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,

Table 1. List of orchid genera which have been lumped into other genera by recent authors affecting the nomenclature of the orchids of Panama.

Genus	Reduced under	Reference
Acostaea Schltr.	*Specklinia* Lindl.	Pridgeon & Chase (2001)
Ada Lindl.	*Brassia* R.Br.	Chase & Whitten (2011)
Amparoa Schltr.	*Rhynchostele* Rchb.f.	Hágsater & Soto (2003)
Areldia Luer	*Specklinia*	This paper
Chelyorchis Dressler & N.H.Williams	*Rossioglossum* (Schltr.) Garay & G.C.Kenn.	Chase *et al.* (2008)
Cohniella Pfitzer	*Trichocentrum* Poepp. & Endl.	Williams *et al.* (2001)
Cucumeria Luer	*Specklinia*	This paper
Goniochilus M.W.Chase	*Leochilus* Knowles & Westc.	Chase *et al.* (2008)
Hexisea Lindl.	*Scaphyglottis* Poepp. & Endl.	Dressler *et al.* (2004a)
Hybochilus Schltr.	*Leochilus*	Chase *et al.* (2008)
Leucohyle Klotzsch	*Trichopilia* Lindl.	Dressler (2004c)
Lophiaris Raf.	*Trichocentrum*	Williams *et al.* (2005)
Mesospinidium Rchb.f.	*Brassia*	Chase & Whitten (2011)
Oerstedella Rchb.f.	*Epidendrum* L.	Hágsater & Soto (2005)
Osmoglossum (Schltr.) Schltr.	*Cuitlauzina* La Llave & Lex.	Dressler & Williams (2003)
Pachystele Schltr.	*Scaphyglottis*	Dressler *et al.* (2004a)
Platyglottis L.O. Williams	*Scaphyglottis*	Dressler *et al.* (2004a)
Pachyphyllum Kunth	*Fernandezia* Ruiz & Pav.	Chase & Whitten (2011)
Pleurothallis R.Br.	*Stelis* Sw.	Pridgeon & Chase (2001)
Psygmorchis Dodson & Dressler	*Erycina* Lindl.	Williams *et al.* (2001)
Restrepiopsis Luer	*Pleurothallopsis* Porto & Brade	Pridgeon & Chase (2001)
Salpistele Dressler	*Stelis*	Pridgeon & Chase (2001)
Scelochilus Klotzsch	*Comparettia* Poepp. & Endl.	Chase *et al.* (2008)
Sigmatostalix Rchb.f.	*Oncidium* Sw.	Chase *et al.* (2008)
Stellilabium Schltr.	*Telipogon* Kunth	Williams *et al.* (2005)
Ticoglossum R.L.Rodr. ex Halb.	*Rossioglossum*	Chase *et al.* (2008)

Table 2. List of orchid genera segregated by recent authors affecting the nomenclature of the orchids of Panama.

Genus	Segregate Genera	Reference
Chondrorhyncha Lindl.	*Benzingia* Dodson	Romero-González & Dodson (2010)
	Daiotyla Dressler	Whitten *et al.* (2005)
	Stenotyla Dressler	Whitten *et al.* (2005)
Elleanthus C.Presl	*Adeneleuterophora* Barb. Rodr.	Dudek & Szlachetko (2010)
	Evelyna Poepp. & Endl.	Dudek & Szlachetko (2010)
Eltroplectris Raf.	*Callistanthos* Szlach.	Szlachetko & Rutkowski (2008)
Epidendrum	*Coilostylis* Raf.	Whitner & Harding (2004)
Erythrodes Blume	*Aspidogyne* Garay	Ormerod (2007), Ormerod (2009)
	Kreodanthus Garay	Ormerod (2008)

continues

TABLE 2. *Continues*.

Genus	Segregate Genera	Reference
Erythrodes Blume	*Microchilus* C.Presl	Ormerod (2002)
	Platythelys Garay	Ormerod (2007)
Habenaria Willd.	*Bertauxia* Szlach	Szlachetko (2004a)
	Habenella Small	Szlachetko & Kras (2006)
	Platantheroides Szlach.	Szlachetko (2004b)
Kefersteinia Rchb.f.	*Senghasia* Szlach.	Szlachetko (2003)
Ligeophila Garay	*Aspidogyne* Garay	Ormerod (2007) Meneguzzo (2012)
Lycaste Lindl.	*Selbyana* Archila	Archila (2010)
Malaxis Sol. ex Sw.	*Microstylis* (Nutt.) Eaton	Szlachetko & Margońska (2006)
Masdevallia Ruiz & Pav.	*Acinopetala* Luer	Luer (2006)
	Alaticaulia Luer	Luer (2006)
	Buccella Luer	Luer (2006)
	Diodonopsis Pridgeon & M.W.Chase	Pridgeon & Chase (2001)
	Fissia (Luer) Luer	Luer (2006)
	Reichantha Luer	Luer (2006)
	Spilotantha Luer	Luer (2006)
	Zahleria Luer	Luer (2006)
Maxillaria Ruiz & Pav.	*Adamanthus* Szlach.	Szlachetko & Śmiszek 2006[2007]
	Calawaya Szlach. & Sitko	Szlachetko & Sitko (2012)
	Camaridium Lindl.	Blanco *et al.* (2007)
	Chaseopsis Szlach. & Sitko	Szlachetko & Sitko (2012)
	Chelyella Szlach. & Sitko	Szlachetko & Sitko (2012)
	Christensonella Szlach., Mytnik, Górniak & Śmiszek	Szlachetko, Mytnik, Górniak &
	Heterotaxis Lindl.	Ojeda, Carnevali & Romero (2005)
	Inti M.A.Blanco	Blanco *et al.* (2007)
	Laricorchis Szlach.	Szlachetko & Sitko (2012)
	Mapinguari Carnevali & R.B.Singer	Blanco *et al.* (2007)
	Maxillariella M.A.Blanco & Carnevali	Blanco *et al.* (2007)
	Mormolyca Fenzl	Blanco *et al.* (2007)
	Nitidobulbon Ojeda, Carnevali & G.A.Romero	Ojeda, Carnevali & Romero (2009)
	Ornithidium Salisb. ex R. Br.	Blanco *et al.* (2007)
	Pseudocymbidium Szlach. & Sitko	Szlachetko & Sitko (2012)
	Pseudomaxillaria Hoehne	Szlachetko & Sitko (2012)
	Psittacoglossum La Llave & Lex.	Szlachetko & Sitko (2012)
	Rhetinantha M.A.Blanco	Blanco *et al.* (2007)
	Sauvetrea Szlach.	Blanco *et al.* (2007)
	Viracocha Szlach. & Sitko	Szlachetko & Sitko (2012)
	Xanthoxerampellia Szlach. & Sitko	Szlachetko & Sitko (2012)
Oncidium Sw.	*Brevilongium* Christenson	Christenson (2006b)

