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 leaflike, 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*, *Rossioglossum*, *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*