Orchids

Botanical Jewels of the Golfo Dulce Region, Costa Rica

Orchids: Botanical Jewels of the Golfo Dulce Region, Costa Rica

Imprint

Publisher: Verein zur Förderung der Tropenstation La Gamba, University of Vienna, Rennweg 14, 1030 Vienna, Austria, www.lagamba.at, tropenstation.botanik@univie.ac.at

Editors: D. Rakosy, M. Speckmaier, A. Weber, W. Huber, A. Weissenhofer

Authors (alphabet.): C. Gegenbauer, W. Huber, F. Pupulin, D. Rakosy, M. Speckmaier, W. Wanek, A. Weber, A. Weissenhofer

Illustrations: see credits p. 198

Layout: M. Ringler

Language Editing: C. Dixon, A. Luck

Printing: Rema-Print, Vienna

Date of publication: June 2013

ISBN: 978-3-9502996-3-2

Book may be referenced as: Rakosy, D., Speckmaier, M., Weber, A., Huber, W., Weissenhofer, A. (eds) 2013. Orchids: Botanical Jewels of the Golfo Dulce Region, Costa Rica. Verein zur Förderung der Tropenstation La Gamba. Vienna, Austria.

Orchids

Botanical Jewels of the
Golfo Dulce Region, Costa Rica

Authors

for affiliations see page 136

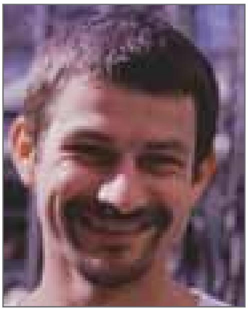
Christian Gegenbauer

Werner Huber

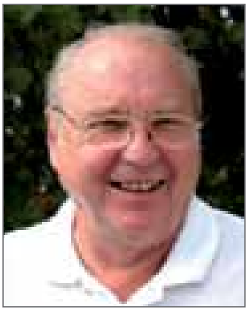
Franco Pupulin

Demetra Rakosy

Manfred Speckmaier



Wolfgang Wanek



Anton Weber

Anton Weissenhofer

Contents

The Tropical Research Station La Gamba

Wolfgang Wanek

The La Gamba Tropical Research Station is located near the small village of La Gamba, on the edge of the Esquinas rain forest. The Esquinas rain forest exists thanks to the conservation work of Michael Schnitzler, who collected financial donations in Austria and forwarded them to the Costa Rican government, which in turn purchased large tracts of forest from landowners in south-western Costa Rica. This rain forest, which is also known as the *Regenwald der Österreicher* ("Rainforest of the Austrians"), has since become part of the Parque Nacional Piedras Blancas and is a valuable link in the impressive chain of national parks in Costa Rica. The La Gamba Tropical Research Station is situated close to the national park and its luscious primary tropical rain forests. Being located near the village of La Gamba also means that the station allows access to a mosaic of managed land, including oil palm and tree plantations, pastures, rice fields and residential gardens. It therefore offers easy access to a wide range of natural and man-made ecosystems. The station is run by the *Verein zur Förderung der Rettung des Esquinas-Regenwaldes in Costa Rica* ("Association for the advancement of the La Gamba Tropical Research Station"), an Austrian non-profit organisation dedicated to fostering research and teaching at the station. With the financial support of Schnitzler's original foundation – the *Verein Regenwald der Österreicher* – and of the *Verein zur Förderung der Rettung des Esquinas-Regenwaldes in Costa Rica*, the Austrian Ministry of Science and Research and the University of Vienna, the station has been variously expanded and improved during the last ten years, and now comprises several buildings (including an air-conditioned laboratory) and a botanical garden. It provides comfortable living and research facilities for over 30 visitors at a time. Thanks to this infrastructure, the station is on the threshold of becoming an internationally established research institution and educational centre, focusing on the scientific exploration and conservation of Neotropical rain forests. Since its foundation, many scientists have used it to carry out field research in the Esquinas rain forest, while visitors have enjoyed its beautiful surroundings.

Numerous scientific publications have resulted from research performed at the La Gamba Tropical Research Station, including around 70 doctoral and master's theses. This scientific work focused initially on the flora and vegetation of the forest, but has since broadened to include a wide range of other topics, such as animal–plant interactions, herpetology, ornithology, entomology, limnology, plant ecophysiol-


Main building of the Tropical Research Station La Gamba

ogy, biogeochemistry, ecosystem ecology, geography and sociology. Around 60 field courses and excursions have been held, enabling students and scientists from universities all over the world to visit and study the Piedras Blancas National Park. Much of the biological data that has recently been gathered, as well as older research, indicates that these lowland forests rank among the most diverse and productive lowland rain forest ecosystems in Central America.

As well as supporting research and teaching activities, the station works with the inhabitants of La Gamba through a series of projects aimed at improving their living conditions. These projects are run partly in collaboration with the nearby Esquinas Rainforest Lodge, an example of sustainable ecotourism also founded by Michael Schnitzler.

The Association is particularly keen to provide our visitors, as well as all those who love and are fascinated by the tropics, with information about the biology and ecology of the local and regional rain forests and the adjacent cultivated land. In 2001, the station published an *Introductory Field Guide to the Flowering Plants of the Golfo Dulce Rain Forests, Costa Rica*, followed by a series of 11 full-colour brochures: *The Amphibians and Reptiles of the Golfo Dulce Region, Costa Rica*; *The Birds of the Golfo Dulce Region, Costa Rica*; *Das Leben hier und dort – La vida aquí y allá*; *Ecosystem Diversity in the Piedras Blancas National Park and Adjacent Areas (Costa Rica)*; *Fruits in Costa Rican Markets*; *Corbiculate Bees of the Golfo Dulce Region, Costa Rica*; *Dragonflies of the Golfo Dulce Region, Costa Rica*; *Butterflies of the Golfo Dulce Region, Costa Rica*; *Stream Ecosystems of Costa Rica*; *Lichens of the Golfo Dulce Region, Costa Rica*; and *Creating a Forest – Creando un Bosque*. A scientific monograph, *Natural and Cultural History of the Golfo Dulce Region, Costa Rica*, was also published in 2008.

We are now pleased to add a new full-colour booklet to this series, covering the orchids of the Golfo Dulce region. The booklet offers an insight into the general biology and flower morphology of orchids, as well as their pollination mechanisms, systematics, habitat adaptation and cultivation. Orchids are the most diverse plant family in Costa Rica and this booklet describes around 70 species from the Golfo Dulce region. We hope that it will be a source of information and joy to all those who love the tropics and its orchid flora, as well as scholars, students, teachers and researchers at universities, and – of course – all the friends of the Rainforest of the Austrians and the La Gamba Tropical Research Station.

The orchid garden of the Tropical Research Station La Gamba

For further information, see:
www.lagamba.at
www.regenwald.at

The Rainforest of the Golfo Dulce Region

Werner Huber & Anton Weissenhofer

The Golfo Dulce region is located at the southern corner of Costa Rica's Pacific coast, near the border with Panama, in an area containing the Corcovado and Piedras Blancas (Esquinas forest) national parks. The region's forests are the only remaining moist and wet evergreen lowland forests on the Pacific slope of Central America. The elevation of the region ranges from sea level to 745 m on the Cerro Rincón, Peninsula de Osa, and 579 m on the Cerro Nicuesa in the Esquinas forest. Annual precipitation is about 6000 mm, with a short dry season from December to March. The relief is strongly structured at the landscape level and contains many microhabitats and niches. The region contains diverse soil types, and it has high vegetation dynamics (i.e. many forest gaps). All of these factors, together with the biogeographical position of the Golfo Dulce region, have produced a highly species-rich forest, with about 2.700 species of higher plants and around 145 mammals, 50 amphibians, 90 reptiles, 370 birds and numerous insects.

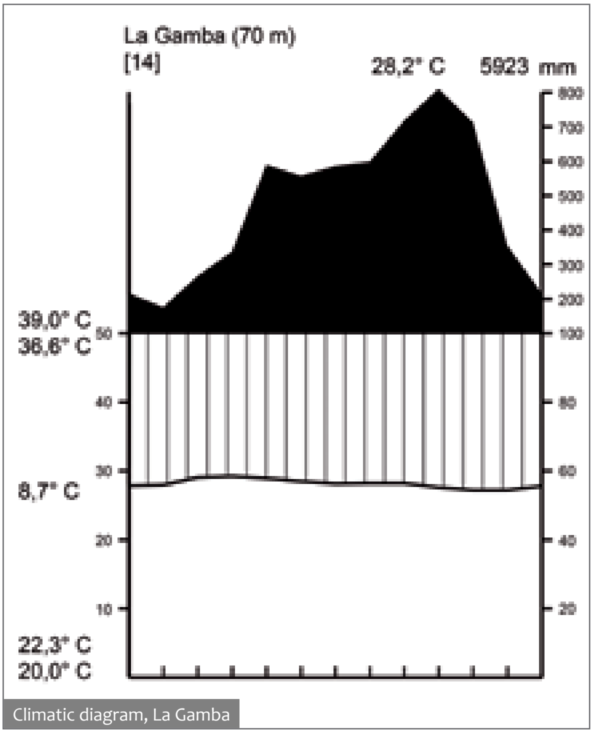
The moist and wet evergreen lowland forests contain trees up to 60 m high, including *Anacardium excelsum* (Anacardiaceae), *Parkia pendula* (Fabaceae–Mimosoideae), *Carapa guianensis* (Meliaceae), *Brosimum utile* (Moraceae) and *Caryocar costaricense* (Caryocaraceae) – most of which retain their foliage throughout the year. Palms are a typical feature of the Esquinas forest, which contains around 45 species, including *Socratea exorrhiza*, *Iriartea deltoidea*, *Welfia regia* and *Asterogyne martiana*. *Heliconia* herbs grow conspicuously near streams and in forest gaps. Lianas, such as *Bauhinia* sp. (Fabaceae–Caesalpinioideae) and *Entada* sp. (Fabaceae–Mimosoideae), vines and epiphytes (Bromeliaceae, Orchidaceae) are often found on trees. About 233 species of orchids and 40 species of bromeliads are distributed in the region. Hemiepiphytic plants of the genus *Clusia* are abundant in the very wet parts of the forest, while fig trees (*Ficus*) are more frequent in the drier parts (e.g. on the Corcovado plains). Epiphyllic plants such as mosses and lichens are abundant, mainly in the very wet gorges. On the coast, the coconut palm (*Cocos nucifera*) and the tropical almond tree (*Terminalia catappa*, Combretaceae) are the most conspicuous plants; in the mangroves, it is the red mangrove (*Rhizophora mangle*, Rhizophora-

The Chorro waterfall near La Gamba

ceae) and the tea mangrove (*Pelliciera rhizophorae*, Pellicieraceae). As well as the various types of primary and secondary forest, the area contains other kinds of habitat such as pastures, pools, rivers, cultivated land and various plantations (such as oil palm, teak and manioc).

Orchids are abundant in the forest, especially as epiphytes. Many local and exotic species can be found at the Casa Orquideas on the coast of the Golfo Dulce, where Trude and Ron McAllister have compiled a fascinating collection of orchids (and other plants) in their garden. A large variety of local orchids are also grown in the orchid garden "Casa Richard Weixler" at the La Gamba Tropical Research Station.

Costa Rica's geographical position on the "bridge" between North and South America, and the fact that some parts of the country – like the region close to the Golfo Dulce region – formed a kind of refuge for tropical animals and plants during the last ice age, has led to remarkable biogeographical patterns. The region contains numerous range-restricted plants and animals, many of which reach their northern limits in southern Costa Rica. An extensive system of trails in the Corcovado and Piedras Blancas national parks (La Gamba) offers wonderful insights into tropical rain forests, and the region is an excellent place for naturalists to learn about tropical nature.



Climatic diagram, La Gamba

A giant Kapok tree (*Ceiba pentandra*) in the Piedras Blancas National Park

Welcome to the Fascinating World of Golfo Dulce Orchids

Demetra Rakosy, Manfred Speckmeier & Anton Weber

Plant lovers and botanists alike have long been fascinated by orchids. This results from three main factors: the enormous number of species; the wide variation in the size, form and coloration of the flowers; and the incredible ingenuity of the flowers in ensuring pollination.

Nobody knows the exact number of orchid species. According to recent analyses, it probably lies between 22,000 and 26,000 (with some estimates even reaching 35,000). This would mean that the orchid family comprises around 10% of all flowering plant species, which is rivalled only by the daisy family (Asteraceae). Orchids are classified into just under 900 genera. Some of these genera are large, comprising more than 1000 species (such as *Bulbophyllum*, *Epidendrum* and *Pleurothallis*), while others are smaller, or even monospecific.

Many orchids have large, colourful and sometimes quite bizarre flowers, so it is no wonder that they generate enormous horticultural interest. In contrast to the terrestrial orchids of temperate regions, tropical orchids are relatively easy to grow and hybridise, and more than 100,000 hybrids and cultivars have been created to date through selection and artificial hybridisation. Not all orchids have received equal attention, however. Many of them, known as "botanical" orchids, have small and inconspicuous flowers, but – when seen under a lens or stereo-microscope – they reveal themselves to be as just beautiful as their showier relatives.

Orchids are found all over the world, except in the very coldest and hottest regions (i.e. on the Arctic and Antarctic ice shields and in certain deserts). The richest concentrations of genera and species are in the tropics of the Old and New Worlds. For instance, while temperate North America contains some 25 genera, tropical America is home to almost ten times as many (200–250). Within tropical America, Costa Rica is something of an orchid hot-spot. With over 1300 species (in about 180 genera) recorded so far, orchids represent the most species-rich family of flowering plants in the country (out of 324 families, 2350 genera and roughly 10,000 species are represented). On average, every eighth Costa Rican plant species is an orchid!

This booklet covers the orchids of the Golfo Dulce region of Costa Rica. Situated in the southwestern part of the country, and encompassing the distinctively shaped Osa Peninsula, the region is a paradise for nature and for nature lovers. It measures *c.* 1300 km^2 and contains two national parks – Corcovado National Park, (established in 1975 and measuring 424 km^2) and Piedras Blancas National Park (established as a separate national park in 1999 and measuring 148 km^2) – two major forest reserves (the Golfo Dulce Forest Reserve, with an area of *c.* 600 km^2, established in 1979 and connecting the Corcovado and Piedras Blancas national parks; and Golfito National Wildlife Refuge, established in 1985 and measuring 28 km^2) and privately owned protected areas. Although the Golfo Dulce region covers only 2.5% of the area of Costa Rica, it harbours over 230 orchid species in 65 genera – i.e. around 18% of the total number currently known from the whole country. This is even more remarkable given the lack of montane and upper montane forests with cool climate and permanent cloud cover, which are significant orchid habitats elsewhere. The highest elevations in the area – Cerro Rincón on the Osa Peninsula, and Cerro Nicuesa in the Piedras Blancas National Park – are only *c.* 750 m and 580 m a.s.l., respectively. Such altitudes are too low, and the associated areas too small, to harbour a rich and specialised montane orchid flora.

The booklet contains descriptions of over 70 species, accompanied by colour photos and drawings. As with any selection, the one presented here is somewhat arbitrary, although we have tried to include those orchids that visitors to the Golfo Dulce region are most likely to encounter. Most are "botanical orchids", without large or spectacular flowers. Some of the species are relatively common and can often be seen growing epiphytically on fruit trees or on trees along roads, but most are restricted to primary forests and often grow high up in the trees. These can only be seen with binoculars, or when rotten branches that house epiphytes fall to the ground. Terrestrial orchids are the easiest ecological group to spot in the forest, but these are relatively rare, and most species are epiphytes. Some other orchids have been included in the booklet because of their peculiar pollination biology.

The species are arranged alphabetically by scientific name. Each description has the following format: (1) name and first publication of the currently accepted species name (the basionym is given where appropriate; synonyms are cited only in exceptional cases, such as when a genus has been split quite recently; English and Spanish names are given where available); (2) etymology (i.e. the meaning of the generic name and the specific epithet; the generic name is explained only for the first species of each genus); (3) taxonomic history and/or further information; (4) classification (i.e. the position of the genus in terms of subfamily, tribe and subtribe); (5) description; (6) distribution; (7) ecology (i.e. habitat, altitude, etc.); (8) flowering (because some species lack sufficient data, the flowering times given are mostly estimates); (9) pollination biology (if no data is available, the pollination biology of related species or the genus is given instead; general information on the genus is only given for the first species of each genus); (10) further remarks (e.g. how the species can be distinguished from related species in the same area); (11) references (in short form; full references are provided at the end of the booklet).

The booklet also includes some more general chapters on orchids, covering subjects such as the morphology of the plant body, growth patterns, flower structure, pollination, fruit structure, seed dispersal, history, classification and cultivation. The main text does not include extensive references, since general information can be found in most books on orchids. More scientific sources that are recommended for further reading include van der Pijl & Dodson (1966), Dodson & Gillespie (1967), Arditti (1992), Pridgeon (1992), Dressler (1993a), Endress (1994), van der Cingel (1995, 2001) and Pridgeon *et al*. (2003–2009). Spanish-speaking readers will find the most important general information (including on horticulture) in Fischer (2006), Freuler (2006, 2008) and Rollke (2008, 2011), while good German-language sources include Brieger *et al*. (1970–2002, based on Schlechter, 1915), Bechtel *et al.* (1985), Senghas (1993) and Dressler (1997).

At the end of the booklet is a glossary, a full list of references and, as an appendix a checklist of all orchid species reported so far from the Golfo Dulce region. Note that it is likely that many more species are yet to be discovered and recorded, especially in the less accessible parts of the Corcovado National Park. If you are visiting the national parks and forest reserves, we encourage you to keep your eyes peeled and to carry a camera with you in case you spot anything new! Please do not be tempted, however, to pick or collect any orchids. If you find something interesting, take a photograph and tell us about it. Remember that the best way to appreciate orchids is to see them in their natural habitat and conserve them for future generations.

We hope you find this booklet interesting, and that you enjoy visiting the natural paradise that is the Golfo Dulce!

Platystele sp. (encountered by M. Speckmaier and T. Rennebarth)

Plant Body, Growth Patterns and Inflorescence Structure of Orchids

Anton Weber & Manfred Speckmaier

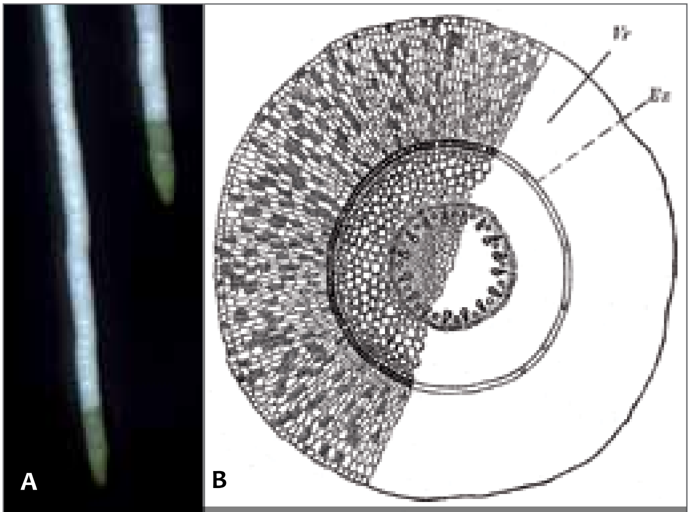
Plant organs

As in almost all flowering plants, the plant body of orchids is composed of three basic organs: leaves, stem (axis) and roots. The leaves are the primary photosynthetic organs, the stem is the structure bearing the leaves and serves for conducting water and nutrients, and the roots primarily serve for water and nutrient uptake and to anchor the plant. Both the stem and the roots, however, may serve other functions.

Leaves. The leaves emerge at the "nodes" of the stem. They are undivided, with parallel or curved veins (rarely net-veined) and are often somewhat fleshy. The leaf base is often widened into a distinct sheath. The leaves are alternately arranged, usually forming two ranks (distichy; e.g. → *Arundina graminifolia*), but sometimes forming a flat plane (→ *Dichaea poicillantha*) or a fan (→ *Ornithocephalus bicornis*). In terrestrial orchids, the leaves are often arranged spirally or in a basal rosette (e.g. → *Pelexia funckiana,* → *Prescottia stachyodes*). The leaf-blade may be filiform (thread-like), grass-like, lanceolate (lance-shaped), ovate (egg-shaped), cordate (heart-shaped) or orbiculate (round) in shape. In most orchids, the leaves are perennial, living for several years. In some tropical orchids with pseudobulbs, the leaves are shed seasonally and new leaves are formed with the new pseudobulb. For orchids that lack green leaves entirely, see below.

Stem, pseudobulbs. The stem may be elongate (with long internodes) or short, bearing the leaves in close succession. In many epiphytic orchids, it is thickened and forms a pseudobulb that stores water and nutrients. Because there are no stomata, photosynthesis seems to be limited. In homoblastic orchids, the thickening covers several internodes (e.g. → *Mormodes*, → *Caularthron* – here the pseudobulbs are hollow and house ants); in heteroblastic orchids, the thickening is restricted to a single internode (e.g. → *Leochilus*, → *Maxillaria*, → *Oncidium*). In the latter case, the leaves are borne at the base and/or at the apex of the pseudobulb.

Roots, aerial roots. Terrestrial orchids have roots that are buried in the ground and exhibit the typical anatomy of a root. Epiphytic orchids have "aerial roots", serving two functions: clinging to the bark of the stem or branches of a host tree, and thus anchoring the plant in the substratum, and water (and nutrient) uptake and storage. The aerial roots are thick, cylindrical, and anatomically highly modified. They are white or grey when dry, and green when filled with water. The water is stored in the spongy outer cell layers – the so-called *velamen* or *velamen radicum*. These layers, a multiple epidermis, consist of dead cells that are able to absorb moisture and nutrients from the atmosphere. The green colour of the water-filled roots comes from the chloroplasts in the living cells below the velamen. The surface of the roots of-



A Aerial roots of an epiphytic orchid; note silvery, air-filled surface tissue (velamen radicum) below the green, growing tip. **B** Cross-section. Ex = exodermis, Vr = velamen radicum. From Troll (1943: Fig. 2148).

ten exhibits distinctive "track marks" known as pneumatodes. These structures perform a similar function to stomata, allowing the roots to exchange gases and thus to perform photosynthesis. While, in leafy species, the aerial roots play only a marginal role in photosynthesis, in leafless epiphytic orchids – with the leaves reduced to tiny, functionally irrelevant scales – they are the only photosynthetic organs. This condition is found, amongst others, in the genera *Taeniophyllum* and *Dendrophylax* (which includes the Cuban ghost orchid, *D. lindenii* – not to be confused with the Holy Ghost orchid, *Peristeria elata*, the national flower of Panama). In some cases, the aerial roots are associated with symbiotic fungi or bacteria. In the latter case, the orchid takes up nutrients from bacteria that fix nitrogen from the air.

Life forms and growth patterns

All orchids are fundamentally perennial herbs. While orchids of the wet tropics can grow, flower and fruit continuously, those that live in seasonal climates have developed distinct strategies to survive in adverse environmental conditions.

Terrestrial, epiphytic and lithophytic orchids. Frosty and hot/dry periods can be best survived through structures that lie buried in the ground during the unfavourable season. This is commonly achieved with underground corms (e.g. *Orchis* spp.) or short rhizomes with fleshy roots (e.g. → *Pelexia funckiana*, → *Wullschlaegelia aphylla*). Compared to epiphytic orchids, terrestrial orchids are rare in tropical forests. Examples from the Golfo Dulce region include → *Habenaria monorrhiza*, → *Pelexia funckiana*, → *Sobralia decora* and → *Wullschlaegelia aphylla*.

Non-terrestrial orchids occur only in the tropics and subtropics, in the form of epiphytes. These orchids normally grow high up on the trunks and branches of trees. The advantage is the higher light intensity available in the canopy (only 1%–2% of the sunlight reaches the forest floor); the disadvantages are the loss of soil contact, entailing problems of anchorage and water supply. Epiphytic orchids are, therefore, permanently threatened by fall and/or desiccation. Orchids have developed remarkable strategies to minimise the danger of drying out, namely the formation of water storage structures such as aerial roots and pseudobulbs. Extreme cases of epiphytic growth are the obligate twig epiphytes (e.g. → *Erycina crista-galli*, → *Notyllia barkeri* and → *Trizeuxis falcata*). These orchids grow exclusively on the twigs and small branches of trees and are characterised by their minute size, often with a fan-like arrangement of laterally compressed, unifacial leaves (e.g. → *Ornithocephalus bicornis*), a highly abbreviated life cycle (6–12 months) and hooked seeds (Chase and Palmer 1997).

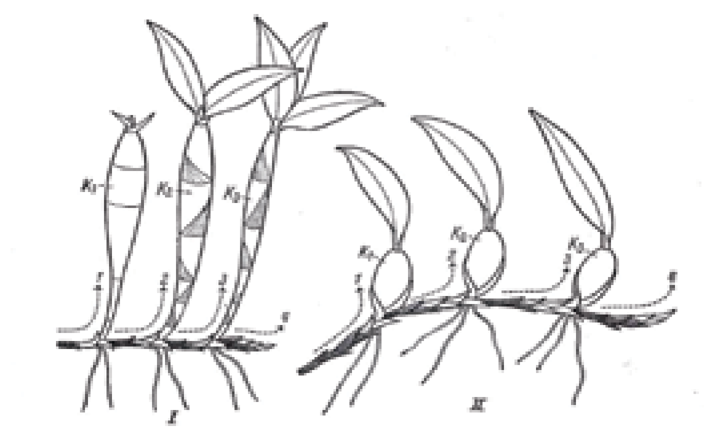
The terrestrial and epiphytic growth patterns are not always sharply separated. There are many tropical orchids that grow partly on the ground or epiphytically at the base of tree trunks (e.g. → *Sobralia* spp., → *Warrea costaricensis*). Other species are lithophytic, being adapted to growth on rocks or gravel. Most of these species are facultative lithophytes, growing also as terrestrials or epiphytes (e.g. → *Epidendrum schlechterianum*, → *Prescottia stachyodes*).

Autotrophic and myco-heterotrophic (parasitic) orchids. There are several terrestrial genera, scattered over different alliances of the monandrous orchids, that do not produce normal green leaves, but only pale yellowish or brownish scales along the stem. These orchids are called "mycotrophic" or "myco-heterotrophic". They are basically parasites that exploit fungi, which is remarkable as it is the reverse of the usual situation: the fungus is normally the parasite (taking up organic compounds through the mycelium) and the host is the plant/animal. Orchids have turned the tables: they parasitise the mycelium of saprophytic fungi and steal the organic matter produced by the fungus. There are two such species in the Golfo Dulce region, → *Wullschlaegelia aphylla* and *W. calcarata*.

In principle, every orchid is a part-time parasite. The tiny, dust-like seeds have no repository of energy and need a fungus for germination. The plant only becomes self-sustaining, and is no longer completely dependent on the fungus partner, after the first green leaves have developed. In mycotrophic species, this exploitative relationship is maintained throughout the orchid's life.

Monopodial and sympodial growth. The growth patterns of epiphytic orchids can be classified into two categories: monopodial and sympodial. The term *monopodium* (adj. monopodial) is derived from the Greek

Campylocentrum micranthum, a monopodial orchid; note growing plant apex and axillary position of inflorescences



Sympodial growth of homoblastic (I) and heteroblastic orchids (II); for explanations, see text. From Troll (1937: Fig. 624)

monopous (= one-footed, consisting of a single foot or single unit) and means that the stem of a plant consists of a single, dominant stem that grows continuously. The continuous growth may be temporarily interrupted (if the plant needs to survive a climatically adverse period), but is resumed from the same meristem when favourable conditions return. Consequently, monopodial orchids have a leafy stem that grows continuously over many years (theoretically indefinitely). Inflorescences are produced from the axils of the leaves. Monopodial epiphytic orchids are relatively rare, a good example from the Golfo Dulce region is → *Campylocentrum micranthum*.

The sympodial pattern is very different (*sympodium* literally means a structure consisting of several "feet"). Here, the plant stem is composed of successively formed units, and each unit represents the axillary shoot of the preceding unit. Growth continues by the formation of an axillary bud situated near the top or at the base of the unit. Sympodial growth is characteristic of epiphytic orchids that form pseudobulbs (e.g. species of → *Bulbophyllum*, → *Maxillaria* and → *Oncidium*). A succession of pseudobulbs is thus a succession of axillary shoots, each ending in a pseudobulb.

Though sympodial growth is characteristic of orchids with pseudobulbs, it is not restricted to that group. For example, in → *Pleurothallis* and allied genera, the consecutive branches resemble complete unifoliate plants and are called 'ramicauls'.

Inflorescence structure

The inflorescences of orchids are fairly uniform. They usually form spikes – inflorescences with an elongated axis and sessile lateral flowers (the long, rod-like inferior ovary of the flower often resembling a pedicel).

All orchid flowers are lateral in origin, but the uppermost flower may curve upwards and may seem to occupy a terminal position. This is often the case when the inflorescence is reduced to a single flower.

The number of flowers per inflorescence varies considerably, ranging from one to several hundred. The production of more flowers can be through elongation of the inflorescence axis (with a relatively dense succession of flowers), branching, or both. Branched inflorescences are often referred to as "panicles", but in correct botanical terminology they represent double spikes, triple spikes, and so on (→ *Lockhartia acuta*, → *Oncidium polycladium*). The arrangement of the flowers along the rachis is either in a spiral (e.g. → *Pelexia funckiana*) or, more commonly, in two opposite ranks (distichous arrangement).


Caularthron bilamellatum, homoblastic pseudobulbs


Trigonidium egertonianum, heteroblastic pseudobulbs in close succession

The sequence of flower opening may be successive or roughly simultaneous. Successive opening allows for a longer time of flower presentation to pollinators, while simultaneous blooming increases the showiness of the inflorescence (the "big bang effect"). Large flowers are expected bloom successively, and small ones simultaneously, but this rule-of-thumb is often broken.

The longevity of the orchid flowers is strongly correlated with pollination. Unpollinated flowers may remain open for several weeks, while pollinated flowers wither quickly, as one can see readily with ornamental orchids. The main events that trigger floral senescence are removal of the pollinia, deposition of pollen on the stigma, or a combination of the two.

There are some orchids where the flowers last for only one day (e.g. species of → *Sobralia*). To ensure pollination, all individuals in a given region open on the same day. This is triggered by environmental factors.

The Orchid Flower

Anton Weber & Demetra Rakosy

Although there are an incredible number of orchid species and a wide diversity of flower forms, orchid flower architecture shows a surprising uniformity. Firstly, it is important to note that the orchid flower can be interpreted as a variant of the lily flower. J. W. von Goethe was among the first to notice their common structure, asking "Who could blame us if we referred to orchids as monstrous lilies?" Like lilies, orchids have two alternating whorls of tepals, each consisting of three segments, primitively six stamens (also in two whorls of three), and a gynoecium composed of three carpels. There are, however, significant modifications that may represent a significant evolutionary progression, as follows. (1) The floral symmetry switched from radial symmetry to monosymmetry (zygomorphy); this is manifested especially in one of the inner petals, known as the "lip" (see below). (2) The fertile stamens were reduced in number to three, two or one; the others remain as staminodes or are absent. (3) The gynoecium changed its position from superior to inferior. These elementary progressions are accompanied by numerous subtle differences in the construction of the flower, the most significant of which are discussed below.

Flower symmetry. All orchid flowers are monosymmetrical (zygomorphic), but the degree of symmetry shows considerable variation. In the most primitive orchids (such as those with three fertile stamens: the Malesian genus *Neuwiedia*), the lip is almost identical to the other tepals. The degree of zygomorphy increases with the evolutionary elaboration of the lip. In many orchid flowers, the lip is the largest and structurally most elaborate part of the flower, and, in terms of coloration and showiness, it is also the most conspicuous and eye-catching. In other orchids, the lip is reduced to a tiny structure surrounded by large tepals and the monosymmetry appears to have reverted to radial symmetry (e.g. → *Stelis*).

Resupination. When seen from the front, the lip of an orchid flower usually points downwards. This position, and the associated orientation of the flower, is a secondary development. In ontogeny, the lip actually starts as the uppermost of the three inner tepals. By bending over (in the case of pseudoterminal solitary flowers such as *Cypripedium* spp.) or, more frequently, by rotating the inferior gynoecium through 180°, the flower is brought into an inverted position, with the lip pointing downwards. Through this "resupination", the flower is brought into an advantageous functional position. The lip is no longer just an eye-catching structure that helps to attract pollinators, but also serves as a landing area and site of activity for those pollinators.

Some orchid flowers are not resupinate, and their flowers (with the lip in an upright position) operate differently (→ *Catasetum maculatum*, → *Prescottia stachyodes*). Interestingly, a few orchid flowers turn their flowers through 360°, which again results in an upright lip position (known as "hyper-resupination").

Perianth. This is the collective term for the sterile phyllomes of a flower. In most monocotyledons, the perianth consists of two whorls of three, and this is also the case in the orchid family. The segments of the outer whorl are known as the outer tepals, and those of the inner whorl are known as the inner tepals. Although morphologically problematical, orchidologists are accustomed to referring to the outer tepals as the "sepals" and to the inner tepals as the "petals". This convention is followed here for convenience, but note that the sepals and petals of orchids are not homologous with the sepals and petals of dicotyledons (i.e. they did not evolve from the same ancestral organs).

Although the lip is morphologically a segment of the perianth, it is conventionally seen in contrast to the other five segments of the perianth. In open, spreading flowers, these other tepals may form a kind of shield that contrasts with the lip in structure and coloration.

Sepals. The sepals may be similar in size, shape and coloration, narrow or broad, blunt, acute or (in some fly-pollinated or wasp-pollinated species) long-acuminate or tailed. The dorsal sepal (in resupinate flowers) can be quite different from the lateral ones and must be treated separately in the descriptions. The two lower (= lateral) sepals are sometimes fused at the margins to form a synsepal (e.g. → *Lepanthes* spp.,

Oeceoclades maculata, resupinate flower

Catasetum maculatum, non-resupinate flowers

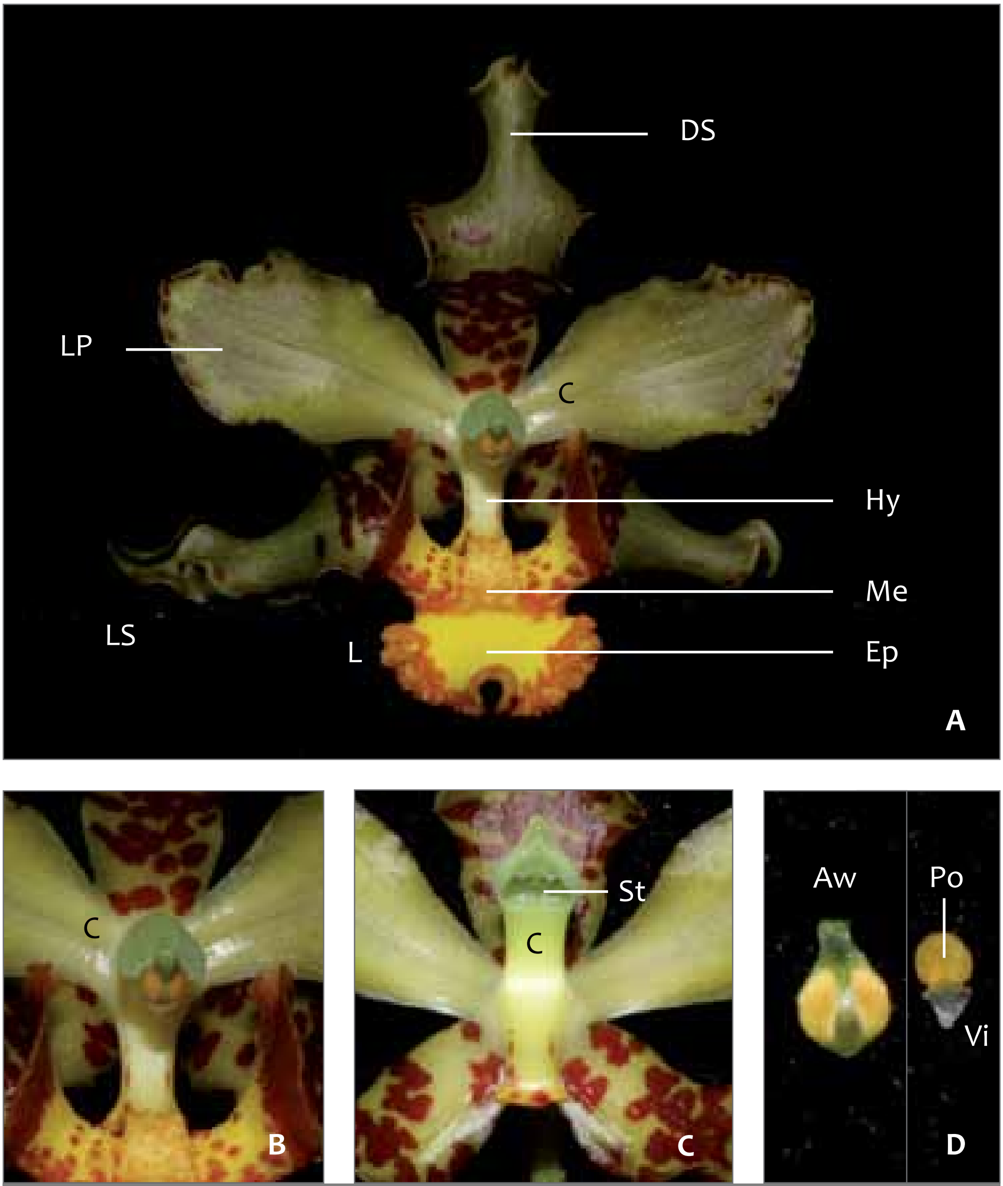
→ *Specklinia* spp.). In such flowers, the petals and the lip are often small, and the flower thus becomes distinctly bilabiate.

Petals. The petals correspond to the inner tepals of other monocotyledons. Technically, the lip is a petal, but because of its (usually) more elaborate structure, it is generally treated separately. The two remaining petals are in a lateral position. They may resemble the sepals in size, shape and coloration, but they usually differ from them in some way.

Lip (labellum). The lip is the most interesting and distinctive segment of the perianth. It is not immediately obvious that the lip corresponds to a perianth segment. Charles Darwin was the first to suggest that the lip was a composite structure that also includes parts derived from the androecium, a theory that was supported by some 20th-century orchidologists. In recent decades, however, study of floral ontogenesis using scanning electron microscopy has shown that Darwin's interpretation is flawed: like the other segments of the perianth, the lip takes its origin from a single primordium and there is no indication that other floral organs are involved in its formation (Kurzweil 1999, Kurzweil and Koczyan 2002). Staminode primordia other than those associated with the fertile stamen(s) may appear during floral ontogenesis, but are not associated with the lip.

In most orchids, the lip is a highly modified structure, differing from the remaining perianth segments in many ways. It may be spreading or, with considerable modification and specialisation, transformed into a slipper-shaped pouch, as in *Cypripedium* or *Phragmipedium* (Cypripedioideae). In many alliances, the lip is articulated into three portions – the hypochile (basal portion), the mesochile (intermediate or middle portion) and the epichile (terminal portion) – and each may be further subdivided; for instance, the epichile may be divided into two or three lobes. The upper surface of the lip may show distinct excrescences, such as fleshy lumps, ridges, keels or plates, which are collectively referred to as *calli* (singular *callus*).

Stamens and staminodes. Of the six stamens of the lily flower, only a subset are retained in orchid flowers, either as fertile stamens or as sterile, rudimentary staminodes. Three groups of orchids can be distinguished, based on the number of fertile stamens. The triandrous group (three fertile stamens) is represented by the single genus *Neuwiedia* (Apostasioideae). The diandrous orchids, with two fertile stamens and a distinctive staminode between, are represented by *Apostasia* (Apostasioideae) and the slipper orchids (Cypripedioideae). The large majority of orchids (99%) are monandrous. In these



Structure of a complex, monandrous orchid flower (*Cyrtopodium willmorei*). **A** Total view; **B** Central part with column enlarged; **C** Column with anther wall and pollinarium removed, note stigma; **D** Anther wall and pollinarium enlarged. DS Dorsal sepal, LS Lateral sepal, LP Lateral petal, L Lip, Hy Hpochile, Me Mesochile, Ep Epichile, C Column, St Stigma, Aw Anther wall, Po Pollinarium, Vi Viscidium

species, the single fertile stamen is flanked by two staminodes (i.e. the reverse of diandrous orchids). The remaining staminodes are fairly inconspicuous or absent.

Column. There is always some degree of fusion between the stamens, the staminodes and the style in the orchids. In triandrous orchids, only the basal parts of the filaments and the style are fused, and the distal parts – filaments bearing the anthers, and a style with a three-parted stigma on top – remain free. In the diandrous and monandrous orchids, the stamens are seamlessly fused to a structure known as the column. The column is often laterally winged, the wings partly representing staminodes. In the monandrous orchids, the anther is seated in a clearly defined area at or near the top of the column, known as the clinandrium. An important feature of this group is the modification of one of the stigma lobes into the rostellum. The rostellum is thin-walled and a sticky substance is produced in its interior. In some orchids (e.g. *Listera*, *Neottia*) the rostellum wall becomes lacerated when it comes into contact with a visiting insect, and the viscid contents are released explosively, catapulting them onto the insect's head. On contact with the anther, the glue attaches the pollen to the insect's head. In more elaborate examples, a viscidium (a small sticky pad or thin lamella with a sticky base) is formed, which is connected by a short stalk (caudicle or frenicle; see below) to the compact pollen mass (pollinium) of a theca or pollen sac. The 1–8 pollinia, the stalk(s) and the viscidium collectively form a structure known as a pollinarium. The pollinarium is the transport unit for one or more pollinia from flower to flower, with the pollinator being the vehicle.

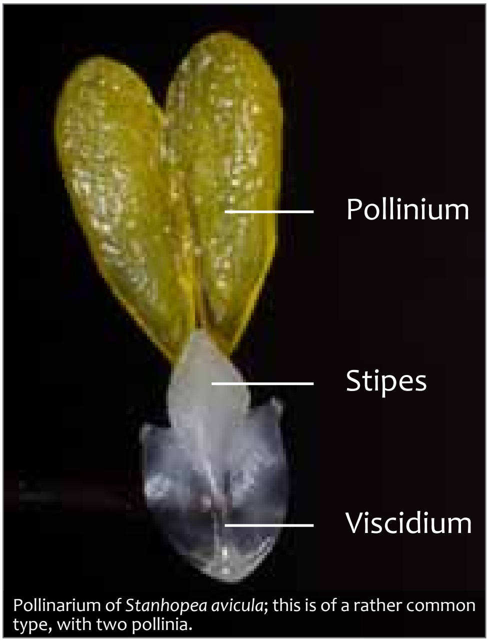
Column foot. In many orchids, the base of the column forms a ventral extension to which the lip is attached. The bases of the lateral sepals, as well as those of the petals, are attached to this extension and are thus conspicuously broadened. A prominent column foot is most characteristic of the large Asiatic genus *Dendrobium* (of which many species are grown as ornamentals). Examples from the Golfo Dulce orchids include → *Bulbophyllum oerstedii*, → *Christensonella uncata* and → *Scaphyglottis behrii*.

Anther: structure and position. Anthers are found on top of distally free filaments only in the primitive orchids *Neuwiedia* and *Apostasia*; in other taxa, they are incorporated into the column. Each of the two halves of an anther (theca) has two locules, inside which the pollen grains are produced (after meiosis of the pollen mother cells). Each locule then produces a pollinium, making two per theca and four per anther. In most orchids, however, the two locules of a theca fuse in the course of pollen development (by degeneration of the locular wall), so that each theca produces a single pollinium (i.e. two pollinia per anther). In rare cases, the pollen locule is further subdivided into two halves so that eight chambers and pollinia are formed in total.

The anther either opens along longitudinal slits (as in Orchidoideae), or its frontal wall falls off completely when touched. Anther opening is necessary in order for the pollinia to be freed from the anther after the viscidium has come into contact with a pollinator.

In some monandrous orchids, the position of the anthers is upside-down, such that the top of the anther bends down by almost 180°, whereby the apex of the anther and the pollinia become associated with the rostellum and the viscidium, respectively. This type of anther is called acrotonic, and is characteristic of the subfamily Orchidoideae. In contrast, in the basitonic anthers/orchids, the position of the anthers is normal and the viscidium is connected with the base of the pollinium.

Pollen, pollinium and pollinarium. The pollen of orchids is never powdery; the pollen grains always stick together in some way, although there is considerable variation in the degree of coherence. The more primitive orchids have sectile pollen, in which the pollen grains stick together loosely and only a portion of the contents of a theca or pollen sac is removed by a pollinator. In most monandrous orchids, the contents of a theca or pollen sac form a compact, globose, ovoid or club-shaped body, consisting of pollen grains firmly glued together (known as a pollinium). In some cases, the transport unit is the "naked" pollinium. In the majority of orchids, however, the pollinium has a short stalk (caudicle or frenicle), which is associated with a sticky pad or lamella. This composite structure is called the pollinarium. Depending on the taxon, a pollinarium may comprise a single pollinium (in the case of two separate pollinaria produced by the anther, as



Pollinarium of *Stanhopea avicula*; this is of a rather common type, with two pollinia.

in Orchidoideae), or (in case of complex pollinaria, as found in most tropical groups) two, four or even eight pollinia.

Note that the stalk connecting the pollinium with the viscidium is different in the acrotonic and basitonic orchids. In the former, it consists of coherent sterile and degenerated pollen grains (the stalk is then called a frenicle or *freniculum*); in the latter, it is a product of the tapetum, a transitive cell layer lining the pollen locule (the stalk is then called a caudicle or *caudicula*).

Pollinaria show considerable diversity in their number of pollinia, the number and the nature of the stalks, and the structure carrying the stalks and pollinia. A survey of orchid pollinia and pollinaria is found in Johnson and Edwards (2000).

Ovary, ovules and stigma. The orchid gynoecium (ovary; ovule-bearing part of the flower) is composed of three fused carpels. It is always inferior. As it is usually slender and cylindrical, the gynoecium is often mistaken for a flower stalk (pedicel). A true pedicel may be present, but it is generally short and inconspicuous.

In cross-section, the ovary is tri-symmetrical. In the Apostasioideae and the Neotropical genera of Cypripedioideae, three septa divide the ovary into three locules, and placentation is axile. In all other orchids, including all those found in the Golfo Dulce, there are no septa and the ovules are attached to "parietal" placentae, located at the fusion lines of the carpels.

The ovules are microscopic and produced in huge numbers (see "Fruits and seeds" below). They are reduced to the absolute minimum: a single-layered integument and a few-celled nucellus comprising the embryo sac with the egg cell. After fertilisation, the ovules develop into seeds. The integument develops into a single-layered reticulate testa and the egg cell develops into an embryo, which is merely an aggregation of diploid cells, globular in shape and lacking any differentiation.

In order to develop into a seed, an ovule must be fertilised by a pollen grain. Given the huge number of ovules present in an ovary, it is not enough for a pollinator to transport a small number of pollen grains to the flower. In most orchids, therefore, the pollen grains of a pollen sac or theca are glued together and transported as a unit.

The apex of the gynoecium is represented by the stigma. This consists of three lobes, the median lobe of which is usually somewhat larger and in most cases transformed into a special structure – the rostellum. All three of the stigmatic lobes in primitive orchids – or the lateral two lobes in others – are covered by mucilage consisting of macerated cells embedded in a slimy matrix. The mucilage is viscous and its stickiness ensures the adhesion of the pollinia.

The rostellum is a projecting, cup-shaped part of the column. In its interior, a sticky substance (homologous with the stigmatic mucilage of the lateral stigmatic lobes) is produced, forming a sticky disc. This allows the pollinia or pollinarium to be attached to the head or abdomen of an insect pollinator. In more primitive orchids, the sticky disc and the pollinia are completely separated; in the more advanced orchids, a "stalk" (caudicle or frenicle – see above) is produced to connect the two structures and combine them into a single functional unit.

Floral structures for rewarding pollinators: nectaries, elaiophores and osmophores. The principal reward offered by orchid flowers to their pollinators is nectar. In the most obvious cases, it is produced in a spur – a slender cylindrical or sac-like extension of the lip or another segment of the perianth. It may also be secreted in a tubular structure, formed by the fused bases of the perianth segments, situated above the ovary (e.g. → *Epidendrum hellerianum*). In many orchids, nectar is simply secreted in a shallow depression on the lip or between the column and the lip, such as in → *Stelis* or → *Pleurothallis* species.

Among the significant floral rewards discovered in recent decades are fatty oils and perfumes, produced by "elaiophores" and "osmophores", respectively. Details on these structures and their exploitation by highly specialised bees are given in the chapter "Pollination".

Many orchid flowers do not offer any reward to their pollinators, and attraction is by deceit. This phenomenon is also discussed in the pollination chapter.

Pollination Biology of Orchids

Anton Weber & Demetra Rakosy

Pollination is a crucial event in the life history of every plant. Orchids have evolved particularly diverse and intriguing pollination strategies, including some of the most bizarre relationships between flowers and pollinators known in plants.

The first naturalist to study the pollination of orchids was Christian Konrad Sprengel (1793). He was succeeded more than 60 years later by Charles Darwin, who, in *The various contrivances by which British and foreign orchids are fertilised by insects* (1877), described some of the more sophisticated relationships between European and tropical orchids and their pollinating insects. An enormous amount of research work on the subject has accumulated since then (summarised by van der Cingel 1995, 2001) and is still being carried out. For a historical survey of orchid pollination, from Linnaeus to present, see Fay and Chase (2009) and Michenau *et al.* (2009).

Self- and cross-pollination (auto- and allogamy), pollinators

Most orchid species are cross-pollinated (allogamous), relying on a variety of insects (bees, wasps, ants, flies, butterflies, moths, beetles) and birds (hummingbirds) for pollination. Ant and beetle pollination is only known in a few orchids, and does not seem to occur in the Golfo Dulce orchids. Bats have been mentioned as potential orchid-pollinators, but so far there is no reliable proof for this behaviour.

Obligate or facultative self-pollination is rare in orchids and seems to have evolved mainly in species growing in habitats where access to pollinators is limited. Obligate self-pollinating species usually have small, inconspicuous flowers, which often do not or not fully open (*Wulschlaegelia aphylla*). Facultative self-pollination is an important strategy that guarantees fruit set when pollinators' visits are scarce. This occurs in in many orchids. Notable are species which produce both selfing and outcrossing flowers (→ *Caulathron bilamellatum*).

Floral attractants, rewards and deception

In insect-pollinated flowers, pollinators are usually attracted over long distances by scent (olfactory cues). Of the two classic floral rewards – nectar and pollen – only nectar is relevant. Pollen is not provided as a reward because (1) pollen is exclusively collected by bees and used (mixed with nectar) as brood feed, and (2) rather than being powdery, the pollen of most orchid genera is glued together in pollinia – this makes it difficult to harvest or mix with nectar, and therefore unusable as a brood feed. As a functional replacement, pseudopollen is produced in a small number of orchids (see below).

Nectar is usually produced in a spur, more rarely (in fly-pollinated species) externally as a droplet on the lip. The composition (content and ratio of hexose to sucrose, presence of amino acids, etc.), sugar concentration and quantity of nectar vary widely, depending on the animals being attracted.

Floral rewards that have only been discovered in recent decades, also play an important role: fragrances (volatile oils) and fatty oils. These substances are collected by highly specialised bees. A recently discovered third class of floral rewards, resin, is also produced by some orchids. A much longer-known substance with similar consistency and utility is wax.

A large proportion of orchids – about one third of the species – offer no reward. These orchids rely on deception and mimic signals which are associated by the insects with either food, mates, competitors, nesting- or sleeping sites. The most sophisticated and fascinating pollination strategy that has evolved in orchids, is "sexual deceit". The flowers mimic the olfactory, visual and tactile cues of females of particular species of bees, wasps or flies, and attract males searching for females. While attempting to copulate with the "false females", the males inadvertedly remove the pollinia from the flower or deposit the pollinia brought along. An enormous amount of literature dealing with sexual deception in orchids has accumulated; recent surveys include Schiestl (2005), Jersáková *et al.* (2006), and Gaskett (2010).

Pollination by bees (melittophily)

Bees play a most significant role in the pollination both of temperate and tropical orchids. Of particular importance in the Neotropics are the euglossine bees (Apidae: Euglossini). Of the five genera (*Euglossa*, *Eulaema*, *Eufriesea*, *Exaerete* and *Aglae*), *Euglossa* is the largest, with over 100 species; the others are less speciose or even, in the case of *Aglae*, monotypic. Except for *Eulaema*, the species of which resemble temperate bumblebees, the bees' bodies are a metallic green, gold, red or blue colour. The group is also characterised by the proboscis, which is often longer than the body and is carried in a reflexed position between the legs during flight. It is important to note that the males and females exhibit striking morphological and behavioural differences in adaptation to exploitation of floral rewards (see below).

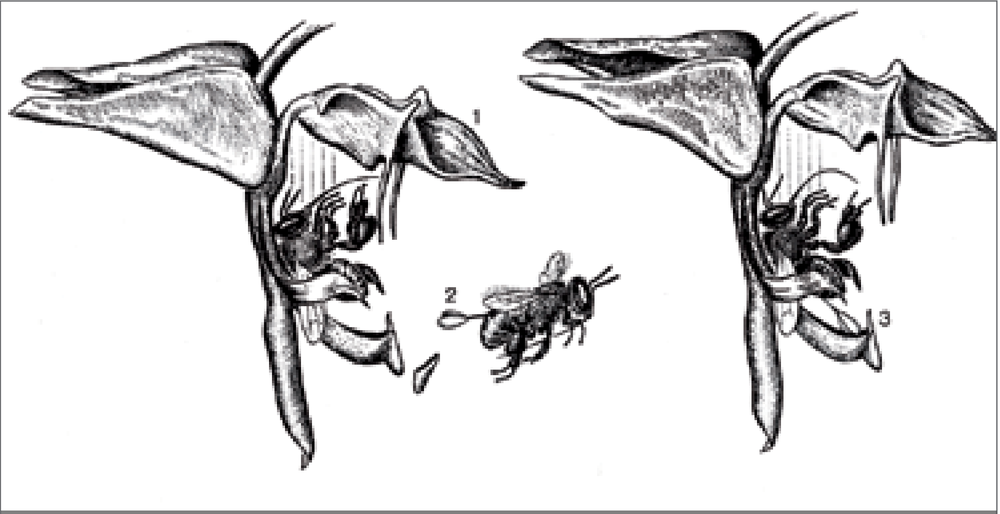
Another highly specialised group of bees are the centridinid bees (Apidae: Centridini). The main genera are *Centris* (> 100 species) and *Epicharis* (*c.* 40 species). They are remarkable in having structural devices to collect and transport fatty oil from flowers (see below).