continues

TABLE 2. *Continues*.

Genus	Segregate Genera	Reference
Oncidium Sw.	*Chelyorchis* Dressler & N.H.Williams	Dressler & Williams (2000), Carnevali *et al.*
	Heteranthocidium Szlach., Mytnik & Romowicz	Szlachetko, Mytnik & Romowicz (2006)
	Otoglossum (Schltr.) Garay & Dunst.	Williams *et al.* (2001)
	Rossioglossum (Schltr.) Garay & G.C.Kenn.	Chase *et al.* (2008)
	Stacyella Szlach.	Szlachetko (2006)
	Trichocentrum Poepp. & Endl.	Williams *et al.* (2001)
	Vitekorchis Romowicz & Szlach.	Romowicz & Szlachetko (2006)
Pleurothallis R.Br.	*Aberrantia* Luer	Luer (2005)
	Acronia C.Presl	Luer (2005)
	Acianthera Scheidw.	Pridgeon & Chase (2001)
	Anathallis Barb.Rod.	Pridgeon & Chase (2001), Hágsater & Soto
	Ancipitia (Luer) Luer	Luer (2004)
	Apoda-prorepentia (Luer) Luer	Luer (2004)
	Areldia Luer	Luer (2004)
	Crocodeilanthe Rchb.f. & Warsz.	Luer (2004)
	Cucumeria Luer	Luer (2004)
	Didactylus Luer	Luer (2005)
	Dracontia (Luer) Luer	Luer (2004)
	Echinella Pridgeon & M.W.Chase	Pridgeon & Chase (2001)
	Echinosepala Pridgeon & M.W.Chase	Pridgeon & Chase (2002)
	Effusiella Luer	Luer (2007)
	Elongatia (Luer) Luer	Luer (2004)
	Empusella (Luer) Luer	Luer (2004)
	Gerardoa Luer	Luer (2006)
	Kraenzlinella Kuntze	Luer (2004), Hágsater & Soto (2003)
	Lankesteriana Karremans	Karremans (2014)
	Lalexia Luer	Luer (2011)
	Loddigesia Luer	Luer (2006)
	Lomax Luer	Luer (2006)
	Muscarella Luer	Luer (2006)
	Niphantha Luer	Luer (2010)
	Pabstiella Brieger & Senghas	Luer (2007)
	Panmorphia Luer	Luer (2006)
	Phloeophila Hoehne & Schltr.	Pridgeon & Chase (2001), Luer (2006)
	Rhynchopera Klotzsch	Szlachetko & Margońska (2001)
	Ronaldella Luer	Luer (2006)
	Sarcinula Luer	Luer (2006)
	Specklinia Lindl.	Pridgeon & Chase (2001), Hágsater & Soto
	Stelis Sw.	Pridgeon & Chase (2001)

continues

Table 2. *Continues*.

Genus	Segregate Genera	Reference
Pleurothallis R.Br.	*Tribulago* Luer	Luer 2004, Luer (2006)
	Sylphia Luer	Luer (2006)
	Unciferia (Luer) Luer	Luer (2004)
	Unguella (Luer) Luer	Luer (2005)
	Zosterophyllanthos Szlach. & Marg.	Szlachetko & Margońska (2001), Szlachetko & Kulak (2006)
Prosthechea Knowles & Westc.	*Anacheilium* Rchb.f. ex Hoffmanns.	Withner & Harding (2004)
	Hormidium (Lindl.) Heynh.	Withner & Harding (2004)
	Panarica Withner & P. A. Harding	Withner & Harding (2004)
	Pollardia Withner & P. A. Harding	Withner & Harding (2004)
	Pseudencyclia Chiron & V.P. Castro	Chiron & Castro-Neto (2003)
Stanhopea Frost ex Hook.	*Stanhopeastrum* Rchb.f	Szlachetko (2007)
Trichosalpinx Luer	*Tubella* (Luer) Archila	Archila (2000)

