

A MONOGRAPH OF THE GENUS *LOCKHARTIA* (ORCHIDACEAE: ONCIDIINAE)

By

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To my parents, who have always supported and encouraged me in every way.

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LIST OF ABBREVIATIONS

3'ycf1	1500 base-pair region near the 3' end of the putative gene <i>ycf1</i> (plastid DNA)
5'ycf1	1200 base-pair region near the 5' end of the putative gene <i>ycf1</i> (plastid DNA)
bp	base pairs
CI	consistency index
cm	centimeters
cult.	cultivated (in specimen citations)
FAA	formalin-alcohol-acetic acid solution (0.5:9:0.5)
FLD	field locality data
H	height
ITS	internal transcribed spacer (nuclear DNA)
km	kilometers
kV	kilovolts
L	length
LM	light microscope or light microscopy
LS	longitudinal section
m	meters
mg	milligrams
min	minutes
mL	milliliters
ML	maximum likelihood
mm	millimeters
mM	millimolar
MP	maximum parsimony

ng	nanograms
OTU	operational taxonomic unit
RI	retention index
s	seconds
SD	standard deviation
SEM	scanning electron microscope
sp.	species (singular)
spp.	species (plural)
trnH-psbA	intergenic spacer between the <i>trnH</i> and <i>psbA</i> genes (plastid DNA)
trnL-F	intergenic spacer between the <i>trnL</i> and <i>trnF</i> genes (plastid DNA)
TS	transverse section
W	width
μg	micrograms
μL	microliters
μm	micrometers
μM	micromolar

Abstract of Dissertation Presented to the Graduate School
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A MONOGRAPH OF THE GENUS *LOCKHARTIA* (ORCHIDACEAE: ONCIDIINAE)

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The Neotropical orchid genus *Lockhartia* is morphologically very distinct from others in the subtribe Oncidiinae. Although a few taxonomic revisions of this genus have been published in the past, the species circumscriptions have heretofore remained unsatisfactory, and the evolutionary relationships among them have remained unknown. No detailed morphological or anatomical survey focused on the genus has been carried out before. The present monographic treatment aims to improve our understanding of this group of plants.

A review of the taxonomic history of the genus is presented, which explains the fragmentary state of knowledge prior to the beginning of this project. It details the contrasting views of different taxonomists on the systematic position of these plants, which reflects their unusual morphological traits. It also lists the existing floristic works that deal with the genus, which often apply inconsistent species delimitations and unsatisfactory keys for their identification. It also provides a summary of the various phylogenetic studies that have included species of *Lockhartia*.

A taxonomic revision of the genus is presented, which provides updated species circumscriptions, detailed morphological descriptions and geographic distribution

summaries, and exhaustive herbarium specimen citations. Twenty-nine species are recognized, including five new species: *Lockhartia compacta* R. Vásquez & M. A. Blanco, *L. endresiana* M. A. Blanco, *L. oxyphylla* M. A. Blanco, *L. rugosifolia* M. A. Blanco, and *L. tenuiflora* M. A. Blanco.

A detailed morphological and anatomical survey of the genus is presented. The structure of roots, stems, leaves, inflorescences, flowers, fruits, seeds, and seedlings is documented and discussed. The unusual shoot morphology of these taxa is unlike that of any other members of subtribe Oncidiinae. Particular attention is given to the strange structure of the inflorescences (for which the term “pseudocyme” is coined), which appears to be unique among the angiosperms. On morphological grounds, the genus *Lockhartia* can be divided in two subgenera, *Lockhartia* and *Pseudobulbosa*. The former is subdivided into three informal phenetic groups: the Parthenocomos group, the Longifolia group, and the Imbricata group. In turn, the latter is subdivided into three subgroups: the Imbricata subgroup, the Oerstedii subgroup, and the Acuta subgroup.

A phylogenetic study of the genus is presented. Separate analyses using DNA sequences and morphological data have contrasting results, with the morphological analysis resulting in much less resolved cladograms. Molecular analyses indicate that the major groups mentioned above may not be monophyletic, and thus they are not formally recognized as subgeneric taxa. Morphological analyses provide some support for the hypothesis that *Lockhartia genegeorgei* (the sole member of subgenus *Pseudobulbosa*) may be an intergeneric hybrid, but this cannot be confirmed in the absence of molecular data. Finally, the evolution of selected morphological characters is

traced on a cladogram adapted from the results of molecular analyses, and their putative ecological and evolutionary significance is discussed in this context.

CHAPTER 1 GENERAL INTRODUCTION

Orchids of the genus *Lockhartia* are naturally distributed from central-western Mexico to southeastern Brazil (Fig. 1-1). They are epiphytes that belong in the subtribe Oncidiinae, a group that contains ca. 1600 species throughout the Neotropics (Pridgeon *et al.*, 2009). Most species have a very particular vegetative morphology, with elongate stems completely covered by imbricate, laterally flattened leaves. The shoots resemble hair braids, and for this reason species of *Lockhartia* are often called “braided orchids”.

Historically, the systematic position of this genus has been controversial, although recent phylogenetic studies based on molecular data have confirmed its relatively isolated position within the subtribe Oncidiinae (Taxonomic History, Chapter 2).

For many years, *Lockhartia* has been considered a taxonomically confusing genus even when plants are occasionally cultivated as ornamentals or botanical curiosities (Hawkes, 1965). The detailed morphology and anatomy of these plants are very incompletely known, as are the evolutionary relationships among its species.

The present study, designed as a traditional botanical monograph, aims to resolve these knowledge voids. The information presented here will hopefully prove useful for future studies on the biology and conservation of these plants.

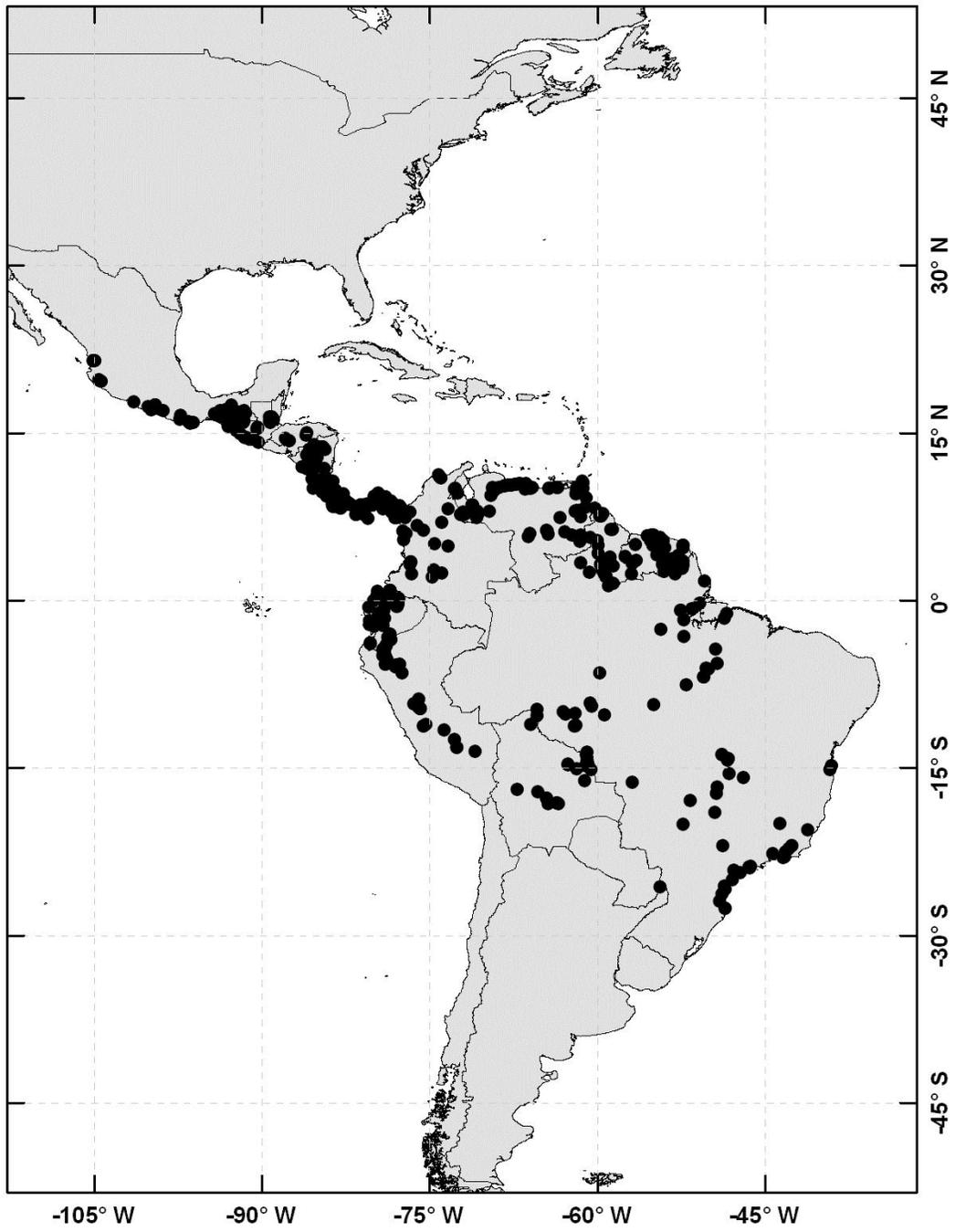


Figure 1-1. Geographic distribution of the genus *Lockhartia*, based on herbarium specimen records. See Taxonomic Revision (Chapter 3) for details.

CHAPTER 2 TAXONOMIC HISTORY

The earliest known collections of *Lockhartia* were made by Jean-Baptiste Patris (1764 to 1783, French Guiana) and by Hipólito Ruiz and José Antonio Pavón (1776, Peru). Other early collections were made by Jean Baptiste Leblond (1784 to 1789, French Guiana), by Martín de Sessé y Lacasta (1789, Mexico), Alexander von Humboldt and Aimée Bonpland (1799, Venezuela), and by Juan Tafalla (1803, Ecuador).

In 1783, Lamarck described the first species of *Lockhartia* as *Epidendrum imbricatum*, based on Patris's collection. However, Lamarck did not cite a type specimen, and his description was quite simplistic and lacked an illustration; as a result, the true identity of *E. imbricatum* remained in obscurity until 1952, when Hoehne concluded it must have been a species of *Lockhartia*. The specimens on which Lamarck based his description were identified only during the preparation of the present monograph (Taxonomic Revision, Chapter 3).

In 1792, Richard described the same species as *Epidendrum biserra* based on Leblond's collection. Live plants of this species were sent to the United Kingdom by David Lockhart, the first superintendent of the Royal Botanic Gardens in Trinidad; when one of these flowered in cultivation in 1827, William Jackson Hooker described it as *Lockhartia elegans* in his honor, establishing the genus. However, a few months later, George Loddiges (who also managed to flower a plant in his commercial greenhouse), transferred *L. elegans* to *Fernandezia* Ruiz & Pav., a genus described in 1794.

Even though Ruiz and Pavón never described any species of *Lockhartia* under their genus *Fernandezia*, they annotated their own collection of *Lockhartia* from Peru

and the Mexican specimen of Sessé with the generic name *Fernandezia*. That probably influenced Loddiges. Lindley (1833) followed this circumscription, and from 1836 to 1846 he described three species of *Lockhartia* under the genus *Fernandezia* (*F. acuta*, *F. lunifera*, and *F. longifolia*). Lindley (1846) placed *Fernandezia* in an unranked group he called Vandeeae, subgroup Brassidae.

At first, Heinrich Gustav Reichenbach also included *Lockhartia* in *Fernandezia* and described *F. parthenocomos* in 1852; however, a few weeks later he transferred that species to *Lockhartia*, and went on to describe a remarkable 16 additional species in that genus throughout his life. Reichenbach (1855) was also the first to publish a revision of the genus (reprinted in Reichenbach, 1864), in which he recognized 10 species. Reichenbach placed *Lockhartia* in his "Subordo Epidendreae" (roughly corresponding to the currently accepted subfamily Epidendroideae; Chase *et al.*, 2003). However, Reichenbach's important contribution to the taxonomy of *Lockhartia* was eclipsed by the provision in his will to lock up his herbarium for 25 years after his death (1889–1914). As a consequence, his specimens were not available for study during that period and several synonymous names were published by Schlechter and Kraenzlin.

Bentham (1881) followed Lindley in placing *Lockhartia* in tribe Vandeeae, but he elaborated Lindley's classification by dividing each tribe into subtribes. Bentham's tribe Vandeeae contained eight subtribes, including the Oncidieae and the Sarcantheeae (endings for suprageneric taxa were not yet standardized then). Bentham divided tribe Sarcantheeae into three "series", and placed *Lockhartia* in the first series along with *Centropetalum* Lindl. (currently *Fernandezia*), *Pachyphyllum* Kunth, and four other

Asiatic genera. Bentham acknowledged that his subtribe Sarcantheae was based mostly on vegetative characters and that its subdivisions were probably too artificial.

Soon after, Pfitzer (1882), Möbius (1887), and Ridley (1896) expressed that *Lockhartia* was better classified in the Oncidieae, instead of the Sarcantheae. Pfitzer (1887, 1889), in his own family-wide classification of the Orchidaceae, placed *Lockhartia* in a group called the "Monandrae-Oncidiinae-Odontoglossae".

In his famous horticultural and systematic treatment of the orchid family, "Die Orchidee", Schlechter (1914) listed the species of *Lockhartia* found in cultivation in Europe at the time. Schlechter considered that *Lockhartia* was very distinct morphologically, and created a subtribe exclusively for it, Lockhartiinae. Later, Schlechter (1926) placed *Lockhartia* in a tribe of its own (Lockhartieae), in subfamily Monandrae, division Acrotonae, tribe Kerosphaerae, series Pleuranthae, subseries Sympodiales (a system modified from that of Pfitzer). Despite other classifications proposed during the following decades (below), Schlechter's (1926) classification of the Orchidaceae was the most widely accepted until the 1960's (e.g., Schweinfurth, 1959).

Kraenzlin (1923) published a second revision of *Lockhartia*; he recognized 29 species, although not exactly the same ones recognized in the present monograph. Kraenzlin described four new species of *Lockhartia*, two of which are considered synonyms here. He illustrated most species, although several of his drawings are somewhat inaccurate and thus not very useful for identification (Garay, 1970b).

Kraenzlin (1923) did not recognize the tribe Lockhartiinae, and instead placed *Lockhartia* in an unranked group called the "Pseudomonopodiales", within the monandrous orchids. Besides *Lockhartia*, this group included the genera *Pachyphyllum*,

Centropetalum (currently *Fernandezia*), *Dichaea* Lindl., *Orchidotypus* Kraenzl. (currently a synonym of *Pachyphyllum*), and *Pterostemma* Kraenzl. These genera share a "pseudomonopodial" growth habit (i.e., shoots with seemingly indeterminate apical growth, but that normally stop growing once they reach a certain length and then generate daughter shoots from the base). *Lockhartia*, however, differs from the others in that its stems have the potential to produce terminal inflorescences, and thus have truly determinate growth. It is unclear if Pfitzer or Kraenzlin realized this. Hawkes (1952), while considering the merits of Kraenzlin's classification, felt that *Lockhartia* was misplaced in this group and suggested that it was better kept in Schlechter's subtribe Lockhartiinae.

Mansfeld (1937) was the next orchidologist to propose a family-wide classification, and he followed Schlechter in recognizing a subtribe Lockhartiinae within tribe Vandeeae. Aside from this, he did not make any contributions to the taxonomy of *Lockhartia*.

Dressler and Dodson (1960) proposed a completely new classification of the Orchidaceae, and put *Lockhartia* in the "*Oncidium* alliance". They remarked that "*Lockhartia* is distinctive in habit, but has no other consistent feature to distinguish it from the other genera of this group."

Wirth (1964) acknowledged that *Lockhartia* is likely an isolated lineage within the Oncidiinae, but suggested that it could be related to *Oncidium* Sw. section *Walueuwa* (Regel) Schltr. (the latter currently lumped with *Gomesa* R. Br.; Pridgeon *et al.*, 2009).

Garay (1963) hypothesized that *Lockhartia* is closely related to *Oncidium* section *Iridifolia* (Kraenzl.) Garay (= *Psygmorchis* Dodson & Dressler, currently placed in *Erycina* Lindl.; Pridgeon *et al.*, 2009) because of the shared lack of an abscission layer in the

leaves and their superficially similar flowers. Dodson and Dressler (1972) argued against this view and pointed out significant differences in the pollinarium structure of both taxa and suggested that *Lockhartia* could be related to *Centropetalum* (= *Fernandezia*). Dressler (1974) modified his original classification accordingly and transferred *Lockhartia* in subtribe Lockhartiinae, tribe Pachyphyllae Dressler.

Later, Dressler (1981) moved *Lockhartia* to subtribe Oncidiinae Benth., although in a subgroup of its own. Finally, Dressler (1993a) suggested that *Lockhartia* might be closely related to *Fernandezia*, *Pachyphyllum*, and *Raycadenco* Dodson (groups he also moved to subtribe Oncidiinae), based on their similar pollinarium morphology.

Senghas (1995) published a synopsis of *Lockhartia* as part of the posthumous “third edition” of Schlechter's “Die Orchidee”. He synonymized many names and only accepted 19 species. However, this treatment was obviously prepared in haste, and several of the photographs are misidentified. Senghas resurrected Schlechter's subtribe Lockhartiinae, and placed it with several other subtribes in a special group (“Tribella Bipolliniata”) within tribe Oncidieae. This group includes all the oncidoid genera with two pollinia per pollinarium (those with four pollinia were grouped under “Tribella Tetrapollinata”); however, it is not monophyletic according to DNA sequence data (Williams *et al.*, 2001).

Szlachetko (1995) also recognized subtribe Lockhartiinae within tribe Oncidieae, and he also included *Raycadenco*; Senghas (1995) put that genus in its own subtribe, Raycadencoinae.

In a cladistic analysis of morphological data of 98 genera of Orchidaceae, Freudenstein and Rasmussen (1999) recovered *Lockhartia* as sister to *Dichaea* (the

latter genus is nested in subtribe Zygopetalinae Schltr. according to molecular data; Pridgeon *et al.*, 2009, and references therein). They acknowledged that many of their results were probably caused by convergence of morphological traits, and did not make any taxonomic decisions based on them.

Chase and Palmer (1989; 1992) published the first molecular studies (analyzing plastid DNA restriction site variation) of subtribe Oncidiinae, but did not include species of *Lockhartia*. The first molecular phylogenetic study to include *Lockhartia* was that of Freudenstein and Chase (2001), for an assessment of the phylogenetic utility of the mitochondrial *nad1b-c* intron in Orchidaceae; they sampled only five species of subtribe Oncidiinae (as circumscribed by Pridgeon *et al.*, 2009, the classification followed here). *Lockhartia amoena*, the only species of the genus included in the latter study, was recovered as sister to a species of *Rodriguezia* Ruiz & Pav.

Williams *et al.* (2001a,b) published phylogenetic analyses of DNA sequence data of a larger number of taxa of the Oncidiinae, including two species of *Lockhartia*. Their results showed that *Lockhartia* formed a clade, nested within the subtribe but without good support for an exact placement. A similar result (with one species of *Lockhartia*) had been obtained previously in a phylogenetic analysis of subtribe Stanhopeinae and related groups (Whitten *et al.*, 2000).

Zelenko and Chase (2002) published a preliminary cladogram of subtribe Oncidiinae (probably produced before those published by Williams *et al.*, 2001), in which *Lockhartia* appears as sister to the Excavatum group of *Oncidium* (*Oncidium* section *Excavata* Kraenzl., now *Vitekorchis* Romowicz & Szlach., *pro parte*). Another cladogram showing this relationship was published by Chase *et al.* (2005) as a

summary of previous studies. However, a sister relationship between *Lockhartia* and the *Oncidium excavatum* group was neither shown or mentioned by Williams *et al.* (2001), nor was it recovered in any of their subsequently published analyses. *Vitekorchis* appears to be an isolated lineage within the Oncidiinae, but more closely related to *Oncidium* and related genera than to *Lockhartia* (Pridgeon *et al.*, 2009; Whitten *et al.*, in prep.).

A recent cladistic study of the Oncidiinae, based exclusively on morphological and anatomical data (Stern & Carlswald, 2006), included two species of *Lockhartia* but resulted in cladograms that were either unresolved or weakly supported.

Williams *et al.* (2005) cited unpublished analyses in which *Lockhartia* appeared as sister to a clade formed by the *Telipogon* Kunth, *Pachyphyllum*, and *Ornithocephalus* Hook. groups, and used two species of *Lockhartia* as an outgroup for their analysis of the *Telipogon* alliance. A similar relationship was found by Sandoval-Zapotitla *et al.* (2010b) with a combination of molecular and morphological characters. However, additional analyses using a much larger sample of taxa in the Oncidiinae and additional DNA regions (Whitten *et al.*, unpublished; preliminary results in Pridgeon *et al.*, 2009) have shown that *Lockhartia* represents an isolated group within the Oncidiinae (as previously hypothesized by Chase, 1986), separate from the clade formed by *Fernandezia*, *Pachyphyllum*, and *Raycadenco*, and apparently not sister to the above mentioned clades.

An interesting development in the taxonomy of *Lockhartia* was the discovery of *L. genegeorgei* D.E. Benn. & Christenson, described in 1998. The vegetative morphology of this taxon is highly aberrant for the genus; it has pseudobulbs and articulated,

conduplicate leaves, although the inflorescence and floral morphology is very similar to that of *Lockhartia* (Taxonomic Revision, Chapter 3). Bennett and Christenson established the subgenus *Pseudobulbosa* to accommodate this species (the only subgeneric division proposed to date), while Senghas (2001) considered it too distinct from *Lockhartia* and segregated it to the genus *Neobennettia* Senghas. Chase (2009) hypothesized that *L. genegeorgei* is simply a species of *Lockhartia* that shows several plesiomorphic character states. Another possibility is that *L. genegeorgei* is a natural hybrid between a species of *Lockhartia* and a species of *Oncidium*. Unfortunately, *L. genegeorgei* is rare and attempts to extract DNA from the few herbarium specimens available have failed. This species is provisionally accepted as a member of *Lockhartia* in the present treatment, pending analyses of molecular data (when available).

Annotated treatments of *Lockhartia* (often within larger floristic works, and not including unannotated or unvouchered checklists) have been published for various countries or regions: Belize (Ames and Correll, 1953; McLeish *et al.*, 1995), Brazil (Cogniaux, 1906), Central America (Hemsley, 1882-1886; Williams, 1956), Costa Rica (Ames, 1937; Dressler, 1993b; Atwood and Mora de Retana, 1999; Pupulin, 2002; Dressler, 2003), French Guiana (Lemée, 1955; Christenson, 1997), Guatemala (Ames and Correll, 1953), the Guyana Highland (Schweinfurth, 1967), Honduras (Nelson Sutherland and Ortiz Kafati, 2007), Mexico (Williams, 1951; McVaugh, 1985), Nicaragua (Hamer, 1984a; Hamer, 2001), Panama (Standley, 1928; Allen, 1949; Dressler, 1993b), Peru (Schweinfurth, 1961), Suriname (Werkhoven, 1986), Trinidad (Grisebach, 1864; Cogniaux, 1910; Schultes, 1960, 1967), and Venezuela (Ernst, 1878; Foldats, 1970).

The nomenclature and species circumscription in most of these differs from the present taxonomic revision.

Lockhartia is still poorly understood in Colombia, despite the large size of that country and its central position in the overall geographic distribution of the genus. This stems from a lack of a modern floristic treatment of Orchidaceae for that country, and the paucity of herbarium collections (in both Colombian and foreign herbaria).

CHAPTER 3 TAXONOMIC REVISION

The genus *Lockhartia* is one of the most distinctive among the Neotropical epiphytic orchids. Unlike most of its relatives in subtribe Oncidiinae, the plants lack pseudobulbs (except in one species) and have elongate stems with imbricate, equitant, unifacial leaves without an abscission layer. Inflorescences are produced from both the apex of the stem and the axils of the leaves. The inflorescences are also unique in the Orchidaceae in that they are pseudo-cymose (Schneckenburger, 1993), that is, they have sympodial development but clearly are derived from an ancestral raceme (the prevailing type of inflorescence among orchids). The structurally complex flowers are medium-sized to small, either white or yellow with brown blotches, and subtended by perfoliate floral bracts. Chapter 4 (Morphology and Anatomy) treats the morphology and architecture of the plants in more detail.

Species of *Lockhartia* occur from southern Mexico to Bolivia and Brazil; they are absent in the Caribbean, except for the island of Trinidad. Plants of *Lockhartia* can be found near sea level to ca. 2800 m elevation, in forests that do not experience a pronounced dry period.

William Jackson Hooker described the genus *Lockhartia* in 1827. To date, 56 basionym names have been validly published (8 of them in the last 20 years). Despite several attempts to revise the genus (Reichenbach, 1855; Reichenbach, 1864; Kraenzlin, 1923; Senghas, 1995), several species remain insufficiently characterized and/or poorly delimited. The present revision aims to provide a clear view of the taxonomy of the genus.

Materials and Methods

Materials

This revision is based on the study of herbarium material complemented by collections made in the field and from cultivated plants. The study of living material was critical to my understanding of morphological differences between several species. Approximately 2275 individual herbarium specimens (sheets with specimens and/or illustrations and jars with material preserved in liquid, representing 1514 different collections) from 67 herbaria were studied. The vast majority of these was examined directly; approximately 5% of the specimens were studied indirectly through photographic images, and many of these were duplicates of specimens studied directly.

The following herbaria provided specimen loans (§), images (†), and/or were visited (*). Acronyms follow Index Herbariorum (Thiers, 2011): AAU[‡], AMO[‡], B[‡], BH[‡], BM*, BR^{§‡}, BRIT[‡], C[‡], CAS* (including DS), CAY[§], CICY[§], CINCH[‡], COL[‡], CR*, DAV[‡], DUKE*, E[‡], F[§], FLAS*, FTG*, FSU[‡], G^{§*}, Harvard University Herbaria^{§‡} (A, AMES, GH, ECON), HLDG[‡], HOXA[‡], HUA[‡], INB*, INPA[‡], IRBR[‡], JAUM[‡], JBL*, K^{§‡*}, L[§], M*, MA^{‡*}, MEXU[§], MG^{‡§}, MICH[§], MO^{§*}, MOL[‡], NY^{§*}, OXF[‡], P*, PMA*, PH[§], QCA*, QCNE*, RB[‡], RENZ*, RSA[‡], S[‡], SCZ*, SEL^{§*}, SP[‡], TEX[§] (including LL), TRIN[§], U[§], UC^{§*}, US[§], USJ*, USM[‡], VEN[‡], W*, WIS[‡], WU*, XAL[§], and Z*.

Herbarium Methods

Specimens were compared to each other, to the type specimens (when these were available), to descriptions in the protologues (for all 55 validly published basionym names attributable to *Lockhartia*), and to descriptions in various floristic treatments (Taxonomic History [Chapter 2] has a complete list of floristic works consulted). The flowers of ca. 25 specimens were rehydrated by soaking them in concentrated ammonia

(NH₄OH) at room temperature (ca. 25°C) for 12–24 hrs and then washing them in tap water (Taylor, 1976). Rehydrated flowers were drawn (whole and dissected) using a dissecting microscope with a camera lucida attachment. Copies of the drawings were attached to the specimens.

The overall morphological variation was assessed visually, and selected morphological characters were measured (quantitative characters; Figs. 4-3A and 4-16) or scored (qualitative characters). Specimens that share a certain amount of similarity in these characters were assigned to morphospecies. These morphospecies were compared to type specimens and to literature descriptions, and names (and synonyms) were assigned to each. Descriptions for each accepted species were prepared, taking into account the variation observed in the available material (herbarium specimens and live plants), and all herbarium sheets were annotated.

After dehiscence, the fruits of *Lockhartia* rapidly dehydrate and shrink substantially, and their valves become reflexed. Undehisced fruits may shrink a little in diameter upon drying, but the length is not affected in a significant way. Thus, the shape and dimensions of fruits in the species descriptions are based on non-dehisced, presumably mature fruits from herbarium specimens (dehisced fruits were not measured), and also on mature fruits measured in life, when these were available.

Species Concepts and Circumscription

It would be difficult in the limited amount of time available for this study to carry out population genetic analyses in most natural populations of *Lockhartia*. Thus, a morphological concept has been adopted for the practical delimitation of species (i.e., a phenetic species concept *sensu* Judd *et al.*, 2008). It is assumed that the resulting morphospecies correspond to independent evolutionary lineages (i.e., the “evolutionary”

or various “phylogenetic” species definitions; Judd *et al.*, 2008). The possibility of limited hybridization or introgression among these presumed lineages is not excluded, as some of the observed morphological variation suggests this possibility for a few species pairs. However, it is assumed that these lineages have maintained a genetic pool mostly independent from each other (thus, the theoretical cohesion species concept is also implicitly accepted; Templeton, 1989).

For the most part, the analyses based on molecular data (obviously based on a relatively small set of individuals and an incomplete set of species) agree with the species circumscriptions that resulted from the taxonomic revision (Phylogeny, Chapter 5). The species recognized here are not necessarily assumed to be monophyletic; monophyly is not an appropriate criterion for species recognition because reticulate, nonhierarchical, and nondivergent relationships among conspecific individuals are incompatible with grouping by monophyly (Davis, 1999; Judd *et al.*, 2008).

Phenology

The flowering phenology of each species in its natural habitat is summarized in the species descriptions.

The collecting date of flowering specimens (including those that did not have any flowers present in the herbarium sheet, but whose labels indicated the presence of flowers) was recorded and entered in a Microsoft Excel spreadsheet. Specimens prepared from plants in cultivation were excluded to avoid introducing artifacts of abnormal flowering times caused by artificial environmental conditions.

For each species, the number of specimens in flower per month was plotted to obtain an indication of the intensity of flower production throughout the year (data not shown). The data for most species for which numerous (>25) flowering specimens are

available indicate that flowering occurs throughout the year, although with definite highs and lows depending on the season.

The phenology of fruit production was not described, mainly because fruits often remain attached to the inflorescences even after dehiscence, and, in some cases, it can be difficult to distinguish dehisced fruits from fruits that have split open due to pressing upon collection. Also, orchids that bear only fruits in the field are rarely collected for the herbarium because of the difficulty of identification; thus, fruiting specimens are undersampled. Fruit production, however, necessarily follows flower production (with an obvious delay for dehiscence and seed dispersal). Fruits generated through artificial pollinations tend to mature in 2 to 4 months after initiation.

Distribution

The geographic distribution for each species is summarized in the species descriptions. An estimated 50% of the herbarium specimens examined that have field locality data (FLD) have geographic coordinates (latitude and longitude). These were entered in a Microsoft Excel spreadsheet. For the rest of the specimens with FLD but without coordinates, these were found, whenever possible, with the aid of gazetteers, various online databases (e.g., www.geonames.org, www.biogeomancer.org), or the program Google Earth version 5.2.1 (www.google.com/earth/).

Whenever there was ambiguity as to the exact locality of a specimen, or if the coordinates given in the label were not in agreement with the indicated locality, the specimen was not used for mapping the distribution of the species. In a few cases where only a major political subdivision was indicated (e.g., province or municipality) and no other records of that species were available for the region, the coordinates of the approximate center of that political unit were entered as an approximation, as any

deviation from the actual point of collection would be minuscule in the scale of the resulting distribution maps of the entire species.

All obtained coordinates were transformed from their original format (commonly in degrees, minutes and seconds) to decimal degrees, and entered in the program ArcGIS version 9.3.1 (Esri, Redlands, California) to generate distribution maps for each species.

Taxonomic Treatment

Twenty-nine species of *Lockhartia* are recognized, including the anomalous *L. genegeorgei* (which is placed in a different genus by some authors; see comments under that species). Thus, 26 validly-published names have been assigned to synonymy (several of these for the first time). Five species new to science are also included among the 29 recognized species.

Geographic coordinates were obtained for a total of 982 collections (ca. 66% of all specimens examined). Many of the rest are collections prepared from cultivated plants with either no or vague original locality data.

The appendix has an index to all numbered collections examined and their assigned species. Abbreviations for authors of plant names follow Brummitt and Powell (1992) and the International Plant Name Index (www.ipni.org) throughout.

Genus *Lockhartia*

Lockhartia Hook., Bot. Mag. 54: t. 2715. 1827. TYPE SPECIES: *Lockhartia elegans* Hook. (= *Lockhartia imbricata* (Lam.) Hoehne).

Lockhartia subgen. *Pseudobulbosa* D.E. Bennett & Christenson, Lindleyana 13: 51 (1998). TYPE SPECIES: *Lockhartia genegeorgei* D.E. Bennett & Christenson.

Neobennettia Senghas, J. Orchideenfreund 8(4): 364 (2001 [preprint distributed 12 Sept. 2001]). TYPE SPECIES: *Lockhartia genegeorgei* D.E. Bennett & Christenson

Genus description

Caespitose, sympodial, rhizomatous epiphytes (rarely lithophytes). Stems of most species elongate, of determinate growth, not branched (or rarely producing daughter shoots with roots at the base) erect or pendent, oval in cross section, usually completely covered by the leaf sheaths; one species (*L. genegeorgei*) with a pseudobulb at the apex of the erect portion of each stem. Roots white, cylindrical, not(or rarely) branched, normally arising only from the rhizome, occasionally from the upper nodes as well. Leaves always distichous, glabrous, with entire margins, in most species laterally flattened and unifacial (except for the sheath), without an abscission line, more or less triangular in outline, acute to rounded apically, arranged in two rows, with imbricating bases, completely covering the stem (leaves bifacial, conduplicate, and with an abscission layer in *L. genegeorgei*). Inflorescences terminal and/or axillary, 1–30-flowered pseudo-cymes, often several per shoot and then either simultaneously or sequentially produced (normally in a basipetal fashion); inflorescence bracts triangular, conduplicate and folded along midvein to suborbicular, amplexicaul and expanded, in some species showing a morphological gradient from base to apex of the rachis. Flowers widely open to campanulate, normally resupinate, with no apparent preferred orientation in some small-flowered species, or flowers facing down in some species with pendent stems, or by bending of the pedicel in some species with erect stems; perianth and column white or yellow, frequently with orange and/or brown spots or blotches on the labellum and column, without detectable fragrance. Sepals valvate, widely ovate to oblong, obtuse to acute, frequently with a minute, near-apical keel on the abaxial surface, flat to slightly concave, the median sepal similar to the lateral ones. Lateral petals widely ovate to oblong, round to acute, frequently with slightly undulating

(scalloped) margins; some species with petals arched toward the front of the flower and with reflexed margins. Labellum suborbicular to markedly 3-lobed, the lateral lobes (if present) obscure to elongate; if elongate then wide-oblong to linear, frequently arching toward the front of the flower; midlobe (when present) pandurate to (rarely) subquadrate, frequently divided in four lobules; callus present or absent; when present either (1) a glabrous or tuberculate thickening extending from near the base to the middle of the labellum, commonly with a concave cushion-like thickening at the base, with minute secretory hairs within, located near the point of attachment of the labellum, (2) a raised, concave central area, often surrounded by a toothed keel, with a trapezoid projection at the base that bears minute glandular hairs, or (3) a transverse, irregular ledge in the central part of the labellum. Column relatively short, subtruncate, straight to slightly curving upward, trigonous to hemispherical in cross section, winged or not, devoid of a clinandrium; anther terminal, anther cap subhemispherical, with an apical beak, glabrous to micropapillate, with two internal septae; pollinarium with two pyriform pollinia, each one with a caudicle that connects to a branch of a narrow, bifid tegular stipe, which in turn has an apical, exposed (not covered by the anther cap) sticky, round viscidium (each pollinium with a longitudinal groove and the stipe lanceolate and entire in *L. genegeorgei*). Fruit a dehiscent capsule, pendent (nodding in species with erect stems), subspherical, fusiform or elongately pyriform, smooth, glabrous, glaucous in some species, dehiscing by three longitudinal slits while still green, but soon becoming dry; each valve soon becoming reflexed, with many hygroscopic hairs attached near the margin of each valve on the internal surface. Seeds minute, fusiform, with elongated testa cells arranged longitudinally.

Key to the species of *Lockhartia*

- 1a. Leaves linear, usually >10 cm long, conduplicate and bifacial to the apex, with an abscission layer; stems with a terminal, exposed, oblong pseudobulb; pollinarium stipe lanceolate and entire; plants from Peru (subgenus *Pseudobulbosa*) 9. *L. genegeorgei*
- 1b. Leaves more or less triangular in side view, <6 cm long, bifacial and conduplicate only at the base, the rest unifacial and isobilateral, without an abscission layer; stems elongate and narrow, devoid of pseudobulbs, hidden by the imbricating leaves; pollinarium stipe linear and bifid; plants from anywhere in the neotropics (subgenus *Lockhartia*) 2
- 2a. Leaves relatively thick (ca. 1–1.5 mm at the middle) and leathery, often apiculate; inflorescence openly branched, wiry, divaricate, with suborbicular, amplexicaul, small (2-4 mm) bracts; rachis internodes 4 times as long as the bracts or longer; flowers 6–10 mm tall, creamy white, with two parallel, minutely pilose keels on the labellum1. *L. acuta*
- 2b. Leaves relatively thin (ca. 0.5–1 mm at the middle) and soft or firm, but not leathery, not or rarely apiculate; inflorescence never wiry and divaricate; rachis internodes no more than twice as long as the bracts; flowers not as above..... 3
- 3a. Labellum suborbicular when spread flat, with lateral lobes much wider than long, raised around the column at anthesis (“Parthenocomos group”)..... 4
- 3b. Labellum suborbicular or not, with lateral lobes either absent or not much wider than long, or labellum suborbicular but convex 8
- 4a. Flower base color white..... 5
- 4b. Flower base color yellow 6

- 5a. Leaves acute, plants pendent; labellum with a longitudinally elongate, oblong callus; plants from NE Venezuela20. *L. oblongicallosa*
- 5b. Leaves obtuse to round, plants erect; labellum with a transverse, ledge-like callus; plants from Peru3. *L. bennettii*
- 6a. Leaf surface minutely rugose; sepals \leq 12 mm long, Peru and Ecuador26. *L. rugosifolia*
- 6b. Leaf surface smooth; sepals \geq 16 mm long, Venezuela and Guyana..... 7
- 7a. Labellum with a transverse, ledge-like callus; plants from the Venezuelan Coastal Range24. *L. parthenocomos*
- 7b. Labellum devoid of a callus, only with a central area covered with minute hairs; plants from the Guiana Shield 15. *L. latilabris*
- 8a. Labellum suborbicular to oblong, devoid of lateral lobes; callus consisting only of a concave depression near the base of the labellum, surrounded by a raised rim; flowers yellow or white; stems flexuous, pendent or with a tendency to become descending with age (“Longifolia group”)..... 9
- 8b. Labellum various, but often with conspicuous lateral lobes near the base; callus rarely absent, or more commonly present and consisting of a tuberculate thickening that extends from the base to the middle portion of the labellum; flowers always yellow; stems rigid, usually erect (“Imbricata group”, *pro parte*) 12
- 9a. Leaves obtuse, widely elliptic to ovate; flowers >16 mm in diameter, plants from Panama and Colombia21. *L. obtusata*
- 9b. Leaves acute, narrowly triangular; flowers <12 mm in diameter, plants from anywhere in the Neotropics 10

- 10a. Flowers white with an orange callus; rim of callus provided with a pair of prominent teeth distally..... 12. *L. hercodonta*
- 10b. Flowers yellow with an orange callus; rim of callus with a single hooked, conical, or tuberculate tooth distally, or tooth absent 11
- 11a. Mature stems consistently pendent, usually >30 cm long; leaves curved toward stem apically, often sigmoid; labellum suborbicular; rim of callus with a hooked, conical, or tuberculate tooth distally..... 17. *L. longifolia*
- 11b. Mature stems pendent or not, usually <30 cm long; leaves curved away from stem, never sigmoid; labellum oblong to pandurate; rim of callus devoid of a distal tooth, or this very subtle25. *L. parthenoglossa*
- 12a. Plants from Mexico and Central America 13
- 12b. Plants from South America (including Trinidad) 21
- 13a. Labellum apex obtuse to retuse; column one third to one half as long as the labellum; plants from Costa Rica6. *L. dipleura*
- 13b. Labellum apex emarginate and bilobed; column less than one third as long as the labellum; plants from anywhere in Mesoamerica..... 14
- 14a. Column wings wider near the base of the column; plants from Costa Rica and Panama 15
- 14b. Column wings wider near the middle or near the tip of the column; plants from anywhere in Mesoamerica..... 16
- 15a. Distal part of callus forming a mass of low, verrucose tubercles 11. *L. grandibractea*
- 15b. Distal part of callus forming 5–7 longitudinal toothed keels.....7. *L. endresiana*

- 16a. Flowers \leq 12 mm tall; labellum midlobe \leq 5 mm wide at its widest point; lateral lobes of labellum absent to elongate; callus smooth or merely papillate 17
- 16b. Flowers \geq 12 mm tall; labellum midlobe \geq 9 mm wide at its widest point; lateral lobes of labellum always elongate; callus tuberculate (rarely papillate)..... 18
- 17a. Flowers 10–12 mm tall, 1 or (rarely) 2 open at once per inflorescence; inflorescences usually few (1–3) per stem.....4. *L. cladoniophora*
- 17b. Flowers 5–8 mm tall, often 3 to 6 open at once per inflorescence; inflorescences usually several (\geq 4) per stem.....19. *L. micrantha*
- 18a. Labellum midlobe subquadrate to obscurely pandurate when flattened, wider across the basal lobules, and wider than long 2. *L. amoena*
- 18b. Labellum midlobe markedly pandurate when flattened, wider across the apical lobules, and longer than wide 19
- 19a. Callus of labellum covered with cone- or teeth-like tubercles; shoots (stems and leaves) relatively narrow (8–13 mm), at least distally22. *L. oerstedii*
- 19b. Callus of labellum covered with cushion-like tubercles to almost smooth; shoots (stems and leaves) relatively wide (10–25 mm) 20
- 20a. Callus of labellum relatively thick and wider distally, not bifid or only obscurely so; inflorescence bracts almost perpendicular to the rachis and markedly distichous, the inflorescences thus appearing scalariform; leaves frequently straight or slightly curved toward stem; plants from the Sierra Madre de Chiapas range (including Guatemala and extreme E Oaxaca)29. *L. verrucosa*
- 20b. Callus of labellum relatively low and oblong, bifid; inflorescence bracts imbricate, spirally arranged, the inflorescences thus not appearing scalariform; leaves

- frequently curved away from stem; plants from W Mexico (Nayarit to central Oaxaca)8. *L. galeottiana*
- 21a. Callus of labellum smooth or seemingly absent; flowers usually <8 mm tall 22
- 21b. Callus of labellum tuberculate or with cushion-like thickenings; flowers usually >8 mm tall 24
- 22a. Labellum unlobed; plants from Pará state in Brazil 14. *L. ivainae*
- 22b. Labellum commonly with lateral lobes; plants from elsewhere in the Neotropics .. 23
- 23a. Callus of labellum formed by a single low keel; plants from Bolivia....5. *L. compacta*
- 23b. Callus of labellum formed by 2 subparallel keels; plants from Colombia and Venezuela.....19. *L. micrantha*
- 24a. Plants from anywhere W of the Andes 25
- 24b. Plants from anywhere E of the Andes 26
- 25a. Flowers 12–14 mm tall; column longer than wide; plants from NW Ecuador (and probably SW Colombia)..... 23. *L. oxyphylla*
- 25b. Flowers 17–22 mm tall; column wider than long; plants from W Ecuador and NW Peru..... 27. *L. serra*
- 26a. Plants from the E slopes of the Andes in Colombia, Ecuador, Peru, and Bolivia .. 27
- 26b. Plants from the Bolivian or Venezuelan lowlands (500 m or less) or anywhere in Brazil or the Guianas 28
- 27a. Column dolabriform, wider than long, with flabellate wings 16. *L. lepticaula*
- 27b. Column rhombic, as long as wide, with triangular wings28. *L. tenuiflora*

- 28a. Lateral lobes of labellum absent to 2 mm long, less than half as long as midlobe; labellum midlobe suboblong; callus oblong; plants from the Guianas, Venezuela, and N Brazil..... 13. *L. imbricata*
- 28b. Lateral lobes of labellum 3–5 mm long, subequal to midlobe in length (rarely shorter); labellum midlobe pandurate; callus wider distally; plants from Bolivia and Brazil (S of the Amazon)..... 29
- 29a. Flowers usually 7–10 mm tall; plants from the Brazilian planalto or the S Amazon basin in Brazil and Bolivia..... 10. *L. goyazensis*
- 29b. Flowers usually 12–18 mm tall; plants from the Atlantic Forest (Mata Atlântica) biome of E and SE Brazil..... 18. *L. lunifera*

Species Treatment

***Lockhartia acuta* (Lindl.) Rchb. f.**

1. *Lockhartia acuta* (Lindl.) Rchb. f., Bot. Zeit. 10: 767. 1852. *Fernandezia acuta* Lindl., Bot. Reg. 21: tab. 1806. 1836. TYPE: [TRINIDAD & TOBAGO:] Trinidad, June 1836, *Ex Hort. Thomas A. Knight s.n.* (voucher not found; lectotype, here designated: illustration in Bot. Reg. 21: tab. 1806. 1836).

Lockhartia pallida Rchb. f., Bonplandia (Hanover) 2(2): 14. 1854. SYNTYPES: [VENEZUELA]. Carabobo, *Ex Hort., H. Wagener 103 sub Keferstein s.n.* (lectotype, here designated: W-Reich.-Orch.-44377; drawings of lectotype: W-Reich.-Orch.-419, AMES-39379; possible iso-lectotype: K-Lindl.-78998, excluding *Fendler 1431, Wagener 3, Keferstein s.n.* and type illustration of *Fernandezia acuta*); and [PANAMA]. Port Chagres, sent by Dr. Beer, *Keferstein s.n.* (possibly “Keferstein s.n.” in K-Lindl.-78998).

Lockhartia lasseri Schnee, Rev. Fac. Ing. Agron. (Maracay) 1: 120. 1952. TYPE: VENEZUELA. Barinas, Río Paguey, 1942, *T. Lasser* 752 (holotype: VEN [image seen]; isotype: VEN [flowers in spirit, not seen]).

Stems erect or descending, rigid, 14–76 cm long when reproductive, with 32–74 leaves; shoots (stem and leaves) 8–18 mm wide. Leaves marcescent, unifacial, laterally flattened, triangular in side view, with straight to slightly incurving margins, imbricate and completely covering the stem, obliquely acute to apiculate or mucronate (rarely truncate or praemorse), exposed part of largest leaves 15–38 × 3–9 mm. Inflorescences both terminal and axillary from the distalmost leaves, 1–7 per stem (produced sequentially), with 3–30 flowers produced more or less simultaneously; exerted portion 4–10 cm long, internodes 10–18 mm long; inflorescence bracts amplexicaul, cordate, acute, the distal ones rounder, 3–4 × 2–4 mm; pedicel and ovary 8–9 mm long. Flowers resupinate, widely open, 8–12 mm tall, white; the labellum occasionally tinged yellow or pale orange, the anther cap white to yellow. Sepals elliptic to ovate, slightly concave, obtuse, 4–5 × 3–3.5 mm. Petals long elliptic to oblong, flat to slightly concave, apically rounded, 4–4.5 × 2–2.5 mm. Labellum subpandurate, with 4 lobules on the distal half, emarginate, straight to slightly reflexed near the middle, 5.5–6 mm long, 4–5 mm wide near the distal end, 3 mm wide near the middle; lobules round to acute; callus composed of 2 parallel ridges, merged at the base, minutely pilose, 2–3 mm long, and a tuft of longer, orange hairs at the very base of the labellum, 0.5 mm long. Column winged, 2–3 mm long, 2.5–3 mm wide; the wings subrectangular, ascending, 0.5–1 × 1–1.5 mm, with an entire margin; stigmatic cavity narrowly elliptic to pandurate, 1 × 0.5

mm; anther cap galeate, 0.7–1 mm long; pollinarium 0.8 mm long, stipe bifid. Fruit ellipsoid to obovoid (rarely subspherical), glaucous, 6–15 × 5–7 mm.

Nomenclatural notes: *Fernandezia acuta* was based on a plant imported and cultivated by Thomas Andrew Knight (1759-1838), but this plant was probably never vouchered. The only sheet labeled as *F. acuta* in the Lindley herbarium at Kew (K-Lindl.-78998) has a copy of the original illustration in color, an entire plant (*Fendler 1431*), two plant fragments (*Wagener 3* and *Keferstein s.n.*), and a packet with flowers. Neither of those three plant collections corresponds to Knight's plant, and they were not cited in the protologue. The original illustration is thus designated as lectotype.

One of the plant fragments mounted on that sheet (*Keferstein s.n.*) probably came from the same cultivated plant used by Reichenbach f. to describe *Lockhartia pallida* (the annotation, in Reichenbach f.'s handwriting, reads "*Lockhartia pallida* Ex Panam. [illegible] Keferstein c. Rchb. f."); however, it lacks the number "103" present in the material at W; thus, I am reluctant to consider it an isotype. It could be "clonotype" material (prepared later from the same cultivated plant as the type). The other fragment was collected by Wagener, but in "Santa Marta" (Colombia?), not Carabobo.

A number for Wagener's collection was not mentioned in the protologue of *Lockhartia pallida*, but it is written on the label of the only herbarium sheet with an actual plant fragment with the name *L. pallida* in the Reichenbach f. herbarium (W-Reich.-Orch.-44377), and this specimen has locality information consistent with the protologue. The only other sheet at W with the name *L. pallida* (W-Reich.-Orch.-419) only has drawings (originals?) of the illustrations published in the protologue.

Phenology: Flowering plants have been collected throughout the year, but more abundantly during the months of December, January, and February.

Distribution: Distributed from southern Costa Rica (Golfo Dulce region, Puntarenas province) to Venezuela and Trinidad & Tobago (present in Trinidad, but absent from Tobago), from sea level to 900 m (Figure 1). A sterile specimen that strongly resembles *L. acuta* from the province of Jinotega in Nicaragua (*Rueda & Coronado 7868*, MO) is included here, although it could conceivably be a stout plant of *L. oerstedii*. Daniel Jiménez (pers. comm., 2010) observed (but did not voucher) plants of *L. acuta* in Pital de San Carlos (Costa Rica), a locality on the Caribbean side of the continental divide, which, together with the putative Nicaraguan record, suggests that *L. acuta* occurs (rarely) in eastern Costa Rica and Nicaragua.

Additional specimens examined: COLOMBIA. Without locality: *Ospina Hernández 770* (JAUM); *Saunders 2068* (W-Reich). Magdalena: Parque Nacional Tayrona, alrededores de Pueblito en la zona Arqueológica, cerca de la quebrada "Las Lajas"; "La Boquita" y "El Tigre", 250 m, 1979, *Moreno 497* (COL); Santa Marta, 457 m, 11 Jul. 1903, *Smith 2374* (BM, F, G, GH, K, MICH, MO, NY, P); Santa Marta, Minca, 610 m, *Wagner s.n.* (K-Lindl, G), 600 m, 30 Jun. 1933, *Giacometto 106* (AMES). Meta: without specific locality, 25 Feb. 1937, *Renz 3013* (RENZ), 500 m, Dec. 1937, *Renz 3014* (RENZ); P.N.N. Tinigua, Río Duda, Serranía Chamusa, Centro de Investigaciones Ecológicas La Macarena, trocha baño después del 3er caño (R11 1200 m), 350 m, Oct. 1996, *Stevenson 1935* (COAH, COL); Sierra de la Macarena, Plaza Bonita, 400 m, 16 Nov. 1949, *Philipson et al. 1434* (BM, COL, UC); Cordillera La Macarena, trocha entre el Río Guejar y el caño Guapayita, Caño Yerli, 500 m, 20 Dec. 1950, *Idrobo & Schultes*

759 (AMES, COL); Caño Entrada, 500 m, 22 Dec. 1949, *Philipson & Idrobo 1856* (BM, NY, UC), 24 Dec. 1949, *Philipson & Idrobo 1901* (BM, COL, UC). Santander: Vicinity of Barranca Bermeja, Magdalena Valley, between Sogamoso and Colorado Rivers, 100 m, 27 Feb. 1935, *Haught 1593* (AMES). COSTA RICA. Without province or locality: Cultivated, *Tonduz s.n.* (G), 6 Jun. 2005 (cult.), *Pupulin 4375* (JBL-spirit); "Lado del Pacífico", Feb. 1921, *Span 19* (CR). Puntarenas: Esquinas Forest Preserve, 0 m, 10 Jan. 1951, *Allen 5761* (SEL); Golfito, P.N. Piedras Blancas, La Bolsa, near the river, 70 m, 12 May 2001, *Huber & Weisserhofer 2548* (CR, WU); Golfito, Puerto Jiménez, P.N. Esquinas, Fila Way, 200 m, 17 Feb. 2000, *Wania 94* (CR); Osa Peninsula, about 5 km W of Rincón de Osa, N and W of the airfield, 50 m, 9 Jan. 1970, *Burger & Liesner 7245* (F); Osa, El Campo, subiendo por la fila entre Aguabuena y Baneguitas, cuenca superior de Quebrada Banegas, bajando hasta la Quebrada Digo-Digo, 350 m, 13 Jan. 1991, *Herrera 4812* (MO); Osa, Sierpe, Los Mogos, 200 m, 11 Dec. 1990, *Herrera 4765* (CR, INB, MO); P. N. Piedras Blancas, sendero Fila (near La Gamba), 200 m, 16 Mar. 2002, *Arauz Suárez 3149* (WU); Refugio de Vida Silvestre de Corcovado, 30 Jul. 1988, *Campos s.n.* (USJ); Reserva Forestal Golfo Dulce, cabeceras de Quebrada Vaquedano, 400 m, 28 Dec. 1991, *Aguilar & Herrera 799* (INB, MO); Osa Peninsula, about 5 km W of Rincón de Osa, 50 m, 24 May 1973, *Burger & Gentry 9022* (CR, F).

NICARAGUA. Jinotega: Municipio de Bocay, Reserva Bosawas, faldas del Cerro Wizo, 200 m, 18 Feb. 1998, *Rueda & Coronado 7868* (MO). PANAMA. Without province or locality: 3 May 2004 (cult.), *Blanco 2567* (FLAS); 4 Mar. 1912 (cult.), *Pring s.n.* (MO); 28 Jul. 1880, *Jelski s.n.* (W-Reich); 1976, *Taylor 10* (K-spirit); *Pittier 255* (AMES); Cultivated, *Powell 51* (K); Cultivated, *Powell s.n.* (AMES); Canal Zone, *Silvestre s.n.*

(MO); Cruces Hills, 1894, *Fawcett s.n.* (BM); Nature trail at Camp 1 on Madden Dam Highway, 1 Apr. 1939, *Elmore J3* (RSA). Colón: Bohío, 11 Apr. 1910, *Crawford 525* (PH); Manzanilla Island near Aspinwall, 1861, *Hayes 106* (BM, K); Near Gatún, 1859, *Hayes s.n.* (AMES); NW part of Canal Zone, area W of Limón Bay, Gatún Locks and Gatún Lake, N of Mindi Hills, along Quebrada Morito, 28 Mar. 1956, *Johnston 1740* (AMES); Río Gatuncillo, vicinity of Santa Rosa, 25 m, 24 Feb. 1947 (cult.), *Allen 4253* (G). Panamá [including Canal Zone]: Around Culebra, 50 m, 1911 (cult.), *Pittier s.n.* (AMES); Balboa, cultivated at Gamboa, *Powell 52* (K); Barro Colorado Island, Jan. 1939, *Brown 151* (F), 20 Feb. 1969, *Croat 8056* (DUKE, F, MO, NY, SCZ), Aug. 1928, *Chickering 60* (MICH), Dec. 1933, *Avilés 34* (F), 3 Oct. 1973, *Montgomery 161* (MO), 16 Jul. 1971, *Croat 15569* (MO), 27 Oct. 1931, *Shattuck 234* (F, MO), 22 Mar. 1971, *Croat 14042* (MO); Cerro Jefe, 700 m, 23 Feb. 1970, *Dressler 3824* (PMA); Chiva-Chiva, 0 m, 23 Jan. 1923 (cult.), *Powell 52* (AMES), 3 Dec., *Christopher s.n.* (AMES); Drowned forests of Quebrada Tranquila and its branches, 70 m, 8 Jan. 1935, *Dodge & Allen 17325* (K); Foot hills E of City, 0 m, cultivated at Gamboa, *Powell 52* (AMES, K, MO); Gigante Bay, 19 Mar. 1932, *Shattuck 837* (F, MO); Past Río Ipeti, along Panamerican Highway about 4-5 km E, 9 Feb. 1977, *Folsom & Collins 1677* (MO); Pedro Miguel, 0 m, Nov. 1922 (cult.), *Powell 52* (AMES, S); San José Island, Perlas archipelago, Gulf of Panama, about 55 mi SSE of Balboa, 22 Jan. 1946, *Johnston 1217* (AMES, US); Trail from Río Espavé toward Río Agua Clara, 23 Jan. 1972, *Gentry 3775* (MO); Upper Chagres River, Quebrada Melgada, 70 m, 13 Jan. 1935, *Steyermark 17515* (AMES, BM, G, K, MICH, S, U, UC); El Llano-Cartí road, km 19, 350 m, 3 Feb. 1986, *Nevers et al. 6881* (MO), km 24.5-30, 200 m, 23 Jan. 1985, *Nevers et al. 4589* (MO). TRINIDAD

& TOBAGO. Trinidad [without specific locality]: 18 Jan. 1905, *Bradford 5305* (BM, K); 12 Mar. 1895 (cult.), *Bonsall s.n.* (K); 3 Mar. 1918 (cult.), *Broadway 8765* (TRIN); 22 Apr. 1890 (cult.), *Broadway 4030* (TRIN); *anonymous s.n.* (K-spirit); *anonymous s.n.* (W-Reich); *Ryan s.n.* (C). San Juan-Laventille: Caura Valley, outside Caura Caves, 14 Jun. 1988, *Chaboo s.n.* (TRIN). Siparia: Siparia, 22 Mar. 1957 (cult.), *Downs s.n.* (AMES); St. Anne's, 1892, *Broadway s.n.* (AMES). VENEZUELA. Anzoátegui: [near border between Anzoátegui and Sucre]: Between Río León of Quebrada Danta and Río Zumbador, NE of Bergantín, 500 m, 24 Feb. 1945, *Steyermark 61123* (AMES, F). Aragua: Prope Coloniam Tovar, 1854, *Fendler 1431* (AMES, K, K-Lindl). Barinas: without specific locality, 300 m, 4 Feb. 1953, *Renz 7901* (RENZ); Reserva Forestal Caparo, Unidad I, parte sur entre pica 7 y 9, 16-18 kms SE del campamento Cachicamo, E de El Cantón, 100 m, 9 Apr. 1968, *Steyermark et al. 101993* (VEN); Reservas Forestales de Ticoporo, 7 Nov. 1977, *Fernández 2836* (F); Río Michay, Reserva Forestal de Ticoporo, 5 May 1966, *Marcano Berti 905* (MO). Guárico: Guatopo, 610 m, *Dunsterville 449* (K). Lara: Barquisimeto, 1893, *Mocquerys s.n.* (AMES, P, S); Cumbre del Cerro Gordo, al N de Barquisimeto, 900 m, Jan. 1924, *Saer 107* (NY, VEN); Distr. Palavicini, 60 m, 16 May 1959, *Renz 9465* (RENZ). Miranda: Cerros del Bachiller, near E end, between base and summit, above Quebrada Corozal, S of Santa Cruz, 10 km (by air) W of Cupira, 60 m, 25 Mar. 1978, *Steyermark & Davidse 116725* (MO); Distr. Acevedo, 900 m, 7 Feb. 1960, *Renz 9784* (RENZ); Distrito Paez, drainage of the Río Guapo, Cerro Riberón between Río Guapo and Río Chiquito, 44.5 km directly (in a straight line) SE of Caucagua, 200 m, 1 Jun. 1977, *Davidse & González 13613* (MO, VEN); Dto. Paez, Qda. Chaguaramas, 7 Jun. 1977, *González & Davidse 950* (VEN).

Yaracuy: Distr. Nirgua, 200 m, 7 Sep. 1959, *Renz 9685* (RENZ). Zulia: without specific locality, 200 m, 21 Jan. 1951, *Renz 6602* (RENZ), 500 m, 17 Dec. 1950, *Renz 6579* (RENZ), 26 Oct. 1950, *Renz 6550* (RENZ); Distrito Perijá, 200 m, 12 Feb. 1947, *Renz 4198* (RENZ); Río Negro, Perijá, 1 Feb. 1954, *Aristeguieta & Montoya 2077* (VEN); Sierra de Perijá, Río Yasa, abajo de "Kasmera" (Estación Biológica de la Universidad de Zulia), al SO de Machiques, 270 m, 24 Aug. 1977, *Steyermark & Fernández 99691* (VEN). CULTIVATED [without original locality data]: *anonymous s.n.* (K-spirit); 1870, *anonymous s.n.* (K); Jan. 1878, *anonymous s.n.* (K); Sep. 1888, *anonymous s.n.* (K); Mar. 1889, *anonymous s.n.* (K); Oct. 1895, *anonymous s.n.* (K); 4 May 1899, *anonymous s.n.* (G); 23 Feb. 2009, *Blanco 3221* (FLAS); 2 Dec. 1908 (cult.), *Nash 24685* (NY); 8 Feb. 1905, *Smith s.n.* (BM).

Commentary: *Lockhartia acuta* is easily recognizable by its relatively thick and rigid shoots, coriaceous leaf epidermis, leaf apices often apiculate to subpraemorse, open, wiry inflorescences with long (4–10 cm) internodes and small (3–4 mm) bracts, and small, whitish flowers. There is slight geographic variation in the shape of the labellum lobules (e.g., round in Costa Rican plants vs. acute in those from Venezuela and Trinidad), but the morphology is otherwise very homogeneous.

***Lockhartia amoena* Endrés & Rchb. f**

2. *Lockhartia amoena* Endrés & Rchb. f., Gard. Chron. 666. 1872. TYPE: COSTA RICA. *Endrés s.n.*, *Ex Hort.* Hamburg Botanic Garden, Feb. 1872 (lectotype, here designated: W-Reich.-Orch.-44339; drawing of holotype: AMES-24870, line drawings in pencil, excluding color drawing of flower).

Lockhartia costaricensis Schltr., Repert. Spec. Nov. Regni. Veg. 3(31-32): 81. 1906. TYPE: COSTA RICA. [San José: Pérez Zeledón], Los Palmares [de El General,

Pérez Zeledón, Repunta, ca. 616 m, 9°19'N 83°40'W; *fide* Gazetteer of Costa Rican Plant Collecting Locales], January 1897, *H. Pittier, Inst. Phys.-Geogr. Cost. 10592* (holotype: B, [destroyed, drawing of holotype: AMES-23170]; lectotype, here designated: BR, image seen; original floral analysis by Schlechter published by Mansfeld in *Repert. Spec. Nov. Regni Veg. Beih.* 49: T. 79, Nr. 313. 1931).

Stems erect or descending, more or less rigid, 8–62 cm long when reproductive, with 20–74 leaves; shoots (stem and leaves) 8–20 mm wide. Leaves marcescent, unifacial, laterally flattened, triangular in side view, with straight (occasionally incurving or outcurving) margins, obtuse to (rarely) acute, exposed part of largest leaves 12–40 × 4–11 mm. Inflorescences both terminal and axillary from the distal half of the stem, 1–6 per stem (produced either simultaneously or sequentially), with up to 7 inflorescences per stem (sequentially produced), with 1–14 flowers produced more or less simultaneously; exerted portion 1.5–6 cm long, internodes 2–8 mm long; inflorescence bracts amplexicaul, widely ovate, cordate, obtuse, nearly flat to infundibuliform, 3–11 × 3–10 mm; pedicel and ovary 5–15 mm long. Flowers resupinate, widely open, 10–14 mm tall, yellow, the labellum and column heavily spotted with purple brown; the labellum often with white areas around the callus; the anther cap white to yellow. Sepals ovate, slightly concave, obtuse, 6–7 × 4.5–5 mm. Petals long elliptic to oblong, curved toward the front, margins reflexed, apically obtuse or rounded, 6–9 × 4.5–5 mm when flattened. Labellum 3-lobate, 7–10 mm long, 13–16 mm wide across lateral lobes when flattened; lateral lobes elongate, oblong, obtuse apically, curved toward front, 6–7 × 1–1.5 mm; midlobe obscurely divided in 4 lobules, subquadrate, emarginate, wider across the basal lobules when flattened, margin irregularly undulate, 6–8 × 9–12 mm, the basal

lobules folded backwards, the distal lobules projected forward; callus elongate, more or less rectangular; basal part forming a concave cushion with a basal tuft of short, glandular hairs, 1.5–2.5 × 2–2.5 mm; the distal portion forming a mass of low tubercles, sometimes appearing as several low keels. Column broadly winged, 2–2.5 mm long, 4–4.5 mm wide; wings obliquely subquadrate, 1.5 × 1–1.5 mm, with a denticulate to lacerate margin; stigmatic cavity elliptic to pandurate, 0.8 × 0.5 mm; anther cap galeate, 1 mm long; pollinarium 1 mm tall, stipe bifid. Fruit not seen.

Nomenclatural notes: The sheet with the type specimen of *Lockhartia amoena* (W-Reich.-Orch.-44339) has a piece of paper inside the bluish packet with the annotation “N. 2527”, and there is a drawing by Endrés on a separate sheet (W-Reich.-Orch.-44351) with the same number. However, the labellum in the drawing has an undivided midlobe, and possibly represents *L. dipleura*.

Because the type of *Lockhartia amoena* was simply cited as having been collected by Endrés in Costa Rica, without an associated collection number, and the confusing state of the Endrés collections in W, the specimen W-Reich.-Orch.-44339 is designated as lectotype.

One specimen (*Endrés s.n.*, AMES-26068) might be part of the same field gathering, but is not type material because the type specimen was prepared from cultivation at the Hamburg Botanic Garden.

The only extant specimen of *Pittier, Inst. Phys.-Geogr. Cost. 10592* (the type specimen of *Lockhartia costaricensis*; see Pittier, 1923, for this notation) is at BR and has a piece of paper, attached directly to the plant, that reads: “Palmares 159 única.” There are no flowers with this specimen, but at AMES there is a copy of a drawing from

the Schlechter herbarium in Berlin with a floral dissection and a single piece of stem. This indicates that the specimen at BR was originally a unicate, but that Schlechter took a piece (including all the flowers) with him to Berlin. This fragment, now destroyed (Ames, 1944), should be considered the holotype. The remaining specimen at BR is designated here as lectotype.

Phenology: Flowering plants have been collected throughout the year, but more abundantly during the months of December, January, and February.

Distribution: Costa Rica and Panama, from 300 to 1800 m on the Pacific slope (Figure 2). The locality data of a specimen prepared from a cultivated plant (supposedly collected in Pacayas in Cartago province, Costa Rica) is probably erroneous (and thus excluded from the distribution map); no other collections are known from this well-botanized Caribbean slope locality.

Hamer (1984b) reported *Lockhartia amoena* from Nicaragua and possibly Guatemala, but no specimens from those countries have been seen; the Nicaraguan specimen cited by Hamer is actually a plant of *L. micrantha*, and the voucher for the illustration is a Costa Rican plant of *L. grandibractea*. Schweinfurth (1961) listed *L. amoena* for Peru, based on a misidentified specimen of the then undescribed *L. lepticaula*.

Additional specimens examined: COSTA RICA. Without locality: 12 Nov. 1936 (cult.), *anonymous s.n.* (K); 6 Jan. 2009 (cult.), *Bogarín 3989* (JBL-spirit); *Endres 302* (W-Reich); *Endres s.n.* (W-Reich, multiple sheets); *Mason 2397* (K-spirit); *Pfau 79* (W-Reich); *Endres 214* (W-Reich). Alajuela: Naranjo, Cerro Espíritu Santo, 1245 m, Sep. 1922, *Brenes s.n.* (NY); San Carlos, Quesada, Puente de Casas, 400 m, 6 May 1978,

Todzia 251 (CR, F); San Ramón, Alto Calera, 7 Jan. 1930, *Brenes 11599* (NY); San Ramón, camino a Piedades Sur, 6 Feb. 1989, *Retana s.n.* (USJ); Colinas de San Ramón, 14 Nov. 1927, *Brenes 1672* (F), 19 Nov. 1927, *Brenes 3427* (NY), 21 Jan. 1925, *Brenes 1193* (AMES, BH, NY); San Ramón, El Socorro, 1120 m, 18 Jan. 1924, *Brenes 825* (CR); San Ramón, La Palma, 1270 m, 12 Jan. 1928, *Brenes 1672* (CR, NY); San Ramón, Los Angeles, 1100 m, 21 Dec. 1936, *Solís Rojas 502* (BM, CR, F); San Ramón, Mondongo a Santiago, 825 m, 9 Jan. 1930, *Brenes 11599* (AMES, F); San Ramón, Río Jesús, 850 m, Dec. 1921, *Brenes 212* (AMES, CR); San Ramón, San Pedro, 990 m, 23 Jan. 1925, *Brenes 2436* (CR, F); San Ramón, Santiago, Cerros del Mondongo, 925 m, 7 Jan. 1930, *Brenes 11599* (CR). Cartago: Pacayas, Jun. 1986 (cult.), *Mora 32* (USJ; questionable locality). Puntarenas: Aguabuena, 3.5 km W of Rincón, four-hectare permanent sample plot 1 km N of BOSCOA station, 350 m, 12 Jan. 1993, *Thomsen & Korning 224* (C, CR, K); Along Río Sonador, near Panamerican Highway, El General Valley, 600 m, 31 Jan. 1965, *Williams et al. 28789* (F); Along the Río Cacao above Pan American Highway, El General Valley, 900 m, 30 Jan. 1965, *Williams et al. 28665* (F); Coto Brus, Cordillera de Talamanca, Agua Caliente, Ribera Río Cotón y alrededores aguas termales, 1000 m, 1 Feb. 1995, *Villalobos 27* (CR, FLAS, INB, MO); Coto Brus, P. I. La Amistad, Cordillera de Talamanca, Estación Pittier, Río Cotón, Aguas Calientes, 1680 m, 1 Feb. 1995, *Alvarado 23* (INB, F, K, MO); Coto Brus, Z.P. Las Tablas, Cordillera de Talamanca, Límite Zona Protectora Las Tablas, sendero a Quebrada Gemela, 1650 m, 30 Jan. 1995, *Chinchilla 28* (FLAS, INB, MO); Coto Brus, zona no protegida, cuenca Térraba-Sierpe, Finca Cafrosa, Fila Palmital, 1800 m, 31 May 1998, *Gamboa 2198* (INB); Golfito, near and along trail leading from

Km 3/Torres rd. to Quebrada Culebra (tributary of Río Sorpresa), ca. 2.5 km (by air) NE of Golfito, 300 m, 1 Feb. 1992, *Grayum et al. 10089* (INB, MO); Golfito, P.N. Corcovado, Península de Osa, Cerro Rincón, 745 m, 30 Jan. 1998, *Gamboa et al. 2138* (INB); Guavín, Haut-Cabagra, près de Buenos Aires, 650 m, Mar. 1892, *Pittier (I.P.G.C.R.) 6598* (BR); Hills above Palmar Norte, trail to Buenos Aires, 830 m, 17 Feb. 1951, *Allen 5888* (SEL); Osa, Sierpe, San Juan, Fila Casaloma, siguiendo la trocha a Sierpe, estribaciones Cerros Chocuaco, 500 m, 28 Jan. 1991, *Herrera 4883* (CR, F, INB, MO); Cordillera de Tilarán, Monteverde, headwaters of Queb. Amapala, 3 km SE from the village of San Luis, Pacific slope moist forest, 1200 m, 28 Jan. 1993, *Haber et al. 11424* (CR, INB, MO); Río Sirena [Río Sereno?], Sabalito, 1991, *Soto s.n.* (USJ-spirit). San José: Coronado, Cascajal, 8 Nov. 2005 (cult.), *Schug 270* (JBL-spirit); Dota, E slope and crest of Cerro Nara, 1100 m, 31 May 2005 (cult.), *Pupulin et al. 1162* (JBL-spirit); Dota, R.F. Los Santos, cuenca del Savegre, San Isidro de Dota, sendero La Flecha, por sendero a Fila Mora, 700 m, 24 Jan. 2003, *Morales & González 10236* (INB); Edge of Río Sonador, 36 km S of San Isidro El General, 533 m, 27 Feb. 1966, *Molina et al. 17932* (F); Reserva de Vida Silvestre Boracayán, Fila Costeña, near Prov. Puntarenas border, ca. 10 km E of Dominical, southern Fila Tinamastes near Cuesta Yeguas, 6 Mar. 2006 (cult.), *Clark 141 sub Blanco 3212* (FLAS); Tarrazú, estribaciones del Cerro Hormiguero, 900 m, 23 Mar. 1999, *Estrada & Binder 2086* (CR); Tarrazú, San Lorenzo, estribaciones SE de Cerro Toro, 900 m, 4 Apr. 1997, *Estrada et al. 724* (CR); Vicinity of El General, 900 m, Dec. 1935, *Skutch 2316* (AMES, K, MICH, MO, NY, S, SEL, US). PANAMA. Without locality: 17 Feb. 2009 (cult.), *Blanco 2556* (FLAS); 12 Nov. 1976 (cult.), *Dodson s.n.* (SEL). Chiriquí: Without locality, Jan. 1982, *Micklow s.n.* (MO); 12

mi. W of Potrerillos, 1067 m, 30 Mar. 1934, *Brown s.n.* (AMES); E of Cuesta Piedra along Río Macho Monte, 950 m, 12 Feb. 1985, *Luer et al. 10520* (MO). Coclé: El Valle, 22 Jan. 1984, *Chase 84101* (K-spirit); Hills N of El Valle de Antón, vicinity of La Mesa, 1000 m, 21 Jan. 1941, *Allen 2313* (AMES); Mountains beyond La Pintada, 400 m, *Hunter & Allen 586* (AMES, MO); Río Coclé del Norte, 457 m, 14 Jan. 1958 (cult.), *Newcomb s.n.* (AMES, BH, F, G, K, M, MO, NY, UC, US). Herrera: Chepo de las Minas, 650 m, 17 Dec. 1977, *Dressler 5749* (FLAS); Hill above Chepo de las Minas, 700 m, 19 Dec. 1977, *Folsom et al. 6962* (MO, PMA, SEL). Panamá: Cerro Campana, 1000 m, Dec. 1951, *Cope s.n.* (AMES); Cerro Campana, 26 Jun. 1968, *Dressler 3526* (PMA); Cerro Campana, 8.6 miles SW of Capira, 700 m, 29 Jun. 1970, *Luteyn 1016* (DUKE, GH). Veraguas: 2/10 mi beyond fork in road at Escuela Agrícola Alto Piedra on road to Río Calovébora, 750 m, 3 Apr. 1976, *Croat & Folsom 33917* (MO); 5 mi W of Santa Fe on road past Escuela Agrícola Alto Piedra on Pacific side of divide, 800 m, 18 Mar. 1973, *Liesner 870* (MEXU, MO, NY, SEL, TEX); Above Santa Fe and above Alto de Piedra, on ridge-trail to top of Cerro Tute-Arizona, 1150 m, 6 Feb. 1988, *McPherson 12088* (MO); Vicinity of Escuela Agricultura Alto Piedra near Santa Fe, trail to top of Cerro Tute, 975 m, 6 Oct. 1969, *Antonio 1995* (F, MO). CULTIVATED [without original locality data]: *anonymous s.n.* (K-spirit); *Chase 8167* (K-spirit).

Commentary: *Lockhartia amoena* is diagnosed by the combination of long labellum side lobes, subquadrate (obscurely tetralobulate) labellum midlobe with heavy brown spotting and whitish areas on the basal lobules (the last trait easily overlooked), and a wider-than-long column with obliquely subquadrate wings.

As a member of the Imbricata group, *L. amoena* can be difficult to distinguish from other congeners if flowers are not available. It is a vegetatively variable species; plants from central Panama have relatively robust stems and numerous flowers per inflorescence, while those from southern Costa Rica have narrower, more flexible stems with fewer (up to 5) flowers per inflorescence. However, the floral morphology is rather uniform. The relative robustness of the plants is also apparently related to the elevation, with the more robust plants occurring at higher places.

Several authors have treated *Lockhartia grandibractea* as a synonym of *L. amoena* (e.g., Hamer, 1984a; Mora and Atwood, 1992b; Atwood and Mora de Retana, 1999; Dressler, 2003). Both species are superficially similar, and have overlapping geographic and elevational distributions. The inflorescence bracts of both species can be almost as large as the flowers (they are the largest in the genus), although there are populations of both species with much smaller bracts. However, the column of *L. grandibractea* is visibly longer and has smaller and differently shaped wings; the labellum midlobe is also narrower and more clearly tetralobulate. Stout plants of *L. amoena* tend to have larger, more open inflorescences than plants of *L. grandibractea*. Both species also have contrasting phenologies; the flowering peak of *L. amoena* occurs during the dry season (December to February), while that of *L. grandibractea* occurs during the middle of the rainy season (June to September). No intermediate forms have been detected.

Atwood & Mora de Retana (1999) also included *L. dipleura* in the synonymy of *L. amoena*, but the former species is considered distinct in this treatment (see notes under *L. dipleura*).

It is remarkable that no fruiting collections are known among the numerous ones studied; perhaps successful pollination and/or fertilization are uncommon in this species.

***Lockhartia bennettii* Dodson**

3. *Lockhartia bennettii* Dodson, Icon. Pl. Trop., ser. 2, 1: t. 88 (1989). TYPE: PERU. Amazonas: Bóngara, 5 km North of the North end of lake Pomacocha on the road to La Rioja, 2000 m, 8 Oct. 1964, collected live only, pressed 1 fl. 14 Jan. 1965, by D.E. Bennett in Lima, Peru, *P.C. Hutchinson 6813 sub D.E. Bennett s.n.* (lectotype, here designated: UC-299010, mounted on right side of sheet).

Stems erect or pendent, more or less rigid, 20–45 cm long when reproductive, with 26–42 leaves; shoots (stem and leaves) 13–23 mm wide. Leaves marcescent, unifacial, laterally flattened, triangular in side view, with straight to slightly incurving margins, obtuse to (rarely) acute, exposed part of largest leaves 22–35 × 6–9 mm. Inflorescences both terminal and axillary from distal part of the stem, with 1–4 flowers produced sequentially; exerted portion 2–3 cm long, internodes 2–4 mm long; inflorescence bracts amplexicaul, conduplicate, ovate, obtuse to acuminate, campanulate, 5–7 × 3–5 mm; pedicel and ovary 9–11 mm long. Flowers resupinate, openly campanulate, 10–20 mm across, white, the labellum with a large, central yellow blotch almost completely covered with orange or brown reticulations; the column wings yellow dotted with brown, and the anther cap white. Sepals elliptic to oval, concave, obtuse, 8–10 × 4–6 mm. Petals obovate, apically obtuse or rounded, 10–13 × 6–10 mm. Labellum suborbicular, obscurely 3-lobate, 8–11 mm long, 14–16 mm wide when flattened; side lobes wider than long, transversely oval, curving around the column, 4–6

× 8–10 mm; midlobe wider than long, transversely oval, retuse, margin gently undulate, 3–5 × 9–12 mm; callus rectangular, smooth, puberulous, gradually increasing in thickness distally, occupying the entire central portion of the labellum, forming an irregularly undulate ledge at the base of the midlobe, 6–7 × 4–5 mm. Column narrowly winged, 3–3.5 × 3 mm, the wings obliquely lanceolate and pointed forward, 1 × 2 mm; anther cap galeate, 1 × 1.5 mm; pollinarium 1 mm tall, stipe bifid. Fruit not seen.

Nomenclatural notes: The sheet annotated as the type by Dodson (UC-299010) has two different gatherings prepared from the same plant in cultivation. No mention was made about this in the protologue, where the collection was cited as “*P.C. Hutchinson 6813-1*”. Both gatherings have their own label, but the suffix “-1” is not present on either. Only one of these gatherings has the locality “Amazonas, Bongara” on its label (same as in the protologue), and thus it is designated as lectotype. It consists of a single pressed flower in a paper packet.

Bennett prepared several “clonotypes” (herbarium specimens presumably prepared from the same cultivated plant, but at a different date than the original type specimen), all of them under Hutchinson’s collection number 6813. One of these is mounted on the same sheet as the holotype. Although they can be considered “biological duplicates”, these “clonotypes” cannot be treated as isotypes because they represent different gatherings (collected at different dates) (McNeill *et al.*, 2006).

Phenology: The few field collections available indicate that the species flowers at least in March and July. Several other collections do not indicate a month of preparation or were made from plants in cultivation. Dodson and Bennett (1989b) indicated the

flowering period to be from June to August, an observation probably based on cultivated plants in Lima.

Distribution: Endemic to Peru in the departments of Amazonas, Cajamarca, and Huánuco (expected in San Martín), from 1800 to 2700 m on the eastern (Amazonian) side of the Andes (Figure 3). It might occur also in extreme southern Ecuador in the Zamora-Chinchipe province, but I have not seen any Ecuadorian collections.

Additional specimens examined: PERU. Without locality data: 1877, *Vidal-Sénègue s.n.* (P); Cultivated, *Whitten 99232* (FLAS). Amazonas: Bongará, 5 km N of the N end of Lake Pomacocha on the road to La Rioja, 2000 m, 31 Aug. 1965 (cult.), *Hutchinson 6813 sub D.E. Bennett s.n.* (UC, mounted on left side of holotype sheet, possible clonotype), 16 Jul. 1966, *Hutchinson 6813 sub Bennett s.n.* (SEL, possible clonotype), 15 Jan. 1965 (cult.), 16 Jul.—17 Sep. 1966 (cult.), *Hutchinson 6813 sub Bennett 2843* (AMES, possible clonotype), 15 Jan. 1965 (cult.), *Hutchinson & Wright 6871* (UC); Chachapoyas, 2700 m, 4 Jul. 1978, *López & Aldave 8553* (HUT). Cajamarca: Jaén, Jaén, 1986 m, 16 Mar. 2009, *Vásquez 218* (MOL); Jaén, Jaén, Rinconada, San José de la Alianza, 2000 m, 18 Mar. 2009, *Vásquez 231* (MOL). Huánuco: Muña, 2 Mar. 1959, *Woytkowski 5228* (MO); Near Muña, 1830 m, *Bennett 53* (SEL). CULTIVATED [without original locality data]: *anonymous s.n.* (K-spirit); 22 Feb. 2004, *Blanco 2554* (FLAS); 25 Jan. 2000, *Whitten et al. 1704* (FLAS).

Commentary: *Lockhartia bennettii* is one of five species of campanulate-flowered lockhartias. It is immediately distinguished from the others by its white flowers with a large orange-brown area at the base of the labellum. The protologue of *L. bennettii* indicates a pendent habit, and I have seen photographs of a plant with pendent stems;

however, all the plants I have seen in cultivation have clearly erect or ascending stems. This might be a variable character in this species.

There are relatively few field collections of *Lockhartia bennetii*, which is surprising given its relatively showy flowers and that it is not too rare in cultivation.

***Lockhartia cladoniophora* Rchb. f.**

4. *Lockhartia cladoniophora* Rchb. f., Flora 71: 150-151. 1888. TYPE: [COSTA RICA. *Endrés 2526*], *Ex Hort.* Hamburg Botanic Garden, 2 January 1875 (holotype: W-Reich.-Orch.-44364, including five different sets of illustrations, apparently made from the original plant in cultivation, or possibly from more than one plant).

Stems erect, more or less rigid, 4–30 cm long when reproductive, with 12–48 leaves; shoots (stem and leaves) 7–12 mm wide. Leaves marcescent, unifacial, laterally flattened, triangular to subfalcate in side view, with straight (occasionally incurving) margins, obtuse to round apically (rarely acute), exposed part of largest leaves 7–23 × 2–5 mm. Inflorescences both terminal and axillary from the distal or middle portion of the stem, with 1–3-flowers produced sequentially; exerted portion 0.5–1.5 cm long, internodes 1–3 mm long; inflorescence bracts amplexicaul, widely ovate, cordate, obtuse, 3–5 × 3–4.5 mm; pedicel and ovary 5–10 mm long. Flowers resupinate, widely open, 8–11 mm tall, yellow, the labellum spotted with reddish brown around the callus; the column with a reddish brown infrastigmatic bar. Sepals ovate, slightly concave, obtuse, 4.5–5 × 2–2.5 mm. Petals elliptic to oblong, obtuse, 4.5–5 × 2 mm. Labellum 3-lobate, 6–7 mm long, 6–7 mm wide across lateral lobes when flattened; lateral lobes oblong, obtuse apically, bent toward front, 2–3 × 1–1.5 mm; midlobe divided in 4 lobules, pandurate, emarginate, wider across the basal lobules when flattened, 5 ×

5–5.5 mm, the basal lobules slightly folded backwards, the distal lobules straight; callus formed by two subparallel low keels that converge distally, extending from the base to the middle of the labellum, 2.5–3 × 1–1.5 mm; the base with a minuscule pad of glandular trichomes. Column winged, 1.5 mm long, 2 mm wide; wings rhombic, 0.5 × 0.5 mm, with an entire to crenulate margin; stigmatic cavity 0.5 × 0.5 mm; anther cap galeate, 1 mm long; pollinarium 1 mm tall, stipe bifid. Fruit not seen.

Nomenclatural notes: The sheet annotated as the type (W-Reich.-Orch.-44364) has a stem with one flower, a packet, and five pieces of paper (four with pencil drawings, one with a watercolor). These pieces of paper have (clockwise from top left): 1) pencil drawings of flowers from front and back, inflorescences, labellum, column, and elaiophore trichomes; written with “*L. Bl. Endes*” (Endrés?), “2/76”, “2.77”, [illegible phrase], “*cladoniophora*”; 2) pencil drawing of dissected flower, and “*End. 2526, 1875, 2 Jan*”. (Endrés?); 3) pencil drawing of inflorescence, flower, and flower parts, and “1876. 3 Jan”, “*Endres 1 5*” (?); 4) drawing of flower, lip and column, and “2526”; and 5) watercolor of flower in life and column from above, and “*cladonioph. Dec. 86*”. There is a scrap of rag paper glued to the bottom left that reads in Reichenbach f.’s handwriting: “*cladoniophora Rchb. f. 17 Jan 77* [illegible].”

The protologue makes no mention of a collector or collection number, but three of the illustrations on the type sheet have “Endres” written on them, and one (considered here as the type on the basis of the year being the same as that in the protologue) has the annotation “*End. 2526.*” Augustus Endrés collected in Costa Rica until he left for Colombia in 1875 (Ossenbach *et al.*, 2010); thus, he must have collected the live plant in Costa Rica before he sent it to Hamburg, where it flowered in January 2, 1875. The

other illustrations glued to the sheet are almost certainly “clonotypes”, prepared from the same plant cultivated in Hamburg during subsequent flowerings in 1876, 1877, and 1886.

Phenology: Flowering plants have been collected from January to March and June to October, but flowers are probably produced throughout the year.

Distribution: Endemic to Costa Rica, from 600 to 1100 m on the Caribbean slopes of the Guanacaste, Tilarán, and Central Cordilleras (Figure 4).

Additional specimens examined: COSTA RICA. Alajuela: 27.6 km NE of Liberia in forested pass area between Volcán Santa María and Volcán Miravalles, eastern lower slopes of Volcán Santa María, 800 m, 28 Feb. 1978, *Utley 5914* (DUKE); Beside Laguna María Aguilar, 780 m, 28 Mar. 1969, *Lent 1522* (F); Parque Nacional Rincón de la Vieja, rd. to Colonia Blanca by Quebrada Rancho Grande, 700 m, 10 Oct. 1978, *Todzia 478* (CR); Santa María National Park, road down Caribbean slope, ca. 1 km W of E end of park, 7 km E of colored house at junction of road to Hacienda Santa María, 600 m, 8 Feb. 1978, *Liesner 5184* (CR, MO); Upala, Aguas Claras, Hotel Termalés Azules, 700 m, 28 Jan. 2005, *Karremans et al. 290* (JBL-spirit); Upala, Zapote, desvío a la izquierda después del puente sobre el Río Zapote, en sentido Bijagua-Pueblo Nuevo, ladera E del Volcán Miravalles, siguiendo la margen del Río Zapote, 675 m, 12 Feb. 2007, *Bogarín et al. 2352* (JBL-spirit). Cartago: Turrialba, La Esperanza, camino a Simari, 1100 m, 18 Jun 2010, *Morales 19167* (INB); S of Taus, along Río Pejibaye, 750 m, 7 Oct. 1979, *Todzia 802* (CR). CULTIVATED [without original locality data]: 23 Jan. 1981, *Chase 81010* (K-spirit); 19 Oct. 1979, *White s.n.* (SEL).

Commentary: *Lockhartia cladoniophora* is most similar to *L. micrantha*, but it is distinguished from that species by the inflorescences produced sequentially (instead of simultaneously) with larger, more widely open flowers produced sequentially on each inflorescence. As expected, both species are sister taxa according to DNA data.

Lockhartia cladoniophora is rare and is known from relatively few collections.

Until recently, *Lockhartia cladoniophora* was an obscure name, possibly overlooked because of the omission in the protologue of the collector or country of origin, the type is an unicate, and Kraenzlin's (1923) published drawing is too inaccurate and stylized to be useful. Herbarium specimens have been misidentified as *L. micrantha*, and more recently, as *L. chocoensis* (Bogarín *et al.*, 2008); the later name is here considered a synonym of *L. micrantha*.

***Lockhartia compacta* R. Vásquez & M.A. Blanco**

5. *Lockhartia compacta* R. Vásquez & M.A. Blanco, *sp. nov.* TYPE: BOLIVIA. Santa Cruz: Prov. Florida, El Sillar, 1350 m, Parque Nacional Amboró, epífita en bosque tucumano-boliviano, 3 Julio 1995, R. Vásquez 2522 (Holotype: LPB).

Lockhartia micrantha Rchb.f. affinis, sed callo ligulato simplici (non bifido).

Stems apparently erect, 5–10 cm long when reproductive, more or less rigid, completely covered by the leaves, each one with 20–24 leaves. Leaves marcescent, unifacial, laterally flattened, triangular in side view, with straight to slightly incurving margins, acute to obtuse apically, exposed part of largest leaves 3–16 × 1–8 mm wide. Inflorescences axillary (and probably also terminal) from the distal half of the stem, with 1–2 flowers produced sequentially; exerted portion 5–9 mm long, internodes 1–2 mm long; inflorescence bracts amplexicaul, infundibuliform, cordate-acute when flattened,

2.5–3 × 2–3 mm; pedicel and ovary 4–5 mm long. Flowers resupinate, widely open, 7–8 mm tall, yellow with scant brown markings at the base of the lateral lobes of labellum and dark brown at base of column; labellar callus pale brown. Sepals elliptic to obovate, slightly concave, apex apiculate and navicular, 4–4.5 × 2.5 mm. Petals elliptic, flat, apically rounded, 4.5 × 3 mm. Labellum trilobate; the lateral lobes oblong, gradually diminishing in width, erect, 3 × 1 mm, apically rounded; midlobe distally tetralobulate, apically emarginate, 6 mm long, 2.5–3 mm wide at the base, 4.5 mm at the widest part near the apex, with a slightly concave disk 1 × 1.5 mm at the base (with glandular hairs); prolonged into a simple oblong callus, 2.5 × 1 mm. Column triangular, subequilateral, 1.5–2.5 mm wide at base, 2 mm tall without anther cap, stigmatic cavity ovate, 7–8 mm long, rostellum remnant digitiform, protruding into apical part of stigma; anther cap not seen; pollinarium 0.5 mm tall, viscidium triangular, stipes bifid, with two pollinia, pollinia ellipsoid, 0.2 mm long. Fruit not seen.

Phenology: flowering at least in July and September.

Etymology: named for the very compact vegetative and floral habit of the plants.

Distribution: Endemic to the province of Florida, department of Santa Cruz, in the eastern side of the eastern Andean cordillera in Bolivia, from 1000 to 1300 m (Figure 5).

Additional specimens examined: BOLIVIA. Santa Cruz: Prov. Florida, Refugio Los Volcanes, Río Elvira, 1000 m, 17 Sept. 2001, *Vásquez et al.* 4259 (Herb. R. Vásquez); *Vásquez et al.* 4281 (Herb.R. Vásquez).

Commentary: *Lockhartia compacta* is very similar to *L. micrantha*, but differs from that species in the simple (not bifid), ligulate labellar callus. Also, the lateral lobules of

the midlobe are positioned more distally in the labellum of *L. compacta*. The ranges of both species are separated by thousands of kilometers.

Lockhartia compacta could be confused with *L. goyazensis*, which also occurs in Bolivia, but in Bolivia that species is restricted to lower elevations in the Humid Evergreen Forest and Humid Amazonian Forest biomes (*sensu* Vásquez and Ibisch, 2000). *Lockhartia goyazensis* has slightly larger flowers with longer, narrower labellum lateral lobes and a massive, tuberculate callus that covers a large portion of the midlobe.

