

## ORCHIDS WITHOUT BORDERS: STUDYING THE HOTSPOT OF COSTA RICA AND PANAMA

DIEGO BOGARÍN<sup>1,2,3</sup>, FRANCO PUPULIN<sup>1,3,4</sup>, CLOTILDE ARROCHA<sup>2</sup> & JORGE WARNER<sup>1</sup>

<sup>1</sup>Jardín Botánico Lankester, Universidad de Costa Rica. P.O. Box 302-7050 Cartago, Costa Rica, A.C.

<sup>2</sup>Herbario UCH, Universidad Autónoma de Chiriquí, 0427, David, Chiriquí, Panama

<sup>3</sup>Centro de Investigación en Orquídeas de los Andes “Ángel Andreetta”,  
Universidad Alfredo Pérez Guerrero, Ecuador.

<sup>4</sup>Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts, U.S.A.  
and Marie Selby Botanical Gardens, Sarasota, FL, U.S.A.

**ABSTRACT.** The Mesoamerican region is one of the richest in orchid diversity in the world. About 2670 species, 10% of all orchids known have been recorded there. Within this region, most of the species are concentrated in the southernmost countries. Costa Rica with 1598 species (or 0.030 spp/km<sup>2</sup>) and Panama with 1397 species (0.018 spp/km<sup>2</sup>) stand at the top of endemic species list of all Mesoamerica, with 35.37% and 28.52%, respectively. These figures, however, are misleading, as political boundaries do not have any relationship to orchid diversity. If we ignore the political frontier, there is a common biogeographic area. However, if we put the border back, the numbers in terms of scientific production and research change dramatically. Costa Rica has increased the knowledge of its orchid flora through the establishment of a successful research system, whereas Panama has lacked a similar process. To address this problem, the Lankester Botanical Garden at the Universidad de Costa Rica and the Universidad Autónoma de Chiriquí, Panama, established a new research center focused on the study of orchids. The aim of the cooperation is to provide the methodology, information, and expertise for a long-term project on taxonomy and systematics of the orchids of Panama

**KEY WORDS:** Orchidaceae, Mesoamerica, Costa Rica, Panama, floristics, taxonomy

The Mesoamerican region is one of the richest in orchid diversity in the world. About 2670 species, 10% of all orchids known, have been recorded there. The distribution of orchids in the region is not uniform. Diversity at country level depends on geological, climatic, and orographic factors as well as territorial extension. However, when examining the diversity index for Orchidaceae (calculated as number of species/km<sup>2</sup>), a trend is evident. The southern regions of the isthmus, with Costa Rica and Panama, head the list with rates of 0.03 and 0.018, respectively (Fig. 1). These numbers are also reflected in terms of absolute diversity, with 1598 and 1397 orchid species of Orchidaceae recorded for this two countries, respectively, the highest values in the region (Ossenbach *et al.* 2007; Fig. 2). Phylogenetic studies on the evolution of the family show that both countries currently have a floristic contingent of different origins, joining the rich Andean flora with the large number of taxa from nuclear Mesoamerica,

which disappear quickly in the South American flora (Fig. 3). From a phylogeographical point of view, and the peculiarity of its geological history, Costa Rica and Panama represent a laboratory for the evolution of orchids, and a critical examination of their orchid floras is of scientific priority under both the study and conservation of biodiversity (D’Arcy & Correa 1985; Dressler 2003).

Despite its geological and floristic similarities, the political boundary has affected knowledge and scientific production. A strong imbalance between the two countries is evident. In the last 10 years, about 170 scientific papers for the orchid flora of Costa Rica were published. In contrast, about 70 scientific papers were devoted to the orchids of Panama. Costa Rica has increased the knowledge of its orchid flora through the establishment of a successful research system, whereas Panama has lacked a similar process. The latest, in-depth studies on the orchids of Panama took place more

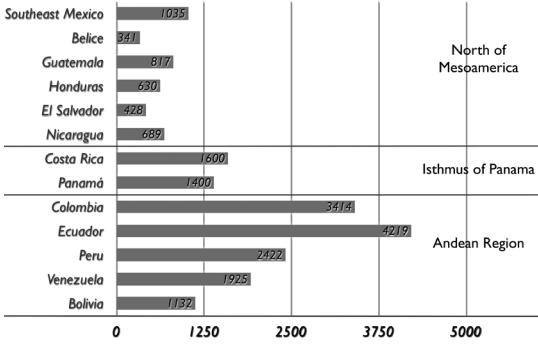


FIGURE 1. Comparison of the number of species/ km<sup>2</sup> between northern Mesoamerica, Isthmus of Panama, and the Andean countries.

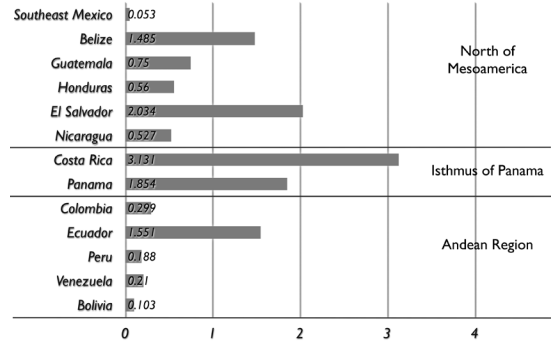


FIGURE 2. Comparison of the number of species between northern Mesoamerica, Isthmus of Panama, and the Andean countries.

than 20 years ago; recent information has been produced sporadically by researchers based in other countries (Dressler 1993; Williams & Allen 1946-1949). In this paper, we analyze the future and challenges of orchid research in the isthmus of Costa Rica and Panama. We present the main objectives of the scientific cooperation between Jardín Botánico Lankester of the Universidad de Costa Rica and the Universidad Autónoma de Chiriquí, Panamá.