87.7% of the genera and more than 90% of the species. Ten tribes (62.5%) contain less than three genera and ten species (Table 5). These groups also encompass the most diverse subtribes. Of the 27 recorded, Pleurothallidinae has 30 genera and 405 spp. (by far the most diverse), Laeliinae 16 genera and 292 spp., Oncidiinae 29 genera and 157 spp. and Maxillariinae with 18 genera and 132 spp. are the most numerous in terms of species richness and endemism. All these subtribes together surpass 100 species and account for 50% of the genera and 72% of species. Seven subtribes (26%) have more than ten species while ten (37%) contain less than ten species. A comparison among the most diverse subtribes is shown in Table 6. Recent estimates of the age of the Orchidaceae based on molecular clock calculations by Ramírez *et al.* (2007) and subsequent recalibration by Gustafsson *et al.* (2010) and Guo *et al.* (2012) show that the common ancestor of Orchidaceae existed in the Late Cretaceous 80-90 Mya. From this perspective, current subfamilies diverged before the mass extinction of the Cretaceous/Paleogene (K-Pg). Most notably, after this period, Epidendroideae and also Orchidoideae diversified in the numbers that we know today (Ackerman 2014). The diversification of the Pleurothallidinae, Laeliinae, Oncidiinae and Maxillariinae, the largest subtribes within Epidendroideae, may have occurred about 15-20 Mya in the Early Miocene. This diversification coincided with geological events that shaped the tropical Andes and the Isthmus of Panama and were perhaps key geological events in the evolutionary history of these groups. In fact, they are the two best represented subfamilies in the tropical Andes and Costa Rica-Panama. The uplift of the Cordillera de Talamanca, resulting in the final closure of the isthmus about 3.5 Mya in the Pliocene as well as the abrupt appearance of the Andes between 6-10 Mya created new environments, isolation of regions and local climate changes (appearance of cold and humid regions, where the highest number of species and endemism are found) thus promoting rapid diversification by allopatric speciation. Further work is required to study the biological processes that could boost radiations of diverse groups (see discussion of endemic species). Other groups did not diversify and contain few species in the region. For example, Cypripedioideae, has only three representatives on the isthmus. *Selenipedium chica* Rchb.f. is the sole member of the subfamily with plicate leaves in Central America and is found only from central Panama to the southeast (Fig. 7A). Guo *et al.* (2010) indicate that the isthmus served as a corridor for species that managed to diversify in South America but not in Costa Rica and Panama. *Selenipedium* Rchb.f. evolved during the Paleocene, while representatives with conduplicate leaves (*Phragmipedium* Rolfe) originated around the Eocene. Vanilloideae is a pantropical group with few representatives in Panama, but the isthmus could also be used as a bridge for future dispersion between the two land masses. Other representatives of Old World diverse

TABLE 3. Classification of the Orchidaceae of Panama, species number and endemism.

Taxa	Species number	Endemism
Subfamily VANILLOIDEAE		
Tribe Vanilleae		
Subtribe Pogoniinae		
Cleistes	1	
Subtribe Vanillinae		
Vanilla	8	
Subfamily CYPRIPEDIOIDEAE		
Phragmipedium	2	
Selenipedium	1	
Subfamily ORCHIDOIDEAE		
Tribe Cranichideae		
Subtribe Cranichidinae		
Gomphichis	1	
Pseudocentrum	1	
Pterichis	1	
Solenocentrum	1	
Baskervilla	2	1
Prescottia	2	
Ponthieva	4	
Cranichis	6	
Subtribe Goodyerinae		
Aspidogyne	5	1
Goodyera	2	
Kreodanthus	3	2
Microchilus	12	6
Platythelys	3	
Subtribe Spiranthinae		
Beloglottis	2	
Brachystele	1	
Coccineorchis	7	
Cyclopogon	9	1
Discyphus	1	
Eurystyles	3	
Pelexia	4	1
Sacoila	1	
Sarcoglottis	4	1
Stenorrhynchos	1	
Tribe Orchideae		
Subtribe Orchidinae		
Habenaria	20	4
Subfamily EPIDENDROIDEAE		
Tribe Arethuseae		
Subtribe Arethusinae		
Arundina	1	
Tribe Calypsoeae		
Govenia	4	1
Wullschlaegelia	2	
Tribe Collabieae		
Calanthe	1	
Spathoglottis	1	
Tribe Cymbidieae		
Subtribe Catasetinae		
Catasetum	3	
Clowesia	1	
Cycnoches	9	3
Dressleria	3	3
Galeandra	2	
Mormodes	7	2
Subtribe Coeliopsidinae		
Coeliopsis	1	
Peristeria	3	
Subtribe Cyrtopodiinae		
Cyrtopodium	1	
Subtribe Eriopsidinae		
Eriopsis	1	
Subtribe Eulophiinae		
Eulophia	1	
Oeceoclades	1	
Subtribe Maxillariinae		
Camaridium	48	8
Christensonella	2	
Cryptocentrum	7	1
Heterotaxis	4	
Inti	2	
Lycaste	9	1
Mapinguari	1	
Maxillaria	21	3
Maxillariella	11	
Mormolyca	5	1
Neomoorea	1	
Nitidobulbon	1	
Ornithidium	6	1
Rhetinantha	3	
Rudolfiella	1	
Teuscheria	2	
Trigonidium	3	
Xylobium	5	
Subtribe Oncidiinae		
Aspasia	2	
Brassia	8	1
Cischweinfia	4	2
Comparettia	2	
Cuitlauzina	2	
Cyrtochiloides	2	
Eloyella	1	
Erycina	3	
Fernandezia	3	
Ionopsis	2	
Leochilus	5	
Lockhartia	9	
Macradenia	1	
Macroclinium	10	2
Miltoniopsis	2	
Notylia	4	1
Oncidium	32	6
Ornithocephalus	7	3
Otoglossum	2	
Plectrophora	1	
Psychopsis	1	
Rhynchostele	1	
Rodriguezia	2	
Rossioglossum	4	
Systeloglossum	2	1
Telipogon	23	17
Trichocentrum	9	1
Trichopilia	12	5
Trizeuxis	1	
Subtribe Stanhopeinae		
Acineta	4	1

TABLE 3. *Continues*.