Lockhartia compacta is known from very few collections and is seemingly rare and restricted to a small area of the Bolivian-Tucuman Forest biome. This area appears to be the southern limit of distribution of the genus *Lockhartia* in the Andes (*L. lunifera* and *L. goyazensis* occur farther south in Brazil). Plants of *L. compacta* are likely overlooked by collectors because of their small flowers.

***Lockhartia dipleura* Schltr.**

6. *Lockhartia dipleura* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 69-70. 1923. TYPE: COSTA RICA. [San José: Barva], San Jerónimo [de Moravia], 1350 m, [ca. 10°01'N 84°01'W; *fide* Gazetteer of Costa Rican Plant Collecting Locales], 1922, C. Wercklé 102 (holotype: B [destroyed]; neotype, designated [as lectotype] by Pupulin in Bot. J. Linn. Soc. 163: 140. 2010: drawing of holotype, AMES-31614).

Lockhartia integra Ames & C. Schweinf., Schedul. Orchid. 10: 108. 1930. TYPE: COSTA RICA. Guanacaste: El Silencio, near Tilarán, 750 m, [10°28'49"N, 84°54'12"W, *fide* Gazetteer of Costa Rican Plant Collecting Locales], 13 Jan 1926, P.C. Standley & J. Valerio 44675 (holotype: AMES; isotype: US).

Stems erect to descending, more or less rigid, 17–35 cm long when reproductive, each one with 36–50 leaves, each one with 32–50 leaves; shoots (stem and leaves) 7–13 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly and obliquely lanceolate in side view, with straight to slightly incurving margins, acute, exposed part of largest leaves 18–22 × 3–5 mm. Inflorescences both terminal and axillary from the distal part of the stem, with 1–3 flowers produced sequentially; exerted portion 1–2 cm long, internodes 1–5 mm long; inflorescence bracts amplexicaul, infundibuliform, cordate-acute when flattened, 3–6 × 2–5 mm; pedicel and ovary 7–10 mm long. Flowers resupinate, widely open, 7–9 mm tall; yellow with chocolate brown blotches on the labellum and column; labellar callus mostly brown. Sepals elliptic to obovate, acute to obtuse, 5–6 × 3–4 mm. Petals elliptic, curved toward front, obtuse, 5–6 × 3–4 mm. Labellum trilobate; 5–7 mm long, 5–7 mm wide across lateral lobes when flattened; the lateral lobes oblong, 3–5 × 1 mm, acute; midlobe subpandurate, obtuse to slightly retuse, 5–6 mm long; callus subrectangular, the basal part forming a subquadrate concave cushion with a basal tuft of short, glandular hairs, 2 × 1.5 mm, the distal part forming 2 or 3 subparallel, tuberculate, low keels 3 × 1.5 mm. Column winged, 2.5–3 × 2.5–3 mm, the wings more or less rhombic, with serrulate margins; stigmatic cavity ovate, 1 × 0.5 mm, rostellum remnant digitiform, protruding into apical part of stigma; anther cap galeate, 1 mm long; pollinarium 1 mm tall, stipe bifid. Fruit obovoid, 8–12 × 5–7 mm.

Nomenclatural notes: It appears that the type specimen of *Lockhartia dipleura* was a unicate (no duplicates have been found), and it was destroyed during World War II (Ames, 1944). Schlechter and Ames had an active exchange program, and an artist

was hired to make copies of Schlechter's drawings and to make tracings of type specimens of orchid species described by Schlechter, all under Schlechter's supervision (Ames, 1944). This activity continued even after Schlechter's death in 1925. The drawings at AMES made under Schlechter's supervision are indicated with a special label in red ink that reads "DRAWINGS AND ANALYSES FROM HERB. SCHLECHTER MADE UNDER SUPERVISION OF RUDOLF SCHLECHTER." The ones that do not have this label must be those done after Schlechter's death. The drawing of the type of *Lockhartia dipleura* at AMES does not have this label, and thus it cannot be considered original material (that is, not seen by Schlechter), and cannot be designated as a lectotype. Thus, Pupulin's designation should be treated as a neotypification, not a lectotypification.

Lockhartia integra was described from a specimen with a flower in bad condition (and no longer present on the sheet), and the isotype does not have flowers. Louis O. Williams noted (*in sched.*) that the only flower apparently had "broken lines" where the side lobes should be, and suggested that this entity could be the same as *L. micrantha*. Later, Atwood and Mora de Retana (1999) put *L. integra* in the synonymy of *L. pittieri* Schltr. (= *L. parthenoglossa* Rchb. f.). However, the vegetative morphology of the type of *L. integra* is different from that of most plants of *L. micrantha* and *L. parthenoglossa*. The callus with three longitudinal ridges, the basal, subquadrate, concave disc, and the relatively large column suggests that *L. integra* is conspecific with *L. dipleura*. On the other hand, the possibility remains that the type collection of *L. integra* is a stout plant of *L. micrantha*, and that the above-mentioned features represent artifacts from a poorly preserved, rehydrated flower.

Phenology: The few field collections available indicate that the species flowers at least in January, May, and July.

Distribution: Endemic to Costa Rica, where it grows from 500 to 1350 m on the Caribbean slope of the Tilarán and Central Volcanic Cordilleras (Figure 6). A report from Corcovado National Park (near sea level, on the Pacific coast in the Osa Peninsula of Costa Rica) is based on a plant flowered in cultivation at Lankester Botanical Garden; this locality is questionable and the collecting data for that plant were probably erroneous.

Additional specimens examined: COSTA RICA. Without locality: 1 Aug. 1994 (cult.), *anonymous s.n.* (USJ-spirit). Alajuela: Reserva Biológica Monteverde, Río Peñas Blancas, 800 m, 8 May 1989, *Bello 880* (CR); Reserva de San Ramón, May 1989 (cult.), *Mora s.n.* (USJ); S of Aguas Zarcas, above the Río Aguas Zarcas, 500 m, 20 May 1968, *Burger & Stolze 5104* (F); San Carlos, Cordillera de Tilarán, falda N del Volcán Arenal, camino a Tabacón, 500 m, 18 Jan. 1994, *Lépiz et al. 121* (INB); San Ramón, Reserva Biológica A.M. Brenes, 10 Jun. 1994 (cult.), *Mora s.n.* (USJ-spirit, 2 jars); Upala, C.B. Guanacaste-Rincón de la Vieja, Cuenca del Pizote, San Cristóbal, sendero al vivero por el Río Cucaracho, 620 m, 31 Jan. 1998, *Quesada 528* (INB). Cartago: Jiménez, Pejibaye, Taus, Río Pejibaye, 1 km after the school of Taus, 700 m, Aug. 2009 (cult.), *Pupulin et al. 7734* (JBL-spirit). Puntarenas: Sirena de Corcovado, Jul. 1989 (cult.), *Morúa s.n.* (USJ; questionable locality).

Commentary: *Lockhartia dipleura* is distinguished from other species in the “*Oncidium*-like flower” group by its obtuse (non emarginated or retuse) labellum provided with three parallel, verrucose keels, and a somewhat cucullate column. The

leaves tend to be acute and narrower than in other Costa Rican species (except for *L. oerstedii*, which often has darker green leaves and much larger flowers). It is most similar to the South American *L. imbricata*, which has a callus composed of numerous, tiny tubercles not organized in files, shorter (often non-existent) lateral lobes, and a proportionally smaller column.

The drawing of *L. dipleura* published by Mora & Atwood (1992c) includes a dissected flower whose parts were not flattened, and thus the labellum appears deceptively narrower. Schlechter's drawing (destroyed, but with a copy in AMES, published by Pupulin, 2010) of a rehydrated flower better shows the shape of the flattened labellum.

Lockhartia dipleura was put in the synonymy of *L. amoena* by Atwood and Mora de Retana (1999), but that species has a much wider, subquadrate, retuse labellum midlobe and much wider, flabellate column wings. No intermediates seem to occur between both taxa. Dressler (2003) considered *L. dipleura* a synonym of *L. micrantha*, but the latter species has much smaller flowers produced simultaneously.

Lockhartia dipleura is apparently a rare species, judging from the few collections available.

***Lockhartia endresiana* M.A. Blanco**

7. *Lockhartia endresiana* M.A. Blanco, *sp. nov.* TYPE: COSTA RICA. Alajuela: San Ramón, camino a Colonia Palmareña, 600 m, 10°51'06"N 84°31'06"W, collected without flowers on 23 Jan. 2001 by M. Blanco, R. Moran, E. Watkins & E. Vargas, flowered in cultivation at Lankester Botanical Garden on 15 Jul. 2002, *M. Blanco 1803* (Holotype: USJ-79983; clonotype, flowered 23 January 2001: FLAS).

Lockhartia grandibracteata Kraenzl. affinis, sed callo constans ex carinis octo parallelis denticulatis, et lobis basalibus labelli angustioribus.

Stems erect, more or less rigid, 15–35 cm long when reproductive, with 28–48 leaves; shoots (stem and leaves) 8–20 mm wide. Leaves marcescent, unifacial, laterally flattened, triangular in side view, acute, with straight to incurving margins, exposed part of largest leaves 5–19 × 3–6 mm. Inflorescences both terminal and axillary from the distal part of the stem, with 1–3 flowers produced more or less simultaneously; exerted portion 1–3 cm long; inflorescence bracts amplexicaul, infundibuliform, subrotund, cordate, obtuse to round apically, 8 × 8–9 mm; pedicel and ovary 14 mm long. Flowers resupinate, widely open, 14–18 mm tall; yellow with dark chocolate-brown markings on the lateral lobes, disk, and central keels of callus of the labellum, and a dark brown line at the base of the column; occasionally spotted on the upper part of the column and at the base of the petals. Sepals ovate to elliptic, slightly concave, obtuse, 6–7 × 4–5 mm. Petals oblong-elliptic, slightly incurved, with revolute margins, rounded to truncate apically, 7–7.5 × 4–4.5 mm when flattened. Labellum trilobate; the lateral lobes oblong, incurved, 6 × 1.5 mm, apically obtuse to rounded; midlobe divided in 4 lobules (the two basal ones triangular and projected backward, the two distal ones rounded when flattened), apically emarginate, 10.5–11 mm long, 10.5–11.5 mm wide (across the widest part of midlobe when flattened); callus subpandurate, the basal part forming a subquadrate concave cushion with a basal tuft of short, glandular hairs, 2 × 2 mm, the distal part formed by 6–8 high (to 1.5 mm tall), subparallel, denticulate keels, 4 × 3.5 mm when labellum is flattened. Column hastate, truncate, held perpendicular to the

labellum, 3-3.5 mm long, 4.5-5 mm wide at base, 2.3 mm wide distally; anther cap hemispherical, 1-1.3 mm in diameter; pollinarium not seen. Fruits not seen.

Phenology: field collections indicate that flowering occurs from March to September, during Costa Rica's rainy season.

Etymology: the epithet honors Augustus R. Endrés (1838-1874) (Ossenbach *et al.*, 2010), who first illustrated this species. Endrés also collected the type specimens (or sent live plants that were used to prepare the types) of several other names in *Lockhartia* (e.g., *L. amoena* Endrés & Rchb. f., *L. cladoniophora* Rchb. f., *L. grandibractea* Kraenzl., *L. hercodonta* Rchb. f. ex Kraenzl., and *L. odontochila* Kraenzl.).

Distribution: presently known only from Costa Rica, from 600 to 1450 m on the Caribbean slope of the Guanacaste and Tilarán cordilleras and on the Pacific side of the Talamanca cordillera (Figure 2).

The collections from the Zona Protectora Las Tablas suggest that this species also occurs in adjacent Chiriquí province of Panama, but no collections from that country have been identified yet. It is possible that some Panamanian herbarium specimens without flowers, annotated as *Lockhartia* cf. *grandibractea* Kraenzl. during this study, are actually *L. endresiana*; both species cannot be distinguished without flowers.

Additional specimens examined: COSTA RICA. Without locality: 19 Oct. 1994 (cult.), *LeDoux & Stern 355* (MO). Alajuela: Guatuso, Cote, Lago Cote, 640 m, 4 Jun. 2004, *Gómez-Laurito 14314* (USJ); San Carlos, Quesada, Puente de Casa, 400 m, 6 May 1978, *Todzia 251* (CR, 2 sheets). Cartago: Turrialba, Guayabo, 16 Sep. 1991, *Mora s.n.* (USJ spirit-57678); Turrialba, Tayutic, Vereh, Grano de Oro, 2 km al E,

camino a Llanos del Quetzal, 1200 m, 28 Jul. 1995, *Herrera & Cascante 8163* (CR, F, K). Guanacaste: Guatuso, Cordillera de Tilarán, Lago Coter, 700 m, 18 May 1997, *Rivera 3080* (CR); Liberia, Parque Nacional Guanacaste, Estación Cacao, 1100 m, 2 Jun. 1990, *Carballo 40* (CR). Puntarenas: Buenos Aires, Boruca, 700-1000 m, Jul. 1976, *Ocampo 1423* (CR); Coto Brus, San Vito, Estación Biológica Las Cruces, Sendero Ridge, 28 Aug. 2008, *Oviedo-Brenes 214* (HLDG), 1219 m, 16 Aug. 1967, *Raven 21820* (F), 1 mile due S of San Vito de Java, 1067 m, 18 Aug. 1967, *Raven 21906* (CR, DUKE, F, PMA, SEL, U); Río Sirena [Río Sereno?], Sabalito, 1991, *Soto s.n.* (USJ-spirit); Zona Protectora Las Tablas, Finca Las Alturas, road from Las Alturas to Fila Tigre, 1450 m, 3 Jul. 2004 (cult.), *Pupulin et al. 4493* (JBL-spirit), 22 Mar. 2003 (cult.), *Pupulin et al. 4518* (JBL-spirit).

Commentary: *Lockhartia endresiana* is most similar to *L. grandibractea*, with which it shares the general shape of the labellum and column. However, it differs by the structure of the callus (composed of eight parallel denticulate keels, vs. a compact mass of low tubercles in *L. grandibractea*), and by the narrower basal lobes (arms) of the labellum. There are intermediate forms between both species in the area around the Costa Rican-Panamanian border, and it is likely that there is hybridization between them, especially because both species flower mostly during the rainy season. However, the morphological extremes are different enough to justify, in my opinion, their treatment as different species. In the absence of flowers, it is practically impossible to tell the two species apart, and difficult to distinguish either of them from *L. amoena*.

Endrés prepared a detailed drawing of *Lockhartia endresiana* (*Endrés 302*, W-Reich.-Orch.-33697), which includes a stem with an inflorescence, front and side view

of the flower, a detail of the callus base with the elaiophore, six details of the column, and the pollinarium with detached pollinia. At the bottom and on the right side there are drawings of a column with wide, flabellate wings, possibly of *L. amoena*. There is no indication of the original locality for any of these elements in the drawing, and their corresponding vouchers have not been found and may have not been preserved.

***Lockhartia galeottiana* A. Rich. ex Soto Arenas**

8. *Lockhartia galeottiana* A. Rich. ex Soto Arenas, Icon. Orchid. 10: plate 1038, xvii-xviii. 2008. Based on *Ophrys imbricata* Sessé & Mociño, Pl. Nov. Hisp., ed. 2: 142. (1887?-)1890. Non *Orchis imbricata* Sessé & Mociño (Fl. Mexic., ed. 2: 199. 1894 or 1896?), nec *Epidendrum imbricatum* Lam. (*Lockhartia imbricata* (Lam.) Hoehne). TYPE: [MEXICO. Guerrero: Chilpancingo de los Bravo], mountains of Acahuizotla, July [1789], M. Sessé s.n. (lectotype, designated by Soto Arenas, Icon. Orchid. 10: plate 1038. 2008: “20-1 *Epidendrum imbricatum* de México,” from the original labels of the Expedición Real de Botánica, No. 4335 in the “modern labels” and with the negative No. 40963 of the Chicago Natural History Museum, MA-4335 [photo seen], photo: F; probable isoelectotype: sheet annotated as “*Fernandezia imbricata* de Mexico” in J. A. Pavón’s handwriting [“Mexico, Herb. Pavon” written on back of sheet, Sessé s.n. (his name not written on the specimen; see Nomenclatural notes below)], BM-000534515. Painting of putative type collection in life: “277, 20-1, *Serapias imbricata* Sp.N.”, Hunt Institute for Botanical Documentation (Pittsburgh, PA, USA), Torner Collection No. 6331.0183 [photo seen], copy (hand painted) in G [DC. plate no. 1197; photo: Chicago Natural History (Field) Museum negative no. 30867; prints in F, MICH, MO]).

Stems erect or descending, rigid, 13–46 cm long when reproductive, with 26–54 leaves; shoots (stem and leaves) 10–25 mm wide. Leaves marcescent, unifacial,

laterally flattened, narrowly triangular in side view, subfalcate, with outcurving to straight (rarely incurving) margins, obtuse (rarely obliquely acute), exposed surface of largest leaves 14–41 × 4–9 mm. Inflorescences both terminal and axillary from upper portion of the stem (produced sequentially along the stem), with 1–3 flowers produced sequentially, exerted portion 0.5–1.7 cm long, internodes 1–4 mm long; inflorescence bracts amplexicaul, widely ovate, cordate, obtuse, apiculate, 2–5 × 2–4 mm, appressed or oblique (forming an acute angle) to the rachis, imbricate; pedicel and ovary 10–15 mm long. Flowers resupinate, widely open, 14–25 mm tall, yellow, the labellum and column heavily spotted with reddish brown; the lateral lobes with oblique-longitudinal brown stripes; the anther cap white to yellow. Sepals ovate to elliptic, slightly concave, obtuse, 6–7.5 × 4–5 mm. Petals long elliptic to oblong, curved toward the front, margins reflexed, apically obtuse to subtruncate, 7–9.5 × 4.5–6 mm when flattened. Labellum 3-lobate, 8–17 mm long, 10–16 mm wide across lateral lobes when flattened; lateral lobes elongate, oblong, obtuse apically, curved toward front, 4–6 × 1–1.5 mm; midlobe divided in 4 lobules, pandurate, emarginate, wider across the distal lobules when flattened, margin irregularly undulate, 8–14 × 8–14 mm, the basal lobules folded backwards, the distal lobules flared obliquely downward; callus elongate, suboblong; basal part forming a concave cushion with a basal tuft of short, glandular hairs, 2 × 1.5–2 mm; the distal portion forming an oblong mass of low tubercles, 4 × 1–3 mm, wider and bifid distally. Column broadly winged, 2 mm long, 4.5 mm wide; wings suboblique, subquadrate ovate, 2 × 2 mm, with an entire to denticulate margin; stigmatic cavity oblong to pandurate, 1 × 0.5 mm; anther cap galeate, 1–1.5 mm long; pollinarium 1 mm tall, stipe bifid. Fruit obovoid, 10–12 × 5–7 mm.

Nomenclatural notes: The specimen cited here as the probable isotype of *Ophrys imbricata* does not have Sessé's name on it, but was annotated by Pavón as "*Fernandezia imbricata* de Mexico", a name that was never published. It is well known that Pavón sold thousands of specimens from the Sessé and Mociño herbarium to private, mainly British collectors (McVaugh, 1977), many of which ended up in BM. It was unusual for Pavón to modify the names of Sessé and Mociño, but he probably recognized the specimen as a member of *Fernandezia* (as originally circumscribed by Ruiz and himself), and he probably changed it from either *Ophrys* or *Epidendrum* and discarded the original label. Pavón never collected in Mexico.

The painting of the type cited above was made by Atanasio Echeverría y Godoy (one of the artists of the Sessé expedition) directly from the live plant in the field. The original is now deposited in the archives of the Hunt Institute for Botanical Documentation in Pittsburgh. A hand-painted copy (DC. plate 1197, part of the copy set commissioned by Augustin Pyramus de Candolle) is held at G, with photos in several herbaria (e.g., F, MICH, MO, from the Field Museum negative no. 30867). The number "20-1", present in both the lectotype and the paintings, refers to the Linnaean class and order "Gynandria-Monandria" and is not a collection number (McVaugh, 1985).

The detailed locality data and year for the type collection of *Ophrys imbricata* are inferred from the Sessé and Mociño expedition itinerary presented by McVaugh (1977). The plant was collected by Sessé in 1789 during the expedition's "second excursion"; Mociño did not join the team until the "third excursion" (McVaugh, 1977). The results of the expedition (including valid species descriptions) were published posthumously a

century later. McVaugh (1977) discussed the complexities and uncertainties of the true dates of these publications, which do not always match the year printed on them.

The detailed locality data and date of collection of “*Fernandesia galeottiana* A. Rich.” were obtained by comparing the locality name in the painting with Galeotti’s itinerary, published by McVaugh (1978).

Phenology: Flowering plants have been collected throughout the year, but more abundantly during the months of May, June, and July; no flowering collections have been made in August.

Distribution: Endemic to western Mexico, in the states of Guerrero, Jalisco, Nayarit, and Oaxaca, from 550 to 1500 m in the Sierra Madre del Sur and the southern portion of the Sierra Madre Occidental (Figure 7). A watercolor of this species by Galeotti and currently in P (not seen, but cited by Soto Arenas in the protologue) was apparently made from a plant collected in Juquila (Oaxaca), and has a note stating that the elevation was “6500 ft.” (1980 m); thus, it is possible that *L. galeottiana* occurs (rarely) as high as 2000 m.

Additional specimens examined: MEXICO. Without locality: *anonymous* 10 (K-spirit); Aug. 1888 (cult.), *Bull s.n.* (K); *Karwinski* 3041 (G). Guerrero: 1 mi N of Agua de Obispo, 1006 m, 1 Jul. 1952, *Rowell* 2995 (F, MICH); Agua del Obispo, 975 m, 11 Jun. 1954, *Ryan & Floyed* 34 (LL); Atoyac-El Gallo, km 54, 27 Sep. 1981 (cult.), *Hágsater* 4770 (AMO, 4 sheets); Atoyac, El Ranchito, 11 km al NE de El Paraíso, 1100 m, 25 May 1986, *Soto Núñez & Solórzano* 12799 (MEXU); Atoyac, El Ranchito, 13 km al NE de El Paraíso, 1100 m, 22 Apr. 1985, *Soto Núñez & Aureoles* 8432 (E, MEXU); Camino Atoyac-El Gallo, arriba de Paraíso, km 54, 3 Aug. 1987 (cult.), *Hágsater* 4770 (AMO, 2

sheets), 8 Jun. 1984 (cult.), *Hágsater 4770* (AMO, 5 sheets), 26 Sep. 1986 (cult.),
Hágsater 4770 (AMO, 3 sheets), 27 Feb. 1977 (cult.), *Hágsater 4771* (AMO);
Chilpancingo, 22 Jun. 1977 (cult.), *Ackerman 870* (SEL), 7 Jul. 1978 (cult.), *Ackerman*
1213 (SEL), 7 Apr. 1978 (cult.), *Pridgeon s.n.* (F); Galeana, Plan de Carrizo, 750 m, 14
Oct. 1939, *Hinton et al. 14640* (AMES); Galeana, Sierrita, 800 m, 28 Jun. 1939, *Hinton*
et al. 14366 (AMES); Km 339-40 between Acahuizotla and Agua de Obispo in highway
to Acapulco, 914 m, 1 Oct. 1949, *Moore 5145* (AMES, BH); Mexico-Acapulco road, km
341-342, Jul. 1941, *Sawyer 103* (F); Near Cantiles de Joveritos, km 353 road México-
Acapulco, 900 m, 3 Mar. 1932 (cult.), *Oestlund 2687* (AMES, MEXU, MO, S, US); Near
end of road to El Fresno Microondas, turnoff to which is 2 mi S of El Rincón on
Acapulco-Iguala Hwy. (#95), 1100 m, 28 Sep. 1983, *Chase 83253* (AMO, K-spirit,
MICH, MO, SEL); Near Jaltianguis, 550 m, 21 Jun. 1934 (cult.), *Oestlund 1720* (AMES,
BM, S, US); Region of Acahuizotla, Jul. 1942, *Sawyer 680* (F); Region of Joveritos, 800
m, 19 Mar. 1936 (cult.), *Oestlund 3280* (AMES, MO); San Luis Acatlán, 20 km al N de
Miahuichán, 1050 m, 24 May 1983, *González Loera & Castaneda 324* (MEXU); Sierra
Madre, above La Providencia, Acapulco, 21 Nov. 1882, *Hancock 4* (K, 2 sheets).
Jalisco: 10 miles S of Autlán toward La Resolana, 1463 m, 15 Jul. 1949, *Wilbur &*
Wilbur 1728 (DS, DUKE, F, MEXU, MICH, WIS); Purificación, La Estancia, Sierra de
Purificación, 1450 m, 20 Nov. 1987, *Díaz Luna 19346* (AMO); Road W of Autlán, 1311
m, Jun. 1955, *Johnson 1254-40* (SEL); SW of Autlán, toward Manzanillo, 1200 m, 9
Apr. 1949, *McVaugh & Wilbur 10223* (AMES, G, MEXU, MICH, NY, US). Nayarit: Ca.
10 mi W of Tepic on road to Jalcocotán, 26 Dec. 1949, *Dressler 1007* (US); Jocolcotán,
20 Dec. 1946, *Dawson s.n.* (RSA); Near La Yerba, ca. 20 km NW of Tepic on

Jalcocotán road, 12 Jul. 1961, *Dressler & Wirth 2704* (AMES, BRIT, MO, UC, US); Xalisco, El Astal, cerca de la capilla en el ejido El Cuarenteno, 1450 m, 22 May 1996, *Alvarado & Ibarra 352* (MEXU); Xalisco, La Carbonera, 16 Jun. 1992, *Alvarado 51* (MEXU). Oaxaca: Pluma Hidalgo, Pochutla, Cerro Espino, al E de la finca cafetalera Monte Cristo, 1250 m, 24 Feb. 1988, *Campos 1499* (MEXU); Pochutla, Cal. S. Antonio, Cerro del Machete, 1500 m, Feb. 1941, *Reko 6061* (AMES, MEXU, RSA); Pochutla, Finca Monte Cristo, Cerro Espino, 1000 m, 8 Feb. 1977, *Souza & Soto 7139* (MEXU); Pochutla, San Miguel del Puerto, 50 m al N del casco de la finca Monte Carlo, 900 m, 29 Mar. 2002, *Saynes et al. 2907* (MEXU); Pochutla, San Miguel del Puerto, Finca Montecarlo, al N rumbo al Rancho Las Lobas, 1210 m, 31 May 2001, *Saynes et al. 2191* (MEXU); Teoxomulco, *Karwinski s.n.* (G). COUNTRY UNKNOWN: C. America (cult.), *Renz 14492* (RENZ). CULTIVATED [without original locality data]: 24 Jul. 1983, *Chase 83147* (K-spirit); 2 Jun. 1932, Ecuador, below Quito, *Oestlund 2688* (AMES, S; locality likely erroneous).

Commentary: *Lockhartia galeottiana* is most similar to *L. verrucosa*, from which it is distinguished by the leaves often slightly curved away from the stem (vs. straight to incurved), the usually shorter, congested inflorescences with spiral phyllotaxy produced sequentially (basipetally) along the stem (vs. generally several produced simultaneously), often more than one flower produced in each inflorescence (vs. usually only one), and the narrower, bifid callus of the labellum. The apical lobules of the labellum midlobe tend to be somewhat wider than in *L. verrucosa*. The distinctive leaf shape is, however, somewhat variable (even in the same plant), and some collections (or individual stems) can appear more similar to those of *L. oerstedii* (with long, narrow

shoots with straight leaves) or *L. verrucosa* (with leaves slightly curved toward the stem). The floral differences, however, are consistent.

Lockhartia galeottiana and *L. verrucosa* are allopatric (the former occurs in the Sierra Madre del Sur and the southern part of the Sierra Madre Occidental in western Mexico, while the latter occurs in the Sierra Madre de Chiapas in southern Mexico and Guatemala), and their ranges are separated by the Chivela Pass in Oaxaca. *Lockhartia galeottiana* is the northernmost species in the genus, and it is not sympatric with any other species of *Lockhartia*.

Collections of *Lockhartia galeottiana* have traditionally been treated as *L. oerstedii* in the literature (e.g., McVaugh, 1985) and annotated as such in herbaria. However, *L. oerstedii* has narrower stems, a wider callus, taller callus tubercles, and occurs from Chiapas to Panama.

***Lockhartia genegeorgei* D.E. Benn. & Christenson**

9. *Lockhartia genegeorgei* D.E. Benn. & Christenson, Lindleyana 13: 53, fig. 15. 1998. *Neobennettia genegeorgei* (D.E. Benn. & Christenson) Senghas, J. Orchideenfr. 8: 364. 2001. TYPE: PERU. Huanuco: Leoncio Prado, 3 Km SW of Cueva de Pavas, Alturas de Huachipa, September 1992, *E. Jara P. sub D.E. Bennett 5199* (lectotype, here designated: specimen annotated as “isotype” on label but marked as “holotype” on sheet, with the following label data: PERU. Huanuco: Leoncio Prado, 3 kms from the road to Tingo María, Alturas de Huachipa, 5 January 1992, *D.E. Bennett 5199-24*, NY-4660; isotype: USM, transferred to MOL *fide* E.A. Christenson, not found in either herbarium, probably a “clonotype” and thus not a true isotype).

Stems erect or arching, 5–11 cm long when reproductive (to the apex of the pseudobulb), covered by 4–5 imbricate, progressively longer, foliaceous bracts and

terminated by a single pseudobulb; pseudobulb narrowly elliptic, more or less flattened, truncate to slightly oblique apically, 2–5 × 0.4–0.6 cm, with a single apical leaf. Leaves (including foliaceous bracts of stem) conduplicate, linear, acute, with an abscission layer; sheaths folded lengthwise, 10–40 × 3–6 mm (in profile), blades 3–15 cm × 3–6 mm; apical leaf without a sheath, conduplicate but folded lengthwise for ca. half of its length, 7.5–30 cm × 3–6 mm. Inflorescences axillary from the leaf immediately subtending the pseudobulb, with 4–15 flowers produced more or less simultaneously; exerted portion 6–20 cm long, internodes 2–5 mm long; peduncular bracts narrowly triangular, acute, subappressed to the peduncle, 5–7 × 2–4 mm; rachis bracts amplexicaul, subrotund, cordate, obtuse, apiculate, expanded, 4–6 × 4–6 mm, not imbricate; pedicel and ovary 8–11 mm long. Flowers resupinate, widely open, 12–15 mm tall, yellow with two orange bands on the callus, the column yellow with orange lines on the wings and a pale white anther. Sepals elliptic, slightly concave, acute, the laterals slightly oblique, 5–6 × 2–3 mm. Petals elliptic, apically round to subtruncate, 5–6 × 3–3.5 mm. Labellum sigmoid in profile, obscurely lobed, lacking arm-like basal lobes, obscurely pandurate when flattened but much wider below the middle, retuse, the margins reflexed in life except near the apex, 7–9 mm long, 5–6 mm wide when flattened; callus consisting of two parts; the basal part a concave, elliptic cup 3 × 2 mm, with a dense, oblong pad of very short (<0.5 mm) glandular trichomes in the middle; the distal part formed by 2 raised (1 mm), smooth, convergent keels, together 2 × 1.5 mm. Column broadly winged, 3 mm long, 3.5 mm wide; wings oblique, subquadrate, each with a raised midvein, 1.5 × 2 mm, with a slightly irregular margin; stigmatic cavity teardrop-shaped, acuminate toward the anther, 2 × 0.6 mm; rostellum elongate, 0.7 mm long; anther cap slightly surpassing

column wings, galeate, subrostrate apically, 1.7×1 mm; pollinarium 1.7 mm tall, stipe elongate, subspathulate, entire, wider near the pollinia 1×0.2 mm. Fruit not seen.

Nomenclatural notes: David E. Bennett (1923-2009) frequently prepared “duplicate” herbarium specimens from his plants in cultivation in Lima, at different dates. Each pseudo-duplicate was given a suffix number after the collection number assigned to the cultivated plant, and the date of preparation was indicated on the label. Several such pseudo-duplicates were designated as isotypes for orchid species that Bennett described together with Eric A. Christenson. However, because these pseudo-duplicates cannot be considered part of the same gathering (in the sense used by the International Code of Botanical Nomenclature; McNeill *et al.*, 2006), such specimens are not true isotypes and should be treated simply as paratypes.

The four known dry specimens of *Lockhartia genegeorgei* prepared by Bennett (four in NY, one in FLAS) have label data that are partially inconsistent with the protologue (the paratype in spirit at MOL does not have a label with it, other than the collector’s number). The specimen here chosen as lectotype has the suffix “24”, and the date of preparation disagrees with that given in the protologue. However, it is the most complete specimen. The date mentioned in the protologue probably refers to the date of preparation of the description and/or illustration.

Another possibility is that Bennett’s prefix number refers to the species and not to individual plants. This idea is supported by the following sentence from the protologue: “Both collections represent large populations and many clones of each were brought into cultivation and flowered in Lima.” All four dry specimens of *L. genegeorgei* seen by me have the Bennett prefix number “5199” followed by different numerical suffixes; it is

improbable that all of these were prepared from the same cultivated plant, especially because the type illustration shows a rather small plant. In any case, none of the additional specimens at NY or FLAS can be considered true duplicates.

The herbarium collections of David Bennett previously deposited in USM and in Bennett's own personal herbarium have been transferred to MOL (Eric Christenson, pers. comm. 2009), but the isotype of *L. genegeorgei* has not been found at any of these herbaria (Delsy Trujillo, pers. comm., 2010). The only specimen in MOL is in spirit, and has a different Bennett number (7321) than the type collection.

Phenology: All four known herbarium specimens (including the type) were apparently prepared from plants in cultivation in Lima, where they flowered in January, September, and December.

Distribution: Endemic to Peru, where it has been collected only in Huánuco department, province of Leoncio Prado, at 1200 m (Figure 5).

Additional specimens examined: PERU. Huánuco: Leoncio Prado, heights above Huachipa, 3 km from the road to Tingo María, 1200 m, 5 Jan. 1992 (cult.), *E. Jara sub Bennett 5199-13* (NY); Leoncio Prado, heights above Huachipa, 3 km from Cueva de Las Pavas, 20 Dec. 1991 (cult.), *Jara sub Bennett 5199-19* (FLAS); Leoncio Prado, heights above Huachipa, 3 km from the road to Tingo María, 1200 m, 12 Sep. 1992 (cult.), *Jara sub Bennett 5199-6* (NY); "Same general locality as the type", Oct. 1995, *Jara sub Bennett 7321* (MOL-spirit).

Commentary: *Lockhartia genegeorgei* is immediately recognizable by its relatively short stems terminated by a pseudobulb, linear, articulated, conduplicate leaves that are much longer than those of any other species of *Lockhartia*, strictly axillary

inflorescences, long (up to 12 cm) inflorescence peduncles, labellum without lateral lobes but with a large elaiophore (about 1/3 the length of the labellum) and a strange, folded callus, elongate rostellum, and elongate and entire (non bifid) stipe.

Lockhartia genegeorgei is the most deviant species in the genus, so much so that Bennett and Christenson (1998) put it in a subgenus of its own (*Pseudobulbosa* D.E. Benn. & Christenson), and Senghas (2001) erected the genus *Neobennettia* for it. However, this species also has a number of traits that are diagnostic of *Lockhartia*: the pseudo-cymose inflorescence development, the amplexicaul, widely ovate and expanded inflorescence bracts (as in most species of the Imbricata group of subgenus *Lockhartia*), and the elaiophore (putatively functional) formed by a field of minute trichomes in a depression at the base of the labellum.

Chase (2009) suggested that *Lockhartia genegeorgei* has reverted to an ancestral vegetative morphology more typical of other members of subtribe Oncidiinae, implying that the other species of *Lockhartia* show a paedomorphic condition. It may also be that *L. genegeorgei* is sister to the remainder of the genus and that it retained several plesiomorphic traits. Yet a third possibility is that *L. genegeorgei* is a natural hybrid (or a lineage of hybrid origin) between a species of *Lockhartia* (probably the sympatric *L. lepticaula*) and a species of *Oncidium*. Unfortunately, *L. genegeorgei* remains a rare species (very few herbarium collections are known, all from the same area) and no live material or DNA has been available to test these hypotheses; repeated attempts to extract DNA from herbarium specimens have failed.

***Lockhartia goyazensis* Rchb. f.**

10. *Lockhartia goyazensis* Rchb. f., Bot. Zeit. 10: 768. 1852. TYPE: BRAZIL.
Goyaz [Goiás]: between Arrayas [sic; Tocantins: Arraias] & São Domingos [sic; Goiás:

São Domingos], May 1840, *G. Gardner* 4360 (holotype: W; isotypes: BM, CGE [not seen], E [image seen], G [3 sheets], K, K-Lindl. [mounted on the right side of the type sheet of *Lockhartia lunifera*], OXF [image seen], W. Possible type fragment: single flower in packet of unaccessioned sheet at W, annotated “*Gardner*” inside packet; rehydrated by Kraenzlin).

Stems erect or descending, rigid, 5–38 cm long when reproductive, with 18–80 leaves; shoots (stem and leaves) 10–17 mm wide. Leaves marcescent, unifacial, laterally flattened, triangular in side view, with outcurving (occasionally straight) margins, obtuse to truncate (commonly rounded), exposed part of largest leaves 8–24 × 4–7 mm. Inflorescences both terminal and axillary from the distal part of the stem, with 1–3 flowers produced sequentially; exerted portion 0.3–1.7 cm long, internodes 1–2 mm long; inflorescence bracts amplexicaul, widely ovate, cordate, obtuse, apiculate, nearly flat to infundibuliform, 3–4 × 2–4 mm; pedicel and ovary 8–10(17) mm long. Flowers resupinate, widely open, 8–10 mm tall, yellow, the labellum with reddish brown spots and lines around the callus and on the lateral lobes, and an open V-shaped dark brown infrastigmatic band. Sepals elliptic, slightly concave, obtuse, 4–6 × 2.5–3 mm. Petals widely elliptic, apically rounded to subtruncate, 4.5–6 × 2.5–3 mm. Labellum 3-lobate, 5–6.5 mm long, 6–10 mm wide across lateral lobes when flattened; lateral lobes short to elongate, oblong to linear, obtuse to acute apically, curved toward front, 2–4 × 0.5–1 mm; midlobe divided into 4 lobules, more or less pandurate, emarginate, margin irregularly undulate, 4–5 × 3.5–5 mm, the basal lobules folded backwards, the distal lobules projected downward; callus more or less triangular or drop-shaped; basal part forming a concave cushion with a basal tuft of short, glandular hairs, 1.5–2 × 1.5–2 mm;

the distal portion forming a widely obovate mass of tubercles. Column winged, 2–2.5 mm long, 1.5–2.5 mm wide; wings directed downward, giving the column a hooded appearance, oblique, 0.5–1 × 1–1.5 mm, with an entire to denticulate margin; stigmatic cavity rhombic to hemispheric, 0.8 × 0.8 mm; anther cap not seen; pollinarium not seen. Fruit obovoid, 8–12 × 3–6 mm.

Nomenclatural notes: George Gardner collected the type in 1840 somewhere between the towns of Arraias and São Domingos (in southeastern Tocantins and northeastern Goiás states, in their current delimitation); both towns are ca. 77 km apart. Tocantins was not established as a separate state until 1988, and it was part of Goiás at the time of Gardner’s explorations. In the account of his travels in Brazil, Gardner (1846) described that part of his voyage in pages 376-379 (Chapter XI). The type was likely collected on May 8th 1840, when Gardner traveled between Fazenda Gamelleira and Fazenda Mangê, still closer to Arraias than to São Domingos (and thus probably still in Tocantins state). Part of the entry for that day describes the locality where the type was likely collected:

“Soon after leaving Gamelleira, we entered a virgin forest quite unlike any I had seen since leaving the Province of Rio de Janeiro, and which I little expected to find in the district where we were now travelling. It contained many large trees, covered with numerous parasitical Orchideae.”

Although this particular patch of forest might no longer exist, Gardner’s detailed description of the landscape could allow someone familiar with the area to locate the site.

One of the isotypes of *Lockhartia goyazensis* at G has the year 1841 instead of 1840; this is probably a typographic error as it still bears Gardner’s collection number 4360.

The name “*Lockhartia macrocarpon* L.C. Rich.” (written on *Maciel et al. 1475*, MG), was never published, and to my knowledge, was never even proposed by Louis Claude Richard. However, this name probably originated from a *Lockhartia* plant, mislabeled as “*Catasetum macrocarpon*”, which flowered at Kew sometime before 1817 and on which the genus *Lockhartia* was established (Lindley, 1824, and nomenclatural notes under *L. imbricata*). How this name came to be associated with a recent collection of *L. goyazensis* is a mystery.

Phenology: Plants have been collected in flower mostly from April to August, and occasionally in other months of the year.

Distribution: Central Brazil and eastern Bolivia, at least from 150 to 900 m (Figure 8). However, most collections lack elevational data. *Lockhartia goyazensis* is a common species in the Brazilian planalto and the southern Amazon basin in the states of Goiás (including the Distrito Federal Brasília), Mato Grosso, Minas Gerais, Rondônia, and southern Pará. It has been collected a few times in the Brazilian state of Amazonas. In Bolivia, it is known from the eastern Amazonian lowlands in the states of Beni, Pando, and Santa Cruz.

Additional specimens examined: BOLIVIA. Beni: Vaca Diez, 20.8 km E of Riberalta on road to Guayaramerín, 230 m, 25 Sep. 1981, *Solomon 6413* (MO, SEL); Vaca Diez, camino de Riberalta hacia Guayaramerin, desviando al camino a Cahuela, 150 m, 15 Aug. 2000, *Kromer & Acebey 1442* (LPB). Pando: W bank of Rio Madeira between Cachoeiras Madeira and Misericordia, 29 Jul. 1968, *Prance et al. 6604* (INPA, K, NY); W bank of Rio Madeira, 4 km above Abuna, 23 Jul. 1968, *Prance et al. 6264* (COL, F, GH, INPA, K, MG, NY, S, U). Santa Cruz: Guarayos, 5 km al S de las

instalaciones de Perseverancia, Riberas del Río Negro, 275 m, 16 Jul. 1992, *Vargas et al. 1701* (NY); Guarayos, Reserva de Vida Silvestre Ríos Blanco y Negro, Río San Martín (Concesión Oquiriquia), 300 m, 4 Sep. 1993, *Vargas & Tagua 2728* (F); Ñuflo de Chávez, Perseverancia, vecindad del Río Negro, tributario del Río Baures, a 75 km S del límite del Dpto. de Beni y 150 km O del Río Paragua, 200 m, 16 May 1991, *Mostacedo & Foster 84* (F); Ñuflo de Chávez, Reserva de Vida Silvestre "Ríos Blanco y Negro", Laguna Pajalar, 14 Aug. 1992, *Saldías et al. 2177* (LPB); Velasco, campamento El Refugio, a 1500 m al N de la casa, yendo al cerro por el camino de la ribera del Río Paragua, 180 m, 26 Jun. 1994, *Guillén 1946* (MO, NY); Velasco, Parque Nacional Noel Kempff M., Cataratas Federico Ahlfelt, Río Paucerna, 210 m, 11 May 1994, *Vásquez et al. 2203* (LPB-Vasq); Velasco, Parque Nacional Noel Kempff M., Río Itenez, Flor de Oro, Río Itenez, 200 m, Jun. 1993, *Vásquez et al. 2126* (LPB-Vasq); Velasco, Parque Nacional Noel Kempff Mercado, camino a El Encanto, 260 m, 6 Nov. 1995, *Rodríguez & Foster 765* (MO); Velasco, Parque Nal. Noel Kempff Mercado, campamento en Lago Caimán, tramo de bosque desde el Río Itenez hasta el lago, 250 m, 4 Oct. 1995, *Vargas et al. 4040* (F); Velasco, Río Paragua, 200 m, Apr. 1984, *Moreno sub Vásquez 911* (LPB-Vasq); [Velasco], beim Río Tarvo, km 8.1, 30 Aug. 1951, *Schmidt 2* (M).

BRAZIL. Without state or locality, or state uncertain: "Brasilia" [not the Brazilian capital, which was founded in 1960], 1841, *Duparquier s.n.* (BM); "Jarú, Rio Branco, Amazonas", 1913, *Kuhlmann 3464* (RB). Amazonas: In flumine Madeira et in arbor sylvae sapurensis, Flum. Nigri, *Martius 2694* (M); Rio dos Pombos, by waterfall about 4 hours by canoe N of the intersection with Transamazon Highway and 74 km E of Aripuana river, 23 Jun. 1979, *Calderón et al. 2651* (INPA, K). Brasília: APA de

Cafuringa, Fazenda Palestina, margem esquerda do Rio Sal, 2 Oct. 1992, *Pereira & Alvarenga 2271* (K, SP). Goiás: without locality, Apr. 1844, *Weddell 2581* (P); "Goyaz", Jun. 1920, *Herter 6930* (L); Cabeceiras de Goiás, Fazenda Raizama, km 20 da rodovia GO, 850 m, 29 Mar. 1994, *Pereira 2588* (K, SP); Goiânia, Dec. 1936, *Brade s.n.* (RB); Niquelandia, estrada de acesso a Lt CODEMIM, Serra da Mesa, 17 km apos a entrada para Rosariana, 11 Jul. 1996, *Pinho dos Santos et al. 487* (SP); Niquelandia, estrada de terra vicinal a GO-237 (Niquelandia/Colinas), entrada a 600 m da ponte sobre o bagagem a 40 km desta, 410 m, 14 Apr. 1992, *Walter et al. 1294* (RB); Niquelandia, Macedo, Mata ca. 03 km abaixo da mina de níquel, 28 Jun. 1996, *Azevedo et al. 1011* (SP); Próximo a Cromenia, 28 Aug. 1978, *Magnano 287* (RB, 2 sheets); Region of the southern Serra Dourada, 20 km E of Formoso, 16 May 1956, *Dawson 14865* (RSA); Region of the southern Serra Dourada, 21 km SE of Formosa, E of Amaro Leite, 14 Jan. 1965, *Dawson 14952* (UC); Serra do Caiapó, ca. 50 km S of Caiaponia, road to Jataí, 900 m, 27 Jun. 1966, *Irwin et al. 17870* (F, K). Mato Grosso: Aripuanã, Dardanelos, parte baixa da cachoeira das Andorinhas, 26 Sep. 1975, *Lisbôa et al. 285* (INPA); Aripuanã, Projeto Juina, arredores do aeroporto, 12 Jun. 1979, *Silva & Rosario 4879* (MG, NY); Cupim prope Palmeiras, 20 Dec. 1893, *Lindman A2457* (S, 2 sheets); Margem esquerda do Rio Juruena, arredores do acampamento da promessa, terreno de rocha de granito, SC 21 VC, 19 Jun. 1977, *Rosa & Santos 2143* (INPA, MG, MO, RB, U, US); Sandy E bank of Rio Aripuana, N of Humboldt Campus, 9 Oct. 1973, *Prance et al. 18303* (INPA, NY); Sta. Cruz, Nov. 1891, *Moore 692* (BM, K, NY); Tres Lagoas, km 85 da estrada para Alto Sucuriú, Fazenda Barreirinho, margens do Rio da Prata (afluente do Rio Sucuriú), 29 Aug. 1985, *Barros 1163* (SP); Tres Lagoas, margem

direita do Sacuriú, 18 Jun. 1964, *Correa Gomes 1948* (SP). Minas Gerais: without locality, Apr. 1915, *Vincent 6930* (L); Estação Experimental Agua Limpia, 9 Mar. 1949, *Granofremas 2555* (RB); Horto Florestal de Paraopeba (EFIEX-IBDF), Munic. de Paraopeba, 700 m, 11 May 1974, *Martinelli & Fernandes da Silva 320* (RB); Ituiutaba, Fazenda do Fundai, 7 Jul. 1950, *Macedo 2466* (NY, RB, S [2 sheets], SP, UC); Unai, localidade denominada Palmital, na confluencia do correjo das Lages com o Rio Preto, 27 Apr. 1993, *Pereira & Alvarenga 2493* (K). Pará: Agua Azul, em campina cortada pela estrada que vai de Xinguará a São Félix do Xingú, km 55 na margem esquerda do Rio Agua Preta, 1 Jun. 1994, *Silva et al. 331* (MG); Altamira, Rio Iriri, margem direita do Rio Iriri, cachoeira do Desvío (Amaro Velho), 18 Aug. 1986, *Vasconcelos et al. 15* (MG); Itaituba, Base Aérea do Cachimbo, km 792, 19 Apr. 1983, *Silva et al. 36* (INPA, NY); Marabá, Carajás, N-1, lado S da estrada, 14 Sep. 1984, *Silva & Santos 7* (MG); Pau D'Arco, Marajoará, 15 Aug. 1998, *Grogan 355* (INPA); Prope Porto de Moz in ripa flu. Xingú, [10 Sep. 1819], *Martius 2694* (M, W-Reich); Serra dos Carajás, 12 km W of camp ECB on the ferrovia, ca. 57 km W of road BR 150, 26 Jun. 1982, *Sperling et al. 6349* (K, NY); Serra dos Carajás, 6 km SE of AMZA camp N-1, 19 May 1982, *Sperling et al. 5731* (F, K, MG, NY). Rondônia: Alvoradá do Oeste, Linha 64, a 07 km da BR-429 em direção a Costa Marques, 1 May 1987, *Cid Ferreira 9001* (INPA); Ariquêmes, cultivated in Munich Botanical Garden, *Gerlach s.n.* (FLAS, M); Cacoal, BR 364, rodovia Cuiaba-Porto Velho, km 234, ao N da cidade, morro da torre da EMBRATEL, 23 Jun. 1984, *Cid et al. 4753* (INPA, K, MG, NY, SEL); Ji-Paraná, Rio Jarú, 20 Jul. 1987, *Martuscelli s.n.* (SP); Porto Vehlo to Cuiaba highway, 4 km S of Nova Vida, 15 Aug. 1968, *Forero & Wrigley 7074* (NY); Presidente Médici, BR-364, km 14, 17 May 1985,

Maciel et al. 1475 (MG); Rodovia Presidente Médici-Alvoradá, Rio Muqui, 18 Jun. 1983, *Silva 6217* (INPA, RB [2 sheets]). CULTIVATED [without original locality data]: Jul. 1896, *O'Brien s.n.* (K).

Commentary: *Lockhartia goyazensis* is most similar to *L. lunifera*, from which it can be distinguished by the leaves that often curve slightly away from the stem, the slightly smaller flowers, the elaiophore cushion often provided with a pair of distal rounded tubercles, and the narrower distal lobules of the labellum midlobe. The two species are largely allopatric, with *L. goyazensis* distributed in the Brazilian planalto and southern Amazon basin (including eastern Bolivia), and *L. lunifera* having a more coastal distribution, from southern Bahia to Santa Catarina. Herbarium specimens of *L. goyazensis* are occasionally misidentified as *L. lunifera*.

In the northern part of its distribution, *Lockhartia goyazensis* is parapatric (has limited overlap) with *L. imbricata*, and it is possible that there is some hybridization between them. Plants identified as *L. goyazensis* from that region tend to have wider and shorter labellum side lobes than those from farther south, although the callus morphology is uniform throughout the species range.

Lockhartia goyazensis was illustrated in Dodson and Vásquez (1989) as *L. ludibunda* (a synonym of *L. lunifera*).

***Lockhartia grandibractea* Kraenzl.**

11. *Lockhartia grandibractea* Kraenzl., Pflanzenr. (Engler) IV, 50 (Heft 83): 15, fig. 2H. 1923. TYPE: COSTA RICA. [Cartago, Dec.] *A.R. Endrés s.n.* (lectotype, here designated: drawings by A. R. Endrés of *Endrés 629*, W-Reich.-Orch.-33713; isolectotype: W-Reich.-Orch.-33709; voucher not found; epitype, here designated:

COSTA RICA. Alajuela: Reserva Biológica Monteverde, Río Peñas Blancas, Quebrada Gemelas, 800 m, 10°19'N 84°43'W, 10 Sep. 1989, *E. Bello* 1224 (INB; iso-epitype: MO).

Lockhartia triangulabia Ames & C. Schweinf., *Schedul. Orchid.* 8: 80-81. 1925.

Lockhartia amoena var. *triangulabia* (Ames & C. Schweinf.) C. Schweinf. & P.H. Allen, *Bot. Mus. Leaf.* 13(6): 150. 1948. TYPE: PANAMA. Chiriquí: [Boquete], Palo Alto Hill [in isotypes], 4000-5000 ft. [1220-1524 m], December 1923 [in potential isotypes], *C.W. Powell* 362a (holotype: AMES; potential isotypes: AMES, MO [both as "*C.W. Powell* 362", without the suffix "a"]).

Stems erect to descending, more or less rigid, 13–43 cm long when reproductive, with 20–60 leaves; shoots (stem and leaves) 10–23 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, acute to obtuse (occasionally rounded), with straight to incurving margins, exposed part of largest leaves 17–40 × 4–10 mm. Inflorescences both terminal and axillary from the distal part of the stem, with 3–10 flowers produced more or less simultaneously; exerted portion 2–8 cm long, internodes 4–10 mm long; inflorescence bracts amplexicaul, infundibuliform, subrotund, cordate, obtuse to apiculate, glaucous, 7-11 × 5-10 mm; pedicel and ovary 11–17 mm long. Flowers resupinate, widely open, 12–18 mm tall; yellow with orange-brown markings on the lateral lobes and on and around the callus, and a dark brown line at the base of the column; basal lobules of labellum midlobe often with a white background. Sepals ovate to elliptic, slightly concave, obtuse, 7-8 × 4-5 mm. Petals oblong-elliptic, slightly incurved, with revolute margins, rounded to truncate apically, 7-8 × 4-5 mm when flattened. Labellum trilobate, 11-12 × 14-15 mm (across lateral lobes); the lateral lobes oblong, incurved, 7-9 × 1.5 mm, apically obtuse to

rounded; midlobe divided in 4 lobules (the two basal ones triangular and projected backward, the two distal ones rounded when flattened), apically emarginate, 8-9 mm long, 11-12 mm wide (across the widest part of midlobe when flattened); callus suboblong, wider distally, the basal part forming a subquadrate concave cushion with a basal tuft of short, glandular hairs, 2 × 2 mm, the distal part formed by an irregular mass of tubercles 5 × 4 mm when labellum is flattened. Column hastate, truncate, narrowly winged, wider near the base, held perpendicular to the labellum, 3-3.5 mm long, 3.5 mm wide across the wings, 2 mm wide distally; anther cap hemispherical, 1-1.3 mm in diameter; pollinarium not seen. Fruit obovoid, non-glaucous, 17-23 × 7-8 mm.

Nomenclatural notes: Kraenzlin mentioned Endrés as the only collector in the protologue of *L. grandibractea*; thus only a collection by him can be considered as the type. However, Kraenzlin only annotated two specimens collected by Hübsch as “types”. It is well known that Kraenzlin frequently annotated as types specimens that cannot possibly be considered type material in the modern sense (Christenson, 1994).

The only material at W that can be convincingly matched to Kraenzlin’s description are drawings of *Endrés 629*, mounted on two sheets. The voucher for these drawings has not been found, but there is a handwritten description by Endrés (W-Reich.-Orch.-33713) with the number 629 and data “Cartago, Dec., [illegible]”. It is possible that *Endrés s.n.* (W-Reich.-Orch.-45080, without flowers) is the voucher (if the original label was lost), but this specimen was annotated by Kraenzlin as *L. amoena*, and presently there is no way to confirm or reject this possibility.

Kraenzlin's description of the species could apply to either *L. grandibractea* (as circumscribed here) or *L. endresiana*, but the protologue drawing shows a labellar callus made up of a mass of low tubercles, which is diagnostic of the former.

The name *Lockhartia triangulabia* is based on *Powell 362a* (holotype at AMES). Another specimen at AMES, *Powell 362* (without the suffix "a") looks vegetatively different and appears to be *L. endresiana*. The suffix "a" after Powell's collection number was probably assigned by Ames and Schweinfurth to distinguish between both specimens. There is a previously undetected duplicate number (*Powell 362*) in MO, which is vegetatively identical to *Powell 362a*. In annotations made to the specimens in AMES, R.L. Dressler suggested that *L. triangulabia* might represent a hybrid complex between *L. oerstedii* and *L. amoena*, a conclusion I disagree with.

Phenology: Flowering plants have been collected throughout the year, but more abundantly during the months of June, August, and September (middle of the rainy season in the region).

Distribution: Costa Rica and western Panama, from 500 to 1700 m (Figure 2). In northern and central Costa Rica it is found almost exclusively on the Caribbean slopes of the Guanacaste, Tilarán, and Central Volcanic cordilleras, but in the Talamanca Cordillera of southern Costa Rica and western Panama it is found almost exclusively on the Pacific slopes.

Additional specimens examined: COSTA RICA. Without locality: 26 Nov. 1936 (cult.), *anonymous s.n.* (K); 28 Oct. 1922 (cult.), *anonymous s.n.* (K); *anonymous s.n.* (K-spirit, 2 jars); *Endres s.n.* (W-Reich, sterile); 1882, *Huebsch s.n.* (W-Reich, 2 sheets); 24 Oct. 1950 (cult.), *Lankester s.n.* (K); 2 Oct. 1950 (cult.), *Lankester s.n.* (K);

Cultivated, *Lankester s.n.* (BM); 19 Sep. 2004 (cult.), *Pupulin 2953* (JBL-spirit);
Cultivated, *Rowlee & Rowlee 292* (AMES). Alajuela: Cataratas de San Ramón, Jun.
1988, *Retana s.n.* (USJ); Monteverde Cloud Forest Reserve in Peñas Blancas Valley,
just above the "German's", 900 m, 12 Dec. 1989, Atwood & Morris 4111 (SEL);
Monteverde Reserve, Peñas Blancas river valley, Atlantic slope, 800 m, 3 Oct. 1986,
Bello ex Haber 5705 (MO); Monteverde, confluencia Quebrada Leona y Río Peñas
Blancas, Aug. 1989, *Campos s.n.* (USJ); P. Nac. Rincón de la Vieja, Colonia Blanca, 7
km al S en Finca Los Mora, Quebrada Mora, 600 m, 3 Aug. 1991, *Rivera & Jiménez*
1514 (CR, INB); Reserva Biológica Alberto Brenes, 1200 m, 21 Jun. 2007 (cult.), *Rojas*
et al. 7021 (JBL-spirit); Reserva Biológica Monteverde, Río Peñas Blancas, Finca
Cornelio, 950 m, 18 Sep. 1987, *Haber & Bello 7588* (INB); Reserva Biológica
Monteverde, Río Peñas Blancas, Laguna y Quebrada Celeste, 850 m, 4 Nov. 1989,
Bello 1452 (INB); Reserva de San Ramón, aprox. 30 km NNO de San Ramón, 8 Dec.
1984, *Dressler & Biologia-350 296* (USJ); Reserva Forestal Arenal, Río Peñas Blancas,
Quebrada Agua Gata, Finca Francisco, 1200 m, 19 Sep. 1990, *Obando 118* (F, INB, K,
USJ); Reserva San Ramón, Jun. 1986, *Retana s.n.* (USJ); San Ramón, cuenca del San
Carlos, de San Miguel sobre carretera de lastre, ruta a Laguna Pocosol, ca. 1.5 km
antes del puente del Río San Lorenzo, 500 m, 23 May 2001, *Rodriguez & Lépiz 7362*
(INB); Upala, P.N. Guanacaste, Cordillera de Guanacaste, Estación San Ramón, Dos
Rios, Sendero El Níspero, 550 m, 4 Apr. 1995, *Quesada 306* (INB). Cartago: Atlantic
rainforest of Río Birris canyon, 1000 m, 20 Oct. 1959 (cult.), *Horich sub Blydenstein s.n.*
(UC); Cachí, Aug. 1989, *Castelfranco s.n.* (USJ); La Fuente, 1110 m, 20 Sep. 1923,
Lankester s.n. (AMES); La Fuente, E Turrialba, 1200 m, 23 Aug. 1925, *Alfaro 74*

(AMES); Pejibaye, La Selva, 1100 m, 7 Jan. 2001 (cult.), *Pupulin* 2794 (USJ); Río Birrís canyon, 1000 m, 16 Oct. 1961 (cult.), *Horich sub Hutchinson* s.n. (MO); Río Navarro, forests above Orosi, 1524 m, 26 Nov. 1946 (cult.), *Allen* 3832 (SEL); Turrialba, 1 Apr. 1924, *Alfaro* 39971 (AMES, US), *Alfaro* 40231 (AMES); Turrialba, 1000 m, 20 Jun. 1932, *Kupper* 1628 (M); Turrialba, entre Santa Cruz y Pacayas, Oct. 1990 (cult.), *Cambronero* s.n. (USJ); Turrialba, Guayabo, Aug. 1989, *Retana* s.n. (USJ, 2 sheets); Turrialba, Moravia de Chirripó, 1000 m, 17 Feb. 2004 (cult.), *Pupulin et al.* 3626 (JBL-spirit); Turrialba, Moravia de Chirripó, 3 km después de un albergue en Hacienda Moravia, 1100 m, 30 Jul. 2005 (cult.), *Karremans & Ferreira* 875 (JBL-spirit); Turrialba, Pejibaye, Selva, 1100 m, 22 Feb. 1996, *Blanco et al.* 657 (CR); Turrialba, Platanillo, 700 m, 21 Mar. 1954, *León* 4352 (USJ); Turrialba, San Antonio, orillas del Río Guayabito, Quebrada Loca, 1450 m, 26 Sep. 2004 (cult.), *Karremans & Karremans* 400 (JBL-spirit); Turrialba, Santa Cruz, El Retiro, 1400 m, Jan. 1941, *Valerio* 1287 (CR, F); Vicinity of Orosi, 30 Mar. 1924, *Standley* 39686 (AMES), *Standley* 39908 (AMES, US), *Standley* 39942 (AMES, US). Guanacaste: La Tejona, N of Tilarán, 600 m, 25 Jan. 1926, *Standley & Valerio* 46014 (AMES); Las Nubes de Río Chiquito, 1200 m, *Chase* 15882 (K-spirit); Las Nubes, Tilarán, 1.5 km N Las Nubes on road to Tilarán, 1300 m, 6 Aug. 1988, *Haber & Atwood* 8564 (CR); Tilarán, Cerro Frio, zona Monteverde, vertiente Pacífica, 1100 m, 30 Jun. 1987, *Haber & Bello* 7329 (MO). Limón: Región SE del Lago Dabagri, cruzando las filas hacia Telire (Laguna Tiestos y Fila de los Aguacatillos), 5 Nov. 1984, *Gómez et al.* 23191 (MO, SEL); Talamanca, Lago sin nombre al pie de Fila Lleskila, 1160 m, 4 Nov. 1984, *Gómez et al.* 23117 (MEXU, MO). Puntarenas: [Coto Brus], Between Las Cruces Botanical Garden and Río Jaba, ca. 3 km SE of San Vito de

Coto Brus, 1050 m, 11 Jul. 1985, *Grayum 5591* (MO); [Coto Brus], 1 mile due S of San Vito de Java, 1067 m, 18 Aug. 1967, *Raven 21906* (CR, DUKE, F, PMA, SEL, U); [Coto Brus], Wilson's finca, 6 km S of San Vito de Java, 1219 m, 16 Aug. 1967, *Raven 21820* (F); Coto Brus, 1000 m, 23 Feb. 1992, *Pupulin s.n.* (USJ); Coto Brus, cuenca Térraba-Sierpe, Z.P. Las Tablas, Estación Biológica Las Alturas, sendero a Fila Tigre, 1360 m, 26 Jun. 1999, *Alfaro 2452* (INB); [Coto Brus], San Vito de Java, 22 Sep. 1968, *Mathias sub Rodríguez 1183* (USJ); Coto Brus, Zona Protectora Las Tablas, Finca Las Alturas, road from Las Alturas to Fila Tigre, 1450 m, 6 Jun. 2005 (cult.), *Pupulin et al. 4515* (JBL-spirit); Coto Brus, Zona Protectora Las Tablas, Las Alturas de Cotón, Las Alturas Biological Station, S slopes of Cerro Chai, 1500 m, 2 Jul. 2007 (cult.), *Pupulin et al. 5834* (JBL-spirit); Entre Agua Buena y San Vito de Java, 1200 m, 22 Oct. 1964, *Jiménez 2471A* (F); [Coto Brus], Finca Las Cruces, 6 km S of San Vito de Java, 1220 m, 10 Feb. 1971, *Gills & Plowman 10095* (A); Monteverde, Río San Luis valley, Pacific slope below Monteverde, 900 m, 14 Jul. 1988, *Haber 8526* (CR, MO); Monteverde, upper San Luis river valley on Pacific slope below Monteverde, 1300 m, 23 Aug. 1986, *Haber 5393* (SEL), *Haber 5397* (MO); Puntarenas, Cordillera de Tilarán, San Luis, Buen Amigo, Monteverde, 1100 m, 10 Nov. 1993, *Fuentes & Fuentes 566* (CR, INB); Puntarenas, Sendero La Catarata, por el río, 1100 m, 5 Mar. 1993, *Fuentes 200* (CR, INB). San José: Acosta, Cangrejal, Escuadra, Tiquires, Hacienda Tiquires, 1200 m, 4 Apr. 2007 (cult.), *Valverde et al. 2009* (JBL-spirit), *Valverde et al. 2020* (JBL-spirit); Acosta, cuenca del Pirrís-Damas, Acosta, Fila Zoncuano, Tiquires, en el sendero a Tiquiritos por la fila, 1000 m, 13 May 2001, *Morales 8059* (INB); Acosta, cuenca del Pirrís-Damas, Fila Ayarales, falda NE, Quebrada Ayarales, camino al Cornelio, 1250 m,

13 May 2001, *Morales 8025* (INB). PANAMA. Without locality: *Powell s.n.* (AMES).
Chiriquí: Without specific locality, 914 m, Jan. 1919 (cult.), *Powell 75* (AMES, MO); Al E
del sitio de presa en Fortuna, 6 May 1976, *Mendoza 310* (PMA); Between Pinola and
Quebrada Seco on the Chiriquicito-Caldera trail, 21 Apr. 1968, *Kirkbride & Duke 1017*
(MO [2 sheets], NY); Boquete, Palo Alto Hill, 1220 m, Dec. 1923 (cult.), *Powell 362*
(AMES), Camino hacia la Finca Landau, NE del campamento de Fortuna (sitio de
presa), 1100 m, 9 Jun. 1976, *Correa et al. 2164* (PMA); Camp Hornito, Fortuna Dam
site, 1000 m, 13 Aug. 1976, *Dressler 5342* (FLAS, PMA); Cerro Hornito, 1700 m, 14
Dec. 1976, *Luer et al. 1314* (SEL); E del sitio de presa en Fortuna, 17 Feb. 1976,
Mendoza et al. 128 (PMA); E of the Fortuna main campsite, 1200 m, 12 Sep. 1977,
Folsom et al. 5273 (CR, MO); Fortuna Dam area, Fortuna-Chiriquí Grande, 0.7 m, NW
of center of dam, 1080 m, 27 Jun. 1994, *Croat & Zhu 76487* (MO); Fortuna watershed,
3-4 km beyond AOKI camp, 1200 m, 5 Jun. 1980, *Folsom et al. 8062* (TEX); La Fortuna
hydroelectric project, 1040 m, 19 Mar. 1978, *Hammel 1987* (MO); NO del campamento
Fortuna, 1000 m, 23 Sep. 1976, *Correa 2618* (DUKE, MO, PMA); Vicinity of Guálaca,
8.6 mi from Planes de Hornito, La Fortuna on road to dam site, 1219 m, 9 Jul. 1980,
Antonio 5004 (MO, PMA); Watershed for the Fortuna Project Dam, above dam site,
1300 m, 7 Jun. 1980, *Folsom et al. 8195* (TEX); Watershed for the Fortuna Project
Dam, at first stream below the AOKI camp, 1100 m, 6 Jun. 1980, *Folsom et al. 8127*
(TEX). CULTIVATED [without original locality data]: 17 Jan. 1916, *anonymous s.n.* (K);
2 Nov. 1920, *anonymous s.n.* (AMES); 5 Oct. 1914, *anonymous s.n.* (K); MBG 59-67-
17, *anonymous s.n.* (SEL); MBG 60-8-19, *anonymous s.n.* (SEL); *anonymous s.n.* (K-
spirit, 2 jars); 28 Dec. 1914, *anonymous s.n.* (K); 25 Jan. 1927, *anonymous s.n.* (K); 23

Mar. 1925, *anonymous s.n.* (K); 23 Mar. 2004, *Blanco 2559* (FLAS); 9 Dec. 1964, *Fisulnauz s.n.* (WU); 18 Jul. 1987, *Whitten 3432* (FLAS); 17 Jun. 1984, *Whitten s.n.* (FLAS).

Commentary: *Lockhartia grandibractea* is most similar to *L. endresiana*, from which can be distinguished by the callus of the labellum made up by an irregular mass of round, low tubercles (instead of several longitudinal, toothed keels). However, both species are extremely similar otherwise (see commentary under *L. endresiana*).

Lockhartia grandibractea has been synonymized under the superficially similar *L. amoena* by several authors (Hamer, 1984a; Mora and Atwood, 1992b; Senghas, 1996; Atwood and Mora de Retana, 1999; Dressler, 2003), but the floral structure of both species is consistently different. The labellum midlobe of both *L. grandibractea* (and *L. endresiana*) is more pronouncedly tetralobulate and narrower in profile than that of *L. amoena*. There are also important differences in the column, with that of *L. grandibractea* and *L. endresiana* being longer than that of *L. amoena*, and with small triangular wings restricted to the base. Plants of *L. grandibractea* tend to be stouter and have larger inflorescence bracts than those of *L. amoena*. However, there is some overlap between both species in these traits, and stout plants of *L. amoena* can be difficult to distinguish from *L. grandibractea* in the absence of flowers.

Illustrations of *Lockhartia grandibractea* have been published by Hawkes (1953) and Senghas (1996, line drawing), both as *L. amoena*. The voucher for the illustration of “*L. amoena*” published by Hamer (1984b) is actually a plant of *L. grandibractea*, but the drawing, which was obviously done from the dried specimen, is highly stylized and shows a floral morphology not consistent with that of the actual specimen.

***Lockhartia hercodonta* Rchb. f. ex Kraenzl.**

12. *Lockhartia hercodonta* Rchb. f. ex Kraenzl., Pflanzenr. (Engler) IV, 50 (Heft 83): 8, fig. 2A. 1923. TYPE: COSTA RICA. [Escazú?], A.R. *Endrés* s.n. [number not indicated] (lectotype, here designated: *Endrés 167*, W-Reich.-Orch.-18012; isolectotypes: W-Reich.-Orch.-2985, W-Reich.-Orch.-2993, W-Reich.-Orch.-2994, W-Reich.-Orch.-2999, W-Reich.-Orch.-33683 [drawing], W-Reich.-Orch.-33704 [drawing, with locality “Camino de los Escazús”], W-Reich.-Orch.-33708 [drawing], W-Reich.-Orch.-44372 [one flower and drawings], W-Reich.-Orch.-338 [original pencil drawing by *Endrés* and inked version; copy at AMES]).

Stems descending to pendent, more or less flexible, 9–45 cm long when reproductive, with 16–50 leaves; shoots (stem and leaves) 15–30 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly and obliquely lanceolate and falcate to slightly sigmoid in side view, with incurving margins toward the apex, acute, exposed part of largest leaves 20–58 × 2–8 mm. Inflorescences both terminal and axillary from the distal half of the stem, with 1–5 flowers produced sequentially; exerted portion 0.5–4.5 (rarely up to 7) cm long, internodes 1–10 mm long, rachis often nodding; inflorescence bracts amplexicaul, conduplicate, narrowly triangular in side view, acute to acuminate, appressed to the rachis and imbricate, 2–16 × 0.5–2 mm (folded), often transitioning from leaves in elongate inflorescences; pedicel 6–8 mm long. Flowers resupinate or non resupinate, or more commonly pendent (facing down), widely open, 6–9 mm tall, white (reportedly yellow in some Ecuadorian collections) frequently tinged with yellow on the callus and tepal bases and with orange blotches on the trichome field of the callus and the tips of the callus teeth. Sepals ovate, concave, acute, 3–5 × 2–3

mm. Petals obovate to oval, apically obtuse or rounded, slightly concave and projected obliquely forward, 3.5–6 × 2–3 mm. Labellum suborbicular, convex, obscurely 3-lobate, truncate to retuse, 4–6 mm long, 5–7 mm wide when flattened; callus suborbicular to oval, located on the central-proximal portion of the labellum, concave, surrounded by 4 elevated (2 mm high) teeth, with an oblong field of glandular trichomes in the central area and on a trapezoid ledge pointed toward the base of the labellum, 3–4 × 2.5–3.5 mm. Column winged, 2.5 × 3 mm (including wings), the wings obliquely subquadrate with an entire to denticulate margin, 1.5 × 1 mm; anther cap galeate, 1 × 0.7 mm; pollinarium 0.7 mm tall, stipe apparently bifid. Fruit globular to obovoid, 4–13 × 3–10 mm.

Nomenclatural notes: In the protologue of *L. hercodonta*, Kraenzlin stated that the type was collected by Endrés; however, he did not specify a collection number and failed to annotate any specimens as types. Thus, a lectotype is designated here (from material annotated by Kraenzlin).

The numbers associated with collections by Endrés likely represent species numbers, not collection numbers in the modern sense (C. Ossenbach, pers. comm. 2010). Thus, other specimens that have the same number as the lectotype (167) are not necessarily iso-lectotypes. Two drawings of *L. hercodonta* made by Endrés have other numbers associated with them (1324, W-Reich.-Orch.-32256, and 2528, W-Reich.-Orch.-35156), but no actual specimens with those numbers exist in the Reichenbach herbarium in W.

Kraenzlin further indicated in the protologue that Reichenbach intended to describe this species but never got to publish it; Reichenbach had even prepared a

lithographic illustration of the species. Copies of this unpublished illustration are deposited in AMES and W.

Phenology: Flowering plants have been collected throughout the year, but much less abundantly from April to July.

Distribution: From Belize and Guatemala to Ecuador, from 300 to 2000 m (Figure 9). No collections from El Salvador and Colombia are known, but it is expected to occur in those countries as well. In Central America, *L. hercodonta* occurs on both sides of the continental divide (although in Panama it has been collected only on the Pacific side). In Ecuador (and presumably in Colombia) it occurs only on the western (Pacific) side of the Andes.

This species tends to grow in deep shade and windy locations (Mora and Atwood, 1992e; Atwood and Mora de Retana, 1999).

Additional specimens examined: BELIZE [formerly BRITISH HONDURAS]. Cayo: Maya Mountain divide in the vicinity of Doyle's Delight (DD), along North Ridge Trail, 0.1-0.5 km N of DD, 1000 m, 22 Aug. 2007, *Holst 8921* (SEL). Toledo: without specific locality, *Adams K56* (K-spirit); Camp 2, 6-8 km SE of Union Camp, trail from Camp 2 to Camp 3, 665 m, 15 Feb. 1997, *Hawkins 1428* (MO); Helicopter landing site 500 (HLS 500), 3.5 km E of Union Camp, area 1 km ENE of helicopter landing pad on main ridge of SW end of Little Quartz Ridge, 940 m, 19 Feb. 1997, *Hawkins 1489* (MO, SEL); In high ridge, on base of hill beyond Union Camp, Edwards Road beyond Columbia, 13 Mar. 1948, *Gentle 6469* (LL, NY). COSTA RICA. Without locality: *anonymous s.n.* (K-spirit); 4 Aug. 2002 (cult.), *Blanco 2284* (USJ); 5 Sep. 1963 (cult.), *Dodson 2549* (SEL); *Horich s.n.* (MO); Oct. 1915, *Lankester s.n.* (K); 1913, *Lankester*

s.n. (K); 27 May 2007 (cult.), *Ossenbach s.n.* (JBL-spirit); 8 Nov. 2005 (cult.), *Schug 247* (JBL-spirit). Alajuela: La Balsa area, 10 Aug. 1976 (cult.), *Marshall s.n.* (SEL); Parque Nacional Rincón de la Vieja, rd. to Colonia Blanca by Quebrada Rancho Grande, 7 Jul. 1978, *Todzia 431* (CR); Puntarenas, R. B. Monteverde, Cordillera de Tilarán, Estación Alemán's, 1000 m, 10 Sep. 1991, *Bello et al. 4039* (INB); Res. Forestal de San Ramón, 800 m, 17 Feb. 1989, *Merz 233* (CR); Reserva Biológica Monteverde, Río Peñas Blancas, 800 m, 14 Jan. 1988, *Haber & Bello 8092* (CR), 900 m, 25 Mar. 1988, *Haber & Bello 8336* (CR); Reserva Biológica Monteverde, Río Peñas Blancas, Laguna de Poco Sol, 750 m, 5 Aug. 1989, *Bello 1049* (INB, MO), 700 m, 14 Dec. 1989, *Bello 1649* (CR); Reserva Biológica Monteverde, Río Peñas Blancas, Manuel Rojas Finca, 850 m, 2 Nov. 1989, *Bello 1434* (INB); Reserva Biológica Monteverde, San Ramón, Estación Alemán's, 900 m, 17 Oct. 1991, *Bello et al. 4098* (INB); Reserva de San Ramón, along the course of Río Lorencito, W to the refuge, 1050 m, 21 Aug. 1991, *Germani 70* (USJ); Reserva de San Ramón, along the path to the refuge, 1050 m, 18 Aug. 1991, *Pupulin 92* (USJ); Reserva de San Ramón, along the upper course of the Río Lorencito, 1200 m, 22 Aug. 1991, *Pupulin 133* (USJ); San Carlos, La Fortuna, Finca El Jilguero, sector basal y medio de Volcán Chato, 900 m, 20 Nov. 1992, *Herrera 5524* (CR, K, US); San Ramón, 25 Jul. 1928, *Brenes 945* (NY); San Ramón, La Palma, 1800 m, 29 Oct. 1922, *Brenes 365* (CR), 1190 m, 30 Oct. 1922, *Brenes 365* (AMES), 1175 m, 2 Jan. 1924, *Brenes 783* (CR), 29 Aug. 1924, *Brenes 1034* (NY), 1175 m, 29 Aug. 1924, *Brenes 2284* (CR), 1175 m, 5 Oct. 1927, *Brenes 2638* (CR), 1180 m, 30 Oct. 1922, *Brenes 2894* (NY), 1984, *Mora s.n.* (USJ-spirit), 3 Aug. 1935, *Quirós 245* (F), *Quirós 304* (CR, F); San Ramón, Los Angeles, Reserva

Biológica de San Ramón, Las Rocas, 2 km al O de Finca de Carlos González, 1000 m, 16 Feb. 1994, *Herrera & Mora 6879* (CR, USJ); San Ramón, Los Lagos, entrada a la Reserva Biológica Alberto Brenes, 800 m, 23 Jan. 2001, *Blanco et al. 1792* (USJ); San Ramón, R.B. Monteverde, Cordillera de Tilarán, San Ramón, Río Peñas Blancas, Refugio Eladio's, Sendero Eston's, 800 m, 5 Mar. 1992, *Bello et al. 4548* (INB); San Ramón, Reserva Biológica Alberto Brenes, 1000 m, 4 Sep. 2004 (cult.), *Bogarín 982* (JBL-spirit), 900 m, *Bogarín 1887* (JBL-spirit); San Ramón, San Pedro, 1200 m, Nov. 1921, *Brenes 192* (CR); San Ramón, San Rafael, 24 Feb. 1945, *Echeverría 4110* (CR, F); Sarapiquí, Cariblanco, 11 Sep. 1957, *Lankester 2* (CR, 2 sheets). Cartago: El Muñeco, S of Navarro, 1400 m, 8 Feb. 1924, *Standley 33740* (AMES); Jiménez, Bajos de El Humo, entre ríos Humo y Vueltas, ladera E de Cerros Duán, 1400 m, 1 Apr. 2009 (cult.), *Bogarín et al. 5769* (JBL-spirit); Navarro, 24 Jul. 1924, *Lankester 905* (AMES); Turrialba, Las Abra, ladera SE del Volcán Turrialba, puente sobre el Río Guayabo, 2000 m, 2 Sep. 2008 (cult.), *Bogarín & Kisel 4927* (JBL-spirit); Turrialba, San Antonio, 1400 m, 10 Feb. 2004 (cult.), *Bogarín et al. 703* (JBL-spirit); Vicinity of Orosi, 30 Mar. 1924, *Standley 39957* (AMES). Guanacaste: Abangares, Upper San Gerardo Valley, 5 km N of Monteverde, Atlantic slope/continental divide, 1500 m, 12 Oct. 1989, *Haber & Zuchowski 9552* (CR); Area de Conservación Guanacaste, Estación Pitilla, Fila Orosilito, 700 m, 12 Nov. 1990, *Ríos 189* (CR); Cordillera de Tilarán, 1 km al N de Las Nubes de Río Chiquito, zona Monteverde, Atlantic slope, 1300 m, 4 Sep. 1988, *Haber & Zuchowski 8699* (CR); Las Nubes de Río Chiquito, 1 km NW of village on continental divide, hilltop, 1300 m, 27 Mar. 1989, *Haber & Atwood 9164* (CR); Liberia, P.N. Guanacaste, Cordillera de Guanacaste, Estación Cacao, sendero a la cima del volcán,

1100 m, 17 Sep. 1995, *Espinoza 1373* (INB); Liberia, SW (Pacific) slope of Cerro Cacao, Cordillera de Guanacaste, 1350 m, 9 Aug. 2007, *Grayum et al. 12545* (INB); Liberia, W (Pacific) slope of Cerro Cacao, between Estación Cacao and Casa Fran(k), headwaters of Quebrada Florcita, 1100 m, 12 Aug. 2007, *Grayum & García 12659* (INB); P. Nac. Rincón de la Vieja, colecta en el Mirador, Río Negro, 1 Oct. 1990, *Rivera 697* (CR); Parque Nacional Guanacaste, Estación Cacao, 1100 m, 25 Nov. 1990, *Espinoza 104* (INB); Tilarán, San Gerardo Abajo, Río Caño Negro, Fincas Quesada y Arce, 1100 m, 5 Dec. 1991, *Bello & Cruz 4290* (INB, MO). Heredia: An 2 Ostabhangen der Barba [sur les pentes orientales du Barba], 1200 m, 22 Dec. 1881, *Lehmann 1058* (BM, G); Sarapiquí, Colonia Virgen del Socorro, camino a Cariblanco, Río San Fernando, 750 m, 13 Feb. 2004 (cult.), *Bogarín et al. 732* (JBL-spirit); Yerba Buena, NE of San Isidro, 2000 m, 22 Feb. 1926, *Standley & Valerio 49263* (AMES). Limón: Limón, Almirante, cuenca superior del Río Xichiari, 1300 m, 14 Aug. 1995, *Herrera 8486* (CR, K); Siquirres, Las Brisas de Pacuarito, subiendo por la fila superior de la margen izquierda de Quebrada Jesus, hasta Cerro Tigre, 1550 m, 2 Nov. 1995, *Herrera et al. 8659* (CR, K, MEXU). Puntarenas: Monteverde Reserve, 2 km SW Station, in leeward cloud forest, 1500 m, 7 Apr. 1993, *Ingram & Ferrell 1793* (SEL); Monteverde Reserve, Sendero Nuboso, 1550 m, 1 Nov. 1993, *Atwood et al. 5027* (USJ); Monteverde, on property of Jan Lowther known as the "Paja", 1425 m, 27 Nov. 1989, *Atwood & Morris 4019* (SEL); [Buenos Aires], Piedra del Convento, 850 m, Feb. 1891, *Pittier [I.P.G.C.R.] 3857* (BR); Puntarenas, Guacimal, Altos de Río Veracruz, Finca Brenes, 1300 m, 12 Jan. 1990, *Bello 1782* (INB); Reserva Biológica Monteverde, trail to Peñas Blancas, near the Refugio Alemán, 910 m, 26 Mar. 2000, *Pupulin 2251* (USJ); Río San Luis,

Monteverde, Cordillera de Tilarán, 1100 m, Sep. 1977, *Dryer 1633* (CR). San José:
 About 1 mi beyond divide between San Isidro del General and coastal town of
 Dominical, 900 m, 22 May 1976, *Croat 35290* (MO, SEL); Concepción, 1500 m, 4 Nov.
 1978, *Todzia 515* (CR); La Hondura, 1700 m, 2 Mar. 1924, *Standley 36280* (AMES); La
 Hondura, 1300 m, 15 Aug. 1933, *Valerio 801* (CR, F); La Palma, 1400 m, 7 Oct. 1960
 (cult.), *Horich sub Hutchinson s.n.* (UC); La Palma, 1600 m, 17 Mar. 1924, *Standley*
38270 (AMES); Paso de La Palma, Jul. 1986, *Mora s.n.* (USJ); San Marcos de Tarrazú,
 1927, *Valerio 18* (F); Tarrazú, Nápoles, estribaciones al O de Cerro Pito, 1200 m, 30
 Nov. 1995, *Herrera et al. 8781* (CR); Vásquez de Coronado, Parque Nac. Braulio
 Carrillo, along sendero La Botella, 750 m, 13 Jan. 1991, *Ingram & Ferrell 856* (CR,
 SEL); Vicinity of El General, 1190 m, Dec. 1935, *Skutch 2334* (AMES), 1100 m, Aug.
 1936, *Skutch 2844* (AMES); Zurquí, 28 Oct. 1969, *Gómez 2412* (F). ECUADOR.
 Without locality: 29 Sep. 2003 (cult.), *Whitten et al. 2383* (FLAS). Esmeraldas: From Lita
 to Alto Tambo, 600 m, Mar. 1999 (cult.), *Hirtz 7436* (SEL). Imbabura: Above Río
 Chalguayaco, below Magnolia, lower Intag Valley, 1372 m, 17 Sep. 1944, *Drew E-642*
 (AMES); Along trail from García Moreno to Magnolia, 1585 m, 11 Sep. 1944, *Drew E-*
566 (AMES); Along trail to Río Chalguayaco, below Magnolia, lower Intag Valley, 1372
 m, 12 Sep. 1944, *Drew E-575* (AMES); Trail to San Luis de la Vega, below García
 Moreno, 1067 m, 9 Sep. 1944, *Drew E-555* (AMES). Manabí: Pedernales, Cerro Pata
 de Pájaro, 10 km E of Pedernales, Finca of the family Arroyo, 300 m, 19 Jun. 1996,
Clark et al. 2670 (GH, MO, QCNE, SEL). GUATEMALA. Sololá: S slopes of Volcán
 Atitlan above Finca Moca, along Río Bravo below Aposento woods, 1250 m, 21 Jun.
 1942, *Steyermark 48039* (AMES, F). HONDURAS. Olancho: Unión de los ríos de El

Pinol, El Tigre, y Las Cantinas, 1200 m, 29 Jan. 1993, *Nelson & Andino 14502* (GH).

NICARAGUA. Without locality: *Heller 3790* (SEL); *Heller s.n.* (SEL); 914 m, 28 Jul. 1975 (cult.), *McCullough s.n.* (SEL); 13 Aug. 1968 (cult.), *Warr 15* (K). Boaco: Monte Azul, San José de los Remates, 1000 m, 12 Feb. 1983, *Moreno 20276* (MO). Granada: Lado NW del Volcán Mombacho, Finca San Joaquín, 800 m, 15 May 1981, *Moreno & Henrich 8498* (MO); Near summit of extinct volcano Mombacho, 1345 m, 9 Apr. 1971, *Atwood 5468* (BM, BRIT, GH, MICH, MO, NY, SEL [2 sheets]); Volcán Mombacho, 15 Feb. 1977, *Atwood 77153* (SEL). Jinotega: 2 mi N of Santa María Ostumas, 1219 m, 1960, *Heller 1271* (SEL, 2 sheets); Bocay, Reserva Natural Kilambé, comunidad Santa Teresa de Kilambé, 900 m, 8 Jan. 2001, *Rueda et al. 15572* (MO); Cerro Grande, 1234 m, *Heller 1271* (SEL); Macizos de Peñas Blancas, top and N slope of steep ridge SW of finca of Manuel Estrada (El Cielo), S of Río Gusaneras, 1200 m, 16 Jan. 1979, *Stevens 11584* (MO); Weuili, comarca Aguas Rojas, Reserva Natural Kilambé, 1250 m, 19 Mar. 2001, *Rueda et al. 15854* (MO), *Rueda et al. 15940* (FLAS, MO); Wiwili, Reserva Cerro Kilambé, 1100 m, 29 Aug. 2000, *Rueda et al. 14756* (MO). Matagalpa: Along road to La Fundadora about 5 km N of Sta. María de Ostuma, Cordillera Central de Nicaragua, 1400 m, 16 Jan. 1965, *Williams et al. 27714* (F); Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradón, peak WNW of Hda. San Martín, 1400 m, 20 Jan. 1982, *Stevens et al. 21195* (MO, SEL); Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradón, slopes N and W of Hda. San Martín, 1000 m, 18 Jan. 1982, *Stevens et al. 21097* (MO). Zelaya [Región Autónoma Atlántico Norte]: Along trail from Cerro El Inocente toward Cerro Saslaya, reaching saddle between the peaks and at this point near the source of Caño Majagua, 1050 m, 8 Mar. 1978, *Stevens 6698* (MO);

Siuna, Reserva de BOSAWAS, Cerro La Albóndiga, ubicado al frente del Cerro Saslaya en dirección E, 1200 m, 15 Apr. 1999, *Rueda et al. 10738* (MO). PANAMA. Without locality: 15 May 2004 (cult.), *Blanco 2575* (FLAS); 7 Sep. 2009 (cult.), *Blanco 3232* (FLAS); *Dressler 102* (K-spirit); *Taylor 63* (K-spirit); 15 Nov. 2006 (cult.), *Whitten 3345* (FLAS). Chiriquí: Camp Hornito, Fortuna Dam site to Cerro Fortuna, 1200 m, 16 Aug. 1976, *Dressler 5397* (FLAS); Cerro Colorado, about 50 km N of San Félix, 1300 m, 19 Aug. 1975, *Dressler 5126* (FLAS); Trail W from Fortuna Dam Camp to La Fortuna, 1300 m, 23 Feb. 1985, *Hampshire & Whiteford 36* (BM); Vicinity of Fortuna Dam, along ridge at southern boundary of watershed, 1250 m, 28 Apr. 1986, *McPherson 9119* (MO); Vicinity of Fortuna Dam, along roadside and in forest between road and reservoir, 1100 m, 5 Dec. 1987, *McPherson 11812* (MEXU, MO, PMA). Coclé: Above El Valle, 900 m, 20 Feb. 1985, *Luer et al. 10646* (MO); Alto Calvario, 800 m, 20 Apr. 1977, *Folsom & Jaslon 2711* (MO); Hills above El Valle de Antón, 3 Oct. 1967, *Dressler 3051* (PMA). Panamá: Along trail to Cerro Brewster from Río Pacora valley, 670 m, 19 Nov. 1985, *McPherson 7514* (MO); Area surrounding Rancho Chorro, mountains above Torti Arriba, Cañazas mountain chain, 400 m, 3 Dec. 1977, *Folsom et al. 6667* (MO, 2 sheets); Campo Tres, 3 mi NE of Altos de Pacora, 500 m, 10 Mar. 1973, *Liesner 563* (MO); Cerro Jefe, 1000 m, 2 Mar. 1976, *Luer et al. 702* (SEL), 900 m, 2 Mar. 1976, *Taylor 13205* (K, K-spirit); In high ridges of the Serranía de Majé, S of the village of Ipetí, ca. 5 hrs. walk from the village, 650 m, 31 Mar. 1982, *Huft et al. 1680* (MO); La Eneida, region of Cerro Jefe, 21 Dec. 1969, *Dressler 3769* (FLAS); Old Chepo Rd, turn off to Cerro Azul, 900 m, 14 Jan. 1984, *Chase 84004* (K-spirit). Veraguas: Near first branch of Río Santa María, about 8 km NE of Santa Fe, 21 Dec. 1975, *Dressler 5231*

(FLAS); On Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fe, 700 m, 18 Mar. 1973, *Liesner 962* (MO); Vicinity of continental divide, third branch of Río Santa María to drop-off to lowlands, 12-15 km NW of Santa Fe, 650 m, 16 Nov. 1974, *Dressler 4837* (FLAS). CULTIVATED [without original locality data]: 28 Aug. 1958, *anonymous s.n.* (K-spirit); *anonymous s.n.* (K); *anonymous s.n.* (K-spirit, 2 jars); 6 Sep. 2002, *Blanco 2286* (FLAS); *Whitten 99232* (FLAS).

Commentary: *Lockhartia hercodonta* is most similar to the Andean *L. longifolia*, from which can be distinguished by the generally shorter stems and leaves, the white flowers, and the labellum callus with two basal and two distal teeth instead of only one. It is also similar to *L. parthenoglossa* (which has a similar geographic distribution) but that species has leaves that curve away from the stem, slightly larger, yellow flowers, and an elongate labellum.

Some collections of *Lockhartia hercodonta* from NW Ecuador (e.g., *Drew E-555*) are described as having yellow flowers, and the two apical teeth of the callus in these specimens are partly fused. Likewise, some specimens of *L. longifolia* from that region resemble *L. hercodonta* vegetatively. This suggests that hybridization between both species occurs there.

