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WHY ARE THERE SO MANY ORCHID SPECIES?

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At the present time we have cataloged 3,784 species of orchid naturally occurring in Ecuador, the smallest country in Andean South America. When one considers the size of the country of Ecuador, in comparison with that of Brazil or Colombia, the total numbers seem to express an error on the part of the counter. Brazil had an estimated total of 2,600 species in 1994. Colombia had, according to Father Ortiz, 3,264 species as of the year 2000. Colombia is a much larger country than Ecuador but with similar topography. In any case, we are left wondering why Ecuador is so surprisingly blessed (table 1).

One frequently hears that intensive work on the flora of Colombia has declined dramatically over the last 30 or so years due to guerrilla activity, the devastation to botanical research wrought by CITES (ostensibly designed to control trade in native species but applied heavily to legitimate biological research), and legal and political barriers. That is all true. Collecting and taxonomic work in Ecuador, on the contrary, expanded just as dramatically with the efforts of the Scandinavian botanists in conjunction with botanists of the Catholic University of Quito, and the Missouri Botanical Garden botanists working with the Ecuadorian National Herbarium. Ecuador has had a relatively benign CITES authority, no guerrilla activity, and political problems that did not affect plant taxonomy. The orchid collections in the Ecuadorian herbaria now surpass other herbaria in the world with more than 12,000 specimens of native Ecuadorian orchids. More than 20% of the vascular plants that have been recorded from Ecuador are orchids. Consequently one may attribute the large number of orchids documented to occur in Ecuador to greater collecting effort. That still begs the question; why are there so many species of orchids in Ecuador?

Table 1. Some large orchid genera in Ecuador: Note that of the 13 largest genera of orchids in the Ecuador flora, seven are members of the pleurothallid alliance. The members of the pleurothallid alliance, with a total of more than 1,650 species in Ecuador, make up more than 44% of the total number of orchid species reported to occur in Ecuador.

Genus	Approximate Total Species	Species in Ecuador
Pleurothallis	1,300	473
Epidendrum	1,200	452
Lepanthes	700	336
Maxillaria	650	200
Stelis	600	258
Masdevallia	500	208
Oncidium	500	97
Telipogon	135	50
Dracula	105	50
Platystele	85	52
Cyrtochilum	65	36
Cranichis	62	24
Brachionidium	50	23

We believe that there are several reasons, often working together, that might explain why orchid speciation has been so explosive in the neotropics (see Gentry & Dodson 1987, for a more extensive discussion).

A. PHYSICAL FACTORS

1. **Characteristics of orchids that lend to rapid adaptive radiation**:

A. *Epiphytism*. The majority of the orchid genera that have had an extremely high level of speciation grow normally as epiphytes. The epiphytic habit allows for adaptation to divergent locations in trees.

B. *Wind borne seed dissemination*. Orchid seed is extremely small with an undeveloped mass of cells surrounded by a papery chaff that can be easily transported by wind for substantial distances. Invasion by micorhizal fungi provides the initial nutrition that makes possible the development of a protocorm from the undeveloped cell mass.

C. *Extremely numerous seed production from a single pollination event*. A single deposition of a pollinarium on the stigma of a compatible flower can lead to production of literally millions of viable seeds. Flowers of the majority of flowering plant families produce fewer than 100 seed per pollination. Therefore, with the production of millions of seed an orchid flower may produce a substantial number of viable progeny with mutations. Some of those mutations may be beneficial and result in new avenues of species development.

D. *Preadapted pollinators*. Orchids have had a tendency to adapt to limited numbers of pollinators (often a single species of pollinator for a single species of orchid) so that pollinator specificity plays an important role in reproductive isolation of species. Potential but unused pollinators commonly are available in the habitat as a result of similar explosive speciation by insects, comparable to that of the orchids.

E. *Pollinator specificity through deception*. Numerous examples of mimicry in orchid flowers have been published, ranging from food mimicry, pseudocopulation, pseudoantagonism, to pseudoprey.

F. *Potential genetic flexibility*. The genetic controls that tend to maintain the nature of a species and reduce variability can be broken. For example, African Violets had very little variability prior to the 1920's when selection of variants and interbreeding resulted in the incredible variety that we know today. Orchids may pass naturally through similar phenomena.

The characteristics of the orchids mentioned above are true of orchids in any part of the world. Those features predispose the orchids in the Andes, and other mountainous regions, to be able to adapt to the shifting nature of the habitats in those regions. In areas such as Amazonia with tall tree forests and homogeneous habitats seldom does one find more than 100 species of orchid in a given locality. From one locality to another the orchid flora will differ slightly but the number of species stays about the same. In the Andes, however, localities are known with more than 300 species of orchid. In addition, the species diversity is extremely high between habitats so that very similar appearing habitats on the eastern side of the Andes in Ecuador, at the same elevation and with similar rainfall, that are 100 km apart may have only 10% commonality of species (Gentry & Dodson 1987).