Taxa	Species number	Endemism
Coryanthes	4	2
Gongora	10	1
Horichia	1	
Houlletia	2	
Kegeliella	2	
Lacaena	1	
Paphinia	2	1
Polycycnis	5	1
Sievekingia	3	1
Stanhopea	10	2
Subtribe Zygopetalinae		
Benzingia	1	
Chaubardiella	1	
Chondroscaphe	3	1
Cochleanthes	1	
Cryptarrhena	2	
Daiotyla	2	
Dichaea	26	3
Euryblema	1	1
Galeottia	1	
Huntleya	2	
Kefersteinia	11	4
Koellensteinia	1	
Pescatoria	2	
Stenotyla	3	1
Warczewiczella	2	
Warrea	1	
Warreopsis	1	
Tribe Epidendreae		
Subtribe Bletiinae		
Bletia	2	
Subtribe Chysinae		
Chysis	3	2
Subtribe Coeliinae		
Coelia	1	
Subtribe Laeliinae		
Acrorchis	1	
Barkeria	1	
Brassavola	2	
Cattleya	1	
Caularthron	1	
Dimerandra	1	
Dinema	1	
Encyclia	7	1
Epidendrum	206	53
Guarianthe	1	
Homalopetalum	1	
Jacquiniella	6	1
Laelia	1	
Nidema	2	
Prosthechea	21	2
Scaphyglottis	39	5
Subtribe Pleurothallidinae		
Acianthera	13	1
Anathallis	4	
Barbosella	5	1
Brachionidium	12	5
Diodonopsis	1	
Dracula	6	3
Dresslerella	4	3
Dryadella	6	2
Echinosepala	6	1
Kraenzlinella	1	
Lalexia	1	
Lankesteriana	4	
Lepanthes	66	21
Lepanthopsis	2	1
Masdevallia	26	9
Muscarella	3	
Myoxanthus	7	
Octomeria	5	
Pabstiella	1	
Phloeophila	2	1
Platystele	20	3
Pleurothallis	54	23
Pleurothallopsis	2	
Restrepia	3	
Scaphosepalum	4	1
Specklinia	34	7
Stelis	88	23
Trichosalpinx	18	4
Trisetella	4	1
Zootrophion	3	
Subtribe Ponerinae		
Helleriella	1	
Isochilus	3	
Nemaconia	1	
Tribe Gastrodieae		
Uleiorchis	1	
Tribe Malaxideae		
Crossoglossa	5	2
Liparis	3	
Malaxis	15	2
Tribe Neottieae		
Palmorchis	4	
Tribe Dendrobieae		
Subtribe Bulbophyllinae		
Bulbophyllum	2	
Tribe Sobralieae		
Elleanthus	23	2
Sobralia	39	16
Tribe Triphoreae		
Subtribe Triphorinae		
Monophyllorchis	1	
Psilochilus	3	1
Triphora	4	
Tribe Tropidieae		
Corymborkis	1	
Tribe Vandeae		
Subtribe Aeridinae		
Phalaenopsis	1	
Subtribe Angraecinae		
Campylocentrum	9	
Subtribe Polystachyinae		
Polystachya	2	
TOTAL	1365	296

Table 4. Number of taxa, percentage of total (%) and endemism in each subfamily recorded in Panama.

Subfamily	Tribes	Subtribes	Genera	Species	Endemism
Epidendroideae	13 (81.3)	21 (77.8)	159 (85.5)	1257 (92.1)	278 (94.3)
Orchidoideae	2 (12.5)	4 (14.8)	24 (12.8)	96 (7.0)	17 (5.8)
Vanilloideae	1 (6.3)	2 (7.4)	2 (1.1)	9 (0.7)	0 (0)
Cypripedioideae	0 (0)	0 (0)	2 (1.1)	3 (0.2)	1 (0)
Total	16	27	187	1365	296

Table 5. Genera, species, endemism and percentage of total (%) in the 16 tribes present in the orchid flora of Panama.

Tribe	Genera	Species	Endemism
Epidendreae	52 (27.8)	708 (51.9)	174 (58.8)
Cymbidieae	87 (46.5)	427 (31.3)	81 (27.4)
Cranichideae	23 (12.3)	76 (5.6)	13 (4.4)
Sobralieae	2 (1.1)	62 (4.5)	18 (6.1)
Malaxideae	3 (1.6)	23 (1.7)	4 (1.4)
Orchideae	1 (0.5)	20 (1.5)	4 (1.4)
Vandeae	3 (1.6)	12 (0.9)	0 (0.0)
Vanilleae	2 (1.1)	9 (0.7)	1 (0.0)
Triphoreae	3 (1.6)	8 (0.6)	1 (0.3)
Calypsoeae	2 (1.1)	6 (0.4)	1 (0.3)
Neottieae	1 (0.5)	4 (0.3)	0 (0.0)
Collabieae	2 (1.1)	2 (0.1)	0 (0.0)
Dendrobieae	1 (0.5)	1 (0.1)	0 (0.0)
Arethuseae	1 (0.5)	1 (0.1)	0 (0.0)
Gastrodieae	1 (0.5)	1 (0.1)	0 (0.0)
Tropidieae	1 (0.5)	1 (0.1)	0 (0.0)

Table 6. Genera, species, endemism and percentage of total (%) in many different subtribes in the orchid flora of Panama.

Subtribe/Tribe*	Genera	Species	Endemism
Pleurothallidinae	30 (16)	405 (29.6)	110 (37.2)
Laeliinae	16 (8.6)	292 (21.4)	62 (21.0)
Oncidiinae	29 (15.5)	157 (11.5)	39 (13.2)
Maxillariinae	18 (9.6)	132 (9.7)	15 (5.1)
Sobralieae*	2 (1.1)	62 (4.5)	18 (6.1)
Zygopetalinae	17 (9.1)	61 (4.5)	10 (3.4)
Stanhopeinae	11 (5.9)	44 (3.2)	9 (3.1)
Spiranthinae	10 (5.3)	33 (2.4)	3 (1.0)
Goodyerinae	5 (2.7)	25 (1.8)	9 (3.1)
Catasetinae	6 (3.2)	25 (1.8)	8 (2.7)
Malaxideae*	3 (1.6)	23 (1.7)	4 (1.4)
Orchidinae	1 (0.5)	20 (1.5)	4 (1.4)

subtribes (Angraecinae and Bulbophyllinae) have their centers of diversity in other regions such as Brazil and not on the Isthmus of Panama. On the other hand, groups such as Eriopsidinae, Gastrodieae, Ponerinae, and Triphorinae, are not diverse in the Neotropics.