***Lockhartia imbricata* (Lam.) Hoehne**

13. *Lockhartia imbricata* (Lam.) Hoehne, Arq. Bot. Estado São Paulo, n.s., form. maior, 2: 139. 1952. : *Epidendrum imbricatum* Lam., Encycl. (Lamarck) 1: 189. 1783. Non *Epidendrum imbricatum* Lindley, Gen. Sp. Orchid. Pl. 110. 1831, nec *Epidendrum imbricatum* var. *angustifolium* Cogn., Fl. Bras. (Martius) 3(5): 171. 1898. TYPE: [FRENCH GUIANA]. Cayenne, [1764-1783], from Herb. L'Heritier, *J.B. Patris s.n.* (Lectotype, here designated: G, unnumbered sheet with several plants and two old

labels, one of which reads “*Epidendrum? Cayenne, leg. Patris Herb. L’Héritier*”;
isolectotype: G).

Epidendrum biserrum Rich., Actes Soc. Hist. Nat. Paris 1: 105, 112. 1792; as
‘*Biserra*’. *Lockhartia biserra* (Rich.) Christenson & Garay, Lindleyana 11: 17. 1996.
TYPE: [FRENCH GUIANA]. Cayenne, “in veici in *Crescentia cujete*”, August [1784-
1789], *J.B. Leblond s.n.* [414 in G] (Lectotype, here designated: P-456058;
isolectotypes: G, P-00456059).

Lockhartia elegans Hook., Bot. Mag. 54: tab. 2715. Feb 1827; *Fernandezia*
elegans (Hook.) G. Lodd., Bot. Cab. 13: tab. 1214. Jun 1827. TYPE: [TRINIDAD &
TOBAGO:] Trinidad, *D. Lockhart s.n.*, *Ex Hort.* Royal Botanic Gardens Kew, [flowered
on or before 1817?], (holotype: drawing based on live plant, BM?, not found; voucher
not found. Lectotype, here designated: illustration in Bot. Mag. 54: tab. 2715. 1827).

Lockhartia weigelti Rchb. ex Rchb. f., Bot. Zeit. 10: 767. 1852. TYPE: SURINAM.
Paramaribo [*fide* isotype at G], [1827-1828], *C. Weigelt s.n.* (holotype: W-Reich.-Orch.-
44366 [excluding *Fr. W.R. Hostmann 366*], microfiche seen; isotypes: BM-534528, G,
K-Lindl.-79006, PH-1071506; possible isotype: NY [Surinam, *Ex herb. Schweinitz*]).

Lockhartia obtusifolia Regel, Ann. Sci. Nat. Bot. sér. 4, 6: 378. 1856. Non
Fernandezia obtusa Lindl. ex L. Linden, Ill. Hort. 29: 51. 1882. TYPE: COLOMBIA
[probably VENEZUELA]. *Lansberg s.n.* [probably J. G. van Lansberge], *Ex Hort.* St.
Petersburg Botanic Garden, March 1856 (holotype: LE, image seen; photos of holotype:
K, NY).

Lockhartia floribunda Rchb. f., Hamburger Garten- Blumenzeitung 16: 179. 1860.

TYPE: Original locality unknown, *Ex Hort.* Professor Fregge in Abtuaundorf near Leipzig (Germany), 1860 (holotype: W-Reich.-Orch.-44373 [excluding *Jelski 8*]).

Stems erect, more or less rigid, 3.5–35 cm long when reproductive, with 14–60 leaves; shoots (stem and leaves) 6–14 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, obtuse to round apically, with (mostly) straight margins, exposed part of largest leaves 7–20 × 3–7 mm. Inflorescences both terminal and axillary from the distal half of the stem, with 1–3 flowers produced sequentially; exerted portion 0.5–2 cm long, internodes 3–5 mm long; inflorescence bracts amplexicaul, infundibuliform, ovate, cordate, acute to apiculate, 2.5–5 × 1.5–3.5 mm; pedicel and ovary 9–10 mm long. Flowers resupinate, widely open, 7–11 mm tall, yellow with dark chocolate-brown markings on and around the labellum callus, and a dark brown line at the base of the column. Sepals ovate to elliptic, slightly concave, obtuse to acute, 3.5–4.5 × 2.5–3 mm. Petals oblong-elliptic, widely spread, with slightly revolute margins, rounded to truncate apically, 4–5 × 2–2.5 mm when flattened. Labellum entire to trilobate, 4.5–6 × 2.5–6 mm (across lateral lobes or widest point of labellum); the lateral lobes (when present) triangular to oblong, slightly incurved, acute, 0–2.3 × 0.7 mm; midlobe entire, subspathulate to obscurely pandurate, obtuse to retuse, 3–4 mm long, 2.5–3.5 mm wide (across the widest part of midlobe when flattened); callus oblong to subpandurate, the basal part forming a subquadrate concave cushion with a basal tuft of short, glandular hairs, 1.5 × 2 mm, the distal part formed by a mass of minute tubercles, 3 × 1.5–2 mm. Column winged, 2.5 mm long, 3 mm wide (including wings),

the wings trapezoid, with a denticulate margin, 1.5×2 mm; anther cap hemispherical, 1 mm in diameter; 1 mm long, with a bifid stipe. Fruit obovoid, $5-16 \times 2-6$ mm.

Nomenclatural notes: *Lockhartia imbricata* has a complicated nomenclatural history. First, the identity of the type specimen of *Epidendrum imbricatum* Lam. has heretofore remained unclear. Lamarck based his description on a dry specimen (“v.[.]” = “vue sèche”, seen dry) from Cayenne, but unfortunately he did not indicate the name of the collector nor in whose herbarium he saw it. Although vague, the description in the protologue almost certainly applies to a species of *Lockhartia* (as convincingly argued by Hoehne (1952), and *L. imbricata* (as circumscribed here) is the only species of the genus known to occur in French Guiana, where it is very common.

Schweinfurth (1967) erroneously listed the type of *L. imbricata* as having been collected in Trinidad, without any additional data. Christenson (1996) also assumed the type was collected in Trinidad, and cited P as the herbarium of deposition. Romero-González (2005) correctly cited the type of *L. imbricata* as having been collected in French Guiana, although deposited in P-Lam. (indicated as not seen but with a photograph at AMES; this photograph has not been found and this citation was probably erroneous). Moreover, there are no *Lockhartia* specimens in the general collection at P old enough to have possibly been studied by Lamarck on or before 1783, and there are no *Lockhartia* specimens at all in the historical herbaria of either Lamarck or Jussieu (also studied by Lamarck) in Paris. Wilson Hoehne (Federico C. Hoehne’s son) had already searched for the type specimen in P and failed to find it (Hoehne, 1952). Thus, the type has to be searched in the other herbaria studied by Lamarck.

One of such herbaria was that of Charles Louis L'Héritier, eventually acquired by Augustin Pyramus de Candolle and now in Geneva. Lamarck based many of his species on material from L'Héritier's herbarium (Stafleu and Cowan, 1979). The collection, identified here as the type of *L. imbricata* (Patris s.n., G, 2 sheets), is to my knowledge the only extant *Lockhartia* specimen that could have possibly been collected before 1783 and examined by Lamarck before the publication of the protologue (see below). Both duplicates have the locality "Cayenne" written on their labels and have a few fruits but lack flowers (Lamarck's description did not mention any flowers). Lamarck did not annotate either sheet, but I have little doubt that he based his *Epidendrum imbricatum* on this collection.

Jean Baptiste Patris arrived in Cayenne on December 19, 1764. He explored some parts of the interior of French Guiana in 1766-1767, and lived in Cayenne until his death in 1786 (Chaïa, 1970).

Richard's description of *Epidendrum biserrum* is extremely simple; the information concerning locality and collector are taken from the first page of the article (Richard, 1792), where it is clearly indicated that all the plants described there were sent from Cayenne by Leblond. Jean-Baptiste Leblond collected in various places in French Guiana during the years 1784-1789 (Pouliquen, 2001) (1786 to 1803 according to Lescure, 1998). The isotype at G has a label clearly annotated "*Epidendrum biserra* Richard, Act. Soc. Hist. Nat., Cayenne, Herb. Leblond", and a small piece of rag paper glued to the label, in the same handwriting (probably Richard's) that reads "414 Epid. biferra."

Two sheets in P are labeled as holotype and isotype of *Epidendrum biserrum*, although these annotations are recent. The sheet marked as holotype has a label that indicates it belonged to the herbarium of Louis Claude and Achille Richard. The sheet marked as isotype belonged to the herbarium of E. Drake (part of the Richard herbarium came to P via the Drake del Castillo collection; (Stafleu and Cowan, 1983).

The protologue of *Lockhartia elegans* implies that Hooker based his description on a drawing (in Aiton's collection) of a plant flowered at Kew years before, not on the live plant nor on a herbarium specimen. This drawing has not been found, and thus the illustration published in the protologue is designated as lectotype.

In fact, it appears that the plant on which that drawing was based, which was the plant sent by David Lockhart from Trinidad, flowered in cultivation at Kew on or before 1817 (at least 10 years before the publication of the species), according to Lindley (1824), who, while commenting about the genus *Catasetum*, mentioned:

“... the *C. macrocarpon* of Richard being scarcely known except by name. Before the publication, however, of the work of M. Kunth, in which the genus was established, two other plants had been seen in this country, both of which still remain to be recorded; the one was a plant which, some time before 1817, flowered in the garden at Kew, where it was called *Lockhartia*, but which has not been since seen in any other collection ...”

It must be noted, however, that Lockhart first arrived in Trinidad in 1818, not 1817, and immediately became superintendent of the botanic garden. Lindley's comments imply that by 1824 the plant was no longer alive, and all that remained for Hooker to study was the drawing in Aiton's collection. Romero-González (2005) cited the type of *L. elegans* as “*Lockhart ex Hort. Kew s.n., K*”, but such specimen has not been found, and even if it existed, it could not be considered the type because Hooker did not base his description directly on it.

The voucher for Loddiges' 1826 painting of *Fernandezia elegans* is mounted (along with a copy of the painting) on the same sheet as the isolectotype of *Lockhartia micrantha* (*Hinds s.n.*) in the Lindley herbarium at Kew; however, this is not a type. It is a different plant of the same species, as explicitly mentioned by Loddiges. Loddiges did not attempt to describe a new species, but simply transferred Hooker's name to *Fernandezia*. A fragment of the latter specimen is in W.

A specimen fragment at M, labeled as "*Lockhartia elegans* Hook. *Bot. Mag. tab. 2715. Trinidad*" in what appears to be Lindley's handwriting, could be a voucher for the plant on which the original drawing was prepared. However, there is no way to know for sure. This fragment is mounted on the same sheet as another fragment labeled as *Lockhartia lunifera* in the same handwriting.

An unnumbered specimen in NY (Surinam, *Ex. herb. Schweinitz*) is likely an isotype of *Lockhartia weigelti*. Lewis David von Schweinitz (1780-1835) frequently discarded collectors' original labels "in favor of his own copied tickets" (Stafleu and Cowan, 1985).

Regel republished the description of his *Lockhartia obtusifolia* in 1857 (*Gartenflora* 6: 131) along with an illustration not originally included in the protologue. The number on the illustration was erroneous (191 vs. 190), but it is the only illustration of a species of *Lockhartia*, and it clearly corresponds to *L. imbricata*. In the illustration, the species name was also erroneously transcribed ("*Lockhartia obtusa* Rgl."); this probably led some authors to assume that this combination was based on the then yet unpublished name "*Fernandezia obtusa* Lindl.", a combination published much later by Linden. The locality "Columbia" likely refers to "Gran Colombia", a short-lived republic that

encompassed the modern countries of Colombia, Venezuela, Panama, and Ecuador, from 1819 to 1831. In fact, Ernst (1878) cites *L. obtusifolia* for Caracas, Venezuela, and not from Colombia.

Phenology: Flowering plants have been collected throughout the year, but more commonly from August to November, and with a minor peak in March.

Distribution: Venezuela, Trinidad, the Guianas, and northern Brazil (states of Amapá, Pará, and Roraima), from sea level to 800 m (Figure 8). A specimen from Colombia (*anonymous s.n.*, P), consisting of only flowers mixed with others of a different species, is likely based on a cultivated plant with erroneous locality information.

Lockhartia imbricata is very abundant in the Guianas and eastern Venezuela; it is apparently rare in the adjacent northern portions of the Amazon basin (Brazilian states of Pará and Roraima, and the southern portion of Amapá), although one collection of confirmed identity is known from southern Pará state (close to the border with Mato Grosso, on the southern part of the Amazon basin). Another collection from Portuguesa state in western Venezuela, which is relatively isolated from other known populations, lacks specific locality data and its locality information could be erroneous.

Early reports from Mexico and Panama (as *L. elegans*) can be traced to misidentified specimens of *L. galeottiana* and *L. micrantha* cited by Lindley (1834), Grisebach (1864), and Hemsley (1882-1886).

Additional specimens examined: BRAZIL. Without locality: Cultivated, *anonymous s.n.* (K); *Hoffmannsegg s.n.* (B-Willd.); *Pohl 172* (M). Amapá: Bacia do Oiapoque, Rio Camopi, 20 Aug. 1960, *Irwin et al. 47678* (MG); Coastal region, along road to Amapá, vic. Km 108, Rio Pedreira, 0 m, 18 Jul. 1962, *Pires & Cavalcante 52197*

(NY); Mouth of Rio Iaue, 21 Aug. 1960, *Irwin & Westra 47683* (B, F, GH, MG, MICH, NY, U); Rio Araguari, at mouth of Anicahy, above camp 14, 8 Oct. 1961, *Pires et al. 51564* (NY); Rio Araguari, Cachoeira Pedra Fina, Camp 13, 9 Oct. 1961, *Pires et al. 51590* (K, NY); Rio Oiapoque, lower and middle slopes of Mt. Bagotte, 3 km SE of Boa Esperança, 100 m, 19 Aug. 1960, *Egler 47678a* (NY); Serra do Navío, Rio Amapari, Macaco Ore Body, 8 Nov. 1954, *Cowan 38169* (NY). Pará: without specific locality, 1835, *Home s.n.* (K); 1 km ao S de Gorotire, 500 m de Rio Preto, 20 Aug. 1985, *Gély 439* (MG); Almeirim, Monte Dourado, estrada do S de Pacanari, 5 Dec. 1978, *Santos 475* (INPA, MG, U); Amazonas-Gebiet, Taperinha bei Santarém, 28 Jul. 1927, *Ginzberger & Zerny 680* (F, W, WU); Barcarena, praia do Caripy, Baía do Marajó, 19 Jun. 1984, *Lins et al. 423* (MG); Ilha do Mosqueiro, near Pará, 0 m, 3 Nov. 1929, *Killip & Smith 30552* (AMES, NY, US); Itaboca [cachoeiras], *Burchell 9200* (K); Rio Jari, Moute Dourado, Planalto B. (Pilao), 23 Oct. 1968, *Silva 1304* (NY, SP). Roraima: Caracaraí, Parque Nacional do Viruá, na beira da Estrada Perdida, 27 Nov. 2006, *Carvalho et al. 931* (INPA); Rio Branco, Serra de Carauma, Nov. 1908, *Ule 7733* (G, K); SEMA Ecological Reserve, Ilha de Maracá, N end of the Trilha de Preguica (very close to the Furo de Santa Rosa), 27 Jan. 1988, *Ratter & Milliken 6126* (K). COLOMBIA. Without locality: *anonymous s.n.* (P; questionable origin, possibly cultivated). FRENCH GUIANA. Without locality: Mar. 1847 (cult.), *anonymous s.n.* (P). Commune unknown: Camp no. 3, Roche no. 1, Akouba Booka goo Soula, Bassin du Ha, 500 m au SO, 160 m, 26 Aug. 1987, *Granville et al. 9733* (CAY); Fleuve Approuague, Rivière Arataye, Saut Parare, ilet pres du camp de base, 29 Oct. 1978, *Sastre 6261* (CAY); Fleuve Approuague, Rivière Arataye, Saut Parare, zone a prelevements non limités, 13 Mar.

1978, *Sastre 5843* (CAY, NY, P, U); Kutaka, 134 m, 17 Dec. 1991, *Veth 206* (CAY, U); Maroni River above mouth of Marouini River, island in river near Antecum Pata, 140 m, 18 Aug. 1987, *Weitzman 206* (MO, NY, U, US); Mont Saint-Marcel, zone centre-E du massif, forêt sommitale du sommet de 500 m ENE, 450 m, 28 Jul. 2002, *Granville et al. 15543* (CAY); Saint-Eloi, Region de Saül, a 3 km a l'E de Saint-Eloi, sur le layon vers le pic Matecho, 200 m, 21 Sep. 2000, *Granville et al. 14343* (CAY, NY). Apatou: Region de Paul Isnard, Montagne Lucifer, versant sud, a 3.5 km NNE de Citron, 450 m, 11 Nov. 1982, *Granville 5258* (CAY, P). Camopi: En amont du confluent Oyapock-Yawe, haut Oyapock, 29 Aug. 1985, *Prévost & Grenand 2014* (CAY, P); Sommet de l'innselberg, 3-4 km ENE du Grand Croissant, N de Camopi, 265 m, 3 Dec. 1983, *Feuillet 1132* (CAY, P). Cayenne: Cayenne, 1839, *Leprieur 134* (G), *Rothery 246* (K), 1846, *Rothery 1853* (K). Maripasoula: Dans les ilots de l'Itany, en aval d'Antecume Pata, confluent de l'Itany (Haut Maroni) et du Marouini, 20 Nov. 1977, *Cremers 5093*, (CAY [2 sheets], P), 27 Mar. 1979, *Cremers 5522* (CAY); Montagne Bellevue de l'Inini, extrémité S, versant NW, 350 m, 11 Sep. 1985, *Granville et al. 8150* (CAY); Plante rameiree des iloli de l'Itany en aval d'Antecume Pata, 1979, *Cremers 6009* (CAY); Plante rameiree du Saut Domosoula, amont de Touinki (HI Itani), Oct. 1979, *Cremers 6008* (CAY); Rivière Grande Ouaqui, a 8 km en amont de son confluent avec la Petite Ouaqui, rive droite, 13 Jul. 1973, *Granville 4960* (CAY, P); Rivière, Grand Inini en aval et en amont de Degrad Fourmi, 13 Sep. 1985, *Granville et al. 8204* (CAY, P, U); Saut Macaque, 12 Sep. 1961, *Schnell 12158* (P). Roura: Roura, 1858, *Sagot s.n.* (P, 2 sheets), 1858, *anonymous s.n.* (K). Saint Laurent du Maroni: St. Jean du Maroni, 11 Mar. 1914, *Benoist 850* (P). Saül: 2 km SW of Saül, blue track, 180 m, 27 Aug. 1986, *Ek & Montfoort 135* (CAY); 2 km SW

of Saül, track Limonade, 180 m, 9 Aug. 1986, *Ek & Montfoort 251* (NY, U), 11 Aug. 1986, *Ek & Montfoort 252* (NY, U); Fleuve Grand Inini, en aval de Degrad Fourmi Bord de la crique Adolphe, 140 m, 11 Aug. 1985, *Granville 7421* (CAY); La Carbet Mais-trail, 8 Sep. 1989, *Mori et al. 20857* (NY); La Fumeé Mountain Trail, 350 m, 13 Aug. 1987, *Mori & Gracie 18710* (NY); La Fumeé West, 250 m, 26 Aug. 1989, *Mori & Ek 20725* (NY); Saül, 20 m, 12 Aug. 1986, *Freiberg 15* (B); Saül village, 13 Oct. 1976, *Veyret 1410* (CAY, P); Saül, autour du village, 13 Oct. 1972, *Granville 4576* (CAY, P).

GUYANA [formerly BRITISH GUIANA]. Without locality: 1869, *Jelski s.n.* (WU). Barima-Waini: Sebai Ck., Kaituma River, 18 Mar. 1945, *Fanshawe 2420* (K, NY, U, US). East Berbyce-Corentyne: Corentyne River, Nov. 1879, *Jenman 147* (P). Pomeroon-Supenaam: Pomeroon River, Pomeroon District, 17 Dec. 1922, *de la Cruz 3108* (NY, US). Upper Takutu-Upper Essequibo: Acarai Mts., 10 km S of Sipu River, upper slopes of highest peak in central Acarai Mts., 800 m, 5 Sep. 1998, *Clarke et al. 7491* (US); Along side of newly cleared right-of-way, 15-20 km NE of Surama Village Rd., 90 m, 1 Mar. 1990, *McDowell et al. 2094* (US); Kanuku Mts., Rupununi River, Puwib River, near "the farm" of the Captain of Sandcreek, 80 m, 14 Feb. 1985, *Jansen-Jacobs et al. 211* (B, U); Kanuku Mts., slope of Nappi Mt., Camp 2, 450 m, 13 Nov. 1987, *Jansen-Jacobs et al. 919* (U); Kuyuwini River watershed, Bat Mt; N and NE slopes of inselberg, 300 m, 19 Sep. 1993, *Henkel et al. 3061* (CAY, GH, MO, NY, U, US); Kuyuwini River watershed, between headwaters Toucan & Marudi creeks, 2-4 km S of Marudi Mtn., 250 m, 16 Sep. 1993, *Henkel et al. 2972* (GH, MO, US); NW slopes of Kanuku Mountains, in drainage of Moku-moku Creek (Takutu tributary), 150 m, 31 Mar. 1938, *Smith 3586* (AMES, F, K, NY, P, U, W); Rewa River, 0-5 km S of Great Falls, 90 m, 20 Sep. 1997,

Clarke et al. 6615 (CAY, NY, U); Rewa River, Spider Mountains, 400 m, 23 Sep. 1999, *Jansen-Jacobs et al. 6122* (U); Rupununi River, betw. Kwattamang Landing & Rewa Village, 100 m, 29 Sep. 1997, *Clarke et al. 6775* (US), *Clarke et al. 6780* (CAY, US); Rupununi, E Kanuku Mountains, NE of Warimure, 200 m, 27 Jan. 1991, *Jansen-Jacobs et al. 2261* (U); Rupununi, foothills of NW Kanuku Mts., near Moco-Moco village, 100 m, 28 Oct. 1979, *Maas & Westra 3892* (U); S Rupununi Savanna, Aishalton Mts; 2 km S of Aishalton village, 200 m, 12 Oct. 1993, *Henkel et al. 3447* (GH); SE Kanuku Mts., Makaparima Mtn. foothills, 4 km NNE of Crabwood Creek camp, 400 m, 26 Oct. 1981, *Hoffman 400* (NY, US); Upper Rupununi River, near Dadanawa, 14 Jun. 1922, *de la Cruz 1503* (AMES [2 sheets], F, MO, NY, PH); Western extremity of Kanuku Mountains, in drainage of Takutu River, 600 m, 4 Mar. 1938, *Smith 3290* (NY). SURINAME.

Without locality: Mar. 1842, *Hostmann 366* (BM, G, K [2 sheets], OXF, P); *Hostmann 685* (G, P [2 sheets], S [2 sheets]); *Tulleken 384* (L). Brokopondo: Brownsberg Forest, 450 m, Mar. 1981, *Ingham sub Kimnach s.n.* (AMES). Commewijne: Lower Suriname River tributary, Paulus Creek, 31 Dec. 1950, *Florschutz & Florschutz 902* (U).

Marowijne: Anansitabbetje, Granholosoela, Tapanahony River, 2 Aug. 1973, *Teunissen & Teunissen 1117* (U); In Montibus, qui dicuntur Nassau; border of Marowijne R. above base camp, 27 Feb. 1949, *Lanjouw & Lindeman 2334* (AMES, U); Via secta ab Moengo tapoe ad Grote Zwiebelzwamp, along Djai-creek, W of camp, 5 Oct. 1948, *Lanjouw & Lindeman 662* (U). Nickerie: Area of Kabalebo Dam project, forest E of road km 26, 30 m, 11 Sep. 1980, *Lindeman et al. 337* (U). Para: Agila, N of Auca along Surinam river, distr. Suriname, 1 May 1977, *Teunissen & Teunissen 1240* (U); Berlyn, 11 Mar. 1830, *Splitgerber 721* (L). Sipaliwini: Upper Coppename R., Raleigh Falls, 25 Aug. 1920, *Pulle*

345 (AMES, U); Wilhelmina Gebergte area, Lucie River, on small granitic islands in river, near confluence of Oost Rivier, 225 m, 12 Sep. 1963, *Irwin et al.* 55650 (NY, U); Wilhelmina Gebergte, 1 km SE of Juliana Top, headwaters of West River, 800 m, 27 Aug. 1963, *Irwin et al.* 55135 (NY). TRINIDAD & TOBAGO. Trinidad [without specific locality]: Feb. 1876 (cult.), *anonymous s.n.* (K); *anonymous s.n.* (M); *Cruger 1523* (TRIN); *Cruger 2246* (K); Mar. 1913 (cult.), *Hill 23* (K); Cultivated, *Loddiges s.n.* (K-Lindl). Corporation/county unknown: Matchepoorie, 11 Mar. 1921, *Britton & Britton 2223* (NY). Couva-Tabaquite-Talparo: Near Piparo Settlement, Williamsville, 29 Nov. 1919, *Broadway s.n.* (AMES, BH, G, K, NY). Princess Town: Moruga, 19 Mar. 1921, *Britton & Broadway 2442* (AMES, NY). Siparia: Siparia, Nov. 1954, *Downs s.n.* (AMES).

VENEZUELA. Anzoátegui: Between Río León of Quebrada Danta and Río Zumbador, NE of Bergantín, 500 m, 24 Feb. 1945, *Steyermark 61123* (AMES, F, G [2 sheets], VEN). Bolívar: Canaima, *Dunsterville 348* (AMES [drawing], K, K-spirit); El Palmar, Fundo La Esperanza, a unos 15 km al S de El Palmar, 200 m, 23 Jun. 1998, *Díaz et al.* 3725 (VEN); Padre Chien, a 24 km de El Palmar en la vía hacia Río Grande, 275 m, 12 Apr. 1997, *Díaz et al.* 3184 (SEL); Padre Chien, El Palmar, Río Grande, 300 m, 14 Apr. 1997, *Chacón 786* (SEL, VEN); Piar, Ciudad Piar, Orinoco, 350 m, 16 Nov. 1958, *Renz 9207* (RENZ); Río Caura, 5-20 km S (río arriba) del campamento Las Pavas (Salto Pará), 220 m, May 1983, *Morillo & Liesner 8805* (MO, VEN); Río Caura, arriba del Salto Pará, en las islas 2-3 km arriba del campamento Las Pavas, 250 m, 14 Jan. 1977, *Steyermark et al.* 112959 (VEN); Sierra Imataca, Río Toro (Río Grande), between Río La Reforma and Puerto Rico, N of El Palmar, between Río Reforma and rapids above Río Reforma, 200 m, 14 Dec. 1960, *Steyermark 88069* (AMES, VEN); Sifontes, 28 km

al N de Tumeremo, entre cabeceras del Río Guarán y Fundo Caratal al S de la Serranía de Nuria, 200 m, May 1986, *Fernández 3139* (VEN); Sucre, Río Caura, sitio AC12, Cerro del Puerto, 200 m, 30 Nov. 2000, *Díaz et al. 4886* (SEL). Delta Amacuro: Between La Margarita and Puerta Miranda, Río Acure, 80 m, 26 Nov. 1960, *Steyermark 87814* (NY); Río Cuyubini, along lower section of river, upstream from Casa Cuyubini, 90 m, 12 Nov. 1960, *Steyermark 87486* (VEN). Distrito Capital: "Caracas" [possibly cultivated], 1851, *Hermens s.n.* (P). Portuguesa: Without specific locality, 350 m, 13 Nov. 1951, *Renz 7529* (RENZ). Territorio Federal Amazonas: Atures, Río Coro-Coro, stream and slope E of river, W of Serranía de Yutaje, 6 km N of settlement of Yutaje, 320 m, 22 Feb. 1987, *Liesner & Holst 21315* (MO). CULTIVATED [and/or without original locality data]: 1 Feb. 1951 (cult.), *anonymous 2605* (U); 15 Apr. 1918 (cult.), *anonymous s.n.* (K); 22 Feb. 1961 (cult.), *anonymous s.n.* (NY); 20 Sep. 1889 (cult.), *anonymous s.n.* (G); *anonymous s.n.* (K-spirit, 2 jars); 7 Feb. 1986 (cult.), *Granville 8302* (CAY); 13 Dec. 1973 (cult.), *Lee 150* (BH); 6 Dec. 1972 (cult.), *Magrum 167* (BH); *Mason 1811* (K-spirit); 22 Sep. 1979, *Pires 16995* (MG).

Commentary: *Lockhartia imbricata* is most similar to the Costa Rican endemic *L. dipleura*, from which can be distinguished by its (generally) more obtuse leaves, the labellum with shorter, wider lateral lobes and callus not organized in longitudinal keels, and the proportionately smaller column.

Lockhartia imbricata is variable in the degree of development of the lateral lobes of the labellum (although, when present, they are very short). However, the other floral features appear to be reasonably uniform through most of the geographic range of the species. Only in the SE portion of its range is there any morphological variation that

suggests the possibility of hybridization with *L. goyazensis* (although collections from this region are relatively few).

Lockhartia imbricata is very common in the Guianas, judging by the number of collections made there. The only other species of *Lockhartia* in the region is *L. latilabris*, which has pendent stems, longer, acute leaves, larger, campanulate flowers, a subentire labellum devoid of a callus, and a much more restricted geographic distribution (see notes under that species).

***Lockhartia ivainae* M.F.F. da Silva & A.T. de Oliveira**

14. *Lockhartia ivainae* M.F.F. da Silva & A.T. de Oliveira, Biol. Mus. Paraense Emílio Goeldi, Bot. 17(2): 263-267. "2001" (publ. 2002). TYPE: BRASIL. Estado do Pará, município de Água Azul do Norte, na margem do Rio Água Azul, Jun. 1999, A.T. de Oliveira 03 (holotype: MG, photo seen).

Stems descending or pendent, 14–22 cm long when reproductive, with 28–34 leaves; shoots (stem and leaves) 7–17 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, obtuse to round apically, with outcurving margins, exposed part of largest leaves 7–20 × 3–6 mm. Inflorescences both terminal and axillary from the distal part of the stem, with 1(–3) flowers produced sequentially; exerted portion 4–8 mm long, internodes 1–2 mm long; inflorescence bracts amplexicaul, campanulate to widely open, suborbicular to ovate, cordate, acute to obtuse, 4–5 × 3–4.5 mm; pedicel and ovary 9 mm long. Flowers resupinate, widely open, 7–8 mm tall, yellow with a few reddish brown spots on the callus and on each side of the stigmatic cavity. Sepals oval to oblong, obtuse, reflexed, 4–5 × 3 mm. Petals ovate to oblong, acute, 5 × 2.5 mm. Labellum entire, ovate, emarginate, 5.5 × 4 mm;

callus a subtle, oblong thickening with a basal tuft of minute glandular hairs in a slight depression, $4 \times 1.5\text{--}2$ mm. Column winged, widely rhomboid, 2 mm long, 2.5 mm wide (including wings); the wings triangular, 0.5×1 mm; anther cap hemispherical, 1 mm in diameter; pollinarium 0.7 mm tall, apparently with a bifid stipe. Fruit not seen.

Phenology: The only two specimens known have been collected in flower in July.

Distribution: Known only from the municipality of Agua Azul do Norte in Pará state, Brazil (Figure 8). The elevation in the area ranges from ca. 250 to 500 m.

Additional specimen examined: BRAZIL. Pará: Agua Azul, em campina cortada pela estrada que vai de Xinguará a São Félix do Xingú, km 55 na margem esquerda do Rio Agua Preta, 1 Jun. 1994, *Silva et al.* 330 (MG).

Commentary: *Lockhartia ivainae* is cautiously accepted here as a valid species. Only digital images of the type were available for study, and the paratype does not have any flowers. The floral morphology (based on the illustration published in the protologue and a photograph published by Ferreira Fernandes da Silva & Fernandes da Silva, 2010) seems distinctive enough to warrant specific recognition; however, it could also represent a prematurely opened bud or malformed flower of *L. imbricata* or *L. goyazensis*. The vegetative morphology, with the leaves gently curving away from the stem, agrees with that of *L. goyazensis*. If it is indeed a valid species, the tiny, inconspicuous flowers could explain the paucity of collections.

Lockhartia ivainae can be recognized by its tiny (7–8 mm) flowers and very simple labellum (the least elaborate in the entire genus). The callus consists merely of a pair of subtle, smooth keels that merge distally, barely thicker than the rest of the labellum. The floral bracts are also very small.

***Lockhartia latilabris* C. Schweinf.**

15. *Lockhartia latilabris* C. Schweinf., Fieldiana, Bot. 28(1): 200-203, fig. 41. 1951.

TYPE: VENEZUELA. Bolívar, Salto de Iwaracarú-merú, at western end of Sororopántepuí, 1615 m, 15 Nov. 1944, J.A. Steyermark 60222 (holotype: F, isotype: AMES).

Stems descending to pendent (occasionally suberect when young), more or less flexible, 15–58 cm long when reproductive, with 26–60 leaves; shoots (stem and leaves) 13–22 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, with straight margins (slightly incurving near the tip), obliquely acute, exposed part of largest leaves 23–35 × 4–7 mm. Inflorescences both terminal and axillary from distal part of the stem, with 1(–3) flowers produced sequentially; exerted portion 0.5–1.5 cm long, internodes 1–3 mm long; inflorescence bracts amplexicaul, conduplicate to campanulate, narrowly triangular to ovate, 4–7 × 1.5–3 mm; pedicel and ovary 6–9 mm long. Flowers non-resupinate, campanulate, 14–16 mm across, yellow, the labellum either completely yellow or with a large central area blotched in reddish brown, the column either completely yellow or with reddish brown blotches. Sepals oval to ovate, concave, acute to obtuse, 9–10 × 5–6 mm. Petals obovate, apically obtuse to rounded, 11–12 × 7–8 mm. Labellum entire, suborbicular to obreniform, wider than long, retuse, campanulate, margin minutely undulate, 9–11 mm long, 14–16 mm wide when flattened; callus represented by a slightly thickened, smooth, puberulous area in the central portion of the labellum, 5 × 9 mm, with a subtle apical transverse depression 2 mm wide (callus otherwise absent). Column narrowly winged, 2 × 3 mm, the wings triangular, 1 × 0.5 mm; anther cap galeate, 1 × 0.7 mm; pollinarium not seen. Fruit obovoid, 10–12 × 6–7 mm.

Phenology: The few flowering specimens available have been collected during the months of August, September, and November.

Distribution: West-central Guyana and eastern Bolívar state in Venezuela, from 490 to 1615 m (Figure 10). Apparently also present in Brazil, on the basis of a plant illustrated by Ferreira Fernandes da Silva and Fernandes da Silva (2010), where it is reported as a new species record for that country. No specific locality data are given for that plant (it is only stated that it was collected “in gallery forest above 1000 m”), but judging from the distribution of other collections, the species is expected to occur in the northern portion of the Brazilian state of Roraima. This species is apparently restricted to the Pacaraíma Mountains and the Gran Sabana formation in the Guiana Shield.

Additional specimens examined: GUYANA. Cuyuni-Mazaruni: Upper Mazaruni River basin, Mt. Ayanganna, talus at base of cliff, along NE side, 900 m, 1 Aug. 1960, *Tillett & Tillett 44961* (NY, VEN); Upper Mazaruni River basin, Kako River, along Pat Bailey's line to top of Karowtipu, 490 m, 20 Sep. 1960, *Tillett & Tillett 45470* (NY). Potaro-Siparuni: Mt. Kopinang, along creek near camp, 1350 m, 7 Apr. 1988, *Hahn et al. 4296* (MO). VENEZUELA. Without locality: *Dunsterville 245A* (K [description and drawing only, no voucher found]). Bolívar: Km 120 S of El Dorado on the road to Sta. Elena de Uairén, 1100 m, *Dunsterville 1243* (K [description only, no voucher found]); Piar, summit of Amaruay-tepui, SE quarter of tepui, 550 m, 12 May 1986, *Liesner & Holst 20847* (VEN).

Commentary: *Lockhartia latilabris* is most similar to *L. parthenocomos*, from which can be distinguished only by the lack of an irregular distal ledge in the callus. The callus of *L. latilabris* is so subtle that some authors have described the species as not

having one. Both species are extremely similar and impossible to distinguish vegetatively (without locality data), and even if flowers are present the labellum has to be studied in detail. However, they are allopatric, separated hundreds of kilometers by the lowlands of the Orinoco basin. *Lockhartia latilabris* occurs in the region around the intersection of the borders of Venezuela, Brazil, and Guyana, while *L. parthenocomos* is restricted to the Venezuelan Coastal Range.

***Lockhartia lepticaula* D.E. Benn. & Christenson**

16. *Lockhartia lepticaula* D.E. Benn. & Christenson, Icon. Orchid. Peruv. plate 678. 2001. TYPE: PERU. Huanuco: Leoncio Prado, above Cueva de Las Pavas, 950 m, 10 Nov. 1991, *E. Jara P. ex Bennett* 5326 (holotype: Herb. Bennettianum, transferred to MOL according to Eric A. Christenson, pers. comm. 2009, not found, probably never prepared; lectotype, here designated: plate 678 in Icon. Orchid. Peruvianum. 2001).

Stems erect or descending, more or less rigid, 17–74 cm long when reproductive, with 22–85 leaves; shoots (stem and leaves) 8–13 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, with straight to slightly incurving margins, acute to narrowly rounded apically, exposed part of largest leaves 15–30 × 4–7 mm. Inflorescences both terminal and axillary from the distal half of the stem, with 1–7 flowers produced more or less simultaneously, exerted portion 1–5 cm long, internodes 2–8 mm long; inflorescence bracts amplexicaul, widely ovate to suborbicular, cordate, obtuse to apiculate, expanded to campanulate, 3–7 × 3–5.5 mm; pedicel and ovary 10–15 mm long. Flowers resupinate, widely open, 12–17 mm tall, yellow, the petals occasionally whitish yellow, the labellum with reddish brown to purplish-brown spots around the callus and on the lateral lobes, the callus mostly

orange. Sepals elliptic, slightly concave, acute to obtuse, 5–7 × 3–4 mm. Petals oval to suboblong, round to subtruncate apically, 5–8 × 3–4.5 mm. Labellum 3-lobate, 7–10 mm long, 8–12 mm wide across lateral lobes when flattened; lateral lobes elongate, narrowly oblong to sublinear, attenuate, acute, curved toward front, 4–7 × 1 mm; midlobe divided into 4 lobules, pandurate, emarginate, margin irregularly undulate, 6–8 × 5–10 mm, the basal lobules folded backwards, the distal lobules straight; callus oblong, the base forming a concave cushion with a tuft of short, glandular hairs, 1.5–2 × 2 mm; the distal portion forming a mass of low tubercles, 2.5–3.5 × 1–1.5 mm. Column widely winged, dolabriform, 2–2.5 mm long, 3–4 mm wide; wings obliquely flabellate, with an irregularly denticulate margin, 1.5 × 2 mm, with an entire to denticulate margin; stigmatic cavity subpandurate, 0.8 × 0.8 mm; anther cap galeate, 1 mm in diameter; pollinarium 0.8 mm tall, stipe bifid. Fruit not seen.

Phenology: The relatively few specimens available indicate that the species flowers at least from May to November.

Distribution: Bolivia and Peru, from 670 to 1320 m, on the eastern (Amazonian) side of the Andes (Figure 5). The sole Bolivian record cited here was identified from a photo of the herbarium specimen and an illustration by Roberto Vásquez; its flowers seem to be somewhat smaller than those of Peruvian collections.

Additional specimens examined: BOLIVIA. Santa Cruz: Florida, Río La Junta, entre La Angostura y Bermejo, 15 Oct. 1993, *Vásquez et al. 2119* (LPB-Vasq). PERU. Without locality: *Bennett 4601* (MOL-spirit); 8 Jun. 2010 (cult.), *Blanco 3237* (FLAS). Cajamarca: San Ignacio, Huarango, Localidad Romerillo, 1170 m, 8 Nov. 1997, *Campos 4558* (HAO [destroyed, photo seen], MO, USM). Huánuco: Huánuco, Monzón,

cerca Tingo María, 700 m, 21 Jun. 1953, *Ferreyra 9313* (AMES, UC, USM), 14 Sep. 1954, *Ferreyra 10078* (AMES, UC, USM); Leoncio Prado, Rupa Rupa, al O de Tingo María, 700 m, 22 Aug. 1978, *Schunke 10514* (BRIT, MO); Tingo María, 670 m, 29 Oct. 1948, *Carpenter 106* (AMES); Tingo María, Río Huállaga, 4 Oct. 1972, *Croat 21087* (F, FTG, MO, SEL). Pasco: Oxapampa, Distr. Chontabamba, camino a Pusapno, 1800 m, 6 Apr. 2005, *Becerra et al. 1014* (HOXA). San Martín: Rioja, Pardo Miguel, 1.5 km al O del centro poblado Aguas Verdes, 1320 m, 24 Jun. 1997, *Sánchez Vega & Dillon 9013* (CPUN, HAO [destroyed, photo seen], SEL). Ucayali: Padre Abad, Boquerón de Padre Abad, 1000 m, 24 May 1993, *Jara sub Bennett 6026* (NY). CULTIVATED [without original locality data]: 9 May 2004, *Blanco 2573* (FLAS); 27 Sep. 1988, *Whitten 3433* (FLAS).

Commentary: *Lockhartia lepticaula* is most similar to the primarily Ecuadorian *L. tenuiflora*, from which is distinguished by its wider labellum midlobe and flabellate column wings. The two species appear to be parapatric, and no intermediates have been detected.

Lockhartia lepticaula is also similar to *L. serra*, which can have similarly flabellate column wings, but that species has much larger flowers, petals more pronouncedly arched forward, and relatively longer, obtuse labellum side lobes. Further, the two species occur on opposite sides of the Andes.

***Lockhartia longifolia* (Lindl.) Schltr.**

17. *Lockhartia longifolia* (Lindl.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 6: 99. 1919. : *Fernandezia longifolia* Lindl., Orchid. Linden. 13. 1846. TYPE: VENEZUELA. Mérida: neighborhood of Mérida [city], 5000 ft [1524 m], July 1842, *J. Linden 660* (holotype: K-Lindl.; isotypes: BR, G, P, W-Reich.-Orch.).

Lockhartia platyglossa Rchb. f., *Linnaea* 41: 106. 1877. TYPE: [COLOMBIA. Antioquia:] Medellín, [1872-1875], *G. Wallis s.n.* (W-Reich.-Orch.-44350).

Lockhartia hologlossa Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 7: 199. 1920. TYPE: [COLOMBIA]. Cauca [Possibly Valle del Cauca]. Ca. 1800 m, *M. Madero s.n.* (holotype: B, destroyed. Lectotype, here designated: Tab. 71, Nr. 274 in *Repert. Spec. Nov. Regni Veg. Beih.* 57. 1929).

Lockhartia unicornis Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 7: 200. 1920. TYPE: [COLOMBIA.] Cauca [now Valle del Cauca]: Cali, West Cordillera, 1500-2000 m, 6 Aug 1883, *Lehmann 3290* (holotype: B, destroyed. Lectotype, here designated: K-000078997; isotypes: AMES, BM, G [photos: AMES, F, MO, SEL], NY).

Lockhartia tuberculata D.E. Benn. & Christenson, *Brittonia* 46: 241, 243, fig. 9. 1994. TYPE: PERU. Junín: Chanchamayo, headwaters of Río Toro near Puente San Félix, 29 Feb. 1992, *O. del Castillo ex Bennett 5403* (holotype: USM *fide* protologue, MOL *fide* E. Christenson, pers. comm., not found; lectotype, here designated: NY).

Stems descending to pendent, more or less flexible, 13–80 cm long (and possibly longer) when reproductive, with 20–72 leaves; shoots (stem and leaves) 9–45 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular and falcate to slightly sigmoid in side view, with incurving (rarely straight) margins toward the apex, acute, exposed part of largest leaves 21–80 × 3–9 mm. Inflorescences both terminal and axillary from the distal fourth of the stem, up to 7 per stem (produced simultaneously or sequentially); with 1–5 flowers produced sequentially; exerted portion 0.5–4.5 cm long, internodes 1–4 mm long; inflorescence bracts amplexicaul, conduplicate, narrowly triangular in side view, acute to acuminate, appressed to the

rachis and imbricate, 3–8 × 1–2 mm (folded); pedicel 5–7 mm long. Flowers resupinate or non resupinate, or more commonly pendent (facing down), widely open, 6–18 mm tall, yellow with brick red spots on the callus. Sepals ovate to oval, concave, acute to obtuse, 3–7 × 1–4 mm. Petals obovate to elliptic (occasionally suboblong), apically obtuse, subtruncate or apiculate, projected obliquely forward, 4–10 × 2–8 mm. Labellum suborbicular, convex, obtuse to shallowly retuse, 4–12 mm long, 4–11 mm wide when flattened; callus suborbicular to oblong, located on the central-proximal portion of the labellum, concave, surrounded by an elevated ridge (to 1 mm high) and a single tooth (to 2 mm tall) at the apex, with an oblong field of glandular trichomes in the central area and on a trapezoid ledge pointed toward the base of the labellum, 3–5 × 2.5–3.5 mm. Column winged, 2.5–3 × 3–3.5 mm (including wings), the wings obliquely subquadrate with an entire to denticulate margin, 1.5 × 1.5 mm; anther cap galeate, 1.3 × 1.3 mm; pollinarium 0.8 mm tall, stipe bifid from the base. Fruit globular to obovoid, 9–14 × 5–9 mm.

Nomenclatural notes: Although clearly a species of *Lockhartia*, the exact identity of Lindley's *Fernandezia longifolia* remained in obscurity for 130 years. The holotype in Lindley's herbarium at K had a single flower apparently hidden behind the stem. This is evident from Lindley's remark in the protologue: "*The structure of the flowers unknown to me.*" The isotype at P lacks flowers; the isotype in the Reichenbach herbarium at W has one flower, but Reichenbach seemingly failed to notice that it was an isotype of *F. longifolia*, and annotated the specimen as *L. parthenocomos*. This specimen was also overlooked as a type when the Reichenbach f. herbarium was photographed for the IDC microform (Burns-Balogh, 1988). Reichenbach (1857) initially listed *F. longifolia* as a

synonym of his own *Lockhartia parthenocomos*, and later (Reichenbach, 1855; Reichenbach, 1864) as a species of uncertain identity (“*species obscurissima et ob florum defectum non recognoscenda, igitur delenda*”). Kraenzlin (1923) also listed *L. longifolia* as a putative synonym of *L. parthenocomos*, while Dunsterville and Garay (1959) and Foldats (1970) listed *L. parthenocomos* as a synonym of *L. longifolia*.

It was not until 1973 when, at the request of Dunsterville and Garay (1976), Peter Taylor rehydrated the flower from the holotype of *L. longifolia* and both species were recognized as different from each other.

The illustration selected here as lectotype of *Lockhartia hologlossa* is the original drawing prepared by Schlechter, but it was not published until after Schlechter’s death by Mansfeld (1929). Mansfeld also published the original drawing by Schlechter of *L. unicornis* in the same publication.

According to the protologue of *Lockhartia tuberculata*, the holotype (the only specimen cited) was deposited in USM. According to Eric Christenson (pers. comm., 2009), all the types of orchids described by Bennett and Christenson that were originally deposited in USM were transferred to MOL, although a search for them in either herbarium failed to find the type of *L. tuberculata* (Delsy Trujillo, pers. comm. 2010). However, an unmarked type specimen of *L. tuberculata* was found in NY; this specimen is probably the only extant voucher, and thus will be designated as lectotype.

Phenology: Flowering plants have been collected throughout the year, but more abundantly during January and February.

Distribution: From Colombia and western Venezuela south to Bolivia, from 750 to 2800 m on both sides of the Andes (but only on the eastern side in Peru and Bolivia) (Figure 9).

Additional specimens examined: BOLIVIA. Without locality: *Bang* 2286 (AMES, BM, E, F, G [2 sheets], GH, K [2 sheets], M, MICH, MO, NY [4 sheets], PH, W, WU, Z). Cochabamba: Río Juntas, 800 m, 13 Apr. 1892, *Kuntze s.n.* (NY, 2 sheets). La Paz: Inquisivi, near the pass above Circuata, "Polea", 2500 m, 30 Jan. 1983, *Luer et al. 8654* (SEL). Santa Cruz: Yungas de San Mateo, 2000 m, 11 Apr. 1911, *Herzog 1988b* (L). COLOMBIA. Antioquia: Parque Nacional Natural "Las Orquídeas", sector Calles, margen derecha del Río Calles, arriba de la confluencia con el Río Polo, 1400 m, 28 Mar. 1988, *Cogollo et al. 2737* (JAUM). Boyacá: Municipio Santa María, vertiente oriental de la Cordillera Oriental, 1400 m, 15 Aug. 2010 (cult.), *Giraldo 206* (COL). Caquetá: without specific locality, 1200 m, 26 Feb. 1979, *Renz 4007* (RENZ). Cauca: Popayán, *Lehmann s.n.* (W-Reich). Magdalena: Sierra Nevada de Santa Marta, on trail between finca Reflejo and finca Cecilia in quebrada E of Quebrada Indiana, 1700 m, 1 Sep. 1972, *Kirkbride 2043* (COL [2 sheets], NY). Norte de Santander: Ocaña, 1500 m, 1849, *Schlim 1026* (K). Tolima: Entre Murillo y El Líbano, 15 km de Murillo, 2000 m, 8 Apr. 1984, *Albert de Escobar et al. 4208* (HUA). Valle del Cauca: Cordillera Occidental, vertiente oriental, Hoya del Río Cali, Pichinde, Alto de Miravalle, hacia la Leonera, dehesas, 2020 m, 28 Oct. 1944, *Cuatrecasas 18319* (AMES, F); Cordillera, arriba de Saladito, cerca al cerro de la televisora, 2000 m, 27 Jan. 1970, *Espinal 3735* (COL); Farallones de Cali, 2000 m, 15 Oct. 1882, *Lehmann 2020* (G, 4 sheets); San Antonio, Estación de la Televisora de Cali, 1900 m, 16 Oct. 1962, *Schmidt-Mumm 149* (COL, 2

sheets). ECUADOR. Without locality data, or province unknown: Huacapamba [?], 19 Jan. 1883, *Poortman 482* (K, P [2 sheets]); *anonymous s.n.* (K-spirit); 25 Jan. 2000 (cult.), *Whitten et al. 1646* (FLAS), 29 Sep. 2003 (cult.), *Whitten et al. 2385* (FLAS).

Azuay: Along road from Gualaceo to Chiguinda, Jan. 1989, *Hirtz et al. 4004* (MO).

Bolívar: Huaranda [Guaranda], [Jun. 1803], *Tafalla 444* (G, W-Reich). Cotopaxi: 3 km E of El Palmar on road Quevedo-Latacunga, 800 m, 5 Apr. 1980, *Dodson & Gentry 10198* (SEL); Bosque Integral Otonga, 1400 m, 21 Apr. 1999, *Muñoz & Tapia 130* (SEL), 22 Apr. 1999, *Muñoz & Tapia 231* (QCNE), 1450 m, 18 May 1999, *Muñoz & Tapia 392* (QCNE); Tenefuerste, Río Pilalo, km 52-53, Quevedo, Latacunga, 750 m, 21 Feb. 1982, *Dodson & Gentry 12788* (MO, QCA, SEL). Imbabura: Reserva Los Cedros, 1300 m, 3 Jul. 1999, *Endara & Cooper 308* (QCA). Loja: Cachaco on road from Yangana to pass on road to Valladolid, 2450 m, 1 Jul. 1982 (cult.), *Dodson et al. 13296* (SEL); Cachaco, near pass between Yangana and Valladolid, 2400 m, Mar. 1985, *D'Alessandro 373* (SEL); Ramos pamba road Vilcabamba-Valladolid, Sep. 1980, *D'Alessandro 373* (SEL); Yangana, *André s.n.* (K). Morona-Santiago: Chihinda [Chiguinda?], 1861, *Pearce s.n.* (BM). Napo: Along Río Borja, 1700 m, 16 Feb. 1990, *Dalström 1346* (SEL); Baeza, 1500 m, *Hirtz 8* (SEL); Baeza, al pie del Río Quijos, 2500 m, 2 Sep. 1995, *Cornejo & Bonifaz 4497* (AAU); Baeza, riverside approx. 1 km SW of the village, 2000 m, 20 Oct. 1976, *Ollgaard & Balslev 10212* (AAU, AMES, F, MO, NY, SEL); Desviación Baeza-Lago Agrio 2 km antes de Baeza, al margen del Río Papallacta, 1900 m, 21 Aug. 1989 (cult.), *Hágsater & Dodson 8922* (AMO, 4 sheets). Pichincha: 5 km E of the Río Toachi at km 33 on road Santo Domingo to Quito, 1000 m, 1 Feb. 1987, *Dodson & Hirtz 16908* (MO); Along the mining road above Minas Toachi, 1200 m, 27 Feb. 1982, *Hirtz & León*

111 (SEL); Quito-Sto. Domingo via Chiriboga, km 85, 1200 m, 16 Feb. 1991, *Dodson et al.* 18675 (MO, QCNE); Palanda, Región de la Cordillera del Cóndor, sector Sur, Parroquia San Francisco de Vergel, cuenca alta del Río Vergel, Pica Sangola, 2200 m, 12 Mar. 2005, *Quizhpe et al.* 995 (QCNE), Pica de Sol Naciente, 2100 m, 15 Mar. 2005, *Quizhpe et al.* 1070 (QCNE); Quito, Nanegal, Hacienda El Carmen, c. 5 km airline SE of Nanegal, 1200 m, 9 Jul. 1991, *Webster et al.* 28964 (DAV); Quito, Nanegal, Bosque Protector Maquipucuna, along trail from guava plantation to Río Tulambi, 1300 m, 10 Jul. 1992, *Webster et al.* 29301 (DAV, QCNE). Zamora-Chinchipe: Cerro Colorado, S of Nambija, 17 Feb. 2002, *Hirtz et al.* 8007 (SEL); Zamora-Cenepa, ca. km 25- km 33, 1700 m, 5 Dec. 1957, *Dodson* 242 (SEL); Zumba, 1200 m, 10 Nov. 2001 (cult.), *Hirtz* 7817 (SEL). PERU. Without locality: *Bennett* 6427 (MOL-spirit); 1876, *Vidal-Senege s.n.* (P). Cajamarca: San Ignacio, San José de Lourdes, base del Cerro Picorana, 2010 m, 20 Jan. 1999, *Díaz et al.* 10352 (CPUN, GH, MO, SEL); San Ignacio, San José de Lourdes, Campamento Zural, camino al Cerro Picorana, 2010 m, 28 Jan. 1999, *Díaz et al.* 10552 (MO). Cusco: Chirumbia, 2000 m, Dec. 1956, *Vargas* 11381 (CUZ; photos: F, NY); Quispicanchis, Ttio to Murayaca, Marcapata, 1960 m, 28 Jan. 1943, *Vargas* 3138 (AMES, CUZ [photos: F, NY]); Urubamba, 101 km from Cuzco between Pampacahua and Cedrobamba, Quebrada and Río Pachachoca, Santuario Histórico Machu Pichu, 2800 m, 8 Jul. 1989, *Núñez et al.* 11107 (MO); Urubamba, Machu Picchu, 2020 m, 4 Jan. 1946, *Vargas* 5546 (AMES). Huánuco: Muña, 1830 m, *Bennett* 15 (SEL); Muña, *Ruiz s.n.* (BM, MA). Junín: Huacapistana, 25 Apr. 1964, *Bennett* 462 (AMES, UC); Huacapistana, 1800 m, 6 Jun. 1929, *Killip & Smith* 24296 (AMES, F, G, K, NY, UC, USM); Satipo, Cordillera Vilcabamba, Northern Cordillera Vilcabamba, E slope, upper

River Poyeni watershed, 2050 m, 23 Jun. 1997, *Boyle et al. 4568* (F, USM). Pasco: Oxapampa, Distr. Oxapampa, sector Muchuymayo, zona de amortiguamiento del Parque Nacional Yanachaga Chemillen, 2024 m, 23 Mar. 2010, *Perea et al. 4126* (HOXA). VENEZUELA. Mérida: without specific locality, 1200 m, 19 Dec. 1961, *Renz 5138* (RENZ, 2 sheets). Táchira: 18 km SW of La Fundación, 950 m, 14 Mar. 1981, *Liesner & González 10567* (VEN); On road from San José de Bolívar to La Mesa, 1500 m, *Dunsterville 1273* (K). COUNTRY UNKNOWN: Rio de Cachaco, *André s.n.* (K). CULTIVATED [and/or without original locality data]: 19 Aug. 2010 (cult.), *Blanco 3215* (FLAS); *Pavón s.n.* (G); 4 Apr. 2000 (cult.), *Whitten 3434* (FLAS).

Commentary: *Lockhartia longifolia* is most similar to *L. hercodonta*, but that species has white flowers (commentary under *L. hercodonta* lists further differences). *Lockhartia parthenocomos*, which has been confused with *L. longifolia* in the past, occurs in the Venezuelan Coastal Range and has much larger flowers with a concave labellum and a non-crateriform callus. *Lockhartia rugosifolia*, which has been confused with *L. longifolia* in herbaria, also has a concave labellum with a non-crateriform callus, although the flowers are much smaller than those of *L. parthenocomos*; its leaves are rugulose, while those of *L. longifolia* are smooth.

The leaf morphology of *Lockhartia longifolia* is variable throughout its geographical range. Populations from Venezuela and NE Colombia have straight or incurved, “strict” leaves (i.e., that form a narrow angle with the stem), plants from elsewhere in Colombia, Ecuador, and Peru tend to have longer leaves that are slightly sigmoid and that diverge from the stem at a wider angle, giving the shoots a more “loose” appearance. Collections from Bolivia have relatively straight leaves. Some collections from NW

Ecuador vegetatively resemble *L. hercodonta*, which suggests there could be hybridization between both taxa (commentary for *L. hercodonta*). The type of *L. tuberculata* from central Peru has unusually incurved leaf tips.

Moreover, the flowers of *Lockhartia longifolia* are quite variable in size, with a 3-fold difference between extremes (e.g., the type of *L. tuberculata* from Peru has flowers 6 mm across, while *Cuatrecasas 18319* from Colombia has flowers 18 mm tall). However, this variation is continuous and the morphology of the floral parts, including the callus and column, are relatively uniform. Schweinfurth (1955) also commented on the variable flower size of this species (as *L. hologlossa*).

***Lockhartia lunifera* (Lindl.) Rchb. f.**

18. *Lockhartia lunifera* (Lindl.) Rchb. f., Bot. Zeit. 10: 767. 1852. : *Fernandezia lunifera* Lindl. Edwards's Bot. Reg. 25: misc. 91-92, 1839. SYNTYPES: BRAZIL. [São Paulo:] Bananal [22°40'50"S, 44°19'25"W, ca. 450 m], *J.T. Descourtilz s.n.* (plate 60 in Descourtilz's "Epidendres des forêts vierges du Brésil", Bibliothèque de L'Institut de France, Paris); BRAZIL. Without further locality data, *Ex Hort. G. Loddiges s.n.* (lectotype, here designated: K-Lindl.-79001 [including watercolor of flower in life near the bottom left corner of the sheet; excluding *Gardner 4360*, *Jamieson s.n.* and *Jameson s.n.*]); and BRAZIL. [Bahia], near Ilheos [Ilhéus], [probably collected between 10 Nov. 1818 and 18 Feb 1819], *C.F. von Martius s.n.* (not found; not in BR, K, or M).

Lockhartia ludibunda Rchb. f., Bot. Zeit. 15: 159. 1857. TYPE: [BRAZIL. Santa Catarina:] near Joinville, *Ex Hort. Consul Schiller* [near Hamburg], *Schiller s.n.* (holotype: W-Reich.-Orch.-44340; possible isotypes: W-Reich.-Orch.-44341 and -44342).

Stems erect or descending, more or less rigid, 7–46 cm long when reproductive, with 22–63 leaves; shoots (stem and leaves) 10–17 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, with slightly outcurving (occasionally straight) margins, obtuse to truncate (commonly rounded) apically; exposed part of largest leaves 12–27 × 4–6 mm. Inflorescences both terminal and axillary from the distal half of the stem, with 1–3 flowers produced sequentially; exerted portion 0.3–1 cm long, internodes 1–2 mm long; inflorescence bracts amplexicaul, ovate to suborbicular, cordate, obtuse to acute or apiculate, nearly flat to infundibuliform, 2–5 × 1.5–4 mm; pedicel and ovary 9–13 mm long. Flowers resupinate or nutant (facing down), widely open, 9–16 mm tall, yellow, the labellum with large reddish brown blotches and lines around the callus and on the lateral lobes; and an open V-shaped infrastigmatic dark brown band. Sepals elliptic to widely oval or ovate, slightly concave, obtuse, reflexed, 4–6 × 2.5–4.5 mm. Petals widely oval, apically rounded to subtruncate, curving toward the front, with reflexed margins, 4.5–6.5 × 3–5 mm when flattened. Labellum 3-lobate, 6.5–8.5 mm long, 9–13 mm wide across lateral lobes when flattened; lateral lobes elongate, straight to falcate (curving upwards) when flattened, oblong, obtuse to round apically (often crenulate near the apex), curved toward front, 4.5–7 × 1–1.5 mm; midlobe divided in 4 lobules, pandurate, emarginate, margin irregularly undulate, 4.5–7 × 4–8 mm, the basal lobules folded backwards, the distal lobules projected downward or somewhat flaring; callus more or less triangular, becoming wider and slightly bifid distally; basal part forming a concave cushion with a basal tuft of short, glandular hairs, 1 × 2 mm; the distal portion forming a subtriangular mass of tubercles. Column winged, 2 mm long (with anther cap), 3–4 mm wide; wings

expanded, obliquely quadrate to subtrapezoid, wider at the base, 0.5–1 × 1 mm, with a minutely crenulate margin; stigmatic cavity narrowly pandurate, 1 × 0.3 mm; anther cap galeate, 1 mm long; pollinarium 0.8 mm tall, stipe bifid. Fruit obovoid to ellipsoid, glaucous, 7–12 × 4–6 mm.

Nomenclatural notes: Only two of the three elements cited in the protologue of *Fernandezia lunifera* have been found. The specimen present in Lindley's herbarium at K is designated as the lectotype.

There are three additional collections mounted on the same sheet as the lectotype. These are: 1) *Jameson s.n.* from Peru, a stem with an attached flower, possibly of *Lockhartia lepticaula*; 2) *Jamieson s.n.* from Nanegal (Ecuador), collected in 1854; a stem without flowers, vegetatively reminiscent of *L. serra*; and 3) *Gardner 4360* from Brazil, which is an isotype of *L. goyazensis*. There is also a small watercolor of the flower in life, apparently of Loddiges's plant, near the bottom left corner of the sheet; this is too part of the lectotype.

There are three extant *Lockhartia* specimens collected by von Martius in M, but none of these has the locality "Ilheos" written on its label.

The Descourtiz mentioned by Lindley in the protologue is not Michel Etienne Descourtiz (1775-1835), who worked mostly in the Caribbean, but his son, Jean Théodore Descourtiz (?-1855), who worked for the National Museum of Rio de Janeiro. His watercolors and (informal) descriptions of Brazilian orchids (Descourtiz, 1825-1855) were bound in three volumes (21 "livraisons") and are deposited in the Bibliothèque de L'Institut de France in Paris. It appears that Lindley examined these paintings and described several species based on them.

A specimen from the H.G. Reichenbach herbarium (W-Reich.-Orch.-44329) is annotated as the type of *Lockhartia lunifera*, but it does not correspond to any of the original elements cited by Lindley in the protologue. Reichenbach (1855) clearly stated:

“Unsere Abbildung nach der Pflanze aus dem gräfflich Thun-Hohenstein’schen Garten zu Tetschen, cultivirt vom Herrn Schlossgärtner Josst. Auch aus Herrn Van Houtte’s Garten von Herrn Kegel mitgetheilt.”

The sheet at W has two stems, one of them labelled “*h. Houtt. Gard., Oct. 1848, H. Kegel*”, which is clearly the second plant mentioned by Reichenbach above. The other stem must be the plant cultivated by Josst. None of these two collections are types.

There are three specimens at W-Reich.-Orch. labeled *Lockhartia ludibunda*, apparently in H.R. Reichenbach’s hand. The specimen cited here as the holotype seems to be the one first sent by Consul Schiller to Reichenbach, and the one that Reichenbach used to describe the species. It has two stems with detached flowers (in a packet), and a piece of paper with several drawings in pencil of different parts of the plant. Although Reichenbach f. never published these drawings, Kraenzlin (1923) published very stylized drawings, but clearly based on Reichenbach’s.

A second specimen in Vienna (W-Reich.-Orch.-44341) has a number “68” written on its label, here interpreted to be the year 1868, and thus eliminating it as possible type material of *L. ludibunda*. The third specimen (W-Reich.-Orch.-44342) has no indication of the date of preparation, but a detached flower in the packet is clearly the one on which the drawing attached to the holotype was based.

The combination “*Fernandezia robusta* Klotzsch” was explicitly mentioned by Reichenbach (1855; 1864) as a name used for a plant in cultivation by Senator Martin Johann Jenisch II (1793-1857) of Hamburg. Reichenbach also made clear that this unpublished name corresponds to *Lockhartia lunifera*. The combination “*Fernandezia*

robusta Klotzsch ex Rchb. f.” is occasionally cited, but it is not validly published under Article 34.1 of the Code (McNeill *et al.*, 2006). Reichenbach (1855) mentioned the existence of a herbarium specimen (“Hab. sp. sicc. et vid. viv. c.”), which was probably destroyed in Berlin along with many other Klotzsch collections; however, a probable duplicate (a fragment consisting of a single flower), originally part of the Meisner herbarium, exists in NY. The combination *Fernandezia robusta* (Bateman) Schltr. is a synonym of *L. verrucosa*, and its homonym *F. robusta* (Schltr.) Senghas is a synonym of *Fernandezia sanguinea* (Lindl.) Garay & Dunst.

Phenology: Flowering plants have been collected throughout the year, but more abundantly from December to March.

Distribution: Southwestern Brazil (from southern Bahia to Santa Catarina), and possibly in northeastern Argentina (in Misiones province), from sea level to at least 700 m (very few specimens have elevational data) in Atlantic Forest (Mata Atlântica) biome (Figure 8).

The sole Argentinian record (from Iguazú National Park) is based on a specimen that lost its flowers, but its vegetative and inflorescence morphology and Atlantic Forest habitat strongly suggest that it is *L. lunifera*, although it could also be *L. goyazensis*. Notably, no species of *Lockhartia* have been reported for the Argentinian or Brazilian portions of the Iguazú Falls area (Johnson, 2001; Cervi and Borgo, 2007).

Additional specimens examined: ARGENTINA. Misiones: P. Nal. Iguazú, 26 Jan. 1997, *Ospina 1435* (COL; identification tentative). BRAZIL. Without locality: *anonymous s.n.* (K-spirit); *anonymous s.n.* (M); 15 Aug. 1920 (cult.), *Doring 5174* (M); *Glaziou 1120* (P); 1817, *Raddi s.n.* (G). State unknown: Rio Macabe, 1845, *Riedel 8*

(P). Bahia: Jaguaquara a Apuerema, 4 Oct. 1972 [1973?], *Pinheiro s.n.* (INPA); Una, estrada Sao José-Una, entre os kms 40 e 45 a partir da BR, 8 Oct. 1992, *Amorim et al.* 821 (NY, U); *Erskine* 235 (K-spirit). Espírito Santo: Sta. Isabel, 9 Jan. 1947, *Krieger & Roth* 1120 (RB). Minas Gerais: Serra do Gongo-Socco [Serra do Gandarela], 4 Mar. 1922, *Hoehne s.n.* (SP). Paraná: Alexandra, 11 May 1909, *Dusén* 8107 (AMES, F, NY, S); Caioba, 10 Jan. 1936, *Hoehne s.n.* (SP); Fazenda Marumby, 14 Jan. 1914, *Dusén* 14274 (K, MICH, S); Jacarehy, 11 Jan. 1915, *Dusén* 16333 (AMES, S), 9 Feb. 1916, *Dusén* 17692 (MO, S); Rio Imbuguassú, 22 Apr. 1910 (cult.), *Dusén s.n.* (L, P, S). Rio de Janeiro: Without specific locality, 1 Jun. 2004 (cult.), *Bocayuva s.n.* (RB), *Gaudichaud s.n.* (G); Bords de la riv. Paquequer, Feb. 1889, *Neves Armond* 41 (AMES, BR); Carmo, *Neves Armond* 294 (BR); Carmo de Cantagallo, 1938, *Neves Armond s.n.* (RB); Petrópolis, Bairro de Matto Grosso, Feb. 1928, *Spannagel* 131 (SP); Rio-Serra de Carioca, 700 m, 22 Mar. 1951, *Pabst* 1284 (AMES); Sebastianópolis [Rio de Janeiro], Dec., *Martius* 2237 (M); Serra da Carioca, Estrada do Sinmeré, 600 m, 22 Apr. 1951, *Pabst* 1034 (S). Santa Catarina: Ad ripas fluvii Pirahy, 19 Sep. 1897, *Schwacke* 13226 (RB); Blumenau, 10 Feb. 1941, *anonymous s.n.* (RB); Sacco Grande, Insula St. Catharina, 3 Sep. 1950, *Rohr* 42 (AMES); Saco Grande, Insula, Dec. 1950, *Pabst* 819 (M). São Paulo: without specific locality, 19 Jul. 1996 (cult.), *Müller* 1987/96 (RENTZ); "Alto da Serra, Rio Grande, etc.", 1904, *Edwall (Comm. Geogr. Geol. S. Paulo)* 1877 (BR); "Brasilia prope San Paulo", *Bowie & Cunningham s.n.* (BM); Cananeia, Ilha do Cardoso, ao vilarejo de Maruja, 22 Jun. 1989, *Romaniuc Neto et al.* 846 (HUEFS, RB); Cubatão, 30 Dec. 1923 (cult.), *Gehrt* 14606 (NY); Iguapé, Estação Ecológica Jureia-Itatins, Serra da Jureia, ao redor da cachoeira do Salto, 12 Dec. 1990, *Gomes da Silva*

et al. 103 (SP); Iguapé, Reserva da Jureia, trilha para a figueira grande, 14 Mar. 1990, Rossi *et al.* 556 (SP); Iguapé, Rio Peroupava, Boa Vista, 1 Jan. 1919, Brade 8527 (K, M, NY); Prope Raiz da Serra, 20 m, Jun. 1901 (cult.), Kerner 22 sub Wettstein & Schiffner s.n. (WU, 2 sheets); Santos, Sonomocabas, 30 Mar. 1875, Mosén 3800 (S). CULTIVATED [and/or without original locality data]: 27 Aug. 1922 (cult.), Ames s.n. (AMES); anonymous 1670 (W-Reich); 8 Nov. 1922 (cult.), anonymous s.n. (BR); 6 Jun. 2004 (cult.), Blanco 2576 (FLAS); 16 Aug. 2004 (cult.), Blanco 2670 (SEL-spirit); 14 Aug. 2004 (cult.), Blanco 2688 (FLAS); 16 Nov. 2006 (cult.), Blanco 3219 (FLAS); Chase 82231 (K-spirit); 28 Jul. 1983, Chase 83157 (K-spirit, supposedly from Costa Rica but must be erroneous); Oct. 1848 (cult.), Kegel s.n. (W-Reich); 13 Dec. 1912 (cult.), Lambach 1139 (BR); 30 Nov. 1994 (cult.), LeDoux & Stern 379 (MO).

Commentary: *Lockhartia lunifera* is very similar to *L. goyazensis*, but it can be distinguished from that species by the usually shorter, straighter leaves, larger flowers, and wider labellum midlobe (see more details under *L. goyazensis*). It is also similar to the Central American *L. amoena*, which is vegetatively variable, can have multiple flowers open simultaneously in each inflorescence, and has a subquadrate labellum midlobe.

Lockhartia lunifera is the southernmost species in the genus, and it is not sympatric with any other *Lockhartia*.

***Lockhartia micrantha* Rchb. f.**

19. *Lockhartia micrantha* Rchb. f., Bot. Zeit. 10: 768. 1852. Non *Lockhartia macrantha* Lem. SYNTYPES: PANAMA. Veragua [Veraguas], [15-20 March 1837], R. Hinds s.n. (lectotype, designated by Atwood in Icon. Pl. Trop. pl. 1449. 1992, here narrowed down: W-Reich.-Orch.-55160 [excluding *Cuming* s.n.]; Isolectotypes: K-78996,

K [excluding *Wood s.n.*], K-Lindl.-78999 [excluding *Loddiges s.n.*], W); and PANAMA [erroneously “Chili” or “Chile” in some labels], Chiriquí, 1828-1830 [erroneously 1831, 1833, 1834 or 1835 in some labels], *H. Cuming s.n.* [or 20, 1297, or 1298] (BM-534525, BR-681386, K [3 sheets], OXF, W, W-Reich.-Orch.-55160 [excluding *Hinds s.n.*]).

Lockhartia chiriquiensis Schltr., Repert. Spec. Nov. Reg. Veg. 12: 215. 1913.

TYPE: PANAMA. Chiriquí: vicinity of San Felix, 0-120 m, December 1911 [“January 1912” in herbarium labels], *H. Pittier 5286* (holotype: US, drawing and photo of holotype: AMES; isotypes: B [destroyed, drawing: AMES-26840], BM, NY).

Lockhartia chocoënsis Rchb. f. & Triana ex Kraenzl., Pflanzenr. (Engler) IV, 50 (Heft 83): 19, fig. 2E. 1923. TYPE: COLOMBIA [“Nouvelle Grenade” in isotype at P]. Prov. de Chocó: “Forêts de Choco,” 1851-1857. *J. Triana s.n.* (holotype: W-Reich.-Orch.-44328; isotype: P-456060).

Lockhartia lankesteri Ames, Schedul. Orchid. 5: 36. 1923. TYPE: COSTA RICA. [Alajuela:] San Carlos, Aguas Zarcas [10°23'N, 84°20'W, 490 m], 30 Mar 1923, *C.H. Lankester 448* (holotype: AMES).

Lockhartia pandurata Pupulin, Rev. Biol. Trop. 46(4): 998. 1998. TYPE: COSTA RICA. Puntarenas: Aguirre, Parque Nacional Manuel Antonio, 80 m, 11 July 1995, *F. Pupulin 313* (holotype: USJ; isotype CR, not found).

Stems erect, horizontal or descending, more or less rigid, 4–46 cm long when reproductive, with 14–70 leaves; shoots (stem and leaves) 7–14 mm wide. Leaves marcescent, unifacial, laterally flattened, triangular in side view, with straight (rarely incurving or outcurving) margins, obtuse to obliquely truncate apically (sometimes round or subpraemorse), exposed part of largest leaves 8–22 × 3–7 mm. Inflorescences both

terminal and axillary from from the distal three fourths of the stem, up to 12 per stem (produced simultaneously, or rarely sequentially), with 1–9 flowers produced more or less simultaneously; exerted portion 0.5–1.5(2.7) cm long, internodes 1–5 mm long; inflorescence bracts amplexicaul, widely ovate to suborbicular, cordate, acute to obtuse and apiculate, 2–5 × 1–4.5 mm; pedicel and ovary 3–9 mm long. Flowers resupinate, widely open, 5–10 mm tall, completely yellow, or the labellum with pale reddish brown spots around the callus and/or the column with a reddish brown infrastigmatic series of dots or a single bar. Sepals ovate to oval, slightly concave, obtuse to apiculate, 3–4 × 2–3 mm. Petals elliptic to suboblong, obtuse, 3–4.5 × 2–3 mm. Labellum entire to 3-lobate, 3.5–6 mm long, 2.5–9 mm wide across lateral lobes (or widest part, when lateral lobes absent) when flattened; lateral lobes (when present) very short and obscure to elongate and oblong, obtuse to round apically, bent toward front if elongate, 0–4 × 0–1 mm; midlobe entire to obscurely 4-lobulate, subovobate to rhombic, emarginate, wider near the apex, 2.5–4 × 2.3–5 mm; callus suboblong; the basal part a concave cushion, subquadrate, 1 × 1 mm, with a small tuft of glandular trichomes; the distal part formed by two subparallel, smooth to obscurely tuberculate, low keels that converge distally (often not detectable in rehydrated flowers), 1.5 × 1 mm. Column winged, 2–2.5 mm long (with the anther cap), 2–3 mm wide; wings triangular to deltoid, 0.5–1 × 1 mm, with an entire to crenulate margin; stigmatic cavity 0.6 × 0.2 mm; anther cap galeate, 1 mm long; pollinarium 1 mm tall, stipe bifid. Fruit subglobose to obovoid, glaucous, 4.5–8 × 2.5–5 mm.

Nomenclatural notes: Reichenbach f. cited two collections in the protologue of *Lockhartia micrantha*, which should therefore be considered syntypes: “*Veragua Hinds*”

and "*Panama Cuming*". Both of these were collected in modern-day Panama. The former region of "Veragua" roughly corresponds to the modern province of Veraguas. "Panama" probably refers to the region around Panama City. At the time, modern-day Panama was part of Colombia.

Richard Hinds was a naturalist on board of the *H.M.S. Sulphur* during a mission to survey the Pacific coast of the New World. The Sulphur surveyed the coast of Veraguas on March 15-20, 1837; the coastal localities of Bahia Honda and Pueblo Nuevo (both of them in the modern province of Veraguas) are mentioned by Belcher (1843) as part of the ship's itinerary.

Hugh Cuming explored the Pacific coast of South and Central America during his "second voyage" on board of the schooner *Discoverer* in 1828-1830 (Dance, 1980). Cuming was based in Chile (a country outside of the natural distribution of *Lockhartia*), and several duplicates of the syntype bear labels with the pre-printed locality "Chili" or "Chile" (which should be considered an error). Some syntype duplicates indicate different years on their labels (1831, 1833, 1834 and 1835), which do not represent collecting dates (Cuming stayed in England from 1831 until 1835 (Dance, 1980). Those years probably represent dates of distribution of Cuming's sets of botanical collections, which were taken care of by William Jackson Hooker. Several sheets have numbers written on their labels: 20 (W), 1297 (one sheet at K), and 1298 (one sheet at BM and two sheets at K). Hooker most likely assigned these numbers while he organized the distribution of Cuming's sets of plant collections; Cuming seemingly did not use field collection numbers, and his specimens often have conflicting numbers and locality names (Rolfe 1908; Johnston 1936). Even if there are several gatherings represented

among Cuming's specimens of *L. micrantha*, all of them can be considered syntypes as Reichenbach f. likely studied all of them before he described the species.

The one sheet in Reichenbach f.'s personal herbarium has fragments of both Hinds's and Cuming's collections, most likely "kleptotypes". The fragments from the Cuming collection have an annotation in Reichenbach's hand that reads "*Cuming 1298*", an indication that they were taken from either the specimen at BM or from the specimens at K. None of the other sheets of either collection has any remaining flowers. Lindley (1834) cited *Cuming 1298* as *Fernandezia elegans*.

Mora and Atwood (1992d) cited *Hinds s.n.* at W as the type of *Lockhartia micrantha* (effectively designating a first-step lectotype) but there are two sheets currently at W; the lectotype is here restricted to the sheet that belonged to Reichenbach's herbarium, the only sheet that contains flowers (Art. 9.15 of McNeill *et al.*, 2006).

Christenson (1995) made the argument that Pittier's Panamanian collections of Orchidaceae at US should be regarded as holotypes. In 1913, a set of type fragments (apparently including *Lockhartia chiriquiensis*) was sent from US to B at the request of Ignatz Urban (then director of B); these isotypes were destroyed during WWII (Ames, 1944). The collecting date on the specimen labels of *Pittier 5286* (type of *Lockhartia chiriquiensis*, including the drawing at AMES) is January 1912, but this must be an error; Pittier was in San Félix twice in December of 1911, but not in January of 1912 (Dwyer, 1973). Schlechter was aware of this, because in the protologue he cited the collection date as December 1911.

Both holotype and isotype of *L. chocoensis* have labels that read “*Lockhartia chocoënsis* Rchb. f. & Triana, Forêts de Choco” in H.G. Reichenbach’s handwriting. This indicates that Reichenbach intended to publish this species jointly with Triana, although he never did it. A later annotation on the holotype by Kraenzlin reads “*Lockhartia chocoensis* Rchb. f. et Kränzlin.” Reichenbach f. had rehydrated the flowers (as mentioned in the protologue by Kraenzlin) and dissected one; the two remaining entire flowers are in bad shape. Unfortunately, the isotype specimen has no flowers.

Ames only cited “Costa Rica, San Carlos” (a large county in the Costa Rican province of Alajuela) as the type locality for *L. lankesteri*, but a paper slip in the packet of the type specimen has an annotation in Lankester’s hand that reads “*Lockhartia, Aguas Zarcas San Carlos*”.

Phenology: Flowering plants have been collected from November to August, with well-marked maximum in January, February, and March (the peak of the dry season in most of the species geographic range). No flowering collections have been made in September or October, which normally are the rainiest months.

Distribution: From Nicaragua to Colombia and Venezuela, from sea level to 1500 m (Figure 4). Collections from Colombia and Venezuela occur at generally higher elevations (700–1500 m) than most Central American ones (0–1200 m). In the 1850’s, Fendler prepared a Venezuelan collection supposedly from the state of Aragua; no other collections are known from that state, and it is possible that Fendler’s plant was actually brought from Táchira to Aragua and flowered there in cultivation.

A specimen supposedly from Suriname (*Chase 86194*, K-spirit) lacks specific locality data and was likely prepared from a cultivated plant with erroneous information.

Foldats (1970) also listed Suriname and Guyana in the geographic range of *L. micrantha*, but he cited no vouchers, and his reports are likely based on misidentified specimens of the vegetatively similar *L. imbricata*, cited by Cogniaux (1906), Kraenzlin (1923), and Maguire (1948).

Additional specimens examined: COLOMBIA. Boyacá: Municipio de Santa María, vertiente oriental de la Cordillera Oriental, 1400 m, Feb. 2011 (cult.), *Giraldo 230* (COL). Caquetá: San Vicente del Caguán, carretera de Neiva a San Vicente, entre los sitios Sibate y las Morras (kms. 110-116), Cordillera Oriental, Vertiente Oriental, 1000 m, 27 Nov. 1990, *Betancur & Churchill 2226* (COL, HUA, US). COSTA RICA. Without locality, or locality questionable: *Endres s.n.* (W-Reich); *Sanford 6* (K-spirit); “Communicated to C.H. Lankester, said to have been collected by Abel Delgado on the Atlantic coast of Costa Rica, near sea level,” Jan. 1965, *Williams et al. 28866* (F, NY). Alajuela: Orotina, 250 m, Nov. 1923, *Lankester 782* (AMES, 2 sheets); Surubres près de San Mateo, 27 Jan. 1892, *Biolley 7093* (BR, G); Trinchera [Finca], *Endres s.n.* (W-Reich); Vicinity of Capulín, on the Río Grande de Tárcoles, 80 m, 2 Apr. 1924, *Standley 40201* (AMES). Cartago: Turrialba, grounds of Instituto Interamericano, 610 m, 12 Dec. 1947, *DeWolf 303* (AMES); Vicinity of Pejivalle, 900 m, 7 Feb. 1926, *Standley & Valerio 47034* (AMES, US), *Standley & Valerio 47100* (AMES). Guanacaste: Above Río Las Cañas, 500 m, 14 Feb. 1930, *Thomas 7905* (AMES); Aguilares, 600 m, 29 Jan. 1926, *Standley & Valerio 46377* (AMES, US); Hills S of farmhouse, Hacienda Granadilla, 500 m, 11 Feb. 1930, *Dodge & Thomas 7182* (AMES); Hojancha de Nicoya, 200 m, 29 Jan. 1942, *León 963* (CR [2 sheets], F); Quebrada Grande, SE of Tilarán, 650 m, 27 Jan. 1926, *Standley & Valerio 46097* (AMES), *Standley & Valerio 46118* (AMES, US);

Tilarán, 250 m, 20 Mar. 1923, *Valerio 1* (CR); Upper portion of cañón of Río San José, 460 m, 12 Feb. 1930, *Dodge & Thomas 7892* (AMES); Vicinity of Líbano, 260 m, 15 Jan. 1926, *Standley & Valerio 44927* (AMES, US); Vicinity of Tilarán, 500 m, 10 Jan. 1926, *Standley 44161* (AMES, US), *Standley 44271* (AMES, US), *Standley & Valerio 44989* (AMES). Heredia: Magsasay, sendero entre el campamento Canta Rana y Río Peje, 400 m, 14 Jan. 1983, *Chacón 75* (CR, MO). Puntarenas: Buenos Aires, Ujarrás, orilla Río Ceibo, 300 m, 29 Dec. 1981, *Ocampo 3423* (CR); Corcovado Nat. Park, near Estación Sirena, 3 Dec. 1989, *Merz 406* (CR); Esquinas Forest, area between the Río Esquinas and Palmar, 30 m, 1 Dec. 1949, *Allen 5366* (F, SEL); Golfito, P. N. Piedras Blancas, Valle de Coto Colorado, Río Bonito, 100 m, 12 Apr. 1996, *Fletes et al. 255* (INB); Golfito, P.N. Corcovado, Península de Osa, Estación Sirena, Sendero Sirena, 10 m, 12 Jun. 1994, *Aguilar 3376* (CR, INB); Golfito, Parque Nacional Corcovado, Estación Biológica Sirena, 100 m, 6 Jan. 2005 (cult.), *Bogarín et al. 1241* (JBL-spirit); Golfito, Parque Nacional Corcovado, Península de Osa, Estación Sirena, Sendero Ollas, 10 m, 12 Feb. 1994, *Aguilar 3115* (CR, INB, FLAS, MO); Isla Violín, Jul. 1974, *Poveda & Gómez 4715* (CR, 3 sheets); Manuel Antonio, Quepos, 26 Jan. 1989, *Morúa s.n.* (USJ); NE of Sabalito along road to La Unión, 800 m, 17 Jan. 1967, *Burger & Matta 4534* (CR, F); Near Rincón de Osa, 100 m, 17 Feb. 1974, *Liesner 2202* (MO); On Maxwell Cone's "El Volcán" farm at the junction of Río Angel and Río Volcán, El General Valley, 450 m, 2 Feb. 1963, *Williams et al. 24231* (CR, F, GH); Osa, El Campo, subiendo por la fila entre Aguabuena y Baneguitas, cuenca superior de Quebrada Banegas, bajando hasta la Quebrada Digo Digo, 350 m, 13 Jan. 1991, *Herrera 4812* (CR, MO); Osa, Península de Osa, Rancho Quemado, 200 m, 20 Jan. 1993, *Quesada 377* (INB); Osa, Puerto

Jiménez, 5 m, 7 Apr. 1930, *Brenes 12216* (CR, F); Parque Nacional Corcovado, Estación La Leona, junto a Quebrada La Leona, 0 m, 21 Jan. 1993, *Aguilar 1642* (CR, INB); Parque Nacional Corcovado, Sirena, Jack's 800 Trail, 150 m, 15 Feb. 1988, *Kernan 150* (INB); Península de Osa, cerca del Río Volcán, Feb. 1989 (cult.), *Campos s.n.* (USJ); Playa Blanca road near Rincón de Osa, 0 m, 15 Feb. 1974, *Liesner 2156* (CAS, MO, NY); Playa Blanca, Golfo Dulce, 0 m, 25 Feb. 1933, *Valerio 369* (F); Punta Quepos, 3 km S of Puerto Quepos, cove at NE base of península, up to main ridge, 80 m, 21 Jan. 1987, *Grayum 7975* (CR, MO); Reserva Marengo, Península de Osa, 23 Feb. 1992, *Pupulin s.n.* (USJ); Rincón de Osa, 7 Dec. 1966 (cult.), *Rodríguez 1044* (USJ); Rincón de Osa, Osa Peninsula, about 5 km W of Rincón de Osa, 50 m, 24 May 1973, *Burger & Gentry 9022* (CR); Santo Domingo de Golfo Dulce [Puerto Jiménez], Mar. 1896, *Tonduz [I.P.G.C.R.] 10053* (BR); Vicinity of Tinoco Station, area between the Río Esquinas and Palmar Sur de Osa, 30 m, 16 Mar. 1950, *Allen 5489* (F, US). San José: Santa María, Jun. 1869, *Endres 543* (W-Reich); Turrubares, Pacific side, 225 m, 6 Mar. 1926, *Alfaro 265* (AMES); Z. P. La Cangreja, Santa Rosa de Pursical, en las faldas de la Fila La Cangreja, 500 m, 6 Jan. 1993, *Morales 1016* (INB). NICARAGUA. Without locality: 1867, *Tate 459* (K). Chontales: Between Acoyapa and San Miguelito, 366 m, Aug., *Heller 2385* (SEL, 3 sheets). Managua: Sierra de Managua, Río Masigua, 600 m, Apr. 1938, *Garnier 1831* (AMES, F). Matagalpa: Río Blanco, "El Bálsamo", 1 km al W de Río Blanco, 200 m, 17 Mar. 1984, *Moreno 23609* (MEXU, MO, SEL). Río San Juan: El Castillo, comunidad Boca de Escalera, 1 km al O, 100 m, 4 Feb. 2005, *Urbina 832* (MO); San Bartolo, 28 Jul. 1972, *Robbins 6135* (MO, SEL). Zelaya [now Región Autónoma Atlántico Norte]: Along new road to Mina Nueva América (leading more or

less W from ca. 14.3 km N of El Empalme on main road to Rosita), ca. 6.3 km from main road, 29 Apr. 1978, *Stevens 8433* (MO); Along new road to Mina Nueva América (leading more or less W from ca. 14.3 km N of El Empalme on main road to Rosita), ca. 7.7 km from main road, 29 Apr. 1978, *Stevens 8429* (MO); Along new road to Mina Nueva América (leading more or less W from ca. 14.3 km N of El Empalme on main road to Rosita), ca. 8.6 km from main road, 27 Apr. 1978, *Stevens 8362* (MO); Along road between El Empalme and Limbaika, ca. 1.5 km SE of Palmera, 60 m, 24 Feb. 1979, *Stevens 12946* (MO, SEL); Siuna, Comarca El Hormiguero, trocha El Hormiguero, 7 Jan. 1983, *Ortiz 602* (MO, SEL). Zelaya [now Región Autónoma Atlántico Sur]: Along new road from Río Blanco to Río Copalar, ca. 31 km E of Río Blanco, 13 Feb. 1979, *Stevens 12140* (MO, SEL); El Zapote, 40 km al NE de Nueva Guinea, camino al NE de San Martín, 130 m, 26 Feb. 1984, *Sandino 4745* (MO). PANAMA. Without locality, or locality ambiguous: 28 Jan. 1908 (cult.), *anonymous 153* (K); 6 Dec. 1978 (cult.), *Atwood 78134* (SEL); 23 Mar. 2004 (cult.), *Blanco 2558* (FLAS); 20 Aug. 2004 (cult.), *Blanco 2671* (FLAS); 22 Nov. 1977 (cult.), *Henderson s.n.* (SEL); 28 Nov. 1978 (cult.), *Medina s.n.* (SEL); Cultivated, *Powell 51* (K); 7 Apr. 1978 (cult.), *Pridgeon s.n.* (SEL); 28 Apr. 2001 (cult.), *Silvera 18* (FLAS); 9 Apr. 2002 (cult.), *Silvera 72* (FLAS); "Hills E of city and in the province of Chiriquí, sea level to 4000 ft. Blooms in January and February", cultivated, *Powell 51* (AMES, MO). Province unknown: Cruces, 0 m, 22 Nov. 1922 (cult.), *Powell 3189* (AMES); Milaflores, 0 m, Jan. 1923 (cult.), *Powell 3203* (AMES); Ojo del Agua, 0 m, Dec. 1922 (cult.), *Powell 3048* (AMES); Santa Lucía, Mar. 1839, *Barclay 2800* (BM). Chiriquí: Without specific locality, 1219 m, Dec. 1923 (cult.), *Powell 3476* (AMES); Burica Peninsula, San Bartolo Límite, 18 km W of

Puerto Armuelles, 450 m, 24 Feb. 1973, *Bussey 584* (MEXU, MO, SEL). Coclé: 2 mi N of Cerro Pilón, 900 m, 16 Mar. 1973, *Liesner 722* (MO); A few km above El Valle, 1000 m, 6 Mar. 1976, *Luer et al. 752* (SEL), *Luer et al. 764* (SEL); Cerro Gaital, 7 Mar. 2009 (cult.), *Blanco 3223* (FLAS); Cerro Pajita, hills N of El Valle de Antón, Fld. Gamboa, 1000 m, 18 Feb. 1947, *Allen 4259* (BM, BR, G [2 sheets], F); Crest of Cerro Pajita, N of El Valle, 1200 m, 2 Jan. 1947, *Allen 3939* (AMES, G); El Valle de Antón, 1000 m, 16 Mar. 1946, *Allen 3420* (MO); El Valle de Antón, slopes of Cerro Gaital, 14 Nov. 1999 (cult.), *Whitten 99233* (FLAS); Hills above El Valle de Antón, 23 Nov. 1967, *Dressler 3194* (PMA); Hills N of El Valle de Antón, vicinity of La Mesa, 1000 m, 21 Jan. 1941, *Allen 2318* (AMES); On the Mesa above El Valle, 900 m, 5 Dec. 1983, *Luer et al. 9259* (SEL); Penonomé, 15 m, 23 Feb. 1908, *Williams 623* (NY, 3 sheets); Region N of El Valle de Antón, 1000 m, 13 Jan. 1942, *Allen 2903* (AMES). Colón: Upper Río Piedras headwaters, along trail from end of Santa Rita Ridge Road, ca 11 km SW of Cerro Braja, 600 m, 2 May 1981, *Sytsma et al. 4210* (MO). Darién: 10 km NE of Jaqué, ridge and steep slopes at headwaters of Río Pavarandó, 427 m, 30 Jan. 1981, *Sytsma & D'Arcy 3345* (MO); 10 km NE of Jaque, ridge to headwaters of Río Pavarandó, 365 m, 1 Feb. 1981, *Sytsma & D'Arcy 3444* (PMA, SEL); Cerro Sapo, 488 m, 1 Feb. 1978, *Hammel 1181* (MO); E slope of Cerro Sapo, 762 m, 3 Feb. 1978, *Hammel 1282* (MO); Ensenada del Guayabo, along shoreline and lagoons on NW coast, 18 km SE Jaqué, 0 m, 11 Jan. 1983, *Garwood et al. 159* (BM). Los Santos: Vicinity of Tonosí, Guánico, 36 m, 27 Feb. 1963, *Stern et al. 1836* (MO, US). Panamá [including Canal Zone]: 1 km al E del campamento de los guardabosques de INRNARE, sendero de interpretación, 800 m, 29 Apr. 1993, *Correa et al. 9502* (F, PMA); 2-3 mi S of Goofy Lake, rd. to Cerro Jefe,

610 m, 10 Dec. 1966, *Lewis et al.* 295 (MO); Along telephone cable trail between splice S16 and S49, Río Indio, 12 Jan. 1935, *Steyermark & Allen* 17437 (AMES, BM, G, MICH), *Steyermark & Allen* 17440 (BM); Altos de Pacora, 800 m, 4 Mar. 1976, *Taylor* 13224 (K, K-spirit); Area entre Cerro Jefe y La Eneida, 900 m, 12 Feb. 1971, *Correa et al.* 1736 (PMA); Balboa, Nov. 1923, *Standley* 25494 (AMES); Barro Colorado Island, 17 Feb. 1939, *Zetek s.n.* (MO); Cerro Campana, 500 m, 20 Feb. 1984, *Churchill & de Nevers* 4975 (MO); Cerro Campana, 5 Mar. 1969, *Dressler* 3610 (PMA, FLAS), 400 m, 13 Jan. 1967 (cult.), *Hutchinson & Dressler* 2881 (AMES, UC), 850 m, 11 Mar. 1973, *Liesner* 597 (MO); Cerro Campana, near tower, 30 Mar. 1977, *Folsom et al.* 2301 (MO); Cerro Jefe, 17 Aug. 1967, *Dressler* 3022 (PMA), 21 Jan. 1967, *Dwyer* 8367 (MO), 800 m, 23 Feb. 1977, *Folsom et al.* 1864Z (MO), 1000 m, 2 Mar. 1976, *Luer et al.* 703 (SEL), 1000 m, 13 Feb. 1977, *Luer & Luer* 1407 (SEL), 700 m, 30 Aug. 1977, *Maas et al.* 2714 (U), *Taylor* 65 (K-spirit); Cerro Jefe, 1.5 mi along first right fork near summit, 850 m, 22 Nov. 1980, *Sytsma & Antonio* 2337 (MO); Drowned forests of Quebrada Tranquila and its branches, 70 m, 8 Jan. 1935, *Dodge & Allen* 17325 (AMES, G, K, MICH, MO); In vicinity of Cerro Campana, 884 m, 14 Feb. 1978, *Utley* 5706 (DUKE); Kanal-Zone, 11 Jan. 1965 (cult.), *Fuernkranz s.n.* (WU); La Eneida, region of Cerro Jefe, 1 Jan. 1968, *Dressler* 3302 (PMA); Mountains N of Cerro Jefe, 26 Aug. 1967, *Stimson et al.* 5421 (NY); NE slope of Cerro Jefe on road to Buenos Aires, 792 m, 27 Jan. 1966, *Tyson et al.* 3258 (SCZ); Parque Nacional Altos de Campana, sendero de interpretación, parcela 5-5, 1 Apr. 1989, *Pérez* 363 (PMA); Pedro Miguel, 0 m, Nov. 1922 (cult.), *Powell* 3049 (AMES, 2 sheets); Río La Maestra, 25 m, 4 Dec. 1936, *Allen* 61 (AMES, MO [2 sheets], NY, PH, US); Río Pedro Miguel, near East Paraíso, 7 Jan.

