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Interactions of the Cerrado Palms *Butia paraguayensis* and *Syagrus petraea* with Parasitic and Pollinating Insects

I Silberbauer-Gottsberger[1], SA Vanin[2], G Gottsberger[1]

1 - Universität Ulm, Ulm, Germany.

2 - University of São Paulo - USP, São Paulo, Brazil.

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Corresponding author
Ilse Silberbauer-Gottsberger
Botanischer Garten und Herbarium
Universität Ulm, Hans-Krebs-Weg
89081 Ulm, Germany
E-Mail: ilse.silberbauer@uni-ulm.de

Abstract

The two cerrado palms *Butia paraguayensis* and *Syagrus petraea* were studied with regard to parasitizing and pollinating insects that visit their reproductive organs. At the study site in Botucatu, São Paulo State, both species occurred together, while at the study site in Indianópolis, Minas Gerais state, only *S. petraea* was growing. Bees of the subfamily Meliponinae and Halictinae were the main pollinators of *B. paraguayensis* and several beetles and flies were additional pollinators. The visiting beetles divided up in more exclusive parasites, such as the weevils *Tripusus leiospathae* and *Petalochilus lineolatus*, and the Colydiidae *Bitoma palmarum*, which bored and oviposited the closed spathe and whose larvae fed on the flower buds, as well as species of the weevil *Microstrates*, which bred in staminate flowers. Differently, the curculionids *Anchylorhynchus bicolor*, *Parisoschoenus* sp., *Dialomia* sp., and species of *Mystrops* (Nitidulididae) behaved as parasites and pollinators. On the other hand, *S. petraea* shows more evident adaptations for pollination by beetles. This species has *Trigona spinipes* as prominent bee pollinator, but otherwise beetles dominated as visitors, being them either parasites, pollinators or both. Although several identical beetle genera occur on both palms, at the species level they are different, as for example *Anchylorhynchus camposi* on *S. petraea.* At the two distant study sites of *S. petraea* in Botucatu and Indianópolis, several species, especially of the parasitic insects, are identical, indicating that parasitism is a stronger bond than pollination in this species which is characterized by a generalist pollination mode.

Introduction

Palms are prominent, characteristic and abundant components of most tropical and subtropical landscapes. They are known to attract and to shelter many insects (Lepesmé, 1947, Howard et al., 2001). Therefore, palms are also hotspots of insect abundance and diversity in any vegetation type. Responsible for this are, among others, the commonly large inflorescences and infructescences, which carry many flowers and fruits and thus provide abundant food for insects in form of pollen, nectar and tissue. The other reason for insect richness on palms are the many possibilities for them to hide between the hard or woody leaf bases and the large inflorescence structures, which themselves have an extended developmental time and thus provide ample possibilities for insects to oviposit and breeding.

One of the early Brazilian pioneers working on palms and their insects was Gregorio Bondar, who noted that a considerable entomological fauna of Hemiptera, Lepidoptera and Coleoptera has evolved on the native palms of Brazil, some of them damaging or destroying leaves, flowers and fruits. Bondar (1964) elaborated that of Coleoptera, especially Hispinae (Chrysomelidae) and Curculionidae have segregated on American palms a large number of genera and species. "Each genus of native palms, and at times, each species, has its own entomological fauna, and by means of the insects collected, one can determine the genus and species of the palm." (Bondar, 1964).

Palms are mainly pollinated by insects (Henderson,

1986) and many palm species are visited jointly by an array of different insects, which are of varying importance in pollination. However, often a predominance of one group of insects as pollinators can be observed (Silberbauer-Gottsberger, 1990, Gottsberger & Silberbauer-Gottsberger, 2006b). Certain morphological and physiological differentiation patterns of flowers or inflorescences and scent emissions are correlated with this predominance of pollinators. Palms are frequently associated with beetles, which may take advantage of different vegetative and floral organs for mating and reproduction. Several of these beetles are involved in pollination. They may act as additional, predominant or exclusive pollinators.

In the World Checklist of Palms by Govaerts and Dransfield (2005), 2364 species in 190 genera are accepted. Sixty-seven genera and 550 species are said to occur naturally in the Americas (Henderson et al., 1995), and of these, 210 species are native to Brazil (Lorenzi et al., 2004). Based on the last mentioned authors, 20 species are native to the Central Brazilian cerrado *sensu lato* vegetation (see Gottsberger & Silberbauer-Gottsberger, 2006a). The distribution of the cerrado species among its six genera is the following: *Acanthococos* (1 species), *Allagoptera* (2 spp.), *Astrocaryum* (1 sp.), *Attalea* (4 spp.), *Butia* (4 spp.) and *Syagrus* (8 spp.) (Lorenzi et al., 2004).

