNEBY (Syn. *Cassia multijuga* L. C. RICH.; Tab. 1), which bear flowers with two erect stamens with long filaments. These species are also pollinated by large bees (Tab. 2). In flowers of *Senna pendula* (WILLD.) IRWIN & BARNEBY var. *glabrata* (VOG.) IRWIN & BARNEBY (Syn. *Cassia indecora* H. B. K. var. *glabrata* VOG., *C. coluteoides* COLLAD.;

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Fig. 2), the two longer stamens with their long filaments and brown anthers are bent against each other, forming a kind of "gateway" (Fig. 4). Four medium sized stamens occupy the flower center, while the three staminodes are located on the upper, adaxial part of the androecium. As in the other *Senna* species, large bees vibrate the central anthers and receive pollen on their ventral side (Fig. 4 a). The vibration is also transmitted to the two upwardly directed stamens, from which pollen is ejected onto the dorsal side of the bees. They receive the pollen in front of the thorax and on the wings (Fig. 4 c). The gynoecium, also curved upwards, during the bees' visits often touches the bees or is closely positioned near the bees' body just at the parts where the pollen from the two "gateway" stamens is deposited. As pollen from these two long stamens happens to stick on two opposite places of the thorax, as well as on the whole thorax, enantiostyly in this species seems to be non-functional as a means for guaranteeing pollination. Small Augochlora bees vibrate each anther separately. In order to reach the pollen, Trigona bees bite holes into the anthers (Fig. 4 d).

In *Senna obtusifolia* (L.) IRWIN & BARNEBY (Syn. *Cassia obtusifolia* L.), a pantropical herb with small flowers, the stamens appear undifferentiated and are almost all of the same size. In this species the gynoecium is strongly recurved, so that the stigma and the anther openings nearly contact each other (DELGADO SALINAS & SOUSA SÁNCHEZ 1977; Fig. 2).

Chamaecrista Species

Chamaecrista desvauxii (COLLAD.) IRWIN & BARNEBY var. *glauca* (CHOD. & HASSL.) IRWIN & BARNEBY (Syn. *Cassia latistipula* BENTH.) is a half meter tall perennial herb with a few-flowered inflorescence and relatively large flowers as compared with the other *Chamaecrista* species studied (Tab. 1). The deeply yellow-colored flowers, one per inflorescence, in March 1977 opened at 6:15 in the morning and closed their petals at 12:30. The innermost petal is dish-like and in an upward position right or left of the flower's mid line, and alternating with the opposed gynoecium (see also the other variety *parvifoliola* on Fig. 5 a). Three of the four longer stamens are in front of this differentiated petal, while the fourth and the other smaller six stamens are bundled but separated from the three. Corresponding with the size of the stamens and the gynoecium (the latter is 1.5 times as long as the longest stamens, Tab. 1), large bees belonging to the genera Epicharis, Bombus, and Ptiloglossa vibrate the stamens bundlewise, and are the most effective pollinators (Tab. 2). A smaller bee species, Exomalopsis fulvofasciata, also was observed to vibrate some of the stamens and may function as an occasional pollinator. A small Augochlora bee vibrates the stamens one by one and Trigona spinipes (FABRICIUS) bites holes into the anthers to reach the pollen. Very small bees like Thectochlora alaris

Tab. 2. Vibrating bee species and the *Cassiinae* species visited. Abbreviations: Bot = Botucatu, Par = Pardinho, Bel = Fazenda Bela Tanda, Tre = Fazenda Treze de Maio; camp = *campestris*, cath = *cathartica*, flex = *flexuosa*, glau = *desvauxii* var. *glauca*, lab = *labouriaeae*, parv = *desvauxii* var. *parvifoliola*.

	Senna								Chamaecrista					
	affinis			multijuga	pendula			rugosa		camp	cath	lab	glau	parv	flex
	Bot	Par	Bel	Bot	Bot	Tre	Par	Tre	Bel	Tre	Tre	Tre	Tre	Tre	Tre
Andrenidae: Oxaeinae															
Oxaea flavescens KLUG	•	•	•			•		•		•	•		•		
Anthophoridae: Anthophorinae															
Centridini:															
Centris (Xanthemisia) bicolor (LEPELETIER)		•													
C. (Melanocentris) dorsata LEPELETIER						•		•							
C. (Trachina) longimana FABRICIUS									•						
C. (Melanocentris) pectoralis BURMEISTER	•					•		•		•					
C. (Ptilotopus) scopipes FRIESE			•					•							
Centris (Ptilotopus) sp.								•							
C. (Centris) varia ERICSON										•					
Epicharis (Epicharitides) cockerelli FRIESE													•		
E. (Anepicharis) dejeanii LEPELETIER		•		•	•			•					•		
E. (Epicharis) rustica flava FRIESE	•	•	•												
E. (Triepicharis) cf. schrottkyi (FRIESE)													•		
Exomalopsini:															
Exomalopsis (Megamalopsis) fulvofasciata (SMITH)						•		•			•	•	•	•	•
Eucerini: *Florilegus (Floriraptor) atropos* (SMITH)										•	•			•	
Xylocopini:															
Xylocopa (Neoxylocopa) brasilianorum (LINNAEUS)		•					•								
X. (Megaxylocopa) frontalis (OLIVIER)	•	•	•					•		•					
X. (Neoxylocopa) hirsutissima MAIDL			•					•							
X. (Schoenherria) macrops LEPELETIER						•		•							
X. (Neoxylocopa) ordinaria SMITH	•			•	•	•									
X. (Neoxylocopa) virescens autorum MOURE & CAMARGO in press		•	•		•		•		•						
Apidae: Bombinae:															
Bombini: *Bombus (Fervidobombus) atratus* FRANKLIN			•											•	
Bombus (Fervidobombus) morio (SWEDERUS)	•	•			•		•	•			•	•	•	•	•
Euglossini:															
Euglossa (Euglossa) melanotricha MOURE											•				
Halictidae: Halictinae:															
Augochlorini:															
Augochloropsis aurifluens (VACHAL)															•
A. cf. *cupreola* (COCKERELL)												•			•
A. smithiana (COCKERELL)						•								•	•
Augochloropsis sp.													•		
Pseudaugochloropsis graminea (FABRICIUS)	•	•			•					•			•	•	
Pseudaugochloropsis sp.		•													
Colletidae: Diphaglossinae:															
Ptiloglossa hemileuca MOURE													•		

