

## *Selenicereus wittii* (Cactaceae): an epiphyte adapted to Amazonian Igapó inundation forests\*

WILHELM BARTHOLOTT, STEFAN POREMBSKI, MANFRED KLUGE, JÖRN HOPKE, and  
LOKI SCHMIDT

Received August 7, 1996; in revised version September 23, 1996

**Key words:** *Cactaceae*, *Selenicereus wittii*. – Igapó, Amazonia, epiphytes, dispersal, pollination, anatomy, ecophysiology, crassulacean acid metabolism (CAM), fragrance.

**Abstract:** The biology, ecology, and distribution of *Selenicereus* (*Strophocactus*) *wittii*, one of the least known taxa of *Cactaceae*, are described. This epiphyte climbs appressed to tree trunks with leaf-like, flattened stems and is found exclusively along the high waterline of black water rivers (Rio Negro, Vaupés, Apaporis) in the Igapó inundation forests of Amazonia. Ecophysiologicaly, *S. wittii* is a crassulacean acid metabolism (CAM) plant. It bears white, nocturnal flowers 25 cm in length which emit a fragrance consisting mainly of benzylalcohol, benzyl benzoate, and benzyl salicylate. They exhibit an extreme sphingophilous syndrome as an adaptation to pollination by probably only two species of hawk-moth from the genera *Amphimoena* and *Cocytius*. The seeds, aberrant for the family, contain air-filled chambers and are water-dispersed. Thus, *S. wittii* represents the paradoxical life form of an hydrochorous epiphytic cactus which withstands periodical inundation.

*Selenicereus wittii* (SCHUMANN) G. ROWLEY is, together with *Epiphyllum phyllanthus* (L.) HAW. and *Rhipsalis baccifera* (J. F. MILL.) W. T. STEARN, one of only three species of *Cactaceae* occurring in Central Amazonia. It is one of the most enigmatic members of the family. It is rare even in larger herbaria, which house, if at all, only fragments of sterile material.

The species was discovered in the Igapó-forests of the Rio Negro close to Manaus (Brazil) in 1899 at the time of the “rubber boom” by N.H. WITT, a German businessman and amateur collector. Subsequently, specimens were sent to K. SCHUMANN in Berlin-Dahlem, the monographer of the family, who described it as *Cereus wittii* (SCHUMANN 1900). SCHUMANN was already aware of its questionable systematic position within *Cereus*. Consequently, BRITTON & ROSE (1913), when splitting most of the large artificial genera into smaller taxa, established a

---

\* Dedicated to emer. Univ.-Prof. Dr FRIEDRICH EHRENDORFER on the occasion of his 70th birthday

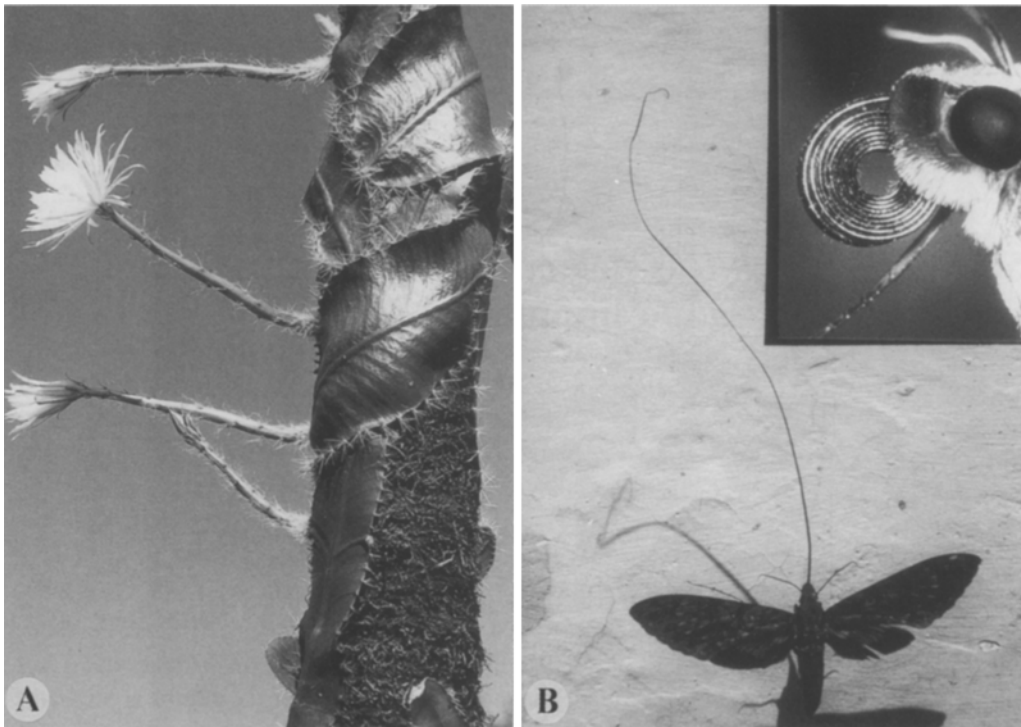


Fig. 1. *A* *Selenicereus wittii*, salverform, flowers 25 cm in length; *B* *Cocytius cruentus* (*Sphingidae*), one of two possible pollinators, with a proboscis length of 25 cm