The genera with the most species are shown in Tables 3 and 7. The most diverse are: *Epidendrum*, 206 spp. (70% of Laeliinae and alone exceeding 100 species), *Stelis* (88 spp.), *Lepanthes* Sw. (66 spp.) and *Pleurothallis* (54 spp.) (together accounting for 50% of Pleurothallidinae), *Camaridium* 48 spp., *Scaphyglottis* and *Sobralia* Ruiz & Pav. with 39 spp. Of the 187 genera recorded, 159 (85%) have fewer than ten species and represent 52% of the flora, while the remaining 15% of the genera contains 48% of the species (Fig. 20–26). Similar to its geological history, Panama and Costa Rica show a strong floristic relationship with the Tropical Andes. When analyzing the most numerous genera of the Pleurothallidinae (the most diverse Neotropical subtribe) that reach the highest number of species in the Andes such as *Lepanthes*, *Pleurothallis s.l.*, *Stelis s.l.* as well as *Brachionidium* Lindl. and *Platystele* Schltr., we found a clear trend. These genera are more diverse in Costa Rica and Panama than in other regions of Central America. When comparing the floristic data of Panama with the flora of Ecuador, one of the most intensively studied Andean countries (Dodson 2003), we found that there is proportionately the same trend. The genera with the most species are *Epidendrum*, *Pleurothallis* (> 400 spp.), and *Stelis s.s.*, *Lepanthes* (> 300 spp.). Other groups with high number of species in

Table 7. The most diverse orchid genera in Panama.

Genera	Species number	Percentage of the flora
Epidendrum	206	15.09
Stelis	88	6.45
Lepanthes	66	4.84
Camaridium	48	3.96
Pleurothallis	48	3.52
Scaphyglottis	39	2.86
Sobralia	39	2.86
Specklinia	34	2.49
Oncidium	32	2.34
Dichaea	26	1.90
Masdevallia	26	1.90
Telipogon	23	1.68
Elleanthus	23	1.68
Maxillaria	21	1.54
Prosthechea	21	1.54
Habenaria	20	1.47
Platystele	20	1.47
Trichosalpinx	18	1.32
Malaxis	15	1.10

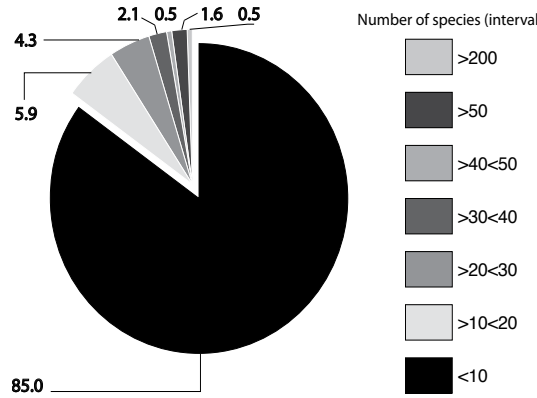

Figure 20. Percentage of the number of genera with their respective number of species.

the Andes include *Fernandezia* Lindl., *Telipogon* Kunth and terrestrial genera such as *Aa* Rchb.f. and *Petrichis* Lindl. are other examples of Andean influence (Dodson 2003, García-Castro *et al.* 1993). The results found are similar to that of Costa Rica in terms of number of taxa (Dressler 2003c). The definition of LCA treating Costa Rica and Panama as two areas with high biological similarity is supported by our data. Unpublished results on the floristic affinities of LCA with other areas of the Neotropics show that Panama shares at least 70% of its orchid flora with Costa Rica (Bogarín *in prep*.). Floristic inventories in Costa Rica have also revealed a strong component of Panamanian species mainly in the region of the Cordillera de Talamanca, strengthening a close biological relationship (Bogarín *et al.* 2008, Karremans *et al.* 2012, Fernández *et al.* 2014). Most species of *Epidendrum*, *Lepanthes*, *Pleurothallis*, and *Stelis* found in both countries are in the region of Talamanca. However, the whole country does not have close relations with Costa Rica. The central regions (Coclé), and southeastern Panama (Panama, Darién and comarcas Emberá, Guna Yala, Kuna de Madugandí and Kuna de Wargandí) show more affinities to South American taxa, which are not distributed in Costa Rica or even in the western provinces (Chiriquí and Bocas del Toro and part of Veraguas). Among them we can mention *Houlletia odoratissima* Linden ex Lindl. & Paxton, *Huntleya fasciata* Fowlie, *Kefersteinia mystacina* Rchb.f., *Lycaste campbellii*, *Lycaste powellii* Schltr., *Miltoniopsis roezlii* (Rchb.f.) God.-Leb., *Selenipedium chica* and genera such as *Eloyella* P. Ortiz, *Euryblema* Dressler, *Koellensteinia* Rchb.f., *Neomoorea* Rolfe and *Rudolfiella* Hoehne, absent in northern Central America (Dressler 2003c).

The Southern Pacific region of Panama is geologically and biologically more related to the Department of Chocó in Colombia. Recent studies in the Serranía del Baudó support this floristic relationship. Misas (2005) documented from this region with several species described from Panamanian material. Of the 357 species recorded, 167 (48%) are also found in Panama, mostly in the central and southeast. Among the species recorded are: *Epidendrum flexuosissimum* C.Schweinf., *Lockhartia obtusata* L.O. Williams, *Lycaste campbellii*, *L. powellii*, *Scaphyglottis coriacea* (L.O. Williams) Dressler and *Specklinia areldii* (Luer) Pridgeon & M.W. Chase among others. Additionally, we determined a specimen of *Cryptocentrum misasii* P. Ortiz & Carnevali, recently described from Serranía del Baudó by Carnevali *et al.* (2012) that was collected in

the Darién National Park. These data demonstrate that the increasing collecting efforts and the publication of floristic treatments in the border provinces of Panama and Colombia will help to better understand its narrow phytogeographical relationships. There are few groups with greater diversity in northern Mesoamerica than is found in Panama. *Barkeria* Knowles & Westc. with about 20 species in Mesoamerica and *Rhynchostele* Rchb.f. with a center of diversity in Mexico and Guatemala, among others, contain a single species in Panama. LCA can be seen as a biotic unit, but it could in turn be subdivided on its orchid diversity into biogeographic provinces proposed for other groups such as fish, insects and birds (Myers *et al.* 2000).

