

# **Systematics and evolution of the genus *Pleurothallis* R. Br. (*Orchidaceae*) in the Greater Antilles**

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***Pleurothallis obliquipetala* Acuña & Schweinf.**

**Für Jakob und Julius,**

die nichts unversucht ließen, um das Zustandekommen dieser Arbeit zu verhindern.

## **Zusammenfassung**

Die antillanische Flora ist eine der artenreichsten der Erde. Trotz jahrhundertelanger floristischer Forschung zeigen jüngere Studien, daß der Archipel noch immer weiße Flecken beherbergt. Das trifft besonders auf die Familie der Orchideen zu, deren letzte Bearbeitung für Cuba z.B. mehr als ein halbes Jahrhundert zurückliegt.

Die vorliegende Arbeit basiert auf der lang ausstehenden Revision der Orchideengattung *Pleurothallis* R. Br. für die Flora de Cuba. Mittels weiterer morphologischer, palynologischer, molekulargenetischer, phytogeographischer und ökologischer Untersuchungen auch eines Florentails der anderen Großen Antillen wird die Genese der antillanischen *Pleurothallis*-Flora rekonstruiert.

Der Archipel umfaßt mehr als 70 Arten dieser Gattung, wobei die Zahlen auf den einzelnen Inseln sehr verschieden sind: Cuba besitzt 39, Jamaica 23, Hispaniola 40 und Puerto Rico 11 Spezies. Das Zentrum der Diversität liegt im montanen Dreieck Ost-Cuba – Jamaica – Hispaniola, einer Region, die 95 % der antillanischen Arten beherbergt, wovon 75% endemisch auf einer der Inseln sind. Da die meisten Arten entweder endemisch oder pankaribisch verbreitet sind, bleiben die floristischen Bezüge zwischen den Inseln und zu den kontinentalen Nachbargebieten nur schwach ausgeprägt. Immerhin lassen sich einige Verbindungen unter den Inseln der Großen Antillen und besonders zu Mittelamerika erkennen. Diese Affinitäten steigen von Ost nach West.

Molekulargenetische und (mikro-)morphologische Daten als phylogeographisches Werkzeug zeichnen dieses Muster deutlicher. Danach lassen sich die antillanischen Arten hinsichtlich ihrer Genese in drei Gruppen einteilen. 25% der Arten ist pankaribisch verbreitet, wobei der Großteil der antillanischen Populationen vom mittelamerikanischen Festland stammt. Ebenfalls aus dieser Region stammen weitere 25%, die jedoch auf den Inseln neue Arten gebildet haben (Anagenese). Die verbleibenden 50% der großantillanischen Sippen sind autochthon und das Ergebnis adaptiver Radiation auf den Inseln. Diese intensive Kladogenese beschränkt sich auf drei Verwandtschaftskreise innerhalb der Gattung *Pleurothallis* in den Untergattungen *Antilla* Luer und *Specklinia* Lindl. Es stellte sich heraus, daß der überwiegende Anteil der Artbildungsprozesse allopatrischer Natur ist. Sympatrie konnte nur in einem einzigen Fall direkt belegt werden.

Das Ergebnis der allopatrischen Speziation sind zwei Typen von Vikarianz, räumlich geographischer und geologischer. In Cuba sind überraschenderweise fast 80% der endemischen Arten an einen Gesteinstyp gebunden, überwiegend an Serpentin. West-Hispaniola, wo viele Schwesternarten cubanischer Sippen beheimatet sind, besteht fast ausschließlich aus Kalkstein. Geographische Vikarianz ist daher oft geologisch unterlegt, eine Bindung die für Epiphyten kaum vermutet wurde. Hinter der Geologie verbergen sich

jedoch eher Bestäuberareale und weniger physiologische Anpassung als limitierender Faktor. Eine Verfrachtung in Vegetation auf anderem petrologischen Untergrund scheint damit der Hauptauslöser für Artbildungen gewesen zu sein. Grundlage waren höchstwahrscheinlich individuenarme Gründerpopulationen die den Bedingungen eines *founder events* ausgesetzt waren.

Neben den reichen geologischen Verhältnissen im Dreieck Ost-Cuba – Jamaica – Hispaniola wird die intensive Artbildung durch weitere spezifisch lokale Bedingungen unterstützt. Karibische Wirbelstürme dürften entlang der Hauptrouten für eine häufige Verfrachtung von Samen oder Pflanzen von Mittelamerika auf die Großen Antillen sowie zwischen den Inseln selber verantwortlich sein. Ein zweiter günstiger Umstand für erfolgreiche Migration innerhalb des Dreiecks besteht in der räumlichen Nähe der Inselgebirge und deren optimalen klimatischen Bedingungen für die Besiedlung durch mikrophytische Epiphyten.

Molekulargenetische Daten lieferten weiterhin wertvolle Informationen in Bezug auf die beiden aktuell diskutierten Systeme der *Pleurothallidinae*, einer streng morphologischen (Luer) und einer fast ausschließlich auf DNA-Sequenzen (Pridgeon & Chase) basierenden Klassifikation. DNA-Sequenzen der cubanischen Arten stützen das neue System von Pridgeon & Chase weitestgehend, zeigen aber noch Widersprüche in einigen der neuen oder wiedererrichteten Taxa.

Angesicht dessen, daß die karibische Florenregion leider nicht nur durch ihre Biodiversität zu den zehn globalen *hot spots* zählt, sondern auch durch die großflächige Zerstörung von Primärvegetation, war es auch ein Anliegen der vorliegenden Arbeit, ein erstes detailliertes Bild von Genese und Verbreitung antillanischer Orchideen zu vermitteln. Diese Daten können direkt für die Gestaltung und das Management von karibischen Schutzgebieten eingesetzt werden, da Orchideen in der Naturschutzpolitik einen hohen Argumentationswert besitzen.

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# 1 Introduction

## 1.1 Subtribe *Pleurothallidinae* – an introduction

The orchidaceous subtribe *Pleurothallidinae* forms one of the most diverse natural groups of this family (Dressler 1993a). The ~30 (sensu Luer 1986a) resp. 35 genera (sensu Pridgeon & Chase 2001) comprise more than 3500 species (Luer, pers. commun.), i.e. ~15% of the world's orchid flora.

### *Distribution*

The ecological centre of diversity of these exclusively neotropical orchids lies in the (sub)montane rain- and cloudforests of the Central American Sierra Madre chain and the South American Andes. Yet pleurothallids are found from Florida to Bolivia and N Chile, including the Antillean Arc. Growing primarily in epiphytic habitats, many taxa can be found in rupicolous and (pseudo)terrestrial niches as well.

### *Morphology*

The subtribe consists mostly of microphytic plants. Due to the minor horticultural role, these plants have long been excluded from detailed studies in every respect. Only recently pleurothallids have been the target of morphological and anatomical studies (Pridgeon & Williams 1979; Pridgeon 1981a,b,c; Pridgeon & Stern 1982, 1983, 1985; Stern & al. 1985; Neyland & Urbatsch 1993; Stenzel 2000). Two features are usually considered to delimit the subtribe (Fig. 1): the nonbulbous secondary stems (ramicauls) and the persistent pedicel with an abscission layer just below the ovary and not at the base of the pedicel as in all other orchids (Luer 1986a). A third notable macromorphological feature is a ring-like structure above the abscission layer, the annulus (Fig. 1). This character of still unknown function (Stern & al. 1985, Luer 1986a) is found only in the more derived genera (Pridgeon & al. 2001).

Within the subtribe there are the world's smallest orchids (Luer 1990) as well as species measuring several meters in height. All stages from densely caespitose to long creeping habits can be found. The ramicaul may be reduced or may be elongate. Except for *Fronitaria* Luer, it bears a single terminal leaf. The erect or pendent inflorescence, usually inserted below the abscission layer, arises from the rhizome in some groups, while it is merged into the leaf blade in others, resembling a phylloclade as in *Ruscus*. Floral organs are very diverse. There is a wide array of ornamentations and appendages such as warts, scales, hairs etc. Sepals show various degrees of connation. Both sepals and petals may carry osmophores at their tips. The lip may be simple or lobed and often forms a complex,



3-dimensionally elaborated structure. It is hinged either to the base of the column or to a foot, which is formed by an extension of ovary and column. The labellum is often mobile or even actively motile in some cases. The column carries the anther, stigma and rostellum at its distal end. The anther may be hooded and ventral (facing the lip) or apical. The stigma is usually entire; only in some genera we find stigmatic lobes or even bi-partitioned stigmas.

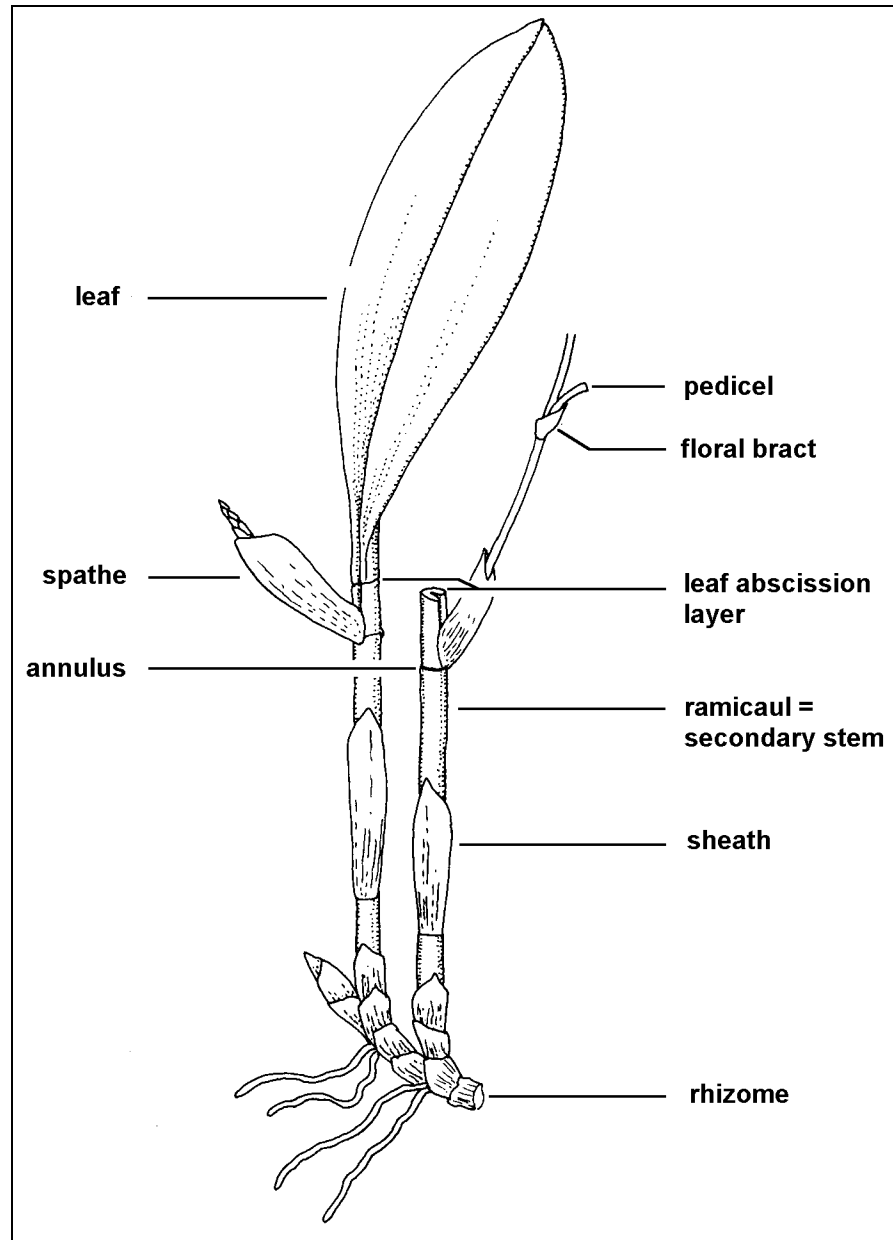


Fig. 1: General morphology of a pleurothallid orchid. Adapted from Luer (1986a).

A widespread feature of pleurothallid orchids is succulence, although the classic storage organs in orchids, the stems, are not thickened into pseudobulbs. Succulent tissues may be found in all organs, i.e. they are not confined to vegetative parts of the plant. This is the result of adaptation to xeric conditions of the epiphytic and epilithic habitat.

The enormous richness of vegetative and reproductive features in *Pleurothallidinae* is equally reflected in microscopical characteristics. Such an amazing variety of **palynological** differentiation as in *Pleurothallidinae* (Stenzel 2000) can be found nowhere else in higher orchids (*Epidendroideae* s.l. Dressler 1993a). The number of pollinia, 2, 4, 6, or 8, differs substantially between genera, with the majority of taxa having only one pair. It is widely agreed now that reduction in number proceeded from 8 to 2 pollinia (Dressler 1993a, Stenzel 2000, Pridgeon & al. 2001). However, this evolutionary process is not necessarily accompanied by a sporodermal differentiation. Thus, there can be taxa with 8 (*Octomeria*) or 4 (*Barbosella*) pollinia with a highly elaborated sporoderm in the outer tetrads, while other genera with 2 pollinia still show an ancient state of sporodermal sculpture (Stenzel 2000). These “inconsistencies” illustrate once more the complex morphological evolution within the subtribe.

Although clearly heterobathmic constellations complicate the picture of palynological evolution, individual features were found to be usually consistent with generic boundaries. Yet there is one striking exception: *Pleurothallis*. This large genus (sensu Luer 1986b) shows virtually all sculpture types found elsewhere in the subtribe (Stenzel 2000), strongly suggesting polyphyly in Luer’s system.

#### *Taxonomy and Systematics*

The earliest revision of pleurothallid orchids was published by J. Lindley in several fascicles of his *Folia*, with the most extensive one covering the genus *Pleurothallis* (Lindley 1859). F. Kränzlin treated some masdevalliid genera in his “Monographien der Gattungen *Masdevallia*, *Lothiana*, *Scaphosepalum*, *Cryptophoranthus*, und *Pseudoctomeria*” (1925). Another 60 years passed until C. Luer started his *Icones Pleurothallidarum* with a generic survey (Luer 1986a). All these classifications were morphologically based. Pridgeon (1982b) and Neyland & al. (1995) tried to liberate pleurothallid systematics from subjective weighting by using numerical analysis, still being based on morphological characters. Finally, Pridgeon, Solano & Chase (2001) presented molecular data and radically changed the pleurothallid system in a subsequent paper (Pridgeon & Chase 2001, with nomenclatural corrections in Pridgeon & Chase (2002). Yet, even the new system, introduced by Pridgeon and Chase with about 500 taxonomic changes, i.e. transfers for the most part, seems to be partially questionable. It was completely turned down by Luer (2002) and critical reviews have been published both in papers and on the Internet (Hammel & al. 2002, Jost & Endara 2002).

Morphological traits that have been traditionally employed in pleurothallid systematics comprise number of pollinia, presence or absence of the annulus, shape of the ramicaul and the transition area with the leaf base, degree of sepalous connation, floral

appendages and osmophores, shape and adnation of the lip as well as special floral structures, e.g. motile lips. In most cases it is not just one synapomorphic character, but a combination of different traits, that distinguishes taxa. This high level of parallel evolution and the subsequent “homoplasy rife” (Pridgeon & al. 2001: 2286) has made so difficult the distinction between homologous and analogous characteristics. Consequently, distinct features used in taxonomy form often merely “key characters” instead of true synapomorphies. This applies to both macro- and micromorphological and anatomical traits (Pridgeon 1982a, Stenzel 2000, Pridgeon & al. 2001).

Palynological data has already been successfully applied earlier in phylogenetic investigation in orchids (reviewed in Stenzel 2000) and has been found to be useful in delimiting pleurothallid genera (Stenzel 2000). However, it must be used with care when discussing relationships. The molecular based system proposed by Pridgeon & Chase (2001) has made palynological patterns much more consistent with generic boundaries, especially in the re-defined genera *Pleurothallis* and *Stelis* (Stenzel 2004b). Yet, the new concept comprises again new or resurrected genera that show palynologically discordant traits, as was found in initial studies at the outset of this thesis. With additional DNA sequences and further palynological data, especially from the “genus” *Pleurothallis*, I investigate whether the molecular based system introduced by Pridgeon & Chase has provided pleurothallid systematics a convincing frame work reflecting natural evolution.

## 1.2 *Pleurothallis* of the Greater Antilles

The Greater Antilles form the northernmost boundary of pleurothallid orchids. Only a few species have been found further N at the S tip of Florida.

The first *Pleurothallis* described, *Pleurothallis ruscifolia* (Jacq.) R. Br., was based on Antillean material, i.e. Martinique (Jacquin 1763). It is the type of the largest natural orchidaceous group world-wide. The next species of this genus were published in 1788 by the Swedish botanist O. Swartz and, like *P. ruscifolia*, they were placed in the genus *Epidendrum*. After R. Brown had established the genus *Pleurothallis* (in Aiton & Aiton, 1813), J. Lindley from the Royal Botanical Gardens Kew united the genera *Lepanthes*, *Octomeria*, *Pleurothallis* (incl. *Specklinia*) and *Stelis* in the subtribe *Pleurothallidinae* Lindl. The majority of the Antillean taxa described in the 19<sup>th</sup> century were published by Lindley. Apart from a few taxa that had been described by him earlier, he benefited from the extensive field work by Charles Wright in Cuba in the late 50ies (Lindley 1858: 9 epithets). H. G. Reichenbach added another 5 species based on Wright’s set that was sent to W. J. Hooker (Reichenbach 1865). Parallely, Grisebach had also worked on Wright’s material. However, Reichenbach’s publication made most of his pleurothallid epithets “Makulatur” (i.e. superfluous; Griseb. in lit. according to Howard 1988: 251). The next century started with several new species from Jamaica described by W. Fawcett and A. B. Rendle

(1909a,b), after Fawcett had already described *P. uncinata* (*Myoxanthus uncinatus* (Fawc.) Luer) in 1895. A. C. Cogniaux published several Antillean taxa of *Pleurothallis* (1909-1910), mainly based on Wright's collections, that either had been overlooked or misinterpreted by Lindley and Reichenbach. Meanwhile, the Swede E. Ekman had started his extensive field work in Cuba. His material served as a base for many orchid species published by R. Schlechter, then curator in the Botanical Garden Berlin-Dahlem. However, merely one species of *Pleurothallis* was published from Ekman's material, the Cuban *P. ekmanii*. Another 50 years passed until D. D. Dod started investigations on Hispaniola, a work that resulted in the publication of no less than 17 epithets attributed to *Pleurothallis* from this island (Dod 1976, 1977, 1978, 1984b, 1989a). H. Dietrich added another epithet for Cuba (1984a). As the most recent contribution, Luer (1998c, 1999a) and Stenzel (2001, 2002) described 13 species from Cuba and Hispaniola referable to *Pleurothallis*. This shows that the Greater Antilles still host a treasure of taxa new to science, despite intensive scientific work in this neotropical region for several hundred years now.

Although the subtribe *Pleurothallidinae* represents essentially a continental taxon, it comprises at least ~150-200 species in the Greater Antilles. There are ~10 genera on the islands of the arc, the diversity of which is distributed very unevenly. Only a few species rich genera (*Pleurothallis*, *Lepanthes*, *Lepanthopsis*) contrast a majority of poorly represented taxa (*Barbosella*, *Brachionidium*, *Myoxanthus*, *Octomeria*, *Platystele*, *Stelis*, *Trichosalpinx*, *Zootrophion*). *Pleurothallis* seems to be by far the most diverse genus. It may be dethroned, however, once *Lepanthes* is thoroughly revised on all islands.

In any case, *Pleurothallis* is the morphologically most diverse pleurothallid group in the Arc. While the other pleurothallid genera, except *Lepanthes*, were revised in the last decade in Luer's *Icones*, *Pleurothallis* has been treated thoroughly only for Puerto Rico (Ackerman 1995, 1997) and Jamaica (Adams 1972). Concerning the species rich, large islands Cuba and Hispaniola, however, "only" several new descriptions were published by H. Dietrich for Cuba and D. D. Dod for Hispaniola. Thus, a taxonomic revision is still pending.

This status quo does not concern *Pleurothallis* alone. Cuba's latest revision of the orchid family dates back to the 40ies of the last century (León & Schweinfurth 1946) and there are many other plant families that have not been treated since then either. To create a modern Flora, Cuba, in collaboration with the GDR and Hungary, had launched therefore the ambitious Nueva Flora de la República de Cuba project in the early 70's (Lepper 1992). This collaboration is based mainly on scientific exchange between the Jardín Botánico Nacional de La Habana, the Friedrich-Schiller-University Jena, the Humboldt-University Berlin, and, since the 1990's, the Botanical Museum Berlin-Dahlem. Since then, a substantial stock of herbarium material as well as phytogeographical and ecological

data has been gathered in numerous field trips. Both, physical and non-physical material and data on *Orchidaceae* (Dietrich 1979, 1980, 1982, 1983, 1984c, 1985, 1988, 1992) were considered to provide an excellent base for a revision of the genus *Pleurothallis* as well as further studies. While several plant families have been treated as part of the Flora Cuba Project since the mid 90's, *Orchidaceae* have not been tackled yet. The revision of the main orchid genus *Pleurothallis*, as part of this study, can be considered the starting point of a series of taxonomic treatments of this important family in one of the floristic hotspots of the world. It will form the base for all further studies that make up the present thesis.

### **1.3 Biogeography of the Antillean Arc**

Island biogeography has fascinated evolutionary scientists since Darwin, who dedicated a whole chapter to the "inhabitants of oceanic islands" (Darwin 1859]. Some general traits of island biotas, like low diversity and high endemism compared to similar continental areas, were already stated by him. Other questions that arise when it comes to issues of island floras or faunas and their evolution depend heavily on the archipelago and the taxon in concern. Questions as origin, dispersal and speciation cannot be detached from the specific geological and climatic history, as well as their present constellation, dispersal capabilities of the taxon in question, ecological demands and reproductive traits.

Islands are often chosen as a geographical unit, because they combine some specific features not found in continental areas: "small, isolated, and relatively simple systems to most continental situations" (Baldwin & al. 1998 quoted from Carlquist 1965). Although the prevalence of these traits is questionable and may be heavily influenced by our anthropogenic view, islands do have some advantages for biogeographical studies: (1) they are geographically clearly defined, (2) political borders are mostly identical with island limits, i.e. the geographical limits of local Floras are naturally defined, (3) the age can often be easier determined than in continental areas, especially in the case of volcanic islands (Baldwin & al. 1998).

However, in some cases not even these advantages may be present. The West Indies, for instance, are an archipelago that has a complex geological history (Hedges 2001, Iturralde-Vinent & MacPhee 1999]. In the recent past, Caribbean palaeogeography and biogeography were discussed in close connection by aligning one with the other. In this attempt, biogeographical aspects were studied most intensively in animals. In contrast, the number of Antillean phytogeographical works is comparably small (Samek 1988, Howard 1974). Other studies are confined to single islands (Alain 1978, Samek 1973, Borhidi 1996) or form little more than introductory chapters of floral works. The two most recent and comprehensive publications on West Indian biogeography (Woods 1989,

2001) contain merely one botanical study each. Thus, phytogeographical issues are mainly dealt within floristic studies, which focus naturally on a very limited geographical scope.