monotypic genus, *Strophocactus*, and placed it within the *Hylocereeae* (BRITTON & ROSE 1920) – a systematic position unchallenged until the present (BARTHOLOTT & HUNT 1993). The floral structure of *Strophocactus wittii* (SCHUMANN) BRITTON & ROSE suggests a close affinity to the hylocereoid genus *Selenicereus*, which comprises some 20 climbing species with large nocturnal flowers, found in the Caribbean and tropical America. In general, the species is, therefore, currently treated as *Selenicereus wittii* (SCHUMANN) G. ROWLEY.

Until now, published information on the biology, ecology, and vegetative and reproductive structures of this remarkable plant is practically non-existent. Colour illustrations and observations were published by the late MARGARET MEE in the description “Moonflower” in her “Flowers of the Amazon Forests” (MEE 1988).

The authors had the opportunity to study *Selenicereus wittii* not only in its natural habitat near Manaus (L. S.), but also over many years in cultivation (W. B., S. P., L. S.). The morphology, anatomy, and in particular the seed and pollen ultrastructures (W. B., S. P.) were examined, as was the ecophysiology (M. K.) and the chemical analysis of its fragrance (J. H.).

#### Material and methods

**Living material.** The study encompassed three clones cultivated in the Botanical Gardens of Bonn, Darmstadt, and Heidelberg (FRG): (1) a collection from the type locality near

Manaus was received from BEATRIX ORSSICH (Teresopolis, BRA) in 1986, (2) an undocumented clone from the Botanical Garden of Munich in 1974, and (3) a third plant of undocumented origin studied at the Botanical Garden in Berlin-Dahlem in 1984. The plants grew well under hothouse conditions (30 °C day/25 °C night, RH 80%) and usually flowered in winter (November-February). The plant did not survive for a longer period under succulent-house conditions, which may be the reason for its rarity in cactus collections. A fresh ripe fruit collected along the Rio Negro was sent to us by M. MEE. Voucher specimens of the material received from B. ORSSICH conserved in spirit are deposited in Bonn (BONN).

**Herbarium material.** An annotated list of 21 collections of *S. wittii* in American herbaria was provided by MYRON KIMNACH (Huntington Botanical Gardens, CA) and analysed for the distribution pattern of the species.

Brazil: ALENCAR, L. 276 (NY); COOPER 44 (US); MADISON, KENNEDY, MONTEIRO & BRAGA 6046 (F); POOLE, J. M. 1824 (HNT); WITT, N. H. s.n. (US, lectotype).

Colombia: LIESNER, R. & CLARK, K. 9030 (MO); LUETZELBURG 22272 (M); SCHULTES, R. E. & CABRERA, I. 13750 (US).

Peru: CROAT, T. B. 20404 (MO, US); DAVIDSON, C. 9494 (HNT); DAVIDSON, C. 9532 (HNT); HONES, J. 9494 (MO); KILLIP & SMITH 27885 (NY); KILLIP & SMITH 29394 (NY); SOLOMON, J. 3524 (MO); ZARUCCHI 1616 (US).

Ex horto: UCBG 51.950-1 (US).

**Microscopy.** For light microscopy, living material was fixed in FAA, dehydrated by standard methods, and embedded in Paraplast for serial sections with a rotating microtome. Staining was implemented with safranin and astra blue. For scanning electron microscope (SEM) studies, fresh material was fixed in 2% glutaraldehyde in phosphate buffer (pH 7.0). Ethanol was used for dehydration. Subsequent drying was done using the critical point method. The material was coated with gold (Balzer SCD 040 sputter) and observed in a SEM (Cambridge Stereoscan 200).

**Ecophysiology.** For gas exchange measurements, the middle part of a stem was enclosed in situ in a fully climatized plexiglass chamber of an open compact system (Walz; Effeltrich; Germany) as described by GRAMS & al. 1996. The conditions inside the cuvette were maintained at exactly those in the greenhouse, to which the plant parts remaining outside the cuvette were exposed. Net CO<sub>2</sub> exchange ( $J_{CO_2}$ ) and transpiration ( $J_{H_2O}$ ), together with photosynthetic photon flux density (PPFD), air humidity, and leaf and air temperature were recorded continuously. From these data, the leaf/air water vapour pressure difference (dN) and the conductance for water vapour ( $G_{H_2O}$ ) were calculated according to FARQUHAR & SHARKEY (1982) and LÜTTGE & al. (1986).