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(VACHAL) and Ceratalictus cf. theius (SCHROTTKY), as well as wasps, ants and bugs, lick on exudates of leaf nectaries.

Very similar in flower construction, but with smaller flowers and smaller leaves, appears another variety, *Chamaecrista desvauxii* (COLLAD.) IRWIN & BARNEBY var. *parvifoliola* (IRWIN) IRWIN & BARNEBY (Syn. *Cassia langsdorfii* KUNTH. var. *parvifoliola* IRWIN; Fig. 2, 5 a). It is an about 50 cm tall perennial herb from the cerrados. Stamen and gynoecium length correspond with each other, being both about one centimeter long (Tab. 1). Small bees, vibrating the stamens bundlewise or individually (Tab. 2), are perfect pollinators of these small flowers. The most frequent and effective pollinator is Exomalopsis fulvofasciata, which occupy different positions within the flowers. Consequently, the bees receive pollen on their ventral as well as on their dorsal side and on the wings; contact of these pollen-carrying parts of the bees with the stigma occurs. Augochloropsis and Pseudaugochloropsis bees vibrate one stamen after the other and are principally covered with pollen on their ventral side. They also receive pollen on the wings or on the dorsal abdomen. Contact of the stigma both with the ventral and dorsal side of the bees was observed. Species of Florilegus and Bombus are only occasional visitors of this variety.

The flowers of the perennial herb *Chamaecrista flexuosa* (L.) GREENE (Syn. *Cassia flexuosa* L., Fig. 2, 5 b) are about the same size as the above mentioned variety. In this species the flowers are resupinate, the innermost disk-like petal is positioned in the lower, abaxial half of the flower, always right or left from the median symmetry line. The gynoecium is slightly longer than the longest stamen (Tab. 1).

On flowers of this species we could not observe larger bees; they were pollinated only by small Exomalopsis and Augochloropsis species (Tab. 2) which carried pollen in large amounts on their ventral side and in less quantity also on the dorsal side of the abdomen or on the wings. An unidentified Augochlorini species collected pollen which had fallen in the low dish-like petal (Fig. 5 b).

Flowers very similar to those of *Ch. flexuosa* are found in the low perennial species *Chamaecrista nictitans* (L.) IRWIN & BARNEBY var. *ramosa* (VOG.) IRWIN & BARNEBY (Syn. *Cassia patellaria* L.) and *Chamaecrista repens* (VOG.) IRWIN & BARNEBY var. *repens* (Syn. *Cassia apaensis* CHOD. & HASSL.), on which, however, no pollinators could be observed.

The small flowers of the half meter tall herb *Chamaecrista campestris* IRWIN & BARNEBY (Syn. *Cassia camporum* BENTH., Fig. 5 c) are resupinate. The innermost petal has a thicker tissue than the other petals and is folded into a tube-like structure in such a way that the pores of the anthers of all stamens, which are of about the same small size (Fig. 2), are directed towards the inner larger opening of the folded petal. The style, curved either to the left or the right, is located opposite to this specialized petal. The ovary

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itself is shorter than the stamens and is surrounded by them. Ovary and style, together, are more or less the same length as the tubular petal (Tab. 1). The larger sized Xylocopa and Centris, as well as Florilegus and Oxaea bees (Tab. 2), can vibrate these small flowers because the folded and thickened petal is a mechanically sufficient strong support for the settling of these large bees. During vibration, pollen ejected from the anthers passes through the tubular petal and is deposited afterwards on the ventral side of the bees' thorax or abdomen (the same mechanism as in *Chamaecrista hispidula* Fig. 7). If smaller bees like Pseudaugochloropsis vibrate the stamens they may collect some pollen, but the larger amount of pollen passes through the tube formed by the differentiated petal and is lost. Such behavior of small bee species does not usually lead to contact with the stigma and therefore pollination does not occur.