Similar to the insufficient taxonomic treatment of the *Orchidaceae*, the phytogeographical patterns of this family in the Antilles are only rarely dealt with (Dietrich 1989a, Trejo-Torres & Ackerman 2001, Ackerman & al. in press). Zooming further into the family, the situation gets even worse: there are no phytogeographical studies dealing with any of the Antillean orchid groups. Considering the poor taxonomic knowledge that notoriously accompanies this family this is not surprising. Even the introduction of molecular techniques has not triggered further biogeographical studies. Most studies using genetic markers are aimed at the “re”-revision of the orchidaceous system, with little or no attention being paid to geographical issues. Ironically, the introduction of this new and powerful tool may even postpone its application in a phytogeographical context, since both the new systematic revision as well as the introduction of nomenclatural consequences are very time-consuming. Moreover, the discussion on morphological vs. molecular systems, further distract the attention from the fact that molecular methods have proven to be very powerful in the phytogeographical field, too (Baldwin & al. 1998). *Pleurothallidinae* provide an excellent example for this barren conflict (Pridgeon & Chase 2001, Luer 2002).

The phytogeography of the Greater Antilles has long focused on comparing species richness and endemism, and assessing putative channels of floristic exchange based on floristic similarity. Only recently have been introduced cladistic methods (Judd 2001, Trejo-Torres & Ackerman 2001: PAE and PAD) to make floristic affinities between areas more lucid. However, apart from Judd (2001) no phylogeographical study has been published to my knowledge, so far. While molecular data has already been used in the study on the genesis of other island floras (reviewed in Baldwin & al. 1998) there are virtually no data available for the Antilles.

Patterns of orchidaceous phytogeography in the Greater Antilles are still poorly known too. Orchids serve often as a “political tool” employed in conservation issues when defining the floristic value of an area. Detailed knowledge about distribution, host specificity and other ecological correlation rarely exists, unfortunately. This is especially the case in endemic taxa with a limited distribution. The endemic portion in the genus *Pleurothallis* was estimated at ~60% for Cuba (Acuña Galé 1939, León & Schweinfurth 1946); however, distribution data given in these treatments and more recent data from field work within the Flora Project often do not coincide. Moreover, it is a well-known fact, that endemism, local or regional, is often a collection artefact or is simply overestimated. Dietrich (Dietrich 1989a), referring to some highly endemic pleurothallid genera, takes the view that “every more or less isolated mountain chain has its own species”. Initial

sampling and collecting as well as herbarium studies prior to this study had indicated a probably much wider distribution than actually considered in many taxa. Likewise, field observations prior to this study had indicated that taxa of wider, e.g. Circum-Caribbean, distribution grow in a great array of different habitats, i.e. spatial distribution seems to be correlated with less ecological specialisation. Unfortunately, there is almost no data on ecological preferences of orchids (Freiberg 1992). The predominance of pleurothallids in moist habitats is the only correlation that is usually stated. H. Dietrich (pers. commun.) reported the observed association of orchids with certain petrologic features (limestone). To test these hypotheses, Cuba with its diverse ecological and geological patterns, provides an excellent background.

#### **1.4 Goals of this study**

It is surprising that both an area and a plant family that have been attracting scientists for centuries now, still show blank areas. As was shown in the previous chapters, several factors have influenced the decision to choose the genus *Pleurothallis* for a study on the genesis of the Caribbean orchidaceous flora. The main objectives of the present study are the following:

1. Revision of the genus *Pleurothallis* (sensu Luer 1986a,b) for the Flora of Cuba. Macro- and micromorphological, i.e. palynological, characterisation of the members of this genus.
2. Comparison of Antillean molecular and palynological data with the results of recent taxonomic changes in *Pleurothallidinae* by Pridgeon & Chase (2001). Are the genera of the new system monophyletic?
3. Genesis of the Greater Antillean taxa of *Pleurothallis*. Has the island arc been colonised via the Lesser or via the Greater Antilles? How are these orchids distributed along the island chain, both horizontally and vertically? Are endemic taxa as restricted as stated in literature?
4. Discussion of the ecological distribution of *Pleurothallis* in the Antilles. Are endemic taxa as stenoecious and are widespread species as euryoecious as assumed?

## 2 Materials and Methods

### 2.1 Materials

This study is primarily based on the Cuban and Antillean species of the genus *Pleurothallis* (sensu Luer 1986b). For palynological and phytogeographical studies, however, taxa from other pleurothallid genera were added to provide a broader view on these orchids. *Pleurothallis ekmanii* Schltr., *Pleurothallis excentrica* (Luer) Luer (bas. *Octomeria excentrica* Luer) and *Pleurothallis* 'flabelliformis' nom. prov. (bas. *Octomeria prostrata* H. Stenzel), three species of uncertain phylogenetic position, were treated under the generic name *Pleurothallis*, which, unfortunately, made the employment of an unpublished name unavoidable.

Material was collected in Cuba, Jamaica, the Dominican Republic, and Puerto Rico during the years 1997 - 2001. The vast majority of the samples was gathered during a 6-month stay in Cuba in 1998 (Tab. 1), another in 1999, and a third one of 3 months in 2000 in Jamaica and Puerto Rico. Initially, localities which should be visited were chosen from herbarium data and from information found in literature. Additional suggestions came from Dr. M. A. Díaz (HAJB), Dr. H. Dietrich (JE) and Dr. A. Urquiola Cruz (HPPR) resulting from former field trips within the Flora de Cuba Project (hereafter FCP).

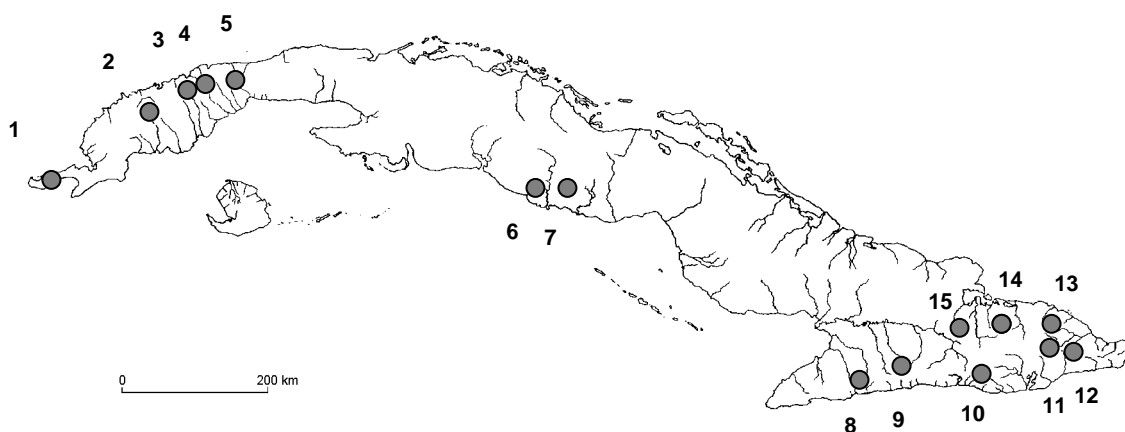


Fig. 2: Collecting areas in Cuba.

1 – Guanahacabibes; 2 – Sierra de los Órganos; 3 – Cajalbana; 4 – Pan de Guajaibón; 5 – Taco Taco, Rangel; 6 – Montañas de Trinidad; 7 – Sierra de Banao; 8 – Turquino Massif; 9 – Guisa, Victorino; 10 – Gran Piedra; 11 – Palenque, Bernardo, Pico Galán; 12 – Sierra de Imías; 13 – Meseta del Toldo; 14 – Sierra del Cristal; 15 – Sierra de Nipe.

The majority of the more than 1300 vouchers collected belongs to the family *Orchidaceae*, with almost 500 representing taxa of the subtribe *Pleurothallidinae*. Collecting and transfer of the material took place in accordance with Cuban law and CITES criteria. In general, collecting of entire populations was avoided. In concordance with the rules of the FCP, herbarium material belonging to *Pleurothallis* will be split between HAJB and JE.



Holotypes and vouchers consisting of single specimens will be deposited in HAJB in any case. Material in spirit, CARNOY as well as silica dried samples belong to the personal collections of the author. All material that does not belong to *Pleurothallis* will be housed in HAJB.

Tab. 1. Survey of the field work in Cuba.

Province	Area	Date	collections H. Stenzel
PR	Sierra del Rosario	III- 1998	400-414
PR	El Moncada; Pan de Guajaibón; Cajálbana	IV- 1998	415-429
Ho	Sierra de Nipe	IV- 1998	430-493
Ho	Sierra de Moa: Reserva de Jaguaní	V- 1998	494-503
Ho	Sierra del Cristal: Río Levisa	V- 1998	504-547
Ho	Sierra de Moa; between El Piloto and El Toldo	VI- 1998	558-601
Ci, SS	Sierra de Escambray	VII- 1998	602-618
Gr	Sierra Maestra: Victorino	VIII- 1998	619-640
Gr, SC	Sierra Maestra: Turquino Massif	VIII- 1998	641-663
SC	Santiago de Cuba: Gran Piedra	VIII- 1998	664-680
PR	Sierra del Infierno	III- 1999	710-716
PR	Mantua: La Cana	III- 1999	716-721
Ho	Sierra de Nipe	IV- 1999	722-743
Ho	Sierra del Cristal	IV- 1999	744-778
Gr, SC	Sierra Maestra: Turquino Massif	IV- 1999	780-839
Gu	Palenque; Piedra La Vela	IV,V 1999	839-849
Gu	Yateras: Pico Galán	V- 1999	850-874
Gu	Yateras: Bernardo	V- 1999	875-876
Gu	Sierra de Imías: Los Calderos	V- 1999	877-880
Gu	Sierra de Imías: La Yamagua	V- 1999	881-916
PR	Sierra de Quemado: El Moncada	VI- 2001	1100-1112, 1139-1166, 1211-1249
PR	Sierra de Cajálbana, S slope	VI- 2001	1113-1138
	Guanahacabibes: Cabo Corrientes	VI- 2001	1167-1174, 1210
PR	Guanahacabibes: road to Cabo San Antonio	VI- 2001	1175-1209, 1323
PR	Pan de Guajaibón	VI- 2001	1250-1299
PR	Sierra de Cajálbana, N slope	VI- 2001	1300-1322

Besides these personal collections, material of the following herbaria was examined: AJBC, BSC, HAC, HAJB, HPPR, JE, B, BM, BR, DUKE, G, GH (AMES), GOET, IJ, K (including K-L), NY, S, UPRRP, and W. Xerocopies or scanned images of material of the following herbaria was included, too: B-W (IDC-copies), GH (AMES), M, S.

#### *Collection of plant material*

Plants were dried in a portable press in the field. To preserve the details of the delicate and fragile generative organs, part of the material was conserved in spirit.

As far as possible, each voucher was completed by information on

1. plant characteristics in vivo (colours, scents, growing habit, inflorescence and flower posture, flower characteristics);
2. population characteristics (number of individuals, ~ flowering individuals);
3. the locality (geographic position with GPS data), altitude, elevation above ground in the case of epiphytic populations (higher levels of trees etc. were examined by

eye and binoculars), cardinal point of the growing site on bark or rock, geological and edaphic characteristics;

4. bio-ecological data (phorophytes, accompanying flora, vegetation type, observations of potential pollinators).

Mature flowers for palynological studies were separately dried in paper envelopes.

Slide images were taken of the natural environment and the collected plants.

Samples for molecular analyses were taken from fruits as well as from young and mature leaves. They were externally cleaned with ethanol (70%), cut into pieces to facilitate dehydration and stored in perforated paper envelopes in silica gel. In the first run (1998) desiccated material was stored only at (subtropical) room temperature. Later, material was maintained under cool conditions as soon as the pieces were dry. Even small intervals of time (from one month on!) under subtropical conditions led to severe deterioration concerning quality and amount of extractable DNA.

## **2.2 Methods**

### *Descriptions and drawings*

Descriptions were made including all material examined. Since the majority of the species could be collected in flowering condition, flower sections were carried out based mostly on personal spirit collections of the author. In most cases type material was not dissected, for many of the unique historical collections by Jacquin, Wright or Schlechter, are poor in generative material. Dry herbarium material was rehydrated in boiling water. Spirit material was dissected without further preparation. Pencil drawings were later copied with ink and scanned at high resolution. Scanned images were then arranged in position and size and provided with scales. All drawings are done by the author.

### *Reproductive biology*

Phenological information was gathered from observations in the field and from herbarium material.

### *Ecological and phytogeographical patterns*

**General phytogeography** – Data of distribution was collected from herbarium sheets in the herbaria mentioned above and was completed by information from the following sources: Ackerman 1995, 1997; Adams 1971, 1972, & pers. comm.; Ames & Correll 1952; Carnevali & al. 2001; Correll 1965; Dix & Dix 2000; Dietrich s. p. 10; Dod 1974, 1984b, 1986b, 1989b; Foldats 1970; Dressler 1993b; Garay & Sweet 1974; Gloudon & Tobisch

1995; Hamer 2001; Luer 1975a, 1975b, 1990, 1998b, 1998c, 1999a, 1999b, 2000; MacLeish & al. 1995; Nir 2000; Stehlé 1939; Williams 1951; Williams & Allen 1946; Williams & al. 1980. Additional information from the NYBG West Indian *Orchidaceae* Specimens database (<http://www.nybg.org/bsci/hcol/wior/orchidchecklist.html>) and the MBG W3TROPICOS database (<http://mobot.mobot.org/W3T/Search/vast.html>) was taken into consideration.

This analysis is aimed at the comparison of the Greater Antilles islands with adjacent Lesser Antilles and continental areas. It includes all species of *Pleurothallis* found in the Greater Antilles. Variables are: West Cuba, Central Cuba, East Cuba, Jamaica, Hispaniola, Puerto Rico, Lesser Antilles, Central America, and South America.

**Vertical distribution** – Data of the vertical distribution of Cuban *Pleurothallis* species was gathered from personal observations and herbarium material. Occurrence of taxa was recorded in altitudinal belts of 100 m. Gaps within the vertical distribution were interpolated, which did not alter the graph qualitatively.

**Geology** – The distribution of the Cuban species of *Pleurothallis* in vegetation on three distinct types of rock (limestone, magmatic or volcanic rock, serpentine) was analysed. Petrologic (type of rock) data was obtained from personal observations and information on herbarium sheets. These facts were compared with Borhidi (1996), Samek (1973). Serpentine, though representing only one of the ultrabasic rock types is used in the broader sense of the latter hereafter. In the case of volcanic rock, the data may comprise actually a variety of types, which could not be differentiated. In fact, this category is more a negative circumscription: in no case it does contain stands, neither on ultrabasic rock nor on limestone. These stands are limited to the Sierra Maestra chain.

**Vegetation types** – Data concerning vegetation types are based on personal observations and information on herbarium sheets. These were compared with Samek (1973), Borhidi (1996), and Capote & Berazaín (1984). Assigning epiphytes to the vegetation types suggested by these authors turned out to be problematic occasionally. First, herbarium data is very scarce. *Pleurothallis* is distributed almost exclusively in colline to montane areas, where vertically and horizontally interlocked vegetation types can change within a few meters. Information from herbarium sheets, apart from their second hand character, are often too general. Second, classification of vegetation types may differ substantially between authors. Three problems occurred: 1) types were partially incomparable because of inconsistent methods used by the authors and due to inaccurate descriptions, 2) there were cases of general misapplication of terms, and 3) some types turned out to be useless in classifying epiphytes (*Pleurothallidinae*). The latter was detected only in the course of the present study and will be discussed in detail later.

In the present study vegetation types sensu (Borhidi 1996) were used, however, with

some changes. Considering the differences that exist in the usage of even such common terms as “elfin” and “montane” (Capote & Berazaín 1984; Borhidi 1996) it seems reasonable to define the terms used in this study.

- **Elfin vegetation** – dwarf forests, thickets and shrubwoods with cloud forest appearance (rich in different kinds of epiphytes; branches, stems and rocks covered by mosses and lichens). Found on isolated peaks and crests: Pan de Guajaibón; Sierra del Escambray: Pico Potrerillo, Lomas de Banao; Pico Cristal; Pico Galán; Turquino Massif: N-slopes, crests, and summits; summit of Loma del Gato; Gran Piedra. Includes rocky habitats (epilithic life forms).
- **Montane rainforests** – sensu Borhidi (1996) p.p. (includes some stands of Borhidi’s montane karstic forests). Sierra del Escambray (Pico Potrerillo, San Juan?), Sierra Maestra, Sierra del Purial.
- **Montane rainforests on serpentine** - sensu Borhidi (1996) p.p. (includes Borhidi’s submontane rainforests on serpentine in the Moa-Toa-Duaba area). Sierra de Nipe (lower W slope, EILM), Sierra del Cristal (N-E-slope, lower W-slope), Moa, Toa, Duaba.
- **Submontane seasonal rainforests** – sensu Borhidi (1996) p.p. This includes the humid karstic forests of Oriente, which may be debatable. Therefore, the mogote complex is added further down as a separate unit. Vegetation of the mogotes in Oriente (Sierra de Nipe belt, N of Sierra Maestra, Yunque de Baracoa); vegetation in mesoclimatic niches in Pinar del Río and (hoyos and below shaded slopes), Sierra Maestra between 200-800 m.
- **Semi-deciduous mesophytic forests** – sensu Borhidi (1996). Mogotes (surrounding forests).
- **Dry (microphilous) evergreen forests** – sensu Borhidi (1996). Coast of Guanahacabibes peninsula.
- **Dry (thorny) lowland serpentine shrubwoods (cuabal)** – sensu Borhidi (1996). Cajalbana, Canasí.
- **Semi-dry (semi-thorny) serpentine shrubwoods (charrascal)** – sensu Borhidi (1996) p.p. (comprises Borhidi’s semi-dry lowland and montane shrubwoods). East Cuba: lowlands and hills N of Sagua-Baracoa; summit and SE+N-slope of La Mensura; S-slope of Sierra del Cristal 700-1000 m; Toldo massif; Alto de la Iberia.
- **Karstic forests** – although this is a mosaic of interlocked forest types already included in this list, I think it is important to include this traditional Cuban vegetation complex as a separate unit. It comprises the mogote systems of West, Central and East Cuba.

- **Xerothermic *Pinus cubensis* forests on serpentine** – sensu Borhidi (1996). East Cuba: serpentine areas of northern and eastern Oriente.
- **Pine forests on limestone** – sensu Borhidi (1996). Occurs only on the edge of pine forests on serpentine in Monte Cristi Borhidi (1996)
- **Montane pine forests** – sensu Borhidi (1996): isolated patches in the Turquino region and Gran Piedra.
- **Gallery forests and shrubwoods** – the term (hereafter as gallery forests) comprises colline, submontane and montane river banks and creeks. It should be stressed that headwaters are included.
- **Secondary forests** – the term appears only in the Spanish summary of Borhidi (1996). In the present study it refers to secondary mogote vegetation (stands of former seasonal evergreen forests) and cupeyales in the Sierra de Nipe (originally montane rainforests on serpentine).
- **Secondary thickets** – refers to a *Gleichenia*(?) – *Dicranopteris* – treefern shrubwood (Borhidi 1996: matorrales seminaturales) on the summits of Los Calderos (Sierra de Imías).
- **Cultivations** – coffee plantations are the only cultivations where species of *Pleurothallis* have been found so far.

#### *Computing and representation of the data in diagrams*

*Dendrograms* – Data was set up in matrices in which species were coded as present (1) or absent (0). Species represented by single collections (*Pleurothallis appendiculata*, *P. ghiesbreghtiana*, *P. aristata*) or questionable classification (*P. murex* was described from sterile material) are not included in the matrices that were used to show correlations. To assess and show groupings of variables, Maximum Parsimony (MP) analyses were conducted. Dendrograms were initially rooted with a hypothetical outgroup with all species coded absent (Lundberg rooting), which was abandoned in a second run (see p. 80). Computation was carried out with the PHYLIP package (Felsenstein, J. 1989: PHYLIP (Phylogeny Inference Package) version 3.5c). This algorithm follows largely PAE (parsimony analysis of endemism) introduced by Rosen & Smith (1988). See Trejo-Torres & Ackerman (2001) for a detailed discussion of this method.

*3-dimensional diagrams* – Most ecological variables, e.g. types of rock, vegetation, and vertical amplitude, were examined as to their correlation with overall horizontal distribution of the taxa. Although the same data was statistically evaluated, too, 3-dimensional diagrams were chosen for presentation, because of the intriguing and lucid way they convey information. In order to present the diagram in a clearly arranged manner, species

were classified according to their occurrence in  $n$  locations (i.e. frequency) in the Caribbean (6 locations: West Cuba, Central Cuba, East Cuba, Jamaica, Hispaniola, Puerto Rico) and adjacent areas (GA-SA: Lesser Antilles, Central America, South America). The latter, because of its vast area, does not represent a 7<sup>th</sup> location. Thus, species of distribution outside the Greater Antilles, may or may not be present in all 6 inner Antillean localities. Again, in order to avoid overloading the diagrams, ecological amplitudes were classified, too, usually in three units representing the growing amplitude. Hence, horizontal distribution is growing on the x-axis from left to right and the ecological amplitude from the foreground towards the background (see Fig. 56 e.g.).

*Statistics (correlation)* – As just mentioned, an association between horizontal distribution and the ecological amplitude was examined. Species were grouped according to the number of areas they occur in (see previous paragraph for a definition). All correlations were performed with the SPSS 10.0 package,  $r_s$  represents the Spearman's rank correlation coefficient (Sokal & Rohlf 1995),  $N$  the number of species,  $P$  is the significance value. The significance criterion for all tests was set at  $\alpha=0.05$ , therefore  $P$ -values smaller than  $P=0.05$  are considered as significant.

### *Palynology*

The material included in the study of pollen morphology comprises ~100 samples of 72 pleurothallid and 2 other orchidaceous species (Tab. 2). The latter were used in the molecular study by (Pridgeon & al. 2001) as outgroup taxa. All but three Cuban species (*Pleurothallis caymanensis*, *P. oricola*, *P. nummularia*) currently treated as *Pleurothallis* could be included. With the exception of *Brachionidium parvum* and *Pleurothallis aristata*, from Puerto Rico, all Cuban taxa were represented by one local voucher at least. The Cuban endemic *Pleurothallis grisebachiana*, a widespread species variable in size and flower coloration, is represented by 10 samples from 9 different localities (Fig. 45), to test the degree of variation in pollen morphology. The same applies to *Pleurothallis mucronata* (Fig. 46) and *P. ekmanii* (Fig. 47) three Cuban localities each), *P. ghiesbreghtiana* (three samples from Central America, and one each from Cuba, Jamaica and Puerto Rico) and *Pleurothallis ruscifolia* (Jacq.) R. Br. (5 samples). The only subgenus of *Pleurothallis* that is endemic in the Antilles (~10 species, Luer 2000), subg. *Antilla* Luer, is represented by 7 species with 3 being restricted to Cuba.

Antillean material from closely related genera (*Brachionidium*, *Lepanthes*, *Lepanthopsis*, *Platystele*, *Stelis*, *Trichosalpinx*, *Zootrophion*) as well as from presumed sister or outgroup taxa in previous cladistic studies of *Pleurothallidinae*, *Arpophyllum* (Neyland & al. 1995, Pridgeon & al. 2001) and *Dilomilis* (Pridgeon & al. 2001) was included for comparative purposes.

All dry specimens were rehydrated for 1-5 min in hot water. All spirit material (Stenzel 482, Stenzel 765, Stenzel 1298) was dissected directly. Pollinia were removed, mounted on double tape and dried at room temperature. Pollinia were finally gold sputtered 100 s at 30 mA and a distance of 6 cm from the electrode.

Pollinia were examined with a JEOL SM 6300 SEM at the Palynological Laboratory of the Natural History Museum Stockholm and at the Museum of Natural History Berlin. Working data is as follows: Acceleration voltage 15 kV, probe current  $3 \times 10^{-11}$  A, distance 8-12 mm. Since the upper half of the pollinium tends to be more stable (Schill & Pfeiffer 1977) and generally free of elastoviscin (Stenzel 2000), data of this area was used for comparison. Caudicular regions were documented as well. If not indicated otherwise, photos show the entire pollinarium and details on the side of the upper pollinium which faces the tapetum. Pollen terminology, if adequate, was applied according to Punt & al. (1994). For description of additional terms see glossary (p. 172).