2. **Geography and Climatology**:

During the past several thousand years the tectonic plates that form the Andes have constantly clashed resulting in uplifting of the mountains and the continued production of volcanic activity. The uplifting, the volcanic activity, and the constant wearing away of the mountains produces new habitats. The position of Ecuador in reference to the ocean currents adds another factor. The cold Humboldt current colliding with the warm California current at the midpoint of western Ecuador produced by the annual wobble of the earth makes remarkable change in climate for a tropical region located on the equator.

Historically, the climate of Ecuador has gone through striking change with advancing and receding glacial periods and consequent change in temperatures. Only ten thousand years ago the region came out of a glacial period where the average temperatures in the Andes and Amazonia were 5 degrees centigrade lower than those of present day Ecuador (Colinvaux 1987). That difference in temperatures from present day resulted in permafrost in the area above Quito (the present capital city of Ecuador at 2750 m elevation) and the upper Amazon region was clothed with coniferous forests. Clearly, the orchid populations were not where they are now. It is estimated that they would have had to recede to a position at least 1000 meters lower than they are now in order to survive. Some refugia may have occurred at higher elevations. A lesser glacial period occurred about 3000 years ago. The orchid populations surely must have changed position many times over geological history.

Volcano's have erupted constantly over the past millennia and in fact are erupting now. The consequent deposition of lava, lajars and volcanic ash, sometimes to considerable depths over broad areas, has a devastating effect on the local floras. The often-extensive areas that are inundated in volcanic debris quickly kill the existing plant cover and provide new habitat for invasion by all manner of plants. Orchids are among the first pioneers and can travel long distances.

Features of the climatology of Ecuador:

A. The equatorial position of Ecuador means that the sun is nearly directly overhead all year long. In fact, it passes over the equator twice each year at the spring and autumnal equinoxes. The climate tends to be benign and the annual fluctuations are minimal. Plants that occur on north or south facing slopes will get their share of sunlight.

B. The coastal region has a pronounced seasonal character based on rainfall affected by the annual movement of the offshore Humboldt and California currents. The southern half of the coastal region has cool dry conditions for half the year. This is due to overcast clouds (without rain) produced by the cold Humboldt Current and lasting from May to November. In December the warm California current moves sufficiently south to cause heavy rainfall and warm temperatures in the southern half of coastal Ecuador.

C. The Amazon region has a fairly constant climate with the winds blowing east to west and depositing heavy rain on the eastern slopes of the Andes from April to October. There is a drier season from November to March.

D. The western slope of the western range of the Andes is very abrupt while the eastern slope of the eastern range is more gently sloped. This is due to the uplifting created by the west to east sliding of the tectonic plates. Between the western and eastern ranges an interandean depression exists that is mostly deforested now.

E. Rainfall and temperatures are affected by elevation. Even in the coastal plain elevations of more than 400 meters have humid forests due to the nocturnal deposition of mist from overhanging clouds. From mid Ecuador south along the western slope of the Andes a band of humid forest exists (existed?) corresponding to the position of the overhanging clouds. The band is several hundred meters wide in mid Ecuador but only a few meters wide in southern Ecuador.

F. North- and south-facing slopes have substantially different climatic conditions from north- and south-running ridgelines.

Given the nature of the orchids (subject to long range dispersal, potential of beneficial mutations resulting from high numbers of seed per pollination, strong pollinator specificity resulting in effective reproductive isolation, etc.,) and the changing geology and microclimates of Ecuador, rapid change in the genetic nature of populations leading to explosive speciation is possible.

To provide an idea of the extent of the devastation caused by geological activity a few examples can suffice. In 1987 an earthquake of a 7.2 magnitude on the Richter scale struck north-central Ecuador with the epicenter near Volcán Reventador, about 40 miles northeast of Quito in a direct line. Damage to buildings in Quito was extensive but not catastrophic. On the face of Volcán Reventador a landslide occurred that was 40,000 hectares in area. The slide caused a temporary dam on the Rio Napo that broke after a couple of days. The ensuing wall of water that came down the Rio Napo devastated indigenous communities all the way to the Amazon River and the death toll was incalculable. The bald area is now recovering. Eighty thousand years ago the Volcán Chalupas exploded leaving a crater 40 km in diameter and a baby volcano appeared in the crater that we now call Volcán Cotopaxi. The explosion covered with ash what we now know as 5 provinces of central Ecuador to a depth of 30 m. The Volcán Tungurahua, which now has 12 species of Telipogon occurring on its slopes, is only 3,000 years old. An eruption of Volcán Pululagua 3,500 years ago left the province of Pichincha covered in 1.5 m of ash. Volcán Pululahua is about 20 km northwest of Quito.

