Scientific work of Austrian students in the "Austrian rainforest" (Piedras Blancas National Park, Costa Rica), with special regard to pollination studies

Trabajo científico de los estudiantes en el "Bosque lluvioso de los Austriacos" (Parque Nacional Piedras Blancas, Costa Rica), con especial consideración en los estudios de polinización

Anton WEBER

Abstract: In the "Austrian rainforest" ("Bosque de los Austriacos", parts of Piedras Blancas National Park), research work continues to be carried out by students of Austrian universities. A survey of the numerous departments involved, and of the broad range of topics covered in doctoral, diploma and baccalaureal theses is given. In context with the preceding papers in this volume, special attention is paid to studies of pollination and reproduction of Golfo Dulce plants. The results of three selected theses are given in some detail.

Key words: Costa Rica, Piedras Blancas National Park, Esquinas rainforest, Austrian rainforest, doctoral, diploma and baccalaureal theses, universities, pollination.

Resumen: En la "Bosque lluvioso de los Austriacos" (parte del Parque Nacional Piedras Blancas), numerosos trabajos de investigación ha sido y son llevado a cabo continuamente por los estudiantes de las universidades austriacas. Se realiza un estudio de los departamentos implicados y de la amplia gama de temas elaborados en las tesis de doctorado, diplomado y master. En el contexto del anterior trabajos de este volumen, se presta especial atención a los estudios de la polinización y de reproducción de las plantas de Golfo Dulce. Se hace referencia con algún detalle a los resultados de tres tesis seleccionadas.

Palabras clave: Costa Rica, Parque Nacional Piedras Blancas, bosque lluvioso Esquinas, Bosque lluvioso de los Austriacos, tesis de diplomado y master, doctorado, universidades, polinización.

Introduction

The Golfo Dulce area is associated with Austria and Austrian people in a special way. Firstly, a 1930 Austrian expedition under the leadership of Otto Porsch visited the Osa peninsula and carried out important studies on the flora and the pollination of plants (see papers of DÍAZ 2008 and WEBER 2008, this volume). Secondly, 60 years later, by the initiative of the musician Michael Schnitzler, Austrian people contributed essentially to the conservation of the area which is now Piedras Blancas National Park. With their donations, large areas of rainforest could be purchased from the owners, ceded to the Costa Rican goverment and thus saved from logging. The government of Costa Rica officially declared these parts as "Bosque de los Austriacos" and encouraged research work in the area. This work was made possible at a larger scale through the foundation of the "Tropenstation La Gamba". In recent years, a good deal of research work has been carried out by Austrian (and other) students, mostly in the format of diploma and doctoral theses. More recently, baccalaureal theses have also been carried out or are in progress.

One of the greatest benefits of the "Tropenstation La Gamba" is that facilities are not only available to established scientists, but that university students are enabled to carry out scientific work at different levels. Even pupils at secondary schools can gain insight into scientific work at a tropical field station. Students come from all over the world. There is no national restriction, and indeed, doctoral and diploma theses have been carried out by students of several German universities (Düsseldorf, Essen, Mainz, Ulm), as well as from US universities (University of Montana, Cornell University). Unfortunately, no Costa Rican students have yet used the station for writing a thesis, but this is cer-

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tainly only a question of time, as the station is increasingly being used by Costa Rican scientists and institutions (e.g., INBio). Nonetheless, and unsurprisingly, most students using the station are from Austria, with quite a considerable number of universities and institutes or departments involved.

In the first part of the paper, a survey is given of the diploma and baccalaureal theses that have been carried out by students of Austrian institutions. The list (Appendix) documents the numerous institutions that have been and are involved.

In context with the previous paper in this volume, which presents an overwiew on the diversity of pollination strategies found in the Golfo Dulce plants, the theses relating to pollination biology are singled out and three of them are reviewed in some detail. Pollination studies have been conducted so far from students of the universities of Vienna, Salzburg and Graz.

Theses of Austrian students carried out in the "Austrian rainforest"

In this section, a survey is given of the doctoral, diploma and baccalaureal theses already carried out or still being carried out by students of Austrian universities. This is in the form of a simple list, without comments about the content and scientific results (Appendix). Abstracts and publications emanating from some of these theses can be found in the "Scientific Report" ("Wissenschaftlicher Bericht"), which is edited every year in updated form by the "Tropenstation".

The list shows not only the considerable number of students and institutions involved, but also the enormously wide range of topics. Indeed, the spectrum of sciences involved is very broad, including botany, zoology, ecology, ecophysiology, pharmacognosy, agriculture, soil science, geography, ethnology, sociology, history and others. Mainly for historical reasons, scientific work on plants is dominant, but a steadily increasing number of theses in other disciplines are being published. As far as plants are concerned, studies on the flora (systematic treatment of groups such as ferns, palms, legumes, melastomes, Rubiaceae etc.), vegetation (floristic, statistical and structural analyses of ecologically different plots), special ecological groups (e.g., epiphytes, hemiepiphytes, myrmecophytes), ecophysiology (nutrient transport, litter decomposition, etc.), and reproductive ecology have been performed or are still under way.