Tab. 2: Plant material used for palynological studies (species present in Cuba in bold type).

\* – CR = Costa Rica, CU = Cuba, DR = Dominican Republic, EC = Ecuador, HA = Haiti, JA = Jamaica, NI = Nicaragua, PR = Puerto Rico, SU = Surinam, VE = Venezuela. \*\* – Gr = Prov. Granma, Gu = Prov. Guantánamo, Ho = Prov. Holguín, PR = Prov. Pinar del Río, SC = Prov. Santiago de Cuba, SS = Prov. Santi Spíritus.

Species	Voucher	Country* & Locality**
<i>Arpophyllum giganteum</i> Hartw. ex Lindl.	Hort. Kew. (1932-18801)	? ?
<b><i>Brachionidium parvum</i> Cogn.</b>	Stenzel 1005	PR Carribean Nat. Forest, Pico de Este, W slope
<b><i>Dilomilis elata</i> (Benth. &amp; Hook.) Summerhayes</b>	Stenzel 765	CU Ho: Sierra del Cristal, S slope, near summit
<b><i>Lepanthes diaziae</i> Luer</b>	Stenzel 480	CU Ho: Sierra de Nipe, Cayo Las Mujeres, W slope
<b><i>Lepanthes dorsalis</i> Schltr.</b>	Stenzel 481	CU Ho: Sierra de Nipe, Arroyo Woodfred, S bank
<b><i>Lepanthes dressleri</i> Hesp.</b>	Stenzel 410	CU PdR: mogotes E of Río Taco Taco, S of El Rangel
<b><i>Lepanthes fulva</i> Lindl.</b>	Stenzel 624	CU Gr: Sierra Maestra, Bayamo, Victorino, El Gigante, summit
<b><i>Lepanthes melanocaulon</i> Schltr.</b>	Stenzel 457	CU Ho: Sierra de Nipe, Cayo Las Mujeres (Alto de la Torre)
<b><i>Lepanthes obliquilobia</i> Hesp.</b>	Stenzel 401	CU PdR: Sierra del Rosario, Mogote Peña Blanca
<b><i>Lepanthes silvae</i> Dietrich</b>	Stenzel 561	CU Ho: Sierra de Moa, Meseta del Toldo, along headwaters of Río Piloto
<b><i>Lepanthes trichodactyla</i> Lindl.</b>	Stenzel 72	CU Gr: Sierra Maestra, Turquino Massif, below La Aguada de Joaquín
<b><i>Lepanthes trichodactyla</i> Lindl.</b>	Stenzel 447	CU Ho: Sierra de Nipe, La Mensura, north slope
<b><i>Lepanthes turquinoensis</i> Schltr.</b>	Stenzel 76	CU Gr: Sierra Maestra, Turquino Massif, below La Aguada de Joaquín
<b><i>Lepanthopsis microlepanthes</i> (Griseb.) Ames</b>	Stenzel 664	CU SC: Sierra Maestra, Santiago de Cuba, La Gran Piedra
<b><i>Lepanthopsis pygmaea</i> C. Schweinf.</b>	Stenzel 632	CU SC: Sierra Maestra, Bayamo, Victorino, El Gigante, summit
<b><i>Platystele hyalina</i> H. Stenzel</b>	Stenzel 569	CU Ho: Sierra de Moa, Meseta del Toldo, NE of abandoned miner's camp El Piloto, along creek
<b><i>Platystele ovalifolia</i> (Focke) Garay &amp; Dunsterv.</b>	Stenzel 860	CU Gu: Yateras, N ridge of Pico Galán
<b><i>Pleurothallis alpestris</i> (Sw.) Lindl.</b>	Stenzel 959	JA John Crow Mountains, Cuna Cuna Pass
<b><i>Pleurothallis appendiculata</i> Cogn.</b>	PFC 63808 ex HAJB	CU Gr: Sierra Maestra, Buey Arriba, near Barrio Nuevo
<b><i>Pleurothallis aristata</i> Hooker</b>	Stenzel 1000	PR Río Grande, Río Sonadora, 1,5 km upstream from Rd. 186
<b><i>Pleurothallis aristata</i> Hooker</b>	Luer & Luer 12227	SU Montagne de Kaw
<b><i>Pleurothallis bissei</i> Luer</b>	Stenzel 482	CU Ho: Sierra de Nipe, Woodfred, along N bank of creek
<b><i>Pleurothallis brighamii</i> S. Wats.</b>	Stenzel 473	CU Ho: Sierra de Nipe, behind EIIM station and Sabina trail
<b><i>Pleurothallis brighamii</i> S. Wats.</b>	Stenzel 505	CU Ho: Sierra del Cristal, lower Río Levisa, gallery forest
<b><i>Pleurothallis caymanensis</i> C.D.Adams</b>	Stenzel 1209	CU PR: Guanahacabibes, Barra de la Sorda, E from lighthouse Roncali
<b><i>Pleurothallis claudii</i> D.D.Dod</b>	Dod 527 ex NY09199	DR S side of the road Hondo Valle, towards Sierra de Neiba, km 204, km 190, 1300m
<b><i>Pleurothallis cordatifolia</i> Dod</b>	Stenzel 192	DR Sierra de Bahoruco, near border with Haiti, above military base El Aguacate
<b><i>Pleurothallis corniculata</i> (Sw.) Lindl.</b>	Stenzel 472	CU Ho: Sierra de Nipe, behind EIIM station and Sabina trail

<b><i>Pleurothallis corniculata</i> (Sw.) Lindl.</b>	Stenzel 477	CU	Ho: Sierra de Nipe, base of Salto de Guayabo, N bank
<i>Pleurothallis curtisii</i> D.D.Dod	ex NY 60792		
<i>Pleurothallis delicatula</i> Lindl.	Stenzel 958	JA	John Crow Mountains, Cuna Cuna Pass
<b><i>Pleurothallis denticulata</i> Cogn.</b>	Stenzel 644	CU	SC: Sierra Maestra, Turquino massif, ascent to La Aguada de Joaquín, above Loma del León
<b><i>Pleurothallis denticulata</i> Cogn.</b>	Wright "bbbb" ex W 42704	CU	"Oriente, prope Monte Verde"
<b><i>Pleurothallis domingensis</i> Cogn.</b>	Stenzel 662	CU	SC: Sierra Maestra, Macizo del Turquino, Pico Real
<b><i>Pleurothallis domingensis</i> Cogn.</b>	Lippold s.n. ex JE 16133	CU	Gr: S. Maestra, Pico Bayamesa, N slope
<b><i>Pleurothallis domingensis</i> Cogn.</b>	Stenzel 197	DR	Sierra de Neiba, summit of ridge
<b><i>Pleurothallis domingensis</i> Cogn.</b>	Tuerckheim 3331 ex NY 60844	DR	Constanza
<b><i>Pleurothallis domingensis</i> Cogn.</b>	Alain 18269 ex NY 60836	DR	Constanza, Alto Casabito
<b><i>Pleurothallis ekmanii</i> Schltr.</b>	Stenzel 517	CU	Ho: Sierra del Cristal, south side of Pico Cristal, upper Río Levisa, epiphytic in dwarf gallery forest
<b><i>Pleurothallis ekmanii</i> Schltr.</b>	Stenzel 762	CU	Ho: Sierra del Cristal, south side of Pico Cristal, trail to the peak, elfin thicket, on rocks
<b><i>Pleurothallis ekmanii</i> Schltr.</b>	Stenzel 573	CU	Ho: Sierra de Moa, Meseta del Toldo, epiphytic dwarf gallery forest along headwaters of Río Piloto
<b><i>Pleurothallis excentrica</i> (Luer) Luer</b>	Stenzel 466	CU	Ho: Sierra de Nipe, La Mensura, north slope, broadleaf forest
<b><i>Pleurothallis 'flabelliformis'</i> H. Stenzel</b>	Stenzel 507	CU	Ho: Sierra del Cristal, lower Río Levisa, gallery forest
<i>Pleurothallis formondii</i> D.D.Dod	ex NY 9205		
<b><i>Pleurothallis gelida</i> Lindl.</b>	P. Herrera ex HAC 3356	CU	SC: La Gran Piedra
<b><i>Pleurothallis gelida</i> Lindl.</b>	Endres ex K	CR	?
<b><i>Pleurothallis gemina</i> H. Stenzel</b>	Stenzel 464	CU	Ho: Sierra de Nipe, La Mensura, north slope
<b><i>Pleurothallis ghiesbreghtiana</i> A. Rich. &amp; Galeotti</b>	Hort. Kew. (1999-2869)	EC	?
<b><i>Pleurothallis ghiesbreghtiana</i> A. Rich. &amp; Galeotti</b>	Hort. Kew. (1968-22804)	NI	?
<b><i>Pleurothallis ghiesbreghtiana</i> A. Rich. &amp; Galeotti</b>	S.A. Marshall & D. A. Neill 6685 ex B	NI	Chontales
<b><i>Pleurothallis ghiesbreghtiana</i> A. Rich. &amp; Galeotti</b>	Stenzel 1298	CU	PR: Pan de Guajaibón, summit area
<b><i>Pleurothallis ghiesbreghtiana</i> A. Rich. &amp; Galeotti</b>	Stenzel 967	PR	Maricao, Maricao Forest Reserve, Monte de Estado, Rt. 120, km 16.85
<b><i>Pleurothallis ghiesbreghtiana</i> A. Rich. &amp; Galeotti</b>	"Hort. Lodd. s.n., 1824" ex K	JA	?
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 489	CU	Ho: Sierra de Nipe, headwaters of Río Piloto, gallery forest, serpentine
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 496	CU	Ho: Sierra de Moa, Jaguaní Reserve, Arroyo Prieto, serpentine?
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 504, 538	CU	Ho: Sierra del Cristal, lower Río Levisa, gallery forest, serpentine
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 600	CU	Ho: Sierra de Moa, Toldo Massif, road to Moa, gallery forest, serpentine
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 605	CU	SS: Sierra de Escambray, Pico de Potrerillo, summit, limestone
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 612	CU	SS: Sierra de Escambray, Cascada de Vegas Grandes, limestone
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 619	CU	Gr: Sierra Maestra, Victorino, mogote at road, limestone
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 865	CU	Gu: Yateras, Pico Galán, N slope, gallery forest, serpentine
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	Stenzel 882	CU	Gu: Sierra de Imías, La Yamagua, charrascal along creek, serpentine
<i>Pleurothallis grobyi</i> Batem. ex Lindl.	G. Vargas & al. 1543	CR	Puntarenas, Cantón de Osa
<i>Pleurothallis haitiensis</i> D.D.Dod	ex NY 9207	HA	
<b><i>Pleurothallis helenae</i> Fawc. &amp; Rendle</b>	Stenzel 637	CU	Gr: Sierra Maestra, Victorino, El Gigante, summit
<i>Pleurothallis hirsutula</i> Fawc. & Rendle	C. Whitefoord 1394 ex BM 82345	JA	Trelawny, on damp rock outside Windside Cave
<i>Pleurothallis lanceola</i> (Sw.) Lindl.	Maxon 9536 ex NY 59959	JA	St. Thomas, Maccasucker Bump
<i>Pleurothallis laxa</i> (Sw.) Lindl.	Morris s.n. ex K	JA	Blue Mountains
<b><i>Pleurothallis llamachoi</i> Luer</b>	Stenzel 583	CU	Ho: Sierra de Moa, Meseta del Toldo, road to Moa, gallery forest at creek
<b><i>Pleurothallis longilabris</i> Lindl.</b>	Stenzel 895	CU	Gu: Sierra de Imías, La Yamagua, centre of valley above creek
<i>Pleurothallis miguelii</i> Schltr.	ex NY 59972		
<i>Pleurothallis mitchellii</i> D.D.Dod	ex NY 9209		



<i>Pleurothallis mucronata</i> Lindl. ex. Cogn.	Stenzel 478	CU	Ho: Sierra de Nipe, Cayo Las Mujeres, W slope, broadleaved dwarf forest
<i>Pleurothallis mucronata</i> Lindl. ex. Cogn.	Stenzel 520	CU	Ho: Sierra del Cristal, S slope, along upper Río Levisa
<i>Pleurothallis mucronata</i> Lindl. ex. Cogn.	Stenzel 560	CU	Ho: Sierra de Moa, Meseta del Toldo, along headwaters of Río Piloto
<i>Pleurothallis murex</i> Rchb. f.	Martinez-Falcon s.n. ex HAC 41200	CU	SS: Yaguajay, Lomas de Canoa
<i>Pleurothallis obliquipetala</i> Acuña & C. Schweinf.	Stenzel 653	CU	Gr: Sierra Maestra, Turquino Massif, below La Aguada de Joaquín
<i>Pleurothallis obovata</i> (Lindl.) Lindl.	Stenzel 692	CU	?
<i>Pleurothallis odontotepala</i> Rchb. f.	Stenzel 67	CU	Gr: Sierra Maestra, Turquino Massif, Alto de Naranjo (Pico Mella)
<i>Pleurothallis oricola</i> H.Stenzel	Stenzel 1210	CU	PR: Guanahacabibes, trail from María la Gorda to Cabo Corrientes
<i>Pleurothallis papulifolia</i> Luer	Stenzel 483	CU	Ho: Sierra de Nipe, Woodfred, along N side of creek
<i>Pleurothallis prostrata</i> Lindl.	Stenzel 581	CU	Ho: Sierra de Moa, Meseta del Toldo, unpaved road to Moa, gallery forest along a dry creek
<i>Pleurothallis pruinosa</i> Lindl.	Splitgerber 527	SU	?
<i>Pleurothallis pruinosa</i> Lindl.	Herrera 6330 ex K	CR	Alajuela, Bijagua
<i>Pleurothallis pubescens</i> Lindl.	Ackerman 2041 ex UPRRP 6289	PR	Mun. Utuado, Cerro Morales
<i>Pleurothallis quisqueana</i> D.D.Dod	Alain 15483 ex NY 59544	DR	
<i>Pleurothallis quisqueana</i> D.D.Dod	ex NY 59709		
<i>Pleurothallis aff. racemiflora</i> (Sw.) Lindl.	Stenzel 888	CU	Gu: Sierra de Imías, La Yamagua, charrascal and gallery forest along creek on serpentine
<i>Pleurothallis racemiflora</i> (Sw.) Lindl.	Stenzel 643	CU	Gr: Sierra Maestra, Turquino Massif, below La Aguada de Joaquín, Rascaciolo
<i>Pleurothallis rubroviridis</i> Lindl.	Stenzel 880	CU	Gu: Sierra de Imías, Los Calderos, ridge E from the valley
<i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.	s.n.	?	Botanical Garden Munich
<i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.	C.K.Horich s.n. (Univ. Calif. B.G. Berkeley acc# 59.270-1) ex K	CR	Cerro Cedral
<i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.	ex NY 59721	?	
<i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.	ex NY 59720		
<i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.	ex NY 59783		
<i>Pleurothallis sertularioides</i> (Sw.) Spreng.	Stenzel 603	CU	SS: Sierra de Escambray, Pico de Potrerillo, summit
<i>Pleurothallis shaferi</i> Ames	Stenzel 453	CU	Ho: Sierra de Nipe, La Mensura, N slope
<i>Pleurothallis simpliciflora</i> D.D.Dod	ex NY 9215		
<i>Pleurothallis testaeifolia</i> (Sw.) Lindl.	Stenzel 75	CU	SS: Sierra Maestra, Turquino Massif, below La Aguada de Joaquín
<i>Pleurothallis tribuloides</i> (Sw.) Lindl.	Stenzel 634	CU	Gu: Sierra Maestra, Victorino, El Gigante, Barril forest at summit
<i>Pleurothallis trichophora</i> Lindl.	Wright 659 ex K-L	CU	E Cuba
<i>Pleurothallis trichyphus</i> Rchb. f.	Stenzel 620	CU	Gr: Sierra Maestra, Victorino, mogote at road
<i>Pleurothallis velaticaulis</i> Rchb. f.	Fendler 1472 ex K-L	VE	?
<i>Pleurothallis velaticaulis</i> Rchb. f.	L. Williams & A.H.G. Alston 300 ex BM 82425	VE	El Avila
<i>Pleurothallis wilsonii</i> Lindl.	Stenzel 845	CU	Gu: Palenque, Piedra La Vela, gallery forest along Arroyo Sonador
<i>Pleurothallis wrightii</i> Rchb. f.	Stenzel 442	CU	Ho: Sierra de Nipe, La Mensura, N slope
<i>Stelis pygmaea</i> Cogn.	Stenzel 669	CU	SC: Sierra Maestra, Santiago de Cuba, La Gran Piedra
<i>Trichosalpinx dura</i> (Lindl.) Luer	PFC #66454 ex HAJB	CU	SS: Sierra de Escambray, Pico de Potrerillo
<i>Zootrophion atropurpureum</i> (Lindl.) Luer	s.n.	?	living collection I. Bock, Naumburg
<i>Zootrophion atropurpureum</i> (Lindl.) Luer	Stenzel 811	CU	Gr: Sierra Maestra, Turquino Massif, between Loma de León and La Aguada de Joaquín

Plant material used in this study is listed in Tab. 3. All but 2 of the 39 *Pleurothallis* species (*Pleurothallis appendiculata*, *P. murex*) currently known to occur in Cuba could be included, i.e. the range is limited geographically. One of the 33 species successfully sampled could not be recollected in Cuba, i.e. material from other islands had to be employed (*Pleurothallis aristata* from Puerto Rico). Two species are represented by two accessions each. *P. trichophora* with material from East and Central Cuba which marks the phytogeographical limits of this plant, and *P. ghiesbreghtiana* with one voucher from West Cuba and the other from Puerto Rico.

Tab. 3: Plant materials used in molecular studies.

\* – CU = Cuba, HA = Haiti, PR = Puerto Rico. \*\* – Gr = Prov. Granma, Gu = Prov. Guantánamo, Ho = Prov. Holguín, PR = Prov. Pinar del Río, SC = Prov. Santiago de Cuba, SS – Prov. Sancti Spiritus.

Species	Voucher	Country* & Locality**
<i>Pleurothallis aristata</i> Hooker	Stenzel 996	PR Mun. Río Grande, El Yunque, trail from Caimitillos to Mt. Britton
<i>Pleurothallis bissei</i> Luer	Stenzel 730	CU Ho: Sierra de Nipe, Woodfred, along N bank of creek
<i>Pleurothallis brighamii</i> S. Wats.	Stenzel 740	CU Ho: Sierra de Nipe, behind EIM station and Sabina trail
<i>Pleurothallis corniculata</i> (Sw.) Lindl.	Stenzel 889	CU Gu: Sierra de Imías, La Yamagua
<i>Pleurothallis domingensis</i> Cogn.	Stenzel 662	CU SC: Sierra Maestra, Turquino Massif, Pico Real
<i>Pleurothallis ekmanii</i> Schltr.	Stenzel 762	CU Ho: Sierra del Cristal, S slope of Pico Cristal, trail to summit
<i>Pleurothallis excentrica</i> (Luer) Luer	Stenzel 752	CU Ho: Sierra del Cristal, S slope of Pico Cristal, along upper Río Levisa
<i>Pleurothallis flabelliformis</i> H. Stenzel	Stenzel 745	CU Ho: Sierra del Cristal, S slope of Pico Cristal, along upper Río Levisa
<i>Pleurothallis gemina</i> H. Stenzel	Stenzel 452	CU Ho: Sierra de Nipe, La Mensura, north slope
<i>Pleurothallis ghiesbreghtiana</i> A. Rich. & Galeotti	Stenzel 967	PR Maricao, Bo. Maricao Afuera, Maricao Forest Reserve
<i>Pleurothallis ghiesbreghtiana</i> A. Rich. & Galeotti	Stenzel 1298	CU PR: Pan de Guajabón, summit
<i>Pleurothallis grisebachiana</i> Cogn.	Stenzel 619	CU Gr: Sierra Maestra, Victorino, mogote at road
<i>Pleurothallis helenae</i> Fawc. & Rendle	Stenzel 766	CU Ho: Sierra del Cristal, Pico Cristal, elfin forest on peak
<i>Pleurothallis llamachoi</i> Luer	Stenzel 545	CU Ho: Sierra del Cristal, lower Río Levisa, gallery forest
<i>Pleurothallis longilabris</i> Lindl.	Stenzel 895	CU Gu: Sierra de Imías, La Yamagua, centre of valley above creek
<i>Pleurothallis mucronata</i> Lindl. ex. Cogn.	Stenzel 478	CU Ho: Sierra de Nipe, Cayo Las Mujeres, W slope
<i>Pleurothallis nummularia</i> Rchb. f.	Stenzel 896	CU Gu: Sierra de Imías, La Yamagua, centre of valley above creek
<i>Pleurothallis obliquipetala</i> Acuña & C. Schweinf.	Stenzel 789	CU Gr: Sierra Maestra, Turquino Massif, below La Aguada de Joaquín
<i>Pleurothallis obovata</i> (Lindl.) Lindl.	Stenzel 840	CU Gu: Palenque, Mogote de Buena Vista, along crest
<i>Pleurothallis odontotepala</i> Rchb. f.	Stenzel 784	CU Gu: Turquino Massif, trail from Alto de Naranjo to La Aguada de Joaquín
<i>Pleurothallis papulifolia</i> Luer	Stenzel 483	CU Ho: Sierra de Nipe, Woodfred, along N side of creek
<i>Pleurothallis prostrata</i> Lindl.	Stenzel 856	CU Gu: Yateras, W slope of Pico Galán
<i>Pleurothallis pruinosa</i> Lindl.	Stenzel 890	CU Gu: Sierra de Imías, La Yamagua, Monte Oscuro
<i>Pleurothallis racemiflora</i> (Sw.) Lindl.	Stenzel 783	CU Gr: Sierra Maestra, Turquino Massif, below La Aguada de Joaquín
<i>Pleurothallis rubroviridis</i> Lindl.	Stenzel 893	CU Gu: Guantánamo, Sierra de Imías, La Yamagua
<i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.	Stenzel 635	CU Gr: Sierra Maestra, Bayamo, Victorino, peak of El Gigante
<i>Pleurothallis sertularioides</i> (Sw.) Spreng.	Stenzel 843	CU Gu: Palenque, Mogote de Buena Vista, along crest
<i>Pleurothallis shaferi</i> Ames	Stenzel 453	CU Ho: Sierra de Nipe, La Mensura, N slope
<i>Pleurothallis testaeifolia</i> (Sw.) Lindl.	Stenzel 656	CU SS: Sierra Maestra, Turquino Massif, below La Aguada de Joaquín
<i>Pleurothallis tribuloides</i> (Sw.) Lindl.	Stenzel 634	CU Gu: Sierra Maestra, Victorino, El Gigante
<i>Pleurothallis trichophora</i> Lindl.	Stenzel 606	CU SS: Trinidad, Pico Potrerillo
<i>Pleurothallis trichophora</i> Lindl.	Stenzel 630	CU Gu: Sierra Maestra, Victorino, El Gigante
<i>Pleurothallis trichyphus</i> Rchb. f.	Stenzel 620	CU Gr: Sierra Maestra, Victorino, mogote at road
<i>Pleurothallis wilsonii</i> Lindl.	Stenzel 621	CU Gr: Sierra Maestra, Victorino, mogote at road
<i>Pleurothallis wrightii</i> Rchb. f.	Stenzel 733	CU Ho: Sierra de Nipe, Cayo Las Mujeres, W slope

*Material* – Since it was not possible to extract DNA from existing herbarium collections, material for molecular investigations had to be collected in the wild. Outside ITS sequences for outgroup comparison were kindly provided by Dr. A. M. Pridgeon. They were originally published by Pridgeon & al. (2001) and will be cited hereafter, if necessary, under the GenBank accession number.