Bee-pollinated orchid flowers are mostly characterized by a violet, purple, yellow or white colour, often with markings on the lip serving as nectar guides, and a strong smell emitted during the day. The flowers are often of the gullet or lip type, for which the marked zygomorphy is an important prerequisite. For reaching the nectar (if present), the bees often have to enter deeply the flower.

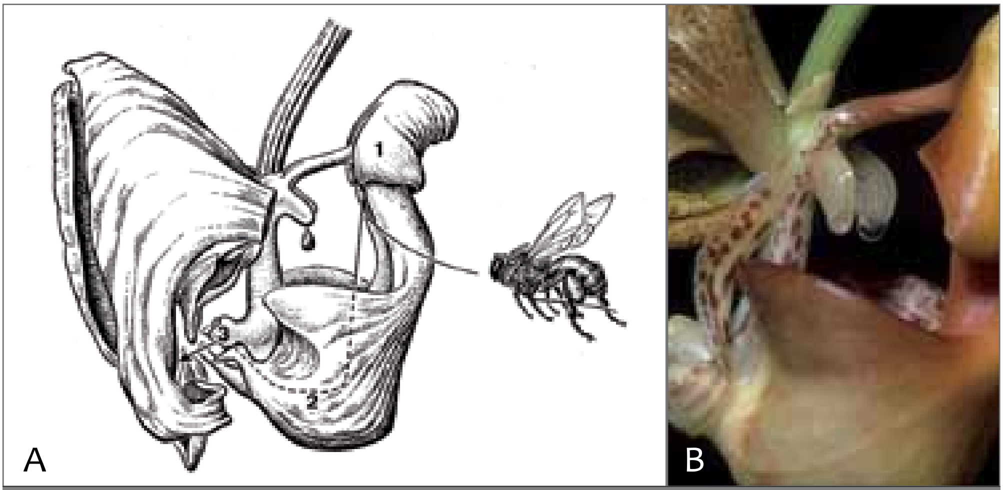
Nectar flowers. Nectar is taken up by many groups of bees, including the euglossine and centridinid bees (both males and females). In bee-pollinated flowers, the sugar concentration of the nectar is generally higher than in bird-pollinated, butterfly-pollinated or moth-pollinated flowers. Examples of nectar-rewarding species include → *Pelexia funckiana* or species of the genus *Maxillaria* (s. l.).

Deceptive nectar flowers. Flowers with a conspicuous, but empty spur are well known from *Orchis* and related genera (see survey of Dafni 1987), and are likely to occur also in bee-pollinated orchids of the Golfo Dulce region.

Flower of *Gongora* sp. with male euglossine bee scraping the lip surface in an upside down position in order to collect perfume droplets; note pollinia on the bee's back.



Accidentally, the bee slips and falls down. The lateral appendages of the column guide the sliding bee to the column tip. When passing the tip, the pollinia are affixed to its back. If the bee is already carrying pollinia from another flower, these are scraped from the bee's back and attached to the stigma. From Barth (1982).



A Pollination of *Coryanthes*. The lip is modified to form a liquid-filled bucket. When collecting fragrances at the lip base **(1)**, the male euglossine bee accidentally slips and falls down into the liquid **(2)**. It can only exit the flower through a narrow passage formed by the lip tip and the column apex **(3)**. When passing this passage, the pollinarium is affixed to the bee's back. If the bee carries a pollinarium along, this is scraped from its back and attached to the stigma. From Barth (1982) **B** *Coryanthes kaiseriana*, detail of flower centre. The two central projections secrete a slimy fluid that collects in the bucket.

Flowers presenting pseudopollen. Although there are no true pollen flowers in the orchids, some species offer a floral reward in the form of "pseudopollen", a yellow-white farinaceous powder. This is derived from disintegrating hairs on the labellum, and is rich in proteins and starch. Examples of orchids that produce pseudopollen include species of → *Maxillaria* (s. l.) and → *Polystachya*. Discovery was by Janse (1886), detailed morpho-anatomical studies have been carried out more recently by Davies *et al*. (2000, 2002).

Deceptive pollen flowers. Although orchids do not provide pollen as a floral reward, deceptive pollen flowers do exist (*Calypso*, *Arethusa*); none are found in the Golfo Dulce area.

Perfume flowers. Fragrances commonly serve as olfactory cues for attracting pollinators over long distances, but do not themselves represent floral rewards. In the 1960s, the German-Austrian biologist Stefan Vogel (1966) became aware that floral scents can also serve directly as a reward. There is no or only a non-functional nectary in these flowers; it is functionally replaced by a scent-emitting structure called the osmophore. The scent is secreted in the form of tiny droplets of volatile oils consisting of monoterpenes and benzenoids. The fragrant flowers attract only male euglossine bees. The scent droplets are collected by the bee using feathery brushes on its tarsi, and are stored in conspicuous pouches on the hind legs called tibial organs. Within the pouch, the flower fragrance is apparently mixed with the bee's own secretions, and is thereby transformed into an apparently characteristic, species-specific (possibly even individual-specific) perfume. This perfume may play a rôle in territorial display and courtship (olfactory marking of the swarm routes).

Early summaries of pollination of perfume flowers have been given by Williams (1982) and Williams and Whitten (1983). Presently, much work on euglossine bees and their rôle in pollination is carried out by Thomas Eltz and collaborators, at the University of Bochum (e.g. Eltz *et al*. 2007, Zimmermann *et al*. 2006).

At present, more than 50 orchid genera are known to include perfume flowers, many of which are represented in the Golfo Dulce forests. These include four of the most bizarre genera in terms of flower architecture and pollination strategy: → *Catasetum*, → *Coryanthes*, → *Gongora* and → *Stanhopea*.

Oil flowers. Fatty oil is another floral reward that was discovered by Stefan Vogel (1969). Since its discovery, a huge amount of information has accumulated. To date, more than 1500 species, in 10 angiosperm families, are known to reward pollinators with oils.

There are two types of elaiophore – epithelial or trichome – both of which occur in the orchids. In epithelial elaiophores, the oil is produced by secretory epidermal cells, and collects below the cuticles of the cells, which then burst and release the oil. Epithelial elaiophores occur in many species of *Oncidium* (→ *O. polycladium*) and related genera (e.g., *Trichocentrum*, Pansarin and Pansarin 2011). In the trichome elaiophore, the oils is secreted by a dense felt of seriate or glandular hairs and is stored in the capillary interstices of the hairs. Trichome elaiophores are characteristic of *Ornithocephalus* (→ *O. bicornis*), a genus of > 50 dwarf species with minute flowers. The chemical composition of the oil is complex and variable; it is principally a mixture of C16 and C18 fatty acids that usually possess a hydroxyl or acetyl residue in the β-position. Detailed studies on the chemistry of the oil have been recently carried out by Reis *et al*. (2000, 2007), and on the structure of orchid elaiophores by Stpiczyńska *et al*. (2007, 2008) and Pacek *et al*. (2012).

The oil is principally collected by female "anthophorid" bees of the tribes Centridini (especially species of *Centris* and *Epicharis*), Tetrapediini and Tapinotaspidini. The bees have remarkable morphological adaptations for collecting oil: combs consisting of densely packed, flattened bristles on the side of the first tarsal segments of the front and middle legs, or velvety pads to absorb the oil. The oil is only collected by the female bees, whereas both females and males visit various other flowers to take up nectar or – in the case of the females – pollen.

Deceptive oil flowers. Although many *Oncidium* flowers look similar, some species do not offer oil (or nectar). Vogel (1974) was the first to assume that these flowers mimic the oil flowers of Malpighiaceae, more recent studies include Silvera (2002), Powell *et al*. (2003), Renner and Schaeffer (2010) and Vale *et al*. (2011). Intrageneric mimicry is also a possibility.

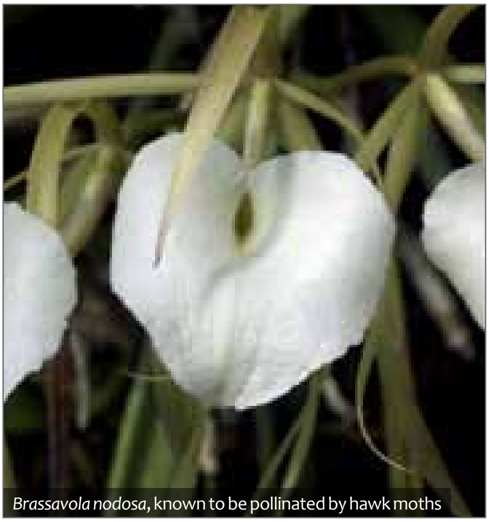
Wax and resin flowers. Porsch (1909) was the first to observe that wax platelets on the lip of *Maxillaria* (s. l.) species are collected by bees and that the wax apparently replaces the "honey" (nectar) as a floral reward. The wax is probably used in nest construction. The same applies to resin, which is also offered by species of *Maxillaria* s. l. (Singer and Koehler 2004). Other species of the same genus are believed to perform resin-mimicry (Davies and Stpiczyńska 2012). It is unknown whether there are any wax-offering or resin-offering orchids in the Golfo Dulce region.

Sexually deceptive bee flowers. Sexually deceptive orchids are adapted to attract male insects (particularly bees and wasps) that are deceived into attempting to mate with orchid flowers and inadvertently act as pollinators. The most familiar example may be the European genus *Ophrys*, but less is known about sexually deceptive orchids in Central and South America, and many deceptive species may remain to be discovered and studied. Old reports of pseudocopulation in → *Trigonidium* by males of the meliponid bee *Plebeia droryana* were confirmed by Singer (2002), who also documented the removal and deposition of the pollinaria. Another well-documented case is *Mormolyca ringens* from Brazil, the flowers of which are pollinated through pseudocopulation by *Nannotrigona* and *Scaptotrigona* bees (Singer *et al*. 2004).

Pollination by wasps

Like bees, wasps are dependent on energy-rich substances and thus use floral rewards such as nectar and pollen for their own needs. In contrast to bees, however, they do not use pollen for feeding the brood, but use living prey

Fly with pollinarium (arrow) visiting a flower of *Masdevallia rechingeriana* (Brazil)



Brassavola nodosa, known to be pollinated by hawk moths

Habenaria distans, probably pollinated by noctuid or related moths

(captured insects or spiders) instead. Some orchids were inventive enough to exploit the feeding behaviour of wasps by performing prey mimicry:

Prey-deceptive wasp flowers. The flowers mimic insect prey partly by their form and coloration, and particularly by chemical cues such as alarm pheromones (Brodmann *et al.* 2008a,b, 2009). → *Brassia caudata* is a striking case that occurs in the Golfo Dulce area (Pupulin and Bogarin 2005). The victims of deception are female spider wasps (species of *Pepsis* and *Campsomeris*), which would normally sting and paralyze a spider, drag it to her nest and lay an egg in the anaesthetised body, which then serves as living food for the developing larva. The flowers of *Brassia* mimic spiders, probably by the emission of a specific scent. By the wasp's efforts to sting or grasp the flower, the pollinarium is attached to its head and is then carried another flower. It remains unclear whether the long sepals and petals mimic spider webs in order to attract the wasps visually from afar.

Sexually deceptive wasp flowers. Orchid pollination by wasps through pseudocopulation is well known in *Ophrys* in Europe, and in *Drakea* and *Cryptostylis* in Australia and South East Asia. Knowledge of equivalents in the Americas remains poor by comparison. One of the most exciting cases, confirmed recently, is that of *Geoblasta pennicillata*, a terrestrial orchid from subtropical South America which is pollinated by male *Campsomeris bistrimacula* (Scoliidae) wasps (Ciotek et al. 2006). No sexually deceptive wasp-pollinated orchids are yet known from the Golfo Dulce area.

Pollination by flies (myiophily)

An survey on fly pollination in orchids, which is frequent in tropical species, has been given by Christensen (1992). The Golfo Dulce orchids include a number of taxa adapted to that group of pollinators – species of *Dresslerella*, *Dryadella*, *Lepanthes*, *Masdevallia*, *Macroclinium*, *Pleurothallis*, *Stelis* and *Trichosalpinx*. In simple cases, the orchid flowers are little more than generalist flowers that are visited by various small insects, including (or with some dominance of) flies. These flowers are usually small and of drab colour – brownish, red-brown, olive or yellowish, and often speckled or striped (e.g. → *Acianthera*, → *Pleurothallis* and → *Specklinia*). They emit a faint, sweetish scent, present a landing platform (the lip, fused sepals held beneath the lip, and/or a leaf held beneath the flower) and provide easily accessible nectar.

In some orchids, floral structures can be observed which are strongly associated with fly-pollination – tail-like appendages and so-called *Flimmerkörper*. The tails are long, drawn-out tips of the tepals (especially sepals) and serve as osmophores (e.g. → *Masdevallia lata*); *Flimmerkörper* are hair- or club-shaped appendages on the tepals or the lip, or a very small, hinged lip. A slight breeze is sufficient to set the *Flimmerkörper* into motion. A detailed survey of these structures (occurring in four families of angiosperms) was recently presented by Vogel (2002). The functional interpretation is that the flowers mimic female flies in flight and attract males.

In some specialised flowers, flies are attracted by a disagreeable odour. In these cases, the flowers mimic a brood site, namely carrion or dung. Strictly speaking, only in the "carrion flowers" exist intimate relations between flowers and pollinating flies ("sapromyiophily").

Flies (Diptera) are a hugely varied group of insects and very different taxa have become involved in pollination. Of special interest are the orchids that are pollinated by fungus-gnats (Mycetophilidae, Sciaridae), first described by Vogel (1973, 1978). These orchids (species of *Dracula*, *Corybas* and *Cypripedium*) mimic fungi in which these insects normally lay their eggs. The lip bears sometimes parallel and branched crests that mimic the lamellae of a mushroom. So far, no such orchids, which are largely bound to moss and cloud forests at high elevations, have been reported from the Golfo Dulce area.

Sexually deceptive fly-pollinated flowers. Fly-pollination by sexual deceit is the predominant, or possibly exclusive, mode of pollination in the large genus → *Lepanthes*. The details have been studied recently in *L. glicensteinii* (Blanco and Barbosa 2005). The tiny flowers are pollinated through pseudocopulation of fungus-gnats (*Bradysia floribunda*, Sciaridae). When visiting a flower, the fly curls its abdomen under the labellum and grabs the appendix with its genital claspers, before dismounting the flower and turning to face away from it. During this pivoting manoeuvre, the pollinarium is attached to the abdomen of the fungus-gnat.

Pollination by butterflies (psychophily)

In general, butterflies tend to visit coloured flowers which are fragrant, bloom during the day and provide nectar. The flowers typically have a long, narrowly cylindrical tube and a radially symmetrical or slightly zygomorphic, flat limb, where the butterfly can alight and rest while sucking the nectar. Flowers of this type are rare among tropical orchids and butterfly-pollination is accordingly rare. Some (especially terrestrial) *Epidendrum* species have been reported to be butterfly-pollinated (e.g. *E. fulgens* and *E. secundum* in Brazil, Pansarin and Amaral 2008). For a survey on butterfly pollination in orchids see van der Cingel (2007).

Deceptive butterfly-pollinated flowers. As the floral reward for butterflies is typically nectar, deceit is commonly employed, through the general similarity of the flower to a nectariferous flower. A striking example is the nectarless terrestrial orchid *Epidendrum radicans* (not yet recorded from the Golfo Dulce area, but common at higher elevations in Costa Rica). It has been suggested that it forms a floral mimicry complex with *Lantana camara* and *Asclepias curassavica* (Bierzychudek 1981). *Asclepias* and *Lantana* are presumed to be Müllerian mimics of each other, while the nectarless *Epidendrum* is thought to be a Batesian mimic. A test of this hypothesis (Boyden 1980), however failed: the presumed Batesian mimic *Epidendrum* was not visited more often when interspersed with the model than when alone.

Pollination by moths (sphingophily, phalaenophily)

This is more common in tropical orchids than pollination by butterflies. Moths usually fly at night, and features such as flowering at night, the emission of a strong sweetish scent in the evening and night-time, the presence of nectar and the lack of colourful flowers are characteristic of moth-pollinated flowers. The flower colour is white, cream, yellowish or greenish, in order to contrast with a dark background. In terms of shape, moth flowers are similar to butterfly flowers, having a long spur or cavity for nectar secretion and storage, and a distinct limb. The function of the latter and the length of the spur depends on the kind of moths visiting the flowers. In flowers pollinated by hawkmoths (Sphingidae), the limb only serves as a visual signal. The hawk moths do not alight, but

Scaphyglottis (*Hexisea*) *imbricata*, apparently pollinated by hummingbirds take up nectar – via a thin and sometimes extremely long proboscis – while hovering in front of the flowers, thereby making contact with the anther and stigma. As flight and hovering are energy-intensive, a relatively high amount of nectar must be provided by the flowers to fuel the high metabolic rates. Typical sphingophilous flowers are found in → *Brassavola nodosa* and many *Epidendrum* species (e.g. → *E. nocturnum*). Other groups of moths (especially Noctuidae, Pyralidae, and Geometridae) alight on the – usually smaller and often densely arranged flowers – and take up the nectar while sitting on the flower. Example of phalaenophilous orchids include → *Campylocentrum micranthum*, → *Habenaria monorrhiza, H. distans*, and → *Prescottia stachyodes*.

Deceptive moth-pollinated flowers. That which applies to deceptive butterfly-pollinated flowers also applies to moth-pollinated flowers. The flowers of some *Epidendrum* species exhibit the character syndrome of sphingophilous flowers, but do not produce nectar. The flowers of → *Brassavola nodosa* produce very little nectar and with low sugar concentration, and therefore seems to be part-way towards developing a nectar-deceptive flower.

Pollination by birds (ornithophily)

Bird-pollination is not uncommon in orchids. The main group of birds involved in the Neotropics are the hummingbirds (Trochilidae) (for a nice survey on that subject see Siegel 2011). They visit the flowers to take up nectar, the presence and appropriate quality of which (rather watery, with low sugar concentration) is an important part of the pollination syndrome. Another significant characteristic is optical conspicuousness (vivid coloration, with colours such as red, orange, yellow and combinations thereof). Fragrance is of no significance, as hummingbirds have no sense of smell. The most striking examples from the Golfo Dulce region are → *Scaphyglottis bidentata* and *S. imbricata*, which were for a long time placed in a genus of their own, *Hexisea*. The flowers of both species are bright red, those of *S. imbricata* having a yellow callus on the lip. The nectary structure has been studied by Stpiczyńska *et al*. (2005).

Deceptive bird-pollinated flowers. → *Epidendrum pseudepidendrum* is thought to be hummingbird-pollinated, but does not produce nectar and seems to rely on deceit.

Pollination by bats (chiropterophily)

The only orchid genus in which bat-pollination might appear is *Vanilla*. Indeed, bat-pollination has been mentioned as a possibility and there exist some vague and untraceable reports that Mexican *Vanilla* species are bat-pollinated (fide Havkin-Frenkel and Belanger 2011). The flowers are large, robust, whitish-greenish and strongly fragrant, but lack the most significant reward for bats – nectar. Therefore, reports on visitation/pollination of *V. planifolia* and *V. pomposa* by euglossine bees are much more plausible (Lubinsky *et al*. (2006, Soto Arenas and Dressler 2010). The reason why bats are apparently not involved in orchid pollination, is probably that these hairy animals lack any suitable surfaces for pollinarium attachment (Dressler 1993a).

Concluding remarks

This survey can only be a glimpse into the fantastic variety of orchid pollination mechanisms. Pollination is central to research into ecosystems and the interactions between plants and animals, and orchids make use of a wide range of animals to secure their reproduction and survival. The many fertilisation strategies used by orchids are the result of a long coexistence and coevolution between plants and animals. So far, relatively little work has been carried out into orchid pollination in the Golfo Dulce rain forests, and interested researchers (particularly biology students) are encouraged make this area of study a priority.

There is great public interest in orchids, and many excellent reasons to protect them. However, this can only happen if their pollinators are also protected, which is why pollination studies are so important for conservation projects and conservation management programmes. The protection of the habitats in which these plants and their pollinators live therefore needs to be one of the fundamental goals of any conservation effort.

Fruit Structure and Seed Dispersal of Orchids

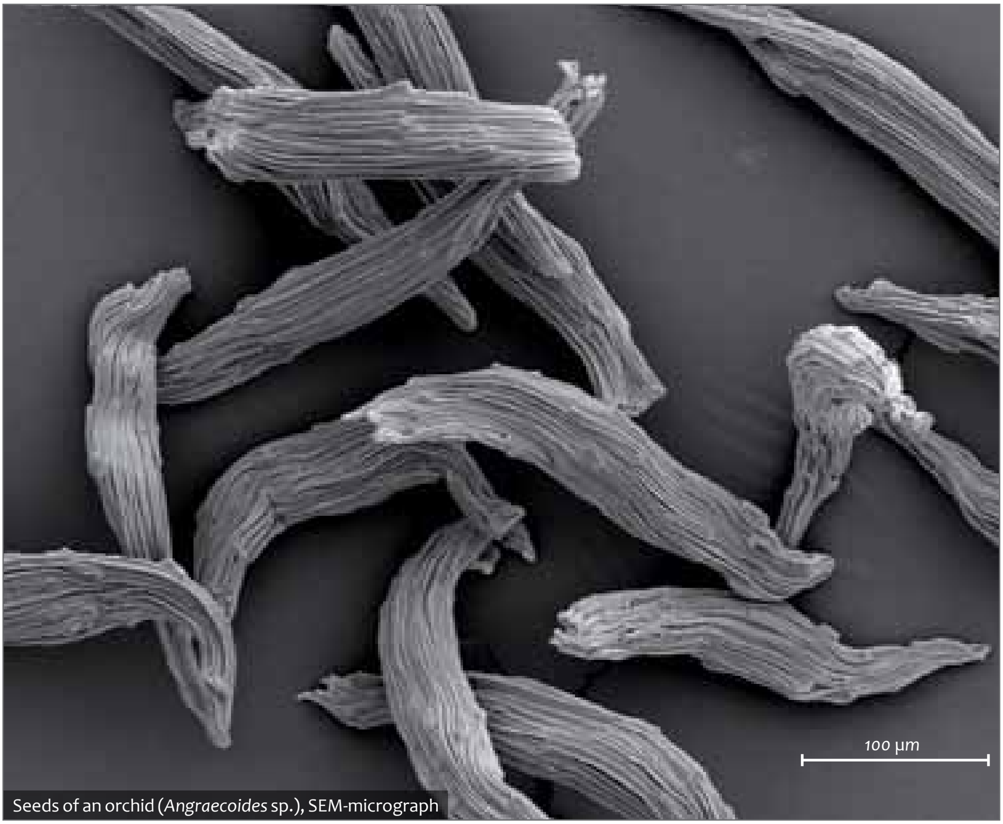
Anton Weber & Manfred Speckmaier

In contrast to the enormous diversity of floral forms and colours, the fruit of orchids is surprisingly uniform. It is almost always a dry capsule that opens along longitudinal slits to release the dust-like, wind-dispersed seeds. The capsules open either along three lines (the sutures of the three fused carpels) or along six lines (the sutures and the midribs of the carpels). Usually the carpels or carpel halves remain coherent at the base and at the tip. They thus form a kind of cage, from which the seeds are blown by the wind. The time required for the fruit to ripen varies greatly among the taxa, ranging from several weeks to 18 months.

The only fruits that do not fully conform to this general pattern are those of *Vanilla*, where the fruits are thick-walled and tardily dehiscent. The relatively hard-shelled and sticky seeds are not blown out by the wind, but mostly remain in the fruit until it decays. During the process of ripening and drying, phenolic compounds (with the main and commercially important components vanillin and ethylvanillin in the cultivated *Vanilla fragrans*) crystallize, and these fine crystals give the capsule a diamond-dusted appearance and emit the distinctive vanilla smell; the seeds themselves are flavourless. For commercial purposes, vanilla fruits are harvested just before ripening, when the fruits are still closed.

There is a long-standing debate about the natural dispersal of vanilla seeds. The structure of the fruits and seeds suggests dispersal by animals. Different groups of dispersers have been suggested and (partly) observed: euglossine bees, bats and birds. There are several reports that male euglossine bees (*Eulaema* spp.) visit the fruits and collect the fragrance. The seeds stick to their body and are transported away. Whether this is more than a chance event remains to be seen. Bat-dispersal of fruits has been suggested for *V. insignis* and was recently observed in *V. pomposa* in Peru (Soto Arenas & Dressler, 2010). Red-fruited *Vanilla* species from Asia are thought to be bird-dispersed.

Ripe, open fruits of *Maxillaria* sp.; note mass of dust seeds inside



Seeds of an orchid (*Angraecoides* sp.), SEM-micrograph

Seeds

Orchids produce among the greatest numbers of seeds per fruit of any plants. The number ranges from several hundred to hundreds of thousands. In some species, over a million seeds per capsule have been estimated. Such a vast number can be only reached if the seeds are microscopic and if the structures making up the living part of the seed are reduced to the absolute minimum. In fact, an orchid seed consists only of a single-layered testa, which loosely covers the inner part (forming a minute balloon that is readily transported by the wind), and the embryo. The embryo is a tiny, globose body that lacks any differentiation (e.g. a cotyledon or subsequent leaf primordia). It is simply a tiny ball of meristematic cells. The endosperm, which would normally supply energy in the earliest stages of germination, is absent. The seed must enter a symbiotic/parasitic relationship with a mycorrhizal fungus, which provides the energy necessary for germination and juvenile development. As the probability of a seed coming across a suitable fungus is very small, only an extremely small portion of the seeds grow into mature plants.

Orchid Diversity and Classification, with a Focus on the Golfo Dulce Region, Costa Rica

Franco Pupulin & Demetra Rakosy

Orchid history

Reliable fossil evidence has long been considered essential when assessing the temporal origin and diversification of orchids, but molecular dating of the Orchidaceae was until recently hampered by the complete absence of unambiguous fossils. In the last few years, however, a small amount of irrefutable evidence concerning the early history of orchids has come to light: orchid pollinia have been described from the West Indies (Ramírez *et al.*, 2007), and two orchid leaves have been found in Early Miocene deposits of New Zealand (Conran *et al.*, 2009). These findings have allowed the first direct calibration of orchid phylogeny, superseding the large discrepancies in age estimates obtained in the last decade. Using these fossils as internal calibration points, and departing from the phylogenetic trees previously obtained from DNA sequences, the origin of Orchidaceae has now been estimated at *c.* 77 million years ago (Ma). This supports an "ancient" origin of the most recent common ancestor of all extant orchids in the Late Cretaceous (Gustafsson *et al.*, 2010).

An extinct stingless bee, covered with pollinia from an orchid species belonging to the subtribe Goodyerinae, was found in an amber deposit in Hispaniola, Greater Antilles in 2007. This showed not only that orchids were well established in the Americas 15–20 Ma, but also that all the major lineages of the family were already formed by this time, with an estimated crown age of the five orchid subfamilies of between *c.* 57 Ma for the Vanilloideae and *c.* 32 Ma for the "higher epidendroids" (which includes most of the extant orchid genera and species). This indicates that the history of the orchids in the Americas is long enough to account for the astonishing diversity that the family exhibits in the Neotropical regions today.

Distribution and diversity

The Americas are home to around 13.000 species of orchids, with more than 93% of all the species restricted to the tropics. The orchid flora of the American isthmus – including the southern end of the North American continent and the land bridge connecting it to South America – is particularly rich, with the southern portion of the isth-

Dichea morrisii

mus showing the highest orchid diversity in the world. Of the five subfamilies of Orchidaceae, four (Cypripedioideae, Epidendroideae, Orchidoideae and Vanilloideae) are represented in the southern portion of the isthmus; only the very primitive and strictly Asian members of Apostasioideae are absent. Costa Rica and Panama (which mostly share a common geological history) together harbour over 3000 species of Orchidaceae (1519 in Costa Rica, and probably around the same number in Panama). This is as many as Brazil, which is hundreds of times larger, and almost as many as the entire African continent. Even though the northern regions of the Andes have a higher number of orchid genera and species, a simple estimate based on the recorded number of taxa and the sizes of the countries shows that southern Mesoamerica is packed with orchids in all possible environmental niches.

Orchid distribution in the narrow isthmus is greatly influenced by the climatic conditions caused by the presence of two oceans and the continental division that forms the backbone of the isthmus. From northern Mexico to central Panama, orchid diversity is highest along the Caribbean drainage, due to the more constant availability of water and the shorter (or non-existent) dry season, both of which favour epiphytism. Conversely, the climate of the continental division's Pacific drainage is characterised by a well-defined and often prolonged dry season that can last over eight months in some regions. Although highly fragmented, dry and seasonally dry forests stretch along the Pacific coast from southern Chiapas (Mexico), through Guatemala, El Salvador, Honduras and Nicaragua to north-western Costa Rica, to reappear in the lowlands of the Gulf of Panama.

Because drought tolerance is key to survival in the driest habitats, the epiphytic flora of the Pacific regions of Central America is less diverse than its Caribbean counterpart. Orchid diversity is reduced along the Pacific plains and lowlands, which usually host a limited number of species, mostly characterised by broad geographical distributions. The ranges of *Brassavola nodosa, Catasetum maculatum*, *Caularthron bilamellatum*, *Encyclia cordigera*, *Epidendrum sculptum* and *E. stamfordianum* are almost uninterrupted from Mexico to Panama and to the dry regions of Venezuela, Colombia, Ecuador and Peru; the distribution of *Dimerandra emarginata* runs from Mexico to Panama, and again along the dry regions of South America from Colombia to the Guianas and down to Brazil; *Cyrtopodium macrobulbon* and *Nidema boothii* span from Mexico to Panama; *Chelyorchis ampliata* and *Nitidobulbon nasutum* are found from Guatemala to Peru, while *Aspasia epidendroides* ranges from Guatemala to northern South America; *Laelia rubescens* is distributed from Mexico to Costa Rica, where it disappears at the point where the seasonal forest merges with the humid forest close to the mouth of the Río Grande de Tárcoles. Although it may include local endemics, some of which are restricted to narrow areas, the orchid flora of the Pacific lowlands of Mesoamerica is largely uniform in terms of genera and species. All of these widespread, Pacific lowland elements of the Neotropical orchid flora also occur in the Golfo Dulce region, mainly in the mangrove and palm swamps, and in the swamp forests along the coast.

The rugged physiography of the area, however, with elevations ranging from sea level to over 700 m, has favoured the establishment of a number of other ecosystems and vegetation types, including large areas of epiphyte-rich uplands and cloud forests. These are home to an extraordinarily diverse orchid flora, which includes a large number of endemic species found nowhere else in the world. They include: *Dichaea globosa*; *Epidendrum montis-narae*, *E. pseudepidendrum* and *E. zunigae*; *Gongora boracayanensis*; *Lycaste bruncana*; *Macroclinium alleniorum*; *Masdevallia borucana*; *Maxillaria atwoodiana*; *Polycycnis blancoi*; and *Triphora ravenii*. Most of these taxa were described fairly recently – mainly in the last 20 years – as a direct result of increased botanical exploration in a region that was previously difficult to access.

The area's steep and rugged terrain, as well as the unique diversity of the orchids found here, is mostly due to its geological history. The Golfo Dulce region exhibits a jigsaw of ecosystems and biotopes, which has resulted in suitable habitats for a large number of orchid species usually restricted to higher and cooler environments. These include: *Coccineorchis bracteosa*; *C. standleyi*; *Dichaea morrisii*, species of *Lepanthes*; *Masdevallia* cf. *calura*; *Platystele oxiglossa*; *Pleurothallis volcanica*; *Stelis janetiae*; and *S. lecucopogon*.

The geographical position of the Golfo Dulce region, in the middle of the land bridge that connects the North and South American continents, is an additional reason for its orchid richness. In general terms, the flora of southern Central America is influenced both by elements that originate in nuclear Mesoamerica – a region better defined today as "mega-Mexico" – and by a contingent derived from Andean and western Amazonian ancestors, the latter being the more important contributor. As the land bridge was completed very recently in geological terms – probably around 3 Ma – a corridor was formed, increasing species migration between the two continental masses.

Species of *Laelia*, such as *L. rubescens* and *L. undulata*, species of *Epidendrum* of the "*E. difforme* group", *Guarianthe aurantiaca* and *G. skinneri*, *Encyclia alata*, as well as species of the genera *Arpophyllum*, *Barkeria*, *Brassavola*, *Ionopsis*, *Isochilus*, *Jacquiniella*, *Rhynchostele*, and *Rossioglossum* – to mention just a few – are among the most obvious elements in the orchid flora of Costa Rica whose distributions are centred in the northern regions of the isthmus or, less frequently, in the Antillean arc. Only about 10% of the orchid species recorded in Costa Rica has their southernmost distribution limit in that country. The presence of these species in Costa Rica is, however, mostly restricted to the dry or seasonally dry regions of the north, and few of them reach the southern part of the country and the humid areas of the Golfo Dulce region.

Far more frequent in Costa Rica are those elements that show a close relationship with the montane orchid flora of the Andes. Several genera reach their northern limit of distribution here, including: *Koellensteinia*; *Miltoniopsis*; *Otoglossum*; *Peristeria*; *Pescatoria*; *Plectrophora*; *Psychopsis*; *Telipogon*; and *Warreopsis*. This "Andean connection" is even clearer if we take into account the fact that the distributions of around 20% of all orchid species found in Costa Rica do not extend to Nicaragua; instead, the mountainous regions of the country represent their northern distribution limit. The Andes are the centre of diversity for genera including: *Aspasia*; *Benzingia*; *Chondroscaphe*; *Dresslerella*; *Gongora*; *Lepanthes*; *Lockhartia*; *Masdevallia*; *Mormolyca*; *Peristeri*; *Pleurothallis*; *Stelis*; *Trichocentrum*; *Trichopilia*; *Xylobium*; and *Warrea.* All these genera are well represented in the flora of Costa Rica and are also relatively frequent in the gallery forests and cloud forests of the Golfo Dulce region.


Gongora boracayanensis

Orchid classification

The taxonomically relevant history of orchid classification starts with Carolus Linnaeus (1707-1778), who (in the *Species Plantarum*, vol 2: 939-954, ed. 10, 1753) recognised eight genera (*Orchis*, *Satyrium*, *Ophrys*, *Serapias*, *Limodorum*, *Arethusa*, *Cypripedium* and *Epidendrum*) which he placed in "Classis XX. Gynandria. Diandria". Remarkably, Linnaeus attributed all tropical orchids known to him to a single genus, *Epidendrum,* which then contained the ridiculous number of only 14 species, 11 from the Old World tropics (mostly from India) and 3 from the New World tropics (*E. vanilla = Vanilla fragrans*; *E. nodosum = Brassia nodosa*, and *E. guttatum = Tolumnia guttata*). Strangely Linnaeus considered the epiphytic species as parasites.

The family Orchidaceae was formally established by the French botanist A.L. de Jussieu (1748-1836) in his *Genera Plantarum* (1789), under the name "Orchideae". The first comprehensive classification was developed by the "father of orchidology", the British botanist John Lindley (1799-1865), who (in T*he Genera and Species of Orchidaceous Plants*, 1835) used the number of fertile anthers (one or two) and pollen structure (waxy or powdery, granular and sectile) to subdivide the orchid family into 8 tribes. The first to use both vegetative and floral characters for orchid classification was the German botanist Ernst Pfitzer (1846-1906), who, after publishing an *Entwurf einer natürlichen Anordnung der Orchideen* (1887) treated the orchid family in Engler & Prantl's epoche-making *Die Natürlichen Pflanzenfamilien* (Part II/6, 1889). Another German orchidologist, Rudolf Schlechter (1872-1925), developed in his monumental handbook *Die Orchideen, ihre Beschreibung, Kultur und Züchtung* (1915; a third and completely new edition is presently being published by Brieger, Maatsch & Senghas 1988 onw.) one of the most

Specklinia cornicula

influential orchid classifications, subdividing the family into 4 tribes and 80 subtribes, based on a combination of both floral and vegetative characters. Schlechter's system has been used for several decades, until Robert L. Dressler (1927-) published a new classification (in T*he Orchids: Natural History and Classification* 1981, 1986, 1990, and *Phylogeny and Classification of the Orchids* 1993), subdividing the family into 6 subfamilies (Apostasioideae, Cypripedioideae, Epidendroideae, Orchidoideae, Vandoideae, Spiranthoideae) and 21 tribes, based on column and pollen structure and vegetative (anatomical) characters. Later, by integrating data on seed structure, he included the subfamily Vandoideae into Epidendroideae. Other authors differed from Dressler's classification by including the orchids into a separate order, Orchidales with 3 subfamilies, Aposatsiaceae, Cypripediaceae and Orchidaceae (Rassmussen 1985, Szlatchetko 1995) based a combination of floral (column structure) and vegetative traits (leaves, velamen, etc.).

The use of molecular markers led to significant changes in the orchid classification at the subfamilial and tribal level. More recently, the combination of molecular and morphological analyses resulted in major rearrangements at generic level, especially in the species rich genera *Maxillaria*, *Pleurothallis* (e.g. *P. corniculata* → *Specklinia corniculata*; *P. descipiens* → *Ascianthera descipiens*) and *Stelis*.

The present account follows the classification presented in Pridgeon *et al.* (2003-2009), which is essentially based on molecular data (e.g. Chase *et al.* 1994, Cameron *et al.* 1999, Chase *et al.* 2003, Freudenstein *et al.* 2003, Cameron 2007), although morphological and anatomical data are incorporated where available. Here the Orchidaceae are divided into 5 subfamilies, 17 tribes and 42 subtribes, with the following interrelationships between the subfamilies: [Apostasioideae [Vanilloideae [Cypripedioideae [Epidendroideae, Orchidoideae]]]]. Morphologically the five subfamilies have been differentiated mainly (but by no way exclusively) by the androecium and column structure. The Apostasioideae, comprising only two genera *Neuwiedia* and *Apostasia*, are sister to the remainder of the Orchidaceae and are characterized by having only slightly zygomorphic flowers, an undifferentiated lip, 2 or 3 fertile anthers and powdery pollen. The relationship of Vanilloideae and Cypripedioideae to the remaining Orchidaceae has not been well supported in the earliest molecular analysis, but now it is clear that Vanilloideae are sister to the Cypripedioideae plus all other Orchidaceae with 1 fertile anther. This indicates that monandrous flowers evolved twice in orchids, once in Vanilloideae and once in the common ancestor of the Epidendroideae and Orchidoideae.

In the following, a short, general description of the four subfamilies present in Costa Rica (with the exception of introduced taxa) will be given together with a list of the tribes, subtribes and genera found in the Golfo Dulce region (the descriptions follow those in Pridgeon *et al.* 2003-2009). Detailed descriptions of the subtribes and tribes are given in Dressler (1993a) and Pridgeon *et al.* (2003-2009).

Subfamily Vanilloideae

Description: Plants terrestrial, monopodial or sympodial, vines or herbs, sometimes achlorophyllous mycotrophs. **Stem** erect, glabrous, sometimes elongate and climbing. **Leaves** one or many, alternate or whorled, often fleshy or coriaceous, sometimes reduced, green or achlorophyllous. **Inflorescence** a single terminal flower, terminal or axillary raceme or panicle. **Flowers** mostly showy, resupinate, one coloured. **Sepal**s free, fleshy, spreading, yellow, white, green, pink, or brown. **Petals** free, fleshy or membranous, spreading to incurved, sometimes forming a false floral tube, similar in colour to the sepals. **Lip** free or with the lateral margins fused to the column, forming a floral tube, entire or often trilobed, with complex hairs, bristles, scales, papillae or crests. **Column** slender, straight, sometimes arched, stigma emergent, rostellum acute, bent forward, column apex often hooded, then with distinct appendages on either side of the terminal anther; fertile anther one, staminodes two; pollen mostly loose, shed in monads, rarely tetrads or forming true pollinia without secondary structures. 1 tribe, 2 subtribes, 15 genera, *c.* 250 species, pantropical.


Acianthera decipiens

Representatives in the Golfo Dulce Region:
Tribe Vanilleae
  Subtribe Vanillinae
    Vanilla

Subfamily Cypripedioideae

Description: Plants terrestrial, sometimes epiphytic or lithophytic herbs with creeping rhizomes. **Shoots** erect, leafy, clustered to well spaced, terete, basally enclosed by a few sheathing bracts, one to several leaves above. **Leaves** usually plicate or conduplictae, spreading to suberect, thin textured, fleshy or coriaceous, green or marked with dark and light green or maroon. **Inflorescence** terminal, one to many-flowered, terete, bracts leaf-like, but smaller than the uppermost leaf. **Flowers** large, showy, one or two coloured. **Dorsal sepal** free, erect or forming a hood over the lip. **Lateral sepals** usually fused into a concave synsepal, similar to the dorsal sepal. **Petals** free, flat, inflexed or reflexed, spreading or pendent, sometime spiralling. **Lip** deeply pouched, inflated, slipper- or urn-shaped. **Column** short, stigma stalked to subsessile, tripartite; anthers two, staminode one, terminal to column, shield-like; pollen powdery or viscid. 5 genera, *c.* 120 species, northern hemisphere and tropics.

Representatives in the Golfo Dulce Region:
Phragmipedium (expected)

Subfamily Orchidoideae

Description: Plants mostly terrestrial, tuberous (root or stem tubers, sometimes rhizomes) herbs, sometimes mycotrophic with the leaves reduced to achlorophyllous sheaths. **Leaves** deciduous, rarely persistent, spirally arranged, one to many, often forming a basal rosette, upper leaves smaller, bract-like, usually green, sometimes spotted or veined with white, red or gold. **Inflorescence** terminal, erect or arching, one to many flowered. **Flowers** usually small, sometimes larger, often showy, usually resupinate, flat to tubular, white, yellow, green, pink, purple, red or brown. **Dorsal sepal** free, often adnate to the petals, forming a hood over the column. **Lateral sepals** free, sometimes forming a spur-like mentum. **Petals** entire or two-lobed. **Lip** deflexed, entire, three-, five-lobed or bipartite, often basally saccate or with a spur-like nectary. **Column** with one fertile anther, staminodes two, lateral; stigma entire or two lobed, rostellum two or three lobed, shorter or as long as the anther, pollinia 2 or 4, sectile, with secondary structures. 4 tribes, >200 genera, >3,600 species, almost cosmopolitic.

Representatives in the Golfo Dulce Region:
Tribe Cranichideae
  Subtribe Cranichidinae
    Prescottia
  Subtribe Goodyerinae
    Microchilus, *Platythelys*
  Subtribe Spiranthinae
    Coccineorchis, *Cyclopogon*, *Pelexia*, *Sarcoglottis*, *Schiedeella*
Tribe Orchideae
  Subtribe Orchidinae
    Habenaria

Subfamily Epidendroideae

Description: Plants terrestrial, epiphytic or lithophytic, perennial herbs, rarely mycotrophic with reduces leaves, sympodial or monopodial. **Stems** usually leafy, one or more basal internodes swollen to form a pseudobulb. **Leaves** entire, alternate, often distichous, frequently fleshy or coriaceous. **Inflorescence** erect to pendulous, spicate, racemose or paniculate, one to many flowered, basal, lateral or terminal. **Flowers** minute to large, often showy, mostly resupinate, variously coloured. **Sepals** usually free, sometimes variously adnate, dorsal sepal often dissimilar to lateral sepals, lateral sepals sometimes adnate to the column foot, foming a saccate, conical or spur-like mentum or connate, forming a synsepal. **Petals** free, rarely adnate to sepals, often showy. **Lip** entire or variously lobed, two- to three-partite, with or without calli, ridges, hairs or crests, with or without a basal spur. **Column** short to long, with or without a foot, sometimes apically winged; anther one, ± terminal to the column; staminodes two; stigma 3-lobed, concave, viscous; rostellum usually transverse; pollen in tetrads, usually in discrete pollinia, pollinia mealy or waxy, 2, 4, 6 or 8, with secondary structures. 19 tribes, >570 genera, *c.* 18,000 species, almost cosmopolitic.

Representatives in the Golfo Dulce Region:
(Higher Epidendroids)
Tribe Cymbidieae
  Subtribe Stanhopeinae
    Coryanthes, *Gongora*, *Polycycnis*, *Stanhopea*
  Subtribe Maxillariinae
    Camaridium, *Christensonella*, *Cryptocentrum*, *Heterotaxis*, *Inti*, *Lycaste*, *Mapinguari*, *Maxillaria*, *Maxillariella*, *Mormolyca*, *Nitidobulbon*, *Ornithidium*, *Rhetinantha*, *Trigonidium*, *Xylobium*
  Subtribe Zygopetalinae
    Cryptarrhena, Dichaea, Galeottia, *Warrea*
  Subtribe Oncidiinae
    Aspasia, *Brassia*, *Erycina*, *Ionopsis*, *Leochilus*, *Lockhartia*, *Macroclinium*, *Notylia*, *Oncidium*, *Ornithocephalus*, *Rossioglos sum*, *Trichocentrum*, *Trichopilia*, *Trizeuxis*
  Subtribe Catasetinae
    Catasetum, *Clowesia*, *Dressleria*, *Mormodes*
  Subtribe Eulophiinae
    Eulophia

Tribe Vandeae
  Subtribe Angraecinae
    Campylocentrum
  Subtribe Polystachyinae
    Polystachya

Tribe Epidendreae
  Subtribe Bletiinae
    Bletia
  Subtribe Bulbophyllinae
    Bulbophyllum
  Subtribe Pleurothallidinae
    Acianthera, *Anathallis*, *Dresslerella*, *Dryadella*, *Echinosepala*, *Lepanthes*, *Masdevallia*, *Octomeria*, *Pabstiella*, *Platystele*, *Pleurothallis*, *Specklinia*, *Stelis*, *Trichosalpinx*, *Trisetella?*
  Subtribe Laeliinae
    Brassavola, *Caularthron*, *Dimerandra*, *Encyclia*, *Epidendrum*, *Jacquiniella*, *Nidema*, *Prosthechea*, *Scaphyglottis*

Tribe Neottieae
    Palmorchis

Tribe Triphoreae
    Monophyllorchis, *Triphora*

  Tribe Calypsoeae
    Wullschlaegelia

(lower Epidendroids)
Tribe Sobralieae
    Elleanthus, *Sobralia*

Orchids and Ants

Christian Gegenbauer

Ants are among the most ecologically important organisms on earth, and are almost ubiquitous in tropical regions. A large number of orchids, as well as many other plant species, show some degree of interaction with ants. This usually involves the ants coming into contact with small nectar glands on the plant known as extrafloral nectaries, located on vulnerable spots such as flower stalks, seed pods or young shoots. As the ants are attracted to this food source, their numbers on the plant increase, which may deter herbivores and other threats to the plant.

Two orchid genera found in the Esquinas rain forest – *Coryanthes* and *Caularthron* – show a more complex symbiotic relationship with ants. They provide them with food and nesting space, and receive protection and nutrients in return.

The genus *Coryanthes* is found almost exclusively in arboreal ant nests – the so-called "ant gardens". The plant provides food in its extrafloral nectaries and its roots help to stabilise the ants' nests. In return, the ants not only provide fertiliser through their faeces, and shield the orchid against herbivores, but also protect it against pathogens by acidifying the environment and by secreting antimicrobial substances. Without ants, *Coryanthes* is prone to microbial infections, making it difficult to grow in horticulture (Gerlach 2011).

In the genus *Caularthron*, the water-rich tissue of young pseudobulbs desiccates upon maturation, forming a hollow chamber which ants can use as a nesting space. During this process, a vertical slit opens at the base of the pseudobulb, creating a natural entrance for the ants. This does not seem to cause significant damage to the plant and the pseudobulbs remain alive while they are inhabited.

As well as providing nesting space, *Caularthron* attracts ants through extrafloral nectaries on its reproductive structures (flower stalks, flowers and seed pods), on developing shoots and – uniquely among orchids – on mature leaf bases, thereby providing nectar throughout the year.

The ants inhabiting these orchids clearly benefit from this association by gaining a secure nesting space, and may obtain up to half of their nutritional needs from the extrafloral nectaries of their host plants. This association is not, however, highly specific: more than 30 different ant species were found to inhabit the hollow pseudobulbs of *Caularthron bilamellatum*.

The benefits to the orchid of being associated with ants are more complex and are still poorly understood. While many ant species – such as those of the genus *Azteca* – fiercely defend their host plant against disturbances, and some even prune nearby vegetation to protect their host

Natural openings at the base of *Caularthron bilamellatum* pseudobulbs from being overgrown, other ants remain completely passive to attacks on their host orchid. Ants also frequently farm aphids on orchids. Whether this behaviour should be considered a form of parasitism depends on the value of any other benefits the orchids may receive from their inhabitants.

Experiments suggest that plants occupied by ants produce significantly more flowers and fruit than those with ants and ant debris removed. The reasons for this are still not fully understood, but it is likely to be linked to nutrients that the orchids receive from the ants. Larger ant colonies produce significant quantities of nutrient-rich, humus-like waste, which the ants usually store in the apical regions of hollow pseudobulbs. Some ant species use single pseudobulbs as "waste chambers", which may become completely filled with humus.

Isotopic labelling experiments conducted on *Caularthron* have shown that the plants are capable of taking up nutrients in large quantities from inside the hollow pseudobulbs, and of transferring them to reproductive structures such as the seeds (Gegenbauer *et al.* 2012). Even though it is not yet known how important this is compared to the usual uptake through the root system, it is likely to be highly valuable, considering that these orchids live in nutrient-poor environments.


Cut through a hollow pseudobulb of *Caularthron bilamellatum*


Caularthon bilamellatum growing epiphytically on a tree

Cultivation of Orchids in the Tropics

Manfred Speckmaier

Greenhouses, climatic conditions and substrates

It is widely assumed that orchids can be cultivated more easily in the tropics than in temperate zones, due to the warmer climate. However, although no artificial heating is required in the tropics, most inhabited areas actually require artificial cooling systems to grow orchids, since they are located at much lower altitudes than the plants' natural habitats. Environmental humidity is also much lower in inhabited areas than in the rain forest, especially within large cities. In any case, greenhouses in the tropics rarely use air conditioning, as artificial cooling is much more expensive than artificial heating and also unsuitable for local greenhouses, which usually do not have walls but do have a plastic roof covering to reduce light intensity. The options for successfully cultivating orchids from other climatic zones are therefore limited. In temperate zones, it is easier to simulate any kind of artificial climate, so greenhouses have generally been adapted to the cultivation of tropical orchids.

In the Golfo Dulce region there are two orchid gardens, the "Casa Orquideas" owned by Ron and Trudy MacAllister and the smaller orchid garden of the La Gamba field station. La Gamba lies about 70 m a.s.l., so it enjoys a hot tropical climate with extremely high humidity, and minimal variation between day and night temperatures. The only orchids that can be successfully cultivated in the research station's orchid garden are therefore those from the surrounding area; any other species, such as those from the nearby Fila Costeña or other mountainous parts of Costa Rica, die relatively quickly under the unfamiliar climatic conditions. Only indigenous orchids from the surrounding area should be grown in the orchid garden for scientific purposes, in order to avoid confusion and misidentification.

Most orchids in the tropics – including those found in the Golfo Dulce region – are epiphytes. They therefore need to be cultivated on a surface that allows their roots access to enough light, ventilation, humidity and nutrients. Sections of tree-fern trunks, pieces of durable bark, and the inner fibrous surface of a coconut shell

M. Speckmaier and T. Rennebarth working in the orchid garden of the Tropical Research Station La Gamba can all provide suitable surfaces. The latter is the best material under an ecological aspect, but the least durable, since coconut fibre decays very quickly. Pieces of tree-fern trunk are the most durable, but should be used sparingly, to avoid damaging the critically endangered tree-fern populations. Whether to use pieces of bark or whole branches depends on the tree species and also on the orchid species being grown. Most species of *Mormodes*, *Catasetum* and (to some extent) *Gongora* and *Stanhopea*, for example, grow best on a surface with access to decomposing wood for their roots, but others, such as *Brassavola nodosa*, *Caularthron bilamellatum* and many *Epidendrum* and *Oncidium* species (especially twig epiphytes), need a durable surface that dries out quickly after watering or rainfall.

The terrestrial orchid species belonging to the Spiranthinae, and the semi-terrestrials such as *Sobralia* and *Vanilla* species, should be grown on substrates that retain water relatively well, such as the inner surface of coconuts. On the other hand, the members of the Spiranthinae respond best when planted in loose substrate in the hollow of a coconut shell after the fibres have been removed. *Sobralia* species, and related species such as *Elleanthus*, can be fixed on top of the coconut shell if their root systems are relatively intact. A pole or access to a living tree trunk is necessary for *Vanilla* species, which are climbers that need a surface to attach to. Terrestrial orchids can also be grown in pots, using a loose material that does not rot too quickly.

Orchids commonly cultivated in the Golfo Dulce region

Like in other regions of the world, the most commonly cultivated orchids in the Golfo Dulce region are those which have large, showy flowers. Also some cultivated species are native to the region, most are exotic species or hybrids. There are however no records of invasive orchid species in the Golfo Dulce region. Among the spectacular native orchids, the most often cultivated species is the national flower of Costa Rica, *Cattleya skinneri* (Guaria Morada). The second species of *Cattleya*, known from Costa Rica is *C. dowiana*, but it is seldom grown by the people, as it is very rare and difficult to cultivate. Besides *Cattleya*, species as *Sobralia decora*, *Encyclia cordigera*, *Schomburgkia lueddemanniana* and several *Oncidium* species can be observed in private gardens and yards. Much more popular are exotic orchid species, most of which originate from Asia: *Papilionanthe (Vanda) teres*, *Arundina graminifolia*, *Aerides odorata*, *Spathoglottis plicata* or *Phaius tankervilliae*. *P. teres* and *A. graminifolia* are very commonly cultivated in the Golfo Dulce region, as these two species prosper best in hot and very humid climate without any special care.

Propagation of orchids

Orchid capsules contain large numbers of seeds – from several hundred to 5 million, while the seeds are among the world's smallest and lightest (100 000 seeds weigh only *c.* 1 g) and can be easily distributed by the wind. However, their small size also means that they have virtually no endosperm and therefore lack the resources needed for germination and/or seedling establishment. Orchid seeds are therefore dependent on the association with mycorrhizal fungi, which provide them with sugars as energy source and probably other essential compounds required for germination and/or seedling establishment. The association with the fungus usually lasts throughout the orchid's life in terrestrial orchids (especially in achlorophyllous species), but in epiphytic orchids it may be only maintained till the orchid seedling reaches the photosynthetic state. The specificity of the relationship varies and may range from orchid roots being associated only with a restricted group of fungal partners to a broad association with different fungal groups. The fungi do not seem to benefit from the association (also some evidence exists that in some cases the fungus received C from the plant), in most cases the orchids therefore parasitize their fungal partner.