In this paper we compare two cerrado palms, *Butia paraguayensis* and *Syagrus petraea*, with respect to the insects visiting and feeding on still closed and already opened inflorescences, flower buds and open flowers, as well as immature and mature fruits. In a previous paper a detailed account of the phenology, the growth and duration of the inflorescences and infructescences, of anthesis, and the morphology and functioning of extrafloral nectaries of *Butia* (under the old, now invalid name *B. leiospatha*) was given (Silberbauer-Gottsberger, 1973). It was also mentioned that principally bees, beetles and flies were the visitors and pollinators of this species, but most insects at that time were not identified to genera and species and observations on their behavior have been scarce. Also *S. petraea* (under the synonym *S. loefgrenii*) was already shortly mentioned as being pollinated by bees and beetles (Silberbauer-Gottsberger, 1990), again without being able at that time to provide details about visitors and their importance as pollinators and parasites.

One aspect of the present paper was to distinguish for both species between insects which are flower visitors without being pollinators and others which are effective pollinators. Another aspect was to verify, by direct observation and, additionally, by information from the literature, the level of parasitism of certain insect species; which one is an exclusive harmful floral parasite, destroying floral tissue without contributing to pollination and which one is a parasite and an effective pollinator at the same time? At one study site, in the state of São Paulo, both studied species occurred sympatrically, which provided the opportunity to verify similarities and differences in the attracted parasitic and pollinating insects. In another study site in the state of Minas Gerais, only *S. petraea* occurred.

Since the open, unspecialized palm flowers often have a generalist pollination system (Gottsberger & Silberbauer-Gottsberger, 2006b), we hypothesized that in distant sites of the same palm species, the parasitic insects, living inside and nourishing themselves of floral or fruit tissue, should be more specific than the pollinating insects which mainly collect and feed only on pollen and nectar.

Material and methods

The two species studied have a quite vast distribution. *Butia paraguayensis* (Barb. Rodr.) L.H. Bailey is distributed from the Brazilian states of Minas Gerais, Mato Grosso do Sul, São Paulo, Paraná and Rio Grande do Sul, to Paraguay, Argentina, and northern Uruguay. This species occurs mainly in cerrado *s.l.* vegetation on sandy soils, at 500-900 m elevation (Henderson et al., 1995, Lorenzi et al., 2004). *Syagrus petraea* (Mart.) Becc. has an even more northern distribution, occurring from the Brazilian states Pará, Maranhão, Piauí, Bahia, Minas Gerais, Tocantins, Goiás, Rondônia, Mato Grosso, Mato Grosso do Sul, and São Paulo, to eastern Bolivia and eastern Paraguay. Also this species grows mainly in cerrado *s.l.* vegetation, however, apparently in more open physiognomies than *B. paraguayensis* (pers. observation), on sandy to red clayey soils, but also in open, semideciduous forests on stony soils, at 600-1000 m elevation (Henderson et al., 1995, Lorenzi et al., 2004).

There were principally two study sites for the two species, one was in the municipality of Botucatu in São Paulo state, where both species occurred together, and the other was in the municipality of Indianópolis, Minas Gerais, where only *S. petraea* occurred. The climate of the Botucatu region (city coordinates 22°53´9´´S, 48°26´42´´W, alt. 756 to 920 m) is characterized by an average yearly precipitation of about 1300 mm. The seasonal distribution of precipitation indicates that 37% of the total annual rainfall occurs in spring, 44% in summer, 10% in autumn and only 9% in winter, that is, a warm rainy season from October to March alternates with a cooler dry season from April to September (Tubelis et al., 1975). The daily temperature means throughout the year ranged from about 16 to 25°C, with the lowest in July and the highest in February. The yearly average temperature is about 21°C. The exact place of the Botucatu study site, Treze de Maio, where both species occurred, about 8 km northwest of the city of Botucatu, consisted of a mixture of several, more closed and more open, cerrado *s.l.* physiognomies and lies at 650 m alt. The other study site of *S. petraea* was close to Indianópolis (city coordinates 19°2´20´´S, 47°55´1´´W, alt. c. 800 m) at Fazenda Bela Taanda and neighboring fazendas. The temperatures in the more northern Indianópolis site are somewhat higher than in Botucatu.

In *B. paraguayensis* in Botucatu, 20 flowering individu-

als were marked in 1970/1971. These individuals served for studying the phenology, the duration of flowering of staminate and pistillate flowers, the fruit development and ripening, as well as the approach to and the behavior of insects at the inflorescences and infructescences. To verify the duration of development during the colder and drier versus the warmer and more humid periods of the year, inflorescence buds were weekly measured (length and circumference) from a length of 30 cm on until their opening. Visitors were partly observed and collected during blocks of 30 minutes at different times of the day to obtain a more equilibrated picture of occurrence of insects on this palm during whole days. Additional and complementing observations on this species occurred in the years 1977, 1980, 1983, 1989, 1990, 2007 and 2009.

For studies of *S. petraea* in Botucatu in 1980, 1981, 1983, 1985 and 1990, 35 flowering individuals were selected and investigated at the same site as for *B. paraguayensis*. At the other site in Indianópolis, similar comparative studies of *S. petraea* were done on 26 flowering individuals in 1983, 1985 and 1990.