Stable carbon isotope composition ( $\delta^{13}C$ -values) was determined by mass spectrometry after combustion of approximately 10 mg dried plant material to CO<sub>2</sub> using standard conditions (ZIEGLER & al. 1976). The results are expressed as a deviation from the standard (PDB). The sample under analysis was derived from a plant cultivated in the greenhouse.

**Fragrance analysis.** The collection of volatiles was performed by means of an open-loop-stripping technique: a flow of air containing the flower volatiles was passed through a charcoal trap (1.5 mg, CLSA-Filter, Winterthur, Switzerland). The air stream was generated by a miniature circulation pump (Fürgut in Aitrach, FRG) which was connected in line with the charcoal trap (enclosed in stainless steel holder) as previously described for a closed system (KAISER 1991, DONATH & BOLAND 1995). The air was primed in close vicinity to the opening of the blossom and the stream of air first passed the charcoal trap before entering the pump.

The collection was maintained for 24 hours using two different traps during the night (7 p.m.–7 a.m.) and day (7 a.m.–7 p.m.). The volatiles were eluted from the charcoal traps

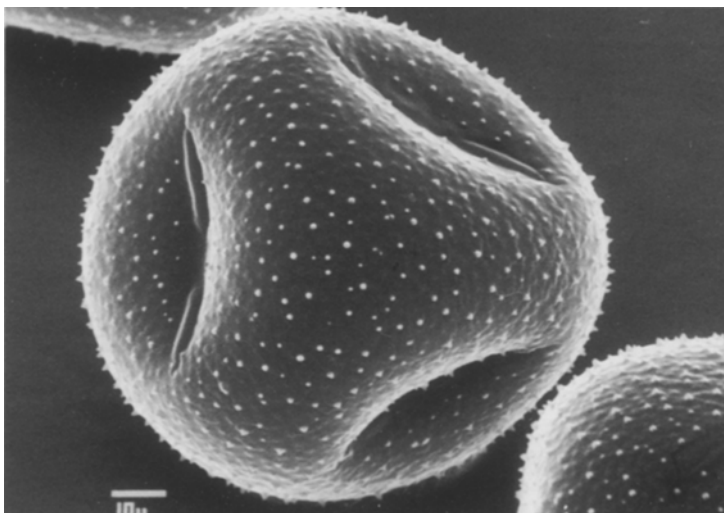


Fig. 2. Pollen of *Selenicereus wittii*, diameter 105  $\mu\text{m}$

by  $\text{CH}_2\text{Cl}_2$  (2' 15  $\mu\text{l}$ ) and analysed immediately by GC/MS (MD 800, FISONS). Compounds were separated on a fused silica column (SE 30, 15 m' 0.32 mm) under temperature programmed conditions from 50 °C (for 2 min) at 10 °C  $\times$  min<sup>-1</sup> to 200 °C, then at 30 °C  $\times$  min<sup>-1</sup> to 280 °C (for 3 min). Carrier gas: He; interface temperature: 280 °C; source temperature: 250 °C; scan range: 35–350 Da; ionisation mode: EI, 70 eV.

## Results and discussion

**Vegetative adaptations Morphology.** *Selenicereus wittii* is an epiphyte with flattened stems (Fig. 1 A) which twine and climb by aerial roots on the side, appressed to tree trunks. The roots are inserted along the mid-nerve and lateral nerves entering the areoles. The plant stems exposed to direct sunlight usually are a dull red as a result of intense betalain pigmentation. They are flat as a leaf, 6–14 cm wide, up to 60 cm long, and only 2–4 mm thick. The areoles are small, set at close intervals only 5–8 mm apart along the entire margin of the joints, and they bear up to 20 short, whitish spines.

**Anatomy.** The overall leaf-like appearance of the stem is reinforced by its anatomy. The phyllocladodia show leaf-like dorsiventral organisation, differentiated into an underside (appressed to the tree) and an upper side (exposed to sunlight). The upper side is characterized by a thick (4  $\mu\text{m}$ ) cuticle and a thick (50  $\mu\text{m}$ ) layer of dark-green hypodermal cells with numerous chloroplasts.