1924, *Standley 29984* (AMES, US); Serranía de Majé, trail between headwaters Río Ipetí Grande and Charco Rico, 700 m, 27 Jan. 1984, *Churchill & de Nevers 4411* (MO); Slopes of Cerro Jefe beyond Cerro Azul between 4-8 miles, 25 Jan. 1970, *Wilbur & Weaver 11380* (DUKE); Summit of Cerro Campana, 31 Mar. 1969, *Porter et al. 4932* (MO). Veraguas: Bahía Honda, 28 Mar. 1939, *Elmore H23* (F, MICH), 21 Feb. 1934, *Taylor 1510* (AMES, MICH, RSA); Sona, Bahía Honda, Playa del Sol, 2 m, 3 Jul. 2001, *Castroviejo et al. 16162* (MA); Vicinity of Santa Fe, Río Santa María, 305 m, 26 Mar. 1947, *Allen 4429* (G). SURINAME. Without specific locality: 13 Nov. 1986, *Chase 86194* (K-spirit, possibly cultivated, country of origin likely erroneous). VENEZUELA. Aragua: Prope Coloniam Tovar, 1854, *Fendler 1432* (K, K-Lindl). Táchira: 10 km E of La Fundación, ca 15 km by road, above Represa Dorada, 800 m, 14 Mar. 1981, *Liesner & González 10529* (MO [2 sheets], VEN); Río San Buena, 10 km E of La Fundación, around Represa Dorada, 700 m, 13 Mar. 1980, *Liesner et al. 9620* (MO, VEN); Road from San Cristóbal to Macanillo, 1500 m, Nov. 1972, *Dunsterville & Dunsterville 1255* (K, VEN), Mar. 1977 (cult.), *Dunsterville & Dunsterville s.n.* (VEN); San Cristóbal, 1350 m, 29 Nov. 1959, *Renz 9739* (RENZ, 2 sheets). CULTIVATED [and/or without original locality data]: *anonymous s.n.* (K-spirit, 2 jars); 18 Apr. 2004 (cult.), *Blanco 2561* (FLAS), *Blanco 2562* (FLAS); 8 Feb. 2009 (cult.), *Blanco 3220* (FLAS); *Chase 8170* (K-spirit); 22 Mar. 1977 (cult.), *Cheekwood s.n.* (SEL); *Endres s.n.* (W-Reich); 9 Dec. 1987 (cult.), *LeDoux & Stern 154* (MO); 6 Jan. 1988 (cult.), *LeDoux & Stern 170* (MO); 9 Mar. 1988 (cult.), *LeDoux & Stern 218* (MO); 17 Mar. 1975 (cult.), *Mason 14* (K, K-spirit); *Mason 14P* (K-spirit); 24 Mar. 1976 (cult.), *McDiarmid s.n.* (SEL); 22 Feb. 1988 (cult.), *Ploch s.n.* (SEL); 20 Jan. 1912 (cult.), *Shaffer s.n.* (K).

Commentary: *Lockhartia micrantha* is easily recognizable by its small floral bracts and flowers, several flowers open at once per inflorescence, the often simultaneously produced inflorescences, and the small, subspherical fruits (*L. hercodonta* and *L. parthenoglossa* can have fruits of similar shape and size, but their leaf shape is completely different). The stems and leaves of *L. micrantha* are variable in size; many collections have quite small shoots (which facilitates identification), but others are more robust and can be difficult to distinguish from other species of *Lockhartia* when inflorescences are absent. Plants with very short (juvenile?) shoots can produce flowers (e.g., *Dressler et al. 764*, SEL, has a flowering shoot only 4 cm tall!). The shape of the labellum is also variable; the side lobes can be well developed or completely absent, although individual plants produce flowers of consistent shape.

Lockhartia micrantha is very similar to *L. cladoniophora*, a rare species with slightly larger and fewer flowers (see discussion under that species for further differences).

Lockhartia chocoensis is interpreted here as conspecific with *L. micrantha* and different from plants from northwestern Ecuador that have been known by that name (treated here as *L. oxyphylla*). The drawing attached to the holotype sheet of *L. chocoensis* (probably made by H.G. Reichenbach) is somewhat stylized and shows a callus formed by three longitudinal keels, possibly an artifact from rehydration. Furthermore, the leaf shape in the holotype and isotype of *L. chocoensis* are more similar to those of *L. micrantha* than to *L. oxyphylla*, and the isotype shows an inflorescence (without flowers) arising from the central portion of the stem. Even when no modern collections of *L. micrantha* from the Colombian department of Chocó have

been seen, there are collections from the adjacent Pacific coast of Darién province in Panama. Garay (1970a) published a photograph of a Colombian plant of *L. micrantha* (as *L. chocoensis*). Costa Rican material identified as *L. chocoensis* by Bogarín *et al.* (2008) corresponds to *L. cladoniophora*.

It is perplexing that in Central America *L. micrantha* is more abundant below 500 m elevation, while in Colombia and Venezuela (from where relatively few collections are known) the same species seemingly occurs only at or above 700 m. The South American plants do not differ morphologically in any significant way from the Central American ones, and thus they are here considered conspecific.

***Lockhartia oblongicallosa* Carnevali & G.A. Romero**

20. *Lockhartia oblongicallosa* Carnevali & G.A. Romero, Orchids Venezuela, ed. 2: 1138, unnumbered figure on page 460. 2000. TYPE: VENEZUELA. Monagas: near Caripe, flowering in cultivation, originally collected by T. Odehnal, March 1976, *T. Odehnal s.n.* sub *G. C. K. Dunsterville 1352* (holotype: drawing at AMES; voucher not found and possibly never prepared; copy of type drawing: K, and published in the protologue).

Stems descending to pendent (occasionally suberect when young), 28–45 cm long when reproductive, with 30–40 leaves; shoots (stem and leaves) 18–25 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular to suboblong in side view, with mostly straight margins (slightly incurving near the tip), obliquely acute, exposed part of largest leaves 34–40 × 4–7 mm. Inflorescences axillary from the distal third of the stem and possibly also terminal, 1-flowered; exerted portion 4–6 mm long, internodes 1–3 mm long; inflorescence bracts amplexicaul, campanulate, narrowly

triangular to suborbicular, 4–8 × 2–8 mm; pedicel and ovary 2–5 mm long. Flowers pendent, campanulate, ca. 10 mm across, white with a yellow callus and a pale pink band at the distal end of the callus. Sepals ovate, concave, obtuse, 7 × 5 mm. Petals obovate, apically obtuse to rounded, slightly concave and projected forward, 7–8 × 5 mm. Labellum entire, suborbicular, concave and difficult to spread, retuse, margin entire, 7–8 mm long, 8–9 mm wide when flattened; callus an oblong, raised ridge from the base to the middle of the labellum, covered with yellow glandular trichomes, 4.5 × 1.5 mm, with a somewhat bifid apex. Column narrowly winged, 2.5 × 3 mm, the wings obliquely rectangular, 1 × 2 mm; anther cap galeate, 1 mm in diameter; pollinarium stipe bifid from the base, 1 mm tall. Fruit subglobular, 6–7 mm × 5–6 mm.

Nomenclatural notes: Although not obvious from the phrasing of the protologue, the designated type is the drawing prepared by G.C.K. Dunsterville deposited at AMES (G. Carnevali and G. Romero, pers. comm. 2009). The voucher for this illustration has not been found at AMES, K or VEN (which hold most of Dunsterville's collections), and was possibly never prepared.

Phenology: The type is the only collection with flowers, but it produced them in cultivation in Caracas. A small plant cultivated at the Muenchen-Nymphenburg Botanische Garten (Munich) produced flowers infrequently.

Distribution: Endemic to the mountains around the city of Caripe, in Mónagas state, Venezuela (Figure 10). The only specimen with elevational data was collected at 1300 m.

Additional specimens examined: VENEZUELA. Mónagas: Caripe, [Sep. 1799], *Humboldt & Bonpland 571* (B-Willd., image seen); Caripe, Hacienda La Cuchilla, 16

Jan. 2009, *Leopardi 311* (IRBR); Summit of Cerro de la Cueva de Doña Anita, south of and bordering valley of Caripe, 1300 m, 7 Apr. 1945, *Steyermark 61930* (C, F, VEN).

Commentary: *Lockhartia oblongicallosa* is a narrow endemic of the area around Caripe in Mónagas state, Venezuela. It is similar to both *L. latilabris* and *L. parthenocomos*, but those two species have much larger, yellow flowers with a transverse callus, and do not occur in the same area. The oblong callus is unique among the campanulate-flowered species of *Lockhartia* (i.e., the *Parthenocomos* species group).

***Lockhartia obtusata* L.O. Williams**

21. *Lockhartia obtusata* L.O. Williams, Amer. Orchid Soc. Bull. 9: 209, f. 8. 1941.
TYPE: PANAMA. Coclé: Hills north of El Valle de Antón, 1000 m, 23 June 1940, *P.H. Allen 2160* (holotype: AMES).

Stems descending to pendent, more or less flexible, 20–41 cm long when reproductive, with 23–33 leaves; shoots (stem and leaves) 25–45 mm wide. Leaves marcescent, unifacial, laterally flattened, obliquely oblong to elliptic in side view, with straight to outcurving margins, obtuse to round with a subapical notch (at the apex of the sheath), rarely acute in relatively narrow leaves; exposed part of largest leaves 24–48 × 6–12 mm. Inflorescences both terminal and axillary from the distal two thirds of the stem, up to 7 per stem (produced simultaneously), with 1–3 flowers produced sequentially; exerted portion 0.5–2 cm long, internodes 1–5 mm long; inflorescence bracts amplexicaul, ovate, acute to acuminate, loosely appressed to the rachis and imbricate, 3–6 × 2.5–4 mm; pedicel 4–9 mm long. Flowers non-resupinate, widely open, 15–20 mm tall, yellow with orange spots on the callus and column wings, and a white or

yellowish white area around the callus; anther cap yellowish white. Sepals ovate to oval, concave, acute, 9–10 × 6–7 mm. Petals oval, obtuse to round apically, projected obliquely forward, 9–11 × 5–7 mm. Labellum suborbicular, convex, obtuse to shallowly retuse, 9–11 mm long, 12–14 mm wide when flattened; callus suborbicular, located on the central-proximal portion of the labellum, concave, surrounded by a low ridge (0.5 mm high) and a single tooth (2 mm tall) at the apex, with an oblong field of glandular trichomes in the central area and on a trapezoid ledge pointed toward the base of the labellum, 11–13 × 6 mm. Column winged, dolabriform, 2.5 × 4.5 mm (including wings), the wings flabellate, with an entire to crenulate margin, 1.5 × 2 mm; anther cap galeate, 1.3 × 1.2 mm; pollinarium 0.8 mm tall, stipe bifid from the base. Fruit obovoid, dark green, not glaucous, 12–14 × 5–8 mm.

Phenology: Flowering plants have been collected in January and June, but flowers are likely produced at other times of the year as well.

Distribution: Known only from the mountains around El Valle de Antón (Coclé province, Panama) and Cerro Mutatá (Chocó department, Colombia), from 500 to 1000 m (Figure 11).

The sole Colombian record is based on a drawing and a photograph published by Misas Urreta (2005). Although I have not seen the specimen, the illustrations clearly represent *L. obtusata*.

Additional specimens examined: COLOMBIA. Chocó: Serranía del Baudó, Cerro Mutatá, 500 m, *Misas Urreta 306* (HPUJ, drawing seen). PANAMA. Without locality: 9 May 2004 (cult.), *Blanco 2572* (FLAS); 23 Dec. 2009 (cult.), *Blanco 3025* (FLAS). Coclé: Cerro Gaital, above El Valle de Antón, 10 Jun. 1999 (cult.), *Whitten*

99231 (FLAS); El Valle, 22 Jan. 1984 (cult.), *Chase 84102* (K-spirit); El Valle de Antón, N Hills, 29 Jun. 1946, *Allen 3550* (G); El Valle de Antón, vicinity of La Mesa, 1000 m, 22 Jun. 1941, *Allen 2579* (SEL); Valle de Antón, 15 Jun. 2002 (cult.), *Blanco 2106* (USJ, USJ-spirit).

Commentary: *Lockhartia obtusata* is immediately recognizable by its elliptic to widely oblong leaves and large, yellow flowers with a crateriform callus. No other species of *Lockhartia* has similar leaves, and the other three species with a crateriform callus have much smaller flowers (although a few collections of *L. longifolia* have flowers that are nearly as large).

There are very few field collections of *Lockhartia obtusata*; it is probably a rare species.

***Lockhartia oerstedii* Rchb. f.**

22. *Lockhartia oerstedii* Rchb. f., Bot. Zeit. 10: 767-768. 29 October 1852, *nom. cons. prop.* (Taxon 59: 1895. 2010). TYPE: COSTA RICA. [Heredia], Barva, 7000 ft [2133 m], 7 Mai 1846 [5/47 in K], A.S. *Oersted s.n.* [7056 in C] (holotype: W-Reich.-Orch.-44337; isotypes: C, G, K-Lindl.-79002 [excluding *Fendler 1432*; photo: AMES-23432]); possible isotype: W-Reich.-Orch.-44338; drawing of type: W-Reich.-Orch.-44336 [copy of drawing: AMES-24875; photo: AMES-23432]).

Oncidium mirabile Rchb. f., Bot. Zeit. 10: 697. 1 October 1852. *Lockhartia mirabilis* (Rchb. f.) Rchb. f., Xenia Orchid. 1: 100, 106. 1855, *nom. rej. prop.* (Taxon 59: 1895. 2010). TYPE: PANAMA. Chiriqui, *Warszewicz s.n.* (holotype: W-Reich.-Orch.-44335; drawing of holotype: AMES-24874).

Lockhartia lamellosa Rchb. f., Hamburger Garten- Blumenzeitung 21: 300. 1865. TYPE: MEXICO. [probably Chiapas], *Ex Hort. Consul Schiller, Schmidt s.n.* (lectotype,

designated by Soto Arenas, *Icon. Orchid.* 10: xvii-xviii. 2008, to be corrected: W-Reich.-Orch.-44332 [erroneously cited by Soto Arenas as "W-44232"], colored illustration annotated "2/7 64", excluding the two pencil illustrations; photo: AMES-24873).

Lockhartia odontochila Kraenzl., *Pflanzenr.* (Engler) 4, Fam. 50 (Heft 83): 17. 1923. TYPE: COSTA RICA. *Endrés s.n.* (holotype: W-Reich.-Orch.-58236; drawing of holotype: AMES-41424).

Stems erect (rarely descending), more or less rigid, 7–47 cm long when reproductive, with 18–54 leaves; shoots (stem and leaves) 8–13 mm wide, often becoming markedly narrower distally. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, with straight to slightly incurving margins, obtuse to acute apically, exposed part of largest leaves 13–33 × 3–8 mm. Inflorescences both terminal and axillary from the distal half of the stem, up to 9 per stem (produced sequentially, or rarely simultaneously), with 1–7 flowers produced more or less sequentially; exerted portion 5–20 mm long, internodes 2–5 mm long; inflorescence bracts amplexicaul, subtriangular to ovate, cordate, acute to apiculate, frequently sigmoid or recurved in side view, conduplicate to expanded, held more or less perpendicular or oblique with respect to the rachis, rarely imbricate, 4–6.5 × 2.5–5.5 mm; pedicel and ovary 10–14 mm long. Flowers resupinate, widely open, 14–24 mm tall, yellow, the labellum and column heavily spotted with reddish brown; the lateral lobes with oblique-longitudinal brown stripes or dots forming lines; the anther cap white to yellow. Sepals ovate to elliptic, slightly concave, obtuse, 5.5–9 × 5–6 mm. Petals oval to suboblong, curved toward the front, margins reflexed, apically obtuse to subtruncate, 7–9 × 5–6 mm when flattened. Labellum 3-lobate, 9–16 mm long (from the base to the

distal margin, excluding the lateral lobes which curve toward the base when flattened), 14–16 mm wide across lateral lobes when flattened; lateral lobes elongate, oblong to obovate, obtuse to round apically, curved toward front, 7–10 × 2.5–6 mm; midlobe divided in 4 lobules, pandurate, emarginate, wider across the distal lobules when flattened, margin irregularly undulate, 11–14 × 12–15 mm, the basal lobules folded backwards, the distal lobules flared obliquely downward; callus obovate; basal part forming a concave cushion with a basal tuft of short, glandular hairs, 1.5–2 × 1.5–2 mm; the distal portion forming a spatulate mass of low tubercles, 4–5 × 3–5 mm, wider distally. Column winged, dolabriform, 2.5–3 mm long, 3–4 mm wide; wings suboblique, subquadrate ovate, 1.5 × 1–1.5 mm, with an entire to denticulate margin; stigmatic cavity oblong to subpandurate, 1 × 0.5 mm; anther cap galeate, 1–1.2 mm long; pollinarium 1 mm tall, stipe bifid. Fruit obovoid, glaucous, 9–15 × 5–6 mm.

Nomenclatural notes: Reichenbach published *Oncidium mirabile* one month before he published *Lockhartia oerstedii*. He eventually transferred *O. mirabile* to *Lockhartia*. The name *L. mirabilis* has heretofore remained in relative obscurity, probably because its type consists of a single, partially dissected flower, while the name *L. oerstedii* has been widely applied to this species. A proposal for conservation of the name *L. oerstedii* against *O. mirabile* has been presented (Blanco and Williams, 2010).

In the protologue of *L. oerstedii*, Reichenbach indicated the locality for Oersted's collection simply as "Barba [sic.] in Costa Rica", but later (Reichenbach, 1864) he provided more data on the type collection ("Auf dem Vulcan Barba in Costa Rica bei 7000' Seehöhe am 7. Mai von Herrn Dr. Oersted gesammelt"). All four duplicates also indicate the elevation as 7000' (feet). The specimen label at W has the date "7 Mai

1846”, while the one at K says “5/47”. It is likely that both are true duplicates and the year in one of these is erroneous. The specimen at C does not indicate the date, but has the number 7056 (absent in the other specimens).

The name *Lockhartia lamellosa* is based on a cultivated plant of Mexican origin. A sheet with three drawings in W seems to be the only material that is congruent with the protologue; one of those drawings was designated as lectotype by Soto Arenas (2008), but he cited the wrong herbarium accession number. The correct accession number is indicated above.

Mora and Atwood (1992a) and Atwood & Mora-Retana (1999) listed Stange (one of the gardeners of the consul Schiller) as the collector of the type specimen of *L. lamellosa*. However, Reichenbach only cited Schiller and his chief gardener Schmidt in the protologue. The actual person that sent the plant from Mexico is unknown.

The drawing at AMES of the type specimen of *Lockhartia odontochila* (probably prepared in the 1920’s or 1930’s) clearly shows a flower near the tip of the tallest stem, but that flower is now missing from the type specimen in Vienna. The drawing does not show the critical structure of the labellum, but the vegetative morphology and the description in the protologue clearly indicate that it is the same as *L. oerstedii*.

The provisional name “*Lockhartia tzelta*” was used by Soto Arenas for at least some of the populations considered here to belong in *L. oerstedii*.

Phenology: Flowering plants have been collected throughout the year, but much more abundantly during the months of May, June, and July (the beginning of the rainy season throughout most of the species’ range).

Distribution: Southern Mexico (Chiapas state) to western Panama (Chiriquí province), from 600 to 2200 m, on both sides of the continental divide (Figure 7). No collections are known from El Salvador, and only one collection is known from Nicaragua. It is apparently rare in Guatemala and Honduras, but it is very common in Costa Rica and western Panama.

Additional specimens examined: COSTA RICA. Without locality: *anonymous s.n.* (VEN); 4 Aug. 2002 (cult.), *Blanco 2283* (USJ); 26 Jul. 2003 (cult.), *Blanco & Whitten 2462* (JBL-spirit); 11 Jun. 2007 (cult.), *Bogarín 3937* (JBL-spirit); 1 Sep. 1932, *Kupper 32* (M); 28 Aug. 1922, *Lankester s.n.* (AMES); 18 Dec. 2000 (cult.), *Pupulin 2741* (JBL-spirit); 19 Jun. 2001 (cult.), *Pupulin 2813* (USJ); 21 May 2002 (cult.), *Pupulin 3854* (USJ); 2 Jun. 2002 (cult.), *Ruiz 8* (USJ); 10 Nov. 2005 (cult.), *Schug 246* (JBL-spirit); 8 Jun. 1896 (cult.), *Tonduz s.n.* (G); 29 Aug. 1932, *Valerio 145* (CR, F). Alajuela: Alfaro Ruiz, Guadalupe de Zarcero, 1650 m, 30 May 1938, *Smith 688* (AMES, F, K, NY); Reserva de San Ramón, 1000 m, Aug. 1989, *Retana s.n.* (USJ); San Ramón, Reserva Biológica Alberto Brenes, 900 m, 1 Jun. 2000 (cult.), *Blanco 1520* (USJ); San Ramón, San Pedro, 3 Jun. 1987, *Núñez Rivas 8* (USJ); Valverde Vega, Bajos del Toro, Hacienda Río Toro, Reserva Biológica Privada Bosque de Paz, 1500 m, 19 Sep. 2008 (cult.), *Karremans & Muñoz 1965* (JBL-spirit); Valverde Vega, cuenca del Río Toro, Reserva Biológica Bosque de Paz, Jardín de Orquídeas Dr. Stephen H. Kirby, 1450 m, 1 Sep. 2004, *Muñoz 04-102* (USJ). Cartago: without specific locality, 1265 m, 1888, *Cooper 5967* (BR); 8 Jun. 1933, *Valerio 192* (CR, F); Agua Caliente del Llano, 1300 m, 11 May 1906, *Brenes s.n.* (NY); Bord du Río Reventado, 23 Jun. 1906, *Brenes s.n.* (NY); Cartago, 8 Jun. 1933, *Brenes s.n.* (NY); Copalchí [Colpachí], Candelaria, 1854,

Nov., *Endres 302* (W-Reich); Oreamuno, Cipreses, 1850 m, 1 Jun. 2000 (cult.), *Pupulin 798* (USJ), 23 Jun. 1988, *Pupulin et al. 834* (USJ); Orosi, Jul. 1924, *Alfaro s.n.* (AMES, US), 20 Jun. 1924, *Alfaro s.n.* (AMES, US); Pacayas, 26 Jun. 1987, *Ruiz Boyer 18* (USJ); Tierra Blanca, 2200 m, 22 May 1932, *Kupper 1414* (M); Tres Ríos, Pizote, Los Lotes, 24 Jun. 1967, *Rodríguez 1068* (USJ); Tres Rios, San Ramón, El Pizote, 1770 m, 19 Jun. 1984, *Gómez & Herrera 23035* (CR, DUKE, F, MEXU, MICH, MO, NY, WIS); Tres Ríos, Tiribí, Estación del ICE, 4 Jun. 1987, *Vargas 24* (USJ); Turrialba, 11 Jun. 2006 (cult.), *Pupulin 3605* (JBL-spirit); Vicinity of Cartago, 1425 m, Feb. 1924, *Standley 39282* (AMES, US). Heredia: Barba [Barva], 1100 m, 20 Jul. 1941, *León 851* (CR, 2 sheets); Barva, camino hacia Calle Higuierón, a orilla del Río Macarrón, 1800 m, 25 Jan. 2004 (cult.), *Bogarín & Prendas 676* (JBL-spirit); Barva, Lajas del Roble, Mar. 1993, *Cruz s.n.* (USJ); El Roble, 1500 m, 10 May 1938, *Valerio 2595* (AMES); Fuentes de Pérez, San José de la Montaña, 1475 m, 12 Apr. 1957, *Jiménez 7* (CR); Rancho Flores [slopes of Volcán Barva], 22 Feb. 1890, *Pittier I.P.G.C.R. 2342* (BR); San Rafael, camino a Las Chorreras, orilla del Río Segundo, 1600 m, 14 Jan. 2003 (cult.), *Bogarín 44* (JBL-spirit); Sarapiquí, 1000 m, Aug. 1989, *Retana s.n.* (USJ); Upper Río Porros above San José de la Montaña, 1700 m, 4 Dec. 1959 (cult.), *Horich sub Blydenstein s.n.* (UC), 23 Sep. 1960 (cult.), *Horich sub Hutchinson s.n.* (MO), 5 Oct. 1963 (cult.), *Horich sub Hutt s.n.* (AMES), 24 Jun. 1964 (cult.), *Horich sub. Hutt s.n.* (US); Vara Blanca, 7 Jun. 1987, *Sánchez 8* (USJ). Puntarenas: without specific locality, 1500 m, 1 Mar. 1984, *Chase 84327* (K-spirit); Buenos Aires, Cuenca Térraba-Sierpe, Estación Tres Colinas, Finca Víctor Arias, 1680 m, 12 Sep. 1996, *Alfaro 824* (INB, MO); Buenos Aires, Cuenca Térraba-Sierpe, Potrero Grande, Tres Colinas, bajando hacia

Helechales, 1700 m, 25 Apr. 2006, *Rodríguez et al. 10137* (INB); Buenos Aires, R.I. Ujarras, Cordillera de Talamanca, Ujarras, margen izquierda de Quebrada Dorora, camino a Río Lori, 1520 m, 11 Mar. 1993, *Herrera 5863* (CR, INB, MO); Coto Brus, Cuenca Térraba-Sierpe, Zona Protectora Las Tablas, sobre Fila Palmital, 1440 m, 24 May 1999, *Alfaro 2304* (INB); Coto Brus, Z.P. Las Tablas, Cordillera de Talamanca, Límite Zona Protectora Las Tablas, Cerro Quijada del Diablo, 2100 m, 22 Mar. 1996, *Navarro 280* (INB, MO); [Monteverde], on farms of Joe Stucky and Marvin Rockwell, 1370 m, 5 Jul. 1989, *Atwood 89278* (AMES, SEL [2 sheets]); Monteverde Cloud Forest Reserve and community, Cordillera de Tilarán, 1400 m, 30 Jul. 1981, *Neill 5068* (BM, CR, MO); Monteverde, in community near cliff edge, 1350 m, 15 Jun. 1989, *Atwood 89184* (SEL); Parque Nacional Amistad, Las Tablas, near the upper Río Cotón, 1400 m, 14 Jul. 1982, *Todzia 1922* (CR). San José: Acosta, Cerro el Dragón, 1800 m, 2 Nov. 2005 (cult.), *Valverde 600* (JBL-spirit), 1600 m, 2 Nov. 2005 (cult.), *Chinchilla sub Valverde 636* (JBL-spirit); Aserrí, Z.P. Caraigres, cuenca del Pirrís-Damas, Aserrí, Parrita, Quebrada Concha, 1550 m, 6 Dec. 2002, *Morales et al. 8848* (INB); Cañon, 1300 m, 1 May 1932, *Kupper 1088* (M); Parque Bolívar, 28 Apr. 1935 (cult.?), *Valerio 1011* (F); Pérez Zeledón, Herradura, 1000 m, Aug. 1989, *Retana s.n.* (USJ); Pérez Zeledón, San Isidro, cerca Río General, 1000 m, Aug. 1989, *Retana s.n.* (USJ); Santa María, 15 May 1928, *Stork 2100* (AMES, MO), 25 May 1928, *Chacón sub Stork 2324* (AMES, MO), 1524 m, 15 Apr. 1928, *Danielson sub Stork 1495* (AMES [2 sheets], MO); Santa María [de Dota], May, *Endres 543* (W-Reich); Vicinity of Santa María de Dota, 1500 m, 14 Dec. 1925, *Standley 41610* (AMES), *Standley 42822* (AMES).

GUATEMALA. Without locality: Jun., *Hamer s.n.* (F, MO). Alta Verapaz: Cobán, 1219

m, 5 Sep. 1920, *Johnson 727* (AMES, US); Rd. Chama-Cobán, 914 m, 1 Aug. 1920, *Johnson 556* (AMES); San Cristóbal, Sep. 1870, *Bernoulli & Cario 566* (RENZ, 2 sheets); San Cristóbal A.V., carretera a Baleu, 1000 m, 28 Jul. 1994, *Véliz et al. 943886* (MEXU). Huehuetenango: Between Las Palmas and Chacula, Sierra de los Chucumatanes, 1400 m, 1 Sep. 1942, *Steyermark 51744* (AMES, F). HONDURAS. Comayagua: Jicarito, 610 m, 23 Jul. 1933, *Edwards 469* (AMES, 2 sheets); Siguatepeque, Cicirinteca, 1219 m, 24 Sep. 1932, *Edwards 256* (AMES). Olancho: (El Guamil), Agalta National Park, 19 km NNW of Catacamas, 1300 m, 4 Jun. 1992, *Hawkins et al. 479* (EAP, MO). MEXICO. Chiapas: without specific locality, 700 m, 10 Jul. 1991, *Cribb s.n.* (K-spirit); Comitán, Los Lagos, 35 mi SE of Comitán, road San José to Montebello, 15 Apr. 1949, *Carlson 1798* (F); E of Comitán, 1400 m, *Nagel & Monzón 6991* (F); La Trinitaria, 13 km al E de Tziscaco, camino a Pacayal, 5 km al E de Colonia Cuauhtemoc, 1000 m, 9 Aug. 1985, *Chehaibar et al. 206* (MEXU); Ocosingo, *Schmeling 6250* (F); Ocosingo, a 2 km al N de Naja, camino a Palenque, 840 m, 23 Sep. 1988, *Martínez & Stevens 23964* (MEXU); Ocosingo, comunidad Lacandona de Naha, 27 km al SE de Palenque, por la carretera fronteriza hasta el cruce Chancala, después 55.6 km por el camino de terracería hacia Monte Líbano, 950 m, 26 Dec. 1993, *Durán & Levy 10* (MEXU); Ocosingo, Laguna Ocotál Grande, 800 m, 6 Feb. 1973, *Breedlove 33022* (DS); Ocosingo, Laguna Ocotálito a 12 km al N de Monte Líbano camino a Chancala, 980 m, 2 Feb. 1986, *Martínez 17162* (MEXU, MO); Ocosingo, limestone area near Laguna Ocotál Grande, ca. 25-30 km SE of Monte (Cerro) Líbano (which is ca. 45 km E of Ocosingo), 950 m, 20 Jul. 1954, *Dressler 1482* (AMES, MEXU, MICH, US). NICARAGUA. Without locality: *Heller s.n.* (SEL; possibly

the same as *Heller 1796* or *10804*, known only by drawings at SEL, reportedly from Nueva Segovia: N of Jalapa, 690 m). PANAMA. Without locality: 18 Apr. 2004 (cult.), *Blanco 2563* (FLAS-spirit); 23 Dec. 2009 (cult.), *Blanco 2565* (FLAS); *Powell s.n.* (AMES); Jun. 1936, *Purdom s.n.* (AMES); 18 Jul. 1997 (cult.), *Whitten 99234* (FLAS). Chiriquí: without specific locality, 914 m, 17 Mar. 1919 (cult.), *Powell 75* (K, MO); 1219 m, May 1923 (cult.), *Powell 3352* (AMES); Apr. 1858, *Wagner s.n.* (M); 16 km above town at Volcán, along N side of savanna, 1798 m, 13 Feb. 1978, *Hammel 1575* (MO); 2 mi N of El Hato del Volcán, 30 May 1970, *Croat 10648* (CAS, MO); 3 mi N of el Volcán, 1524 m, 28 Jun. 1969, *Tyson 5853* (MO, 2 sheets); Along road to Cerro Azul, ca 2 km above Escuela Jaramillo Arriba #3 E of Boquete, 1450 m, 11 Aug. 1974, *Croat 26741* (MO, SEL); Along stream near FSU Field camp at Cerro Punta, 25 Apr. 1969, *Lazor 2821* (MO); Along upper end of the Horquete road above Boquete, 1524 m, 17 May 1971, *Proctor 31959* (LL); Behind the Florida State University cabin, 2.2 mi below Cerro Punta on the W side of Volcán Chiriquí, 1830 m, 22 Jun. 1970, *Luteyn 873* (DUKE); Boquete, Bajo Mono, 1372 m, 19 Apr. 1938, *Davidson 584* (AMES, BM, F, US); Boquete, slopes below Cerro Horqueta, along Quebrada Horqueta, 1600 m, 22 Jun. 1971, *Webster 16714* (DAV); El Boquete, 1300 m, 1912, *Maxon 5096* (F), 1000 m, 2 Mar. 1911, *Maxon 5097* (F); Guadalupe, 2000 m, 15 Mar. 1985, *Hampshire & Whitefoord 622* (BM); Hill E of Audubon Cabin, S of Cerro Punta, 1400 m, 12 Jul. 1983, *Hamilton & Krager 3866* (MO); Llano del Volcán, 1500 m, 27 May 1946, *Allen 3502* (AMES, BM, G); Llano E of El Hato del Volcán, 2012 m, 5 Apr. 1979, *Hammel et al. 6778* (MO); Near Costa Rican border, 13 km by road S of Río Sereno, Finca Hartmann, 1400 m, 12 May 1991, *Henshold & McPherson 1014* (F, K, MA, MO, NY); Ridges south

of Finca Lérica, 1828 m, 26 Jul. 1947, *Allen 4764* (G, P); Slopes above Los Llanos, above Volcán, 2000 m, 4 Jun. 1986, *McPherson 9316* (MO); Slopes on Cerro Horqueta, 1650 m, 13 Aug. 1974, *Croat 29942* (MO); Valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, 1300 m, 27 Jun. 1935, *Seibert 132* (MO), *Seibert 133* (BM), *Seibert 186* (AMES, K [2 sheets], MO, NY, WIS); Vcty. Boquete, lumber road into the hills E of the Río Caldera, 1372 m, 23 Jul. 1947, *Allen 4666* (G); Vcty. Finca Lérica, upper S slopes of the Quebrada Velo, 1524 m, 25 Jul. 1947, *Allen 4743* (F, G, U); Vicinity of Boquete, Finca Collins, 1676 m, 24 Jul. 1959, *Stern et al. 1125* (MO, 2 sheets); Vicinity of Casita Alta, Volcán Chiriquí, 1500 m, 28 Jun. 1938, *Woodson et al. 966* (AMES, BM, US); Vicinity of Cerro Punta, 2000 m, 24 May 1946, *Allen 3493* (BM); Vicinity of Finca Lérica, 1750 m, 7 Jul. 1940, *Woodson & Schery 236* (AMES, MO); W-facing slope, E of Río Macho de Monte, ca. 6 km NE of El Hato del Volcán, 1700 m, 9 Feb. 1986, *Grayum 6480* (MO, SEL). CULTIVATED [without original locality data]: *anonymous s.n.* (K-spirit, 5 jars); *anonymous s.n.* (W-Reich, 2 sheets); 2 Jul. 1909 (cult.), *Beauvard 6930* (G); 3 May 2004 (cult.), *Blanco 2566* (FLAS, 2 sheets); 4 May 1977 (cult.), *Marshall s.n.* (SEL); 1886 (cult.), *O'Brien s.n.* (BM); 19 Oct. 1979 (cult.), *White s.n.* (SEL).

Commentary: *Lockhartia oerstedii* is very similar to *L. galeottiana* and *L. verrucosa*, but it differs from them in its generally narrower shoots, narrower labellum isthmus, more pronounced callus tubercles, and more southern distribution. *Lockhartia oerstedii* and *L. verrucosa* are sympatric in parts of Guatemala and Chiapas and both species experience their peak flowering during the same months (May to July); however, I have not seen any intermediate specimens that suggest hybridization.

Many collections of *Lockhartia oerstedii* have tall shoots that become progressively narrower distally, and leaves that are very appressed against the stem (i.e., diverging at a narrow angle from it). The leaves also tend to be darker green (both in life and in the herbarium) than other sympatric species of *Lockhartia*.

Lockhartia oerstedii is one of the most common species in the genus in southern Central America, although it seemingly becomes less abundant farther north, judging from the fewer collections.

***Lockhartia oxyphylla* M. A. Blanco**

23. *Lockhartia oxyphylla* M. A. Blanco, *sp. nov.* TYPE: ECUADOR. Esmeraldas: Quininde, Fundación Paraíso de Papagayos, Centro de Rescate de Aves y Mamíferos, km 2 via Esmeraldas, 6 Jul. 1996, J.L. Clark, N. Binder & W. Naranjo 2796 (holotype: QCNE; isotypes: MO, SEL).

Lockhartia micrantha Rchb.f. affinis, sed foliis longioribus acutis, inflorescentiis succedaneis, floribus grandioribus et succedaneis, et callo verrucoso.

Stems erect, horizontal or descending, more or less rigid, 15–41 cm long when reproductive, with 29–74 leaves; shoots (stem and leaves) 8–14 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, with straight to slightly incurving (rarely slightly outcurving) margins, acute (rarely obtuse or rounded), exposed part of largest leaves 11–26 × 3–5 mm. Inflorescences both terminal and axillary from from the distal three fourths of the stem (produced sequentially), with 1–3 flowers produced sequentially; exerted portion 0.5–1.8 cm long, internodes 1–5 mm long; inflorescence bracts amplexicaul, narrowly lanceolate to widely ovate, subcordate, acute to acuminate, apiculate, 4–8 × 2–6 mm; pedicel and ovary 6–10 mm long.

Flowers resupinate, widely open, 11–13 mm tall, yellow with orange-brown spots on most of the labellum (except on the distal midlobe lobules). Sepals elliptic, slightly concave, acute to apiculate (apex navicular), 5 × 2.5 mm. Petals suboblong to narrowly obovate, obtuse to round, 5 × 2 mm. Labellum 3-lobate, 6–7 mm long, 10 mm wide across lateral lobes when flattened; lateral lobes elongate, suboblong to attenuate, acute, curved toward front of flower, 3.5–4 × 1–0.8 mm; midlobe 4-lobulate, pandurate, wider across the basal lobules, 4.5–5 × 6–7 mm; callus suboblong; the basal part a concave cushion, subquadrate, 1 × 1.5 mm, with a small tuft of glandular trichomes; the distal part formed by a mass of low (1 mm tall) tubercles, 3 × 1.5 mm. Column narrowly winged, widely oval, 2.5–3 mm long (without the anther cap), 2.3 mm wide; wings decurrent, hemispherical, 0.5 × 1 mm, with an entire margin; stigmatic cavity oval, 1 × 0.7 mm; anther cap not seen, pollinarium not seen. Fruit globular to obovoid, 7–9 × 5 mm.

Phenology: Flowering plants have been collected from May to November.

Distribution: Northwestern Ecuador (provinces of Esmeraldas, Imbabura, and Pichincha), on the Pacific slope of the Andes, from 100 to 1550 m (Figure 12). Expected in the adjacent department of Nariño in Colombia.

Additional specimens examined: ECUADOR. Without locality: *Sodiro s.n.* (QPLS, 2 sheets); 29 Sep. 2003 (cult.), *Whitten et al.* 2382 (FLAS), *Whitten et al.* 2441 (FLAS). Esmeraldas: Bocana de Ene, 50 m, 22 Apr. 2003, *Cornejo & Bonifaz* 7701 (QCNE); Km 12 on road under construction from Lita to Alto Tambo (21 kms), 725 m, 20 May 1987, *Dodson et al.* 17138 (MO, QCNE); Km 8 Lita-Altotambo, 740 m, 19 Jul. 1988, *Dodson & Gentry* 17512 (MO, QCNE); Quinde, Bilsa Biological Station,

Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabel, 400 m, 5 May 1995, *Clark & Watt 804* (QCNE); Quininde, The Mache-Chindul Ecological Reserve, Bilsa Biological Station, 35 km W of Quinindé, 5 km W of Santa Isabel, 500 m, 17 Nov. 1996, *Clark 3660* (SEL). Imbabura: Below García Moreno, lower Intag Valley, 1219 m, 19 Sep. 1944, *Drew E-674* (AMES); Between Lita and Alto Tambo, *Blanco 2488* (SEL-spirit); La Unión, lower Intag Valley, 1311 m, 20 Sep. 1944, *Drew E-690* (AMES). Pichincha: Nanegal, 1854, *Jamieson s.n.* (K-Lindl); Parroquia Nanegal, Loma Cachillacta, 6-6.5 km airline SE of Nanegal, 1540 m, 7 Sep. 1993, *Webster et al. 30408* (QCNE), 1550 m, *Webster et al. 30428* (DAV, QCNE); Valle Nanegal, 8 Aug. 1874, *Sodirol s.n.* (QPLS).

Commentary: *Lockhartia oxyphylla* has been known by the name *L. chocoensis* (Dodson, 2004), the latter treated here as a synonym of *L. micrantha* (see comments for that species). *Lockhartia oxyphylla* differs from *L. micrantha* in its more elongate, acute leaves, stems with few, sequentially produced inflorescences, much larger flowers produced sequentially on each inflorescence, and a verrucose-tuberculate callus. In addition, the shoots of *L. oxyphylla* tend to be relatively longer and narrower than those of *L. micrantha*. The two species do not appear to be sympatric.

***Lockhartia parthenocomos* (Rchb. f.) Rchb. f.**

24. *Lockhartia parthenocomos* (Rchb. f.) Rchb. f., Bot. Zeit. 10: 767. 29 Oct 1852. : *Fernandezia parthenocomos* Rchb. f., Bot. Zeit. 10: 639. 10 Sep 1852. SYNTYPES: [VENEZUELA]. Caracas, *Ex. Hort., Keferstein s.n.* (not found); and [VENEZUELA]. Caracas, *Ex. Hort., Leipzig, 52* [1852], *Wagner 102 sub Keil s.n.* (lectotype, here designated: W-Reich.-Orch.-44365; possible iso-lectotype: K-Lindl.-79003, excluding *Fendler 2443*).

Lockhartia parthenocomos var. *purpurata* Rchb. f., *Bonplandia* (Hanover) 3: 215, 1855. TYPE: VENEZUELA. [Caracas], imported by Senator [Martin Johann] Jenisch, cultivated by Mr. Kramer and by Mr. Geitner, *Ex Hort.* Erdbranden near Planitz [Zwickau, Saxony, Germany] (holotype: W-Reich.-Orch.-44355; possible isotype: W-Reich.-Orch.-44356).

Stems pendent, more or less flexible, 17–50 cm long when reproductive, with 22–48 leaves; shoots (stem and leaves) 13–22 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, with straight to slightly incurving margins, obliquely acute, exposed part of largest leaves 20–37 × 4.5–7 mm. Inflorescences both terminal and axillary from the distal one third of the stem (produced sequentially), with 1–3 flowers produced sequentially; exerted portion 0.5–1.5 cm long, internodes 1–3 mm long; inflorescence bracts amplexicaul, ovate to lanceolate, acute to acuminate, conduplicate to campanulate, 5–7 × 2–5 mm; pedicel and ovary 9–11 mm long. Flowers apparently non-resupinate, campanulate, 10–15 mm across, cream to yellow, the labellum often brownish and the callus and column occasionally with purplish spots. Sepals ovate to elliptic, concave, acute to obtuse, 8–10 × 4–5 mm. Petals obovate, apically obtuse or rounded, 7–12 × 5–9 mm. Labellum suborbicular to subreniform, obscurely 3-lobate, 8–11 mm long, 13–15 mm wide when flattened; side lobes wider than long, transversely oval, curving around the column, 3–4 × 7–8 mm; midlobe wider than long, transversely suboval to reniform, retuse, margin gently undulate, 4–5 × 8–10 mm; callus rectangular, smooth, puberulous, occupying the entire central portion of the labellum, forming an irregularly toothed ledge at the base of the midlobe, 4–5 × 6–8 mm. Column narrowly winged, subrhombic, 2.5 × 3 mm (excluding

anther cap), the wings obliquely lanceolate and pointed forward, 1 × 2 mm; anther cap galeate, 1.2 × 0.8 mm; pollinarium 1 mm tall, stipe bifid from the base. Fruit subglobose to obovoid, 12–16 × 8–10 mm.

Nomenclatural notes: In the protologue of *L. parthenocomos*, Reichenbach mentioned two plants flowered in cultivation, and thus both should be considered syntypes. Reichenbach did not specify the original field collector nor the country of origin in the protologue, but later revealed that the plant had been collected by “Wagener” (probably Hermann Wagener, 1823-1877) in Caracas, Venezuela (Reichenbach, 1855). Only one of the syntypes has been found, and it will be formally designated as the lectotype.

The specimen at K-Lindl. cited here as a possible isotype is annotated as “*Lockhartia parthenocomos* Rchb. f.” in H.G. Reichenbach's handwriting, but has no further data. It might be a type fragment given to Lindley by Reichenbach. It is mounted on the same sheet as *Fendler 2443*, also *L. parthenocomos*.

Lockhartia parthenocomos var. *purpurata* is here considered to be a mere color variation of *L. parthenocomos*. The flowers in the type specimen have no noticeable distal teeth on the callus (thus resembling the very similar *L. latilabris* from the Guiana Shield), although that could be an artifact of the drying process. In the protologue, Reichenbach did not indicate from where in Venezuela the plant originated; however he later stated that the plant also came from Caracas (Reichenbach, 1855).

No type material for *Lockhartia parthenocomos* var. *crispula* has been located, and the meager original description is insufficient for confirming the identity of this taxon (Poorly Known Taxa, below).

Phenology: The few flowering field collections available have been made in March, June, October, November, and December. Flowers are probably produced sporadically throughout the year.

Distribution: Endemic to Venezuela, in the states of Aragua, Carabobo, and Miranda, from 750 to 1600 m in the Venezuelan Coastal Range (Figure 10). The locality of the two syntypes was cited as “Caracas”, although probably this was just the shipping port for the plants.

Additional specimens examined: VENEZUELA. Aragua: without specific locality, 1000 m, 12 Dec. 1953, *Renz 8137* (RENZ, 2 sheets); Hacia la cumbre de Rancho Grande, Parque Henri Pittier, 29 Oct. 1980, *anonymous s.n.* (VEN); Parque Nacional Pittier, on steep slopes facing N (seaward) between summit of pass and Choroni, 1200 m, 3 Nov. 1962, *Steyermark 55398* (VEN); Parque Nacional Pittier, slope facing N (seaward) between summit of pass and Choroni, 1200 m, 3 Nov. 1962, *Steyermark 90994* (AMES); Prope Coloniam Tovar, 1856, *Fendler 2443* (K, K-Lindl). Carabobo: Above Hacienda Cura, between Valencia and Maracay, 1600 m, 8 Jan. 1939, *Alston 6195* (BM); Bejuma, al O de la carretera Bejuma-Canoabo, entre la Cumbre Paraguito y Cerro El Marquero, 1000 m, 27 Jun. 1999, *Meier & Kunert 5000* (VEN), *Meier & Kunert 5004* (VEN); Laderas arriba de las cabeceras del Río San Gián, arriba de Los Tanques y La Toma, entre Quebrada No. 2 y Quebrada de Los Verros, al S de Borburata, 750 m, 29 Mar. 1966, *Steyermark 95293* (VEN). Miranda: Without specific locality, *anonymous 1552* (W-Reich); Los Guayabitos, *Dunsterville 245* (K).

Commentary: *Lockhartia parthenocomos* is diagnosed by the pendulous habit, the large, campanulate, yellow flowers with a concave labellum, and the transversely

oriented callus with an irregularly toothed distal ledge. It is most similar to *L. latilabris*, which lacks a callus ledge. It has also been confused with both *L. longifolia* and *L. rugosifolia*; see comments under those species for distinguishing characters.

Lockhartia parthenocomos is the only member of the genus present in the Venezuelan Coastal Range west of Caracas.

***Lockhartia parthenoglossa* Rchb. f.**

25. *Lockhartia parthenoglossa* Rchb. f., Hamburger Garten- Blumenzeitung 21: 300. 1865. TYPE: Without original locality data, *Ex Hort.* Consul Schiller [near Hamburg, Germany], 9 April 58 [1858], *Stange s.n.* (holotype: W-Reich.-Orch.-44352).

Lockhartia pittieri Schltr., Repert. Spec. Nov. Regni Veg. 12: 216. 1913. TYPE: PANAMA. Colón: Bohio ["Bohis" in protologue], *Ex Hort.* Mrs. Rosseau in Culebra, April 1911, *H. Pittier 3401* (mixed collection; lectotype, here designated: plant on right side of sheet, excluding plant of left side, US; isotype: B [destroyed]; drawing of holotype: AMES).

Lockhartia variabilis Ames & C. Schweinf., Schedul. Orchid. 8: 81-82. 1925. TYPE: PANAMA. [Colón]: Wooded hills near Frijoles, 0 m, *Ex Hort.* Powell's Horticultural Garden, Jan-Feb 1924, *C.W. Powell 355* (Lectotype, here designated: AMES-28131; isolectotype: AMES-spirit, not seen).

Stems ascending to pendent, more or less flexible, 5–45 cm long when reproductive, with 12–50 leaves; shoots (stem and leaves) 21–40 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular and subfalcate in side view, with outcurving (rarely straight) margins, acute (the apex occasionally minutely round), rugulose-foveolate; exposed part of largest leaves 19–40 × 3–6 mm. Inflorescences

both terminal and axillary from the distal half of the stem, up to 10 per stem (produced simultaneously or sequentially), with 1–5 flowers produced sequentially; exerted portion 0.5–1 cm long; internodes 0.5–3 mm long; inflorescence bracts amplexicaul, conduplicate to flat, narrowly lanceolate, acute to acuminate, held obliquely from the rachis, 1.5–3 × 1–2 mm; pedicel and ovary 7–9 mm long. Flowers resupinate, widely open, 9–15 mm tall, pale to intense yellow, the callus orange to brown. Sepals elliptic, slightly concave, obtuse to apiculate, 3–4 × 2–3 mm. Petals obovate to elliptic (occasionally suboblong), obtuse to acute, 4–5 × 2.5–3.5 mm. Labellum suboblong to subelliptic, rarely subpandurate, emarginate, flat to slightly convex, 6–8 mm long, 4–5.5 mm wide when flattened; callus elliptic, located on the central-proximal portion of the labellum, concave, surrounded by an elevated ridge (up to 0.5 mm high), often with a single distal tooth (up to 1.5 mm tall) and a proximal trapezoid, glabrous ledge (1 mm long) pointed toward the base of the labellum, the ridge and part of the central area glandular-pubescent, 2 × 1.5 mm. Column winged, subrhombic, 2–2.5 × 2–3 mm (including wings), the wings subtriangular with an entire margin, 0.5 × 1 mm; anther cap galeate, 1.3 × 1 mm; pollinarium 0.7 mm tall, stipe bifid from the base. Fruit subglobular to obovoid, 4–9 × 3–5 mm.

Nomenclatural notes: This species has been known for many years by the name *Lockhartia pittieri*. The type specimen of *L. pittieri* at US has an annotation in pencil that says “Fragment sent to Berlin 9/19/13, [unreadable signature]”. This fragment was sent at the request of Ignatius Urban after Schlechter had examined the specimen and returned it to US; thus the specimen at US must be considered the holotype (Christenson, 1995). However, there are two stems mounted on the type sheet,

representing two different species. The sterile stem on the left is probably *L. micrantha*, and is clearly not what Schlechter described. The stem on the right side is formally designated here as the lectotype to preserve the circumscription of this species.

The flower in spirit of *Powell 355* at AMES is effectively a duplicate, and thus the dry specimen is designated as lectotype of *L. variabilis*.

Phenology: Flowering plants have been collected throughout the year.

Distribution: From Guatemala and Belize south to northwestern Colombia, from sea level to at least 700 m (Figure 11). A collection based on a cultivated plant (*Valerio s.n.*, USJ) indicates an elevation of 1350 m, which does not coincide with the known elevation of the indicated locality, and is thus probably erroneous.

The sole Ecuadorian specimen was prepared from a cultivated plant owned by an orchid grower who traveled to Panama on a frequent basis. The locality data reported by the plant owner is probably erroneous; no field collections of *L. parthenoglossa* are known from Ecuador.

Additional specimens examined: BELIZE. Toledo: without specific locality or date, *Adams K57* (K-spirit); Blue Creek, above Blue Creek village, 40 m, 19 Feb. 1979 (cult.), *Adams B12* (K, K-spirit); Ca. 40 km SW of Punta Gorda, Dolores Estate, 1 Feb. 1990, *Balick et al. 2567* (NY, SEL); In high ridge, on hill top beyond Central Camp, Edwards Road beyond Columbia, 11 Jun. 1951, *Gentle 7363* (LL); In high ridge, on hill top near Carmelita Camp, Edwards Road beyond Columbia, 1 May 1951, *Gentle 7321* (LL); Vicinity of Sapote Camp, c. 6.5 mi due W of Medina Bank, 244 m, 23 Apr. 1976, *Proctor 35940* (MO). COLOMBIA. Antioquia: Chigorodó, vereda Malagón, Caño Malagón abajo (El Cocuelo), 220 m, 11 Jan. 1986, *Rentería et al. 4573* (JAUM); Turbo,

carretera Tapón del Darién, sector Río León-lomas aisladas, 40 m, 26 Nov. 1983, *Brand & González 599* (JAUM), 29 Dec. 1983, *Brand & Escobar 806* (COL, JAUM, MO), 28 Feb. 1984, *Brand & González 954* (JAUM); Turbo, Tapón del Darién, 50 m, 16 Apr. 1985, *Rentería et al. 3812* (COL, JAUM). Chocó: Bahía Solano, 0 m, 13 Feb. 1947, *Haught 5570* (COL); Riosucio, Parque Natural Nac. Los Katyos, Río Cacarcas a Cristales, 70 m, 2 Dec. 1976, *León 656* (COL, MO); Norte de la Costa Pacífica [Serranía del Baudó], 100 m, Jul. 1988, *Misas Urreta 186* (COL, HUA, JAUM). COSTA RICA. Without locality: 18 Apr. 1967, *Hespenheide s.n.* (USJ). Alajuela: San Carlos, 1923, *Lankester 681* (AMES); San Carlos, Bijagua, Zapote, camino a Bijagua centro cerca del Río Zapote, 510 m, 15 Dec. 2005 (cult.), *Bogarín & Pupulin 2241* (JBL-spirit), *Bogarín & Pupulin 2242* (JBL-spirit); San Carlos, cerca de Ciudad Quesada, 1350 [350?] m, 7 Nov. 1993, *Valerio s.n.* (USJ-spirit), 16 Feb. 1994, *Valerio s.n.* (USJ). Guanacaste: Parque Nacional Guanacaste, Estación Pitilla, sendero El Mismo, Finca La Pasmompa, 700 m, 9 Dec. 1990, *Ríos 246* (INB). Limón: Cerro Coronel, E of Laguna Danto, 20 m, 15 Sep. 1986, *Stevens & Montiel 24610* (MO); Sixaola, hills between headwaters of Quebrada Mata de Limón and upper branches of Quebrada Tigre, and lowland forest of Quebrada Tigre drainage, Finca Anai, 25 m, 18 Nov. 1984, *Grayum et al. 4456* (MO). Puntarenas: Coto (Golfo Dulce), 0 m, 17 Feb. 1933, *Valerio 574* (F); Esquinas Forest, area between the Río Esquinas and Palmar, 30 m, 30 May 1950, *Allen 5555* (SEL); Golfito, Esquinas, La Gamba, bosque de los Austriacos, Tropenstation, 200 m, 22 Sep. 2008 (cult.), *Blanco & Serrano 2653* (JBL-spirit); Golfito, P.N. Piedras Blancas, Sendero Fila (near the Tropenstation La Gamba), 200 m, 18 Apr. 2002, *Olbrecht & Arauz Suárez 3335* (CR, WU); Osa, Rancho Quemado, sector SE,

Sierpe, 400 m, 4 Nov. 1991, *Marín 252* (INB); Osa, San Juan, 24 Sep. 2004 (cult.), *Cambronero sub Pupulin 2615* (JBL-spirit); Osa, Sierpe, Los Mogos, cabeceras de la Quebrada Taboga, 200 m, 14 Dec. 1990, *Herrera 4783* (INB); Parque Nacional Corcovado, Cerro Brujo, 600 m, 24 Jan. 1991, *Castro 256* (USJ); R.F. Golfo Dulce, Península de Osa, Aguabuena O, cerca de casa de Don Beto, 50 m, 21 Nov. 1992, *Aguilar 1497* (INB). ECUADOR. Guayas: Near Bucay, 20 Oct. 1979 (cult.), *Estrada sub Dodson et al. 9235* (SEL; locality questionable; plant probably from Panama).

GUATEMALA. Petén: Los Arcos-Cadenas road, km 142/143, E, 16 Dec. 1969, *Contreras 9369* (CAS, LL [2 sheets]). NICARAGUA. Chontales: without specific locality, *Tate 492* (K); 3 mi E of La Libertad, 670 m, *Heller 5824* (SEL). Río San Juan: El Castillo, comunidad Las Maravillas, 5 km al N, 100 m, 11 Nov. 2004, *Guzmán 1066* (MO); El Castillo, Reserva Indio-Maíz, a lo largo del caño El Pavón, a 3 km de su desembocadura en el Río Bartola, 1 Jan. 1997, *Rueda et al. 5228* (MO). Zelaya [now Región Autónoma Atlántico Norte]: Along new road to Mina Nueva América (leading more or less W from ca. 14.3 km N of El Empalme on main road to Rosita), ca. 10 km from main road, 23 Feb. 1979, *Stevens 12691* (MO). PANAMA. Without locality data: *Braga 2074* (RB); 1967, *Bristan 1508* (MO); May 1991 (cult.), *Dressler 9573* (USJ-spirit). Province unknown: Cativa-Porto Bello trail, 0 m, Jan. 1924 (cult.), *Powell 361* (AMES). Colón: 1-2 km from the Portobelo Highway up the Río Guanche, 50 m, 17 Feb. 1982, *Knapp & Schmalzel 3618* (MO); 10 mi SW of Portobelo, 2-4 mi from coast, 24 Mar. 1973, *Liesner 1098* (MO); Ft. Sherman and mouth of Chagres R trail, 0 m, Jan. 1924 (cult.), *Powell 372* (MO); Navy Reservation, N of Gamboa, upper Río Mendoza, 7 Feb. 1969, *Dressler 3605* (PMA); Near Gatún Station, P. Rail Road, 4 Feb. 1860, *Hayes*

524 (NY, 2 sheets); Santa Rita lumber road, ca. 15 km E of Colón, 20 Apr. 1971, *Dressler & Williams 3974* (PMA); Santa Rita lumber road, E of Colón, 23 Feb. 1968, *Dressler 3392* (PMA), 20 Mar. 1969, *Dressler 3621* (FLAS); Santa Rita ridge, 500 m, 17 Feb. 1986, *McPherson 8468* (MO); Santa Rita Ridge near Agua Clara rain gauge, 4 Mar. 1973, *Kennedy 2726* (MO); Santa Rita Ridge Rd., 20-22 km from Transmithica Hwy., 305 m, 25 Sep. 1980, *Sytsma 1345* (MO), *Sytsma 1363* (MO); Santa Rita Ridge, ca. 7 mi from Transisthmian Highway, 198 m, 21 Dec. 1981, *Wilbur et al. 15070* (DUKE); Trail from end of Santa Rita Ridge Road to Río Piedras, 600 m, 16 Feb. 1980, *Antonio 3776* (MO). Darién: 10 km NE of Jaque, headwaters of Río Pavarandó, 427 m, 31 Jan. 1981, *Sytsma & D'Arcy 3370* (MO); 10 km NE of Jaque, ridge and steep slopes at headwaters of Río Pavarandó, 427 m, 30 Jan. 1981, *Sytsma & D'Arcy 3342* (MO); Darien, 2-3 mi SE of Pijibasal on Río Paraseneco, ca. 9-10 mi S of El Real, 18 Dec. 1980, *Hartman 12073* (MO, PMA); Hills SE of Río Chico, ca. 10 km upstream from Nazareht, 300 m, 20 Dec. 1980, *Hahn 138* (MO); Marragantí and vicinity, 3 m, 3 Apr. 1908, *Williams 1008* (AMES, NY). Panamá [including Canal Zone]: Barro Colorado Island, 4 Dec. 1980 (cult.), *Ackerman s.n.* (FLAS); El Llano-Cartí highway, 10-12 km N of El Llano, 2 Mar. 1974, *Dressler 4621* (FLAS, PMA); Km 12-13 on the El Llano-Cartí road, 380 m, 25 Feb. 1976, *Kennedy & Dressler 3523* (F); Parque Nacional Soberanía, Río Agua Salud, entre el puente y el vertedero, 50 m, 11 Mar. 1997, *Mitre 342* (PMA, SCZ). CULTIVATED [without original locality data]: 26 Jan. 1907 (cult.), *Nash 24686* (NY); 31 May 1911 (cult.), *Nash 24686* (NY); 3 Mar. 1915 (cult.), *Nash 24686* (NY).

Commentary: *Lockhartia parthenoglossa* is most similar to *L. hercodonta*, but that species has smooth leaves that curve inward distally and white flowers with a

suborbicular labellum. It can also resemble *L. longifolia*, which also has longer stems and leaves, sigmoid, smooth leaves that curve inward distally, and a suborbicular labellum.

Even when not in flower, plants of *Lockhartia parthenoglossa* can be distinguished from other *Lockhartias* by their leaves noticeably curving away from the stem and rugulose-foveolate texture (the last character shared with *L. rugosifolia*, although not as pronounced as in that species). Plants with juvenile foliage can resemble a narrow-leaved *L. hercodonta*, but that species has smooth leaves.

***Lockhartia rugosifolia* M.A. Blanco**

26. *Lockhartia rugosifolia* M.A. Blanco, *sp. nov.* TYPE: PERU. Amazonas: [Bongará?], Utcubamba river floodplain forest near Jazan (below Shipasbamba), 1400 m, 29 Jun. 1962, *J.J. Wurdack 1090* (Holotype: AMES-104844; isotypes: NY, USM).

Lockhartia parthenocomos (Rchb.f.) Rchb.f. affinis, sed foliis rugulosis, bracteis inflorescentiarum complanatis lateraliter, et floribus valde parvioribus.

Stems completely pendulous, more or less flexible, 28–84 cm long when reproductive, with 38–72 leaves; shoots (stem and leaves) 13–25 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular in side view, with straight to slightly incurving or outcurving margins, acute, rugulose-foveolate; exposed part of largest leaves 11–56 × 2–9 mm. Inflorescences both terminal and axillary from distal half of the stem, resembling grass spikelets, up to 11 per stem (sequentially produced?), with 1–4 flowers produced more or less sequentially; the rachis completely obscured by the bracts; exerted portion 1–2 cm long, internodes 1–2 mm long; inflorescence bracts amplexicaul, conduplicate, narrowly triangular to ovate, acute,

scarious, 5–11 × 1–4 mm; pedicel and ovary 5–7 mm long, hidden by the floral bract. Flowers pendulous to resupinate, campanulate, 6–11 mm across, dark yellow with several pale brownish-orange horizontal bars across the center of the labellum (under the trichome pad). Sepals ovate, slightly concave, acute, 5–6 × 3–4 mm. Petals widely elliptic, flat, apically rounded, 6 × 5 mm. Labellum suborbicular, shallowly 3-lobate, 7–8 mm long, 10–11 mm wide when flattened; side lobes wider than long, transversely elliptic, slightly concave, 3 × 6–7 mm; midlobe wider than long, bilobulate, retuse, slightly reflexed, 2–3 × 5–6 mm; callus merely a rectangular, smooth, puberulous area occupying the central portion of the labellum, not markedly thickened, 4 × 2.5 mm. Column narrowly winged, subrhombic to spatulate, 3 × 2 mm, the wings obliquely oval and decurrent, wider distally, 0.5 × 1.5 mm; anther cap galeate, 1 × 1 mm; pollinarium not seen. Fruit obovoid, 12–15 × 7 mm.

Phenology: field collections indicate that the plants flower at least in the months of January, May, June, August, and October, and probably throughout the year.

Distribution: Presently known from the Peruvian department of Amazonas, in the provinces of Bongará, Chachapoyas, and Rodríguez de Mendoza, in the Utcubamba river basin, from 1200 to 1600 m, on the eastern (Amazonian) side of the Andes (Figure 3). Apparently also present in the southeastern Ecuadorian province of Zamora-Chinchipec, on the basis of *Hirtz et al.* 7329 (from a cultivated plant) and *D'Alessandro* 753 (RPSC, not found, identified as *L. parthenocomos* in www.tropicos.org); see commentary below.

Additional specimens examined: ECUADOR. Without locality data: 3 May 2004 (cult.), *Blanco* 2568 (FLAS), *Blanco* 2569 (FLAS), *Blanco* 2570 (FLAS); 25 Jan. 2000

(cult.), *Whitten et al. 1645* (FLAS); 29 Sep. 2003 (cult.), *Whitten et al. 2432* (FLAS, QCA). Zamora-Chinchipe: Zumba, Mar. 2000 (cult.), *Hirtz et al. 7329* (SEL). PERU. Without locality data: *anonymous s.n.* (K-spirit); 18??, *Mathews s.n.* (BM). Amazonas: Búngara, vicinity of Campomiento Ingenio 1-3 km up road to Pomacocha from Puente Ingenio, 1300 m, 27 Jan. 1964, *Hutchinson & Wright 3837* (AMES, UC), 5 May 1964 (cult.), *Hutchinson 3837* (AMES, UC); Campomiento Ingenio on Río Utcubamba, 300 km E of Olmos, 1250 m, 10 Oct. 1964, *Hutchinson & Wright 6849* (UC 2 sheets); Chachapoyas, Jazán (Ingenio-Chachapoyas), en ribera derecha del Utcubamba, 1200 m, 28 May 1963, *López et al. 4275* (AMES, HUT); [Rodríguez de Mendoza], Mendoza, 1600 m, 8 Aug. 1963, *Woytkowski 8172* (GH, MO, SEL).

Commentary: *Lockhartia rugosifolia* has been confused with both *L. longifolia* and *L. parthenocomos*, both of which it resembles vegetatively. It differs from *L. longifolia* in its straight, verruculose leaves, campanulate flowers, concave labellum and non-crateriform callus. The floral morphology is more similar to that of *L. parthenocomos*, although that species has smooth leaves, much larger flowers, and occurs only in the Venezuelan Coastal Range.

The spikelet-like condensed inflorescences with strongly conduplicate, distichous bracts and the rugulose leaf texture are diagnostic of *L. rugosifolia*. The leaves of *L. parthenoglossa* are also rugulose, but much less pronouncedly so (and apparent only under magnification).

Dodson and Bennett (1989a) and Dodson (2002: 453) published illustrations of this species, identified as *Lockhartia parthenocomos*.

***Lockhartia serra* Rchb. f.**

27. *Lockhartia serra* Rchb. f., Otia Bot. Hamburg. 1: 6. 1878. TYPE: ECUADOR. Guayas: Guayaquil, Litoral-Ebene, Mai 1876, *F.C. Lehmann* 92 (number from holotype label) (holotype: W-Reich.-Orch.-44331; photo: RPSC) .

Lockhartia schunkei D.E. Benn. & Christenson, Icon. Orchid. Peruvianum 3: plate 486. 1998. TYPE: PERU. Tumbes: Zarumilla, 10 Km E of El Caucho, Bosque Nacional de Tumbes, 580 m, 15 Mar. 1993, *M. Cavero B. 314 ex D.E. Bennett* 6563 (holotype: MOL-spirit; isotype: USM, not found).

Stems erect to descending, more or less rigid, 9–47 cm long when reproductive, with 20–74 leaves; shoots (stem and leaves) 8–20 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular to obliquely lanceolate in side view, apically rounded; exposed part of largest leaves 15–39 × 3–7 mm. Inflorescences both terminal and axillary from the distal third of the stem, up to 4 per stem (sequentially produced), with 1–13 flowers produced more or less sequentially; exerted portion 1–6 cm long, internodes 1–3 mm long; inflorescence bracts amplexicaul, widely ovate to suborbicular, cordate, obtuse to apiculate, expanded to campanulate, 5–9 × 3–8 mm; pedicel and ovary 17–20 mm long. Flowers resupinate, widely open, 16–22 mm tall, yellow, the labellum with brown to purplish-brown spots around the callus and on the lateral lobes (the latter almost solid brown), the callus mostly orange; the column with dark brown dots on the wings and a V-shaped infrastigmatic line. Sepals ovate to elliptic, slightly concave, acute to obtuse, apex navicular abaxially, 8–11 × 5–6 mm. Petals suboblong to obovate, round to subtruncate apically, markedly arched forward, margins reflexed, difficult to spread flat, 9–11 × 4.5–5.5 mm. Labellum 3-lobate, 12–13

mm long (from the base to the tip of the midlobe apical lobules), 14–18 mm wide across lateral lobes when flattened; lateral lobes elongate, oblong, obtuse to subtruncate, slightly falcate, arched toward front, 7–10 × 1.5–3 mm; midlobe divided into 4 lobules, markedly pandurate, emarginate, margin irregularly undulate, 9–11 × 10–12 mm, the basal lobules folded backwards, the distal lobules flared; callus suboblong; the base forming a concave cushion with a tuft of short, glandular hairs, 1.5 × 2 mm; the distal portion forming a mass of low tubercles, wider distally, 4–5 × 1–3 mm. Column winged, more or less dolabriform, 1.5–3 mm long, 4–5.5 mm wide; wings obliquely flabellate, with an irregularly denticulate margin, 1.5 × 2 mm, with an entire to denticulate margin; stigmatic cavity subpandurate, 1.2 × 0.7 mm; anther cap galeate, 1.5 mm in diameter; pollinarium 1.4 mm tall, stipe bifid. Fruit obovoid to narrowly pyriform, glaucous, 8–25 × 6–9 mm.

Nomenclatural notes: The holotype of *L. schunkei* consists of a single flower in spirit at MOL, and the isotype at USM (which should have been transferred to MOL) has not been found. However, the original description and illustration of *L. schunkei* clearly indicate that this name is synonymous with *L. serra*, which is widespread and common in the coastal forests and adjacent lowlands of western Ecuador.

Phenology: Flowering plants have been collected throughout the year, but with a higher frequency from April to June.

Distribution: Central and southern Ecuador and extreme northwestern Peru (Tumbes department), from sea level to 720 m, on the coastal lowlands west of the Andes (Figure 12).

In Ecuador, *L. serra* is relatively common in humid forests in the provinces of Guayas and Los Ríos. One historical collection is known from Manabí, a province that has been heavily deforested in recent decades. It is expected to occur also in El Oro province.

One collection (*Asplund 16454*, S, included in Figure 12) was supposedly collected in the province of Esmeraldas. However, this is a questionable locality; no other collections of *L. serra* are known from this province, which is dominated by a much more humid rain forest, and the specimen appears to have been prepared from a cultivated plant (possibly with erroneous data).

Additional specimens examined: ECUADOR. Without locality: 22 Jun. 1977 (cult.), *Ackerman 878* (SEL); 9 May 2004 (cult.), *Blanco 2574* (FLAS); 11 Aug. 2004 (cult.), *Blanco 2669* (FLAS); 30 Jun. 2009 (cult.), *Blanco 3228* (FLAS); 22 Mar. 1976 (cult.), *Brenner 10* (SEL); "Bauas" [Guayas?], *Lehmann H.K. 1143* (K); *Lehmann 8905* (K); 12 Feb. 1919 (cult.), *Powell 50* (K); *Sodiño s.n.* (QPLS; without label); 26 Sep. 1991 (cult.), *Wagner s.n.* (USJ); 29 Sep. 2003 (cult.), *Whitten et al. 2431* (FLAS).
Esmeraldas: Timbre, 24 May 1955 (cult.?), *Asplund 16454* (S; locality questionable).
Guayas [including Santa Elena]: 10 km W of Pedro Carbo, 23 Jul. 1940, *Haught 3083* (AMES, NY); Bosque Protector Cerro Blanco, 300 m, May 1993, *Cornejo 20* (QCNE); Capeira, km 21 Guayaquil to Daule, 70 m, 18 Sep. 1981, *Dodson & Dodson 11350* (MO, SEL); Cerro La Camarona, Cord. Colonche, 150 m, 6 Sep. 1979, *Valverde 1823* (SEL); Guayaquil, 10 Jan. 1842, *I.K.C. s.n.* (K); Guayaquil, Bosque Protector Cerro Blanco, carretera a Salinas, km 15, 350 m, 15 Aug. 1991, *Rubio et al. 1766* (QCNE), *Rubio et al. 1818* (QCNE); Guayaquil, Bosque Protector Cerro Blanco, carretera

Guayaquil-Salinas, km 15, 100 m, 6 May 1992, *Tipaz et al.* 836 (QCNE, 2 sheets);
 Guayaquil, Cerro Azul, vía a la costa, km 12, 500 m, 18 Mar. 1992, *Palacios & Rubio*
 9981 (QCNE); Guayaquil, esclusas de Puerto Nuevo, 0 m, 10 May 1964, *Valverde* 306
 (COL, US); Hacienda Barcelona, 12 km from Guayaquil on road to Salinas-Playas, 20
 Apr. 1962, *Gilmartin* 683 (US); Prop. Puente de Chimbo, *Sodiro* 128 (QPLS); Road
 Guayaquil-Quevedo, along river at La Toma, 20 m, 15 Apr. 1960, *Dodson* 22 (MO, SEL,
 US). Los Ríos: 41.5 km S of Quevedo, Nuevo Zapotal, 9 Jun. 1971, *MacBryde* 419
 (AMES, MO, NY, QCA, SEL); Hacienda Clementina, 30 m, 19 Dec. 1945, *Harling* 94
 (S); Hacienda Clementina, Cerro Samama, above Río Mombe, ca 38 km NE of
 Babahoyo, 200 m, 23 May 1994, *Stahl & Knudsen* 1186 (S); Quevedo, 15 Aug. 1964
 (cult.), *Bennett & Dodson s.n.* (AMES, UC); San Antonio de Columa, km 39, on the road
 Puebloviejo-Guaranda, 250 m, 20 Apr. 1980, *Holm-Nielsen* 22932 (AAU); Vinces,
 Jauneche forest, between Mocachí and Palenque on the Estero Peñafiel, 70 m, 3 Oct.
 1979, *Dodson et al.* 8735 (MO, SEL), 24 Jan. 1981, *Gentry et al.* 30772 (MO, QCA,
 SEL); Zapotal, km 56 Babahoyo to Quevedo, 220 m, 8 Jun. 1974 (cult.), *Dodson* 5588
 (SEL), 2 Aug. 1976 (cult.), *Dodson* 5588 (QCA). Manabí: Bahía de Caraquez, Jun.
 1903, *Lehmann B.T.*95 (AMES, GH, K, L, NY). PERU. Tumbes: Matapalo, El Caucho-
 Campoverde, parcela de evaluación permanente del Proyecto Flora de Perú, bajando a
 la quebrada, 16 Mar. 1995 (cult.), *Vargas & Salviz* 972 (USM); Zarumilla, entre P.C. El
 Caucho y P.C. Campoverde, Bosque Nacional de Tumbes, Reserva de Biosfera del
 Norveste, 720 m, 7 Jul. 1992, *Díaz et al.* 4702 (B, HUT, MO, USM). CULTIVATED
 [without original locality data]: 28 Jul. 2004, *Blanco* 2668 (FLAS); 20 Sep. 1958, *Dress*
 7015 (BH); 16 May 1893, *Linden s.n.* (BR); 22 Jan. 1978, *Robledo 5 sub Luer* 2805

(SEL); 18 Dec. 1909, *Nash 28294* (NY), 23 Dec. 1910, *Nash 28294* (NY); 9 Apr. 2002, *Silvera 73* (FLAS); 18 Jul. 1997, *Whitten 99235* (FLAS); 17 Jun. 1984, *Whitten s.n.* (FLAS).

Commentary: *Lockhartia serra* resembles the Central American *L. oerstedii* in vegetative morphology and flower size and appearance. However, the leaves of *L. serra* tend to be obtuse or rounded apically and less appressed to the stem (i.e., they diverge at a wider angle). The inflorescence bracts of *L. serra* are generally bigger and not recurved; the labellum side lobes are almost solid brown (vs. dotted in *L. oerstedii*), and the callus tubercles are much lower.

This is the species of *Lockhartia* that occurs farthest south in the lowlands west of the Andes, in seasonally dry forest, most of which has been destroyed. It is replaced by *L. oxyphylla* in the much wetter lowland and middle elevation forests of northwestern Ecuador. To the south of Tumbes (Peru), the lowland forests become too dry for most epiphytes and no species of *Lockhartia* occur there.

***Lockhartia tenuiflora* M.A. Blanco**

28. *Lockhartia tenuiflora* M.A. Blanco, *sp. nov.* TYPE: ECUADOR. Prov. Sucumbios [actually Prov. Napo: Cantón El Chaco, Parroquia Gonzalo Díaz de Pineda]: Road from Las Palmas to El Chaco, km. 10.9, 1777 m, 00°17'40.3"S, 77°46'22.7"W, 11 Feb. 2004, *M. Whitten, N. Williams, M. Blanco, K. Neubig & A. Reynolds 2719* (Holotype: FLAS; isotype: QCA).

Lockhartia lepticaula D.E. Benn. & Christenson affinis, sed mediolobo labelli angustiore et alis gynostemii triangulari et parviore.

Stems apparently erect, more or less rigid, 14–51 cm long when reproductive, with 38–55 leaves; shoots (stem and leaves) 10–19 mm wide. Leaves marcescent, unifacial,

laterally flattened, narrowly triangular in side view, with straight to slightly incurving or outcurving margins, obtuse to rounded apically, exposed part of largest leaves 10–29 × 3–9 mm. Inflorescences both terminal and axillary from the distal half of the stem, with 1–6 flowers produced more or less simultaneously; exerted portion 1–2.5 cm long, internodes 2–5 mm long; inflorescence bracts amplexicaul, widely ovate to suborbicular, cordate, obtuse to apiculate, expanded to campanulate, 6–7 × 3–6.5 mm; pedicel and ovary 11–15 mm long. Flowers resupinate, widely open, 12–16 mm tall, yellow, the labellum with reddish brown to purplish-brown spots around the callus and on the lateral lobes, the callus mostly orange. Sepals elliptic, slightly concave, acute to obtuse, 6–6.5 × 3–3.5 mm. Petals elliptic to suboblong, round to subtruncate apically, slightly curved forward, the margins recurved, 6 × 3.5 mm. Labellum 3-lobate, 8–11 mm long, 13–15 mm wide across lateral lobes when flattened; lateral lobes elongate, narrowly oblong to sublinear, attenuate, acute, curved toward front, 5.5–6.5 × 1 mm; midlobe divided into 4 lobules, pandurate, emarginate, margin irregularly undulate, 6.5–7.5 × 5.5–6.5 mm, the basal lobules folded backwards, the distal lobules straight; callus suboblong, the base forming a concave cushion with a tuft of short, glandular hairs, 1.5 × 1.5 mm; the distal portion forming a mass of low tubercles, 3–4 × 2–2.5 mm. Column winged, rhombic, 3 mm long, 3 mm wide; wings subtriangular, with an irregularly denticulate margin, 1 × 1.5 mm; stigmatic cavity subpandurate, 1 × 0.4 mm; anther cap galeate, 1.3 × 1 mm; pollinarium 1 mm tall, stipe bifid. Fruit fusiform to obovoid, 14–16 × 6–7 mm.

Phenology: the few field collections available indicate flowering at least during the months of February, July and November. Cultivated plants are known to flower in March, August, and September.

Distribution: Ecuador, and possibly Colombia, from 1100 to 1900 m on the eastern (Amazonian) side of the Andes (Figure 12). Expected in northern Peru.

The two Colombian collections have somewhat deteriorated flowers or no flowers at all. Their identification as *L. tenuiflora* is tentative, based on their vegetative morphology.

Etymology: from the Latin *tenuis* (slim) and *floris* (flower), in reference to the slim appearance of the flowers in front view, due to the folding back of the lateral lobules of the labellum midlobe.

Additional specimens examined: COLOMBIA. Department unknown: West. Cordillera, Observatorio, 2600 m, Sep. 1941, *Dryander 2527* (US; identification tentative). Cundinamarca: Vergara, Vda. El Palmar, 1590 m, 14 Jun. 1993, *Chaparro de Barrera & Barrera Torres 168* (COL; identification tentative). ECUADOR. Without locality data: 11 March 2005 (cult.), *Blanco 3012* (FLAS), 25 Aug. 2009 (cult.), *Blanco 3231* (FLAS); 29 Sep. 2003 (cult.), *Whitten et al. 2430* (FLAS, QCA). Morona-Santiago: Gualaquiza, Vertiente occidental de la Cordillera del Cóndor, arriba del Valle del Río Quimi, 1600 m, 11 Dec. 2000, *Freire 4314* (QCNE); Plan de Milagro, road Cuenca to Limón, ca. 15 km SW of Limón, 1900 m, 20 Nov. 1989, *Dodson et al. 17878* (MO, QCNE). Napo: 23 km E of El Chaco, Quito-Lago Agrio road, 1700 m, 7 Nov. 1974, *Gentry 12596* (MO, NY). Zamora-Chinchipe: Zamora–Cenepa, River Zamora, 1100 m, 26 Jul. 1960, *Dodson 182* (MO, SEL); Loyola, 1800 m, Apr. 2001 (cult.), *Hirtz 7687* (SEL, mixed with *Epidendrum* sp. on separate sheet).

Commentary: *Lockhartia tenuiflora* is very similar to the primarily Peruvian *L. lepticaula*, but that species has a wider labellum midlobe and flabellate column wings (see comments under *L. lepticaula* for further information).

A color photograph of *Lockhartia tenuiflora* was published by Dodson (2002: 451) as *L. biserra* (Rich.) Christenson & Garay.

***Lockhartia verrucosa* Lindl. ex Rchb. f.**

29. *Lockhartia verrucosa* Lindl. ex Rchb. f., Hamburger Garten- Blumenzeitung 15: 53-54, 1859. TYPE: *Ex Hort.* Consul Schiller, *Stange s.n.* (lectotype, here designated: W-Reich.-Orch.-44327).

Fernandezia robusta Bateman, Bot. Mag. 92: t. 5592. 1866; '*Fernandesia robusta*'. *Lockhartia robusta* (Bateman) Schltr., Repert. Spec. Nov. Regni. Veg. 3: 82. 1906. Non *Fernandezia robusta* (Schltr.) Senghas, Schlechter Orchideen I/B (31): 1926. 1995. SYNTYPES: GUATEMALA. *Skinner s.n.* (not found, or possibly K-Lindl.-000079005, annotated by Lindley as "*Fernandezia verrucosa*", without further data [photo: AMES-23426]); and GUATEMALA. [Izabal: Puerto Barrios?], Vera Cruz, [1860-1864], *Ex Hort.* Royal Botanic Gardens Kew, May 1864, *O. Salvin s.n.* (mixed collection; lectotype, here designated: K-000078995, excluding 3 flowers of *Lockhartia imbricata*, originally in upper packet together with 2 flowers of *F. robusta*, now moved to a new, separate packet on right side of sheet; voucher for illustration in Bot. Mag. 92: t. 5592).

Stems erect (rarely descending), more or less rigid, 16–62 cm long when reproductive, with 24–68 leaves; shoots (stem and leaves) 14–25 mm wide. Leaves marcescent, unifacial, laterally flattened, narrowly triangular to oblong in side view, with straight to slightly incurving margins, acute to subtruncate (rarely subpraemorse); exposed part of largest leaves 22–50 × 4.5–10 mm. Inflorescences both terminal and

axillary from the distal half of the stem, up to 10 per stem (produced more or less simultaneously), with 1-(2) flowers produced sequentially; exerted portion 0.5–2.5 cm long, internodes 2–4 mm long; inflorescence bracts amplexicaul, narrowly triangular to widely ovate, cordate, acute to apiculate, expanded and held more or less perpendicular to the rachis, non-imbricate, distichous, 4–8 × 3–6 mm; pedicel and ovary 10–20 mm long. Flowers resupinate, widely open, 12–26 mm tall, yellow, the labellum and column heavily spotted with reddish brown; the lateral lobes with oblique-longitudinal brown stripes or dots forming lines; the column with brown dots on the wings and an open V-shaped infrastigmatic line; the anther cap white to yellow. Sepals ovate to oval, slightly concave, obtuse, 6–8 × 5–6 mm. Petals oval to suboblong, apically obtuse to subtruncate, curved toward the front, margins reflexed, difficult to spread flat, 7–8 × 4–5 mm when flattened. Labellum 3-lobate, 12–16 mm long (from the base to the distal margin, excluding the lateral lobes which curve toward the base when flattened), 13–18 mm wide across lateral lobes when flattened; lateral lobes elongate, oblong to slightly obovate, obtuse to round or subtruncate apically, curved toward front, 6–9 × 2–3.5 mm; midlobe divided into 4 lobules, pandurate, emarginate, margin irregularly undulate, 9–11 × 9–13 mm, the basal lobules folded backwards, the distal lobules flared obliquely downward; callus obovate; basal part forming a concave cushion with a basal tuft of short, glandular hairs, 2 × 2 mm; the distal portion forming a spatulate mass of low tubercles, 4–5 × 3–5 mm, wider distally. Column widely winged, dolabriform, 3–4 mm long, 5–6 mm wide; wings round to flabellate, 1.5 × 2 mm, with an entire to denticulate margin; stigmatic cavity oval to subpandurate, 1 × 0.4 mm; anther cap galeate, 1.2 mm long; pollinarium 1 mm tall, stipe bifid. Fruit narrowly obovoid, 13–19 × 6–7 mm.

Nomenclatural notes: In the protologue of *Lockhartia verrucosa*, Reichenbach stated that this species was introduced from Joinville (Brazil: Santa Catarina) by Consul G.W. Schiller; however, this species is only known from southern Mexico and Guatemala. The provenance given to Reichenbach by Schiller is obviously erroneous, and Reichenbach (1869) later confirmed that the species is of Guatemalan origin.

A specimen in the Lindley herbarium at Kew (K-Lindl.-000079005), which lacks collection data, was annotated by Lindley as "*Fernandezia verrucosa*", but he never published that name. Reichenbach undoubtedly saw this specimen and used the specific epithet when he described *L. verrucosa* ("*Fernandezia verrucosa* Lindl., Herb. Mss!"). Rolfe annotated this specimen as the type of *L. verrucosa*, but it cannot be considered a type in the modern sense because Reichenbach did not cite it in the protologue (although it may be a syntype of *Fernandezia robusta*, see below).

The name "*Fernandezia verrucosa*" is erroneously listed by some (e.g., the W3TROPICOS website) as having been validly published, attributed to "Lindl. ex Kraenzl." However, Kraenzlin (1923) explicitly cited that name under the synonymy of *L. verrucosa* as one used by Lindley and never published.

Bateman mentioned two collections in the protologue of *Fernandezia robusta* (one by Skinner, and another by Salvin) without designating either as the type, and thus both are to be considered syntypes. Salvin's specimen at K will be designated as the lectotype; it includes three flowers of *Lockhartia imbricata*, in addition to the flowers of the actual plant mounted on the sheet. These three flowers have now been placed in a separate packet. The specimen labeled "*Fernandezia verrucosa*" in the Lindley

herbarium (mentioned above) could be the plant collected by Skinner, but it has no indication of the collector.

The specimen collected by Salvin has the undated annotation “Vera Cruz, O. Salvin Sr.” This locality is probably the Guatemalan town of Veracruz (Department of Izabal, Municipality of Puerto Barrios), not the Mexican state (Salvin visited Guatemala several times, but as far as it is known he never collected in Mexico, and no species of *Lockhartia* are known to naturally occur in the Mexican state of Veracruz). However, such a lowland site (ca. 20 m) is also an unlikely natural locality for *L. verrucosa*, a species that normally occurs above 900 m elevation; it was probably either cultivated there or simply shipped from the neighboring port of Puerto Barrios.

The unpublished name “*Fernandezia robusta* Klotsch”, occasionally (but erroneously) cited as a validly published name, was merely listed by Reichenbach (1855; 1864) as one used for a plant of *Lockhartia lunifera* cultivated by Jenisch (nomenclatural notes under *L. lunifera*).

Phenology: Flowering plants have been collected throughout the year, but much more frequently during the months of May, June, and July.

Distribution: Southern Mexico (Chiapas and eastern Oaxaca) and Guatemala, from 800 to 2200 m (Figure 7). *Lockhartia verrucosa* is geographically isolated from its putative sister species, *L. galeottiana*, by the Chivela Pass, which separates the Sierra Madre del Sur from the Sierra Madre de Chiapas.