The obligate association between orchids and especially orchid seeds and mycorrhizal fungus has made artificial propagation of orchids at a large scale difficult. The first to succeed to germinate orchid seeds was David Moore (1807-1879), director of the Glasnevin Botanical Gardens in Ireland, who had sown the seeds in pots with already established orchid plants, without suspecting the reason for the success of his attempts. This method allowed for the first time the rearing of orchids from seeds, however it was not very productive and still had a high rate of failure. The first

Orchid seedlings cultivated in coconut shells

to discover the obligate association of orchids with mycorrhizal fungi was Noel Bernard (1874-1911) in 1899. The first symbioytic method for orchid seed germination was developed by Joseph Charlesworth (1850/51-1920) and John Ramsbottom (1885–1974) and constituted a major advance in orchid propagation. In 1904, the German botanist Hans Burgeff (1883-1976) was the first to attempt to germinate orchid seeds by sowing them in an agar tube that was previously inoculated with a mycorrhizal fungus under sterile conditions. In 1922, the American plant physiologist Lewis Knudson (1884-1958) developed a much easier asymbiotic method, in which sucrose is provided directly to the seeds along with several other macro- and microconstituents dissolved in an agar-based medium (Richter 1974). As sugars are the most widespread and effective energy suppliers in nature, the seeds need to be disinfected and sown out on a sterilised medium under aseptic conditions in order to prevent the growth of any other opportunistic microorganisms that may be more competitive than the orchid seeds. Even though this asymbiotic method has its difficulties, it has been modified by various scientists and hobbyists since its discovery, and is still a standard method for propagating orchids.

Another way to propagate orchids, especially cultivars and hybrids, is through micropropagation. This is considered to be more advantageous than raring orchids from seeds because plants with identical characters to the parental plant can be obtained (clones), which will flower more rapidly than those obtained from seeds (which often require several years to flower). Gavino Rotor Jr. (1917-2005) was the first to produce clonal plantlets from *Phalaenopsis* flower stalks in 1949, however his work has gone widely unnoticed. Today a great variety of methods for orchid micropropagation exist, which use either shoot tips, leave segments, inflorescences, rhizomes, roots or just a small tissue fragment on different culture media as starting materials. These methods have greatly contributed to the development of the orchid market, which has developed into one of the most successful horticultural trades. For details on the history of orchid micropropagation and an overview of the methods the reader may consult: e.g., Arditti (2009), Samira *et al.* (2009), Yam and Arditti (2009), Hossain *et al.* (2012).

The Spice Vanilla

Manfred Speckmaier

Vanilla is the second most expensive spice (after saffron) and is widely used throughout the world, yet few people know that the vanilla pod is the fruit of an orchid. In fact, it is the only one of the estimated 25 000–30 000 species of orchids which is cultivated on a major scale for its fruits. The genus *Vanilla* comprises over 100 species, distributed throughout the tropics, except in Australia. Most species occur in the Americas (52) and in SE Asia and New Guinea (31), while Africa (17), the islands of the Indian Ocean (7) and the Pacific area (3) harbour far fewer species (Cameron 2011). It was originally thought that the centre of diversity of the genus lay in the Indo-Malaysian region, but recent studies have shown that the genus probably originated in Central America.

Although 95% of all commercialised vanilla is produced from a single species – *Vanilla planifolia* – about 35 species of *Vanilla* are known or

Vanilla cultivation at the “Casa Orquidea”, Piedras Blancas National Park thought to be aromatic. *Vanilla planifolia* is indigenous to lowland forests of tropical Mesoamerica, but is cultivated throughout the tropics.

Both vanilla pods and the vanilla flavouring come from *Vanilla planifolia*, and the unique smell and taste are mainly due to the phenolic aldehyde vanillin. This compound was first isolated and identified by the French chemist Nicolas-Theodore Gobley in 1858; since 1874, it has been obtained in larger amounts from pine resin extracts, and from 1876 onwards by chemical synthesis. These alternative sources initially caused the commercial use of natural vanilla to decrease significantly. Nowadays, most of the vanilla flavouring used in cosmetics and in the food industry comes from alternative sources, but true vanilla has recently regained its importance, because it contains a number of minor constituents that are essential for its unique taste and fragrance. It is therefore irreplaceable in the production of perfumes such as the famous Chanel No 5. Natural vanilla is also growing in importance in the food industry, as the market price has dropped and consumers have learnt to appreciate the differences between real and artificial flavourings.

Today, vanilla is one of the most popular spices, and is found in nearly all sweet foods, ice creams and drinks, and in perfumes and many cosmetic products. The global production of vanilla is estimated to be 7000 tons annually, with the main producing countries being Indonesia, Madagascar and China.

The indigenous people of the south-eastern part of modern-day Mexico were the first to use *Vanilla planifolia* as a spice. The Aztecs used vanilla to aromatise *xocolatl*, a drink made from ground cacao, ground maize and chilli peppers and only consumed by the nobility. The fruits were also supposedly used for perfumes and medicinal purposes. Despite this, neither cacao trees nor vanilla orchids grew in the high altitudes and dry climate of the Aztec empire, so both vanilla and cacao beans had to be obtained through tribute payments from the peoples of the southern lowlands, especially the Totonac. In the Totonac culture, vanilla was considered a sacred plant and was often used as a divine offering to the gods. There are several legends about the origin of the orchid. The best known may be that of Tzacopontziza (=”morning star”), the beautiful daughter of King Tenitzill III. In order to hide her beauty from the sight of men, she was consecrated to the cult of Tonacayohua, the goddess of fertility, but a young prince fell in love with the princess and kidnapped her from the temple. The priests found the young couple and killed them as a punishment for breaking the oath of chastity given by the princess to the goddess. From the place of their death, a tree and an orchid emerged, the orchid winding itself around the branches of the tree, as if embracing it. When the orchid bloomed, its flowers were enveloped in a sweet smell, which was even stronger in its ripe fruits. The priests believed that the tree and the vine were born from the blood of the prince and princess and thereafter considered the vanilla a sacred plant, and a symbol of love.

Europeans first came into contact with vanilla through the *xocolatl* offered to the Spanish conquerors by the Aztec king. In 1510, the first vanilla pods arrived in Spain. At that time, the Spanish did not know where these aromatic pods came from (Rain 1986). The first illustration of a vanilla plant dates from 1522 and was published in the *Codex Badianus* under its Nahuatl name *tlilxochitl* (= “black flower”, referring to the colour of the mature, fermented seed pods) alongside the recipe for a perfume. This was the first drawing of an orchid from the New World. Meanwhile, the Spanish conquerors had subjugated the Aztec empire, and the vanilla-flavoured chocolate drink became fashionable among the European nobility. In 1571, as demand for vanilla grew, Francisco Hernández de Toledo was sent by the Spanish King Felipe II to Mexico to learn about the harvesting and processing of vanilla. He described its medicinal properties in his *Rerum Medicarum Novae Hispanie Thesaurus*, which was published posthumously in Rome in 1651. At that time, vanilla was used mainly to flavour chocolate drinks, although some people, including Queen Elizabeth I of England, were so fascinated by its flavour that they also used it as a spice in all kinds of dishes (Escobar *et al.* 1991).

The first record of vanilla plantations, established by the Totonac people in what is now Mexico, dates from 1767. By 1793, the first plants had been taken to Réunion in the Indian Ocean. Although the plants could grow and flower outside their natural range, they never produced fruit, as their natural pollinators were absent. Techniques for artificially pollinating vanilla were developed at the beginning of the 19th century by Charles F. A. Morren in Liège (1836) and by Joseph H. F. Neumann in Paris (1838), but the

Drying of vanilla pods in Madagascar

technique widely used today was developed in 1841 by Edmond Albius, a former slave, on Réunion (the former "Île Bourbon", hence the name "Bourbon vanilla" used for the finest vanilla pods from the Indian Ocean area). The method was also used in the native range of the vanilla, as the natural fruit set is very low (often below 1%). Vanilla plantations were soon started in Madagascar, Mauritius, the Seychelles and the Comoros Islands, before expanding into Asia, especially India, Sri Lanka, Java and the Philippines. The cultivation of vanilla has also had a long tradition in Tahiti – a French dependency in the Pacific Ocean – which gave rise to the somewhat mysterious "*Vanilla tahitensis*", probably a selected cultivar of a hybrid between *Vanilla planifolia* and *V. odorata*.

Unfortunately, achieving fructification is only half the work, because neither the young nor the mature fruits contain the desired vanillin unless they are processed in a particular way. The unprocessed fruits contain a non-volatile glycosylated form of vanillin, known as glucovanillin. During ripening and processing of the fruits, glucovanillin is enzymatically hydrolysed to vanillin and glucose. There are different methods of curing, which all consist of four basic steps: "killing", "sweating", "drying" and "conditioning". The "killing" step can be performed with either dry or moist heat, which destroys the cell membranes to initiate the enzymatic activities that degrade glucovanillin into vanillin and glucose, leading to the darkening of the fruits. During the "sweating" step, the fruits are exposed to high temperatures in a humid environment in order to achieve the desired texture and flexibility. In the "drying" step, the fruits are desiccated in the shade at ambient temperature. In the final, "conditioning" step, the fruits are stored for several months in closed containers at ambient temperature, in order to develop the required taste and smell. Afterwards, the seed pods are separated according to quality and bundled for export. Extracts and other products are mostly produced in the importing countries.

There are several other species which are cultivated besides *Vanilla planifolia*, although none matches the commercial value of this species: *Vanilla pompona*, *V. chamissonis*, *V. claviculata*, *V. griffithii* and *V. abundiflora* are cultivated in America (mainly Mexico). The latter two species are also cultivated in Asia, together with "*V. tahitensis*", which seems to be an artificial hybrid and has never been found growing in the wild.

Trichosalpinx blaisdellii - drawing by Margareta Pertl

Selected Orchids of the Golfo Dulce Region

Demetra Rakosy, Manfred Speckmaier, Anton Weber

Ornithocephalus bicornis - drawing by Stefan Vogel

Acianthera pantasmi *(Pleurothallis pantasmi)*

Acianthera pantasmi (Rchb.f.) Pridgeon & M.W.Chase, Lindleyana 16: 245 (2001).
Basionym: *Pleurothallis pantasmi* Rchb.f., Bonplandia (Hannover) 3: 224 (1855).
E.: Mt. Pantasmo *Pleurothallis*. **Sp.:** -

Etymology: The generic name is formed from the Latinised Greek *akis* (= point, beak) and the Latin *anthera* (= anther), referring to the species' somewhat pointed anther. The epithet is derived from Mt. Pantasmo, a volcano in the north of Nicaragua, where the first specimens of the species were collected.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Acianthera pantasmi

Taxonomic notes: The genus *Acianthera* comprises *c.* 200 species formerly placed in the subgenera *Acianthera*, *Arthrosia*, *Sarracenella* and *Specklinia* of *Pleurothallis s.l.*

Description: Plants epiphytic, medium-sized, creeping to caespitose, pseudobulbs lacking. **Stems** erect, sharply 3-winged, 10–18 cm long, gradually broadening towards the leaf blade and basally enclosed by 2–3 tubular sheaths. **Leaves** fleshy, erect, coriaceous, narrowly ovate, acute, the blade gradually narrowing towards the base, uniting at the margins with the wings of the stem; blade 3.5–8 cm long, 1–1.7 cm wide, much shorter than the stem. **Inflorescence** very short, racemose, emerging from the base of the leaf blade, consisting of a cluster of 2–4 small flowers that bloom simultaneously. **Flowers** fleshy, dark red to brownish, minutely pubescent outside. **Dorsal sepal** free, narrowly obovate, obtuse, 3-veined, 0.5 cm long, 0.2 cm wide. **Lateral sepals** connate into a slightly bifid, elliptical, obtuse, 6-veined synsepal, 0.45 cm long, 0.4 cm wide. **Petals** ovate, acute, 3-veined, 0.2 cm long, 0.1 cm wide. **Lip** tongue-shaped, trilobed, apex oblong, acute, lateral lobes erect and rounded, emerging below the middle of the lip. **Column** slender, with a pair of conspicuous, descending, obtuse wings, 0.2 cm long.

Distribution: Nicaragua to Costa Rica.

Ecology: Very wet forests, between 50 m and 600 m. Can often be found growing in exposed places, e.g. on trees bordering paths or roads.

Flowering: Throughout the year.

Pollination biology: Nothing is known about the pollination biology of this species. *Acianthera* species have myiophilous flowers and are pollinated by flies of the families Phoridae and Chloropidae. Those pollinated by Phoridae flies provide rewards (droplets of nectar on the lip), whereas those pollinated by Chloropidae are rewardless. The pollinators are so small that they have to enter the flower almost completely in the search for rewards, the lip acting as a lever, pushing the fly against the rostellum and thus ensuring the attachment of the pollinarium. The plant-pollinator relationship appears to be species-specific in some species, while others show a more generalised relationship.

References: Luer in Hammel *et al.* (2003: 433), de Melo *et al.* (2010), de Melo *et al.* (2011).

Acianthera pantasmi

Acianthera pantasmi

Arundina graminifolia

Arundina graminifolia (D.Don) Hochr., Bull. New York Bot. Gard. 6: 270 (1910).
Basionym: *Bletia graminifolia* D.Don, Prodr. Fl. Nepal. 29 (1825).
E.: Bamboo orchid, bird orchid. **Sp.:** Orquídea bambú.

Etymology: The generic name is derived from the Latin *arundo* (= reed). The epithet is formed from the Latin *gramen*, gen. *graminis* (= grass) and *folium* (= leaf), alluding to the grass-like leaves of the plant.

Classification: Subf. Epidendroideae, Tr. Arethuseae, Subtr. Arethusinae.


Arundina graminifolia

Description: Plants terrestrial. **Stems** erect, rigid, cane-like, up to 2.5 m tall, growing in clumps. **Leaves** many, alternate, leathery, grass-like, with overlapping sheaths; blades 8–30 cm long, 0.5–2 cm wide. **Inflorescence** terminal, with up to 15 flowers, with only one or two open at a time. **Flowers** large, similar to those of *Cattleya* or *Sobralia*, resupinate, white to pink, with a purple lip. **Sepals** lanceolate to narrowly ovate, the lateral sepals converging and hidden behind the lip; *c.* 3 cm long, 1 cm wide. **Petals** broadly ovate, 3 cm long or longer, 2.5 cm wide. **Lip** trilobed, crenate, lateral lobes forming a 4–5 cm long tube that encompasses the column and broadens apically, middle lobe crenate, apically cleft, with a basal yellow spot and 3 longitudinal, pubescent crests. **Column** straight, winged, white to pink.

Distribution: Natural distribution in Asia, ranging from northern and southern India through Malaysia and Indonesia to Tahiti. It has been introduced as an ornamental in Hawaii, Puerto Rico, Costa Rica, Guatemala, Panama, Jamaica and Guadeloupe, where it has become partly naturalised.

Ecology: Open, sunny, wet or boggy places. In its native range, *Arundina* often occurs in natural or anthropogenic forest clearings, on steep, rocky hillsides, and on roadsides. In Costa Rica, it is often grown in gardens or in pots as an ornamental.

Arundina graminifolia

Flowering: Throughout the year, with a peak between September and October.

Pollination biology: *Arundina graminifolia* appears to rely on a form of deception, as its flowers do not produce nectar. Pollinators are reported to be bees of the genus *Xylocopa*. In Japan, various lepidopteran and hymenopteran species have been observed to visit (but not pollinate) the flowers. Occasionally, the species appears to reproduce autogamously through cleistogamy. In Costa Rica, no insect visitation or pollination has been recorded, but as the species is not native here, it is likely that its legitimate pollinators are also missing. According to Pridgeon *et al.* (2005), this species possesses extrafloral nectaries, attracting mainly wasps (as it does in Costa Rica) and ants, which may protect the plant from herbivores.

Remarks: (1) In its native range, *Arundina graminifolia* exhibits high floral variability, which has led to the description of several varieties. These have even been considered as full species by some authors. The most widely accepted view, however, is that *Arundina* is monospecific, comprising only the florally variable *A. graminifolia*. (2) In traditional Chinese medicine, extracts of the rhizome are used for detoxification and to treat arthritis. (3) In Costa Rica, *Arundina graminifolia* can be easily confused with *Sobralia* species because of their similar growth habit and flower shape, but the narrow, smooth and shiny leaves are distinctive (in *Sobralia* they are much broader, plicate and matt). (4) *Cattleya*, which has similar flowers in some species, can be distinguished by its epiphytic habit, short stems, usually fleshy leaves and the presence of pseudobulbs.

References: Gargiullo *et al.* (2008), Goldman in Pridgeon *et al.* (2005: 18–22), Hsuan *et al.* (1998: 69), Teoh (2005: 67).

Aspasia epidendroides

Aspasia epidendroides Lindl., J. Bot. 1: 6 (1834).
E.: *Epidendrum*-like *Aspasia*. **Sp.:** -

Etymology: The generic name is derived from the Greek *aspázesthai* (= welcoming, embracing), referring to the lip embracing the column foot. The epithet refers to the similarity of its flowers to those of *Epidendrum*.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Description: Plant epiphytic. **Pseudobulbs** conspicuous, up to 13 cm long and 6 cm wide, light green, strongly compressed, with a narrow stem-like base, which is normally totally enclosed by the distichous leaf sheaths. **Basal leaves** 2 or 3, oblanceolate, base conduplicate, apex acuminate, 6–13 cm long, 2–3 cm wide. **Apical leaves** always 2, lanceolate to ligulate, base conduplicate, apex acuminate, up to 30 cm long and 5 cm wide, but usually somewhat smaller. **Inflorescences** lateral from the base of the pseudobulb, normally 2 emerging from between the 2 uppermost leaf sheaths (= bases of the basal leaves) and the edges of the pseudobulb, usually shorter than the apical leaves, up to 8-flowered, 10–25 cm long. **Flowers** conspicuous in size and colour, resupinate, fragrant, opening in succession from the base towards the tip, 2–3 flowers open at a time. **Sepals** oblanceolate to narrowly obovate, apiculate, green, with irregular coffee-brown blotches, but sometimes entirely maroon to olive-green, 2.5 cm long, 0.8 cm wide, the lateral sepals somewhat shorter. **Petals** sometimes shaped and coloured like the sepals, but more often unicoloured, usually with a pronounced dark rose-red hue, 2.0 cm long, 0.8 cm wide. **Lip** white, with an irregularly shaped pink to intense lilac centre, subquadrate to pandurate, somewhat concave, with 2 basal yellow calli and 4 yellow, divergent elongate crests, the inner crests being longer than the outer ones. **Column** white, with some of the same pink-to-lilac coloration of the lip on its underside, attached to the base of the lip, 1.7–2.1 cm long.

Distribution: From Guatemala throughout Central America to western Colombia (although not yet found in Belize). Locally very common.

Aspasia epidendroides

Aspasia epidendroides

Ecology: Normally grows in humid to very humid evergreen lowland forests, from sea level up to 1000 m. In the Golfo Dulce region, the plants are found in deep shade on tree trunks and lower branches, often 2–4 m above the forest floor.

Flowering: Throughout the year, with a peak between January and May.

Pollination biology: The flowers emit a sweet perfume during the day and have a false nectary. Pollinators are nectar-foraging euglossine bees.

Remarks: (1) *Aspasia epidendroides* is the type species of the small genus *Aspasia*, which contains 8 species ranging from southern Mexico to southern Brazil. (2) When not in flower, the species can be easily confused with *Brassia caudata*, the only other species of similar habit and size growing in the crepuscular light of the forest. The two species can be distinguished by the shape of the pseudobulbs and (if present) the inflorescences. The pseudobulbs of *Aspasia epidendroides* are conspicuously stipitate at their base. If inflorescences are present on the plants, those of *Aspasia* are usually much shorter than the plant and bear 4–8 flowers, while those of *Brassia caudata* bear many more flowers and are as long as, or longer than, the plant.

References: Dodson and Escobar (1993: 50–51), Dressler in Hammel *et al.* (2003: 21-22), Escobar *et al.* (1991: 38–39), Genaust (2005), Hamer (1982: pl. 604), Pupulin (1998).

Aspasia epidendroides

Brassavola nodosa

Brassavola nodosa (L.) Lindl., Gen. Sp. Orchid. Pl.: 114 (1831).
Basionym: *Epidendrum nodosum* L., Sp. Pl. 2: 953 (1753).
E.: Lady of the Night. **Sp.:** Huelenoche, Brassavola común.

Etymology: The generic name commemorates the Venetian physician and botanist Antonio Musa Brassavola (1500–1550). The epithet is derived from the Latin *nodosus* (= knotted, knobbly), referring to the knobbly appearance of the stems.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Taxonomic notes: The Neotropical genus *Brassavola* comprises 17 species, the best-known and most widespread being *Brassavola nodosa*. Carl Linnaeus (1707-1778) described the species in 1753 under the genus *Epidendrum*, in which he subsumed all tropical orchids of epiphytic habit.

Description: Plants epiphytic or lithophytic, caespitose, growth sympodial, pseudobulbs lacking. **Stems** 4–15 cm long, slender, terete; concealed by tubular, papery sheaths. **Leaves** solitary, erect, linear, acute, fleshy, channelled on the upper surface, 5–15 cm long, 0.5–1.5 cm wide. **Inflorescence** terminal, bearing one to several flowers, up to 24 cm long. **Flowers** white to greenish, with purple spots at the base of the lip. **Tepals** linear, acute, 5–9.5 cm long, 2–5 cm wide. **Lip** tubular at base, gradually broadening into the spreading lamina; lip lamina subcordate, acute, with greenish veins, outer margins recurved, lip 5–6.2 cm long, 2.5–3.5 cm wide. **Column** short, completely enclosed by the lip.

Brassavola nodosa

Brassavola nodosa

Distribution: The distribution of *Brassavola nodosa* largely matches that of the genus, ranging from Mexico throughout Central America to Columbia, Venezuela and Peru. It has also been reported from several islands in the West Indies (ABC Islands, Trinidad and Tobago). Common.

Ecology: Prefers mangrove forests and rocky coasts. The plants commonly grow on the trunks and branches of red, black and white mangrove (*Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*, respectively).

Flowering: Throughout the year.

Pollination biology: Although this species is self-compatible, self-pollination does not occur in nature, and the species relies exclusively on insects for pollination (allogamy). The buds usually start opening in the evening. If they are not pollinated, the flowers remain open for up to 34 days. If pollination is successful, they wither immediately. The white-greenish flowers emit a strong, pleasant scent in the evening and during the night, the main component of which is 1,8-cineole. The strong nocturnal scent, the whitish coloration and the tubular basal constriction of the lip suggest that pollinators are hawk moths (Sphingidae). Interestingly, the flowers produce little nectar of poor quality (5% sugar concentration), or no nectar at all, which raises the question of whether this species is food-deceptive. There are additional nectaries at the base of the sepals, probably attracting ants, which may protect the flowers from herbivores.

Remarks: *Brassavola nodosa* was among the first tropical orchids to be brought to Holland from the Caribbean island of Curaçao in 1698. Its successful propagation laid the foundations of orchid cultivation in botanical gardens all over the world.

References: Ames and Correll (1953: 423–425), van der Cingel (2001: 118), Dodson *et al.* (1969), Dressler in Hammel *et al*. (2003: 34), Escobar *et al*. (1991: 50-51), Fisher and Zimmerman (1988), Haber and Frankie (1989), Hills *et al.* (1968), Murren and Ellison (1996), van der Pijl and Dodson (1966: 28), Pridgeon (1992: 40), Roebuck and Steinhart (1978), Schemske (1980), Williams (1981).

Brassia caudata

Brassia caudata (L.) Lindl., Bot. Reg. 10: t. 832 (1824).
Basionym: *Epidendrum caudatum* L., Syst. Nat. (ed. 10) 2: 1246 (1759).
E.: Spider orchid. **Sp.:** Orquidea araña, Ballarina, Chapulin.

Etymology: The generic name commemorates William Brass (d. 1783), a botanical illustrator and plant collector who worked mainly in West Africa. The epithet is derived from the Latin *caudatus* (= tailed), referring to the long-tailed sepals of the flowers.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Description: Plants epiphytic, up to 40 cm tall. **Pseudobulbs** strongly compressed, up to 12 cm long and 3 cm wide, but usually smaller, apex with 2 leaves, basally enclosed by several sheaths, the uppermost sheaths sometimes bearing a small leaf. **Leaves** elliptic–oblong, obtuse to slightly acute, coriaceous, 17–23 cm long, 3–4.2 cm wide. **Inflorescence** lateral, emerging between the pseudobulb and the upper leaf sheath, ± horizontal to slightly arching, racemose, bearing 6–12 flowers arranged distichously, up to 35 cm long. **Flowers** large and eye-catching, sweetly fragrant, almost all flowers opening simultaneously. **Dorsal sepal** yellowish green, with irregular maroon blotches, the blotches usually being denser at base and fading towards the apex. Basal part of sepal ovate, becoming narrowly elongate, tip acuminate, 4–9 cm long and *c.* 0.5 cm broad at the widest part, near its base. **Lateral sepals** with same coloration as the dorsal sepal, but usually 3× longer, 12–30 cm long. **Lip** unilobular, 3–5 cm long, 1–2 cm wide,

Brassia caudata

white, becoming faintly yellowish towards the edges, marked with chestnut-brown blotches at its base, margins somewhat folded back along the central part, the apical part ± triangular with an elongate acuminate tip, base of lip adnate to the column and with 2 parallel swollen calli with several deep yellow markings. **Column** stout, *c.* 0.5 cm long.

Distribution: The distribution of *B. caudata* largely matches that of the genus, ranging from Mexico and Florida through Central America to the northern half of South America. Widespread but not common.

Ecology: *Brassia caudata* normally grows in warm, humid to very humid evergreen lowland forests, from sea level up to 750 m. In the Golfo Dulce region, the plants are found on tree trunks, large branches and lianas, not always high above the ground level, but always in deep shade.

Flowering: April to July.

Brassia caudata

Brassia caudata

Pollination biology: The flowers emit a sweet perfume during the day which apparently serves to attract pollinators. In several *Brassia* spp., large wasps of the genera *Pepsis* and *Campsomeris* have been observed to pollinate the flowers. The wasps attempt to sting the lip and thereby remove/deposit the pollinia. It has been suggested that the flowers exhibit prey-mimicry (particularly mimicking spiders), thus attracting wasps hunting for living prey for their brood. Visual signals, i.e. the shape of the flowers and the long sepals, may play some role, but attraction is mainly through chemical cues.

Remarks: The genus *Brassia* comprises c. 30 species, with four occurirng in Costa Rica, and only *B. caudata* in the Golfo Dulce region. Sterile plants may be confused with *Aspasia epidendroides*.

References: Allen in Woodson and Schery (1949: 170–173), Atwood and Mora de Ratana in Burger (1999: 117), Dodson and Escobar (1993: 82–85), Dressler in Hammel *et al.* (2003: 35), Escobar *et al.* (1991: 52–53), Genaust (1996), Hamer (1982: pl. 623), van der Pijl and Dodson (1966: 38), Pupulin and Bogarin (2005).

Bulbophyllum oerstedii

Bulbophyllum oerstedii (Rchb.f.) Hemsl., Biol. Cent.-Amer., Bot. 3(16): 213 (1884).
Basionym: *Bolbophyllaria oerstedii Rchb.f.,* Bonplandia 3: 223 (1855).
E.: Rat-tailed orchid. **Sp.:** -

Etymology: The generic name is formed from the Greek *bulbos* (= bulb) and the Latin *phyllum* (= leaf), referring to the presence of pseudobulbs furnished with leaves. The epithet commemorates the Danish naturalist Anders Sandøe Ørsted (1816–1872), who carried out pioneering biological work in Central America.

Bulbophyllum oerstedii

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Bulbophyllinae.

Description: Plants epiphytic, up to 20 cm tall. **Pseudobulbs** slender, 4-angulate, well separated on the creeping rhizome, basally covered by a few tubular sheaths, 2.5–4 cm long, *c.* 2.5 cm wide. **Leaves** 2, coriaceous, linear-lanceolate, acute, up to 20 cm long, 1–2.5 cm wide. **Inflorescence** lateral, pendent, with a thick and fleshy rachis, 12–25 cm long, bearing several small and inconspicuous flowers. **Flowers** pale green to yellowish green, spotted with purple, apex of the lip purple. **Dorsal sepal** free, concave, ovate, acute, 0.6 cm long, 0.35 cm wide. **Lateral sepals** slightly connate at base, ovate-acuminate, 0.7 cm long, 0.3 cm wide. **Petals** elliptic, obtuse, 0.25 cm long, 0.1 cm wide. **Lip** entire, ligulate, obtuse, fleshy toward the apex, geniculate, contracted at the base and articulate to the foot of the column, 0.25 cm long, 0.1 cm wide. **Column** subterete, trilobed at apex, with a distinct foot, about 0.18 cm long.

Distribution: Widely distributed (but not common) in the lowlands of Central and South America.

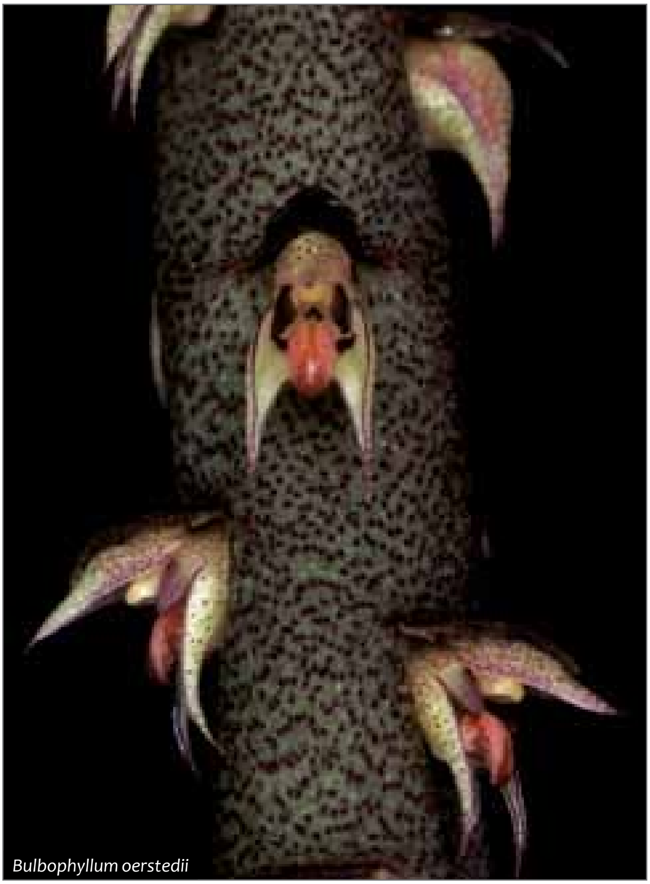
Ecology: This epiphyte occurs mostly in warm, wet tropical forests, from sea level up to 500 m.

Flowering: December to January.

Pollination biology: Nothing is known about the pollination biology of this species. Most species of the genus seem to be fly-pollinated, several are autogamous.

Remarks: (1) *Bulbophyllum* is one of the largest plant genera, comprising more than 2800 species. (2) Some authors use the name *Bulbophyllum pachyrachis* (A.Rich.) Griseb. for this species, but that name actually refers to a species from the West Indies.

References: Allen in Woodson and Schery (1949: 9–10), Dressler in Hammel *et al.* (2003: 37), Pupulin (1998).


Bulbophyllum oerstedii


Bulbophyllum oerstedii

Campylocentrum micranthum

Campylocentrum micranthum (Lindl.) Maury, J. Bot. 3: 273 (1889).
Basionym: *Angraecum micranthum* Lindl., Edward's Bot. Reg. 21, t. 1772 (1835).
E.: Fairy bent-spur orchid, tiny-flowered *Campylocentrum*. **Sp.:** -

---

Etymology: The generic name is formed from the Latinised Greek *kampylos* (= twisted, curved) and *kentron* (= spur), alluding to the curved spur of the lip in several species. The epithet is formed from the Latinised Greek *mikros* (= small) and *anthos* (= flower), alluding to the tiny flowers.

Classification: Subf. Epidendroideae, Tr. Vandeae, Subtr. Angraecinae.

Description: Plants epiphytic, with monopodial growth. **Stems** erect or pendent (depending on size), distichously leafed throughout and completely enclosed by leaf sheaths that become brown after the basal leaves have dropped; continuously elongating, reaching up to 75 cm, frequently branched. **Roots** numerous, mostly aerial, irregularly wavy, tangling, silvery-grey, growing from the nodes along the whole stem, always directed towards the opposite side from the leaf at the same level. **Leaves** elliptic to oblong, with an asymmetrical tip, dull green, 3.5–8.0 cm long, 1.0–1.5 cm wide. **Inflorescence** straight, produced from lower stem nodes, always pointing away from the leaf at the same level, often level with a root, axis slightly conical, as long as or shorter than the leaves. **Flowers** small, many, in dense distichous arrangement, resupinate, white to faintly rose-red, becoming pale orange when fading. **Tepals** lanceolate, narrowly acuminate, 0.4–0.5 cm long, up to 0.1 cm wide at base, lateral sepals tending to be slightly longer than the dorsal one. **Lip** inconspicuously trilobed, lateral lobes auriculate, 0.4–0.5 cm long, 0.15 cm broad; spur conspicuous, translucent greenish white to orange-white, curved, slightly saccate with a rounded apex, (often visibly) filled with nectar for one third to half of its length. **Column** stout, 0.1 cm long.

Campylocentrum micranthum

Distribution: This is the most widespread species of the genus, ranging from southern Florida and the Bahamas to Brazil and Peru. Not uncommon.

Ecology: The plants usually grow in humid to wet evergreen lowland forests, from sea level to 750 m. In the Golfo Dulce region, they are found in shady places, mostly on lower branches and twigs of trees. The plants often grow on cultivated trees such as citrus (*Citrus*), cocoa (*Theobroma*), guava (*Psidium*) and calabash (*Crescentia*). Sometimes the plants appear to be suspended in the air, as they are attached to the host tree by only a few roots.

Flowering: Mainly from January to June, but may occur sporadically throughout the year.

Pollination biology: No particulars are known for the species. The white flowers and the long, nectar-filled spur suggest pollination by sphingid or noctuid moths.


Campylocentrum micranthum

Remarks: (1) *Campylocentrum* is a remarkable genus because its species are the only truly monopodial orchids in Costa Rica, and in Central and South America as a whole. Other monopodial genera are found in Mexico and the Caribbean, but include only a few species, whereas *Campylocentrum* contains 64 species. (2) Although some species occur in Asia (Sri Lanka), the centre of diversity of subtribe Angraecinae is in the African tropics, where the closest relatives of the genus *Campylocentrum* are found. (3) Although superficially resembling some *Epidendrum* species, *Campylocentrum* cannot be confused with that or any other genus. The persisting lateral inflorescences about the length of the leaves are characteristic. Such inflorescences are not found in the species of *Epidendrum* found in the Golfo Dulce region. (4) The full name of the species is sometimes given as *Campylocentrum micranthum* (Lindl.) Rolfe, but Rolfe's transfer (1903) is antedated by that of Maury (1889).

References: Dodson and Escobar (1993: 92), Dressler in Hammel *et al.* (2003: 39–40), Escobar *et al.* (1991: 54–55), Hamer (1982: pl. 627).

Catasetum maculatum

Catasetum maculatum Kunth, Syn. Pl. 1: 331 (1822).
E.: Spotted *Catasetum*. **Sp.:** Torito, Zapatico.

Etymology: The generic name is formed from the Greek *kata* (= below) and *seta* (= bristle), referring to the characteristic bristles at the base of the column. The Latin epithet *maculatum* (= spotted, speckled) alludes to the spotted flowers.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Catasetinae.

Taxonomic notes: This species was first collected in Colombia in 1801 by the famous naturalists and explorers Alexander von Humboldt (1769–1859) and Aimé Bonpland (1773–1858), but only described 20 years later by one of Humboldt's German collaborators in Paris, Carl S. Kunth (1788–1850).

Description: Plants epiphytic, caespitose, stems ascending, up to 70 cm tall. **Pseudobulbs** subfusiform–conical, covered by thin, membranous, imbricating sheaths, 8–30 cm long, 1.5–8 cm wide, leafless pseudobulbs spiny at the apex. **Leaves** several per pseudobulb, deciduous, distichously arranged, elliptic-lanceolate, plicate, strongly nerved and acute, 30–45 cm long, 5–12 cm wide. **Inflorescence** emerging at the base of the pseudobulbs, racemose, erect to arching, up to 40 cm long, bearing 3 to 14 flowers. **Flowers** non-resupinate, dimorphic, unisexual, monoecious, but functionally dioecious, the plants producing either male or female flowers during a flowering season; bisexual inflorescences are rarely encountered. **Male flowers** yellowish green, spotted with purple; **tepals** membranaceous, elliptic to lanceolate, acuminate, 4–4.6 cm long, 1.6–2.1 cm wide; **lip** fleshy, saccate, margins of the basal part of the orifice ciliate; column concave, with 2 slender, elongate antennae curving downwards and extending into the lip. **Female flowers** yellowish green, spotted with purple at the base of the petals; **sepals** reflexed, fleshy, broadly tongue-shaped, apiculate at apex, 2.8 cm long, 2 cm wide; **petals** reflexed, fleshy, elliptic–lanceolate, acute, 2.5 cm long, 1.9 cm wide; **lip** similar to that of male flowers, but margins of the orifice not ciliate; column without antennae.


Catasetum maculatum

Catasetum maculatum

Distribution: Mexico to Colombia.

Ecology: Fairly common in Neotropical forests at lower elevations.

Flowering: July to September.

Pollination biology: As with *Stanhopea* and *Gongora*, males of euglossine bees visit the flowers of *Catasetum* in the search of fragrances. However, unlike other scent-rewarding species, this genus has unisexual flowers, which means that each flower performs either the male or female function. Although they differ morphologically, the fragrances produced by the flowers are the same. In male flowers, fragrance production starts 2–3 days after anthesis, whereas female flowers may take up to 4 days before the scent is emitted. When visiting male flowers, the bees alight on the lip and enter the lip cavity upside-down. While trying to scrape off the fragrance (tiny droplets of terpenes), they come into contact with the antennae, which are under strong tension. When touched, the antennae cause an explosive release of the pollinarium, which is catapulted against the bee and affixed to its back. After *c.* 20 min, the anther cap falls off and the stalks of the pollinia straighten into an upright position. When the bee then visits a female flower, it again enters the lip cavity upside-down in order to gather the fragrance. When trying to leave the flower, the pollinia become caught in the stigmatic opening and pollination is ensured. In both male and female flowers, scent production stops soon after the pollinia have been removed or pollination has taken place. Euglossine bees known to pollinate *Catasetum maculatum* are *Eulaema cingulata*, *E. meriana* and *E. polychroma*.

Remarks: *Catasetum* plants normally produce either male or female flowers during a season (functional dioecy), but the same plant may produce both male and female flowers during its lifetime (monoecy). Vigorous plants, growing in light-exposed places with plenty of nutrients typically produce female flowers, whereas male flowers are more commonly produced by smaller plants in nutrient-poor, shady habitats.

References: van der Cingel (2001: 83–89), Dodson (1962), Dressler in Hammel *et al.* (2003: 41), Fulop (2009), Hamer (1982: pl. 629), Higgs *et al.* (1972), Pupulin (1998).

Caularthron bilamellatum

Caularthron bilamellatum (Rchb.f.) R.E. Schultes, Bot. Mus. Leafl. 18(3): 92, t. 14 (1958).
Basionym: *Epidendrum bilamellatum* Rchb. f., Ann. Bot. Syst. 6: 345 (1862).
E.: Two-ledged *Caularthron*, little virgin. **Sp.:** Hormigero, Bacgaquero (both meaning "ant-nest", for reasons given below).

Etymology: The generic name is formed from the Latinised Greek *kaulos* (= stem) and *arthron* (= articulation, joint), referring to the nodal articulation of the swollen stem. The epithet is formed from the Latin *bi* (= two) and *lamellatus* (= lamellate), alluding to the callus of the lip, which is shaped into two gills (ribs).

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Taxonomic notes: The genus *Caularthron*, described by the French botanist Constantine S. Rafinesque (1783–1840) in 1837 and revived by Richard E. Schultes (1915–2001) in 1958, currently comprises 4 species. The genus is related to *Schomburgkia* and *Myrmecophila*, which also live in association with ants (myrmecophytic).

Description: Plants epiphytic. **Pseudobulbs** fusiform, with several nodes and internodes when fully mature, hollow inside, up to 20 cm long and 5 cm wide, young pseudobulbs completely covered by green sheaths, adult pseudobulbs covered by light beige, dead sheaths. **Leaves** 2–3, on top of pseudobulb, coriaceous, linear, somewhat conduplicate, obtuse to subacuminate, *c.* 8 cm long, 2 cm wide. **Inflorescence** terminal, 12–20 cm long, apically loosely few-flowered (up to 10 flowers). **Flowers** resupinate, white or sometimes with a pinkish hue, most flowers in an inflorescence, cleistogamous, a few chasmogamous, about 1.5–2.2 cm in diameter. **Tepals** of similar size and shape, sepals with a more rigid texture than the petals, petals more spathulate than sepals, *c.* 1.2 cm long, 0.6 cm wide. **Lip** narrowly ovate, slightly trilobed, 0.9 cm long, 0.4 cm wide, with 2 prominent triangular, hollow, ± yellow-coloured calli. **Column** almost as broad as the lip, 0.7–0.8 cm long.

Distribution: From Guatemala throughout Central America to northern South America and Trinidad.

Ecology: *Caularthron bilamellatum* is a typical epiphyte of trees growing on beaches (it is, for instance, abundant in the Manuel Antonio National Park, where it grows on the small tree *Hippomane mancinella*, Euphorbiaceae). In the Golfo Dulce region, it is quite rare; here, it grows in the crowns of large trees, especially emergent trees that are not too bushy. The plants are normally difficult to spot and to see in flower, unless the plants or flowers have fallen to the forest floor.


Caularthron bilamellatum

Flowering: Mainly February to April.

Pollination biology: *Caularthoron bilamellatum* has a mixed mating system, relying on both


Caularthron bilamellatum

selfing and insects for pollination. Normally, the plants produce a varying number of cleistogamous and a few chasmogamous flowers. The cleistogamous flowers do not open, and self-pollination takes place inside the closed flower. The chasmogamous flowers open fully and are available for cross-pollination. The cleistogamous flowers are predominantly white and are abundant in plants growing on more shady branches, whereas chasmogamous flowers are usually pale pink and predominate in plants growing in open, sunny places. The chasmogamous flowers bloom successively, with several opening at a time. Anthesis of these flowers lasts for about one week. Large carpenter bees of the genus *Xylocopa* have been reported as pollinators, but other bee species may also be involved. The mixed mating system is probably an adaptation to increase reproductive success in habitats where pollinators are limited.

Remarks: The hollow pseudobulbs of *Caularthron bilamellatum* are usually inhabited by ants. In Panama, up to 11 ant species have been found to live in association with this species. The relationship is a fairly opportunistic one. In order to grant access to the interior, a small hole opens at the base of the pseudobulbs when they reach their mature size. The ants use the hollow pseudobulbs as nesting sites. There is some evidence that they "fertilise" the plants with their nutrient-rich detritus. The ants also seem to protect the orchids from herbivores while patrolling the extrafloral nectaries at the base of the leaves and on the peduncles, buds and pedicels. Quite rare in the area.

References: van der Berg et al. in Pridgeon *et al*. (2005: 218–222), Dodson and Escobar (1993: 110–111), Dressler in Hammel *et al*. (2003: 43), Escobar *et al.* (1991: 52), Fisher and Zimmerman (1998), Gegenbauer *et al.* (2012), Genaust (1996), Hamer (1982: pl. 623), McLeish *et al.* (1995: 162–163), Schultes (1958).


Caularthron bilamellatum

Christensonella uncata (*Maxillaria uncata*)

Christensonella uncata (Lindl.) Szlach., Mytnik, Górniak & Smiszek, Polish Bot. J. 51: 59 (2006).
Basionym: *Maxillaria uncata* Lindl., Edwards's Bot. Reg. 23: t. 1986 (1837).
E.: Hook-shaped *Maxillaria*. **Sp.: -**

Etymology: The generic name commemorates the American orchidologist Eric A. Christenson (1956–2011), who contributed greatly to the knowledge of the genus *Maxillaria*. The epithet is derived from the Latin *uncatus* (= hooked), alluding to the hooked shape of the column when viewed from the side.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Taxonomic notes: The 21 species of the genus *Christensonella* were formerly included in the genus *Maxillaria*, which was shown to be highly polyphyletic in recent molecular and morphological analyses.

Description: Plants epiphytic, small, caespitose, creeping, with short to elongated rhizomes, *c.* 15 cm high. **Pseudobulbs** cylindrical, smooth, concealed by scaly bracts, unifoliate, 0.5–3 cm long. **Leaves** linear to oblong–lanceolate, fleshy, flat to terete, acute, 1.5–10 cm long, 0.1–2 cm wide. **Inflorescence** axillary, solitary, 1-flowered, *c.* 1 cm long. **Flowers** waxy, white to light purple, with pink to purple or reddish maroon stripes, lip whitish, not fragrant. **Dorsal sepal** oblong, 0.7–1.4 cm long, 0.2–0.5 cm wide. **Lateral sepals** oblong-ovate, triangular, apiculate, forming a prominent mentum, 0.9–1.5 cm long, 0.2–0.5 cm wide. **Petals** linear-oblong, acute, 0.6–1.5 cm long, 0.1–0.5 cm wide. **Lip** slender spathulate, simple, margin crenulate, basally

Christensonella uncata

channelled, concave, distal quarter constricted, tip slightly undulate, 0.9–1.9 cm long, 0.2–0.4 cm wide; callus oblong to clavate. **Column** with pronounced foot, almost as long as the column, with conspicuous wings at the apex, 0.5–1.4 cm long.

Distribution: Southern Mexico, Central America, the West Indies, the Amazon region of northern South America, and Bolivia. *Christensonella uncata* is the most widespread species of the genus, and is the only representative of *Christensonella* in Central America. It is frequent in the southern part of its distribution range, but becoming rare in the northern part of its range.

Ecology: Epiphytes on larger branches of trees, in seasonally dry and wet forests at elevations up to 1700 m.

Flowering: Throughout the year.

Christensonella uncata

Pollination biology: *Christensonella uncata* does not produce nectar or any kind of reward, although related species are known to produce wax and resin-like secretions. The pollinator species are as yet unknown, but *C. uncata* is most likely to be bee-pollinated.

Remarks: (1) *C. uncata* is the only representative of the genus *Christensonella* in Costa Rica, and can be easily distinguished from other Maxillariinae by its narrow, coriaceous leaves, white-lavender flowers with pinkish, reddish to maroon stripes, the simple lip with crenulate margins, elongate column foot and slender column with conspicuous wings, which give it the appearance of a hook. (2) The species is highly polymorphic throughout its wide range, and may actually represent a species complex consisting of several narrowly-distributed species. (3) *Christensonella* species have a unique type of pollinarium, distinct from all other types found in the Maxillariinae: the stipe is formed from the whole rostellum and detaches entirely when the pollinarium is removed (for details, see Singer and Koehler 2004).

References: Atwood and Mora de Retana in Burger (1999: 80–81), Atwood in Hammel *et al.* (2003: 330), Blanco *et al.* (2007), Koehler *et al.* (2008), Koehler *et al.* (2012), Singer and Koehler (2004), Szlachetko *et al.* (2006), Whitten *et al.* (2007).

Coryanthes kaiseriana

Coryanthes kaiseriana Gerlach, Lankesteriana 8: 23–27, f. 1A–D, t. 1–3 (2003).
E.: Kaiser's bucket orchid. **Sp.:** -

Etymology: The generic name is formed from the Greek *korys* (= helmet) and *anthos* (= flower), meaning helmet-flower. The epithet commemorates the Swiss chemist Roman Kaiser (b. 1945), who pioneered the head-space technology for fragrance analysis and contributed greatly to the understanding of plant fragrances, including those of orchids.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Stanhopeinae.

Taxonomic notes: This showy orchid was described only in 2003, by Günter Gerlach from the Munich Botanical Garden. The type specimen had been collected in 1967, in the area around San José, but had been misidentified as *C. speciosa*, *C. maculata* and *C. picturata,* respectively.

Description: Plants epiphytic. **Pseudobulbs** aggregated, narrow oblong-ovoid to oblong-conical, with a brown ring at the apex, covered when young by membranous leaf sheaths, up to 14.5 cm long, 2.2 cm wide. **Leaves** 2 at the apex of the pseudobulb, narrowly elliptical to linear-lanceolate, acute, up to 41 cm long, 5.5 cm wide. **Inflorescence** pendent, with several bracts, up to 80 cm long. **Flowers** brightly coloured and morphologically complex. **Tepals** dull greenish yellow, with reddish brown spots; sepals and lateral petals bent backwards. **Lip** slightly compressed dorsally, divided into three sections: hypochile, mesochile and epichile; hypochile orange-yellowish, with a touch of red, apex sinuate, semicircular, 3.5 cm high, 3.2 cm long, 4.2 cm wide; osmophores beneath the hypochile; mesochile semitubular in section,

Coryanthes kaiseriana

yellow with red sides; internal part of epichile yellow, with purplish red spots, exterior part yellowish red, 3.0 cm high, 3.4 cm long, 4.4 cm wide. **Column** white, with red speckles.

Distribution: The species is only known from the Pacific slopes of Costa Rica and Panama.

Ecology: Like other representatives of the genus *Coryanthes*, this species grows in humid lowland forests, being most frequently found along rivers and creeks.

Coryanthes kaiseriana

Flowering: Observed in flower in May, but likely flowers much longer.

Pollination biology: The short-lived flowers emit a strong, pleasant odour. *Coryanthes kaiseriana* belongs to the group of "perfume orchids", which reward their pollinators not with nectar, but with perfumes. These substances are collected by male euglossine bees that incorporate the perfumes into their courtship signalling. In general, the relationship between perfume orchids and their pollinators is specific, and this has also been observed in *C. kaiseriana*, which is pollinated by *Euglossa allenii* and *E. flammea*. Males of these species are attracted and rewarded by the fragrance, while the removal of pollinia and pollination is mediated by the intricate morphology of the flowers. As in lady's-slipper orchids, the lip is modified to form a liquid-filled trap. Once caught, the bees can only exit the flower through a narrow passage formed by the tip of the lip and the column apex, thereby passing the stigma and removing the pollinarium with their thorax. The whole pollination process can last 10–30 minutes. Self-pollination is prevented by the spatial separation of the stigma and the anther, as well as by the size of fresh pollinia, which are too large to fit onto the stigma.

Remarks: (1) The genus *Coryanthes* comprises *c.* 40 species, distributed from Guatemala to Bolivia. It is one of the few orchid genera known to form an obligate mutualistic partnership with ants. The plants grow in so-called "ant gardens", consisting of soil particles, detritus and plant parts, which are built between the branches of trees. The resulting clumps are up to 80–100 cm in diameter. The orchids obtain nutrients from the ant gardens and are protected from herbivores and potential competitors by the ants. It has also been hypothesised that the ants might contribute to seed dispersal, since the minute seeds have lipid deposits which may serve as food for the ants. Another source of nutrients is the nectar produced in extra-floral nectaries located in the most vulnerable parts of the plant, such as new shoots, bracts or flower buds. The most common ant genera associated with *Coryanthes* species are *Crematogaster*, *Azteca* and *Camponotus*.

References: Gerlach and Dressler (2003), Gerlach (2011).

Dichaea panamensis

Dichaea panamensis Lindl., Gen. Sp. Orchid. Pl.: 209 (1833).
E.: Panamanian *Dichaea*. **Sp.:** -

Etymology: The generic name is formed from the Greek *di* (= two) and *keio* (= to divide), referring to the distichous leaf arrangement. The epithet refers to Panama, the country from which the species was first described.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Zygopetalinae.

Description: Plants epiphytic, caespitose, without pseudobulbs. **Stems** of up to 20 cm long, flattened, spreading to suberect or pendent, unbranched or rarely producing lateral shoots. **Leaves** 2-ranked, with base clasping the stem, oblique to spreading, subcoriaceous, narrowly elliptic to lanceolate, acute, 1.2–4 cm long and 0.2–0.5 cm wide, varying in length along the stem. **Inflorescence** solitary, emerging below the leaves, 1-flowered. **Flower** variable in colour, sepals and petals usually greenish white, with purple spots of different size and shape, lip white, spotted towards the apex. **Dorsal sepal** lanceolate-ovate, dorsally carinate, 0.6–0.9 cm long, 0.2–0.3 cm wide. **Lateral sepals** similar in shape to the dorsal sepal, 0.6–1.2 cm long, 0.4 cm wide. **Petals** obliquely ovate, acute, wider than the sepals, 0.4–0.9 cm long, 0.3–0.5 cm wide. **Lip** anchor-shaped, 0.7–1 cm long, 0.6–0.9 cm wide when spread, bipartite: hypochile inversely cuneate, epichile broadly triangular, trilobed, lateral lobes narrowly triangular, acute, spreading, retuse. **Column** greenish white, anther cap with a purplish hue, erect, 0.3–0.6 cm long, with a distinct foot.

Distribution: Widely distributed in the Neotropics, ranging from Mexico through Central America to Peru, Ecuador and Brazil. Common.

Ecology: The plants grow in moist to wet forests at up to 1100 m, usually preferring shady places on the trunks of forest trees.

Flowering: Throughout the year.

Pollination biology: *Dichaea* species appear to be pollinated by male euglossine bees, which collect fragrances. The flowers are nectarless.


Dichaea panamensis

Pollinia of *D. panamensis* have been found on various species of *Euglossa* and *Eufriesea*, although it is still uncertain what fragrant substances, if any, are produced by the flowers.

References: Allen in Woodson and Schery (1949: 240), Dressler in Hammel *et al*. (2003: 77), Pupulin (2010: 36–37).


Dichaea panamensis


Dichaea panamensis


Dichaea panamensis

Dichaea poicillantha

Dichaea poicillantha Schltr., Repert. Spec. Nov. Regni Veg., Beih. 19: 73 (1923).
E.: Colourful-flowered *Dichaea* **Sp.:** -

Etymology: The epithet is formed from the Latinised Greek *poikilos* (= many-coloured, varied, spotted) and *anthos* (= flower), in reference to the flowers' strongly spotted sepals and petals.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Zygopetalinae.

Description: Plants epiphytic, caespitose, without pseudobulbs. **Stems** completely enclosed by imbricating leaf sheaths, pendent, dorsoventrally flattened and loosely branched, up to 90 cm long. **Leaves** distichous, usually expanded, ovate-elliptic to oblong, apiculate, medium-green to olive-green or bronze-green, 7–20 cm long, 3–7 cm wide. **Inflorescences** solitary, 1-flowered, emerging below the foliage, 0.8–1.6 cm long. **Flowers** bowl-shaped to completely spreading, sepals and petals grey-orange, spotted violet, lip white, with violet shoulders and a solid violet epichile. **Sepals** oblong-elliptic, acute, dorsal sepal often curved over the column, 0.65–1.4 cm long, 0.35–0.6 cm wide. **Petals** elliptic to oblong, bent, acute, similar to or larger than sepals. **Lip** anchor-shaped, bipartite: hypochile square, broadly inversely cuneate, with broadly rounded shoulders; epichile transversally elliptic, broadly obtuse, provided with long attenuate, spreading to retuse lateral lobes. **Column** yellow-green, wings violet, suberect to erect, 0.35–0.4 cm long, column foot subterete at base, with 2 ciliate semi-elliptic, rounded wings, apically dilated into a petaloid, erect clinandrium.