Voucher specimens of both species are deposited in the herbaria Botucatu (BOTU), Brasília (B) and Ulm (ULM). The insects collected at the palms are deposited in the insect collection of Sergio Vanin at the Department of Zoology, University of São Paulo (USP), in São Paulo, and in the private collection of the authors in Ulm.

Results

Flowering and anthesis

Adult individuals of *Butia paraguayensis* in Botucatu are erect palms and can attain a maximum stem height of 1.5 to 2 m (Gottsberger & Silberbauer-Gottsberger, 2006b); individuals become already sexually mature having a stem height of only half a meter. On the other hand, *Syagrus petraea* is a so-called "acaulous" short palm. It has subterranean ramified stems. The apical part of the shoot, were the leaves and inflorescences are formed, emerges from the soil in an inclined position and may grow to a height of 20-40 cm (Gottsberger & Silberbauer-Gottsberger, 2006b). When growing in a larger population of ca. 30-50 plants, both species are flowering and fruiting practically year-round.

The flowers are unisexual and the inflorescences are monoecious. The pistillate flowers together with staminate ones are arranged in triads more at the basal part of the rachillae (inflorescence ramification of the first order), while staminate flowers alone occupy the apical part. There are about 30-40 rachillae with about ten times more staminate than pistillate flowers. Flower number is variable and apparently depends on the size of the inflorescence. One inflorescence of *B. paraguayensis* can carry about 1200-2500 staminate and 120-200 pistillate flowers. *S. petraea* has smaller and less ramified inflorescences (up to 8 rachillae) and with about five times more staminate than pistillate flowers. One inflorescence can carry about 150-250 staminate and 30-50 pistillate flowers. Some inflorescences at the Indianópolis site had only staminate flowers.

We detected a considerable seasonal difference in the rate of reproductive organ development in *B. paraguayensis*. Development of inflorescences, flowers and fruits was faster during the warm rainy season than during the cool dry season. In 30 cm long inflorescence buds, the time until spathe opening decreased from June to December, this is from mid-dry season to mid-rainy season. Also from September onwards, there was an increase in the number of inflorescences produced by an individual. Flowering and fruiting time also accelerated. For example, inflorescences which opened in June, July or August took 111 days (on average) to produce ripe fruits, those which opened in September and October took 93 and those in November and December only 57 days.

The inflorescences of each individual of *B. paraguayensis* and *S. petraea* developed one after the other. Only very rarely are staminate and pistillate flowers, either within or between inflorescences of the same plant, simultaneously in a functional stage. For this reason, these palms are mostly functionally dioecious.

Anthesis in both species begins in the morning with the longitudinal splitting of the woody peduncular bract, the spathe, which can be up to 80 cm long in *B. paraguayensis* and ca. 20 cm long in *S. petraea.* With the opening of the spathe the inflorescence is released. The rachillae are spread. The staminate flowers are functioning first, viz. the inflorescence is protandrous. In *Butia* about 1/3 of staminate flowers open at the first day, while this was 1/10 in *Syagrus petraea*. In both species the staminate phase of an inflorescence lasts for about fifteen days (or even longer in the dry season), while one individual flower lasts for one or two days only. Only after the last staminate flower has withered, followed by a non-flowering interval of 10 to 15 days, the pistillate flowers become receptive. In *Butia* the stigmas are spread apart, while in *Syagrus* they keep together. All the pistillate flowers in *Butia* enter their receptive phase within two to three days, in *S. petraea* within 5 to 7 days, while an individual pistillate flower may be receptive for one or two days only.

In the population of *Butia* there existed individuals with grayish purple staminate and pistillate flowers, and others with yellow flowers. The flowers emit a faint, pleasant, sweet scent. The flowers of *S. petraea* are pale yellow, the pistillate ones turning to orange yellow when sexually active. Both sexes emit a similar odor, which is faint and straw-like during the day, gradually becoming stronger in the afternoon, as well as gaining spermatic- and mushroom-like notes; this stronger odor persists overnight. Staminate flowers in both species have a reduced, sexually non-functional, central gynoeceum, known as pistillode. Nectar is produced by septal nectaries in both staminate and pistillate flowers, less abundant in *S. petraea* than in *B. paraguayensis.*

Insects visiting Butia paraguayensis

The insects observed visiting the reproductive organs of *B. paraguayensis*, from unopened inflorescences to ripe fruits, belong to 6 orders. The more frequent visitors were of the orders Hymenoptera, Diptera and Coleoptera, while the Hemiptera, Orthoptera and the enigmatic order Strepsiptera were less represented (Table 1). More than 45 different insect species, representing 15 families were found visiting the reproductive organs of *B. paraguayensis*.

The most common insects visiting both staminate and pistillate flowers, and thus being the effective pollinators, were bees, especially Meliponinae, but also Halictidae and Apinae. *Trigona hyalinata* and *T. spinipes* were frequent and about twice as abundant at staminate than at pistillate flowers, whereas the more rare *Paratrigona lineata lineata* and the introduced *Apis mellifera* sometimes visited the pistillate flowers more frequently. Other bee species that visited both the staminate and pistillate flowers were *Ceratalictus theius,* and *Chloralictus* cf. *opacus*. Bee species of the genera *Augochlora*, *Augochlorella*, and *Augochloropsis* were seen at staminate and sometimes also more frequently on pistillate flowers and therefore are also effective pollinators.

