Floral Biology and Insect Visitors of the Understory Palm *Synechanthus warscewiczianus* at the Pacific Coast of Colombia

ROBERT SIEFKE
University of Applied Sciences Eberswalde
Alfred-Moeller-Str. 1
16225 Eberswalde, Germany
herrlich2@web.de
AND
RODRIGO BERNAL
Instituto de Ciencias Naturales
Universidad Nacional de Colombia
Apartado 7495, Bogotá, Colombia
rbernalg@unal.edu.co

***Synechanthus warscewiczianus*, an understory palm growing near Tumaco, on the Pacific coast of Colombia, is shown to be pollinated principally by flies.**

Synechanthus is a genus of small understory palms of the wet forests of Central America and the northwest of South America. It belongs to the tribe Hyophorbeae in the subfamily Ceroxyloideae (Uhl & Dransfield 1987), and consists of two species (Moore 1971) – *S. fibrosus* and *S. warscewiczianus*. The latter is distributed at elevations below 1400 m, from the Atlantic coast of Nicaragua to the Pacific coast of Ecuador. It has no known commercial use and is only locally used by some indigenous people who are reported to eat the cooked fruits and use the leaves to dye textile black. It is apparently not as common in cultivation as its relative *S. fibrosus*. So far no detailed study of the pollination of this genus has been published. This paper provides data on the reproductive biology and insect visitors of *Synechanthus warscewiczianus* (Fig. 1) in Colombia.

Study Site

This study was carried out during July and August 1999 in a slightly disturbed primary wet forest (bosque húmedo tropical in Holdridge's [1982] system) at 50 m elevation in Finca Guacaray near Tumaco in the Department of Nariño, at the Pacific coast of south-western Colombia (1º26' N, 78º36' W) (Fig. 2). The finca comprises an area of 236 ha, out of which about 100 ha are wet forests. Annual rainfall in this area is 3279 mm (average for 1995–1997, measured at the finca) and temperature ranges between 22ºC and 32ºC, with an average of 27ºC.

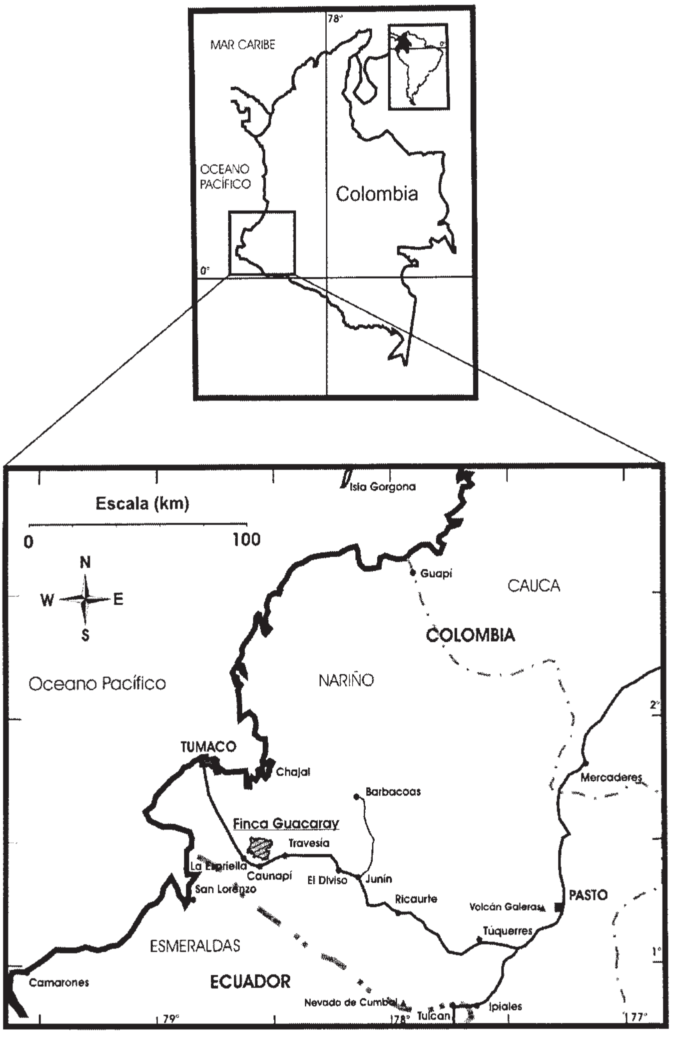
Methods

We numbered all 30 individuals of *S. warscewiczianus* found in the finca and marked them with red flagging tape. Every inflorescence,