Distribution: Nicaragua to Panama, perhaps also in Mexico.

Ecology: Widespread in shady places in the understorey of lowland to submontane wet forests, 200–2500 m. Like all *Dichaea* species, *D. poicillantha* is a shade-loving plant, growing mostly under low light conditions on the main trunk and large branches of trees, where the plants may form large clumps.

Dichaea poicillantha

Flowering: Throughout the year, with a peak between May and July.

Pollination biology: The pollinator of *D. poicillantha* is unknown, but it seems that species of *Dichaea* are generally pollinated by fragrance-collecting male euglossine bees.

Remarks: The problematic identity of this variable species (the type material was lost and only the original drawing of the flowers has survived) was only recently clarified.

References: Dressler in Hammel *et al*. (2003: 77), Neubig *et al*. (2009), Pupulin in Pridgeon *et al.* (2009: 489–494), Pupulin (2010: 38).

Dichaea poicillantha

Dichaea poicillantha

Dresslerella hispida

Dresslerella hispida (L.O.Williams) Luer, Selbyana 3(1): 4 (1976).
Basionym: *Pleurothallis hispida L.O.Williams,* Ann. Missouri Bot. Gard. 27(3): 277 (1940).
E.: Hispid *Dresslerella*. **Sp.: -**

Etymology: The generic name commemorates the American orchidologist Robert L. Dressler (b. 1927). The epithet is derived from the Latin *hispidus* (= hairy), referring to the hairy leaf margins and sepals.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants epiphytic, caespitose, up to 5 cm tall, pseudobulbs lacking. **Stems** prostate, 1–4 cm long, with a single leaf, enclosed by several leathery, ciliate sheaths, the upper one reaching to the base of the leaf. **Leaves** narrowly elliptic, coriaceous, obtuse, minutely ciliate at the margins, 1–6.5 cm long, 1–2.5 cm wide. **Inflorescence** short, one- to few-flowered, emerging at the base of the leaf blade, from beneath the last sheath. **Flowers** dark purple, covered by white hairs, almost closed, with only an apical opening between the dorsal sepal and the synsepal. **Dorsal sepal** lanceolate, acute, connate for half its length to the lateral sepals, 0.5–1 cm long, 0.2–0.3 cm wide. **Lateral sepals** connate to their tips, forming a boat-shaped synsepal, 0.6–1.1 cm long, 0.4–0.6 cm wide. **Petals** linear-oblong, acute, 0.4–0.7 cm long, 0.1–0.2 cm wide. **Lip** sagittate-lanceolate, obtuse, with erect lateral lobes. **Column** auriculate-winged towards the apex, 0.25 cm long.

Distribution: Nicaragua, Costa Rica, Panama, Colombia. Rare.

Ecology: Epiphyte in wet forests, from 450 m to 500 m.

Dresslerella hispida

Flowering: Plants have been observed in flower in July, September and October, but the flowering period might be longer.

Pollination biology: There are no records of the pollination biology of this genus. The flower colour and size suggest fly-pollination. The dorsal sepal and the petals of some species bear osmophores, which apparently serve to attract pollinators. In addition, the small size of the opening between the dorsal sepal and the synsepal may act as a barrier to larger insects.

Remarks: The genus *Dresslerella* comprises 8 species, which are quite variable in both plant habit and flower colour, making identification difficult. The species is easy to differentialte from all other pleurothalids in the Golfo Dulce region due to its glaucous velvety leaves.

References: Luer in Hammel *et al.* (2003: 85), Medina and Pupulin (2010), Pridgeon in Pridgeon *et al.* (2005, 352–354).

Dresslerella hispida

Dresslerella hispida

Dryadella odontostele

Dryadella odontostele Luer, Lindleyana 11 (2): 54–55 (1996).
E.: - **Sp.:** -

Etymology: The generic name probably alludes to the *dryades* (= dryads, female tree spirits) of Greek mythology. The epithet is formed from the Greek *odon* (= tooth) and *stele* (= column), referring to the toothed column of the species.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants miniature epiphytes, growing in dense turfs, pseudobulbs lacking. **Leaves** erect, coriaceous, narrowly elliptic to obovate, 1–2.5 cm long, 0.3–0.35 cm wide. **Inflorescence** solitary, racemose, producing one solitary, inconspicuous flower at a time. **Flowers** translucent green, with some red areas. **Dorsal sepal** ovate, concave, obtuse, connate to the lateral sepals, forming a cup, 0.35–0.4 cm long, 0.2–0.25 cm wide. **Lateral sepals** ovate, oblique, obtuse, 0.3 cm long, 0.2 cm wide. **Petals** green, usually with a red mid-vein, subsagittate, obtuse, 0.15 cm long, 0.13 cm wide. **Lip** greenish, reddish at the base, blade elliptical, slightly curved, apically rounded, base ending in 2 recurved appendages, 0.13 cm long, 0.1 cm wide. **Column** green, with pink spots, with a pair of acute, descending tooth-like, 0.15 cm long processes near the apex.

Distribution: From Costa Rica to Colombia. Not uncommon.

Ecology: Found in humid forests between 50 m and 900 m.

Flowering: September to October.

Pollination biology: The pollinators and pollination mechanism of this species are not yet known, but the flowers are assumed to be fly-pollinated.

Remarks: This is the only species of *Dryadella* in Costa Rica to have the column morphology described above.

References: Luer (1996), Luer in Hammel *et al.* (2003: 89).

Dryadella odontostele

Elleanthus graminifolius

Elleanthus graminifolius (Barb.Rodr.) Løjtnant, Bot. Not. 129: 447 (1977).
Basionym: *Adeneleuterophora graminifolia* Barb.Rodr., Gen. Sp. Orchid. 2: 171, t. 797 (1882).
E.: Grass-leaved *Elleanthus*. **Sp.: -**

Etymology: The meaning of the generic name is unclear. The first part of the name may refer to the Greek mythological women *Helle* – after whom the Hellespont (Dardanelles) is named – or to *Helena*, the wife of Menelaus of Sparta, whose abduction by Paris caused the Trojan War – but it is more likely that it refer to the Greek *helene* (= torch), which in combination with *anthos* (Latinised *anthus*, = flower) alludes to the inflorescence, which may suggest a torch with flame-like flowers. The epithet is formed from the Latin *gramineus* (= graminaceous, grass-like) and *folium* (= leaf), referring to the grass-like leaves.

Classification: Subf. Epidendroideae, Tr. Sobralieae.

Description: Plant epiphytic, growing in dense clumps, pseudobulbs lacking. **Stems** slender, *c.* 30 cm long. **Leaves** narrowly linear, apically tridentate, varying in length along the stem, 4–5.5 cm long, 0.08–0.2 cm wide. **Inflorescence** terminal, racemose, with a subtending leaf-like bract, somewhat exceeding the inflorescence in length, bearing one to several flowers. Floral bracts distichous, ovate, acute. **Flowers** white, with a greenish throat, opening ± successively. **Sepals** lanceolate-ovate, acute, 0.3–0.4 cm long, 0.1–0.15 cm wide. **Petals** falcate, margins erose, 0.3–0.4 cm long, 0.1–0.15 cm wide. **Lip** saccate at the base, broadening apically into a somewhat erose lamina, with 2 fleshy, elliptic calli at the base, 0.3–0.35 cm long, 0.4–0.45 cm wide. **Column** short, with an apical tooth, *c.* 0.2 cm long.

Distribution: Mexico, the West Indies to Peru and Brazil.

Ecology: *Elleanthus graminifolius* prefers wet forests in a warm climate, up to 1200 m, usually growing in large clumps on the higher branches of trees.

Flowering: Throughout the year, with a peak in October.

Pollination biology: Several species of the genus are hummingbird-pollinated and *E. brasiliensis* is known to be protandrous. No particulars are known about the pollination of *E. graminifolius.*

Remarks: The genus comprises c. 115 species, native to the Neotropics. In the Golfo Dulce region three other species are known, from which *E. graminifolius* can be distinguished by its small size, grass-like leaves, flattened inflorescences and superimposed bracts.

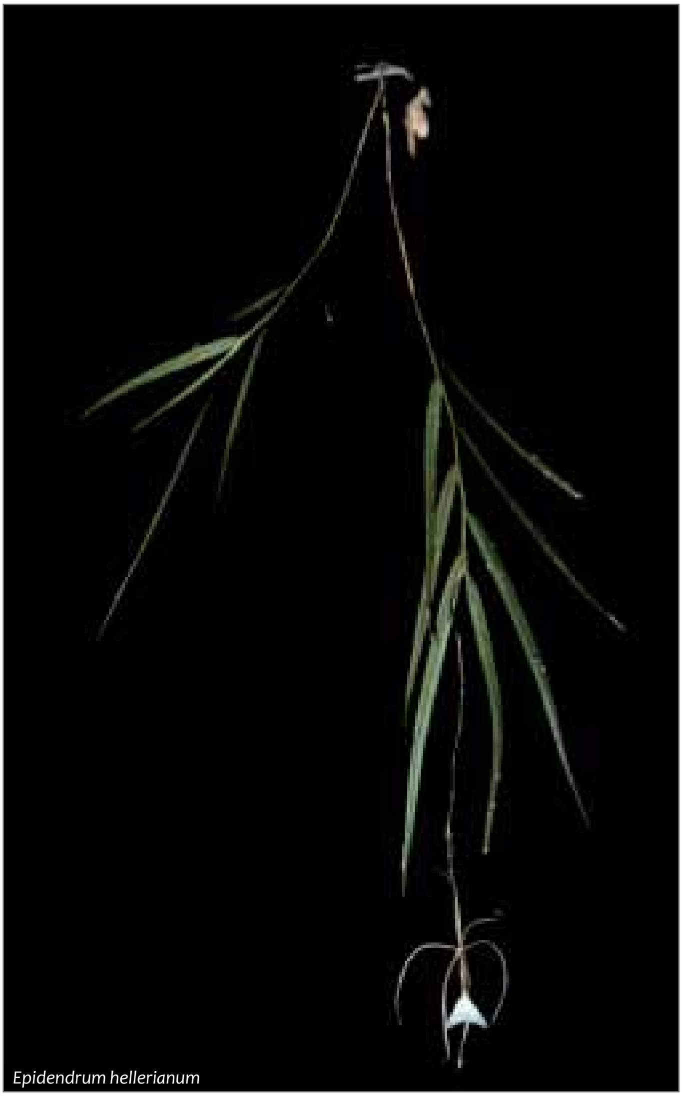
References: Dressler in Hammel *et al.* (2003: 93), Hamer (1982: pl. 674), Singer (2003).

Elleanthus graminifolius

Epidendrum hellerianum

Epidendrum hellerianum A.D.Hawkes, Orchid Digest 30(8): 258–259 (1966).
E.: Heller's *Epidendrum*. **Sp.:** -

Etymology: The generic name is formed from the Greek *epi* (= on, upon) and *dendron* (= tree), referring to the epiphytic growth of the plants. The genus was established by Carl Linnaeus (1707-1778) in 1753 and originally included all the epiphytic orchids known at the time. The specific epithet commemorates the American mining engineer and amateur botanist Alfonse H. Heller (1894–1973), who was the first to collect specimens of the species in Nicaragua.



Epidendrum hellerianum

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Description: Plants epiphytic, with long, pendent shoots up to 50 cm, pseudobulbs absent. **Stems** slender, unbranched, with leaves only in the upper part. **Leaves** articulate, narrowly linear, acute, grass-like, 15 cm long, 3–0.5 cm wide. **Inflorescence** terminal, pendent, peduncles filiform, fractiflex, up to 8 cm long, with nodes at intervals of *c.* 1.5 cm, concealed by sheathing bracts. Pedicels short, filiform. Ovary translucent, basally inflated, narrowing towards the junction with the column. **Flowers** white, occasionally with a reddish tint on the sepals, petals and ovary, pendent, solitary, produced successively; up to 6 cm broad when fully spreading. **Sepals** linear-oblanceolate, acute, forming a narrow tube at the base, 3 cm long, 0.3–0.4 cm wide. **Petals** similar to sepals, 3 cm long, 0.1–0.2 cm wide. **Lip** with 2 erect calli at the base, trilobed above the middle, apex lobe strongly reflexed, 1.6 cm long,1.6 cm wide when spread; lateral lobes dolabriform, obtuse, midlobe triangular, acute. **Column** elongate, clavate, apically 3-lobed, 1.4–1.7 cm long, 0.1–0.4 cm wide.

Distribution: From Nicaragua to Panama.

Ecology: *Epidendrum hellerianum* grows as an arching to pendent epiphyte in deep shade in very wet rain forests at low elevations, from sea level to 600 m. It is not common around Golfo Dulce.

Flowering: Sporadically throughout the year.

Epidendrum hellerianum

Pollination biology: Most *Epidendrum* species are known to be pollinated by butterflies and moths, but several species attract hummingbirds. Species adapted to moths have white or green, star-shaped flowers, deep nectaries and produce fragrances mostly at night. Butterfly pollinated species are brightly coloured and produce only a faint scent, while hummingbird pollinated species have bright orange, red to purple flowers and are often scentless. Some species have also been reported to be autogamous. The genus comprises mostly food-deceptive species. In the case of *E. hellerianum*, the most likely pollinators are moths, because the mainly white flowers are probably fragrant at night. Additionally, the flowers have a very long (*c.* 6 cm), translucent, saccate spur adnate to the ovary, suggesting adaptation to the long proboscis of moths.

Remarks: (1) The genus Epidendrum comprises c. 1500 species. All of the species originally included in the genus by Linnaeus have since been included into other genera. (2) E. hellerianum is easily recognised by its narrow sepals and petals and its prominent, translucent ovaries. Vegetatively, *E. hellerianum* can only be confused with *E. turialvae*, which grows in the same ecological niche but is a much more robust plant, with stems that are leafy throughout, while those of *E. hellerianum* bear few leaves on the upper portions of the stems.

References: van der Cingel (2001: 74-75), Hágsater, García-Cruz and Sánchez Saldaña in Hammel *et al.* (2003: 134), Hágsater *et al.* in Pridgeon *et al.* (2005: 236-251), Hamer (1982: pl. 718).

Epidendrum nocturnum

Epidendrum nocturnum Jacq., Enum. Syst. Pl. 29 (1760).
E.: Star orchid, San Pedro orchid. **Sp.:** Orquidea Estrella.

Etymology: The Latin epithet *nocturnum* (= nocturnal, nightly) alludes to the species' nocturnal fragrance emission.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Taxonomic notes: This orchid was among the first Neotropical species to be described. The description was prepared by the famous Austrian botanist Nikolaus Joseph Freiherr von Jacquin, founder of the Botanical Garden of Vienna, and was published in the epoch-making book *Enumeratio systematica plantarum, quas in insulis Caribaeis vicinaque Americes continente detexit novas, aut jam cognitas emendavit* in 1760.

Description: Plants epiphytic, lithophytic or sometimes terrestrial, with ± upright shoots, pseudobulbs lacking. **Stems** terete at base, becoming somewhat flattened toward the apex, 15–70 cm long, completely covered by sheaths and bearing leaves only along the upper portion of the stem. **Leaves** 4–10, linear-elliptic to ovate-elliptic, apex obtuse to retuse, leaf blade *c.* 10 cm long, 4 cm wide. **Inflorescence** terminal, short and compact, completely covered by dead sheaths, producing several flowers in succession, with one flower opening at a time. **Flowers** large and star-shaped. **Sepals** greenish yellow to yellowish white, narrow, acute, with recurved margins, 4–6.5 cm long, 0.5–0.8 cm wide. **Petals** like the sepals, but slightly narrower. **Lip**


Epidendrum nocturnum

white with 2 yellow calli, attached to the column up to its apex, trilobed; lateral lobes elliptical to ovate, white, 0.4–0.7 cm long, 1.0–1.5 cm wide; central lobe linear-filiform, narrowly acuminate, white, sometimes turning greenish or yellowish towards the tip, 2.5–4.5 cm long, *c.* 0.3 cm broad. **Column** straight to slightly curved, somewhat thicker towards the apex, white, 1.5 cm wide, 0.5 cm broad.


Epidendrum nocturnum

Distribution: From Florida to southern South America.

Ecology: *Epidendrum nocturnum* grows mostly as an epiphyte, but can also be found growing on rocks and escarpments or even on fence poles (as seen in the photograph). The species is found in forests at altitudes of 0–800 (–1500) m. It is, however, heliophilous, and can even survive in places with full sun. In the Golfo Dulce region, it is more common in disturbed places with secondary vegetation than in the dense primary forest. Here, the plants grow in the canopy of the trees, where they are difficult to spot.

Flowering: Throughout the year.

Pollination biology: Most *Epidendrum* species with white or light-coloured flowers are known to be pollinated by moths. This probably also applies to *E. nocturnum*, which is known to emit a strong fragrance at night. Cleistogamous individuals and populations of *E. nocturnum* are also known, but have not yet been encountered in the area under consideration.

Remarks: *Epidendrum nocturnum* is quite variable in the size and shape of the lip. Several varieties and forms have been recognised, which, in more recent molecular genetic studies, have proved to be true species. However, all the plants found so far in the Golfo Dulce region seem to belong to *E. nocturnum* s. str. The species can be confused with *E. oerstedii* and *E. longicolle*, but the former has prominent 1–2-leaved pseudobulbs, whereas the latter has stems with a greater number of much narrower leaves. Neither *E. oerstedii* nor *E. longicolle* has yet been collected in the Golfo Dulce region.

References: Escobar *et al.* (1991: 168-179), Hágsater, García-Cruz and Sánchez Saldaña in Hammel *et al.* (2003: 145), Hamer (1982: pl. 723), van der Pijl and Dodson (1966: 127).

Epidendrum pseudepidendrum

Epidendrum pseudepidendrum Rchb.f., Xenia Orchid. 1: 160, t. 53 (1856).
Basionym: *Pseudepidendrum spectabile* Rchb.f., Bot. Zeitung (Berlin) 10(42): 733–734 (1852).
E.: False *Epidendrum*. **Sp.:** -

Etymology: The epithet is formed from the Greek prefix *pseudo* (= false, deceptive, having a close resemblance to) and the generic name *Epidendrum* (see *E. hellerianum*). Reichenbach originally thought that the species belonged to a genus that was different from (but resembled) *Epidendrum*, which he named *Pseudepidendrum*. When transferring it to *Epidendrum*, he used that name as the specific epithet (since the epithet *spectabile* of the basionym was no longer available).

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Description: Plants epiphytic, caespitose, pseudobulbs lacking. **Stems** erect, cylindrical, 50–200 cm tall, completely covered by sheaths, bearing 5–10 leaves in the apical third. **Leaves** elliptical to oblanceolate, acute, somewhat coriaceous, 5.0–20 cm long, 1.5–5 wide. **Inflorescence** subterminal, racemose, sometimes branched, several-flowered, mostly not more than 4 opening at the same time, arching to overhanging while elongating, about 15 cm long, axis completely covered by imbricate bracts, floral bracts much shorter than the ovaries. **Flowers** small to medium-sized, but showy because of the bright orange lip contrasting with the dark green tepals, weakly scented. **Sepals** similar in size and shape, oblanceolate, acute, concavely spathulate near their apices, 2.4–3.2 cm long, 0.4–0.7 cm wide, the lateral sepals usually somewhat narrower. **Petals** of similar length to the sepals, but narrower (*c.* 0.3 cm broad). **Lip** unguiculate, the long claw attached to the column, subquadrate to ± bilobate, apically recurved, lobes subquadrate, obtuse, edges crenulate to lacerate; disc with short calli at the base and a central one with 1, 3 or up to 5 ridges running along the centre from the base to the apex. **Column**, straight, clubbed, green at the base, turning yellow, pink or magenta towards the apex.

Distribution: Known to occur in southern Costa Rica and northern Panama.

Epidendrum pseudepidendrum

Ecology: *Epidendum pseudepidendrum* occurs in fairly wet forests on the Pacific slope, from 200 to 1700 m. The plants usually grow on the main branches of large trees, where access to light is better than inside the forest; the plants are therefore hard to spot. The species seems to be quite rare and can be found only at the highest elevations in the Golfo Dulce region.

Flowering: December to January.

Pollination biology: *Epidendum pseudepidendrum* is a hummingbird-pollinated species, pollinator attraction being ensured by the bright and showy orange lip of the flowers. The flowers do not produce any kind of reward (food deception), but may mimic co-occurring rewarding species.

Remarks: Due to the large size of the plants and the distinctively green and orange coloured flowers, this species cannot be confused with any other orchid growing in the Golfo Dulce region. The species is much sought after by orchid collectors for its showy flowers, and, unfortunately, over-collecting has led to a decline of natural populations. Given its small area of distribution, *E. pseudepidendrum* is also threatened by the destruction of its habitat and is considered an endangered species.

References: van der Cingel (2001: 121), Hágsater, García-Cruz and Sánchez Saldaña in Hammel *et al.* (2003: 155–156), Morales (2009: 128), van der Pijl and Dodson (1966: 95), Williams in Woodson and Schery (1946: 367).

Epidendrum pseudepidendrum

Epidendrum schlechterianum

Epidendrum schlechterianum Ames, Schedul. Orchid. 7: 9, fig. I (1924).
Basionym: *Epidendrum brevicaule* Schltr., Feddes Repert. Beihefte 17: 30 (1922) 30, non Schltr. Feddes Repert. Beihefte 9: 81 (1921).
E.: Schlechter's *Epidendrum*. **Sp.: -**

Etymology: The epithet commemorates the German orchidologist Rudolf Schlechter (1872–1925), who first described the species under the illegitimate name *E. brevicaule*.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Taxonomic notes: Due to several erroneous descriptions and taxonomic rearrangements, the species can often be found as either *Nanodes discolor* Lindl., *Nanodes congestioides* (Ames & C.Schweinf.) Brieger or *Epidendrum congestoides* Ames & C.Schweinf. in numerous publications.

Description: Plants small, epiphytic or lithophytic, densely caespitose, many-branched, without pseudobulbs. **Stems** 3–7 cm long, stout, densely leaved throughout, concealing the surface of the stem. **Leaves** succulent, green with a ± purple suffusion (depending on the intensity of insolation), densely imbricate, distichous, oblong to ovate, obtuse, with minutely rugose margins, 1–2 cm long, 0.6–1.0 cm broad. **Inflorescence** apical, racemose, emerging from the axils of the apical leaves, shorter or slightly longer than the leaves. **Flowers** usually two, opening simultaneously, large compared to the small size of the plant, almost the same colour as the leaves, ± yellowish–reddish green and usually shinier than the leaves. **Sepals** widely spreading, dorsally carinate, carinae of the lateral sepals minutely denticulate, *c.* 1.0 cm long, 0.4 cm broad. **Petals** widely spreading, pointing diagonally downwards, almost parallel to the lateral sepals, margins minutely dentate to erose, *c.* 0.8 cm long, 0.3 cm broad. **Lip** succulent, adnate to the column, reniform, mucronate, often of a more intense reddish or even slightly bluish-green colour and a velvety appearance, margins erose to minutely denticulate, *c.* 0.5–0.8 cm long, 0.5. cm broad. **Column** cylindrical, fimbriate at apex, *c.* 0.5 cm long.


Epidendrum schlechterianum

Epidendrum schlechterianum

Distribution: Widespread from Mexico to northern South America, extending as far as Guyana, French Guiana, Trinidad and Tobago.

Ecology: The species occurs in very wet lowland forests, preferring light-exposed places on solitary trees or high branches in the canopy. Plants can occasionally be found on exposed, mossy rocks. They are also commonly seen in secondary forests or in plantations of fruit trees.

Flowering: Throughout the year, with a peak between January and June.

Pollination biology: No particulars known.

Remarks: The plants closely resemble *Epidendrum congestum*, a species endemic to Costa Rica, but that species has so far been found only at altitudes between 1000 m and 2000 m, and thus seems to be ecologically well separated. *Epidendrum congestum* usually produces 3–4 flowers opening at a time at the stem apex, and the flowers have a cordate rather than reniform lip.

References: Ames (1924: 9, fig. 1), Hágsater, García-Cruz and Sánchez Saldaña in Hammel *et al.* (2003: 125–126, as *E. congestoides*), Hamer (1984: pl. 882), Williams in Woodson and Schery (1946: 372–373).

Epidendrum turialvae

Epidendrum turialvae Rchb.f., Gard. Chron. 1871: 1678 (1871).
E.: Turrialba *Epidendrum*. **Sp.:** -

Etymology: The epithet is derived from *turialva* (= Turrialba, also spelled Turialva), the name of a volcano and its adjacent area in the province of Cartago (Costa Rica).

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Description: Plants epiphytic, shoots erect, overhanging or pendent (depending on the size of the plant), pseudobulbs lacking. **Stems** terete, ± leafy throughout or bearing leaves in the apical half only, 30–60 cm long. **Leaves** 6 to 11, narrowly lanceolate, elongate–acuminate, about 10–20 cm long, 0.5–2.5 cm broad. **Inflorescence** terminal, arching to pendent, completely covered by large flattened sheaths, up to 15 cm long; rachis racemose, few-flowered, flowers opening from the base to the tip, one to three open at a time; over the year, a peduncle may produce more than one raceme, each arising from a different node. **Flowers** resupinate, relatively small and inconspicuous compared to the size of the plant; sepals and petals light green, occasionally with a purplish hue, strongly reflexed, sometimes even touching the ovary with their outer surface. **Sepals** spathulate, concave, 1.0–1.3 cm long, 0.3–0.5 cm broad; lateral sepals carinate with slightly asymmetric, acuminate tips. **Petals** filiform, 1.0–1.2 cm long, 0.02–0.1 cm broad (0.1 cm at the broadest part of the conspicuously spathulate and acuminate apex). **Lip** white or greenish white, subquadrate, nearly as long as wide, 0.9–1.1 cm long, 1.0–1.2 cm wide, trilobate; the central lobe conspicuously winged, wings broad and truncate; lateral lobes dolabriform with rounded apices; disc with 2 porrect, oblong and obtuse calli near the base, followed by a prominent central crest that extends to the apex of the lip, accompanied by 2 smaller and shorter parallel crests on both sides. **Column** clubbed, adnate to the lip, *c.* 1 cm long.


Epidendrum turialvae

Distribution: Some authors consider *E. turialvae* to be endemic to Costa Rica, but it has also been collected in adjacent Nicaragua.

Epidendrum turialvae

Ecology: This forest species occurs within a wide range of altitudes, from sea level up to 1100 m. The plants grow epiphytically low down on tree trunks and on thicker branches in relatively shady places inside the forest.

Flowering: Throughout the year.

Pollination biology: Most *Epidendrum* spp. with inconspicuously coloured flowers are known (or assumed) to be pollinated by moths. The pollinators of *E. turialvae* are, as yet, unknown. Since the coloration of the lip varies from pure white to deep purple or violet, the flowers cannot be assigned to a specific (insect) pollination syndrome.

Remarks: (1) This species is quite variable in the coloration of the lip. Most flowers have a ± purplish violet blotch in the centre of the lip, while others have an entirely white or entirely deep violet lip, sometimes even with an almost bluish hue where the coloration of the blotch is very faint. (2) With its mostly overhanging shoots, the species can hardly be confused with any other orchid occurring in the Golfo Dulce region. Smaller plants (with erect shoots) may resemble *E. hellerianum*, which grows in similar ecological conditions, but the stems are more robust. When in flower, it is possible to distinguish *E. turialvae* by the reflexed greenish sepals and petals, which usually contrast with the colour of the lip and the trilobed labellum, with a bilobed midlobe.

References: Hágsater, García-Cruz and Sánchez Saldaña in Hammel *et al.* (2003: 168), Hamer (1982: pl. 742), Morales (2009: 160).

Epidendrum turialvae

Epidendrum vulgoamparoanum

Epidendrum vulgoamparoanum Hágsater & L.Sánchez, Icon. Orch. 8, Pl. 898 (2006).
E.: - **Sp.:** Plástico.

Etymology: The epithet is formed from *vulgo* (= generally, in the sense of common people; from the Latin *vulgus* = people) and *amparoanum*, a name alluding to Doña Amparo de Celedón, who sent a consignment of orchid material from Costa Rica to Rudolf Schlechter in Berlin (Germany) for identification and investigation in *c.* 1900. For a long time, the species was mistaken for *E. amparoanum*, but was then recognised as a different and new species, hence the specific name beginning with *vulgo*.

Epidendrum vulgoamparoanum

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Description: Plants epiphytic, shoots of young plants erect to horizontal or overhanging, caespitose, with sympodial branching, pseudobulbs lacking. **Stems** few, about 15–35 long, laterally compressed, distichously leaved throughout, losing their leaves when old. **Leaves** 4–9, light green, succulent and stiff, elliptic to ovate, slightly conduplicate and dorsally carinate, 3–7 cm long, 1.5–3 cm broad, the largest leaves in the upper third of the stem, but the last one conspicuously smaller and enclosing the inflorescence. **Inflorescence** very short and entirely enclosed by the sheath of the apical leaf, few- to many-flowered. **Flowers** large, usually 3–5 in an inflorescence, resupinate, opening simultaneously, light green to yellowish green, becoming dull yellow when fading, fragrant. **Dorsal sepal** elliptic, acute, with ± recurved, entire margins, 2–3 cm long, 0.5–1 cm broad. **Lateral sepals** well separated, opening widely, similar to the dorsal sepal in shape and size, but tending to be somewhat broader. **Petals** elliptic to oblanceolate, acute, somewhat smaller than the sepals, flat, slightly curved and pointing forwards. **Lip** coriaceous, rigid, basally adnate to the column, 2.5–3.0 cm long, 1.5–2.0 cm broad, reniform, obscurely trilobed, with a furrowed callus, margins somewhat undulate. **Column** straight, short, *c.* 1.3 cm long, forming


Epidendrum vulgoamparoanum

a deep tube together with the base of the lip; tube elongated, forming a thin capillary nectary into the ovary.

Distribution: From the Pacific coast of Costa Rica southwards to the northern part of Panama, at altitudes of up to 500 m. Common.

Ecology: The species grows mainly in the lowlands, in wet to seasonally dry forests. It prefers semi-shaded to exposed sites on branches and trunks of mostly solitary trees or trees growing at the forest edge. It is therefore not uncommon to find it on trees along roadsides and in plantations of fruit trees. Exotic trees such as old mango trees (*Mangifera indica*) are, for example, common host trees.

Flowering: Sporadically throughout the year.

Pollination biology: Owing to the strong smell of the flowers (resembling hot plastic or rubber, and also present to a certain extent during the day; pers. obs.), the inconspicuous flower colouring and the deep nectariferous tube, moths are the most likely pollinators, as with many other species of the *Epidendrum difforme* group.

Remarks: *Epidendrum vulgoamparoanum* belongs to the *Epidendrum difforme* group, which is characterised by small to medium-sized cane-like epiphytic species with a short apical, usually many-flowered, inflorescence of green, whitish or yellowish green, sometimes somewhat translucent and ± coriaceous flowers, which are strongly fragrant at night. As many of these *Epidendrum* species look very much alike, there has been much taxonomic confusion. *Epidendrum vulgoamparoanum* seems to be the only species of the *E. difforme* group that occurs in the Golfo Dulce region, but a closer examination may bring other species to light.

References: Hágsater and Soto Arenas (2002: pl. 898), Hágsater, García-Cruz and Sánchez Saldaña in Hammel *et al.* (2003: 114), van der Pijl and Dodson (1966: 86–87).

Erycina crista-galli *(Oncidium crista-galli)*

Erycina crista-galli (Rchb.f.) N.H.Williams & M.W.Chase, Lindleyana 16: 136 (2001).
Basionym: *Oncidium crista-galli* Rchb.f., Bot. Zeitung (Berlin) 10: 697 (1852).
E.: Dancing lady. **Sp.:** Dama danzante.

Etymology: The generic name is derived from the Greek *Erykine* (= a sobriquet for Aphrodite, the goddess of love and beauty in Greek mythology), probably referring to the beautiful flowers. The epithet is formed from the Latin *crista* (= crest) and *gallus* (= cock), referring to the resemblance of the lip callus to a cock's comb.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Description: Plants epiphytic, small, spreading, up to 10 cm tall. **Pseudobulbs** small, ovoid, somewhat compressed, totally enclosed by imbricating sheaths, the upper ones bearing conspicuous leaves (the apical leaf aborted), 1–2 cm long, 0.5–1 cm wide. **Lateral leaves** 2–3 on each side of the pseudobulb, distichous, linear to narrowly elliptic, dorsally carinate, acuminate, 2–8 cm long, 0.5–1 cm wide. **Inflorescences** lateral, with several inflated, foliose sheaths, somewhat longer than the leaves, usually 1-flowered or with flowers produced in succession, up to 5 in total. **Flowers** large compared to the size of the plant, yellow with brown spots. **Sepals** similar, yellow, the lateral ones almost totally hidden by the lip, 0.2–0.6 cm long, 0.2–0.4 cm wide. **Petals** yellow, transversely maroon-blotched, oblong–subquadrate to obovate-subquadrate, margins undulate, truncate to rounded at the apex, 0.65–1.0 cm long, 0.35–0.5 cm wide. **Lip** yellow, dominating the flower, trilobed, the central lobe ± 4-lobed, usually slightly wider than long, 1.4–2.3 cm long, 1.3–2.2 cm wide. Disc ± white, marked by irregular maroon blotches; callus raised, basally winged and apically shaped like the tail (fluke) of a whale, ± spotted by maroon markings. **Column** short, thick, 0.2–0.4 cm long, with 2 conspicuous wings.

Distribution: Mexico to Peru. Widespread, but not common.


Erycina crista-galli

Ecology: *Erycina crista-galli* is a twig epiphyte, preferring small branches in relatively exposed positions on single, often small trees. The species often grows on fruit trees such as *Psidium guajava* or *Citrus* spp., or on ornamental trees and shrubs such as *Crescentia cujete* (calabash tree) or *Hibiscus rosa-sinensis*.

Flowering: Throughout the year.

Pollination biology: It has been suggested that the flowers rely on food-deception for pollination, possibly mimicking flowers of co-occurring Malpighiaceae. Bees of the genus *Centris* have been observed visiting the flowers. *Erycina glossomystax* – another fan-shaped species of the genus– has been reported to be pollinated by *Epicharis rustica*, also an oil-collecting bee.

Remarks: (1) The genus comprises 10 species, all of which were formerly included in the genus *Oncidium*. (2) In the Golfo Dulce region there are two additional species, from which *E. crista-galli* can be distinguished by its carinate leaves, the presence of a pseudobulb and the characteristic callus.

References: Allen in Woodson and Schery (1949: 189), Ames and Correll (1953), Chase in Pridgeon et al. (2009: 265-269), van der Cingel (2001: 120), Damon and Valle-Mora (2008), Dodson (2003: 883), Dressler in Hammel *et al.* (2003: 360), Hamer (1984: pl. 1054), Pérez-Hérnandez *et al.* (2011).

Erycina crista-galli

Gongora boracayanensis

Gongora boracayanensis Jenny, Dalström & Higgins, Selbyana 28(2): 99–102 (2007).
E.: - Sp.: -

Etymology: The generic name commemorates the viceroy of New Granada (Colombia), Don Antonio Caballero y Góngora (1723–1796). The epithet alludes to the private wildlife refuge of Boracayán in Costa Rica, where the holotype of this species was collected.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Stanhopeinae.

Taxonomic notes: The genus comprises c. 60 taxonomically challenging species, distributed in the Neotropics. For a long time, *G. boracayanensis* was misidentified as *Gongora quinquenervis*, the type species of the genus. By chance, a seedling was introduced to the Lankester Botanical Garden (Costa Rica) in the pot of a *Lycaste* plant. After blooming in 2006, it was ascertained that this specimen, as well as collections by Rudolf Jenny, belonged to a new species distinct from *G. quinquenervis*.

Description: Plants large epiphytes. **Pseudobulbs** clustered together, conical, strongly ridged, 2-leaved, 7 cm long and 4–5 cm wide. **Leaves** shortly petiolate, lanceolate to ovate, acute, 25–35 cm long, 12–15 cm wide. **Inflorescence** pendulous, arising from the base of a pseudobulb, 30–70 cm long, usually bearing 10–15 flowers. **Flowers** with pale red to maroon sepals with darker spots near the base, gradually turning into stripes at the apex, petals greenish red with red spots, lip white, with a few red spots on the epichile and the hypochile. **Dorsal sepal** lanceolate, reflexed, acute, 2.4–2.6 cm long, 0.5–0.6 cm wide. **Lateral sepals** triangular, acute, reflexed with revolute edges, 2.6–2.9 cm long, 1.1–1.3 cm wide. **Petals** united for two-thirds of their length with the column, free at the tips; tips ending in 2 oblong, acute bristles, 1.7–1.9 cm long. **Lip** tripartite, hypochile triangular when viewed from the side, with short, straight, basal, lateral horns, tips acute; mesochile tip ex-


Gongora boracayanensis

tended, acute, with a distinct hump; epichile high, acute. **Column** pale red-green, with narrow dark red bars, slightly curved, triangularly winged at apex, 1.8–2 cm long.

Distribution: Endemic to Costa Rica. So far, the species is only known from the Fila Costeña (Alto de San Juan, Fila Costeña Norte; Cordillera Brunqueña; Río Pacuare) and the area around the La Gamba Field Station.

Ecology: Epiphyte in warm and humid rain forests, between 600 m and 1000 m.


Gongora boracayanensis

Flowering: March to May, but the flowering period is probably longer.

Pollination biology: The first observations on the pollination biology of the genus *Gongora* were made by Crüger (1865) in Trinidad. However, Crüger wrongly interpreted the behaviour of the pollinators as gnawing on the flowers. In fact, *Gongora* – like other representatives of the Stanhopeinae – are pollinated exclusively by males of euglossine bees (Apidae, Euglossini), which are attracted by the specific fragrances produced by the flowers. The bees have specialised collection organs on their legs, which enable them to brush the fragrance droplets from the lip surface and store them for transport. The pollination mechanism is similar in all species of the genus: the flowers hang upside-down, being formed such that the pollinator, after landing on the top of the labellum, has to crawl onto the underside in order to collect the fragrance, which is produced by osmophores located at the base of the labellum. The bee collects the fragrance droplets with the brush-like hairs on the tarsi of its front legs. It then flies a short distance away and transfers the fragrance into the saccate tibial organ on its hind legs. However, because the lip surface is smooth, the bee sometimes slips and falls along a kind of chute formed by the petals and the column of the flowers. This guides the pollinator to the stigma and the pollinarium, which gets attached to the scutellum of the pollinator. The flowers are protandrous, at least in some species, the stigma becoming receptive only after the pollinarium has been removed. The relationship between these so-called “perfume orchids” and their male bee pollinators is highly specific, with only one or a few pollinators visiting a certain species. For *G. boracayanensis*, the pollinator is currently unknown, but the authors have observed a single male specimen of *Euglossa* carrying pollinaria and collecting fragrance from a plant near the La Gamba Field Station. Unfortunately, it was not possible to identify the bee based on the photographs taken.

Remarks: Due to the morphological similarity between most species of the genus, and especially of those belonging to the subgenus *Gongora*, identification of the species is difficult. The best characters for species discrimination seem to be the floral scent and the pollinators, which are, however, often unavailable. *Gongora boracayanensis* is very similar to the co-occurring *G. claviodora*., from which it can be distinguished by the short and straight horns of the hypochile and the overall coloration pattern.

References: van der Cingel (2001: 99–101), Crüger (1865), Dressler (1968), Jenny *et al.* (2007), Martini *et al.* (2003).

Gongora claviodora

Gongora claviodora Dressler, Orquideologia 7: 75 (1972).
E.: Clove-scented *Gongora*. **Sp.:** Orquídea góngora, torito.

Etymology: The epithet is formed from the Latin *clavus* and *odorus* (= odorous, fragrant). The Romans used the word *clavus* – literally "nail" – to designate cloves (the dried flower buds of *Syzygium aromaticum*, Myrtaceae); the epithet thus means "smelling of cloves", alluding to the strong clove-like scent, characteristic of the flowers of this species.

Gongora claviodora

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Stanhopeinae.

Description: Plants epiphytic, large. **Pseudobulbs** oval to globose, deeply ridged, bifoliate, 3.5–9 cm long, 2.4–4.5 cm wide. **Leaves** shortly petiolate, broad, lanceolate, acute, 15–45 cm long, 5–15 cm wide. **Inflorescence** emerging laterally, pendent, up to 40 cm long, bearing 8–25 flowers, opening simultaneously. **Flowers** uniformly wine-red to dark red, with a velvet surface on the inner side of the petals and the lip base. **Dorsal sepal** broadly ovate, rolled up at the edges (revolute), reflexed, acute, adherent to the back of the column for a quarter of its length, 1.9–3.3 cm long, 0.6–0.9 cm wide. **Lateral sepals** narrowly oval, acute, reflexed, with revolute edges, 2.7–3 cm long, 1.4–1.7 cm wide. **Petals** united with the column for two-thirds of their length, but free at the tips, here narrowing into 2 acute bristles. **Lip** tripartite, 2–2.3 cm long, 0.7 cm wide; hypochile bulbous at the base, curving into small, blunt tips; mesochile with acute tips, pointing diagonally forward; epichile high, acute, with a ± distinct hump. **Column** subterete, 2–2.8 cm long.

Distribution: Nicaragua to Panama.

Gongora claviodora

Ecology: Grows in very humid forests, at up to 1600 m.

Flowering: January to June.

Pollination biology: In Costa Rica, the strongly scented flowers are pollinated by males of *Euglossa viridissima*. For details on the pollination biology of the genus, see the description of *G. boracayanensis*.

Remarks: Like most other *Gongora* species, *G. claviodora* may vary in colour, which makes identification difficult, especially from photographs. The most characteristic feature is its clove-like scent, which distinguishes it from the co-occurring *G. boracayanensis*, *G. histronica* and *G. unicolor*.

References: Chase and Palmer (1997), Dressler in Hammel *et al.* (2003: 186–187), Jenny and Sommer (1993: 45-46).

Gongora histrionica

Gongora histrionica Rchb.f., Bonplandia 2: 92 (1854).
E.: Enchanting *Gongora*. **Sp.:** Orquídea góngora, torito.

Etymology: The epithet is derived from the Latin *histrionicus* (= dramatic, enchanting), referring to the beautifully coloured flowers of this species.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Stanhopeinae.

Description: Plants epiphytic, large. **Pseudobulbs** oval to globose, deeply ridged, bifoliate, 7 cm long, 3–5 cm wide. **Leaves** shortly petiolate, broadly lanceolate, acute, 40 cm long, 12–15 cm wide. **Inflorescence** emerging laterally, pendent, up to 40 cm long, bearing up to 25 flowers that open simultaneously. **Flowers** speckled with dark red on a yellow to yellow–orange background, but coloration may be much lighter. **Dorsal sepal** ovate, rolled up at the edges, acute, pointing downwards, adherent to the back of the column for a quarter of its length, 3–3.1 cm long, 2.3–2.4 cm wide. **Lateral sepals** triangular, acute, reflexed and with rolled-up edges, 2.5–2.6 cm long, 1.4–1.6 cm wide. **Petals** fused to the column for two-thirds of their length, but free at the tips, where they narrow into 2 acute bristles. **Lip** clearly tripartite; hypochile bulbous at the base, tips right-angled and blunt; horns broad, rounded, bent sideways and then curving downwards; mesochile distinct, pointing forward, with acute tips; epichile high, acute, with a distinct hump. **Column** subterete, 2.2–2.5 cm long.

Distribution: Costa Rica, Panama and Colombia.

Gongora histrionica

Ecology: Growing in very humid forests, between 100 m and 750 m.

Flowering: Reports are from February, but the flowering season is likely to be longer.

Pollination biology: The pollinators of this species are males of an unidentified *Euglossa* species. For details on the pollination biology of the genus, see *G. boracayanensis*.

Remarks: *Gongora histrionica* can be distinguished from the co-occurring *G. claviodora*, *G. boracayanensis* and *G. unicolor* by the characteristic horns and the colour pattern.

References: Jenny and Sommer (1993: 45-46).

Gongora histrionica

Gongora histrionica

Habenaria monorrhiza

Habenaria monorrhiza (Sw.) Rchb.f., Ber. Deutsch. Bot. Ges. 3: 274 (1885).
Basionym: *Orchis monorrhiza* Sw., Prodr. Veg. Ind. Occ.: 118 (1788).
E.: Tropical bog orchid, single-rhizome bog orchid. **Sp.: -**

Etymology: The generic name is derived from the Latin *habena* (= strap), alluding to the strap-like lobes of the petals and lip of some species. The epithet is derived from the Latinised Greek *monorrhizus* (= one- or single-rooted), probably alluding to the single tuber of the original collection.

Classification: Subf. Orchidoideae, Tr. Orchidieae, Subtr. Orchidinae.

Description: Plants terrestrial, 18–120 cm tall. **Stems** leafy throughout, leaf sheaths ± darkly maculate. **Leaves** obovate–lanceolate, elliptic–lanceolate or oblong–lanceolate, acute or acuminate, margins undulate, scarious; 4–14 cm long, 2–4 cm wide. **Inflorescence** racemose, ± elongate, dense, many-flowered, up to 22 cm long. **Flowers** showy, white, variable in size. **Dorsal sepal** ovate or suborbicular–ovate, concave, 0.5–1.4 cm long, *c.* 0.5 cm wide. **Lateral sepals** obliquely ovate or elliptic, 0.6–0.8 cm long, *c.* 0.4 cm wide. **Petals** bipartite, anterior lobe filiform, 0.5–0.7 cm long; posterior lobe narrowly oblong to elliptic, obtuse, 0.6–0.8 cm long, 0.2–0.3 cm wide. **Lip** deeply tripartite, midlobe narrowly ligulate, 0.65–1 cm long, *c.* 0.1 cm wide; lateral lobes filiform, 0.75–1.2 cm wide; spur cylindrical, slender, 1.8–2.3 cm long. **Column** 2.5 cm long.

Habenaria monorrhiza

Distribution: From Mexico to Brazil. Common.

Ecology: Terrestrial plants growing in wet meadows and thickets, woody hillsides, open slopes and roadsides, at up to 1800 m.

Flowering: Throughout the year.

Pollination biology: The genus *Habenaria* comprises mainly phalaenophilous (moth-pollinated) species, although pollination by crane-flies has been reported in the South American *Habenaria parviflora*. Pollinaria are deposited on the pollinator's eyes or proboscis, and the filiform lobes of the petals and lip seem to play a role in guiding the pollinator to the appropriate position for the removal and/or deposition of pollinia. The flower structure, nectar and nocturnal scent production suggest that *H. monorrhiza* is phalaenophilous, however the specific pollinators are still unknown.

Remarks: The genus comprises c. 600 species. In the Golfo Dulce region only two species have been recorded. *Habenaria monorhizza* can be distinguished from *H. distans* by the blackish markings on the stem, the scarious leaf margins and white flowers.

References: Ames and Correll (1952: 38), van der Cingel (2001: 81–82), Dressler in Hammel *et al.* (2003: 198), Schweinfurth (1958: 29–30), Singer (2001).

Habenaria monorrhiza

Heterotaxis maleolens *(Maxillaria maleolens)*

Heterotaxis maleolens (Schltr.) I.Ojeda & Carnevali, Novon 15: 580 (2005).
Basionym: *Maxillaria maleolens* Schltr., Repert. Spec. Nov. Regni Veg., Beih. 19: 233 (1923).
E.: Foul-smelling *Maxillaria*. **Sp.: -**

Etymology: The generic name is formed from the Greek prefix *hetero-* (= other, different) and *taxis* (= arrangement), possibly referring to the pseudobulbs, which differ from that of the genus *Maxillaria*. The epithet is formed from the Latin *malus* (= bad) and *olens* (= smelling), referring to the characteristic scent of the flowers, which resembles a mix of naphthalene and coconut and is, despite the name, rather pleasant.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Taxonomic notes: The genus *Heterotaxis* was established in 1826 by the British orchidologist John Lindley (1799–1865), based on *Heterotaxis crassifolia* Lindl. In 1854, he established the genus *Dicrypta* based on the same species. Later, however, the genus was sunk into *Maxillaria*. Recent phylogenetic analyses have shown that the genus *Maxillaria* is highly polyphyletic. One of the species groups that proved to be not closely related to the core species of *Maxillaria* was Lindley's *Heterotaxis crassifolia* (which had, however, already been described as *Epidendrum sessile* in 1788 by the Swedish botanist Olof P. Swarz). Further morphological and phylogenetic analyses resulted in the re-establishment of the genus *Heterotaxis* Lindl., comprising about 20 species. The correct name of the type species is thus *Heterotaxis sessilis* (Sw.) F.Barros. However, in many publications, even more recent ones, the species is still referred to as *Maxillaria crassifolia* (Lindl.) Rchb.f.

Description: Plants epiphytic, large, caespitose, *c.* 45 cm high. **Pseudobulbs** ovate, laterally compressed, smooth, unifoliate, 5–9 cm long

Heterotaxis maleolens

Heterotaxis maleolens

and 2.5–3.5 cm wide. **Leaves** subtended by 2 or more leaf-bearing sheaths, blade oblong–ligulate, leathery, tough, oblong, tip obtuse, sometimes bilobed, petioles varying in length, blade 16–42 cm long, 2.2–5.5 cm wide. **Inflorescence** emerging at the base of the pseudobulbs, single-flowered, apiculate, 4–5 cm long. **Flowers** leathery, greenish yellow, lip paler, marked with red, fragrant. **Sepals** narrowly ovate, angular, cuspidate, 2–2.6 cm long, 1–1.1 cm wide. **Petals** elliptic–oblong to lanceolate–ovate, obliquely spathulate, forming a hood over the column, acute, 1.8–2.1 cm long, 0.5–0.6 cm wide. **Lip** hinged to the foot of the column, parallel to the column, clearly trilobed in the middle, middle lobe triangular, lateral lobes erect, oblong, rounded, clasping the column, 1.8–2.2 cm long, 1.4 cm wide; callus bib-like, extending to the middle, where it is superposed with a second linear callus, a third, ovate callus on the midlobe. **Column** arcuate, foot obsolete, 1.4–1.5 cm long.

Distribution: Mexico and Honduras to Columbia, probably also occurring in Guatemala. Widespread, but uncommon.

Ecology: Large epiphyte of wet pre-montane rain forests, at elevations between 50 m and 1150 m.

Flowering: Throughout the year.

Pollination biology: There is no specific information on the pollination biology of this species. Several species of the genus are known to produce pseudopollen and resin as rewards. Others have been reported to be cleistogamous. Pollinators are mainly bees of the genus *Trigona*, which remove the pollinia on their scutellum.

Remarks: *Heterotaxis maleolens* is quite similar to *H. crassifolia* when not in flower, but can be distinguished from the latter by the more robust plant with much broader leaves.

References: Atwood and Mora de Retana in Burger (1999: 63), Atwood in Hammel *et al.* (2003: 317), Blanco *et al.* (2007), Carnevali and Carnevali (1993), Hamer (1983: pl. 858), Ojeda *et al.* (2003, 2005), Szlachetko *et al.* (2012), Whitten *et al.* (2007).

Heterotaxis sessilis *(Maxillaria crassifolia)*

Heterotaxis sessilis (Sw.) F.Barros, Hoehnea 29: 112 (2002).
Synonym: *Maxillaria crassifolia* (Lindl.) Rchb.f., Bonplandia (Hannover) 2: 16 (1854).
Basionym: *Epidendrum sessile* Sw., Podr. Veg. Ind. Occ. P. 22 (1788).
E.: Hidden orchid. **Sp.:** -

Etymology: The epithet is derived from the Latin *sessilis* (= sessile), apparently referring to the short petioles of the flowers.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Description: Plants epiphytic, sympodial, caespitose, *c.* 30 cm tall. **Pseudobulbs** reduced, narrowly oblong, compressed, covered by imbricating sheaths, unifoliate, *c.* 3 cm long, *c.* 1 cm wide. **Leaves** linear–oblong, fleshy, apex unequally bilobed, 7–40 cm long, 1.3–3 cm wide, shortly petiolate at the base, petiole triangular in cross-section. **Inflorescence** 1- to few-flowered, flowers barely emerging from the leaf axil. **Flowers** uniformly white or yellow. **Sepals** elliptic to ovate, thickened, apex fleshy, acute, 1.3–1.8 cm long, 0.5–0.6 cm wide. **Petals** erect, oblanceolate to spathulate, acute, 10–15 cm long, 0.3–0.4 cm wide. **Lip** whitish yellow with purple spots on the margins, ovate–elliptic, erect, fleshy, articulate to the column foot, somewhat constricted below, uppermost third appearing trilobed, with the side lobes curved towards the column, 1.0–1.5 cm long, 0.4–0.6 cm wide; calli two, yellow, mealy, one between the lateral lobes, the second along the midlobe. **Column** somewhat bent, cylindrical, broadening above, with a poorly defined foot, 0.7–1 cm long.

Heterotaxis sessilis

Distribution: Widespread in southern Florida, Central America, Jamaica, Cuba and South America.

Ecology: Epiphyte on large branches and trunks of trees in warm and wet primary and secondary forests, at elevations up to 1300 m.

Flowering: Throughout the year, with a peak in December to February.

Pollination biology: It has been suggested that the genus *Heterotaxis* is adapted to wasp-pollination. Pseudopollen or wax may be offered as a reward. *Heterotaxis sessilis* has been reported to be cleistogamous, but all individuals observed in the Golfo Dulce region had fully opened flowers, suggesting that the flowers were allogamous. It is possible that the species has a mixed mating system.

References: Atwood and Mora de Retana in Burger (1999: 53–54), Atwood in Hammel *et al.* (2003: 30), Hamer (1983: pl. 848).

Heterotaxis sessilis

Heterotaxis sessilis

Ionopsis utricularioides

Ionopsis utricularioides (Sw.) Lindl., Coll. Bot.: t. 39A (1826).
Basionym: *Epidendrum utricularioides* Sw., Prodr. Veg. Ind. Occ.: 122 (1788).
E.: Delicate violet *Ionopsis*. **Sp.:** Confites.

