

# Otto Porsch and the scientific goals and results of the Austrian Costa Rica expedition 1930

## Otto Porsch y los objetivos y resultados científicos de la expedición Austriaco-Costarricense de 1930

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**Abstract:** As a complement to the historical paper of DÍAZ (this volume), a brief survey is given of the life and career of Otto Porsch (1875-1959) and the scientific goals and results of the Austrian Costa Rica Expedition (1930) he organised and directed. Porsch had broad scientific interests and was an eminent expert and pioneer in the field of pollination biology. Little was known at his time on the pollination of tropical plants by birds, bats and other vertebrates. Based on experiences from an expedition to Java (1913-1914), Porsch wanted to expand his studies on bird pollination to the neotropics. He chose Costa Rica as a destination because of its richness in hummingbirds. Here, he conducted extensive field studies and was able to confirm and deepen many of his former predictions. PORSCH was probably the first to fully realise the significance of hummingbirds for the evolutionary differentiation of the neotropical flora. Moreover, he was the first to prove definitively the existence of bat-pollinated flowers. In addition to various other anthecological studies, Porsch carried out valuable vegetation studies, publishing them in volume 23/4-5 of KARSTEN & SCHENCK's "Vegetationsbilder". To document the wide range of Porsch's interests and research fields, a list of his papers is published here for the first time.

**Key words:** Otto Porsch, biography, list of publications, Costa Rica expedition 1930.

**Resumen:** Como un complemento a la publicación histórica de DÍAZ (este volumen), se entrega una breve investigación de la vida y carrera de Otto Porsch (1875-1959) y los objetivos científicos y resultados de la expedición Austriaco Costarricense (1930) organizada y dirigida por él. Porsch tuvo un gran interés científico y fue un experto y pionero en el campo de la biología de la polinización. Poco se conocía en esos tiempos sobre la polinización de plantas tropicales por aves, murciélagos y otros vertebrados. Basado en la experiencia de una expedición a Java (1913-1914), Porsch busco extender sus estudios sobre polinización por aves a los neotrópicos. Él eligió Costa Rica como destino, debido a la riqueza en picaflares. Aquí él condujo extensos estudios en terreno y fue capaz de confirmar y profundizar muchas de sus ideas iniciales. Porsch fue probablemente el primero en confirmar en su totalidad el significado de los picaflares para la diferenciación evolutiva de la flora neotropical. Por otra parte, él fue el primero en comprobar definitivamente la existencia de flores polinizadas por murciélagos. Además de varios otros estudios relacionados con la ecología de flores, Porsch realizó importantes estudios vegetacionales, publicados en el volumen 23/4-5 de KARSTEN & SCHENCK's "Vegetationsbilder". Para registrar el amplio rango de intereses e investigaciones de campo de Porsch, se incluye una lista de todos sus trabajos.

**Palabras clave:** Otto Porsch, biografía, lista de publicaciones, expedición a Costa Rica 1930.

### Introduction

It is little known that in the scientific exploration of Costa Rica and the Golfo Dulce region, Austrian scientists played a pioneering role. The first Austrian scientists who visited Costa Rica were the traveller and pioneer photographer Emanuel Ritter von Friedrichsthal (1809-1842), the naturalist and explorer Karl (Carl) Ritter von Scherzer (1821-1903) and the meteorologist Julius von Hann (1839-1921). Friedrichsthal made extensive plant collections and is commemorated in many plant names, e.g., the orchid *Maxillaria*

*friedrichsthalii*, the bromeliad *Aechmaea friedrichsthalii* and the ornamental gesneriad *Chrysothemis friedrichsthaliana*. Scherzer travelled with the German zoologist and writer Moritz Wagner (1838-1903) and co-authored a remarkable book on "The Republic of Costa Rica" (WAGNER & SCHERZER 1856). He is also commemorated in the name of a well-known ornamental plant: the aroid *Anthurium scherzerianum*.

