Left, Figure 15. Robert L. Dressler on a field trip to Cerro Arizona (Tute), Veraguas in 1975. Courtesy of Kerry A. Dressler.

Above, Figure 16. Robert L. Dressler, Jane Luer and Carl A. Luer on a field trip to Cerro Colorado in 1985. Courtesy of Kerry A. Dressler.

Materials and methods

Study area. *Geography*–. Panama lies in the south-east of Central America (9°38'N-7°12'N, 83°03'N-77°09'W) and comprises the narrowest and lowest land strip of America separating the Atlantic from the Pacific oceans (Figs. 17, 18, 19). The country is well known because of the Panama Canal, which allows the trade between the two oceans and is placed along the narrowest point of Panama that is less than 50 km wide. Panama runs from west to east and comprises 75, 517 km^2 of land and 2, 210 km^2 of territorial waters. Politically, it is divided in ten provinces: Bocas del Toro, Coclé, Chiriquí, Colón, Darién, Herrera, Los Santos, Panamá Oeste, Panamá, Veraguas and five indigenous "comarcas" or regions: Emberá, Guna Yala, Kuna de Madugandí, Kuna de Wargandí and Ngöbe-Buglé. Panama is usually divided in western, central and eastern Panama. Western Panama is the continuation of the Cordillera de Talamanca, which spans much of Costa Rica and extends to Chiriquí and Veraguas. This mountain range has the highest elevations of the isthmus, usually above 3000 m. No active volcanoes are found in this range. It is mostly protected by the La Amistad International Park. The highest peaks are found there close to the border with Costa Rica: Volcán Barú (3475 m), Cerro Fábrega (3335 m), Itamut (3293 m) and Echandi (3162 m). The Cordillera de Talamanca crosses the provinces of Bocas del Toro, Chiriquí, Veraguas and Comarca Ngöbe-Buglé. It loses elevation towards central Panama in the provinces of Veraguas and Coclé where it is also known as Serranía del Tabasará. Its main slope is: Cerro Santiago (2127 m). The provinces of Herrera, Los Santos and part of Veraguas are called central provinces and comprise mostly the Península de Azuero. Here the highest point is Cerro Hoya (1559 m), which is isolated from the Cordillera de Talamanca and Tabasará by the dry plains of Veraguas. Colón, Panama and Panama Oeste are in Central Panama, on the narrowest stretch of the country where elevations are relatively low, usually less than 1000 m. The area includes the slopes of Cerro Azul (571 m), Brewester (899 m), Campana (1030 m), Gaital (1185 m), Jefe (1007 m) and Nombre de Dios (587 m). Eastern Panama comprises the provinces of Darién (the easternmost province and adjacent to Colombia) and Panama towards the boundary with Colombia and the comarcas Emberá, Guna Yala, Kuna de Madugandí and Kuna de Wargandí. The Pan-American highway