Additional specimens examined: GUATEMALA. Without locality: May 1866, *Bernoulli* 316 (BR [2 sheets], G, K, W-Reich); May 1866, *Bernoulli & Cario* 489 (S). Alta Verapaz: Cobán, 10 Jan. 1941, *Dodge* 1980 (AMES), 1372 m, 14 May 1940, *Lewis* 225

(AMES). Quezaltenango: Along old road between Finca Pirineos and Patzulín, 1200 m, 9 Feb. 1941, *Standley 86984* (AMES, F [2 sheets]). Sacatepéquez: Volcán de Agua, 14 May 1942, *Steyermark 46397* (F). San Marcos: Above Finca El Porvenir, up Loma Bandera Shac, lower S-facing slopes of Volcán Tajumulco, 1300 m, 9 Mar. 1940, *Steyermark 37333* (AMES, F). Santa Rosa: Zamorora, 1500 m, Apr. 1893, *Heyde & Lux 4616* (AMES, BR, F, K, M, NY). Suchitepéquez: SW lower slopes of Volcán Zunil, between Finca Montecristo and Finca Asturias, SE of Santa María de Jesus, 1200 m, 1 Feb. 1940, *Steyermark 35271* (F); Volcán Santa Clara, between Finca El Naranjo and upper slopes, 1250 m, 23 May 1942, *Steyermark 46596* (AMES, F). MEXICO. Without locality: Jan. 1960, *anonymous s.n.* (K-spirit); 20 Jul. 1967 (cult.), *Nevling & Gómez-Pompa 295* (A, MEXU). Chiapas: 6 mi N of Ocozocoautla, along gravel road to Apitpac, 1000 m, 9 Jul. 1977, *Croat 40551* (MO); 6-10 km NE of La Soledad along road from Las Margaritas to Campo Alegre, 1600 m, 7 Dec. 1986, *Breedlove et al. 66245* (CAS); About 1 mi NE of Hwy 190 from a point about 2.3 mi NW of Comitán, 20 Jul. 1971, *Stevens 1277* (MO); Amatenango del Valle, 1 km above Aguacatenango, 1800 m, 5 Jun. 1988, *Breedlove 68954* (CAS, MO); Amatenango del Valle, 1 km N de Col. Benito Juárez, 5 km S desvío carr. a Amatenango, 1780 m, 11 May 1993, *Ochoa-Gaona et al. 4106* (CAS); Angel Albino Corzo, between Finca Cuxtepeque and Finca Cabañas, 1100 m, 9 May 1988, *Breedlove & Bourell 67501* (CAS); Berriozabal-Las Vistas, 12 Jun. 1950, *Miranda 6372* (MEXU); Coapilla, Panteón de Coapilla, 1700 m, 4 Jul. 1991, *Cabrera Cachon 159* (CAS [2 sheets], MEXU), 25 Aug. 1994, *Cabrera Cachon 224* (MEXU); Comitán, 2 km SE Llano Largo, carretera Villa Las Rosas-Comitán, 11 May 1993, *Ochoa-Gaona et al. 4126* (CAS, CICY); Comitán, Los Lagos, 35 mi SE of

Comitán, road San José to Montebello, 15 Apr. 1949, *Carlson 1797* (F, 3 sheets); Honduras, near Siltepec, 1500 m, 9 Jul. 1941, *Matuda 4369* (AMES, F, LL, MEXU, MO, NY, SEL); Jiquipilas, Los Alpes, 1200 m, 25 May 1995, *Castillo 686* (MEXU); La Concordia, 8 km adelante del Rancho Las Cabañas, 1150 m, 10 May 1988, *Cabrera Cachón 67* (MEXU); La Concordia, Cerro El Venado, Poligono V, 1654 m, 19 Apr. 2005, *Gómez Dominguez 952* (CAS); La Independencia, 6-10 km NNE of La Soledad along logging road from Las Margaritas to Campo Alegre, 1600 m, 1 Jul. 1981, *Breedlove 51267* (CAS); La Trinitaria, 4 km E of La Trinitaria along Mex 190, 1480 m, 8 Jul. 1990, *Hampshire et al. 1173* (BM, MEXU); Las Margaritas, 8 km E of Las Margaritas along road to La Soledad, 1700 m, 15 Sep. 1974, *Breedlove 37894* (AMES, DS); Mapastepec, El Triunfo Reserve, mule trail W of Cañada Honda towards El Tomatal, c. 1 km from Cañada Honda, 1450 m, 28 Feb. 1990, *Hampshire et al. 783A* (BM, MA); Montebello Lake district, 1524 m, Oct. 1953, *Johnson 353-104* (SEL); Near Hacienda Santa María de los Arcos, E of Comitán, 1500 m, 26 May 1936, *Nagel sub Oestlund 4541* (AMES); Ocozocoautla de Espinoza, 18-20 km N of Ocozocoautla along road to Mal Paso, 800 m, 20 Oct. 1971, *Breedlove & Thorne 21075* (DS); Ocozocoautla, 7 km de Horizonte a Ciprés, al Cerro El Banadero, 1200 m, 10 Jun. 1983, *Vásquez 939* (XAL); Ocozocoautla, Reserva del Ocote, al NE del Rancho Corocito, ladera del Cerro La Colmena, 850 m, 27 Apr. 1983, *Calzada 9676* (XAL); Pueblo Nuevo Solistahuacán, 3 km NW of Pueblo Nuevo Solistahuacán, on the slopes below Hy. 195 in the vicinity of Clínica Yerba Buena, 1646 m, 14 Jun. 1971, *Fathrop 7502* (DS, RSA); Road above Teopisca on route to San Cristóbal de las Casas, 4 May 1952, *Moore 6462* (BH); Totolapa, Rancho Ch'a ha' 5-6 km W of Teopisca, 2200 m, 18 Jul. 1972, *Breedlove*

26177 (AMES, DS, MO, NY, SEL); Venustiano Carranza, 3 mi S of Aguacatenango along road to Pinola Las Rosas, 1707 m, 25 Jun. 1965, *Breedlove 10550* (DS, F, LL, MICH, NY), 15 Jul. 1966, *Breedlove 14545* (DS, F, MEXU, WIS); Villa Las Rosas, km 12.3 de la carretera Villa Las Rosas-Comitán, 1630 m, 15 May 1995, *Mejía & Luna 478* (CICY); Yola, 6 Nov. 1959 (cult.), *Alava sub Blydenstein s.n.* (MO), 14 Jan. 1965 (cult.), *Alava sub Hutchinson s.n.* (UC), 16 Oct. 1961 (cult.), *Alava sub Hutchinson s.n.* (UC), 18 Sep. 1961 (cult.), *Alava sub Kimnach s.n.* (UC). Oaxaca: San Miguel Chimalapa, Arroyo entre Cerro Verde y Cerro Amargo, al S del camino Benito Juárez-La Ciénaga, ca. 8 km en línea recta al SE de Benito Juárez, ca. 32 km en línea recta al NNE de San Pedro Tapantepec, 1200 m, 4 Aug. 1986, *Maya 3722* (MEXU, MO), San Miguel Chimalapa, cabecera del Arroyo Caracol, Cerro Guayabitos, al NO de Congregación Benito Juárez, ca. 40 km en línea recta al N de San Pedro Tapantepec, 1450 m, 7 Aug. 1984, *Maya 376* (CAS, MEXU, MO); Santa María Chimalapa, cañada al lado S del Cerro El Quetzal (cerro ca. 4 km al N de Cerro Guayabitos), ca. 8 km en línea recta al NO de Benito Juárez, ca. 44 km en línea recta al N de San Pedro Tapanatepec, 1600 m, 11 Jul. 1986, *Maya 3581* (MEXU, MO). CULTIVATED [and/or without original locality data]: Cultivated, *anonymous s.n.* (BR); cultivated, *anonymous s.n.* (G); *anonymous s.n.* (K-spirit); *anonymous s.n.* (W-Reich); *anonymous s.n.* (K-Lindl; photo: AMES); cultivated, *anonymous s.n.* (W-Reich); 28 Dec. 1914 (cult.), *anonymous s.n.* (K); cultivated, *anonymous s.n.* (W-Reich); 6 Jun. 2004 (cult.), *Blanco 2667* (FLAS); 4 Jun. 2009 (cult.), *Blanco 3218* (FLAS); 4 Jun. 2009 (cult.), *Blanco 3227* (FLAS); 27 Jul. 2009 (cult.), *Blanco 3230* (FLAS); 1 Jul. 1976 (cult.), *Dodson s.n.* (SEL); *Gailer 18* (K-spirit); *Gower s.n.* (E); 11 Aug. 2000 (cult.), *Mally 105* (CAS); *Mason 1194* (K-spirit);

Sessé s.n. (G); 20 Jun. 1984 (cult.), *Staal s.n.* (SEL); Cultivated, *Veitch 443* (W-Reich); May 1889 (cult.), *Veitch s.n.* (K).

Commentary: *Lockhartia verrucosa* is most similar to *L. galeottiana*, which has much shorter, congested inflorescences with spiral phyllotaxy and a narrower labellum callus. It also resembles *L. oerstedii*, which has narrower shoots and taller teeth in the callus. See notes under those species for further information.

Poorly Known Taxa

***Lockhartia macrantha* Lem.**

Lockhartia macrantha Lem., Ill. Hort. 12: misc. 57-58. 1865. Non *Lockhartia micrantha* Rchb.f. TYPE: MEXICO. Ex Hort. Ambroise Verschaffelt (Ghent), [1865?], Ghiesbreght s.n. (not found).

The name *Lockhartia macrantha* has hitherto been ignored, although it is validly published, probably because of its similar spelling to Reichenbach's *L. micrantha*, or because Lemaire compared it with *L. lunifera*. However, Lemaire explicitly described *L. macrantha* as a new species.

Lemaire based his description from a live plant cultivated in Ghent, sent from Mexico by Ghiesbreght. However, no corresponding herbarium material has been found (possibly it was never prepared), and no illustration of it was published. The description can apply equally to *L. galeottiana*, *L. oerstedii*, and *L. verrucosa*, all of which occur in Mexico. Ghiesbreght collected in Chiapas (where both *L. oerstedii* and *L. verrucosa* occur; Roriosa, 1887), but he also traveled extensively through other Mexican states, where he could have collected *L. galeottiana*. In any case, all three of those names (or their basionyms) were published earlier, and thus *L. macrantha* would be a synonym.

***Lockhartia parthenocomos* var. *crispula* Regel**

Lockhartia parthenocomos var. *crispula* Regel, Ann. Sci. Nat., Bot. sér. 4, 6: 378. 1856; Index Seminum [St. Petersburg (Petropolitanus)] 1856: 23. 1856. TYPE: COLOMBIA [probably VENEZUELA]. [*Ex Hort. St. Petersburg Botanical Garden?*], *Lansberg s.n.* (holotype: LE?, not found).

This name is based on a plant reportedly collected in Colombia (but more likely in Venezuela; see nomenclatural notes of *L. imbricata*) by someone named Lansberg (possibly J.G. van Lansberge, who collected in Venezuela (Chaudhri *et al.*, 1972), apparently cultivated in the St. Petersburg Botanical Garden in Russia under the name “*Bothriostigma distichophyllum*” (as evidenced by its listing in their Index Seminum). No type material has been found in LE (which holds the main set of Regel’s collections) or elsewhere. It may correspond to the illustration (sent to Linden’s horticultural firm in Ghent by Lansberg) mentioned by Reichenbach (1855) as *Fernandezia longifolia*. That illustration has not been found either.

Although the specific epithet suggests it is a species with campanulate flowers (i.e., a member of the Parthenocomos group), the brief description of the flower in the protologue is more consistent with that of a species with long, incurved labellum lateral lobes (i.e., a member of the Imbricata group). However, it is impossible to reconstruct the detailed floral morphology from the meager original description.

Excluded Name: *Fernandezia obtusa* Lindl. ex Linden

Fernandezia obtusa Lindl. ex Linden, Ill. Hort. 29: 51. 1882. “[*Fernandezia*] *obtusa*, Ldl., Colombie, 1844.” *Nomen nudum*.

Linden listed this name for a cultivated plant from Colombia, without a description or a diagnosis. No type specimen or illustration attributable to this name has been

found. Reichenbach (1855; 1864) listed this name as dubious, at the end of his enumeration of the species of *Lockhartia*.

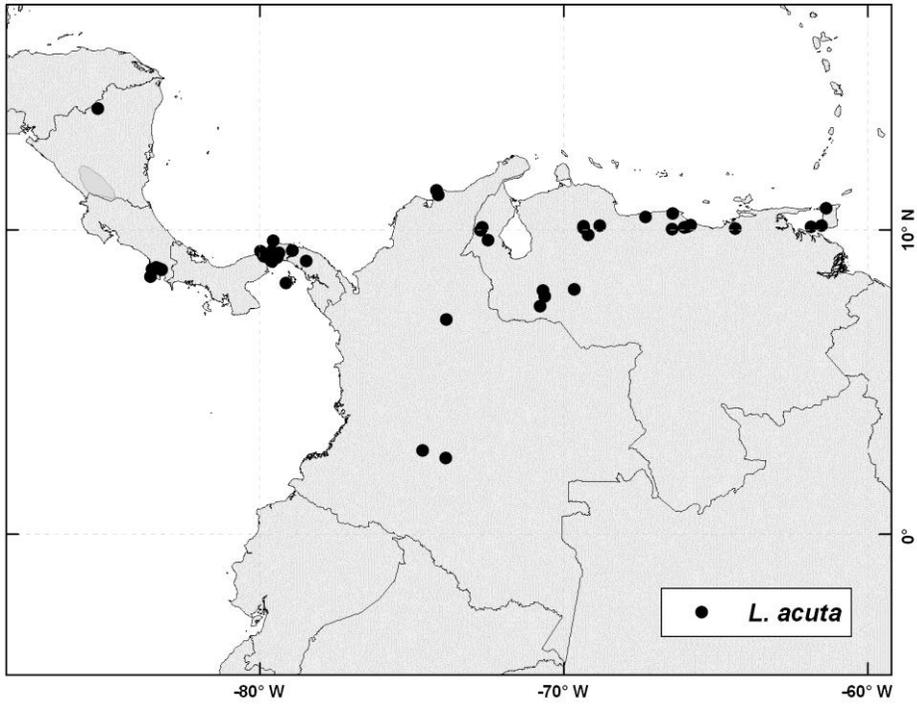


Figure 3-1. Distribution of *Lockhartia acuta*.

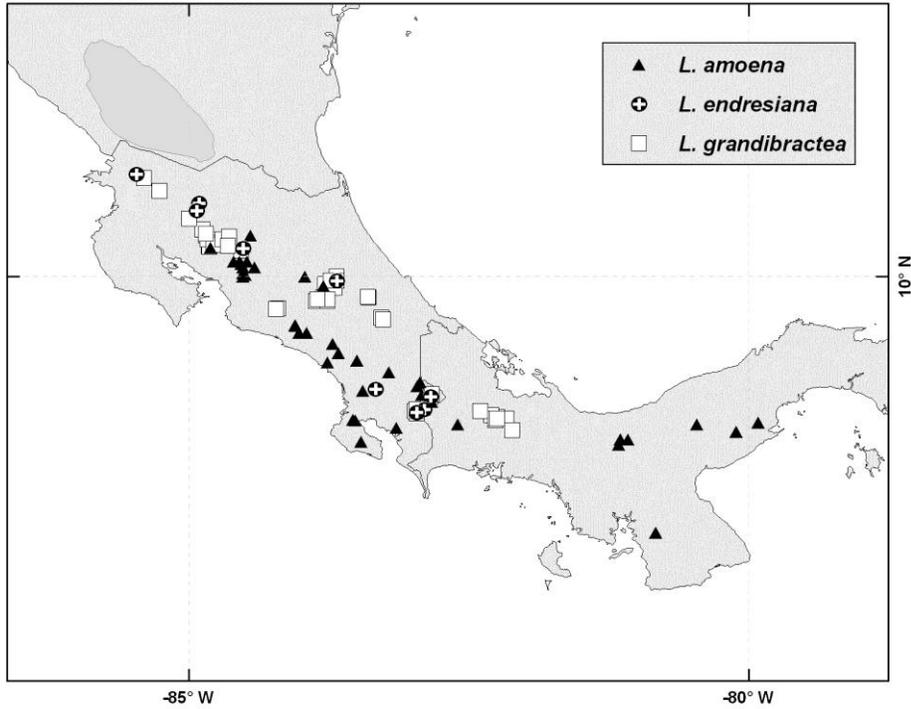


Figure 3-2. Distribution of *Lockhartia amoena*, *L. endresiana*, and *L. grandibractea*.

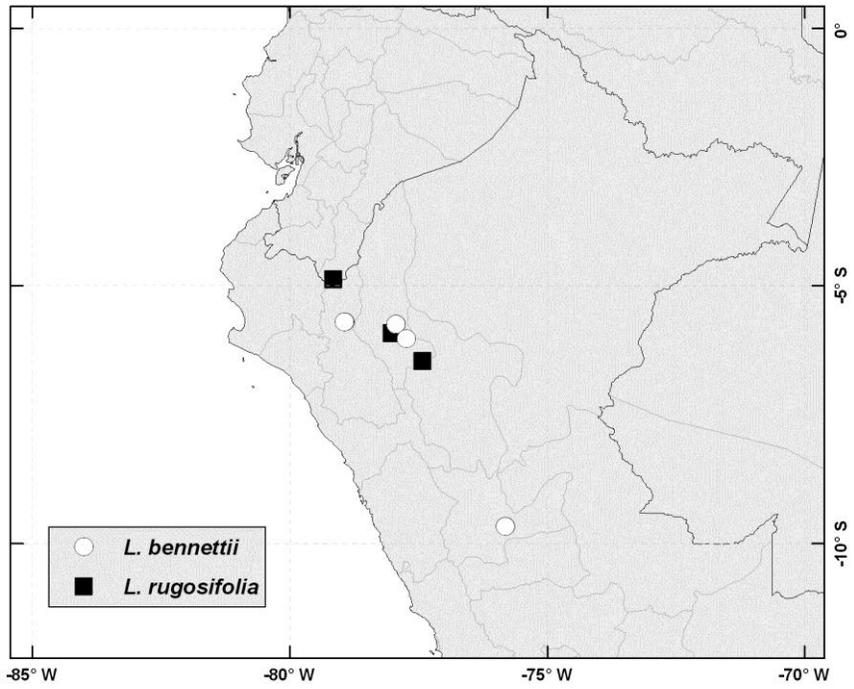


Figure 3-3. Distribution of *Lockhartia bennettii* and *L. rugosifolia*.

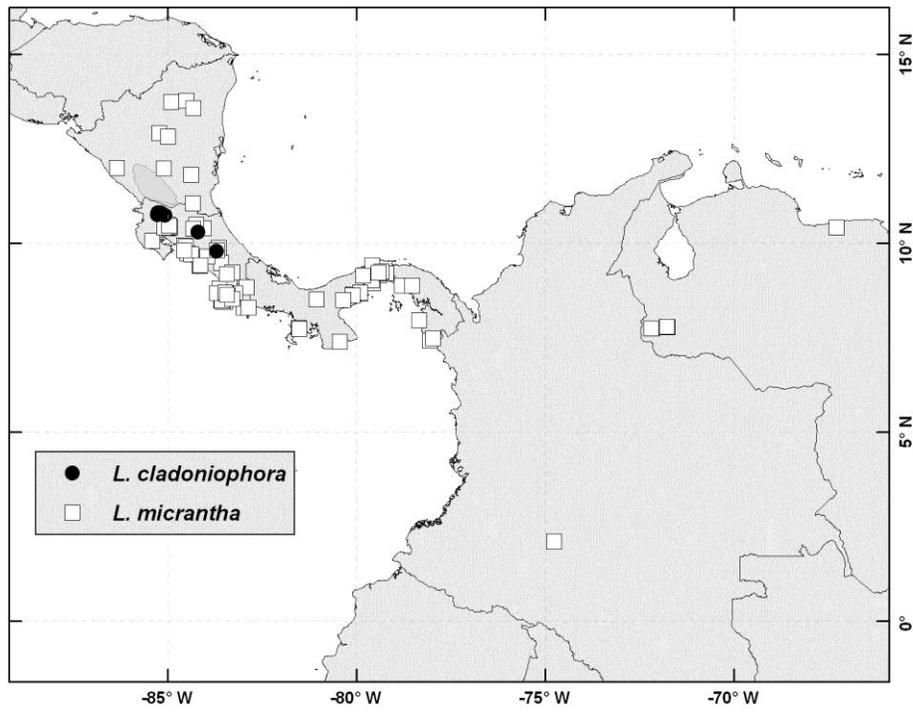


Figure 3-4. Distribution of *Lockhartia cladoniophora* and *L. micrantha*.

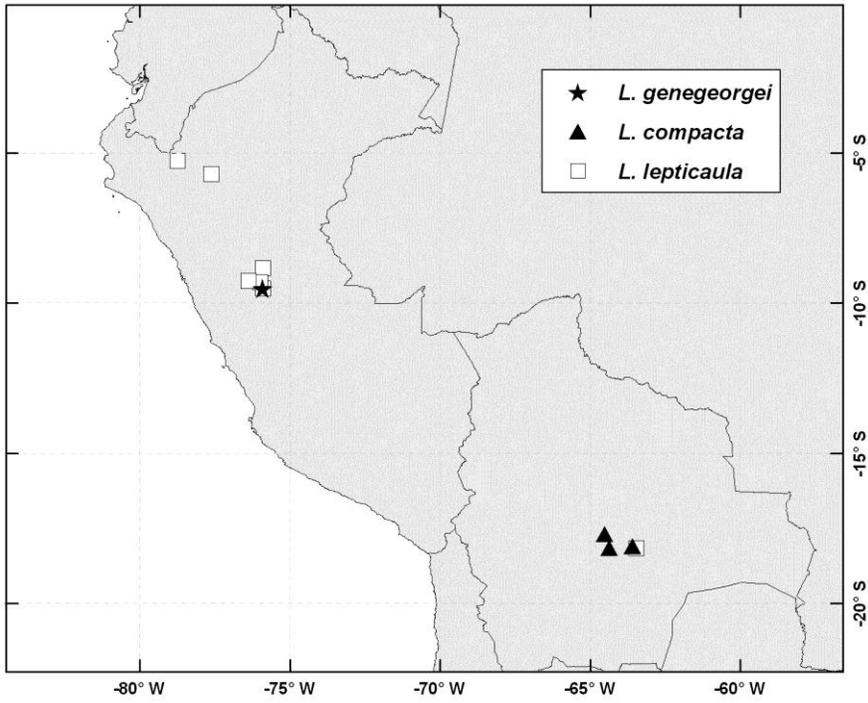


Figure 3-5. Distribution of *Lockhartia compacta*, *L. genegeorgei*, and *L. lepticaula*.

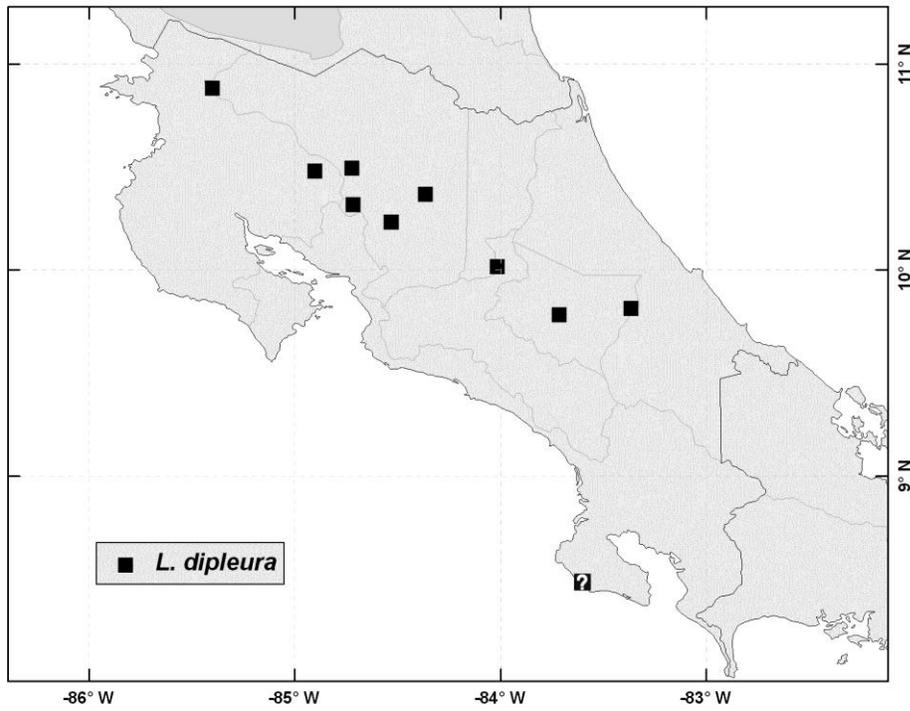


Figure 3-6. Distribution of *Lockhartia dipleura*.

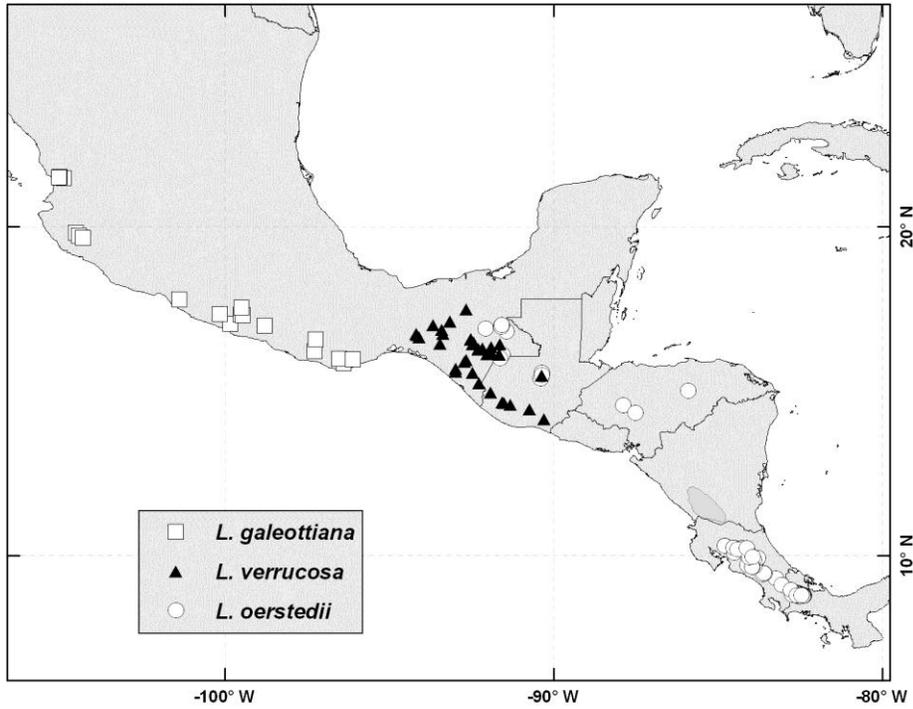


Figure 3-7. Distribution of *Lockhartia galeottiana*, *L. oerstedii*, and *L. verrucosa*.

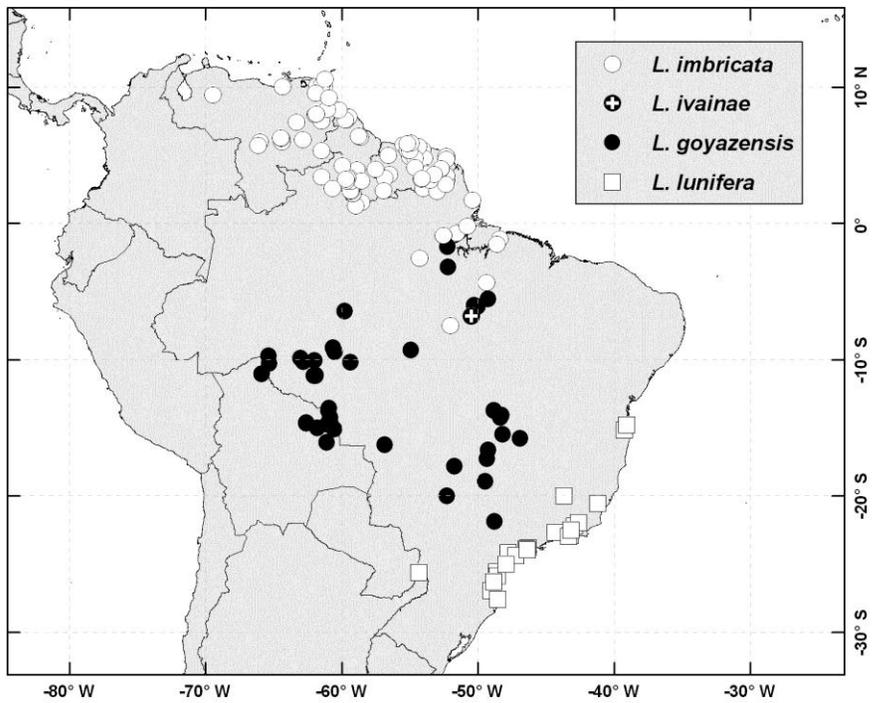


Figure 3-8. Distribution of *Lockhartia goyazensis*, *L. imbricata*, *L. ivainae*, and *L. lunifera*.

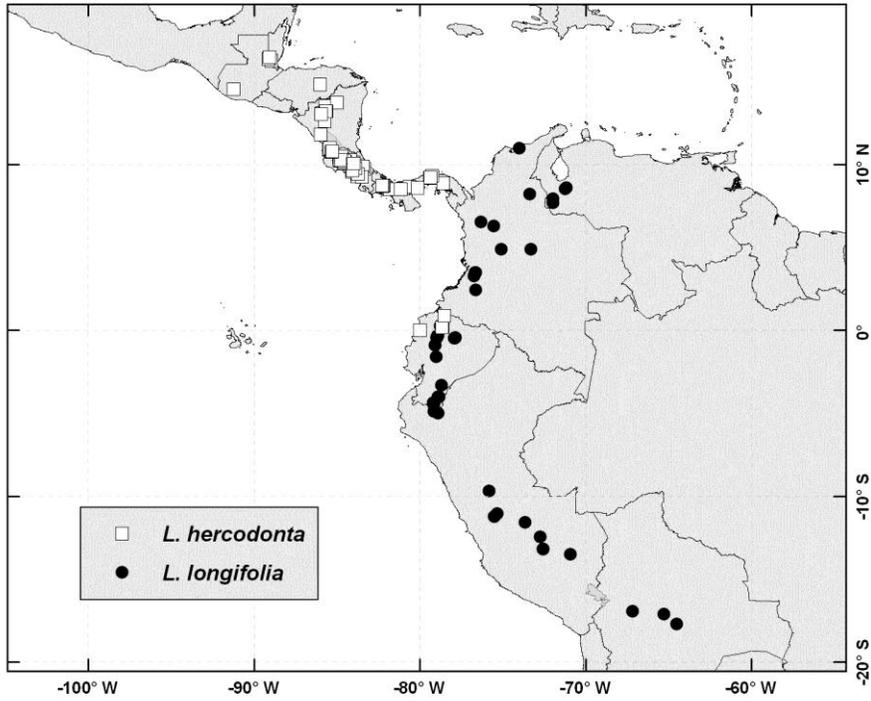


Figure 3-9. Distribution of *Lockhartia hercodonta* and *L. longifolia*.

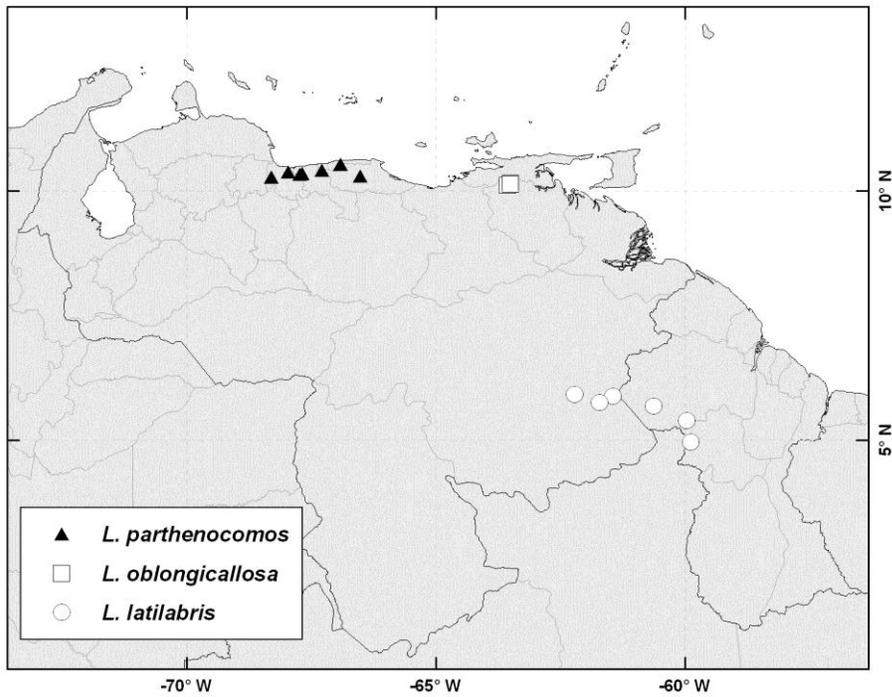


Figure 3-10. Distribution of *Lockhartia latilabris*, *L. oblongicallosa*, and *L. parthenocomos*.

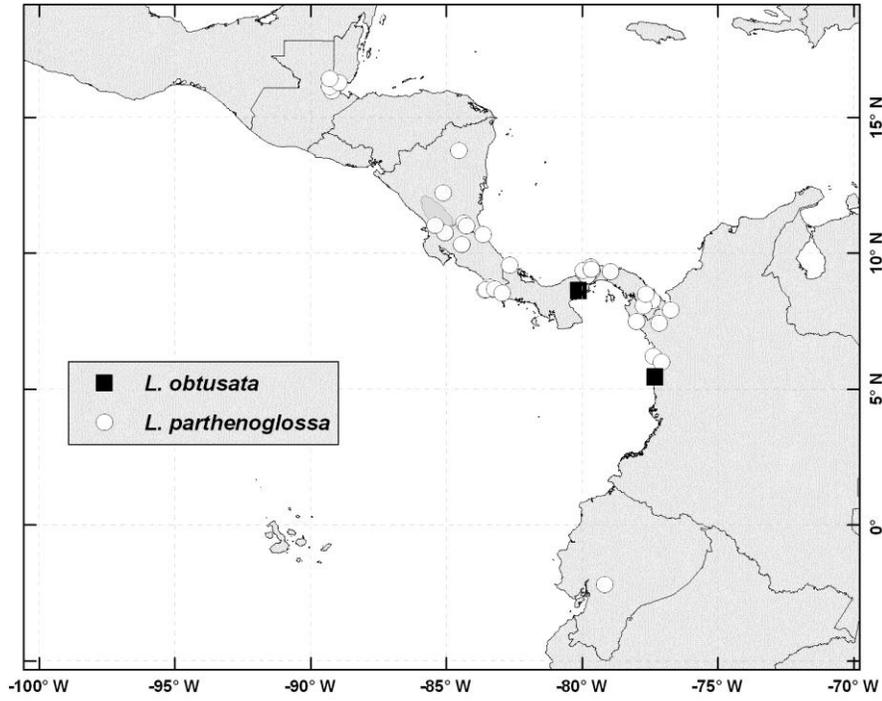


Figure 3-11. Distribution of *Lockhartia obtusata* and *L. parthenoglossa*.

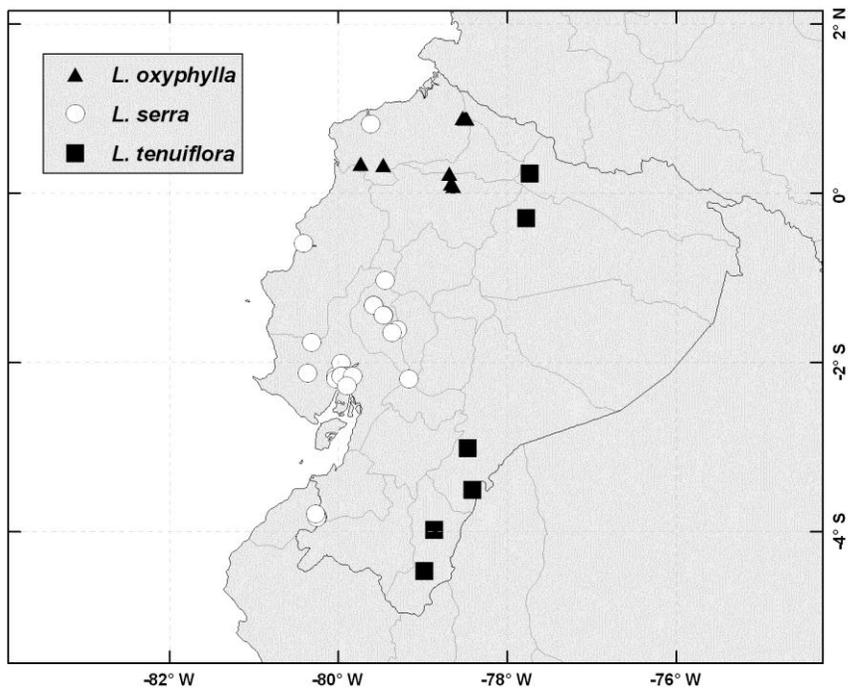


Figure 3-12. Distribution of *Lockhartia oxyphylla*, *L. serra*, and *L. tenuiflora*.

CHAPTER 4 MORPHOLOGY, ANATOMY, AND PHYTOCHEMISTRY

Based on their general morphology, the species of *Lockhartia* are classified in two subgenera; subgenus *Lockhartia*, which contains all but one species; and subgenus *Pseudobulbosa*, which has only one member, *L. genegeorgei* (which is immediately distinguished from the other species by its vegetative morphology). Subgenus *Lockhartia* can be subdivided into three informal phenetic groups (Table 4-1): the “Imbricata” group (19 species), the “Longifolia” group (four species), and the “Parthenocomos” group (five species). The Imbricata group can be subdivided into three subgroups: the Imbricata subgroup (15 species), the Acuta subgroup (with one species, *L. acuta*), and the Oerstedii subgroup (three species).

Plants of subgenus *Lockhartia* are easy to assign to either of the Imbricata, Longifolia, or Parthenocomos groups, especially when flowers are available. However, these groups are not monophyletic according to molecular data (Phylogeny, Chapter 5), and the status of *L. genegeorgei* as a legitimate member of the genus is still unclear (several of its morphological traits suggest it may be a recent intergeneric hybrid between a species of *Lockhartia* and a species of the genus *Oncidium*). The species in the Parthenocomos group tend to be underrepresented in herbaria and are rarely found in cultivation; thus, some details of their morphology and anatomy are still unknown.

Various features of the anatomy of *Lockhartia* species have been reported by Möbius (1887), Wetz (1897), Williams & Broome (1976), N. H. Williams (1979), Ziegler (1981), Pridgeon *et al.* (1983), Møller & Rasmussen (1984), Pridgeon (1987), Chase & Phippen (1988), Porembski & Barthlott (1988), Stern & Carlswald (2006), Szlachetko & Mytnik-Ejsmont (2009), and Sandoval-Zapotitla *et al.* (2010b), always as part of surveys

of larger taxonomic groups. Many of these authors did not prepare or cite voucher specimens for their study plants, and thus their specific identity cannot be verified. This is significant because many *Lockhartia* plants, both in cultivation and in herbaria, were found to be misidentified during the course of this investigation.

In the following discussion, the classifications of Chase *et al.* (2003) for Orchidaceae, and of Pridgeon *et al.* (2009) for subtribe Oncidiinae, are followed.

Materials and Methods

The study of each organ is here divided into morphology (external, macroscopic structure, observable with the naked eye) and anatomy (both external and internal microscopic structure, observable with light microscopy and scanning electron microscopy).

Morphology

Plants of *Lockhartia* were studied from live specimens cultivated at the Florida Museum of Natural History (approximately 45 plants representing 17 different species), additional plants cultivated and observed at other institutions, and from ca. 2275 herbarium specimens representing ca. 1514 different collections (Taxonomic Revision, Chapter 3).

Flowers, fruits, and vegetative portions of living plants (and a few rehydrated organs from herbarium specimens) were photographed and/or drawn using a Wild M5 dissecting microscope with a camera lucida attachment.

Anatomy

Roots, stems, leaves, flowers, and fruits from some of the cultivated plants were fixed in FAA (70% ethanol, acetic acid, and formalin, 9:0.5:0.5) from two to six days, and then washed in water and stored in 70% ethanol until sectioned. Transverse

sections of stems, leaves, and fruits (75–150 μm thick, depending on the structure) were made with a sliding microtome. Roots and flowers were embedded in paraffin wax and transverse sections (25–75 μm thick) were made with a rotary microtome. Sections were stained with Heidenhain's iron-alum haematoxylin and counter-stained with safranin (Johansen, 1940). Epidermal leaf scrapings were made following Cutler's method (Cutler, 1978). Sections and scrapings were mounted on glass slides with Canada balsam, and were observed and photographed with a Zeiss Axioskop 40 compound microscope.

The length and width of ten guard cells were recorded in one sample each of 10 species (one young leaf per plant per species; taken five to 10 leaves below stem apex from an actively growing stem).

Seeds of nine plants representing eight species were either fixed in FAA and stored in 70% ethanol, or rehydrated from dry material by placing them in water for five minutes. The length and width of ten seeds per plant were measured using a compound microscope with a calibrated stage micrometer.

The leaf surface of one species, the flower surface of five species, and the seeds of three species of *Lockhartia* were observed with an Hitachi S-4000 Scanning Electron Microscope (SEM) at 6 or 8 kV following dehydration with an ethanol gradient, critical point drying, and sputter coating with platinum.

Results and Discussion

In the rest of this section, the various plant structures are described in general for species of subgenus *Lockhartia*, and those of *L. genegeorgei*, if different, are pointed out accordingly. The anatomy of *L. genegeorgei* has not been studied previously nor in the present study, and it is possible that it differs in some details from that of the other

species. Therefore, any generalizations about the anatomy of *Lockhartia*, both in the following paragraphs and the cited literature, should be interpreted accordingly.

General Habit

Plants of *Lockhartia* are always epiphytes, with a sympodial mode of growth (Holttum, 1955; Dressler, 1981; H. Rasmussen, 1986). All species in subgenus *Lockhartia* have the same general vegetative structure, with elongate, narrow stems with many internodes (always more than 14 in fully grown adult stems, up to 74 in a few cases), that are concealed by the imbricating, non-articulated, isobilateral leaves (Chase, 2009; personal observation). This condition is similar to that found in some other, unrelated genera of epiphytic orchids, such as *Dendrobium* sections *Aporum* and *Rhizobium* (Carlsward *et al.*, 1997), and some species of *Angraecum*, *Epidendrum*, *Jacquinella*, *Oberonia*, and *Podochilus* (Fig. 4-1B). This is in sharp contrast to the growth habit of most other members of subtribe Oncidiinae, which have heteroblastic pseudobulbs (comprised of a single swollen internode) with one to four dorsiventral leaves at the apex and a similar number of leaves at the base (Fig. 4-1A).

Lockhartia genegeorgei has an intermediate condition between that of subgenus *Lockhartia* and that of most other members of Oncidiinae; it has relatively short stems that terminate in a heteroblastic (single internode) pseudobulb, and has articulated, linear, conduplicate leaves (Bennett & Christenson, 1998), (Fig. 4-1C).

Roots

Morphology

As in most other members of subtribe Oncidiinae and most epiphytic orchids in general, the roots of *Lockhartia* are cylindrical, glabrous, have green growing tips and a white velamen (Pridgeon, 1987). They are relatively thin, ca. 1–1.5 mm in diameter. The

roots are almost always unbranched or only sparsely branched. Only in rare cases do the roots show regular branching. The only herbarium specimen of *L. genegeorgei* with roots shows frequent root branching.

Normally, roots are borne from the basal, rhizome-forming portion of the stem. However, some species (e.g., *L. amoena*, *L. grandibractea*, *L. longifolia*) occasionally produce roots from more distal portions of the stem. In either case, the roots emerge directly from the base of the axillary bud (usually one per bud, but rarely more). These roots occasionally break through the base of the leaf.

The roots produced from the rhizome invariably grow tightly appressed against the surface of the substrate; only the roots that are rarely produced from the upper parts of the stem hang free.

The external morphology of the roots offers no useful taxonomic characters.

Anatomy

Root transverse sections of three species of *Lockhartia* (*L. serra*, *L. tenuiflora*, and *L. verrucosa*) were studied with light microscopy.

The velamen consists of three to five cell layers (three to four layers found by Pridgeon, 1987; Porembski and Barthlott, 1988). Five cell layers were observed in the velamen of *L. serra* (Fig. 4-2).

Porembski and Barthlott (1988) distinguished 10 major types of velamen in the roots of Orchidaceae; *Lockhartia*, as all members of tribe Cymbidieae (sensu Chase *et al.*, 2003), has the “*Cymbidium* type” of velamen. This velamen type is characterized by the epivelamen cells slightly smaller than those of the endovelamen (but otherwise not too different from them), the cells somewhat elongated radially, cell walls with thin, long-sinuate thickenings (and these interrupted by numerous large pores in the non-

thickened wall portions), exodermis cells smaller than those of the endovelamen and with thickened outer tangential walls, and cortex frequently containing tracheoidal idioblasts (but the latter are absent in *Lockhartia*, (Porembski & Barthlott, 1988). In root transverse sections of *Lockhartia lunifera* and *L. oerstedii*, Stern and Carlsward (2006) observed isodiametric epivelamen cells and isodiametric to anticlinally (radially) elongated endovelamen cells, which agrees with Porembski and Barthlott's (1988) characterization.

The exodermal cells have U-shaped wall thickenings: the anticlinal and internal-periclinal walls are thickened; this was also reported by Stern and Carlsward (2006).

The cortex consists of two (in *L. verrucosa*) or three cell layers. The cortical cells are parenchymatous, isodiametric, and the diameter of the innermost ones is more than twice that of the exodermal cells. There are conspicuous intercellular spaces where the walls of three or more cortical cells meet. Stern and Carlsward (2006) remark that the walls of the water storage cells of the root cortex are smooth (those in the leaves are banded).

Stern and Carlsward (2006) reported isodiametric cells with thickened walls in both the endodermis and pericycle of *Lockhartia*. Clear observation of those structures was not possible in the microscopic slides prepared for the present study, due to the excessive thickness of the sections. Like most members of subtribe Oncidiinae, roots of *Lockhartia* lack tilosomes (Pridgeon *et al.*, 1983; Stern & Carlsward, 2006).

The stele consists of a solid cylinder of small-diameter xylem cells (apparently tracheids and/or very narrow vessels) on the periphery, with seven major and seven minor groups of phloem cell bundles. Stern and Carlsward (2006) reported a hexarch

root stele in their samples of *Lockhartia*, although they did not publish any illustrations. The major phloem bundles are located about two or three cell layers inside the xylem cylinder and alternate with the more peripheral minor phloem bundles. The core of the stele consists of fibers (with thicker walls than the xylem cells, with no intercellular spaces (also reported by Stern & Carlswald, 2006).

Stems

Morphology

Each unit or branch of the sympodial system is divided into a proximal, short (2-4 internodes, ca. 5 mm long) rhizome segment, which grows appressed to the substrate and has very small bracts, and a distal, elongate (up to 85 internodes and 85 cm long in some species), erect or pendulous leafy portion. In most species of *Lockhartia* (except in *L. genegeorgei*), the stem axis has the potential to continue growing past the leaf-bearing portion and become a terminal inflorescence (Inflorescences, below).

In most species, stems are more or less rigid and have a tendency to grow erect. Large plants of these species, however, often produce stems that grow downward (although they remain rigid), probably to avoid shading by other stems of the same plant. Some species that normally produce erect stems in cultivation (e.g., *L. acuta*) are described as pendent in many herbarium collections. Other species have relatively flexible stems that may initially grow upward, but invariably become pendulous as they increase in length (e.g., *L. longifolia*, *L. obtusata*, *L. parthenocomos*). The orientation of the stems with respect to gravity, or more specifically, the relative rigidity of the stems, is taxonomically important. One species (*L. bennettii*) seems to be variable in this respect, with some plants producing pendent stems and others having erect stems.

The length of the stem is variable, depending on the age of the plant, its relative strength, and the environmental conditions. Seedlings and juvenile plants produce progressively taller stems; these juvenile stems cease their growth before the next stem is produced from their base. At some point, one of the stems (the first adult stem) produces inflorescences after it stops elongating. Subsequent adult stems continue to become taller until they reach a height that is characteristic of the species or population. In the species descriptions (Taxonomic Revision, Chapter 3), the stem length is reported only for adult, mature stems (those with inflorescences or inflorescence remnants). Adult stems are here defined as those that have attained the potential to produce an inflorescence.

Adult, mature stems of *Lockhartia imbricata* and *L. micrantha* can be very short (e.g., only 3.5 cm long in *Granville 5258, CAY, L. imbricata*), but both of these species can also produce much longer stems (up to 35 or 46 cm long, respectively). On the other extreme are the pendent stems of *L. longifolia* and *L. rugosifolia*, which can reach up to 80 and 84 cm long. In the latter case, these are lengths measured from live plants, as the entire length of the longest stems in these species is rarely included in herbarium specimens; it is likely that the stems of these species can become much longer in natural conditions. The relative length of the stem is not necessarily related to its orientation (erect or pendent) or relative strength (rigid or flexible); for example, *L. acuta* and *L. lepticaula* typically produce rigid, erect stems that can grow up to 76 and 74 cm long, while in *L. obtusata* and *L. parthenoglossa*, which have flexible, mostly descending to pendent stems, the maximum recorded lengths are 41 and 45 cm, respectively.

The stems of *Lockhartia genegeorgei* are unique in the genus in having a pseudobulb formed by the last internode (Fig. 4-1C). This pseudobulb is 2–5 cm long and 4–6 mm wide (measured from dry herbarium specimens; the width may be slightly larger in live plants), and somewhat flattened. The rest of the erect part of the stem has only 4 or 5 internodes.

Normally, the stems do not branch. In rare occasions, however, branches do develop from an axillary bud, and these may produce basal roots and additional shoots in sympodial fashion (Senghas, 2001). These “keikis” (as they are known in horticultural circles) can eventually become established, and probably constitute an (infrequent) mode of vegetative propagation in nature. These “keikis” form mostly in stems whose base or apical meristem has been damaged; they rarely form in young, healthy stems. In cultivation, the formation of “keikis” can reportedly be induced by cutting a shoot from the base and placing it on top of moist *Sphagnum* moss (Hawkes, 1958).

The stem axis is entirely, or almost entirely, concealed by the overlapping leaves (Fig. 4-3A). The apical part of each internode is infrequently exposed between the sheaths of the two lower leaves. Only rarely do some internodes grow longer than the subtending leaf sheath and get almost completely exposed.

Each stem and its leaves form a distinctly flattened, ancipitous shoot. Therefore, the term “shoot” throughout this treatment refers to the stem and leaves together. The shoot width (measured as the distance between the outermost leaf portions on opposite sides of the shoot; Fig. 4-3A) is reported for each species in the Taxonomic Revision (Chapter 3).

Probably because it is normally hidden within the leaves, the stem epidermis is devoid of stomata. The stem surface, however, is never adnate to the inner epidermis of the leaf sheath (but see below for an alternative interpretation). Stems are somewhat compressed in cross section (often appearing ancipitous), with the two edges aligned with the leaf midribs and axillary buds (i.e., the parastichies). The stem surface is always glabrous and smooth.

The leaves are decurrent on the stem, so that each internode is somewhat wider distally. This is not normally apparent unless the leaves are removed from the stem; after this, the distal end of the internode forms a ledge between it and the narrower base of the next internode. This ledge is slightly wider on the side of the next leaf axil, and supports a small axillary bud, which is completely hidden in the leaf sheath. There is always a visible line that marks the leaf insertion (where the tissues of the stem and leaf separate and diverge); this line can be whitish to purple, and is often partially or completely hidden by the sheaths of the preceding leaves.

Anatomy

In cross section, the stem presents three main zones: epidermis, a non-vascularized cortex, and a vascular “core” (Fig. 4-4A,B). In thick sections, the cortex appears translucent, while the vascular core appears opaque. A similar organization of stem tissues in *Lockhartia* was noticed by Weltz (1897) and Stern and Carlswald (2006). Among other genera in the Oncidiinae, a clear distinction between stem cortex and vascular core has been reported in *Aspasia lunata* Lindl., *Gomesa crispa* (Lindl.) Klotzsch ex Rchb. f., *Warmingia* Rchb. f. sp., *Oncidium baueri* Lindl. (Stern & Carlswald, 2006), and *O. sphacelatum* Lindl. (Withner *et al.*, 1974). It is unknown if the stem tissues of *Lockhartia genegeorgei* are organized into core and cortex.

The epidermal cells are ca. 20–30 μm wide, 5–10 μm tall (periclinally flattened) in cross section (Fig. 4-4C). Their external surface is smooth and devoid of stomata. The lack of stomata (or their occurrence in low densities) is actually a common trait of the epidermis of the pseudobulb (and probably stems in general) in many orchids (Solereeder & Meyer, 1969).

The cortex is composed by 3–4 cell layers perpendicular to the stem wings, and 6–15 layers parallel to the wings. The number of cortical cell layers is reduced at the base of the internode (in the segment surrounded by the closed portion of the leaf sheath). The cells are parenchymatous, isodiametric, have thin walls and small intercellular spaces (Fig. 4-4C). Their walls have banded thickenings (reported as smooth by Stern and Carlswald, 2006). They can be much larger than the epidermal cells (up to 150 μm in diameter), and probably function as water-storage cells. Vascular traces in the form of isolated vascular bundles can be observed in the wing portion of the cortex.

The vascular core contains 30–40 vascular bundles embedded in a matrix of small, thick-walled parenchyma cells (Fig. 4-4D). The latter are isodiametric, 25–35 μm in diameter, and each cell contains numerous amyloplasts (at least in young, actively growing stems; no old stems were sampled for anatomy).

The vascular bundles are collateral, with a cap of fibers facing the outside of the stem, several xylem vessels facing the center, and a few phloem sieve elements in the middle (completely surrounded by the fibers and vessels) (Fig. 4-4D). The vessels are quite narrow (10–15 μm wide). The fibers have conical stegmata (small cells almost completely filled with a relatively large silica body) appressed to their outer-facing walls

(Møller & Rasmussen, 1984; Stern & Carlswald, 2006). Only the fiber caps on the periphery of the vascular core have associated stegmata; the inner vascular bundles lack stegmata.

Homology

For practical purposes, both stem cortex and stem core are both treated here as part of the stem (also in the species descriptions of the taxonomic revision, Chapter 3). However, it is plausible that the cortex represents the proximal part of the leaf sheath that has become completely adnate to the stem. A similar condition is found in other groups of monocotyledons with isobilateral leaves, such as *Acorus* L., *Jacquiniella* Schltr., and many Iridaceae (Arber, 1921; Arber, 1925). According to this interpretation, the vascular core represents the stem proper, which has lost its epidermis, and the axillary buds have moved up the stem to the new leaf axils. The stem-leaf fusion hypothesis is supported by the divergence of the leaf traces from the vascular “core” several millimeters below the leaf axil. As in most other taxa in the Oncidiinae, the leaf bases of *Lockhartia genegeorgei* are not decurrent on the stem.

Leaves

Morphology

As in most other genera in tribe Cymbidieae, the leaves of *Lockhartia* have a distichous arrangement along the stem. The leaves of all species in subgenus *Lockhartia* are markedly flattened laterally and lack an abscission layer. In the species descriptions (Taxonomic Revision, Chapter 3) and elsewhere in this chapter, the leaf shape for species in subgenus *Lockhartia* is described as seen in lateral view. If a leaf ceases to be functional, it dries up still attached to the stem (i.e., the leaves are

marcescent); it may eventually disintegrate in place or break away from the stem if pulled.

The stem wings are probably of foliar origin (see above); however, for practical purposes the base of the leaf is defined here as the point where it diverges from the stem. Usually, there is a change in color and/or texture at this point, and some species (e.g., *L. serra*) may have a purple line marking the leaf insertion.

Leaves of subgenus *Lockhartia* have three main zones (Fig. 4-3B): 1) an amplexicaul, tubular, closed sheath that tightly clasps the next internode; 2) an elongate bifacial, open sheath, that gradually diminishes in depth distally, and 3) an isobilateral, unifacial “blade” that extends beyond the open sheath. The closed portion of the sheath is relatively short (2–12 mm), and is normally hidden by the open sheath of the preceding leaf. The length of the open sheath and unifacial blade is variable, depending on the species. In Chase’s (1986) survey of leaf types in the Oncidiinae, such leaves are categorized as “Type III”.

Because the leaves of subgenus *Lockhartia* lack an abscission layer and may be partially fused to the stem, it is unclear what part is homologous with the blade of other Oncidiinae (defined here as the portion of the leaf above the abscission layer). Some other members of subtribe Oncidiinae with isobilateral leaves have an abscission layer that divides the open sheath from the unifacial blade (e.g., *Macroclinium*, *Ornithocephalus* spp.). It is possible that the thin line that marks the leaf insertion represents the remnant of the abscission layer, which is no longer functional. According to this interpretation, the stem wings are homologous with the leaf sheath, which has become fused to the stem, and the entire “leaf” above the insertion point (including the

closed and open sheaths, and the unifacial blade) is homologous with the leaf blade proper of other Oncidiinae.

Leaf size is variable within species. There is usually a gradient along individual stems; typically the leaves near the base of the shoot (just above the rhizome) are much smaller than those of the middle portion. In many species, the leaves also decrease in size toward the distal portion of the stem (Fig. 4-1B). This is especially noticeable in *L. oerstedii*, which thus has characteristically “flagelliform” shoots. Other species, like *L. galeottiana* and *L. verrucosa*, do not normally show a distal reduction in leaf size. These are only trends, however, as there is substantial variation in the vegetative morphology of every species. In the species descriptions prepared for the present work (Taxonomic Revision, Chapter 3), the leaf dimensions are reported for the largest leaf in each stem, which is usually located near the middle or the basal third of the stem. The leaf length was measured as a straight line (even if the leaf was curved) from the apex to the most basal visible part, usually located in the angle formed by the two previous leaves (the base of the leaf is usually completely hidden by the sheath of the previous leaf, which would require dissection of every specimen to measure the total length). The leaf width was measured as the straight line that reached the widest visible part of the leaf (at or near the top of the tubular sheath), perpendicular to the outer leaf margin (Fig. 4-3A).

Lockhartia genegeorgei (subgenus *Pseudobulbosa*) has elongate, linear, conduplicate leaves, provided with an abscission layer that divides the sheath from the blade (Fig. 4-1C). The terminal leaf on the pseudobulb of this species lacks a sheath, but it has an abscission layer at the base. Chase (1986), who surveyed the main leaf

types present in the Oncidiinae, classified these leaves in his “Type V” (the most common type of leaf in the subtribe).

In subgenus *Lockhartia*, overall leaf shape is taxonomically useful to distinguish some species, but there is extensive interspecific overlap among most others. All species of the Longifolia group have unique leaf shapes that almost always can be used reliably for identification (*L. longifolia* has elongate, sigmoid leaves; those of *L. hercodonta* are usually shorter and slightly incurved distally; in *L. parthenoglossa* they curve outward, and *L. obtusata* has oblong to widely elliptic, obtuse leaves). The leaves of *L. galeottiana* and *L. goyazensis* also curve away from the stem. Those of *L. acuta* (Acuta subgroup) are relatively thick and are usually subpraemorse just below the apex, which is often apiculate and sharp to the touch.

The leaves of most other species (especially those in the Imbricata group) are more or less obliquely triangular and less useful for taxonomic identification. There are some differences among species in the leaf relative length, apical shape, angle of divergence from the stem, and even color, but these are not always consistent and are not reliable by themselves for species identification.

The surface of the leaf is always glabrous, and in most species it is smooth. In *Lockhartia parthenoglossa* and *L. rugosifolia*, however, the surface is rugulose, like that of some species of *Macroclinium*. The leaves of *L. rugosifolia* are more markedly rugose than those of *L. parthenoglossa*; in the later case, the leaf surface has to be observed under magnification to detect the wrinkly surface. In both cases the wrinkles form a reticulating pattern, delimiting smooth areoles that contain one or a few stomata. In subgenus *Lockhartia*, the leaf is smooth but has a pattern (more evident under

magnification and toward the leaf base) of tiny, dark green dots in a pale, greyish-green background. The dark green dots appear to be the stomatal subsidiary cells and possibly other surrounding cells. This gives these leaves a characteristic glaucous-like appearance from a distance. This dotting is frequently retained in herbarium material, but appears to be absent in the available herbarium specimens of *L. genegeorgei*.

The angle of divergence between the stem axis and the leaf base (using its adaxial leaf margin as a guide) is a taxonomically useful character in some cases. Most species have moderate divergence angles (15–30°), but some species tend to have narrower angles (5–15°), so that the leaves look very appressed to the stem (e.g., *L. oerstedii*, *L. rugosifolia*). Other species have leaves that are widely divergent from the stem (30–45°), which gives the entire shoot a “feathery” look (e.g., *L. galeottiana*, *L. hercodonta*, *L. longifolia*, *L. parthenoglossa*).

Anatomy

Möbius (1887) was the first to study the leaf anatomy of *Lockhartia*, as part of his family-wide survey of foliar anatomy. He illustrated a leaf cross section of *L. lunifera* (Möbius, 1887; plate XXIV-2). Other authors that studied the leaf anatomy of *Lockhartia* include Wertz (1897), N.H. Williams (1979), Møller and Rasmussen (1984), Stern and Carlswald (2006), and Sandoval-Zapotitla *et al.* (2010a, b).

The abaxial epidermis has abundant stomata (Fig. 4-5). The epidermal cells range from approximately isodiametric to axially elongate in surface view (ca. 25–50 µm long), have straight to irregular anticlinal walls, and are usually nucleated. Stomata are flush with the epidermis (or, in *L. parthenoglossa* and *L. rugosifolia*, at the center of wide “areoles” formed by the raised epidermal parts that form the rugose leaf texture) and have prominent cuticular ledges, with a fusiform-shaped slit for an opening. The inner

wall of the guard cells (the one facing the mesophyll) is conspicuously thickened. As reported by N. H. Williams (1979), each stoma usually has four subsidiary cells (two lateral and two polar; i.e., tetracytic), although divided lateral or polar subsidiaries are not uncommon (resulting in five subsidiary cells). The subsidiaries are similar in shape to other epidermal cells, but they often have a higher concentration of chloroplasts and they often stain slightly darker than other epidermal cells. The stomata of *Lockhartia* range from 21 to 33 μm long and from 15 to 33 μm wide (subsidiary cells excluded); thus, they rank among the smallest stomata found in Orchidaceae (compare with data in Rasmussen, 1987). Table 4-2 provides detailed stomatal dimensions for 10 species of *Lockhartia*.

The adaxial epidermis is similar to the abaxial one, except that it is completely devoid of stomata (i.e., the leaf is hypostomatic). The adaxial epidermal cells of *Lockhartia longifolia* are visibly longer than those of other species (ca. 100 μm long). In cross section, the epidermal cells (both abaxial and adaxial) are anticlinally flattened (ca. 10 μm tall; Fig. 4-7E).

The three parts of the leaf (closed sheath, open sheath, and isobilateral blade; Fig. 3-3B) are clearly recognizable in cross section (Fig. 4-7A–D). The mesophyll is clearly divided in two zones; an abaxial chlorenchymatous zone, formed by two or three layers of relatively small cells (ca. 25–30 μm in diameter) densely filled with chloroplasts, and a water-storage zone, formed by three to five layers of relatively large cells (up to 100 μm in diameter) devoid of chloroplasts. This differentiation of the mesophyll was originally noticed by Möbius (1887). Stern and Carlsward (2006) reported the presence of an adaxial hypodermis in *Lockhartia*, which likely corresponds to the non-

chlorenchymatous water storage zone. The mesophyll is solid, with minimal intercellular spaces; most cells are approximately isodiametric, and are not arranged in either palisade or spongy parenchyma (a common feature in plants with crassulacean acid metabolism [CAM] photosynthesis; Nelson *et al.*, 2005). Substomatal chambers are extremely reduced (usually smaller than adjacent chlorenchyma cells, a common feature among epiphytic orchids; Rasmussen, 1987; Fig. 4-8). Bundles of calcium oxalate raphides are found in some cells of the chlorenchymatous mesophyll (also reported for *Lockhartia* by Sandoval-Zapotitla *et al.*, 2010a).

A variable number of longitudinal vascular and fiber bundles is found along the boundary that separates the chlorenchyma from the water-storage mesophyll (and thus closer to the abaxial epidermis). Fiber bundles are usually placed closer to the abaxial epidermis than the vascular bundles. The vascular bundles are collateral, and have prominent abaxial fiber caps that surround the phloem cells, and a few adaxial xylem cells (Fig. 4-8). As in the stem, the fibers have longitudinal rows of stegmata with conical silica bodies on their abaxial side (Møller & Rasmussen, 1984).

In the closed and open sheath portions of the leaf, the median vascular bundle (midrib) runs close to the adaxial epidermis, but in the isobilateral blade it runs approximately in the middle (in between the upper and lower edges; Fig. 4-7B–D).

Inflorescences

Morphology

Inflorescences of *Lockhartia* can be both apical and axillary, even on the same shoot (Figs. 4-9). In most orchids, this is usually a consequence of developmental accidents (e.g., Goh, 1976). Few orchid genera produce both terminal and lateral inflorescences (Arditti, 1992), and species that normally produce both types on the

same shoot (being simultaneously acranthous and pleuranthous, *sensu* Dressler, 1961) are very rare (e.g., several species in the *Epidendrum alberti* Schltr. subgroup; Hágsater, 1985). *Lockhartia* and *Telipogon* Kunth are the only genera in the Oncidiinae that are normally able to produce terminal inflorescences (although in *Telipogon*, individual species produce either lateral or terminal inflorescences, not both, and it is unknown if their terminal inflorescences are truly terminal or pseudoterminal). It appears that *Lockhartia* and *Telipogon* are not particularly closely related (Whitten *et al.*, in preparation), and the capability to produce terminal inflorescences likely evolved independently in both genera.

In some cases, seemingly terminal inflorescences of *Lockhartia* are actually subterminal; careful dissection of the terminal leaves reveals their axillary position (Fig. 4-9B). In such cases, the abortive apical bud is completely hidden by the sheaths of the last two leaves. However, truly terminal inflorescences are often revealed by this method (Fig. 4-9A). In some cases, an axillary inflorescence develops from the axil of the last foliaceous leaf next to the terminal inflorescence, and this can potentially be misinterpreted as a case of dichotomous branching (e.g., as in Andersen *et al.*, 1988).

Mature stems have the potential to produce several inflorescences. A few species (e.g., *L. micrantha*, *L. lepticaula*, *L. obtusata*) normally produce several inflorescences more or less simultaneously on the same shoot. Most other species usually produce inflorescences sequentially, in a basipetal manner (i.e., progressively down the stem from the apex; Fig. 4-10A). In *L. hercodonta*, *L. longifolia*, and *L. parthenoglossa*, the inflorescences are produced basipetally along the stem, but each inflorescence can remain active for many weeks to a few months, and mature stems with several active

inflorescences can give the false impression of having simultaneously developed inflorescences. In at least *L. hercodonta*, *L. longifolia*, *L. oblongicallosa*, and *L. obtusata*, individual mature stems have the potential of producing inflorescences over at least two consecutive years (as observed in cultivated plants).

Some species (e.g., *L. amoena*, *L. micrantha*, *L. verrucosa*) rarely produce terminal or pseudoterminal inflorescences, but their axillary inflorescences are still initiated in a basipetal manner along the stem (except for *L. micrantha*, which has simultaneous inflorescences; Fig. 4-9D).

The sequence of inflorescence initiation along the shoot (for those taxa with the potential to produce more than one inflorescence per stem) has not received much attention in the Orchidaceae. However, most of the taxa that can produce multiple inflorescences per shoot have either simultaneous or acropetal inflorescence initiation. Species of *Dendrobium* Sw. sections *Phalaenanthe* Schltr. and *Spatulata* Lindl. have basipetal inflorescence initiation, although subsequent inflorescences develop in different years (Wood, 2006).

Inflorescences of *Lockhartia* are also peculiar in their unique branching pattern (Wirth, 1964; Schneckenburger, 1993). Once the first flower is produced in the axil of a bract, the inflorescence apical meristem aborts, and further extension growth occurs from the axillary bud located one internode below the floral bract. This branch (coflorescence) produces two to four internodes before producing another flower, and then another branch is produced from the axillary bud located one internode below. This secondary branch usually has a reduced number of internodes, but it may continue the process (Fig. 4-10B). In rare cases, the inflorescence can grow almost indeterminately

through repeated axillary branching. Axillary buds located further down on the main axis of the inflorescence have the potential to produce additional branches, also in a basipetal manner. In *Lockhartia acuta*, the second-order branches have only one internode before the flower (Fig. 4-10C), which gives the inflorescence a somewhat more open appearance. This branching pattern is highly conserved in *Lockhartia*, and I have not seen the apical meristem adjacent to a flower continue the growth of the main axis, either in live plants or in herbarium specimens.

Most species of *Lockhartia* have inflorescences with proleptic branching (i.e., a branch develops only after a flower has been produced by its subtending axis), and thus have sequentially produced flowers (fig. 4-10B). However, some species of the Imbricata group (e.g., *L. acuta*, *L. lepticaula*, *L. micrantha*) have inflorescences with sylleptic branching (i.e., all the branches develop simultaneously), and thus they have simultaneously produced flowers; these inflorescences do not develop any further (Fig. 4-10C). *Lockhartia amoena* is dimorphic for this character, with lowland populations having proleptic inflorescence branching, and those from higher elevations having sylleptic inflorescence branching. In inflorescences with proleptic branching, subsequent daughter branches are always produced in a basipetal fashion (the first from the node immediately below the floral bract, the second from the node below that one, etc.).

The pattern of branch initiation in compound inflorescences of orchids has not received much attention, although acropetal development seems to be the rule (pers. obs.). Basipetal branch development (as expressed in *Lockhartia* species with proleptic branching) is relatively rare among Orchidaceae, although *Oncidium sotoanum* R. Jiménez & Hágsater is one example (Light, 1997, as *O. ornithorhynchum* Kunth), and

apparently *O. melanops* Rchb.f. as well (Dunsterville & Garay, 1972). The basipetal branch initiation of *Lockhartia* inflorescences was first noted by Pfitzer (1882), although he did not elaborate further on the inflorescence architecture of the genus.

Because a flower is the last fully developed structure produced by any given axis, and additional growth of the inflorescence occurs only through branching, the inflorescence of *Lockhartia* has been called a cyme (e.g., Grisebach, 1864; Dressler, 1981; Pridgeon, 1992; Dressler, 1993). However, true cymes have determinate development, in which the apical meristem eventually turns into a flower (Weberling, 1989). This is not the case in *Lockhartia*. Careful inspection of the floral bract base often reveals a filamentous “appendix” opposite the bract axil (Schneckenburger, 1993; Fig. 4-10B,C). This appendix represents the remnant of the aborted apical bud, and demonstrates that the inflorescence of *Lockhartia* is developmentally indeterminate (i.e., polytelic), at least in principle. Thus, the inflorescence of *Lockhartia* is a modified raceme that is always branched (i.e., a compound raceme) whenever it has more than one flower¹.

¹ Branched inflorescences in orchids are frequently called panicles. As defined by European botanists, however, a panicle is a branched determinate inflorescence (e.g., a cyme), which does not occur in the Orchidaceae (Weberling, 1989; Prenner *et al.*, 2009). The raceme (a monopodial floriferous axis; Bell, 2008) is the basic type of inflorescence throughout the Orchidaceae, sometimes highly modified (Schneckenburger, 1993). American botanists explicitly define panicle as a compound raceme (e.g., Judd *et al.*, 2008). Even single-flowered orchid inflorescences usually

It is noteworthy that the developmental pattern of the *Lockhartia* inflorescence appears to be unique, not only among orchids, but (as far as I know) also among angiosperms. Kraenzlin (1923) struggled to categorize it under one of the known inflorescence types, and he compared it to both a corymb and a dichasium. In Weberling's (1989) terminology, the inflorescence of *Lockhartia* can be described as polytelic, with single-flowered main florescence and coflorescences. However, it does not fit any of the inflorescence types described by Weberling. Thus, I propose the term "pseudocyme," which is used throughout the present treatment. Even when it is clearly a modified raceme (polytelic in the strict sense), it has sympodial development (characteristic of cymose, or monotelic, inflorescences).

Dressler (1981, 1993) hypothesized that *Lockhartia* evolved from an ancestor with single-flowered inflorescences, and when more flowers per inflorescence were eventually selected for, these evolved by lateral branching instead of continued apical growth. Another possibility is that it is an adaptation to produce multiple flowers with minimal length extension of the inflorescence axis, which may be important for the mechanical stability of the long shoots that support those inflorescences.

The basal internodes of the inflorescence are usually somewhat flattened, but the more distal internodes are terete. There is usually a rapid transition between the laterally flattened, decurrent leaves and the dorsiventral, non-decurrent bracts in terminal inflorescences (Fig. 4-9).

have an aborted shoot apical bud opposite the flower bract, which reveals their racemose nature.

The base of axillary inflorescences is also somewhat flattened because of the tight space within the leaf sheath. The axillary bud is often slightly displaced to the side, so that it partially overlaps with the base of the next leaf sheath (the preceding leaf has to be dissected in order to see this). There is a minuscule (< 1 mm long) prophyll near the base, opposite the main stem axis. The prophyll and the next two or three bracts are tiny and clasping, and are usually hidden inside the supporting leaf sheath.

Depending on the species, the exposed parts of the inflorescence can have two types of bracts. Most species have widely ovate to subrotund, cordate bracts, which usually are widely expanded and nearly perpendicular to the inflorescence axis. These inflorescences have a very characteristic appearance, and the bracts can be almost as large as the flowers (although they are always pale green). In contrast, other species (e.g., *L. hercodonta*, *L. longifolia*, *L. parthenoglossa*, *L. rugosifolia*) have imbricate, lanceolate, strongly conduplicate bracts that clasp the inflorescence axis. Inflorescences of the second type are very compact and inconspicuous; their pseudo-cymose branching is apparent only upon dissection under magnification. A few species (e.g., *L. bennettii*, *L. obtusata*) have bracts that are somewhat intermediate in shape, being more or less infundibuliform, although this is a variation of the subrotund shape.

Anatomy

The internal anatomy of the inflorescence axis and bracts of *Lockhartia* has not been investigated. The anatomy of the inflorescence rachis is probably similar to that of the “core” portion of the stem, although much less sclerenchymatized (inflorescences are much more flexible and narrower than the stems).

Flowers

Morphology

The flowers of *Lockhartia* are 5–30 mm tall (many species have flowers that are markedly taller than wide). They have been described as very complex, although they are really of average complexity when compared to those of other genera in the Oncidiinae. In fact, *Lockhartia ivainae* and the species of the Parthenocomos group have relatively simple flowers. Only some of the species of the Imbricata group have labella with relatively complex lobes, folded lobes, and calluses.

Flowers of *Lockhartia* probably produce some kind of fragrance to attract pollinators although these are not detectable by most humans. Individual flowers remain open for five to 10 days, after which they wilt and fall if they have not been pollinated. Fitch (1960) reported that flowers of *L. oerstedii* can remain open for more than 10 days. There are no visible changes in the structure of the column during anthesis, and the stigma is presumably receptive during most of this period.

Most (maybe all) species of *Lockhartia* secrete oils from specialized trichomes on the labellum (see below). Thus, even when careful observations on the natural mode of pollination are lacking, it is safe to assume that the pollinators are oil-collecting bees. Such bees are diverse in the Neotropics, and the females collect floral oils as an important dietary component for their larvae (Vogel, 1973; Buchman, 1987; Alves dos Santos *et al.*, 2007).

The pedicel is not sharply differentiated from the inferior ovary. During anthesis, the ovary is only slightly thicker and darker than the pedicel, but usually much shorter (typically ca. 1–2 mm long). Together, the pedicel and ovary can measure from 2 to 20 mm; in the species descriptions, the length of the pedicel includes the ovary (excluding

the description of the fruit, see below). The pedicels in *Lockhartia micrantha* are short (3–9 mm), while those of *L. serra* are long (17–20 mm). However, there is significant inter- and intraspecific variation in the length of this structure, and thus the taxonomic value of this character is limited.

Almost invariably, the pedicel and ovary do not show any torsion, and thus the floral bract is aligned with the dorsal sepal (i.e., opposite the labellum). The pedicel is often bent so that the flower faces obliquely downward, probably an adaptation to prevent raindrops from obstructing access of the flowers to pollinators. In most species of the Imbricata group, the labellum is positioned on the lower side of the flower, regardless of stem orientation, and thus the flowers are resupinate (Dressler, 1981). This is achieved by either torsion of the inflorescence axis, and/or bending of the pedicel to the appropriate side. In *L. micrantha*, a species that produces multiple simultaneous flowers per inflorescence, the labellum seemingly does not have a preferential orientation with respect to gravity; as a group, however, the flowers tend to face mostly downward. In the Longifolia group, *L. hercodonta* and *L. longifolia* have pendent flowers that face mostly or completely down; *L. parthenoglossa* has mostly resupinate flowers, and *L. obtusata* has non-resupinate flowers. In the Parthenocomos group, most species seemingly have pendulous or obliquely resupinate flowers, although *L. parthenocomos* reportedly has a geniculate pedicel and non-resupinate flowers, and *L. bennettii* has resupinate flowers. The flowers of *L. genegeorgei* are resupinate.

The structure of the perianth (especially that of the labellum) of the three major groups of subgenus *Lockhartia* is so different from each other that they probably would

have been described as different genera, if their vegetative morphology were not so uniform and different from that of other Oncidiinae (Figs. 4-11 to 4-13).

The flowers of most *Lockhartia* species are yellow. Four species have white flowers: *L. acuta* (Imbricata group, Acuta subgroup), *L. hercodonta* (Longifolia group), and *L. bennettii* and *L. oblongicallosa* (Parthenocomos group). Almost all the species of the Imbricata and Oerstedii subgroups have brown spots and/or dots on various parts of the labellum and column, and very rarely at the base of the petals. However, *L. ivainae* has completely yellow flowers (although this species is poorly known), and some collections of *L. micrantha* also have unspotted flowers. *Lockhartia longifolia* often has tiny to large brown dots on the ventral surface of the column wings, but none of the other species of the Longifolia group have any brown spotting; however, they all may have orange spots on various parts of the callus rim. In the Parthenocomos group, *L. bennettii* and *L. parthenocomos* have a central area of the labellum with heavy brown spotting (absent in some plants of *L. parthenocomos*), and their column wings can also be spotted.

The sepals are ovate, elliptic, ovate, or obovate, rarely oblong, and are often somewhat concave. They have a small subapical keel near the apex, which may make the sepal look shortly acuminate. The sepals may be only partially expanded (like in the campanulate flowers of the Parthenocomos group), more or less perpendicular to the ovary (e.g., in *L. micrantha* and the Longifolia group), or even completely reflexed from the base, leaning against the pedicel when fully open (e.g., in most members of the Imbricata group). The three sepals are similar in shape, although the lateral sepals may

be slightly oblique at the base (the side of each sepal adjacent to the labellum slightly wider than the opposite side).

The lateral petals (called simply “petals” from here on) may be oblong, elliptic, ovate, or obovate, and either more or less flat or folded along the midline so that their margins are bent backwards. In the latter case, the main axis of the petal is often curved forward, making the petals three-dimensionally falcate, like “bull horns” (e.g., most of the larger-flowered species in the Imbricata group: *L. amoena*, *L. endresiana*, *L. galeottiana*, *L. grandibractea*, *L. oerstedii*, *L. serra*, and *L. verrucosa*; Fig. 4-11A,B). In *L. hercodonta*, *L. longifolia*, and *L. obtusata*, the lateral petals are flat but partially projected forward (Fig. 4-12A).

The structure of the labellum is best described separately for each group. In the Imbricata group, the labellum is variously lobed and often longer than wide (Fig. 4-11A,B). Most species have a pair of lateral lobes located at the base of the labellum; these range from short and obscure (e.g., in some morphs of both *L. imbricata* and *L. micrantha*) to markedly elongate (in most species). In the latter case, the side lobes often curve forward, their tips almost touching each other in some species, and resemble embracing arms; their likely function is to force the pollinator to place its head squarely straight in front of the column.

The three species of the Oerstedii subgroup (*L. galeottiana*, *L. oerstedii*, and *L. verrucosa*) have relatively wide lateral lobes that are often wider near the apex. Other species (e.g., *L. cladoniophora*, *L. compacta*, *L. dipleura*) have lateral lobes of intermediate length and are only partially curved forward. Both *L. imbricata* and *L. micrantha* have morphs with or without lateral lobes, including various degrees of

development when present. The labella of *L. acuta* and *L. ivainae* lack lateral lobes. Most species with long, embracing lateral lobes have brown markings on their adaxial surface (*L. amoena*, *L. endresiana*, *L. goyazensis*, *L. grandibractea*, *L. lepticaula*, *L. lunifera*, *L. oerstedii*, *L. serra*, *L. tenuiflora*, and *L. verrucosa*); the pattern of these markings is often diagnostic of the species or group. For example, the lateral lobes of *L. serra* are almost solid brown, except for the margins, and the species in the *Oerstedii* subgroup have three or four series of oblique, interrupted, semi-parallel lines. The labellum midlobe is usually longer than the lateral lobes, and is often subdivided into two pairs of lobules; these are here called “basal lobules” and “distal lobules”. The basal lobules are usually strongly bent back, so much so that in some cases they touch each other behind the labellum; they often have brown spots (in *L. acuta*, *L. ivainae*, and *L. micrantha*, however, the basal lobules are not strongly bent back nor have spots). The two distal lobules are usually straight or flare out, and do not have any spots; together, they delimit a notch at the apex of the labellum. The callus is formed by a thick ridge that extends from the base to the middle of the labellum, more or less to the level of the isthmus that separates the basal lobules from the distal lobules. The surface of the callus is covered by folds and tubercles of various shapes, either grouped into a single mass or arranged into five or seven parallel keels. *Lockhartia acuta*, *L. cladoniophora*, *L. compacta*, *L. ivainae*, and *L. micrantha* have a much simpler callus that consists of two parallel, slightly raised, wide keels; in *L. ivainae*, the callus is almost non-existent. In most species of the group, the basal part of the callus consists of a cushion-shaped pad with a slight depression at its center. Located in this depression, and immediately under the column, is a patch of tiny glandular hairs that secrete small quantities of oil (Silvera,

2002). The term “elaiophore cushion” is used here for the entire structure. *Lockhartia acuta*, *L. cladoniophora*, *L. compacta*, *L. ivainae*, and *L. micrantha* have either a very reduced elaiophore cushion or none at all, although they all have the pad of secretory hairs at the base of the labellum. The species with a well-formed elaiophore cushion have two kinds of elaiophore hairs (fig. 4-16A,B). One type is relatively long and thick, with clavate tips (up to 400 μm long, ca. 20 μm in diameter at the base, and 40 μm in diameter near the tip; the apex sometimes bifid and then wider); these hairs are restricted to the central part of the elaiophore (immediately beneath the stigma), are parallel to each other, and lie on the surface of the labellum. Their tips are visibly adnate to each other. The second type of hair is much shorter, thinner, and of uniform girth (100 μm long or less and 10 to 15 μm in diameter). These shorter hairs cover the entire surface of the elaiophore, including the areas flanking the central portion (where the long hairs are located). The long hairs often cover the short ones that occur beneath them. The species with a poorly defined elaiophore cushion appear to have elaiophore hairs of a uniform, intermediate length. The elaiophore hairs of 10 species of the Imbricata group that have been histochemically tested have all stained positively with Sudan IV, indicating that they are the source of the oils. The entire surface of the callus in *L. acuta* is covered by much smaller trichomes that also stain positively with Sudan IV (Fig. 4-16C).

In the Longifolia group, the labellum is suborbicular to oblong or even slightly pandurate (obscurely lobed in *L. hercodonta*), but is always entire and slightly to strongly convex (Fig. 4-12). The callus is always crateriform (consisting of a raised, irregular rim that encircles a concavity). The rim can be either high and sharp or low and

more or less rounded, and has either one, two, or four teeth or bulges. Most species of the group (except *L. hercodonta*) have secretory trichomes that line various parts of the rim; these trichomes stain weakly with Sudan IV, indicating that there is a weak production of lipids in them. There is a minute trapezoid ledge at the base of the concavity that is raised proximally and slopes down distally. The bottom surface of the concavity, including part of the trapezoid ledge, is covered with very short hairs that also stain weakly with Sudan IV. The entire callus of the Longifolia group is probably homologous with the elaiophore cushion of the Imbricata group.

The labellum of the Parthenocomos group is concave, suborbicular to obreniform when flattened, and obscurely three-lobed (Fig. 4-13). The lateral lobes are much wider than long and curve up, to partially surround the column. The apex of the midlobe is either straight or slightly convex. Four of the five species in this group have a callus that consists simply of a slightly thickened area at the center of the labellum, which forms an irregularly toothed transversal ledge at the level of the separation of the lateral lobes. The callus of *L. oblongicallosa* is markedly different, consisting of an oblong, longitudinal thickening that is covered with short, orange hairs (probably secretory).

The labellum structure of *Lockhartia genegeorgei* is superficially similar to that of species in the Imbricata group; however, it lacks lateral lobes, has an elongate “elaiophore cup”, and there are two keels that converge in the middle (Fig. 4-14). The elaiophore cup of *L. genegeorgei* is different from the elaiophore cushion of the Imbricata group in that it is not a wide, rounded structure, but it is an oblong concavity surrounded by a pair of sharp keels. In life, the entire labellum is strongly sigmoid in lateral view, a condition not found in any species of subgenus *Lockhartia*.

The column (gynostemium) in most *Lockhartia* species is relatively short and wide (1.5–3.5 × 1.5–6 mm; usually about as long as wide or shorter), sessile, winged, and either straight or somewhat arched upwards to expose the ventral surface (Figs. 4-11C, 4-15). *Lockhartia endresiana* and *L. grandibractea* have columns that are seemingly longer than wide, but that is partly caused by their very narrow column wings. In cross section, the column is more or less flat on the ventral side, and moderately convex on the dorsal side. There is no *tabula infrastigmatica*, a callus-like thickening found at the base of the column in many yellow-flowered taxa in the Oncidiinae. The putative function of the *tabula infrastigmatica* is to allow the bee pollinator to grab it with its mandibles while it attempts to collect oils secreted by the lateral lobes of the labellum with its front and middle legs. Because *Lockhartia* species secrete the oils on the base or center of the labellum, the pollinating bees likely use a different method for holding to the flower while visiting the flowers (the presence of a *tabula infrastigmatica* is often associated with clawed petals, which do not occur in *Lockhartia* either). Many species of *Lockhartia*, however, including most of the members of the Imbricata group, have a characteristic dark brown band at the base of the column immediately below the stigma, shaped like a wide V. The name “infrastigmatic line” is used in the species descriptions for this character. In *L. acuta* and *L. micrantha*, the infrastigmatic line is usually faint, or made up by two brown spots on either side of the base of the column. The column of *L. rugosifolia* lacks an infrastigmatic line, but the disc of the labellum has several transverse, brown bands, the most basal of which is darker and resembles the infrastigmatic line of other species. The function of the infrastigmatic line is unknown, although it probably functions as a visual “oil guide” for the visiting bees.

The wings of the column vary from small and triangular or hemispherical (e.g., in *L. acuta*, *L. hercodonta*, *L. latilabris*, *L. parthenocomos*, and *L. parthenoglossa*), to greatly enlarged and flabellate (e.g., in *L. amoena*, *L. galeottiana*, *L. lepticaula*, *L. longifolia*, *L. obtusata*, *L. oerstedii*, and *L. verrucosa*; Fig. 4-11C). The wings of *L. endresiana* and *L. grandibractea* are triangular and widest at the base of the column. In most species, the column wings expand horizontally on the same plane, rendering the ventral surface of the column flat. *Lockhartia dipleura*, however, has column wings projected downward, giving the column a hooded appearance. The margins of the column wings can be either entire, denticulate, or praemorse. The function of the column wings is probably to guide any pollinia attached to the head of a visiting bee towards the stigma.

The stigma, like that of most Epidendroid orchids, is concave and sticky. Most species of *Lockhartia* have an oblong stigma that is about two to three times as long as wide, often slightly narrower at the center, and slightly deeper than wide. This makes the stigma almost slit-like. In some flowers, the stigma is so narrow that only one pollinium can be inserted at a time, unless the entire pollinarium is rotated to be perpendicular in relation to the stigma. This suggests that normally only one pollinium of the pair is inserted in the stigma. The width of the stigma did not change 72 hours after removal of the anther and pollinarium from the column in three species of *Lockhartia* that were so tested; thus, there is no evidence for structural protandry. The stigma is deep enough for two pollinia to be completely inserted in it, with only the stipe and viscidium remaining outside. *Lockhartia goyazensis* has a much wider, subcircular

stigma, and that of *L. genegeorgei* is teardrop-shaped (ovate with an apical narrow extension).

In subgenus *Lockhartia*, the rostellum (as defined by Dressler, 1989) is a minute (ca. 0.2–0.3 mm), subrectangular tissue flap that projects backwards from the distal wall of the stigma (Fig. 4-11D). The external margins of the rostellum are replicate and clasp the viscidium and the distal portion of the stipe during anthesis (Szlachetko & Mytnik-Ejsmont, 2009). The rostellum of *L. genegeorgei* is much longer (1 mm), sublinear, and curved outward (Fig. 3-14).

As in the vast majority of members of tribe Cymbidieae, the anther is terminal and incumbent (*sensu* Dressler, 1981). The anther bed is relatively flat, smooth, and sits at an angle with respect to the ventral surface of the column (Fig. 4-15). The anther cap is hemispherical, galeate, slightly bilobed at the base (which is located at the apex of the column), and has short apical beak over the rostellum; it measures 0.8 to 1.4 mm in diameter in most species. The anther cap of *L. genegeorgei* is elongate (ca. 2 mm), almost twice as long as wide, with an apical beak that covers the long rostellum. In all species, the external surface of the anther cap is characteristically micropapillate, except for the smooth middle line. Internally, the anther cap has a basal, triangular septum that supports the terminal part of the pollinia. Two short triangular projections (ca. 0.3 mm tall) flank the anther cap on the ventral side of the column, and probably help in holding the anther cap in place. When the anther cap is removed, these projections appear as little “horns”.

The pollinarium in subgenus *Lockhartia* is unusual (although not unique) among members of subtribe Oncidiinae because of its bifid stipe and elongate caudicles. Each

one of the two pollinia are linked to one tip of the bifid stipe by a caudicle. There is a viscidium (*sensu* Dressler, 1989) at the apex of the stipe. As in the rest of tribe Cymbidieae, the stipe is tegular (i.e., it is formed by the epidermal cells -or their periclinal walls- of the dorsal surface of the rostellum; F.N. Rasmussen, 1986). Thus, the stipe is much thinner than the caudicles that connect it to the pollinia (Fig. 4-15). The caudicles are formed inside the anther; this can be clearly seen in the microscopical sections of the anther of an unidentified species of *Lockhartia* presented by Szlachetko and Mytnik-Ejsmont (2009). When a pollinarium of *Lockhartia* (even if freshly removed) is seen from the front, a distinction is not always clear between the stipe and the caudicles. However, if seen from the side (when freshly removed), the caudicles are clearly thicker than the very thin stipe. The pollinia are obpyriform and from 0.2 to 0.5 mm long, depending on the species. The caudicle is an attenuate, basal extension of the pollinium, and there is no sharp delimitation between the pollinium and the caudicle. The stipe is usually shorter than the pollinia and caudicles (Fig. 4-15). After several minutes of removal from the anther, the thin stipe usually collapses upon the viscidium. Thus, it may be difficult to detect the presence of a stipe, and the pollinarium in this condition could be confused with that of a pleurothallid orchid. Bentham (1881) commented on finding pollinia in dry specimens of *Lockhartia* either free or connected by just a viscidium, decidedly an artifact caused by a collapsed stipe. The viscidium is elliptic, and 0.1–0.2 mm long. The entire pollinarium is 0.8–1.3 mm long. The stipe of *Lockhartia genegeorgei* is elongate (ca. 1 mm), entire (not bifid), and slightly wider on the end that supports the pollinia; the entire pollinarium is ca. 2 mm

long. The pollinia in all species are yellow, obovoid, with an acute base, and about 0.4–0.6 mm long.

If one or two pollinia (from the same or a different plant) are deposited on the stigma, the later closes and engulfs the pollinia in a matter of several hours. If the pollinia are from a compatible plant (most species tested are self-incompatible), the ovary enlarges substantially and the perianth withers (Fig. 4-19A).

Figure 4-16 illustrates how the measurements of the various floral parts reported in the species descriptions (Taxonomic Revision, Chapter 3) were made.

Anatomy

The young ovary is nearly cylindrical in cross section, with its wall having approximately 10 cell layers (Fig. 4-20A). The single locule shows three paired, parietal, placental ridges. As in most other orchids, the ovules are not differentiated during anthesis (Clements, 1999).

The labellum is ca. 500–600 μm thick, and, at least near its base, has approximately 12–14 cell layers (Fig. 4-18A–C). The ground tissue is parenchymatous, with minimal intercellular spaces. The epidermal cells are smooth and anticlinally flattened. No stomata were detected in the floral organs. Five to seven vascular bundles are visible in the labellum cross section. The cells of yellow flowered species contain numerous yellow chromoplasts, and the cells on parts of the flower that have brown spots seemingly have these pigments (probably anthocyanins) in vacuoles.

Lockhartia oerstedii has prominent callus tubercles, and these were also studied in cross section. The tubercles are filled with a solid parenchyma, the cells of which are somewhat elongated in the same direction as the point of the tubercle (Fig. 4-18C,D).

The epidermal cells are papillose. Many other species of the Imbricata group also have tubercles in the callus, but not as prominent.