*DNA extraction* – DNA was extracted at Friedrich-Schiller-University in Jena from 0.01-0.5g of dried leaves or fruits, following a modified 2%-CTAB (hexadecyltrimethylammoniumbromide) procedure of Doyle & Doyle (1987) and Hellwig & al. (1999). DNA was purified using Qiagen tip-20 columns (Qiagen Inc., Hilden, Germany) following the manufacturer's protocols. Purified DNA extracts are stored in HUB.

*Amplification* – All PCRs were run using Taq DNA Polymerase Kit from Qiagen (Qiagen Inc.). Initially, Baldwin's (1992) primers P1 (=ITS5" sensu Baldwin), P2 (=ITS2"), P3 (=ITS3"), P4 (=ITS4") were employed. They yielded two fragments. One was the result of primers P1 (5'-GGA AGT AAA AGT CGT AAC AAG G-3') and P2 (5'-CTC GAT GGA ACA CGG GAT TCT GC-3'). It covered ITS1 and 2/3 of 5.8S gene with a total length of ~380 bp. The other fragment of ~440 bp included 2/3 of the 5.8S gene and ITS2. It was the product of primers P3 (5'-GCA TCG ATG AAG AAC GCA GC-3') and P4 (5'-TCCTCCGCTTATTGATATGC-3'). Both fragments are overlapping in the 5.8S region, so by combining the two, the complete ITS1-5.8S-ITS2 (hereafter ITS) sequence could be achieved.

Tab. 4: *Pleurothallis gemina*: 17SE (p.p.), ITS1, 5,8S, ITS2, and 26SE (p.p.) sequences. Noncoding (ITS) regions in lower case, primer target regions underlined, primer pair P1/P2 in red, primer pair P3/P4 in blue, amplification direction of primers indicated by „<“ and „>“. Base mismatches in primers in bold type.

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T**GGAAGTAAAAGTCGTAACAAGG**>TTTCCGTAGGTGAACCTGCGGAAGGATCATTGtcgagaccg  
aatatatcgagcgattcgagaaacctgtgaatgaatgagcggcgccatcgctcgcgcaaatgccgcctccatcgccggcctgtttaa  
gcgccgtcgatgagaggcgatgaaaactcaaaccggcgagctgcgcgccaaggaaatacaatacacgatcctgtattgggttc  
ggtggcgtggagtgcagtcgcacaccacacggataAAAACGACTCTCGGCAATGGATATCTCGGCTCTC**CGAT**  
**CGATGAAGAGCGCAGC**>GAAATGCGATACGTGGTGCGAATT<**GCAGAATCCCGCGAACCATC**  
**GAG**AATTTGAACGCAAGTTGCGCCCGAGGCCAGCCGGCCAAGGGCACGTCCGCCTGGGCGT  
CAAGCgttacgtcgctccgtgccagctccatgccaccgacgggtgtgtatggggaggggtcgatgtgcagagtggctcgtcgtgcc  
gcgggcgtggcgggctaagatcgggatcgctcgtgtgccacgaacgataaggggtgatgaaaattgtcctgtgtgtatcgtggcga  
cgtgagaagagattgtaccagcagatgatccaatctaagcgtcgtccacagacgtcggttggaatGCGACCCAGGATG  
GGCGAGGCCACCCGCTGAGTTTAA<**GCATATCAATAAGCGGAGGAAA**GAACTTACAAG

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Tab. 4 illustrates the position of each primer within the nrDNA region of interest. Baldwin's primers gave ad hoc excellent results in ITS1 (P1-P2) but less so in the case of ITS2 (P3-P4). Adjusting of the annealing temperature did not improve the quantity and quality of the products. Since the PCR with P1-P4 gave the same blurred PCR products as P3-P4, I

assumed that the P4 must include bases mismatching the 26SE target region. However, this cannot explain the notorious difficulty amplifying ITS2. Rather than base mismatches, secondary structures could explain those problems, for later usage of P4 in nested cycle sequencing with templates gained from non-P1-P4 PCR, showed no problems at all.

Sequence analyses revealed a three base mismatch in primer P2 compared with the actual 5.8S target region in all species examined, whereas primer P3 has one base mismatch (Tab. 4). Cycle sequencing functioned well despite these incongruities.

In those cases where PCR with Baldwin's primers failed, a second set of oligos was employed (Sun & al. 1994). Using the primers "17SE" (5'-ACG AAT TCA TGG TCC GGT GAA GTG TTC G-3') and "26SE" (5'-TAG AAT TCC CCG GTT CGC TCG CCG TTA C-3') PCR yielded a fragment of ~ 900 bp comprising ITS1, 5.8S gene, and ITS2 along with ends of the bordering coding regions. Since these oligos anneal further outwards from primers P1 and P4, P1-P4 could be used for nested cycle sequencing.

The amplification was conducted via the following thermal cycle profile: 150s95°C/ 28-34x [30s95°C/60s50-58°C/ 60s72°C]/ 300s72°C/ 4°C. PCR products were purified using the QiaQuick® PCR Purification Kit (Qiagen Inc.).

*Cycle sequencing* – Both strands of the amplified gene fragments were directly cycle sequenced in 10 µl volumes containing 2 µl of ABI Prism BigDye Terminator cycle sequencing reaction mix (ABI Biosystems), 0.5 µM primer, 2 µl dd H<sub>2</sub>O and 4 µl DNA. Sequencing products were purified following the ABI standard protocol adjusted to 10 µl reaction volume by addition of dd H<sub>2</sub>O. Sequences were obtained by running the sequencing products on an Perkin Elmer ABI 377 automated sequencer. The resulting sequence electropherograms of both strands were corrected manually for misreads and merged into one sequence file using BioEdit (version 5.0.9.; Hall 1999) for Windows 95, which was generally used to store and manage sequences.

*Alignment and phylogenetic analysis* – The question of homology is a crucial problem in inferring phylogenetic relationships from nucleotide sequence data (Doyle & Davis 1998), i.e. the insertion of gaps is one of the most critical steps in molecular analysis. To compare the influence of the extent of indels, sequences were initially aligned using CLUSTAL W (Thompson & al. 1994) employing different delay values and gap costs and then adjusted by eye (see appendix for sequences). Unambiguous indels that seem to be duplications of upstream sequences (e.g. ATAT → ATATAT) were coded as single events. From each matrix an additional set with ambiguous indel regions being excluded was drawn. A fifth matrix was created by stripping an aligned set of all columns containing gaps. Cladistic analysis was conducted with these 5 data sets using sequence AF262915 (*Dilomilis montana* (Sw.) Summerh.) from (Pridgeon & al. 2001) as outgroup.

Substitution patterns were analysed by comparing observed and expected substitutions

among all sequences. The number of expected substitutions was calculated from base frequencies. Substitution saturation was evaluated by plotting portions of transitions and transversion against distance.

Phylogenetic trees were built using parsimony algorithms (Maximum Parsimony – MP hereafter). Computation was accomplished with PAUP\* version 4.0b8 (Swofford 2000). The following settings were chosen: Fitch parsimony (Fitch 1971), heuristic search, gaps as fifth character, 100 replicates of random sequence addition, tree bisection-reconnection (TBR) branch swapping, MulTree.

Relative support of the topologies found was evaluated with 1000 bootstrap subsets of each of the 5 matrices.

Sequence editing and statistical analysis were performed using BioEdit and DAMBE (version 4.1.19; Xia & Xie 2001).

### *Taxonomy*

Although profoundly challenged by molecular data (Pridgeon, Solano & Chase 2001, Pridgeon & Chase 2001) the morphological concept of Luer (1986c) will be the basis of this work. The main reasons are

1. less than 60 % of the supraspecific taxa proposed by Luer and included in that molecular study were represented by the type species.
2. Pridgeon & Chase (2001) based their ~500 nomenclatural transfers on the sequences of 187 pleurothallid specimens. Those epithets not sequenced were transferred merely on the basis of Luer's morphological system. A great number of taxa of Luer's system, however, had been shown to be paraphyletic in the same molecular study.
3. 15 of the 39 Cuban species were transferred to other genera, however, only 3 species were effectively included in the molecular screening.

There are more reasons why to handle the new system with extreme care. In order not to anticipate the results of this work they will be discussed later (p. 113).

### *General rules*

Authority abbreviations follow those of Brummit & Powell (1992) and abbreviations of herbaria are in concordance with those of the Index Herbariorum (<http://www.nybg.org/bsci/ih/searchih.html>). Name of the Cuban provinces were abbreviated according to the rules of the FCP (Greuter & al. 2002): PR – Pinar del Río, SS – Santi Spíritus, Ci – Cienfuegos, Ho – Holguín, Gr – Gránma, SC – Santiago de Cuba, Gu – Guantánamo.

### **3 RESULTS**

#### **3.1 Morphology**

The Cuban species of *Pleurothallis* reflect the morphologically diverse conditions of the entire genus (Luer 1986b) to a great extent. Morphological descriptions along with figures and data on distribution and ecological preferences are presented in the following. They represent a literal translation of the Spanish manuscript submitted for the Flora de Cuba (Stenzel 2004a).

***Pleurothallis* R. Br.** in Aiton, Hortus Kew. ed. 2. 5: 211. 1813.

Type: *Pleurothallis ruscifolia* (Jacq.) R. Br. (*Epidendrum ruscifolium* Jacq.).

= *Cryptophoranthus* Barb. Rodr. Type: *Cryptophoranthus fenestratus* (Barb. Rodr.) Barb. Rodr. (*Pleurothallis fenestrata* Barb. Rodr.).

**Herbs**, epiphytic, lithophytic, or pseudoterrestrial. **Rhizome** very short or elongated. **Ramicauls** reduced or elongated, simple, superposed (not in Cuba) or branched (not in Cuba), terete to winged or channeled, erect to pendent, partially or entirely covered by scarious sheaths, glabrous or with trichomes, tubular or infundibuliform; with or without an annulus. **Leaves** usually thick, glabrous or variably papillose or tomentose; margin entire or variably papillose, crenate dentate or serrate. **Inflorescence** fasciculate or racemose, solitary to numerous, single to multi-flowered, (sub)terminal, erect or pendent, subtended at the base by a sheath or spathe more or less developed; peduncle very short or elongated with various bracts; anthesis successive, almost simultaneously. **Floral segments** membranous to thickened, glabrous or variably papillose, verrucate, or pubescent; margin entire, variably papillose, ciliate, or cut; apex acute to rounded, truncate to caudate, sometimes thickened or cucullate. **Sepals** free or variously connate. **Petals** usually shorter than the sepals, free. **Labellum** simple, 3- or 5-lobed, base in various forms hinged to the base or foot of the column. **Column** stout or slender, straight to arcuate, base often elongated into a foot; clinandrium winged, entire or variably incise. **Anther** apical to subapical; pollinia 2, 6 (not in Cuba) or 8. Stigma apical (not in Cuba) to ventral, entire to bilobed (not in Cuba). **Ovary** glabrous or variably verrucate, papillose or pubescent.

**Distribution:** The same as that of the subtribe. About 1200 species (C. A. Luer, personal communication); 39 in Cuba. Centre of diversity in the (sub)montane rainforests and cloud forests of Central and South America and the Greater Antilles.

**Reproduction biology:** The same as that of the subtribe. In Cuba there are at least 4 species showing autogamy.

#### Key to the species.

- |    |  |                        |
|----|--|------------------------|
| 1  | Ramicauls > 1,0 cm long .....  | 2                      |
| 1* | Ramicauls < 1,0 cm long .....  | 17                     |
| 2  | Sheaths of the ramicauls with purplish red scales .....                      | <i>P. bissei</i>       |
| 2* | Sheaths of the ramicauls glabrous .....                                      | 3                      |
| 3  | Ramicauls separated by > 0,5 cm .....  | 4                      |
| 3* | Ramicauls separated by < 0,4 cm .....  | 5                      |
| 4  | Ramicauls 2-3-articulated, leaves acute .....                                | <i>P. wilsonii</i>     |
| 4* | Ramicauls 4-5-articulated, leaves obtuse to rounded or emarginate .....      | <i>P. obovata</i>      |
| 5  | Inflorescence fasciculate, multi-flowered .....                              | <i>P. ruscifolia</i>   |
| 5* | Inflorescence racemose, 2- to multi-flowered .....                           | 6                      |
| 6  | Inflorescence axis shorter than ½ of the leaf .....                          | 7                      |
| 6* | Inflorescence axis longer than ½ of the leaf .....                           | 8                      |
| 7  | Ramicauls > 4,0 cm long, longer than leaves .....                            | <i>P. rubroviridis</i> |
| 7* | Ramicauls < 4,0 cm long, shorter than leaves .....                           | <i>P. odontotepala</i> |
| 8  | Plants > 10,0 cm long .....  | 9                      |
| 8* | Plants < 10,0 cm long .....  | 12                     |
| 9  | Inflorescence shorter than the leaf .....                                    | 10                     |
| 9* | Inflorescence longer than the leaf .....                                     | 11                     |
| 10 | Leaf < 3,5 cm wide, pedicel shorter or of the same length as the bract ..... | <i>P. domingensis</i>  |

- 10\* Leaf > 3,5 cm wide, pedicel longer than the bract ..... *P. gelida*
- 11 Leaf without longitudinal middle fold (involute vernation) ..... *P. ghiesbreghtiana*
- 11\* Leaf with longitudinal middle fold (plicate vernation) ..... *P. racemiflora*
- 12 Inflorescence axis shorter or of the same length as the leaf ..... *P. pruinosa*
- 12\* Inflorescence axis longer than the leaf ..... 13
- 13 Foliar proportions 3:2-1:1 (length:width), leaf profoundly denticulate or crenulate with crenae up to 1,0 mm long, sepals < 4,0 mm long ..... *P. murex*
- 13\* Foliar proportions 5:1-3:2, leaf at most denticulate or crenulate with crenae < 0,5 mm long, sepals > 5,0 mm long ..... 14
- 14 Uppermost sheath of the ramicaul reaching the base of the leaf (upper part of the ramicaul not visible) ..... 15
- 14\* Uppermost sheath of the ramicaul not reaching the base of the leaf (upper part of the ramicaul visible) ..... 16
- 15 Margin of the leaf entire; sepals > 11,0 mm long ..... *P. appendiculata*
- 15\* Margin of the leaf minutely serrate; sepals < 11,0 mm long ..... *P. prostrata*
- 16 Pedicel as long as the bract, fused with the axis up to the middle; ramicauls basally articulated; labellum basally biauriculate ..... *P. denticulata*
- 16\* Pedicel much longer than the bract, free; ramicauls basally and in the middle articulated; labellum basally without lobes ..... *P. trichophora*
- 17 Sheaths of the ramicauls purplish red hirsute ..... *P. nummularia*
- 17\* Sheaths of the ramicauls glabrous ..... 18
- 18 Ramicauls separated by > 1 mm (plants repent) ..... 19
- 18\* Ramicauls separated by < 1 mm (plants ± caespitose) ..... 24
- 19 Leaves > 0,5 cm wide ..... *P. testaeifolia*
- 19\* Leaves < 0,5 cm wide ..... 20
- 20 Ramicauls separated by > 2 mm (plants conspicuously repent); peduncle > 1 cm long ..... *P. sertularioides*
- 20\* Ramicauls separated by < 2 mm (plants indistinctly repent); peduncle < 0,5 cm long ..... 21
- 21 Leaves acuminate or mucronate ..... *P. oricola*
- 21\* Leaves obtuse or subacute ..... 22
- 22 Ramicauls reduced (inflorescence apparently basal); flowers thickened; outside of the sepals convex; 8 pollinia present ..... *P. excentrica*
- 22\* Ramicauls 1,0-2,5 mm long (terminal inflorescence); flowers membranous; outside of the sepals plane or concave; 2 pollinia present ..... 23
- 23 Inflorescence axis shorter than ½ of the leaf, several inflorescences (1-)2-3, single flowered; flowers purple ..... *P. wrightii*
- 23\* Inflorescence axis longer than ½ of the leaf, inflorescence solitary, 2-flowered; flowers whitish ..... *P. gemina*
- 24 Inflorescence axis at most as long as the leaf ..... 25
- 24\* Inflorescence axis longer than the leaf ..... 30
- 25 Pedicel shorter than the bract ..... 26
- 25\* Pedicel longer than the bract ..... 28
- 26 Ramicauls > 2 mm long (inflorescence emerging from the apex of the ramicaul); sepals verrucate; 2 pollinia ..... *P. tribuloides*
- 26\* Ramicauls < 2 mm long (inflorescence apparently emerging from the base of the ramicaul); sepals glabrous; 8 pollinia ..... 27
- 27 Leaves 0,2-0,4 cm wide, oblanceolate, flowers purplish ..... *P. excentrica*
- 27\* Leaves 0,7-1,5 cm wide, spatulate, flowers whitish and mottled with purple .....



.....	<i>P. 'flabelliformis'</i>	
28 Inflorescence axis longer than ½ of the leaf, inflorescence two-flowered, flowers whitish .....		
.....	<i>P. gemina</i>	
28* Inflorescence axis shorter than ½ of the leaf, flowers purple .....		29
29 Inflorescence solitary, two-flowered; tip of the sepals caudate, yellow .....		
.....	<i>P. obliquipetala</i>	
29* Inflorescences two or three, single flowered; tip of the sepals thickened, purple .....		
.....	<i>P. wrightii</i>	
30 Inflorescences single flowered (sometimes with an aborted bud) .....	<i>P. corniculata</i>	
30* Inflorescences with more than one flower (apparently one-flowered in species with successive anthesis!) .....		31
31 Inflorescence congested (axis not visible between flowers) .....		32
31* Inflorescence distantly flowered (axis visible between flowers) .....		33
32 Leaves < 1,5 cm long, apiculate or mucronate, margin entire .....	<i>P. trichyphiss</i>	
32* Leaves > 1,5 cm long, tridentate, margin minutely denticulate .....	<i>P. brighamii</i>	
33 At least some pedicels > 3 mm long .....		34
33* Pedicels generally < 3 mm long .....		37
34 Flowers cleistogamous .....	<i>P. helenae</i>	
34* Flowers with normal anthesis .....		35
35 Leaves up to 0,9 cm long, base short cuneate .....	<i>P. mucronata</i>	
35* Leaves 0,7-2,7 cm long, base elongated cuneate .....		36
36 Sepals < 5,0 mm long .....	<i>P. longilabris</i>	
36* Sepals > 6,0 mm long .....	<i>P. aristata</i>	
37 Leaves with distinct warts on the upper side, rounded or emarginate ...	<i>P. papulifolia</i>	
37* Leaves glabrous or at most rough, acute to obtuse .....		38
38 Ramicauls < 0,5 mm long or absent; column without foot; 8 pollinia present .....		
.....	<i>P. ekmanii</i>	
38* Ramicauls > 1,5 mm long; column with foot; 2 pollinia present .....		39
39 Leaves rigid, acuminate or apiculate, base short cuneate; inflorescence erect or ascending .....		
.....	<i>P. caymanensis</i>	
39* Leaves slightly thickened, but not rigid, obtuse, acute or mucronate, base elongated cuneate; inflorescence erect, ascending, pendent or prostrate on the substrate ....		40
40 Flowers 3(-4), simultaneous anthesis, whitish .....	<i>P. shaferi</i>	
40* Flowers 3-12, successive anthesis, yellowish or purple .....		41
41 Margin of the leaf denticulate, inflorescence pendent or repent on the substrate, flowers whitish with dense purple stripes, lateral sepals slightly caudate, connate up to the middle .....		
.....	<i>P. llamachoi</i>	
41* Margin entire, inflorescence freely pendent or ascending, flowers yellow with stripes of red, lateral sepals acute, connate almost up to the tip .....	<i>P. grisebachiana</i>	

***Pleurothallis appendiculata* Cogn.** in Urban, Symb. Antill. 7: 174. 1912. Holotype: "Santo Domingo [Dominican Republic], prope Constanza", 1400 m, IV-1910, Türrckheim 3233 ex herb. Cogniaux (BR No 843457!). – Fig. 3.

**Herbs**, caespitose, 3,5-7,5 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** ascending or pendent, distinctly surcate with margins passing into the margins of the leaf, 2-3,5 cm long, 3-articulated below the middle, entirely covered by three scarious sheaths, apically oblique and carinate; without an annulus. **Leaves** slightly

coriaceous, narrow ovate to elliptic, acute to subacuminate, 1,5-4 × 0,5-1,5 cm, green, glabrous; base cuneate to attenuate; margin entire. **Inflorescence** a terminal raceme, pendent, up to six per stem, with 2-6 flowers; subtended at the base by a narrow ovate sheath of 0,5 cm in length; peduncle 1-3,5 cm long, with two bracts; axis flexuosus, 0,5-4 cm long. **Pedicels** 2 mm long, fused up to the middle with the axis; bract membranous, oblique-infundibuliform, acute, carinate, often reddish, up to 0,4 cm long. **Flowers** resupinate?, anthesis successive. **Sepals** membranous, slightly thickened along the nerves, green-yellowish with purple stripes, carinate; **dorsal** sepal basally connate 1 mm with the lateral ones, narrow oblanceolate, acute, 3-veined, 1,3 × 0,2 cm; margin entire to slightly papillose; the **lateral** ones basally connate 4 mm but adnate almost up to the tip, the base forming a mentum with the ovary, synsepal (broadly) ovate, acute, bifid, 6-veined, 1,1-1,2 × 0,8-0,9 cm; margin entire or slightly papillose. **Petals** membranous, light reddish, subulate, slightly falcate, acute, 1-veined, 5-6 × 1,2 mm; margin entire to slightly crenulate. **Labellum** slightly thickened, light reddish to purple, spatulate, trilobate, obtuse, 4-5 × 2,5 mm when expanded, midlobe suborbicular, the lateral ones basally slightly thickened and antrorse, apically broad, membranous, revolute; upper side with two lengthwise calli beyond the middle, apically papillose; base clawed, with two auricles connected by a transverse callus; margin entire below the middle, somewhat sinuate, crenulate or papillose above. **Column** light reddish, slightly curved inwards, carinate, winged beyond the middle, 4-4,5 mm long; foot 1-1,5 mm long, with a depression elongated; clinandrium winged; margin profoundly dentate. **Anther** apical; pollinia 2, obtuse-triangular, slender. Stigma ventral. **Ovary** 2-2,5 mm long, papillose to verruculate. **Capsule** verrucate. – Fl.: V, Fr.: V-VI.

**Distribution:** Greater Antilles (except Jamaica). Present in East Cuba: Gr (Sierra Maestra: Buey Above, Barrio Nuevo). Epiphytic; prefers shady and humid conditions in montane rainforests about 1400 m, in vegetation on soils derived from volcanic rock. Very rare, known only from one locality.

***Pleurothallis aristata* Hook.** in Ann. Mag. Nat. Hist., ser. 2, 11: 329. 1839. = *Specklinia aristata* (Hook.) Pridgeon & M. W. Chase in Lindleyana 16: 256. 2001. Lectotype (designated here): “*Pleurothallis aristata*” [based on material from Demerara, Guyana, cultivated in Liverpool by Parker] in Ann. Mag. Nat. Hist., ser. 2, 11: t. 15. 1839. – Fig. 4.

= *Pleurothallis urbaniana* Rchb. f. in Ber. Deutsch. Bot. Ges. 3: 279. 1885. Holotype: “Puerto Rico, Maricao, Indiera Fría”, 3-XII-1884, Sintenis, Plantae portoricenses No. 503 (W ex herb. Reichenbach Orch. No. 25575!).