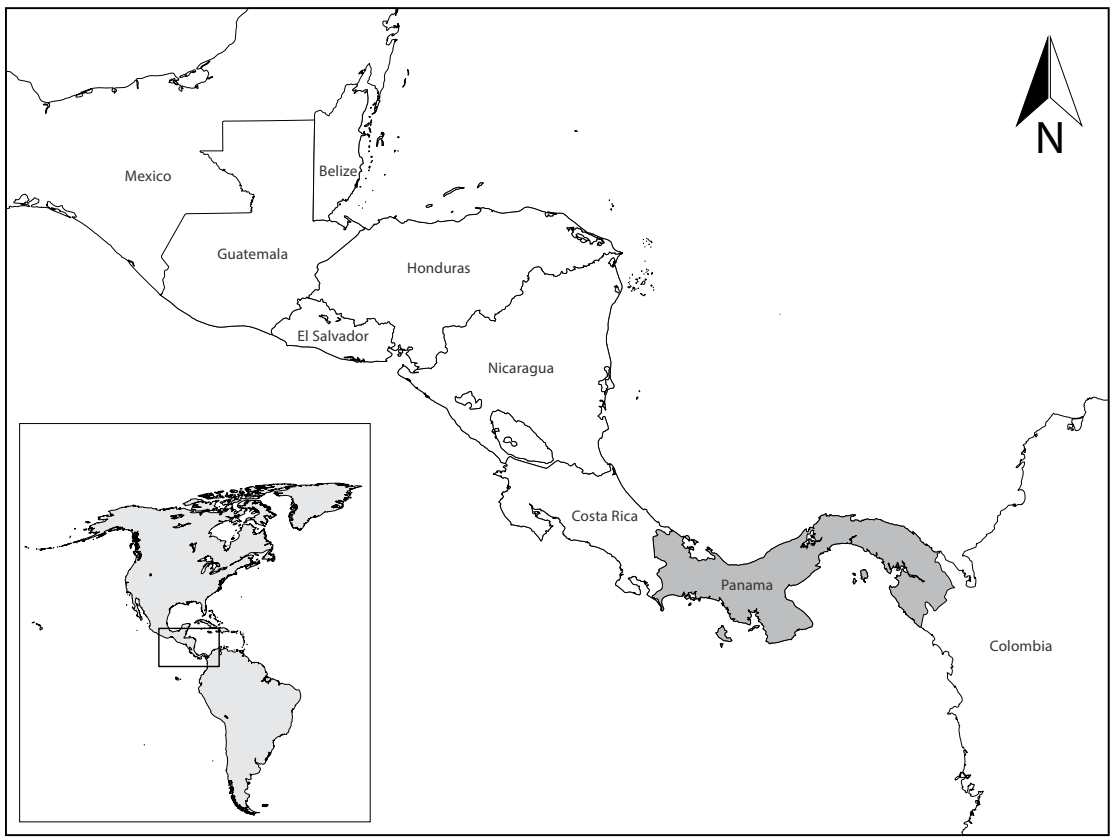

Figure 17. Panama lies in the southeastern part of Central America.

terminates at Yaviza in Darién. There is no connection by road with Colombia after this point. The ridge of Darien which extends along the Atlantic has the highest peaks of eastern Panama: Sasardi (610 m), Bell (1046 m), Chucurtí (1695 m), Gandi (1160 m), Armila (1421 m), Tanela (1421 m), Tacarcuna (1875 m) and Nique (1550 m). Serranía de San Blas along the Kuna Yala extends along the coast from central to the southeastern point, with Cerro Habú (747 m), Ebitan (736 m) and Diablo (518 m), among the highest points. Along the Pacific side, the main ranges are Majé with its highest points Cerro Chucantí (1430 m) and Pechito Parado (591 m), which is isolated from Serranía del Sapo with Cerro La Piña (1580 m); Jurado with Cocalita (1052 m), Bagre and Pirre with Cerro Pirre (1569 m). This area of Darién is perhaps the richest in plant species but the least known botanically. Panama has over 480 rivers. The most important are Changuinola, Cricamola and Teribe in Bocas del Toro; Caldera, Chiriquí, Chiriquí Viejo and Piedra in Chiriquí; Tabasará in Comarca Ngöbe-Buglé; Santa María in Coclé and Herrera; Balsas, Chagres, Chucunaque (the longest with 231 km) and Tuira in central-eastern Panama. There are three main lakes: Alajuela (also known as Madden), Bayano and Gatún (artificial). The main islands are all off the Pacific coast: Cébaco (80 km²) in Montijo Bay, Coiba (493 km²) and Isla del Rey (234 km²) in the Archipiélago de Las Perlas. Coiba is the largest island in the Pacific of Central America (IGTG 2007).

Geology –. Panama lies on the Costa Rica-Panama microplate, a complex area of interaction of three tectonic plates: Nazca, Cocos and Caribe. Panama emerged as an archipelago of islands about 15 Mya ago in the middle Miocene. However, the complex evolution leading to the formation of the Isthmus started during the Late Cretaceous and ended about 3.5 Mya in the Pliocene, resulting in the complete closing of the isthmus separating the Atlantic and Pacific oceans. The ranges of Costa Rica and Panama together with those of western Colombia are among the youngest in