The folded petal in the flowers of *Chamaecrista cathartica* (MART.) IRWIN & BARNEBY var. *cathartica* (Syn. *Cassia cathartica* MART. var. *cathartica*, Fig. 5 d) are even more closed and more tube-like. The resupinate flowers exhibit a standard-like petal (about 2 cm long) in an upward, adaxial position, two lateral "wing"-petals, and one petal in the low abaxial position. The tubular petal is the innermost one and surrounds the openings of the anthers of the ten stamens, which are more or less equal in length (Fig. 2). This modified petal is opposite to the gynoecium; a reciprocal change of position between the gynoecium and the stamens and the modified petal (enantiostyly) occurs also in this species. Large bees of the genera Euglossa, Bombus, Florilegus and Oxaea (Tab. 2) vibrate the tubular petal and stamens jointly. Just as in *Ch. campestris*, the folded petal functions as an elongation of the stamens in projecting the pollen to the level of the stigma; the outer petal-tube opening and the stigma reach about the same length. Small bees like Augochloropsis or Pseudaugochloropsis were not seen to visit the flowers of this species (Tab. 2); even when visiting they would be largely excluded from contact with the anther openings and, consequently, would not reach the pollen.

In the herbaceous, about one meter tall perennial, *Chamaecrista labouriaeae* (IRWIN & BARNEBY) IRWIN & BARNEBY (Syn. *Cassia labouriaeae* IRWIN & BARNEBY), the folded petal does not envelop the openings of all anthers. The ten stamens are very short and of the same length as the ovary (Tab. 1). Style extension and length of the tube-like petal correspond with each other. Thus, also in this species, the function of the modified petal as a stamen prolongation is obvious. Although the flower size belongs to the smallest ones in the genus, Bombus is a frequent visitor and effective pollinator. However, also in this species, the smaller bees, such as Exomalopsis and Augochloropsis, are pollinators when settling or leaving the flowers (Tab. 2).

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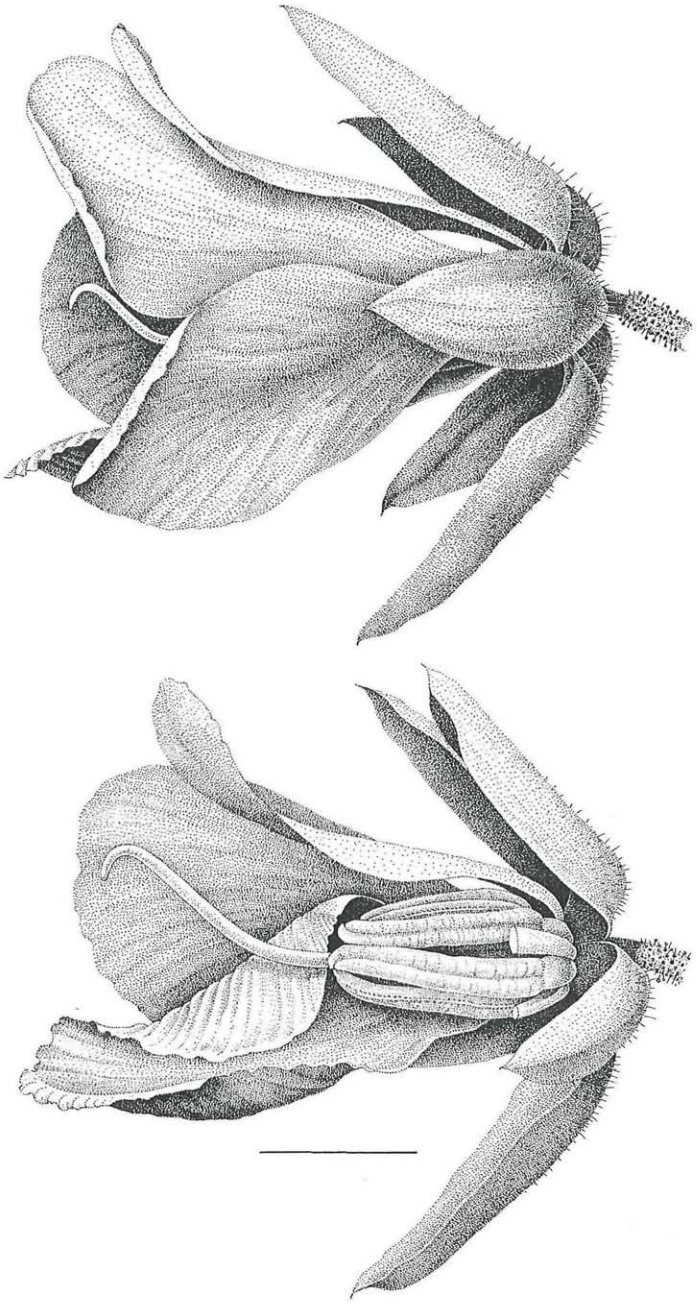

Fig. 6. *Chamaecrista hispidula* flowers. – a) Entire flower. – b) Flower with two petals removed, showing the cone of stamens, whose pores are directed into the tube-like petal. Style curved towards the viewer. Bar: 0.5 cm. (From bot. Jahrb. Syst. 109: 486).