A further, not identified *Chloralictus* species was seen

Table 1. Insects on reproductive organs of *Butia paraguayensis* in Botucatu, SP. +++ very frequent, ++ frequent, + rare, pc pollen collecting, pf pollen feeding, nf nectar feeding, pnf pollen and nectar feeding, ff fruit feeding, m mating, op ovipositing.

Order, family, subfamily, tribe	Genus, species	Inflor. bud	Flowers		Fruits	
			staminate	pistillate	unripe	ripe
COLEOPTERA						
Corylophidae	indet.		+			
Colydiidae	*Bitoma palmarum*	+/op?	+/pf			
Chrysomelidae						
Galucerinae	indet.		+/pf/nf	+/nf		
Curculionidae						
Anthonominae						
Anthonomini	*Anthonomus* sp. 2		+			
Baridinae	indet.	+/op?	++/pf			
Centrinini	sp. 2		++			
	Centrinaspis sp.		+/pf			
	Dialomia sp. 1		+			
	Revena rubiginosa		+		+/op	
Madarini	*Angelocentris schubarti*		++/pf/nf	+/nf/op?		
	Tripusus leiospathae	+/op?	+++/pf			
	Parisoschoenus sp.		+/pf	+/op?		
	Microstrates rufus		+/pf/op?			
	Microstrates sp. nov.		++/pf/op?			
	Gen. 1		+			
Erirhininae						
Derelomini	*Anchylorhynchus bicolor*		+++/pf	+/mop		
Molytinae						
Conotrachelini	*Conotrachelus* sp. 6		+			
Petalochilinae	*Petalochilus lineolatus*		+			
Nitidulidae	*Mystrops palmarum*		+/pf/op?	+		
	Mystrops sp. 2		++/pnf			
	Mystrops sp. 4		++/pnf	++		
	Mystrops sp. 6		++/pnf			
Scarabaeidae						
Rutelinae	*Antichira capucina* group				+/ff	
Scarabaeinae	*Ateuchus* sp.					+/op
Silvanidae	*Silvanus* sp. 1		++/pf			
Tenebrionidae						
Alleculinae	*Prostenus cyaneus*		+/pf			

Table 1. [Continued]. Insects on reproductive organs of *Butia paraguayensis* in Botucatu, SP. +++ very frequent, ++ frequent, + rare, pc pollen collecting, pf pollen feeding, nf nectar feeding, pnf pollen and nectar feeding, ff fruit feeding, m mating, op ovipositing.

DIPTERA	3 spp. (Muscidae, Calliphoridae)	+/nf	+/nf
HEMIPTERA			
Cydnidae	indet.	+/nf	+
Coreidae	indet.	+/nf	
HYMENOPTERA			
Apidae			
Apinae	*Apis mellifera*	+/pc	+/nf
Meliponinae			
Trigonini	*Paratrigona lineata lineata*	+/pc/nf	+/nf
	Trigona hyalinata	+++/pc/nf,	++/nf
	Trigona spinipes	+++/pc/nf	++/nf
Halictidae			
Halictinae			
Augochlorini	*Augochlora* sp.	+/pc	++/nf
	Augochlorella michaelis	+/pc	
	Aurochloropsis aurifluens	+/pc	
	Aurochloropsis cleopatra	+/pc	
	Ceratalictus theius	+/nf	++/nf
Lasioglossini	*Chloralictus* cf. *opacus*		++/nf
	Chloralictus sp. 1		+/nf
Formicidae	several spp. indet.	+/nf	+/nf
Vespidae	indet.	+/nf	+/nf
ORTHOPTERA			
Proscopiidae		+	
STREPSIPTERA	indet.	+	

only on staminate flowers. In staminate flowers, bees principally collected pollen, but fed also a little on nectar, whereas in pistillate ones only nectar was available for them. Additionally, several fly, wasp and ant species visited both types of flowers and therefore at least the flies and wasps have to be considered effective pollinators as well. At our study site in Botucatu, the two *Trigona* species were very abundant and aggressive, and other bees, even the often dominant *Apis mellifera*, as well as occasionally also wasps and flies were attacked and chased away by them.

A recently opened inflorescence was often inhabited and visited by many species and individuals of beetles. Sometimes we counted up to ten species of beetles in one inflorescence represented by more than 40 individuals. Half of them were often made up by very small beetles, different species of *Mystrops* (Nitidulidae) and *Microstrates* (Curculionidae) or by the somewhat larger (8 mm) weevil *Anchylorhynchus bicolor*.