**Geography**

Costa Rica and Panama are situated in the southeast of Central America (11°15'N-7°10'N, 85°56'N-77°09'W) and comprise a narrow land strip called the Isthmus of Panama that links North and South America, separating the Atlantic from the Pacific Ocean (Fig. 4). In the north of Costa Rica along the border with Nicaragua, floodplain lands separate the mountain ranges of Guanacaste from northern Central America. These chains are formed by active volcanoes such as the Rincón de la Vieja (1916 m) and Arenal (1670 m). The Cordillera Volcánica Central in Costa Rica has higher elevations with active volcanoes: Poás (2708 m), Irazú (3432 m), and Turrialba (3340 m). To the southeast lies the Cordillera de Talamanca, an intricate mountain range with the highest elevations of the isthmus, usually above 3000 m. This mountain range has no active volcanoes and is protected mostly by the La Amistad International Park. The highest peak is Cerro Chirripó (3820 m) followed by the peaks of Buenavista (3491 m), Durika (3281 m), Kamuk (3549 m), and Echandi (3162 m) in Costa Rica. Close to the border lie the highest peaks of Panama:

Volcan Barú (3475 m), Cerro Fábrega (3335 m), and Cerro Itamut (3293 m) (Fig. 5). The Cordillera de Talamanca loses elevation towards central Panama in the provinces of Veraguas and Coclé. Central Panama is the narrowest stretch of the isthmus, and elevations are relatively low. It includes Cerro Azul (571 m), Campana (1030 m), Gaital (1185 m), and Jefe (1007 m). Towards Colombia, the ridges of San Blas and Darien extend along the Pacific with the highest peak, Cerro Tacarcuna (1875 m). Along the Atlantic side, the main ranges are Sapo, Bagre, and Jurado. Other important geological formations are the peninsulas of Azuero, Burica, Osa, and Nicoya, comprising lower-elevation mountain ranges but relatively isolated from Talamanca.

**Geology**

Costa Rica and Panama act as a geological unit. Both countries lie mostly on the Costa Rica-Panama microplate, a complex area of interaction of three tectonic plates: Nazca, Cocos, and Caribe (Fig. 6). According to Coates *et al.* (1992), three major events led the tectonic evolution of the southern Central American isthmus. First is the volcanic activity favored by the convergent tectonics of the eastern Pacific subduction zone, one of the primary forces that produced the volcanic arc that extends from North America to the south. Another tectonic effect is the subduction of the Cocos Ridge on the Pacific. This submarine range led to the rise of the isthmus from the Arenal Volcano in Costa Rica to nearby Cerro Campana and Gaital at El Valle, Panama. From this region, the Cordillera de Talamanca emerged and

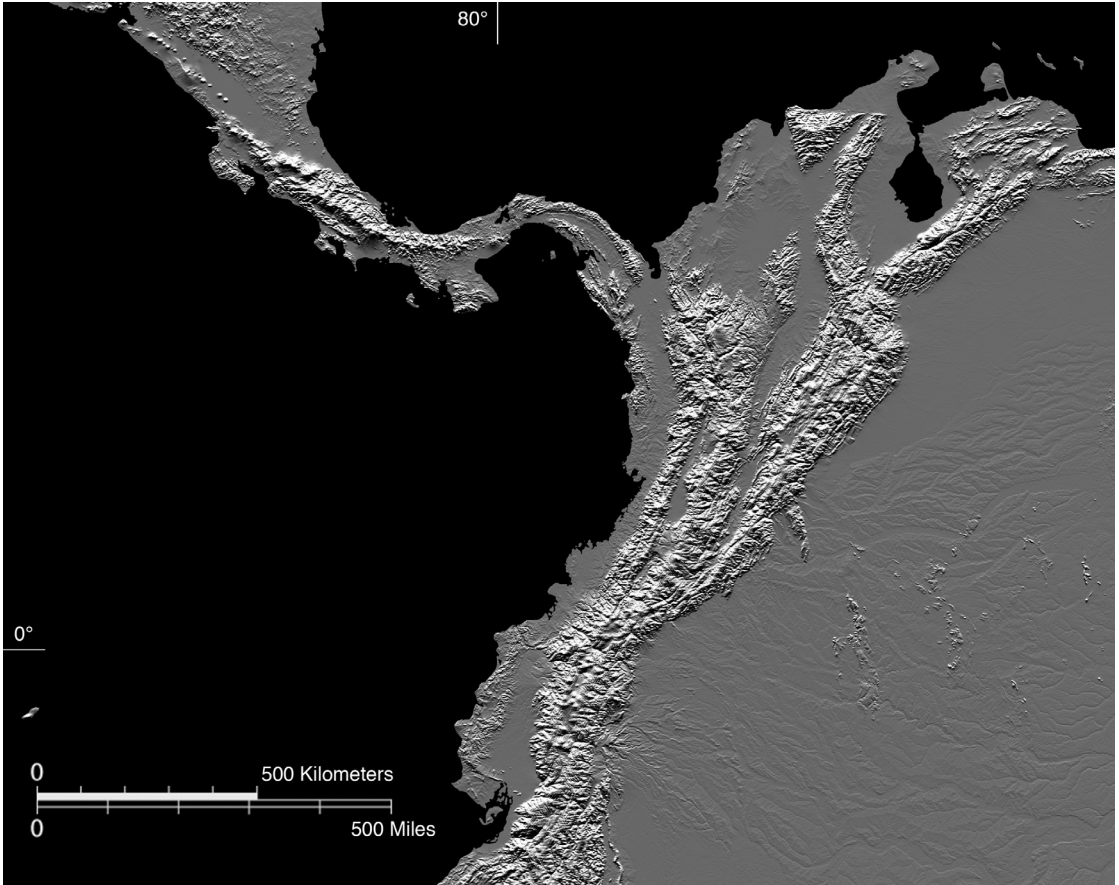


FIGURE 3. Costa Rica and Panama lie close to the Equator between North and South America.