**Herbs**, caespitose, 1,5-3 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** ascending, 1-3 mm long, 2-articulated, entirely covered by two membranous sheaths; annulus present. **Leaves** slightly thickened, narrow elliptic to oblanceolate, acute to subobtuse, tridentate with the middle tooth being elongated, 1,4-2,7 × 0,4-0,5 cm, green, glabrous; base narrow attenuate; margin entire. **Inflorescence** a terminal raceme, ascending, two per stem, 2-6 flowers; subtended at the base by a lanceolate and conduplicate sheath of 0,5-1 mm in length; peduncle 2,5-4,5 cm long, with two bracts; axis 0,5-1,5 cm long. **Pedicels** up to 9 mm long, fused 0,7 mm with the axis; bract membranous, tubular to infundibuliform, 1,4-1,7 mm long. **Flowers** with successive anthesis. **Sepals** membranous, greenish with purple stripes; margin papillose; **dorsal** sepal free, lanceolate, caudate, 3-veined, 6,5 × 1,5 mm; the **lateral** ones connate basally 1 mm, lanceolate, carinate, caudate, 2-veined, 6,5 × 1,3 mm. **Petals** membranous, hyaline with a purple nerve, oblique spatulate, acute, 1-veined, 3 × 1 mm; margin profoundly fimbriate to lacerate. **Labellum** slightly thickened, purple, oblong, trilobate, obtuse to retuse, 2,3 × 1,3 mm when expanded, midlobe suborbicular, papillose to pilose, the lateral ones denticulate, antrorse; upper side with a central lengthwise depression on the lower half, apically papillose; lower side distinctly carinate; base truncate; margin papillose, verrucate, revolute. **Column** whitish, slightly curved inwards, 2 mm long; foot 0,5 mm long, with two orbicular calli; clinandrium slightly winged, margin serrate. **Anther** apical; pollinia 2, pyriform, sculpture punctate. Stigma ventral. **Ovary** 1-1,5 mm long,

glabrous. **Capsule** 6 mm long, glabrous and ribbed. – Fl.: V-VII, Fr.: V-VIII.

**Distribution:** Tropical America and Antilles. Present in east Cuba: SC (Sierra Maestra: falda sur of the Pico Turquino). Epiphytic; prefers shady and humid conditions in cloud or montane rainforests about 1800 m. Known from a single collection.

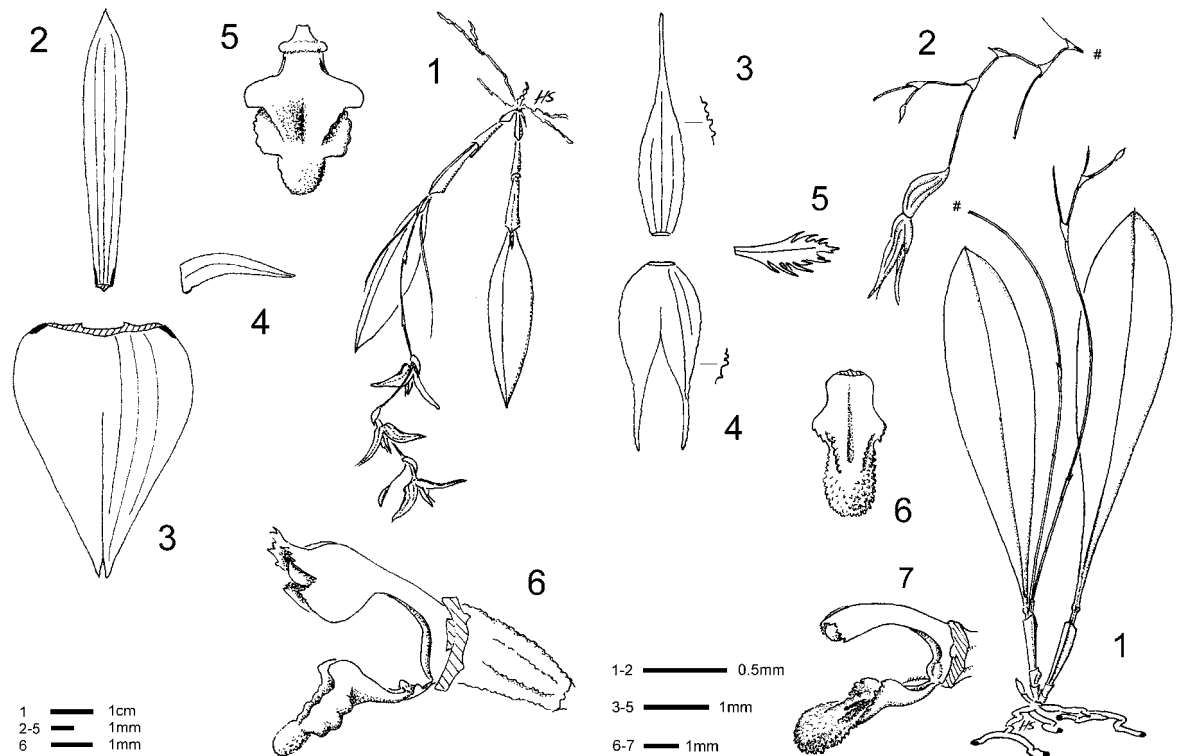


Fig. 3: *Pleurothallis appendiculata* Cogn.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip. 6 – Lip, ovary and column in natural position.

Fig. 4: *Pleurothallis aristata* Hooker.  
1 – Plant. 2 – Inflorescence, upper part. 3+4 – Sepals. 5 – Petal. 6 – Lip. 7 – Lip, ovary and column in natural position.

***Pleurothallis bissei* Luer** in Lindleyana 14: 108. 1999. Holotype: “Cuba, Holguín, Mayarí, lower Sierra de Nipe, Loma la Mensura”, 31-X-1977, Bisse & al. (HAJB!). – Fig. 5.

**Herbs**, subrepent, 2,5-8,5 cm high (excluding the inflorescence). **Stems** with tubular sheaths which are densely covered with scale-like, erect, brownish red hairs. **Rhizome** slightly elongated, separating the ramicauls by 2-4 mm. **Ramicauls** erect or ascending, 1-4,5 cm long, 3-articulated; without an annulus. **Leaves** coriaceous, narrow elliptic, acute to subobtusate, often tridentate, 1,4-4 × 0,4-0,7 cm, yellowish green and uneven on the upper side, green and glabrous on the lower side; base cuneate; margin finely serrate. **Inflorescence** a terminal raceme, ascending, two per stem, with 2-3 flowers, subtended at the base by an ovate and conduplicate sheath of 1-2 mm in length; peduncle 0,3-0,4 cm long, with two bracts; axis 0,4-1 cm long. **Pedicels** 1-1,5 mm long, fused below the middle with the axis; bract membranous, tubular, 1-1,3 mm long. **Floral segments** membranous, 3-veined, acute; anthesis successive. **Sepals** whitish, with the nerves reddish; margin slightly asper; **dorsal** sepal basally connate 1 mm with the lateral ones, (narrow) elliptic, 6,9-7,2 × 2,2-2,4 mm; the **lateral** ones basally connate 1 mm but adnate up to beyond the middle, the base forming a mentum with the ovary, narrow elliptic-ovate, 6,9-7,2 × 2-2,1 mm. **Petals** whitish, oblanceolate, 4,5 × 1,7 mm; margin apically serrulate. **Labellum** slightly thickened to membranous, reddish to deep red, narrow oblong, rounded, 4-4,2 × 1,1-1,2 mm when expanded; upper side with two lengthwise calli above the middle; base truncate; margin antrorse below the middle, crenulate above. **Column** white, slender, slightly curved inwards, 3 mm long; foot up to 1 mm long; clinandrium slightly winged, margin entire. **Anther** apical; pollinia 2, lentiform, sculpture granulate. Stigma ventral. **Ovary** 1 mm long, glabrous. **Capsule** 5 mm long, glabrous with prominent and verrucate ribs. – Fl.: XI-II, Fr.: XI-IV.

**Distribution:** Endemic in eastern Cuba: Ho. Lithophytic; prefers open places like the banks of rivulets, in gallery forests from 700 to 900 m, on serpentine rock. Rare.

**Ecology:** Plants growing on river banks stand temporal inundations during the rainy season.

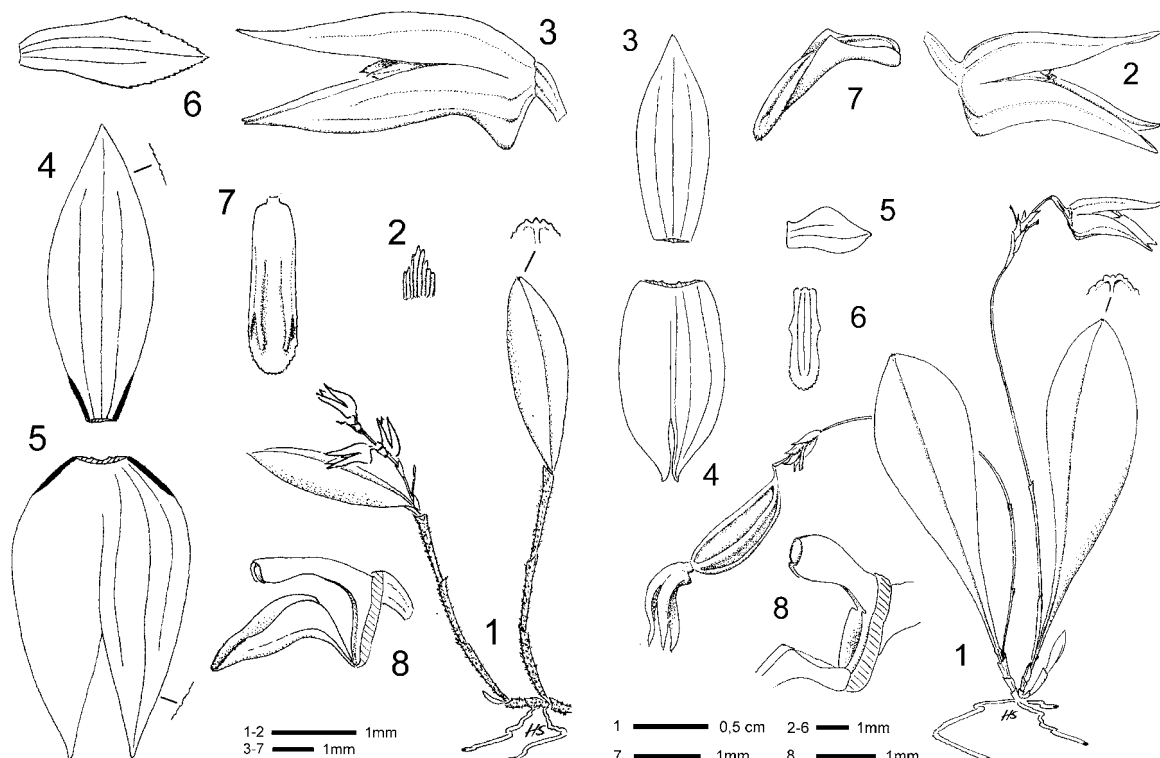


Fig. 5: *Pleurothallis bissei* Luer

1 – Plant. 2 – Scale. 3 – Flower. 4+5 – Sepals. 6 – Petal. 7 – Lip. 8 – Lip, ovary and column in natural position.

Fig. 6: *Pleurothallis brighamii* S. Wats.

1 – Plant. 2 – Flower. 3+4 – Sepals. 5 – Petal. 6+7 – Lip. 8 – Base of lip, ovary and column in natural position.

***Pleurothallis brighamii* S. Watson** in Proc. Amer. Acad. Arts 23: 285. 1888.  $\equiv$  *Specklinia brighamii* (S. Watson) Pridgeon & M. W. Chase in Lindleyana 16: 256. 2001. Holotype: "Guatemala: eastern portion of Verapaz and Chiquimula, [flowering] Cambridge - Aug. 1887" [Chocón], VIII-1887, Watson (AMES No. 72461 [photo!]). – Fig. 6.

**Herbs**, caespitose, 2-3,5 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, straight, 0,9-2,2 mm long, 3-articulated, entirely covered by three scarious and tubular sheaths; annulus present. **Leaves** slightly thickened and somewhat coriaceous, spatulate, acute or obtuse, slightly tridentate, 1,5-3,3  $\times$  0,3-0,6 cm, green, glabrous; base narrow attenuate; margin entire. **Inflorescence** a terminal congested raceme, solitary, few-flowered; peduncle 2,4-3,7 cm long, with two or three bracts; axis 1-3 mm long. **Pedicels** 2,5-3 mm long, free; bract membranous, tubular, acuminate, up to 2 mm long. **Flowers** with a successive anthesis. **Sepals** y petals membranous to slightly thickened, yellow with red stripes, carinate, acute; margin entire; **dorsal** sepal free, oblong-elliptic to narrow obovate, 3-veined, 5,8-6,2  $\times$  2-2,3 mm; the **lateral** ones connate to 2/3, the base forming a mentum with the ovary, synsepal elliptic, bifid, 6-veined, 5,9-6,2  $\times$  3-3,4 mm; **petals** oblique, spatulate, 2-veined, 2,5  $\times$  1,3 mm. **Labellum** slightly thickened, yellow with a red margin, oblong, recurved, rounded, 2,8-3  $\times$  1 mm when expanded; upper side with two lengthwise calli above the middle, apically minutely papillose; base subcordate; margin with two straight auricles in the middle, tip papillose. **Column** stout, yellowish with red margin, 1,5 mm long; foot  $\pm$  1 mm long, with a suborbicular depression and two acute auricles close to the base; clinandrium slightly winged, bidentate. **Anther** apical; pollinia 2, broadly obovate, sculpture punctate to granulate. Stigma ventral. **Ovary**  $\pm$  1 mm long, glabrous. **Capsule** 6-8 mm long, ribbed. –

Fl.: II-VIII, Fr.: II-X.

**Distribution:** Central America from México to Costa Rica, Greater Antilles (except Puerto Rico). Present in West Cuba: PR (Sierra of the Rosario: Río Taco Taco); Central Cuba: Santi-Spirit. Mts., Sierra Caballete; East Cuba: Ho, SC, Gu. Epiphytic or lithophytic; prefers humid and shady places generally close to water in gallery forests, montane rainforests, cloud forests and secondary forests (cupeyales) from 350 to 700 m, in vegetation on soils derived from limestone or serpentine rock. Rare.

**Ecology:** Frequently in association with *Pleurothallis corniculata*.

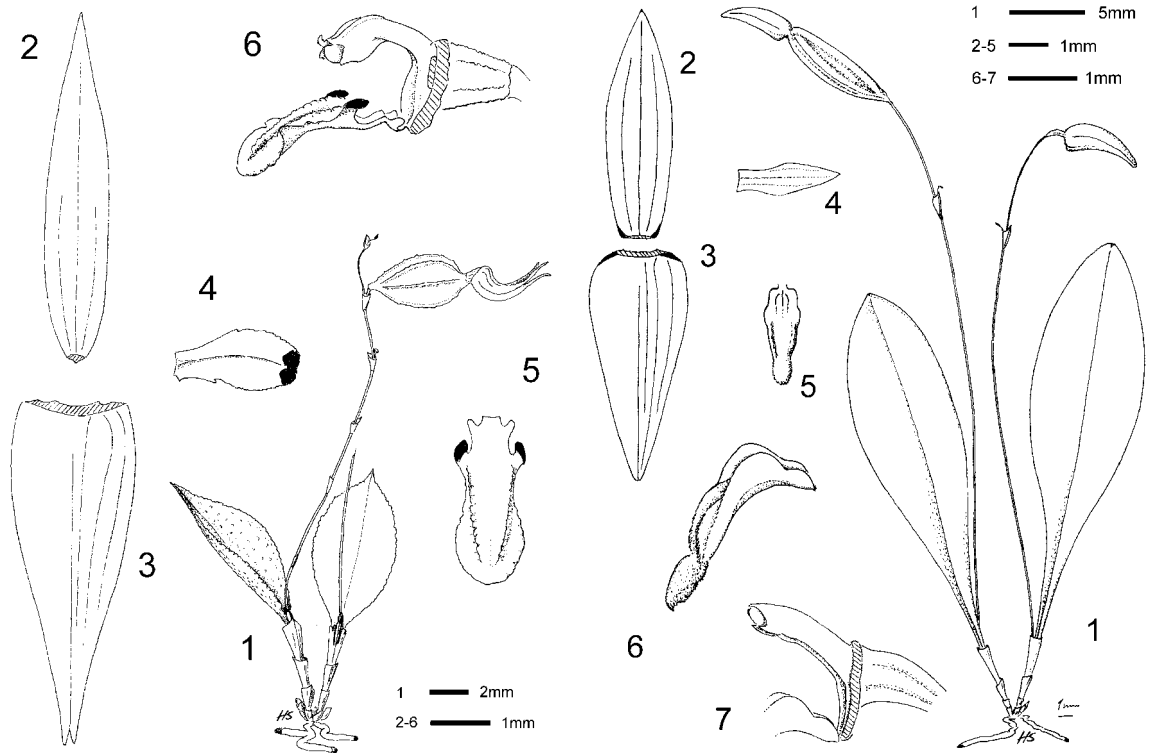


Fig. 7: *Pleurothallis caymanensis* C.D. Adams. 1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip. 6 – Lip, ovary and column in natural position.

Fig. 8: *Pleurothallis corniculata* (Sw.) Lindl. 1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip. 6 – Lip. 7 – Base of lip, ovary and column in natural position.

***Pleurothallis caymanensis* C. D. Adams** in Orquideologia 6: 146. 1971. Holotype: "Grand Cayman: along road to North Side, 0.4 mile [650 m] SE of Old Man Village, rocky limestone woodland", 9-VI-1967, Proctor 27983 (J!). – Fig. 7.

**Herbs**, subcaespitose, 1-2 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** up to 6 mm long, 3-articulated below the middle, entirely covered by two scarious sheaths; without an annulus. **Leaves** thickened and rigid, ovate to broadly elliptic or suborbicular, conduplicate, acute, acuminate or apiculate, 6-12(-14) × 4-7 mm, yellowish green and verrucate on the upper side, green and rough on the lower side; base cuneate; margin crenulate to erose. **Inflorescence** a terminal raceme, ascending, two per stem, (1-)2-3 flowers, subtended at the base by a lanceolate sheath of 1 mm in length; peduncle 1-2,5 cm long, with 2-4 bracts; axis 0,5-1 cm long. **Pedicels** 1-1,2 mm long, free; bract membranous, tubular or slightly infundibuliform, loosely verrucate, basally reddish, 1 mm long. **Flowers** with a successive anthesis. **Sepals** membranous, slightly thickened along the nerves, greenish yellow with purple stripes, carinate; **dorsal** sepal free, lanceolate, acute, 3-veined, 5-5,7 × 0,9-1,1 mm; margin entire; the **lateral** ones connate basally but adnate up to the tip, the base forming a mentum with the ovary, synsepal lanceolate, acute, bifid, 6-veined, 5-5,3 × 2-2,3 mm; margin entire. **Petals** membranous, whitish with a reddish nerve and a deep red dot at the apex, spatulate, rounded to emarginate, 1-veined, carinate, 2 × 1 mm; margin irregularly serrate.

**Labellum** slightly thickened, reddish and deep purple, oblong to spatulate, rounded, 2,7 × 1 mm when expanded; upper side with two lengthwise, verrucate calli; base attenuate, biauriculate; margin entire or crenulate and with two purple lobes. **Column** light reddish and apically purple, curved inwards, 1,5 mm long; foot 1 mm long, with an elongated depression; clinandrum winged and serrate. **Anther** subapical; pollinia 2?. Stigma ventral. **Ovary** 1 mm long, rough. **Capsule** 5-6 mm long, verrucate on the ribs. – Fl.: III-VII, Fr.: III-VIII.

**Distribution:** Greater Antilles (Cuba and Grand Cayman). Present in West Cuba: PR (Guanahacabibes: Barra la Sorda). Epiphytic; prefers humid places in semideciduous forests at low elevations, generally in vegetation on limestone. Known from one locality.

***Pleurothallis corniculata* (Sw.) Lindl.** in Bot. Reg. 28: misc. 83, no. 110. 1842 (excl. syn.). ≡ *Epidendrum corniculatum* Sw., Prodr.: 123. 1788. ≡ *Dendrobium corniculatum* (Sw.) Sw. in Nova Acta Regiae Soc. Sci. Upsal. 6: 83. 1799. ≡ *Cymbidium corniculatum* (Sw.) Spreng., Syst. Veg. 3: 722. 1826. Lectotype (Fawcett & Rendle 1910: 61, specified here): “*Epidendrum corniculatum* Swartz, Jamaica”, Swartz (BM!; isoelectotypes?: S ex herb. Alstroemer [foto!], W ex herb. Reichenbach Orch. No. 26609!). – Fig. 8.

= *Pleurothallis nubigena* Lindl. in Ann. Mag. Nat. Hist., ser. 3, 1: 326. 1858 [as “rubigena”]. Lectotype (designated here): “in Cuba Orientali, 1856-7” [blue label], Wright 657 (K-L!; isoelectotypes?: G ex herb. Barbey-Boissier!, K!).

– “*Pleurothallis hymenantha*” sensu Lindley (1860: 219) (non *Pleurothallis hymenantha* Lindl.).

**Herbs**, caespitose, 2-5 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, straight, 3-6 mm long, 4-articulated, entirely covered by 4 scarious, tubular or slightly conduplicate sheaths; annulus present. **Leaves** slightly coriaceous, elliptic to oblanceolate or spatulate, acute to obtuse, tridentate, 1,7-4,5 × 0,5-0,7 cm, green, glabrous; base attenuate; margin entire. **Inflorescence** terminal, solitary, single flowered, straight, subtended at the base by an ovate and acute sheath of 1-1,7 mm in length; peduncle 2,5-3,5 cm long, with one bract. **Pedicels** 0,6-1 cm long; bract membranous, conduplicate, short apiculate, 1,8-2,1 mm long. **Sepals** membranous to slightly thickened, yellowish green, carinate, slightly papillose on the outside along the nerves; **dorsal** sepal basally connate with the lateral ones, narrow elliptic, acute, 3-veined, 5-6 × 1,6-1,8 mm; margin entire; the **lateral** ones connate only basally but adnate up to the tip, the base forming a mentum with the ovary, synsepal narrow ovate, acute, 6-veined, 4,5-5,5 × 2,2-2,6 mm; margin glabrous. **Petals** membranous, whitish, elliptic, oblique in the upper part, acute, 3-veined, 2,5-2,8 × 0,7-0,9 mm; margin entire. **Labellum** slightly thickened, whitish, narrow ovate to lanceolate, rounded, 2,5 × 1 mm when expanded; upper side with two lengthwise, papillose calli above the middle, apically papillose; lower side papillose along the nerves; base truncate, short clawed; margin entire, antrorse below the middle, ciliate or papillose above. **Column** whitish, slightly curved inwards, 1,6 mm long; foot 0,6 mm long; clinandrum slightly winged, bidentate. **Anther** apical; pollinia 2, generally amorph with a reduced sculpture, or rarely, in flowers open (xenogamous), oblong to obovate with a granular sculpture. Stigma ventral. **Ovary** 1 mm long, glabrous or verrucate along the ribs. **Capsule** 6,5-7 mm long, with slightly verrucate ribs. – Fl.: I-XII, Fr.: I-XII.

**Distribution:** Central America from Belize to Costa Rica (Pánama?), Greater Antilles (Cuba, Jamaica), Hispaniola (Dod 1984b: 107). Present in West Cuba: PR; Central Cuba: Ci (Sierra de Escambray), SS; East Cuba: Ho, Gr, SC, Gu. Epiphytic or lithophytic; prefers humid and shady or open conditions in vegetation of the mogotes, montane rainforests, gallery forests, and in degraded forms of these forest types like in secondary forests (cupeyales), from 300 to 800 m, usually associated with the vegetation on limestone. Common.

**Ecology:** Frequently in association with *Pleurothallis sertularioides*, *Pleurothallis*

*tribuloides* and *Pleurothallis wilsonii*.