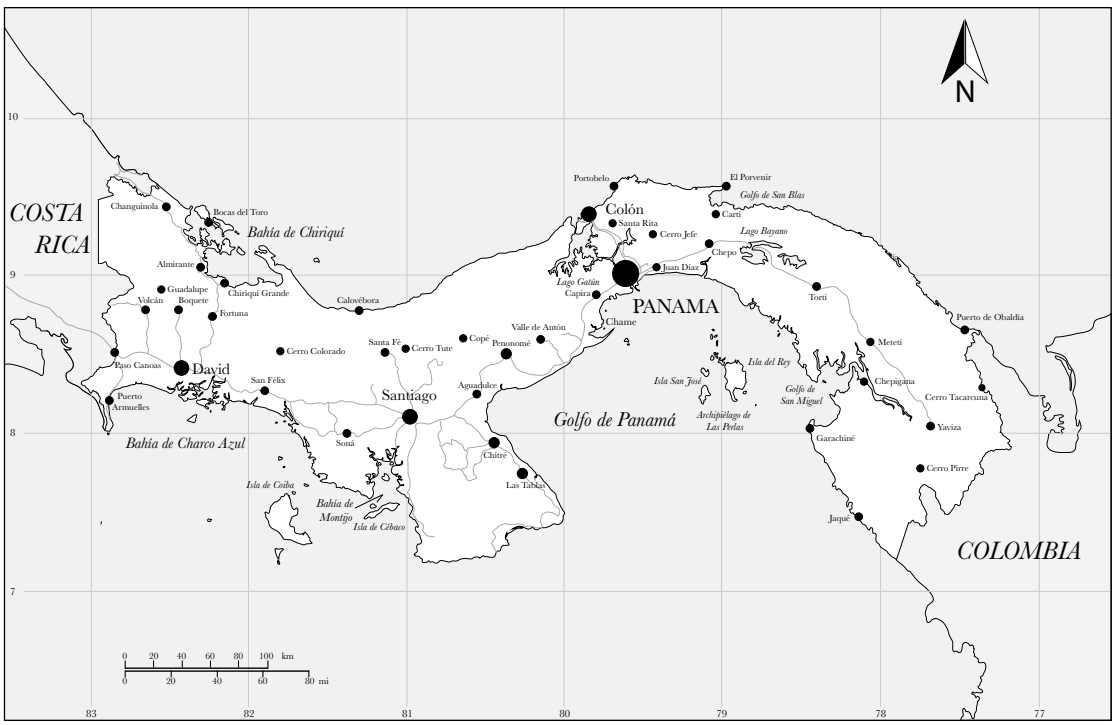

FIGURE 18. Map of Panama showing some of the most important cities and places visited by botanists. Map by D. Bogarín.

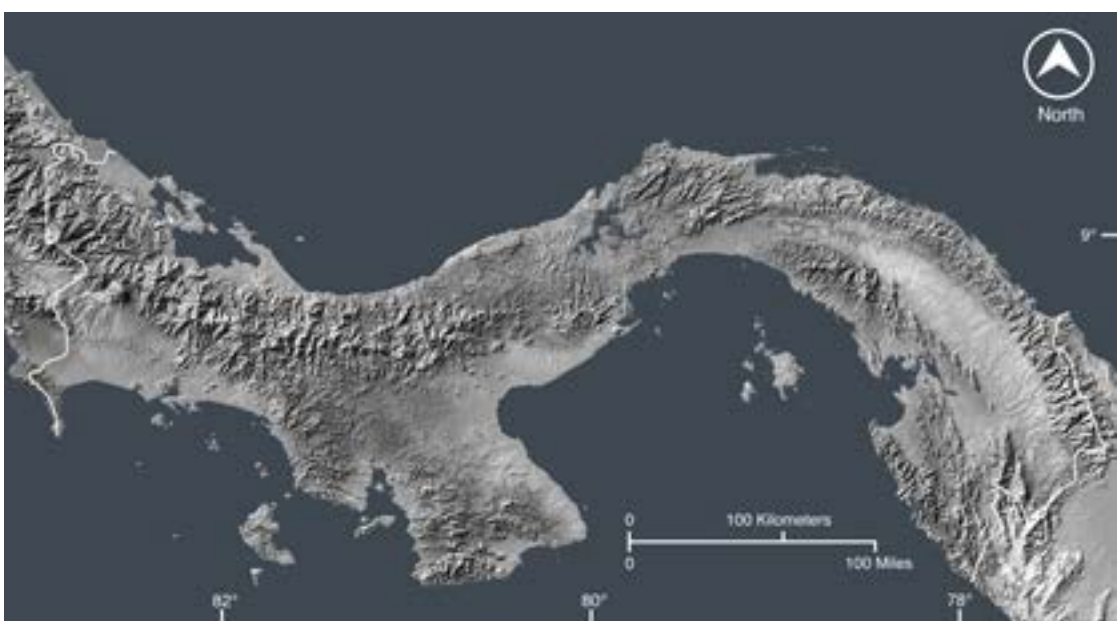

FIGURE 19. Geomorphology of Panama. Modified from false-color image of Panama by the Shuttle Radar Topography Mission, NASA/JPL/NIMA/SRTM Team.