Although at genus level there is a similarity with neighboring areas of the isthmus, at the species level the picture may be different for some groups. By analyzing the most diverse genera we noted that few species (mainly in the Pleurothallidinae) are shared between the tropical Andes and LCA. For example, of the nearly 150 species of *Lepanthes* of Costa Rica and Panama, only two species are shared with Colombia and Ecuador, countries whose floras each reported over 300 species (Luer 2006, Luer & Thoerle 2012). Again floristic work intensification in the southeastern region of Panama may change this scenario. However, it is clear that there are certain trends towards more specific biogeographic characterization for LCA. The other diverse groups such as *Maxillaria*, *Pleurothallis* and *Stelis* have been subject to nomenclatural changes and generic recircumscriptions (Pridgeon & Chase 2001, Luer 2002a, Blanco *et al.* 2007). Furthermore, *Epidendrum* (206 spp.), the largest genus in Panama, is accepted as a broadly defined genus. However, because of their heterogeneity, about 35 genera proposed so far are currently reduced in synonymy (Hágsater & Salazar 1993, Hágsater 1999, 2001, 2010, 2013, Hágsater & Sánchez 2004, 2006, 2007, 2008, 2009, Hágsater & Soto Arenas 2005). All these nomenclatural issues suggest that the phytogeographic conclusions should be interpreted in context.

A distribution analysis of species recorded in this study reveals that Panama shares the majority of taxa with: Costa Rica (90.6%), Colombia (15.6%), Ecuador (12.5%) and northern Mesoamerica (9.3%). In the past decade 108 species, belonging to 38 genera, were described based on Panamanian material. Some species described prior 2004 were not included by Correa *et al.* (2004). About 44.9% of these records are still endemic to Panama, 47.3% are shared with Costa Rica, 6.7% with Colombia and 2.4% with other regions of the Neotropics. These data support the narrow floristic relations between Costa Rica and Panama formerly discussed. However, we must also consider that there is some bias regarding botanical exploration, with most expeditions undertaken of greater intensity in the provinces bordering Costa Rica and less intense toward the provinces bordering Colombia. Despite the low percentage of species that Panama shares with Colombia and Ecuador in terms of new floristic contributions of the last decade, it is expected that an increase in botanical exploration in the province of Darién and surrounding areas will reveal more species in common. Unfortunately, the access to this area is restricted and problematic, hampering research efforts. It is likely that the number of records now regarded as endemic will decrease with the increasing botanical explorations in regions neighboring Costa Rica and Colombia.

Ecologically, the family is more diverse at elevations from 1500 to 2800 m where most of the species are found. Regions such as the dry lowland areas of Azuero at sea level are poor in orchid species. The highlands of Volcán Barú, Cerro Echandi, Cerro Fábrega and Cerro Itamut are less diverse as they are located above 3000 m elevation; however, they are the only places in Panama where it is possible to observe some genera such as *Pterichis* or some species of *Telipogon*. About 173 (12,7%) of the species recorded are terrestrials and 1193 (87,3%) are epiphytes. Some species (*Eriopsis* Lindl., or some species of *Epidendrum*, *Sobralia* and *Elleanthus*) exhibit both habits, existing as either terrestrials and / or epiphytes. Other species such as *Vanilla* Mill. with eight species can be considered climbing or scandent vines. Some species of Pleurothallidinae, Laeliinae, Maxillariinae can be seen in rocky, humid, mossy areas but they cannot be considered strictly terrestrials.

So far we have analyzed some of the biological, evolutionary and geological factors behind the numbers found in the flora of Panama. However, the knowledge of a region involves an analysis of the level of effort that the scientific community has undertaken in order to understand the diversity of a particular site.

A total of 686 taxa described (658 species, 3 subspecies and 25 varieties) in 131 genera were based

Table 8. Authors who published most of the basionyms of Panama.

Author	Standard form	Number of species
Carlyle A. Luer	Luer	148
Rudolf Schlechter	Schltr.	117
Robert L. Dressler	Dressler	112
Heinrich G. Reichenbach	Rchb.f.	64
Eric Hágsater	Hágsater	55
Oakes Ames	Ames	51
Louis Williams	L.O.Williams	43
Charles Schweinfurth	C.Schweinf.	34
John T. Atwood	J.T.Atwood	13
John Lindley	Lindley	9

on type material collected in Panama. Of the total, 392 (57.2%) names are accepted as names lacking synonyms, 158 (23.0%) are accepted as homotypic synonyms and 136 (19.8%) have been treated as heterotypic synonyms. The genera with most species described are: *Epidendrum* (112 spp.), *Pleurothallis* (86 spp.), *Lepanthes* (45 spp.), *Sobralia* (33 spp.), *Maxillaria* (31 spp.), *Oncidium* and *Stelis* (30 spp.). The authors that published most species of orchids in the flora of Panama are shown in Table 8. Luer, Schlechter and Dressler are the major contributors to the taxonomy of Orchidaceae of Panama (Figs. 12C, 15, 16). Schlechter through C.W. Powell managed to describe several species in the early stages of orchid research in Panama (Figs. 11, 12C). Dressler's major contributions were made during his more than 20 years at the STRI in Balboa, Canal Zone and Luer contributed with the taxonomy of Pleurothallidinae, the largest subtribe in Panama. The most important herbaria for the orchid flora of Panama in terms of type specimens are summarized in Table 9. Most of the type specimens of the species described by Schlechter were lost in Berlin (Christenson 1991a, 1991b, 1991c). We recorded 97 names that have been lectotypified. Most of the specimens that were lost at Berlin correspond to Powell's collections described by Schlechter. Duplicates are mostly found at AMES, BM, K, MO, S and W (Christenson 1991b). AMES is an important herbarium because it houses copies of Schlechter's original drawings of types made under his supervision (Ames 1944) as well as the majority of

Table 9. Number of type specimens deposited in the most important herbaria for Panama.