A potential example of a group that may owe its diversity to macro devastation of habitat and changing temperatures is that of the genus *Telipogon*. The genus consists of something over 135 species. It occurs from Costa Rica to Venezuela and south along the Andes from Colombia to Bolivia. None of the

Central American species occur in South America. Fewer than 4 species are widespread in distribution, e.g., Venezuela to Peru. Most species are local endemics. Fifty of the 135 species are known from Ecuador. Populations frequently have high numbers of species occurring sympatrically (15 species in the Nudo de Pasto in Colombia just north of the border with Ecuador and 12 species in the Nudo de Sabanilla in southern Ecuador). The genus is characterized by having the appearance of an insect in the center of the usually roundish flower. The column is usually provided with spine-like hairs in clusters or covering the whole upper surface. A few species have columns that are bald. Many of the species have protruding calli under the column that are covered in shorter, spiny hairs. Many species are brightly colored with yellow, brown and red spots, blotches, vein-lining and reticulations.

Telipogon belongs to the Subtribe Telipogoninae with 3 other genera. *Stellilabium* has about 25 species, some of which have flowers so insect-like that the natives call them "La Mosca" ('the fly' in Spanish). The species tend to be distributed at slightly lower elevations than *Telipogon* and are known from Mexico to Bolivia. The genus only differs from *Telipogon* by smaller flowers. *Trichoceros* is a genus of 4 or 5 species distributed from central Ecuador to Bolivia. All of its species have obvious pseudobulbs with elongate rhizomes between the pseudobulbs so that the plants are subviney. The flowers are very insect-like. *Hofmeisterella* is a monotypic genus occurring in the Andes from Venezuela to Bolivia. Its flowers are bald and only in recent years has been recognized that the genus belongs to the Telipogoninae. All species of the Subtribe have a viscidium that is hook-shaped to catch on the legs of the pollinator.

All species of *Telipogon* appear to be pollinated by flies of the family Tachinidae. Tachinid flies are nearly universal in the tropics, it being one of the largest fly families. Many species are usually present in any habitat. The flies are of varying size and most of them have spines on their dorsal abdomen (similar to those of the column or callus of many species of *Telipogon*). The flies are characterized by males that establish territories, spend the day patrolling their territory, and attack and drive away any other insects that fly through. The females encounter the males in their territories and copulation takes place at the site. Female flies are also parasitic on other insects, grabbing and laying an egg on the prey while in flight. The hatching larva consumes the tissues of the prey as it develops.

Members of the genus *Telipogon* and its allies occur at upper elevations of cloud forest rarely lower than 1500 m with some species reaching páramo at 3600 m. Populations are usually small with few individuals spread over restricted areas. Curiously, distribution can be spotty. For example, *T. vieirae* (the only *Telipogon* with an obviously winged column) has a population east of Medellín at La Union in Colombia and another at La Planada on the Colombia/Ecuador border. No specimens have been collected in the intervening 800 km. Some species are strictly terrestrial in habit and occur in páramo (e.g., *T. boisserianus, T. ionopogon, T. nervosus,* and *T. venustus*) but most are epiphytic. Even though several species may occur together in a particular habitat, no natural hybrids have been reported. Clearly reproductive isolation by way of adaptation to specific pollinators has been very effective.

The evidence seems fairly clear that none of the species of *Telipogon* would have been able to occupy their present day range during the glacial periods. Surviving populations would have occurred below 1500 meters during the cold periods. They probably formed small populations in refugia at the lower edge of the much lower páramo. As the glaciers receded vast areas would have been available for migration of the pioneering survivors. Due to the fractured nature of the montane habitat the survivors would probably have constituted small populations, had built-in pollinator specificity, and thus strong reproductive isolation. Due to the S.Wright (1977) effect, small interbreeding populations promote gene fixation (Terborg & Winter 1982). Any mutants with preadaptive selection of existing pollinators would have become quickly fixed and will have developed into new species very rapidly. Fixing of variants would have led to the explosive speciation that we see today. It seems likely that many of the species that we find now have developed since the last major glaciation period.

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Calaway H. Dodson, Ph.D., received his Doctorate in 1959 from the Rancho Santa Ana Botanic Garden after doing graduate work at the Missouri Botanical Garden. He immediately took a teaching and research position at the University of Guayaquil and established the Instituto Botanico there. In 1960, he returned to the Missouri Botanical Garden as Curator of Living Plants. In 1964 he took a position as Professor of Botany at the University of Miami, Coral Gables Florida, where he was a pioneer in the development of chemical analysis of floral fragrances of orchids. In 1973, he left the University of Miami to take the position of founding director of the Marie Selby Botanical Garden in Sarasota, Florida. After 10 years at Selby Gardens he returned to the Missouri Botanical Garden as a research scientist stationed in Ecuador. The overwhelming number and diversity of orchids led to the development of a computerized database to organize the massive quantity of information. For this reason, he prepared a data set containing 35,000 records of orchid specimens located in herbaria of the world that were collected in Ecuador.