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Fig. 7. *Chamaecrista hispidula.* – a) flower being visited and vibrated by Pseudaugochloropsis pandora; note that the cloud of pollen grains ejected from the poricidal anthers passes through the tube of the folded petal and is lost for the bee. – b) Xylocopa carbonaria, touching the stigma during visitation. Bar 0.5 cm. (From bot. Jahrb. Syst. 109: 487).

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Chamaecrista ochnacea (VOG). IRWIN & BARNEBY var. *purpurascens* (BENTH.) IRWIN & BARNEBY (Syn. *Cassia ochnacea* VOG. var. *purpurascens* BENTH.), studied at the Minas Gerais site, also shows a flower construction in which the folded petal is an important and integral part of its functional success. Larger bees are also the pollinators in this species.

Chamaecrista hispidula (VAHL) IRWIN & BARNEBY (Syn. *Cassia hispidula* VAHL, *C. tetraphylla* MARTYN), from the beach dunes of Northeast Brazil, has flowers with the same petal construction (Fig. 6). Large Xylocopa and Centris species are able to vibrate and pollinate these small flowers because the folded petal is a sufficiently strong support during their visits (GOTTSBERGER & al. 1988; Fig. 7). In this species small bees are obviously not pollinators.

The androecium of the creeping herb, *Chamaecrista rotundifolia* (PERSOON) GREENE var. *rotundifolia* (Syn. *Cassia rotundifolia* PERSOON), is completely different. In the very small flowers only five stamens are fertile and the anthers open by slits. Between the fertile stamens five staminodes are formed. The ovary has more or less the same length as the stamens. Augochloropsis bees were seen to explore the anthers and to collect pollen apparently without any vibration. The frequency of bee visitation at these flowers was very low.

Morphological Details of the Flower

The flower size of the studied species varies (Tab. 1) from small in *Chamaecrista*, with less than 1 cm length of the longest petal (*Ch. labouriaeae*), to about 1.5 cm in *Ch. campestris* and *Ch. flexuosa*, and even 2 cm in *Ch. desvauxii* var. *glauca*. All flowers of *Senna* that we examined had petals longer than two centimeters; *S. affinis* reached even three centimeter petal length. Petals and gynoecium in some species of *Senna* and *Chamaecrista* may have the same length, but the gynoecium sometimes is shorter or also somewhat longer (in *S. pendula*), or may reach at the maximum 1.3 times the length of the longest petal, as in *S. multijuga* and *Ch. labouriaeae*. The gynoecium of the studied *Senna* species consists nearly in its total length of the ovary, while the style is very short; a gynophore is also weakly developed. In contrast, the *Chamaecrista* species studied do not have a gynophore and the style is a prominent part of the gynoecium, being of about the same length as the ovary. In the species of *Chamaecrista* with the tube-like modified petal the style is still more extended, being two times the ovary, which is as short as the stamens.

The character of stamens with different length in the *Senna* and *Chamaecrista* species is more or less constant, although the species often show a particular pattern (Tab. 3). In *Chamaecrista flexuosa* different flowers may have a different pattern (Tab. 3). In some flowers we found five longer stamens, one of them even 1 mm longer than the others, and five

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shorter ones, while other flowers had two longer stamens accompanied by the gynoecium, three opposite medium stamens and five shorter ones, one of them also positioned together with the gynoecium.

Tab. 3. Length of the fertile stamens in centimeters of *Senna* and *Chamaecrista* species.

S.affinis	*S.rugosa*	*S.multijuga*	*S.pendula*	*Ch.desvauxii var.glauca*	*Ch.desvauxii var.parvifoliola*	*Ch.flexuosa*	*Ch.flexuosa*	*Ch.hispidula*	*Ch.campestris*	*Ch.labouriaeae*
1.60	1.73	1.64	3.40	1.17	0.95	1.03	0.92	0.75	0.64	0.33
1.40	1.70	1.62	3.15	1.16	0.86	0.93	0.90	0.70	0.63	0.32
1.40	1.60	1.01	1.50	1.16	0.75	0.93	0.75	0.70	0.61	0.31
1.06	0.95	0.78	0.88	1.16	0.73	0.91	0.75	0.61	0.53	0.30
1.06	0.94	0.78	0.84	0.96	0.59	0.90	0.74	0.60	0.51	0.30
0.89	0.93	0.76	0.78	0.93	0.57	0.55	0.50	0.59	0.50	0.28
0.89	0.93	0.70	0.72	0.86	0.55	0.50	0.42	0.57	0.48	0.28
----	----	----	----	0.85	0.52	0.48	0.42	0.54	0.47	0.28
----	----	----	----	0.82	0.51	0.43	0.41	0.52	0.47	0.27
----	----	----	----	0.80	0.50	0.36	0.41	0.52	0.44	0.23

There is a tendency in *Senna* and *Chamaecrista* species for at least the longest stamens to attain about the same length as the gynoecium. In some species the gynoecium may be, however, 1.5 to 2 times longer than the stamens; only in *Senna pendula* it was sligthly shorter. The real difference between gynoecium length and stamen length does not exceed 1.3 cm, as happens in *S. affinis* and *Ch. labouriaeae*. In the other species studied, this difference is always less than one centimeter. Certainly such differences are more significant in smaller than in larger flowers. A trend observed is that the longer the gynoecium the higher is the number of ovules which it contains. Such a correlation is not absolute nor linear, but seems quite evident in the genus *Senna* (Fig. 8).