In 1930, a group of Austrian biologists, under the leadership of Otto Porsch (1875-1959), visited Costa Rica, including the Osa Peninsula, and carried out sig-

nificant studies regarding the interactions of flowers and pollinating animals and the neotropical vegetation. In the preceding paper of this volume, the Costa Rican historian R.E. DÍAZ deals with the historical aspects of this expedition. He describes the historical-political circumstances under which the expedition was planned and carried out, lists the members of the expedition, sketches the travelling route (see Map 1), and highlights the co-operation and mutual benefits of the Austrian and local scientists (especially José F. Tristán, Alberto M. Brenes and Ludwig Leipold).

The present paper is intended to complement that of DÍAZ (2008) in two respects. Firstly, it presents some personal details on the expedition leader, Otto Porsch. This seems appropriate, as Porsch's name is scarcely known to the younger generation of floral ecologists. It is, therefore, a good opportunity to remember here this eminent biologist and pioneer of tropical anthecology. Secondly, it gives some details on the scope and the scientific results of the expedition.<sup>1</sup>

Porsch was not only a gifted specialist in the field of pollination biology, but had a broad range of interests and published papers on many research topics. To document this wide range, a list of his publications is published here (Appendix). Though Porsch was celebrated in some birthday articles and festschriften, such a list apparently has never been compiled and is published here for the first time.

### Otto Porsch (1875-1959) – life, career and research

A few months from now, we will reach the 50<sup>th</sup> anniversary of Porsch's death (Jan. 2, 1959). This and the fact that Porsch's name and scientific work is little known by contemporary scientists (especially in the Anglo-American region) served as a motive to present some biographical data and reflections. Most of Porsch's scientific findings, especially of the pollination of tropical plants by birds and bats, have become commonplace among the last generations of floral ecologists, and only few people remember the tiresome route which led to these insights. Moreover, as nearly all of his publications are in German, and are published in Austrian or German journals (some of which, such as "Biologia generalis", which Porsch edited for more than 10 years, no longer exist, some of difficult access or appearing under another title).

<sup>1</sup> The Costa Rica expedition was also briefly addressed in an earlier paper by BAUERNFEIND (1996, in German), but with essential focus on Moriz Sassi and the ornithological studies.

### Life and career

Otto Porsch was born on Sept. 12, 1875 in Vienna. He studied botany (under A. Kerner von Marilaun, J. Wiesner, K. Fritsch, G. Beck von Mannagetta and R. von Wettstein) and zoology (under A. Hatschek and K. Grobben) at the University of Vienna. In 1901, he completed his degree "Doctor of Philosophy". In the same year, he moved to the University of Graz, where he became a scientific assistant to Prof. G. Haberlandt. Two years later (1903), he moved back to Vienna to take a post under Prof. R. von Wettstein. In 1909, he became head of the Botanical Garden of the University of Czernowitz (the easternmost university of the Austro-Hungarian monarchy, now in the Ukraine) and became full professor there in 1914. In 1920, he moved back to Vienna and was appointed as a full professor (o. Prof.) and director of the Institute of Botany and Botanical Garden of (what is now) the University of Natural Resources and Applied Life Sciences, Vienna. During his 25 years at this institution, he was twice its head ("rector", 1932-1933, and 1939-1940). In 1945, Porsch retired at the age of 70. On Jan. 2, 1959, at the age of 84, he passed away.

### Research

Porsch was an extraordinarily fruitful and multifaceted researcher. His main research area was floral ecology (pollination biology), but he also contributed substantial papers to the fields of morphology, systematics, anatomy, plant geography and evolution. In pollination ecology, he dealt with all groups of animal pollinators: insects (Porsch was an excellent entomologist, with a profound knowledge of insect diversity; his study on ancient insect types as flower visitors, published in 1957, twelve years after his retirement, is still a classic), birds (Porsch published numerous papers on bird pollination, before he was able to study hummingbird-pollination in the field in Costa Rica), bats (first field observations related to cultivated *Kigelia africana* in Java; in Costa Rica Porsch was able to provide definitive proof that flowers adapted to bat pollination really do exist) and other (non-flying) vertebrates. In addition, classical studies include those on the pollination of *Ephedra* and other Gnetales, the sweet chestnut (*Castanea sativa*), the horse chestnut (*Aesculus hippocastanum*) and cacti. The papers presenting the results of the Costa Rica expedition will be addressed in some more detail below.