Herbaria (Acronym)	Holotypes	Isotypes	Lectotypes
MO	157	53	4
B	115	0	0
SEL	104	10	0
AMES	97	37	81
W	54	0	6
US	37	7	0
AMO	33	6	0
PMA	20	47	0
K	14	13	5
F	11	10	0
FLAS	9	6	0
CR	5	5	0
NY	4	6	0

lectotypes (Table 9). Syntypes are cited for ten names, all described by Schlechter or Reichenbach. Seven herbaria in the United States keep more than 60% of the holotypes, 10% is kept in Europe (about 17% were lost in B), 5% in Mexico at AMO (mostly *Epidendrum*) and only 3% are kept in Panama (all at PMA herbarium). The MO herbarium is the most important in terms of type specimens for the orchid flora of Panama (Table 9). Figure 17 shows some locations where type specimens have been collected in Panama.

Some genera have traditionally been studied more intensively than others. In addition to the recognized contributions of Schlechter, Ames and L.O. Williams to the Panamanian orchids, Dressler promoted the study of Orchidaceae of the Isthmus in a broad sense. He made major contributions in *Sobralia* and *Elleanthus*, *Chysis* Lindl., *Oncidium*, *Trichopilia* and *Telipogon* among others. Hágsater and colleagues have led to a better understanding of *Epidendrum*, Atwood in *Maxillaria s.l.* and Luer in Pleurothallidinae. The decreasing activity of these scientists in the flora of Panama, has led to a slowdown in terms of scientific publications in comparison with neighboring countries such as Costa Rica (Bogarín *et al.* 2013b). Furthermore, many areas remain unexplored for orchids. The most urgent areas to be explored are the Cordillera de Talamanca, on both Pacific and Caribbean slopes, indigenous comarcas

Table 10. Twenty genera with the most endemic species in the orchid flora of Panama.

Genus	Endemic species	Total species
Epidendrum	53 (18.0)	206
Pleurothallis	23 (7.8)	54
Stelis	23 (7.8)	88
Lepanthes	21 (7.1)	66
Telipogon	17 (5.8)	23
Sobralia	16 (5.4)	39
Masdevallia	9 (3.1)	26
Camaridium	8 (2.7)	48
Specklinia	7 (2.4)	34
Oncidium	6 (2.0)	32
Microchilus	6 (2.0)	12
Scaphyglottis	5 (1.7)	39
Brachionidium	5 (1.7)	12
Trichopilia	5 (1.7)	12
Habenaria	4 (1.4)	20
Trichosalpinx	4 (1.4)	18
Kefersteinia	4 (1.4)	11
Dichaea	3 (1.0)	26
Maxillaria	3 (1.0)	21
Platystele	3 (1.0)	20

Table 11. Relationship between the number of endemic species and the total of species of the genera with most endemic species.

Genus	Endemics/total
Telipogon	73.9
Microchilus	50.0
Pleurothallis	42.6
Brachionidium	41.7
Trichopilia	41.7
Sobralia	41.0
Kefersteinia	36.4
Masdevallia	34.6
Lepanthes	31.8
Stelis	26.1
Epidendrum	25.7
Trichosalpinx	22.2
Specklinia	20.6
Habenaria	20.0
Oncidium	18.8
Camaridium	16.7
Platystele	15.0
Maxillaria	14.3
Scaphyglottis	12.8
Dichaea	11.5

(albeit with inherent problems obtaining collection permits), the Caribbean side of Veraguas, Colón, Panama and the foothills of Majé, San Blas, Sapo and Darién. Panama is a privileged country biologically; however we estimate that much work remains to complete a floristic treatment that reveals more realistic data on the orchid flora that the country hosts. This checklist is a starting point in this direction and we hope that this contribution will encourage and boost orchid research on the Isthmus of Panama and the surrounding regions. We are still working to develop a taxonomic illustrated treatment covering all the Orchidaceae of Panama (Bogarín *et al.* 2013b).

Endemism. A total of 296 (21.7%) endemic species in 69 (36.9%) genera were recorded (Table 3). This percentage of endemism is superior to other Central American countries except Costa Rica and southern Mexico (Ossenbach *et al.* 2007). The high number of species in the most diverse taxa of the flora of Panama is proportionally reflected in the number of endemic species. For example, Epidendroideae concentrates 94.3% of the endemic species, the tribes Epidendreae (58.8%) and Cymbidieae (27.5%) and subtribes Pleurothallidinae (37.2%), Laeliinae (20.9%) and Oncidiinae (13.2%) are the groups with the most endemic species in the country (Tables 4,5,6). The genera with the highest number of endemic species are *Epidendrum* (53 spp., 18%), *Pleurothallis* (23 spp., 7.8%), *Stelis* (23 spp., 7.8%), *Lepanthes* (21 spp., 7.1%), *Telipogon* (17 spp., 5.8%) and *Sobralia* (16 spp., 5.4%). These six genera account for 50% of endemic species (Table 10). The remaining genera have less than ten endemic species and 31 (45%) of the genera have only one endemic species. The percentages of endemism within Pleurothallidinae are

high. It is likely that the complex pollination systems propitiated narrow distributions in some genera. According to Ackerman (2014), the exploitation of highly diverse groups of pollinators such as Diptera (Pleurothallidinae), Lepidoptera (*Epidendrum*) and Hymenoptera (*Sobralia*) is one of the possible reasons for the diversification of Neotropical orchids. Clear examples are the genera pollinated by sexual deception such as *Lepanthes* and *Telipogon* that "exploit" highly diverse groups of insects belonging to Sciaridae and Tachinidae respectively (Dodson 2003, Blanco & Barboza 2005). Both groups are quite diverse in the Andes and the highlands of Costa Rica and Panama where the levels of endemism are also high.