The numerous individuals of *Mystrops* and *Microstrates* species were mostly feeding on pollen, sometimes took profit also of the nectar, also oviposited in the stamens and visited pistillate flowers only sporadically, thus not being of great importance in pollination. The frequent Derelomini weevil *Anchylorhynchus bicolor* (sometimes represented by up to 20 individuals in one inflorescence) also fed on pollen and on nectar but visited the pistillate flowers more frequently and were also pollinating. These beetles were always present in the inflorescences, hidden at the base of the spathe, when either staminate or pistillate flowers were active, respectively. They left the inflorescences in the "inactive" interval phase. However, besides pollinating, they parasitized the pistillate flowers after mating and ovipositing the ovary. The larvae developed inside the gynoeceum and were eating the ovule. The destroyed flowers fell to the ground, where the beetles continued their development to pupae and adults. About 30 to 50% of the pistillate flowers were attacked and did not develop to fruits. The more rare visitors of the pistillate flowers, *Angelocentris schubartii* and *Parisoschoenus* sp., were also pollinators and we suspect them to parasitize the pistillate flowers too.

In the open inflorescences of *Butia,* in some years, *Anchylorhynchus bicolor* was represented by two morphs. There was a common form of one color (gray-magenta) and another one with black longitudinal stripes. In another year an additional third black morph with one yellowish line surrounding the wings appeared. In 19 inflorescences in the

staminate stage, 109 individuals of the one colored morph, 42 striped ones and only one of the dark morphs were counted. In ten inflorescences in pistillate phase, 8 one colored, eleven striped individuals and one dark individual were present.

The *Microstrates* species oviposited in the stamens and their larvae fed on the anthers; they were only occasionally seen to visit the pistillate flowers. At midday the pollen became powdery, thus pollination by wind apparently occurs as well.

Before opening, the inflorescence bud often was parasitized by the small Colydiidae *Bitoma palmarum* (2 mm long), the weevil *Tripusus leiospathae* (3.5 mm long and with a 2.5 mm long proboscis), and a not identified further weevil of the subfamily Baridinae (5.5 mm long with a 1.2 mm long proboscis). They made holes into the bud spathe and layed their eggs into the spathe. These holes were always closed by the plant by a resinous substance. *Bitoma* larvae developed in the spathe tissue, while *Tripusus* and the Baridinae larvae probably fed on staminate flower buds in the interior of the inflorescence. When the inflorescence bud had recently opened, beetle larvae were present in between the flowers, and often had destroyed and eaten many of them. Unfortunately, we could not rear the larvae to adults. As these species were never seen on pistillate flowers, they are probably no

Table 2. Insects on reproductive organs of *Syagrus petraea* in Botucatu, SP and Indianópolis, MG. +++ very frequent, ++ frequent, + rare, pc pollen collecting, pf pollen feeding, nf nectar feeding, pnf pollen and nectar feeding, tf tissue feeding, m mating , op ovipositing, search searching on the flower.

Order, family, subfamily, tribe	Genus, species	Botucatu Flowers		Indianópolis Flowers	
		staminate	pistillate	staminate	pistillate
COLEOPTERA					
Chrysomelidae					
Cassidinae	indet.			+	
Hispinae	*Imatidium* sp.			+	
Cleridae	indet.			+	
Cucujidae	indet.				+
Colydiidae	*Bitoma palmarum*	+/pf			++
Curculionidae					
Baridinae					
Baridini	*Cryptobaris sulcata*			+	
Centrinini	*Dialomia* sp. 1	+			
	Ladustes speciosus				+
	Palmocentrinus cf. *lucidulus*	+			+
Madarini	*Hustachea campestris*	+++	++/tf	+++/op?	+++
	Microstrates cocos-campestris	+++			
	Microstrates sp. nov.	+++/pf	+	+++/pf/op?	+
	Parisoschoenus plagiatus			+	
Cryptorhynchinae					
Cryptorhynchini	*Coelosternus* sp. 1			+	
Erirhininae					
Derelomini	*Anchylorhynchus camposi*	+++/pf	++	+++/pf	+++/nf/m/op
	Phytotribus sp. 1	+/pf		++/pf/m/op	+
	Phytotribus sp. 2	+/pf	+		
Molytinae					
Hilobiini	*Heilus* sp. 1			+	
Nitidulidae	*Mystrops* sp. 3			+/pnf/op	+/nf
	Mystrops sp. 5	+/pnf	+/nf	+/pnf/op	+/nf
Silvanidae	*Silvanus* sp. 2	+	+	+/pnf	+/nf
DIPTERA	indet.				+/nf
Phoridae	indet.	+/nf	+/nf		
HYMENOPTERA					
Apidae					
Apinae	*Apis mellifera*			+/pc	
Meliponinae					
Trigonini	*Trigonisca pseudogreaffii*			+	
	Paratrigona lineata lineata			+/pc	+
	Trigona spinipes	++/pc	+/search	+++/pc	+/search
Halictidae					
Augochlorini	indet.	+/pc			
Formicidae	indet.		+/nf		+/nf
BLATTODEA	indet.			+	

pollinators. Also the maiority of the other insects found in the inflorescence visited only the staminate flowers. Many of the observed insects just crawled around or were sitting on the flowers and it was not possible to obtain informations about their behavior or their specific importance for the plant.