In all species studied, the floral trichomes present on the labellum are unicellular and formed by an extension of an epidermal cell. The nucleus of the cell is normally located in the trichome extension. As seen with the SEM, the floral trichomes have a smooth cuticle, although sometimes the apical portion of the trichome has crystalline deposits of unknown nature (probably lipoidal). The long elaiophore hairs of *L. oerstedii* and *L. oxyphylla* (of the Imbricata species group) are swollen and even bifid at the tip, while the short hairs are never bifid (Fig. 4-17).

Williams and Broome (1976) studied the surface of the pollinia of a variety of orchids with SEM, including two species of *Lockhartia*. Like in most other members of Oncidiinae, the pollinia of *Lockhartia* have a smooth, unsculptured surface, other than well-defined divisions between either tetrads or individual pollen grains (interpreted as tetrads by Pridgeon, 1999) that form a mosaic-like pattern. Dressler (1986), who probably interpreted the bifurcate portion of the *Lockhartia* stipe as part of the caudicles, indicated that the latter are formed almost purely by elastoviscin and are devoid of pollen tetrads. However, Senghas (2001) published SEM images of the pollinarium of *Lockhartia* cf. *amoena* (probably *L. oerstedii*, judging from other misidentified photos in the same article) that clearly show the bifid stipe formed by epidermal cells of the rostellum (or their periclinal walls) and the caudicles made up by somewhat elongate pollen tetrads.

Fruits

Morphology

Fruits of *Lockhartia* are smooth, glabrous, nearly round in cross section, globular to long obovoid (attenuate basally, and rounded to truncate apically), and pendulous (Fig. 4-19A). They range in size from 4 to 25 mm long, and from 3 to 10 mm in diameter. *Lockhartia hercodonta*, *L. micrantha*, and *L. parthenoglossa* have small (ca. 4–7 mm long), subglobose fruits. The fruits of some species (e.g., *L. acuta*, *L. lunifera*, *L. micrantha*, *L. oerstedii*, *L. serra*) are glaucous, covered by a whitish waxy bloom that is easily rubbed off if touched. Other species have non-glaucous fruits (e.g., *L. grandibractea*, *L. obtusata*). The presence of glaucousness is apparent only in live fruits, and thus the state for this character is unknown in species for which fruits are only known from herbarium material. The fruits of other species (e.g., *L. amoena*, *L. bennettii*, *L. cladoniophora*, *L. compacta*, *L. endresiana*, *L. genegeorgei*, *L. ivainae*, and *L. lepticaula*) are unknown, although they are probably similar in structure to those of other species.

Like the fruits of most other orchids, those of *Lockhartia* are unilocular capsules with parietal placentation and loculicidal dehiscence (i.e., the dehiscence lines run along the midrib of each carpel; Rasmussen & Johansen, 2006; Figs. 4-19, 4-20). A diagram of a fruit cross section of *L. acuta* was first published by Eichler (1875: 182; as *Fernandezia acuta*), and an entire unopened fruit of *L. lunifera* was first illustrated by Barbosa Rodrigues (1883).

Upon maturation, the three valves separate from each other from the apex while they are still green, and then recurve, exposing the paired placental ridges located along the middle line of each valve (Fig. 4-19B,C). Because the fruit is pendulous, the

inner surface with the placentae remains protected from raindrops. Hygroscopic endocarpic trichomes line the inner margins of each valve and assist in the dispersal of the seeds by dislodging them from the placentae. The mode of dehiscence of *Lockhartia* fruits was first described by Prillieux (1857) for *L. acuta* (as *Fernandezia acuta*), and illustrated by Eichler (1875: 182; as *Fernandezia acuta*) and Pfitzer (1882). It is the same in all species of *Lockhartia* for which dehisced capsules have been observed. Most other members of Oncidiinae have fruits that dehisce through three lateral slits, but in which the valves remain attached to each other at the apex.

The open capsules dry up in a matter of a few days after dehiscence, shrinking substantially in the process. An open capsule can shrink to almost half of its original size. Unopened capsules do not shrink so much when dried for the herbarium; thus, all measurements of fruits in the species descriptions are taken exclusively from unopened capsules, either from live material or from herbarium specimens. Only seemingly mature capsules were measured.

Anatomy

Anatomical studies of orchid fruits are few (Rasmussen & Johansen, 2006, and references cited therein). Transverse sections of an unopened fruit of *Lockhartia serra* (*Blanco 2574*, FLAS) were studied for the following description (Fig. 3-20). The fruit anatomy of other species of *Lockhartia* has not been studied but is likely similar. The terminology and structural interpretation of orchid fruits proposed by Rasmussen and Johansen (2006) is followed here.

The fruit wall is formed by ca. 12–16 cell layers, including the external and internal epidermises. The external epidermis consists of anticlinally flattened cells (Fig. 4-20C). The ground tissue of the internal cell layers is parenchymatous; the cells are

approximately isodiametric in the region under the paired placental ridges (i.e., in the region of fusion of two adjacent carpels). However the parenchymatous cells are transversely stretched (and thus thinner) in the areas between the paired placental ridges. A consequence of this is that the fruit wall is thinner between placental ridges than under those ridges (ca. 1.0 mm thick in its thinnest part, ca. 1.8 mm under the ridges). Large brachysclereids are scattered through the fruit wall, although they are more numerous close to the external epidermis (Fig. 4-20C). These idioblasts are slightly elongate with their long axis aligned radially from the center of the fruit, and two to five times as large as the surrounding parenchyma cells. These sclereids possibly serve as a defense against chewing herbivores.

The internal epidermis of the fruit between the placental ridges is formed by a layer of thin-walled, globular cells, which are lignified (as evidenced by their positive staining with safranin; Fig. 4-20D). This layer of cells becomes thinner near the placental ridges and eventually disappears at their base. At the center of the areas between placental ridges (i.e., along the midribs of the carpels, where these split apart) there is a narrow zone of emergence of endocarpic trichomes. These are hollow and also have lignified walls. The endocarpic trichomes are absent in the young ovary (Fig. 4-20A); thus, they probably develop concurrently with the seeds.

The placental ridges are irregularly branched, ca. 0.8–1.2 mm long, and are formed by much smaller parenchymatous cells. Each major branch of the placenta bears a few dozen ovules. The fruit locule is wide enough (ca. 4.5 mm at its widest point) that the branches of one placental ridge do not touch those of other ridges.

At either side of the base of the placental ridges, thick, dark masses can be seen; these are remnants of pollen tube aggregations (Fig. 4-20B; Rasmussen & Johansen, 2006).

Seeds

Most orchids have wind-dispersed “dust seeds”, which vary in length from 50 μm to 6 mm; in most cases they consist of a simple, fusiform seed coat with a loose embryo and suspensor inside (Molvray & Chase, 1999; Arditti & Ghani, 2000, and references therein). Species in subtribe Oncidiinae are rather uniform in their seed morphology; in general, their seeds are similar to those of subtribe Maxillariinae, although usually relatively longer (Chase & Pippen, 1988).

The seeds of *Lockhartia* are typical of those of the Oncidiinae, and are unremarkable within the subtribe. Chase and Pippen (1988) illustrated the seed of *L. galeottiana* (as *L. oerstedii*) with SEM, and seeds of three other species were observed with SEM for the present study (Fig. 4-21). In addition, length and width were measured for seeds of nine different collections representing eight species. The seeds were rehydrated for a few minutes in tap water, put on a microscope slide, and ten seeds from each collection were randomly selected and measured for each collection (Table 4-3). Chase and Pippen (1988) observed a 25–40% decrease in seed width (but no change in length) after drying; it is unclear if rehydrated orchid seeds recover their original width, and the width measurements reported here should be interpreted with caution.

The seeds of *Lockhartia* are fusiform, with a slightly wider to truncate micropylar pole. The testa cells are oval and elongate, with thickened anticlinal walls. The ends of the testa cells are round, and the anticlinal walls are sinuate in the zone of overlap of

contiguous testa cells. The external periclinal walls are very thin and collapse at maturity, with the result that the anticlinal walls form a network of ridges over the entire testa. Aside from these anticlinal cell ridges, there are neither cell wall extensions nor sculpturing of any kind. This agrees with the seed characters for the genus reported by Ziegler (1981) and Chase and Pippen (1988).

The measured length of *Lockhartia* seeds varies from 162 μm (in *L. oerstedii*) to 475 μm (in *L. longifolia*), and the width varies from 56 μm (in *L. micrantha*) to 125 μm (in *L. lunifera*). The mean length:width ratio varies from 2.1 (*L. oerstedii*) to 5.35 (*L. longifolia*) (Table 4-3). No reliable conclusions can be drawn about patterns among species groups due to the sparse sampling, but these data probably provide a good indication of the seed size variation in the genus.

Seedlings

Seedlings of *Lockhartia lunifera* and *L. serra* were studied (Fig. 4-22). These were acquired from the commercial firm Troy Meyers Conservatory (Poulsbo, Washington, USA), which provides orchid seed germination services. The seedlings of *L. serra* were from seeds produced during the present study (*Whitten 2431* \times *Blanco 3228*).

Several protocorms were observed. These are yellowish, ca. 1.5–2 mm in diameter, almost spherical to slightly elongate (never more than 1.5 times as long as wide), and with a somewhat irregular surface. A greenish leaf primordium occurs on a rounded part of the protocorm (the epicotyl); the opposite “pole” (the hypocotyl) is somewhat bluntly pointed. In some cases, the protocorm forms a chain of two or three connected globular structures before producing a leafy shoot (Fig. 4-22E).

One or two leafy shoots can emerge directly from a protocorm. These juvenile shoots already show the morphology typical of adult shoots of subgenus *Lockhartia*

(i.e., without pseudobulbs, and with imbricating, isobilateral leaves), which is frequently observed in herbarium specimens that have juvenile stems still attached to the mature ones. This supports Chase's (2009) hypothesis that the vegetative morphology of *Lockhartia* represents a pedomorphic condition (several other genera in the Oncidiinae have seedlings with isobilateral leaves and adults with dorsiventral, conduplicate leaves).

The first shoot produced by the protocorm is short, with up to 10 leaves. The next shoot is produced from one of the basal nodes of the first shoot in typical sympodial fashion. Each new shoot is usually taller than the previous one and has several more leaves. This progressive growth of new stems continues, and eventually one of the new stems produces a terminal inflorescence (see description of inflorescences above).

The first two to four juvenile shoots produced by the protocorm have a characteristic morphology, with proportionally narrower leaves (as measured from the abaxial to the adaxial edges) with a much wider angle of divergence from the stem (compared with the adult leaves of the same species). This is particularly apparent in some herbarium specimens that still retain their juvenile stems alongside the adult ones (Fig. 4-22F,G). This form of heteroblasty has been observed in most species for which abundant herbarium material is available and facilitates the recognition of seedlings.

Cytogenetics

The chromosome number of *Lockhartia* seems to be $x=28$ ($2n=56$); this is based on counts of *L. micrantha* (Charanasri & Kamemoto, 1975) and *L. goyazensis* (Pessoa Félix & Guerra, 2000). This is the most common chromosome number in Oncidiinae, and it may be plesiomorphic for the subtribe (Chase & Palmer, 1992). An early count of $2n=14$ in *L. oerstedii* (Garay, 1963) is probably erroneous (Chase, 2009). An attempt

was made during the present study to obtain additional chromosome counts in several species, but unfortunately no mitotic figures could be found.

Several successful intergeneric crosses involving *Lockhartia* have been registered by the Royal Horticultural Society (this organization only registers artificial hybrids that have produced flowers); the other parental taxa are *Gomesa crispa* (Lindl.) Klotzsch ex Rchb.f., *Leochilus scriptus* (Scheidw.) Rchb.f., *Oncidium cheiroporum* Rchb.f., *Oncidium pictoides* M.W. Chase & N.H. Williams, *Otoglossum harlingii* (Stacy) N.H. Williams & M.W. Chase, *Tolumnia triquetra* (Sw.) Nir, and *Trichopilia marginata* Henfr. Some of these species have published chromosome counts of $2n=56$; however, *Tolumnia triquetra* has a published count of $2n=42$. The chromosome number and mitotic behavior of these hybrids is unknown.

The genome size of *Lockhartia oerstedii* was reported as 1.80 pg/1C nucleus (DNA mass in the unreplicated gametic nucleus) by Chase *et al.* (2005). According to that study, genome size in the Oncidiinae ranges from 1.10 to 7.70 pg/1C nucleus.

Phytochemistry

The phytochemistry of *Lockhartia* has been only sparsely studied. The first analyses were performed by Raffauf (1962), who tested herbarium specimens of several species (including *L. acuta*, *L. grandibractea*, *L. imbricata*, *L. hercodonta*, *L. micrantha*, and *L. oerstedii*) for the presence or alkaloids (Raffauf did not include a list of species or specimens tested, but several herbarium specimens at AMES bear a stamp that indicate their use in the experiment and the result of the test). Only *L. oerstedii* tested positive, although Raffauf's method could detect alkaloids only if these were in concentrations of over 0.01% (dry weight basis).

Lüning (1967), working with fresh plant tissues, detected alkaloids in *L. oerstedii* (at ca. 0.001% of fresh weight) but not in *L. parthenoglossa* (as *L. pittieri*). The identity of these alkaloids was not determined.

Finally, C. A. Williams (1979) detected the presence of quercetin in leaves of *L. acuta*. Interestingly, this flavonoid was not detected in any other species of subtribe Oncidiinae, or even tribe Cymbidieae (*sensu* Pridgeon *et al.*, 2009). Williams took this as support for the separation of *Lockhartia* from Oncidiinae.

Table 4-1. Major morphological groups of *Lockhartia* and their constituent species. See text for details.

Subgenus <i>Lockhartia</i>			Subgenus <i>Pseudobulbosa</i>
Imbricata group	Longifolia group	Parthenocomos group	
<i>L. acuta</i> ¹	<i>L. hercodonta</i>	<i>L. bennettii</i>	<i>L. genegeorgei</i>
<i>L. amoena</i>	<i>L. longifolia</i>	<i>L. latilabris</i>	
<i>L. cladoniophora</i>	<i>L. obtusata</i>	<i>L. oblongicallosa</i>	
<i>L. compacta</i>	<i>L. parthenoglossa</i>	<i>L. parthenocomos</i>	
<i>L. dipleura</i>		<i>L. rugosifolia</i>	
<i>L. endresiana</i>			
<i>L. galeottiana</i> ²			
<i>L. goyazensis</i>			
<i>L. grandibractea</i>			
<i>L. imbricata</i>			
<i>L. ivainae</i>			
<i>L. lepticaula</i>			
<i>L. lunifera</i>			
<i>L. micrantha</i>			
<i>L. oerstedii</i> ²			
<i>L. oxyphylla</i>			
<i>L. serra</i>			
<i>L. tenuiflora</i>			
<i>L. verrucosa</i> ²			

¹ Acuta subgroup

² Oerstedii subgroup

Table 4-2. Stomatal dimensions of selected species of *Lockhartia*, from ten randomly chosen stomata per collection. All values are expressed in micrometers (μm). Means are rounded to the nearest μm .

Species	Collection ¹	Length range	Length mean	Length SD	Width range	Width mean	Width SD	Mean L:W ratio
<i>L. acuta</i>	Blanco 3221	25–33	28	2.2	25–30	28	1.6	1.00
<i>L. amoena</i>	Blanco 2556	22–25	23	1.1	26–29	27	0.9	0.85
<i>L. hercodonta</i>	Blanco 3232	21–25	22	1.1	25–29	27	1.6	0.81
<i>L. longifolia</i>	Whitten 2385	23–26	25	0.9	22–27	24	1.5	1.04
<i>L. micrantha</i>	Blanco 3223	22–26	24	1.4	15–29	27	1.1	0.89
<i>L. obtusata</i>	Blanco 3025	23–29	26	1.3	27–30	28	1.0	0.93
<i>L. oerstedii</i>	Blanco 2565	27–30	29	0.9	30–33	31	0.9	0.93
<i>L. serra</i>	Blanco 3228	23–27	26	1.0	26–27	27	0.7	0.96
<i>L. tenuiflora</i>	Blanco 3231	25–27	26	0.8	25–29	26	1.2	1.00
<i>L. verrucosa</i>	Blanco 2667	23–29	27	1.8	27–33	29	1.7	0.93

¹ All vouchers deposited in FLAS.

Table 4-3. Seed dimensions of selected species of *Lockhartia*, from ten randomly chosen seeds per collection. All values are expressed in micrometers (μm). Means are rounded to the nearest μm .

Species	Collection ¹	Length range	Length mean	Length SD	Width range	Width mean	Width SD	Mean L:W ratio
<i>L. acuta</i>	Blanco 2567	250–294	273	13.8	62–81	69	6.9	3.96
<i>L. grandibractea</i>	Blanco 2559	250–306	277	16.7	87–106	94	6.6	2.95
<i>L. longifolia</i>	Kuntze s.n.	400–475	433	21.8	69–94	81	6.9	5.35
<i>L. lunifera</i>	Blanco 2688	237–350	287	31.7	106–125	116	6.7	2.47
<i>L. micrantha</i>	Blanco 2561	181–269	241	25.7	56–94	76	10.8	3.17
<i>L. micrantha</i>	Blanco 2562	219–306	260	29.2	75–100	91	7.4	2.86
<i>L. oerstedii</i>	Blanco 3024	162–231	202	22.4	87–112	96	8.3	2.10
<i>L. serra</i>	Blanco 2669	212–263	246	19.3	75–106	92	11.0	2.67
<i>L. verrucosa</i>	Blanco 3227	250–338	288	27.0	81–100	92	5.7	3.13

¹ All vouchers deposited in FLAS, except *Kuntze s.n.* (NY).

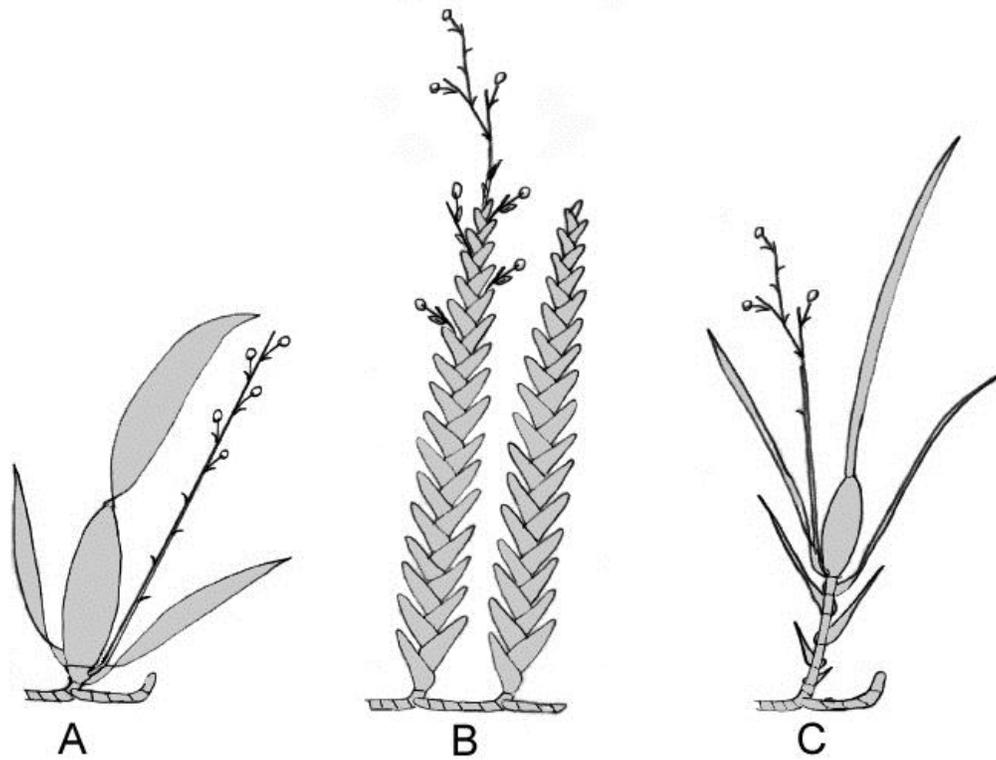


Figure 4-1. Generalized growth habits of *Lockhartia* and related taxa, schematic. Length of rhizome segments exaggerated for clarity; roots and rhizome bracts not shown. (A) Typical member of subtribe Oncidiinae (hypothetical ancestral habit). (B) *Lockhartia* subgenus *Lockhartia*. (C) *Lockhartia* subgenus *Pseudobulbosa* (*L. genegeorgei*).

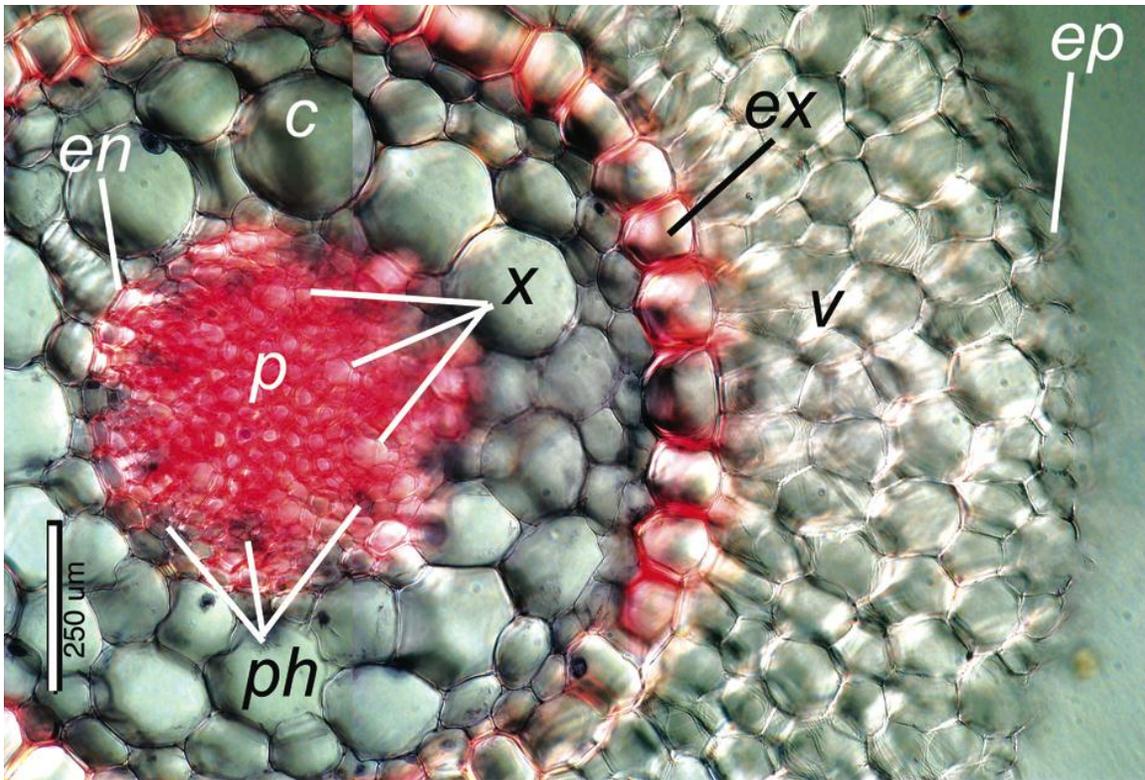


Figure 4-2. Root cross section of *Lockhartia serra* (Blanco 3228, FLAS). Abbreviations: *c*, cortex; *en*, endodermis; *ep*, epidermis; *ex*, exodermis; *p*, pith (sclerified); *ph*, phloem; *v*, velamen; *x*, xylem.

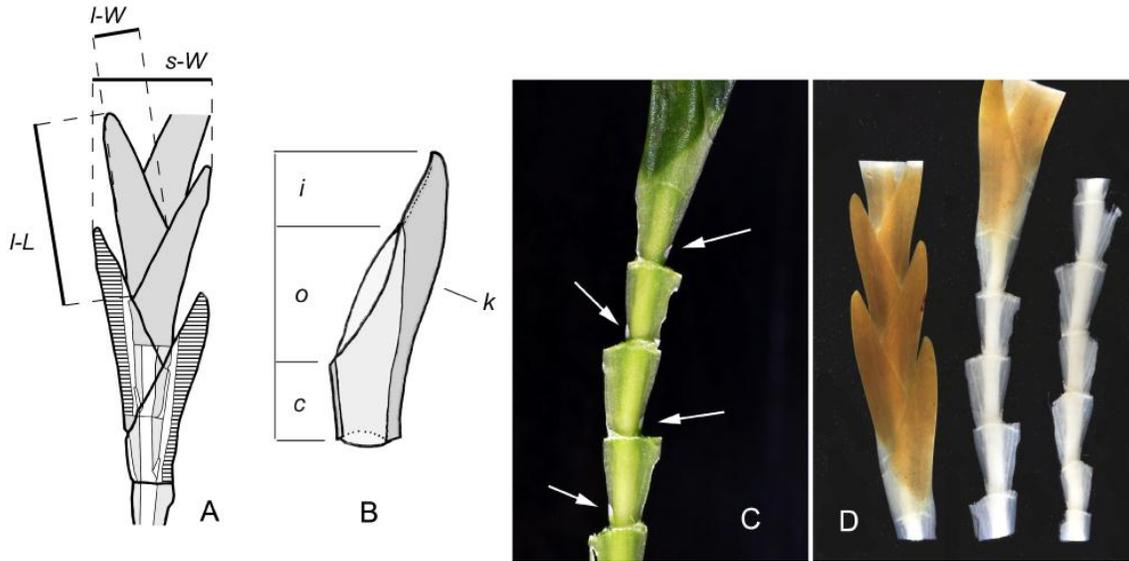


Figure 4-3. Stem and leaf structure of *Lockhartia* subgenus *Lockhartia*. (A) Schematic representation of a shoot segment with the lowermost leaf removed for clarity and the internal stem structure indicated for the three lower internodes; isobilateral portion of the leaf (including keel) shown with horizontal hatching; stem vascular core and axillary buds shown in white. Also indicated are standard measurements of leaf length (*I-L*), leaf width (*I-W*), and shoot width (*s-W*) as reported in the species descriptions (see text for details). (B) Leaf parts, schematic: closed portion of leaf sheath (*c*), open portion of leaf sheath (*o*), isobilateral blade (*i*), and isobilateral keel (*k*). (C) Stem segment with leaves removed; arrows point to axillary buds. (D) Three stem segments preserved in ethanol, the one at left with leaves attached. Notice opaque vascular core, translucent cortex, and leaf traces emerging from the base of each internode (i.e., the previous node). All based on *L. oerstedii* (Blanco 2565, FLAS).

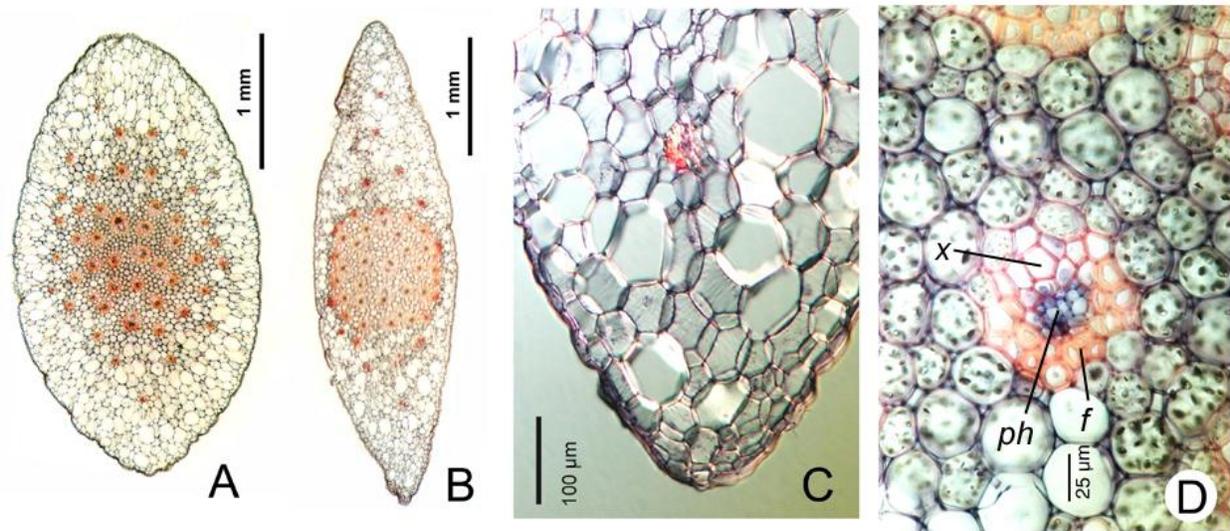


Figure 4-4. Stem anatomy of *Lockhartia*, TS. (A) *L. obtusata* (Blanco 3025, FLAS) and (B) *L. longifolia* (Whitten 2385, FLAS); notice vascular core surrounded by cortex. (C) Detail of epidermis and cortex; notice isolated vascular bundle of leaf trace near center, and some cortex cells showing banded wall thickenings; *L. serra* (Blanco 3228, FLAS). (D) *L. obtusata* (Blanco 3025), detail of vascular core in central part of stem; vascular bundle surrounded by amyloplast-containing parenchyma. Abbreviations: *f*, fibers; *ph*, phloem; *x*, xylem.

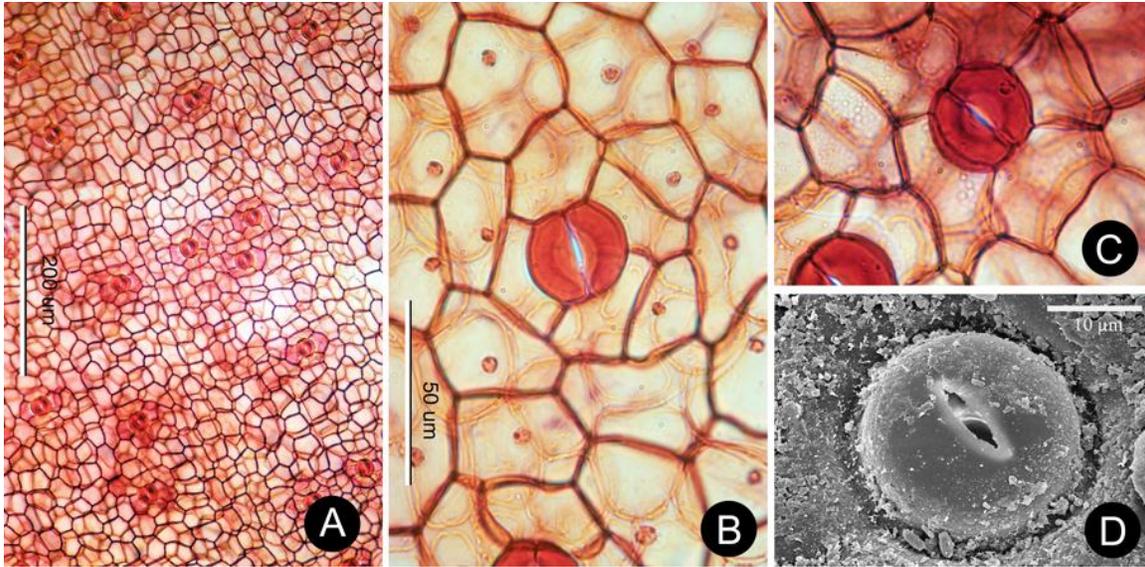


Figure 4-5. Leaf abaxial epidermis of *Lockhartia*. (A) *L. micrantha* (Blanco 3223, FLAS), general view of abaxial epidermis, notice abundant stomata; scale bar = 200 μm . (B) *L. oerstedii* (Blanco 2565, FLAS), tetracytic stoma and adjacent cells; scale bar = 50 μm . (C) *L. longifolia* (Whitten 2385, FLAS), stoma with five subsidiary cells; same scale as B. (D) *L. lunifera* (Blanco 3219, FLAS), SEM showing cuticular ledge covering stoma (edge of guard cell visible through slit); scale bar = 10 μm .

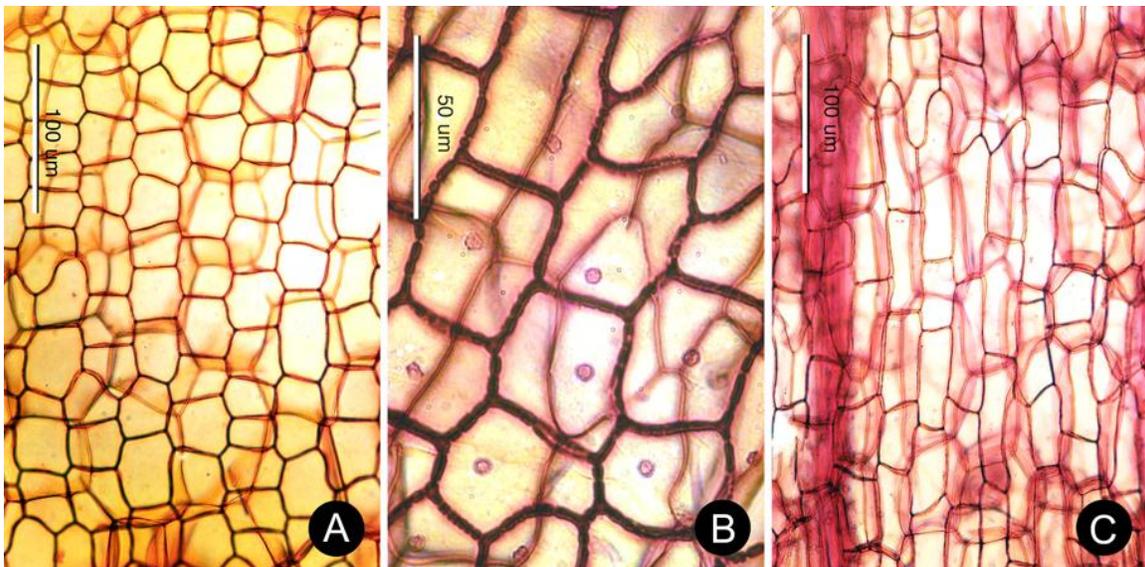


Figure 4-6. Leaf adaxial epidermis of *Lockhartia*. (A) *L. verrucosa* (Blanco 2667, FLAS). (B) *L. acuta* (Blanco 3221, FLAS). (C) *L. longifolia* (Whitten 2385, FLAS), notice vascular bundle along left side of image.

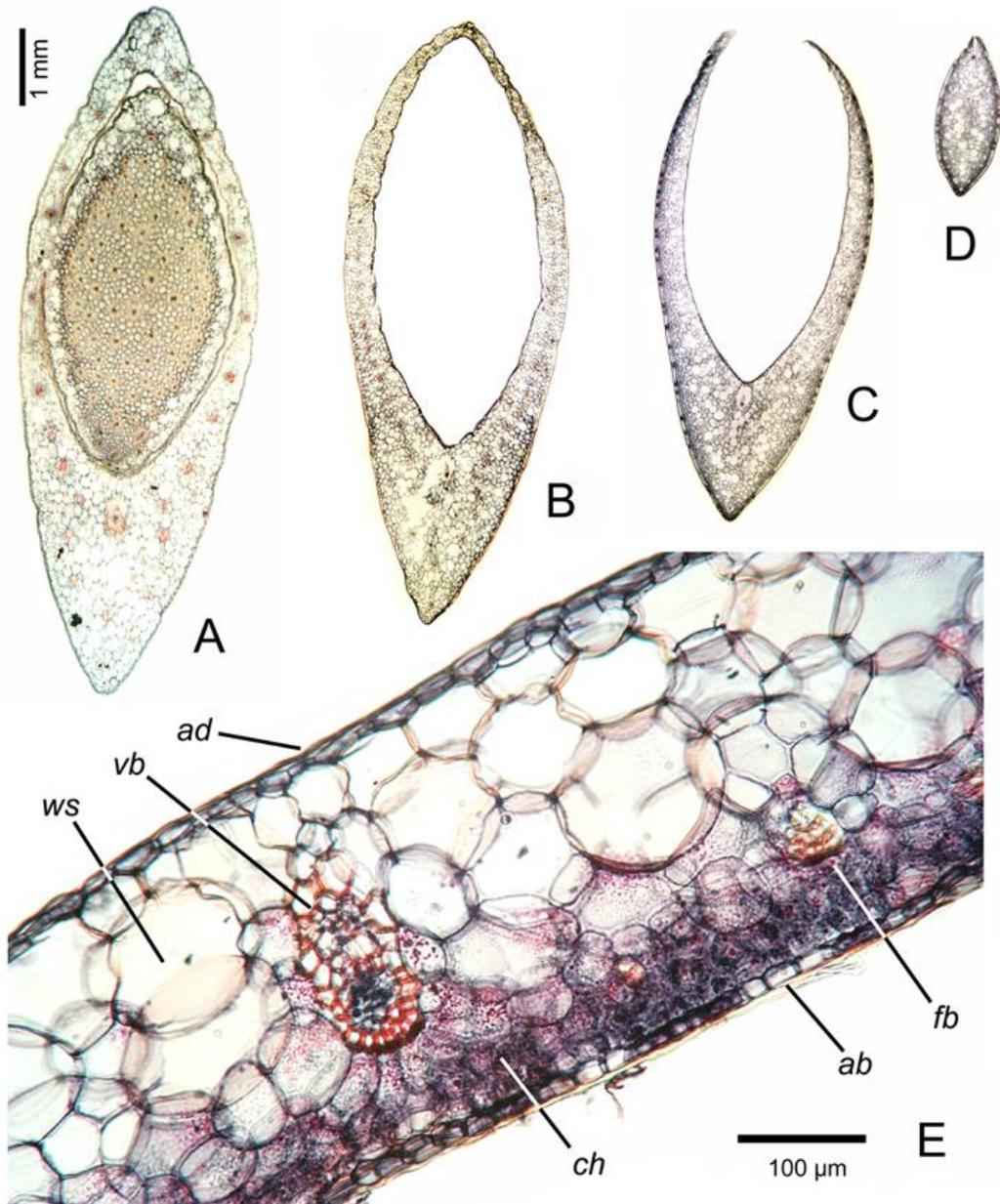


Figure 4-7. Leaf anatomy of *Lockhartia*, TS. (A) *L. serra* (Blanco 3228, FLAS), base of leaf, corresponding to closed portion of sheath, enclosing stem; notice distribution of vascular bundles in leaf. (B–D) *L. acuta* (Blanco 3221, FLAS); B, closed sheath; C, open sheath; D, isobilateral portion of blade; same scale as for A. (E) *L. obtusata* (Blanco 3025, FLAS), detail of leaf cross section. Abbreviations: *ab*, abaxial epidermis; *ad*, adaxial epidermis; *ch*, chlorenchymatous mesophyll; *fb*, fiber bundle; *vb*, vascular bundle; *ws*, water-storage mesophyll.

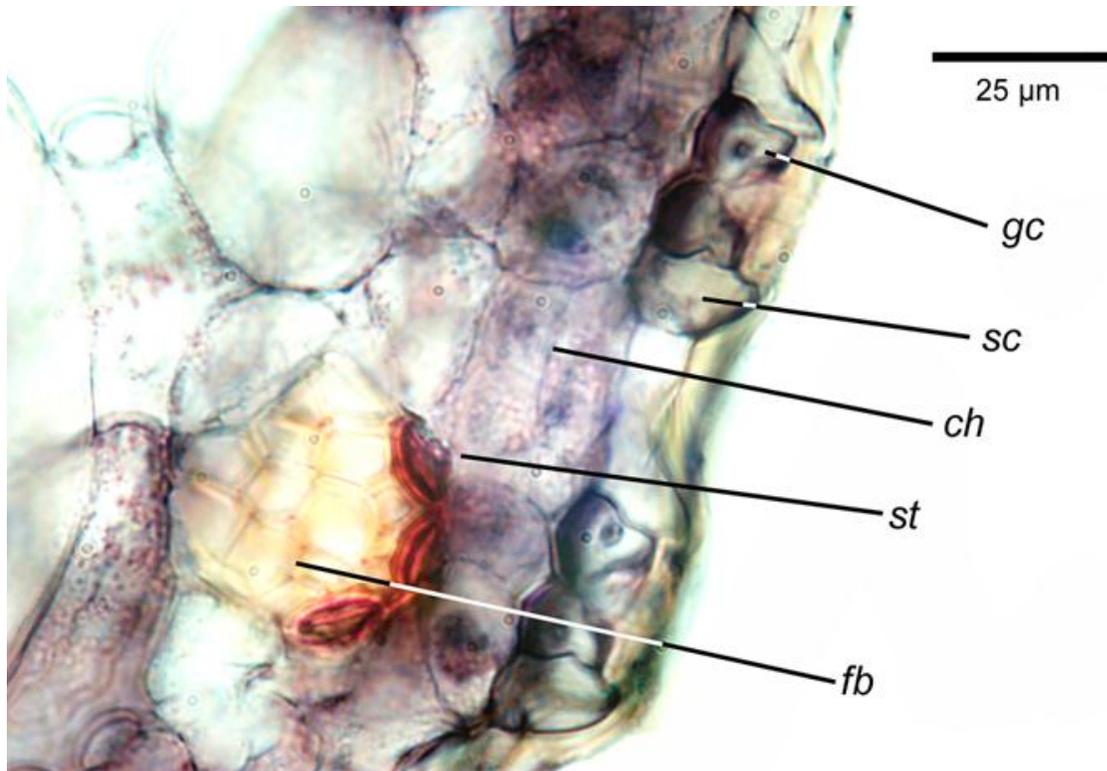


Figure 4-8. Abaxial epidermis and associated subepidermal tissues of *Lockhartia longifolia* (Whitten 2385, FLAS), TS. Notice apparent absence of substomatal chambers (possibly an artifact of excessive thickness of section) and stegmata on abaxial side of fiber bundle. Abbreviations: *ch*, chlorenchymatous mesophyll; *fb*, fiber bundle; *gc*, guard cell; *sc*, subsidiary cell; *st*, stegmata.

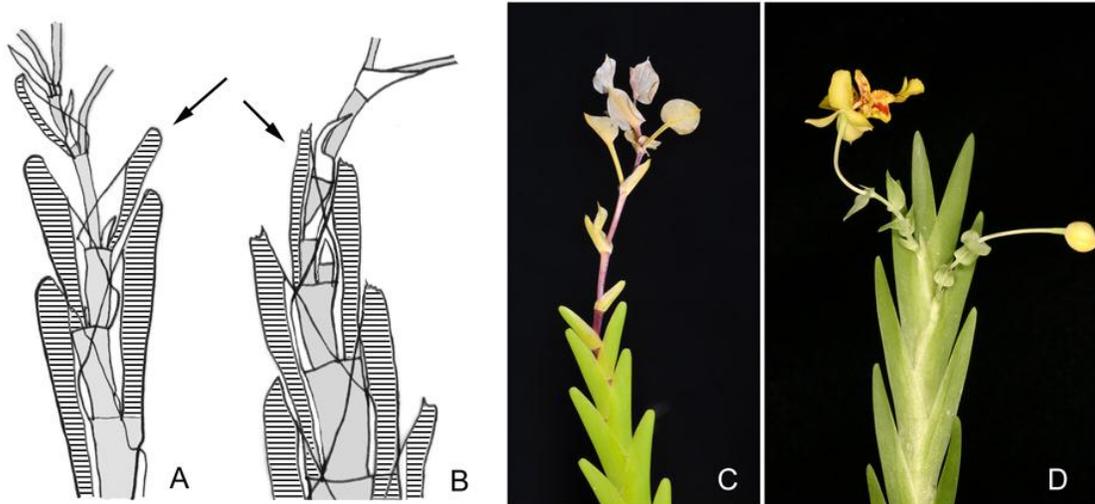


Figure 4-9. Variations in inflorescence position in *Lockhartia* subgenus *Lockhartia*. (A) Schematic representation of a truly terminal inflorescence; notice undeveloped axillary bud from last foliaceous leaf (indicated by arrow). Based on shoot dissection of *L. serra* (Blanco 2669, FLAS). (B) Schematic representation of a pseudoterminal inflorescence; notice the aborted shoot apical bud hidden by the sheath of the last foliaceous leaf (indicated by arrow), and the inflorescence originating from the axil of the same leaf. Based on shoot dissection of *L. acuta* (Blanco 3221, FLAS). (C) Old, terminal inflorescence in *L. serra* (Blanco 2669). (D) Two axillary inflorescences and no terminal inflorescence in *L. verrucosa* (Blanco 3227, FLAS).

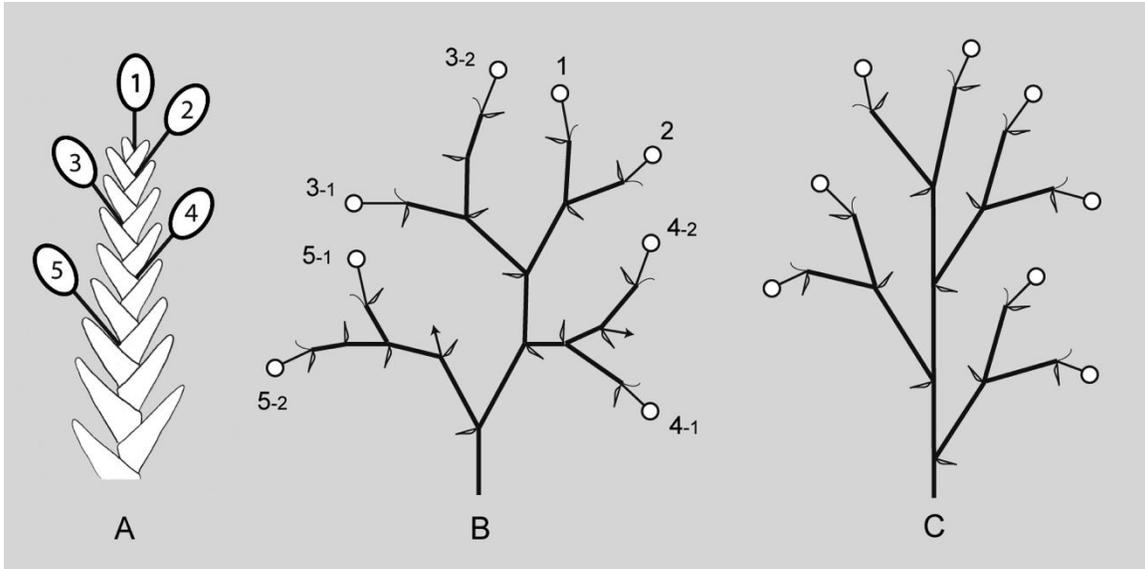


Figure 4-10. Mode of inflorescence development in *Lockhartia*. (A) Basipetal inflorescence initiation along a stem, the most common condition in the genus (a few species have simultaneous inflorescence initiation); ovals represent inflorescences; numbers indicate order of inflorescence initiation. (B) Structure of a *Lockhartia* pseudocyme, schematic. Proleptic branching represented by numbers; large numbers indicate the order of primary branch initiation (including primary axis, 1); small numbers indicate the order of secondary and tertiary branch initiation and flower opening on each branch; arrows represent recently initiated branches. (C) Structure of pseudocyme of *L. acuta*, schematic. This species has sylleptic (simultaneous) branching and a single internode per secondary branch. Notice filament representing abortive apical meristem opposite each floral bract in B and C.

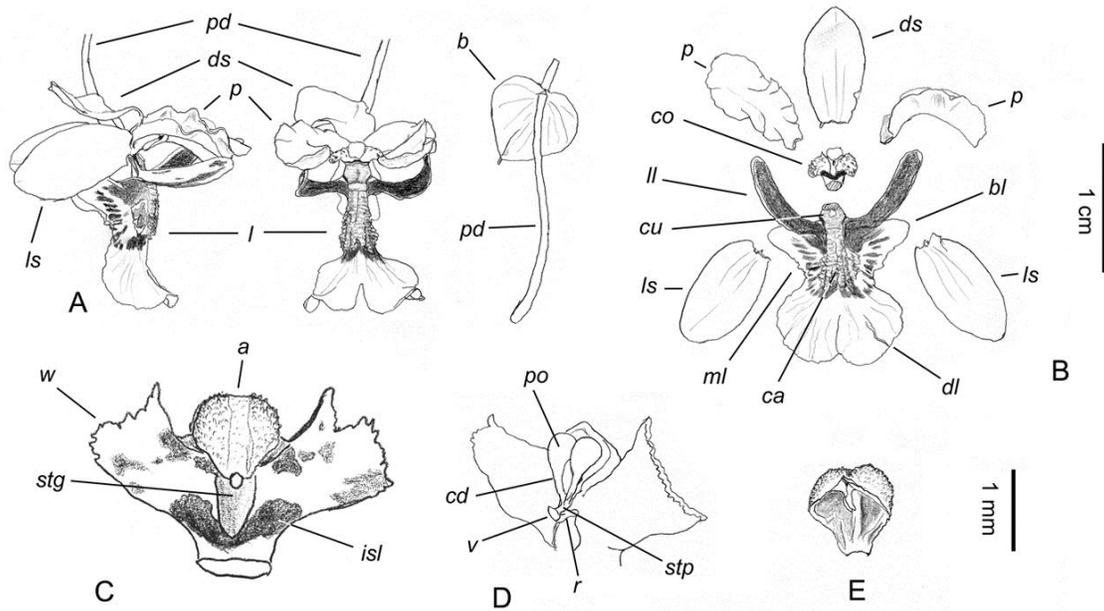


Figure 4-11. Floral morphology of the Imbricata group of *Lockhartia* subgenus *Lockhartia*; A–B: *L. serra* (Blanco 2669, FLAS), C–E: *L. amoena* (Blanco 2556, FLAS). (A) Flower in lateral view (left), front view (center), and pedicel with floral bract (right). (B) Dissected flower; perianth parts flattened except for petal on the right side (shown in its natural configuration); flattened petal distorted. (C) Column, ventral view. (D) Schematic representation of column with anther cap removed to show the pollinarium; oblique view. (E) Anther cap from behind. Abbreviations: a, anther cap; b, floral bract; bl, basal lobule of labellum midlobe; ca, callus; cd, caudicles; co, column; cu, elaiophore cushion; dl, distal lobule of labellum midlobe; ds, dorsal sepal; isl, infrastigmatic line; l, labellum; ll, lateral lobe of labellum; ls, lateral sepal; ml, midlobe of labellum; p, petal; pd, pedicel and ovary; po, pollinium; stg, r, rostellum; stigma; stp, stipe; v, viscidium; w, column wing.

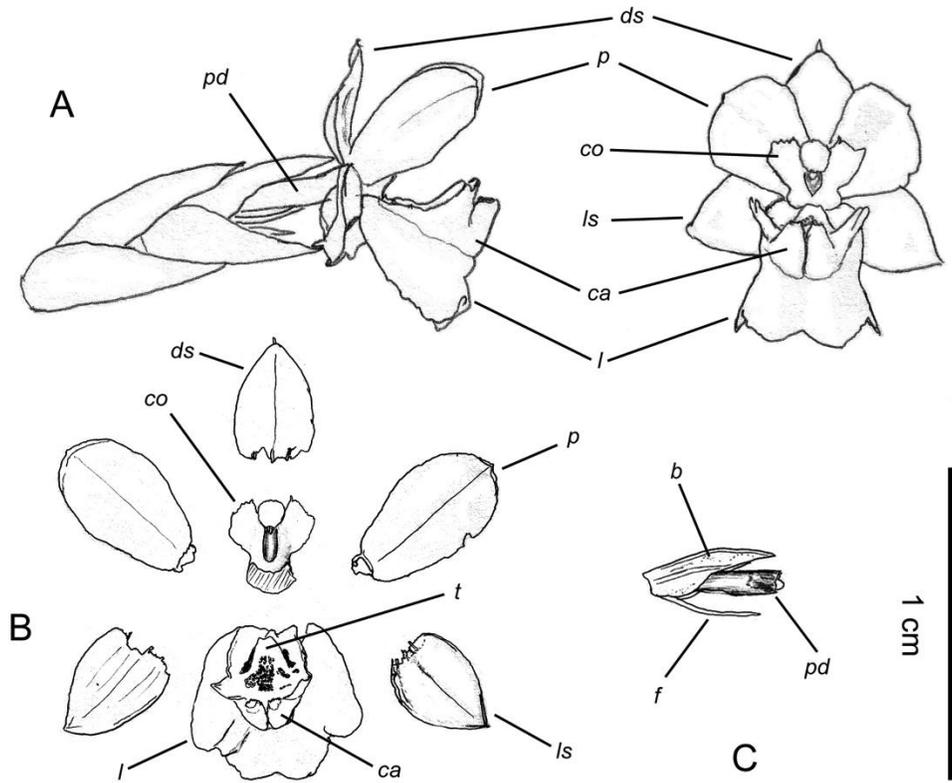


Figure 4-12. Floral morphology of the Longifolia group of *Lockhartia* subgenus *Lockhartia*; *L. hercodonta* (Blanco 3232, FLAS). (A) Flower in lateral view (left) and front view (right). (B) Dissected flower; perianth parts flattened. (C) Floral bract and pedicel, and abortive filament. Column parts are similar to those in Figure 4-11 C–E. Abbreviations: *b*, floral bract; *ca*, callus; *co*, column; *ds*, dorsal sepal; *f*, abortive filament; *l*, labellum; *ls*, lateral sepal; *p*, petal; *pd*, pedicel and ovary; *t*, trapezoid ledge.

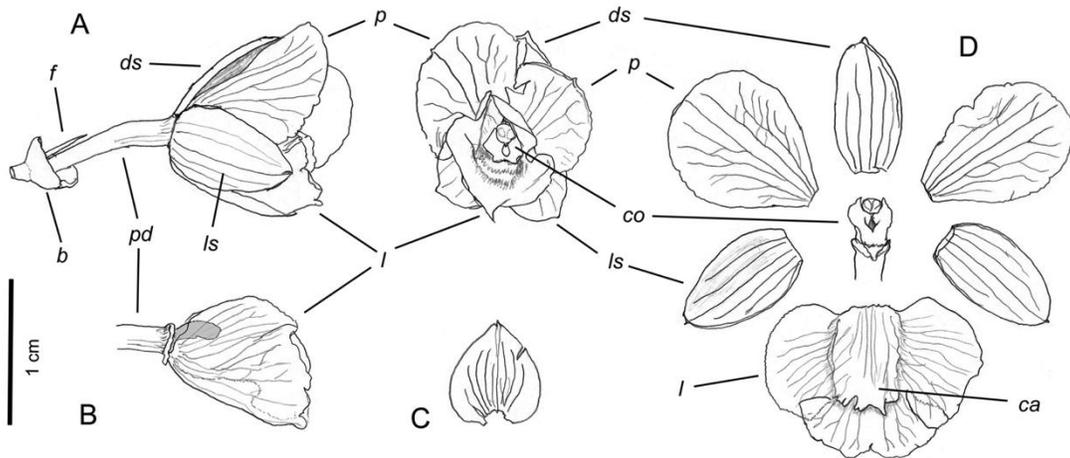


Figure 4-13. Floral morphology of the Parthenocomos group of *Lockhartia* subgenus *Lockhartia*; *L. bennettii* (Blanco 2554, FLAS). (A) Flower in lateral view (left) and front view (right). (B) Flower in lateral view, sepals and petals removed. (C) Floral bract, flattened. (D) Dissected flower; perianth parts flattened. Column parts are similar to those in Fig. X-11 C-E. Abbreviations: *b*, floral bract; *ca*, callus; *co*, column; *ds*, dorsal sepal; *f*, abortive filament; *l*, labellum; *ls*, lateral sepal; *p*, petal; *pd*, pedicel and ovary.

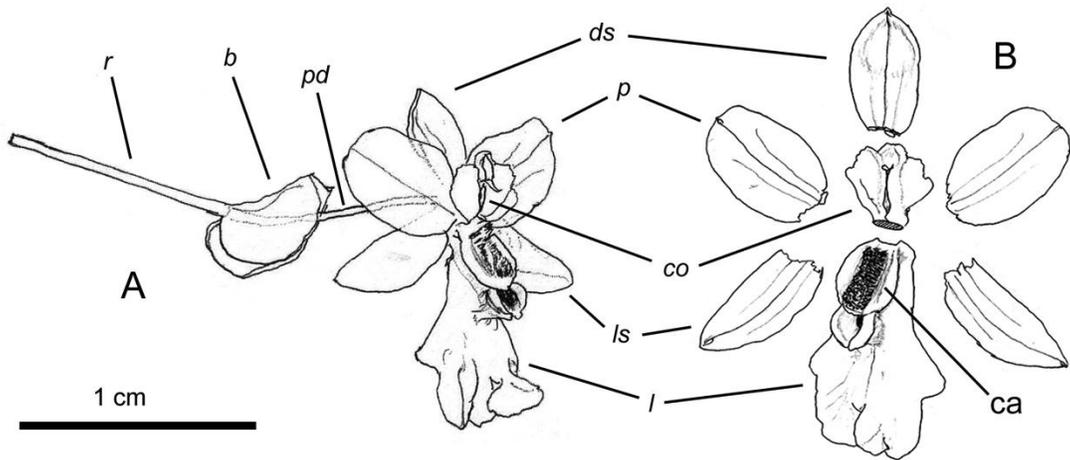


Figure 4-14. Floral morphology of *Lockhartia* subgenus *Pseudobulbosa*; *L. genegeorgei* (Bennett 5199-6, FLAS), rehydrated. (A) Flower in oblique view. (B) Dissected flower; perianth parts flattened (labellum could not be flattened properly). Abbreviations: *b*, floral bract; *ca*, callus; *co*, column; *ds*, dorsal sepal; *l*, labellum; *ls*, lateral sepal; *p*, petal; *pd*, pedicel and ovary; *r*, inflorescence rachis.

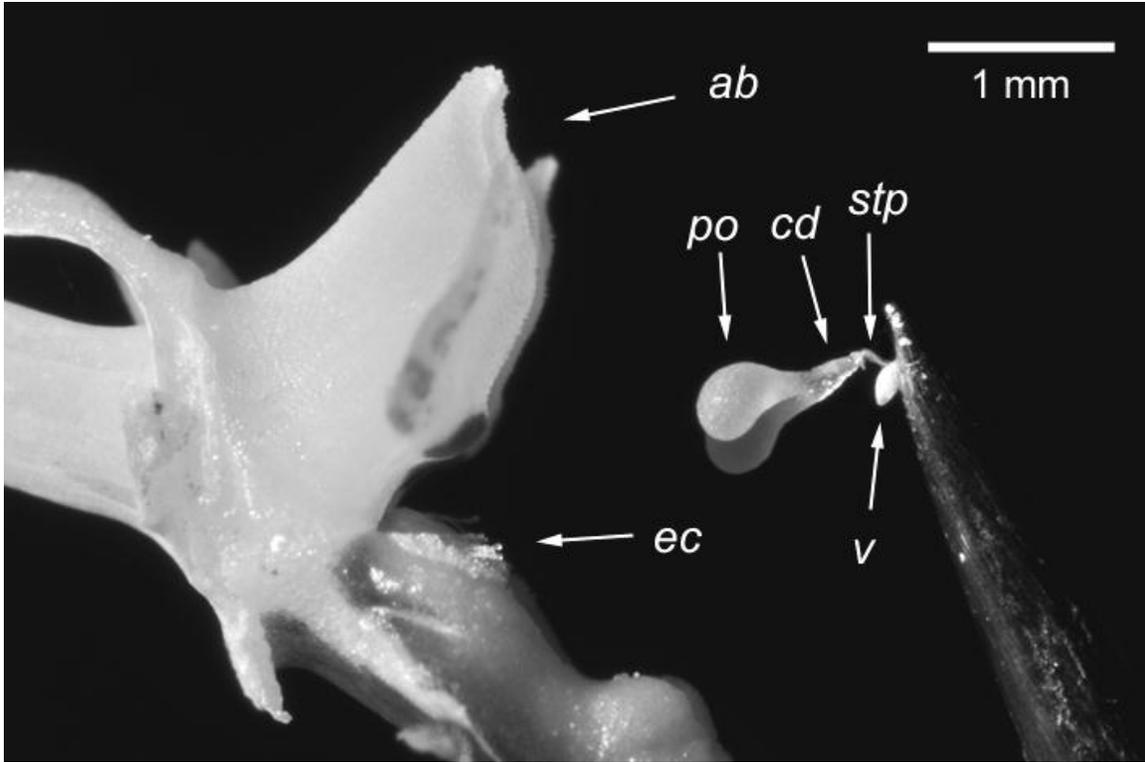


Figure 4-15. Column of *Lockhartia serra* (Blanco 2669, FLAS) with recently removed pollinarium attached to a pin; anther cap not shown. Surface of pollinia that rested on the anther bed is facing down in this image. Sepals and petals removed for clarity. Abbreviations: *ab*, anther bed at column apex; *cd*, caudicles; *ec*, elaiophore cushion at base of labellum; *po*, pollinium; *stp*, stipe; *v*, viscidium.

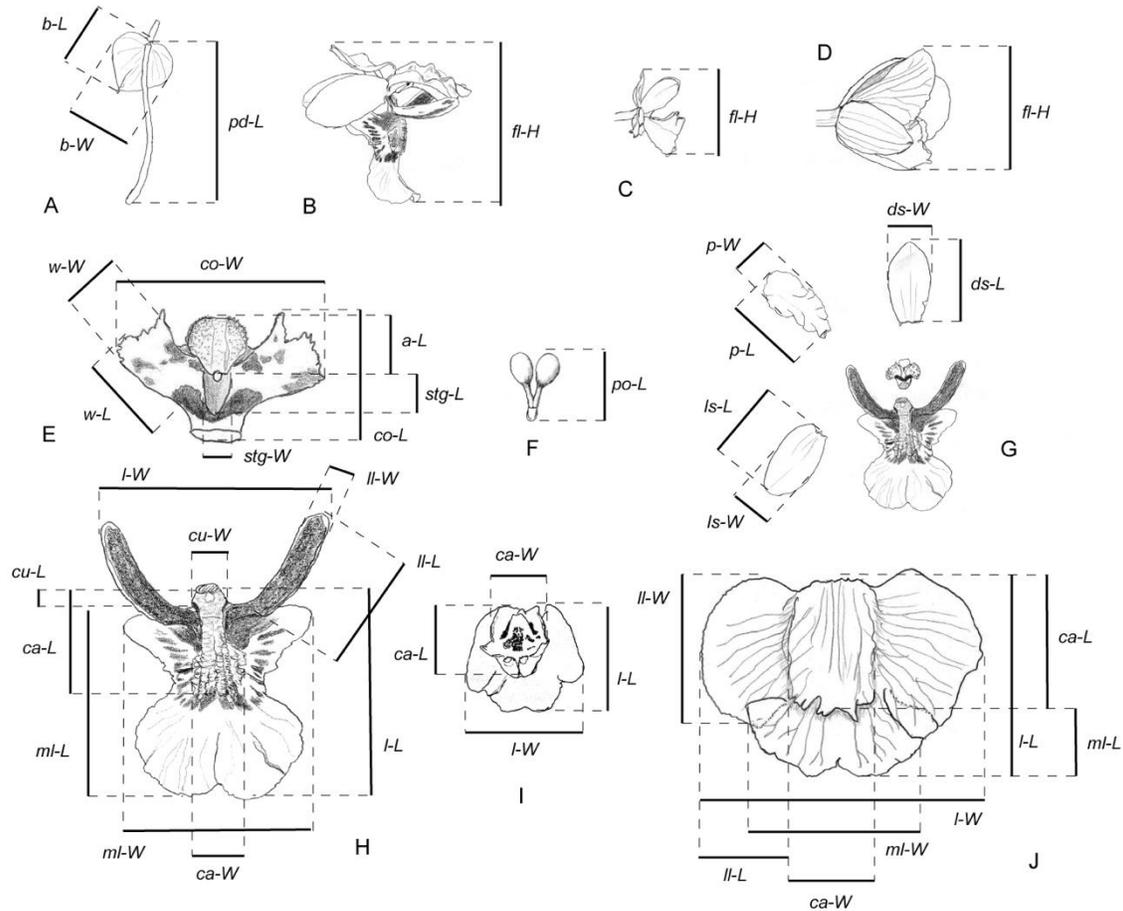


Figure 4-16. Measurements of flowers and floral parts in *Lockhartia*, as reported in species descriptions. (A) Floral bract and pedicel. (B) Flower of the Imbricata group. (C) Flower of the Longifolia group. (D) Flower of the Parthenocomos group. (E) Column. (F) Pollinarium. (G) Sepals and petals. (H) Labellum of the Imbricata group. (I) Labellum of the Longifolia group. (J) Labellum of the Parthenocomos group. For *Lockhartia* subgenus *Pseudobulbosa*, flower height was measured as in B, and labellum dimensions as in I. Abbreviations: *a*, anther; *b*, floral bract; *ca*, callus (callus length includes the elaiophore cushion); *co*, column; *cu*, elaiophore cushion; *ds*, dorsal sepal; *fl*, flower; *l*, labellum; *ll*, lateral lobe of labellum; *ls*, lateral sepal; *ml*, midlobe of labellum; *p*, petal; *pd*, pedicel; *po*, pollinarium; *stg*, stigma; *w*, column wing. Abbreviation suffixes: *H*, height; *L*, length; *W*, width.

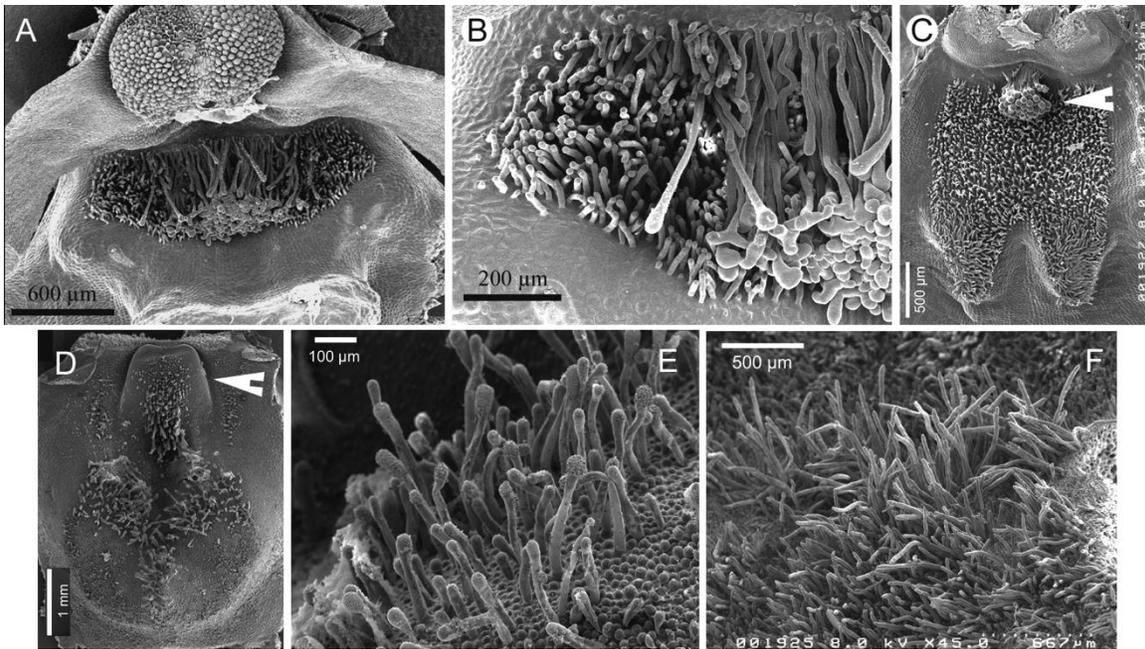


Figure 4-17. Labellar trichomes of *Lockhartia*; SEM images. (A) *L. lepticaula* (Blanco 2573, FLAS); trichomes in depression of elaiophore cushion. Column wings and anther can be seen immediately above trichome field. (B) Detail of A; long trichomes (some of them apically bifid) to the right of image; short trichomes visible to the left and under the long ones. (C) Callus of *L. acuta* (Blanco 2567, FLAS); notice callus body covered by short trichomes and tuft of longer, capitate trichomes at base of labellum (arrowhead). (D) Callus of *L. obtusata* (Blanco 2572, FLAS); trichomes mostly on raised parts of callus; notice trapezoid ledge (arrowhead). (E) Detail of trichomes in D; notice papillate epidermis. (F) Trichomes covering callus in *L. bennettii* (Blanco 2554, FLAS).

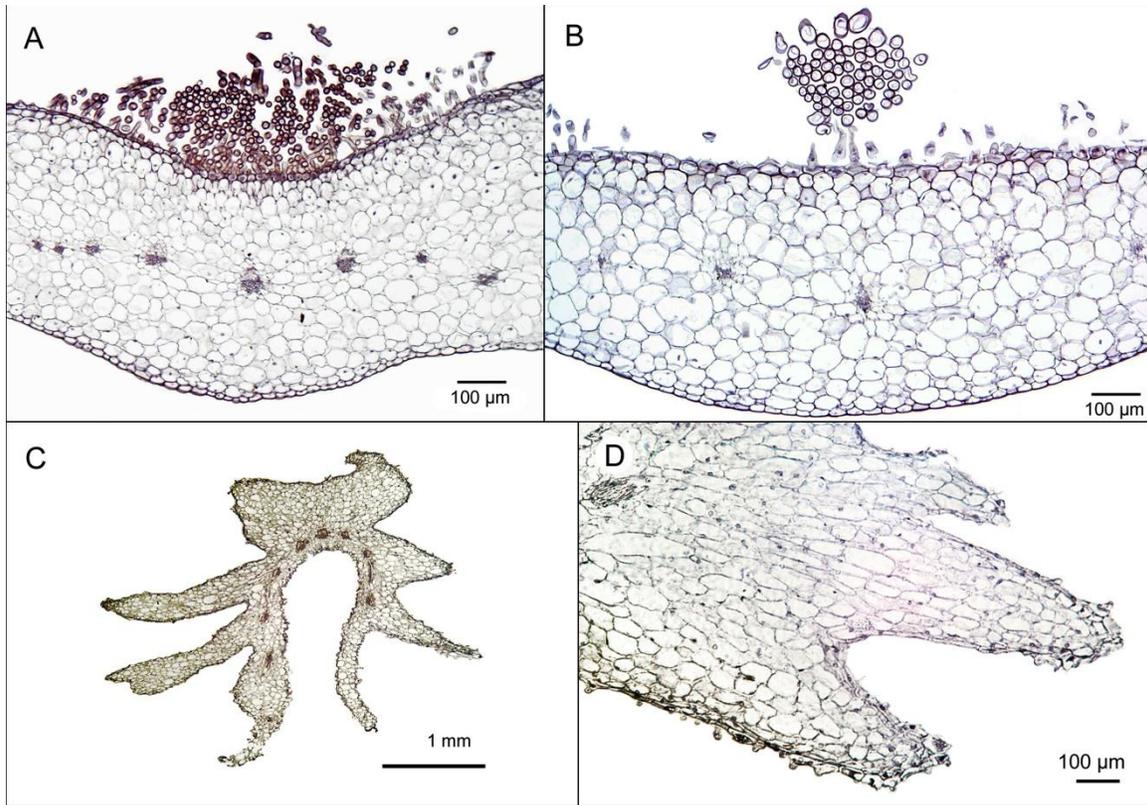


Figure 4-18. Labellar anatomy of the Imbricata group of *Lockhartia* subgenus *Lockhartia*; abaxial surface facing up in A–C. (A) *L. oxyphylla* (Whitten 2382, FLAS), TS at the middle of the elaiophore cushion; long elaiophore trichomes are seen in TS, short elaiophore trichomes in longitudinal or oblique section. (B) *L. acuta* (Blanco 2567, FLAS), TS of base of labellum, through the middle of the long elaiophore trichomes (arrowhead in figure 4-17C). (C) *L. oerstedii* (Blanco 2566, FLAS), TS through the lower portion of the callus; notice the lateral lobules folded back against each other (lower part of the image) and the tall callus tubercles projecting from the labellum. (D) Detail of another section of the same flower; notice cells elongated in the direction of each tubercle and papillate epidermis.

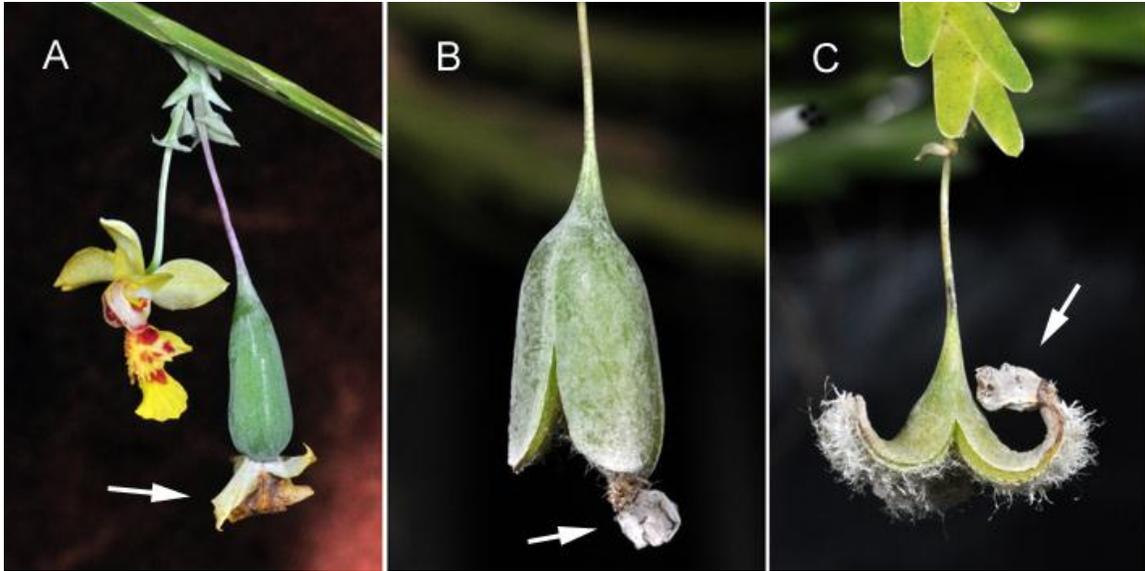


Figure 4-19. Fruit development of *Lockhartia lunifera*. (A) Flower and developing fruit on the same inflorescence; notice that ovary enlarges substantially after pollination, while pedicel does not elongate. (B) Mature capsule at beginning of dehiscence. (C) Capsule completely dehiscent but still green; notice exposed endocarpic trichomes. Arrows indicate perianth remnants attached to the median capsule valve (the one opposite the floral bract). A from *Blanco 2688* (FLAS); B and C from *Blanco 3219* (FLAS).

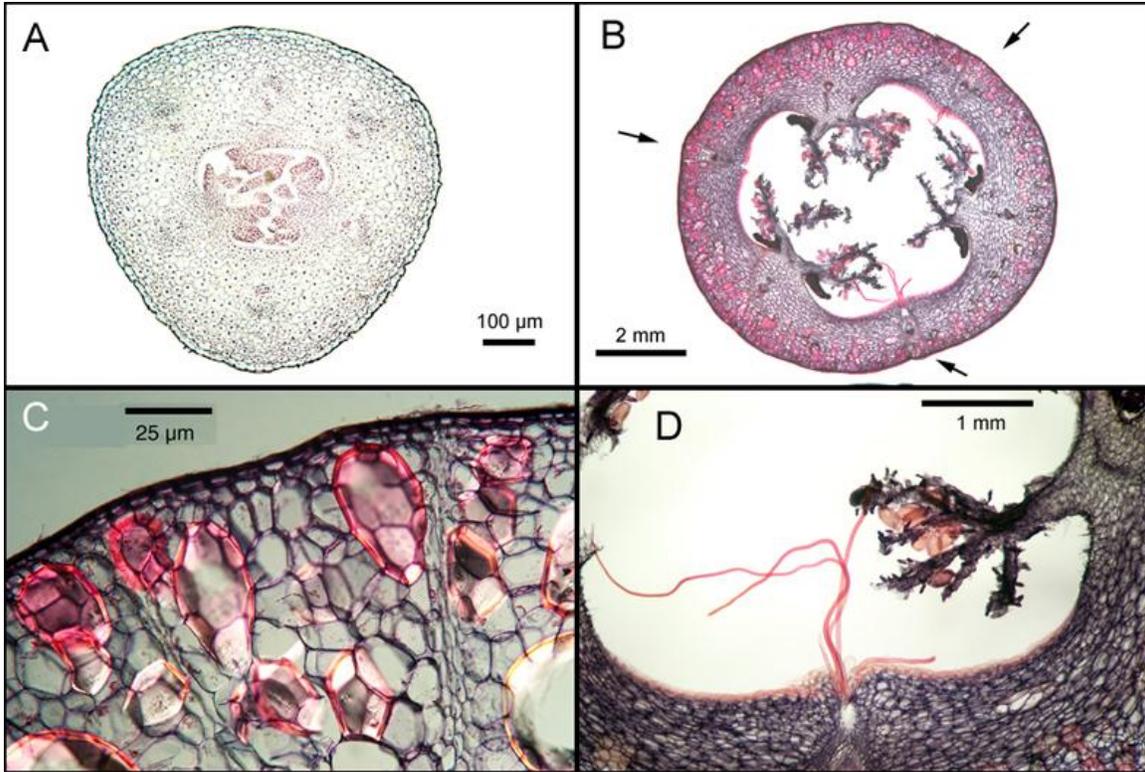


Figure 4-20. Ovary and fruit anatomy of *Lockhartia*. (A) Ovary of *L. acuta* (Blanco 2567, FLAS) at anthesis, TS. B–D: Nearly mature fruit of *L. serra* (Blanco 2572, FLAS), TS. (B) Entire section of fruit; notice three paired placental ridges alternating with three rows of endocarpic trichomes (two rows of trichomes were lost during sectioning). Position of dehiscence lines is indicated by arrows. (C) Detail of the fruit wall; notice large sclereids (stained pink) embedded in the parenchyma. (D) Detail of internal portion of fruit; notice row of endocarpic trichomes (center) and one branched arm of a placental ridge, with several seeds attached (right).

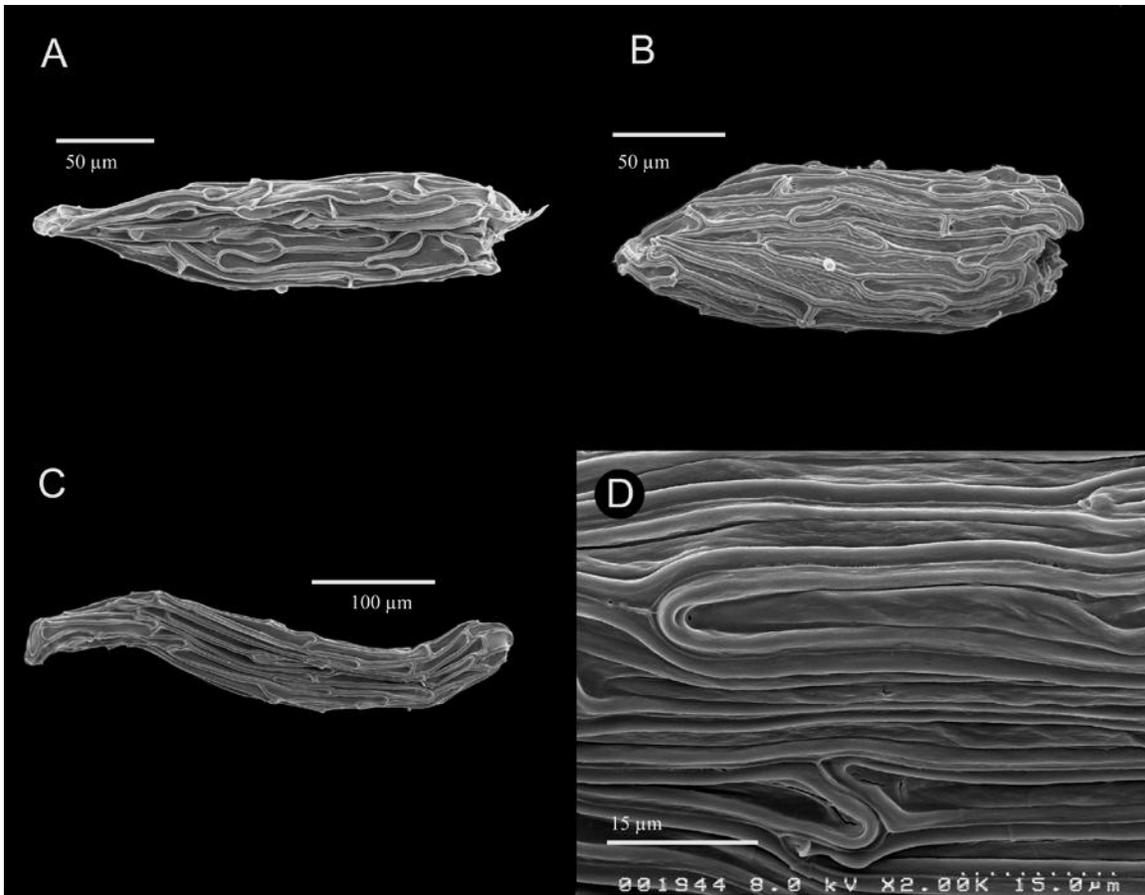


Figure 4-21. Seeds of *Lockhartia*, SEM. (A) *L. oerstedii* (Blanco 2565, FLAS). (B) *L. micrantha* (Blanco 3223, FLAS). (C) *L. longifolia* (Kuntze s.n., NY). (D) Detail of seed coat of *L. micrantha*. Micropylar pole to the right of the image in A, B, and D, and to the left of the image in C.

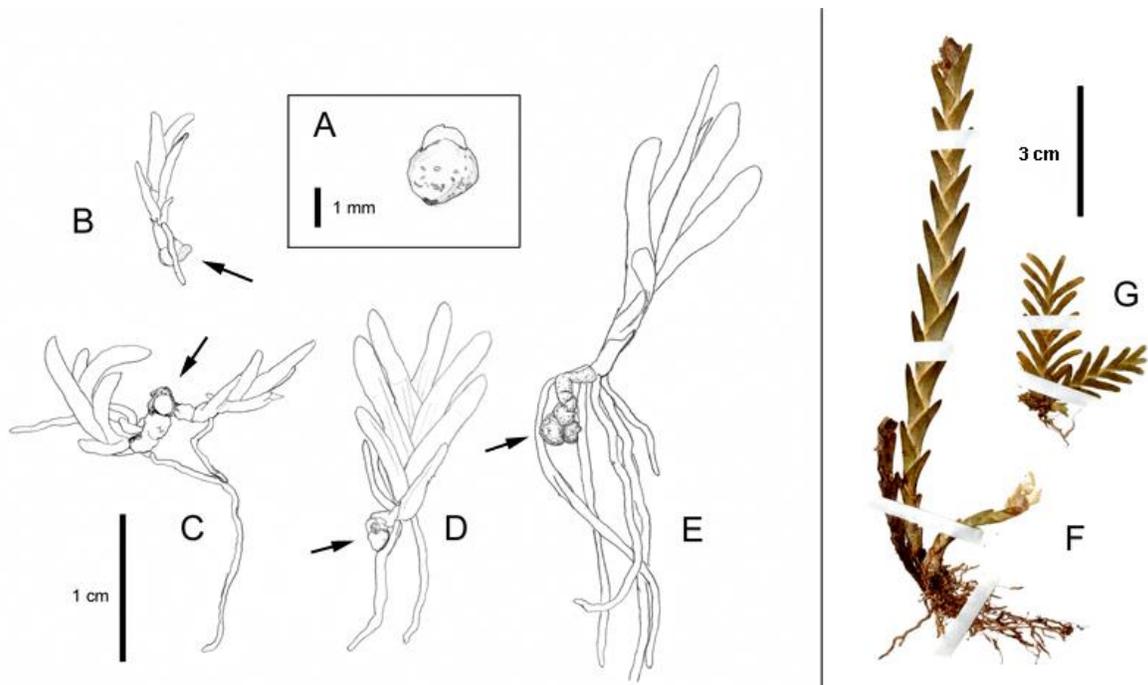


Figure 4-22. Protocorms and seedlings of *Lockhartia*. A–E, *L. lunifera* (unvouchered). (A) Protocorm; epicotyl with leaf primordium on top, hypocotyl below (which produces only absorbing hairs, not roots). (B–E) Seedlings of increasing size with first leafy shoots still attached to protocorms (indicated by arrows); notice two separate leafy shoots produced by a single protocorm in C, and protocorm composed of several globular bodies in E. (F–G) Comparison of adult (F) and seedling (G) shoots of *L. imbricata* from the same herbarium sheet (*Ek & Montfoort 251, U*); notice differences in relative and absolute leaf width, shape, and angle of divergence from the stem.

CHAPTER 5 PHYLOGENY

The genus *Lockhartia* is a member of tribe Cymbidieae, subtribe Oncidiinae (Pridgeon *et al.*, 2009, and references therein). Several cladistic studies, focused on the entire family Orchidaceae or on smaller subgroups, have included species of *Lockhartia* (Freudenstein & Rasmussen, 1999; Whitten *et al.*, 2000; Freudenstein & Chase, 2001; Williams *et al.*, 2001a, b; Williams *et al.*, 2005; Sandoval-Zapotitla *et al.*, 2010b; Neubig *et al.*, in preparation). While a few of these studies (e.g., Williams *et al.*, 2005; Sandoval-Zapotitla *et al.*, 2010b) suggest that the genus *Lockhartia* is sister to a clade that includes the *Ornithocephalus*, *Pachyphyllum* and *Telipogon* groups, most of them recover *Lockhartia* as an isolated lineage of uncertain affinity, or sister to a clade that includes most of the genera of the Oncidiinae (with the exception of *Cuitlauzina* La Llave & Lex., *Grandiphyllum* Docha Neto, *Psychopsis* Raf., *Rossioglossum* (Schltr.) Garay & G.C. Kenn., *Trichocentrum* Poepp. & Endl., and *Trichopilia* Lindl.). A more detailed historical account of the classification and systematic placement of the genus is presented in the Taxonomic History (Chapter 2).

Lockhartia has been divided in two subgenera: subgenus *Lockhartia* (with all but one species) and the monospecific subgenus *Pseudobulbosa* (with *L. genegeorgei* as the only member). Species of subgenus *Lockhartia* have a vegetative architecture that is both remarkably uniform and very different from that of other taxa in subtribe Oncidiinae. Their flowers can be categorized in three disparate morphological types that could arguably be recognized as separate genera by some traditional taxonomists (it is surprising that this has never been proposed). Results from a recent phylogenetic analysis of Oncidiinae that includes 13 species of subgenus *Lockhartia* (a subset of the

ones included in the present analysis; Neubig *et al.*, in preparation) strongly support this subgenus as monophyletic.

Subgenus *Pseudobulbosa* differs from the other species by some floral characters but especially by its vegetative architecture, which is more similar to that of most other taxa in the Oncidiinae. The vegetative morphology of *L. genegeorgei* is so distinct that Senghas (2001) created the genus *Neobennettia* for this species. However, *L. genegeorgei* shares several traits with other species of *Lockhartia*, including a unique inflorescence type called a pseudocyme (Morphology and Anatomy, Chapter 4), which strongly suggest a close phylogenetic relationship between them.

It has been hypothesized that *L. genegeorgei* has reverted to an ancestral vegetative morphology (Chase, 2009). Such a hypothesis implies that its phylogenetic position could be anywhere within the genus (including being sister to the rest of the species). A second possibility is that *L. genegeorgei* inherited the pseudocyme condition from a common ancestor with other species of *Lockhartia*, but retained a plesiomorphic vegetative morphology. According to this scenario, *L. genegeorgei* would necessarily be the sister species of subgenus *Lockhartia*.

Yet a third possibility is that *L. genegeorgei* is a hybrid (or lineage of ancient hybrid origin) between a species of *Lockhartia* (likely *L. lepticaula*, whose geographic range includes that of *L. genegeorgei*) and another taxon of the Oncidiinae, probably a sympatric species of *Oncidium* or *Vitekorchis*. The latter possibility could be confirmed most convincingly by DNA data (e.g., if the plastid and nuclear sequences had strong but incongruent phylogenetic signals pointing to either putative parent). Unfortunately, DNA of this taxon was not available for this study. Morphological data may provide

some indications of hybridization when comparing cladograms from datasets with and without the putative hybrid (e.g., McDade, 1990; 1992).

The major goal of the present chapter is not to delve further into the phylogenetic position of *Lockhartia*, but to investigate the evolutionary relationships among its species, and to explore putative scenarios of morphological evolution within the genus. Specifically, the putative monophyly of the Imbricata, Longifolia, and Parthenocomos groups of subgenus *Lockhartia* will be tested with molecular and morphological data. In addition, morphological data will be used in an attempt to discern which of the three possible evolutionary scenarios mentioned above for *L. genegeorgei* is best supported.

Materials and Methods

Molecular Analyses

Taxon sampling

Specimens were obtained mainly from cultivated plants (most of which lack original collecting data), and a few wild-collected plants. Sixty-five plant accessions were sampled, including 57 plants of *Lockhartia* (Table 5-1). These include 15 of the 19 species of the Imbricata group, all four species of the Longifolia group, and three of the five species of the Parthenocomos group of *Lockhartia* subgenus *Lockhartia* (for a total of 22 out of the 29 species recognized in the Taxonomic Revision, Chapter 3). No DNA could be obtained for *L. genegeorgei*, the sole member of subgenus *Pseudobulbosa* (see below).

To increase the taxon sampling and the number of accessions for some species of *Lockhartia*, an attempt was made to extract DNA from 14 herbarium specimens (including five additional species, *L. genegeorgei* among them). These extractions were

all unsuccessful (they yielded only degraded DNA). Therefore, the molecular analyses only include members of subgenus *Lockhartia* as well as the outgroup taxa (see below).

Lockhartia micrantha exhibits substantial variation in the shape of the labellum; some individuals have elongate, narrow lateral lobes, while others have extremely reduced lateral lobes or none at all (Taxonomic Revision, Chapter 3). Six accessions of *L. micrantha* were sampled, five of which correspond to the morphotype with short lateral lobes, and one to the long lateral lobe morphotype. These two morphotypes are designated by the suffixes “(s)” and “(l)”, respectively.

Because of the isolated (and to a degree, uncertain) phylogenetic position of *Lockhartia* in the Oncidiinae, eight species from various clades within that subtribe were included as part of the outgroup: *Fernandezia tica* Mora-Ret. & García-Castro, *Grandiphyllum hians* (Lindl.) Docha Neto, *Hofmeisterella eumicroscopica* (Rchb.f.) Rchb.f., *Raycadenco ecuadorensis* Dodson, *Rossioglossum ampliatum* (Lindl.) M.W. Chase & N.H. Williams, *Rossioglossum schlieperianum* (Rchb.f.) Garay & G.C. Kenn., *Trichoceros antennifer* (Humb. & Bonpl.) Kunth, and *Trichopilia turialvae* Bateman.

Molecular techniques

DNA was extracted from either fresh tissues or from material preserved in silica gel (Chase & Hills, 1991), using a modified cetyl trimethylammonium bromide (CTAB) technique (Doyle & Doyle, 1987), scaled to a 1 mL volume reaction. Approximately 10 mg of tissue were ground in 1 mL of CTAB 2X buffer and either 8 μ L of β -mercaptoethanol or proteinase-K (25 μ g/mL; Promega, Inc., Madison, Wisconsin, USA). Some total DNAs were then cleaned with QIAquick (Qiagen, Valencia, California, USA) PCR purification columns as a precaution to remove inhibitory secondary compounds,

although no difference in the quality of the obtained total DNA was noted between cleaned and uncleaned samples.

Five DNA regions were selected for the analyses: the nuclear-ribosomal ITS region (encompassing ITS1, 5.8S, and ITS2, heretofore referred simply as “ITS”), and the plastid regions *trnH-psbA* (which includes the intergenic spacer between the *trnH* and *psbA* genes and the *rps19* exon), *trnL-F* (which consists of an intron in the *trnL* [UAA] gene and the intergenic spacer between the *trnL* [UAA] 3' exon and the *trnF* [GAA] gene), and two non-contiguous portions of the putative protein-coding plastid gene *ycf1* (the ca. 1200 bp portion from the 5' end [5'*ycf1*], and the ca. 1500 bp from the 3' end [3'*ycf1*]). These five DNA regions were selected because they are easy to align and phylogenetically informative at the species level in Oncidiinae (e.g., Williams *et al.*, 2001a, b; Williams *et al.*, 2005).

DNA amplifications were done with an Eppendorf Mastercycler EP Gradient S thermocycler (Hauppauge, New York, USA) and reagents from Sigma (St. Louis, Missouri, USA) in 25 μ L volumes with the following reaction components for ITS: 0.5–1.0 μ L template DNA (~10–100 ng), 11 μ L water, 6.5 μ L 5M betaine (added to eliminate the secondary structure of the ribosomal DNA), 2.5 μ L 10X buffer, 3 μ L MgCl₂ (25mM), 0.5 μ L of 10 μ M dNTPs, 0.5 μ L each of 10 μ M primers, and 0.5 units *Taq* polymerase. For all plastid regions, the reaction components were: 0.5–1.0 μ L template DNA (~10–100 ng), 16–18 μ L water, 2.5 μ L 10X buffer, 2–3 μ L MgCl₂ (25mM), 0.5 μ L of 10 μ M dNTPs, 0.5 μ L each of 10 μ M primers, and 0.5 units (0.2 μ L) *Taq* polymerase.