### Research trips and expeditions

Porsch performed many research trips in Europe. Two expeditions led him to the tropics: (1) 1913-1914: Java (Buitenzorg, now Jakarta), enabled by a grant of the Treil-Stiftung of the Austrian Academy of Sciences; (2) 1930: Costa Rica; financed (inter alia) by the Austrian Academy of Sciences, the Austrian Ministry of Sciences and the Museum of Natural History.

## Editorship

Porsch edited the journal “*Biologia generalis*” for more than 10 years (1926-1937). (The journal was founded in 1925 and closed with vol. 19/4 in 1951.)

## Translations

Porsch translated papers which he found to be of particular interest from English and Spanish into German. Those known to the author include a paper by ARBER & PARKIN (1907) on the origin of angiosperms (PORSCH 1908; with critical remarks in a long footnote), and a manuscript of the Costa Rican botanists F. & E. Tristán-Fernández on the pollination of *Sechium edule* (PORSCH 1931).

## Awards, honorary memberships

In 1927, Porsch received the “Lieben” award of the Austrian Academy of Sciences; after 1940, he was a corresponding member of that institution. In 1928, he became a member of the Leopoldinian Academy of Natural Scientists (Halle, Germany).

## Festschriften, biographical notes, obituary

Festschriften appeared on the occasion of Porsch’s 60<sup>th</sup> and 80<sup>th</sup> birthday (ANONYMOUS 1935 and 1955, respectively). Biographical notes appeared in Kürschner’s Deutscher Gelehrten-Kalender (1940/41: 393; 1950: 1579) and Deutsche Biographische Enzyklopädie (1998: vol. 8, p. 38). Short notes on particular steps of Porsch’s career appeared in several places (they are not addressed here). A sensitive obituary was published by SCHIMITSCHEK (1959).

## Plants named for O. Porsch

A number of species from various angiosperm families has been named in honour of Porsch: *Anthurium porschianum* K. KRAUSE (Araceae), *Bactris porschiana* BURRET (Arecaceae), *Restrepia porschii* KRAENZL. = *Barbosella porschii* (KRAENZL.) SCHLTR., now included in *Barbosella cogniauxiana* (SPEG. & KRAENZL.) SCHLTR. (Orchidaceae), *Stelis porschiana* SCHLTR. (Orchidaceae), *Bomarea porschiana* (Alstroemeriaceae) and *Peperomia porschiana* TREL. (Piperaceae). Also a species of lichens bears his name: *Lecidea porschii* (JATTA) J. STEINER (Lecideaceae, Lecanorales).

## Publications

Curiously, none of the festschriften, notes or the obituary includes a list of Porsch’s publications. Such a list has been compiled by S. Sontag and the author and is published here as an Appendix. This seems all the more justified as the papers of 1931 and later are often based on the results of the Costa Rica expedition, and the ear-

lier ones often contain predictions that were later confirmed by that expedition.

## Otto Porsch and the Costa Rica expedition 1930

Details about Porsch’s Costa Rica expedition (dates, participants, travel routes, contacts with local scientists, historical circumstances etc.) are given by DÍAZ (this volume). Here, essentially, the scientific aims and results of the trip are addressed. The main reason for choosing Costa Rica as a destination was the richness of birds, especially hummingbirds. A few years before, PORSCH & SASSI (1928) had carried out studies on the distribution and species richness of hummingbirds in the neotropics, and this formed the basis for planning an expedition to Costa Rica. The start was on Feb. 19, arrival at Porto Limón on March 30, the return was via Hamburg, arriving at Vienna on Sept. 1.