Flower Preference and Visiting Frequency of Bees

In the region of Botucatu, Pardinho and Indianópolis, we caught 31 vibrating bee species on flowers of 10 *Cassiinae* taxa (Tab. 2). The largest bees belong to the tribes Centridini, Xylocopini and Bombini, the medium sized ones to Oxaeini, Eucerini and Euglossini, while the small ones belong to the Exomalopsini and Augochlorini. Flower size

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is related to body size of the bees to a certain extent. The large *Senna* flowers are principally visited by the large bee species, while the small flowers of *Chamaecrista* are only partly visited by small bees only. There is a clear exception in this relationship. The *Chamaecrista* species which bear the modified tubular petal, although they are small-flowered, are visited principally by the larger bee species (Tab. 2).

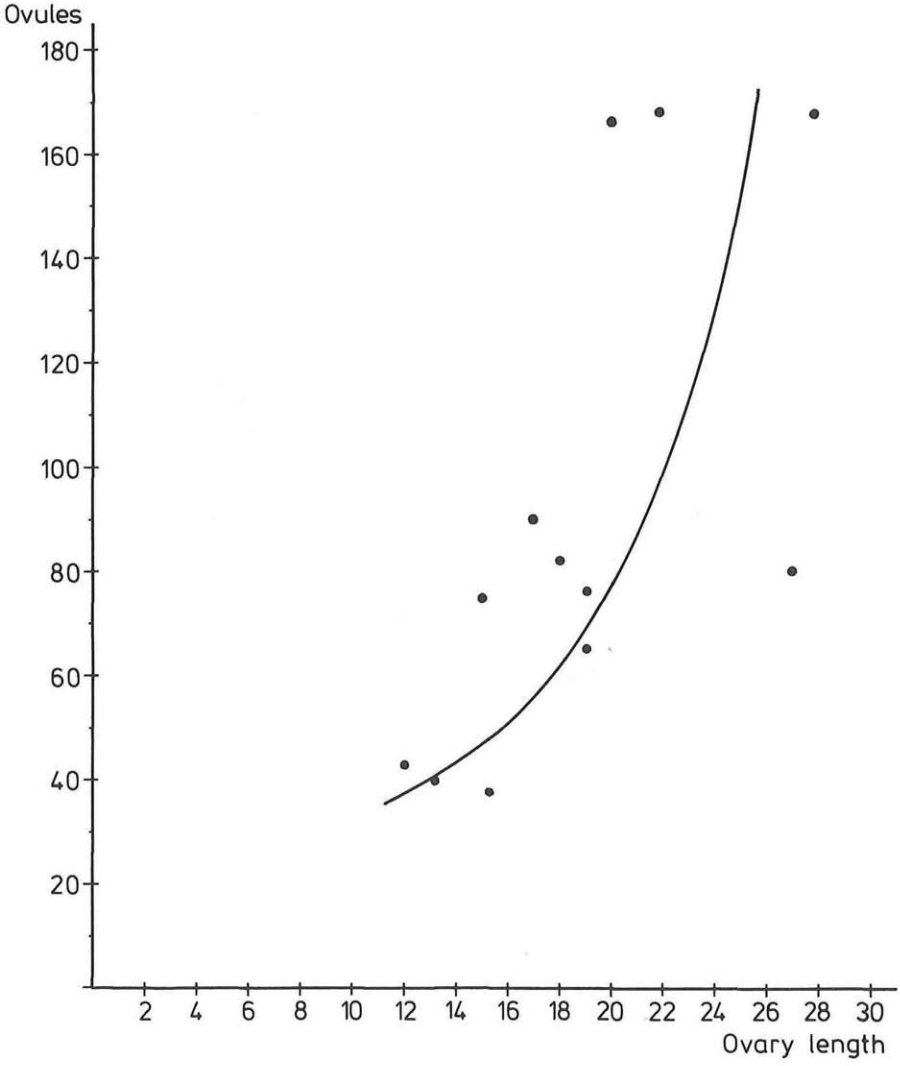

Fig. 8. Relation of ovary length (mm) and number of ovules in *Senna* species (see Tab. 1).