Etymology: The generic name is formed from the Greek *ion* (= violet) and the Greek postfix *-opsis* (= resembling, similar to), referring the similarity of the flowers or the flower colour to violets. The epithet is formed from the Latin *Utricularia* (= the generic name of the bladderworts) and the postfix *-ioides* (= looking like), because of the strong resemblance of the flowers to those of bladderworts.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Description: Plant epiphytic, often only loosely attached to the substrate, thus often appearing suspended in the air. **Pseudobulbs** small, usually leafless or with an inconspicuous small apical leaf, ± completely enclosed by the bases of 2–4 stiff leaves, 1–3 cm long, 0.5–1 cm wide. **Leaves** green to pale purple, depending upon exposure to sunlight, coriaceous, longitudinally sulcate, apically obtuse to cuspidate, 5–15 cm long,


Ionopsis utricularioides


Ionopsis utricularioides

0.7–2 cm wide. **Inflorescence** lateral, emerging between the pseudobulb and the inner leaf, greenish purple, paniculate in its upper third, up to 60 cm long. **Flowers** numerous, up to 100, rose to lavender, sometimes nearly white. **Tepals** forming a kind of bell-shaped funnel, *c.* 5 cm long, 1.8–2.2 cm wide. **Lip** very large compared to the other flower segments, dominating the general shape of the flower, shortly unguiculate and conspicuously bilobed, 9–11 cm long, 7.7–11 cm wide; base of the lip bearing a ± intense violet blotch with 3–5 darker nerves; disc mostly white, with 2 laminar keels. **Column** greenish, *c.* 0.2 cm long.

Distribution: This species is known from Florida, the Caribbean, and all the countries along the Andes (including the Galápagos Islands) as far south as Bolivia, Paraguay and Brazil. It occurs in Costa Rica on both the Atlantic and the Pacific slope. Widespread and not uncommon.


Ionopsis utricularioides

Ecology: The plants grow in wet forests and open sites up to 400 m in relatively exposed and well-ventilated places. They are often found on calabash (*Crescentia* spp.), guava (*Psidium* spp.) and old *Citrus* trees.

Flowering: January to April.

Pollination biology: The species appears to be rewardless, but no particulars are known about its pollination. Based on the floral shape and colour, bee-pollination seems likely.

Remarks: The species is more commonly found in fruit plantations and disturbed areas than in primary forests. In the Golfo Dulce region, it is easily distinguished from all other co-occurring orchids by its somewhat fan-shaped aspect of quite succulent and stiff purplish-green leaves and the many-flowered panicles of reversely cordate flowers. The genus *Ionopsis* comprises only two species; the second, *Ionopsis satyrioides* (Sw.) Rchb.f., has not yet been recorded from the Golfo Dulce region, but may be also present. It can be easily recognised by the small size of the plant body, terete leaves and the short and few-flowered inflorescences. It grows in similar habitats to *I. utricularoides*, but is easily overlooked because of its small size.

References: Dodson (2001: 358–359), Dressler in Hammel *et al.* (2003: 204), Escobar *et al.* (1991: 218–219), Hamer (1984: pl. 782).

Leochilus scriptus

Leochilus scriptus (Scheidw.) Rchb.f., Xen. Orch. 1: 15, t. 6 (1854).
Basionym: *Cryptosanus scriptus* Scheidw., Allg. Gartenzeitung 11: 101 (1843).
E.: Inscribed *Leochilus*. **Sp.: -**

Etymology: The generic name is formed from the Greek *leios* (= smooth) and *cheilos* (= lip), referring to the lack of a prominent callus on the lip (as also seen in *Oncidium*). The epithet is derived from the Latin *scriptus* (= inscribed) and alludes to the brown spots of the flowers, which are reminiscent of hieroglyphs.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Taxonomic notes: The flowers of *Leochilus* superficially resemble those of *Oncidium*, and therefore most *Leochilus* species had for a long time been referred to that genus. However, the genus *Leochilus* proved to be more closely related to genera such as *Rodriguezia*, *Comparetia*, *Notylia* and *Macroclinium* than to *Oncidium*. *Leochilus scriptus* was described in 1844 by the British botanist and orchidologist John Lindley (1799–1856) as *Leochilus herbaceus*, who was unaware of an earlier description by Scheidweiler.

Description: Plants epiphytic, small, with sympodial growth. **Pseudobulbs** unifoliate, ovoid, somewhat compressed, about 2 cm long and 3 cm broad, basally enclosed by 2(–3) sheaths, of which the uppermost bears a leaf that can be as large as the apical one, but is usually smaller. **Leaves** oblong to elliptic, with an acute asymmetrical tip, 5–15.3 cm long, 1.4–2.7 cm wide. **Inflorescence** lateral, borne between the pseudobulb and the leaf-bearing sheath, 4–30 cm long, but usually as long as or shorter than the size of the plant, sometimes branching, but side-branches normally develop when flowering of the main rachis is over, such that flowers can be produced on the same inflorescence several times per year. **Flowers** relatively large, yellowish green to greenish white, all segments ± marked with irregular maroon spots, sometimes along the central nerve of the tepals only. **Dorsal sepal** oblong, concave, somewhat curved forwards, 1 cm long, 0.5 cm wide. **Lateral sepals** free or basally united, lanceolate, 0.9 cm long,


Leochilus scriptus

Leochilus scriptus

0.35 cm wide. **Petals** ovate–elliptic to elliptic–lanceolate, obtuse, 0.8–1.1 cm long, *c.* 0.4 cm wide. **Lip** attached to the base of the column, obovate, cuneate, apically bilobed, *c.* 0.6 cm long, 1.0 cm wide; callus basally saccate and pubescent on the inner surface with some yellow markings, elongating into a subquadrate, sulcate crest. **Column** stout, with 2 lateral protuberances resembling little horns.

Distribution: From Mexico, throughout Central America and nearly all Caribbean islands, to Colombia, Venezuela, Ecuador and Brazil. Widespread, but not common.

Ecology: *Leochilus scriptus* is a typical twig epiphyte, growing on small branches at the edge of the crowns of trees and shrubs. Like other species of the genus *Leochilus*, it can often be found on cultivated trees of guava (*Psidium guajava*), orange and lemon trees (*Citrus* spp.), and even ornamental shrubs such as rose mallow (*Hibiscus rosa-sinensis*). *Leochilus* plants usually grow very quickly and start to flower within a year or two, so that their whole life cycle can be completed before the host twig becomes a branch, which entails considerable ecological changes (e.g. less illumination and a more textured and hence more moisture-retaining surface). *Leochilus scriptus* prefers bright situations, but not full sun, with good air movement. It is commonly found at elevations up to 1000 m.

Flowering: Throughout the year, with a peak between October and February.

Pollination biology: Nothing specific is known about the pollination of the species. *Leochilus* spp. are generally pollinated by small bees and wasps.

Remarks: *Leochilus scriptus* and *L. labiatus* are the only widespread species of the genus, while the other seven are local endemics in Central America and the Caribbean.

References: Chase (1986), Dodson (2001: 378-379), Escobar *et al.* (1991: 228-229), Dressler in Hammel *et al*. (2003:216), Hamer (1982: pl. 799), van der Pijl and Dodson (1966: 38).

Lepanthes spp.

Lepanthes Sw., Nova Acta Regiae Soc. Sci. Upsal. 6: 85, f. 6 (1799).
Type species: *Lepanthes ovalis* (Sw.) Fawc. & Rendle, Fl. Jamaica 1: 71 (1910).
E.: - Sp.: -

Etymology: The generic name is formed from the Greek *lepis* (= scale) and *anthos* (= flower), referring to the tiny, scale-like flowers.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Taxonomic notes: This is one of the largest orchid genera, comprising over 800 species, of which around 93 occur in Costa Rica. Luer (1986) divided the genus into four subgenera based on morphological characters. Recent molecular phylogenies have confirmed the monophyly of the genus, but failed to resolve the infrageneric relationships.

Description: Plants epiphytic, usually minute to small, caespitose, without pseudobulbs. **Stem** erect, enclosed by several tubular, ribbed sheaths, often with ciliate or rough-textured ribs and margins. **Leaf** single, terminal, petiolate, elliptic or ovate, with an obtuse or acute to acuminate tip. **Inflorescence** lateral, racemose, fasciculate or single-flowered. **Flowers** minute, resupinate, brightly coloured and nectarless. **Dorsal sepal** elliptical to oblong, acute to obtuse, free or connate with the lateral sepals. **Lateral sepals** free or connate, forming a synsepal, elliptical to ovate in shape, with an acute to obtuse apex. **Petals** membranaceous or fleshy, triangular to transversely ovate to elongate, or

Lepanthes sp.

Lepanthes sp.

bilobed. **Lip** simple, bilobed or trilobed, lateral lobes embracing the column. Midlobe minute, forming a variously shaped appendix. **Column** semiterete or terete, without a hood or a foot.

Distribution: The genus ranges from Mexico to Bolivia, with a few species in northern Brazil and the Antilles. Many *Lepanthes* species are very locally distributed.

Ecology: These small orchids are mostly twig epiphytes, preferring thin branches covered in moss or leaf mould. They occur at elevations of 100–3300 m in wet and cloud forests.

Flowering: Varies according to species.

Pollination biology: Given the diversity of the genus and the extremely small size of the plants and flowers, it is difficult to observe the pollination of these species. The low level of fruit set observed in several species indicates that they are cross-pollinated. The pollination biology has only recently been accurately described for particular species. In *Lepanthes glicensteinii*, the pollinators were found to be males of the dark-winged fungus gnat *Bradysia floribunda* (Sciaridae, Diptera). As the flowers are nectarless and the pollinators are exclusively males, it appears that this species relies on sexual deception. Although the role of the different floral signals is not yet known, it appears that males rely predominantly on the floral scent for finding the flowers. They approach the flowers from downwind, following the scent plume. When the flies reach the plants, they land on the surface and search for the flowers on foot. When approaching the flowers, the males first walk around them, fanning their wings. They then mount the labellum, facing the dorsal sepal, with the genital claspers grabbing the appendix. The males turn their abdomen by 180°, while still grasping the appendix. During this movement, the pollinia are removed or deposited on the stigma. After a short time, the males release the appendix and fly away, usually without visiting another flower. It is likely that pollination is highly specific, which would explain the low fruit set observed in the genus. Currently, however, it is unclear how widespread sexual deception is in the genus.

References: Blanco and Barboza (2005), Luer (1986, 2010), Luer in Hammel *et al.* (2003: 216–217), Pridgeon and Blanco in Pridgeon *et al.* (2005: 362–365), Vöth (1963).

Lockhartia acuta

Lockhartia acuta (Lindl.) Rchb.f., Bot. Zeitung (Berlin) 10: 767 (1852).
Basionym: *Fernandezia acuta* Lindl., Edwards‘s Bot. Reg. 21: t. 1806 (1836).
E.: Pointed-leafed *Lockhartia*. **Sp.:** -

Etymology: The generic name commemorates the English botanist David Lockhart (1818–1845), the first director of the botanical garden of Port of Spain, Trinidad. The Latin epithet *acuta* (= pointed, acute) refers to the pointed leaves of this species.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Taxonomic notes: The genus comprises *c.* 30 species and occupies a fairly isolated position within the Oncidiinae. Because the species lack articulated leaves and have a pseudo-monopodial growth habit, some authors have placed the genus in a subtribe of its own. However, as the unusual growth habit seems to represent a paedomorphy, most authors include it in Oncidiinae.

Description: Plants epiphytic, up to 40 cm tall. **Stems** arcuate or pendent, laterally flattened, without pseudobulbs, leafy, 20–40 cm long. **Leaves** distichous, densely imbricate, fleshy, laterally triangular, acute, 1.5–3.5 cm long, 0.3–0.9 cm wide. **Inflorescence** terminal or lateral at the apex of the stem, diffusely branched, few-flowered, flowers opening successively, 3–4 cm long. **Flowers** creamy white, 0.5–0.9 cm long, 0.7–0.8 cm wide. **Tepals** rounded or obtuse, free, concave, 0.2–0.4 cm long, 0.2–0.3 cm wide. **Lip** simple or slightly trilobed, subquadrate, with reddish brown marks in the basal half and a pale papillose callus, 0.5–0.65 cm long, 0.3–0.4 cm wide; lip apex with 2 rounded projections. **Column** whitish, with reddish brown markings at the base, distinctly winged, 0.1–0.2 cm long, 0.2–0.3 cm wide.

Lockhartia acuta


Lockhartia acuta


Lockhartia acuta

Distribution: Costa Rica to Colombia, Venezuela, Trinidad and Tobago. Common.

Ecology: In Costa Rica, this epiphytic species occurs in warm, seasonally moist forests of the Pacific slope, at elevations between 50 m and 600 m. It grows preferentially on the trunks and branches of *Poulsenia armata* (Moraceae) trees.

Flowering: December to March.

Pollination biology: The species of *Lockhartia* are probably pollinated by oil-collecting euglossine bees. Nothing is known specifically about the pollination of *L. acuta*.

Remarks: The species may be confused with the co-occurring *L. micrantha*, from which it can be distinguished by its larger, pendent stems, diffusely branched inflorescences, and flower coloration (*L. micrantha* has yellowish flowers).

References: Atwood and Mora de Retana in Burger (1999: 125), Chase et al. in Pridgeon *et al.* (2009: 287–290), Dressler in Hammel *et al.* (2003: 259), Zotz and Schultz (2008).

Lockhartia pittieri

Lockhartia pittieri Schltr., Repert. Spec. Nov. Regni Veg. 12: 216 (1913).
E.: Pittier's *Lockhartia.* **Sp.:** Trenzas.

Etymology: The epithet commemorates the Swiss geographer and botanist Henri François Pittier (1857–1950), who conducted extensive botanical collections in Costa Rica and was invited by the Costa Rican government in 1887 to establish the country's first geographical institute (Instituto Físico-Geográfico). During his residence there, Pittier produced the first detailed map of Costa Rica. His herbarium formed the basis of the first flora of Costa Rica, published between 1891 and 1901 (not completed).

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Description: Plants epiphytic, erect or pendant, lacking pseudobulbs, 15–20 cm tall. **Stems** flattened, unbranched. **Leaves** distichous, densely imbricate, laterally triangular, acute, 2–3.5 cm long, 0.3–0.7 cm wide. **Inflorescence** short, emerging laterally on the upper half of the stem from the leaved axis, one-flowered or few-flowered, 1–1.5 cm long. **Flowers** yellow, with an orange callus at the lip base, *c.* 1.4 cm long, 1 cm wide. **Sepals** concave, elliptic–ovate, reflexed at the base, apex dorsally carinate, acute, 0.4–0.6 cm long, 0.2–0.5 cm wide. **Petals** ovate-lanceolate, dorsally carinate, 0.4–0.8 cm long, 0.3–0.6 cm wide. **Lip** convex, obovate to subquadrate, apex bilobed, 0.6–0.9 cm long, 0.4–0.6 cm wide; callus ovate, with three fleshy keels at base. **Column** stout, with broad, denticulate wings, 0.3 cm long.

Distribution: From Guatemala to Colombia, Ecuador and Guyana. Not uncommon.

Ecology: Epiphyte in the mid-canopies of humid forests, at elevations between 30 m and 800 m.

Lockhartia pittieri

Flowering: November to May.

Pollination biology: Nothing specific is known about the pollination biology of this species. For the pollination biology of the genus, see *L. acuta*.

References: Atwood and Mora de Retana in Burger (1999: 127), Dressler in Hammel *et al.* (2003: 261).

Lockhartia pittieri

Lockhartia pittieri

Macroclinium alleniorum

Macroclinium alleniorum Dressler & Pupulin, Lindleyana 11: 34 (1996).
E.: - Sp.: Manitas.

Etymology: The generic name is formed from the Greek *makros* (= large) and *klinion* (= little bed), referring to the disproportionately large clinandrium that can be observed in most of the species. The epithet commemorates Paul H. Allen (1911–1963) and Dorothy O. Allen (1911–1973), who made an outstanding contribution to the knowledge of Central American orchids.

Classification: Subfam. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Taxonomic notes: The genus *Macroclinium* encompasses about 43 species, distributed throughout the Neotropics. Phylogenetic analyses show that the genus is closely related to *Notylia*, from which this genus differs by its unifacial, dorsally flattened, fan-shaped leaves, and by the attachment point of the lip to the column.

Description: Plants small, sympodial, twig epiphytes, growing in tufts of small fan-shaped shoots. **Pseudobulbs** ellipsoid, strongly compressed, one-leaved, *c.* 0.4 cm long, 0.8 cm wide. **Leaves** green to purplish green, irregularly spotted with dark purple, totally conduplicate, without an inner surface, 1.2–2.5 cm long, 0.3–0.7 cm wide. **Inflorescence** lateral, arching, subumbellate, 1.5–1cm long. **Flowers** several, translucent white, with some violet markings on the petals, resupinate, arranged hemispherically at the apex of the inflorescence. **Tepals** lanceolate, acuminate, 0.55–0.7 cm long, 0.08–0.13 cm wide. **Lip** clawed and arrow-shaped, claw adnate to the column for one-third to one-half of its length, *c.* 5mm long; blade triangular, with serrulate margin and a thickened callus between the lateral lobes. **Column** slender, bent abruptly upwards at the apex, about 0.5 cm long.

Macroclinium alleniorum

Macroclinium alleniorum

Distribution: Endemic to the Golfo Dulce region.

Ecology: *Macroclinium alleniorum* is a twig epiphyte, usually growing in humid to very humid evergreen lowland forests at up to 400 m. It seems to prefer shady places in shrubs and small trees with mossy branches and twigs.

Flowering: December to May.

Pollination biology: Nothing specific is known about the pollination of this species. The tiny flowers of this genus are pollinated by male euglossine bees searching for aromatic compounds. While visiting the flowers, the pollinarium is attached between the bee's eyes. After the pollinarium has been removed, the stigma widens, thus enabling pollination. Unlike other Oncidiinae, the stigma can only receive one pollinium. During the bee's flight to another plant, the stipe bends down so that the pollinia are held horizontally in front of the insect's head. Pollination occurs when one of the pollinia is squeezed into the narrow slit-like extension of the stigma.

Remarks: No other species of *Macroclinium* have yet been found in the Golfo Dulce region, although there are two closely related species – *M. glicensteinii* and *M. generalense* – which could possibly also occur in the area. They differ from *M. alleniorum* in not having such a long clawed lip, with the claw attached to the column up to half of its length, and in bearing hairs or lamellae on the callus.

References: Chase et al. in Pridgeon *et al.* (2009: 291–294), Dodson (2002: 472–473), Dressler in Hammel *et al.* (2003: 266), Escobar *et al.* (1991: 264–265).

Mapinguari longipetiolatus *(Maxillaria longipetiolata)*

Mapinguari longipetiolatus (Ames & C.Schweinf.) Carnevali & R.B.Singer, Lankesteriana 7: 525 (2007).
Basionym: *Maxillaria longipetiolata* Ames & C.Schweinf., Schedul. Orchid. 8: 61 (1925).
E.: Long-petiolate *Mapinguari*. **Sp.: -**

Etymology: The generic name is derived from the Mapinguari, a mythical creature believed to live in the Amazon rain forest, alluding to the cryptic, brownish flowers of the genus. The epithet is formed from the Latin *longus* (= long) and *petiolatus* (= petiolate, bearing a petiole), referring to the characteristic long petiole of the leaves.

Taxonomic notes: The genus *Mapinguari* contains only 4 species, *M. longipetiolatus* being the only representative in Central America. Although the species were included in *Maxillaria* until recently, they were known to be morphologically distinct. Phylogenetic analyses have confirmed the distinctness and the monophyly of the group. However, as advances in the taxonomy of the Maxillariinae are quite recent, the species is found in most publications as *Maxillaria longipetiolata*.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Description: Plants epiphytic, caespitose, 15–30 cm high. **Pseudobulbs** ovoid, unifoliate, 2.5 cm long. **Leaves** linear–lanceolate, subcoriaceous, acuminate, with a distinct slender petiole measuring more than a quarter of the length of the blade, blade 15–27 cm long, 1–2.5 cm wide. **Inflorescence** 1-flowered, emerging laterally at the base of the pseudobulbs, *c.* 1 cm long. **Flowers** dull red, lip slightly darker to blackish red. **Sepals** lanceolate–oblong, acute, 1.8–2 cm long, 0.5–0.8 cm wide. **Petals** linear to elliptic, acute, 1.5–1.8 cm long, 0.3–0.5 cm wide. **Lip** clearly trilobed above the middle, the lateral lobes rounded, erect, middle lobe oblong, rounded, 1.4–1.6 cm long, 0.8 cm wide; callus ligulate, apex forming a rounded "V". **Column** rather small, flattened at the front, 0.8–1 cm long, with a short but clearly visible foot.

Distribution: Costa Rica, Panama, Venezuela and Ecuador. Rare.

Mapinguari longipetiolatus

Habitat: Canopy epiphyte in humid lowland rain forests at up to 600 m.

Flowering: Records are from January, December, June and October. The species probably flowers throughout the year.

Pollination biology: The species of the genus appear to be rewardless and probably rely on some kind of deception. The pollinators are, as in many species of *Maxillaria*, probably bees.

References: Ames and Schweinfurth (1925), Atwood in Hammel *et al*. (2003: 316), Blanco *et al.* (2007), Davies and Stpiczyńska (2012), Whitten *et al.* (2007).

Mapinguari longipetiolatus

Mapinguari longipetiolatus

Masdevallia lata

Masdevallia lata Rchb.f., Gard. Chron. 1877(1): 653 (1877).
E.: Broad-flowered *Masdevallia*. **Sp.: -**

Etymology: The generic name commemorates José Masdevall, a physician and botanist at the court of Charles III of Spain. The epithet is derived from the Latin *latus* (= wide), alluding to the broad lateral sepals of this species.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Taxonomic notes: This species was originally discovered in Costa Rica over a century ago by a collector named Gottlieb Zahn (d. 1870), who unfortunately drowned soon after in a stream. The exact sampling location of the type specimen is therefore unknown. The plants collected by Zahn were sent to Europe, where they were incorporated in the collections of the German orchidologist Heinrich G. Reichenbach (1823–1889), who then described the species. Luer (2006) transferred the species to the genus *Alaticaulia*, based on morphological characters, but this new classification has not been widely accepted. The genus Masdevallia has proven monophyletic in recent molecular studies, currently encompassing more than 400 species.

Description: Plants epiphytic, medium-sized, caespitose, without pseudobulbs. **Stems** slender, erect, enclosed by 2–3 tubular sheaths, 1–1.5 cm long. **Leaves** coriaceous, erect, with a long petiole, 8–13 cm long. Blade narrowly obovate, gradually narrowing towards the base of the petiole, apex obtuse to round, 6–9 cm long and 1.7–2.3 cm wide. **Inflorescence** racemose, few-flowered with successively-blooming flowers on a slender peduncle, 10–15.5 cm long. **Sepals** purple, orange toward the base, glabrous. **Dorsal sepal** narrowly obovate; 1.6–1.8 cm long, 4.5 cm wide; partly connate to the lateral sepals, forming a short tube; free part triangular, narrowing into an acute, erect tail, *c.* 5 cm long. **Lateral sepals** oblique, broadly falcate, partly connate, forming a laterally compressed and deeply arched synsepal, *c.* 2.5 cm long, 2.6 cm wide (expanded); ventral side of the synsepal with 2 pronounced menta, with a conspicuous deflexion in between; apices of the synsepal broadly obtuse, oblique, abruptly contracting into 4 cm-long slender tails. **Petals** white, oblong, obtuse, with a rounded basal callus, 0.6 cm long, 0.2 cm wide. **Lip** ivory-coloured, irregularly spotted with purple, oblong–subpandurate, with marginal folds above the middle, tripartite, 0.5 cm long, 0.18 cm wide; epichile ovate, obtuse, minutely


Masdevallia lata

verrucose; hypochile oblong, subcordate and hinged below. **Column** yellow–white, semiterete, with a short foot, 0.5 cm long.

Distribution: Pacific watershed of Costa Rica and western Panama. Rare.

Ecology: This species occurs in moist lowland forests, at altitudes of up to 800 m, growing on branches of trees that overhang streams.

Flowering: Throughout the year.

Pollination biology: Nothing specific is known about the pollination of this species. Representatives of the genus *Masdevallia* are reported to be either bird- or fly-pollinated. Given the small size of the flowers, it is more likely that the present species is fly-pollinated, possibly performing carrion mimicry.

References: Luer (2000, 2006), Luer in Hammel *et al.* (2003: 283), van der Pijl and Dodson (1966: 109), Pridgeon in Pridgeon et al. (2005: 367-370).

Masdevallia lata

Masdevallia lata

Maxillaria atwoodiana

Maxillaria atwoodiana Pupulin, Orchidee (Hamburg) 54: 563 (2003).
E.: Atwood's *Maxillaria*. **Sp.:** -

Etymology: The generic name is derived from the Latin *maxilla* (= jaw), alluding to the characteristic shape of the joined lip and column-foot of some species, which resembles a jawbone. The epithet commemorates the American orchidologist John T. Atwood (b. 1946), a renowned authority on the genus *Maxillaria*.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Description: Plants epiphytic, erect, up to 15 cm high. **Pseudobulbs** rounded, somewhat flattened, unifoliate, 0.7–0.8 cm long, *c.* 0.7 cm wide. **Leaves** elliptic, subacute, coriaceous, shortly petiolate, 4–12 cm long, 1.2–1.6 cm wide. **Inflorescence** basal, solitary or sometimes 2, erect, single-flowered, peduncle 1.5–1.8 cm long. **Flowers** small, not fully opening, white to cream, lip marked with purple spots, midlobe yellow. **Dorsal sepal** elliptic–lanceolate, obtuse, apiculate, concave, 1.2 cm long, 0.45 cm wide. **Lateral sepals** narrowly elliptic, obtuse, apiculate, concave, 1.7 cm long, 0.45 cm wide. **Petals** obliquely elliptic to lanceolate, acute, apiculate, 1.2 cm long, 0.35 cm wide. **Lip** trilobed, obovate, lateral lobes narrowly elliptic, rounded, erect, midlobe triangular, with a ligulate, glabrous callus extending to about two-thirds of the lip; 1 cm long, 0.65 cm wide. **Column** subterete, clavate when viewed from the side, foot short, androclinium conspicuously fringed, column *c.* 0.9 cm long.

Distribution: Endemic to Costa Rica.

Ecology: Tropical and pre-montane forests of the Pacific watershed, between 200 m and 500 m.

Flowering: January to July.

Pollination biology: The genus Maxillaria s.str. comprises mostly deceptive species, although some may offer pseudopollen as reward. The main pollinators are meliponine bees, which may be attracted by the mimicry of chemical signals involved in the bees foraging or nest defense behaviour.

Remarks: The species can be distinguished from the closely related and co-occurring *M. confusa* by its smaller size, smaller flowers and broader, rounded sepals.

References: Pridgeon *et al.* (2009: 171–173), Pupulin (2003), Whitten et al. in Pridgeon et al. (2009:166-173).

Maxillaria atwoodiana

Maxillariella diuturna *(Maxillaria diuturna)*

Maxillariella diuturna (Ames & C.Schweinf.) M.A.Blanco & Carnevali, Lankesteriana 7: 528 (2007).
Basionym: *Maxillaria diuturna* Ames & C.Schweinf., Schedul. Orchid. 8: 58 (1925).
E.: Long-lived *Maxillaria*. **Sp.: -**

Etymology: The generic name is the diminutive form of *Maxillaria*, referring to its much smaller flowers. The epithet is derived from the Latin *diuturnus* (= long-standing, long-lived), possibly referring to the longevity of the flowers.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Description: Plants epiphytic, usually pendent, successive shoots formed *c.* 3–10 cm apart, with only the lowest forming roots. **Stems** completely covered by imbricating sheaths at the base. **Pseudobulbs** compressed, sharp-edged, ovate–oblong in outline, apically truncate to emarginate, unifoliate, 2.5–4 cm long, *c.* 2.5 cm wide. **Leaves** oblong–elliptic, coriaceous, shortly petiolate, apex acute to obtuse, minutely bilobate, 5.8–9.7 cm long, 1.3–2.2 cm wide, mid-nerve sulcate above and carinate bellow. **Inflorescence** short, reduced to a single flower which is usually covered by a bract of the rhizome. **Flowers** small, campanulate, yellow to greenish yellow, the base of the lip sometimes reddish. **Tepals** ovate–lanceolate, wider at the base, narrowing into an acute apex, forming a distinct mentum with the column foot, 1–1.5 cm long, 0.5–0.7 cm wide. **Lip** slightly trilobed, apically rounded, hinged to the column foot, narrowing at approximately two-thirds from the base, giving it a constricted appearance, c.1.1 cm long, 0.4–0.6 cm wide; lip callus ovate, rounded, fleshy and slightly 3-ridged on the lower half. **Column** arcuate, with a short, broad foot, 0.6–0.8 cm long.

Distribution: Relatively common in Nicaragua, Costa Rica and Panama, probably also occurring in Colombia.

Ecology: Epiphyte, but occasionally found growing terrestrially on steep slopes. The species prefers sunny spots on trees in warm, humid to very humid rain forests, often growing along rivers. Found at 60–1000 (–1600) m.

Flowering: Throughout the year, with a peak between February and June.

Pollination biology: Nothing specific is known about the pollination biology of this species, but some representatives of the genus have been shown to either produce nectar or resins as a reward or to mimic resin-offering species. The rewarding species produce a rather unpleasant smell. The pollinators appear to be stingless bees (Meliponini).

Remarks: This species can be distinguished from other local species of *Maxillaria s.l.* by the long, overhanging shoots that are only rooted at the base, and the apically truncate to emarginate pseudobulbs.

References: Allen in Woodson and Schery (1949: 112), Atwood and Mora de Ratana in Burger (1999: 55–56), Atwood in Hammel *et al.* (2003: 310), Blanco *et al.* (2007), Davies *et al.* (2005), Davies and Stpiczyńska (2012).


Maxillariella diuturna

Maxillariella oreocharis *(Maxillaria oreocharis)*

Maxillariella oreocharis (Schltr.) M.A.Blanco & Carnevali, Lankesteriana 7: 529 (2007).
Basionym: *Maxillaria oreocharis* Schltr., Repert. Spec. Nov. Regni Veg., Beih. 17: 69 (1922).
E.: Mountain *Maxillaria*. **Sp.:** -

Etymology: The epithet is formed from the Greek *oreos* (= mountain) and *charis* (= love, loving), referring to the preferred habitat of this species.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Description: Plants epiphytic, large, climbing, only the lower shoots forming roots, *c.* 40 cm tall. **Pseudobulbs** ovate, laterally compressed, separated from each other by 1–5 cm, apically unifoliate, 1.5–4 cm long, 1–2 cm wide. **Leaves** linear, shortly petiolate, acute, blade 13–30 cm long, 0.5–1.5 cm wide. **Inflorescence** basal, solitary, 1.5–2.5 cm long. **Flowers** with complex colouration, sepals red on the outside, pink inside, petals white to yellow, lip red, with the apical third yellow to white. **Sepals** narrowly ovate–lanceolate, acute, 1.5–1.8 cm long, 0.4–0.5 cm wide. **Petals** obliquely lanceolate, 1.2–1.6 cm long, 0.3–0.5 cm wide. **Lip** hinged to the column foot, oblong, constricted at the base of the apical third, apex fleshy, reflexed, 1.2 cm long, 0.6 cm wide; callus ligulate, reaching beyond the middle. **Column** *c.* 0.9 cm long.

Distribution: Nicaragua, Costa Rica and Panama.

Ecology: Epiphyte in warm, wet forests, growing at altitudes of up to 1100 m.

Flowering: August to December (February).

Pollination biology: Nothing specific is known about the pollination biology of this species. For details on the genus see *M. diuturna*.

References: Atwood and Mora de Ratana in Burger (1999: 67–68), Atwood in Hammel *et al.* (2003: 321), Blanco *et al.* (2007), Davies *et al.* (2005), Davies and Stpiczyńska (2012), Hamer (1982: pl. 862).


Maxillariella oreocharis

Maxillariella oreocharis

Additional common species of *Maxillaria s.l.*

Recent phylogenetic analyses of the genus *Maxillaria s.l.* and closely related genera (*Chrysocycnis, Cryptocentrum, Cyrtidiorchis, Mormolyca, Pityphyllum*, and *Trigonidium)* have led to the splitting of the former genus *Maxillaria* into 12 genera (Whitten et al. 2007). These genera are: *Brasiliorchis*, *Camaridium*, *Christensoniella*, *Heterotaxis*, *Inti*, *Mapinguari*, *Maxillariella*, *Mormolyca*, *Ornithidium*, *Rhetinantha*, *Sauvetrea* and the dwindled genus *Maxillaria*. Several of these genera are also present in the Golfo Dulce region. Amongst them is one of the only two Inti species, which are characterised by their peculiar, fan-shaped plants without pseudobulbs. Further noteworthy species are *Camaridium vittariifolium*, the smallest known species of its genus, and *Mormolyca dressleriana*, which was described as recently as 2007.


Inti bicallosa (*Maxillaria bicallosa*)


Maxillaria porrecta


Mormolyca dressleriana (*Maxillaria dressleriana*)

Rhetinantha aciantha (*Maxillaria aciantha*)

Camaridium vittariifolium (*Maxillaria vittariifolia*)

Mormodes fractiflexa

Mormodes fractiflexa Rchb.f., Gard. Chron. 1872: 141 (1872).
E.: Rolled inward *Mormodes.* **Sp.:** -

Etymology: The generic name is formed from the Greek *mormo* (= a frightful object, hobgoblin) and the postfix *–oides* (resembling), alluding to the unusual appearance of the flowers. The epithet is formed from the Latin *fractus* (= broken) and *flexus* (= bent alternately from one side to the other), referring to the sometimes flexuous inflorescence.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Catasetinae.

Description: Plants epiphytic. **Pseudobulbs** elliptic-oblong, tapering above, covered with papery sheaths when young, c. 15 cm long. **Leaves** several, distichously alternate along the pseudobulb, broadly elliptic, plicate, acute, deciduous, *c.* 20–30 cm long, *c.* 5–10 cm wide. **Inflorescence** lateral, produced from the mature, leafless pseudobulb, racemose, few-flowered. **Flowers** showy, fragrant, pendent, cream to yellow, sepals and petals often with a reddish tint and reddish lines, protandrous. **Sepals** lanceolate-elliptic, acute, 3.3–3.5 cm long, 0.8–1.2 cm wide. **Petals** elliptic, acute, 3.2–3.5 cm long, 1.1–1.4 cm wide. **Lip** bent downwards towards the base of the inflorescence, margins ± parallel beneath, convex, transversally elliptic, entire, rounded or truncate, fleshy, 2.0–2.3 cm long, 2.8–3.1 cm wide. **Column** trigonous below the middle, semiterete above, twisted, pointed, with a finger-like appendage at the tip that touches the lip surface.

Distribution: Costa Rica. Rare.

Ecology: Rainforests and forest edges, growing on the bark of rotting trunks or branches, occasionally also in humus accumulations at the base of palm leaves, at altitudes of 0 to 200 m. The plants are mycotrophic, the seedlings growing over long periods of time in association with fungal hyphae.

Flowering: December to Februrary.

Pollination biology: While the pollinators of *Mormodes fractiflexa* are unknown, other members of the genus have been shown to be pollinated by fragrance-collecting males of the

Mormodes fractiflexa

Mormodes fractiflexa

genera *Euglossa* and *Eufriesea*. The genus *Mormodes* comprises species with either protandrous or functionally dioecious flowers (*M. fractiflexa* is protandrous). In both flower types, the column is strongly bent to the side, so that the stigma faces away from the lip, while the sensitive apical appendage of the column touches the lip surface. In the protandrous flowers the column only straightens approximately 24h after the pollinaria have been removed, so that the stigma then faces the lip and pollinia may be deposited. In functionally dioecious flowers pistillate and staminate flowers can be distinguished, and may be borne simultaneously on the same plant or on separate inflorescences of the same or different plants. In the pistillate flowers, the column straightens shortly after anthesis, whereas the column remains bent in staminate flowers. The removal of pollinaria occurs when a pollinator touches the apical appendage of the column, while scraping the fragrance particles from the lip surface. The appendage acts as a trigger, and when touched, ejects the pollinarium, attaching it to the thorax of the visiting bee. Approximately 15–30 minutes after the pollinarium has been removed, the caudicles straighten, thus allowing the pollination of the next visited flower.

Remarks: (1) Most of the c. 70 species of the genus *Mormodes* are highly variable in colour patterns and flower structure and are therefore difficult to distinguish. In the Golfo Dulce region two other species occur, *M. ignea* and *M. colossus* (however, some authors consider *M. ignea* conspecific with *M. fractiflexa*). (2) Charles Darwin (1809-1882) gave a detailed description of the floral structure and the pollination mechanism of *M. ignea* in his book *The Various Contrivances by which Orchids are Fertilised by Insects.* He was, however, mistaken in claiming that the pollinators gnaw on the lip, when they are actually collecting fragrances.

References: Darwin (1862), Dressler (1993b: 139-141), Salazar *et al.* in Pridgeon *et al.* (2009: 35-39), Salazar-Chávez (1995), Salazar and Dressler in Hammel *et al.* (2003: 335-337).

Mormolyca hedwigiae *(Maxillaria hedwigiae)*

Mormolyca hedwigiae (Hamer & Dodson) M.A.Blanco, Lankesteriana 7: 531 (2007).
Basionym: *Maxillaria hedwigiae* Hamer & Dodson, Icon. Pl. Trop. 8: t. 800 (1982, publ. 1983).
E.: Hedwig's *Mormolyca*. **Sp.: -**

Etymology: The generic name is formed from the Greek *mormo* (= goblin, kobold) and *lycos* (= wolf), referring to the strange shape of the flowers of the genus. The epithet commemorates Hedwig Hamer, the wife of the German orchidologist Fritz Hamer (1912–2004), one of the authorities who first described the species.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Taxonomic notes: The genus *Mormolyca* was established by the Austrian botanist Eduard Fenzl (1808–1879) in 1850, and originally included around 6 species. Recent phylogenetic analyses have confirmed earlier hypotheses based on morphological characters, and show that the *Maxillaria rufescens* alliance (which includes *Maxillaria hedwigiae*) is nested within the genus *Mormolyca*. Under its current circumscription the genus comprises c. 25 species.

Description: Plants epiphytic, sometimes forming large clumps, 20–30 cm tall. **Pseudobulbs** covered by several acute, non-foliate bracts when young, fully-developed pseudobulbs compressed, ovoid–conic, rugose, unifoliate, 2.5–4.5 cm long, 1.5–2.5 cm wide. **Leaves** thin, shortly petiolate, narrowly elliptic, acute, 20–36 cm long, 2–3.5 cm wide. **Inflorescence** short, erect or horizontal, with 3–4 acute bracts, single-flowered, *c.* 3–5 cm long. **Flowers** whitish cream (probably turning greenish with age), lip bright orange, smelling of egg. **Sepals** elliptic, acute, 1.7–1.9 cm long, 0.7–0.9 cm wide. **Petals** elliptic, acute, 1.5–1.7 cm wide, 0.6–0.7 cm wide. **Lip** trilobed, lateral lobes erect, lanceolate, middle lobe fleshy, ovate apex truncated, margins somewhat serrulate; callus broad, oblong, extending to about the middle of the lip. **Column** whitish, slightly bent, with a short foot, winged in the upper half, *c.* 0.9 cm long.

Mormolyca hedwigiae

Mormolyca hedwigiae

Mormolyca hedwigiae

Distribution: From Guatemala to Colombia. Common.

Ecology: Epiphyte, occurring in warm and wet lowland and premontane rain forests, at elevations up to 650 m.

Flowering: October to March.

Pollination biology: The flowers of *M. rufescens*, a close relative of *M. hedwigiae*, are scented and rewarding, in that they produce starch-rich trichomes. Other representatives of the genus are cleistogamous. *Mormolyca ringens* has been shown to rely on sexual deception, attracting males of the meliponine bees *Nannotrigona testaceicornis* and *Scaptotrigona* sp. The flowers of *M. hedwigiae* have a characteristic smell and may be rewarding, but nothing specific is known about its pollination biology.

Remarks: The species is easily distinguished by its whitish cream to greenish colour and orange lip.

References: Atwood and Mora de Retana in Burger (1999: 60), Atwood in Hammel *et al.* (2003: 314), Blanco *et al.* (2007), Bogarin and Pupulin (2010), Carnevali *et al.* (2001), Fernández-Concha *et al*. (2001), Flach *et al.* (2004), Whitten in Pridgeon *et al.* (2009: 177–180), Singer *et al.* (2004), Whitten *et al.* (2007).

Notylia barkeri

Notylia barkeri Lindl., Edwards's Bot. Reg. 24 (Misc.): 90 (1838).
E.: Barker's *Notylia*. **Sp.:** -

Etymology: The generic name is formed from the Greek *notos* (= back) and *tylos* (= hump), alluding to the characteristic form of the column apex. The epithet commemorates the Australian orchid collector George Barker (1880–1965).

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Description: Plants epiphytic, small. **Pseudobulbs** clustered, compressed, oblong, covered by imbricating bracts, unifoliate, *c.* 2.5 cm long, 1 cm wide. **Leaves** elliptic, subacute, coriaceous, *c.* 18 cm long, 0.8–4 cm wide. **Inflorescences** one or two, lateral, arching to pendent, up to 30 cm long, but usually much shorter, dense-flowered. **Flowers** small, white to greenish, sometimes spotted with yellow or orange. **Dorsal sepal** free, linear–lanceolate, concave, subacute, 0.3–0.6 cm long, 0.1–0.2 cm wide. **Lateral sepals** connate and positioned under the lip, rarely free, obliquely subacute, 0.3–0.5 cm long, 0.1–0.2 cm wide. **Petals** linear–lanceolate, acute, 0.25–0.5 cm long, 0.1–0.15 cm wide. **Lip** basally claw-shaped, lamina narrowly triangular, acuminate, with a distinct carinate callus, lip 0.3–0.5 cm long, 0.1–0.2 cm wide. **Column** erect, terete, without a foot, *c.* 0.2–0.3 cm long.

Distribution: Southern Mexico to Panama. Common.

Ecology: This small species is mostly found on twigs of trees or shrubs in dense, humid forests, swamps or even plantations, at altitudes below 1600 m. It usually prefers a warm and humid climate.

Flowering: February to April.

Notylia barkeri

Notylia barkeri

Notylia barkeri

Pollination biology: The genus is pollinated by fragrance-collecting male *Euglossa* bees. The bee removes the pollinaria with the tip of its head when collecting the fragrance. *Notylia barkeri* has been shown to produce approximately 20 olfactory compounds (the main components being β-bisabolene and 1,8-cineole), but it is not yet known which compounds play the major role in pollinator attraction. In Mexico, this species is pollinated by *Euglossa tridentata*, *E. viridissima* and *E. variabilis*. There are no records of the pollinators in Costa Rica.

Remarks: The genus comprises c. 56 species, however the Golfo Dulce region harbours only two species. *Notylia barkeri* can be distinguished from *N. pittieri* by its free lateral sepals and triangular lip.

References: Allen in Woodson and Schery (1949: 231), Dressler (1968), Del Mazo Cancino and Damon (2007).

Oncidium polycladium

Oncidium polycladium Rchb.f. ex Lindl., Fol. Orchid. 6: 47 (1855).
E.: Many-branched *Oncidium*. **Sp.:** lluvia de oro.

Etymology: The generic name is derived from the Ancient Greek *onkos* (= mass, swelling or tumour), alluding to the characteristic callus at the base of the lip. The epithet is formed from the Greek *poly* (= many) and the Latinised Greek *cladium* (= branch), referring to the strongly branched inflorescence of this species.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.


Oncidium polycladium

Description: Plants epiphytic, very large, reaching over 70 cm in height. **Pseudobulbs** subtended by large, scarious sheaths, clustered, ovate–elliptic, laterally compressed, strongly grooved in the dry season, apically 2-leaved, 7–15 cm long, 1.5–4 cm wide. **Leaves** subcoriaceous, erect, linear, acute, caniculate towards the base, 35–50 cm long, 1.5–6 cm wide. **Inflorescence** lateral, emerging erect from the axils of the sheaths, racemose to paniculate with short, dense-flowered branches, up to 100 cm long. **Flowers** yellow, sepals and petals having reddish brown spots and stripes, lip marked by a large brown blotch at the base of the midlobe. **Dorsal sepal** short, unguiculate, elliptic, obtuse, margins undulate, 0.9–1.1 cm long, *c.* 0.4 cm wide. **Lateral sepals** obliquely lanceolate, falcate, acute, 1.1–1.3 cm long, 0.4–0.5 cm wide. **Petals** elliptic–ovate, margins undulate, acute to acuminate, 0.8–1 cm wide, 0.4–0.5 cm wide. **Lip** fiddle-shaped, trilobed, lateral lobes rounded, small, middle lobe with indistinct or very short isthmus, reniform, apex retuse to emarginate, 0.9–1.3 cm long, 0.8–1.3 cm wide; callus of complex shape, with *c.* 7 unequal teeth. **Column** slender, winged, wings narrowly triangular, 0.4–0.5 cm long.

Oncidium polycladium

Distribution: Mexico to Costa Rica, and possibly Panama. Common

Ecology: The species occurs in wet lowland forests at up to 800 m. The plants can often be found high up in the canopy, on the largest branches of the trees.

Flowering: February to April.

Pollination biology: Nothing specific is known about the pollination biology of this species. Most species of the genus are rewardless and are pollinated by either male or female bees of the genus *Centris*. Females visit flowers in search of oils, waxes or food (mimicry of rewarding flowers and food deception), whereas males are attracted either by the mimicry of other males (pseudo-antagonism) or that of conspecific females (sexual deception is known from a single species). Some inconspicuously flowered species are autogamous.

References: Atwood and Mora de Ratana in Burger (1999: 146–147), van der Cingel (2001: 113–114), Dressler in Hammel *et al.* (2003: 364), Pupulin (1998).

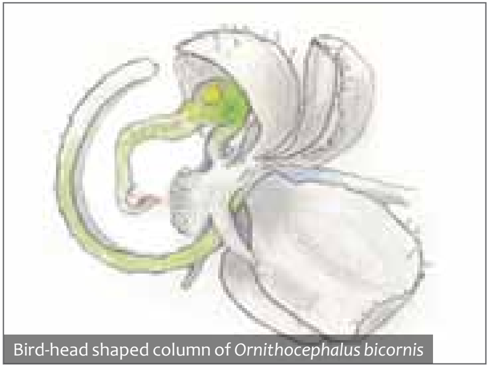
Oncidium polycladium

Ornithocephalus bicornis

Ornithocephalus bicornis Lindl. ex Benth., Bot. Voy. Sulphur 172 (1846).
E.: Two-horned *Ornithocephalus*. **Sp.:** -

Etymology: The generic name is formed from the Greek *ornithos* (= bird) and the Greek *kephalos*, Latinised *cephalus* (= head), referring to the shape of the column, which resembles a bird's head. The epithet is formed from the Latin *bi* (= two) and *cornus* (= horn), referring to the characteristic shape of the lip.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.
Description: Plant a small epiphyte, lacking pseudobulbs, 3.5–12 cm tall. **Stems** very short, usually


Bird-head shaped column of *Ornithocephalus bicornis*


Ornithocephalus bicornis

hidden by the leaves. **Leaves** distichous, fan-shaped, lanceolate to oblong–lanceolate, blades articulate to conduplicate, imbricating, coriaceous, obliquely acute, 1.5–7 cm long, 0.4–1.2 cm wide, leaf sheaths densely congested, imbricate, conduplicate, 1–3 cm long. **Inflorescences** 1–10, emerging from the axil of the leaf sheath, axis slender, racemose, many-flowered, rachis densely hispid, as long as the leaves. **Flowers** greenish white, sometimes yellowish; sepals green, petals and lip white or green. **Sepals** free, suborbicular, concave, obtuse glandular-pubescent on the outside and keeled in the middle, 0.15–0.2 cm long and wide. **Petals** obovate, concave, thin, with a ciliate keel, 0.15–0.2 cm long and wide. **Lip** slender, entire or slightly trilobed, strongly curved inwards, acute, 0.4–0.5 cm long; callus basal, fleshy, papillose, subquadrate to suborbicular, cushion-like, with 2 short, divergent, horn-like lateral appendages. **Column** small, slender, 0.05 cm long, with a rostellum resembling the shape of a bird's beak.

Distribution: Mexico to Panama, Colombia, Venezuela, Ecuador and Peru. Uncommon.

Ecology: Wet forests up to 1500 m.

Flowering: December to May, but occasionally flowering in the wet season.

Pollination biology: The tiny flowers of *O. bicornis* are nectarless, but produce fatty oil as a reward. The pollinator has been reported to be the bee *Paratetrapedia calcarata* (Apidae), which visits the flowers in search of oils as (mixed with pollen) food for their larvae.

References: Allen in Woodson and Schery (1949: 225–226), Ames and Correll (1953: 685–686), van der Cingel (2001: 107–108), Dodson (1967), Dressler in Hammel *et al.* (2003: 368), Silvera (2002).

Ornithocephalus bicornis

Pelexia funckiana

Pelexia funckiana (A.Rich & Galeotti) Schltr., Bot. Jahrb. Syst. 45: 390 (1911).
Basionym: *Spiranthes funckiana* A.Rich & Galeotti, Ann. Sci. Nat., Bot., III, 3: 32 (1845).
E.: Funck's *Pelexia*. **Sp.:** -

Etymology: The generic name is derived from the Greek *pelex* (= helmet), referring to the helmet-shaped structure formed by the united dorsal sepal and petals. The epithet commemorates Nicholas Funck (1816–1896), a famous German orchid collector, who made important contributions to the knowledge of the Central American orchid flora.


Pelexia funckiana

Classification: Subf. Orchidoideae, Tr. Cranichideae, Subtr. Spiranthinae.

Description: Plants terrestrial, slender, reaching up to 45 cm in height. **Leaves** dark green, slightly coriaceous, distinctly petiolate, arranged in a loose basal rosette, leaf blade lanceolate to ovate, acute, 9–26 cm long (including pedicel), 1.5–6 cm wide. **Inflorescence** lax to dense, several-flowered to many-flowered, dorsally pubescent, 10–45 cm long. **Flowers** green to whitish green, lip white. **Dorsal sepals** broad, oblanceolate, acute, dorsally pubescent, 1.4–2.1 cm long, 0.2–0.55 cm wide. **Lateral sepals** linear–oblanceolate, acute, dorsally pubescent, the free upper part strongly recurved, with the basal part forming a spur-like projection, as long and broad as the dorsal sepal. **Petals** united with the dorsal sepal, linear–oblanceolate, acute, 1.4–1.9 cm long, 0.25–0.3 cm wide. **Lip** broadly linear, fiddle-shaped, with 2 retuse auricles at the base. **Column** thick, straight.

Distribution: Mexico to Panama.

Ecology: Terrestrial orchid, occurring in very humid forests, between 300 m and 1500 m.

Flowering: January to June. Common.

Pollination biology: Nothing specific is known about the pollination biology of this species. Other species of the genus have been reported to produce nectar and to be self-compatible, although relying on insects for pollination. Worker bumblebees (*Bombus* sp.) have been observed carrying pollinia on the ventral surface of their labrum.

References: Dressler in Hammel *et al.* (2003: 376–377), Singer and Sazima (1999), Williams *et al.* (1980: 52–52).

Pelexia funckiana

Pelexia funckiana

Platystele speckmaieri

Platystele speckmaieri Luer & Sijm, Icon. Pleuroth. (31): 146 (2010).
E.: Speckmaier's *Platystele*. **Sp.:** -

Etymology: The generic name is formed from the Greek *platys* (= broad) and *stele* (= column), referring to the broadened apical part of the column. The epithet commemorates Manfred Speckmaier (b. 1965), an orchidologist working at the Botanical Garden in Vienna and co-author of the present book. He was the first to notice that the species was probably new to science.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Taxonomic notes: The first person to recognise that the genus *Platystele* was distinct from other pleurothalloid orchids was A. R. Enders, who wrote to Reichenbach in 1869, reporting his observations and providing an illustration of a plant belonging to the genus. However, it was not until 1910 that Rudolf Schlechter (1872–1925), a German taxonomist and orchidologist, established the genus *Platystele* based on *Platystele bulbinella*. For many years, taxonomists failed to note that several species of *Pleurothallis* actually belonged to *Platystele*, and the genus was thought to encompass only a few species. Today, a total of 73 species are included in *Platystele*, and many more may await description.

Description: Plants epiphytic, caespitose, tiny, up to 2.5 cm tall. **Ramicauls** enclosed by 2 tubular sheaths, 0.2–0.3 cm long. **Leaves** erect, petiolate, elliptical–obovate, subacute to obtuse, 0.8–1.2 cm long, 0.2–0.3 cm wide. **Inflorescence** racemose, axis very thin, almost hair-like, at first erect and later arching, *c.* 10 cm long. **Flowers** large for the plant, opening wide, spidery, each with a 1-cm-long stalk, opening successively on the upper quarter or third of the inflorescence, with one flower open at a time. **Sepals** dull reddish translucent, ovate, long-attenuate, slightly thickened at the tips, up to 1.5 cm long, 0.1 cm wide. **Petals** of the same colour as the sepals, lanceolate, sickle-shaped, curved downwards, 0.5 cm long, 0.05 cm wide at their bases. **Lip** of the same dull reddish colour, but more intense


Platystele speckmaieri

and less translucent, distinctly ovate at the base, with a ± long-attenuate, forward-pointing and sometimes curving apex, 0.2 cm long, 0.15 cm wide. **Column** auriculate, 0.08 cm long, 0.08 cm wide.

Distribution: Costa Rica (Golfo Dulce region) and Panama (El Valle de Antón). Rare. The record for Panama may be erroneous due to uncertainty concerning the origin of the type specimen. Since the original description in 2010, the presence of this species in the forests around the La Gamba field station has been confirmed by M. Speckmaier and several other collectors.

Ecology: *Platystele speckmaieri* usually grows on tiny twigs or small branches of trees at shady forest edges, where the light exposure is better than inside the forest, but direct insolation is low. The species therefore appears to be more common along trails and streams. From 60 m to 800 m.

Platystele speckmaieri

Platystele speckmaieri

Flowering: Throughout the year.

Pollination biology: The pollinators of this species are unknown. The small size and dull reddish colour of this and other species of the genus suggest that tiny flies act as pollinators. As in *Stelis* and other related genera, crystalline deposits (probably calcium oxalate hydrate) have been discovered in the flowers. They may play a role in visual signalling.

Remarks: (1) The genus encompasses several of the smallest orchids in the world, with flower diameters sometimes less than 2 mm. (2) *P. speckmaieri* is easily distinguished from all other species due to it's very long caudate sepals.

References: Dodson and Escobar (2003: 744), Escobar *et al.* (415-417), Hammel *et al.* (2003: 381), Luer (1990: 1-4, 2010: 146), Luer in Hammel *et al.* (2003: 381), Luer & Sijm (2010), Pridgeon *et al.* in Pridgeon *et al.* (2005: 383–385).

Pleurothallis homalantha

Pleurothallis homalantha Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 24 (1923).
E.: - Sp.: -

Etymology: The generic name is formed from the Greek *pleuros* (= rib) and *thallos* (= shoot), probably alluding to the thin, rib-like stems of most species. The epithet is formed from the Greek (*h*)*omalos* (= flat) and *anthos*, Latinised Greek *anthus* (= flower), referring to the flat-faced flowers.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Taxonomic notes: In recent phylogenetic analyses, the genus *Pleurothallis* proved to be polyphyletic and was split into several genera: *Acianthera*, *Anthallis*, *Andinia*, *Kraenzlinella*, *Pabstiella*, *Pleurothallis* s. str., *Phloeophila*, *Specklinia* and *Stelis*. *Pleurothallis* s.str. is still one of the largest orchid genera, comprising *c.* 1000 species.