On the underside, the cuticle is thinner (2  $\mu\text{m}$ ) and the cells of the hypodermal layer (30  $\mu\text{m}$  in thickness) contain only very few chloroplasts. Starch is located mainly in the central and lower portion of the section. Mucilage cells are frequent and calcium oxalate idioblasts are scattered throughout. The parallelocytic stomata are not sunken, but in contrast to normal leaves, the number of stomata on the upper- and undersides is identical: about 12 stomata/ $\text{mm}^2$ . This number is extremely low (in *Cactaceae* usually 15–70 stomata/ $\text{mm}^2$ , GIBSON & NOBEL 1986),

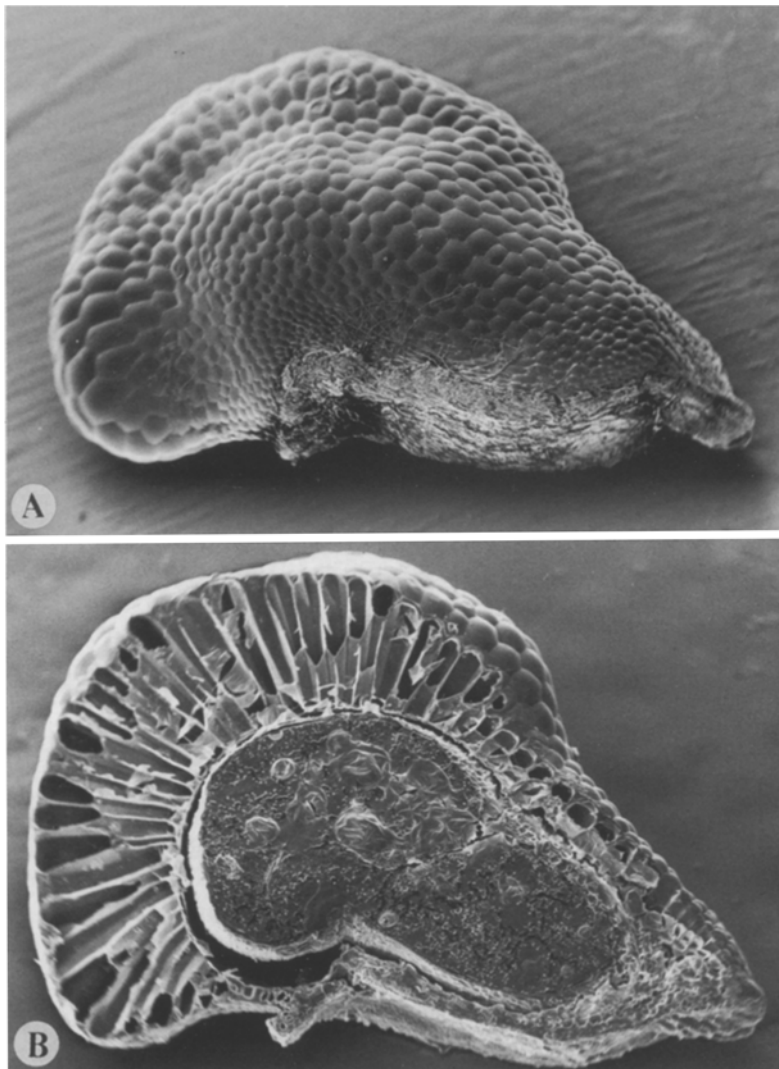


Fig. 3. *Selenicereus wittii*. A Intact seed; B longitudinal section showing the rather small embryo in contrast to the air-filled chambers formed by the apical testa cells. Length of seed 4.1 mm

and seems to be characteristic of flattened, leaf-like epiphytes. For instance, an identical number has been found in *Epiphyllum chrysocardium* ALEXANDER (PEUKERT 1980); only *Blossfeldia liliputana* WERDERM. seems to have a smaller number of stomata (BARTHLOTT & POREMSKI 1996).

**Ecophysiology.** The samples of *S. wittii* obtained from a greenhouse cultivar showed a  $\delta^{13}\text{C}$  value of  $-14,35\text{‰}$ , suggesting that the plant displayed crassulacean acid metabolism (CAM), with fixation of external  $\text{CO}_2$  taking place exclusively during the night (for review on CAM cf., e.g., KLUGE & TING 1978, WINTER & SMITH 1996; for a review on the application of stable carbon isotope analysis in plant ecophysiology RUNDEL & al. 1989). This prediction was fully

supported by the gas exchange patterns displayed by the plant. As Fig. 4 shows, only during the night period of the diel cycle was there net CO<sub>2</sub> uptake, whereas during the day, massive net CO<sub>2</sub> output occurred. This is a typical reaction by CAM plants when exposed to a combination of relatively low light intensity together with high temperature (see the quoted reviews). As expected for a CAM plant, *S. wittii* showed nocturnal opening of the stomata and closure during the day. This is indicated by the values of leaf conductance for water vapour ( $G_{H_2O}$ ), which was high during the night and near zero during the day.