the Neotropics (Kirby 2011). Some exotic lands that were volcanic islands in the ancient archipielago now make up Azuero, Burica and Coiba. These islands were pushed by the Cocos Plate toward the subduction zone with Caribbean Plate along the Pacific coast of Costa Rica and Panama. According to Coates *et al.* (1992)

and Coates & Obando (1996) three major events led the tectonic evolution of the southern Central American isthmus. First, the volcanic activity caused by the convergent tectonics of the eastern Pacific subduction zone, one of the primary forces that created the volcanic arc extending from North America to the south. Another tectonic effect was 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 (which contains the highest points of the isthmus) emerged and reduced its marine connections. The southern region of the isthmus was affected by the collision of the volcanic arc with north-western South America and led to the uplift of eastern Panama (San Blas, and Darién ranges) and northern Andes of Colombia and Venezuela in the late Neogene (Coates *et al.* 2004).

Climate –. The climate of Panama is affected by its geographical position close to the Equator, the narrow strip of land surrounded by two oceans, the mountain chains with different elevation ranges and the prevailing wet winds of the Caribbean. Usually the Caribbean lowlands are moist and warm. Precipitation originates mostly by the trade winds from the Caribbean colliding with the mountain ranges, primarily on the Cordillera de Talamanca and the action of the Inter-tropical Convergence Zone (Kohlmann *et al.* 2002, ANAM 2010). This climate is present from Bocas del Toro, to the Caribbean of Veraguas, Coclé and Colón. Average temperature varies from 25-27°C and precipitation from 2500-4500 mm/y. The Cordillera de Talamanca has broad elevation ranges and the wind system is quite complex. The western Pacific slope of Talamanca, and mid-elevation areas of Coclé, Panamá, San Blas and Darién are wet due to the interaction of local winds with the moist air from the Pacific Ocean. Average temperature varies from 26-28°C and precipitation from 2500-3500 mm/y. The Peninsula de Azuero is warm and dry with marked seasonality and an extended dry season. Average temperature varies from 27-28°C and precipitation is less than 2500 mm/y. In central Panama, there are low hills such as Campana and Gaital and Hoya in Azuero, where montane forests predominate from the interaction of the wet winds. In eastern Panama the climate is warm and rainy, (similar to Chocó in Colombia), and is one of the wettest regions on Earth (Dressler 1993). In general, there are two seasons in Panama: the dry season extending from the late of November to March-April and the wet season from May to November. The wet and dry seasons are better defined on the Pacific slope, while along the Caribbean slope, rains are seasonally variable, with no pronounced dry season (ANAM 2010).

Vegetation –. The flora of Panama is greatly influenced by the biotic exchange between North and South America, resulting in one of the richest countries in terms of plant diversity in the Neotropics. About 3 Mya ago, the vegetation of Panama consisted of open savannas. Some elements of the Laurasian flora colonized the Isthmus: *Alfaroa* Standl., *Alnus* Hill., *Berberis* L., *Billia* Peyr., *Caryocar* L., *Castilleja* Mutis ex L. f., *Magnolia* Juss., *Papaver* L., *Prunus* L., *Quercus* L., *Rubus* L., *Saurauia* Willd., *Ulmus* L. and *Vaccinium* L. At the same time, other southern groups moved northward including, *Drymis* Juss., *Gunnera* L. and *Weinmannia* L. Panama has 12 life zones (ANAM 2010). The most complete account of the flora of Panama by Correa *et al.* (2004) recognizes about 10,444 (91.2%) species of vascular plants and some 924 (8.8%) species are nonvascular. About 80% of the vascular plants are angiosperms. Of all angiosperms, 29.77% are monocotyledons and 60.15% are dicotyledons. Ferns comprise 9.85% but gymnosperms are poorly represented with less than 0.23% of species. The largest families in terms of species number in relation to the total vascular species in Panama are: Orchidaceae (13%), Rubiaceae (5.2%), Fabaceae (5.1%), Poaceae (4.4%), Araceae (3.6%), Melastomataceae (3.2%) and Asteraceae (3.1%). The families with most epiphytic species are Orchidaceae, Araceae, Bromeliaceae (1.9%) and Gesneriaceae (1.8%). Families containing greatest endemism are the Orchidaceae (23.6%), Rubiaceae (8.9%), Araceae (8.6%), Myrsinaceae (6.1%) and Melastomataceae (4.9%). According to the Vegetation Map of Panama (ANAM 2000) there are 24 vegetation types. An estimated of 46% of the territory is covered by forest, where the tropical ombrophile evergreen, latifoliated lowland forest occupies the largest area (24.48%). Regarding the state of conservation of the flora, ANAM (2000) recorded 1,305 endemic