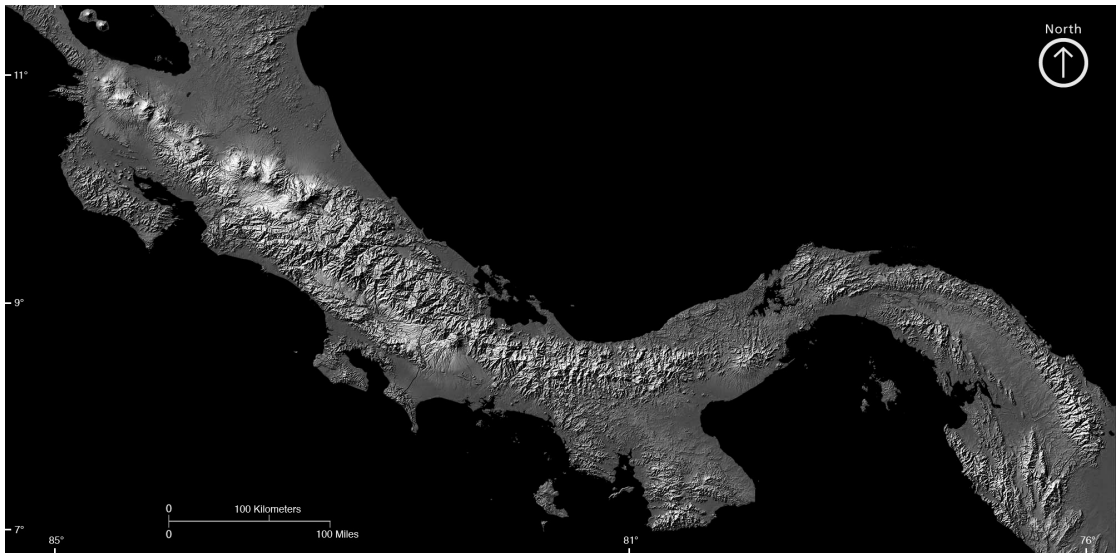


FIGURE 4. Satellite view of Costa Rica and Panama.



FIGURE 5. View of Durika-Utyum peaks at Cordillera de Talamanca in Costa Rica. Clouds are formed by the humid trade winds from the Caribbean. The Pacific side remains relatively clear. Courtesy of Daniel Jiménez.

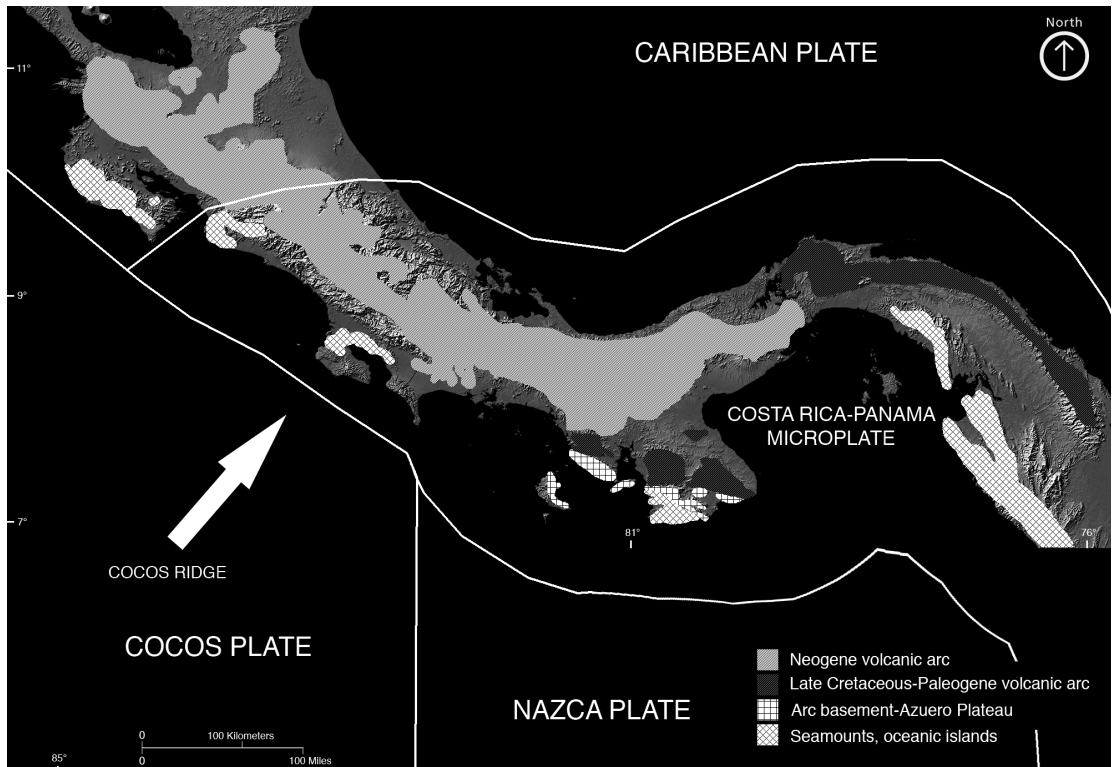


FIGURE 6. Plate tectonic configuration of the Isthmus of Panama. Both countries lie in a complex area of interaction of three tectonic plates: Nazca, Cocos, and Caribe.

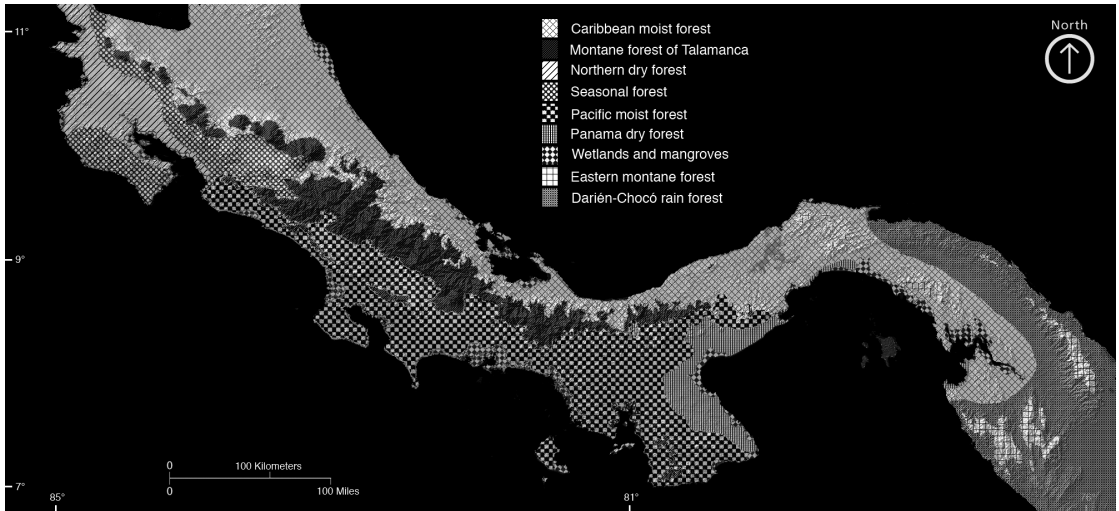


FIGURE 7. Vegetation units of Costa Rica and Panama.