**Reproduction biology:** Some characteristics, like the generally closed flowers (Wright in herb. and pers. observ.), and the amorphous pollinia with a reduced and fragile exinous layer, suggest autogamy and probably cleistogamy in most of the Antillean plants.

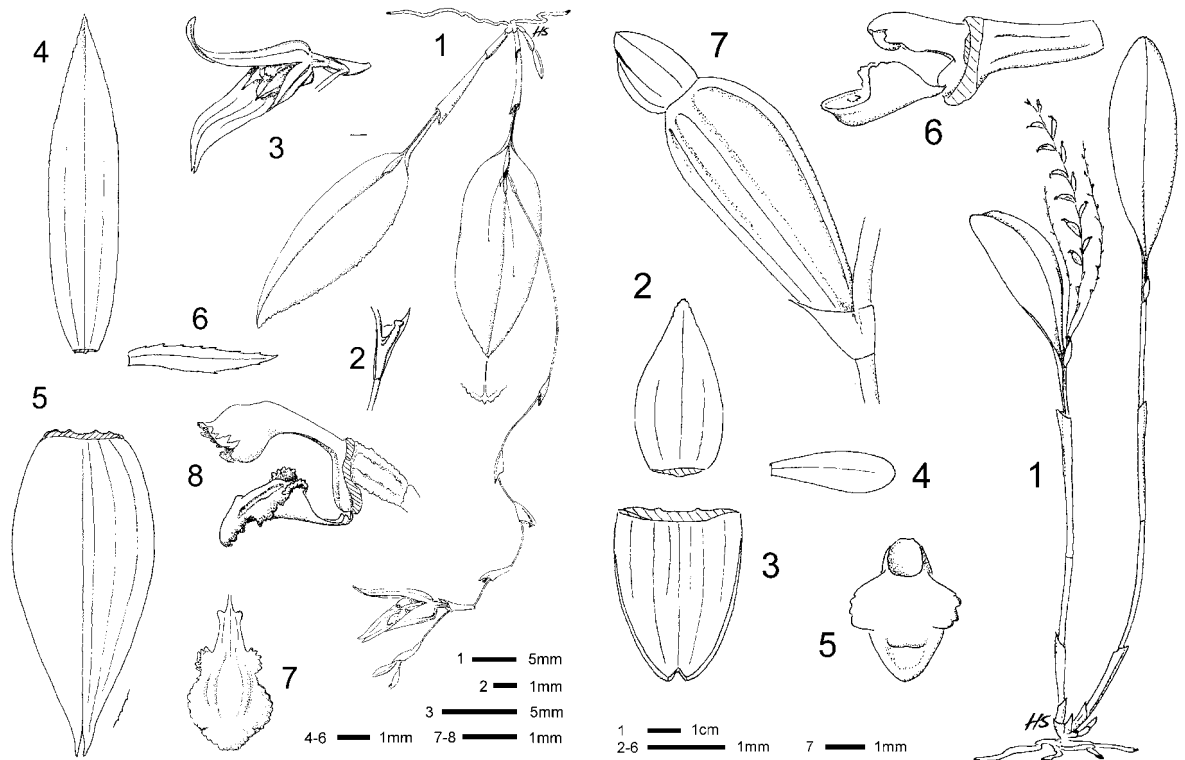


Fig. 9: *Pleurothallis denticulata* Cogn.  
1 – Plant. 2 – Pedicel and bract. 3 – Flower.  
4+5 – Sepals. 6 – Petal. 7 – Lip. 8 – Lip, ovary  
and column in natural position.

Fig. 10: *Pleurothallis domingensis* Cogn.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.  
7 – Fruit with persistent flower.

***Pleurothallis denticulata* Cogn.** in Urban, Symb. Antill. 6: 425. 1909. Lectotype (designated here): “Cuba oriental, prís de Monteverde”, [Loma del Gato, according to Cogniaux (1909)], Wright 657 p.p. ex herb. Cogniaux (BR No. 843468!). – Fig. 9.

= *Pleurothallis parvula* Ames & C. Schweinf. in Sched. Orchid. 8: 30. 1925. Holotype: “Cuba: High Maestra” [Pico Turquino], VII-1922, León 10790 (NY No. 59805 [photo!]; isotype: HAC No. 7209!).

= *Pleurothallis platyglottis* L. O. Williams in Ceiba 1: 228. 1951. Holotype: “Haiti: Guimbi Galata, Mornes des Commissaires”, 1800 m, 21-VI-1942, Holdridge 1287 (AMES [n.v.]).

**Herbs**, caespitose, 2,5-6 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** straight, ascending or pendent, 1-2,5 cm long, basally 2-articulated, to 2/3 covered by two scarious, conduplicate and carinate sheaths; without an annulus. **Leaves** coriaceous, ovate to narrow elliptic, distinctly carinate, acute, tridentate, 1,5-3,5 × 0,7-1,3 cm, green, slightly rough on the upper side, glabrous on the lower side; base short attenuate; margin denticulate, revolute. **Inflorescence** a terminal raceme, pendent, (1-)2-5(-10) per stem, with 2-10 flowers, subtended at the base by an ovate and acute sheath of 1,2-2,5 mm in length; peduncle 1-3,5 cm long, with one bract; axis 2-5,5 cm long. **Pedicels** 2,5-3,1 mm long, fused beyond the middle with the axis; bract membranous, conduplicate, acuminate, 2,5-3,2 mm long. **Flowers** with a successive anthesis. **Sepals** and petals membranous, slightly thickened along the nerves, greenish or yellowish with purple nerves, carinate, acute; margin minutely denticulate; **dorsal** sepal free, linear lanceolate to narrow elliptic, slightly reflexed, 3-veined, 9-10 × 2-2,1 mm; the **lateral** ones adnate almost up to the tip, the base forming a mentum with the ovary, synsepal ovate,

bifid, 6-veined, 9-9,6 × 4-4,2 mm; minutely denticulate on the nerves on the outside. **Petals** membranous, hyaline, light reddish, (narrow) lanceolate, 1-veined, 4-5 × 0,7 mm. **Labellum** thickened, purple with a dark purple margin, obovate to spatulate, slightly lobed, rounded, 2,5-3 × 1,5-1,7 mm when expanded; upper side with two lengthwise calli bordering a central depression; base clawed, biauriculate; margin denticulate and antrorse in the middle, crenulate and revolute in the upper part. **Column** light reddish, clawed, slightly curved inwards, 2,5-3 mm long; foot 0,6 mm long; clinandrium distinctly winged, denticulate. **Anther** apical; pollinia 2, obtusely triangular, sculpture punctate. Stigma ventral. **Ovary** 1,3 mm long, minutely verrucate on the ribs. **Capsule** 6 mm long, with verrucate ribs. – Fl.: V-XI, Fr.: V-XII.

**Distribution**: Greater Antilles (Cuba, Hispaniola). Present in East Cuba: Gr (Sierra Maestra: Pico Turquino; Victorino: Loma El Gigante), SC (Gran Piedra). Epiphytic; prefers humid and shady places close to the ground in montane rainforests, usually in Barril forest (*Cyrtilla racemiflora*) from 900 to 1500 m. Common.

**Variability**: This species is variable regarding form and margin of the leaf and floral segments. The color ranges from greenish and slightly, mottled with purple to entirely purple flowers with only the base being somewhat greenish.

***Pleurothallis domingensis* Cogn.** in Urban, Symb. Antill. 6: 402. 1909. ≡ *Stelis antillensis* Pridgeon & M. W. Chase in Lindleyana 17: 98. 2002. Lectotype (Luer 1998a: 20): “Santo Domingo [Dominican Republic]: Valle Nuevo”, 1900 msm, 29-V-1887, Eggers 2176 (BR [ex herb. Cogniaux] No. 843471!; isoelectotype: K!). – Fig. 10.

– “*Pleurothallis velaticaulis*” sensu Lindley (1860: 219), Alain (1958: 41, 43), Adams (1972: 108) et auct. fl. cub. (non *Pleurothallis velaticaulis* Rchb. f.).

– “*Pleurothallis crassipes*” sensu Cogniaux (1909: 400) (non *Pleurothallis crassipes* Lindl.).

**Herbs**, caespitose, 10-30(-40) cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** ascending, 6-24 cm long, 1-articulated below the middle, partially covered by three tubular sheaths, carinate; annulus present. **Leaves** coriaceous, (broadly) elliptic, obtuse to retuse, 4-16 × 1,5-3,5 cm, green, glabrous; base attenuate; margin entire. **Inflorescence** a terminal raceme, erect, 1-4 per stem, multi-flowered, subtended at the base by a narrow ovate and acute sheath of 0,5-0,8 cm in length; peduncle 0,5-1,5 cm long, with two or three bracts; axis 2,5-11,5 cm long. **Pedicels** 0,5-1 mm long, free; bract membranous, infundibuliform, acute, 2-4 mm long. **Flowers** with a simultaneous anthesis. **Sepals** membranous, greenish to yellowish, rarely with a tint of red, carinate; margin entire or crenulate, involute; **dorsal** sepal free, (narrow) ovate, acute, 3-veined, 2-4,5 × 1,1-1,3 mm; the **lateral** ones adnate up to the middle or close to of the tip, the base forming a mentum with the ovary, synsepal ovate, bifid, 6-veined, 2-4 × 1,5-3,4 mm. **Petals** membranous, hyaline, narrow spatulate or oblanceolate, obtuse to rounded, 1-veined, 1,5-2 × 0,5 mm; margin entire. **Labellum** slightly thickened, whitish, ovate to elliptic, trilobate, obtuse, 1,6-1,8 × 1,2-1,3 mm when expanded, midlobe broadly ovate and patent, the lateral ones antrorse; upper side basally with a circular cavity and a callus in the upper part; base cuneate to obtuse; margin entire to crenulate. **Column** white, straight, 1,3 mm long; foot 0,5 mm long, thickened; clinandrium slightly winged, denticulate. **Anther** apical; pollinia 2, suborbicular to triangular or amorphous, sculpture octomeriform (s. Stenzel 2000). Stigma ventral. **Ovary** 1,5 mm long, surcate. **Capsule** 6 mm long, glabrous, ribbed. – Fl.: VIII-XII, Fr.: VIII-I.

**Distribution**: Greater Antilles and Guadalupe. Present in East Cuba: Ho (Sierra del Cristal: Pico Cristal), Gr, SC, Gu. Epiphytic or Lithophytic; prefers humid and shady places in montane rainforests and cloud forests from 900 to 1500 m. Rare.

**Reproduction biology**: Populations with smaller flowers seem to be autogamous or even cleistogamous. They show fragile and amorphous pollinia. Though open flowers were never observed, plants develop a complete fruit set.



**Variability:** The size of the flowers is quite variable, which may reflect the type of the reproduction biology.

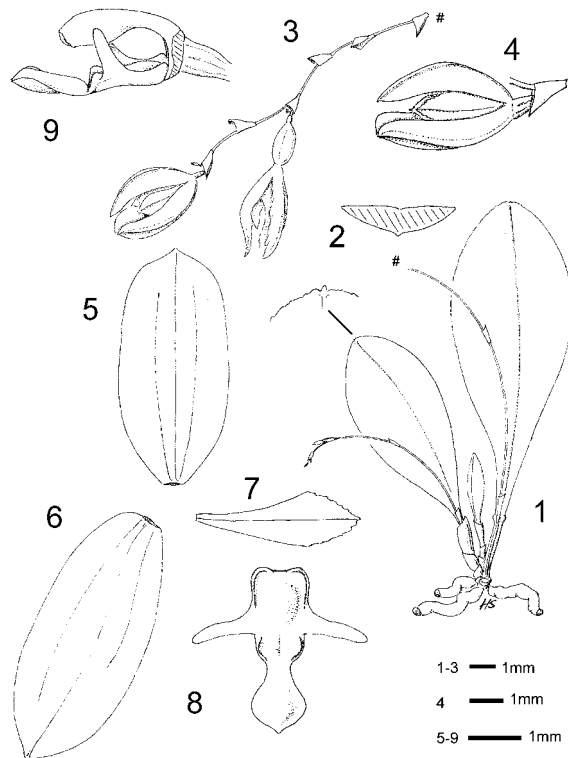


Fig. 11: *Pleurothallis ekmanii* Schltr.  
1+3 – Plant. 2 – Leaf, cross section. 4 – Flower.  
5+6 – Sepals. 7 – Petal. 8 – Lip. 9 – Lip, ovary  
and column in natural position.

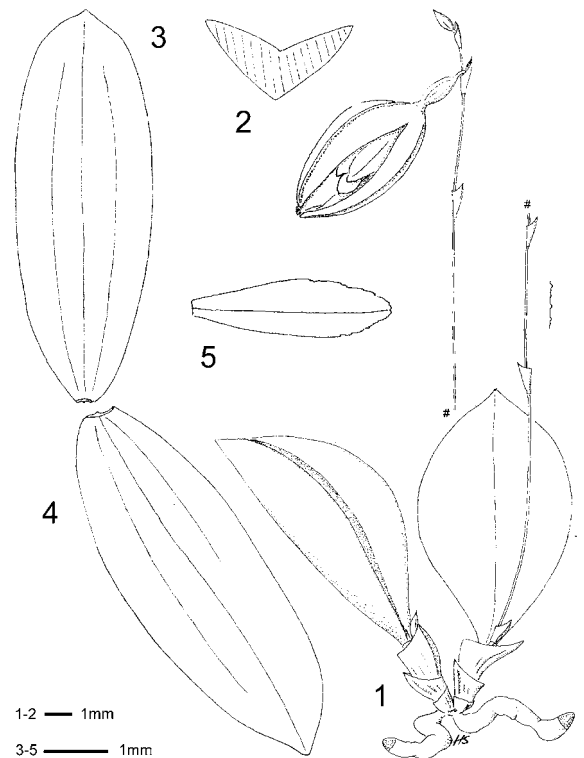


Fig. 12: *Pleurothallis ekmanii* Schltr.  
1 – Plant. 2 – Leaf, cross section. 3+4 – Sepals.  
5 – Petal.

***Pleurothallis ekmanii* Schltr.** in Urban, Symb. Antill. 9: 61. 1923. Holotype: "Cuba: Oriente, Sierra del Cristal, in caumine montis, locis rupestr.", 1325 msm, 08-III-1916, Ekman 6831 (S!). – Fig. 11, Fig. 12

= *Pleurothallis bovilabia* C. Schweinf. in Amer. Orchid Soc. Bull. 15: 234. 1946. Holotype: "Cuba, Oriente, Moa, Monte de la Breña, banks of a rivulet, on chromium rocks", León & al. 22586 (AMES No. 62496!).

**Herbs**, caespitose or subcaespitose, 0,7-1,8 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** up to 0,5 mm long, basally 2-articulated, entirely covered by two scarious, infundibuliform, conduplicate and acute sheaths; without an annulus. **Leaves** coriaceous, obovate to spatulate or (broadly) elliptic, plane or folded, obtuse, acute or subacuminate, tridentate, 0,6-1,7 × 0,3-0,5 cm, green to greyish green on the upper side, green on the lower side; base narrow or short attenuate; margin denticulate in the upper part (sometimes entire). **Inflorescence** apparently basal, a pendent or erect, solitary, 2-few-flowered raceme; peduncle 1,3-7 cm long, with two or three bracts; axis glabrous or minutely verrucate, 0,7-5 cm long. **Pedicels** 0,6-1,2 mm long, fused below the middle with the axis; bract membranous, tubular, acute, slightly conduplicate, 0,8-1,5 mm long. **Flowers** with a successive anthesis. **Sepals** slightly thickened, (greenish) yellow and with a tint of red, convex, 3-veined, apically with minutely verrucate keels; margin entire or minutely denticulate in the upper part; **dorsal** sepal free, elliptic or oblong, obtuse, short acuminate, 3,2-4,5(-5,9) × 1,8-2,1 mm; the **lateral** ones free but often adnate to the tip, (narrow) elliptic to oblong, slightly falcate, obtuse, short acuminate or apiculate, 3,5-5(-6) × 1,8-2 mm. **Petals** membranous, yellowish to reddish, spatulate, acute to obtuse, 1-veined, 2,8-3,1 × 0,9-1 mm; margin apically denticulate or obtuse-serrate. **Labellum** membranous, partially thickened, whitish and with red dark dots, slightly panduriform, trilobate, rounded and short apiculate, 3 × 3,2 mm when expanded, midlobe suborbicular with a circular disc, broadly clawed, the lateral ones elongated,

antrorse; upper side with two calli bordering a central depression; base truncate, with two obtuse, antrorse, dark red lobes; margin entire. **Column** whitish, elongated, curved inwards, 2,2 mm long; foot reduced; clinandrum winged. **Anther** apical; pollinia 8, claviform, sculpture fossulate. Stigma ventral. **Ovary** 1 mm long, glabrous. **Capsule** 5-6 mm long. – Fl.: II-VII, Fr.: II-VIII.

**Distribution:** Endemic in East Cuba: Ho, Gu (Yateras: Pico Galán). Epiphytic or lithophytic; prefers humid places, like the banks of rivulets or foggy mountain crests, in charrascales or gallery forests from 600 to 900 m, exclusively in vegetation on soils derived from serpentine. Rare.

**Variability:** This species is highly variable in its morphology. Fig. 11 and Fig. 12 show extremes in foliar and floral morphology. Observations in the field suggest the existence of various forms. Most distinct differences were found between epiphytic (Fig. 11) and lithophytic or pseudoterrestrial populations (Fig. 12). Lithophytic plants show a very compact habit, erect inflorescences and bigger flowers. Because of these differences, Schweinfurth (1946) published a collection of terrestrial plants as *Pleurothallis bovilabia* C. Schweinf. However, there are intermediate forms and some of the presumed “distinct” characteristics can be found even within the same population.

***Pleurothallis excentrica* (Luer) Luer** in Rev. Soc. Boliviana Bot. 3(1-2): 50. 2001. = *Octomeria excentrica* Luer in Lindleyana 14: 106. 1999. Holotype: “Cuba, Moa, Río Cayuguán”, VII-1949, Alain & al. 896 (AMES [n.v.]; isotype: Herb. Ch. F. Barker No. 15598 [n.v.]). – Fig. 13.

**Herbs**, subrepent. **Rhizome** elongated, separating the ramicauls by 1-2 mm, covered by various scarious and infundibuliform sheaths. **Ramicauls** subreduced, entirely covered by two scarious, infundibuliform, acute sheath; without an annulus. **Leaves** thickened, subprostrate, oblanceolate, obtuse to retuse, tridentate, 0,8-1,5(-2) × 0,2-0,4 cm, green to greyish green or purplish green, rough on the upper side, dark green and rough on the lower side; base cuneate; margin entire. **Inflorescence** apparently basal, a solitary raceme with 1(-2) flowers, subtended at the base by a scarious sheath of 4 mm in length, fused with the peduncle; peduncle erect, up to 4 mm long, with two bracts; axis reduced, barely 1 mm long. **Pedicels** 0,5 mm long, almost entirely fused with the axis; bract membranous, infundibuliform, <1 mm long. **Sepals** thickened, brownish purple, whitish towards the base, connate at the very base, narrow ovate, acute or slightly acuminate, 3-veined, convex, carinate; margin entire; **dorsal** sepal 4,8-5,2 × 2,5-3 mm; the **lateral** ones, 4,8-5,2 × 2-2,4 mm. **Petals** somewhat thickened, purple, oblanceolate, slightly panduriformes, acute, subacuminate, 1-veined, 4,5 × 1,5-1,8 mm; margin minutely crenulate above. **Labellum** thickened, dark purple and whitish, ovate, acute or subobtuse, 4-4,2 × 2,2-2,5 mm when expanded; upper side with a basal circular depression, apically with minute calli and teeth; base truncate; margin below the middle crenulate, in the middle with two antrorse teeth, towards the tip irregularly denticulate. **Column** whitish with purple, slightly curved inwards and apically winged, 2,5 mm long; foot 0,5 mm long; clinandrum winged and crenulate. **Anther** subapical; pollinia 8, pyriform to claviform, sculpture psilate. Stigma ventral. **Ovary** 2 mm long, glabrous. **Capsule** ribbed. – Fl.: IV-VI, Fr.: V-VII.

**Distribution:** Endemic in East Cuba: Ho, SC (Sierra del Cristal: Río Lebisa), Gu. Epiphytic; prefers humid and shady to open conditions, along waterways or foggy mountain crests in gallery forests or montane rainforests from 300 to 800 m, restricted to the vegetation on serpentine rock. Rare.

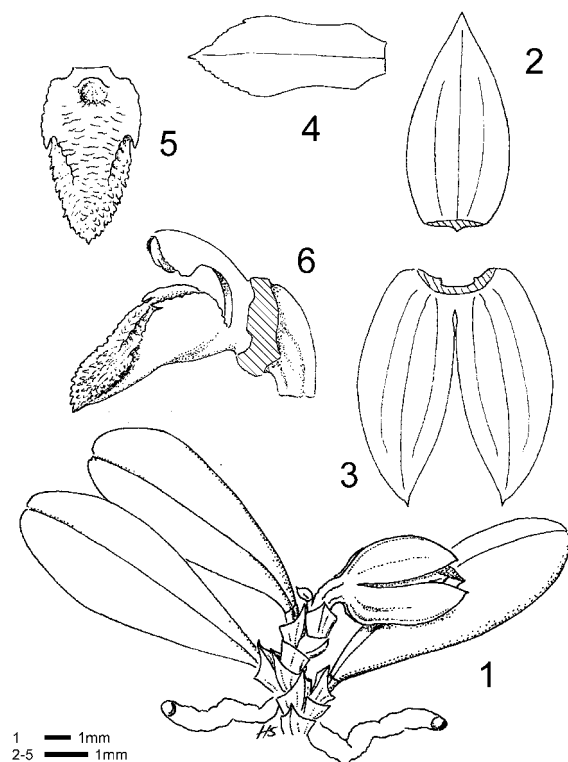


Fig. 13: *Pleurothallis excentrica* (Luer) Luer.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

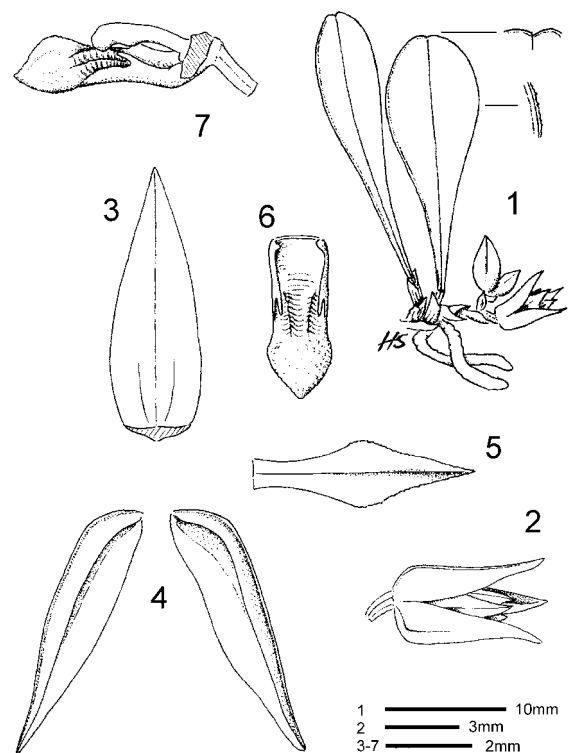


Fig. 14: *Pleurothallis* 'flabelliformis' H. Stenzel  
1 – Plant. 2 – Flower. 3+4 – Sepals. 5 – Petal.  
6 – Lip. 7 – Lip, ovary and column in natural position.

***Pleurothallis flabelliformis* H. Stenzel**, comb. nov. et nom. nov.  $\equiv$  *Octomeria prostrata* H. Stenzel in Lindleyana 16: 26. 2001. Holotype: "Cuba, Holguín, Sierra del Cristal, cabezadas del Río Lebisa, 500 m río abajo desde el campamento base del trillo al Pico, 20°31'39"N, 75°29'10"Oe", 650-700 m, 29-V-1998, Stenzel & Matos 516 (HAJB!; isotype: JE!). – Fig. 14.