species, 3,615 vulnerable, 1,041 endangered and 37 critically endangered. The mountains of Darién, Cerro Tacarcuna, the Cordillera de Talamanca, Cerro Azul and Cerro Jefe are considered the main centers of endemism (Correa *et al.* 2004).

Methods. This checklist was completed from studying specimens strictly collected in Panama and deposited in different herbaria mainly: AMES, CR, F, JBL, K, MO, NY, PMA, SEL, UCH, US and USJ. We included vouchers cited in: several taxonomic treatments (Williams & Allen 1980, Hágsater & Salazar 1993, Hágsater 1999, 2001, 2010, 2013, Dressler 2003c, Hágsater & Sánchez 2004, 2006, 2007, 2008, 2009, Hills 2012, Luer 1986, 1987, 1997a, 1997b, 1998a, 1998b, 1999, 2001a, 2001b, 2004, 2005, 2006, 2007, 2009, 2010, 2011, Ormerod 2004, 2005, 2007, 2008, 2009, 2013, Szlachetko *et al.* 2005, Pupulin 2010, among others), vouchers directly studied in herbaria, other historical collections and specimens collected by the authors in the field.

For the species described on the basis of material collected in Panama preference was given to the type collections as vouchers and the information was obtained directly from protologues (see Literature cited). The main taxonomic and floristic works studied are: Williams (1946a, 1946b), Allen (1949a, 1949b), Williams & Allen (1980) D'Arcy (1987) and Correa *et al.* (2004). Ossenbach *et al.* (2007) was used as reference, though the absence of herbarium vouchers did not allow us to confirm or compare some taxonomic concepts adopted there. Therefore, these examples were not discussed in the excluded species section (see format of the checklist). Some other cases of questionable or misapplied species for the flora of Panama in D'Arcy (1987) and Dressler (1993) were clarified by Correa *et al.* (2004) (see excluded species). Specimen citations, synonyms and information localities cited in the literature were also obtained from the following online electronic databases: EPIDENDRA (The Botanical Databases by Lankester Botanical Garden, http://www.epidendra.org), IPNI (International Plants name Index, http://www.ipni.org) WCSP (World Checklist of Selected Plant Families: Royal Botanic Gardens, Kew, http://apps.kew.org/wcsp/home.do) and TROPICOS (Missouri Botanical Garden Databases, http://www.tropicos.org). Information on publications and protologues was obtained from EPIDENDRA, BHL (Biodiversity Heritage Library, http://www.biodiversitylibrary.org) and the Library of Royal Botanic Gardens, Kew, Lankester Botanical Garden and Herbarium UCH. We added new records collected and documented between January 2012 and August 2014 as part of the activities and preliminary results of the project "Towards a modern orchid flora of Panama" (see introduction). These new records were documented by photographs and by drawings using the techniques described by Pupulin *et al.* (2012) and Bogarín *et al.* (2014). Georeferencing for specimens were obtained using a Garmin eTrex Vista GPS and Google Earth 6.1.0 © and herbarium vouchers were deposited at JBL, UCH and PMA herbaria.

Format of the checklist. Species are presented as an alphabetical list of accepted names with their respective homotypic and heterotypic synonyms and herbarium vouchers. Accepted names are indicated in bold and italics. A herbarium voucher for each accepted name is given. Homotypic and heterotypic synonyms are listed in italics but without bold face and are arranged chronologically. Some species are known to occur in Panama or have been cited in formal taxonomic treatments elsewhere but we have not been able to locate a voucher. The voucher is cited as "not seen" and we refer to the taxonomic work that cited it. In some cases we added a short note warning of a particular case such as species with disjunct distributions with a voucher from a cultivated plant or where we suspect a taxonomic problem.