Shortly after the expedition, PORSCH (1931) addressed briefly the aims and results of that expedition. Details were published in the following months, years and decades. The topics can be broken down as follows:

### Bird pollination

After he had visited Java in 1913-1914, Porsch published pioneering studies on the pollination of tropical plants by birds in the 1920s. Though the focus was on Old World plants (with pollination by perching birds), he made many predictions about neotropical plants, based on the study of cultivated and herbarium material. Porsch wanted to verify and deepen his predictions by field studies and chose Costa Rica for the extraordinary richness of hummingbird species. The aspects studied in the field included the characterisation of the hummingbird pollination syndrome, floral types, flower colours, presence/absence of fragrance, mechanical properties of the flowers, presence/absence of a perching site, nectar production, storage and prevention of nectar loss, dilution by rain, evolution of nectar-flowers in the families of angiosperms, abundance of hummingbird-pollinated flowers in the particular families and in the plant communities, steadiness of hummingbird visitation, visitation times, daily time spent for flower visitation, number of flowers visited per time unit, etc. Porsch and his collaborators were able to bring together an impressive number of facts and observations (with photographic and partly cinematographic documentation) and thus laid the foundation for a critical discussion of the phenomenon of bird pollination in the tropics.

Porsch’s expectations based on his previous investigations were not only confirmed, but by far outmatched. He was probably the first to fully gain the insight that

the neotropical flora is essentially shaped by the existence and involvement of hummingbirds in the pollination of plants, and he correctly interpreted the size and other physical and physiological properties of the hummingbirds as adaptations to flowers (and vice versa).

### Bat pollination

At Porsch's time, almost nothing was known on the pollination of flowers by bats. Though first observations of tropical bats visiting flowers date back to the 18<sup>th</sup> century (DE LA NUX 1772, see BAKER & HARRIS 1957), only the observations of HART (1897), more than one hundred years later, can be qualified as a first scientific record. HART (1897) observed bats visiting and "fertilising" the flowers of *Bauhinia megalandra* and (in a letter to Knuth) *Eperua falcata* (Fabaceae-Caesalpinioideae) in Trinidad. For a long time, these singular observations were either disregarded or considered as a negligible curiosity. Based on observations on cultivated trees of *Kigelia africana* (Bignoniaceae) in Java, PORSCH (1922) added new evidence. It was, however, only on the occasion of the Costa Rica expedition that he was able to provide definitive proof that flowers adapted to bat pollination exist (PORSCH 1931, 1932, 1939). *Crescentia cujete* and *C. alata* (Bignoniaceae) were treated as exemplary cases and visitation/pollination by *Glossophaga soricina* was reported (PORSCH 1931). In addition, PORSCH (1936) regarded (world-wide) *Kigelia*, *Oroxylum*, *Markhamia* and *Illipe* as unambiguous cases of bat pollination, and (correctly) predicted *Ceiba*, *Amphitecna*, *Pachira*, *Vriesea*, *Caryocar*, *Pilocereus*, *Crataeva* and many others as to be bat-pollinated. Today, bat pollination is known from a large number of neo- and palaeotropical plants (see DOBAT & PEIKERT-HOLLE 1985). Regarding the neotropical flora, HELVERSEN (1993) estimates that between 0.5% and 1% of the neotropical angiosperms are pollinated by bats.

### Hawkmoth pollination

Like bat-pollinated flowers, flowers pollinated by hawkmoths (sphingids) are nocturnal. The floral syndromes are similar and sometimes it is difficult to predict the kind of pollinator. During the Costa Rica expedition, Porsch studied a number of cacti and discriminated between the two types of flowers (PORSCH 1938, 1839). He found that the long-tubed flowers of *Epiphyllum*, *Selenicereus*, *Hylocereus*, *Epiphyllum* and many others are pollinated by hawkmoths, while those of *Pilocereus*, *Cephalocereus*, *Pachycereus* and others are pollinated by bats.

### Pollination by non-flying mammals

Porsch discussed the pollination of flowers by non-flying mammals at several occasions (PORSCH 1934,

1935, 1936a,b, 1937) and assumed marsupials to be legitimate pollinators of flowers in Australia. No observations seem to relate to Costa Rican plants. Porsch's idea that the flowers of *Couropita* (Lecythidaceae) might be addressed to mammal pollinators is obsolete; these flowers are deceptive and adapted to the pollination of large bees collecting pollen.