reduced the marine connections. Finally, the southern region of the isthmus was affected by the collision of the volcanic arc with northwestern South America and led the uplift of eastern Panama (San Blas and Darién ranges) and northern Andes of Colombia and Venezuela in the late Neogene. In general terms, the closure of the Isthmus of Panama started some 15 Myr ago in the middle Miocene and was finally closed 3.5 Myr in the Pliocene (Fig. 6).

#### Climate and vegetation

The climate and vegetation of Costa Rica and Panama are affected by their geographical position close to the Equator and surrounded by two oceans, mountain chains with different elevational ranges, and the prevailing wet winds of the Caribbean. Usually the Caribbean lowlands are moist and warm (Fig. 7). Precipitation originates mostly from the trade winds from the Caribbean colliding with the mountain ranges, mostly on the Cordillera de Talamanca and the action of the Intertropical Convergence Zone (Kohlmann *et al.* 2002). Towards the region of central Panama, there are low hills such as Campana and Gaital with montane forests fed by interaction of the wet winds. The Cordillera de Talamanca has broad elevational ranges, and the wind system is complex. The climate varies from humid in the Caribbean watershed to dry and cold at the top of the highest mountains of Talamanca. The Pacific slope of Talamanca is wet from the collision of local winds with the moist air

from the Pacific Ocean. The north Pacific region of Costa Rica and eastern Peninsula de Azuero in Panama are warm and dry with marked seasonality. To the east of Panama the climate is warm and rainy, similar to that of Chocó in Colombia, one of the wettest regions on Earth (Dressler 1993).

#### The orchid flora of Costa Rica and Panama

In general, the orchid flora of Costa Rica and Panama is a reflection of its geological history. Some factors that determine its floristic composition are the location between the great continental floras of north and south, climate, and proximity to the Andes, the most biodiverse area in the Neotropics. The lifting of the Cordillera de Talamanca with elevations up to 4000 m produced new environments for colonizing plant species from the Andean region. Recent studies on the evolution of Orchidaceae (Conran *et al.* 2009; Ramírez *et al.* 2007) support the hypothesis of an ancient origin of the family (76-84 Myr ago). Therefore, during the formation of the Isthmus that began about 15 Myr ago with the emergence of an archipelago, orchids could colonize the islands long before its closure. Some of the endemic species could also be explained by allopatric speciation produced in those ancient islands (Burger 1980). With the closure of the isthmus about 3.5 Myr and the union of the peninsulas of Nicoya, Osa, Burica, and Azuero, other species managed to colonize most of the regions of the isthmus (Fig. 6). These events may be supported by current species



FIGURE 8. Some of the endemic species of *Lepanthes* from Costa Rica and Panama.

composition. For example, most of the genera in Pleurothallidinae (the most diverse subtribe of the Neotropics) from middle and upper elevations (1500-4000 m) such as *Brachionidium* Lindl., *Lepanthes* Sw., *Pleurothallis* R.Br. s.l., and *Stelis* Sw. s.l. are more diverse in Costa Rica and Panama than in other areas of Central America. *Fernandezia* Lindl., *Telipogon* Kunth, and other terrestrial genera such as *Aa* Rchb.f. and *Petrichis* Lindl. are other examples (Dodson 2003; García Castro *et al.* 1995). However, the northern region of Costa Rica and central-southeast Panama have floras with few similarities. The northern region

of Costa Rica has a northern influence, whereas the southeast of Panama is closely related to the flora of Colombia and Ecuador. An exemplary genus to study the evolutionary floristic relationships in the isthmus is *Lepanthes* Sw. Most of the species are found in montane and premontane rain forests at elevations of 1500-2500 m. Many species are endemic to certain ridges or hills, and their distribution is often narrow. In Costa Rica there are about 120 species (Bogarín *et al.* 2012), whereas in Panama 60 species were recorded (Pupulin *et al.* 2009). Both countries share 35 species, all distributed from central and southern Costa Rica

to western Panama. In the region of central Panama, few species are shared (Fig. 8). As an example, *L. schizocardia* Luer, described from the region of Cerro Jefe, was reported for Costa Rica (Dressler 2003). However, a study of the populations from Costa Rica and Panama showed that *L. schizocardia* is an endemic of central Panama, sister of two endemic species from Costa Rica, *L. montis-narae* Pupulin, Bogarín & C.M. Sm. and *L. sotoana* Pupulin, Bogarín & C.M. Sm., both formerly treated as *L. schizocardia* (Pupulin *et al.* 2010). With the advancement of floristic research in both countries we expect to present a more detailed picture of their complex floristic relationships.