1. Recently opened inflorescence of *Synechanthus warscewiczianus*, as well as an infructescence with ripe fruits and one with immature fruits.

either open or in bud, received a number according to the individual and the stem it belonged to. We marked individual staminate and pistillate flowers with a water-based felt-tip pen in order to study their development, and we placed a white cloth under some inflorescences at staminate anthesis to determine the time of abscission of staminate flowers. The highest inflorescences (ca. 4.5 m above ground) were reached by means of small wooden scaffolds. For each individual, the following measurements were taken, when possible: height, diameter (dbh, only for stems over 1m), number of green leaves, number of ramets and number of their leaves, presence of a root cone, length of peduncle, length of rachis, number of rachillae, length of rachillae (average of 15 rachillae per inflorescence), number of staminate flowers per acervulus (average of 15 counts per inflorescence), number of pistillate flowers per rachilla (average of 15 counts per inflorescence), number of developed fruits per rachilla (average of 15 counts per inflorescence).

These figures were used to estimate the total number of staminate and pistillate flowers per inflorescence, and to calculate fruit-set. We tested the presence of nectar using glucose testing paper (Gluco-cinta™, Eli Lilly and Company, Indianapolis, USA). For 18 inflorescences at pistillate anthesis we measured the distance to the nearest palm at staminate anthesis. We observed inflorescences at anthesis at least once per day throughout the day and sometimes at night, at intervals of 0.5–6 hours, depending on their state of development. We observed insect visitors for longer periods of time during all phases of anthesis, and collected in alcohol individuals of every visiting species for further identification.



2. Location of the study site

Some species received generic or species numbers that reflect the respective specialist's own numbering sequence (see Acknowledgments) or that we used for unidentified taxa. We captured separately 13 of the most frequent visitors in order to study their pollen loads. In order to evaluate the occurrence of wind pollination we placed three Vaseline-covered slides on the rachillae of four inflorescences at pistillate anthesis, belonging to four different individuals. We placed six of these slides radially at distances of 0.5 m and 1 m near two inflorescences at staminate anthesis. They were exposed for at least 5 hours without rain. These slides were observed afterwards under a microscope in order to identify and count any pollen grains transported by the wind. Reference pollen was collected from anthers and whole staminate flowers. Morphometric characteristics of this pollen were analyzed. Vouchers of the palm were deposited at COL and PSO.

Results

Morphology. *Synechanthus warscewiczianus* is a small-sized, monoecious undergrowth palm with stems up to 6 m in height (x = 3.8; 1.3 SD; n = 45) and 3.5 cm in diameter (x = 2.8; 0.3 SD; n = 38). Studied palms had 4–11 living leaves per stem (x = 8.1; 1.8 SD; n = 45). Most individuals at the finca (80 %) were cespitose (many, however, with only a few basal shoots), and the majority (83 %), either solitary or cespitose, had a small root cone not exceeding 40 cm in height and 30 cm in diameter. Inflorescences are infrafoliar and they are enclosed in bud by 5–6 peduncular bracts, which dry and become fibrous upon the opening of the inflorescence. The upper part of the stem bears inflorescences and buds at every node, in successive stages of development. The inflorescences measure up to 73 cm (x = 58 cm; n = 21), and they are borne on a long peduncle (x = 41 cm; 7.0 SD; n = 23). The rachis is 9–23 cm long (x = 16.8; 4.2 SD; n = 21) and bears 19–98 unbranched rachillae (x = 70; 22.3 SD; n = 21), each 17–36 cm long (x = 28.5; 5.7 SD; n = 285), and about 2 mm thick. Basal rachillae are the longest. The flowers are arranged in alternating rows (acervuli) on opposite sides of the rachilla, and each rachilla has about 60 acervuli, each with 0–2 pistillate flower proximally and 6–10 (x = 7.8; 1.1 SD; n = 240) staminate flowers distally. Flowers of both sexes are yellowish at anthesis and produce small amounts of nectar but have no perceptible scent. Pistillate flowers are often lacking from the distal acervuli of each rachilla, resulting in about 10 % of exclusively staminate acervuli. In contrast, some of the basal acervuli sometimes have two pistillate flowers, but only one of these develops into fruit. Each rachilla bears 15–101 pistillate flowers (x = 55; 24 SD; n = 255), and 95–1140 (x = 430) staminate flowers. Thus, the number of flowers per inflorescence is very variable – 1264–74,094 staminate flowers (x = 41,491; 22907 SD; n = 16) and 160–8400 pistillate flowers (x = 4420; 2559 SD; n = 17). The staminate/pistillate sex ratio is 14.8/1 (SD 14.8; n = 16).