Not only flowers but also young and ripe fruits of *Butia* were parasitized. One parasite was the weevil *Revena rubiginosa* which oviposited in very young fruits. The large green rutelid beetle *Antichira capucina* was seen to feed on ripe fruits of *Butia*. Under the palm individuals holes in the soil were seen. When digged out, the scarabaeid *Ateuchus* sp. was detected sitting on ripe fruits of *Butia*. It was even possible to observe once an individual of *Ateuchus* rolling a ripe fruit about half a meter away from the palm, digging a hole of about 10 cm depth and than burying a fruit. In some of the holes we found larvae eating the fleshy part of the fruit. The seed inside the hard shell of the inner fruit layer remained intact.

Insects visiting Syagrus petraea

About 30 insect species (from 13 families and 4 orders) were observed and collected on the comparatively smaller inflorescences of *S. petraea*, at the two study sites in Botucatu and Indianópolis together (Table 2). The recently opened inflorescences sometimes sheltered up to hundred individuals of beetles, most of them belonging to small *Mystrops and Microstrates* species, followed by *Anchylorhynchus camposi, Hustachea campestris*, 2 species of *Phytotribus* and one *Silvanus* sp., which all visited staminate and pistillate flowers. They are all pollinators. The other beetle species visited the staminate and/or pistillate flowers only sporadically and were of no real importance in pollination.

Many of the species were already active, even copulating, in the early morning at 5:30 AM, changing the inflorescences also during the day, and increasing their activity in the evening hours. They fed on pollen, on the small amounts of nectar and on flower tissue at the base of the petals of the staminate flowers and on the margins of petals of the pistillate ones. *Mystrops, Microstrates* and *Phytotribus* copulated on the staminate flowers and oviposited them. At different subpopulations and in different years the damage caused by these beetles at staminate flowers could vary from zero to 90%. Of 100 dropped staminate flowers from seven inflorescences counted in September 1990 in Indianópolis, 44% were damaged. In many of these damaged flowers 1.2 mm long larvae were found. In these so infected flowers mostly the anthers were eaten, but also the petals showed gnawing marks on the nutritious tissues.

Anchylorhynchus camposi copulated on the pistillate flowers and oviposited the ovary. This species was present only in inflorescences with sexually active flowers and left the inflorescence during the interval between the staminate and pistillate phases. *Hustachea campestris* was seen on staminate and pistillate flowers, but no copulation or oviposition was detected. Although the spathe of the bud was sometimes damaged, we were unable to detect which one of the insects was responsible for entering the interior of the inflorescence buds.

From the morning on, Meliponinae bees, mainly *Trigona* and *Paratrigona*, frequently collected pollen and also visited the pistillate flowers, where they seemed to search for something but were leaving them soon. However, the bees only visited the flowers from 7:00 AM to 3:00 PM. Diptera and Formicidae were seen on staminate and pistillate flowers in very small numbers.

Discussion

Butia paraguayensis and *Syagrus petraea* are visited by numerous insects, mainly bees and beetles, which play different roles during the development of the inflorescence buds, the flowers and fruits. There are nearly exclusive parasitic beetles, which oviposit and destroy the tissue of the young spathe, as well as staminate flowers and unripe fruits. A second group of insects are parasites and pollinators, and a third group are pure pollinators which only feed on pollen and/or nectar. There is also a forth group of insects, which only visit the staminate flowers, nourishing themselves from pollen and nectar.

Examples of pure parasites in *B. paraguayensis* are the weevils *Tripusus leiospathae* (the former name of this palm was *Cocos leiospatha*!) and an unidentified Baridinae, which bores the spathe and the larvae feed inside the closed inflorescence on staminate flowers. As in nearly all Baridinae, the larvae after dropping of the flowers complete their development in the soil (Costa Lima, 1956). The Colydiidae *Bitoma palmarum* supposedly develops inside the spathe tissue; we found the adult beetle in newly opened inflorescences. Bondar described this beetle as predator of *Attalea funifera* and *Cocos nucifera* (Costa Lima, 1953). Also the weevil *Petalochilus lineolatus* may develop in the interior of the closed spathe. Other species of this genus are mentioned to develop in the inner spathes of the palms of the genera *Diplothemium*, *Attalea* and *Syagrus* (Vaurie, 1954). The larvae of the two *Microstrates* (Curculionidae) species develop in the interior of staminate flower buds, eating anthers and pollen. They complete their development in the fallen flowers at the ground. This was also observed by Bondar for *Microstrates ypsilon* on *Syagrus coronata* and *Cocos nucifera*, and other species, among them *Butia eriospatha* parasitized by *M. hatschbachi*, and *Syagrus flexuosa (*syn. *Cocos campestris*) parasitized by *M. cocos-campestris* (Bondar, 1941, Costa Lima, 1956). *Revena rubiginosa,* which was seen to oviposit young fruits may also be an exclusive parasite. Another species, *R. vagans*, was described by Bondar to bore the young fruits of *Syagrus vagans*, and the growing larva was eating and destroying the whole interior (Lepesmé, 1947).