Within the system of classification followed in this paper we did not document endemic genera for the flora of Panama. However, this conclusion should be viewed with caution. The arbitrary political boundaries of countries and different nomenclatural trends could alter or skew biogeographic interpretations. For example the group of species allied to Salpistele Dressler (= *Stelis s.l.*) is not endemic to Panama as there is one species in Costa Rica and if considered a member of *Stelis s.l.* it would not be endemic to Panama. But nomenclatural issues and political boundaries aside, clearly the *Salpistele* group is endemic to Costa Rica and Panama. Other groups that are more diverse on the isthmus are *Dracontia* Luer and *Unciferia* (Luer) Luer (= *Stelis s.l.*), Certain clades, including *Specklinia*, *Epidanthus* L.O. Williams, *Neowilliamsia* Garay and *Oerstedella*, members of *Epidendrum*; and *Panarica* Withner & P.A.Harding (=*Prosthechea* Knowles & Westc.) among others, can be considered endemic or more diverse in Costa Rica and Panama than in neighboring areas (Dressler 2003c). Other genera that have suffered nomenclatural changes, such as *Camaridium* and *Scaphyglottis*, also show the tendency to have a greater number of endemic species in Costa Rica and Panama (Dressler *et al.* 2004, Kirby 2011). Despite being a geologically young region, the evolution of the orchids on the isthmus is complex. There are several theories that attempt to explain this phenomenon. Some are related to the ancient volcanic arc of islands that created favorable sites for speciation that joined and mixed their floras with the existing continental populations. This is a probable hypothesis to explain the presence of certain lineages on the isthmus but has yet to be tested by integrating molecular and biogeographical data (Burger 1980).

By comparing the ratio of the number of endemic species with the total number of species in the flora of Panama for each genus, the highest percentage of endemism is found in *Telipogon* (73.9%) followed by *Microchilus* (50%), *Pleurothallis*, *Brachionidium*, *Trichopilia* and *Sobralia* (between 41-43%), *Kefersteinia*, *Masdevallia* and *Lepanthes* (between 31-36%), *Epidendrum* and *Stelis* (25–26%), *Trichosalpinx* (22.2%) and the remaining genera have relationships between 7 and 20% (Table 11). Two genera have all their species endemic: *Dressleria* Dodson (3 spp.) and *Euryblema* (1 sp.). *Dresslerella* Luer has four species recorded of which three (75%) are endemic. The high percentage of endemism in *Telipogon* (Dodson & Escobar 1993) should not be surprising considering its complex pollination syndrome (Dodson 2003). However, if we consider that those species were collected very close to Costa Rica, it is likely that some of them will also be found there. On the other hand, the high number of endemic species in *Telipogon*, *Sobralia*, *Epidendrum* and other groups within Pleurothallidinae is also attributable to a greater effort in the study of those genera. The above groups were the preferential study subjects of the taxonomists who made the major contributions to the orchid flora of Panama. It is still necessary to make more comprehensive taxonomic studies, especially in subtribes Laeliinae, Pleurothallidinae, Goodyerinae and Spiranthinae both in Panama and in its neighboring countries, in order to have a more precise conclusion regarding endemism.

Interpretations of endemism evaluated in a context of political boundaries are also biased and lose sense in biological terms. For example, Panama "lost" 11 endemic species of *Lepanthes* because they were recorded in Costa Rica (Fernández *et al.* 2014). However, these collections of *Lepanthes* in Costa Rica come from biogeographical regions related to Panama, such as the Cordillera de Talamanca. Despite the caution required when making interpretations of endemism at the country level, it is nevertheless necessary to record these data because the political decisions on conservation and the sustainable use of natural resources vary from one border to another.

Exotic flora. In Panama, four (0.3%) species are currently recorded as non-native wild populations.

The percentage is low compared to the West Indies but is similar to Costa Rica (Dressler 2003c, Ackerman 2014). At least *Arundina graminifolia* (D. Don) Hochr., *Spathoglottis plicata* Blume from Asia and *Oeceoclades maculata* (Lindl.) Lindl. from Africa and Madagascar are widely dispersed in the Neotropics. *Arundina graminifolia* and *S. plicata* plants are often grown as ornamentals in gardens and naturalization was recorded in Costa Rica, Cuba and Hawaii (Pupulin 2005b, Ackerman 2007). In the case of *A. graminifolia*, the flowers with a trumpet-like shaped lip (similar to *Sobralia*) apparently attract bees that pollinate them. *Spathoglottis plicata* plants are often self-pollinated and do not require native pollinators for reproduction. Both species are terrestrial and grow in places with direct sunlight such as rocky roadsides (Cohen & Ackerman 2009).

Oeceoclades maculata is a fast growing orchid and was classified as an invasive species (Ackerman 2007). It is perhaps the most common introduced orchid in Panama. It is found throughout the Neotropics from Florida (USA) to Brazil. Populations of *O. maculata* are common along both the Caribbean and Pacific lowlands were they are often found among understory vegetation. The adaptation to grow in a wide variety of environments contributes to its invasive prowess. Reproductive success is due to self-pollination (it does not need native pollinators) and high rates of fruit production (Cohen & Ackerman 2009).

The most curious case is perhaps the naturalization of *Phalaenopsis stuartiana* Rchb.f., an endemic orchid from the island of Mindanao in the Philippines (Fig. 26B). It has only been reported from Isla Colón in Bocas del Toro Archipielago where it probably encountered climatic conditions and coastal environments like those on Mindanao. It is the only epiphytic orchid naturalized in Panama. Its introduction, population status and pollination have yet to be investigated. To date, the few herbarium records that exist are all known from this site.

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