The results of a Pearsons product-moment T-test reveal an important component of plant height and a less important component of stem diameter as determinants of the morphologic characteristics of the inflorescences – number of pistillate and staminate flowers per inflorescence, number of rachillae and length of rachis and rachillae (Table 1). This means that taller (and therefore older) palms and those with thicker stems produce bigger inflorescences with more flowers of both sexes. A similar situation has been found to occur in different species of palms (Listabarth 2001). Correlations between rachilla length and plant height and stem diameter are the strongest, with values of 0.555 and 0.608 respectively. In this population we did not find a significant correlation between stem diameter and staminate flowers per acervulus. Correlations between plant height and number of rachillae and length of rachis respectively are high and positive (Table 1). Finally, we found a highly significant correlation between stem diameter and plant height, suggesting sustained primary growth.

In nine infructescences 0–40 fruits developed per rachilla (x = 5.2; 3.3 SD). Thus, fruit-set was 9.4 %. The pollen grains of *S. warscewiczianus* are elliptic and monosulcate (with a longitudinal germinal slit, called sulcus). This sulcus is well defined, nearly as long as the grain itself. The exine is tectate and more or less even, without

Table 1. Comparison of coefficients of correlation (Pearson) between plant height, stem diameter and morphologic measurements for a population of *Synechanthus warscewiczianus* at the Pacific coast of Colombia (only p < 0.05 are shown).

	Length of rachillae	Length of peduncle	Number of rachillae	Length of rachis
Plant Height	0.555		0.533	0.541
DBH	0.608	0.252	0.534	0.425

spines. The grains are 16–27 µm long (x = 23.1; 1.6 SD; n = 100) and 11-20 µm (x = 15.7; 1.7 SD; n = 100) wide (measured in plain view). The length-width ratio is 1.5 (0.2 SD; n = 100).

*Phenology***.** Early development of the inflorescence buds started among the leaves, but the lowest leaf fell off when the enclosed bud did not exceed 3.5 cm. Further growth was slow – during the 30 days of this study the upper buds did not grow at all, whereas the lower, largest buds grew 6–15 cm (x = 10.2 cm; 3.2 SD; n = 24). Upon attaining a length of 46–73 cm, the peduncular bracts started to split longitudinally at the distal end, and the inflorescence opened completely within the next three weeks. At the time of opening all flowers were closed and the rachillae were bright yellow (Fig. 1). They turned green after exposure and then became yellowish again during anthesis. The inflorescence buds were held upright and they leaned gradually to the ground during flower and fruit development.

Synechanthus warscewiczianus is protandrous, and anthesis proceeds basipetally. On the first day of anthesis, only 1–12 (–20) staminate flowers opened at the distal end of those acervuli located at the distal end of the rachillae. In the next few days more and more flowers opened in daily pulses, until all the distal flowers of all acervuli had opened. At the maximum pulse about 8000 staminate flowers opened in one day. The staminate phase lasted 18–25 days (x = 21.2 days; 2.3 SD; n = 12). The last flowers to open were those of the basal acervuli and basal rachillae. This was followed by a pause of 3–5 days (x = 4.2; 0.7 SD; n = 13) during which there were no flowers open. The pistillate phase of the inflorescence lasted 5–9 days (x = 6.6 days; 1.6 SD; n = 8), with the maximum pulse after 2–3 days. The pattern of opening was the same as in the staminate phase.