### A review of the history of the orchidology in Costa Rica and Panama

The botanical exploration of Costa Rica and Panama, which mainly began in the nineteenth century with the visits of E. Arce, G. Barclay and R.B. Hinds, H. Cuming, A.S. Oersted, G. Skinner, J. von Warszewicz, and H. Wendland, led to the discovery of the first orchid species in the region (Ossenbach 2009; Fig. 9). As a side effect of the search for a possible route for the construction of a canal, exploration continued in the nineteenth and early twentieth centuries thanks to a large group of resident naturalists. Efforts by A. Endrés and later H. Pitter, A. Tonduz, A. Brenes, and C. Wercklé among others contributed greatly to reveal the rich flora of the isthmus. Within this group of naturalists, who through their work made Costa Rica the best-known country in Mesoamerica in terms of its orchid diversity profile, was the Charles H. Lankester (Fig. 10). His collection of Orchidaceae, gathered in a period of almost 40 years in the environs of Cartago, the old capital of Costa Rica, was an obligatory stop for botanists who visited Costa Rica and provided countless new species to science. Most of the species were described by Oakes Ames of Harvard and his colleagues over more than three decades of intensive floristic work (Fig. 11). The legacy of C. H. Lankester formed the basis for the creation of the Jardín Botánico Lankester (JBL) in 1973 as part of the Universidad de Costa Rica (UCR) (Fig. 12). With the creation of JBL, Costa Rica secured a permanent institution devoted to the study of orchids. Meanwhile, after the publication of *Orchidaceae Powellianae Panamenses* by Schlechter (1922) and *Flora of Barro Colorado Island* by Standley (1927), Panama received

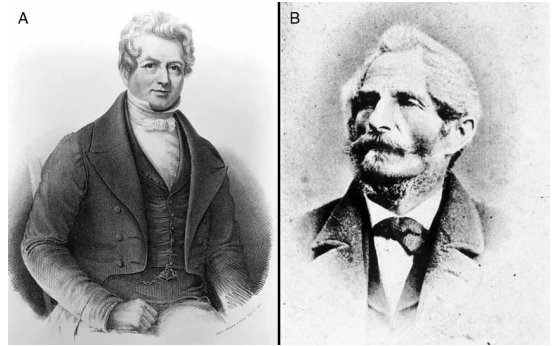


FIGURE 9. **A.** Hugh Cuming (1791-1865). From a lithograph by Hawkins, 1850. Courtesy of Rudolf Jenny. **B.** Josef Ritter von Rawiez Warszewicz (1812-1866). Courtesy of the Hunt Institute for Botanical Documentation.



FIGURE 10. Charles H. Lankester in 1936. Courtesy of Ricardo Lankester.

a strong impetus from L. O. Williams and P. Allen who published the *Flora of Panama: Orchidaceae* (Williams & Allen 1946-1949), the first formal treatment of the country's flora (Fig. 13).

Since 1963 and for over 20 years, R.L. Dressler has undertaken the systematic study of orchids of Panama,

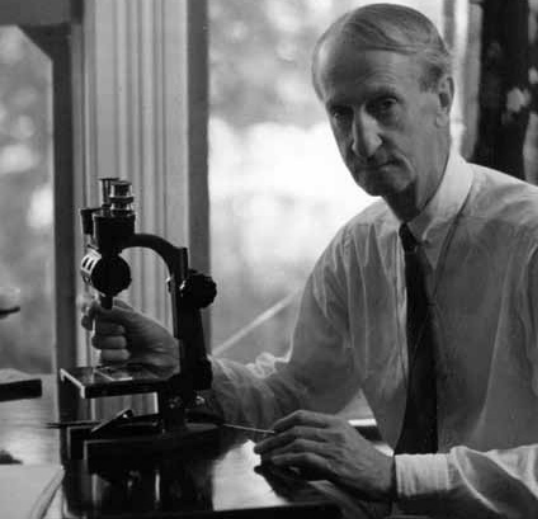


FIGURE 11. Oakes Ames (1874-1950). Courtesy of the Oakes Ames Herbarium, Harvard University.



FIGURE 14. Robert L. Dressler looking for orchids in Ecuador, 2007.



FIGURE 12. Inauguration of the Lankester Botanical Garden on March 2, 1973. Courtesy of Ricardo Lankester.

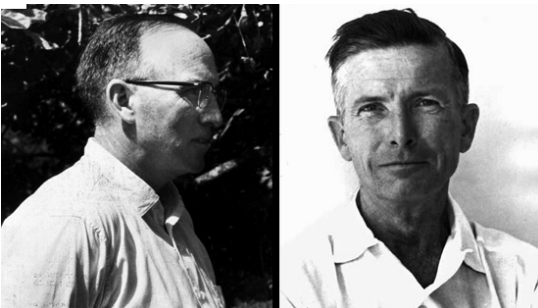


FIGURE 13. A. Louis O. Williams (1908-1991). B. Paul H. Allen (1911-1963). Courtesy of L. D. Gómez.

culminating in the publication of the *Field Guide to the Orchids of Costa Rica and Panama* (Dressler 1980, 1993; Fig. 14). After his retirement from the Smithsonian Tropical Research Institute in 1986, orchid research in Panama was conducted sporadically by visiting researchers without a permanent ongoing plan

of exploration and research (Correa *et al.* 2004). The absence of an active permanent center similar to JBL in Costa Rica slowed the spread of knowledge in Panama. Again, a clear example is *Lepanthes*. In *Flora of Panama*, Williams & Allen (1946-1949) recorded eight species. Later, Dressler (1993) reported 54 species in collaboration with C.A. Luer, who sporadically visited Panama (Luer & Dressler 1986). Since 1993 the number of species did not change significantly, and only six new species were added (Luer 1999). In contrast, about 53 species were recorded from Costa Rica since 1993 to the present (Bogarín *et al.* 2012). *Lepanthes* is just an example of the differences in scientific output between the two countries due to the lack of an ongoing project for the study of Orchidaceae in Panama.

#### **Jardín Botánico Lankester and scientific production in Costa Rica**

Despite their great orchid diversity, tropical regions lack important centers of orchid information. Even today, they are concentrated in Europe and North America. For historical reasons, the study of



tropical plants was performed mainly by European and American botanists in the mid-nineteenth century and the late twentieth century. This produced the information, documents, and type specimens that were deposited in herbaria and libraries far from the countries of origin. To understand and protect their biodiversity, it has become imperative for tropical countries to establish centers or institutions dedicated to the study of living organisms. The AMO Herbarium in Mexico, the Rio Palenque Science Center in Ecuador, and the Jardín Botánico Lankester in Costa Rica are research centers that contributed greatly to the development of scientific projects based on their country of origin (Atwood & Mora de Retana 1999; Dodson 2004; Pupulin 2010; Hágsater *et al.* 2005). It is necessary to expand these efforts to other Neotropical countries with the aim of having an active network of institutions.