**Herbs**, caespitose to subrepent, 2-4 cm high. **Rhizome** subreduced. **Ramicauls** 0,5-1,5 mm long, 2-articulated, entirely covered by two scarious and tubular sheaths; without an annulus. **Leaves** slightly coriaceous, spathulate, obtuse to retuse or emarginate, 1-3,5  $\times$  0,7-1,5 cm, green and plane on the upper side, green and purple and convex on the lower side; base narrow attenuate or cuneate-attenuate; margin minutely crenulate. **Inflorescence** apparently basal, two per stem, a 2-3-flowered receme, subtended at the base by a scarious, acute sheath, of 3 mm in length; peduncle straight, up to 3 mm long, with various bracts; axis 3 mm long. **Pedicels** 0,5 mm long, fused partially with the axis; bract membranous, slightly conduplicate and acute, 2 mm long. **Flowers** resupinate or not, anthesis successive. **Sepals** thickened, whitish with purple towards the tip, narrow ovate to lanceolate, acute, 3-veined, distinctly carinate; margin entire; **dorsal** sepal free, 5,8-6,2  $\times$  2-2,4 mm; the **lateral** ones connate at the very base, slightly falcate, 5,8-6,2  $\times$  2-2,4 mm. **Petals** membranous, whitish, mottled with purple, spathulate, acuminate, 1-veined, 5  $\times$  1,7 mm; margin minutely crenulate or denticulate above. **Labellum** thickened, whitish and purple, panduriform, subacute, 3,5  $\times$  1,3-1,5 mm when expanded; upper side with a basal elongated depression covered by transverse calli, by two verrucate calli in the middle and warts in the upper part; base truncate, subcordate; margin biauriculate and antrorse below the middle, crenulate in the upper part. **Column** whitish or light reddish, elongated, slightly curved inwards, apically winged, 2-2,5 mm long; foot 0,5 mm long; clinandrum winged. **Anther** subapical; pollinia 8, pyriform to claviform, sculpture psilate. Stigma ventral. **Ovary** 1-1,5 mm long, glabrous. **Capsule** slightly ribbed. – Fl.: V-VII, Fr.: V-VIII.

**Distribution**: Endemic in East Cuba: Ho, SC (Sierra del Cristal: Río Lebisa), Gu

(Yateras: Palenque, Loma Bernardo[?]; Maisí). Epiphytic; prefers humid and shady to open conditions like the banks of waterways in gallery forests or, rarely, montane rainforests from 300 to 800 m, restricted to the vegetation on serpentine rock. Rare.

***Pleurothallis gelida* Lindl.** in Bot. Reg. 27: misc. 91, no. 186. 1841.  $\equiv$  *Stelis gelida* (Lindl.) Pridgeon & M. W. Chase in Lindleyana 16: 263. 2001. Holotype: "Loddiges, Nov. 1841" [Jamaica], Loddiges (K-L!). – Fig. 15.

= *Pleurothallis univaginata* Lindl. in Ann. Mag. Nat. Hist., ser. 3, 1: 326. 1858. Lectotype (Luer 2000: 69, specified here): "in Cuba Orientali, 1856-7" [Filantropia or Loma del Gato] [blue label], Wright 656 p.p. (K-L!; isoelectotypes?: G!, K!).

**Herbs**, caespitose, 20-55 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** ascending, 12-30 cm long, 2-articulated, partially covered by three tubular sheaths, carinate; annulus present. **Leaves** coriaceous, obliquely lanceolate to narrow elliptic or oblong, often conduplicate, acute to obtuse, 8-25  $\times$  4-8 cm, green, glabrous; base attenuate; margin entire. **Inflorescence** a terminal raceme, erect or ascending, 1-4 per stem, multi-flowered, subtended at the base by a oblong and falcate sheath of 2-3 cm in length; peduncle glabrous, 0,5-1,5 cm long, with two bracts; axis glabrous, 11-17 cm long. **Pedicels** 3-4 mm long, basally fused by 1 mm with the axis; bract membranous, tubular, 2-3 mm long. **Flowers** resupinate, with an simultaneous? anthesis. **Sepals** membranous, yellowish, 3-veined, basally connate, acute; margin apically crenulate; **dorsal** sepal ovate, 4,9-5,1  $\times$  2,7-2,8 mm; the **lateral** ones forming a mentum with the tip of the ovary, oblique-ovate, 4,9-5,1  $\times$  2,5 mm, the upper part internally papillose. **Petals** membranous, whitish, obovate, rounded or emarginate, 3-veined, 3  $\times$  2 mm; margin apical slightly erose. **Labellum** membranous, partially thickened, whitish, oblong to narrow obovate, slightly trilobate, recurved, rounded, 2,1  $\times$  1 mm when expanded, midlobe suborbicular, the lateral ones less distinct, antrorse; upper side papillose below the middle and with two elongated calli beyond the middle; base short clawed; margin apically slightly crenulate. **Column** whitish, short, slightly curved inwards, up to 2 mm long; foot 0,8-1 mm long; clinandrium somewhat winged and denticulate. **Anther** apical; pollinia 2, broadly ovate, sculpture granulate to subgemmate. Stigma ventral. **Ovary** 1,3 mm long, glabrous. **Capsule** 5-11 mm long, obovate, glabrous, ribbed. – Fl.: X-XII, Fr.: X-I.

**Distribution:** Subtropical and Tropical America from Flórida to South America (Brasil, Bolivia), Greater Antilles. Present in West Cuba: PR (Pan Guajaibón; Sierra del Rosario: Lomas Rangel); Central Cuba: Ci (Sierra de Escambray: Pico San Juan), VC (Escambray: Pico El Tuerto; lomas in the alrededores Manantiales), SS (Trinidad: Pico Potrerillo); East Cuba: Gr, Ho, SC, Gu. Epiphytic or Lithophytic; prefers open to shady places like rocks or tree canopies in vegetation of the mogotes, gallery forests, evergreen mesophyllous forests, montane rainforests and secondary forests (cupeyales). Scattered.

***Pleurothallis gemina* H. Stenzel** in Lindleyana 16: 28. 2001. Holotype: "Cuba, Holguín, Sierra de Nipe, La Mensura, ladera norte, 20°29'30N 75°48'21Oe, bosque latifolia", 850 msm, 24-IV-1998, Stenzel & Matos 452 (Holotype HAJB!; isotype: JE!). – Fig. 16.

**Herbs**, subrepent, 5-10 mm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, ascending, 1-1,5 mm long, 3-articulated, entirely covered by three hyaline sheaths; annulus present. **Leaves** slightly thickened, broadly oblong to obovate or spatulate, obtuse to rounded, minutely tridentate, 4-8  $\times$  2-4,5 mm, green, covered with small warts on the upper side, glabrous on the lower side; base attenuate; margin entire. **Inflorescence** a terminal raceme, erect to ascending, solitary, generally with two simultaneously open flowers; peduncle glabrous, 2-4 mm long, with two bracts; axis glabrous, 2 mm long. **Pedicels** up to 2 mm long, free; bract membranous, tubular or infundibuliform, up to 1 mm long. **Flowers** resupinate, with simultaneous anthesis. **Sepals** membranous to slightly thickened, whitish, 3-veined, acute, tips thickened and greenish; margin entire; **dorsal** sepal free, narrow ovate to lanceolate, 3-3,3  $\times$  1-1,3 mm; the **lateral** ones connate basally, forming a mentum with the tip of the ovary, lanceolate, slightly carinate on the outside, 3-3,3  $\times$  1 mm. **Petals** membranous, white, narrow oblong to

spathulate, obtuse, 1-veined,  $1,7 \times 0,5$  mm; margin entire. **Labellum** slightly thickened, white, entire, narrow elliptic, obtuse,  $2 \times 1$  mm when expanded; upper side with two calli bordering a central depression; base truncate; margin entire, winged and antrorse in basal and central part. **Column** white to greenish white, slender, curved inwards, 1,2 mm long; foot 0,5 mm long, with two minute calli; clinandrium winged, entire. **Anther** apical; pollinia 2, oblique, reni- to lentiform, sculpture psilate to punctate. Stigma ventral. **Ovary** 1 mm long, glabrous. **Capsule** 3-4 mm long, glabrous, ribbed. – Fl.: III-VI, Fr.: III-VII.

**Distribution**: Endemic in East Cuba: Ho, SC (Sierra del Cristal: headwaters of the Río Lebisa). Epiphytic; prefers shady and humid places in montane rainforests, mesophyllous evergreen rainforests and charrascales from 300 to 900 m, exclusively in vegetation on soils derived from serpentine. Scattered.

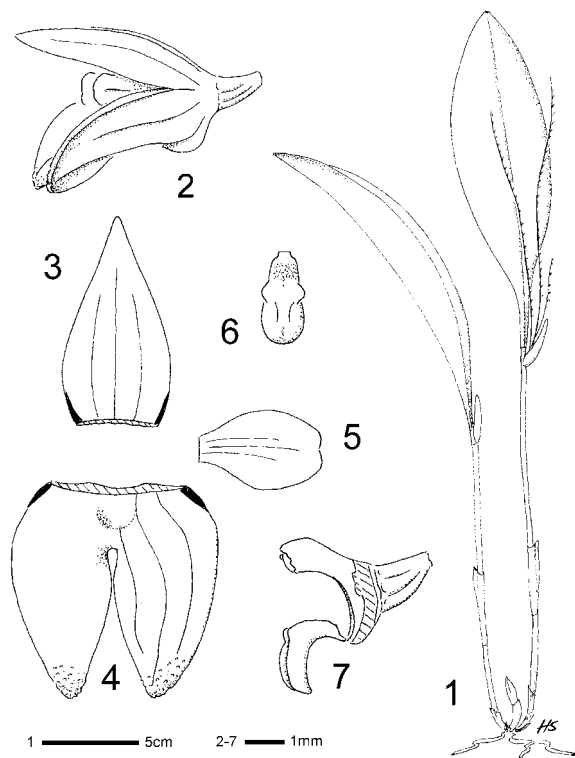


Fig. 15: *Pleurothallis gelida* Lindl.  
1 – Plant. 2 – Flower. 3+4 – Sepals. 5 – Petal.  
6 – Lip. 7 – Lip, ovary and column in natural position.

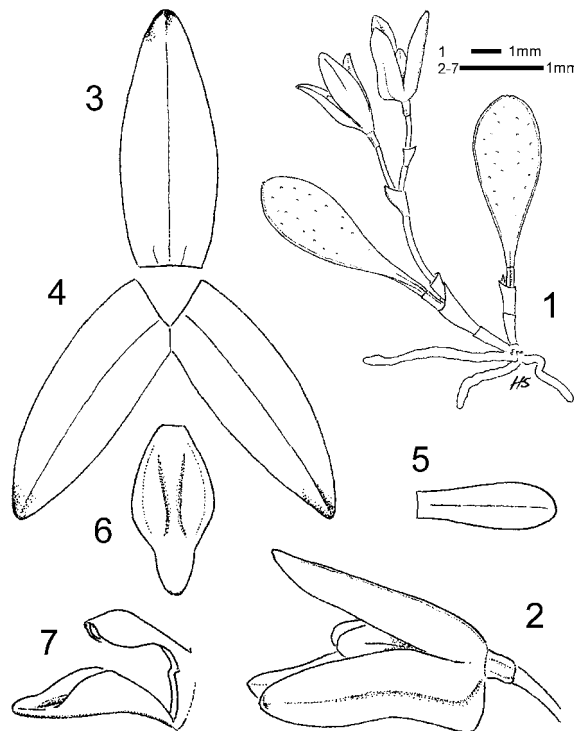


Fig. 16: *Pleurothallis gemina* H. Stenzel  
1 – Plant. 2 – Flower. 3+4 – Sepals. 5 – Petal.  
6 – Lip. 7 – Lip, ovary and column in natural position.

***Pleurothallis ghiesbreghtiana* A. Rich. & Galeotti** in Ann. Sci. Nat., Bot., ser. 3, 3: 16. 1845. Holotype: "Mexique, Province d' Oaxaca", 1842, Ghiesbreght ex herb. Richard (P No. 226376 [photo!], W ex herb. Reichenbach Orch. No. 53684 [fragment of holotype!]). – Fig. 17.

= *Pleurothallis longissima* Lindl., Folia Orchid. *Pleurothallis*: 31. 1859. Holotype: "*Pleurothallis racemiflora* Nob., Hort. Loddiges" [Jamaica, according to Loddiges], 1824, Loddiges (K-L!).

– "*Pleurothallis racemiflora*" sensu Adams (1972: 107), Luer (1975a: 204, 2000: 79), Ackerman (1995: 132), Gloudon & Tobisch (1995: 176), Nir (2000: 299), Pridgeon & Chase (2001: 250) (non *Pleurothallis racemiflora* (Sw.) Lindl., non "*Pleurothallis racemiflora* Lindl. ex Lodd." nom. inval.).

**Herbs**, caespitose and erect, 10-25 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** erect, 4-10 cm long, 2-articulated, completely or partially covered by three scarious sheaths; annulus present. **Leaves** fleshy, narrow elliptic to narrow oblong, obtuse to rounded, minutely tridentate,  $6-12 \times 1,5-3$  cm, shiny green, slightly concave on

the upper side, convex on the lower side; base short attenuate; margin entire. **Inflorescence** a terminal raceme, erect, solitary, multi-flowered, subtended at the base by a conduplicate and acute sheath of 1-1,5 cm in length; peduncle erect, 1-5 cm long, with two bracts; axis erect, 4-11 cm long. **Pedicels** 5 mm long, free; bract membranous, tubular, oblique, acute, 3-4 mm long. **Flowers** resupinate, anthesis subsimultaneous. **Sepals** slightly thickened, yellowish, convex; margin entire; **dorsal** sepal barely basally connate with the lateral ones, narrow ovate, acute, 3-veined, 6-6,3 × 3-3,2 mm; the **lateral** ones connate to 1 mm below the tip, synsepal broadly elliptic to obovate, acute, bifid, carinate with minute warts on the keels, 6-veined, 6-6,3 × 3,5 mm. **Petals** membranous, yellowish, narrow ovate, acute, 3-veined, 5 × 2 mm; margin entire to slightly erose. **Labellum** thickened in the central portion, whitish, panduriform, trilobate, obtuse or retuse, 4 × 2 mm when expanded, midlobe suborbicular, the lateral ones broad, antrorse; upper side with two small calli in the middle; base truncate; margin crenulate to sinuate. **Column** whitish, slightly curved inwards, 3 mm long; foot 0,7 mm long; clinandrium winged with a denticulate margin. **Anther** apical; pollinia 2, obtusely triangular, sculpture punctate-octomeriaeform (s. Stenzel 2000). Stigma ventral. **Ovary** 2,5-3 mm long, glabrous, surcate. **Capsule** 7-8 mm long, ribbed. – Fl.: III-VIII, Fr.: III-X.

**Distribution**: Central America and Venezuela (Luer 2000), Antilles. Present in West Cuba: PR (Pan de Guajabón). Epiphytic, lithophytic or pseudoterrestrial in the litter layer; prefers shady to open places in dwarf forms of the montane rainforests from 600 to 700 m, in vegetation on limestone. Known only from one locality.

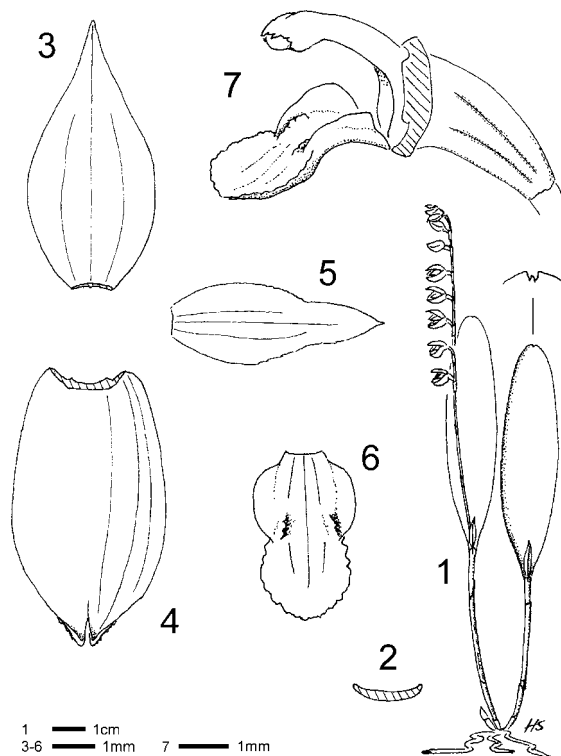


Fig. 17: *Pleurothallis ghiesbreghtiana* A. Rich. & Galeotti.  
1 – Plant. 2 – Leaf, cross section. 3+4 – Sepals. 5 – Petal. 6 – Lip. 7 – Lip, ovary and column in natural position.

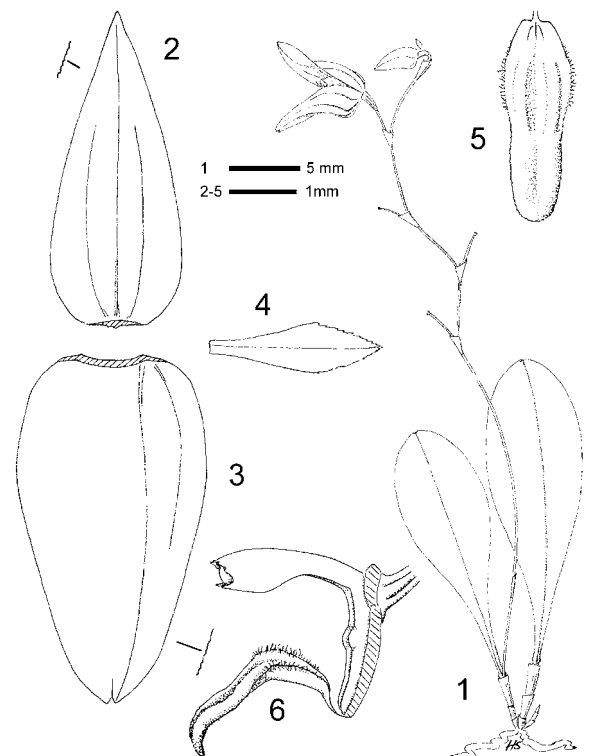


Fig. 18: *Pleurothallis grisebachiana* Cogn.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip. 6 – Lip, ovary and column in natural position.

***Pleurothallis grisebachiana* Cogn.** in Urban, Symb. Antill. 6: 409. 1909. Lectotype (designated here): “prope villam Monte Verde dictam, Cuba Orientali, Jan.-Jul. 1859”, [San André, according to Cogniaux (1909)], Wright 1503 p.p. ex herb. Grisebach (GOET!). – Fig. 18.

= *Pleurothallis blepharoglossa* Luer in Lindleyana 14: 111. 1999. Holotype: “Cuba,

Holguín: Moa, Camino a La Melba, Arroyo Las Comadres", 350 m, 29-XI-1997, Luer & al. 18654 (HAJBI; isotype MO [n.v.]).

– "*Pleurothallis grobyi*" sensu Lindley (1858: 326, 1860: 219), Nir (2000: 289) et auct. fl. cub. (non *Pleurothallis grobyi* Batem. ex. Lindl.).

**Herbs**, caespitose, 0,9-2 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, erect, 1,5-2 mm long, basally 3-articulated, entirely covered by three tubular sheaths; annulus present. **Leaves** slightly thickened, (narrow) spatulate, obtuse, minutely tridentate, 0,5-1,8 × 0,2-0,4 cm, green, glabrous; base narrow attenuate; margin entire or slightly erose in the upper part. **Inflorescence** a terminal raceme, ascending, solitary, 2-5(-10) flowers, subtended at the base by an ovate sheath of 0,5 mm in length; peduncle 0,5-1,5 cm long, with a bract; axis 0,5-3,5 cm long. **Pedicels** 1,2-2,2 mm long, fused to 0,5 mm with the axis; bract membranous, triangular, conduplicate, 0,8-1,1 mm long. **Flowers** resupinate, anthesis successive. **Sepals** membranous to slightly thickened along the nerves, yellow (sometimes with a tint of red), carinate; margin slightly papillose in the upper part; **dorsal** sepal free, narrow ovate, acute, 3-veined, 3,5-4,7 × 1,8-2,1 mm; the **lateral** ones connate to the tip, the base forming a mentum with the ovary, synsepal (narrow) ovate, bifid, 4-veined, 4-5,1 × 2,7-3 mm. **Petals** membranous, yellowish, narrow rhombic to spatulate, acute, 1-veined, 2-2,6 × 0,6-0,8 mm; margin serrulate or slightly crenulate. **Labellum** membranous, partially thickened, yellow with stripes of red, simple, narrow oblong, obtuse, 3-3,2 × 1 mm when expanded; upper side with two (rarely three) lengthwise red calli, bordering a central depression; base short clawed; margin ciliate, antrorse below the middle, papillose and revolute in the upper part. **Column** whitish, slender, carinate, 2,3 mm long; foot 1,4-1,6 mm long, with a elongated cavity and two orbicular calli; clinandrium winged, dentate at the tip; foot reddish. **Anther** apical; pollinia 2, spatulate, sculpture variably psilate or granulate. Stigma ventral. **Ovary** 0,9 mm long, glabrous. **Capsule** 3-4 mm long, glabrous, ribbed. – Fl.: II-VII, Fr.: II-VIII.

**Distribution**: Endemic in Central Cuba: Ci (Sierra de Escambray: lomas al sur of the Pico San Juan), SS; East Cuba: Ho, Gr (Guisa: Victorino; Río Jao), SC, Gu. Epiphytic or lithophytic; prefers shady and humid conditions in vegetation of the mogotes, gallery forests, montane rainforests, mesophyllous evergreen rainforests and secondary forests (cupeyales) from 300 to 800 m; indifferent to the type of the soil, on limestone as in vegetation on serpentine. Scattered.

Dod (1984: 107) includes "*Pleurothallis grobyi*" in a key of the species of *Pleurothallis* from Hispaniola, however, the description of the petals with an entire margin, does not correspond to the characteristics of *Pleurothallis grisebachiana*. There are collection insertion IJ and NY which are annotated as *Pleurothallis grisebachiana*, which in all cases show plants of *Pleurothallis curtisii* D.D.Dod.

**Variability**: Regarding coloration and size this species is highly variable which prompted Luer to publish *Pleurothallis blepharoglossa* Luer as distinct taxon.

***Pleurothallis helenae* Fawc. & Rendle** in J. Bot. 47: 4. 1909. = *Specklinia helenae* (Fawc. & Rendle) Pridgeon & M. W. Chase in Lindleyana 16: 258. 2001. Holotype: [uned. drawing] "*Pleurothallis Helenae*" [drawing by H. A. Wood, folios labelled "Botanical drawings by Miss Ward [sic!]" (IJ!). Epitype (designated here): "Jamaica: Mt. Moses", 1050 msm, Syme, J.P. [Jamaican Plants] 2279 (BM [ex herb. Morris] No. 82290!; isoeotype: NY No. 59937). – Fig. 19.