The staminate flowers opened in the morning between 6.00 and 13.00 hours, with a peak from 10.00 to 11.00 hours. They were at anthesis only for a few hours and abscised in the afternoon of the same day. Individual flowers opened in 10–15 minutes, the anthers flexing back like a steel spring. The pistillate flowers opened during the whole day, from 6.00 to 18.00 hours with a maximum before 9.00 hours. The individual pistillate flowers took much longer than the staminate ones to open completely. During the pause phase of the inflorescence, pistillate buds increased in size and developed their final color. The stigmas remained whitish-yellow and moist for about 2–3 days and were probably receptive that long. Thereafter, they turned brownish and dry, but did not fall off. A few days later it was already possible to distinguish between fertilized and unfertilized flowers, as the former started to develop into fruits.

Out of all 30 individuals found in the finca, 60% flowered and 53% bore developing fruits. The presence of inflorescence buds and infructescences in all stages of development suggests that flowering in this species takes place throughout the year. The distance from an inflorescence at pistillate anthesis to one at staminate anthesis was never shorter than 13 m (x = 21.7; 7.5 SD m; n = 15). In the finca we found three subpopulations of *S. warscewiczianus*. They consisted of 15, 12 and 3 individuals, respectively, and were separated from each other by a distance of at least 1200 m. We found no individuals of this species in the forest between the three patches. In the smallest subpopulation, only one inflorescence came into anthesis during the study period, and did not develop any fruit.

*Pollination***.** The Vaseline-covered slides placed near the inflorescences at anthesis did not receive any pollen grain of *S. warscewiczianus* and received very little pollen of other plants. At least 76 species of insects and other arthropods, belonging to seven orders (Table 2), visited the flowers at anthesis, but only 48 species visited flowers of both sexes. The vast majority of visitors (71) came to the staminate flowers. During the opening of the bracts there were no visitors other than the omnipresent ants and some spiders. In the first days of anthesis, visitors were sporadic. Even at full anthesis there were days without any visitor, especially during rainy days. At night we did not observe any visitors, except for some mosquitoes resting and flying around the rachillae, probably attracted by the flashlight.

The first visitors to arrive at staminate flowers at anthesis were bees (Apidae), which came in small numbers (up to 10 at a time) and busily collected pollen and nectar. They flew spirally around the inflorescence and inspected the rachillae for about 15 seconds each, depending on the amount of pollen available. The activity of the bees was highest in the mornings and decreased as time passed by. Another important visitor group were beetles. They were represented by seven families, out of which Curculionidae and Chrysomelidae were the most diverse. The most conspicuous beetles were the black and yellow *Pyrophorus* sp. 1 (Elateridae), about 3 cm long, and *Cholus* sp. 1 (Curculionidae). The beetles sucked nectar or fed on floral tissue, and some of them were observed only once and in small numbers. The most frequent species were the Alticinae sp. 1 (Chrysomelidae) and Galerucinae sp. 1

Table 2. Insect visitors to staminate and pistillate flowers of *Synechanthus warscewiczianus* at the Pacific coast of Colombia

	Staminate inflorescence	Pistillate inflorescence
Hymenoptera		
Apidae		
Trigona branneri	O	
Trigona tetragona dorsalis	XX	O
Trigona sp. nov.	O	O
Partamona aequitoriana	XX	O
Noguerapis mirandula	O	
Ptilotrigona lurida mocsarya	O	O
Trigonisca sp. 1	O	
Trigonisca sp. nov.	O	O
Formicidae		
Camponotus sp. 1	O	O
Ectatoma sp. 1	O	O
Ectatoma sp. 2	XX	O
Gnamptogenys sp. 1	O	O
Hypoponera sp. 1	XX	XX
Pseudomyrmex sp. 1	XX	XX
Atta cephalotes		O
Paraponera sp. 1	O	O
Paraponera sp. 2	O	
Vespidae		
sp. 1	O	O
sp. 2	O	
Coleoptera		
Chrysomelidae		
Alticinae sp. 1	XX	O
Alticinae sp. 2	O	
Galerucinae sp. 1	O	O
sp. 1	O	
sp. 2	O	
Curculionidae		
Terires sp. 1		O
Phyllotrox sp. 1		O
Cholus sp. 1	O	
Elateridae *Pyrophorus* sp. 1	O	
Cerambicidae sp. 1	O	
Carabidae sp. 1		O
Meloidae sp. 1		O
Lampyridae *Cratomorphus* sp. 1	O	
larva sp. 1	O	O
larva sp. 2	O	O
Diptera		
Conopidae sp. 1	O	
Muscidae		
sp. 1	XX	O
sp. 2	XXX	XXX
Syrphidae		
Metasyrphus sp. 1	O	
Ocyptamus sp. 1	O	
Copestylum sp. 1	XX	XX
sp. 1	O	O
sp. 2	O	O
sp. 3	O	
sp. 4	O	O
sp. 5	O	