One prominent and frequent beetle that is a parasite of the pistillate flowers and at the same time causes pollination in *B. paraguayensis* is *Anchylorhynchus bicolor* (Curculionidae, Derelomini). As this beetle feeds on pollen and passes over several pistillate flowers before ovipositing, it is a relatively effective pollinator. There are many species of *Anchylorhynchus* associated quite specifically with palms (Bondar, 1943, Vaurie, 1954). *Angelocentris schubarti* and *Parisoschoenus* sp. also visit staminate and pistillate flowers and seem to parasitize the pistillate ones. *Parisoschoenus obesulus* is a pest on *Cocos nucifera*, parasitizing the ovary (Sánchez & Nakano, 2003, Moura et al., 2009).

One unidentified *Dialomia* species was found on staminate flowers, but it may belong to the group of parasitic and pollinating insects as well. Larvae of *Dialomia polyphaga* feed on petals and anthers and adult females may lay their eggs in pistillate flowers of palms (Lepesmé, 1947). The nitidulid *Mystrops* species which feed on pollen and nectar apparently parasitize the staminate flower buds. Following Bondar (1940), in *Mystrops palmarum* the larval stage takes 5 to 6 days in the staminate buds and the pupae need 4 to 6 days for their development. The whole cycle of the beetle does not exceed 12 days.

Hymenoptera and Diptera are non-parasitic pollinators and are the most abundant and effective ones in *B. paraguayensis*. The scarab *Ateuchus* functions as a short distance disperser of the fruit. It rolls the ripe fruits a short distance away from the mother individuals and digs holes to bring the fruit underground to oviposit there. The intact fruit is in the right depth for germinating and at the same time it is protected from fire.

The visitor spectrum of *S. petraea* is different from *B. paraguayensis*. Beetles are the most abundant visitors of the inflorescences and flowers, while Hymenoptera and Diptera are less prominent. This species shows adaptations for beetle pollination. The specific floral scent, especially in the afternoon and evening attracts beetles. Some of them are nourished by nutritious tissues on the petals of both the staminate and pistillate flowers. As the flowers produce very low amounts of nectar, they are not that attractive as *B. paraguayensis* for nectar-imbibing insects such as bees and flies.

The only insect species which *S. petraea* were found to share with *B. paraguayensis* are the bees *Trigona spinipes*, *Paratrigona lineata*, and the beetles *Bitoma palmarum*, *Dialomia* sp. 1 and *Microstrates* sp. nov. These species showed on *S. petraea* about the same behavior as on *B. paraguayensis*, with exception of the new *Microstrates* species. In both palm species *Microstrates* sp. nov. developed in the staminate flowers, but visited the pistillate ones only in *S. petraea*, being a pollinator for this species. Otherwise, only the genera of beetles are the same at the two palm species as, for instance, *Anchylorhynchus*, *Parisoschoenus*, *Microstrates, Mystrops* and *Silvanus*, but the species are different ones.

The set of species in *S. petraea* are *Anchylorhynchus camposi*, *Parisoschoenus plagiatus*, *Microstrates cocos-campestris*, *Mystrops* sp. 3, sp. 5, and *Silvanus* sp. 2., while *Anchylorhynchus bicolor*, *Parisoschoenus* sp., *Microstrates rufus*, *Mystrops palmarum*, *Mystrops* sp. 2, sp. 4, sp. 6, and *Silvanus* sp. 1 occur in *Butia paraguayensis*. One of the important pollinating beetles of *S. petraea*, *Hustachea campestris*, did not occur on *B. paraguayensis*. *Hustachea* species appear to parasite staminate flowers; Bondar provided a drawing of *H. bondari*, shown in Lepesmé (1947), piercing and ovipositing the petals of a staminate bud of a palm, with the subsequent development of the larva in its interior. The two *Phytotribus* species also only occurred on *S. petraea*. Species 1 was found at the two sites, ovipositing the staminate flowers in Indianópolis, whereas species 2 occurred only at the Botucatu site.

There are differences in *S. petraea* with regard to the occurrence of several beetle and bee species at the Botucatu and Indianópolis sites. But the parasitic species *Anchylorhynchus camposi*, *Phytotribus* sp. 1, *Microstrates* sp. nov., *Hustachea campestris*, *Mystrops* sp. 5, and *Bitoma palmarum* were found on flowers at both sites. *Anchylorhynchus camposi* was found by Bondar (1941) also on flowers of *Syagrus flexuosa*.

Apparently, there are beetles that have a more restrict occurrence on a small group of palms. To this group certainly belongs the weevil genus *Anchylorhynchus*, visiting the two palm species treated in this paper, and *Petalochilus*, which was found only on *B. paraguayensis*. After the revision of *Anchylorhynchus* by Bondar (1943), Voss (1943) and Vaurie (1954), 16 species of this genus were recognized and five in *Petalochilus* (Vaurie, 1954). Bondar stated that all species of *Anchylorhynchus* develop in palms and as far as verified they breed in flowers of the former genus *Cocos,* which is now subdivided in the monotypic genus *Cocos*, as well as the genera *Butia* and *Syagrus*.