### Pollination of orchids

Like many botanists, Porsch was fascinated by the species richness and bewildering floral diversity of orchids. He studied several insect-pollinated orchids in Costa Rica. He observed *Catasetum* flowers to be visited exclusively by *Euglossa* bees and correctly related the long-distance attraction to the strong fragrance (PORSCH 1955). However, he did not recognise the fragrance as the true floral reward. Porsch was able to confirm bird-pollination in orchids such as *Cattleya*, *Comparettia* and *Aerides* which he had predicted in an earlier paper (PORSCH 1926).

### Vegetation of Costa Rica

In addition to his anthecological studies, Porsch studied and photographed characteristic plants and plant communities at various places and altitudes in Costa Rica. In total, more than one thousand photographs were taken. Soon after his return, PORSCH (1932b) published the results of these studies and a selection of photos in KARSTEN & SCHENCK's multi-volume book series "Vegetationsbilder" (23. Reihe, Heft 4-5).

### Additional aims/results of the Costa Rica expedition

Apart from the expedition leader and botanist Otto Porsch, the expedition party included specialists from various biological fields: Moriz Sassi (ornithology), Otto Koller (mammalogy), Eduard Reimoser (arachnology and entomology), Rudolf Zimara (herpetology), Georg Cufodontis (botany). More technical roles were played by F. Jarkowsky (photographer) and A. Stadler, who prepared and conserved the collected material in situ. W. Moller, a German zoologist, joined the expedition in Costa Rica, after the trip to the Osa Peninsula. All the biological material was collected for and has been deposited at the Natural History Museum in Vienna. In total, nearly 1.200 birds, 250 mammals, 250 amphibians and reptiles, 500 spiders and crustaceans, and over 50.000 insects were collected (BAUERNFEIND 1996). Some living animals were collected for the Vienna Zoo (Schönbrunn).

No attempt has been made here to record completely the papers that comprise the zoological results of the Costa Rica expedition. Inter alia, SASSI (1938/39) pro-

vided an amply annotated list of the bird taxa collected during the expedition. MOLLER (1931) published a remarkable study on the territorial behaviour of hummingbirds. KOLLER (1934) studied the mammals of Costa Rica as to their biogeographical aspects. The herpetological collections of O. Koller and R. Zimara were covered by WETTSTEIN (1934). Though no new taxa were described, this paper contained important additions to the Costa Rican herpetofauna. In particular, it was the first to include records from the Osa Peninsula (SAVAGE 2002). With regard to invertebrates, REIMOSER (1939) published a pioneering paper on the Costa Rican spider fauna. Parts of the zoological collections were examined by external specialists such as ATTEMS (1932; polydesmids) and ROEWER (1932; opilionids). CUFODONTIS (1933-1935) published several papers on the flora of Costa Rica, with descriptions of a considerable number of new species (including two magnificent species of *Heliconia* from the Osa Peninsula: *H. osaensis* and *H. pogonantha*); some Costa Rican plants have also been named in his honour, e.g., *Nectandra cufodontisii*, *Ocotea cufodontisii*, *Chaetolepis cufodontisii*, and REIMOSER (1939) named a spider after him: *Tenedos cufodontii*.

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## Appendix: Publications of Otto Porsch

compiled by S. Sontag & A. Weber

Note: The list may not be complete with respect to talk abstracts and reviews, but surely covers all original publications of scientific importance.

- PORSCH O. (1896): Die Winterknospen des deutschen Waldes. 29 Abb. — *Natur & Haus* **4**: 115-120.
- PORSCH O. (1903): Die Österreichischen *Galeopsis*-Arten der Untergattung *Tetrahit* REICHB.: Versuch eines natürlichen Systems auf neuer Grundlage — *Abh. K. K. Zool.-Bot. Ges. Wien* **2/2**: 1-126, Taf. 1-3.
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- PORSCH O. (1906/1908): Orchidaceae. — In: WETTSTEIN R. v. & V. SCHIFFNER (eds), *Ergebnisse der botanischen Expedition der Kaiserlichen Akademie der Wissenschaften nach Südbrasilien 1901. I. Pteridophyta und Anthophyta*. *Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl.*, **79**: 92-165, Taf. XI-XVIII; Nachtrag 310-311 (1908); preprint (1906).
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