Table 2. Continued

Leptogastridae		
Leptogaster sp. 1	O	O
sp. 2	O	O
Platystomatidae sp. 1	O	O
Empididae		
sp. 1	XXX	XXX
sp. 2	O	O
Drosophylidae		
sp. 1	XXX	XX
Drosophila	XXX	XXX
Syringogastridae *Syringogaster* sp. 1	O	
Otitidae sp. 1	O	O
Mycetophilidae sp. 1	XX	O
Sciaridae sp. 1	XXX	XX
Phoridae sp. 1	O	
Simulidae sp. 1	XX	XX
Diptera sp. 1	O	O
Orthoptera		
Tettigoniidae sp.1	O	O
Gryllidae sp. 1	O	O
Dictyoptera		
Anthocoridae sp. 1	O	O
Arachnida		
unidentified spiders (12 sp.)	O	O
Homoptera sp. 1	O	O
Hemiptera		
Miridae	O	
Pseudoscorpionidae	O	

O = < 5 individuals/inflorescence (simultaneously)

XX = 5–25 individuals/inflorescence

XXX = >25 individuals/inflorescence

(Chrysomelidae), which used the inflorescences as a place to copulate and feed on rachis and floral tissue, but did not move much. There were never more than ten of them, and they were the only species which sometimes remained overnight on the inflorescences.

The most frequent visitors to flowers of both sexes were flies, represented by 25 species in 13 families. Of these, the Syrphidae were the most diverse, with eight species. Muscidae, Drosophilidae, Empididae, and Leptogastridae had two species each. The Drosophilidae sometimes arrived in hundreds to suck nectar and apparently to eat pollen and they used the site to copulate and seemingly to oviposite, although we never observed any Diptera eggs or larvae. The Muscidae sp. 1, Leptogastridae sp. 2, Syrphidae sp. 2, and Syrphidae sp. 3, all of them fat and sometimes metallic-colored flies, came by the dozens, but frequently they were sedentary and with little interest in the flowers. At staminate and pistillate anthesis, it was often possible to find about ten Simulidae sp. 1 and *Copestylum* sp. 1 (Syrphidae) moving rapidly among the flowers and the rachillae, and flying around the inflorescences. They licked nectar and repeatedly touched the anthers and the stigmas. The Muscidae sp. 2, the only species of Sciaridae, and Empididae sp. 1 came frequently in dozens to both sexes to suck nectar and eat pollen, moving from flower to flower. All other species of Diptera came infrequently, in small numbers and did not show much interest in the flowers themselves. Most other visitors were occasional.

Discussion

Due to the absence of pollen grains of *S. warscewiczianus* on the 24 Vaseline-covered slides placed near inflorescences at anthesis, we conclude that wind pollination of this species, if any, is probably insignificant. As a matter of fact, wind in the habitat of the palm is rarely of any significant strength. The production of nectar and the appearance of the inflorescences also indicate entomophily, as do the numerous insect visitors.

Out of the 48 species of insects and other arthropods that visited flowers of both sexes, only beetles, bees and flies deserve any discussion as potential pollinators. All other visitors were occasional or did not move frequently among the flowers. The two chrysomelid beetles (Alticinae sp. 1 and Galerucinae sp. 1) can be ruled out as efficient pollinators, because they came only in small numbers and rarely moved between inflorescences – they remained inactive for hours on the rachis, and only rarely visited the flowers. Their role as pollinators, if any, is probably occasional.

Bees were frequent and collected pollen on the staminate flowers but rarely visited pistillate flowers, where they just licked some nectar and went off. Sometimes they only circled the inflorescence without landing on it.