Thermocycler parameters for amplification of the various regions were as follows. For ITS: a touchdown protocol with 94°C for 2 min; 15 \times (94°C, 1 min; 76°C for 1 min,

reducing 1°C per cycle; 72°C, 1 min); 21x(94°C, 1 min; 59°C, 1 min; 72°C, 1 min); 72°C, 3 min, with primers 17SE and 26SE (Sun *et al.*, 1994). For *trnH-psbA* and *trnL-F*: 94°C for 3 min; 33x(94°C, 1 min; 58°C, 1 min; 72°C, 1 min, 20 s); 72°C, 6 min, with primers F and R (from Xu *et al.*, 2000) for *trnH-psbA*, and primers C and F (or in two separate reactions with primers [C and D] and [E and F], when C and F alone failed to produce a single band) for *trnL-F* (Taberlet *et al.*, 1991). For both portions of *ycf1*: a touchdown protocol with 94°C, 3 min; 8x(94°C, 30 sec; 60°C, reducing 1°C per cycle; 1 min; 72°C, 3 min); 30x(94°C, 30 sec; 50°C, 1 min; 72°C, 3 min); 72°C, 3 min, with primers 1F and 1200R for the 5' portion, and primers 3720F and 5500R (with additional internal sequencing primers intF and intR) for the 3' portion (Neubig *et al.*, 2009).

PCR products were cleaned with Microclean™ (The Gel Company, San Francisco, California, USA) following the manufacturer's protocols, eluted with 50 µL of 10 mM Tris-HCl (pH 8.5) and stored at 4°C. Clean PCR products were then cycle-sequenced using the parameters 96°C, 10 sec; 25x(96°C, 10 sec; 50°C, 5 sec; 60°C, 4 min), with mix of 3 µL water, 1 µL fluorescent Big Dye dideoxy terminator, 2 µL Better Buffer™ (The Gel Company), 1 µL template and 0.5 µL primer. Cycle sequencing products were cleaned using ExoSAP™ (USB Corporation, Ohio, USA) following the manufacturer's protocols. Purified cycle sequencing products were directly sequenced on an ABI 377, 3100, or 3130 automated sequencer according to the manufacturer's protocols (Applied Biosystems, Foster City, California, USA).

Analyses

Electropherograms were assembled and edited with the program Sequencher 4.6™ (GeneCodes, Ann Arbor, Michigan, USA). Sequence data were manually aligned

with the program Se-AI v2.0a11 (Rambaut, 1996). Insertions and deletions (indels) were coded as missing data.

Maximum parsimony (MP) analyses were performed using PAUP*4.0b10 (Swofford, 2003) with Fitch parsimony (unordered characters with equal weights; Fitch, 1971). Heuristic searches consisted of branch swapping by tree bisection reconnection (TBR), stepwise addition with 5000 random-addition replicates holding five trees at each step, and saving multiple trees (MulTrees). Levels of support were assessed using the bootstrap (Felsenstein, 1985). Bootstrap percentages were estimated with 1000 bootstrap replicates, using TBR swapping for five random-addition replicates per bootstrap replicate. For interpretation, bootstrap values of 50–69% are considered weak, those of 70–89% are considered moderate, and those of 90–100% are considered strong.

All MP analyses were performed for datasets including ITS only, plastid regions only, and all data combined. Sequence data for *trnH-psbA* and *trnL-F* could not be obtained for some accessions/species (Table 5-1), but these accessions were still included (with missing data) in the combined matrices. Data congruence was tested by using a partition homogeneity test (Farris *et al.*, 1995) in PAUP*4.0b10. Heuristic searches for the partition homogeneity test were performed using 100 replicates and TBR branch swapping.

A maximum likelihood (ML) analysis of the combined five-region dataset was also performed in PAUP*, assuming a GTR + I + G model (determined by the program JModelTest v.0.1 [Posada, 2008] under the Akaike Information Criterion).

Morphological Analyses

Taxon sampling

For the morphological analyses, species (as circumscribed in the Taxonomic Revision [Chapter 3]), not individual plants, were treated as operational taxonomic units (OTUs). The two morphotypes of *Lockhartia micrantha* (see above) were treated as separate OTUs, for a total of 30 ingroup taxa. The same eight outgroup taxa used in the molecular data matrix were also included in the morphological matrices.

Characters

Forty-four gross morphological characters were scored for all the taxa in the matrix, including 17 vegetative characters (six of them related to inflorescence structure) and 27 reproductive characters (two of them related to the structure of the mature fruit; Table 5-2). This asymmetry reflects the overall vegetative similarity between species of subgenus *Lockhartia* (seven of the vegetative characters are uniform within that subgenus) and the wide variation in their floral structure. Characters were included only if they exhibit variability within the ingroup and/or between the ingroup and the outgroup, and if the variability within individual OTUs (interpreted here as phenotypic plasticity) is minor compared with the variability among OTUs.

Although a survey of anatomical characters was performed as part of this dissertation (Morphology and Anatomy, Chapter 4), they were not included here for several reasons: 1) samples from the species used as outgroups were not available for anatomical study; 2) the anatomical survey was based on only ten species of *Lockhartia* (most of them members of the Imbricata group, and none from either the Parthenocomos group or subgenus *Pseudobulbosa*); 3) little variability among species was detected in most anatomical characters; and 4) anatomical observations were

based on a few sections, usually from a single segment per organ (root, stem, leaf, or flower) of a single plant per species. Thus, the representativeness of the resulting character states for the species would not be guaranteed, and including them in the matrix would amount to pseudo-replication (in contrast to the gross morphological character states, which were scored based on multiple samples). The exclusion of anatomical characters is further justified by the study of Stern and Carlswald (2006), who determined that these provide negligible phylogenetic signal even among different genera of the Oncidiinae. In general, the exclusion of characters because they have missing data is not recommended (Poe & Wiens, 2000), but I feel that the combination of the above-mentioned factors justifies the exclusion of the anatomical characters.

The scoring of character states was based on the examination of 2275 herbarium specimens of *Lockhartia* representing 1514 different collections (Taxonomic Revision, Chapter 3) and several additional specimens for the outgroup taxa, published descriptions (when these were based on illustrated plants or vouchered collections whose identity could be confirmed), and plants in cultivation. Observations of cultivated plants were of particular importance for characters related to the temporal development of structures (e.g., simultaneous vs. basipetal or acropetal inflorescence initiation, etc.). Both unknown and non-applicable character states were scored as missing (PAUP* treats both types of characters in the same way). Live plants of outgroup taxa were not available for cultivation and observation; character states related to the temporal development of structures were inferred from published descriptions, illustrations, and herbarium specimens.

Analyses

Two matrices of morphological data were analyzed using MP as implemented in PAUP* 4.0b10. The first matrix (shown in Table 5-3) consists of 30 binary and 14 multistate characters; of 1672 character state cells, 62 (3.7%) are scored as either missing or inapplicable. This matrix is referred to as the “inclusion” matrix because it includes the anomalous species *Lockhartia genegeorgei*. The second (“exclusion”) matrix is identical to the first except for the exclusion of *L. genegeorgei*. The exclusion matrix consists of 1628 character state cells, of which 59 (3.6%) are scored as either missing or inapplicable. The exclusion matrix was analyzed in order to assess the effect of the presence/absence of *L. genegeorgei* in the ingroup topology.

All characters were treated as unordered and equally weighted (Fitch parsimony). A heuristic search was performed with 10000 tree-bisection-reconnection (TBR) branch-swapping searches; starting trees were obtained from stepwise random addition replicates with five trees held at each step, and saving multiple trees (MulTrees) and steepest descent option not in effect. To assess branch support, a bootstrap analysis was performed with 1000 replicates and 50 TBR branch-swapping searches; starting trees were obtained from stepwise random addition replicates with 5 trees held at each step with MulTrees in effect and steepest descent option not in effect. For interpretation, bootstrap support (BS) of 50–69% was classified as weak, BS of 70–89% as moderate, and BS of 90–100% as strong. The program MacClade version 4.08 (Maddison & Maddison, 2005) was used to examine patterns of character change in the resulting cladograms.

Bayesian inference (BI) analyses were not performed with the molecular datasets. However, BI almost always results in topologies that are essentially congruent with those produced by ML and MP analyses (Rindal & Brower, 2010).

Results

Molecular Analyses

Table 5-4 lists the features of the different DNA datasets used in the MP analyses. Although ITS is the shortest of the five regions, it provided the largest number of potentially parsimony-informative sites and ingroup nodes with moderate to high support. A sample phylogram is shown in Figure 5-1. In the ITS analysis, the three accessions of *Lockhartia amoena* often have relatively long branches (grouped with one accession of *L. tenuiflora* and the sole accession of the long-lobe morphotype of *L. micrantha* in the phylogram of Figure 5-1, although the latter relationship is not always present in all of the most parsimonious trees and is not supported in the 50% majority-rule consensus). Although there are a few bases in the ITS sequences of the three accessions of *L. amoena* that appear different from those of most other members of the genus, this long branch is probably an artifact from the incomplete sequences of these accessions (some of them missing almost 50% of the base data due to repeatedly messy electropherograms from one of the primers).

The 3'*ycf1* region is the longest and it provided the second highest number of potentially parsimony-informative sites and the same number of ingroup nodes with moderate to high support. The 5'*ycf1* and *trnH-psbA* regions provided relatively few potentially parsimony-informative sites and low support for most ingroup nodes; the bootstrap consensus of the 5'*ycf1* analysis supports *Lockhartia* as monophyletic, but there is not strong support for any internal clade (except for several species represented

by more than one accession). The *trnL-F* region is comparable to 5'*ycf1* in terms of proportion of potentially parsimony-informative regions, but it provided the fewest number of ingroup nodes with moderate to high BS.

For the most part, the bootstrap (50% majority rule) consensus trees produced by the analysis of the different DNA regions are topologically congruent, and most of the supported clades make sense from a morphological viewpoint. There are a few accessions that appear as sister to those of a different species in the *trnL-F* and 5'*ycf1* trees, but their subtending branches receive weak BS.

The result of the partition homogeneity test indicates that the different molecular datasets are not statistically incongruent ($p=0.067$), and combined datasets of all four plastid regions and all five DNA regions were analyzed (a representative phylogram of the combined plastid regions is shown in Figure 5-2). There are no hard (i.e., with $\geq 70\%$ BS; Seelanan *et al.*, 1997) topological incongruences between the ITS and combined plastid datasets, and thus the combined five DNA region bootstrap consensus was taken as an acceptable estimate of the phylogeny of the genus. Figure 5-3 shows one of the shortest trees from this analysis, and Figure 5-4 shows the 50% majority rule consensus, with the species that belong to the different morphological groups and subgroups (Table 3-1, Morphology and Anatomy, Chapter 4) indicated by vertical bars (these are not meant to indicate clades).

In the latter tree, *Lockhartia* is strongly (100% BS) supported as monophyletic (it receives $\geq 96\%$ BS in the different DNA region analyses). There is a polytomy on the spine of the tree. None of the three major morphological groups (Imbricata, Longifolia, and Parthenocomos) are supported as monophyletic.

Lockhartia bennettii and *L. rugosifolia* are strongly (88% BS) supported as sister species, although *L. oblongicallosa* does not receive bootstrap support as a member of this clade (Fig. 5-4). However, the putative monophyly of the Parthenocomos group is still a possibility (there are no strongly supported nodes that are incongruent with this hypothesis).

The monophyly of the Longifolia group is strongly contradicted by the results of the combined analysis (Fig. 5-4). Three species of the Longifolia group (*L. hercodonta*, *L. obtusata*, and *L. longifolia*) form a moderately supported clade (82% BS), but the fourth species (*L. parthenoglossa*) is strongly supported (96% BS) as sister to the Imbricata subgroup.

The monophyly of the Imbricata group is also strongly contradicted by the results of the combined analysis, although its subgroups are supported as monophyletic (Fig. 5-4). The two sampled species of the Oerstedii subgroup form a well-supported (99% BS) clade, placed along the spine of the tree. *Lockhartia acuta* (the sole member of the Acuta subgroup) is weakly supported (66% BS) as sister to the (*L. parthenoglossa* + Imbricata subgroup) clade, while the Imbricata subgroup receives low (67% BS) support.

The monophyly of the Imbricata subgroup is weakly supported (67% BS) by the combined molecular analysis (Fig. 5-4). None of the individual molecular datasets provide support for a monophyletic Imbricata subgroup. In the bootstrap consensus of *trnL-F*, ITS, *trnH-psbA*, and *3'ycf1*, the members of the Imbricata subgroup appear in a polytomy that includes *L. parthenoglossa* and (in the last three mentioned regions) *L. acuta*.

For the most part, multiple accessions of individual species are either grouped in the same clade (with >50% BS) or at least not strongly supported as sister to a different species. One accession of *L. endresiana* (Blanco 1803) appears as sister to the only accession of *L. dipleura*, but with low support (60% BS, a relationship also recovered in the 5' *ycf1* and combined-plastid analysis). One accession of *L. lunifera* (Gerlach 141) is weakly supported as sister to the only accession of *L. goyazensis*.

The five short-lobe morphotype accessions of *L. micrantha* form a weakly supported clade (67% BS), although one of the internal nodes receives moderate support (82% BS). The only long-lobe morphotype accession of this species (Blanco 3220) is not part of that clade, but is part of a basal polytomy of the Imbricata subgroup (a pattern also present in the ITS bootstrap consensus). However, in both the 3' *ycf1* and combined-plastid analyses, the long-lobe morphotype accession of *L. micrantha* appears in a weakly supported clade with *L. cladoniophora* (a relationship not recovered by the combined five-gene bootstrap consensus).

The overall topology resulting from the ML analysis of the combined five-gene dataset (not shown) is very similar to that found by parsimony searches, including levels of bootstrap support for individual branches, with only minor differences in the relative placement of individual accessions within the morphological groups and subgroups.

Morphological Analyses

The analysis of the “inclusion” matrix (i.e., including *L. genegeorgei*) produced 467 most parsimonious trees of 182 steps (consistency index [CI] = 0.36, retention index [RI] = 0.74). In the strict consensus (Fig. 5-5) *L. genegeorgei* is placed outside of the genus in an unresolved position with most of the outgroup taxa. In about half of the most parsimonious trees, *L. genegeorgei* appears as sister to subgenus *Lockhartia*, but in

many others it appears as sister to *Raycadenco ecuadorensis* (an outgroup taxon). Subgenus *Lockhartia* is monophyletic with moderate support (84% BS). Only two clades are recovered within subgenus *Lockhartia*: 1) a clade with moderate support (82% BS) formed by the two morphotypes of *L. micrantha*, and 2) a weakly supported clade (54% BS) that includes all members of the Longifolia and Parthenocomos groups. *Lockhartia hercodonta*, *L. longifolia*, and *L. parthenoglossa* (but not *L. obtusata*) form a weakly supported subclade (53% BS).

The analysis of the “exclusion” matrix (i.e., excluding *L. genegeorgei*) produced 38 most parsimonious trees of 168 steps (consistency index [CI] = 0.38, retention index [RI] = 0.76). In the strict consensus (Fig. 5-6), *Lockhartia* is monophyletic with strong support (96% BS) but the intrageneric relationships are unresolved. In contrast to the inclusion matrix, the nine members of the Longifolia and Parthenocomos groups have an unresolved position on the spine of the tree, while the Imbricata group has poor (61% BS) support as a clade.

Discussion

In the following discussion, reference will be made to the groups and subgroups of *Lockhartia* as they were circumscribed in Chapter 4 (Morphology and Anatomy; i.e., the Parthenocomos, Longifolia, and Imbricata groups, the latter divided into the Imbricata, Acuta, and Oerstedii subgroups; Table 4-1). When mention is made about a “member” of one of those groups or subgroups, this does not imply membership in a particular clade.

Molecular Analyses

It is apparent from the molecular analyses that there is strong evidence against the monophyly of the Imbricata and Longifolia groups (Figs. 5-1 to 5-5). The three

accessions of *L. parthenoglossa*, a member of the Longifolia group, are strongly supported as sister to a clade formed by the members of the Imbricata subgroup. This relationship is surprising, given the very homogeneous floral structure of the Longifolia group, in particular the callus structure of their labellum, and suggests that this floral morphology is either plesiomorphic for this group of species or that it evolved twice. *Lockhartia acuta* and the members of the Oerstedii subgroup appear in different positions of the tree, although these positions receive either low support (*L. acuta*, with 67% BS as sister to the *L. parthenoglossa* + Imbricata subgroup clade) or no support at all (the Oerstedii subgroup, placed in a basal polytomy of the genus in the five-gene bootstrap analysis).

All four species of the Longifolia group were sampled, and only four species of the Imbricata subgroup were not sampled for molecular data. The latter four species have clear morphological and geographical affinities to members of the Imbricata subgroup (*L. compacta*, *L. imbricata*, and *L. ivainae*) or to members of the Oerstedii subgroup (*L. galeottiana*). Thus, their inclusion in the analysis would likely have little effect on the relationships among the major groups of the genus. The inclusion of the first three species may or may not provide additional support to the node that supports the Imbricata subgroup, or improve the resolution within that clade. Based on its general morphology and geographic distribution, it is hypothesized that *L. imbricata* would probably group with *L. goyazensis* and *L. lunifera*. It is more difficult to speculate about the putative relationships of *L. compacta* and *L. ivainae* on strictly morphological grounds because of their relatively reduced floral size and simplified callus structure. Taking their geographic distribution into consideration, *L. ivainae* may be closely related

to *L. imbricata* and/or *L. goyazensis*, while *L. compacta* is probably closely related to *L. lepticaula*.

None of the individual or combined molecular datasets provide support for the monophyly of the Parthenocomos group (Fig. 5-5). *Lockhartia oblongicallosa* appears as part of the basal polytomy of the genus in all bootstrap analyses, and a sister relationship between *L. bennettii* and *L. rugosifolia* is only moderately supported (84% BS) by the ITS dataset. However, the results do not provide strong conflict with the possibility of these species forming a clade. Two species of the Parthenocomos group (the Venezuelan-Guyanese *L. latilabris* and *L. parthenocomos*) could not be sampled for DNA data, and their inclusion could potentially change the relationships among the members of this group. *Lockhartia oblongicallosa* is a narrow endemic to northeastern Venezuela and may be closely related to both *L. latilabris* and *L. parthenocomos* (which are probably sister species); however, the strange callus morphology of *L. oblongicallosa* is unique in the genus, and it may be an indication that the latter may, in fact, not belong to a clade formed by other members of the Parthenocomos group. Sampling of both *L. latilabris* and *L. parthenocomos* is necessary to test this hypothesis.

Morphological Analyses

Contrary to my expectations, the analyses of the morphological data were not able to provide resolved and well-supported phylogenies. One possible cause is that many character states are homoplasious as presently coded (Character State Evolution, below). Another factor that likely contributed to this lack of resolution is that several character states are unique to, and/or invariant within, the ingroup (or at least within subgenus *Lockhartia*; e.g., characters 2, 3, 4, 7, 10, 12, 15, 39, 40, 41, 42; Table 5-2).

Such characters provide support for the monophyly of the ingroup, but are practically worthless as sources of internal resolution.

Despite the low resolution of the ingroup, the comparison of the exclusion and inclusion bootstrap trees indicates that the presence/absence of *L. genegeorgei* in the analysis has an effect on the topology of the ingroup. The exclusion analysis provides some support for the monophyly of the Imbricata group, and none for the monophyly of the Longifolia and Parthenocomos groups. In contrast, the inclusion analysis provides some support for a clade formed by members of the latter two groups (and none for the Imbricata group), and places *L. genegeorgei* in an unresolved position with most of the outgroup taxa, even when this taxon was designated as part of the ingroup.

Unfortunately, the placement of *L. genegeorgei* in the inclusion analysis cannot be used to discriminate between the three possible evolutionary scenarios mentioned in the introduction, i.e., that the morphology of *L. genegeorgei* represents a series of reversals, plesiomorphic conditions, or a product of hybridization.

Perhaps some insight about the potential hybrid origin of *L. genegeorgei* can be obtained by comparison of the results obtained here with those of McDade (1990; 1992). She created artificial hybrids of *Aphelandra* (Acanthaceae) and used them in similar exclusion/inclusion cladistic analyses of morphological data to investigate their placement in the cladograms, and to assess their effect on the topology of the ingroup and other tree parameters. McDade found that 1) inclusion of hybrids results in equal or significantly higher consistency indices (CIs); 2) hybrids tend to be placed at or near the base of the clade that includes the most apomorphic parent; 3) hybrids between

distantly related parents resulted in cladograms with low CI and major topological changes.

Comparison of the inclusion and exclusion analyses of the present study reveals very similar CIs for their most parsimonious trees (0.36 and 0.38, respectively), which by itself does not support or conflict with the hypothesis of hybrid origin. The placement of *L. genegeorgei* in the inclusion analysis provides more support for this hypothesis. About half of the most parsimonious trees of the inclusion analysis place *L. genegeorgei* as sister to subgenus *Lockhartia*, while the other half places it as sister to *Raycadenco ecuadorensis*; the latter placement is incompatible with both the reversal and plesiomorphic condition evolutionary scenarios. Finally, the inclusion of *L. genegeorgei* does cause a relatively major topological change in the ingroup, which also agrees with the hypothesis of hybrid origin.

The vegetative morphology of *L. genegeorgei* is rare in the Oncidiinae; each sympodial unit consists of a short horizontal rhizome segment, and an erect stem segment of 4–6 leafy internodes that is terminated by a small pseudobulb. One artificial hybrid between *L. bennettii* and *Oncidium cirrhosum* (Lindl.) Beer, observed at the greenhouses of Ecuagenera Ltda. in Gualaceo, Ecuador, has a similar vegetative morphology (although with shorter leaves). This similar phenotype also suggests that *L. genegeorgei* may be a hybrid between a species of *Lockhartia* and a member of another genus in the Oncidiinae.

Despite all this, morphological data alone do not necessarily confirm the hybrid origin of a taxon. As stressed by McDade (2000), not all cases of character patterns suggestive of hybridization are necessarily due to that process. The strange morphology

of *L. genegeorgei* can also be explained (although less satisfactorily) by the reversal hypothesis and the plesiomorphic state hypothesis. Hopefully, molecular data of this taxon, when available, will help clarify its systematic affinities.

An analysis of combined morphological and molecular data (an approach advocated by Donoghue & Sanderson, 1992) was not carried out, on purpose. Besides the obvious problem of combining two disparate datasets (one with characters obtained from multiple individuals per OTU, the other with characters obtained from single individuals for each OTU), it is apparent that the morphological dataset is plagued by homoplasy and lacks significant phylogenetic signal. The little phylogenetic signal of the morphological dataset also conflicts with that of the molecular dataset. DNA sequences provide a large amount of data with which to test phylogenetic hypotheses that are based on morphological data; combining the morphological and molecular data would most likely introduce phylogenetic noise (due to the different signals) and problems of circularity in the resulting cladograms (Givnish & Sytsma, 1997; Hillis & Wiens, 2000).

Taxonomic Implications

Subgenus *Lockhartia* received strong support as a monophyletic group from all molecular and morphological analyses. Thus, its recognition as a subgenus (or genus, depending on the systematic position of *L. genegeorgei*) is not questioned. Its three major morphological groups, however, either lack support (e.g., the Parthenocomos group) or their monophyly is strongly contradicted by the data (the Imbricata and Longifolia groups, which are paraphyletic). Therefore, despite the intuitive convenience of these groupings, they cannot be formally recognized (e.g., as ranked taxa in a Linnean system) if the principles of phylogenetic classification are applied (Judd *et al.*, 2008).

Two subgroups of the Imbricata group (the Acuta and Oerstedii subgroups) are well supported by the combined molecular analysis. The former, however, is actually monospecific (including only *Lockhartia acuta*, a very distinctive species). The three members of the Oerstedii group (*L. oerstedii*, *L. verrucosa*, and *L. galeottiana*; the last one was not sampled for molecular data but its morphology and geographic distribution strongly suggest that it belongs in this clade) are very similar morphologically to the species of the Imbricata subgroup (which receives low support from the combined molecular analysis). The Acuta and Oerstedii subgroups could be recognized taxonomically (e.g., to sectional level), but there would be little practical gain from this (given that other groups could not be recognized). Thus, at this point, I think it is not advisable to create a subgeneric classification in *Lockhartia*, other than provisionally maintaining the two subgenera until the status of *L. genegeorgei* is clarified.

Character Evolution

In order to explore plausible scenarios of character evolution, a tree was constructed with species for OTUs (including only those species that were sampled for the molecular analysis). The topology of this tree was adapted from that of the phylogram presented in Figure 5-3, and selected characters were traced using MacClade under the accelerated transitions optimization (ACCTRAN).

Morphological variations of the various vegetative and reproductive structures of *Lockhartia* are described in detail in Chapter 4 (Morphology and Anatomy). In the following paragraphs, I will describe features only in relation to putative evolutionary scenarios within the genus, in relation to the outgroup taxa, and in terms of character state delimitation (when necessary). The species not sampled for molecular data (*L. compacta*, *L. galeottiana*, *L. genegeorgei*, *L. imbricata*, *L. ivainae*, *L. latilabris*, and *L.*

parthenocomos) will be mentioned occasionally, but character evolution in relation to them will not be considered at length due to their uncertain position. Character numbers in the figure legends refer to those in Table 5-2.

Stem

Stems of *Lockhartia* can be either erect or pendulous. Large plants of species with erect stems often have individual shoots growing in all directions, but these stems are always relatively rigid. Species with pendulous stems can have stems that are erect when young and not fully-grown, but eventually become pendent because they are more flexible (the stem core is probably less sclerenchymatized than in the erect-stemmed species). According to the suggested evolutionary scenario (Fig. 5-7), the pendulous condition has evolved repeatedly, at least four times (*L. latilabris* and *L. parthenocomos*, not included in the diagram, also have pendulous stems). It appears that the pendulous stem condition occurs in species that grow in less exposed conditions than other congeners. These plants usually hang from horizontal branches, and their pendulous stems probably represents a strategy to exploit the darker but less crowded space under the branch. The leaves of these species tend to be softer than those of erect-stemmed species, but a causal relationship for this is not obvious.

The number of internodes per stem (i.e., per individual sympodial unit) shows a single evolutionary change (from less than eight to more than 13), and represents a synapomorphy for the genus. This change is directly related to the distinctive growth habit of *Lockhartia*. Only one of the outgroup taxa (*Raycadenco*) has more than 13 internodes per stem but it is clearly an independent origin. This character is essentially quantitative but with discrete values. The number of internodes was counted only for mature stems (those that have reached their final vegetative length and have produced

inflorescences; young stems and seedlings can have fewer internodes). Mature stems of *Lockhartia* usually have many more internodes than 13 (up to 74 in some species), while the outgroup taxa rarely have more than six internodes per stem unit. *Lockhartia genegeorgei* has less than 13 internodes.

Leaves

The leaves of subgenus *Lockhartia* have a very uniform and distinctive morphology. Unlike most other taxa in the Oncidiinae, they lack an abscission layer (Fig. 5-8) and thus stay attached to the stem even if they die (i.e., they are marcescent). The loss of an abscission layer appears to be a synapomorphy to subgenus *Lockhartia*. The marcescent condition seems to be related to the origin of leaf decurrence (another apparent synapomorphy for the subgenus; Fig. 5-8), and to isobilateral foliar blades (Fig. 5-9) in *Lockhartia*. These three characters do not seem to be necessarily dependent on each other (some outgroup taxa show various state combinations for them); this justifies their inclusion as separate characters.

Chase (1986, 2009) hypothesized that the evolution of isobilateral (psylgmoid) leaves in the Oncidiinae has occurred repeatedly through neoteny. Several taxa that have open, conduplicate blades as adults often have isobilateral leaves as seedlings, and in some cases they start flowering even before undergoing a vegetative transformation to the adult form. The juvenile morphology has likely been permanently fixed for taxa with isobilateral leaves.

The differential leaf size along the stem (i.e., whether the leaves near the apex of the stem are larger, subequal, or smaller than the leaves near the center of the stem) displays variation among species. Most species have central leaves that are subequal to the apical ones, while others have much smaller apical leaves. The ancestral

condition for the genus is equivocal; central leaves subequal to the apical ones may be either a synapomorphy or a plesiomorphy for the genus (Fig. 5-9). Most outgroup taxa have apical leaves that are much larger than the central ones (a condition also present in *L. genegeorgei*). It must be acknowledged that there is ample intraspecific variation in this character, which makes the delimitation of states somewhat arbitrary (Stevens, 1991; Givnish & Systsma, 1997).

Inflorescences

The inflorescences of *Lockhartia* have several remarkable (although easily overlooked) traits. The pseudocymose condition a clear synapomorphy for *Lockhartia* (it appears to be unique, even among angiosperms; Fig. 5-10).

Axillary inflorescence development is the norm in the Oncidiinae, but plants of subgenus *Lockhartia* can produce terminal inflorescences (i.e., the apical shoot meristem eventually transitions to produce an inflorescence; Fig. 5-10). Also, each shoot can produce multiple inflorescences. By itself, this is not unique in the Oncidiinae, but the order of initiation (basipetal) is highly unusual. Basipetal initiation of inflorescences may be either a synapomorphy or a plesiomorphy of subgenus *Lockhartia*, with several reversals to simultaneous initiation (Fig. 5-11). Most of the outgroup taxa normally produce a single inflorescence per shoot (and thus this character could not be scored for them), but in the few ones that produce multiple inflorescences (*Fernandezia* and *Raycadenco*), the initiation is acropetal. The state for this character could not be scored either for several species of *Lockhartia* (Fig. 5-11), but the character state optimization suggests that the basipetal condition is a synapomorphy for the subgenus.

The proleptic inflorescence branching (i.e., sequential initiation of branches within an inflorescence) is another apparent synapomorphy for subgenus *Lockhartia*, with several reversals to the sylleptic condition (Fig. 5-11). The order of inflorescence initiation is independent of the type of inflorescence branching (Fig. 5-11).

Lockhartia genegeorgei has inflorescences that are exclusively axillary, pseudocymose, and proleptic. It is unknown if it can produce more than one inflorescence per shoot, and if so, in what order.

Perianth color

Many (perhaps most) taxa in the Oncidiinae have yellow flowers (often with spots of darker colors), and this is true of *Lockhartia* as well. The yellow base color of the perianth may be a plesiomorphic condition for the genus, but the placement of *L. oblongicallosa* (a species with white flowers) as sister to the rest of the genus in the sample phylogeny (Fig. 5-12) precludes an unambiguous reconstruction for the ancestral condition of this character in *Lockhartia*. Three other species in the genus have white flowers, suggesting at least three independent evolutionary acquisitions for this character state (Fig. 5-12).

Flower orientation

Resupinate flowers are likely plesiomorphic for *Lockhartia* as indicated by outgroup condition (Fig. 5-12). Most outgroup taxa have resupinate flowers. Six species in the genus have variably-oriented flowers, and only one (*L. obtusata*) has strictly non-resupinate flowers (i.e., with the labellum consistently placed uppermost in the flower). The diagram in Figure 5-12 suggests four independent origins for variable floral orientation occurred in the genus.

Sepals and petals

Sepals of *Lockhartia* can be patent (held more or less perpendicular to the axis of the pedicel) or reflexed against the pedicel (a third state, having the lateral sepals reflexed on the pedicel but the dorsal sepal patent, occurs only in *L. genegeorgei*). The patent condition appears to be plesiomorphic, based on outgroup analysis (Fig. 5-13). The reflexed condition evolved seemingly twice, once in the *Oerstedii* subgroup and another time in the *Imbricata* subgroup, with a secondary reversal in *L. micrantha* and relatives.

Petals of *Lockhartia* can be either straight (held more or less perpendicular to the axis of the pedicel and relatively flat) or arched toward the front of the flower, resembling horns. These two states appear to be highly correlated with the sepal orientation: straight petals occur most often in association with patent sepals, and arched petals occur most often in association with reflexed sepals (Fig. 5-13). This may have to do with alternate strategies of floral visual display; flowers with patent sepals and straight petals present a larger surface area toward the front, while flowers with reflexed sepals and arched petals have a relatively narrow profile if viewed from the front but are more conspicuous if viewed from the side. Only one species (*L. oxyphylla*) has reflexed sepals and relatively straight petals.

Labellum

The relative complexity and structural variability of the callus provided several characters for the morphological analysis, but at the same time makes the exact definition of character states a difficult task. The independence of the various characters associated with the callus is also difficult to guarantee in the absence of developmental

and gene expression studies (e.g., Stevens, 1991; Givnish & Sytsma, 1997; Mabee, 2000).

The labellum of *Lockhartia* can be convex, concave, or relatively flat. Most outgroup taxa have relatively flat labella (Fig. 5-14), but the position of several species of *Lockhartia* with concave labella toward the base of the chosen cladogram, and the common occurrence of the other two conditions throughout the genus prevents an unequivocal reconstruction for the ancestral condition. It is apparent, however, that the labellum configuration is evolutionarily labile.

The relative dimensions of the lateral lobes also show a significant degree of homoplasy within the genus (Fig. 5-14). The chosen cladogram suggests that wider-than-long lateral lobes is the ancestral condition for *Lockhartia*, and this is the condition observed among members of the Parthenocomos group. Lateral lobes that are at least three times as long as wide occur in the Oerstedii subgroup and in most members of the Imbricata subgroup, although some species of the latter developed shorter lobes. The absence of lateral lobes characterizes the grade formed by the Longifolia group and *L. acuta*.

Five callus types can be recognized in *Lockhartia*, but it is unclear if any of these is ancestral to the entire genus (Fig. 5-15). Most species of the Imbricata group have a callus formed by a single tuberculate keel, and some members of the Imbricata subgroup and *L. acuta* have a callus formed by two parallel keels (which likely evolved independently). The crateriform callus type is unique to the species of the Longifolia group; the cladogram in Figure 5-15 suggests that this type of callus may have evolved twice, along with the trapezoid ledge. It is difficult to envision how such a complex

structure evolved twice. The callus is a complex structure, and it could possibly be partitioned in more characters, but the way to delimit these and their respective states is not obvious. Developmental studies of the callus may assist in creating an improved selection of morphological characters.

The callus can also be categorized with respect to its texture (smooth vs. tuberculate) and indument (glabrous vs. pubescent-glandular or pubescent non-glandular), although exactly what constitutes a tubercle is difficult to determine. For the morphological analysis, protuberances with a more or less rounded tip were scored as tubercles, while those with a sharp tip (often elongate) were scored as teeth (character 34, not shown in figures). Tubercles and teeth occur in different types of callus (keeled vs. crateriform, respectively), but it is unclear if they are really independent, non-homologous structures. According to this characterization, the smooth callus seems to be plesiomorphic for the genus, and the pubescent-glandular condition is an apparent synapomorphy (Fig. 5-16). Tuberculate and glabrous calli evolved at least twice (in the *Imbricata* and *Oerstedii* subgroups), although those states are not necessarily dependent on each other (e.g., *L. cladoniophora* and *L. micrantha* have smooth and glabrous calli).

The presence of an elaiophore cushion seems to be correlated with the presence of a basal tuft of secretory hairs in the labellum (Fig. 5-17). The cushion probably functions as a holder for the basal tuft of secretory hairs (and any oil that may be secreted), although two species (*L. acuta* and *L. cladoniophora*) have one structure without the other. The reconstruction on the hypothetical cladogram suggests that the elaiophore cushion evolved twice, but it is unclear regarding the number of times that

the basal tuft of secretory hairs evolved within the genus (the lack of the basal tuft is seemingly plesiomorphic for *Lockhartia*).

Column

The shape of the column wings is quite variable in *Lockhartia*, and this makes the delimitation of discrete states difficult. Five states were scored, plus two additional ones that occur only in outgroup taxa. The “obliquely subquadrate” condition is the most common in the genus, but other states are more or less randomly distributed in the cladogram, making it impossible to infer an unequivocal ancestral state (Fig. 5-18). This underscores the evolutionarily labile nature of the column wings. These structures likely guide the pollinia attached to a pollinator toward the relatively small stigmatic surface during a subsequent floral visit, but the significance of different wing shapes, if any, is unclear. If the detailed shape of the column wings is not that important, then this could explain the high homoplasy apparent in this character.

The stigma of most *Lockhartia* species is narrowly oblong (in contrast to most outgroup taxa), and this appears to be a synapomorphy for the genus (Fig. 5-18). Only one species (*L. goyazensis*) has a relatively wide stigma, which represents a reversal.

Table 5-1. Information for accessions used in the molecular phylogenetic analyses of *Lockhartia*. DNA region sampled are A= ITS, B= *trnH-psbA*, C = *trnL-F*, D= 3'*ycf1*, E= 5'*ycf1*.

Taxon ^a	Voucher	Herbarium ^b	Gene regions
<i>Fernandezia tica</i>	Dressler & Atwood s.n.	FLAS	A,B,C,D,E
<i>Grandiphyllum hians</i>	Chase 86137	K	A,B,C,D,E
<i>Hofmeisterella eumicroscopica</i>	Whitten 2690	FLAS	A,B,C,D,E
<i>Lockhartia acuta</i>	Blanco 2567	FLAS	A,B,C,D,E
<i>Lockhartia acuta</i>	Blanco 3221	FLAS	A,B,D,E
<i>Lockhartia amoena</i>	Blanco 2555	FLAS	A,B,D,E
<i>Lockhartia amoena</i>	Blanco 2556	FLAS	A,B,D,E
<i>Lockhartia amoena</i>	Blanco 3212	FLAS	A,B,D,E
<i>Lockhartia bennettii</i>	Blanco 2554	FLAS	A,B,C,D,E
<i>Lockhartia cladoniophora</i>	Bogarín 2352	JBL	A,D,E
<i>Lockhartia dipleura</i>	Pupulin 7734	JBL	A,B,D,E
<i>Lockhartia endresiana</i>	Blanco 1803	USJ	A,B,C,D,E
<i>Lockhartia endresiana</i>	Pupulin 4518	JBL	A,B,C,D,E
<i>Lockhartia goyazensis</i>	Gerlach 140 ^d	FLAS	A,B,D,E
<i>Lockhartia grandibractea</i>	Blanco 2559	FLAS	A,B,C,D,E
<i>Lockhartia grandibractea</i>	Chase 15882	K	A,D,E
<i>Lockhartia hercodonta</i>	Blanco 1792	USJ	A,B,C,D,E
<i>Lockhartia hercodonta</i>	Blanco 2284	USJ	A,B,C,D,E
<i>Lockhartia hercodonta</i>	Blanco 2286	FLAS	A,B,C,D,E
<i>Lockhartia hercodonta</i>	Whitten 2383	FLAS	A,B,C,D,E
<i>Lockhartia hercodonta</i>	Blanco 2575	FLAS	A,B,D,E
<i>Lockhartia hercodonta</i>	Blanco 3232	FLAS	A,B,D,E
<i>Lockhartia lepticaula</i>	Blanco 2573	FLAS	A,B,C,D,E
<i>Lockhartia lepticaula</i>	Blanco 3237	FLAS	A,D,E
<i>Lockhartia longifolia</i>	Blanco 3215	FLAS	A,B,C,D,E
<i>Lockhartia longifolia</i>	Whitten 2385	FLAS	A,B,C,D,E
<i>Lockhartia lunifera</i>	Blanco 2670	FLAS	A,B,C,D,E
<i>Lockhartia lunifera</i>	Blanco 2688	FLAS	A,B,C,D,E
<i>Lockhartia lunifera</i>	Blanco 3219	FLAS	A,B,C,D,E
<i>Lockhartia lunifera</i>	Gerlach 141 ^d	M	A,B,D,E
<i>Lockhartia micrantha</i> (s) ^c	Blanco 2558	FLAS	A,B,C,D,E
<i>Lockhartia micrantha</i> (s) ^c	Blanco 2561	FLAS	A,B,C,D,E
<i>Lockhartia micrantha</i> (s) ^c	Blanco 2562	FLAS	A,B,C,D,E
<i>Lockhartia micrantha</i> (s) ^c	Blanco 2671	FLAS	A,B,C,D,E
<i>Lockhartia micrantha</i> (l) ^c	Blanco 3220	FLAS	A,B,D,E
<i>Lockhartia micrantha</i> (s) ^c	Blanco 3223	FLAS	A,B,C,D,E
<i>Lockhartia oblongicallosa</i>	Gerlach 142 ^d	M	A,B,D,E
<i>Lockhartia obtusata</i>	Blanco 2106	FLAS	A,B,C,D,E
<i>Lockhartia obtusata</i>	Blanco 2572	FLAS	A,B,C,D,E
<i>Lockhartia oerstedii</i>	Blanco 2283	USJ	A,B,C,D,E
<i>Lockhartia oerstedii</i>	Blanco 2462	JBL	A,B,C,D,E

Table 5-1. Continued

Taxon ^a	Voucher	Herbarium ^b	Gene regions
<i>Lockhartia oerstedii</i>	Blanco 2563	FLAS	A,B,C,D,E
<i>Lockhartia oerstedii</i>	Blanco 2565	FLAS	A,B,C,D,E
<i>Lockhartia oerstedii</i>	Blanco 3224	FLAS	A,B,D,E
<i>Lockhartia oxyphylla</i>	Blanco 2488	FLAS	A,B,C,D,E
<i>Lockhartia oxyphylla</i>	Whitten 2382	FLAS	A,B,C,D,E
<i>Lockhartia oxyphylla</i>	Whitten 2441	FLAS	A,B,C,D,E
<i>Lockhartia parthenoglossa</i>	Aguilar 19	FLAS	A,B,C,D,E
<i>Lockhartia parthenoglossa</i>	Blanco 2653	JBL	A,B,C,D,E
<i>Lockhartia parthenoglossa</i>	Bogarín 2242	JBL	A,B,C,D,E
<i>Lockhartia rugosifolia</i>	Blanco 2570	FLAS	A,B,C,D,E
<i>Lockhartia rugosifolia</i>	Whitten 2432	FLAS	A,B,C,D,E
<i>Lockhartia serra</i>	Blanco 2574	FLAS	A,B,C,D,E
<i>Lockhartia serra</i>	Blanco 2668	FLAS	A,B,D,E
<i>Lockhartia serra</i>	Blanco 2669	FLAS	A,B,C,D,E
<i>Lockhartia serra</i>	Whitten 2431	FLAS	A,B,C,D,E
<i>Lockhartia tenuiflora</i>	Blanco 3012	FLAS	A,B,C,D,E
<i>Lockhartia tenuiflora</i>	Whitten 2430	FLAS	A,B,C,D,E
<i>Lockhartia tenuiflora</i>	Whitten 2719	FLAS	A,B,C,D,E
<i>Lockhartia verrucosa</i>	Blanco 2667	FLAS	A,B,D,E
<i>Raycadenco ecuadorensis</i>	Whitten 3285	FLAS	A,B,C,D,E
<i>Rossioglossum ampliatum</i>	Chase 84104	K	A,B,C,D,E
<i>Rossioglossum schlieperianum</i>	Chase 83449	K	A,B,C,D,E
<i>Trichoceros antennifer</i>	Whitten 2353	FLAS	A,B,C,D,E
<i>Trichopilia turialvae</i>	Whitten 2947	FLAS	A,B,C,D,E

^a Author names are given in Chapter 3 for *Lockhartia* species and in the Materials and Methods section for other taxa.

^b Herbarium acronyms follow Index Herbariorum (Thiers, 2011).

^c For *Lockhartia micrantha*, suffix "(l)" = long lobe morphotype; suffix "(s)" = short lobe morphotype.

^d Gerlach numbers refer to total DNA samples and are listed here for cross-referencing with individual plants; the actual herbarium vouchers are unnumbered (*Gerlach s.n.*).

Table 5-2. Morphological characters and character states used in the phylogenetic analysis of *Lockhartia*. Figures 4-11 to 4-14 and 4-16 (Morphology and Anatomy, Chapter 4) explain the terminology.

Character	Character states
1	Stems erect (0); pendulous (1) ^a
2	Internodes per stem less than eight (0); more than 12 (1) ^b
3	Pseudobulbs absent (0); present (1)
4	Leaf abscission layer absent (0); present (1)
5	Leaf base straight (0); incurved (1); outcurved (2)
6	Leaf apex round to obtuse (0); acute (1); subpraemorse (2) ^c
7	Leaf not decurrent (0); decurrent (1)
8	Leaf sheath terminal notch absent (0); present (1)
9	Central leaves of stem subequal to apical ones (0); central leaves of stem more than three times as long as apical ones (1); apical leaves of stem more than three times as long as central ones (2)
10	Leaf blade conduplicate (0); isobilateral (1)
11	Leaf texture smooth (0); rugulose (1)
12	Inflorescences axillary only (0); both terminal and axillary (1)
13	Inflorescence bracts narrowly triangular (0); widely ovate (1)
14	Inflorescence initiation simultaneous (0); basipetal (1); acropetal (2)
15	Inflorescence racemose or paniculate (0); pseudocymose (1) ^d
16	Inflorescence branching sylleptic (0); proleptic (1)
17	Inflorescence bract appressed to rachis or pedicel (0); free from rachis or pedicel (1)
18	Perianth base color yellow (0); white (1); red or pink (2)
19	Flower resupinate (0); non-resupinate, with labellum uppermost (1); variable orientation (2) ^e
20	Sepals patent (0); reflexed (1); dorsal sepal patent, lateral sepals reflexed (2)
21	Petals straight (0); arched toward front of flower (1)
22	Petals margins approximately flat (0); reflexed (1)
23	Labellum approximately flat (0); convex (1); concave (2)
24	Labellum lateral lobes absent (0); less than twice as long as wide (1); more than thrice as long as wide (2); wider than long (3)
25	Labellum midlobe spotting absent (0); present (1)
26	Labellum apex truncate to acute (0); emarginate to retuse (1)
27	Labellum midlobe distal lobule on same plane as rest of labellum (0); curved forward (1)

Table 5-2. Continued

Character	Character states
28	Callus crateriform (0); single oblong keel (1); twin parallel keels (2); central thickening with transverse apical ridge (3); central thickening without transverse apical ridge (4); absent (5) ^f
29	Labellum midlobe basal lobules absent (0); present (1)
30	Callus texture smooth (0); tuberculate (1)
31	Callus glabrous (0); pubescent-glandular (1); pubescent non-glandular (2)
32	Elaiophore cushion absent (0); present (1) ^f
33	Labellum basal tuft of secretory hairs absent (0); present (1)
34	Callus teeth none (0); one (1); four (2) ^g
35	Callus trapezoid ledge absent (0); present (1)
36	Column straight, continuous with ovary (0); arched away from labellum (1)
37	Infrastigmatic line absent (0); present (1)
38	Column wings absent (0); subtriangular, base attached to entire side of column (1); subtriangular, base restricted to proximal half of column (2); obliquely subquadrate (3); flabellate (4); rounded (5); filiform (6)
39	Stigma round to oval (0); narrowly oblong (1); ovate-acuminate (2)
40	Rostellum less than 0.4 mm long (0); more than 0.8 mm long (1)
41	Anther cap as long as wide (0); twice as long as wide (1)
42	Stipe entire (0); bifid (1)
43	Fruit subglobular (0); obovoid to subcylindric (1)
44	Fruit epidermis lustrous (0); glaucous (1)

^a Stems of species with pendulous habit can be erect when young.

^b This refers to the number of internodes of the erect part of each sympodial unit (excluding the rhizome).

^c This character is scored as if the leaf apex is isobilateral (as is the case in *Lockhartia* subgenus *Lockhartia*) or folded lengthwise; thus, a conduplicate leaf that is obtuse when open can still be scored as acute if folded.

^d The racemose condition includes both branched and unbranched polytelic inflorescences (Morphology and Anatomy, Chapter 4).

^e Flowers are considered resupinate if the labellum is consistently positioned in the lower part of the flower.

^f It is possible that the entire crateriform callus of the Longifolia group of *Lockhartia* is homologous to the elaiophore cushion of the Imbricata group, but in the absence of any developmental study, they are treated here as separate characters.

^g Callus teeth does not include tall, narrow tubercles of the lower part of the callus of the Imbricata group (e.g., *L. oerstedii*).

Table 5-3. Morphological character matrix for *Lockhartia* and outgroup taxa.

Taxon	Character number															
	1				2				3				4			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<i>Fernandezia tica</i>	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	1
<i>Grandiphyllum hians</i>	0	0	1	1	2	0	0	0	1	0	0	0	0	0	0	0
<i>Hofmeisterella eumicroscopica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia acuta</i>	0	1	0	0	1	1	0	1	1	0	0	0	0	1	0	1
<i>Lockhartia amoena</i>	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0
<i>Lockhartia bennettii</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia cladoniophora</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia compacta</i>	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia dipleura</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia endresiana</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia galeottiana</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia genegeorgei</i>	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Lockhartia goyazensis</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia grandibractea</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia hercodonta</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia imbricata</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia ivainae</i>	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia latilabris</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia lepticaula</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia longifolia</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia lunifera</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia micrantha</i> (s)	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia micrantha</i> (l)	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia oblongicallosa</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia obtusata</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia oerstedii</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia oxyphylla</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia parthenocomos</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia parthenoglossa</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia rugosifolia</i>	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Lockhartia serra</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia tenuiflora</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lockhartia verrucosa</i>	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Raycadenco ecuadorensis</i>	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Rossioglossum ampliatum</i>	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Rossioglossum schlieperianum</i>	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Trichoceros antennifer</i>	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Trichopilila turialvae</i>	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0

Table 5-4. Features of DNA regions used in this study in relation to the most parsimonious trees from each MP analysis.

DNA region	No. of species (individuals)	Aligned length (bases)	Potentially parsimony-informative characters	No. of shortest trees	No. of ingroup nodes $\geq 70\%$ BS	Tree length (steps)	CI	RI
ITS	22 (65)	759	128 (17%)	38	11	411	0.35	0.74
<i>trnH-psbA</i>	21 (62)	869	29 (3%)	180	5	82	0.22	0.65
<i>trnL-F</i>	15 (48)	1272	66 (5%)	22	4	221	0.28	0.71
<i>3'ycf1</i>	22 (65)	1528	122 (8%)	84	11	392	0.31	0.69
<i>5'ycf1</i>	22 (65)	974	66 (6%)	220	6	291	0.24	0.62
Plastid regions combined	22 (65)*	4643	283 (6%)	114	14	986	0.33	0.66
All regions combined	22 (65)*	5402	542 (10%)	72	20	1398	0.38	0.68

* All 65 individual accessions were included in the combined matrices even if they had missing data for some regions.

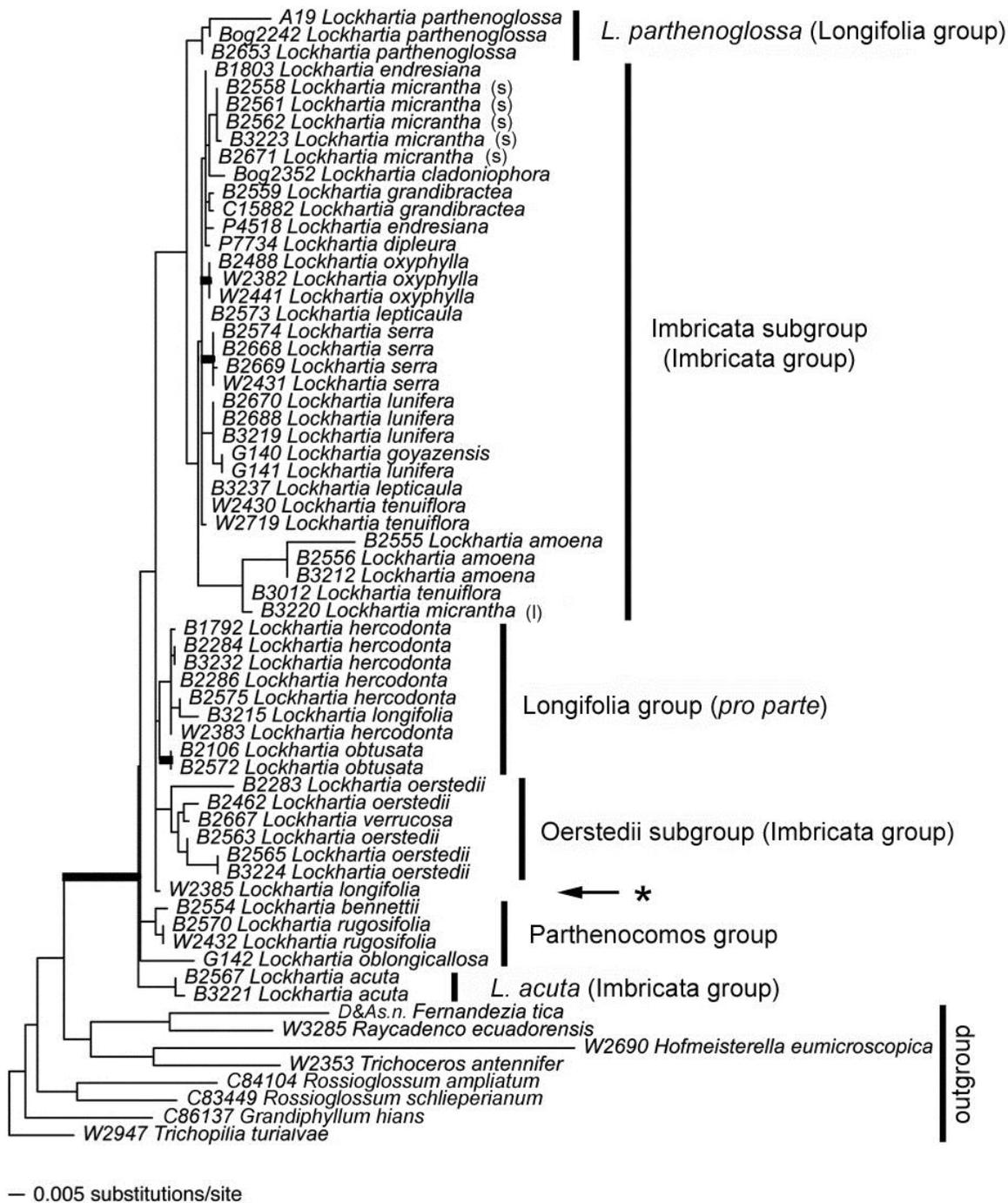
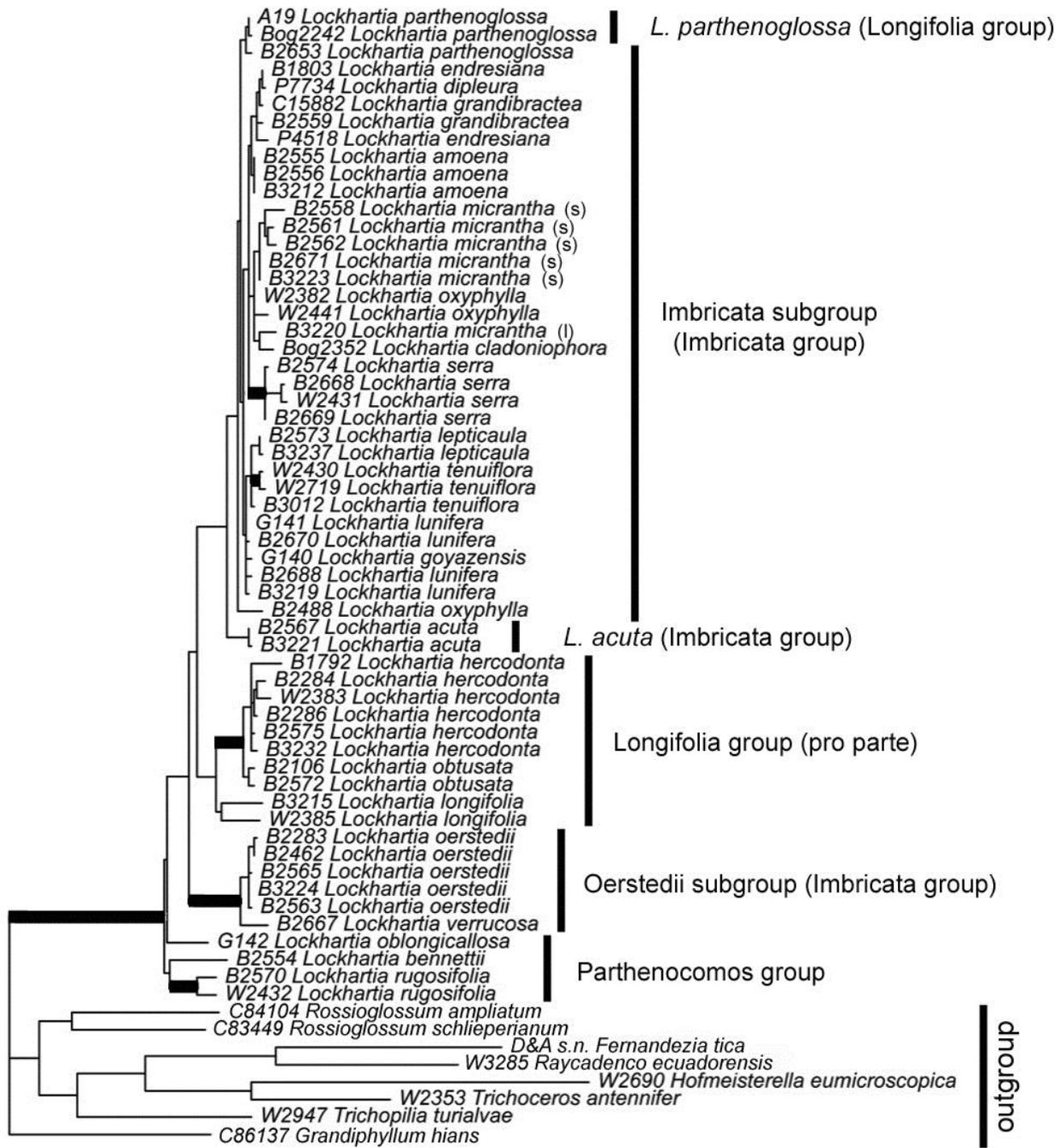


Figure 5-1. Representative phylogram of 38 most parsimonious trees (CI = 0.35, RI = 0.74) of *Lockhartia* based on the analysis of ITS sequences. Branches with strong ($\geq 90\%$) bootstrap support are indicated in bold. The major species groups and subgroups are indicated to the right of the vertical bars. Suffixes “(l)” and “(s)” for *L. micrantha* indicate long- and short-lobe morphotype, respectively. Asterisk indicates one accession of *L. longifolia* that appears separate from other members of the Longifolia group.



— 5 changes

Figure 5-2. Representative phylogram of 114 most parsimonious trees (CI = 0.33, RI = 0.66) of *Lockhartia* based on the analysis of the four combined plastid DNA regions (*trnH-psbA*, *trnL-F*, *3'ycf1*, and *5'ycf1*). Branches with strong ($\geq 90\%$) bootstrap support are indicated in bold. The major species groups and subgroups are indicated to the right of the vertical bars. Suffixes "(l)" and "(s)" for *L. micrantha* indicate long- and short-lobe morphotype, respectively.

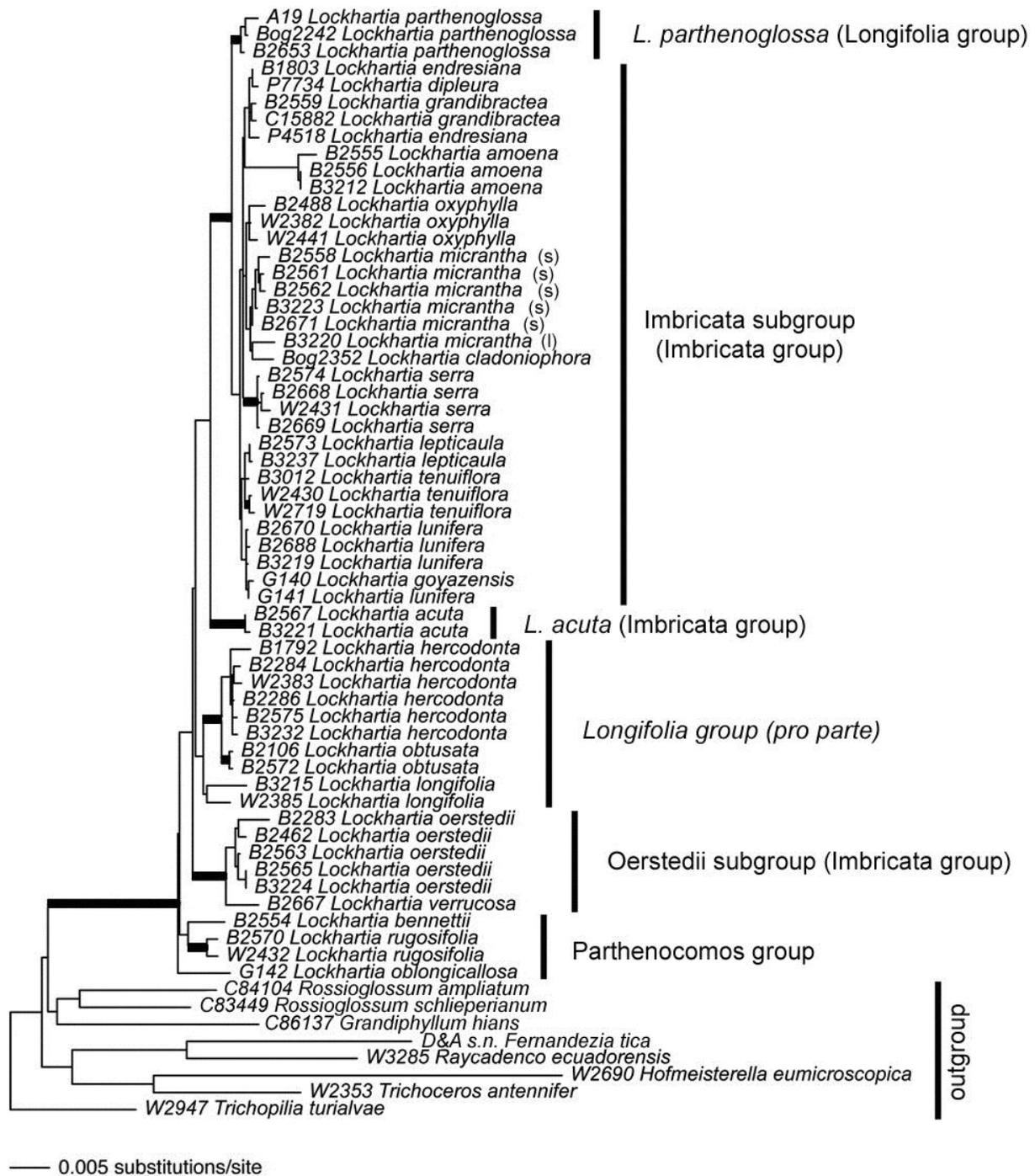


Figure 5-3. Representative phylogram of 72 most parsimonious trees (CI = 0.38, RI = 0.68) of *Lockhartia* based on the analysis of five combined DNA regions (ITS, *trnH-psbA*, *trnL-F*, 3' *ycf1*, and 5' *ycf1*). Branches with strong ($\geq 90\%$) bootstrap support are indicated in bold. The major species groups and subgroups are indicated to the right of the vertical bars. Suffixes "(l)" and "(s)" for *L. micrantha* indicate long- and short-lobe morphotype, respectively. See text for details.

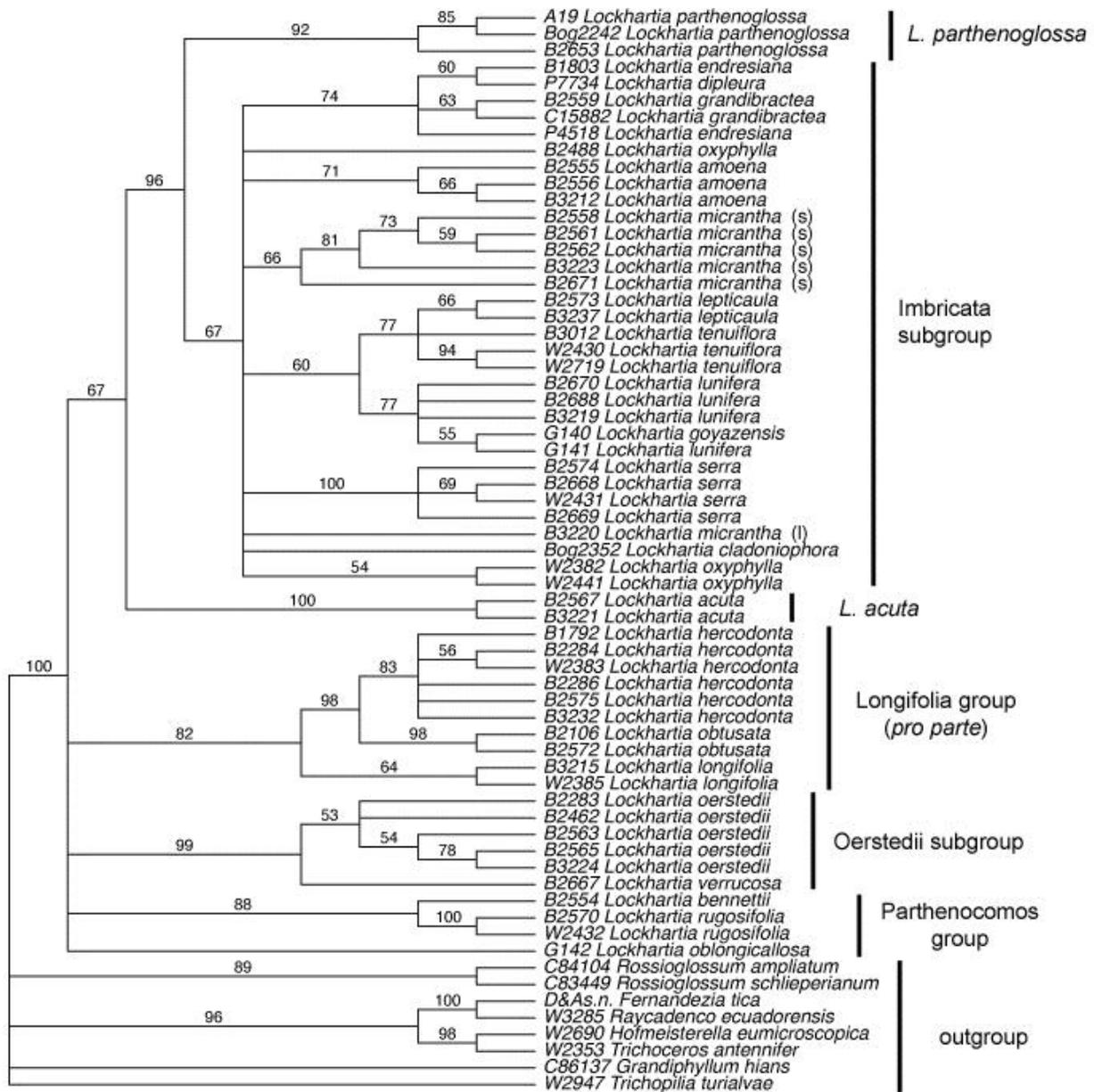


Figure 5-4. Maximum parsimony 50% majority rule consensus for the combined analysis of *Lockhartia* based on five DNA regions (ITS, *trnH-psbA*, *trnL-F*, *3'ycf1*, and *5'ycf1*). Bootstrap support values larger than 50% are indicated above branches. The major species groups and subgroups are indicated to the right of the vertical bars. Suffixes "(l)" and "(s)" for *L. micrantha* indicate long- and short-lobe morphotype, respectively. See text for details.

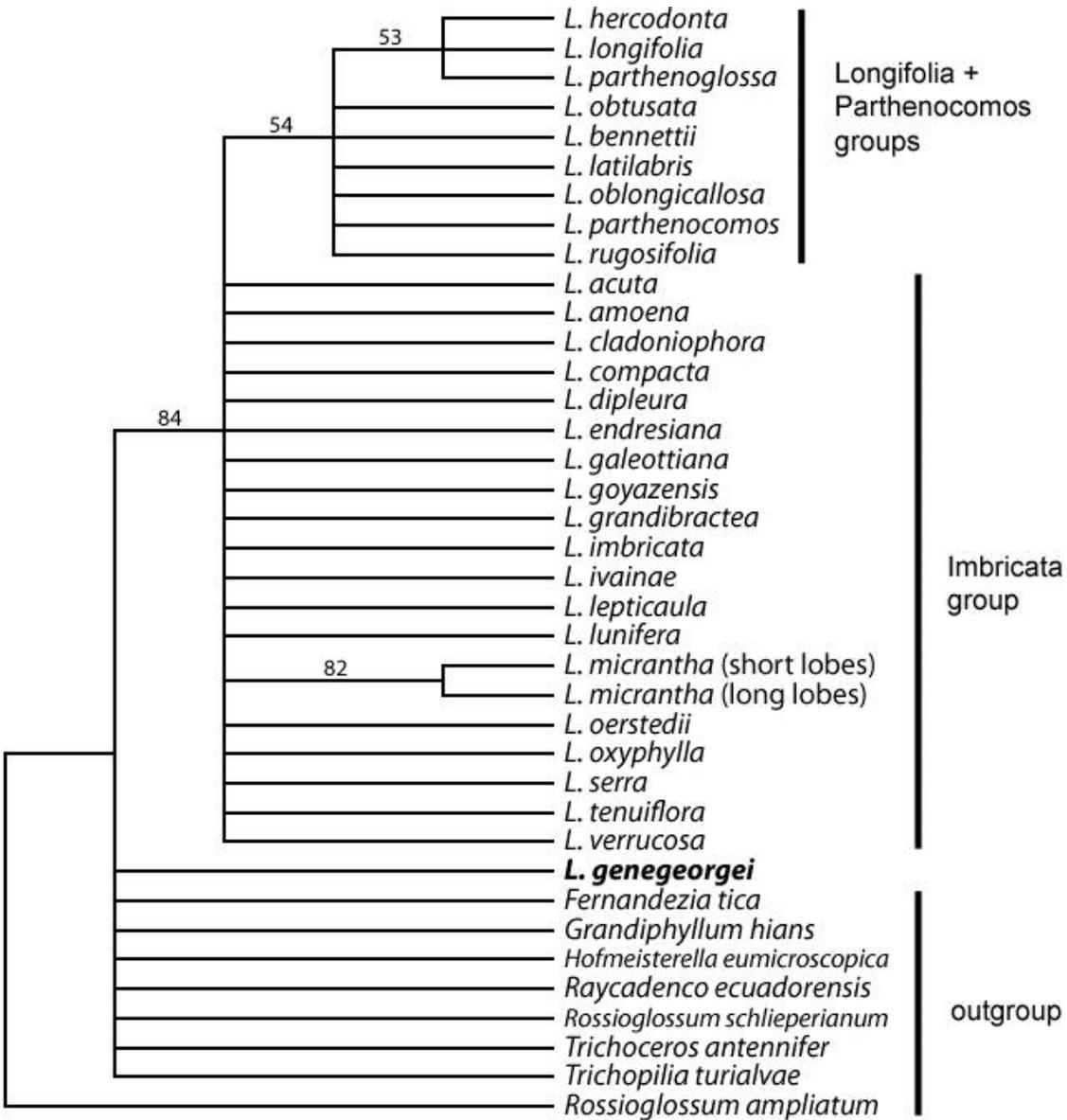


Figure 5-5. Strict consensus of 467 equally parsimonious trees derived from the analysis of 44 morphological characters (length = 182 steps, CI = 0.36, RI = 0.74) of *Lockhartia* (including *L. genegeorgei*, indicated in bold) and outgroup taxa. Numbers above branches indicate bootstrap values above 50%. Major morphological species groups of *Lockhartia* are indicated to the right of the vertical bars. Notice placement of *L. genegeorgei* in an unresolved position together with most outgroup taxa.

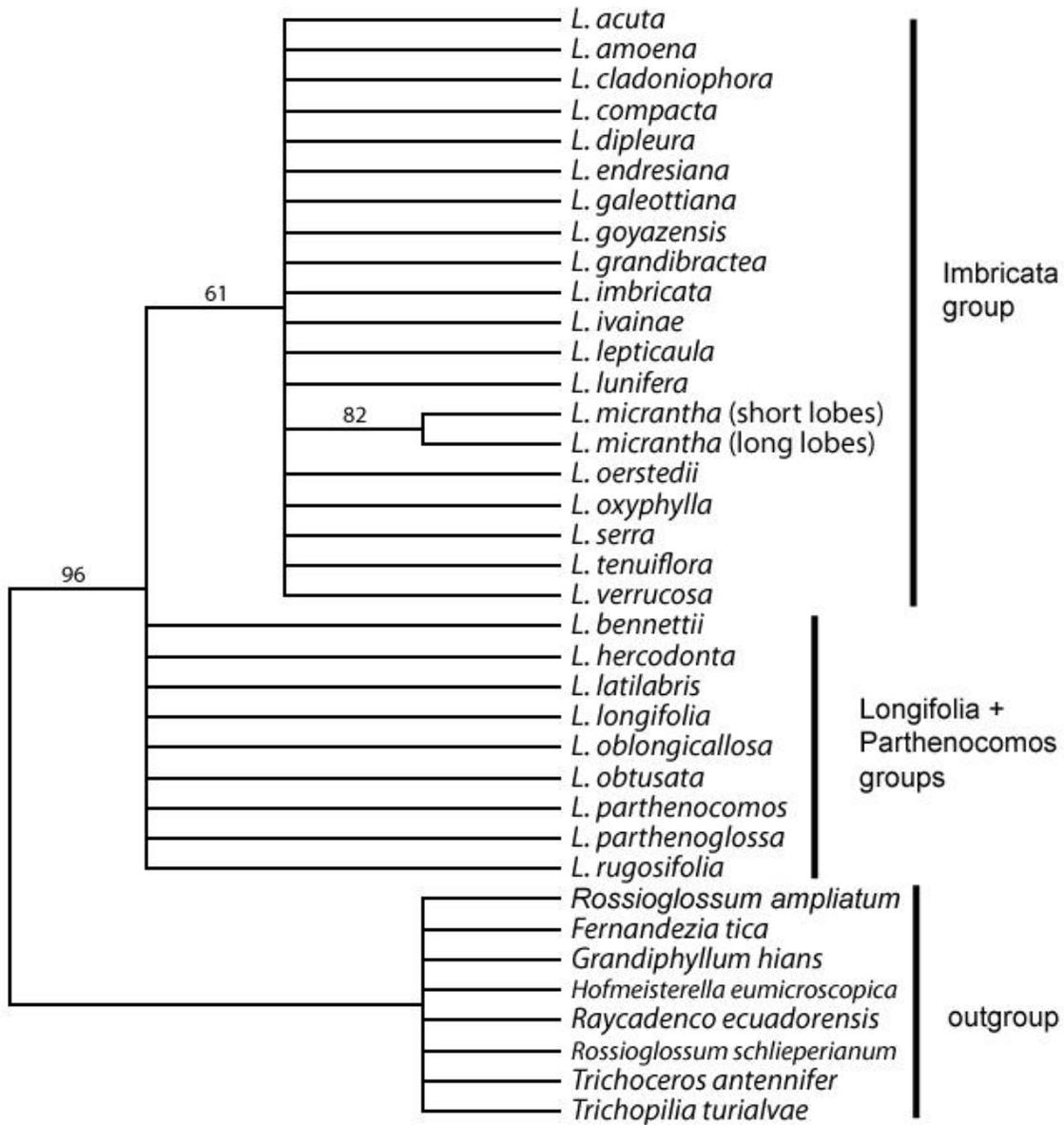


Figure 5-6. Strict consensus of 38 equally parsimonious trees derived from the analysis of 44 morphological characters (length = 168 steps, CI = 0.38, RI = 0.76) for *Lockhartia* (excluding *L. genegeorgei*). Numbers above branches indicate bootstrap values above 50%. Major morphological species groups of *Lockhartia* are indicated to the right of the vertical bars.

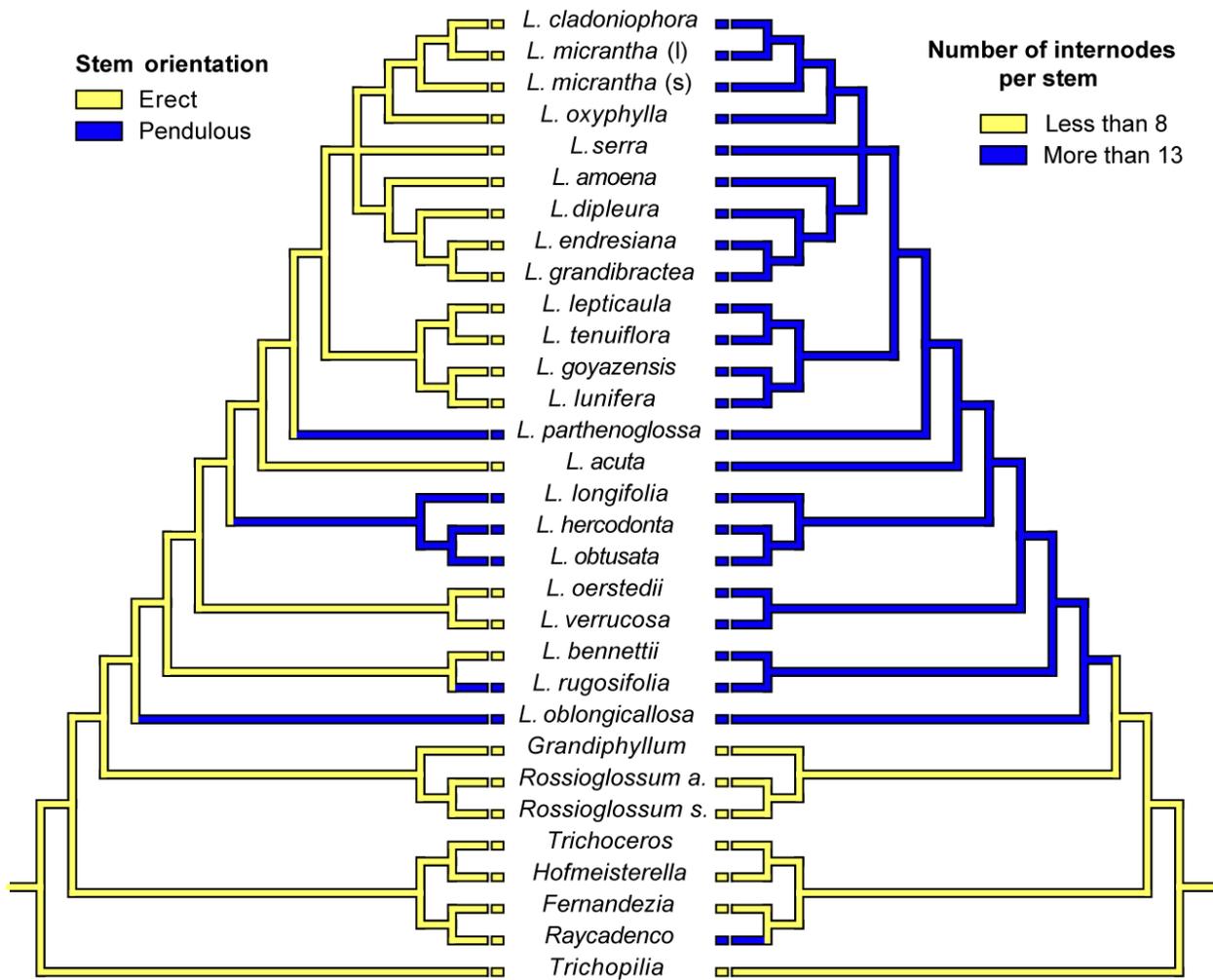


Figure 5-7. Hypothetical evolutionary scenario for stem orientation (character 1) and number of internodes per stem (i.e., individual sympodial unit; character 2) in *Lockhartia*. Outgroup taxa indicated by generic name only (with specific epithet initial for species of *Rossioglossum*).

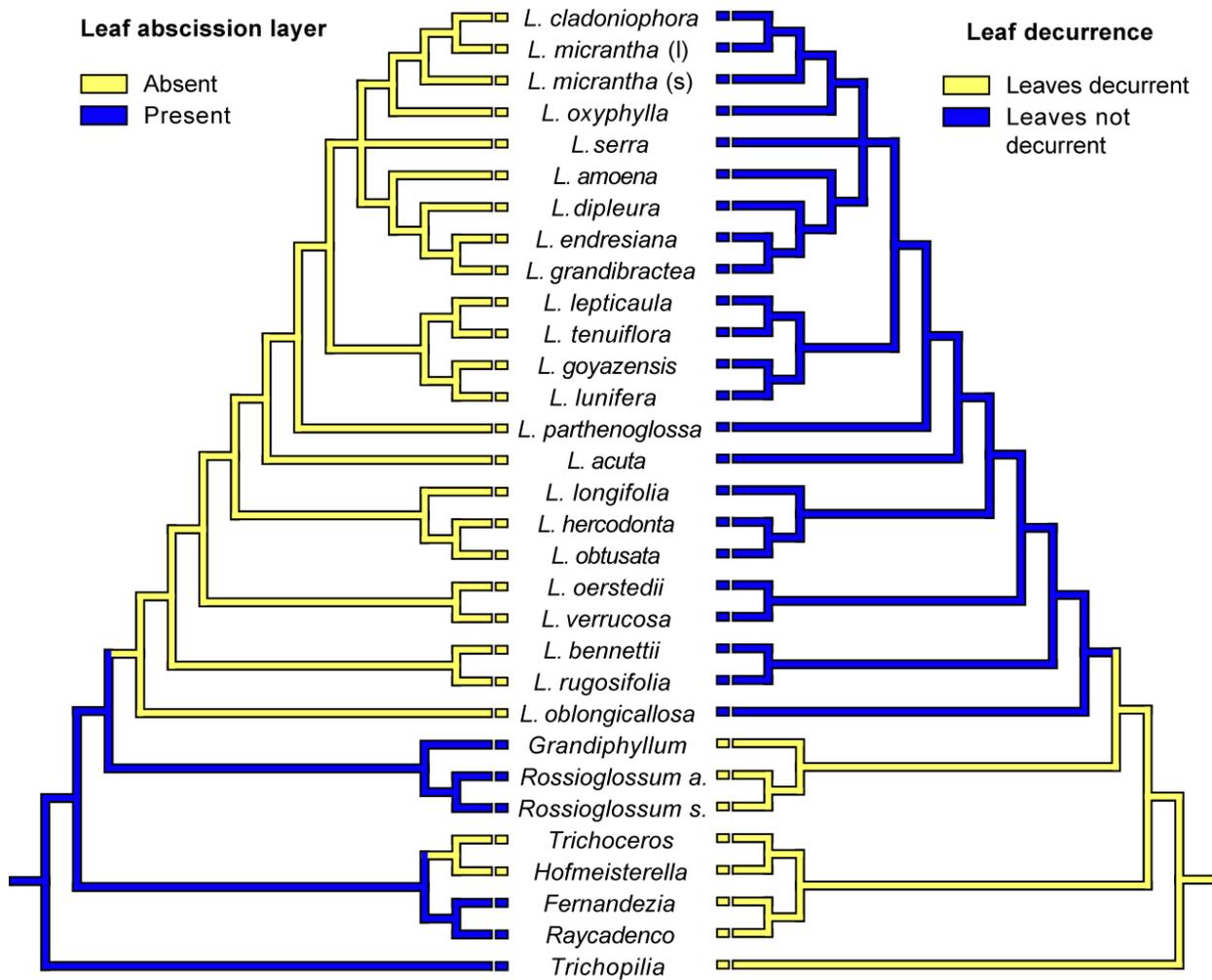


Figure 5-8. Hypothetical evolutionary scenario for leaf abscission (character 4) and leaf decurrence (character 7) in *Lockhartia*.

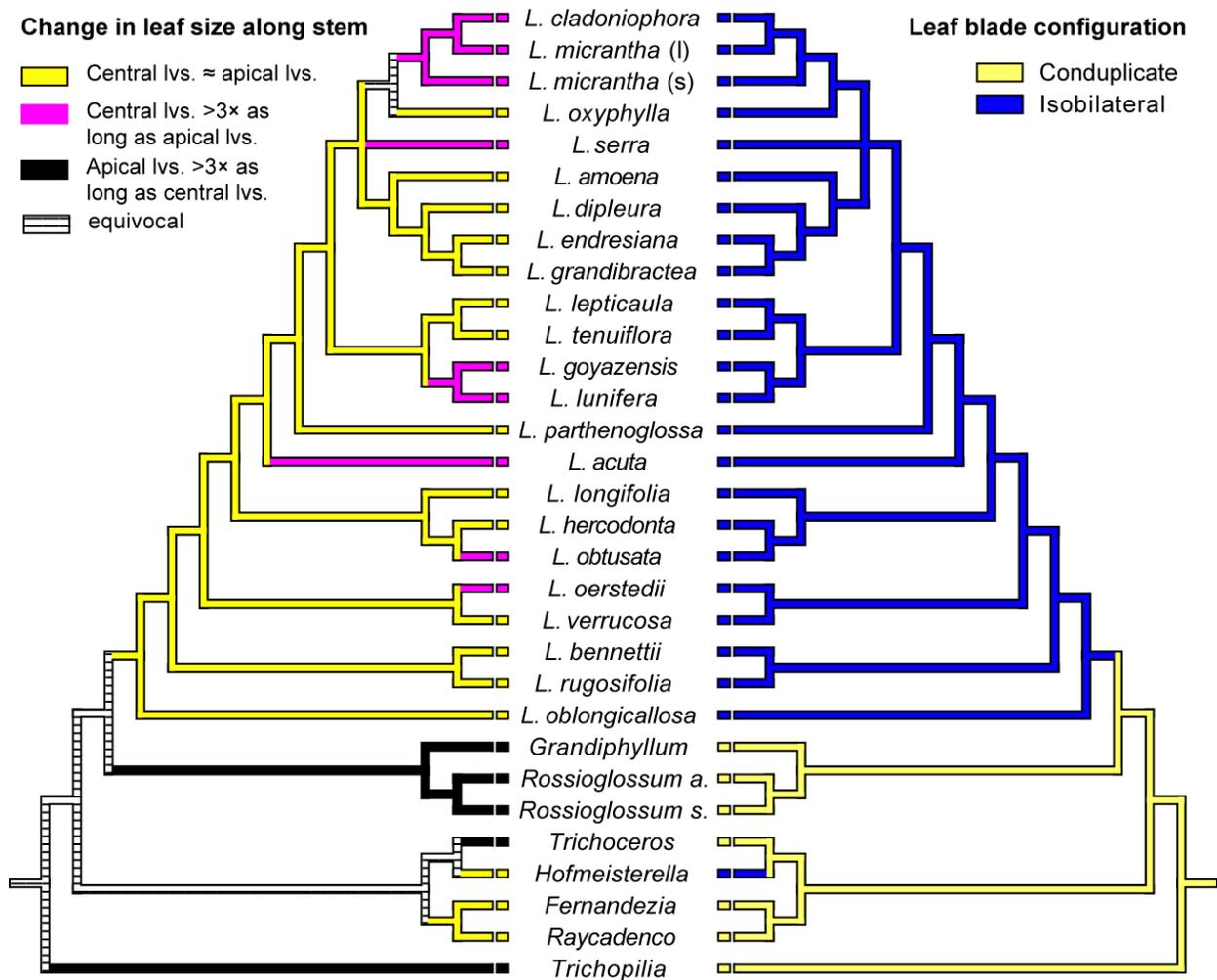


Figure 5-9. Hypothetical evolutionary scenario for differential leaf size along the stem (character 9) and leaf blade configuration (character 10) in *Lockhartia*.

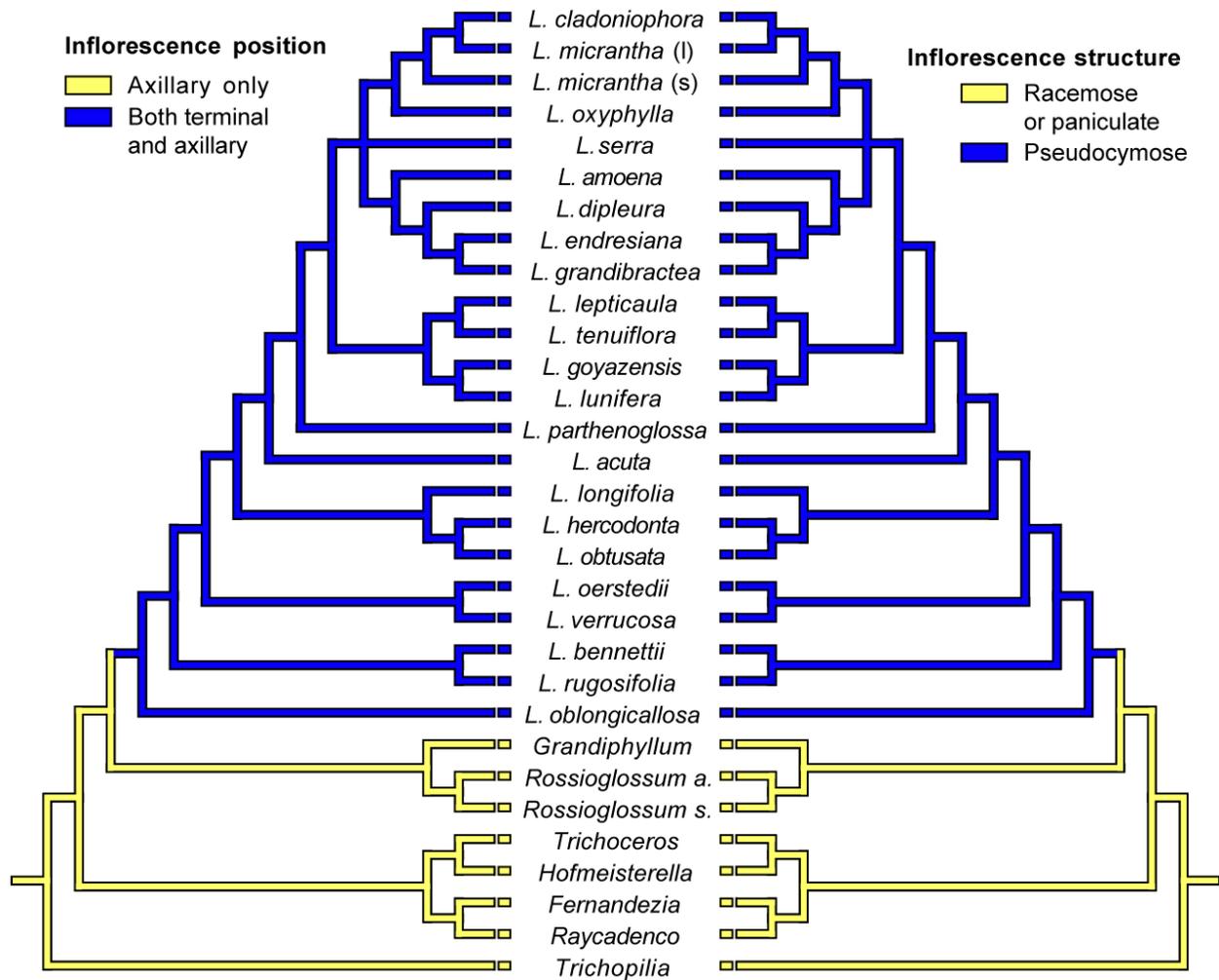


Figure 5-10. Hypothetical evolutionary scenario for inflorescence position (character 12) and inflorescence structure (character 15) in *Lockhartia*.

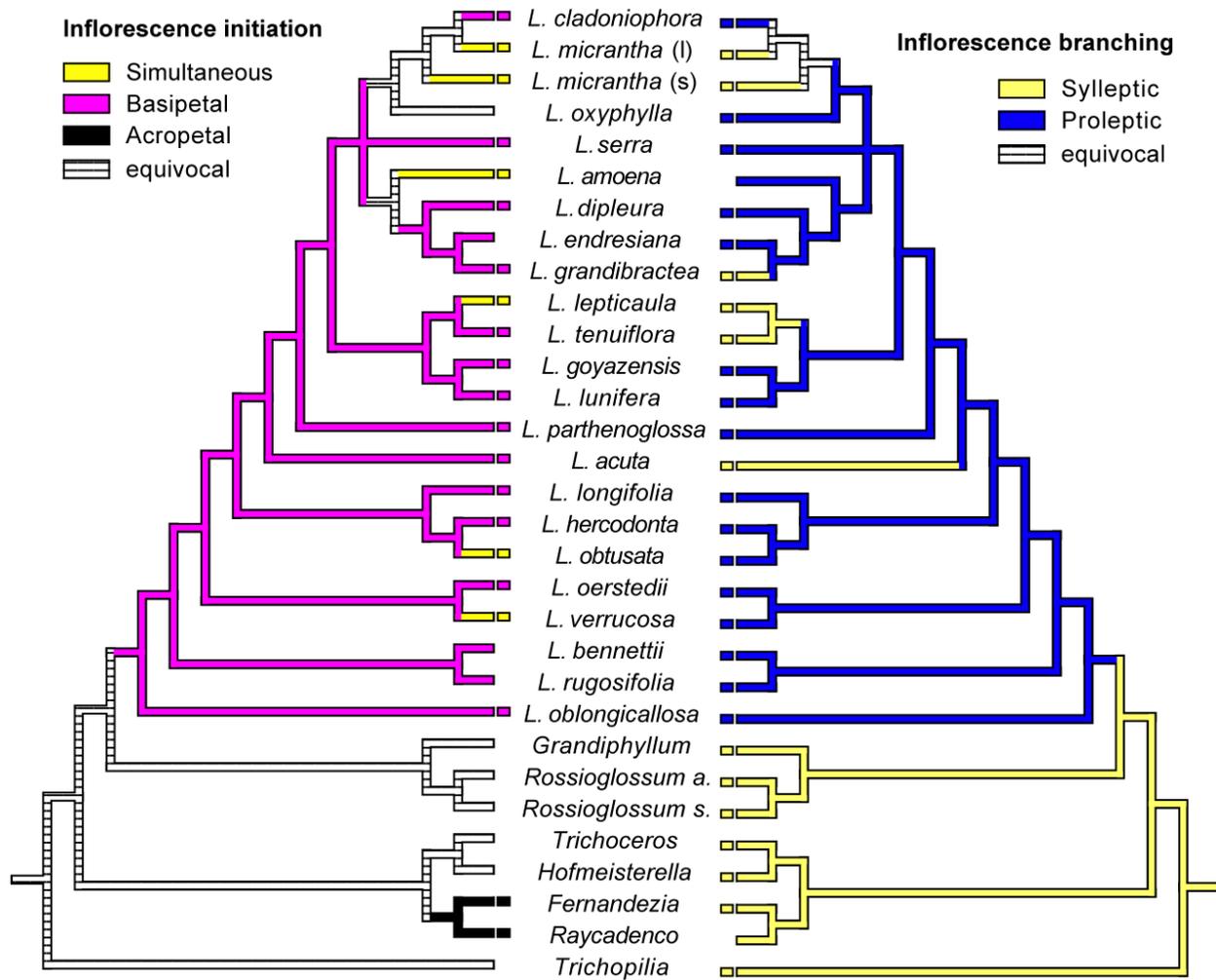


Figure 5-11. Hypothetical evolutionary scenario for inflorescence initiation (character 14) and inflorescence branching mode (character 16) in *Lockhartia*. An empty square at the tip of a branch indicates that the character was not scored for that species, even if the branch color indicates an unequivocal character state.