Pollination studies of Austrian students in the "Austrian rainforest"

Generally, studies on pollination biology – or reproductive ecology more generally – form an integral part of the understanding and use of ecosystems. As was shown in the preceding paper, an enormous diversity of reproductive strategies and plant-pollinator interactions is found in rainforests such as the Golfo Dulce forests. Though a huge amount of information has already been accumulated, we are still at the beginning of a deeper understanding of the functioning of rainforests. Students are encouraged to contribute to this most interesting and rewarding discipline of botany.

In recent years, a number of studies relating to the reproductive ecology of Golfo Dulce plants has been carried out. These theses (one doctoral thesis, several diploma and baccalaureal theses) are marked by an asterisk in the list given in the Appendix. Topics covered include the pollination of *Blakea* (Melastomataceae; SCHEIBER, 2007), *Calathea* (Marantaceae; THURNER 2004), *Clusia* (Clusiaceae; HOCHWALLNER 2004), *Columnea* (Gesneriaceae; KASTINGER 2005), *Episcia* (Gesneriaceae; RAUCH in prep.), *Heliconia* (Heliconiaceae; HORNER 2004), *Pentagonia* and other members of Rubiaceae (CSEKITS, in prep.), *Souroubea* (Marcgraviaceae; RUBIN 2007), and *Tetrathylacium* (Flacourtiaceae/now Salicaceae; SCHMELZ 2006). Zoological aspects (pollen feeding of *Heliconius* butterflies) are covered by the theses of EBERHARD and HIKL (in prep.). Here, three theses of particular scientific relevance have been selected and are considered in greater detail.

Pollination biology of the *Columnea* species (Gesneriaceae) of the Piedras Blancas National Park, Costa Rica

Christoph KASTINGER

Doctoral thesis (in German), approved 2005

With more than 270 species, *Columnea* is the second largest genus of Gesneriaceae and the largest genus of the family occurring in the neotropics. All species are epiphytic and ornithophilous. Six species are fairly common in the Piedras Blancas National Park: *C. angustata*, *C. flaccida*, *C. florida*, *C. polyantha*, *C. raymondii* and *C. segregata*. These were studied with respect to their vegetative and flower morphology, habitat, breeding systems, attraction strategies, nectar production, pollination and fruit set. The background questions are: how do species of an exclusively hummingbird-pollinated genus co-exist, how do they manage competition and how are they adapted to specific hummingbird pollinators, if at all?