Description: Plants epiphytic, medium-sized, caespitose, without pseudobulbs. **Stems** erect, encompassed by 3 sheaths, the upper one reaching above the middle, 10–25 cm long. **Leaf** erect, coriaceous, ovate, cordate at the base, acute, 6–9 cm long, 2.5–4.5 cm wide. **Inflorescence** short, emerging at the base of the leaf, largely concealed beneath a membranous sheath, single-flowered. **Flowers** yellow–green to pale red–brown, glabrous. **Dorsal sepal** free, elliptic–ovate, subacute, 5-veined, 0.8–1.2 cm long, 0.5–0.6 cm wide. **Lateral sepals** fully connate, forming a flat, ovate, subacute, 6-veined synsepal, 0.7–1 cm long, 0.07–0.08 cm wide. **Petals** decurved, oblong, acute, 1-veined, 0.5–0.6 cm long, 0.08–0.1 cm wide. **Lip** elliptic to ovate, entire, obtuse, 0.3–0.4 cm long, 0.2–0.25 cm wide. **Column** solid, slightly terete, 0.2 cm long, 0.2 cm wide.

Pleurothallis homalantha

Pleurothallis homalantha

Distribution: Nicaragua to Panama. Common.

Ecology: Humid forests at higher elevations, between 500 m and 1900 m.

Flowering: December to May.

Pollination biology: Nothing is known about the pollination of this species. Some species of the genus *Pleurothallis* s. lat. produce a small droplet of nectar at the base of the lip, while others are nectarless. The main pollinators are flies (Chloropidae, Bibionidae, Phoridae, Sciaridae and Drosophilidae) and small weevils (Curculionidae). Several species seem to be rewarding, while others perform brood-site mimicry. Brazilian species have been observed to attract female flies exclusively, which – in at least two of the investigated orchid species – laid their eggs on the tepals and lip of the flowers. The females are probably attracted by a combination of olfactory and visual cues. After landing on the flowers or on the leaves, they enter the flowers by pushing the lip down with their bodies. If nectar is present, they feed for several minutes or otherwise probe the lip with their proboscis. It is during this time that oviposition was observed in the rewardless species. The pollinaria are attached to the scutellum of the flies as they try to leave the flowers. The flies often visit the same flowers and individuals several times. The probability of selfing and geitonogamy is, however, reduced, as the species seem to be at least partly self-incompatible. Furthermore, the anther cap remains attached to the pollinia for several minutes in some species, thus preventing the transfer of the pollinia to the stigma. Each species attracts a specific group of closely related pollinators, usually belonging to the same genus. The specificity seems to be higher in the rewardless, brood-site mimicking species.

References: Borba and Semir (2001), van der Cingel (2001: 126–127), Luer in Hammel *et al.* (2003: 422), Pridgeon *et al.* in Pridgeon *et al.* (2005: 385–389).

Pleurothallis phyllocardioides

Pleurothallis phyllocardioides Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 193 (1923).
E.: - Sp.: -

Pleurothallis phyllocardioides

Etymology: The epithet alludes to the resemblance to *Pleurothallis phyllocardia*, which is, however, overall larger.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants epiphytic, small, erect, caespitose, pseudobulbs lacking. **Stems** erect, enclosed by 3 tubular sheaths, unifoliate, 3–15 cm long. **Leaves** spreading, coriaceous, acute, profoundly cordate at base, 3–7 cm long, 1.2–4 cm wide. **Inflorescence** short, emerging from the leaf base, single-flowered. **Flowers** yellow–green, occasionally brown to purple. **Dorsal sepal** free, broadly elliptical to ovate, subacute, 3-veined, 0.3–0.55 cm long, 0.18–0.3 cm wide. **Lateral sepals** fully connate into a ovate, obtuse, 4-veined synsepal, 0.3–0.5 cm long, 0.2–0.3 cm wide. **Petals** narrowly triangular, acute, 1-veined, 0.15–0.3 cm long, 0.03–0.06 cm wide. **Lip** cordate to ovate, obtuse, 0.1–0.2 cm long, 0.1–0.2 cm wide. **Column** semiterete, 0.05 cm long, 0.1cm wide.

Distribution: Guatemala to Panama and throughout the Andes. Common.

Ecology: Humid forests between 150 m and 1150 m.

Flowering: Throughout the year.

Pollination biology: Nothing is known about the pollination biology of this species. For details on the genus, see *P. homalantha*.

References: Hamer (1984: pl. 1119), Luer in Hammel *et al.* (2003: 436).

Pleurothallis phyllocardioides

Pleurothallis phyllocardioides

Polystachya foliosa

Polystachya foliosa (Hook.) Rchb.f. in W.G. Walpers, Ann. Bot. Syst. 6: 640 (1863).
Basionym: *Stelis foliosa* Hook., Ann. Nat. Hist. 2: 330 (1839).
E.: Lesser yellow-spike orchid. **Sp.:** -

Etymology: The generic name is formed from the Greek *polys* (= many, much) and *stachys* (= spike), referring to the inflorescences, which are composed of several spikes in many species of the genus. The epithet is derived from the Latin *foliosus* (= leafy), apparently a general reference to the vegetative aspect of the plants.

Classification: Subf. Epidendroideae, Tr. Vandeae, Subtr. Polystachyinae.

Taxonomic notes: The genus *Polystachya* was established by the English botanist William J. Hooker in 1824, by the description of *Polystachya luteola* (Sw.) Hook., based on *Cranichis luteola* Sw., which obviously did not fit into the genus *Cranichis*. Unfortunately, this description was not valid, because the same species had already been described earlier under several different names. It was only in 1974 that the American botanists Leslie (László) A. Garay and Herman R. Sweet newly combined Jacquin's *Epidendrum concretum* to *Polystachya concreta* (Jacq.) Garay & H.R.Sweet, and established *Polystachya* as a *nomen conservandum*. The genus comprises c. 150 species distributed throughout the Neotropics.

Description: Plant epiphytic. **Pseudobulbs** small, aggregated, ovoid, 2–4 cm long, 1.5 cm wide, covered by leafless and leaf-bearing sheaths. **Leaves** 3–4, distichous, enclosing the inflorescence with their conduplicate bases, size depending on the position of the leaves and the size of the plant, 2–25 cm long, 1.1–2.7 cm wide. **Inflorescence** erect to arching, up to 25 cm long, with several flower-bearing spikes, usually all pointing upwards; spikes cylindrical, many-flowered, with readily visible spaces between the flowers. **Flowers** yellowish green, with a somewhat lighter to nearly white lip, non-resupinate, several flowers opening simultaneously. **Sepals** concave, triangularly ovate, 0.3–0.35 cm long, 0.15–0.2 cm wide. **Petals** lingulate to spathulate, 0.28 cm long, 0.06 cm wide. **Lip** trilobed, *c.* 0.3 cm long, lateral lobes *c.* 0.08 cm long, 0.15 cm wide, central lobe obovate to subquadrate, tip recurved, *c.* 0.15 cm long, 0.15 cm wide;


Polystachya foliosa

callus basal, rounded, covered by glandular hairs with a somewhat icy or crystalline aspect. **Column** pale green, 0.1–0.15 cm long.

Distribution: Mexico to Bolivia and Paraguay. Wide spread and relatively common.

Ecology: The plants grow epiphytically in humid to wet forests at up to 1500 m. *Polystachya foliosa* prefers well illuminated to semi-shaded spots, mostly growing on tree trunks or major branches.

Flowering: July to December.

Pollination biology: All species of the genus *Polystachya* are nectarless, but offer pseudopollen as a reward for pollinators. Female halictid bees have been observed to visit the flowers of *Polystachya flavescens* (now *P. concreta*, a species closely related to *P. foliosa*), collecting the pseudopollen in their scopae. When reversing out of the flower, the bee's thorax touches the column, resulting in the removal/deposition of the pollinia. Some species are known to be self-pollinating or pseudo-cleistogamous.


Polystachya foliosa

Remarks: (1) Three species of *Polystachya* have been recorded in Costa Rica. *Polystachya foliosa* seems to be the only species growing at low altitudes, nevertheless *Polystachya masayensis* may also be found in the more elevated part of the Golfo Dulce region. The plants of *P. masayensis* are considerably smaller than those of *P. foliosa* and usually have a simple, very dense and many-flowered inflorescence with hispidulous–pubescent indumentum. There may be confusion with young specimens of *P. foliosa* that are flowering for the first time. However, even young specimens of *P. foliosa* have an inflorescence of fewer flowers, with flowers growing less densely than in *P. masayensis*. (2) The plant described and illustrated in the *Orchids of Manuel Antonio National Park* (Pupulin, 1998) as *P. masayensis* is *P. foliosa*.


Polystachya foliosa

References: Dressler in Hammel *et al.* (2003: 454–455), Goss (1977), Hamer (1984: pl. 1133), van der Pijl and Dodson (1966: 22–23), Pupulin (1998: 34, pl. 67), Senghas (1989), Speckmaier (1994), Vasquez and Ibisch (2004: 339).

Prescottia stachyodes

Prescottia stachyodes (Sw.) Lindl., Edwards's Bot. Reg. 22: t. 1915 (1836).
Basionym: *Cranichis stachyodes* Sw., Prodr. Veg. Ind. Occ.: 120 (1788).
E.: Spike-like *Prescottia*. **Sp.:** -

Etymology: The generic name commemorates the English physician and botanist J. D. Prescott (1770–1837). The epithet is derived from the Greek *stachyodes* (= spike-like), referring to the inflorescence.

Classification: Subf. Orchidoideae, Tr. Cranichideae, Subtr. Cranichidinae.

Description: Plants terrestrial, rarely epiphytic or lithophytic, up to 1 m high. **Leaves** 1–7, forming a basal rosette, petiole up to 7–27 cm long, leaf blade light green, with a whitish median rib, membranaceous, suberect, elliptic to elliptic–lanceolate, acute, 8–24 cm long, 3–16 cm wide. **Inflorescence** a dense-flowered spike, 40–95 cm long; floral bracts lanceolate, acute, *c.* 0.8 cm long. **Flowers** small, inconspicuous, dome-shaped, not resupinate, pale green, sepals and petals pinkish green. **Sepals** linear–oblong to lanceolate, coiled, obtuse, connate at the base into a short tube, 0.3–0.5 cm long, 0.08–0.13 cm wide. **Petals** linear–lanceolate, obtuse, 0.25–0.5 cm long, 0.02–0.06 cm wide. **Lip** concave or calceiform, margins strongly coiled, 0.4–0.6 cm long, *c.* 0.5 cm wide. **Column** *c.* 0.2 cm long.

Prescottia stachyodes

Distribution: Widely distributed from Florida to northern Argentina and the Antilles.

Ecology: Mostly terrestrial plants, growing in dense shade in the humus layer in rain forests at up to 2100 m.

Flowering: Throughout the year, with a peak between February and August.

Pollination biology: *Prescottia stachyodes* has been reported to be autogamous in Mexico and Puerto Rico. In Brazil, however, recent studies have shown that the species is dependent on pollinators for reproduction, despite being self-compatible. The small flowers produce nectar as a reward for pollinators. These are attracted by the strong, sweet to spicy fragrance which is emitted only at dusk. The flowers are protandrous, with flowers passing through a male phase lasting for about three days before entering the female phase. The anthesis of unpollinated flowers may last 10–12 days. In the male phase, the column is orientated towards the lip, making the stigmatic surface inaccessible to pollinators. In the female phase, the column moves towards the flower entrance, thus exposing the stigmatic surface. At this point, the viscidia dry out, making it impossible to remove the pollinaria. Self-pollination is further prevented by the sequential blooming of the flowers, with pollinators first probing the lowermost flowers and then working their way up to the upper flowers. Thus, during such a visit, the lowermost flowers act as pollinaria receivers and the upper ones as pollinaria donors. The pollinators of *P. stachyodes* have been reported to be moths of the family Pyralidae, which remove the pollinaria with the ventral side of their proboscis while searching for nectar. Reproductive success is usually high, reaching 80%.

References: van der Cingel (2001: 80), Dressler in Hammel *et al.* (2003: 458–459), Hamer (1983: pl. 742), Singer and Sazima (2001), Williams in Woodson and Schery (1946: 41–42).


Prescottia stachyodes


Prescottia stachyodes

Prosthechea pygmaea

Prosthechea pygmaea (Hook.) W.E.Higgins, Phytologia 82: 380 (1997, publ. 1998).
Basionym: *Epidendrum pygmaeum* Hook., J. Bot. (Hooker) 1: 49 (1834).
E.: Dwarf butterfly orchid, clam-shell orchid. **Sp.:** -

Etymology: The generic name is derived from the Greek *prostheke* (= appendage), referring to the characteristic appendage on the back of the column. The epithet is derived from the Latin *pygmaeus* (= dwarf, pygmy), alluding to the small size of the plants and flowers.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Taxonomic history: The species was first described as *Epidendrum pygmaeum* by the British botanist William J. Hooker (1834). Since then it has been transferred to several different genera, including *Hormidium* Lindl. ex Heynh. and *Encyclia* Hook. Based on genetic studies, Wesley E. Higgins (1997, 2002) placed it in the genus *Prosthechea*, which had already been proposed in 1838 by George B. Knowles and Frederick B. Westcott, but considered to be synonymous with *Epidendrum* by later authors. *Prosthechea* now comprises *c.* 89 species formerly belonging to *Encyclidia* subg. *Osmophytum*.

Description: Plants epiphytic, creeping or pendent. **Pseudobulbs** apically bifoliate, cylindrical to elliptic–ovoid, 2–4 cm long, 0.3–0.6 cm wide, standing 1–4 cm apart; rhizome fairly thick, densely covered by leaf sheaths, these becoming brown with age; roots growing along the whole rhizome rather than only under each pseudobulb. **Leaves** thin, elliptic, apex somewhat rounded, 4–6 cm long, 0.6–1.5 cm wide. **Inflorescence** very short, sessile, emerging from the leaf axil, bearing 1–2 flowers, less than 0.5 cm long. **Flowers** small, facing upwards, with a con-

Prosthechea pygmaea

Prosthechea pygmaea

spicuously carinate 0.6-cm-long ovary, greenish to yellowish, sometimes even with a brownish suffusion and nearly white towards the centre. **Sepals** lanceolate, acuminate, the lateral ones connate at the base, 5.5–7 cm long, 0.2 cm wide. **Petals** linear–lanceolate, acuminate, *c.* 4 cm long, 0.8 cm wide. **Lip** adnate for around half of its length to the column, trilobed, lateral lobes embracing the column, *c.* 0.2 cm long, 0.25 cm wide, midlobe with a ± intense magenta blotch at the tip, acuminate, *c.* 1 cm long, 1 cm wide. **Column** straight to somewhat gibbous, middle tooth relatively large, with a fleshy appendage, white, *c.* 0.3 cm long.

Distribution: Florida and the Caribbean to Brazil and Bolivia.

Ecology: The plants grow as epiphytes in semi-shaded, humid places on ± horizontal braches of trees, in wet rain forests at altitudes of 50–1800 m.

Flowering: August to February.

Pollination biology: Nothing specific is known about the pollinators of this species. In general, species of *Prosthechea* are pollinated by bees and wasps; at least one species is bird-pollinated, and several are known to be self-pollinating.

Remarks: The conspicuously scrambling growth-form and the mostly solitary, very small flowers with an acuminate lip distinguish this species from all other species that are similar vegetatively. No other species that could be confused with *Prosthechea pygmaea* is found in the Golfo Dulce region.

References: Berg *et al.* (2000), Dodson (2003: 834), Dressler in Hammel *et al.* (2004: 466), Hamer (1984: pl. 695), Higgins (1997), Higgins (2002), Withner and Harding (2004: 152–157).

Prosthechea pygmaea

Scaphyglottis behrii

Scaphyglottis behrii (Rchb.f.) Benth. & Hook.f. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 219 (1884).
Basionym: *Ponera behrii* Rchb.f., Bonplandia (Hannover) 3: 220 (1855).
E.: Behr's *Scaphyglottis*. **Sp.: -**

Etymology: The generic name is formed from the Greek *skaphe* (= tub) and *glottis* (= languet) which is itself derived from *glossa* (= tongue). It alludes to the concave or tub-like lip of the type species *Scaphyglottis graminifolia*. The epithet commemorates Hans Herman Behr (1818–1904), a renowned German physician, entomologist and botanist.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Taxonomic notes: Molecular analyses have shown the genus (including several other small genera, like *Hexisea*) to from a natural group. In its current circumscription the genus encompasses c. 60 species, with most species occurring in Costa Rica and Panama. **Description:** Plants epiphytic, erect or pendent, without pseudobulbs, up to 45 cm tall. **Stems** slender, densely clustered, simple or superimposed, segments cylindrical to narrowly elliptic or fusiform, finely ridged, apically bifoliate. **Leaves** linear, obtuse, somewhat bilobed at the apex, 5–26 cm long, 0.15–0.45 cm wide. **Inflorescence** a single short raceme or few-flowered fascicle, borne at the apex of the segments of the stem, at the base of the leaves. **Flowers** white, small. **Dorsal sepal** elliptic–oblong to elliptic–oval, obtuse, cucullate, 0.3–0.4 cm long, 0.1–0.15 cm wide. **Lateral sepals** linear–oblong to oblong, acute, 0.35–0.45 cm long, 0.12–0.2 cm wide. **Petals** linear to linear–lanceolate, obtuse, unguiculate, 0.3–0.4 cm long, 0.05–0.1 cm wide. **Lip** spathulate to narrowly obovate, unguiculate, thickly 3-veined, entire to obscurely trilobed, obtuse, 0.35–0.5 cm wide, 0.2–0.35 cm wide. **Column** short, with a prominent foot, narrowly winged, *c.* 0.3 cm long.


Scaphyglottis behrii

Distribution: From Mexico and Guatemala to Venezuela, Brazil, Peru and Ecuador. Not uncommon.

Ecology: Epiphytes on the trunks and branches of high trees, in wet forests at up to 1100 m.

Flowering: December to March, with a peak between January and February.

Pollination biology: Nothing is known about the pollination of this particular species. Most species of the genus produce nectar at the juncture of the column foot and the lip, suggesting that short-tongued insects pollinate the flowers. Some species appear to produce no nectar and are possibly food deceptive), while others are hummingbird-pollinated.

References: van der Cingel (2001: 117–118), Dressler in Hammel *et al.* (2003: 489), Dressler *et al.* in Pridgeon *et al.* (2005: 310–312), Woodson and Schery (1946: 390).


Scaphyglottis behrii


Scaphyglottis behrii

Scaphyglottis bidentata *(Hexisea bidentata)*

Scaphyglottis bidentata (Lindl.) Dressler, Lankesteriana 3: 28 (2002).
Basionym: *Hexisea bidentata* Lindl., J. Bot. (Hooker) 1: 8 (1834).
E.: Bidentate *Hexisea*. **Sp.:** -

Etymology: The generic name of the basionym, *Hexisea*, is formed from the Greek *hexa* (= six) and *isos* (= same), referring to the strong similarity of the six tepals, the lip being scarcely different from the remaining tepals. The specific epithet *bidentata* is formed from the Latin *bi* (= two) and *dentatus* (= toothed, dentate), referring to the cleft apex of the leaves.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Laeliinae.

Taxonomic notes: *Hexisea bidentata*, the type species of the genus *Hexisea*, was first described by the British botanist and orchidologist John Lindley (1799–1865) in 1834, from a plant collected in Panama. He created the small genus *Hexisea* to encompass two Neotropical species, *H. bidentata* and *H. imbricata*. Recently, according to phylogenetic analyses of the genus *Scaphyglottis* and allied genera, the two species were transferred to *Scaphyglottis*.

Scaphyglottis bidentata

Description: Plants epiphytic or lithophytic, caespitose, erect to arching, up to 60 cm long. **Stems** consisting of 3–5(–7) superposed pseudobulbs. **Pseudobulbs** cylindrical to fusiform, conspicuously longitudinally grooved, each bearing 2 apical leaves, green to brownish red depending on the intensity of insolation, becoming almost black with age, shortening towards the apex of the stem, up to 12 cm long, 1 cm in diameter. **Leaves** linear–lanceolate, apically minutely bidentate, enclosing the base of the following pseudobulb with their basal sheaths, 4–10 cm long, 1 cm wide, the lowest and uppermost leaves usually shorter. **Inflorescence** terminal at the uppermost pseudobulb, additional inflorescences occasionally arising from the apices of lower pseudobulbs,


Scaphyglottis bidentata

racemose, bearing 1–7 flowers, inflorescence axis short and completely covered by imbricate sheaths. **Flowers** orange, vivid red to scarlet, with a triangular, dark red callus at the base of the lip, resupinate, opening widely, about 2.5 cm in diameter. **Sepals** linear–lanceolate, subacute to obtuse, about 0.4 cm long, 1.4 cm wide. **Petals** similar in shape, but somewhat smaller, *c.* 0.3 cm long, 1.0 cm wide. **Lip** adnate to the base of the column, forming a hidden sacciform cavity below the column, curving abruptly downwards at the base, 0.4 cm long, 1.0 cm wide. Callus triangular and deep red; **Column** stout, 0.4 cm long.

Distribution: Widespread, ranging from Mexico to Venezuela, Guyana, Colombia and Peru. Not uncommon.

Ecology: Growing as an epiphyte or lithophyte in forests of warm to temperate climates, often found in exposed, sunny spots, at up to 1300 m.

Flowering: Throughout the year, with a peak from December to March.

Pollination biology: *Scaphyglottis bidentata* is probably pollinated by hummingbirds, which are attracted by its brilliantly orange–red flowers and the nectar produced by a conspicuous nectary, formed at the adhesion point of the column to the base of the lip.

Remarks: The species is very similar to the closely allied *S. imbricata* (syn.: *Hexisea imbricata*), but can be vegetatively distinguished by the pseudobulbs, which are blackish-hued, dull, cylindrical and deeply grooved longitudinally in *S. bidentata*, but green, shiny, somewhat flattened and not grooved in *S. imbricata.* When in flower, *S. bidentata* is easily recognised by its widely-opened flowers and the dark red callus on the lip. In contrast, *S. imbricata* has smaller flowers which do not open fully, and the callus is of a yellow–orange colour. So far, *S. imbricata* has not been found in the area of La Gamba, but it is likely that it also grows there. Apart from *S. imbricata, S. bidentata* can hardly be easily confused with any other species of *Scaphyglottis* from this area, because none has blackish-hued pseudobulbs and red flowers (instead, they are white, green or brown).

References: Dressler (2002), Dressler in Hammel *et al.* (2003: 489), Dressler *et al.* (2004), Escobar *et al.* (1991: 206-207), Hamer (1984: pl. 1225), van der Pijl and Dodson (1966: 96).

Sobralia chrysostoma

Sobralia chrysostoma Dressler, Orchids 70: 750 (2001).
E.: Golden-mouthed *Sobralia*. **Sp.:** Flor de un día.

Etymology: The generic name commemorates Francisco Sobral, a contemporary of the Spanish botanists Hipólito Ruiz and José Antonio Pavón, who described the genus in 1794. The epithet is formed from the Greek *chrysos* (= golden yellow) and *stóma* (= mouth, orifice), referring to the yellow throat of the lip.

Classification: Subf. Epidendroideae, Tr. Sobralieae.

Description: Plants mostly terrestrial, sometimes epiphytic. **Stems** thin, leafy, spotted with red–purple, 50–150 cm long. **Leaves** ovate–lanceolate, somewhat plicate, acuminate, mostly remaining for a longer time on the upper two-thirds of the canes, 12–22 cm long, 5–7 cm wide. **Inflorescence** terminal, hidden by several somewhat scaly and hispidulous bracts. **Flowers** short-lived, usually lasting only one day, produced in successions of about 4–6, entirely white with an orange–yellow suffusion on the lip with white veins and a white margin, more intensely coloured towards the throat. **Sepals** oblong, acute, slightly curving backwards at the tips, 6.5–9 cm long, 2.5–3 cm wide. **Petals** oblong–elliptic, acute, margins undulate, 6.5–9 cm long, 3.5–4 cm wide. **Lip** obovate, clasping the column basally, with undulate to crispate margins, 6.5–7.5cm long, 5–7 cm wide. **Column** 4–4.5 cm long.

Distribution: Nicaragua to Panama (Chiriquí province). Not uncommon.

Ecology: The plants grow in hot to warm areas, from close to sea level to 1000 m. Although often growing terrestrially, the species can also be found on large branches or in the forks of branches that are covered with a layer of moss, a web of roots of other plants or a deposit of detritus. The plants can be sometimes found in large numbers on steep road cuts.

Sobralia chrysostoma


Sobralia chrysostoma

Flowering: Throughout the year, with a peak between December and May.

Pollination biology: The pollinators of *Sobralia chrysostoma* are not yet known. Most *Sobralia* spp. are pollinated by *Xylocopa*, *Bombus* and/or large euglossine bees, while two species are adapted to pollination by hummingbirds. As the flowers only last one day, it is often observed that most plants in a given area open their flowers on the same day, making pollination more likely. It has been also suggested that some species may produce fragrances as rewards.

Remarks: (1) *S. chrysostoma* was previously confused with *S. leucoxantha* and *S. powellii*. (2) Of all the *Sobralia* species known from the Golfu Dulce region, this is the only one with large, *Cattleya*-like white flowers with a golden-yellow lip.

References: van der Cingel (2001: 116–117), Dressler (2001), Dressler in Hammel *et al.* (2003: 510), Dressler in Pridgeon et al. (2005: 603-604), Escobar *et al.* (1991: 534), Ortiz (1991: 534), van der Pijl and Dodson (1966: 50, 156).


Sobralia chrysostoma

Sobralia decora

Sobralia decora Bateman, Orchid. Mexico Guatemala: t. 26 (1841).
E.: Beautiful *Sobralia*. **Sp.:** Flor de un día.

Etymology: The epithet is derived from the Latin *decorus* (= graceful, pretty), alluding to the graceful, attractively coloured flowers.

Classification: Subf. Epidendroideae, Tr. Sobralieae.

Description: Plants terrestrial, sometimes epiphytic. **Stems** erect, slender, simple or rarely branching, becoming arching to slightly pendent with an upward-pointed tip while growing, usually only leafy in the upper part, 75–200 cm tall. **Leaves** lanceolate or lanceolate–ovate, plicate, acuminate, coriaceous, underside and leaf-sheaths black, hispidulous, underside purple, 5.5–22 cm long, 1.3–6.5 cm wide. **Inflorescence** apical, sessile, single-flowered or rarely 2-flowered, flowers appearing successively over a long period of time from an elliptic bud formed by several hispidulous bracts. **Flowers** overall lavender to purple in colour, sepals green on the outer side, purple on the inner side, petals purple with a lighter border, lip usually darker than the tepals, especially the throat, with a white base, median stripe and lateral margins. **Sepals** lanceolate, acute, reflexed, 4–5.5 cm long, 1.2–1.7 cm wide. **Petals** elliptic–lanceolate, margins somewhat undulate, acute, reflexed, 3.5–4.7 cm long, 1–1.2 cm wide. **Lip** obovate, margins clasping the column, apex expanded, apical margin undulate–crispate, 4–5.5 cm long, *c.* 3.5 cm wide. **Column** white or purplish, slender, clavate, trilobed at apex, 2–3 cm long.

Sobralia decora

Sobralia decora

Distribution: Mexico to Panama (possibly reaching Colombia), occurring in Costa Rica on both sides of the central mountains. Common.

Ecology: The plants grow in very wet, hot lowland areas from close to sea level to 600 m. Although considered a terrestrial species, *S. decora* can often be found growing epiphytically in the Golfo Dulce region. This can be attributed to the continuous and very high levels of precipitation during the year and the absence of a true dry season.

Flowering: Sporadically throughout the year.

Pollination biology: The pollinator of *S. decora* is so far unknown. For details on the genus, see *Sobralia chrysostoma*.

Remarks: This species is easily distinguished from all other *Sobralia* species of the area by its habit of forming new shoots at the apex of the older stems. In addition, it is the only pink- to red-flowered species in the area.

References: Ames and Correll (1952: 64–65), Dressler in Hammel *et al.* (2003: 510), Hamer (1984: pl. 1164), Ortiz (1991: 534), Williams in Woodson and Schery (1946: 34).

Sobralia decora

Sobralia fragrans

Sobralia fragrans Lindl., Gard. Chron. 1853: 598 (1853).
E.: Fragrant *Sobralia*. **Sp.:** Flor de un día.

Etymology: The epithet is derived from the Latin *fragrans* (= fragrant), referring to the sweet citric scent of the flowers.

Classification: Subf. Epidendroideae, Tr. Sobralieae.

Description: Plants epiphytic or lithophytic, occasionally terrestrial. **Stems** flattened, unifoliate, occasionally bifoliate, 10–35 cm high. **Leaves** narrowly elliptical to broadly lanceolate, coriaceous, plicate, acute, uniformly light green, enclosing most of the stem with the long petiole, 6.5–24 cm long, 1.5–5 cm wide. **Inflorescence** terminal, single-flowered, peduncle long, compressed, enclosed by a leaf-like bract 2–7 cm long, 0.5–2.5 cm wide. **Flowers** fragrant, cream, very light green or entirely white, sepals and petals light greenish white to yellowish white or white, with a slightly darker mid-vein on the outer surface, lip white, with a yellow centre and longitudinal protuberant yellow to greenish yellow, ± fringed nerves. **Sepals** linear to oblong–lanceolate, acute, 3–4 cm long, 0.4–0.7 cm wide. **Petals** lanceolate to oblanceolate–linear, obtuse to acute, 3–4 cm long, *c.* 0.5 cm wide. **Lip** oval to obovate, forming a tube enclosing the column over the basal two-thirds of its length, the apical third forming a roundish lobe with a conspicuously dentate–fimbriate margin, 2.2–4.5 cm long, 1.6–2.5 cm wide. **Column** white, semiterete, clavate, 1.6–1.8 cm long.

Sobralia fragrans

Sobralia fragrans

Distribution: Mexico to Ecuador and Brazil. In Costa Rica, it occurs on both sides of the central mountains. Common.

Ecology: The plants grow epiphytically in wet rain forests at up to 1000 m. *Sobralia fragrans* prefers light-exposed or semi-shaded places, mostly growing high up in large trees in partial shade, often occurring in large bunches.

Flowering: Sporadically throughout the year.

Pollination biology: The pollinator of S. *fragrans* is as yet unknown. For details on the genus, see *Sobralia chrysostoma*.

Remarks: This species is easily distinguished from all other co-occurring *Sobralia* species by its small stature and its mostly single-leaved stems. If in flower, the conspicuously fringed lip and fragrant flowers are also distinctive.

References: Ames and Correll (1952: 66–68), Dressler in Hammel *et al.* (2003: 510), Hamer (1984: pl. 1166), Ortiz (1991: 534), van der Pijl and Dodson (1966: 156), Williams in Woodson and Schery (1946: 31).

Specklinia acrisepala *(Pleurothallis acrisepala)*

Specklinia acrisepala (Ames & C.Schweinf.) Pridgeon & M.W.Chase, Lindleyana 16: 256 (2001).
Basionym: *Pleurothallis acrisepala* Ames & C.Schweinf., Schedul. Orchid. 8: 22 (1925).
E.: - Sp.: -

Etymology: The generic name commemorates the 16th century English plant illustrator Rudolph Speckle, who produced the woodcuts for Leonhart Fuchs' herbal *De Historia Stirpium.* The epithet is formed from the Latin acer (= sharp, pointed) and *sepalum* (= sepal), referring to the acute tips of the sepals.

Taxonomic notes: Recent molecular analyses have shown that *Pleurothallis* subgenus *Specklinia* sensu Luer (2006) is polyphyletic, with the species appearing embedded within several other genera. On the other hand, several species formerly attributed to the subgenera *Empusella* and *Pseudoctomeria* and to the genus *Acostea* have to be included in the new genus *Specklinia*.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants epiphytic, small, caespitose, without pseudobulbs. **Stems** slender, erect, 0.3–1 cm tall, enclosed by 2 thin, tubular sheaths. **Leaves** erect, narrowly elliptical, acute, 4–8 cm long, 0.5–1.3 cm wide. **Inflorescence** a congested fascicle of consecutively blooming flowers, 5–12 cm tall. **Flowers** small, with a complex coloration pattern, the sepals green, spotted with purple, petals solid purple, lip purple or yellow. **Dorsal sepal** membranous, free, oblong–ovate, concave, acute, 0.65–0.9 cm long, 0.2–0.25 cm wide. **Lateral sepals** similar to sepals, but connate to about the middle, with the margins revolute above the lower third, 0.7–0.95 cm long, 0.3–0.4 cm wide. **Petals** thicker than the sepals, ovate, lip margins dilated, apex obtuse, 2-veined, 0.2–0.3 cm long, 0.1–0.2 cm wide. **Lip** fleshy, 3-veined, basally bilobed, lobes reflexed, apex obtuse, baring a spiny callus, *c.* 0.3 cm long, 0.1 cm wide. **Column** yellow–orange, suffused with purple, longitudinally winged, *c.* 0.25 cm long.


Specklinia acrisepala

Distribution: Honduras to Ecuador. Common.

Ecology: Epiphytes in wet lowland forests, at up to 300 m.

Flowering: October and November (to February or March).

Pollination biology: No data is available on the pollination of *S. acrisepala*. The genus *Specklinia* seems to comprise only rewardless species. Some species have been reported to emit a scent resembling rotten fruit and to attract drosophilid flies as pollinators. In Mexico, flies of the families Cecidomyiidae and Phoridae were observed as pollinators, whereas bees of the genus *Plebeia* also visited the flowers. In these cases, food deception seems likely. Because of the insect-like lip, it has been suggested that some *Specklinia* spp. might rely on sexual deception. The removal and deposition of pollinia is facilitated by the articulated lip, which pushes the visiting insect against the column.

References: Blanco and Barboza (2005), Damon and Salas-Roblero (2007), Luer in Hammel *et al.* (2003: 396), Luer (2006: 202–203), Pridgeon *et al.* in Pridgeon *et al.* (2005: 402–405), Pupulin *et al.* (2012).


Specklinia acrisepala


Specklinia acrisepala

Specklinia brighamii *(Pleurothallis brighamii)*

Specklinia brighamii (S.Watson) Pridgeon & M.W.Chase, Lindleyana 16: 256 (2001).
Basionym: *Pleurothallis brighamii* S.Watson, Proc. Amer. Acad. Arts 23: 285 (1888).
E.: Brigham's Specklinia. **Sp.:** -

Etymology: The epithet commemorates the American geologist and botanist William T. Brigham (1841–1926), a friend or colleague of the American botanist Sereno Watson (1826–1892), who described the species in 1888.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants epiphytic, small, caespitose, lacking pseudobulbs, about 10 cm high. **Stems** slender and erect, 0.2–0.6 cm tall, enclosed by 3 thin, tubular sheaths. **Leaves** erect, narrowly obovate–elliptical, slightly tridentate, subacute, 3–9 cm long, 0.5–1.2 cm wide. **Inflorescence** solitary, a congested fascicle of consecutively blooming flowers, few-flowered, 4–10 cm tall. **Flowers** with a complex coloration pattern, sepals dull yellow, marked along the veins with purple, solid purple towards the base, petals yellow, with 2 purple or brown veins, lip deep purple. **Dorsal sepal** membranous, free, oblong–elliptic, acute, 3-veined, 0.5–0.8 cm long, 0.25–0.3 cm wide. **Lateral sepals** connate to above the middle into an obovate to elliptic, acute, bifid, membranous, synsepal 0.5–0.9 cm long, 0.5–0.6 cm wide. **Petals** obovate–spathulate, obtuse, with labellar margins dilated, 2-veined, 0.2 cm long, and wide. **Lip** fleshy, apex rounded, entire, minutely bilobed at the base, 0.25–0.35 cm long, 0.1 cm wide. 2 verrucose calli are found at the base of the lip. **Column** yellow, suffused with purple, longitudinally winged, 0.2–0.3 cm long.

Distribution: Mexico to Panama and the Antilles. Common.

Ecology: Epiphytic or lithophytic plants, preferring humid and shady places on the branches of larger trees, generally close to water, at elevations up to 950 m.

Flowering: December to March.

Pollination biology: No data is available on the pollination of this species. For details on the genus, see *S. acrisepala*.

References: Ames and Correll (1952: 213–214), Luer in Hammel *et al.* (2003: 400), Luer (2006: 206–207), Stenzel (2004: 33–34).


Specklinia brighamii

Specklinia fimbriata *(Pleurothallis setosa)*

Specklinia fimbriata (Ames & C.Schweinf.) Solano, Icon. Orchid. 5–6: t. 671 (2002, publ. 2003).
Synonym: *Pleurothallis setosa* C.Schweinf., Bot. Mus. Leafl. 9: 64 (1941), non *P. fimbriata* Lindl. (1859).
Basionym: *Masdevallia fimbriata* Ames & C.Schweinf., Schedul. Orchid. 10: 18 (1930).
E.: Bristly *Specklinia*. **Sp.: -**

Etymology: The epithet is derived from the Latin *fimbriatus* (= fimbriate, fringed), whereas the epithet of the synonym is derived from the Latin *setosus* (= studded with bristles), both alluding to the hairy flowers of this species.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants epiphytic, minute to small, without pseudobulbs. **Stems** erect, enclosed by 2 short, ribbed sheaths, 0.3–0.5 cm long. **Leaves** erect, coriaceous, linear to narrowly oblong–elliptic, subtriangular in cross section, subacute to obtuse, 0.2 cm thick, 2–2.8 cm long, 0.25 cm wide. **Inflorescence** a prostrate to descending, lax, loosely fimbriate, several-flowered raceme, born laterally from the stem, conspicuously setose–pubescent, up to 5 cm long, flowers opening successively. **Flowers** setose, with translucent greenish white sepals, suffused and spotted with pink or purple, the petals translucent yellow with a brown mid-vein, lip rose to purple. **Dorsal sepal** free, ovate, acute, 3-ridged, 1.1 cm long, 0.25 cm wide, ending in a slender tail, shorter than the sepal blade. **Lateral sepals** partly connate into a broad, oblong, bifid synsepal, 0.8 cm long, 0.7 cm wide, with obtuse apices ending in slender tails, about half as long as the sepals. **Petals** narrowly elliptic, acute, 0.65 cm long, 0.15 cm wide. **Lip** tongue-shaped, laterally angled, rounded at apex, strongly fimbriate, 0.5 cm long, 0.3 cm wide. **Column** semiterete, broadly winged at the base, 0.35 cm long.

Distribution: From Mexico to Costa Rica. Relatively uncommon.

Ecology: Growing as tiny epiphytes in very humid forests, between 150 m and 1200 m.

Flowering: Throughout the year.

Pollination biology: No data is available on the pollination of this species. For details on the genus, see *S. acrisepala*.

References: Ames and Correll (1952: 253–254), Luer in Hammel *et al.* (2003: 445), Luer (2006: 103–104).

Specklinia fimbriata

Specklinia grobyi *(Pleurothallis grobyi)*

Specklinia grobyi (Bateman ex Lindl.) F.Barros, Hoehnea 10: 110 (1983, publ. 1984).
Basionym: *Pleurothallis grobyi* Bateman ex Lindl., Edwards's Bot. Reg. 21: t. 1797 (1835).
E.: Groby's *Specklinia*. **Sp.: -**

Etymology: The epithet commemorates Lord Grey of Groby (1802–1835), a passionate British orchid collector who successfully cultivated the first plants of this species, imported by James Bateman from Guyana.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants epiphytic, small, caespitose, lacking pseudobulbs, *c.* 15 cm tall. **Stem** slender and erect, 0.2–1 cm long, enclosed by 2–3 tubular sheaths, unifoliate. **Leaves** narrowly elliptical to ovate, erect, coriaceous, light to dark green on both sides, or sometimes suffused or spotted with purple, base gradually narrowing into the petiole, blade 2–3 cm long, 0.5–1.5 cm wide. **Inflorescence** lax, flexuous, racemose, 3–15 cm long. **Flowers** membranous, pale yellow, sometimes having a purple or pink tint, flowering simultaneously. **Dorsal sepal** free, ovate, subacute to acute, 3-veined, 0.3–0.6 cm long, 0.2–0.23 cm wide. **Lateral sepals** almost fully connate, forming a slightly bifid, elliptical to ovate, obtuse and slightly concave, 2-veined synsepal, 0.4–0.7 cm long, 0.25–0.3 cm wide. **Petals** membranous, translucent, elliptic, subacute, 1-veined, 0.13–0.2 cm long, 0.05–0.075 cm wide. **Lip** oblong, rounded at the apex, shallowly concave, with 2 longitudinal calli centrally, 0.18–0.25 cm long, 0.075–0.1 cm wide. **Column** winged above the middle, bidentate at apex, 0.18–0.2 cm long.

Distribution: Mexico to southern Brazil. Common.

Ecology: Epiphyte in humid forests up to 950 m.

Specklinia grobyi

Flowering: Throughout the year.

Pollination biology: No data is available on the pollination of this species. For general information on the genus, see the description of *S. acrisepala*.

Remarks: This species is similar to *S. recula*, but can be distinguished by its racemose inflorescence and the broader column wings.

References: Luer in Hammel *et al.* (2003: 421), Luer (2006: 51–52).

Specklinia grobyi

Specklinia recula *(Pleurothallis recula)*

Specklinia recula (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 263 (2004).
Basionym: *Pleurothallis recula* Luer, Lindleyana 11: 92 (1996).
E.: Small *Pleurothallis*. **Sp.: -**

Etymology: The epithet is derived from the Latin *recula* (= small thing, small matter), referring to the minute size of the flowers.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants epiphytic, minute, caespitose, lacking pseudobulbs. **Stems** slender, erect, enclosed by 2 tubular sheaths, 0.1–0.25 cm long. **Leaves** erect, coriaceous, elliptic to obovate, subacute to rounded, 0.5–0.18 cm long, 0.3–0.4 cm wide. **Inflorescence** a fascicle of successive single-flowered pedicels, lateral, 0.15–0.2 cm long. **Flowers** translucent, light yellow with a yellow–orange to yellow–green lip. **Dorsal sepal** free, elliptical to ovate, obtuse, 3-veined, 0.38–0.6 cm long, 0.2–0.3 cm wide. **Lateral sepals** connate to above the middle into an ovate, obtuse synsepal, 0.35–0.6 cm long, 0.25–0.3 cm wide. **Petals** ovate to almost square, obtuse, 1-veined, 0.2 cm long, 1 cm wide. **Lip** elliptical to oblong, arcuate, subacute, 0.18–0.2 cm long, 0.075–0.1 cm wide, with a pair of longitudinal calli near the middle. **Column** deeply winged above the middle, 0.15 cm long.

Distribution: Costa Rica to Ecuador.

Ecology: Very inconspicuous epiphytes, growing on moss-covered branches or trunks in very humid forests, at up to 50 m.

Flowering: Throughout the year.

Pollination biology: No data is available on the pollination of this species. For details on the genus, see the description of *S. acrisepala*.

Remarks: The species is similar to *Specklinia grobyi*, from which it can be distinguished by the fasciculate inflorescences and the elongated wings of the column.

References: Luer in Hammel *et al.* (2003: 441), Luer (2006: 64–65).

Specklinia recula

Specklinia recula

Stanhopea cirrhata

Stanhopea cirrhata Lindl., J. Hort. Soc. London 5: 37 (1850).
E.: Tendril *Stanhopea*. **Sp.:** Torito.

Etymology: The generic name commemorates Sir Philip Henry (1781–1855), 4th Earl Stanhope, who was president of the Royal Medico-Botanical Society in London. The epithet is derived from the Latin *cirr[h]atus* (= with tendrils), alluding to the two bristles at the apex of the column.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Stanhopeinae.

Description: Plants epiphytic. **Pseudobulbs** densely clustered, ovate, strongly ribbed when aged, 2-leaved, 3–6 cm long, 2–4 cm wide. **Leaves** with a rounded, laterally notched petiole, 7–15 cm long; leaf blades leathery, lanceolate, plicate, acute, 40–60 cm long, 11–25 cm wide. **Inflorescence** pendent, growing from the base of the pseudobulb, covered by large, broadly triangular bracts, 2-flowered, 5–7 cm long. **Flowers** with light yellow tepals, without spots and markings, lip yellow to orange, with 2 red to almost black horns, column white, with a greenish back. **Dorsal sepal** concave, acute, upright, 3–4.5 cm long, 1.7–3 cm wide. **Lateral sepals** slightly asymmetric, broadly lanceolate, acute, standing out sideways and not bent backwards, 3.2–4.5 cm long, 1.6–3.5 cm wide. **Petals** oblanceolate, undulate, acute, bent backwards between the dorsal and the lateral sepals, 3–3.5 cm long, 1.2–1.5 cm wide. **Lip** massive, divided into a hypochile and an epichile: hypochile narrower than the epichile, extending sac-like at the base with a flat bottom; upper border of the hypochile with 2 short, laterally emerging, blunt, forward-facing horns; hypochile united with the broadly ovate, acute epichile by a wide but short bridge. **Column** massive, straight, apically broadly winged, 2.5–3 cm long, 0.8–1 cm wide.

Distribution: Panama, Costa Rica and Nicaragua.

Ecology: Epiphyte in lowland rain forests up to 1000 m. Although generally uncommon, it can often be found growing on branches directly above open water.

Flowering: June to September.

Stanhopea cirrhata

Stanhopea cirrhata

Pollination biology: All *Stanhopea* species rely on a similar pollination mechanism. The floral fragrance acts as an exclusive attractant to males of one or a few species of euglossine bees. At close range, the flower colour patterns may act as a visual guide towards the source of the fragrance, at the base of the lip. The flowers are pendent, so that when the bee reaches the source of the fragrance, it is positioned above the narrow channel formed by the apical part of the lip and the column. The bee collects the fragrance droplets with the brush-like hairs on the tarsi and then transfers the fragrance into the saccate tibial organ on its hind legs. The bee seem to be strongly influenced by the fragrance, and slips on the smooth surface of the lip. The lateral horns of the lip ensure that the bee slips through the narrow channel between the lip and the column. If the bee already carries pollinia, these remain attached in the narrow slit of the stigma, ensuring pollination. The bee then comes into contact with the pollinarium, which it carries away on their abdomen. The petals and sepals are bent backwards and are not involved in the mechanical part of the pollination process. Once a flower is pollinated, it withers in a few hours, while unpollinated flowers remain open for several days. The camphor-like fragrance emitted by the flowers consists mainly of α-pinene, β-pinene and 1.8-cineole. It has been found to attract five species of *Euglossa*: *E. championi*, *E. flammea*, *E. gorgonensis*, *E. hansoni* and *E. imperialis*.

Remarks: Non-flowering plants are almost impossible to distinguish from other species of *Stanhopea*. When in flower, however, *S. cirrhata* can be easily identified by its relatively small, paired flowers, short-horned labellum, and bristle-bearing column.

References: Dressler in Hammel *et al.* (2003: 519), Hamer (1984: pl. 1179), Jenny (2004: 33–35).

Stanhopea cirrhata

Other *Stanhopea* species from the Golfo Dulce region

Stanhopea pulla

Stanhopea ecornuta

Stanhopea panamensis

Stelis spp.

Stelis Sw., J. Bot. (Schrader) 1799(2): 239 (1800), nom. cons.
Type species: *Stelis ophioglossoides* (Jacq.) Sw., J. Bot. (Schrader) 1799(2): 239 (1800).
E.: - Sp.: -

Etymology: The generic name is derived from the old Greek name for mistletoe (*Viscum* spp.). At the time the name was given, no difference was made between the semi-parasitic growth of the mistletoes and the epiphytic growth of orchids.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Taxonomic notes: This is one of the largest orchid genera, comprising over 700 species, of which *c.* 80 occur in Costa Rica. Given the minute size of the flowers, identification is extremely difficult, even for orchid experts. The genus was established in 1799 by the Swedish botanist Olof P. Swarz. Based on morphological characters, Leslie A. Garay (1956) recognised three subgenera. Molecular analysis has shown, however, that *Stelis* Sw. is polyphyletic. In order to reach monophyly, several subgenera of *Pleurothallis* had to be included in this genus. Further studies are needed to clarify the circumscription of the genus, and the interspecific relationships within it.

Description: Plants epiphytic, lithophytic or terrestrial, caespitose to creeping, generally small to minute, pseudobulbs lacking. **Stems** erect, enclosed by tubular to concave sheaths. **Leaves** coriaceous to fleshy, elliptical to oblong, acute, sessile to petiolate. **Inflorescence** a few-flowered to rich and densely flowered raceme, emerging from the leaf axil, floral bracts tubular to concave, acute to obtuse. **Flowers** tiny, perianth fleshy, resupinate, the colour ranging from white, yellow or green to dark purple, varying according to species. **Sepals** ovate to triangular, acute to rounded, free or connate, sometimes pubescent or villous. **Petals** sublunate (in section), concave, thickened along the apical margins, much smaller than sepals. **Lip** similar in size to the petals, fleshy, simple or trilobed, variable in shape, often pubescent, basally often with a rounded callus. **Column** terete or semiterete, sometimes winged.

Distribution: South-western Florida, the Antilles and from Mexico to Venezuela, Bolivia, French Guiana and Brazil.

Ecology: The species of this genus are ecologically flexible and occur in a wide range of habitats and elevations. The plants can grow as epiphytes, lithophytes or even as terrestrials. In the Golfo Dulce region, they are mostly encountered as epiphytes on twigs or small trees in wet forests ranging from sea level to the highest peaks. They are frequently found along paths on the branches of trees or on fallen branches or trunks.

Flowering: Varies according to species.

Pollination biology: Some species have been reported to be autogamous. However, most seem to produce nectar, but food deception has also been reported in some species. Pollinators from the following insect groups have been observed: Thysanoptera (thrips), Drosophilidae (fruit flies), Empididae (dagger flies), Sciaridae (dark-winged fungus gnats), Bibionidae (march-flies), Vespidae (wasps), Braconidae (parasitoid wasps), Crysomelidae (leaf beetles), Curculionidae (true weevils), Noctuidae (owlet moths) and Culicidae (mosquitoes). Pollinators are probably attracted by scent and visual signals, including crystals of calcium oxalate hydrate on the petals and lip. The level of pollinator specialisation is unknown.

References: Garay (1956), Karremans *et al.* (2013), Luer in Hammel *et al.* (2003: 521–522), Pridgeon *et al.* in Pridgeon *et al.* (2005: 405–412).

Stelis sp1.

Stelis sp1.

Trichosalpinx blaisdellii

Trichosalpinx blaisdellii (S.Watson) Luer, Phytologia 54: 394 (1983).
Basionym: *Pleurothallis blaisdellii* S.Watson, Proc. Amer. Acad. Arts 23: 284 (1888).
E.: Bonnet orchid, Blaisdell's *Trichosalpinx*. **Sp.:** -

Etymology: The generic name is formed from the Greek prefix *tricho-* (hair-like; from *thrix*, *trichos* = hair) and *salpinx* (= trumpet), referring to the ciliate ribs and margins of the trumpet-shaped leaf-sheaths. The epithet commemorates Frank E. Blaisdell, a plantation manager who assisted Sereno Watson (1826–1892) during his visit to the Chocón in 1885.

Classification: Subf. Epidendroideae, Tr. Epidendreae, Subtr. Pleurothallidinae.

Description: Plants epiphytic, small, caespitose, without pseudobulbs. **Stems** relatively thick, 3–13 cm long, sheathed by 4–7 obliquely truncate, funnel-shaped bracts with clearly visible ciliate veins, terminal bract sheathing the base of the solitary leaf and the racemose inflorescence. **Leaves** elliptical, almost sessile, acute, dark green on the dorsal and purplish on the ventral side, 2–6.5 cm long, 1–3 cm wide. **Inflorescence** solitary, emerging under the apical bract, shorter than the leaf, bearing several simultaneously blooming flowers, 1.5–4 cm long. **Flowers** with glabrous, marginally ciliate sepals, coloration variable, ranging from purple to reddish brown and yellowish brown, petals translucent, yellowish, lip orange–brown to purple. **Dorsal sepal** narrowly ovate, free. **Lateral sepals** connate to about the middle, forming a concave synsepal, 0.4–0.7 (–1) cm long, 0.15–0.2 (–0.3) cm wide. **Petals** oblong, denticulate to ciliate at the apex, 0.15–0.25 cm long, 0.06–0.1 cm wide. **Lip** oblong, obtuse or narrowly rounded, ciliate at the base, with a pair of small deflexed lobes, margins thin, basal half curved, 0.25–0.35 cm long, 0.08–01 cm wide; callus basal, long, reaching to about the middle. **Column** relatively thick, toothed or


Trichosalpinx blaisdellii

Trichosalpinx blaisdellii

fimbriate at the apex, laterally broadly winged, 0.18–0.2 (–0.3) cm long.

Distribution: Southern Mexico to eastern Panama. Widely distributed and nor uncommon.

Ecology: Occurring in wet forests, up to 1800 m.

Flowering: January to March and June to December.

Pollination biology: Nothing is known about the pollination biology of the genus *Trichosalpinx*.

Remarks: The species is variable in both its vegetative and floral characters and may be confused with the co-occurring *T. ciliaris*. It differs from the latter by its somewhat bent stems, narrower leaves and larger flowers.

References: Hágsater and Pridgeon in Pridgeon *et al.* (2005: 415-417). Luer (1983), Luer in Hammel *et al.* (2003: 570–571), Pridgeon *et al.* (2005: 415–417), Watson (1888).

Trichosalpinx blaisdellii

Trigonidium egertonianum

Trigonidium egertonianum Bateman ex Lindl., Edwards's Bot. Reg. 24 (Misc.): 73 (1838).
E.: Dragon-mouth, Egerton's *Trigonidium*. **Sp.:** Boca de dragón.

Etymology: The generic name is derived from the Greek *trigono* (= triangle), referring to the triangular shape of the flowers. The epithet commemorates Sir Philip de Malpas Grey Egerton (1806–1881), an English palaeontologist and grower of exotic plants.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Taxonomic notes: The genus *Trigonidium* was established by the English botanist John Lindley in 1837. The present species was described from a specimen collected by the Scottish merchant, explorer and botanist George U. Skinner (after whom the Costa Rican national flower, *Cattleya skinneri*, is named) at the "Bay of Dulce in Honduras" – actually an old name for the Golfo Dulce region, located on the Pacific coast of Costa Rica.