It is generally accepted that CAM represents an ecophysiological relevant modification of the photosynthetic carbon assimilation pathway. This allows the plants in question to harvest external carbon at low cost of water loss by transpiration (see quoted reviews). Thus, the plants gain the greatest advantage from CAM when photosynthesis takes place while water is in short supply. Presumably this applies also to *S. wittii*. Because of its epiphytic habitat, the cactus grows with virtually no water-storing substrate around the roots. Thus, even short intervals between rains push the plant into water deficiency stress. From an ecophysiological standpoint, CAM represents the most advantageous option of photosynthesis under these conditions.

A further advantage of CAM for *S. wittii* is conceivably the protection against photoinhibition. This can take place if the photosynthetic apparatus is highly energetised while the stomata are closed, since dissipation of excitation energy from the photosystems through the reduction of external CO<sub>2</sub> is not possible. Photographs of *S. wittii* taken in the natural habitat show reddish colouration of the phyllocladodes, presumably due to enhanced synthesis and the accumulation of betalain. This colour change seems to be due to excessive light. The same phenomenon was observed in our greenhouse cultivars when the light intensities accidentally became excessive. With respect to the cactus growing in situ, it is conceivable that it receives, at least temporarily, very high light intensities while the stomata are closed. Thus, external CO<sub>2</sub> is not available to the photosynthetic apparatus. Without protective mechanisms, such a constellation should lead to photoinhibition. OSMOND (1982) proposed that CAM is such a mechanism, because in the light, internal CO<sub>2</sub> is produced by the CAM inside the photosynthesizing cells. This CO<sub>2</sub> is reduced at the expense of assimilatory power derived from the photosynthetic light reaction, thus allowing dissipation of excessive, otherwise destructive excitation energy from the photosystems by chemical action.

In summary, our results clearly indicate that *S. wittii* is a CAM plant. It is reasonable to propose that in situ, CAM offers the cactus twofold protection: (1) against excessive transpiratory water loss during the acquisition of external CO<sub>2</sub> and (2) against photoinhibition induced by high radiation when the stomata remain closed during the day.

**Reproductive adaptations.** Flower. In its natural habitat around Manaus, *S. wittii* flowers mainly in May, as observed by N. H. WITT (SCHUMANN 1902) and confirmed by M. MEE (1988); under European greenhouse conditions, flowering occurs in winter between November and February. Individual flowers open for only one night. Anthesis commences after sunset; flowers are fully expanded about two hours later and start to close again at sunrise. The slender, salverform flower (Fig. 1 A) is up to 27 cm long and 12.5 cm wide; the tepals are pure white and they

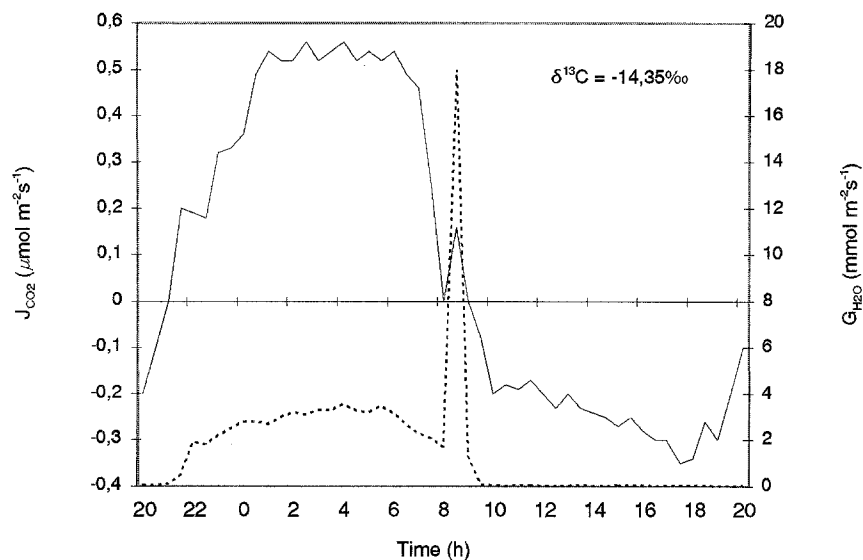


Fig. 4. Net CO<sub>2</sub> exchange ( $J_{CO_2}$ ; continuous line) and water vapour conductance of the epidermis ( $G_{H_2O}$ ; dotted line) in *Selenicereus wittii* held under the conditions outlined in Material and methods. The insert indicates the stable carbon isotope ratio measured in a plant held under similar conditions