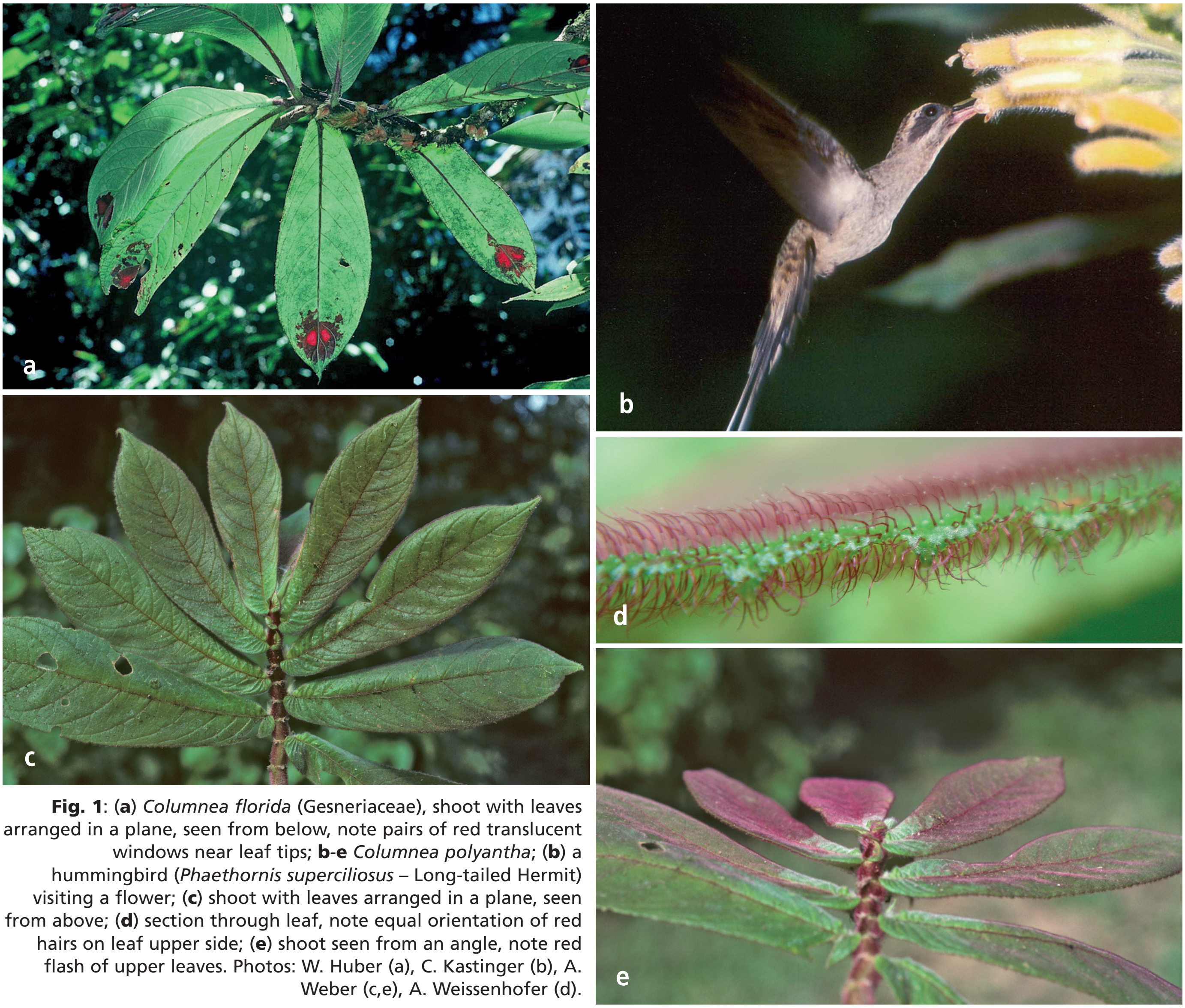

Fig. 1: (**a**) *Columnea florida* (Gesneriaceae), shoot with leaves arranged in a plane, seen from below, note pairs of red translucent windows near leaf tips; **b-e** *Columnea polyantha*; (**b**) a hummingbird (*Phaethornis superciliosus* – Long-tailed Hermit) visiting a flower; (**c**) shoot with leaves arranged in a plane, seen from above; (**d**) section through leaf, note equal orientation of red hairs on leaf upper side; (**e**) shoot seen from an angle, note red flash of upper leaves. Photos: W. Huber (a), C. Kastinger (b), A. Weber (c,e), A. Weissenhofer (d).

Specific differences of the species examined. Kastinger's studies show that each species is distinct in habit, habitat preference, flower morphology, flower coloration and extrafloral cues.

Floral and extrafloral cues. One of the most remarkable features is the stepwise shift in the attractive cues from the flower to the foliage leaves. While two species rely completely on floral cues (large, red, galeate flowers), in the others, leaf markings become increasingly significant. In C. *segregata*, the flowers are small, yellow and rather inconspicuous, but the leaves exhibit red blotches of irregular size and number. These markings reach their culmination is in C. *florida*, in which two distinctly shaped red translucent windows are present near the leaf tips (Fig. 1a). The windows are scarcely seen from above, but of impressive attractiveness when the leaves are held against the light. Apparently, the window effect is mainly operative when the hummingbird flies below the plant. The reverse is true in C. *polyantha*, in which at first sight the leaves seem to be green all over (Fig. 1c). They are, however, covererd by a dense indumentum of reddish hairs, all pointing in the same direction (Fig. 1d). When the leaves or shoots are turned to a certain angle, the whole leaf or shoot flashes an iridescent red (Fig. 1e). The red flash obvisoulsy strikes the eye of a humminbird flying over the plant. As the branches of the richly branched plant point in various directions, many such flashes are produced and can hardly be overlooked by a humminbird searching for nectar.

Course of anthesis. All species examined proved proterandrous, but with conspicuous differenthes in the duration of the male and female stage. In each species, the development and floral timing of all flowers on a shoot was documented. The data reflect interesting strategies and differences in flower presentation which cannot be discussed here.

Nectar secretion. Nectar production was quantitatively studied in selected species. Measurements included the volume of nectar secreted during anthesis (male and female stage) and the sugar concentration of the nectar. Nectar secretion proved to depend strongly on the flowering stage. There is a strong increase during the male stage, and nectar production is highest when the flower enters the female stage. Subsequently, nectar production decreases continuously and ceases when the corolla begins to wilt.

The nectar volume was found to vary considerably. At the peak of secretion, the average volume measured in *C. polyantha* was 4.63µl, while the highest value measured was 13.9µl. The volume of nectar produced was lower in the other species, but with a similar secretion curve.

The measurements of sugar concentration produced values between 25.5% and 32.9%. This is slightly to distinctly higher than the values characteristic of other hummingbird-pollinated flowers (average sugar concentration 20-25%). No correlation between sugar concentration and flowering stage could be found.

Fruit set and breeding system. Fruit set proved very variable in the particular species. In *C. flaccida*, an extremely low fruit set was observed, so that self-pollination can be excluded. This matches with the results of bagging experiments: in case of hand pollination (using pollen from the same plant) no fruits developed. In contrast, *C. polyantha* showed a fairly high fruit set (ca. 40%). However, in 55 of 100 flowers from which a fruit had started to develop, the fruits had dropped before reaching ripeness. In bagging experiments, many fruits developed from hand-pollinated flowers. However, when the anthers were removed before ripeness, no fruits developed. This shows that *C. polyantha* is self-fertile.

The highest fruit set in freely accessible flowers was observed in *C. raymondii* (80%). If a young fruit developed from a flower, this regularly reached maturity. Fruit set was also high in hand-pollinated plants.

In conclusion, one can say that, in the six *Columnea* species, different breeding systems are in operation, ranging from exclusive outcrossing to partial or facultative self-pollination.

Hummingbirds. In the Golfo Dulce area there occur 22 species of hummingbird, which is almost half of the species known for Costa Rica. From these, six species belong to the group of "hermits" (Trochilidae subfam. Phaetornithinae) (Fig. 1b: *Phaetornis superciliosus*), and the remainder to the "non-hermits" (subfam. Trochilinae). Most of the hermit species are frequent in the Golfo Dulce area and are relevant for the pollination of *Columnea*. Of the non-hermits, only *Amazilia tzacatl* proved to be of significance.