Trigonidium egertonianum

Description: Plants epiphytic, erect, robust, densely caespitose, usually forming large clumps, up to 50 cm tall. **Pseudobulbs** aggregated, ovate, conspicuously sulcate and carinate, bifoliate, about 3.5–7 cm long, 1.5–6 cm wide, ± yellowish green depending upon the exposure of the plant to sunlight. **Leaves** linear, acute, with a conduplicate petiole, 20–60 cm long, 1.2–3 cm wide. **Inflorescence** several per pseudobulb, lateral, erect, covered by sheaths, strictly one-flowered, half as long to as long as the leaves. **Flowers** usually facing upwards, somewhat campanulate in appearance, tepals light brownish pink–red to light brownish yellow, with several distinct, dark longitudinal nerves. **Dorsal sepal** spathulate, unguiculate, 7-nerved, conspicuously recurved from the middle of its length, 2.5–4.5 cm long, 1–3.8 cm wide. **Lateral sepals** similar in shape, but slightly smaller in all parts, more strongly recurved and 6-nerved. **Petals** elliptic–lanceolate, unguiculate, much smaller than the sepals, 1.2–2.2 cm long, 0.4–0.6 cm wide, 5-nerved, with a fleshy, shining, azure apex. **Lip** trilobed, white or cream-coloured, 0.5–0.9 cm long, 0.3–0.4 cm wide, central lobe apically recurved, verrucose. **Column** slightly arching, with verrucose margins, 0.5 cm long.

Distribution: Mexico to Ecuador, Brazil and Venezuela. Common.

Ecology: *Trigonidium egertonianum* grows in humid to seasonally dry lowland primary and secondary forests, at altitudes up to 1000 m. It prefers slightly shaded to exposed places on larger trees, where it frequently reaches considerable dimensions. Often, several clumps can be seen on a single tree. In the Golfo Dulce region, the species is quite common, but is rarely observed on a walk through the forest, because the plants grow high up in the canopy. The plants can only be spotted when growing on remnant trees in fields and meadows or along roadsides.

Trigonidium egertonianum

Flowering: November to June.

Pollination biology: As far as is currently known, all species of *Trigonidium* rely on sexual deception for pollination. The pollination mechanism has been described in detail for *T. obtusum*, and is expected to be similar in the other species. The pollinators of this species are males of the eusocial bee *Plebeia droryana* (Apideae, Meliponini), which attempt to copulate with either the petals or the sepals of the flowers. Unlike other sexually deceptive species, *Trigonidium* does not mimic the shape of a female insect. Instead, the flower functions as a trap, the perianth surface being waxy, causing the males to fall into the funnel-shaped flowers. While struggling to escape, they enter the cavity between the lip and the column. Pollinaria are removed when the males try to exit the cavity. Males have been observed to visit the same flowers repeatedly, but self-pollination is unlikely, because fresh pollinia do not fit into the stigmatic cavity. After around 40 minutes, the pollinia dry out and shrink to the appropriate size. The role of olfactory and visual signals in attracting pollinators has not yet been thoroughly assessed, and further research is needed in order to better understand this particular case of sexual deception.

Remarks: (1) *Trigonidium* is a small genus of 13 species. It is closely related to the genus *Maxillaria* and ranges from Mexico throughout Central America and southwards to Brazil and Bolivia. (2) In Costa Rica, three species of *Trigonidium* are known to occur. Of these, *T. riopalenquense* is ecologically similar to *T. egertonianum*, but has not yet been recorded from the Golfo Dulce region. The two species are easily distinguished when in flower: while the inflorescences of *T. egertonianum* are always produced on mature pseudobulbs, those of *T. riopalenquense* flower before the new shoot has developed into a pseudobulb. The light to yellowish green ovoid pseudobulbs bearing two grass-like, long and slender leaves distinguish the species from all other orchids in this area, even when not in flower.

References: Allen in Woodson and Schery (1949: 133), Atwood and Mora de Ratana in Burger (1999: 85), Atwood in Hammel *et al.* (2003: 521–522), Dodson and Escobar (2004: 1070–1071), Escobar *et al.* (1991: 592-593), Hamer (1984: pl. 1189), Singer (2002).

Trizeuxis falcata

Trizeuxis falcata Lindl., Coll. Bot.: t. 2 (1821).
E.: Sickle-like *Trizeuxis*. **Sp.:** -

Etymology: The generic name is formed from the Greek *tri* (= three) and *zeuxis* (= yoke, saddle), probably referring to the shape of the flowers, particularly the synsepal and lip. The epithet is derived from the Latin *falcatus* (= sickle-shaped), referring to the leaves.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Oncidiinae.

Taxonomic notes: John Lindley (1799–1865) obtained this "very curious little … plant" from an orchid collector, who had collected it in Trinidad. Lindley noted the similarity with some species of *Cranichis*, and that it had several distinct characters, which differentiated it from this and all other related genera. Lindley therefore assigned it to a new monotypic genus, *Trizeuxis*. Recent morphological and molecular studies confirm that the genus is not related to *Cranichis*, but belongs to a clade that includes *Macroclinium*, *Notylia*, *Warmingia*, *Macradenia*, *Sutrina*, *Polyotidium* and *Rodriguezia.* Due to poor resolution of the clade, the closest relative of *Trizeuxis* remains unknown.

Description: Plants epiphytic, small, caespitose, up to 10 cm tall, with short distichously foliated stems. **Pseudobulbs** rounded, laterally compressed, completely enveloped by the imbricating leaf bases, up to 1.7 long, 0.7 cm wide. **Leaves** fleshy, laterally flattened, falcate, blades 1–12 cm long, 0.2–1 cm wide, arranged in the form of an open fan. **Inflorescence** produced at the base of the pseudobulb, slender, arcuate to pendent, paniculate, 1.5–2.1 cm long, always exceeding the leaves. **Flowers** greenish yellow to pale yellow, with an orange lip, not resupinate, minute, growing in dense subcapitate or elongate racemes. **Dorsal sepal** ovate, concave, acute, up to 0.3 cm long, 0.23 cm wide. **Lateral sepals** connate for almost their entire length, forming an obovate, bifid synsepal, up to 0.32 cm long, 0.3 cm wide. **Petals** elliptic–ovate, obtuse,


Trizeuxis falcata

Trizeuxis falcata

similar to the dorsal sepal. **Lip** 3-lobed, lanceolate, acute, with erect lateral margins, 0.42 cm long, 0.25 cm wide. **Column** short, stout, subterete, dilated at apex, *c.* 0.1 cm long.

Distribution: Costa Rica to Bolivia, Brazil, the West Indies and Peru. Common.

Ecology: Twig epiphytes in humid areas up to 1000 m. Plants of this species can often be seen on isolated or cultivated trees.

Flowering: February to April.

Trizeuxis falcata

Pollination biology: Some authors have suggested that *Trizeuxis falcata* is autogamous. Records from Ecuador, however, suggest that it is allogamous, the pollinators being small bees of the genus *Trigona*. Whether *Trizeuxis falcata* is rewarding or relies on some kind of deception is not known.

Remarks: *Trizeuxis falcata* is easily recognised by its small, densely clustered, bell-shaped flowers, and the conduplicate fleshy leaves arranged in a fan-shaped alignment.

References: Allen in Woodson and Schery (1949: 145), Atwood and Mora de Retana in Burger (1999: 172), Chase in Pridgeon *et al.* (2009: 383–384), Dressler in Hammel *et al.* (2003: 583), Neubig *et al.* (2012), Pupulin (1998), Williams *et al.* (1980).

Vanilla planifolia

Vanilla planifolia Jacks. ex Andrews, Bot. Repos. 8: t. 538 (1808).
Basionym: *Epidendrum vanilla* L., Sp. Pl. 2: 952 (1753).
E.: Vanilla. **Sp.:** Vainilla.

Etymology: The generic name is derived from the Spanish *vainilla* (= little husk or pod), referring to the characteristic seed capsules. The epithet is formed from the Latin *planus* (= flat) and *folius* (= leaf), referring to the appearance of the leaves.

Classification: Subf. Vanilloideae, Tr. Vanilleae, Subtr. Vanillinae.

Taxonomic notes: In 1753, Carl Linnaeus (1707–1778) described the first *Vanilla* species as *Epidendrum vanilla*, the species now known as *Vanilla planifolia.* The species had already been known for centuries as the source of the vanilla aroma. The first drawing of this species was produced in 1552, by a native Aztec Indian. The drawing was published in the *Codex Badianus*, a book describing the medicinal use of plants by the natives of Mexico. The drawing was the first to depict a New World orchid. In the *Codex Badianus*, the plant was named *tlilxochitl* (= "black flower" in the native Náhuatl language), referring to the colour of the fermented seed pods and not to the colour of the flowers.

Description: Plants hemiepiphytic or rupicolous, climbing vines. **Stem** fleshy, cylindrical, medium to dark green, flexuous, roughly 1 cm in diameter, several metres long, leafy throughout except for the very old parts, nodes 8–11 cm apart, normally bearing a leaf and an aerial root on the opposite side, the roots occasionally growing downwards to the ground and reaching several metres. **Leaves** coriaceous, rigid, elliptic to oblong, acuminate, 9.5–23 cm long, 3.5–7.5 cm broad. **Inflorescences** axillary, racemose, many-flowered, up to 70 flowers in succession, but normally about 10–20, with 1 or 2 open at a time, up to 25 cm long. **Flowers** large, lasting up to one day, light green or whitish green, with a light yellow lip, throat dirty golden–yellow to orange. **Sepals** not opening widely, similar in shape and size, narrowly elliptic, 5.5–6.0 cm long, 1.0–1.3 cm wide. **Petals** not opening widely, long oblanceolate, barely smaller than the sepals, with an elevated flat keel along the middle of the dorsal surface and extending into a 0.2-cm-long, free, cylindrical, acuminate projection. **Lip** unguiculate, attached to the column along its basal half, enclosing the column to form a funnel-shaped tube, cuneate when spread, trilobate, central lobe with 5–7 parallel warty or dentate rows, apically recurved; callus consisting of a rectangular penicillate cushion about 3.5 cm from the base, made up by backward-orientated tufts of lacerate lamellae. **Column** slender, semiterete, pubescent on the inner surface, 3–4 cm long, apically with erose margin. Fruit straight to curved, almost cylindrical, with the thickest part in the apical third, apically acuminate, green and smooth when young, becoming dark brown and rugose during maturation.

Distribution: *Vanilla planifolia* is widely cultivated around the tropics and has frequently escaped from cultivation into the wild. It is, however, probably native to Central America, ranging from Mexico to Costa Rica.

Ecology: *Vanilla planifolia* grows in wet to very wet areas up to 300 m. It prefers exposed places suffused with light in primary and secondary forests, but also grows on rocks and escarpments.

Flowering: Throughout the year, with a peak from December to June.

Pollination biology: Most vanilla species are apparently bee-pollinated. *Vanilla planifolia* appears to have a mixed mating system, with individuals being either autogamous or allogamous. *V. inodora* and *V. palmarum* have been reported to rely solely on self-pollination. Reports of *Melipona* bees as the main pollinators of *Vanilla planifolia* are now considered doubtful; larger bees, such as species of *Euglossa*, *Eulaema* and *Eufriesea*, are probably the true pollinators. In other Neotropical vanilla species, bees of the genus *Centris* and *Xylocopa* may also act as pollinators. Some species seem to produce nectar as a reward, while others, such as *V. planifolia*, rely on food deception for pollination. Olfactory signals seem to play an important role in pollinator attraction. The pollination mechanism in *Vanilla* is quite simple: the flowers of most species form a chamber with an entrance narrowed by the callus. The pollinators can easily enter the flowers, but the backward-facing lamellae of the callus force the pollinators to touch the stigma or the anther when exiting the flowers. In some species, the column touches the lip and the pollinators have to crawl through in order to be able to deposit/remove the pollen. In allogamous species/populations, fruit set is extremely low – sometimes under 1%. In cultivation, vanilla flowers are hand-pollinated in order to ensure high levels of fruit set. Fruit dispersal may occur, depending on the species, either by air or water, or in some species by bats, birds or even bees. However, most cases of zoochory are based only on a few observations and are therefore still speculative.

Vanilla planifolia

Remarks: All *Vanilla* species are very similar and difficult to distinguish, especially when not in flower. *Vanilla planifolia* plants can be distinguished from *V. sarapiquensis* and *V. trigonocarpa* in that they are more robust and have thick, fleshy, rigid leaves. Additionally, the somewhat bell-shaped flowers and the densely many-flowered inflorescences are distinctive.

References: Bory *et al.* (2008), Hamer (1984: pl. 1194), Ortiz and Pedro (1991: 598), van der Pijl and Dodson (1966: 76), Roubik and Ackerman (1987), Soto Arenas and Dressler (2010: 285–354), Soto Arenas and Dressler in Hammel *et al.* (2003: 585–586), Soto Arenas *et al.* in Pridgeon *et al.* (2003: 330–331).

Vanilla sarapiquensis

Vanilla sarapiquensis Soto Arenas, Lankesteriana 9: 342 (2010).
E.: Sarapiquí vanilla. **Sp.:** Vanilla.

Etymology: The epithet is derived from the Sarapiquí river and canton in Costa Rica, from where the species was first described.

Taxonomic notes: This species was described by Mexican botanist Miguel A. Soto Arenas (1963–2009), based on a plant collected in 1995 by Juan F. Morales in the Llanuras de San Carlos, canton Sarapiquí, province of Heredia, in northern Costa Rica. The species was previously confused with *V. pfaviana*.

Classification: Subf. Vanilloideae, Tr. Vanilleae, Subtr. Vanillinae.

Vanilla sarapiquensis

Description: Plants hemiepiphytic, scandent vines. **Stems** fleshy, light to medium green, leafy throughout, relatively slender for the size of the leaves, 0.4 cm in diameter when dry, certainly much thicker when alive, several metres long; nodes about 7–8 cm apart, nodes normally bearing a leaf and a short root on the opposite side. **Leaves** shortly petiolate, elliptic, acuminate, coriaceous, but of a fairly thin texture, 16–20 cm long, 5–7 cm wide. **Inflorescences** mostly axillary, racemose, about 5–6 cm long, usually 4-flowered. **Flowers** showy, opening successively, but lasting long enough for 2 or even 3 to be open at the same time, creamy green, green or light olive-green, with a white lip. **Sepals** opening widely, basally somewhat concave becoming convex toward the backward-curved apex, margins slightly undulate, somewhat recurved in their middle part, elliptic when flattened, sparsely warty on the outer surface, *c.* 2.0 cm long, 4.5 cm wide. **Petals** similar to sepals in shape but narrower, *c.* 1.6 cm wide, outer surface smooth, longitudinally sulcate. **Lip** enclosing the column, forming a narrow, funnel-shaped tube, ovate to orbicular when spread, faintly trilobed; callus formed by 2 conspicuous, basally parallel, broad, apically confluent, irregularly transversal sulcate keels. **Column** basally adnate to the lip, curved, almost cylindrical with a broader apex, 0.4 cm long, 2.1 cm wide.

Distribution: Endemic to Costa Rica. Until now, the species was known only from northern Costa Rica. However, the discovery of *V. sarapiquensis* in the La Gamba area suggests a wider distribution range.

Ecology: *Vanilla sarapiquensis* seems to prefer the edges of primary rain forests at low altitudes, presumably below 100 m. The plants climb up trees from which they then hang down in long garlands. Flowers are usually produced on the more exposed and more brightly illuminated parts of the stem.

Flowering: Possibly throughout the year.

Pollination biology: Nothing is known about the pollination of this species. For details on the genus, see *V. planifolia*.

Remarks: All *Vanilla* species are superficially very similar and difficult to distinguish, especially when not in flower. Nevertheless, *V. sarapiquensis* can be distinguished from *V. planifolia* by its relatively broad, thinly textured leaves and the slender stems, and from *Vanilla trigonocarpa* by its much longer inflorescences. When in flower, *V. sarapiquensis* can be distinguished from all other species known from the Golfo Dulce region by the widely open, somewhat undulate, and strikingly green/white bi-coloured flowers.

References: Lubinsky *et al.* (2006), Soto Arenas *et al.* in Pridgeon *et al.* (2003: 321–333), Soto Arenas and Dressler (2010).

Vanilla sarapiquensis

Vanilla trigonocarpa

Vanilla trigonocarpa Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 1: 126 (1944).
E.: Triangle-fruited vanilla. **Sp.:** Vanilla.

Etymology: The epithet is formed from the Greek *trigono* (= triangle) and the Latin *carpus* (= fruit), referring to the triangular cross-section of the seed capsule.

Classification: Subf. Vanilloideae, Tr. Vanilleae, Subtr. Vanillinae.

Taxonomic notes: This species was described by the Brazilian botanist Frederico C. Hoehne (1882–1959) from a plant collected near Belém in the Brazilian state of Pará. Due to the large gap in the distribution area, the American botanist Robert L. Dressler described a morphologically similar vanilla plant, which he had collected in Panama, as a new species, *V. pauciflora*. Recent genetic studies revealed that *V. pauciflora* and *V. trigonocarpa* are conspecific.

Description: Plants hemiepiphytic, scandent vines. **Stems** fleshy, dark green, slender, 0.7–1.0 cm in diameter, several metres long, leafy throughout, nodes about 5–7 cm apart, normally bearing a leaf and a short root on the opposite side. **Leaves** petiolate, elliptic, oblong or obovate, coriaceous, fairly thin, 15–30 cm long, 5–7 cm broad. **Inflorescence** axillary, racemose, very short (less than 2 cm), 1–4 flowered. **Flowers** comparatively large for the plant, opening widely, white or greenish white, golden to brownish yellow on the inner surface of the lip. **Tepals** somewhat unguiculate, narrowly elliptic to oblong, maximally 12 cm long, 2 cm wide. **Lip** narrowly clawed at the base, forming a relatively long tube which is somewhat inflated towards the apex, inconspicuously trilobed when spread, *c.* 11–12 cm long; callus lamellate, with apically fringed outgrowths, followed by 5–7 parallel furrows toward the apex of the middle lobe. **Column** attached to the lip along its basal two thirds, slightly arching, ventrally papillose and two-winged at the apex. Fruits green, about 1.8 cm in diameter and up to 23 cm long.


Vanilla trigonocarpa

Distribution: Costa Rica, Panama and Brazil.

Ecology: In Panama and Costa Rica, the plants are found in wet lowland forests, between 50 m and 350 m, occurring along the Caribbean and the Pacific coasts.

Flowering: Throughout the year, with a peak between January and February.

Pollination biology: Nothing is known about the pollination of this species. For details on the pollination of the genus, see the description of *Vanilla planifolia*.

Remarks: All *Vanilla* species are very similar and difficult to distinguish, especially when not in flower. *Vanilla trigonocarpa* can be distinguished from the other species co-occurring in the Golfo Dulce region by its very slender stems, and the very short and few-flowered inflorescences that emerge from the basal part of the plants (in the other species, they are produced towards the apex of the growing shoots). When in flower, *V. trigonocarpa* is easily recognised by its very large, widely open flowers made up of fairly slender floral segments.

References: Soto Arenas and Dressler in Hammel *et al.* (2003: 586), Soto Arenas and Dressler (2010).

Warrea costaricensis

Warrea costaricensis Schltr., Repert. Spec. Nov. Regni Veg. 16: 446 (1920).
E.: Costa Rican *Warrea*. **Sp.: -**

Etymology: The generic name commemorates the British orchid collector F. Warr, who collected the first samples of this genus in the early 19th century. The epithet alludes to Costa Rica, the country in which the species was first collected.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Zygopetalinae.

Description: Plants terrestrial or epiphytic, erect, up to 80 cm tall. **Pseudobulbs** ovoid or elliptic, single-leaved, usually covered by papery sheaths, 10–15 cm long. **Leaves** erect, with a short, stout, sheathing petiole, blade elliptic–lanceolate, gradually narrowing towards the base, apex acute, 25–70 cm long, 4–7.5 cm wide. **Inflorescence** a several-flowered (6 or more), erect raceme, emerging from the base of the petiole, as long as or slightly longer than the leaves. **Flowers** pendulous, quite large and showy, sepals and petals orange–yellow, with the colour intensifying to dark red on the outer surface, lip basally white, turning dark red towards the middle, margins yellowish. **Dorsal sepal** ovate–oblong, obtuse, concave, 2.8–3.5 cm long, 1.3–1.5 cm wide. **Lateral sepals** subequal to the dorsal sepal, forming a short mentum with the column foot. **Petals** obovate, obtuse, 2.8–3 cm long, 1.3–1.5 cm wide. **Lip** suborbicular, entire to slightly trilobed, tip retuse, 2.5–3 cm long, 2.5–3 cm wide; callus basal, narrow, white. **Column** slender, arched, with a short foot, 2.2–2.6 cm long.

Warrea costaricensis

Distribution: Guatemala to Panama. Rare.

Ecology: The plants grow in well-shaded places in tropical lowland to premontane forests, between 50 m and 900 m (exceptionally 1500 m).

Flowering: Sporadically throughout the year.

Pollination biology: Although the pollinators of this species are currently unknown, it has been proposed that the genus *Warrea* is pollinated by male euglossine bees that visit the flowers in search of fragrances.

References: Allen in Woodson and Schery (1949: 16), Dressler in Hammel *et al.* (2003: 589), Pupulin (2010: 56–57), Warren (2001).

Wullschlaegelia aphylla

Wullschlaegelia aphylla (Sw.) Rchb.f., Bot. Zeitung (Berlin) 21: 131 (1863).
Basionym: *Cranichis aphylla* Sw., Prodr. Veg. Ind. Occ.: 120 (1788).
E.: Leafless *Wullschaegelia*. **Sp.: -**

Etymology: The generic name commemorates Heinrich R. Wullschlägel (1805–1864) a missionary and later bishop of the Moravian Church in Berthelsdorf (eastern Germany), who compiled an extensive botanical collection from the Caribbean region, Guyana and Nicaragua. The epithet is derived from the Latinised Greek *aphyllos* (= leafless), alluding to the leafless stems.

Classification: Subf. Epidendroideae, Tr. Calypsoeae.

Description: Plant terrestrial, mycotrophic, aphyllous, 15–40 cm tall. **Stem** slender, erect, white to purplish, covered by fine, glandular, white to coffee-coloured hairs, bearing minute scales. **Scales** triangular–lanceolate, acuminate, 0.35–0.5 cm long. **Inflorescence** racemose, slender, covered by fine, glandular hairs, many-flowered. **Flowers** small, not resupinate, fully closed, pale white, erect. **Dorsal sepal** triangular–lanceolate to elliptic–oblong, concave, obtuse, 0.17–0.2 cm long, 0.1–0.15 cm wide. **Lateral sepals** obliquely oblong, basally forming a mentum, subobtuse to acute, 0.17–0.35 cm long, 0.1–0.15 cm wide, forming a spur 0.08–0.15 cm long. **Petals** short, elliptic–obovate to oblong–quadrate, rounded, 0.18–0.2 cm wide, *c.* 0.1 cm wide. **Lip** oblong–quadrate, conduplicate–concave, truncate, erose at apex, 0.3–0.32 cm long, *c.* 0.15 cm wide. **Column** short, with a comparatively long foot.

Distribution: Guatemala and Honduras to the West Indies, southern Brazil and Paraguay.

Habitat: Terrestrial, mycotrophic plants, growing in humus and rotten leaves in the deep shade of dense rain forests, often along water courses, between 100 m and 800 m.

Flowering: Throughout the year.

Pollination biology: *Wullschlaegelia aphylla* is cleistogamous.

Remarks: The genus contains only two, highly similar species, both occurring in the Golfo Dulce region. *Wullschaegelia calcarata* can be distinguished from *W. aphylla* by the brownish, flexuous or basally decumbent stem, somewhat less dense inflorescence and resupinate flowers which are orientated roughly perpendicular to the stem.

References: Ames and Correll (1952), Born *et al.* (1999), Dressler in Hammel *et al.* (2003: 590–591), Schweinfurth (1958: 78).

Wullschlaegelia aphylla

Wullschlaegelia calcarata

WULLSCHLAEGELIA I. aphylla, II. calcarata.

From Martius *et al.,* Flora Brasiliensis, vol. 3(4): Heft 117, t. 57 (1895)

Xylobium foveatum

Xylobium foveatum (Lindl.) G.Nicholson, Ill. Dict. Gard. 4: 225 (1887).
Basionym: *Maxillaria foveata* Lindl., Edwards's Bot. Reg. 25(Misc.): 2 (1839).
E.: Pitted *Xylobium*. **Sp.:** -

Etymology: The generic name is formed from the Greek *xylos* (= wood) and *bios* (= life), referring either to the epiphytic habit ("living on wood") or to the robust and somewhat woody rhizome of the plants. The epithet is derived from the Latin *foveatus* (= having a cavity or depression), referring to the characteristic anther cavity of this species.

Classification: Subf. Epidendroideae, Tr. Cymbidieae, Subtr. Maxillariinae.

Description: Plants epiphytic, robust, up to 40 cm tall. **Pseudobulbs** ovoid or subconical, slightly compressed, smooth or slightly ribbed, bearing 2 or 3 apical leaves, basally enveloped by imbricating sheaths, pseudobulbs 4–9 cm long, 1.5–4 cm wide. **Leaves** elliptic–lanceolate, plicate, subcoriaceous, apex acute, 24–40 cm long, 2.5–7 cm wide. **Inflorescence** growing from the base of the pseudobulbs into an erect, many-flowered raceme, 12–30 cm long. **Flowers** fragrant, creamy white to yellow, lip lined with reddish veins. **Dorsal sepal** free, elliptic to lanceolate, 1–1.4 cm long, 0.3–0.4 cm wide. **Lateral sepals** subfalcate–lanceolate, acuminate, adnate to the foot of the column, 1.2–1.4 cm long, 0.3–0.4 cm wide. **Petals** elliptic, thickening at the apex, 0.8–1 cm long, 0.2–0.3 cm wide. **Lip** articulated at the base with the column foot, 1–1.2 cm long, trilobed, the lateral lobes rounded, erect, middle lobe obtuse, spreading, disc with 3 thickened keels. **Column** very short, semiterete, apex obtuse, *c.* 1 cm long.

Distribution: From Mexico to Peru, Brazil and the Antilles. Not uncommon.

Xylobium foveatum

Ecology: Often found growing on moss-covered branches or cliffs in wet forests, up to 650 m.

Flowering: Possibly throughout the year.

Pollination biology: Nothing is known about the pollination of *X. foveatum*. Species of the genus *Xylobium* do not produce nectar, and so may rely on food deception to attract pollinators. Bees of the genera *Trigona*, *Melipona* and *Partamona* (Apideae, Meliponini) have been reported as flower visitors.

Remarks: Although not strongly fragrant, the scent of the flowers is not unpleasant.

References: Allen in Woodson and Schery (1949: 70–71), Croat (1978), Dressler in Hammel *et al.* (2003: 591), Hamer (1984: pl. 1197), Roubik (2000).

Xylobium foveatum

Glossary and Abbreviations

A

achlorophyllous - lacking chlorophyll

acuminate (leaf) **-** leaf with apex narrowing gradually or abruptly into a pointed tip (acumen)

acute (leaf) - sharply pointed, margins of leaf apex making an angle of less than 90° (cf. obtuse)

adnate - fused to an organ of different kind (e.g. nectar spur to ovary)

allogamy - cross-fertilization, fertilization of a flower by pollen from another plant of the same species

alternate - leaves inserted singly at the stem nodes, arrangement in a spiral or in two opposide rows (distichy)

androecium - entirety of the male parts (stamens) of a flower

androclinium - = clinandrium, cavity at the apex of the column of monandrous orchids, containing the anther

antennae - slender or filiform appendages of column, found in some Catasetum species, causing ejection of pollinarium upon touch

aphyllous - without leaves

apical - at the tip, at the top

apiculate - abruptly ending in a short, acute tip (apiculus)

auricles - ear-like projections, especially of the column

autogamy - self-fertilization, fertilization of a flower by pollen from the same plant, either from the same or a different flower of the same plant (geitonogamy)

B

basal - at the base, at the bottom

basionym - the first name published in association with a type

bipartite, 2-partite - having two parts

bisexual - flowers having both male and female reproductive organs (stamens and carpels)

bract - a usually small, modified leaf subtending an inflorescence or a flower

bristle - stiff, rigid hair

C

c. - circa, roughly

caespitose - growing in dense clusters or forming mats

calceiform - shaped like a shoe or slipper

callus - structure of thickened tissuelocated on the lip or rarely on the tepals

campanulate - bell-shaped

carinate - having a keel or sharp ridge

caudicula, caudicle - stalk-like part of the pollinium, connecting the pollinium with the viscidium

cf. - confer, compare to; in association with a species name: probably, identification not certain

chasmogamy - reproductive strategy in which flowers fully open, relying on cross-pollination

ciliate - fringed, with long hairs

clavate - club-shaped, with narrow base and a thickened apex

cleistogamy - reproductive strategy in which flowers do not open, relying on self-pollination inside the closed bud

clinandrium - = androclinium, cavity at the apex of the column ofmonandrous orchids, containing the anther

column - central structure of orchid flowers, rtesulting from the fusion of the male and female parts

column foot - extension of the base of the column, to which the lip and/or the lateral sepals are attached

column wings - distinct wing-like extensions of the column

conduplicate (leaf) - folded together lengthwise, the inner surfaces facing each other

connate - joined together, fused

cordate (leaf) - heart-shaped

coriaceous (leaf) - leathery, stiff

corm - swollen, fleshy, food-storing, underground stem part; in orchids also: swollen embryo after germination

crenate (leaf) - having margins with short, rounded or obtuse theeth

crenulate (leaf) - with minute rounded teeth

cucullate - having the shape of a hood, hooded

cuneate (leaf) - wedge-shaped

cuspidate (leaf) - narrowing into an acute tip

D

decumbent - lying or growing on the ground, but with ascending or erect distal part

deflexed - abruptly bent or turned downwards

dentate (leaf) - toothed (leaf margin)

denticulate (leaf) - minutely toothed (leaf margin)

diandrous - having two fertile stamens

dicotyledons - group of flowering plants which, among others, are characterized by having two embryonic leaves (cotyledons)

dimorphic - having two distinct shapes, forms or types (e.g., leaves, flowers etc.)

dioecious - having male and female flowers on different plants

disk - area between the lateral lobes and the basal half of the lip

distichous (leaves) - leaves arranged in two rows on opposite sides of the shoot axis

dolabriform (leaf) - shaped like the head of an axe

E

emarginate - having a shallow notch at the tip (e.g. leaf, petal, pseudobulb)

endemic - restricted to a certain region of the world

epichile - terminal (distal) part of a tripartite orchid lip

epiphyte, epiphytic - plant growing on another plant, the host plant being used as a support

erose - irregularly notched, toothed or fringed

ex - follows an author's name when a second author formally describes a taxon, but credits the identification to the first

extrafloral nectary - nectar-secreting gland(s), developing outside of the flower, may be involved in pollination or form part of a defense strategy

F

falcate (leaf) - sickle-shaped

fasciculate - arranged in a bundle

filiform - thread-like

fimbriate - having a fringed margin

flexuous - alternately winding, bending, zig-zag-like

foliaceous - bearing leaves, foliated

food-deception - reproductive strategy involving the mimicry of signals pretending the presence of a reward

fractiflex - sharply zig-zag-like

fusiform - spindle-shaped (e.g. pseudobulb)

G

geitonogamy - fertilisation by pollen from a flower of the same plant

geniculate - abruptly bent

gibbous - bulging, hunched

glabrous - smooth, hairless

H

heliophilous - "light-loving", preferring or adapted to high light intensity

hemiepiphyte, hemiepiphytic - plant which starts life as an epiphyte, but then sends down roots and makes contact with the soil (e.g. fig-trees)

hispidulous - studded with minute hairs or spines

holotype - single herbarium specimen (or illustration) designated by the author describing a new species

hypochile - lower (basal) part of a tripartite lip

I

imbricate - having overlapping edges

indumentum - a collective term for surface coverings, e.g. hair cover of leaf or stem

internode - portion between two successive nodes of a stem

L

labrum - upper part of the lip of arthropods (insects, crustaceans)

lacerate - jagged, as if torn

lamina - leaf blade, usually flat and broadened part of a leaf, also referring to the blade of the orchid lip

lanceolate (leaf) - lance-shaped

ligular - tongue-shaped

ligulate - strap-shaped

lingulate - tongue-shaped, linguiform

lip - the usually specialised upper (by resupination topographically lower) petal of the orchid flower

lithophyte, lithophytic - plants growing on rocks, with nutrients obtained only from rain water and dead plant tissues

M

mentum - chin-like projection of orchid flowers with a column foot, formed by the sepals and the base of the column

melittophily, melittophilous - (syndrome indicating) bee- pollination

membranaceous, membranous (leaf) - thin and rather soft, of pliable texture

meristem - undifferentiated plant tissue, usually located at the growth points (stem or root tips, margin of the primordial leaf), playing an essential role in plant growth and organ differentiation.

mesochile - middle part of a tripartite lip

mimicry - resemblance of an organsim to another in order to escape predators or to attract prey or pollinators

monandrous - having one fertile stamen (99% of the orchids)

monecious - having male and female flowers on the same plant

monocotyledons - group of flowering plants which, among other characters, are characterised by having one embryonic leaf (cotyledon)

monophyletic - Referring to a group comprising all taxa that have a common ancestor

monopodial - plants with a stem continuously growing from a single apical meristem

monotypic (monospecific) - a taxonomic group with only one representative (species)

mucronate (leaf) - ending abruptly in a sharp point

mycotrophic - obtaining nutrients and organic carbon from mycorrhizal fungi (parasitising fungi)

myiophily, myiophilous - (syndrome indicating) fly pollination

myrmecophyte, myrmecophytic - plant living in symbiotic association with ants

N

node - the point on a stem where a leaf is attached

O

oblanceolate (leaf) - lance-shaped, but broadest above the middle and tapering toward the base

oblong (leaf) - having a somewhat elongated form with roughly parallel sides

obovate (leaf) - reversely egg-shaped, with the narrow end attached to the stalk

obtuse (leaf) - blunt or rounded at the apex; converging edges making an angle of more than 90° (cf. acute)

orbicular (leaf) - round, circular

orifice - mouth, opening (of a flower)

ornithophily, ornithophilous - (syndrome indicating) pollination by birds (e.g. hummingbirds in neotropical orchids)

osmophores - tissue or glands producing/emitting a fragrance

P

paedomorphy - state in which juvenile characteristics are retained in the adult form of an organism

pandurate (leaf) - fiddle-shaped

panicle, paniculate - compound inflorescence having a branched inflorescence?

parasite - an organism that grows on and gains its nourishment from another living organsim

phalaenophily, phalaenophilous - (syndrome indicating) pollination by noctuid or pyralid moths

pedicel - stalk of a flower

pedate (leaf) - leaf having palmately divided lobes with the lateral lobes further divided or cleft

peduncle - the (often elongated) internode below an inflorescence

penicillate - having or resembling a small tuft of hairs

perianth - sterile outer segments of a flower (tepals or petals + sepals), surrounding the stamens and the gynoecium

Petiole (leaf) - stalk of leaf lamina

plicate (leaf) - pleated; folded like a fan

phyllome - leaf or a plant structure that corresponds to/has evolved from a leaf

pinnate (leaf) - leaf divided into segments (pinnae) arranged on both sides of the leaf axis (rachis)

pollinarium - pollen transport structure of many orchids, comprising the pollinium or pollinia, caudicle(s) and viscidium

pollinium - coherent mass of pollen grains of an anther locule or fused anther locules of a theca

polyphyletic - a group of taxa having different ancestors

porrect - extended, streching out/forwards

primordium - a plant strucure in its initial stage of development (e.g., leaf or flower primordium)

proboscis - elongated mouth part of insects, especially for sucking nectar

prostrate - growth pattern with shoots trailing on the ground

protandrous - flowers in which the anthers release the pollen before the stigma of the same flower becomes receptive

protuberant - thrusting out from a surface

pseudobulb - swollen, bulb-like, water-storing part of the stem of orchids

pseudocleistogamy, pseudocleistogamous - mixed reproductive system in which chasmogamous and

cleistogamous - flowers co-occur and in which their proportion is determined by environmental factors

pseudopollen - fragments of trichomes formed of starch rich cells, having the appearance of pollen grains and serving as a floral reward for pollinators

psychophily, psychophilous - (syndrome indicating) pollination by butterflies

pubescent - studded with short and/or soft hairs

R

raceme - inflorescence with an elongated main axis and pedicellate lateral flowers

racemose - having the form of a raceme

rachis (rhachis) - axis of a racemose inflorescence

ramicaul - the the unifoliate shoots (branches looking like complete plants) of pleurothallinid orchids

reniform (leaf) - kidney-shaped

resupinate (flower) - 180° turn of a flower, so that the lip points downwards

retuse - rounded or obtuse apex with a slight notch

revolute - margins bent downwards

rostellum - structure formed by the median stigmatic lobe in orchids, containing the viscidium

rugose - wrinkled

rupiculous - growing on or among rocks

S

saccate - pouched, sac-like

sagittate (leaf) - arrow-shaped

saprophyte - an organism that grows on and derives its nourishment from dead or decaying organic matter

scale, leaf scale - leaf reduced to a scale-like structure

scarious - having a dry membranous appearance, but fairly stiff

scopa (plural scopae) - pollen-carrying apparatus on the hind legs of bees, consisting of tufts of hairs

scutellum - triangular structure on the dorsal side of the thorax of insects

self-compatible - capable of self-fertilisation

serrulate (leaf) - having a minutely toothed margin

s.l. - sensu lato, in a broad sense

sessile (leaf, flower) - attached without a stalk

setose - covered with stiff hairs or bristles

sexual deception - reproductive strategy of of plants the flowers of which mimic female insects to such a degree that amorous males are fooled into mating with the flowers, thereby pollinating them.

sheath (leaf) - basal, sheath-like portion of a leaf or bract

sinuate - winding

spathulate (leaf) - having a broad, flat end and tapering into a narrower base.

spike - inflorescence with an elongated main axis and sessile lateral flowers

sphingophily, sphingophilous - (syndrome indicating) pollination by sphingid moths (hawkmoths)

sp. - (in association with a generic name) unidentified species of the respective genus

spp. - species (plural)

spur - tubular projection located at the base and behind the lip of some orchids, usually associated with nectar production

s. str. - sensu stricto, in a narrow sense

stigma - apical structure of the style on which the pollen is deposited

stipes, stipe - lamella of tissue connecting the pollinina (with short caudicle) and the viscidium

stipitate - having a stipe

stipules - small, paired, sometimes leaflike appendages at the base of a leaf or its stalk

staminode - sterile stamen

stomata - minute openings in leaves, stems, or other plant organs enabling gas exchange

subcapitate - almost capitate (gland with stalk and head)

subfusiform - almost spindle-shaped

sublunate - almost crescent-shaped

subquadrate - almost square in shape

subterete - almost terete, almost round in cross-section, inconspicuously angular

subumbellate - forming roughly an umbel

suffusion, suffused - hue, with a hue

sulcate - having narrow, deep furrows or groves

sympodial - growth pattern in which the plant body is formed from successive lateral shoots (usually each ending in a flower or inflorescence)inflorescence

synonym - a scientific name that is, for various reasons, not accepted any longer

synsepal - floral structure formed by the partial or full fusion of twoadjacent sepals

T

tepal - undifferentiated segment of the perianth in flowers (no differentiation into sepals and petals)

terete - cylindrical, round in cross-section, not angular

tarsus - distal part of the insect leg

tibial organ - structure on the hind leg of male euglossine bees serving for storage of fragrances

triandrous - having three fertile stamens

tripartite - divided into three parts

truncate (leaf) - squared off at the apex

twig-epiphyte - epiphytes adapted to dwelling on twigs and small branches of host trees

type species - the species designated to form the type of a genus

U

unguiculate - claw-shaped

unifoliate - having a single leaf

unisexual - a flower having either male parts (stamens) or female parts (carpels, gynoecium) only

V

verrucose - having wart-like projections

viscidium - sticky, pad- or lamella-like portion of a pollinarium serving for attaching the pollinia to a pollinator's body

References

Allen PH (1949). Orchidaceae (part three and four). In Woodson RE, Schery RW (eds). Flora of Panama, fascicles 4 & 5. Annals of the Missouri Botanical Garden 36(1): 1-132, 133-245.

Ames O (1924). Additions to the orchid flora of tropical America with illustrations of *Pleurothallis* and observations on noteworthy species. Schedulae Orchidianae 7: 1-36.

Ames O, Correll DS (1952). Orchids of Guatemala. Fieldiana: Botany 26(1): 1-395.

Ames O, Schweinfurth C (1925). New or noteworthy species of orchids from the American tropics. Schedulae Orchidianae 8: 1–84.

Arditti J (1992). Fundamentals of orchid biology. John Wiley & Sons, New York.

Atwood JT, Mora de Ratana DE (1999). Orchidaceae: Tribe Maxillarieae: Subtribes Maxillariinae and Oncidiinae. In Burger W (ed.). Flora Costaricensis. Family #39. Fieldiana: Botany 40: 1–182.

Barth FG (1982). Biologie einer Begegnung. Die Partnerschaft der Insekten und Blumen. Deutsche Verlags-Anstalt, Stuttgart.

Bechtel H, Cribb P, Launert E (1985). Orchideen-Atlas. Lexikon der Kulturorchideen. Ulmer, Stuttgart.

Berg C, Higgins WE, Dressler RL, Whitten WM, Arenas MAS, Culham A, Chase MW (2000). A phylogenetic analysis of Laeliinae (Orchidaceae) based on sequence data from internal transcribed spacers (ITS) of nuclear ribosomal DNA. Lindleyana 15(2): 96-114.

Bierzychudek P (1981). *Asclepias*, *Lantana* and *Epidendrum*: a floral mimicry complex? Biotropica 13: 54-58.

Blanco MA, Barboza G (2005). Pseudocopulatory pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by fungus gnats. Annals of Botany 95(5): 763-772.

Blanco MA, Carnevali G, Whitten WM, Singer RB, Koehler S, Williams SH, Ojeda I, Neubig KM, Endara L (2007). Generic realignments in Maxillariinae (Orchidaceae). Lankesteriana 7(3): 515-537.

Bogarin D, Pupulin F (2010). Two new species of *Mormolyca* from Costa Rica and Panama. Orchid Digest 74: 43-47.

Borba EL, Semir J (2001). Pollinator specificity and convergence in fly-pollinated *Pleurothallis* (Orchidaceae) species: a multiple population approach. Annals of Botany 88(1): 75-88.

Bory S, Grisoni M, Duval MF, Besse P (2008). Biodiversity and preservation of vanilla: present state of knowledge. Genetic Resources and Crop Evolution 55: 551-571.

Boyden TC (1980). Floral mimicry by *Epidendrum ibaguense* (Orchidaceae) in Panama. Evolution 34: 135-136.

Brieger FG, Maatsch P, Senghas (eds) (1979-2002): Schlechter R, ed. 3: Die Orchideen. P. Parey, Berlin & Hamburg.

Brodmann J, Twele R, Francke W, Ayasse M (2008a). Pollinator-attracting semiochemicals of the wasp-flower *Epipactis helleborine*. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie 16: 171-174.

Brodmann J, Twele R, Francke W, Holzer G, Zhang Q, Ayasse M (2008b). Orchids Mimic green-leaf volatiles to attract prey-hunting wasps for pollination. Current Biology 18: 740-744.

Brodmann J, Twele R, Francke W, Luo Y-B, Song X-Q, Ayasse M. (2009). Orchid mimics honey bee alarm pheromone in order to attract hornets for pollination. Current Biology 19: 1368–1372.

Cameron KM (2007). Molecular phylogenetics of Orchidaceae: the first decade of DNA sequencing. In: Cameron KN, Arditti J, Kull T (eds). Orchid biology: reviews and perspectives. (Memoirs of the New York Botanical Garden 95). New York Botanical Garden Press, New York.

Cameron KM (2011). Vanilla orchids: natural history and cultivation. Timberland Press, Portland & London.

Cameron KM, Chase MW, Whitten WM, Kores PJ, Jarrell DC, Albert VA, Goldman DH (1999). A phylogenetic analysis of the Orchidaceae: evidence from rbcL nucleotide sequences. American Journal of Botany 86(2): 208-224.

Carnevali G, Carnevali IR (1993). New or noteworthy orchids for the Venezuelan flora IX: new taxa, new records, and nomenclatural changes, mainly from the Guayana shield and northern Amazonas. Navon 3(2): 102-125.

Chase MW (1986). A monograph of *Leochilus* (Orchidaceae). Systematic Botany Monographs 14: 1-97.

Chase MW, Palmer JD (1997). Leapfrog radiation in floral and vegetative traits among twig epiphytes in the orchid subtribe Oncidiinae. In Givnish TJ, Sytsma KJ (eds.). Molecular evolution and adaptive radiation. Cambridge University Press. Cambridge.

Christensen DE (1994). Fly pollination in the Orchidaceae. Pp. 415–454. In: Arditti, J. (ed.), Orchid biology: reviews and perspectives. Vol. 6:. John Wiley & Sons, New York etc.

Cingel NA van der (1995). An atlas of orchid pollination, vol 1. European orchids. A.A. Balkema, Rotterdam.

Cingel NA van der (2001). An atlas of orchid pollination, vol. 2. America, Africa, Asia and Australia. A.A. Balkema, Rotterdam.

Cingel L van der (2007). Pollination of orchids by Lepidoptera: outcrossing by long distance transport. Pp. 201-259. In Cameron KM, Arditti J, Kull T (eds.): Orchid biology. Reviews and perspectives, vol. 9. (Memoirs of the New York Botanical Gerden 95). New York Botanical Garden Press, New York.

Ciotek L, Giorgis P, Benitez-Vieyra S, Cocucci AA (2006). First confirmed case of pseudocopulation in terrestrial orchids of South America: pollination of *Geoblasta pennicillata* (Orchidaceae) by *Campsomeris bistrimacula* (Hymenoptera, Scoliidae). Flora 201: 365–369.

Conran JG, Bannister JM, Lee DE (2009). Earliest orchid macrofossils: Early Miocene *Dendrobium* and *Earina* (Orchidaceae: Epidendroideae) from New Zealand. American Journal of Botany 96(2): 466–474.

Croat TB (1978). Flora of the Barro Colorado Island. Stanford University Press, Stanford.

Crüger H (1865). A few notes on the fecundation of orchids and their morphology. Journal of the Linnaean Society (Botany) 8: 127-135.

Dafni A (1984). Mimicry and deception in orchids. Annual Review of ecology and systematics 15: 259-278.

Dafni A (1987). Pollination in *Orchis* and related genera: evolution from reward to deception. In: Arditti J. (ed.). Orchid Biology Reviews and Perspectives. IV. Cornell University Press, London, pp. 79–104.

Damon A, Salas-Roblero P (2007). A survey of pollination in remnant orchid populations in Soconusco, Chiapas, Mexico. Tropical Ecology 48(1): 1-14.

Damon A, Valle-Mora J (2008). Retrospective spatial analysis of the pollination of two miniature epiphytic orchids with different pollination strategies in a coffee plantation in Soconusco, Chiapas, Mexico. Botanical Journal of the Linnean Society 158: 448-459.

Darwin C (1862). On the various contrivances by which British and foreign orchids are fertilized by insects, and on the good effects of intercrossing. Ed. 1. J. Murray, London.

Davies KL, Roberts DL, Turner MP (2002). Pseudopollen and food-hair diversity in *Polystachya* Hook. (Orchidaceae). Annals of Botany 90(4): 477-484.

Davies KL, Stpiczyńska M (2012). Comparative labellar anatomy of resin-secreting and putative resin-mimic species of *Maxillaria* s.l. (Orchidaceae: Maxillariinae). Botanical Journal of the Linnean Society 170(3): 405-435.

Davies KL, Winters C, Turner MP (2000). Pseudopollen: its structure and development in *Maxillaria* (Orchidaceae). Annals of Botany 85(6): 887-895.

Dodson CH (1962). Pollination and variation in the subtribe Catasetinae (Orchidaceae). Annals of the Missouri Botanical Garden 49(1/2): 36-56.

Dodson CH (1967). Relationships between pollinators and orchid flowers. In Atlas do simpósio sôbre a biota amazônica 5: 1-72.

Dodson CH (2001). Native Ecuadorian Orchids, vol. 2: *Dresslerella-Lepanthes*. ColinaLtda, Medellin.

Dodson CH (2002). Native Ecuadorian Orchids, vol. 3: *Lepanthopsis-Oliveriana*. ColinaLtda, Medellin.

Dodson CH, Dressler RL, Hills HG, Adams RM, Williams NH (1969). Biologically active compounds in orchid fragrances. Science 164: 1243-1249.

Dodson CH, Escobar RR (1993). Native Ecuadorian Orchids, vol. 1: *Aa – Dracula*. Colina Ltd., Medellin.

Dodson CH, Escobar RR (2003). Native Ecuadorian Orchids, vol. 4: *Oncidium – Restrepiopsis*. Colina Ltd., Medellin.

Dodson CH, Escobar RR (2004). Native Ecuadorian Orchids, vol. 5: *Rodriguezia – Zygosepalum.* Colina Ltd., Medellin.

Dodson CH, Gillespie RJ (1967). The biology of the orchids. Mid-America Orchid Congress, Nashville.

Dressler RL (1968). Pollination by euglossine bees. Evolution 22(1): 202-210.

Dressler RL (1993a). The orchids: natural history and classification. Cambridge University Press, Cambridge.

Dressler RL (1993b). Field guide to the orchids of Costa Rica and Panama. Cornell University Press, New York.

Dressler RL (1997). Die Orchideen: Biologie und Systematik der Orchidaceae. Bechtermünz, Augsburg.

Dressler RL (2001). Two *Sobralias. Sobralia chrysostoma*is described and the identity of *Sobralia leucoxantha* is resolved. Orchids 70(8): 750-770.

Dressler RL (2002). New species and combinations in Costa Rican orchids, II. Lankesteriana 3: 25-29.

Dressler RL, Whitten WM, Williams NH (2004). Phylogenetic relationships of *Scaphyglottis* and related genera (Laeliinae: Orchidaceae) based on nrDNA ITS sequence data. Brittonia 56(1): 58-66.

Eltz T, Zimmermann Y, Haftmann J, Twele R, Francke W, Quezada-Euan JJG, Lunau K (2007). Enfleurage, lipid recycling, and the origin of perfume collection in orchid bees. Proceedings of the Royal Society B – Biological Sciences 274: 2843-2848.

Endress PK (1994). *Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge.*

Escobar RR, Múnera JM, Ortiz P (eds.) (1991). Orquideas Nativas de Colombia, vol. 1: *Acacallis – Dryadella.* Vol 2: *Elleanthus – Masdevallia*. Vol 4: *Porroglossum – Zygosepalum.* Colina Ltd., Medellin.

Fay MF, Chase MW (2009). Preface. Orchid biology: from Linnaeus via Darwin to the 21st century. *Annals of Botany* 104: 359-364.

Fernández-Concha GC, Carnevali G, Muñoz JLT, Gómez-Juárez M (2001). A synopsis of the *Maxillaria rufescens* complex in Mexico, Central America, and the Greater Antilles. *Brittonia* 53(3): 454-465.

Fischer AL (2008). Cultivo de Orquídeas. Imaginador, Buenos Aires.

Fisher BL, Zimmerman JK (1988). Ant-orchid associations in the Barro Colorado National Monument, Panama. Lindleyana 3(1): 12-16.

Flach A, Dondon RC, Singer RB, Koehler S, Maria do Carmo EA, Marsaioli AJ (2004). The chemistry of pollination in selected Brazilian Maxillariinae orchids: floral rewards and fragrance. Journal of Chemical Ecology 30(5): 1045-1056.

Freudenstein JV, van den Berg C, Goldman DH, Kores PJ, Molvray M, ChaseMW (2004). An expanded plastid DNA phylogeny of Orchidaceae and analysis of jackknife branch support strategy. American Journal of Botany 91(1): 149-157.

Freuler MJ (2006). Orquídeas: una guía esencial para el cuidada y el cultivo de estas increíbles y sofisticadas epifitas. Albatros, Buenos Aires.

Freuler MJ (2008). Orquideas. Editorial Albatros, Buenos Aires.

Fulop D (2009). Biomechanics, pollination, and evolution of *Catasetum* (Catasetinae, Orchidaceae). Dissertation, Harvard University.

Garay LA (1956). Contribution towards a monograph of the genus *Stelis* Sw. Canadian Journal of Botany 34(3): 346-359.

Gargiullo M, Magnuson B, Kimball L (2008). A field guide to plants of Costa Rica. Oxford University Press, New York.

Gegenbauer C, Mayer VE, Zotz G, Richter A (2012). Uptake of ant-derived nitrogen in the myrmecophytic orchid *Caularthron bilamellatum*. Annals of Botany 110(4):757-66.

Genaust H (1996). Etymologisches Wörterbuch der botanischen Pflanzennamen. Birkhäuser, , Basel.

Gerlach G (2011). The genus *Coryanthes*: a paradigm in ecology. Lankesteriana 11(3): 253-264.

Gerlach G, Dressler RL (2003). Stanhopeinae mesoamericanae I. Lankesteriana 8: 23-30.

Goss GJ (1977). The reproductive biology of the epiphytic orchids of Florida 6. *Polystachya flavescens* (Lindley) J.J. Smith. American Orchid Society Bulletin 46: 990–994.

Gustafsson ALS, Verola CF, Antonelli A (2010). Reassessing the temporal evolution of orchids with new fossils and a Bayesian relaxed clock, with implications for the diversification of the rare South American genus *Hoffmannseggella* (Orchidaceae: Epidendroideae). BMC Evolutionary Biology 10: 177.

Haber WA, Frankie GW (1989). A tropical hawk moth community: Costa Rican dry forest Sphingidae. Biotropica 21(2): 155-172.

Hágsater E, Soto Arenas M (2002). Icones Orchidacearum Fasc. 8. The genus *Epidendrum,* part5. Herbario AMO, Mexico.

Hamer F (1982). Icones plantarum tropicarum. Orchids of Nicaragua, fasc. 7, part 1. Marie Selby Botanical Garden Press, Sarasota.

Hamer F (1983). Icones plantarum tropicarum. Orchids of Nicaragua, fasc. 7, part 2; fasc. 8, part 2; fasc. 9, part 3. Marie Selby Botanical Garden Press, Sarasota.

Hamer F (1984). Icones plantarum tropicarum. Orchids of Nicaragua, fasc. 12, part 5; fasc. 13, part 6. Marie Selby Botanical Garden Press, Sarasota.

Hammel BE, Grayum MH, Hererra C, Zamora VN (2003). Manual de Plantas de Costa Rica, vol. 3. Monocotiledóneas (Orchidaceae-Zingiberaceae). Missouri Botanical Garden, St. Louis.

Havkin-Frenkel D, Belanger F (2011). Handbook of *Vanilla* science and technology. Black-Wiley.

Higgs HG, Williams NH, Dodson CH (1972). Floral fragrances and isolating mechanisms in the genus *Catasetum* (Orchidaceae). Biotropica 4(2): 61-76.

Higgins WE (1997). A reconsideration of the genus *Prosthechea* (Orchidaceae). Phytologia 82(5): 370-383.