The constraints to scientific study in the tropics have been the difficulty in access to information and the lack of an appropriate system of enquiry. Scientific progress made by JBL to know and preserve the orchid diversity in Costa Rica was not constant in the beginning. In its early stages, JBL established collaboration with the Chicago Field Museum of Natural History, Harvard University Herbaria, Marie Selby Botanical Gardens, University of Florida, and Royal Botanic Gardens, Kew, among others (Atwood & Mora de Retana 1999; Pupulin & Romero 2003). These projects enriched the access to documentation for conducting orchid research in Costa Rica (Fig. 15). Early in this century, the JBL managed to consolidate its own research system, which laid the foundation for rapid development of its activities in Orchidaceae. This research system is based on some key elements: 1) botanical exploration and cultivation of specimens (Fig. 16); 2) comprehensive plant documentation including interpretation of the natural variation of populations, (Fig. 17); 3) a center with specialized equipment, trained staff, and students involved in the scientific projects; 4) a complex of well-documented collections (live plants, exsiccatae, spirit collections, tissues for DNA extraction, pollinaria, photographs and other digital documentation, botanical illustrations, etc.) (Fig. 18- 20); 5) an electronic system of interrelated databases; 6) complete access to literature and other original documentary



FIGURE 15. Type specimen of *Aspidendrum epidendroides* Lindl., collected in “Panama et Columbia occidentali” by H. Cuming in 1831. Reproduced with permission by the Board of Trustees, Royal Botanic Gardens, Kew.

sources concerning the taxonomy of Neotropical orchids; 7) a commitment to the policies of natural resource conservation and a strict relationship with the Ministry of Environment of Costa Rica; and 8) a network of international scientific cooperation with leading botanical research centers around the world. Through this system the JBL has assumed the role of carrying out the critical study of the orchid flora of Costa Rica. The JBL archival documents for the interpretation of Neotropical orchids are available over the Internet (see the site Epidendrum, [www.epidendrum.org](http://www.epidendrum.org)).



FIGURE 16. Field trip at Fortuna, Chiriquí, Panamá. Photo by Eyvar Rodríguez.



FIGURE 17. Comparison of the flowers of 25 specimens of *Pleurothallis homalantha* Schltr. showing the natural variation among individuals of different populations.

There are many advantages to developing orchid research in the tropics. The almost unlimited access to living material and wild orchid populations allow a more accurate assessment of intra- and interspecific natural variation (compared to the traditional practice of isolated expeditions and transfer of limited amounts of material to herbaria with a poor understanding of natural

variation). It is possible to obtain more comprehensive documentation by studying living organisms. Adequate documentation is a system that includes the preparation of materials such as herbarium specimens, spirit collections, photographs, color botanical plates, ink drawings, and images of pollinaria among others that, compared with protologues and type documents, allow