Species association between hummingbirds and *Columnea*. By far the most frequent visitors of the *Columnea* flowers were hermits. Moreover, a clear association of hummingbirds with particular *Columnea* species could be established (*Glaucis aenea*: *Columnea segregata*, *C. flaccida* and *C. raymondii*; *Phaethornis longirostris*: *C. polyantha* and *C. raymondii*; *Threnetes ruckeri*: *C. flaccida* and *C. segregata*). The only hummingbird observed visiting *C. angustata* was *Amazilia tzacatl* (Trochilinae).

Pollen deposition is principally nototribic. However, contact with the anthers and the stigma, respectively, is with different parts of the head and beak of the hummingbird, depending on the shape and length of the beak and the shape and length of the flower of the *Columnea* visited. Hummingbirds visiting several species of *Columnea* get laden with pollen on different places. An individual of, say, *Glaucis aenea* may thus carry pollen of different *Columnea* species on three places: the middle of the beak (*C. segregata*), between the forehead and the crown (*C. polyantha*) and on the crown (*C. raymondii*) and deliver pollen correctly to the stigma of each *Columnea* species. Thus specific pollen delivery is ensured, even though the flower is visited by different species of hummingbirds.

Frequency of flower visits. On average, the observed hermits returned to the flowers of a particular plant every 50 to 70 minutes and thus showed the well-known trap lining strategy of flower visitation.

Competition, specialisation and adaptation. Since most of the *Columnea* species examined were visited by hermits, there is competition between the sympatric *Columnea* species and competition also arises between the particular species of the hermits. The *Columnea* species with long flower tubes (*C. raymondii* and *C. flaccida*) have obviously specialised in long-billed species of hummingbirds such as *Phaetornis longirostris*. Thus, they have acquired an advantage over competitive bird species with shorter bills. The latter have to dive deeply into the corolla tube to reach the nectar. In contrast, there are disadvantages associated with long corolla tubes: restriction in the number of possible pollinators and nectar robbing by other hummingbirds. The short-tubed flowers (*C. segregata*, *C. florida*) can be visited by any type of hummingbird. However, pollen deposition and transfer from one flower to the other may be less effective, und thus represent a possible disadvantage.

Conclusions. Kastinger's studies show clearly that the six sympatric species of *Columnea* are quite different in their morphology, attraction strategies and pollination requirements. Each is addressed to one or few species of hummingbirds by the combination of different attraction cues (including extrafloral cues), flower size/shape, flower colour, and pollen deposition on various parts of the hummingbird's beak or head. Even if a hummingbird species visits several species of *Columnea*, different location of the pollen ensures correct pollen delivery. Thus, competition is reduced and co-existence both of the sympatric plants and the sympatric hummingbirds is enabled.

Floral morphology, development and pollination of *Clusia valerioi* and *Clusia peninsulae* (Clusiaceae)

Heidrun HOCHWALLNER
Diploma thesis (in English), approved 2004

A first part of this thesis has been published (HOCHWALLNER & WEBER 2006: Flora 201: 407-418), a second part is just being prepared for publication.

This diploma thesis deals with two Costa Rican species of Clusiaceae that offer resin as a floal reward: *Clusia valerioi* and C. *peninsulae*, sp. ined. They were studied both in the field, during a 4-month stay in the "Austrian rainforest" (Piedras Blancas National Park), and subsequently in the laboratory. The field studies related to the phenology, flower structure, course of anthesis, flower visitors, resin collection, pollination process, fruit development and seed dispersal. In the laboratory, the flower structure and floral anatomy (with special reference to the unique stamens and staminodes) and the flower development was studied by means of microtome sections and SEM.

Flower structure. As in all *Clusia* species, the flowers of the two species investigated are unisexual. The perianth consists of five free sepals and five pinkish petals. Petal aestivation is quincuncial, with the two inner petals showing conspicuous imprints of the stamens. In the female flowers, a ring of staminodes surrounds the carpels in the centre (Fig. 2a). The staminodes secrete resin as a floral reward. The male flowers possess a hemispherical androecium made up of numerous tightly packed stamens (Fig. 2b). The entire surface is almost completely covered by a layer of resin. The stamens consist of a thick angular filament column and two anthers situated at the top. The outer anther is annular and surrounds a second, hermispherical anther in its centre. At the periphery, the two anthers are surrounded by a ring-like protuberance of the filament. The gynoecium consists of five or more fused carpels with a sessile stigma on top of each.

Fig. 2: *Clusia valerioi* (Clusiaceae); (**a**) a female flower visited by a meliponid bee (*Trigona* sp.), note ring of staminodia around gynoecium, with surface covered by resin; (**b**) male flower with *Trigona fulviventris*, note packets of resin globules on hind legs. Photos: H. Hochwallner (a), W. Hödl (b).

Stamen/anther interpretation. The peculiar stamen morphology is in need of a morphological derivation from conventional stamens. Three hypotheses have been proposed by Hochwallner, but are not discussed here.