The most common visitors in both staminate and pistillate phases were the flies. The Muscidae sp. 1 and the Mycetophilidae sp. 1 visited flowers of both sexes but their role as pollinators, if any, is probably minor, as they mostly rested among the rachillae. Although the Mycetophilidae are known to carry out pollination in different plant species (Vogel 1978), they have only recently been recorded on palm flowers (Borchsenius 1993).

Drosophilid flies came in hundreds, moved frequently among flowers and rachillae, licked nectar from the flowers, which they frequently touched with their bodies, and used the rachillae as a place to copulate. They have the ability to fly long distances (Bernal & Ervik 1996), but those captured at pistillate flowers did not carry any pollen grains of *S. warscewiczianus*. In other studies, drosophilids have also been found to carry no pollen or only small amounts, when visiting pistillate flowers of the palms *Aiphanes erinacea* (Borchsenius 1993), *Aphandra natalia* (Ervik 1993) and *Phytelephas seemannii* (Bernal & Ervik 1996). Although in some cases they do effect pollination, for example in *Nypa fruticans* (Essig 1973) or *Geonoma macrostachys* (Olesen & Balslev 1990), Schmid (1970) and Borchsenius (1993) ruled them out as pollinators of *Asterogyne martiana* and *Aiphanes erinacea*, respectively. We follow their considerations, but include the drosophilids as potential secondary pollen vectors.

The remaining flies appear to have a more relevant role, and they deserve a more detailed discussion. At both phases of anthesis there were always about ten individuals of Simulidae sp. 1 and *Copestylum* sp. 1 (Syrphidae) running and flying actively among the flowers. They came to lick nectar and maybe to eat pollen. The other syrphids were uncommon and sedentary when visiting the flowers. Syrphid flies and especially the most common *Copestylum* are well known as efficient pollinators of many plant species (Schmid 1970, Borchsenius 1993, Zona 1987). Although Simulidae are not often observed as visitors to palm flowers, they were the only species that carried pollen of *S. warscewiczianus* on their bodies, although in small amounts. The Sciaridae sp. 1, Empididae sp. 1 and Muscidae sp. 2 were common at both phases too, with 25–100 individuals at a time and were highly active around the flowers, eating nectar and pollen, and copulating. They often touched anthers and stigmas with different parts of their bodies. The Sciaridae have been recorded as pollinators in some plants (Vogel 1978) and contribute to it in *Aiphanes erinacea* (Borchsenius 1993). The Empididae have been reported as palm flower visitors in *Asterogyne martiana* (Schmid 1970) and *A. erinacea* (Borchsenius 1993). We therefore suggest that *Copestylum* sp. 1 (Syrphidae), Simulidae sp. 1, Sciaridae sp. 1, Empididae sp. 1 and Muscidae sp. 2 could be the principal pollinators of *S. warscewiczianus* at the study site, because of their high numbers and their activity around the flowers of both sexes.

Fly pollination in *S. warscewiczianus* is not surprising, as this palm exhibits many traits of the myophilous pollination syndrome described by Faegri & Van der Pijl (1979), Henderson (1986) and Borchsenius (1991) – the simple, open form of the small flowers with no depth effect, the easily accessible anthers and stigmas, the yellowish color of the flowers and the rachillae, which is preferred by some flies, the absence of any scent, the diurnal anthesis with relatively long individual phases and the small number of flowers open at a time. Henderson (1986) suggested that fly pollination is frequent in small undergrowth palms. Although the predictive value of pollination syndromes has been challenged (e.g., Consiglio & Bourne 2001, Listabarth 2001) and it is deemed wise to apply them with caution unless complemented with empirical studies and data (Johnson & Steiner 2000), in the case of *S. warscewiczianus*, the pollination syndrome appears to be a good indicator of its pollination mechanism.

In *S. warscewiczianus* fruit set is very low (0.094), compared to the average fruit set of monoecious plants (0.58) (Sutherland 1986). In spite of its low fruit set, however, the average number of fruits per infructescence was high, and sexual reproduction appears to be predominant in this species. This is supported by the high viability of seeds (Bernal pers. obs.). The high proportion of cespitose individuals with only one flowering stem, combined with the temporal separation of staminate and pistillate phases in the inflorescence precludes geitonogamy and favors xenogamy.

Acknowledgments

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