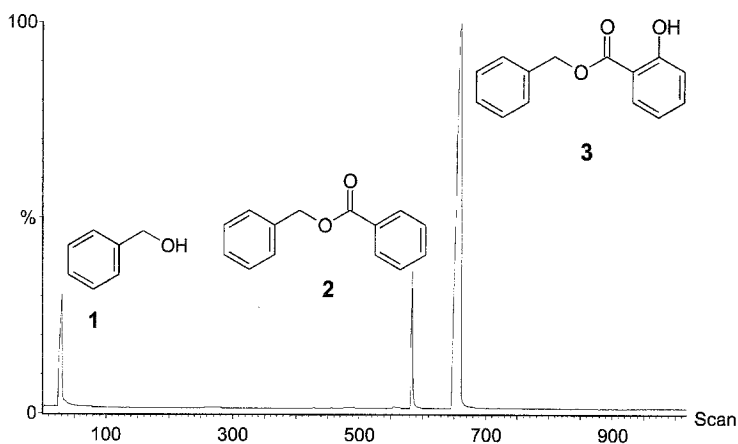


Fig. 5. Gaschromatogram of the volatiles emitted by the blossom of *Selenicereus wittii* during the 12 hour period from 7 p.m. to 7 a.m. (1 benzylalcohol, 2 benzyl benzoate, 3 benzyl salicylate)

strongly reflect ultraviolet light (BURR & BARTHLOTT 1993). The long tube is only 9 mm wide, the pericarp and tube are scaly with hairy spines. The receptacle contains a large amount of clear nectar in its basal part; the 10–14 stigma lobes are papillose as is the lower portion of the style. The numerous stamina produce hexacolpate pollen (Fig. 2) with copious pollenkitt, diameter 95–110  $\mu\text{m}$ ; the exine is tectate, spinulose (spinulae 1.5–2  $\mu\text{m}$ ), anulopunctate (perforations 0.3  $\mu\text{m}$ ). *Selenicereus wittii* differs by six colpae from the usually tricolpate species of the genus (cf. LEUENBERGER 1975); however, apart from the slender salverform shape, the flowers of *S. wittii* generally show all characteristics of *Selenicereus*.

**Flower fragrance.** Prior to full anthesis, the flowers emit a strong perfume which changes (cf. also MEE 1988) approximately two hours after full anthesis into an unpleasant odour. The compounds responsible for the odour were identified as benzylalcohol, benzyl benzoate, and benzyl salicylate (Fig. 5). The emission of these volatiles was more intense during the night, and free benzylalcohol was collected only during the dark period. The identified compounds are typical representatives of the so-called "white-floral-image" (KAISER 1993), which is often indicative of night-active pollinators such as moths.

**Fruit and seeds.** In its natural habitat, the fruit usually ripens within roughly one year (T. MORRISON, pers. comm.). It is a bristly, greenish, oblong berry, approx. 3.5 cm long, dehiscent by a simple longitudinal slit when mature, with numerous seeds embedded in a rather dry pulp.

The shiny black-brown seeds are mussel-shaped (Fig. 3A) and very large ( $4 \times 2$  mm). The hilum and the micropyle are fused into a single, non-sclerified complex. The almost smooth (only reduced cuticular folding patterns occur) testa cells possess the depressed cell-junctions ("interstices") characteristic of all *Hylocereeinae*. The seeds are unusually large for the family (BARTHOLOTT & VOIT 1979) and the longitudinal section (Fig. 3B) reveals an additional unique feature: the curved embryo is rather small and the main body of the seed is made up of a layer of extremely enlarged, dorsal testa cells which are dead and air-filled. When immersed in water the seeds float like cork.

**Pollination ecology.** Certain characteristics (pure white, extremely salverform, scented, nocturnal) of the flower indicate an exclusive pollination by hawkmoths. It thus resembles *Epiphyllum phyllanthus* L. (BARTHOLOTT & RAUH 1975–1976), the only convergent flower within the family. Pollination of *S. wittii* has never been observed in situ. However, because of the extreme length of the floral tube, only two neotropical sphingids come into question: *Cocytius cruentus* CRAMER (Fig. 2) and *Amphimoena walkeri* BOISDUVAL. Both reach a proboscis length of up to 25 cm according to SEITZ (1940) and occur within the natural range of *S. wittii* (D'ARBREIRA 1986). Thus, *Epiphyllum phyllanthus* and *Selenicereus wittii* form the neotropical counterparts of the famous Madagascan orchid *Angraecum sesquipedale* THOURS., whose pollination by the sphingid *Xanthopan morgani* (WALKER) subsp. *praedicta* was predicted by CHARLES DARWIN (1862) 41 years before its discovery (NILSSON & al. 1985). Traplining pollination by large hawkmoths (HABER & FRANKIE 1989) may be an essential prerequisite to maintaining the gene flow between the scattered populations of *S. wittii* along the Amazonian rivers.