Flower anatomy. The resin ducts in the stamens (and staminodes) are remarkable. They are located at the periphery of the filament, and their development is schizogenous. At anthesis, the resin is released from the ring-shaped filament protuberance by bursting the single-layered epidermis.

Flower development. In the early stages, both male and female flowers develop in the same manner. The bracts are distinguished by a decussate arrangement from the five sepals and five petals, which emerge in a spiral manner. In the male flowers, the apical meristem forms five meristematic mounds (common stamen primordia) that are pentagonally arranged in epipetalous

Fig. 3: *Tetrathylacium macrophyllum* (Flacourtiaceae/Salicaceae); (**a**) section of inflorescence, with flowers in female stage; note bulges below tepals, central flowers: bulges with feeding marks; (**b**) nymph of bush cricket (katydid) feeding on flower bulge; flowers in male stage. Photos: V. Schmelz.

position around the apical meristem. From these mounds, the primordia of the proper stamina emerge in 3-5 whorls. Direction is centrifugal. In the centre, five hemispherical bulges arise which develop into carpel primordia. These, however, cease growth very soon, remain rudimentary and are hidden by the stamens in the mature flower. In the female flower, five meristematic mounds produce two tightly packed whorls of staminodes. The development of the staminodes does not differ in essence from that of the fertile stamens, but the staminodes lack the central pollen sac and the anther tissues do not develop into pollen grains.

Flower visitors. The flowers are regularly visited by stingless (meliponine) bees. Five species have been recorded to visit the flowers of *Clusia valerioi* (*Trigona fulviventris*, *T. corvina*, *T. amalthea*, *Tetragona dorsalis*, *Partamona cupira*) and six species to visit *C. peninsulae* (*Trigona fulviventris*, *T. corvina*, *Paratrigona opaca*, *Plebeia frontalis*, *Scaura latitarsis*). All species were observed to collect the resin provided by the flowers. In addition, honey bees (*Apis mellifera*) have been observed to visit the flowers of *C. peninsula*, but these bees appeared clumsy and were not able to handle the resin properly.

Resin collection. The meliponine bees cut off pieces of the resin with their mandibles. Then they form a globule and transfer it via the middle legs to the hind legs. Here the globules accumulate and are transported in packets by the bees (Fig. 2b).

Pollination. The pollen is released by the splitting off of an operculum. Pollen is transferred unintentionally to the female flowers, in which the staminodia also provide resin. This ensures that both sexes are visited by the bees.

Fruit development and opening. After fertilisation, the gynoecium develops into a globose woody fruit, topped by the dark, sessile stigmas. At maturity, the fruits split into a bowl-shaped or star-like capsule, exposing large seeds with an orange-red sarcotesta.

Seed dispersal. Three species of honeycreepers (*Cyanerpes cyaneus*, *C. lucidus* and *Chlorophanes spiza*) have been observed to remove the seeds from the open capsule. They swallow the seeds and transport them internally (endozoochory).

Conclusions. Hochwallner's thesis provides a lot of new information on the structure and development of *Clusia* flowers that offer resin as a floral reward. Details of resin collection and pollination by meliponine bees are communicated for the first time.

Flower morphology, floral development and reproductive ecology of *Tetrathylacium macrophyllum* (Flacourtiaceae/Salicaceae) in the Piedras Blancas National Park, Costa Rica

Verena SCHMELZ

Diploma thesis (in German), approved 2006

This diploma thesis refers to *Tetrathylacium macrophyllum* (Flacourtiaceae, now Salicaceae), a fairly common but little-known understorey tree in the "Austrian rainforest". The tree produces small red-brown flowers in large numbers in bunch-shaped pendent inflorescences. The flowers possess conspicuous bulges below the tepals (Fig. 3a). During earlier excursions, the project supervisor had observed that the bulges often exhibited feeding marks (Fig. 3a, central flowers), suggesting that these bulges possibly represent food bodies and play some role in the pollination of the flowers. Verena SCHMELZ tested this hypothesis and carried out detailed morphological, developmental and anthecological studies.

Inflorescence and flower morphology. The inflorescences represent pendent compound spikes. They consist of ca. 30 partial inflorescences (spikelets) and produce more than 1200 flowers. Anthesis starts 30-32 days after inflorescence initiation. The sessile flowers are consistently tetramerous with a single whorl of wine-red coloured tepals, four stamens with whitish to yellow anthers and a superior syncarpous ovary with a short erect style. The fully grown flowers measure about 5.4 mm in diameter. There are no nectaries or diffusely secreted nectar. Below each tepal, there is a conspicuous lateral bulge of firm tissue. Before and during anthesis, the flowers emit an intense lemon-like fragrance.

Anthesis. Surprisingly, the flowers are nocturnal. They open at dusk, about 4 p.m., entering the female stage (protogyny). The four tepals open only slightly so that the stigma can protrude, while the short style remains hidden in the perianth (Fig. 3a). At about the same time on the second day, the stamens begin to emerge. The anthers slip out and the filaments straighten to reach an upright position. The anthers then recurve to a horizontal position, forming a small platform. The anthers are pale yellow and form a visually strong contrast to the dark red perianth. The pollen is somewhat sticky.