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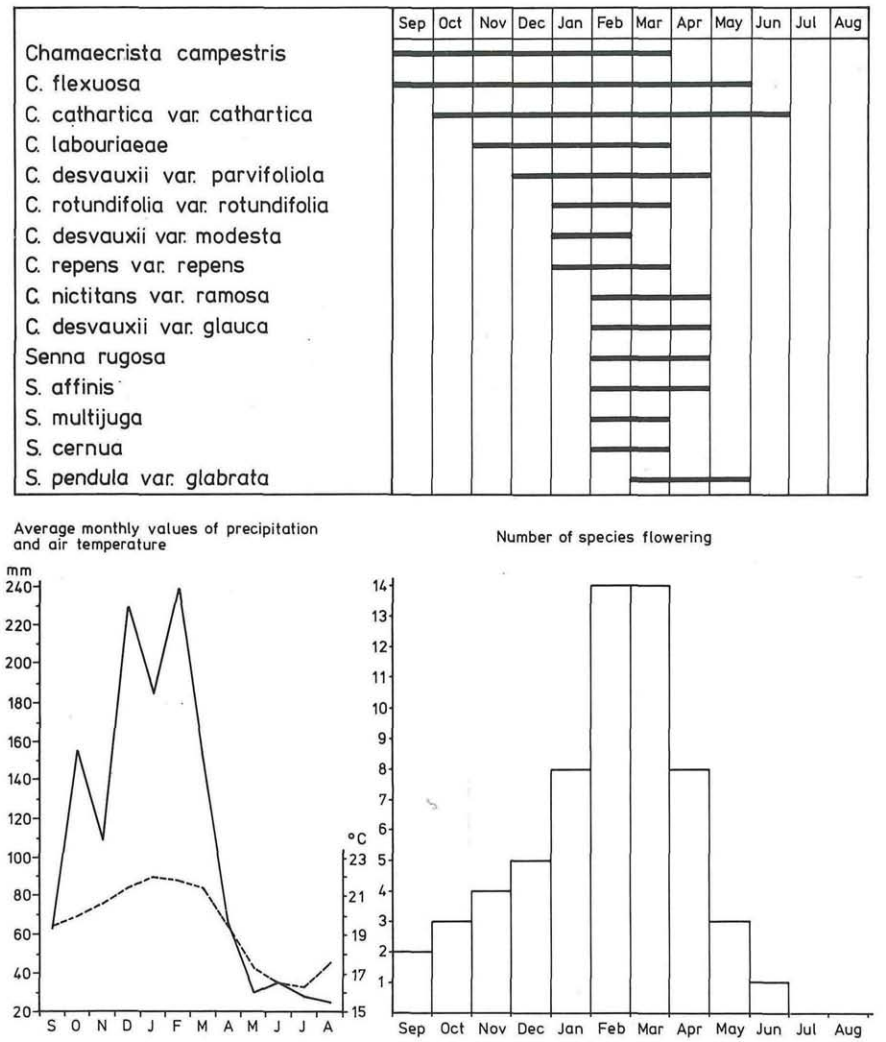

Fig. 9. Flowering periods of *Cassiinae* species in Botucatu, Brazil, during 1973 to 1981, with average monthly values of precipitation and air temperature.

On one species, *Senna rugosa*, we could observe as much as eleven different bee species as flower visitors; in other *Senna* species often eight or nine bee species commonly were seen visiting the flowers (Tab. 2). Although we did not expand on these questions, it was obvious that visiting frequency of bees on the *Senna* bushes with their mass flowering was generally high. Sometimes six or seven individuals of large or medium-sized Xylocopa, Bombus and Oxaea bees could be observed on one 2.5 m tall shrub of *S.*

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affinis. The visitation of flowers started in accordance with the weather conditions; on moist and cool days it began later, 8:30 or 9:00 (e.g. in April 1977) and lasted until about 11:00 or 11:30. Flower visiting frequency was always highest in the middle of the morning at about 10:00.

Frequency of visits to the small annual or perennial species of *Chamaecrista* depends on population size and on how many individuals are in flower at a time. Individuals in a more dense population were visited by more bees and with a higher frequency than when growing as isolated plants. Small-flowered *Chamaecrista* species, with the exception of those species which had the modified petal, often received frequent visits of small bees. Smaller and larger bees were not always constant for one particular *Cassiinae* species. In a mixed population with up to four species of *Senna* and *Chamaecrista* growing together, Bombus, Centris, and Exomalopsis bees were seen to visit different species during one flight.

Phenology

The *Senna* and *Chamaecrista* species flower principally during the hot rainy season of the year (Fig. 9). The reason why flowering of some species on Fig. 9 appears so long is the fact that the data represent a summary of observations over nine years. The species, in fact, do not always flower exactly at the same time, precocity and retardation of flowering periods occur over the years. Thus, the flowering period of one species based on observations from more than one year appears extended. Nearly all *Cassiinae* species in Botucatu show an overlap in their flowering periods. Even in a small cerrado area up to ten species were found flowering at the same time. However, a certain dominance of one or two species, expressed in number of flowering individuals, occurred. For instance, in 1977, *Chamaecrista desvauxii* var, *parvifoliola* was the dominant flowering species in the middle of February, *Ch. flexuosa* was dominant in the first part of March and *Ch. campestris* in the second.