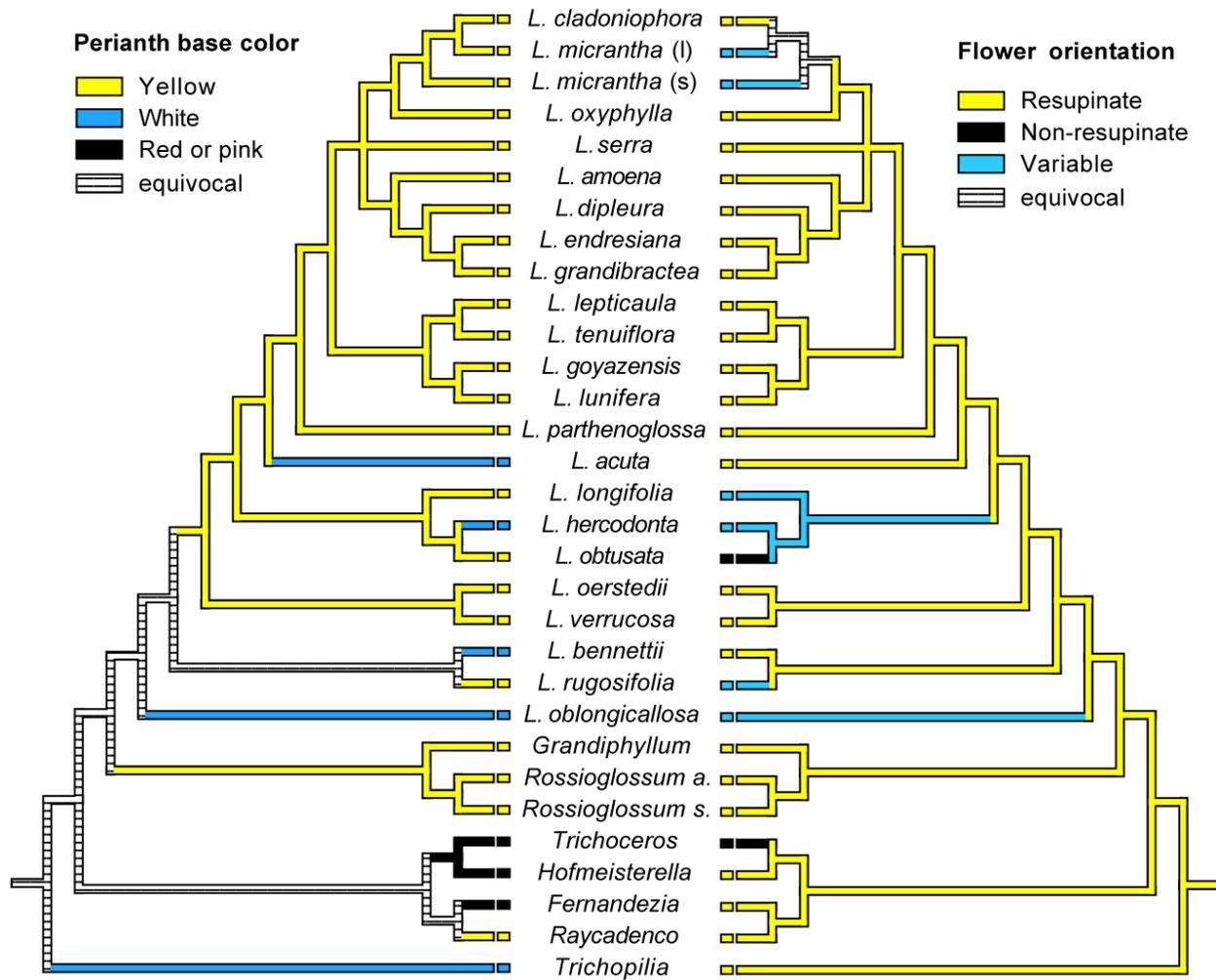


Figure 5-12. Hypothetical evolutionary scenario for perianth base color (character 18) and flower orientation (character 19) in *Lockhartia*.

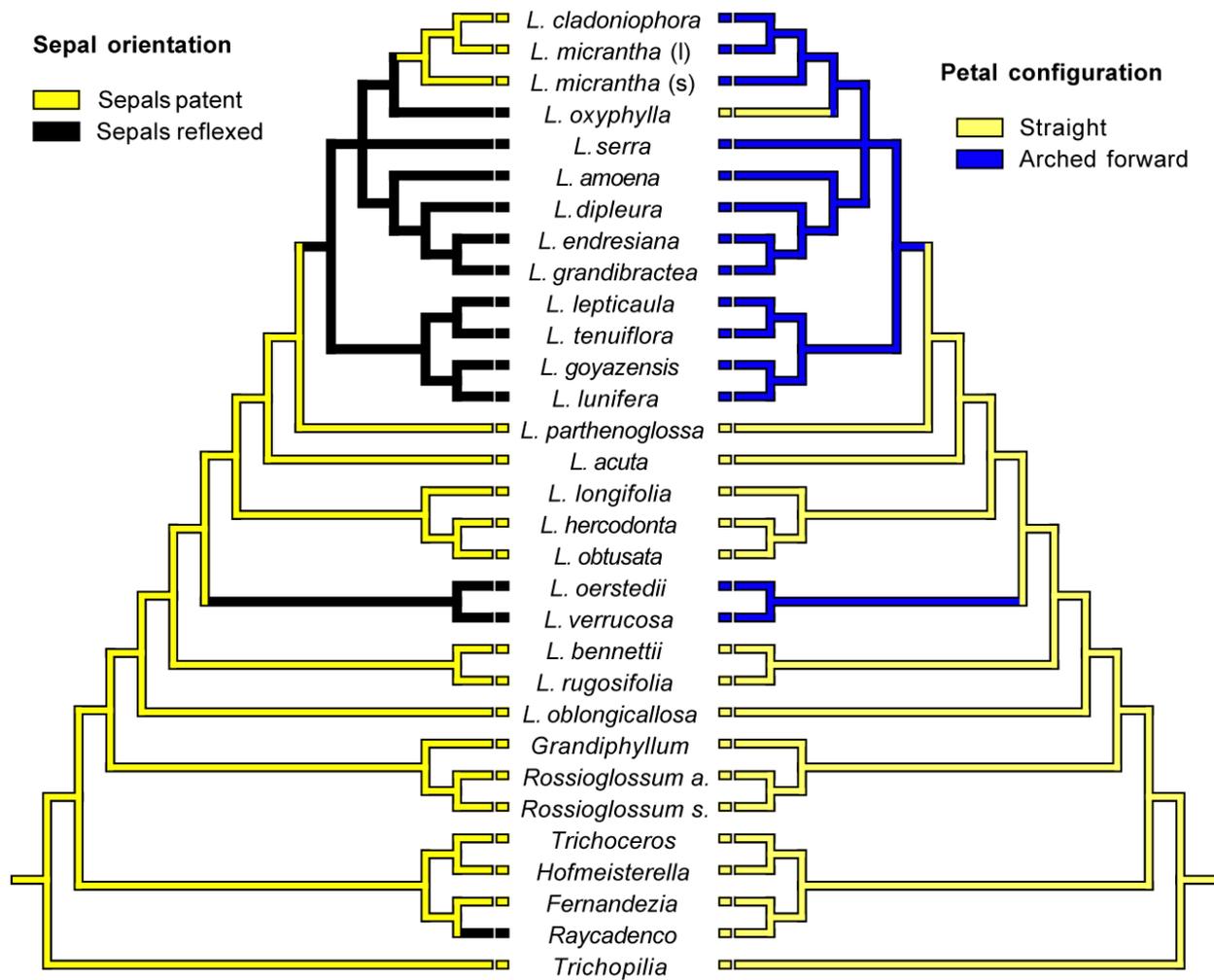


Figure 5-13. Hypothetical evolutionary scenario for sepal orientation (character 20) and petal configuration (character 21) in *Lockhartia*.

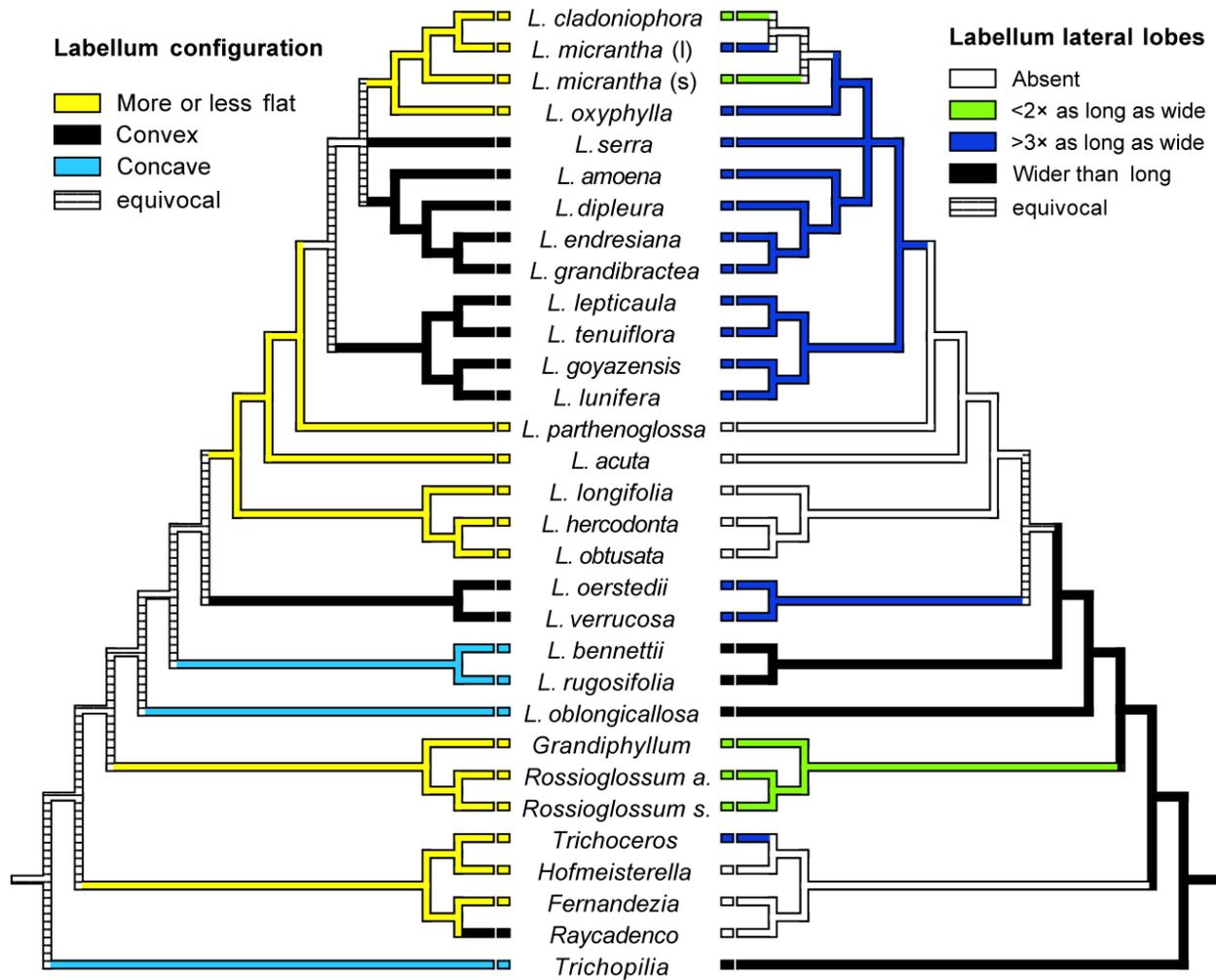


Figure 5-14. Hypothetical evolutionary scenario for labellum configuration (character 23) and labellum lateral lobes (character 24) in *Lockhartia*.

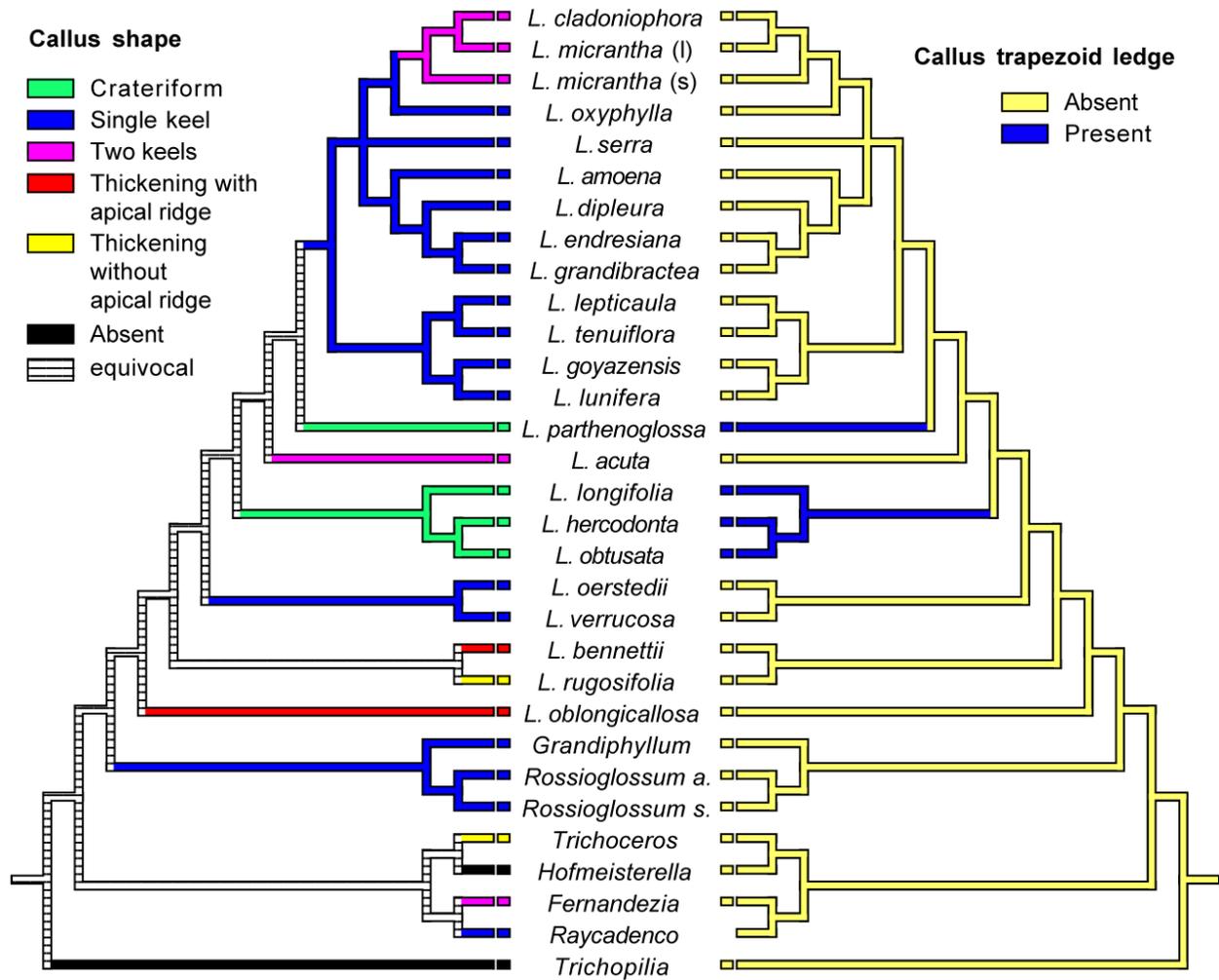


Figure 5-15. Hypothetical evolutionary scenario for callus shape (character 28) and callus trapezoid ledge (character 35) in *Lockhartia*. An empty square at the tip of a branch indicates that the character was not scored for that species, even if the branch color indicates an unequivocal character state.

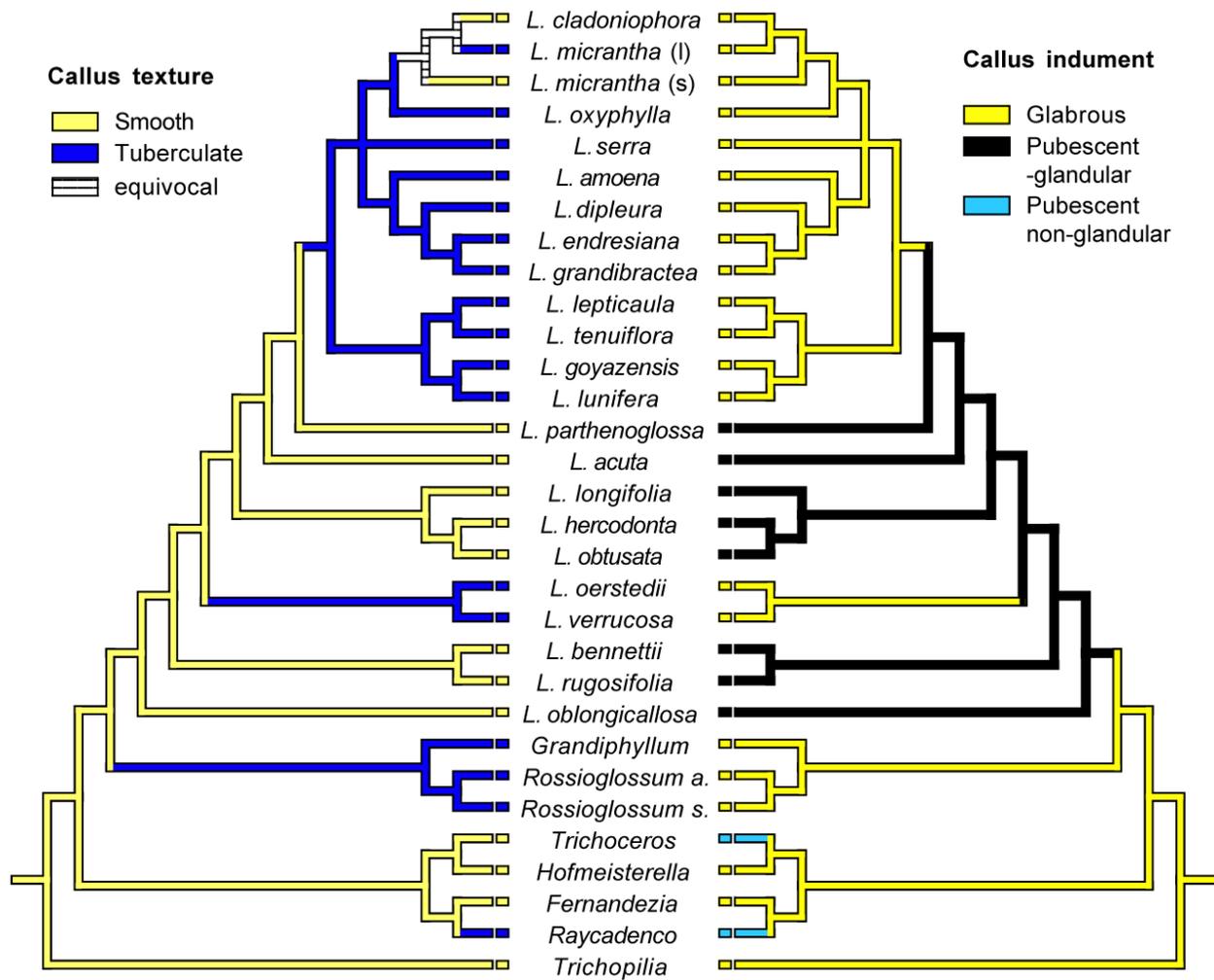


Figure 5-16. Hypothetical evolutionary scenario for callus texture (character 30) and callus indument (character 31) in *Lockhartia*.

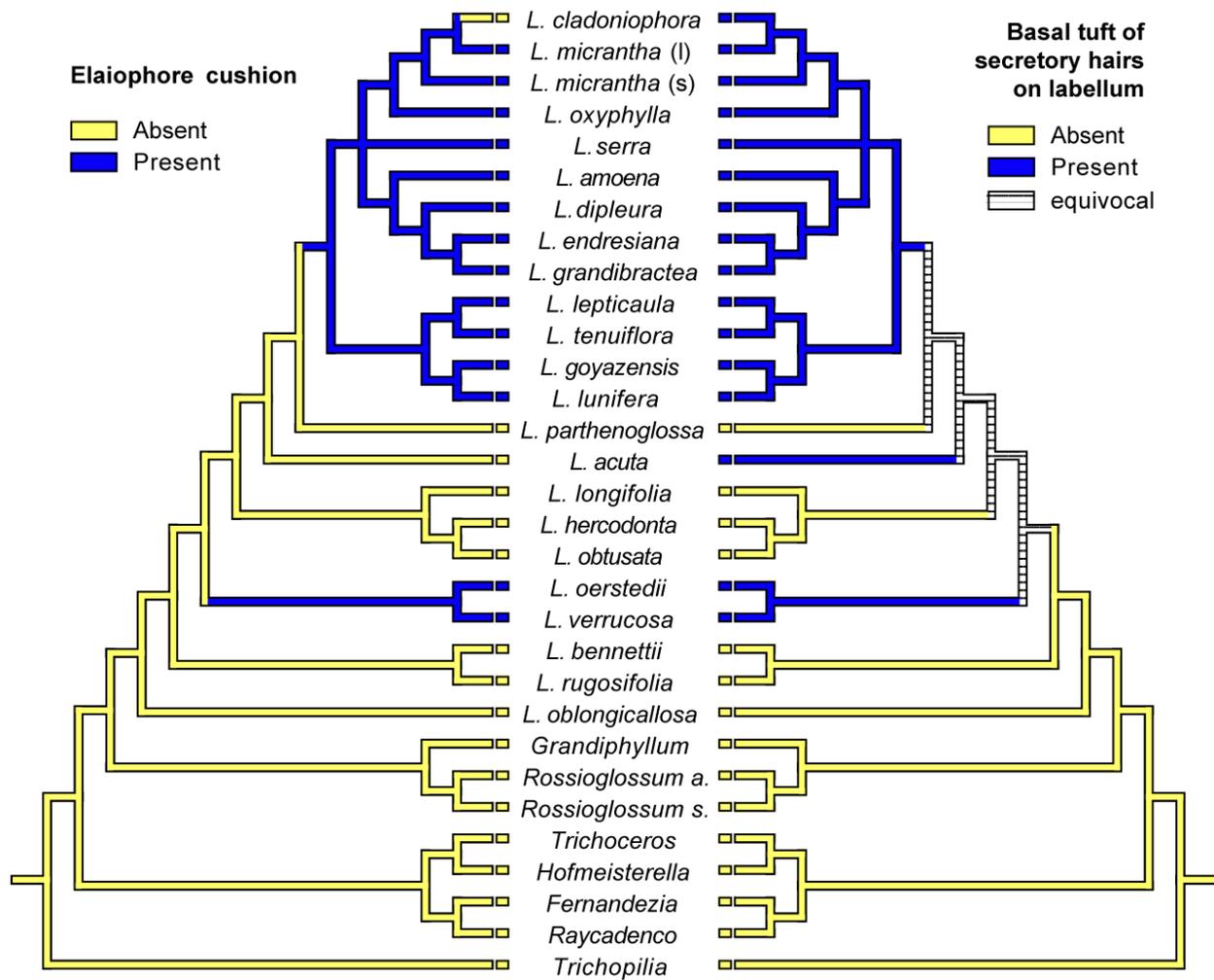


Figure 5-17. Hypothetical evolutionary scenario for the elaiophore cushion (character 32) and the basal tuft of secretory hairs in the labellum (character 33) in *Lockhartia*.

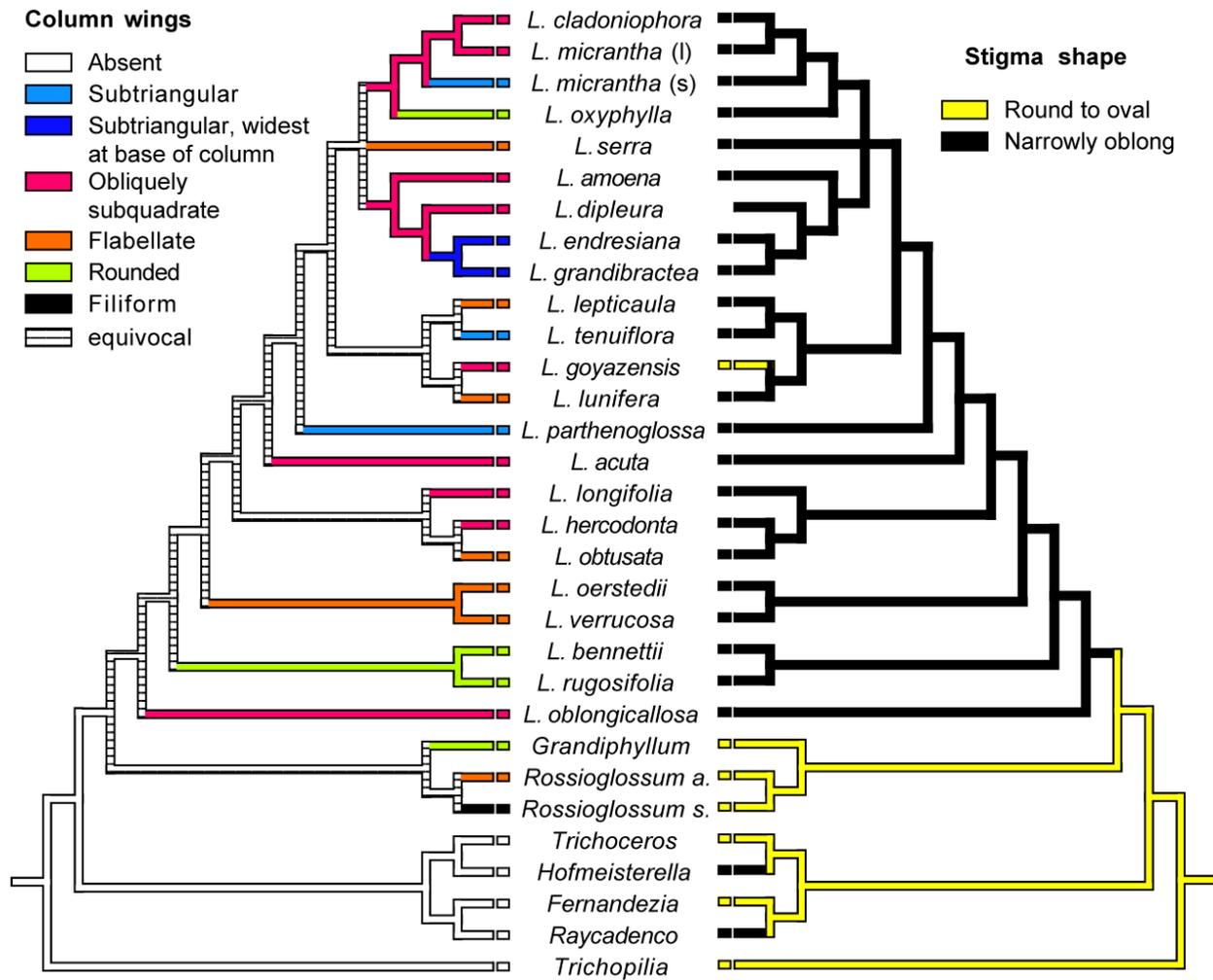


Figure 5-18. Hypothetical evolutionary scenario for column wing shape (character 38) and stigma shape (character 39) in *Lockhartia*. An empty square at the tip of a branch indicates that the character was not scored for that species, even if the branch color indicates an unequivocal character state.

CHAPTER 6 GENERAL CONCLUSIONS

The present study constitutes a monograph of the Neotropical orchid genus *Lockhartia*. It provides a historical review of its taxonomy and systematic relationships, a taxonomic revision based on an exhaustive study of herbarium specimens and cultivated plants, a detailed morphological and anatomical survey, and a study on the evolutionary relationships within the genus and the probable evolutionary trajectory of selected morphological characters.

A total of twenty-nine species of *Lockhartia* are recognized, including five species new to science. Costa Rica, Panama, and Venezuela are the countries with most species (ten, eight, and seven, respectively). Colombia remains the country where the genus is least understood, mainly because of the paucity of herbarium collections.

The morphological study revealed an interesting vegetative architecture, unique in the subtribe Oncidiinae, consisting of elongate stems devoid of pseudobulbs, covered with laterally flattened, imbricate leaves. The stems are ancipitous, and have a central core of densely grouped vascular bundles, which is surrounded by a parenchymatous cortex.

The inflorescence of *Lockhartia*, which can be called a “pseudocyme”, does not fit any of the categories described by Weberling (1989), and appears to be unique among the angiosperms. A detailed account of its morphology and development is presented. The basipetal development of the inflorescences along the shoot, a feature common to many species of *Lockhartia* but rare among orchids, has received little attention in the past.

Based on a phenetic consideration of morphological traits, the species of *Lockhartia* are assigned to two subgenera (*Lockhartia* and *Pseudobulbosa*), and the former is subdivided into three main groups (informally called the Imbricata, Longifolia, and Parthenocomos groups). However, phylogenetic analyses of molecular data indicate that the three species groups of subgenus *Lockhartia* probably are not monophyletic, and thus they should not be formally recognized as sections in a phylogenetic classification. Furthermore, the systematic position of the only species of subgenus *Pseudobulbosa* is unclear; it could either represent a species well nested in the genus but that has partially reverted to an ancestral vegetative morphology, a sister taxon to the rest of the genus, or a natural intergeneric hybrid. A phylogenetic analysis of morphological data suggests that the latter is the case, but this cannot be confirmed in the absence of molecular data (DNA of this species could not be obtained for the present study).

Tracing of morphological characters using parsimony on a cladogram obtained from the molecular phylogenetic analyses indicates that the following characters are probable synapomorphies for the genus (or, at least, for subgenus *Lockhartia*): 1) more than 13 internodes per stem unit, 2) loss of a leaf abscission layer, 3) decurrent leaves, 4) leaves with an isobilateral free portion of the blade, 5) ability to produce both apical and axillary inflorescences, 6) pseudocymose inflorescence structure, 7) proleptic inflorescence branching (with several species having experienced a reversal to the sylleptic branching condition), 8) pubescent-glandular callus indument (with several species having experienced a reversal to the glabrous condition), and 9) stigma narrowly oblong (with one species having experienced a reversal to the oval condition).

Other morphological traits studied appear to be moderately to highly homoplasious within the genus: stem orientation (erect vs. pendulous), leaf size change along the stem, inflorescence initiation (basipetal vs. simultaneous), inflorescence branching (proleptic vs. sylleptic), perianth base color (yellow vs. white), flower orientation (resupinate vs. non-resupinate or variable), sepal orientation (patent vs. reflexed), petal configuration (straight vs. arched), labellum configuration (convex vs. flat or concave), relative size of the labellum lateral lobes, shape of the column wings, and several traits associated with the callus.

APPENDIX
INDEX TO HERBARIUM COLLECTIONS EXAMINED

Numerical List of Species of *Lockhartia*

1. <i>L. acuta</i>	11. <i>L. grandibractea</i>	21. <i>L. obtusata</i>
2. <i>L. amoena</i>	12. <i>L. hercodonta</i>	22. <i>L. oerstedii</i>
3. <i>L. bennettii</i>	13. <i>L. imbricata</i>	23. <i>L. oxyphylla</i>
4. <i>L. cladoniophora</i>	14. <i>L. ivainae</i>	24. <i>L. parthenocomos</i>
5. <i>L. compacta</i>	15. <i>L. latilabris</i>	25. <i>L. parthenoglossa</i>
6. <i>L. dipleura</i>	16. <i>L. lepticaula</i>	26. <i>L. rugosifolia</i>
7. <i>L. endresiana</i>	17. <i>L. longifolia</i>	27. <i>L. serra</i>
8. <i>L. galeottiana</i>	18. <i>L. lunifera</i>	28. <i>L. tenuiflora</i>
9. <i>L. genegeorgei</i>	19. <i>L. micrantha</i>	29. <i>L. verrucosa</i>
10. <i>L. goyazensis</i>	20. <i>L. oblongicallosa</i>	

List of Collections

The numbers in parentheses refer to the Numerical List of Species presented above. More than one species number listed for unnumbered collections represent specimens mounted on separate sheets or clearly marked as a separate collection, unless otherwise indicated. Collector initials are omitted when they are unknown and/or when they are absent from the specimen labels. Many *Lockhartia* collections (including several types) are unnumbered, and they are included here for reference (if this list is used for species determination of unnumbered specimens, their data should be compared with those cited in the text). Anonymous collections (76 in total) are excluded.

- Ackerman, J.D. 870 (8), 878 (27), 1213 (8), s.n. (25).
- Adams, B.R. B12 (25), K56 (12), K57 (25).
- Aguilar, R. 1497 (25), 1642 (19), 3115 (19), 3376 (19).
- Aguilar, R., & G. Herrera 799 (1).
- Albert de Escobar, L., et al. 4208 (17).
- Alfaro, A. 74 (11), 265 (19), 39971 (11), 40231 (11), s.n. (22).
- Alfaro, E. 824 (22), 2304 (22), 2452 (11).
- Allen, P.H. 61 (19), 2160 (21, type of *L. obtusata*), 2313 (2), 2318 (19), 2579 (21), 2903 (19), 3420 (19), 3493 (22), 3502 (22), 3550 (21), 3832 (11), 3939 (19), 4253 (1), 4259 (19), 4429 (19), 4666 (22), 4743 (22), 4764 (22), 5366 (19), 5489 (19), 5555 (25), 5761 (1), 5888 (2).
- Alston, A.H.G. 6195 (24).
- Alvarado, F. 23 (2).
- Alvarado, S. 51 (8).
- Alvarado, S., & S. Ibarra 352 (8).
- Ames, O. s.n. (18).
- Amorim, A.M., et al. 821 (18).
- Andel, T. van, & P. Huyskens 2629 (13).
- André, E.F. s.n. (17).
- Antonio, T. (or T.M.) 1995 (2), 3776 (25), 5004 (11).
- Appun, C. 1646 (13).
- Arauz Suárez, E.G. 3149 (1).
- Aristeguieta, L., & C. Montoya 2077 (1).
- Asplund, E. 16454 (27).
- Atwood, J.T. 5468 (12), 77153 (12), 78134 (19), 89184 (22), 89278 (22).
- Atwood, J.T., & W. Morris 4019 (12), 4111 (11).
- Atwood, J.T., et al. 5027 (12).
- Aubert de la Rue s.n. (13).
- Avilés, S. 34 (1).
- Azevedo, M.L.M., et al. 1011 (10).
- Balick, M.J., et al. 2567 (25).
- Bang, M. 2286 (17).
- Barclay 2800 (19).
- Barros, F. 1163 (10).
- Beauvard 6930 (22).
- Becerra, E., et al. 1014 (16).
- Bello, E. 880 (6), 1049 (12), 1224 (11, epitype of *L. grandibractea*), 1434 (12), 1452 (11), 1649 (12), 1782 (12).
- Bello, E., & E. Cruz 4290 (12).
- Bello, E., et al. 4039 (12), 4098 (12), 4548 (12).
- Bennett, D.E. 15 (17), 53 (3), 462 (17), 4601 (16), 5199 (9, including the type of *L. genegeorgei*; several specimens prepared at different dates, with different number suffixes), 5326 (16, type of *L. lepticaula*), 5403 (17, type of *L. tuberculata*), 6026 (16), 6427 (17), 6563 (27, type of *L. schunkei*), 7321 (9).
- Bennett, D.E., & C.H. Dodson s.n. (27).
- Benoist, R. 850 (13).
- Bernoulli, G. 316 (29).
- Bernoulli, G., & Cario 489 (29), 566 (22).
- Betancur, J., & S. Churchill 2226 (19).
- Biolley, P. 7093 (19, also as Pittier 7093).
- Blanco, M. 1520 (22), 1803 (7, type of *L. endresiana*), 2106 (21), 2283 (22), 2284 (12), 2286 (12), 2488 (23), 2554 (3), 2556 (2), 2558 (19), 2559 (11), 2561 (19), 2562 (19), 2563 (22), 2565 (22), 2566 (22), 2567 (1), 2568 (26), 2569 (26), 2570 (26), 2572 (21), 2573 (16), 2574 (27), 2575 (12), 2576 (18), 2667 (29), 2668 (27), 2669 (27), 2670 (18), 2671 (19), 2688 (18), 3012 (28), 3025 (21), 3212 (2), 3215 (17), 3218 (29), 3219 (18), 3220 (19), 3221 (1), 3223 (19), 3224 (22), 3227 (29), 3228 (27), 3230 (29), 3231 (28), 3232 (12), 3237 (16).
- Blanco, M., & E. Serrano 2653 (25).

- Blanco, M., & M. Whitten 2462 (22), 2463 (11).
- Blanco, M., et al. 657 (11), 1792 (12).
- Blydenstein, J. s.n. (11, 22, 29).
- Bocayuva, M. s.n. (18).
- Bogarín, D. 44 (22), 982 (12), 1887 (12), 3937 (22), 3989 (2).
- Bogarín, D., & Y. Kisel 4927 (12).
- Bogarín, D., & A. Prendas 676 (22).
- Bogarín, D., & F. Pupulin 2241 (25), 2242 (25).
- Bogarín, D., et al. 703 (12), 732 (12), 1241 (19), 2352 (4), 5769 (12).
- Bonsall, J. s.n. (1).
- Bowie & Cunningham s.n. (18).
- Boyle, B., et al. 4568 (17).
- Brade, A.C. 8527 (18), s.n. (10).
- Bradford 5305 (1), 5305 (13).
- Braga, P.I. 2074 (25).
- Brand, J., & M. Escobar 806 (25).
- Brand, J., & M. González 599 (25), 954 (25).
- Breedlove, D.E. 10550 (29), 14545 (29), 26177 (29), 33022 (22), 37894 (29), 51267 (29), 68954 (29).
- Breedlove, D.E., & M. Bourell 67501 (29).
- Breedlove, D.E., & R.F. Thorne 21075 (29).
- Breedlove, E.E., et al. 66245 (29).
- Brenes, A.M. 192 (12), 212 (2), 365 (12), 783 (12), 825 (2), 945 (12), 1034 (12), 1193 (2), 1672 (2), 2284 (12), 2436 (2), 2638 (12), 2894 (12), 3427 (2), 11599 (2), 12216 (19), s.n. (2, 22). Brenes's numbering system is confusing; most labels include several numbers (some in parentheses and/or scratched). The numbers reported here are cautiously interpreted as the "definitive" ones.
- Brenner, J. 10 (27).
- Bristan, N. 1508 (25).
- Britton, N.L., & E.G. Britton 2223 (13).
- Britton, N.L., & W.E. Broadway 2442 (13).
- Broadway, W.E. 4030 (1), 8765 (1), s.n. (1, 13).
- Brown, D.V. s.n. (2).
- Brown, M. 151 (1).
- Bull, D.V. s.n. (8).
- Burchell 9200 (13).
- Burger, W.C., & G. Matta 4534 (19).
- Burger, W.C., & R.G. Stolze 5104 (6).
- Burger, W.C., & R. Liesner 7245 (1).
- Burger, W.C., & J.L. Gentry 9022 (mixed: mostly 1, with 19 in one duplicate).
- Bussey, P. 584 (19).
- Cabrera Cachón, T.G. 67 (29), 159 (29), 224 (29).
- Calderón, C.E., et al. 2651 (10).
- Calzada, J.I. 9676 (29).
- Cambroner, C. s.n. (11).
- Campos, A. 1499 (8).
- Campos, J. 4558 (16).
- Campos, R. s.n. (1, 11, 19).
- Carballo, G., et al. 40 (7).
- Carder, H. s.n. (28).
- Carlson, M.C. 1797 (29), 1798 (22).
- Carpenter, J.B. 106 (16).
- Carvalho, F.A., et al. 931 (13).
- Castelfranco, D. s.n. (11).
- Castillo, J.J. 686 (29).
- Castro, E. 256 (25).
- Castroviejo, S., et al. 16162 (19).
- Chaboo, C. s.n. (1).
- Chacón, I.A. 75 (19).
- Chacón, L. 786 (13).
- Chaparro de Barrera, A., & E. Barrera Torres 168 (28).
- Chase, M.W. 8167 (2), 8170 (19), 15882 (11), 81010 (4), 82231 (18), 83147 (8), 83157 (18), 83253 (8), 84004 (12), 84101 (2), 84102 (21), 84327 (22), 86194 (19).
- Cheekwood s.n. (19).
- Chehaibar, T., et al. 206 (22).
- Chickering, A.M. 60 (1).

- Chinchilla, M., & IV Curso de Parataxónomos 28 (2).
- Christopher s.n. (1).
- Churchill, H.W., & G. de Nevers 4411 (19), 4975 (19).
- Cid, C.A., et al. 4753 (10).
- Cid Ferreira, C.A. 9001 (10).
- Clark, J.L. 3660 (22).
- Clark, J.L., & C. Watt 804 (23).
- Clark, J.L., et al. 2670 (12), 2796 (23).
- Clark, R.B. s.n. (13).
- Clarke, D. 3264 (13).
- Clarke, D., et al. 6615 (13), 6775 (13), 6780 (13), 7491 (13).
- Cogollo, A., et al. 2737 (17).
- Contreras, E. 9369 (25).
- Cooper 5967 (22).
- Cope, W.C. s.n. (2).
- Cornejo, F.X. 20 (27).
- Cornejo, X., & C. Bonifaz 4497 (17), 7701 (23).
- Correa, M.D. 2618 (11).
- Correa, M.D., et al. 1736 (19), 2164 (11), 9502 (19).
- Correa Gomes, J. 1948 (10).
- Cowan, R.S. 38169 (13).
- Crawford, J. 525 (1).
- Cremers, G. 5093 (13), 5522 (13), 6008 (13), 6009 (13).
- Cremers, G., & J.J. de Granville 13947 (13).
- Cremers, G., & F. Crozier 14647 (13), 14919 (13).
- Cribb, P. s.n. (22).
- Croat, T.B. 8056 (1), 10648 (22), 14042 (1), 15569 (1), 21087 (16), 26741 (22), 29942 (22), 35290 (12), 40551 (29).
- Croat, T.B., & J.P. Folsom 33917 (2).
- Croat, T.B., & G. Zhu 76487 (11).
- Cruger 1523 (13), 2246 (13).
- Cruz, J.S. de la 1307 (13), 1503 (13), 3108 (13).
- Cruz, L. s.n. (22).
- Cuatrecasas, J. 18319 (17).
- Cuming, H. 1297, 1298 and s.n. (19, possible syntypes of *L. micrantha*).
- D'Alessandro, D. 373 (17).
- Dalström, S., & Arnby 1346 (17).
- Davidse, G., & A.C. González 13613 (1).
- Davidson, M.E. 584 (22).
- Davis, D.H. 748 (13).
- Dawson, E.Y. 14865 (10), 14952 (10), s.n. (8).
- Delascio Chitty, F.A. 2207 (13).
- DeWolf, G.P. 303 (19).
- Díaz, C., et al. 4702 (27), 10352 (17), 10552 (17).
- Díaz, W., et al. 3184 (13), 3725 (13), 4886 (13).
- Díaz Luna, C.L. 19346 (8).
- Dodge, C.W. 1980 (29).
- Dodge, C.W., & W.S. Thomas 7182 (19), 7892 (19).
- Dodge, C.W., & P.H. Allen 17325 (mostly 19; one duplicate mixed with 1).
- Dodson, C.H. 22 (27), 182 (28), 242 (17), 2549 (12), 5588 (27), s.n. (2, 29).
- Dodson, C.H., & A.H. Gentry 10198 (17), 12788 (17), 17512 (23).
- Dodson, C.H., & P.M. Dodson 11350 (27).
- Dodson, C.H., & A. Hirtz 16908 (17).
- Dodson, C.H., et al. 8735 (27), 9235 (25), 13296 (17), 17138 (23), 17878 (28), 18675 (17).
- Donselaar, J. van, 2099 (13).
- Doring 5174 (17).
- Downs, W.G. s.n. (1, 13).
- Dress, W.J. 7015 (26).
- Dressler, R.L. 102 (12), 1007 (8), 1482 (22), 3022 (19), 3051 (12), 3194 (19), 3302 (19), 3392 (25), 3526 (2), 3605 (25), 3610 (19), 3621 (25), 3769 (12), 3824 (1), 4621 (25), 4837 (12), 5126 (12), 5231 (12), 5342 (11), 5397 (12), 5749 (2), 9573 (25).
- Dressler, R.L., & Biología-350 296 (11).

- Dressler, R.L., & N.H. Williams 3974 (25).
- Dressler, R.L., & M. Wirth 2704 (8).
- Drew, W.B. E-555 (12), E-566 (12), E-575 (12), E-642 (12), E-674 (23), E-690 (23).
- Dryander, E. 2527 (28).
- Dryer, V.J. 1633 (12).
- Dunsterville, G.C.K. 245 (24), 245A (15), 348 (13), 449 (1), 1243 (15), 1273 (17), 1352 (20, type of *L. oblongicallosa* [drawing]).
- Dunsterville, G.C.K., & E. Dunsterville 1255 (19), s.n. (19).
- Duparquier s.n. (10).
- Durán, A., & S. Levy 10 (22).
- Dusén, P. 8107 (18), 14274 (18), 16333 (18), 17692 (18), s.n. (18).
- Dwyer, J.D. 8367 (19).
- Echeverría, J.A. 4110 (12).
- Edwall 1877 (18).
- Edwards, J.B. 256 (22), 469 (22).
- Egler, W.A. 47678a (13).
- Ek, R.C., & D. Montfoort 135 (13), 251 (13), 252 (13).
- Elmore, F.H. H23 (19), J3 (1).
- Endara, L., & M. Cooper 308 (17).
- Endres, A.R. 167 (12, including lectotype of *L. hercodonta*), 214 (2), 302 (mixed: 2, 7, 22), 543 (mixed: 19, 22), 629 (11, drawing, lectotype of *L. grandibractea*), 2526 (4, lectotype of *L. cladoniophora*), s.n. (2, including type of *L. amoena*; 19; 22, including type of *L. odontochila*). Endres's numbering system is confusing; most of his collections are unnumbered.
- Erskine, C.M. 235 (18).
- Espinal, S. 3735 (17).
- Espinoza, R. 104 (12), 1373 (12).
- Estrada, A., & H. Binder 2086 (2).
- Estrada, A., et al. 724 (2).
- Fanshawe, D.B. 2420 (13).
- Fathrop, E.W. 7502 (29).
- Fawcett s.n. (1).
- Fendler, A. 1431 (1), 1432 (19), 2443 (24).
- Fernández, A. 2836 (1), 3139 (13).
- Ferreyra, R. 9313 (16), 10078 (16).
- Feuillet, C. 1132 (13).
- Fisulnauz s.n. (11).
- Fletes, E., et al. 255 (19).
- Florschütz, J., & P.A. Florschütz 902 (13).
- Folsom, J.P., & L. Collins 1677 (1).
- Folsom, J.P., & A. Jaslon 2711 (12).
- Folsom, J.P., et al. 2301 (19), 5273 (11), 6667 (12), 6962 (2), 8062 (11), 8127 (11), 8195 (11), 1864Z (19).
- Forero, E., & B.L. Wrigley 7074 (10).
- Fregge s.n. (13, type of *L. floribunda*).
- Freiberg, M. 15 (13).
- Freire, E. 4314 (28).
- Fuentes, Z. 200 (11).
- Fuentes, Z., & E. Fuentes 566 (11).
- Fuerkranz s.n. (19).
- Gailer, J. 18 (29).
- Gamboa, B. 2198 (2).
- Gamboa, B., et al. 2138 (2).
- Gardner, G. 4360 (10, type of *L. goyazensis*).
- Garnier, H.A. 1831 (19).
- Garwood, N., et al. 159 (19).
- Gaudichaud, C. s.n. (18).
- Gehrt, A. 14606 (18).
- Gély, A. 439 (13).
- Gentle, P.H. 6469 (12), 7321 (25), 7363 (25).
- Gentry, A. 3775 (1), 12596 (28).
- Gentry, A., et al. 30772 (27).
- Gerlach, G. s.n. (10).
- Germani, M. 70 (12).
- Giacometto, J. 106 (1).
- Gillis, W.T., & T.C. Plowman 10095 (11).
- Gilmartin, A.J. 683 (27).
- Ginzberger, A., & H. Zerny 680 (13).
- Giraldo, G.C. 206 (17), 230 (19).
- Glaziou, A. 1120 (18).
- Gómes da Silva, S.J., et al. 103 (18).
- Gómez, L.D. 2412 (12).

- Gómez, L.D., & G. Herrera 23035 (22).
 Gómez, L.D., et al. 23117 (11), 23191 (11).
 Gómez Domínguez, H. 952 (29).
 Gómez Laurito, J. 14314 (7).
 González, A.C., & G. Davidse 950 (1).
 González Loera, J., & J. Castaneda 324 (8).
 Gower s.n. (29).
 Granofremas 2555 (10).
 Granville, J.J. 4576 (13), 4960 (13), 5258 (13), 7421 (13), 8302 (13).
 Granville, J.J., et al. 8150 (13), 8204 (13), 9733 (13), 10515 (13), 14343 (13), 15543 (13).
 Grayum, M. 5591 (11), 6480 (22), 7975 (19).
 Grayum, M., & D. García 12659 (12).
 Grayum, M., et al. 4456 (25), 10089 (2), 12545 (12).
 Grogan, J. 355 (10).
 Guillén, R. 1946 (10).
 Guzmán, R. 1066 (25).
 Haber, W.A. 8526 (11).
 Haber, W.A., & J. Atwood 8564 (11), 9164 (12).
 Haber, W.A., & E. Bello 7329 (11), 7588 (11), 8092 (12), 8336 (12).
 Haber, W.A., ex E. Bello 5393 (11), 5397 (11), 5705 (11).
 Haber, W.A., & W. Zuchowski 8699 (12), 9552 (12).
 Haber, W.A., et al. 11424 (2).
 Hágsater, E. 4770 (8), 4771 (8).
 Hágsater, E., & C.H. Dodson 8922 (17).
 Hahn, W. 138 (25).
 Hahn, W.A., et al. 4296 (15).
 Hamer, F. s.n. (22).
 Hamilton, C., & K. Krager 3866 (22).
 Hammel, B. 1181 (19), 1282 (19), 1575 (22), 1987 (11).
 Hammel, B., et al. 6778 (22).
 Hampshire, R.J., & C. Whitefoord 36 (12), 622 (22).
 Hampshire, R.J., et al. 783A (29), 1173 (29).
 Hancock, W. 4 (8).
 Harling, G. 94 (27).
 Hartman, R.L. 12073 (25).
 Haught, O. 1593 (1), 3083 (27), 5570 (25).
 Hawkins, T., 1428 (12), 1489 (12).
 Hawkins, T., et al. 479 (22).
 Hayes, S. s.n. (1).
 Hayes, Y. 106 (1), 524 (25).
 Heller, A.H. 1271 (12), 2385 (19), 3790 (12), 5824 (25), s.n. (12, 22).
 Henderson, J.L. s.n. (19).
 Henkel, T.W., & R. James 3640 (13).
 Henkel, T.W., et al. 2972 (13), 3061 (13), 3447 (13).
 Henshold, N., & G. McPherson 1014 (22).
 Hermens s.n. (13).
 Herrera, G. 4765 (1), 4783 (25), 4812 (mixed: mostly 19, one duplicate with 1), 4883 (2), 5524 (12), 5863 (22), 8486 (12).
 Herrera, G., & A. Cascante 8163 (6).
 Herrera, G., & V. Mora 6879 (12).
 Herrera, G., et al. 8659 (12), 8781 (12).
 Herter 6930 (10).
 Herzog, T. 1988 (5), 1988b (17).
 Hesperheide, H. s.n. (25).
 Heyde & Lux 4616 (29).
 Hill s.n. (13).
 Hill, A.H. 23 (13).
 Hinds, R. s.n. (lectotype of *L. micrantha*).
 Hinton, G.B., et al. 14366 (8), 14640 (8).
 Hirtz, A. 8 (17), 7436 (12), 7687 (28), 7817 (17).
 Hirtz, A., & J. León 111 (17).
 Hirtz, A., et al. 4004 (17), 7329 (26), 8007 (17).
 Hoehne, F.C. s.n. (18).
 Hoffman, B. 400 (13).
 Hoffman, B., & D. Ardes 3785a (13).
 Hoffmannsegg, J.C.G. s.n. (13).
 Holm-Nielsen, L. 22932 (27).
 Holst, B. 8921 (12).
 Home, E. s.n. (13).

- Horich, C.K. s.n. (12).
 Hostmann 366 (13), 685 (13).
 Huber, W., & A. Weissenhofer 2548 (1).
 Huebsch s.n. (11).
 Huft, M., et al. 1680 (12).
 Humboldt & Bonpland 571 (20).
 Hunter, A.A., & P.H. Allen 586 (2).
 Hutchinson, P.C. 3837 (26), 6813 (3,
 including lectotype of *L. bennettii*),
 s.n. (11, 12, 22, 29).
 Hutchinson, P.C., & R.L. Dressler 2881
 (19).
 Hutchinson, P.C., & J.K. Wright 3837
 (26), 6849 (26), 6871 (3).
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LIST OF REFERENCES

- Allen PH. 1949.** Flora of Panama: Orchidaceae, fourth part. *Annals of the Missouri Botanical Garden* **36**: 133-245.
- Alves dos Santos I, Machado IC, Gaglianone MC. 2007.** História natural das abelhas coletoras de óleo. *Oecologia Brasiliensis* **11**: 544-557.
- Ames O. 1937.** Orchidaceae. In: PC Standley, ed. Flora of Costa Rica. Part I. *Publications of the Field Museum of Natural History, Botanical Series* **18**: 197-306.
- Ames O. 1944.** Destruction of the Schlechter herbarium by bombing. *American Orchid Society Bulletin* **13**: 105-106.
- Ames O, Correll DS. 1953.** Orchids of Guatemala. *Fieldiana, Botany* **26**: 401-727.
- Andersen TF, Johansen B, Lund I, Rasmussen FN, Rasmussen H, Sørensen I. 1988.** Vegetative architecture of *Eria Lindleyana* **3**: 117-132.
- Arber A. 1921.** The leaf structure of the Iridaceae, considered in relation to the Phyllode Theory. *Annals of Botany* **35**: 301-336.
- Arber A. 1925.** *Monocotyledons, a morphological study*. Cambridge University Press: Cambridge, UK.
- Arditti J. 1992.** *Fundamentals of orchid biology*. J. Wiley & Sons: New York.
- Arditti J, Ghani AKA. 2000.** Numerical and physical properties of orchid seeds and their biological implications. *New Phytologist* **145**: 367-421.
- Atwood JT, Mora de Retana DE. 1999.** Flora Costaricensis. Family #39 Orchidaceae: Tribe Maxillarieae: Subtribes Maxillariinae and Oncidiinae. *Fieldiana, Botany New Series* **40**: 1-182.
- Barbosa Rodrigues J. 1883.** *Structure des orchidées: notes d'une étude*. Typographie Nationale: Rio de Janeiro.
- Belcher E. 1843.** *Narrative of a voyage around the world, performed in Her Majesty's Ship Sulphur, during the years 1836-1842. Vol. 1*. Henry Colburn: London.
- Bell AD. 2008.** *Plant form: An illustrated guide to flowering plant morphology*. 2nd Edition. Timber Press: Portland.
- Bennett DE, Christenson EA. 1998.** New species of Peruvian Orchidaceae V. *Lindleyana* **13**: 31-56.
- Bentham G. 1881.** Notes on the Orchideae. *Journal of the Linnean Society, Botany* **18**: 281-360.

- Blanco MA, Williams NH. 2010.** Proposal to conserve the name *Lockhartia oerstedii* against *Oncidium mirabile* (*L. mirabilis*) (Orchidaceae). *Taxon* **59**: 1894.
- Bogarín D, Karremans A, Pupulin F. 2008.** New species and records of Orchidaceae from Costa Rica. *Lankesteriana* **8**: 53-74.
- Brummitt RK, Powell CE. 1992.** *Authors of plant names: a list of authors of scientific names of plants, with recommended standard forms of their names, including abbreviations*. Royal Botanic Gardens, Kew: London.
- Buchman SL. 1987.** The ecology of oil flowers and their bees. *Annual Review of Ecology and Systematics* **18**: 343-369.
- Burns-Balogh P. 1988.** Reichenbach Herbarium, Naturhistorisches Museum, Vienna. Guide to the microform collection. IDC Publishers: Leiden.
- Carlsward BS, Stern WL, Judd WS, Lucansky TW. 1997.** Comparative leaf anatomy and systematics in *Dendrobium*, sections *Aporum* and *Rhizobium* (Orchidaceae). *International Journal of Plant Sciences* **158**: 332-342.
- Cervi AC, Borgo M. 2007.** Epífitos vasculares no Parque Nacional do Iguaçu, Paraná (Brasil). Levantamento preliminar. *Fontqueria* **55**: 415-422.
- Chaia J. 1970.** Jean-Baptiste Patris: médecin botaniste à Cayenne, explorateur de la Guyane (1764-1786). *Actes du 95e Congrès National des Sociétés Savantes* **2**: 189-197.
- Chase MW. 1986.** A reappraisal of the oncioid orchids. *Systematic Botany* **11**: 477-491.
- Charanasri U, Kamemoto H. 1975.** Additional chromosome numbers in *Oncidium* and allied genera. *American Orchid Society Bulletin* **44**: 686-691.
- Chase MW. 1986.** A reappraisal of the oncioid orchids. *Systematic Botany* **11**: 477-491.
- Chase MW. 2009.** *Lockhartia*. In: A Pridgeon, PJ Cribb, MW Chase, FN Rasmussen, eds. *Genera Orchidacearum, Volume 5: Epidendroideae (Part Two)*. Oxford University Press: Oxford, 287-290.
- Chase MW, Hills HH. 1991.** Silica gel: An ideal material for field preservation of leaf samples for DNA studies. *Taxon* **40**: 215-220.
- Chase MW, Palmer JD. 1989.** Chloroplast DNA systematics of lilioid monocots: resources, feasibility, and an example from the Orchidaceae. *American Journal of Botany* **76**: 1720-1730.

- Chase MW, Palmer JD. 1992.** Floral morphology and chromosome number in subtribe Oncidiinae (Orchidaceae): evolutionary insights from a phylogenetic analysis of chloroplast DNA restriction site variation. In: PS Soltis, DE Soltis, JJ Doyle, eds. *Molecular Systematics of Plants*. Chapman and Hall: New York, 324-339.
- Chase MW, Phippen JS. 1988.** Seed morphology in the Oncidiinae and related subtribes (Orchidaceae). *Systematic Botany* **13**: 313-323.
- Chase MW, Freudenstein JV, Cameron KM, Barrett RL. 2003.** DNA data and Orchidaceae systematics: a new phylogenetic classification. In: KW Dixon, SP Kell, RL Barrett, PJ Cribb, eds. *Orchid Conservation*. Natural History Publications: Kota Kinabalu, Sabah, 69-89.
- Chase MW, Hanson L, Albert VA, Whitten WM, Williams NH. 2005.** Life history evolution and genome size in subtribe Oncidiinae (Orchidaceae). *Annals of Botany* **95**: 191-199.
- Chaudhri MN, Vegter IH, De Wal CM. 1972.** Index Herbariorum Part II (3) Collectors I-L. *Regnum Vegetabile* **86**.
- Christenson EA. 1994.** Significant collections of Orchidaceae conserved in Herbarium Hamburgense (HBG). *Brittonia* **46**: 344-354.
- Christenson EA. 1995.** Pittier's Panama collections at US. *Orchid Research Newsletter* **25**: 7-8.
- Christenson EA. 1996.** Notes on Neotropical Orchidaceae - II. *Lindleyana* **11**: 12-26.
- Christenson EA. 1997.** Orchidaceae. In: SA Mori, G Cremers, C Gracie, JJ de Granville, M Hoff, JD Mitchell, eds. *Guide to the Vascular Plants of Central French Guiana. Part 1. Pteridophytes, Gymnosperms, and Monocotyledons*. The New York Botanical Garden: Bronx, 286-342.
- Clements MA. 1999.** Embryology. In: AM Pridgeon, PJ Cribb, MW Chase, FN Rasmussen, eds. *Genera Orchidacearum, volume 1: General introduction, Apostasioideae, Cyripedioideae*. Oxford University Press: Oxford, 38-58.
- Cogniaux A. 1906.** *Lockhartia*. *Flora Brasiliensis* **3(6)**: 450-456, tab. 59.
- Cogniaux A. 1910.** Orchidaceae. *Symbolae Antillanae* **6(3)**: 293-696.
- Cutler DF. 1978.** *Applied plant anatomy*. Longman Group Ltd.: London.
- Dance SP. 1980.** Hugh Cuming (1791-1865), prince of collectors. *Journal of the Society for the Bibliography of Natural History* **9**: 477-501.
- Davis JI. 1999.** Monophyly, populations and species. In: PM Hollingsworth, RM Bateman, RJ Gornall, eds. *Molecular Systematics and Plant Evolution*. Taylor & Francis: London, 139-170.

- Descourtilz JT. 1825-1855.** Epidendres des forêts vierges du Brésil. Unpublished bound paintings, MS6689, Bibliothèque de L'Institut de France: Paris.
- Dodson CH. 2004.** *Native Ecuadorian Orchids, volume V: Rodriguezia-Zygosepalum.* Dodson Publishing: Sarasota.
- Dodson CH. 2002.** *Native Ecuadorian Orchids, Volume III: Lepanthopsis-Oliveriana.* Dodson Trust: Sarasota.
- Dodson CH, Bennett DE. 1989a.** *Lockhartia parthenocomos* Rchb.f. *Icones Plantarum Tropicarum, series II 1989:* plate 0089.
- Dodson CH, Bennett DE. 1989b.** *Lockhartia bennettii* Dodson. *Icones Plantarum Tropicarum, series II 1989:* plate 0088.
- Dodson CH, Dressler RL. 1972.** Two undescribed genera in the Orchidaceae-Oncidiinae. *Phytologia* **24:** 285-292.
- Dodson CH, Vásquez R. 1989.** *Lockhartia ludibunda* Rchb.f. *Icones Plantarum Tropicarum, series II 1989:* plate 0346.
- Donoghue MJ, Sanderson MJ. 1992.** The suitability of molecular and morphological evidence in reconstructing plant phylogeny. In: PS Soltis, DE Soltis, JJ Doyle, eds. *Molecular Systematics of Plants.* Chapman and Hall: New York, 340-368.
- Doyle JJ, Doyle JL. 1987.** A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* **19:** 11-15.
- Dressler RL. 1974.** Classification of the orchid family. In: M Ospina, ed. *Anales de la 7ma Conferencia Mundial de Orquideología / 7th World Orchid Conference Proceedings.* Editorial Bedout: Medellín, 259-279.
- Dressler RL. 1961.** The structure of the orchid flower. *Missouri Botanical Garden Bulletin* **49:** 60-69.
- Dressler RL. 1981.** *The orchids: natural history and classification.* Harvard University Press: Cambridge, Massachusetts.
- Dressler RL. 1986.** Features of pollinaria and orchid classification. *Lindleyana* **1:** 125-130.
- Dressler RL. 1989.** Rostellum and viscidium: divergent definitions. *Lindleyana* **4:** 48-49.
- Dressler RL. 1993a.** *Phylogeny and classification of the orchid family.* Cambridge University Press: Cambridge.
- Dressler RL. 1993b.** *Field guide to the orchids of Costa Rica and Panama.* Cornell University Press: Ithaca.
- Dressler RL. 2003.** Manual de Plantas de Costa Rica: Orchidaceae. *Monographs in Systematic Botany from the Missouri Botanical Garden* **93:** 1-595.

- Dressler RL, Dodson CH. 1960.** Classification and phylogeny in the Orchidaceae. *Annals of the Missouri Botanical Garden* **47**: 25-67.
- Dunsterville GCK, Garay LA. 1959.** *Venezuelan Orchids Illustrated, Volume 1.* Andre Deutsch: London.
- Dunsterville GCK, Garay LA. 1972.** *Venezuelan Orchids Illustrated, Volume 5.* Andre Deutsch: London.
- Dunsterville GCK, Garay LA. 1976.** *Venezuelan Orchids Illustrated, Volume 6.* Andre Deutsch: London.
- Dwyer JD. 1973.** Henri Pittier's botanical activity in Panama. *Taxon* **22**: 557-576.
- Eichler AW. 1875.** *Blüthendiagramme, erster Theil.* Verlag von Wilhelm Engelmann: Leipzig.
- Ernst A. 1878.** Orchideae Venezuelanae. In: JM Spence, ed. *The land of Bolívar, or war, peace, and adventure in the Republic of Venezuela, volume 2.* Sampson Low, Marston, Searle, & Rivington: London, 192-220.
- Farris JS, Källersjö M, Kluge AG, Bult C. 1995.** Testing significance of incongruence. *Cladistics* **10**: 315-319.
- Felsenstein J. 1985.** Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783-791.
- Ferreira Fernandes da Silva M, Fernandes da Silva JB. 2010.** *Orquídeas Nativas da Amazônia Brasileira.* Museu Paraense Emilio Goeldi: Belém.
- Fitch CM. 1960.** The longevity of various orchid flowers. *The Orchid Weekly* **2**: 281-288.
- Fitch WM. 1971.** Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Zoology* **20**: 406-416.
- Foldats E. 1970.** Orchidaceae, Quinta Parte. *Flora de Venezuela* **15**: 598-598.
- Freudenstein JV, Chase MW. 2001.** Analysis of mitochondrial *nad1b-c* intron sequences in Orchidaceae: Utility and coding of length-change characters. *Systematic Botany* **26**: 643-657.
- Freudenstein JV, Rasmussen FN. 1999.** What does morphology tell us about orchid relationships? – A cladistics analysis. *American Journal of Botany* **86**: 225-248.
- Garay LA. 1963.** *Oliveriana* and its position in the Oncidiinae. *American Orchid Society Bulletin* **32**: 19-24.
- Garay LA. 1970a.** Orquídeas colombianas nuevas o críticas. Decena VI. *Orquideología* **5**: 173-183.

- Garay LA. 1970b.** A reappraisal of the genus *Oncidium* Sw. *Taxon* **19**: 443-467.
- Gardner G. 1846.** *Travels in the Interior of Brazil, principally through the Northern Provinces, and the Gold and Diamond Districts, During the Years 1836-1841.* Reeve Brothers: London.
- Givnish TJ, Sytsma KJ. 1997.** Homoplasy in molecular vs. morphological data: the likelihood of correct phylogenetic inference. In: TJ Givnish, KJ Sytsma, eds. *Molecular Evolution and Adaptive Radiation.* Cambridge University Press: Cambridge, U.K., 55-101.
- Goh CJ. 1976.** Reversion of vegetative and reproductive growth in monopodial orchids. *Annals of Botany* **40**: 645-646 + 1 plate.
- Grisebach AHR. 1864.** Orchidaceae. *Flora of the British West Indian Islands* **7**: 606-644.
- Hágsater E. 1985.** Towards an understanding of the genus *Epidendrum*. In: KW Tan, ed. *Proceedings of the 11th World Orchid Conference.* Eleventh World Orchid Conference: Miami, 195-201.
- Hamer F. 1984a.** Orchids of Nicaragua: *Lockhartia* Hooker. *Icones Plantarum Tropicarum* **1984**: plate 824S.
- Hamer F. 1984b.** *Lockhartia amoena* Endres & Rchb.f. *Icones Plantarum Tropicarum* **1984**: plate 1028.
- Hamer F. 2001.** Flora de Nicaragua: Orchidaceae. *Monographs in Systematic Botany from the Missouri Botanical Gardens* **85**: 1612-1860.
- Hawkes AD. 1952.** The pseudomonopodial orchids. *The Orchid Journal* **1**: 287-289.
- Hawkes AD. 1953.** An interesting *Lockhartia*. *The Orchid Journal* **2**: 316-317.
- Hawkes AD. 1958.** *Lockhartia*, a cultural gimmick. *The Orchid Weekly* **1**: 169.
- Hawkes AD. 1965.** *Encyclopaedia of Cultivated Orchids.* Faber and Faber: London.
- Hemsley WB. 1882-1886.** Orchideae. *Biologia Centrali-Americana, Botany* **3**: 197-308.
- Hillis DM, Wiens JJ. 2000.** Molecules versus morphology in systematics: conflicts, artifacts, and misconceptions. In: JJ Wiens, ed. *Phylogenetic Analysis of Morphological Data.* Smithsonian Institution Press: Washington, 1-19.
- Hoehne FC. 1952.** O que vem a ser *Epidendrum imbricatum* Lamarck. *Arquivos de Botânica do Estado de São Paulo* **2**: 137-140.
- Holttum RE. 1955.** Growth-habits of monocotyledons - variations on a theme. *Phytomorphology* **5**: 399-413.

- Hooker WJ. 1827.** *Lockhartia elegans*. Beautiful Lockhartia. *Botanical Magazine* **54**: t. 2715.
- Johansen DA. 1940.** *Plant Microtechnique*. McGraw-Hill Book Company: New York.
- Johnson AE. 2001.** *Las orquídeas del Parque Nacional Iguazú*. L.O.L.A (Literature of Latin America): Buenos Aires.
- Johnston IM. 1936.** A study of the Nolanaceae. *Proceedings of the American Academy of Arts and Sciences* **71**: 1-87.
- Judd WS, Campbell CS, Kellogg EA, Stevens PF, Donoghue MJ. 2008.** *Plant Systematics: A Phylogenetic Approach*, 3 edn. Sinauer Associates: Sunderland, Massachusetts.
- Kraenzlin F. 1923.** IV.50 Orchidaceae-Monandreae-Pseudomonopodiales. *Das Pflanzenreich (Engler)* **83**: 1-66.
- Lamarck JBAPM. 1793.** *Encyclopédie Méthodique, Botanique*. Panckoucke, Paris & Liège.
- Lemée A. 1955.** Orchidacées. *Flore de la Guyane Française* **1**: 368-469.
- Lescure J. 1998.** Les voyageurs et les naturalistes français aux Antilles (XVII^e-XIX^e siècle). In: JL d'Hondt, J Lorenz, eds. *L'exploration naturaliste des Antilles et de la Guyane*. CTHS: Paris, 107-133.
- Light MHS. 1997.** Seed production and germinability in Oncidiinae. *Journal of the Canadian Orchid Congress* **9(1)**: 2-4.
- Lindley J. 1824.** *Catasetum Claveringi* - Capitain Clavering's Catasetum. *The Botanical Register* **10**: 840.
- Lindley J. 1833.** *The genera and species of orchidaceous plants*. Ridgways, Picadilly, London: 207-214.
- Lindley J. 1834.** Catalogue of the Orchideae in Mr. Cuming's collection of South American plants. *Journal of Botany (Hooker)* **1**: 4-8.
- Lindley J. 1846.** *The vegetable kingdom*. Bradbury & Evans: London.
- Lüning B. 1967.** Studies on Orchidaceae alkaloids - IV. Screening of species for alkaloids 2. *Phytochemistry* **6**: 857-861.
- Mabee PM. 2000.** The usefulness of ontogeny in interpreting morphological characters. In: JJ Wiens, ed. *Phylogenetic Analysis of Morphological Data*. Smithsonian Institution Press: Washington, 84-114.
- Maddison DR, Maddison WP. 2005.** *MacClade 4: Analysis of phylogeny and character evolution, version 4.08a*. Sinauer Associates: Sunderland, Massachusetts.

- Maguire B. 1948.** Plant explorations in Guiana in 1944, chiefly to the Tafelberg and the Kaieteur plateau - II. *Bulletin of the Torrey Botanical Club* **75**: 189-230.
- Mansfeld R. 1929.** Figuren-Atlas zu den Orchideenfloren der südamerikanischen Kordillerenstaaten von R. Schlechter. *Repertorium Specierum Novarum Regni Vegetabilis, Beihefte* **57**: 1 + 142 plates and 8-page index.
- Mansfeld R. 1937.** Über das System der Orchidaceae-Monandrae. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* **13**: 666-676.
- McDade LA. 1990.** Hybrids and phylogenetic systematics I. Patterns of character expression in hybrids and their implications for cladistic analysis. *Evolution* **44**: 1685-1700.
- McDade LA. 1992.** Hybrids and phylogenetic systematics II. The impact of hybrids on cladistic analysis. *Evolution* **46**: 1329-1346.
- McDade LA. 2000.** Hybridization and phylogenetics: special insights from morphology. In: JJ Wiens, ed. *Phylogenetic Analysis of Morphological Data*. Smithsonian Institution Press: Washington, 146-164.
- McLeish I, Pearce NR, Adams BR. 1995.** *Native Orchids of Belize*. A.A. Balkema: Rotterdam.
- McNeill J, Barrie FR, Burdet HM, et al. 2006.** International Code of Botanical Nomenclature (Vienna Code). *Regnum Vegetabile* **146**.
- McVaugh R. 1977.** Botanical results of the Sessé & Mociño expedition (1787-1803). I. Summary of excursions and travels. *Contributions from the University of Michigan Herbarium* **11**: 97-195.
- McVaugh R. 1978.** Galeotti's botanical work in Mexico: The numbering of his collections and a brief itinerary. *Contributions from the University of Michigan Herbarium* **11**: 291-297.
- McVaugh R. 1985.** Flora Novo-Galiciana: Orchidaceae. *Contributions from the University of Michigan Herbarium* **16**: 1-366.
- Misas Urreta G. 2005.** *Orquídeas de la Serranía del Baudó, Chocó, Colombia / Orchids from the Serranía del Baudó, Chocó, Colombia*. Corporación Capitalina de Orquideología: Bogotá.
- Möbius M. 1887.** Über den anatomischen Bau der Orchideenblätter und dessen Bedeutung für das System dieser Familie. *Jahrbücher für Wissenschaftliche Botanik* **18**: 530-615.
- Møller JD, Rasmussen H. 1984.** Stegmata in Orchidales: character state distribution and polarity. *Botanical Journal of the Linnean Society* **89**: 53-76.

- Molvray M, Chase MW. 1999.** Seed morphology. In: AM Pridgeon, PJ Cribb, MW Chase, FN Rasmussen, eds. *Genera Orchidacearum, volume 1: General introduction, Apostasioideae, Cyripedioideae*. Oxford University Press: Oxford, 59-66.
- Mora DE, Atwood JT. 1992a.** *Lockhartia oerstedii* Rchb.f. *Icones Plantarum Tropicarum 1992*: plate 1450.
- Mora DE, Atwood JT. 1992b.** *Lockhartia amoena* Endres & Rchb.f. *Icones Plantarum Tropicarum 1992*: plate 1446.
- Mora DE, Atwood JT. 1992c.** *Lockhartia dipleura* Schltr. *Icones Plantarum Tropicarum 1992*: plate 1447.
- Mora DE, Atwood JT. 1992d.** *Lockhartia micrantha* Rchb.f. *Icones Plantarum Tropicarum 1992*: plate 1449.
- Mora DE, Atwood JT. 1992e.** *Lockhartia hercodonta* Reichb.f. ex Kraenzlin. *Icones Plantarum Tropicarum 1992*: plate 1448.
- Nelson EA, Sage TL, Sage RF. 2005.** Functional leaf anatomy of plants with crassulacean acid metabolism. *Functional Plant Biology* **32**: 409-419.
- Nelson Sutherland CH, Ortiz Kafati JC. 2007.** La colección de orquídeas del Herbario TEFH de Honduras. *Ceiba* **48**: 11-59.
- Neubig KM, Whitten WM, Carlsward BS, et al. 2009.** Phylogenetic utility of *ycf1* in orchids: a plastid gene more variable than *matK*. *Plant Systematics and Evolution* **277**: 75-84.
- Ossenbach C, Pupulin F, Jenny R. 2010.** Orchid itineraries of Augustus R. Endrés in Central America: a biographic and geographic sketch. *Lankesteriana* **10**: 19-47.
- Pessoa Félix L, Guerra M. 2000.** Cytogenetics and cytotaxonomy of some Brazilian species of Cymbidioid orchids. *Genetics and Molecular Biology* **23**: 978.
- Pfitzer EHH. 1882.** *Grundzüge einer vergleichenden Morphologie der Orchideen*. Carl Winter's Universitätsbuchhandlung: Heidelberg.
- Pfitzer EHH. 1887.** *Entwurf einer natürlichen Anordnung der Orchideen*. Carl Winter: Heidelberg.
- Pfitzer EHH. 1889.** Orchidaceae. In: A Engler, K Prantl, eds. *Die natürlichen Pflanzenfamilien*. Wilhelm Engelmann: Leipzig, 52-224.
- Pittier H. 1923.** Note on plants collected in tropical America. *Journal of the Washington Academy of Sciences* **13**: 428-431.
- Poe S, Wiens JJ. 2000.** Character selection and the methodology of morphological phylogenetics. In: JJ Wiens, ed. *Phylogenetic Analysis of Morphological Data*. Smithsonian Institution Press: Washington, 20-36.

- Porembski S, Barthlott W. 1988.** Velamen radicum micromorphology and classification of Orchidaceae. *Nordic Journal of Botany* **8**: 117-137.
- Posada D. 2008.** jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution* **25**: 1253-1256.
- Pouliquen M. 2001.** *Les voyages de Jean-Baptiste Leblond, médecin naturaliste du roi, 1767-1802: Antilles, Amérique espagnole, Guyane.* Éditions du C.T.H.S.: Paris.
- Prenner G, Vergara-Silva F, Rudall PJ. 2009.** The key role of morphology in modeling inflorescence architecture. *Trends in Plant Science* **14**: 302-309.
- Pridgeon AM. 1987.** The velamen and exodermis of orchid roots. In: J Arditti, ed. *Orchid biology: reviews and perspectives, IV.* Comstock Publishing Associates: Ithaca and London, 139-192.
- Pridgeon AM. 1992.** *The illustrated encyclopedia of orchids.* Timber Press: Portland, Oregon.
- Pridgeon AM. 1999.** Palynology. In: A Pridgeon, PJ Cribb, MW Chase, FN Rasmussen, eds. *Genera Orchidacearum, Volume 1: General Introduction, Apostasioideae, Cypripedioideae.* Oxford University Press: Oxford, 33-37.
- Pridgeon AM, Stern WL, Benzing DH. 1983.** Tilosomes in roots of Orchidaceae: morphology and systematic occurrence. *American Journal of Botany* **70**: 1365-1377.
- Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN. 2009.** *Genera Orchidacearum Volume 5: Epidendroideae (Part Two).* Oxford University Press, Oxford.
- Prillieux E. 1857.** Observations sur la déhiscence du fruit des Orchidées. *Bulletin de la Société Botanique de France* **4**: 803-809.
- Pupulin F. 2002.** Catálogo revisado y anotado de las Orchidaceae de Costa Rica. *Lankesteriana* **4**: 1-88.
- Pupulin F. 2010.** Orchidaceae Werckleanae: typification of Costa Rican orchid species described from collections by K. Wercklé. *Botanical Journal of the Linnean Society* **163**: 111-154.
- Raffauf RF. 1962.** A simple field test for alkaloid-containing plants. *Economic Botany* **16**: 171-172.
- Rambaut A. 1996.** *Se-Al: Sequence alignment editor, version 2.0a11.* URL: <http://tree.bio.ed.ac.uk/software/seal/>. Accessed August 2007.
- Rasmussen FN. 1986.** On the various contrivances by which pollinia are attached to viscidia. *Lindleyana* **1**: 21-32.
- Rasmussen FN, Johansen B. 2006.** Carpology of orchids. *Selbyana* **27**: 44-53.

- Rasmussen H. 1986.** The vegetative architecture of orchids. *Lindleyana* **1**: 42-50.
- Rasmussen H. 1987.** Orchid stomata - structure, differentiation, function, and phylogeny. In: J Arditti, ed. *Orchid biology, reviews and perspectives, IV*. Cornell University Press: Ithaca, 105-138.
- Reichenbach HG. 1852.** Gartenorchideen. *Botanische Zeitung* **10**: 633-640.
- Reichenbach HG. 1855.** *Xenia Orchidacea - Beiträge zur Kenntniss der Orchideen. Erster Band*. F.A. Brockhaus: Leipzig.
- Reichenbach HG. 1857.** *Catalog der Orchideen-Sammlung von G. W. Schiller*. G. W. Schiller: Hamburg.
- Reichenbach HG. 1864.** *Lockhartia* Hook. *Annales Botanicæ Systematicæ* **6**: 818-822.
- Reichenbach HG. 1869.** *Lockhartia verrucosa*. *Refugium Botanicum* **2**: Tab. 76.
- Richard LCM. 1792.** Catalogus plantarum, ad societatem, ineunte anno 1792, e Cayenna missarum a domino Le Blond. *Actes de la Société d'Histoire Naturelle de Paris* **1**: 105-114.
- Ridley H. 1896.** The Orchideae and Apostaciaceae of the Malay Peninsula. *Journal of the Linnean Society of London, Botany* **32**: 213-416.
- Rindal E, Brower AVZ. 2010.** Do model-based phylogenetic analyses perform better than parsimony? A test with empirical data. *Cladistics* **27**: 1-4.
- Rolfe RA. 1908.** The localities of Cuming's Philippine plants. *Bulletin of Miscellaneous Information, Royal Gardens, Kew* **1908**: 116-119.
- Romero-González GA. 2005.** *Orchidaceae Schomburgkianae*: The orchids collected by R. H. Schomburgk in South America and the Caribbean. *Harvard Papers in Botany* **10**: 231-268.
- Roriosa JN. 1887.** Ghiesbreght, Augustus B., explorador de México; vida y trabajos del naturalista belga. *La Naturaleza, 2da serie (Mexico City)* **1**: 211-217.
- Sandoval-Zapotitla E, Terrazas T, Villaseñor JL. 2010a.** Diversidad de inclusiones minerales en la subtribu Oncidiinae (Orchidaceae). *Revista de Biología Tropical* **58**: 733-755.
- Sandoval-Zapotitla E, García-Cruz J, Terrazas T, Villaseñor JL. 2010b.** Relaciones filogenéticas de la subtribu Oncidiinae (Orchidaceae) inferidas a partir de caracteres estructurales y secuencias de ADN (ITS y *matK*): un enfoque combinado. *Revista Mexicana de Biodiversidad* **81**: 263-279.
- Schlechter R. 1914.** *Die Orchideen*. Paul Parey: Berlin.

- Schlechter R. 1926.** Das System der Orchidaceen. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* **9**: 563-591.
- Schneckenburger S. 1993.** Orchid inflorescences - Descriptive and typological aspects. In: A Pridgeon, ed. *Proceedings of the 14th World Orchid Conference*. HMSO Publications: Edinburgh, 353-360.
- Schultes RE. 1960.** *Native Orchids of Trinidad and Tobago*. Pergamon Press: London.
- Schultes RE. 1967.** Orchidaceae. *Fl. Trinidad & Tobago* **3(1)**: 13-200.
- Schweinfurth C. 1955.** Further notes on American orchids. *Botanical Museum Leaflets (Harvard University)* **17**: 37-64.
- Schweinfurth C. 1959.** Key to the orchids. In: CL Withner, ed. *The orchids – A scientific study*. The Ronald Press Company: New York, 511-528.
- Schweinfurth C. 1961.** Orchids of Peru, Part 4. *Fieldiana, Botany* **30**: 787-1005.
- Schweinfurth C. 1967.** Orchidaceae of the Guyana highland. *Memoirs of the New York Botanical Garden* **14**: 69-214.
- Seelanan T, Schnabel H, Wendel JF. 1997.** Congruence and consensus in the cotton tribe. *Systematic Botany* **22**: 259-290.
- Senghas K. 1995.** 70. Subtribus: Lockhartiinae. In: FG Brieger, R Maatsch, K Senghas, eds. *Rudolf Schlechter Die Orchideen*. 3rd Edition. Blackwell Wissenschafts-Verlag: Berlin, 1929-1937.
- Senghas K. 1996.** *Lockhartia amoena* Endr. & Rchb. f. 1872. *Die Orchidee* **47**: 839-840.
- Senghas K. 2001.** *Neobennettia*, eine neue Gattung aus den peruanischen Anden: mit einem Überblick zur Gattung *Lockhartia*. *Journal für den Orchideenfreund* **8**: 354-364.
- Silvera K. 2002.** *Adaptive radiation of oil-reward compounds among neotropical orchid species (Oncidiinae)*, M.Sc. Thesis, University of Florida, Gainesville, Florida, U.S.A.
- Silvera K, Santiago LS, Winter K. 2005.** Distribution of crassulacean acid metabolism in orchids of Panama: evidence of selection for weak and strong modes. *Functional Plant Biology* **32**: 397-407.
- Solereeder H, Meyer FJ. 1969.** Systematic anatomy of the monocotyledons (Systematische Anatomie der Monokotyledonen), volume VI, Microspermae. Translated by A Herzberg. Israel Program for Scientific Translations: Jerusalem.
- Soto Arenas MA. 2008.** *Lockhartia galeottiana* Soto Arenas. *Icones Orchidacearum* **10**: plate 1038.

- Stafleu FA, Cowan RS. 1979.** Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Vol. II: H-Le. 2nd ed. *Regnum Vegetabile* **98**: i-980.
- Stafleu FA, Cowan RS. 1983.** Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Vol. IV: P-Sak. 2nd ed. *Regnum Vegetabile* **110**: i-1214.
- Stafleu FA, Cowan RS. 1985.** Taxonomic Literature: a selective guide to botanical publications and collections with dates, commentaries and types. Vol. V: Sal-Ste. 2nd ed. *Regnum Vegetabile* **112**: i-1066.
- Standley PC. 1928.** Flora of the Panama Canal Zone. *Contributions from the United States National Herbarium* **27**: 1-416.
- Stern WL, Carlswald BS. 2006.** Comparative vegetative anatomy and systematics of the Oncidiinae (Maxillarieae, Orchidaceae). *Botanical Journal of the Linnean Society* **152**: 91-107.
- Stevens PF. 1991.** Character states, morphological variation, and phylogenetic analysis: a review. *Systematic Botany* **16**: 553-583.
- Sun Y, Skinner DZ, Liang GH, Hulbert SH. 1994.** Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. *Theoretical and Applied Genetics* **89**: 26-32.
- Swofford DL. 2003.** *PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0b10*. Sinauer Associates: Sunderland, Massachusetts.
- Szlachetko DL. 1995.** Systema Orchidarium. *Fragmenta Floristica et Geobotanica Supplementum* **3**: 1-152.
- Szlachetko DL, Mytnik-Ejsmont J. 2009.** Gynostemium Orchidarium IV. Orchidaceae-Vandoideae (Maxillarieae, Cryptorrheneae, Zygopetaleae, Dicheaeae, Telipogoneae, Ornithocephaleae, Oncidieae). *Acta Botanica Fennica* **180**: 1-313.
- Taberlet P, Gielly L, Pautou G, Bouvet J. 1991.** Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* **17**: 1105-1109.
- Taylor, P. 1976.** Orchids brought to life in the herbarium. In: K Senghas, ed. *Tagungsbericht der 8. Welt-Orchideen-Konferenz, Palmengarten Frankfurt, 10.-17. April 1975 / Proceedings of the 8th World Orchid Conference, Palmengarten Frankfurt, 10th-17th April, 1975*. Deutsche Orchideen-Gesellschaft: Frankfurt am Main, 505-509.
- Thiers B. 2011.** Index Herbariorum: A global directory of public herbaria and associated staff. <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>.

- Vásquez R, Ibsch PL. 2000.** *Orquídeas de Bolivia / Orchids of Bolivia, Volumen 1. Subtribu Pleurothallidinae.* Editorial F.A.N.: Santa Cruz de la Sierra, Bolivia.
- Vogel S. 1973.** Ölblumen und ölsammelnde Bienen. *Tropische und Subtropische Pflanzenwelt* **7**: 1-267.
- Weberling F. 1989.** *Morphology of flowers and inflorescences.* Cambridge University Press: Cambridge.
- Weltz M. 1897.** *Zur Anatomie der monandrischen sympodialen Orchideen,* PhD Thesis, Ruprecht-Karls-Universität, Heidelberg.
- Werkhoven MCM. 1986.** *Orchideeën van Suriname.* VACO N.V. Uitgeversmaatschappij: Paramaribo.
- Whitten WM, Williams NH, Chase MW. 2000.** Subtribal and generic relationships of Maxillariinae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. *American Journal of Botany* **87**: 1842-1856.
- Williams CA. 1979.** The leaf flavonoids of the Orchidaceae. *Phytochemistry* **18**: 803-813.
- Williams LO. 1951.** The Orchidaceae of Mexico. *Ceiba* **2**: 1-321.
- Williams LO. 1956.** An enumeration of the Orchidaceae of Central America, British Honduras and Panama. *Ceiba* **5**: 1-256.
- Williams NH. 1979.** Subsidiary cells in the Orchidaceae: their general distribution with special reference to development in the Oncidiaceae. *Botanical Journal of the Linnean Society* **78**: 41-66.
- Williams NH, Broome CR. 1976.** Scanning electron microscope studies of orchid pollen. *American Orchid Society Bulletin* **45**: 699-707.
- Williams NH, Chase MW, Fulcher T, Whitten WM. 2001a.** Molecular systematics of the Oncidiinae based on evidence from four DNA sequence regions: expanded circumscriptions of *Cyrtochilum*, *Erycina*, *Otoglossum*, and *Trichocentrum*, and a new genus (Orchidaceae). *Lindleyana* **16**: 113-139.
- Williams NH, Chase MW, Whitten WM. 2001b.** Phylogenetic positions of *Miltoniopsis*, *Caucaea*, a new genus, *Cyrtochiloides*, and *Oncidium phymatochilum* (Orchidaceae: Oncidiinae) based on nuclear and plastid DNA sequence data. *Lindleyana* **16**: 272-285.
- Williams NH, Whitten WM, Dressler RL. 2005.** Molecular systematics of *Telipogon* (Orchidaceae: Oncidiinae) and its allies: nuclear and plastid DNA sequence data. *Lankesteriana* **5**: 163-184.
- Wirth M. 1964.** *Supra-specific variation and classification in the Oncidiinae (Orchidaceae),* Ph.D. Thesis, Washington University, St. Louis.

- Withner CL, Nelson PK, Wejksnora PJ. 1974.** The anatomy of orchids. In: CL Withner, ed. *The orchids - scientific studies*. John Wiley and Sons: New York, 267-347.
- Wood HP. 2006.** *The Dendrobiums*. A.R.G. Gantner Verlag K.G.: Ruggell, Liechtenstein.
- Xu DH, Abe J, Sakai M, Kanazawa A, Shimamoto Y. 2000.** Sequence variation of non-coding regions of chloroplast DNA of soybean and related wild species and its implications for the evolution of different chloroplast haplotypes. *Theoretical and Applied Genetics* **101**: 724-732.
- Zelenko H, Chase MW. 2002.** Orchids: the pictorial encyclopedia of *Oncidium*. 2nd Edition. ZAI Publications, Quito.
- Ziegler B. 1981.** Mikromorphologie der Orchideensamen unter Berücksichtigung taxonomischer Aspekte. Ph.D. Thesis, Ruprecht Karls Universität, Heidelberg.

BIOGRAPHICAL SKETCH

Mario Alberto Blanco Coto was born in San José, Costa Rica, in 1972. He obtained a Bachelor in Science in biology from the University of Costa Rica (UCR) in 1996. As an undergrad student at UCR, he became very interested in the taxonomy and reproductive biology of plants, particularly orchids. He worked as a research assistant for the late Dora Emilia Mora de Retana, former director of the Lankester Botanical Garden of UCR, in various projects on Costa Rican orchids. In 1997, Mario spent three months as a research intern at the Marie Selby Botanical Gardens in Sarasota, Florida, where he studied the Costa Rican species of *Lepanthes* under the guidance of John T. Atwood. He came to the Botany Department at the University of Florida to pursue a PhD under the guidance of Norris H. Williams. Mario plans to continue doing research in plant systematics, morphology, and reproductive biology, with an emphasis on the Orchidaceae.