Regarding the inflorescence as a whole, the inflorescence is usually in the female stage on the first night and male on the following night. Less commonly it was observed that flowering of an individual inflorescence extended over three nights, with the flowers entering the female stage successively in the first and second night. The non-pollinated flowers fall off quickly during the following days. Receptivity tests carried out in the first evening, in the night, and at dawn the following day showed an intense and rapid reaction. Later in the afternoon (approaching the male stage), the receptivity was clearly reduced.

Flower visitors. Numerous insects were observed to visit the inflorescences and flowers: small dipterans (from the families Drosophilidae, Psychodidae, Phoridae and Sphaeroceridae), small bees (particularly meliponines), and (rarely) small beetles (esp. species of Chrysomelidae-Galerucinae).

After sunset, rather unexpected insects regularly appeared on the inflorescences: bush crickets (called katydids in America; Tettigoniidae subfam. Pseudophyllinae) (Fig. 3b). Both nymphs and adults were observed, possibly belonging to a single species. Their identity is still unknown, but they probably belong to the genus *Pristinotus* (NASKRECKI, pers. comm.). They were observed to arrive singly or in pairs (but never in larger groups) between 8 p.m. and 2 a.m. and spent up to several hours on the inflorescence. These insects could be clearly identified as the insects feeding on the floral bulges and leaving the characteristic feeding marks.

Who are the pollinators? Most of the observed flower visitors cannot be regarded as true pollinators. Bees are restricted to daytime visits, which does not correspond with the nocturnal stigma receptivity and dehiscence of anthers. Moreover, regular bee visits on some inflorescences could not have resulted in pollination, because no fruit developed. Minute dipterans visited the flowers both at day and night, but seem to use the inflorescences primarily for the deposition of eggs and resting. Beetles have not been observed frequently enough to represent regular pollinators. The only insects that were interested in the flowers were the bush crickets. These insects fit the size of the flowers well and seem appropriate to brush off pollen from the anthers and to deposit it on the stigma of flowers in the female stage. The capacity of locomotion and apparent match with flowering phenology lends further support to this idea. Nonetheless, the hypothesis that the bush crickets represent the legitimate pollinators (this would be the first case of orthopteran pollination in the plant kingdom) is much in need of corroboration. Further studies (including studies in other localities of *T. macrophyllum* and chemical analyses of the floral bulges) are needed to answer several open questions.

Appendix: List of doctoral, diploma and baccalaureal theses of students of Austrian universities, with reference to the institutions involved

Due to continuous administrative reform of Austrian universities, the names of the university subunits change permanently. Here the traditional names (used until the end of 2003, usually "Institute of …") and the present name (usually "Department of …") are given where appropriate.

(in prep.) – thesis just being carried out, titles are provisional working titles

* (asterisk) – thesis relating (at least partially) to floral biology

University of Vienna – Institute of Botany / now Faculty Centre of Botany, Department of Palynology and Structural Botany

BRÖDERBAUER D. (in prep.): Diversität und Abundanz von Hemi-Epiphyten in zwei Tieflandregenwaldgebieten in der karibischen und pazifischen Region Costa Ricas. — Diploma thesis.

BURGER S. (2003): Vergleichende Bestandsaufnahme von Ameisenpflanzen entlang eines Transekts im tropischen Tiefregenwald Costa Ricas. — Diploma thesis.

*CSEKITS S. (in prep.): Floral biology of Rubiaceae in the Esquinas rainforest (Piedras Blancas N.P.), Costa Rica. — Diploma thesis.

FISCHER R. (2001): Die Symbiose von *Piper* spp. und *Pheidole bicornis*: ein Nährstoffkreislauf zwischen Pflanzen und Ameisen. — Diploma thesis.

GAAFAR K. (in prep.): Entwicklungsgeschichtliche Untersuchungen zur Anisostipulie und Blütenentwicklung von *Dicraspidia donnel-smithii* (Muntingiaceae). — Diploma thesis.

*HOCHWALLNER H. (2004): Floral morphology, development and pollination of *Clusia valerioi* and *Clusia peninsulae* (Clusiaceae). — Diploma thesis.

HUBER W. (1996): Floristische und biogeographische Untersuchungen in einem Tieflandregenwald in der pazifischen Region von Costa Rica. — Diploma thesis.

HUBER W. (2005): Tree diversity and biogeography of four one-hectare plots in the lowland rainforest of the Piedras Blancas National Park ("Regenwald der Österreicher"), Costa Rica. — Doctoral thesis.

JODL M. (2004): Karyologische Untersuchungen an tropischen Angiospermenfamilien. — Diploma thesis.

*KASTINGER C. (2005): Bestäubungsbiologie der *Columnea*-Arten (Gesneriaceae) im Piedras Blancas Nationalpark, Costa Rica. — Doctoral thesis.

LAUTSCH D. (2000): Ferns and fern allies of the Bosque Esquinas ("Regenwald der Österreicher"), Costa Rica. — Diploma thesis.

LENOTTI C. (in prep.): Diversität und Abundanz von Hemi-Epiphyten in zwei Tieflandregenwaldgebieten an der karibischen und pazifischen Region Costa Ricas. — Diploma thesis.

MAYR E.M. (2005): Floral development in Calceolariaceae: intergeneric variation and comparison with allied groups. — Diploma thesis.

*RAUCH A. (in prep.): Untersuchungen an *Episcia lilacina* im "Regenwald der Österreicher". — Diploma thesis.