Discussion

Ejection of powdery pollen grains from poricidal anthers through vibration functions best during dry weather. Thus, at first it seems amazing that poricidal anthers apparently are manifested most prominently in species from tropical climates (HARRIS 1905), and furthermore in so many genera.

Generally, pure pollen flowers without nectar or oil as additional reward, display open flowers or even flowers with reflexed petals, making the pollen, the only reward, as accessible as possible. This may become a problem, especially in humid tropical regions, where heavy rains may deplete the exposed pollen which is not protected within a flower tube. Phenological studies at two sites, one in Mexico (DELGADO SALINAS & SOUSA

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SÁNCHEZ 1977) and the other (the present study) in Brazil, indeed demonstrated that the majority of the *Cassiinae* species were flowering during the rainy season. In some species of *Senna* we observed that by turgescence the small pores or slits of the apex of the anthers opened or closed accordingly to the ambient humidity. So the ejection of the pollen cloud only functions during appropriate weather conditions. Also the pollinating bees approach flowers only during dry weather. Thus, one important advantage of poricidal anthers is the fact that pollen is well protected within the closed anther-tube. A pollen loss by environmental factors is certainly more critical in flowers with few stamens than in polyandrous ones. So it might become more comprehensible why poricidal anthers occur much more frequently in groups with oligomerized androecium.

Of course, species with poricidal anthers do not flower merely during the wet season and poricidal anthers are not only a device for pollen protection. An economic and effective pollen offer and transfer is certainly at least as important as the other function.

In *Cassiinae*, zygomorphism, heteranthery, enantiostyly and flower resupination, involving morphology and position of the petals and reproductive organs, are well known phenomena. The elongated gynoecium, formed by the ovary and often a long style, projects the stigma away from the flower center. In the *Cassiinae* species, in general, and in the *Senna* species, especially, a longer ovary contains more ovules and so more seeds can be produced. This might confer on those species a reproductive advantage.

In *Cassiinae* flowers there is an obvious tendency of the stamens to be about the same height as the stigma. All the ten stamens can be the same length as the gynoecium. This is the case in some of the small-flowered *Chamaecrista* species where the pollen from all anthers is collected by the bees and may be the pollinating pollen. In many species, however, there is a tendency towards heteranthery, with the differentiation of form and function of the androecium. A few long stamens reach the length of the gynoecium. Shorter stamens in the central part of the flowers are vibrated by the bees and are at the same time used as a support while settling. In order to guarantee pollination, the difference in the level of the stigma and that of the pollinating anthers must not exceed the size of the pollinating bees. The reduced and pollenless staminodes also appear to have some function. The bees sometimes bite into them to cling to the flower. The wounds caused by this biting on staminodes and on pollen-containing anthers were interpreted by previous authors as signs of "milking" of the anthers. A real "milking" (this is squeezing out of pollen) does not occur, certainly not in *Senna*, as the anthers' wall is thick and stiff. The stamen differentiation in *Cassiinae* is accompanied by trends towards zygomorphy of the flowers, which brings about a more stereotypical behavior of the bees during their

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visits. A more precise and economic functioning of the flowers is the consequence of this evolution.

The three genera of the *Cassiinae, Cassia, Senna,* and *Chamaecrista,* apparently have evolved parallel and have attained their evolutionary development in different ways. The pantropical genus *Cassia* sensu stricto, alleged to be the oldest or most primitive genus of the *Cassiinae*, based on morphological characters other than the androecium (BARNEBY pers. comm.), has still elongated dehiscence or pore-like structures at the apex and/or at the base of the anthers. The anthers in this genus have attained the level of the stigma by an elongation of filaments. The bees collect pollen with their mouth organs and legs directly without vibration, but also vibrate, thus facilitating the expulsion of the pollen. The ovary and the style are similarly curved as the three abaxial stamens.

A more stiff structure vibrates more efficiently than such elastic stamens exhibited by the genus *Cassia.* Consequently, the androecium of the *Senna* species appears better constructed and adapted for exploitation by buzzing. The filaments in *Senna* are generally straight or simply incurved and either very short or barely twice as long as the anthers. The latter are voluminous and have thick and stiff walls. The poricidal character is developed best in this genus. Apical pores or small slits not only open and close during changing humidity, but also direct precisely the ejected pollen grains during vibration by the bees. Within the genus there are species with only slightly differentiated stamens, which do not accompany the length of the gynoecium, like *S. surratensis* or *S. obtusifolia.* The stigma and the anther openings reach the same level through the inflection of the gynoecium. The stigma even approximates to the anther openings. Many other *Senna* species have more differentiated male organs. The climax of this development is reached by species with three kinds of stamens: Three longer stamens with at least two of them reaching the length of the gynoecium, four medium-sized ones in the middle of the flower and three adaxial staminodes (*S. affinis, S. rugosa*). The pollination mechanisms are described in this paper. The pollen which the bees receive on their dorsal body side, on the thorax or abdomen, which is mostly pollen from the long stamens, is deposited usually just on those places on the bees' body where the stigma approximates or touches. Additionally, this pollen is with more difficulty brushed off by the bees and functions therefore more as a pollinating pollen. The pollen of the four large central anthers is deposited at the ventral side of the bees' body and is used for the most part by the bees as reward. Only in the middle line of the bees' ventral side, because of the difficulties to brush it off from this place, some pollen does remain, and this may cause pollination too, when the bees are entering or leaving the flowers. The pollen of both kinds of stamens is viable and therefore able to fertilize. The most extreme differentiation of stamens is shown by e.g. *Senna pendula* var.