Several names have been misapplied to the flora of Panama or they have changed since previous taxonomic works. For example species currently accepted under a broad concept that have been redefined or clarified, infraspecific taxa that are now accepted in the range of species or some errors or omissions. To clarify these records, we present a list of excluded species (Appendix 3), in which we discuss the exclusion of doubtful species or the taxonomic clarification of certain concepts that no longer apply to the Panamanian material previously cited in the literature. The endemic species are listed separately. We included only the accepted names for the endemic species list.

A basionym list is presented with the respective accepted name in bold. This list is useful as reference for the species whose type locality is within Panama and for future taxonomic and nomenclatural treatments. Locality data and citations for this list were obtained directly from protologues (see Literature cited).

Nomenclatural considerations. In all cases where it is intended to make a list of the orchid species for a particular region, there are always issues regarding to the classification system followed, mainly from the generic viewpoint. The nomenclature of Orchidaceae has undergone many changes after the publication of several phylogenetic studies (Chase & Palmer 1989, 1992, van den Berg *et al.* 2000, Cameron *et al.* 1999, Cameron 2001, Pridgeon *et al.* 2001a, Chase *et al.* 2003, Salazar *et al.* 2003, Whitten *et al.* 2005 and Williams *et al.* 2005, among others). This list relies largely on the generic concepts proposed in *Genera Orchidacearum* (Pridgeon *et al.* 1999, 2001a, 2001b, 2003, 2005a, 2005b, 2005c). In a few cases we adopted redefined concepts proposed after *Genera Orchidacearum* (Chase & Whitten 2011, Karremans 2014).

To facilitate the understanding of nomenclature issues, we present three tables summarizing the main nomenclatural changes that affected the orchid flora of Panama. Table 1 provides a guide to the genera that have been lumped into other genera and accepted for this work. Table 2 presents the genera that have been segregated into various other genera. As a guide for the reader, Table 3 presents the general classification followed in this checklist with the genera and their respective number of species accepted for Panama including the total of endemic species. The list also provides an overview of the genera that are represented in the country.

This catalog is not intended to discuss the different generic classifications but to serve as a study guide for future taxonomic and floristic works in Panama. Clearly, there are different trends in orchid classification and acceptance of generic boundaries varies from one author to another. Nevertheless, citation of homotypic synonyms will help the reader to determine which names have been proposed by different studies and to easily find the latest changes affecting Panamanian species even if the reader is not familiar with those changes.

Results and discussion

This checklist contains 1,365 taxa (1,360 species, two natural hybrids and three subspecies) in four subfamilies, 16 tribes, 27 subtribes, 187 genera (Figs. 20–26, Table 3). Since the last checklist published in the Catalogue of Vascular Plants of Panama by Correa *et al.* (2004) this is an increase of 210 species published since the last decade. We were able to add 32 records in 17 genera that have not been mentioned so far in the literature. With regard to Ossenbach *et al.* (2007) there is a reduction of 25 species although it was not possible to corroborate the voucher specimens in that treatment. Though we do not yet know the exact number of orchid species that exist in Panama, the country has one of the richest floras of Mesoamerica. The orchid diversity index (calculated as the number of species / km^2) shows 0.018 spp./km^2. The number of species and diversity index are among the highest in the Mesoamerican region together with Costa Rica and southeastern Mexico (Ossenbach *et al.* 2007). The area between Costa Rica and Panama treated as Lower Central America (LCA) is widely recognized for its high number of endemic species, and the number for Orchidaceae is not an exception (Myers *et al.* 2000). Now that we have more accurate numbers, both countries contain a total of 2,030 species of orchids (between 6.5–8% of the global biodiversity of the family) in 130,000 km^2 (about 0.09% of Earth's land area). Some factors explaining this extraordinary diversity are: 1) a natural land bridge uniting three of the 25 recognized hotspots world-wide (Mesoamerica, Choco/Darién/Western Ecuador and Tropical Andes) that.are centers of diversity of many groups of orchids 2) the climatic influence of the Pacific and Atlantic oceans. 3) the orographic and tectonic factors such as the lifting of the Cordillera de Talamanca between Costa Rica and Panama and the formation of foothills of Majé, Darién and San Blas from Panama and western Colombia.

Epidendroideae, with more than 90% of species and over 85% of the genera, is the most diverse group in Panama, significantly outnumbering the other three recorded subfamilies. Orchidoideae contains less than 13% and Vanilloideae and Cypripedioideae less than 1% of the species (Table 4). The most diverse tribes of the 16 recorded are Epidendreae, Cymbidieae, Cranichideae and Sobralieae. These groups make up 25% of tribes,