SCHABER D. (in prep.): *Piper* sp. and its inhabiting ant *Pheidole bicornis*: Do they communicate? — Diploma thesis.

SCHEMBERA E. (2004): The Legume Flora of the Golfo Dulce rainforests, Costa Rica. — Diploma thesis.

*SCHMELZ V. (2006): Bestäubungsökologie von *Tetrathylacium macrophyllum* (Flacourtiaceae). — Diploma thesis.

SCHMIDT M.R. (2001): Interactions between *Tetrathylacium macrophyllum* (Flacourtiaceae) and its live-stem inhabiting ants. — Diploma thesis.

SEHR E.M. 2005: Floral development in Tetrachondraceaea and Oleaceae – two families of basal Lamiales — Diploma thesis.

THURNER M. (2007): Nectar contents and herbivore pressure on *Passiflora* sp. (Passifloraceae) in connection with ants in a tropical rainforest in Costa Rica. — Diploma thesis.

WEISSENHOFER A. (1996): Ökologie und Struktur eines Tieflandregenwaldes in der Pazifikregion von Costa Rica. — Diploma thesis.

WEISSENHOFER A. (2005): Structure and vegetation dynamics of four selected one hectare forest plots in the lowland rainforests of the Piedras Blancas National Park ("Regenwald der Österreicher"), Costa Rica, with notes on the vegetation diversity of the Golfo Dulce region. — Doctoral thesis.

WILL S. (2001): Diversity of the Rubiaceae Juss. (Coffee or Madder Family) in the Esquinas Rainforest, Costa Rica. — Diploma thesis.

University of Vienna – Institute of Ecology and Conservation Biology / Department of Conservation Biology, Vegetation Ecology and Landscape Ecology

PÖLZ E. (in prep.): Bestandesstruktur und -zuwachs eines Tieflandregenwaldes in Costa Rica. — Diploma thesis.

PROMMER, J. (in prep.): Bodenfruchtbarkeit der Hausgärten in Costa Rica. — Diploma thesis.

SCHLUDER J. (in prep): Ökophysiologie der Stickstoffassimilierung von Laub- und Lebermoosen kontrastierender Standorte eines tropischen Tieflandregenwaldes, Costa Rica; "Regenwald der Österreicher". — Diploma thesis.

SONNLEITNER M. (in prep.): Ökologie epiphyller Moose im Esquinas Regenwald, Costa Rica. — Diploma thesis.

STOCKHAMMER J. (1998): Naturvermittlung im tropischen Regenwald, mit einem Konzept für die Esquinas Rainforest Lodge. — Diploma thesis.

University of Vienna – Department of Chemical Ecology and Ecosystem Research

DRAGE S. (2007): Streufall- und Nährstoffrezyklierung im trop. Tieflandregenwald — Diploma thesis.

FÜRNKRANZ M. (2007): Stickstofffixierung von mit Mikroorgansimen assoziierten Epiphyten im Regenwald der Österreicher. — Diploma thesis.

HINKO N. (2007): Mechanismen der Nährstoffdynamik im Kronenraum tropischer Tieflandregenwälder. — Diploma thesis.

HOFHANSL F.(2008): Nährstoffkreisläufe und -recylierung in einem tropischen Regenwald. — Diploma thesis.

PÖRTL K. (2002): Ökophysiologische Auswirkungen der Epiphyllenkolonialisierung auf tropische Unterwuchspflanzen. — Diploma thesis.

RATZER A. (2007): Vergleich der beiden Methoden "ingrowth cores" und "15N-Tracer" zum Schätzen des Feinwurzel-Turnovers. — Diploma thesis.

*RUBIN I. (2007): Blütenbiologische und morphologische Untersuchungen an *Souroubea vallicola* (Marcgraviaceae). — Diploma thesis.

VOGLGRUBER A. (in prep.): Epicuticularkomponenten von Blättern tropischer Unterwuchspflanzen als Regulatoren der Epiphyllengesellschaften. — Diploma thesis.

WANIA R. (2001): Stickstoff-Kreislauf im Kronenraum eines Tieflandregenwaldes. — Diploma thesis.

University of Vienna – Department of Population Ecology

RIEDL I. (in prep.): Die Bedeutung von Galeriewäldern für die Vernetzung von Waldfragmenten. Eine Fallstudie an Vögeln im pazifischen Tiefland von Costa Rica. — Diploma thesis.

SEAMAN B. (in prep.): Gallery Forests in the Pacific lowlands of Costa Rica: an ecological sink for rainforest birds? — Diploma thesis.

University of Vienna – Institute of Zoology / Department of Evolutionary Biology

EBERHARD S. (in prep.): Pollen feeding in butterflies. Evolution of a new mechanism of nutrient extraction. — Doctoral thesis.

HIKL A. (in prep.): Sammeln und Extrahieren von Pollen: Evolution des Verhaltens bei *Heliconius*-Faltern. — Diploma thesis.

KARPFEN U. (2006): Reproductive behaviour and male mating success in the glass frog *Hyalinobatrachium valerioi*. — Diploma thesis.

KEBER A. (1997): Tagfalter-Fauna und Differenzierung der Nahrungssuche an Blüten in der biologischen Station Esquinas (Costa Rica) (Lepidoptera, Papilionoidea). — Diploma thesis.