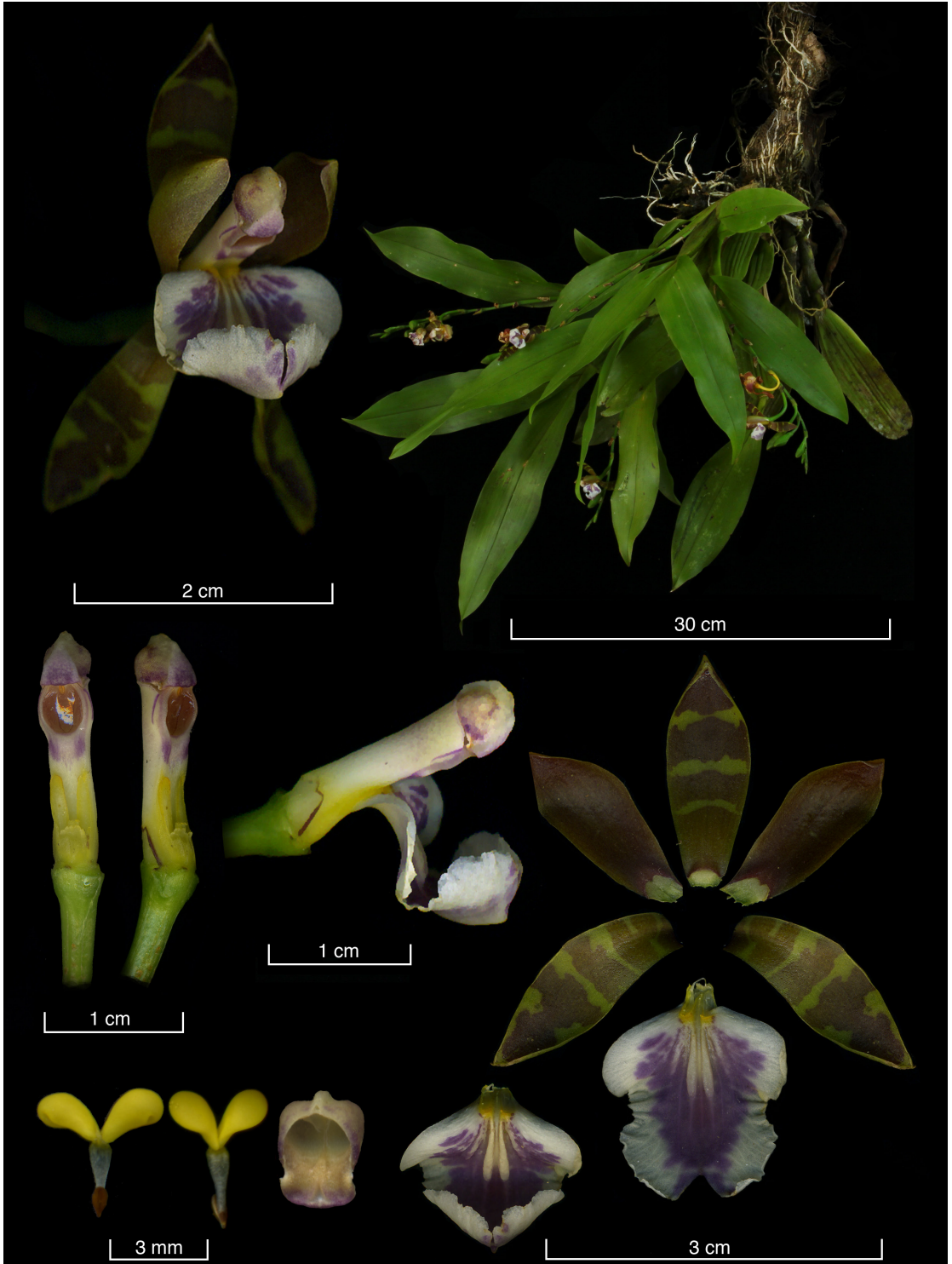


FIGURE 18. Botanical plate of *Aspasia epidendroides* from a plant collected in Chiriquí, Panamá. Courtesy of Herbario UCH.



FIGURE 19. Pollinarium of *Trichocentrum cebolleta* (Jacq.) Christenson, from the pollinaria collection of Herbario JBL.

the development of better taxonomic system (Fig. 15, 18). The development of electronic documentation techniques and the free flow of information through the Internet have contributed positively to increase scientific research (Pupulin 2007, 2009). Botanical exploration activities conducted in the past decade in Costa Rica, far from complete, yielded more than 100 orchid species new to science and several new records. This is a significant accomplishment for a traditionally well-studied orchid flora (Karremans *et al.* 2012).

#### The Orchid Project of JBL and UCH

The establishment of a permanent orchid research center in Panama is essential for the understanding of the flora of the southeastern Mesoamerican isthmus and its relationship with the Andean region. The Jardín Botánico Lankester of the Universidad de Costa Rica and the Herbarium UCH of the Universidad Autónoma de Chiriquí established a research center focused on the study of orchids. The main objectives are to perform a similar task in addition to that of JBL in Costa Rica and address the lack of an active center in Panama. With the adoption of an effective system of documentation of the diversity, JBL provided the methodology, information, and expertise for the long-term project on taxonomy

and systematics (Fig. 21). Essential documents and types that were repatriated in the last 10 years through agreements with other botanical institutions such as AMES, K, W, and MA are now available for the flora of Panama (Fig. 15). The first results including scientific papers and complementary information, photographs, specimens data, and literature of the project are available at EPIDENDRA.

There are many other reasons to implement this task in both countries. Their biological potential and geographical, geological, and floristic affinities are a challenge for science. Geographical proximity allows active communication between the two institutions. The continuous development of research activities, training of students, and reciprocal staff visits are some of the advantages. Their floras are complementary, and the understanding of the species distribution on both sides of the political boundary will lead to more precise conclusions. There are still large areas botanically unexplored. One of the most diverse and least known is the Cordillera de Talamanca, where the emblematic La Amistad International Park, a World Heritage site by UNESCO, protects almost 400,000 hectares of primary forest, the largest montane forest reserve in Central America (Fig. 22). In central and southeast Panama the



FIGURE 20. The spirit collection of Herbario JBL. The collection has almost 10,000 samples of Orchidaceae from the Neotropics.



FIGURE 21. Training of students from Universidad Autónoma de Chiriquí and Universidad de Costa Rica at Fortuna. Photo by Eyvar Rodríguez.

mountain ranges of Bagre, Sapó, Jurado, San Blas, and Darien are critical areas to explore. The proximity of the isthmus to South America also benefits the interpretation of the Andean orchid flora and its relationship to the northern Neotropics.

**ACKNOWLEDGMENTS.** We acknowledge the scientific services of Ministerio del Ambiente, Energía y Mares de Costa Rica (MINAE) and Sistema Nacional de Áreas de Conservación (SINAC) of Costa Rica and Autoridad Nacional del Ambiente (ANAM) of Panama for issuing the scientific permits of this project. This research was enabled by the Project 814-B2-161 “Hacia una moderna flora de orquídeas de Panamá” and by JBL and Herbario UCH. We thank Alec Pridgeon, José Portilla of Ecuagenera, Ltda., Ecuadorian Orchid Association, Guayaquil Botanical Gardens and Expoguayaquil who organized the 4th Scientific Conference on Andean Orchids in Guayaquil, Ecuador.

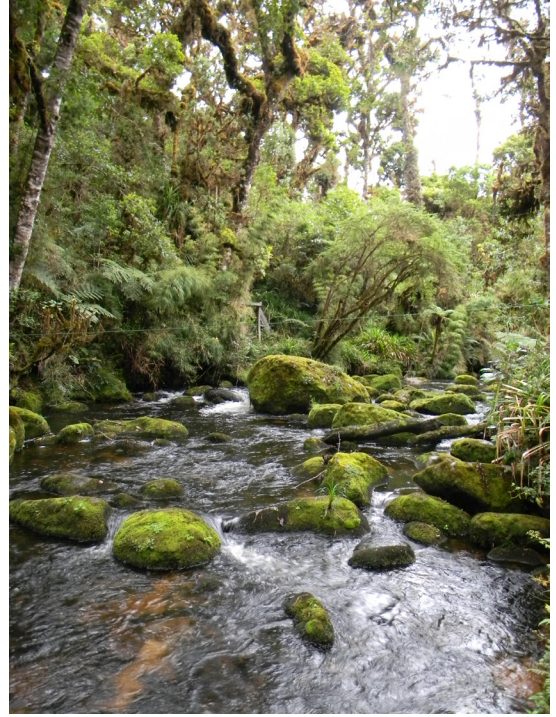


FIGURE 22. Río Terbi at La Amistad International Park. The river begins in Costa Rica and flows into Panama.