Butia is a monophyletic genus of nine species confined to cooler, drier areas in southern Brazil, Paraguay, Uruguay and Argentina. Recently, Martel et al. (2013) verified raphid-containing idioplasts in all *Butia* staminate flower petals sampled, which do not occur in the most closely related genus *Jubaea*, further supporting the cohesive monophyly of *Butia*. *Syagrus* with its 31 species in its present concept apparently is polyphyletic and occurs from Venezuela southwards to Argentina with many species in the Brazilian cerrados and campos rupestris (Dransfield et al., 2008). *Butia paraguayensis* and *B. yatay* are said to be closely related species and being perhaps not distinct from each other (Henderson et al., 1995); at least the beetle breeding on them, in both cases *Anchylorhynchus bicolor*, eventually confirms that the two species are identical. For *Syagrus*, at present recognized as being polyphyletic, future studies may show the whole dimension of the association with *Anchylorhynchus*. It has to be seen after the circumscription of a cohesive monophyletic *Syagrus*, which one of the species still has associations with *Anchylorhynchus*. Meanwhile, besides occurring on species

of *Butia* and *Syagrus*, *Anchylorhynchus* species were detected also on species of *Oenocarpus* in Central Amazonia (Küchmeister, 1997) and in the Colombian Andes (Núnez-Avellaneda and Rojas-Robles, 2008).

On the other side, there are beetles which associate with a multitude of palm genera. Notorious are the genera *Mystrops* (present also on *B. paraguayensis* and *S. petraea*) and *Phyllotrox*, but also, *Celetes*, *Hustachea*, *Andranthobius*, *Dialomia* and others (see e.g., Schmid, 1970, Uhl and Moore, 1977, Beach, 1984, Búrquez et al., 1987, Barfod et al., 1987, Anderson et al., 1988, Scariot & Lleras, 1991, Bernal & Ervik, 1996, Ervik & Feil, 1997, Küchmeister, 1997, Küchmeister et al., 1997, Listabart, 1999, Voeks, 2002, Henderson, 2002). Several of these beetle genera might have numerous (but badly known or undescribed) species which are more or less specific to one or a few palm species. We are beginning to understand that even close-by standing different species of palms often share few visitors and no pollinators because differences in floral scent composition may cause isolation (e.g., Ervik et al., 1999, Knudsen et al., 2001, Núñez et al., 2005).

In many cases palms are parasitized by beetles which afterwards function as pollinators. We then can even say that these palms are breeding their own pollinators. This is an elegant way to make those palms more or less independent for pollination from their surroundings and at the same time this breeding of pollinators shapes the specificity of the beetles for "their" palm species. The nocturnal, thermogenic *Attalea microcarpa*, studied by Küchmeister (1997) in Manaus, provides a most elegant example of a palm breeding its own pollinators. This palm is visited by more than 30 species of Coleoptera, Hymenoptera, Lepidoptera, Diptera and others, but species of staphylinid beetles, *Mystrops* (Nitidulidae), *Groatus*, *Celetes*, *Phyllotrox* and *Belopoeus* (all Curculionidae) are the main pollinators. They are attracted in enormously large numbers (up to 60,000 estimated individuals per inflorescence) during the evening hours by the strongly heated staminate inflorescences which have a fruit- and yeast-like scent emission. The beetles´ activity after entering the semi-closed staminate flowers was pollen eating and oviposition. The larvae develop in the anthers and nourish themselves from pollen grains and anther tissue. Fast growing hyphae of a fungus envolve the totality of the staminate flowers and prevent their dropping to the ground. The fungus holds the withered and loose staminate flowers at the inflorescence, which gives the larvae of the beetles´ time to finish their development in a flushwater-free space above the ground in the heavily raining environment of the palm. The emerging beetles transport pollen grains and fungus spores to other inflorescences. The pistillate flowers also are heating, they emit a similar scent as the staminate ones and attract the same beetle species that visit the staminate inflorescences, however in much lower number. In *A. microcarpa* three organisms or groups of organisms, the palm and its flowers, the beetles and finally a fungus work together to make parasitism and at the same time pollination effective processes.

Not only in *A. microcarpa* but in all palms observed up to now, parasitism by flower beetles is more or less in balance with the number of flowers and inflorescences formed. There always remain enough intact flowers within a palm population to guarantee successful pollination and reproduction.

The two studied cerrado palms, *B. paraguayensis* and *S. petraea*, are visited by insects which are non-pollinators or only occasional pollinators, besides others which are regular and effective pollinators and at the same time parasites. Several of these parasites are effective pollinators. Also these two palms breed several of its pollinating beetle species. Our data confirmed that the parasitic beetles of *S. petraea* found in Botucatu and Indianópolis, two sites about 400 km distant from each other, are more constant visitors than the non-parasitic ones.

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