VOCKENHUBER E. (2008): Reproductive behaviour and parental care in the glass frog *Hyalinobatrachium valerioi.* — Diploma thesis.

University of Vienna – Institute of Pharmacognosy / Department of Pharmacognosy

RADNER K. (in prep.): Die Heilpflanzen von Dona Sara und deren Verwendung. Univ. Wien, Inst. f. Pharmakognosie. Univ. Wien. — Diploma thesis.

WIENERROITHER K. (2000): Medicinal plants of the south of Costa Rica (Area de Conservación Osa). – Diploma thesis.

University of Vienna – Institute of Geography and Regional Research

FRALLER C. (in prep.): Ökotourismus in Costa Rica am Beispiel der Esquinas Lodge in La Gamba. — Doctoral thesis.

University of Vienna – Institute of Social and Cultural Anthropology / Department of Social and Cultural Anthropology

FAHRNBERGER M. (1999): Mit den Augen der Einheimischen. Die Perzeption von Tourismus dargestellt anhand zweier ausgewählter Regionen in Costa Rica mit unterschiedlichem Erschließungsgrad. — Diploma thesis.

University of Natural Resources and Applied Life Sciences, Vienna – Department of Integrative Biology and Biodiversity Research

RAMMLER H. (2004): Physiologische Anpassungen von Epiphyten in Abhängigkeit von ihrer Kronenposition. — Diploma thesis.

University of Natural Resources and Applied Life Sciences, Vienna – Department of Forest- and Soil Sciences, Institute of Soil Science

PAMPERL S. (2001): Der Boden als Standortsfaktor eines baumartenreichen Tieflandregenwaldes in Costa Rica. — Diploma thesis.

University of Natural Resources and Applied Life Sciences, Vienna – Institute of Sanitary Engineering and Water Pollution Control

PICHER C.K. (2007): Naturnahe Abwasserbehandlung in La Gamba, Costa Rica. — Baccalaureal thesis.

University of Natural Resources and Applied Life Sciences, Vienna – Department of Sustainable Agricultural Systems, Division of Organic Farming

LEHMWALD A. (2004): Lokales Wissen über Boden, Bodennutzung und Düngung in Hausgärten im Cantón Golfito, Provincia Puntarenas, Costa Rica. — Diploma thesis.

PEKAREK B. (2004): Die Heilpflanzen in den Hausgärten von La Gamba (Costa Rica): Ethnobotanische Untersuchungen zu Anwendung und Verarbeitung. — Diploma thesis.

University of Salzburg – Institute of Botany / Department of Organismic Biology, Study Group for Diversity and Ecology of Plants

EGGER J. (2005): Morphologische Anpassungen und ökologische Einnischung der Araceen im Bosque Esquinas ("Regenwald der Österreicher"), Costa Rica. — Diploma thesis.

*HORNER G. (2004): Helikonien und ihre Bestäubung durch Kolibris am Beispiel *Heliconia latispatha* im "Regenwald der Österreicher." — Baccalaureal thesis.

MANNEL M. (in prep.): Ameisen-Pflanzen-Interaktion in der Gattung *Inga*. — Baccalaureal thesis.

*THURNER M. (2004): Biologie der Marantaceae (Pfeilwurzgewächse), speziell *Calathea* sp. im "Regenwald der Österreicher." — Baccalaureal thesis.

University of Graz – Institute of Botany / Department of Plant Sciences

BALOCH E. (2006): Phylogeny and selectivity of lichen symbionts on leaves in tropical rainforests with focus on Porinaceae.

*SCHEIBER S. (2007): Bestäubung und Samenverbreitung von *Blakea gracilis* (Melastomataceae) im Piedras Blancas National Park, Costa Rica. — Baccalaureal thesis.

SCHEIDEL A. (2006): Systematische Bestandsaufnahme von Epiphyten in unterschiedlichen Lebensräumen im "Regenwald der Österreicher". — Baccalaureal thesis.

ZACH G. (2006): Palmendiversität im Esquinas-Regenwald – Baccalaureal thesis. ZNIDARIC, N., 2006: Untersuchungen zu Melastomataceae im "Regenwald der Österreicher". — Baccalaureal thesis.

ZNIDARIC N. (in prep.): Die Melastomataceae im Piedras Blancas National Park, Costa Rica. — Baccalaureal thesis.

University of Graz – Institute of Zoology / Department of Zoology

FARKAS A. (2007): Untersuchungen zur Biologie vom endemischen Vogel *Habia atrimaxillaris* im "Regenwald der Österreicher". — Baccalaureal thesis.

University of Insbruck – Institute of Zoology

BEN ROMDHANE K. (2005): Lokomotionsmuster von tropischen, frugivoren Vögeln. — Diploma thesis.

University of Innsbruck – Institute of Geography

KLINGLER M. (2007): Wirtschafts- und siedlungsstruktureller Wandel und seine Folgen in der Gemeinde La Gamba Golfo Dulce Region, Costa Rica. — Diploma thesis.

University of Leoben – Department of Applied GeoSciences and Geophysics

SCHEUCHER L. (2006): Geologischer Aufbau und Verwitterungsbildungen im Regenwald der Österreicher, Costa Rica. — Diploma thesis.

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