**Dispersal, distribution and habitat.** All data from scientific literature, herbarium collections, and personal observation indicate that *S. wittii* is exclusively restricted to the periodically flooded (survey in KUBITZKI 1989) Igapó-forests along Amazonian black water rivers. Not a single specimen was collected along the white water inundated Varzea forests or in non-inundated terra firma forests. The distribution includes the rivers Rio Negro and Japura in Brazil extending into Colombia via the rivers Vaupés, Apaporis, and Caquetá, into Peru with several collections around Iquitos, and probably the southern portion of Amazonian Venezuela. Where *S. wittii* occurs, it is usually abundant and can be easily recognized from a distance by its dull reddish colour.



The peculiar seed structure, a floating device, indicates that *S. wittii* is dispersed by water. Thus, together with the orchid *Galeandra devoniana* SCHOMB in the Igapó of the Rio Negro (KUBITZKI & ZIBURSKI 1994), it represents the paradox of an hydrochorous epiphyte. This is strongly confirmed by its habitat within the Igapó: *Selenicereus wittii* grows exclusively on large tree trunks along the high waterline of the forests. The photo published by M. MEE (1988, 287) documents the location of a plant at the high waterline of the tree trunk, evidenced by the colour of the bark. When T. MORRISON (pers. comm.) revisited the same tree in 1989, the plant was under water, together with many other plants he observed.

Actually, this observation is not new. Both N. H. WITT and SCHUMANN (1900) mentioned it in the original description of the species. As a result, the whole growth form of this epiphyte with flattened stems appressed to tree trunks must be an adaptation to living periodically under torrential water. It should be added that *S. wittii* is a climber, and after the seedling has been established along the high waterline, old plants may grow up to 2 meters above this line.

We are indebted to numerous colleagues for information and assistance: the late MARGARET MEE and, in particular, her publisher TONY MORRISON (Woodbridge, UK), MYRON KIMNACH (formerly curator of Huntington Botanical Gardens, San Marino, USA), the late Countess BEATRIX ORSSICH (Teresópolis, Brazil), JOACHIM ADIS (Plön), GERHARD K. GOTTSBERGER (Ulm); the colleagues at the Entomology Department of the Forschungsinstitut Senckenberg (Frankfurt/Main, Germany) for their advice concerning *Sphingidae* and ERWIN PATZELT (Quito, Ecuador) for providing the illustration of *Cocytius cruentus*; WILHELM BOLAND (Bonn) for enabling the fragrance analysis, HUBERT ZIEGLER (München) for the stable carbon isotope analysis, RÜDIGER SEINE (Bonn) for carefully revising and preparing the manuscript; and last not least, WERNER HÖLLER (Bonn) for the most successful cultivation of *S. wittii* over many years.

## References

- BARTHLOTT, W., HUNT, D. R., 1993: *Cactaceae*. – In KUBITZKI, K., (Ed.): The families and genera of flowering plants, 2, pp. 161–197. – Berlin, Heidelberg, New York: Springer.
- RAUH, W., 1975–1976: Some notes on the morphology, palynology, and geographical variability of *Epiphyllum phyllanthus* (L.) HAW. (*Cactaceae*), the type species of the genus. – Natl. Cact. Succ. J. **29**: 113–115; **30**: 8–10.
- POREMBSKI, S., 1996: Ecology and morphology of *Blossfeldia liliputana* (*Cactaceae*): a poikilohydric and almost astomate succulent. – Bot. Acta **109**: 161–166.
- VOIT, G., 1979: Mikromorphologie der Samenschalen und Taxonomie der *Cactaceae*: Ein raster-elektronenmikroskopischer Überblick. – Pl. Syst. Evol. **132**: 205–229.
- BRITTON, N. L., ROSE, J. N., 1913: Studies in *Cactaceae*. – Contr. U. S. Natl. Herb. **16**: 255–262.
- – 1920: The *Cactaceae*. – Carnegie Inst. Wash. Publ. **248/2**: 211–222.
- BURR, B., BARTHLOTT, W., 1993: Untersuchungen zur Ultraviolettreflexion von Angiospermenblüten II. – Trop. Subtrop. Pflanzenwelt **87**.
- D'ABRERA, B., 1986: *Sphingidae* mundi. Hawk moths of the world. – London: Claxsey.
- DARWIN, C., 1862: On the various contrivances by which British and foreign orchids are fertilized by insects. – London: Murray.
- DONATH, J., BOLAND, W., 1995: Biosynthesis of acyclic homoterpenes: enzyme selectivity and absolute configuration of the nerolidol precursor. – Phytochemistry **39**: 785–790.