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glabrata, where the two longest stamens accompany the gynoecium in length and form and are incurved upwards, directed to each other and forming a kind of gateway. In this case enantiostyly, which occurs also in this species, cannot have the normally attributed function of avoidance of self-pollination. In a flower like that of *S. pendula*, in which one stamen always accompanies the gynoecium, moreover, self-pollination must be the rule and not the exception. In studying similarly constructed flowers, already DULBERGER 1981 doubted about enantiostyly as being always a feature to avoid self-pollination.

The third, primarly American genus *Chamaecrista* shows a strong tendency towards herbaceous plants with a number of species being weedy. The plants carry small flowers of which only one or two open per day.

Differentiation of the androecium is much less apparent than in the other two genera, and staminodes are quite rare. The wall of the anthers is less rigid and the pollen may be pressed out of the pores easily. One petal, the innermost, always different from the others, normally larger, longer and incurved, is called "cucullus" (THORP & ESTES 1975). It is in an upward lateral position in normally oriented flowers and in a low downward position in resupinate ones. Function of this cucullus is not exactly known. It may, however, play some role in orientation and for positioning of the bees during their flower visits. A more obvious function would be better directing of the expulsed pollen grains towards the bees' body. In some *Senna* species also one petal is larger and longer and somewhat dish-like incurved, but in this genus it is the outermost petal which may have some similar function as the cucullus in the *Chamaecrista* species.

The species of *Chamaecrista* with larger flowers are visited and pollinated by large Xylocopa, Bombus, Epicharis and Oxaea species, while the small Augochloropsis, Pseudaugochloropsis, or Exomalopsis bees pollinate these flowers only occasionally. But these small bees are efficient pollinators of the *Chamaecrista* species with smaller flowers (e.g. *Ch. desvauxii* var. *parvifoliola* or *Ch. flexuosa*).

Among the *Chamaecrista* species with small flowers there are several which are visited and pollinated by large bees, as for instance *Ch. campestris, Ch. cathartica* var. *cathartica* or *Ch. hispidula*. A peculiar flower device, only recently described (GOTTSBERGER & al. 1988), exhibits flowers of these species clearly adapted for pollination by large bees. It is the folded tube-like petal which functions as prolongation of the short stamens. With the aid of this petal, pollen is deposited exactly on that part of the bees' body, which during the visitation of the bees is touched by the stigma of a flower of the opposite morph. Furthermore, during settling and vibration, the folded, thickened petal is a good support for the large and heavy bees. In these *Chamaecrista* species, the small bees, only with difficulty obtain some pollen. The structure of this petal and the whole flower construction seems

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to be an adaptation for an avoidance of visitation by small bees. The small bees are largely kept away from the pollen reward and excluded as pollinators. Maybe the larger bee species show more flower constancy and are generally more efficient and precise pollinators.

The present observations revealed that often there was no real contact of the bees' body with the stigma and/or the anther openings, but that there occurred only a close approximation. In recent years, it became evident that electrostatic forces play an important role in pollen transfer via insects (e.g. CORBET & al. 1982). Electrostatic potentials enable pollen to jump from anther to bee and from bee to stigma. Such forces obviously must be especially important during buzz pollination, in which a direct contact of the bees with the reproductive organs only rarely occurs. Without electrostatic forces there would be a lot of pollen dispersion and pollen loss into the air and only occasionally pollen transfer would occur. The probable important role of electrostatics in buzz pollination was already recognized by BUCHMANN 1978, BUCHMANN & HURLEY 1978 and ERICKSON & BUCHMANN 1983.

A modification of the petals and a partial inclusion of the stamens seems to be a general tendency in *Cassiinae*, at least in *Senna* and *Chamaecrista*. However, in *Senna* it is the outermost petal which can be modified and dish-like, whereas in *Chamaecrista* it is the innermost petal which forms the so-called cucullus. This originally adaxial petal, through resupination of the flower, came into an upper or lower lateral position. The curious tube-like petal of some *Chamaecrista* species also is the innermost petal. Such a development to enclose stamens by petals has reached its perfection in the papilionaceous *Fabaceae* flowers, where the two innermost petals are connected to form the keel, enclosing not only the stamens but also the gynoecium. In the *Fabaceae*, the pollen is already well protected by the keel, so poricidal anthers would make no sense. It is obvious that the *Fabaceae* have attained a more perfect way of portioning and exact placement of pollen during flower visitation. Furthermore, they also offer nectar as an additional reward and may develop, therefore, more pollen economy. Evolution for pollen protection and pollen economy with directed pollen placement has occurred in *Cassiinae* as well as in the *Fabaceae*. However, these parallel developments were attained on different morphological grounds.

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