#### LITERATURE CITED

- Atwood, J.T. & Mora de Retana, D.E. 1999. Orchidaceae: Tribe Maxillarieae: Subtribes Maxillariinae and Oncidiinae. In W. Burger (ed.), *Flora Costaricensis*. Field., Bot. n.s. 40:1-182.
- Bogarín, D, C.M. Smith & D. Jiménez. 2012. Illustrations and studies in Neotropical Orchidaceae. 5. *The Lepanthes ovalis* group (Pleurothallidinae) with three new species from Costa Rica. *J. Bot. Res. Inst. Texas* 6(2): 361-373.
- Burger, W.C. 1980. Why are there so many kinds of flowering plants in Costa Rica? *Brenesia* 17: 371-388.
- Coates, A.G., J.B.C. Jackson, L.S. Collins, T.M. Cronin, H.J. Dowsett, L.M. Bybell, P. Jung & J.A. Obando. 1992. Closure of the Isthmus of Panama: The near-shore marine record of Costa Rica and western Panama. *Geol. Soc. Am. Bull.* 104: 814-828.
- Conran, J.G., J.M. Bannister & D.E. Lee. 2009. Earliest orchid macrofossils: early Miocene *Dendrobium* and *Earina* (Orchidaceae: Epidendroideae) from New Zealand. *Amer. J. Bot.* 96: 466-474.
- Correa, M., C. Galdames & M. S. de Stapf. 2004. *Catálogo de las Plantas Vasculares de Panamá*. Panama, Smithsonian Tropical Research Institute.
- D’Arcy, W.G. & M.D. Correa (eds.). 1985. *The botany and*

- natural history of Panama. Missouri Botanical Garden Press, St. Louis, Missouri
- Dodson, C. H. 2003. Why are there so many orchid species? *Lankesteriana* 7: 99-103.
- Dodson, C. H. 2004. Native Ecuadorian orchids. Volume 5: *Rodriguezia-Zygosepalum*. Dodson Publishing, Sarasota, Florida.
- Dressler, R. L. 1980. A checklist of the orchids of Panama as known today. Pp. i-xxvi in: *Orchids of Panama. A facsimile reprint of the Orchidaceae, Flora of Panama*, by L. O. Williams and P. H. Allen. Monographs in Systematic Botany from the Missouri Botanical Garden 4.
- Dressler, R. L. 1993. Field guide to the orchids of Costa Rica and Panama. Cornell University Press, Ithaca.
- Dressler, R. L. 2003. Orchidaceae. Pp. 1-595 in: B. E. Hammel, M. H. Grayum, C. Herrera & N. Zamora (eds.). *Manual de plantas de Costa Rica – Volumen III, monocotiledóneas (Orchidaceae-Zingiberaceae)*. Monogr. Syst. Bot. Missouri Bot. Gard. 93.
- García Castro, J. B., D. E. Mora-Retana & M. E. Rivas Rossi. 1995 [‘1993’]. Lista de orquídeas comunes a Costa Rica y Panamá. *Brenesia* 39-40: 93-107.
- Hágsater, E., M. Á. Soto Arenas, G. A. Salazar Chávez, R. Jiménez Machorro, M. A. López Rosas & R. L. Dressler. 2005. Las orquídeas de México. Instituto Chinoín México, D.F. 304 pp.
- Karremans, A.P., D. Bogarín, M. Fernández, C.M. Smith & M. A. Blanco. 2012. New species and records of Orchidaceae from Costa Rica. II. *Lankesteriana* 12(1): 19-51.
- Kohlmann, B., J. Wilkinson, O. García Valverde & K. Lulla. 2002. Costa Rica desde el espacio. Costa Rica from the Space. Editorial Heliconia, Fundacion Neotropica, San José, Costa Rica.
- Luer, C. A. 1999. Icones Pleurothallidarum XVIII. Miscellaneous new species of *Dryadella*, *Lepanthes* and *Pleurothallis*. Monogr. Syst. Bot. Missouri Bot. Gard. 76: 159-180.
- Luer, C.A. & R.L. Dressler. 1986. Nuevas especies de *Lepanthes* de Panamá. *Orquideología* 16(3): 3-26.
- Ossenbach, C. 2009. Orchids and orchidology in Central America: 500 years of history. *Lankesteriana* 9(1-2): 1-268.
- Ossenbach, C., R. L. Dressler & F. Pupulin. 2007. Orchids of the American isthmus: checklist and conservation status. Ed. Orquideario 25 de mayo, San José, Costa Rica.
- Pupulin, F. 2007. Epidendra, the botanical databases of Jardín Botánico Lankester at the University of Costa Rica. *Lankesteriana* 7(1-2): 178-180.
- Pupulin, F. 2009. Epidendra, la base de datos en línea del Jardín Botánico Lankester de la Universidad de Costa Rica *Orquideología* 26(1): 89-94.
- Pupulin, F. 2010. Orchidaceae: Tribe Cymbidieae: Subtribu Zygopetalinae. *Flora Costaricensis. Fieldiana, Bot. n.s.* 49: 1-60.
- Pupulin, F., D. Bogarín & D. Jiménez. 2009. New species and records in Mesoamerican *Lepanthes*. *Orchid Dig.* 73: 136-145.
- Pupulin, F., D. Bogarín, and C.M. Smith. 2010. Two new species of *Lepanthes* from Costa Rica close to *L. schizocardia* (Orchidaceae: Pleurothallidinae). *Lankesteriana* 9: 423-430.
- Pupulin, F. & G.A. Romero. 2003. Costa Rican Orchidaceae types (Crotypes) digital imaging documentation at AMES, Harvard University. *Lankesteriana* no. 7: 11-16.
- Ramírez S. R., B. Gravendeel, R.B. Singer, C.R. Marshall & N.E. Pierce. 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. *Nature* 448: 1042-1045.
- Schlechter, R. 1922. Orchidaceae Powellianae Panamenses. *Repert. Sp. Nov. Regni Veg. Beih.* 22.
- Standley, P.C. 1927. The flora of Barro Colorado Island. *Smithsonian Misc. Collect.* 78(8): 1-32.
- Williams, L. O. & P. H. Allen. 1946-1949. Orchids of Panama. Monographs in Systematic Botany from the Missouri Botanical Garden.