- FARQUHAR, G. D., SHARKEY, T. D., 1982: Stomatal conductance and photosynthesis. – *Annual Rev. Pl. Physiol.* **33**: 317–345.
- GIBSON, A. C., NOBEL, P. S., 1986: *The cactus primer*. – Cambridge: Harvard University Press.
- GRAMS, T. T. E., BECK, F., LÜTTGE, U., 1996: Generation of rhythmic and arrhythmic behaviour of Crassulacean acid metabolism in *Kalanchoe daigremontiana* under continuous light by varying the irradiance or temperature: Measurements in vivo and model simulations. – *Planta* **198**: 110–117.
- HABER, W. A., FRANKIE, G. W., 1989: A tropical hawkmoth community. – *Biotropica* **21**: 155–172.
- KAISER, R., 1991: Trapping, investigation and reconstitution of flower scents. – In MÜLLER, P. M., LAMPARSKY, D., (Eds): *Perfumes, art, science, technology*. – Elsevier Applied Science **1991**, pp. 213–250. – Amsterdam, Oxford, New York: Elsevier.
- 1993: *The scent of orchids*. – Amsterdam, Oxford, New York: Elsevier.
- KLUGE, M., TING, I. P., 1978: Crassulacean acid metabolism. Analysis of an ecological adaptation. – *Ecol. Stud. Analysis Synth.* **30**. – Berlin, Heidelberg, New York: Springer.
- KUBITZKI, K., 1989: The ecological differentiation of Amazonian inundation forest. – *Pl. Syst. Evol.* **162**: 285–304.
- ZIBURSKI, A., 1994: Seed dispersal in flood plain forests of Amazonia. – *Biotropica* **26**: 30–43.
- LEUENBERGER, B., 1975: *Die Pollenmorphologie der Cactaceae und ihre Bedeutung für die Systematik*. – Diss. Bot. **31**. – Vaduz: Cramer.
- LÜTTGE, M., STIMMEL, K.-H., SMITH, J. A. C., GRIFFITH, H., 1986: Comparative ecophysiology of CAM and C<sub>3</sub> bromeliads. II. Field measurements of gas exchange of CAM bromeliads in the humid tropics. – *Pl. Cell Environm.* **9**: 377–388.
- MEE, M., 1988: *In search of flowers of the Amazon Forests*. – Woodbridge: Nonesuch Expeditions Publisher.
- NILSSON, L. A., JONSSON, L., RASON, L., RANDRIANJOHANNY, E., 1985: Monophily and pollination mechanisms in *Angraecum arachnites* SCHLTR. (*Orchidaceae*) in a guild of long-tongued hawk moths (*Sphingidae*) in Madagascar. – *Biol. J. Linn. Soc.* **26**: 1–19.
- OSMOND, C. B., 1982: Carbon cycling and stability of the photosynthetic apparatus in CAM. – In TING, I. P., GIBBS, M., (Eds): *Crassulacean acid metabolism*, pp. 112–127. – Rockville: American Society of Plant Physiologists.
- PEUKERT, D. E., 1980: Zur Anatomie von *Epiphyllum chrysocardium* ALEXANDER (*Cactaceae*): Epidermis und Stomatogenese. – *Flora* **169**: 1–8.
- RUNDEL, P. W., EHLERINGER, K. A., NAGY, K. A., 1989: Stable isotopes in ecological research. – *Ecol. Stud. Analysis Synth.* **68**. – Berlin, Heidelberg, New York: Springer.
- SCHUMANN, K., 1900: *Cereus wittii* K. SCH. – *Monatsschr. Kakteenk.* **10**: 153–158.
- 1902: Die Blüte von *Cereus wittii*. – *Monatsschr. Kakteenk.* **12**: 137–138.
- SEITZ, A., 1940: *Die Groß-Schmetterlinge der Erde*. **6**. – Stuttgart: Kerner.
- WINTER, K., SMITH, J. A. C., 1996: Crassulacean acid metabolism. – *Ecol. Stud. Analysis Synth.* **114**. – Berlin, Heidelberg, New York: Springer.
- ZIEGLER, H., OSMOND, B., STICHLER, P., TRIMBORN, P., 1976: Hydrogen isotope discrimination in higher plants: correlation with photosynthetic pathway and environment. – *Planta* **128**: 85–92.

Addresses of the authors: W. BARTHOLOTT, S. POREMBSKI, Botanisches Institut der Universität Bonn, Meckenheimer Allee 170, D-53115 Bonn, Federal Republic of Germany.  
– M. KLUGE, Institut für Botanik der Technischen Hochschule Darmstadt, Schnittspahn-

strasse 10, D-64287 Darmstadt, Federal Republic of Germany. – J. HOPKE, Institut für Organische Chemie und Biochemie der Universität Bonn, Gerhard-Domagk-Strasse 1, D-53121 Bonn, Federal Republic of Germany. – LOKI SCHMIDT, Stiftung zum Schutze gefährdeter Pflanzen e.V., Steintorweg 8, D-20099 Hamburg, Federal Republic of Germany.

Accepted September 23, 1996 by M. HESSE and I. KRISAF-GREILHUBER