Higgins WE (2002). Systematics and the segregation of *Encyclia*. Proceedings of the 17th World Orchid Conference, Shah Alam, Malaysia, 24 April-2 May 2002.

Hills HG, Williams NH, Dodson CH (1968). Identification of some orchid fragrance components. American Orchid Society Bulletin 37: 967-971.

Janse JM (1886). Imitirte Pollenkörner bei *Maxillaria* sp. Berichte der Deutschen Botanischen Gesellschaft 4: 277-283.

Jenny R (2004). The genus *Stanhopea*. Caesiana 21-22: 1-291.

Jenny R, Sommer M (1993). The monograph of the genus *Gongora* Ruiz & Pavon. Koelz Scientific Books, Koenigstein.

Jenny R, Higgs WE, Dalström S (2007). An old species finally named and described: *Gongora boracayenensis*. Selbyana 28(2): 99-102.

Jersáková J, Johnson SD, Kindlmann P (2006). Mechansims and evolution of deceptive pollination in orchids. Biological Reviews of the Cambridge Philosophical Society 81(2): 219-235.

Johnson SD, Edwards TJ (2000). The structure and function of orchid pollinaria. Plant Systematics and Evolution 222(4): 243-269.

Karremans AP, Bakker FT, Pupulin F, Solano-Gómez R, Smulders MJ (2013). Phylogenetics of *Stelis* and closely related genera (Orchidaceae: Pleurothallidinae). Plant Systematics and Evolution 299(1): 151-176.

Koehler S, Cabral JS, Whitten WM, Williams NH, Singer RB, Neubig KM, Guerra M, Souza AP, Amaral MCE (2008). Molecular phylogeny of the neotropical genus *Christensonella* (Orchidaceae, Maxillariinae): species delimitation and insights into chromosome evolution. Annals of Botany 102(4):491–507.

Koehler S, Singer RB, Amaral MCE (2012). Taxonomic revision of the neotropical genus *Christensonella* (Maxillariinae, Orchidaceae). Botanical Journal of the Linnean Society 168(4): 449-472.

Kurzweil H (1999). Floral ontogeny of orchids: a review. Beiträge zur Biologie der Pflanzen 71: 45-100.

Kurzweil H, Kocyan A (2002). Ontogeny of orchid flowers. Pp. 83–138. In Kull T, Arditti J (ed.) Orchid biology – reviews and perspectives, vol 8. Kluwer Academic Publishers: Dordrecht, Netherlands.

Linnaeus C (1753). Species plantarum: exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. Laurentius Salvius, Stockholm.

Lubinsky P, Van Dam M, Van Dam A (2006). Pollination of *Vanilla* and evolution in Orchidaceae. Lindleyana 75(12): 926-929.

Luer CA (1983). *Trichosalpinx*, a new genus in Pleurothallidinae. Phytologia 54(5): 393-398.

Luer CA (1986). Icones Pleurothallidinarum I. Systematics of the Pleurothallidinae (Orchidaceae). Monographs in systematic botany, vol. 15. Missouri Botanical Garden, St. Louis.

Luer CA (1990). Icones Pleurothallidinarum VII: Systematics of *Platystele.* Monographs in systematic botany, vol. 38. Missouri Botanical Garden, St. Louis.

Luer CA (1996). New species in the Pleurothallidinae (Orchidaceae)from Costa Rica. Lindleyana 11(2): 54-113.

Luer CA (2000). Icones pleurothallidinarum XIX: Systematics of *Masdevallia* (Part One). *Masdevallia* subgenus *Polyantha*, section *Alaticaules*, section *Polyanthae*. Monographs in systematic botany, vol. 77. Missouri Botanical Garden, St. Louis.

Luer CA (2006). Icones Pleurothallidinarum XXVII: *Dryadella* and *Acronia* section Macrophyllae-Fasciculatae: addenda to *Acianthera*, *Andinia*, *Dracula*, *Dresslerella*, *Lepanthes*, and *Masdevallia*; new taxa, validation of taxa, errata. XXVIII. A reconsideration of *Masdevallia*. Systematics of *Specklinia* and vegetatively similar taxa (Orchidaceae): miscellaneous new taxa in the pleurothallid genera *Acianthera*, *Acronia*, *Arthrosia*, *Colombiana*, *Crocodeilanthe*, *Dracula*, *Dryadella*, *Loddigesia*, *Masdevallia*, *Myoxanthus*, *Ogygia*, *Platystele*, *Porroglossum*, *Restrepia* and *Trichosalpinx*. Monographs in Systematic Botany, vols. 103, 105. Missouri Botanical Garden, St. Louis.

Luer CA (2010). Icones Pleurothallidinarum XXXI. *Lepanthes* of Bolivia. Monographs in Systematic Botany, vol. 120. Missouri Botanical Garden, St. Louis.

Martini P, Schlindwein C, Montenegro A (2003). Pollination, flower longevity, and reproductive biology of *Gongora quinquenervis* Ruiz and Pavon (Orchidaceae) in an Atlantic forest fragment of Pernambuco, Brazil. Plant Biology 5(5): 495-503.

Mayr H (1995). Orchideennamen und ihre Bedeutung. Österreichische Orchideengesellschaft, Wien.

Mazo Cancino A de, Damon A (2007). Fragrance analysis of euglossine bee pollinated orchids from Soconusco, south-east Mexico. Plant Species Biology 22(2): 129-134.

McLeish I, Pearce NR, Adams BR, Briggs JS (1995). Native orchids of Belize. AA Balkema, Rotterdam.

Medina H, Pupulin F (2010). A note on the genus *Dresslerella*. Orchid Digest 74(3): 60-67.

Melo MC de, Borba EL, Paiva EAS (2010). Morphological and histological characterization of the osmophores and nectaries of four species of *Acianthera* (Orchidaceae: Pleurothallidinae). Plant Systematics and Evolution 286(3-4): 141-151.

Melo MC de, Taucce PPG, Borba EL (2011). Reproductive biology and isolation mechanisms in rupicolous species of the *Acianthera prolifera* complex (Orchidaceae) occurring in southeastern Brazil. Plant Systematics and Evolution 293(1-4): 161-176.

Michenau C, Johnson SD, Fay MF (2009). *Orchid pollination: from Darwin to present.* Botanical Journal of the Linnean Society 161: 1–19.

Morales JF (2009). Orchids of Costa Rica, vol 3. Editorial INBio, Santo Domingo de Heredia.

Murren CJ, Ellison AM (1996). Effects of habitat, plant size, and floral display on male and female reproductive success of the neotropical orchid *Brassavola nodosa*. Biotropica 28(1): 30-41.

Neubig K, Williams NH, Whitten WM, Pupulin F (2009). Molecular phylogenetics and the evolution of fruit and leaf morphology of *Dichaea* (Orchidaceae: Zygopetalinae). Annals of Botany 104(3): 457-467.

Neubig KM, Whitten WM, Williams NH, Blanco MA, Endara L, Burleigh JG, Silvera K, Cushman JC, Chase MW (2012). Generic recircumscriptions of Oncidiinae (Orchidaceae: Cymbidieae) based on maximum likelihood analysis of combined DNA datasets. Botanical Journal of the Linnean Society 168(2): 117-146.

Ojeda I, Carnevali G, Williams NH, Whitten WM (2003). Phylogeny of the *Heterotaxis* Lindley complex (Maxillariinae). Evolution of the vegetative architecture and pollination syndromes. Lankesteriana 7: 45-47.

Ojeda I, Fernández-Concha CG, Romero-González GA (2005). New species and combinations in *Heterotaxis* Lindl. (Orchidaceae: Maxillariinae). Navon 15(4): 572-582.

Pacek A, Stpiczyńska M, Davies KL, Szymczak G (2012). Floral elaiophore structure in four representatives of the *Ornithocephalus* clade (Orchidaceae: Oncidiinae). Annals of Botany 110(4): 809-820.

Pansarin ER, Amaral MCE (2008). Reproductive biology and pollination mechanisms of *Epidendrum secundum* (Orchidaceae). Floral variation: a consequence of natural hybridization? Plant Biology (Stuttgart) 10: 211–219.

Pansarin ER, Pansarin LM (2011). Reproductive biology of *Trichocentrum pumilum*: an orchid pollinated by oil-collecting bees. Plant Biology (Stuttgart) 13(4): 576-581.

Pijl L van der, Dodson CH (1966). Orchid flowers: their pollination and evolution. Fairchild Tropical Garden and the University of Miami Press, Coral Gables.

Porsch O (1909). Neuere Untersuchungen über die Insektenanlockungsmittel der Orchideenblüte. Mitteilungen des Naturwissenschaftlichen Vereins der Steiermark 545(2): 346-376.

Powell MP, Pupulin F, Warner J, Chase MW, Savolainen V (2003). Floral mimicry in oncidiod orchids. Lankesteriana 7:109-110.

Pridgeon AM (1992). The illustrated encyclopedia of orchids. Timber Press, Portland.

Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN (2003a). Genera Orchidacearum, vol. 1. General Introduction, Apostasioideae, Cypripedioideae. Oxford University Press, New York.

Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN (2003b). Genera Orchidacearum, vol. 3. Orchidoidae (Part 2), Vanilloideae. Oxford University Press, New York.

Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN (2005). Genera Orchidacearum,vol. 4. Epidendroideae (Part one). Oxford University Press, New York.

Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN (2009). Genera Orchidacearum,vol. 5. Epidendroideae (Part Two). Oxford University-Press. New York.

Pupulin F (1998). Orchid florula of Parque Nacional Manuel Antonio, Quepos, Costa Rica. Revista de biología tropical 46(4): 961-10317.

Pupulin F (2003). *Maxillaria atwoodiana*. Die Orchidee 54(5): 566.

Pupulin F (2010). Orchidaceae: Tribe Maxillarieae: Subtribes Maxillariinae and Oncidiinae. In Burger W (ed.). Flora Costaricensis. Family #39. Fieldiana: Botany 49: 1–60.

Pupulin F, Bogarin D (2005). The genus *Brassia* in Costa Rica: a survey of four species and a new species. Orchids 74(3): 202-207.

Pupulin F, Karremans AP, Gravendeel B (2012). A reconsideration of the empusellous species of *Specklinia* (Orchidaceae: Pleurothallidinae) in Costa Rica. Phytotaxa 63: 1-20.

Rain P (1986). Vanilla cook book. Celestial Arts, Berkeley, California.

Ramírez SR, Gravendeel B, Singer RB, Marshall CR, Pierce NE (2007). Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. Nature 448(7157): 1042-1045.

Reis MG, de Faria AD, Bittrich V, Amaral MC, Marsaioli AJ (2000). The Chemistry of flower rewards – *Oncidium* (Orchidaceae). Journal of the Brazilian Chemical Society (São Paulo) 11(6): 600-608.

Reis MG, de Faria AD, Alves dos Santos I, Amaral MCE, Marsaioli AJ (2007). Byrsonic acid – the clue to floral mimicry involving oil-producing lowers and oil-collecting bees. Journal of Chemical Ecology 33(7): 1421-1429.

Renner SS, Schaeffer H (2010). The evolution and loss of oil-offering flowers: new insights from dated phylogenies for angiosperms and bees. Philosophical Translations of the Royal Society B 365 (1539): 423-435.

Richter W (1974). Orchideen pflegen - vermehren – züchten. J. Neumann-Neudamm, Wien.

Roebuck KI, Steinhart WL (1978). Pollination ecology and the nocturnal scent response in the genus *Brassavola*. American Orchid Society Bulletin 47(6): 507-511.

Rollke F (2008). Orquídeas – rápido y fácil. Hispano-Europea, Buenos Aires.

Rollke L (2011). Orquideas de la A a la Z. Albatros, Buenos Aires.

Roubik DW (2000). Deceptive orchids with Meliponini as pollinators. Plant Systematics and Evolution 22(1-4): 271-279.

Roubik DW, Ackerman JD (1987). Long-term ecology of euglossine orchid-bees (Apidae: Euglossini) in Panama. *Oecologia* 73(3): 321-333.

Salazar-Chávez GA (1995). *Mormodes fractiflexa*. American Orchid Society Bulletin 64(7): 762-765.

Schemske DW (1980). Evolution of floral display in the orchid *Brassavola nodosa*. Evolution 34(3): 489-493.

Schiestl FP (2005). On the success of a swindle: pollination by deception in orchids. Naturwissenschaften 92(6): 255-264.

Schlechter R (1915/1927). Die Orchideen, ihre Beschreibung, Kultur und Züchtung, ed. 1: 1915, ed. 2: 1927. P. Parey, Berlin.

Schultes RE (1958). Orchidaceae Neotropicales: notes on the genus *Caularthron* Raf. Botanical Museum Leafllets of the Harvard University 18(3): 77-102.

Schweinfurth C (1958). Orchids of Peru. Fieldiana: Botany 30(1): 1-260.

Senghas K (1989). *Polystachya concreta* (Jacq.) Garay und Sweet 1974. Orchidee 40(3): 569-572.

Senghas K (1993). Orchideen - Pflanzen der Extreme, Gegensätze und Superlative. P. Parey, Berlin & Hamburg.

Siegel C (2011). Orchids and hummingbirds: sex in the fast lane. Orchid Digest 2011(1): 8-17.

Silvera K (2002). Adaptive radiation of oil-reward compounds among neotropical orchid species (Oncidiinae). Master thesis, University of Florida.

Singer RB (2001). Pollination biology of *Habenaria parviflora* (Orchidaceae: Habenariinae) in southeastern Brazil. Darwiniana 39(3-4): 201-207.

Singer RB (2002). The pollination mechanism in *Trigonidium obtusum* Lindl. (Orchidaceae: Maxillariinae): Sexual mimicry and trap-flowers. Annals of Botany 89(2): 157-163.

Singer RB, Flach A, Koehler S, Marsaioli AJ, Amaral MCE (2004). Sexual mimicry in *Mormolyca ringens* (Lindl.) Schltr. (Orchidaceae: Maxillariinae). Annals of Botany 93(6): 755-762.

Singer RB, Koehler S (2004). Pollinarium morphology and floral rewards in Brazilian Maxillariinae (Orchidaceae). *Annals of Botany* 93(1): 39-51.

Singer RB, Sazima M (1999). The pollination mechanism in the '*Pelexia*' alliance (Orchidaceae: Spiranthineae). Botanical Journal of the Linnean Society 131(3): 249-262.

Singer RB, Sazima M (2001). The pollination mechanism of three sympatric *Prescottia* (Orchidaceae: Prescottinae) species in southeastern Brazil. Annals of Botanny 88(6): 999-1005.

Soto Arenas MA, Dressler RL (2010). A revision of the Mexican and Central American species of *Vanilla* Plumier ex Miller with a characterization of their ITS region of the nuclear ribosomal DNA. Lankesteriana 9(3): 285-354.

Speckmaier M (1994). Elementos florales africanos en Venezuela y el neotropico; género *Polystachya*, parte I. Orquideophilo 2(2): 8-11.

Sprengel CK (1973). Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen. F. Vieweg d. Ä., Berlin.

Stenzel H (2004). Systematics and evolution of the genus *Pleurothallis* R. Br. (*Orchidaceae*) in the Greater Antilles. Dissertation, Humboldt-University.

Stpiczyńska M, Davies KL, Gregg A (2005). Comparative account of nectary structure in *Hexisea imbricata* (Lindl.) Rchb.f. (Orchidaceae). Annals of Botany 95(5): 749-56.

Stpiczyńska M, Davies KL, Gregg A. (2007). Elaiophore diversity in three contrasting members of the Oncidiinae Benth. (Orchidaceae). Botanical Journal of the Linnean Society. 155:135–148.

Stpiczyńska M, Davies KL (2008). Elaiophore structure and oil secretion in flowers of *Oncidium trulliferum* Lindl. and *Ornithophora radicans* (Rchb.f.) Garay & Pabst (Oncidiinae: Orchidaceae). Annals of Botany (London) 101(3): 375–384.

Szlachetko DL, Mytnik-Ejsmont J, Gorniak M, Smiszek M (2006). Genera et species Orchidalium. 15. Maxillarieae. Polish Botanical Journal 51(1): 57-59.

Szlachetko DL, Sitko M, Tukałło P, Mytnik-Ejsmont J (2012). Taxonomy of the subtribe Maxillariinae (Orchidaceae, Vandoideae) revised. Biodiversity: Research and Conservation 25(1): 13-38.

Teoh ES (2005). Orchids of Asia. Times Editions-Marshall Cavendish, Singapore.

Troll W (1937). Vergleichende Morphologie der höheren Pflanzen. Bd. 1, Teil 1. Vegetationsorgane. G. Borntraeger, Berlin.

Troll W (1943). Vergleichende Morphologie der höheren Pflanzen. Bd. 1, Teil 3. Wurzel und Wurzelsysteme. G. Borntraeger, Berlin.

Vale Á, Navarro L, Rojas D, Álvarez JC (2011). Breeding system and pollination by mimicry of the orchid *Talumnia guibertiana* in Western Cuba. Plant Species Biology 26: 163-173.

Vasquez RCh, Ibisch PL (2004). Orquideas de Bolivia. Diversidad yestado de conservación, vol. 2. Fundacion amigos de la naturaleza, Santa Cruz de la Sierra.

Vogel S (1966). Parfümsammelnde Bienen als Bestäuber von Orchidaceen und *Gloxinia*. Österreichische Botanische Zeitschrift 113: 302-361.

Vogel S (1969). Flowers offering fatty oil instead of nectar. Abstracts XI. Int. Bot. Congress Seattle: 229.

Vogel S (1973). Fungus gnat flowers and fungus mimesis. Pollination and dispersal. Pp. 13-18. In Brantjes NBM (ed.), Festschrift van der Pijl. Deptartment of Botany, University of Nijmegen, Nijmegen.

Vogel S (1974). Ölblumen und ölsammelnde Bienen. Tropische und Subtropische Pflanzenwelt 7: 1-267.

Vogel S (1978). Pilzmückenblumen als Pilzmimeten. Flora 167: 329-398.

Vogel S (2002). Flickering bodies: Floral attraction by movement. Beiträge zur Biologie der Pflanzen 72: 89-154.

Vöth W (1963). *Lepanthes wagneri* Rchb.f. Die Orchidee 14(1): 2-5.

Warren SD (2001). Flora de Nicaragua. Missouri Botanical Garden Press, St. Louis.

Whitten WM, Blanco MA, Williams NH, Koehler S, Carnevali G, Singer RB, Endara L, Neubig KM (2007). Molecular phylogenetics of *Maxillaria a*nd related genera (Orchidaceae: Cymbidieae) based on combined molecular data sets. American Journal of Botany 94(11): 1860-1889.

Williams LO (1946). Orchidaceae (second part). In Woodson RE Jr., Schery RW (eds.). Flora of Panama part III, fascicle 3. Annals of the Missouri Botanical Garden 33(1): 315-404.

Williams LO, Allen PH, Dressler RL (1980). Orchids of Panama: a facsimile reprint of the Orchidaceae, Flora of Panama. Missouri Botanical Garden Press.

Williams NH (1981). Floral fragrance components of *Brassavola* (Orchidaceae: Laeliinae). Selbyana5: 279-85.

Williams NH (1982). The biology of orchids and euglossine bees. Pp. 119-171. In Arditti J (ed). Orchid biology: reviews and perspectives 2. Cornell University Press, Ithaca.

Williams NH, Whitten WM (1983). Orchid floral fragrances and male euglossine bees: methods and advances in the last sesquidecade. The Biological Bulletin 164: 355-395.

Withner CL, Harding PA (2004). The Cattleyas and their relatives: the debatable Epidendrums. Timber Press, Portland.

Yam TW, Arditti J (2009). History of orchid propagation: a mirror of the history of biotechnology. Plant Biotechnological Reports 3: 1-56.

Zimmermann Y, Roubik D, Eltz T. (2006). Species-specific attraction to pheromonal analogues in orchid bees. Behavioral Ecology and Sociobiology 60: 833-843.

Zotz G, Schultz S (2008). The vascular epiphytes of a lowland forest in Panama: species composition and spatial structure. Plant Ecology 195(1): 131-141.

Websites

Biodiversity heritage library:
http://www.biodiversitylibrary.org

Epidendra – the global orchid taxonomic website:
www. epidendra.org

Swiss Orchid Foundation:
http://orchid.unibas.ch/site.home.php

The internet orchid species photo encyclopedia (IOSPE):
www.orchidspecies.com

World checklist of selected plant families (WCSP):
http://apps.kew.org/wcsp/home.do

Appendix: Checklist of the Orchid Species in the Golfo Dulce Region

Based on a list of the Lankester Botanical Garden, with incorporation of new records of the Tropical Research Station La Gamba; (?) = in need of confirmation; **bold** = species treated in this booklet

A

Acianthera decipiens (Ames & C.Schweinf.) Pridgeon & M.W.Chase (syn: *Pleurothallis decipiens* Ames & C.Schweinf.)

Acianthera lojae (Schltr.) Luer

***Acianthera pantasmi* (Rchb.f.) Pridgeon & M.W.Chase (syn: *Pleurothallis pantasmi* Rchb.f.)**

Acianthera sicaria (Lindl.) Pridgeon & M.W.Chase (syn: *Pleurothallis sicaria* Lindl.)

Anathallis lewisiae (Ames) Solano & Soto Arenas (syn: *Pleurothallis lewisiae* Ames)

***Arundina graminifolia* (D.Don) Hochr. (cult.)**

***Aspasia epidendroides* Lindl.**

B

Bletia purpurea (Lam.) A.DC.

***Brassavola nodosa* (L.) Lindl.**

***Brassia caudata* (L.) Lindl.**

***Bulbophyllum oerstedii* (Rchb.f.) Hemsl. (syn: *Bulbophyllum pachyrachis* (A.Rich.) Griseb.)**

C

Camaridium inauditum (Rchb.f.) M.A.Blanco (syn: *Maxillaria inaudita* Rchb.f.) (?)

Camaridium neglectum (Schltr.) M.A. Blanco (syn: *Maxillaria neglecta* (Schltr.) L.O.Williams)

Camaridium vaginale (Rchb.f.) M.A.Blanco (syn: *Maxillaria vaginalis* Rchb.f.) (?)

Camaridium vestitum (Sw.) Lindl. (syn: *Maxillaria parviflora* (Poepp. & Endl.) Garay)

Camaridium vittariifolium (L.O.Williams) M.A.Blanco (syn: *Maxillaria vittariifolia* L.O.Williams)

***Campylocentrum micranthum* (Lindl.) Rolfe**

***Catasetum maculatum* Kunth**

***Caularthron bilamellatum* (Rchb.f.) R.E.Schult.**

***Christensonella uncata* (Lindl.) Szlach. (syn: *Maxillaria uncata* Lindl.)**

Clowesia warczewitzii (Lindl. & Paxton) Dodson

Coccineorchis bracteosa (Ames & C.Schweinf.) Garay (syn: *Stenorrhynchos bracteosum* Ames & C.Schweinf.)

Coccineorchis standleyi (Ames) Garay

***Coryanthes kaiseriana* G.Gerlach**

Cryptarrhena guatemalensis Schltr.

Cryptarrhena lunulata R.Br.

Cryptocentrum flavum Schltr.

Cyclopogon elatus (Sw.) Schltr.

Cyclopogon prasophyllum (Rchb. f.) Schltr.

D

Dichaea ciliolata Rolfe

Dichaea globosa Dressler & Pupulin

Dichaea hystricina Rchb.f.

Dichaea morrisii Fawc. & Rendle

***Dichaea panamensis* Lindl.**

***Dichaea poicillantha* Schltr.**

Dichaea trulla Rchb.f.

Dichaea tuerckheimii Schltr.

Dimerandra elegans (Focke) Siegerist (?)

Dimerandra emarginata (G.Mey.) Hoehne

***Dresslerella hispida* (L.O.Williams) Luer**

Dressleria eburnea (Rolfe) Dodson

***Dryadella odontostele* Luer**

Dryadella sp.

E

Echinosepala sp.

Elleanthus caricoides Nash

***Elleanthus graminifolius* (Barb.Rodr.) Løjtnant**

Elleanthus poiformis Schltr.

Elleanthus tillandsioides Barringer

Encyclia cordigera (Kunth) Dressler

Encyclia stellata (Lindl.) Schltr.

Epidendrum anceps Jacq.

Epidendrum baumannianum Schltr.

Epidendrum cf. *blancheanum* Urb. (syn: *Epidendrum acunae* Dressler)

Epidendrum **cf.** *physodes* **Rchb.f.**

Epidendrum curvisepalum Hágsater & Dressler (?)

Epidendrum cystosum Ames

***Epidendrum hellerianum* A.D.Hawkes**

Epidendrum isomerum Schltr.

Epidendrum isthmi Schltr.

Epidendrum macroclinium Hágsater

Epidendrum miserrimum Rchb.f.

Epidendrum montis-narae Pupulin & L.Sánchez

***Epidendrum nocturnum* Jacq.**

Epidendrum octomerioides Schltr.

Epidendrum paniculatum Ruiz & Pav.

***Epidendrum pseudepidendrum* Rchb.f.**

Epidendrum pseudoramosum Schltr.

Epidendrum pumilum Rolfe (syn: *Oerstedella pumila* (Rolfe) Hágsater) (?)

Epidendrum ramosum Jacq.

***Epidendrum schlechterianum* Ames (syn: *Epidendrum congestoides* Ames & C.Schweinf.)**

Epidendrum sculptum Rchb.f.

Epidendrum strobiliferum Rchb.f.

***Epidendrum turialvae* Rchb.f.**

Epidendrum vincentinum Lindl.

***Epidendrum vulgoamparoanum* Hágsater & L.Sánchez**

Epidendrum zunigae Hágsater

***Erycina crista-galli* (Rchb.f.) N.H.Williams & M.W.Chase (syn: *Oncidium crista-galli* Rchb.f.)**

Erycina glossomystax (Rchb.f.) N.H.Williams & M.W.Chase (*Psygmorchis glossomystax* (Rchb.f.) Dodson & Dressler)

Erycina pusilla (L.) N.H.Williams & M.W.Chase (syn: *Psygmorchis pusilla* (L.) Dodson & Dressler)

Eulophia alta (L.) Fawc. & Rendle

G

Galeottia grandiflora A.Rich.

***Gongora boracayanensis* Jenny, Dalström & W.E.Higgins**

***Gongora claviodora* Dressler**

Gongora unicolor Schltr.

***Gongora histrionica* Rchb.f.**

H

Habenaria distans Griseb.

***Habenaria monorrhiza* (Sw.) Rchb.f.**

***Heterotaxis maleolens* (Schltr.) Ojeda & Carnevali (syn. *Maxillaria maleolens* Schltr.)**

***Heterotaxis sessilis* (Sw.) F.Barros (syn: *Maxillaria crassifolia* (Lindl.) Rchb.f.) (?)**

I

Inti sp.

Ionopsis satyrioides (Sw.) Rchb.f. in W.G.Walpers

***Ionopsis utricularioides* (Sw.) Lindl.**

J

Jacquiniella equitantifolia (Ames) Dressler

Jacquiniella globosa (Jacq.) Schltr.

L

***Leochilus scriptus* (Scheidw.) Rchb.f.**

***Lepanthes* sp.**

***Lockhartia acuta* (Lindl.) Rchb.f.**

Lockhartia amoena Endres & Rchb.f.

Lockhartia hercodonta Rchb.f. ex Kraenzl

Lockhartia micrantha Rchb.f.

Lockhartia parthenoglossa Rchb. f.

***Lockhartia pittieri* Schltr.**

Lycaste bruncana Bogarín

M

***Macroclinium alleniorum* Dressler & Pupulin**

***Mapinguari longipetiolatus* (Ames & C.Schweinf.) Carnevali & R.B.Singer (syn. *Maxillaria longipetiolata* Ames & C.Schweinf.)**

Masdevallia calura Rchb.f.

***Masdevallia lata* Rchb.f.**

Masdevallia nidifica Rchb.f.

***Maxillaria atwoodiana* Pupulin**

Maxillaria brachybulbon Schltr.

Maxillaria confusa Ames & C.Schweinf.

Maxillaria porrecta Lindl. (*Maxillaria brunnea* Linden & Rchb.f.)

Maxillaria reichenheimiana Endres & Rchb.f. (syn: *Maxillaria pachyacron* Schltr.)

Maxillaria ringens Rchb.f. in W.G.Walpers

Maxillariella costaricensis (Schltr.) M.A.Blanco & Carnevali (syn: *Maxillaria costaricensis* Schltr.)

Maxillariella diuturna **(Ames & C.Schweinf.) M.A.Blanco & Carnevali (syn: *Maxillaria diuturna* Ames & C.Schweinf.)**

Maxillariella oreocharis **(Schltr.) M.A.Blanco & Carnevali (syn: *Maxillaria oreocharis* Schltr.)**

Maxillariella ponerantha (Rchb.f.) M.A.Blanco & Carnevali

Microchilus calophyllus (Rchb.f.) Ormerod (syn: *Erythrodes calophylla* (Rchb.f.) Ames)

Microchilus nigrescens (Schltr.) Ormerod (syn: *Erythrodes killipii* Ames)

Monophyllorchis microstyloides (Rchb.f.) Garay (syn: *Monophyllorchis maculata* Garay)

Mormodes colossus Rchb.f.

Mormodes fractiflexa Rchb.f.

Mormodes ignea **Lindl. & Paxton**

Mormolyca dressleriana (Carnevali & J.T.Atwood) M.A.Blanco (syn: *Maxillaria dressleriana* Carnevali & J.T.Atwood)

Mormolyca hedwigiae **(Hamer & Dodson) M.A.Blanco (syn: *Maxillaria hedwigiae* Hamer & Dodson)**

Mormolyca moralesii (Carnevali & J.T.Atwood) M.A.Blanco

Mormolyca rufescens (Lindl.) M.A.Blanco (syn: *Maxillaria rufescens* Lindl.)

N

Nidema ottonis (Rchb.f.) Britton & Millsp.

Nitidobulbon nasutum (Rchb.f.) Ojeda & Carnevali (syn: *Maxillaria nasuta* Rchb.f.)

Notylia barkeri **Lindl.**

Notylia pittieri Schltr.

O

Octomeria costaricensis Schltr.

Oeceoclades maculata (Lindl.) Lindl.

Oncidium ansiferum Rchb.f.

Oncidium baueri Lindl.

Oncidium dichromaticum Rchb.f.

Oncidium polycladium **Rchb.f. ex Lindl.**

Oncidium stenobulbon Kraenzl

Ornithidium adendrobium (Rchb.f.) M.A.Blanco & Ojeda (syn: *Maxillaria adendrobium* (Rchb.f.) Dressler)

Ornithocephalus bicornis **Lindl.**

P

Pabstiella aryter (Luer) F.Barros (syn: *Pleurothallis aryter* Luer)

Palmorchis powellii (Ames) C.Schweinf. & Correll

Pelexia funckiana **(A.Rich. & Galeotti) Schltr.**

Platystele speckmaieri **Luer & Sijm**

Platystele caudatisepala (C.Schweinf.) Garay (?)

Platystele ovatilabia (Ames & C.Schweinf.) Garay

Platystele cf. *oxyglossa* (Schltr.) Garay

Platythelys vaginata (Hook.) Garay (syn: *Erythrodes vaginata* (Hook.) Ames)

Pleurothallis correllii Luer (?)

Pleurothallis homalantha **Schltr.**

Pleurothallis phyllocardioides **Schltr.**

Pleurothallis rhodoglossa Schltr.

Pleurothallis rowleei Ames

Pleurothallis ruscifolia (Jacq.) R.Br.

Pleurothallis volcanica Luer

Polycycnis sp.

Polystachya foliosa **(Hook.) Rchb.f.**

Polystachya masayensis Rchb.f.

Prescottia cordifolia Rchb.f.

Prescottia stachyodes **(Sw.) Lindl.**

Prosthechea abbreviata (Schltr.) W.E.Higgins

Prosthechea chacaoensis (Rchb.f.) W.E.Higgins

Prosthechea fragrans (Sw.) W.E.Higgins

Prosthechea pygmaea **(Hook.) W.E.Higgins**

R

Rhetinantha aciantha (Rchb.f.) M.A.Blanco (syn: *Maxillaria aciantha* Rchb.f.)

Rossioglossum ampliatum (Lindl.) M.W.Chase & N.H.Williams (syn: *Oncidium ampliatum* Lindl.)

S

Sarcoglottis sceptrodes (Rchb.f.) Schltr. (syn: *Sarcoglottis hunteriana* Schltr.)

Scaphyglottis behrii **(Rchb.f.) Benth. & Hook.f. ex Hemsl.**

Scaphyglottis bidentata **(Lindl.) Dressler (syn. *Hexisea bidentata* Lindl.)**

Scaphyglottis boliviensis (Rolfe) B.R.Adams (syn: *Scaphyglottis decipiens* C.Schweinf.)

Scaphyglottis fusiformis (Griseb.) R.E.Schult.

Scaphyglottis imbricata (Lindl.) Dressler (syn: *Hexisea imbricata* (Lindl.) Rchb.f.)

Scaphyglottis jimenezii Schltr.

Scaphyglottis laevilabia Ames

Scaphyglottis lindeniana (A.Rich. & Galeotti) L.O.Williams

Scaphyglottis longicaulis S.Watson

Scaphyglottis mesocopis (Endres & Rchb.f.) Benth. & Hook.f. ex Hemsl.

Scaphyglottis minutiflora Ames & Correll

Scaphyglottis panamensis B.R.Adams

Scaphyglottis prolifera (R.Br.) Cogn.

Scaphyglottis stellata Lodd. ex Lindl.

Scaphyglottis tenella L.O.Williams

Schiedeella wercklei (Schltr.) Garay

Schoemburghia sp. (cult.)

Sobralia amabilis (Rchb.f.) L.O.Williams (?)

***Sobralia chrysostoma* Dressler**

***Sobralia decora* Bateman (syn: *Sobralia fenzliana* Rchb.f., *Sobralia neglecta* Schltr.)**

***Sobralia fragrans* Lindl.**

Sobralia labiata Warsz. & Rchb.f.

Sobralia luteola Rolfe

Sobralia macrophylla Rchb.f.

Sobralia mucronata Ames & C.Schweinf.

Sobralia suaveolens Rchb. f.

***Specklinia acrisepala* (Ames & C.Schweinf.) Pridgeon & M.W.Chase (syn: *Pleurothallis acrisepala* Ames & C.Schweinf.)**

***Specklinia brighamii* (S.Watson) Pridgeon & M.W.Chase (syn: *Pleurothallis brighamii* S.Watson)**

Specklinia corniculata (Sw.) Steud. (syn: *Pleurothallis corniculata* (Sw.) Lindl.)

***Specklinia fimbriata* (Ames & C.Schweinf.) Solano (syn: *Pleurothallis setosa* C.Schweinf.)**

***Specklinia grobyi* (Bateman ex Lindl.) F.Barros (syn: *Pleurothallis grobyi* Bateman ex Lindl.)**

***Specklinia recula* (Luer) Luer (syn: *Pleurothallis recula* Luer)**

Specklinia sertularioides (Sw.) Lindl. (syn: *Pleurothallis sertularioides* (Sw.) Spreng.)

Specklinia simmleriana (Rendle) Luer

***Stanhopea cirrhata* Lindl.**

Stanhopea costaricensis Rchb.f.

Stanhopea panamensis N.H.Williams & W.M.Whitten (?)

Stanhopea pulla Rchb.f.

Stanhopea wardii Lodd. ex Lindl.

***Stelis* sp.**

Stelis cucullata Ames (moglich F)

Stelis glossula Rchb.f.

Stelis janetiae (Luer) Pridgeon & M.W.Chase

Stelis multirostris (Rchb.f.) Pridgeon & M.W.Chase (syn: *Pleurothallis racemiflora* (Sw.) Lindl. ex Hook.)

Stelis pardipes Rchb.f.

Stelis quadrifida (Lex.) Solano & Soto Arenas

Stelis superbiens Lindl. (syn: *Stelis leucopogon* Rchb.f.)

T

Trichocentrum caloceras Endres & Rchb.f.

Trichopilia marginata Henfr.

Trichopilia subulata (Sw.) Rchb.f.

***Trichosalpinx blaisdellii* (S.Watson) Luer**

Trichosalpinx caudata Luer & R.Escobar

Trichosalpinx orbicularis (Lindl.) Luer

***Trigonidium egertonianum* Bateman ex Lindl.**

Triphora ravenii (L.O.Williams) Garay

Trisetella dressleri (Luer) Luer (?)

***Trizeuxis falcata* Lindl.**

V

***Vanilla inodora* Schiede**

***Vanilla planifolia* Jacks. ex Andrews**

Vanilla sarapiquensis Soto Arenas

***Vanilla trigonocarpa* Hoehne**

W

***Warrea costaricensis* Schltr.**

Wullschlaegelia aphylla (Sw.) Rchb.f.

***Wullschlaegelia calcarata* Benth.**

X

Xylobium elongatum (Lindl. & Paxton) Hemsl.

***Xylobium foveatum* (Lindl.) G.Nicholson**

Photo Credits

In alphabetic order; t = top, m = middle, b = bottom, l = left, c = center, r = right, tot = total, ins = insert.

Kerry Dressler: 182m, 182b

Traude Duziak: 67tl, 67b, 99b

Thomas Eltz: 93b

Christian Gegenbauer: 13t, 34b, 35t, 35b, 121t, 143bl

Günter Gerlach: 10bl, 17b, 20m, 21tr, 65t, 123t, 181ins

Rudolf Hromniak: 22bl, 22br

Werner Huber: 4b, 7t, 7b, 30bl, 36b, 39b, 86bl, 89t, 108b, 128b, 139t, 148b, 165b, 166t, 166b, 180b

Franz Michelmayer: 157t, 157b

Margareta Pertl: 42tot

Franco Pupulin: 90b, 91t, 93t, 138t

Demetra Rakosy: 109m, 109b, 124b, 125t, 126b, 127b, 162b, 170b, 184b, 185tot

Thorsten Rennebarth: 5t, 70b, 76b, 82b, 113m, 127t, 160b, 174b

Max Ringler: 51t

Anton Sieder: 41t

Manfred Speckmaier: front cover, back cover, 9b, 12t, 13m, 15tl, 15tr, 16t, 16ml, 16mc, 16mr, 23tl 23tr, 24b, 28b, 31t, 32bl, 38t, 48b, 49t, 49b, 52b, 53t, 53b, 54b, 55t, 55b, 56b, 57t, 58b, 59t, 61t, 61b, 62b, 63t, 68b, 69b, 74b, 75t, 77t, 80b, 83t, 83b, 84b, 85t, 86br, 87b, 94b, 95tot, 96b, 98b, 99t, 100t, 100b, 101t, 103t, 110b, 112b, 113b, 116b, 117b, 118b, 119tot, 120ml, 120mr, 120b, 125m, 130b, 131r, 133b, 134b, 135t, 136b, 140b, 141t, 142b, 143br, 144b, 145t, 145b, 147t, 149t, 150b, 151t, 151b, 152b, 153t, 153b, 154b, 155t, 161t, 171b, 172b, 175t, 175b, 177t

Tropenstation La Gamba: 6b

Stefan Vogel: 43m, 130t

Anton Weber: 46b, 132b

Martina Weber: 27t

Peter Weish: 44b, 45b, 47t, 60b, 64b, 67tr, 71m, 71b, 72b, 73b, 78b, 79b, 81t, 92b, 97t, 102b, 104b, 105b, 107t, 107b, 111t, 114b, 115t, 115b, 121b, 122b, 129t, 129b, 135b, 137t, 139b, 141b, 146b, 147b, 156b, 158b, 159b, 161b, 163tot, 164b, 165t, 167tot, 169t, 169b, 171t, 173t, 181b

Anton Weissenhofer: 26b, 45t, 50b, 66b, 69t, 88b, 106b, 133t, 178b, 179r

Authors

Christian Gegenbauer
University of Vienna
Dept of Structural and Functional Botany
Rennweg 14, 1030 Vienna, Austria
Christian.Gegenbauer@gmx.at

Werner Huber
University of Vienna
Dept. of Tropical Ecology and Animal Biodiversity
Rennweg 14, 1030 Vienna, Austria
werner.huber@univie.ac.at

Franco Pupulin
University of Costa Rica
Jardín Botánico Lankester
Apartado 1031-7050 Cartago, Costa Rica
franco.pupulin@gmail.com

Demetra Rakosy
University of Vienna
Dept. of Integrative Zoology
Althanstraße 14, 1090 Vienna, Austria
demetra.rakosy@univie.ac.at

Manfred Speckmaier
University of Vienna
Botanical Garden
Rennweg 14, 1030 Vienna, Austria
manfred.speckmaier@univie.ac.at

Wolfgang Wanek
University of Vienna
Dept. of Chemical Ecology and Ecosystem Research
Althanstraße 14, 1090 Vienna, Austria
wolfgang.wanek@univie.ac.at

Anton Weber
University of Vienna
Dept of Structural and Functional Botany
Rennweg 14, 1030 Vienna, Austria
anton.weber@univie.ac.at

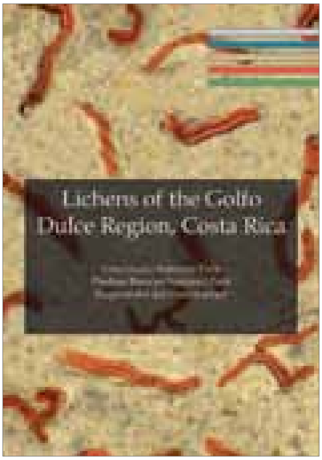
Anton Weissenhofer
University of Vienna
Dept. of Tropical Ecology and Animal Biodiversity
Rennweg 14, 1030 Vienna, Austria
anton.weissenhofer@univie.ac.at

Acknowledgments

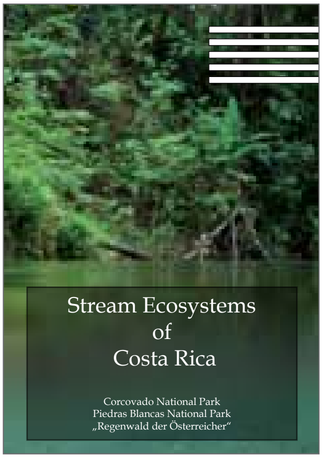
The book could not have been realised without the kind support and help of many people and organisations, and we would like to extend our sincere thanks to all of them. In particular, we thank Susanne Pamperl and Susanne Sontag for technical assistance; Kerry Dressler, Traude Duziak, Thomas Eltz, Florian Etl, Günter Gerlach, Rudolf Hromniak, Thorsten Renebarth, Michael Schnitzler, Anton Sieder, Martina Weber and Peter Weish for providing photos; Margareta Pertl, Friedrich G. Barth and Stefan Vogel for providing drawings; and Peter Stütz for pre-reviewing parts of the manuscript. Last but not least, we gratefully acknowledge the generous support of the Wiener Orchideen Gesellschaft and the Botanical Garden of the University of Vienna.

Creando un bosque
Árboles para corredores biológicos
en la región de Golfo Dulce, Costa Rica

Creating a forest
Trees for biological corridors
in the Golfo Dulce region, Costa Rica

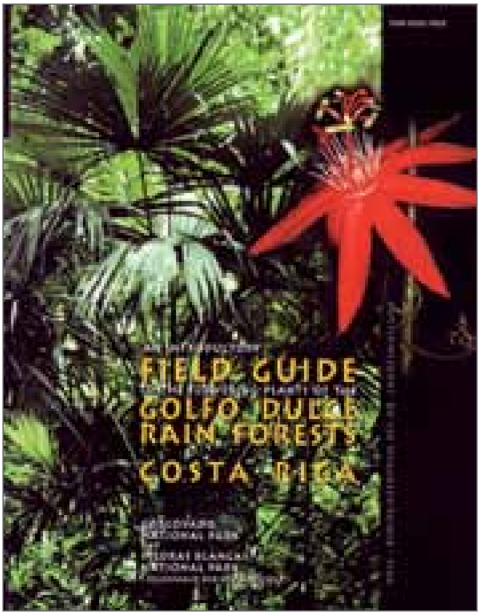


Lichens of the Golfo
Dulce Region, Costa Rica

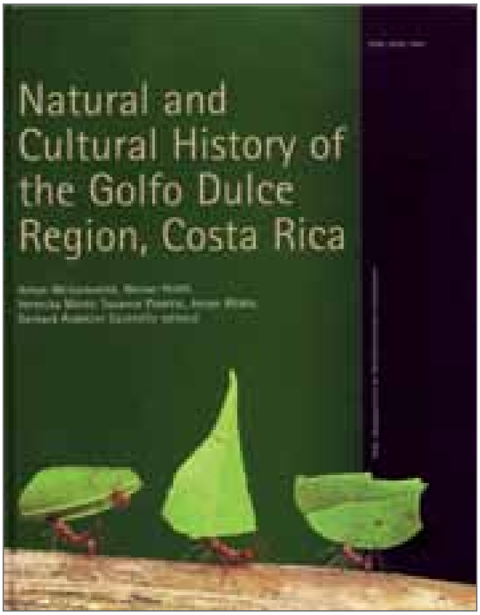


Stream Ecosystems
of
Costa Rica

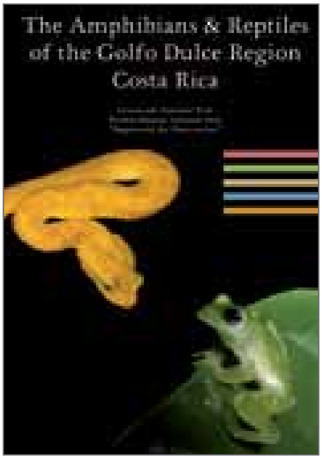
Corcovado National Park
Piedras Blancas National Park
„Regenwald der Österreicher"



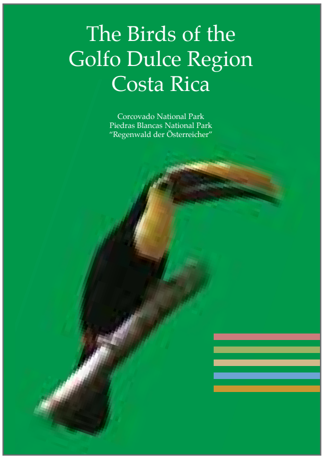
FIELD GUIDE
GOLFO DULCE
RAIN FORESTS
COSTA RICA



Natural and
Cultural History of
the Golfo Dulce
Region, Costa Rica

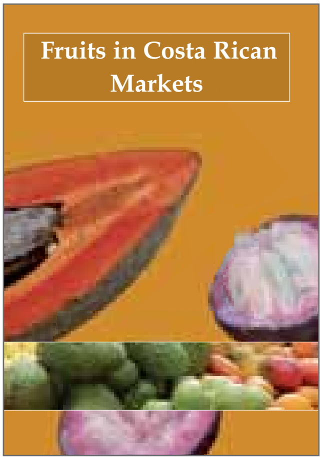


The Amphibians & Reptiles
of the Golfo Dulce Region
Costa Rica

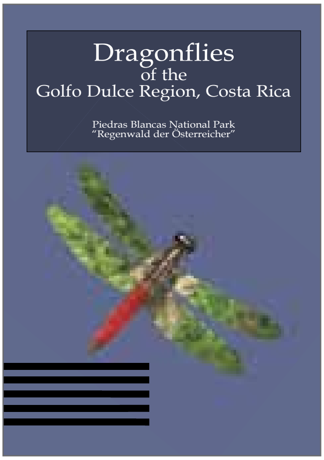


The Birds of the
Golfo Dulce Region
Costa Rica

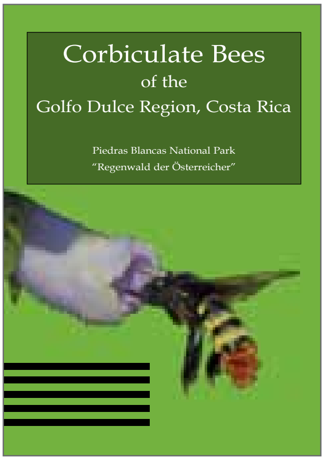
Corcovado National Park
Piedras Blancas National Park
"Regenwald der Österreicher"



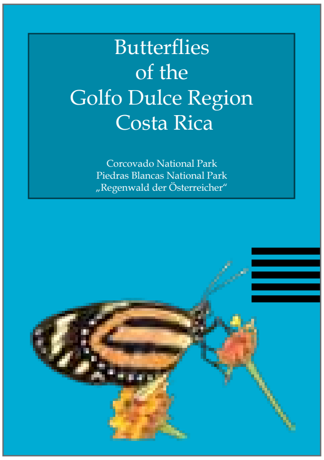
Fruits in Costa Rican
Markets


Dragonflies
of the
Golfo Dulce Region, Costa Rica

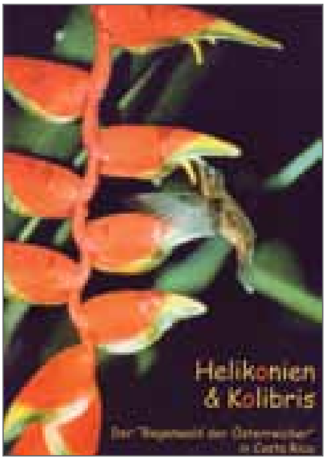
Piedras Blancas National Park
"Regenwald der Österreicher"


Corbiculate Bees
of the
Golfo Dulce Region, Costa Rica

Piedras Blancas National Park
"Regenwald der Österreicher"


Butterflies
of the
Golfo Dulce Region
Costa Rica

Corcovado National Park
Piedras Blancas National Park
„Regenwald der Österreicher"

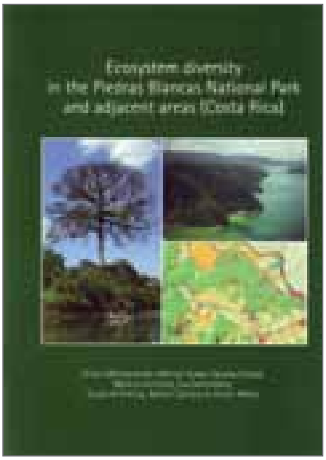

Helikonien
& Kolibris

Der "Regenwald der Österreicher"
in Costa Rica


Das Leben hier und dort
La vida aquí y allá

La Gamba
ein Dorf in Costa Rica
un pueblo en Costa Rica

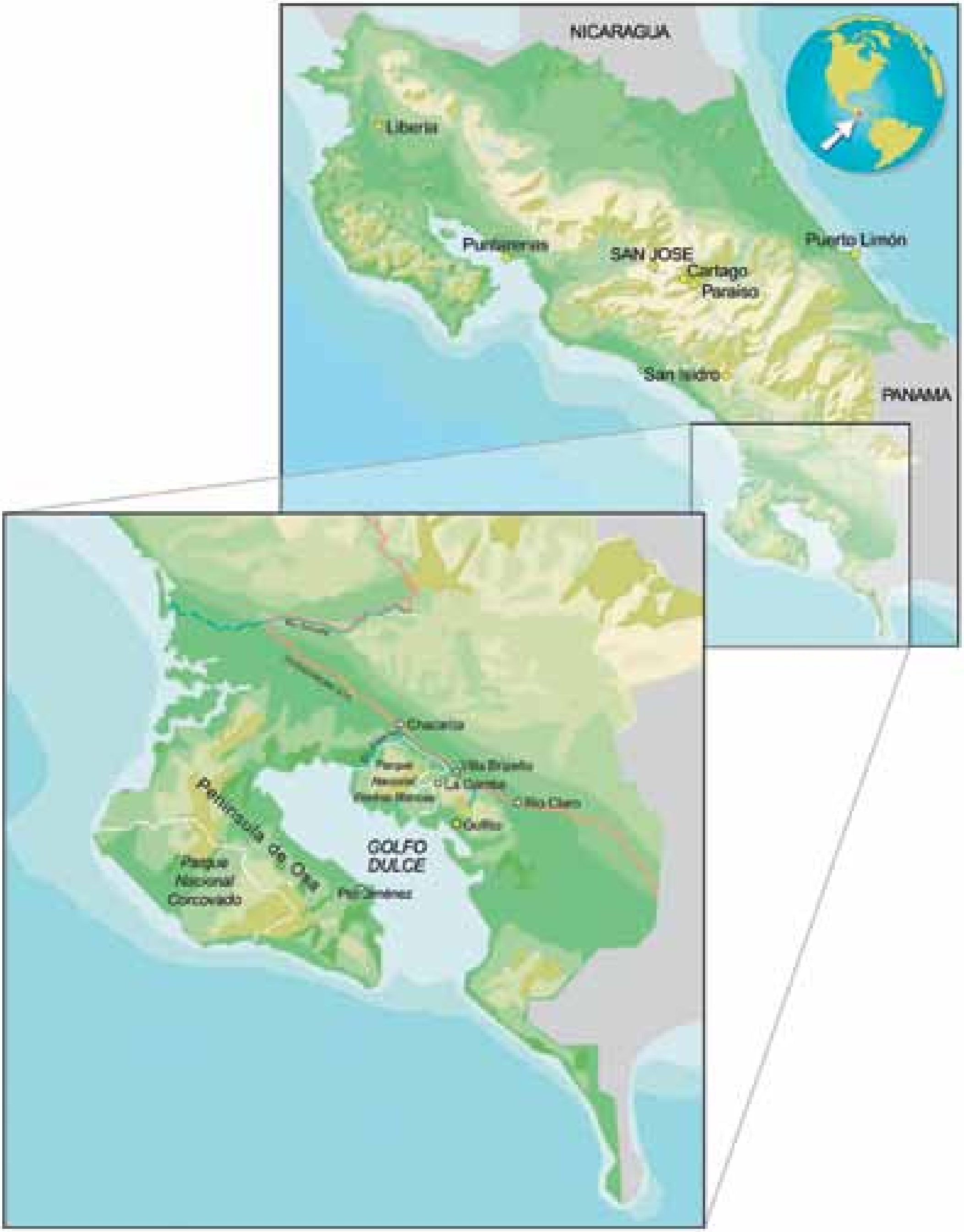
Weibern
ein Dorf in Österreich
un pueblo en Austria


Ecosystem diversity
in the Piedras Blancas National Park
and adjacent areas (Costa Rica)

All books available at:

Verein zur Förderung der Tropenstation La Gamba
University of Vienna
Rennweg 14, A-1030 Vienna, Austria

www.lagamba.at
tropenstation.botanik@univie.ac.at


NICARAGUA
Liberia
Puntarenas
SAN JOSE
Cartago
Paraiso
Puerto Limón
San Isidro
PANAMA
Chacarita
Parque
Nacional
Piedras Blancas
Villa Briceño
La Gamba
Río Claro
Golfito
GOLFO
DULCE
Península de Osa
Parque
Nacional
Corcovado
Pto Jiménez

Orchids are among the most fascinating plants in the rain forest. With over 230 species, they are also the most diverse plant family in the Golfo Dulce region of Costa Rica. This guidebook is an introduction to the world of orchids: the text and numerous colour photographs provide essential information for identifying the most common and conspicuous orchid species in the region. The booklet also includes a general introduction to orchids.

ISBN: 978-3-9502996-3-2