

Orchids

Botanical Jewels of the
Golfo Dulce Region, Costa Rica

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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 lush 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 orchid garden of the Tropical Research Station La Gamba

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.

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-



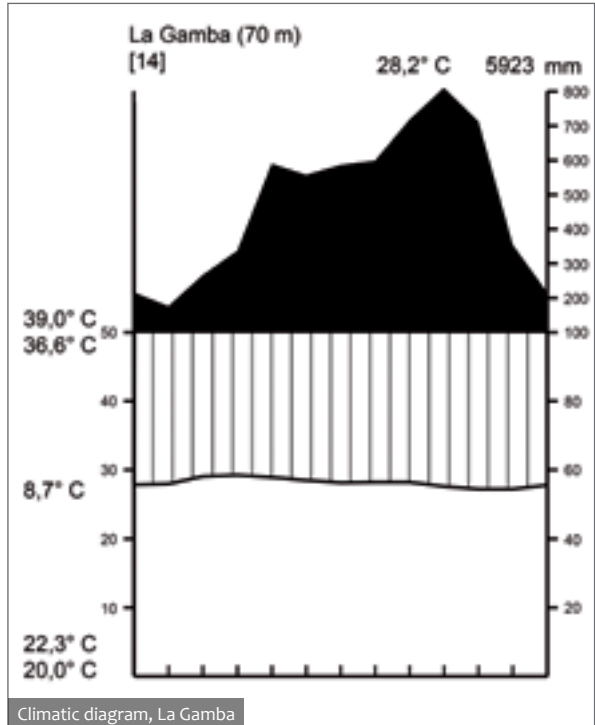
The Chorro waterfall near La Gamba

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.



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 south-western 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 km² and contains two national parks – Corcovado National Park, (established in 1975 and measuring 424 km²) and Piedras Blancas National Park (established as a separate national park in 1999 and measuring 148 km²) – two major forest reserves (the Golfo Dulce Forest Reserve, with an area of c. 600 km², established in 1979 and connecting the Corcovado and Piedras Blancas national parks; and Golfito National Wildlife Refuge, established in 1985 and measuring 28 km²) 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 Na-

tional 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

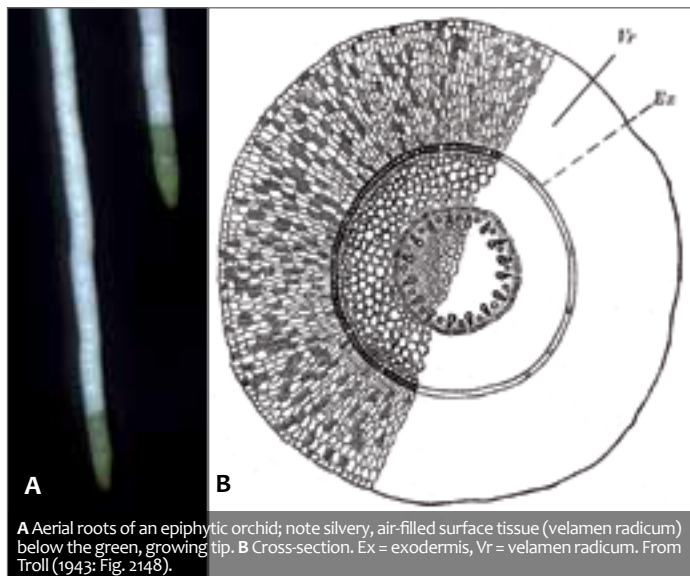
As in almost all flowering plants, the plant body of orchids is composed of three basic organs: leaves, stem (axis) and roots. The leaves are the primary photosynthetic organs, the stem is the structure bearing the leaves and serves for conducting water and nutrients, and the roots primarily serve for 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 funkiana*, → *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*, → *Wulfschlaegelia 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 → *Wulfschlaegelia 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 pseudob-

ulbs. Extreme cases of epiphytic growth are the obligate twig epiphytes (e.g. → *Erycina cristagalli*, → *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, → *Wulfschlaegelia 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

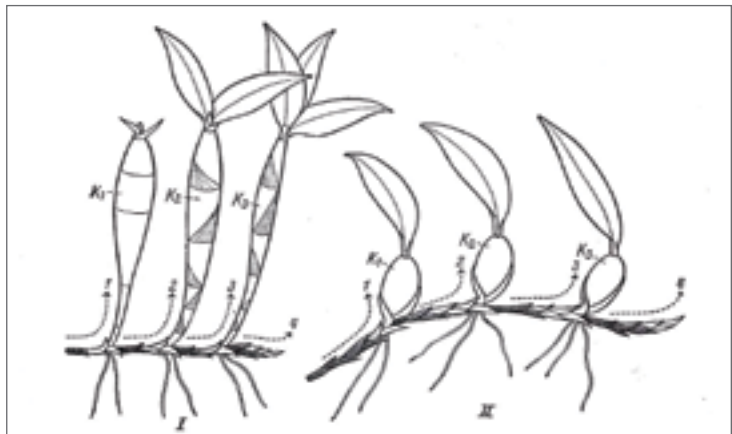
monopous (= one-footed, consisting of a single foot or single unit) and means that the stem of a plant consists of a single, dominant stem that grows continuously. The continuous growth may be temporarily interrupted (if the plant needs to survive a climatically adverse period), but is resumed from the 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’.



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)

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 polycladum*). 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

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.



Trigonidium egertonianum, heteroblastic pseudobulbs in close succession

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.

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

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 Tenitzi 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



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: “kill-

ing”, “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.

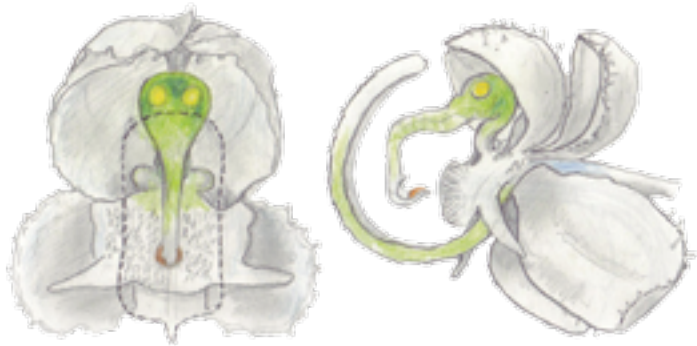
There are several other species which are cultivated besides *Vanilla planifolia*, although none matches the commercial value of this species: *Vanilla pompona*, *V. chamissonis*, *V. claviculata*, *V. griffithii* and *V. abundiflora* are cultivated in America (mainly Mexico). The latter two species 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



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).