**Herbs**, caespitose, 0,7-1,6 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, 0,4-0,7 mm long, basally 2-articulated, entirely covered by two scarious, tubulosas sheaths; annulus present. **Leaves** slightly thickened, (narrow) spatulate, acute to obtuse, tridentate, 0,6-1,6 × 0,2-0,4 cm, green, glabrous; base narrow attenuate; margin entire. **Inflorescence** a terminal raceme, ascending, solitary, 2-6 flowers, subtended at the base by an ovate sheath of 0,4 mm in length; peduncle glabrous, filiforme, 1-1,8 cm long, with one bract; axis glabrous, slender, 0,5-1,7 cm long. **Pedicels** up to 4 mm long, free; bract membranous, triangular, conduplicate, reddish, 0,5-

0,8 mm long. **Flowers** resupinate. **Sepals** membranous, white and reddish, free, narrow ovate, slightly caudate, carinate; margin minutely papillose in the upper part; **dorsal** sepal 3-veined,  $3-3,1 \times 1$  mm; the **lateral** ones slightly falcate, 2-veined,  $3-3,1 \times 1$  mm. **Petals** membranous, hyaline, narrow ovate, acuminate, 1-veined,  $2,5 \times 1,1$  mm; margin profoundly serrate to lacerate. **Labellum** membranous, partially thickened, white, oblong, trilobate, obtuse, short apiculate,  $1,8-1,9 \times 1,1-1,2$  mm when expanded, midlobe thickened, broadly ovate with a circular disc, the lateral ones membranous, antrorse, serrate in the distal part; upper side with two central and short calli bordering a cavity; base truncate; margin minutely papillose in the upper part. **Column** whitish, curved inwards, 1,6 mm long; foot 0,4 mm long, with an elongated cavity; clinandrium slightly winged, denticulate. **Anther** apical; pollinia 2, amorphous, sculpture indistinct. Stigma ventral. **Ovary** 0,9 mm long, glabrous. **Capsule** 5-6 mm long, minutely papillose, ribbed. – Fl.: I-XII, Fr.: I-XII.

**Distribution:** Greater Antilles (except Puerto Rico). Present in East Cuba: Ho (Sierra del Cristal: cumbre), Gr (Victorino: Loma El Gigante), SC (Sierra Cobre: Loma del Gato; Gran Piedra). Epiphytic or lithophytic on twigs or rocks in mosses and lichens; prefers humid and partially open places like foggy mountain crests in elfin forests from 1000 to 1300 m, in vegetation on soils derived from serpentine or on volcanic rock. Rare.

**Reproduction biology:** The flowers set fruit without anthesis which suggests cleistogamy. This is indicated by the amorphous pollinia too.

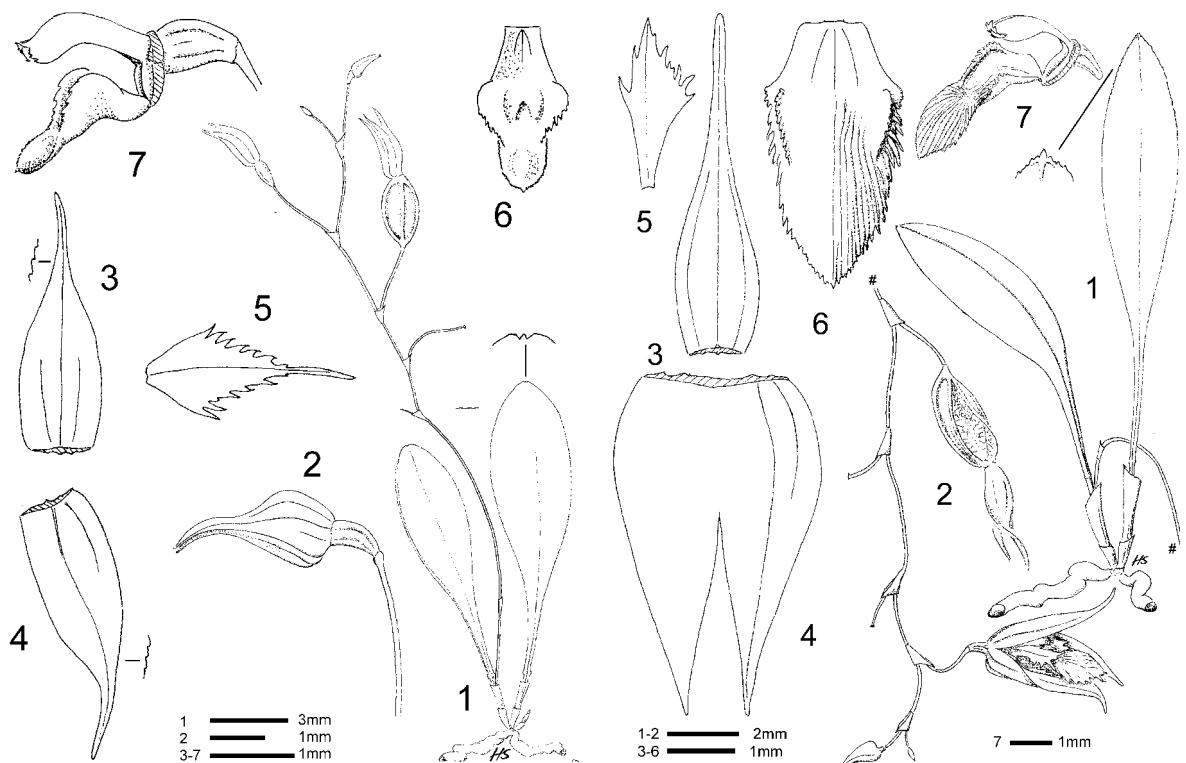


Fig. 19: *Pleurothallis helenae* Fawc. & Rendle  
 1 – Plant. 2 – Flower. 3+4 – Sepals. 5 – Petal.  
 6 – Lip. 7 – Lip, ovary and column in natural position.

Fig. 20: *Pleurothallis llamachoi* Luer  
 1+2 – Plant. 3+4 – Sepals. 5 – Petal. 6 – Lip.  
 7 – Lip, ovary and column in natural position.

***Pleurothallis llamachoi* Luer** in Lindleyana 13: 146. 1998. Holotype: "Cuba: Holguín, Mayarí, Sierra de Nipe, epiphytic in moist forest behind cabins of Agricultural Station", 650 m, 25-XI-1997, Luer & al. 18631 (HAJBI; isotypes: MO [n.v.], UPRRP [n.v.]). – Fig. 20.

**Herbs**, caespitose, 1-2 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, 2-2,4 mm long, basally 2-articulated, entirely covered by two scarious sheaths; annulus present. **Leaves** slightly thickened, narrow elliptic to oblanceolate, acute and short apiculate,  $0,8-1,7 \times 0,2-0,25$  cm, green, glabrous; base



narrow attenuate; margin denticulate beyond the middle. **Inflorescence** a terminal raceme, pendent or repent on or in the substrate, solitary, few-flowered, subtended at the base by an ovate sheath of 0,6 mm in length; peduncle glabrous, hair-like, 0,6-2 cm long, with a bract; axis glabrous, filiforme, 0,4-1,5 cm long. **Pedicels** 1,2-2,4 mm long, free or basally fused with the axis; bract membranous, triangular, conduplicate, reddish, 0,5-0,8 mm long. **Flowers** resupinate, anthesis successive. **Sepals** membranous and slightly thickened along the nerves, yellowish or whitish with purple stripes, lanceolate, carinate; margin entire; **dorsal** sepal free, apically attenuate to slightly caudate, 3-veined, 5-5,1 × 1,2-1,3 mm; the **lateral** ones connate almost to the middle, the base forming a mentum with the ovary, acute, 2-veined, 5-5,1 × 1,4 mm. **Petals** membranous, hyaline with purple nerves, oblique-spathulate, acute, 1-veined, 2,3-2,5 × 1,1-1,2 mm; margin profoundly serrate to lacerate in the upper part. **Labellum** slightly thickened, purple, narrow ovate, acute to subobtusate, 3,8-3,9 × 2-2,1 mm when expanded; upper side with two denticulate calli close to the margin and with purple stripes from the central portion to the marginal teeth; base truncate; margin serrate to fimbriate. **Column** light reddish, slender, curved inwards, 2,1 mm long; foot 0,6 mm long, with an elongated cavity; clinandrium winged and profoundly denticulate. **Anther** apical; pollinia 2, claviform, sculpture psilate. Stigma ventral. **Ovary** 0,7 mm long, glabrous. **Capsule** 3-4 mm long, glabrous, ribbed. – Fl.: III-VI, Fr.: III-VII.

**Distribution:** Endemic in East Cuba: Ho, Gu (Yateras: Pico Galán; Sierra Imías: Alto la Yamagua). Epiphytic; prefers humid and shady places in montane rainforests, gallery forests and charrascales from 400 to 900 m, restricted to the vegetation on serpentine rock. Rare.

***Pleurothallis longilabris* Lindl.** in Ann. Mag. Nat. Hist., ser. 3, 1: 328. 1858. Lectotype (designated here): "Cuba Orientali, 1856-7" [blue label], [Monte Verde, according to Wright in Lindley (1858)], Wright 651 p.p. (K-L!; isoelectotypes?: AMES No. 72372!, G!, G ex herb. Barbey-Boissier!, GOET!, NY No. 59923!). – Fig. 21.

**Herbs**, caespitose, 1-2 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, 1,5-2 mm long, basally 4-articulated, entirely covered by 4 scarious, conduplicate, acute sheaths; annulus present. **Leaves** slightly thickened, narrow elliptic to oblanceolate, acute and short apiculate, 0,8-1,8 × 0,2-0,4 cm, green, glabrous; base narrow attenuate; margin denticulate. **Inflorescence** a terminal raceme, ascending to pendent, solitary, few-flowered, subtended at the base by an ovate sheath of 0,8 mm in length; peduncle glabrous, filiforme, 1-1,5 cm long, with a bract; axis glabrous, flexuosus, filiforme, 1-2,5 cm long. **Pedicels** 3-4,5 mm long, fused to 0,8 mm with the axis; bract membranous, triangular, conduplicate, 0,9-1,2 mm long. **Flowers** resupinate, anthesis successive. **Sepals** membranous and slightly thickened along the nerves, hyaline, purple or with purple stripes, the upper part yellow, narrow ovate, acute, carinate; margin entire; **dorsal** sepal free, 3-veined, 4,8-5 × 1,7-1,8 mm; the **lateral** ones basally connate by 1,5-2 mm, forming a mentum with the tip of the ovary, slightly falcate, 2-veined, 4,8-5 × 1,5-1,6 mm. **Petals** membranous, hyaline, linear, acute, 1-veined, 2,9-3 × 0,9-1,1 mm; margin denticulate to lacerate. **Labellum** membranous, whitish, purple dark and yellow, trilobate, emarginate, 4,4-4,6 × 2-2,1 mm when expanded, midlobe thickened, the lateral ones obtuse-triangular, antrorse, profoundly serrate in the distal portion; upper side with a longitudinal callus, apically covered with papillae and dentiform calli; base truncate; margin serrate in the middle, apically denticulate. **Column** whitish, slender, curved inwards, 2,2 mm long; foot 0,6 mm long; clinandrium winged, margin denticulate. **Anther** apical; pollinia 2, elongated, claviform, sculpture psilate. Stigma ventral. **Ovary** 0,9 mm long, glabrous, red. **Capsule** 3-4 mm long, glabrous, ribbed. – Fl.: III-VI, Fr.: III-VII.

**Distribution:** Endemic in East Cuba: SC (Sierra del Cristal: headwaters of Río Lebisa), Gu (Sierra Imías: Alto la Yamagua). Epiphytic; prefers humid and shady places in mesophyllous evergreen rainforests and montane rainforests from 500 to 600 m, restricted to the vegetation on serpentine rock. Rare.

The collection *Picarda* (IJ) [without flowers] from Haití has the habitus of *P. longilabris*.

However, this morphology is not exclusively confined to the latter but occurs in closely related taxa too (e.g. *Pleurothallis aristata*). It is little probable that a presumed Cuban endemic, that is very rare and restricted in Eat Cuba itself, may occur on the neighbouring island. Dod (1984: 104) too expresses his doubts towards the occurrence of *Pleurothallis longilabris* on Hispaniola.

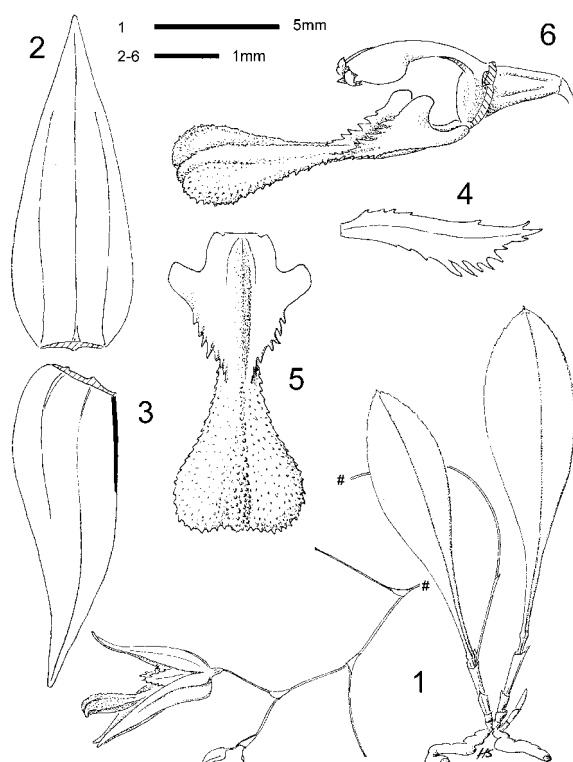


Fig. 21: *Pleurothallis longilabris* Lindl.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

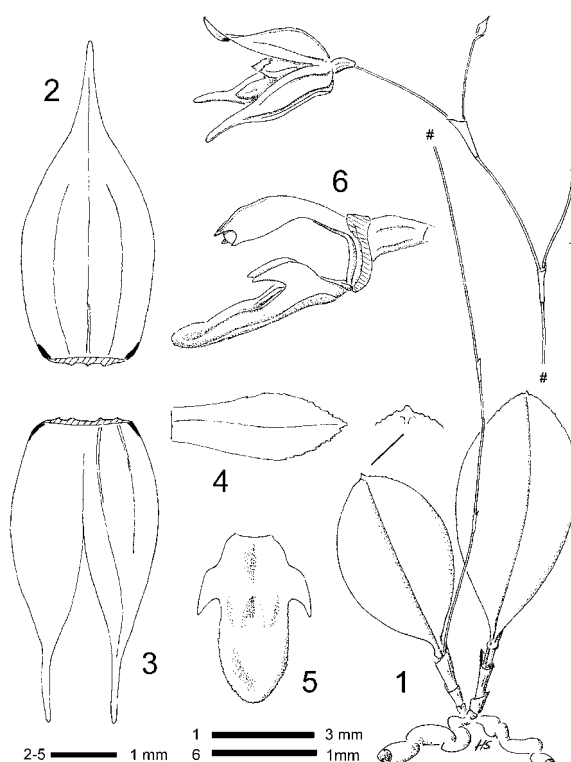


Fig. 22: *Pleurothallis mucronata* Lindl. ex Cogn.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

***Pleurothallis mucronata* Lindl. ex Cogn.** in Urban, Symb. Antill. 6: 424. 1909. Lectotype (designated here): "Cuba", Wright 1504 ex herb. Cogniaux (BR No. 843494!). – Fig. 22.

**Herbs**, caespitose, 0,5-1 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, densely aggregated, 0,8-1 mm long, basally 3-articulated, entirely covered by three membranous tubular and acute sheaths; annulus present. **Leaves** slightly thickened, elliptic to suborbicular, obtuse, short apiculate, 3-7(-9) × 3-3,5 mm, yellowish green and glabrous on the upper side, green and glabrous on the lower side; base short attenuate; margin minutely denticulate. **Inflorescence** a terminal raceme, ± straight, solitary, few-flowered; axis glabrous, filiforme, red, 1-5 cm long, subtended at the base by an ovate sheath of 0,7 mm in length; peduncle, 0,6-3 cm long, with various bracts; axis 0,4-2 cm long. **Pedicels** 2,5-4 mm long, fused to 0,9 mm with the axis; bract membranous, narrow triangular, conduplicate, 1-1,3 mm long. **Flowers** resupinate, anthesis successive. **Sepals** membranous, yellowish or whitish, often with a tint of red or reddish striped, carinate; margin entire; **dorsal** sepal connate basally with the lateral ones, narrow ovate, acuminate, 3-veined, 4-4,7 × 1,9-2 mm; the **lateral** ones connate basally and adnate up to the middle, the base forming a mentum with the ovary, lanceolate, short caudate, 2-veined, 4-4,6 × 1,1-1,2 mm. **Petals** membranous, yellowish and reddish, oblong to oblanceolate, acute, 1-veined, 2,5-2,6 × 1 mm; margin denticulate or crenulate above the middle. **Labellum** membranous and slightly thickened, yellowish and red, oblong, trilobate, subacute to obtuse, 2,5 × 1,6-1,7 mm when expanded, midlobe broadly oblong, slightly thickened, papillose, the lateral ones dentiform, antrorse; upper side with two papillose calli in the middle; base truncate; margin papillose. **Column** whitish, slender, 1,6-1,8 mm long; foot 0,5 mm long, with an elongated cavity; clinandrium winged and dentate in the tip, purple. **Anther** apical; pollinia 2, obtusely triangular,

sculpture psilate. Stigma ventral. **Ovary** 0,6 mm long, glabrous, red. **Capsule** 2-3,5 mm long, glabrous, ribbed. – Fl.: III-VI, Fr.: III-VII.

**Distribution:** Endemic in East Cuba: Ho, SC (Sierra del Cristal: headwaters of Río Lebisa), Gu (Sierra Imías: Alto la Yamagua). Epiphytic; prefers humid and shady to partially open conditions, usually along rivulets in gallery forests or rarely in montane rainforests from 500 to 800 m, restricted to the vegetation on serpentine rock. Scattered.

***Pleurothallis murex* Rchb. f.** in Flora 48: 276. 1865. Holotype: “Cuba, 1860-1864”, Wright 3348 (K!; isotypes?: AMES No. 72375 [photo!], BM No. 82331!, BR No. 843498!, G ex herb. Barbey-Boissier!, G ex herb. de Candolle!, GOET!, HAC ex herb. Sauvalle No. 3175!, W ex herb. Reichenbach Orch. No 54724! [fragment of lectotype?]). – Fig. 23.

– “*Pleurothallis trigonifolia et tuberculata*” according to Lindley (1860: 219) (nomina nuda).

**Herbs**, subcaespitose, 1,5-3 cm high (excluding the inflorescence). **Rhizome** very short, separating the ramicauls by < 1 mm. **Ramicauls** elongated, ascending to pendent, 1-2,2 cm long, basally 1-articulated, covered below the middle by 1-2 scarious sheath; without an annulus. **Leaves** thickened, triangular in transverse section, broadly ovate to suborbicular, rounded to obtuse, short apiculate, 0,5-0,8 × 0,4-0,6 cm, green and verrucate on the upper side, green and rough on the lower side; base obtuse to rounded; margin irregularly denticulate to profoundly crenulate with crenae up to 1 mm long (in sicco). **Inflorescence** a terminal raceme, pendent or ascending, 1-5 per stem, few-flowered, subtended at the base by a conduplicate, carinate and crenate sheath of up to 2 mm in length; peduncle glabrous, 0,7-1,5 cm long, with two or three bracts; axis glabrous, slightly flexuosus, 0,3-1,5 cm long. **Pedicels** 1-1,5 mm long, fused below the middle with the axis; bract membranous, infundibuliform, up to 1 mm long. **Flowers** resupinate, anthesis successive. **Sepals** membranous and slightly papillose along the nerves, yellowish and basally with a tint of red, carinate; margin somewhat papillose; **dorsal** sepal basally connate with the lateral ones, narrow obovate, acute, 1-veined, 2,7 × 1 mm; the **lateral** ones connate to 4/5, synsepal broadly ovate, rounded, bilobed, 4-veined, 2,5 × 2 mm. **Petals** membranous, hyaline, spathulate, apiculate, 1-veined, 1,1 × 0,6 mm; margin serrate in the upper part. **Labellum** membranous, yellowish, spathulate, trilobate, obtuse to rounded, 2 × 1,2 mm when expanded, midlobe oblong-orbicular, the lateral ones rhombic, antrorse, crenulate; upper side with two central and two basal callis; base truncate; margin papillose in the upper part. **Column** whitish, claviforme, 1,5 mm long; foot 0,4 mm long; clinandrium distinctly winged and apically serrate. **Anther** apical; pollinia 2, suborbicular, sculpture vermiculate-granulate. Stigma ventral. **Ovary** 0,5 mm long, papillose. – Fl.: XI, Fr.: XI-XII.

**Distribution:** Endemic in Central Cuba: SS (Yaguajay: Loma la Canoa); East Cuba: Gu (Sierra of the Frijol: Laga of the Galano). Epiphytic; prefers semi open places in vegetation of the mogotes or charrascales in 200 and 1000 m, in vegetation on soils derived from limestone or serpentine rock. Rare. Apart from the type collection only twice recollected.

Dod (1984: 107) and Nir (2000: 295) include *Pleurothallis murex* in the flora of Hispaniola, based on *Dod* 142. However, the fimbriate petals and lip do not coincide with the Cuban plants.

***Pleurothallis nummularia* Rchb. f.** in Flora 48: 276. 1865. ≡ *Phloeophila nummularia* (Rchb. f.) Garay in Orquideologia 9: 118. 1974. Lectotype (designated here): “Cuba: Monte Verde, Jan.-Jul. 1859, Wright 1513” [handwritten label], Wright 1513 (W ex herb. Reichenbach Orch. No. 42681!; isoelectotypes?: GOET!, K!, K-L!). – Fig. 24.

**Herbs**, repent, prostrate. Bracts, sheaths, ovary and capsule generally purplish hirsute. **Rhizome** elongated, separating the ramicauls by 2-4 mm long and covered by three tubular, scarious sheaths. **Ramicauls** very short, 0,2-0,5 mm long, 2-articulated, entirely covered by two scarious sheaths; without an annulus. **Leaves** coriaceous, suborbicular,

rounded to obtuse-retuse, tridentate,  $3-4,5 \times 2-3$  mm, dark green to purple, verrucate; base obtuse to short attenuate; margin slightly crenulate. **Inflorescence** terminal, erect, solitary, single-flowered; peduncle purple, without bracts, 0,8-1,4 cm long, basally subtended by a oblique, conduplicate sheath of 0,8 mm in length. **Pedicels** 2 mm long; bract membranous, infundibuliform, 2 mm long. **Flowers** resupinate. **Sepals** membranous, brownish purple, carinate; margin entire; **dorsal** sepal free, (narrow) ovate, acute, 3-veined,  $5,5-6,0 \times 3,5$  mm; the **lateral** ones entirely connate, synsepal ovate, acute to obtuse, 6-veined,  $5,5-6,0 \times 3,5?$  mm. **Petals** membranous, yellowish green [Wright in herb.], narrow oblong, acute, 3-veined,  $3 \times 0,7$  mm; margin denticulate and ciliate in the upper part. **Labellum** slightly thickened, yellowish green and basally, mottled with purple [Wright in herb.], linguiform to pandurate, slightly trilobate, acute to obtuse,  $2,5 \times 0,8$  mm when expanded; base truncate; margin antrorse below the middle, serrate in the upper part. **Column** yellowish green [Wright in herb.], slender, curved inwards, 2,5 mm long; foot 1 mm long; clinandrium winged. **Anther** apical; pollinia 2. Stigma ventral. **Ovary** 0,5 mm long. **Capsule** 1 cm long. – Fl.: III-VI, Fr.: III-VII.

**Distribution:** Cuba and Jamaica. Present in East Cuba: Ho (Sierra Nipe: Pinares Mayarí, La Caridad), SC (Sierra del Cristal: headwaters of the Río Lebisa), Gu (Sierra Imías: Alto la Yamagua). Epiphytic, on trunks; prefers humid conditions in gallery forests and montane rainforests from 500 to 700 m, in Cuba restricted to the vegetation on serpentine rock. Very rare. There is one collection from Jamaica (*Hesperheide!*: Cockpit Country, on limestone).

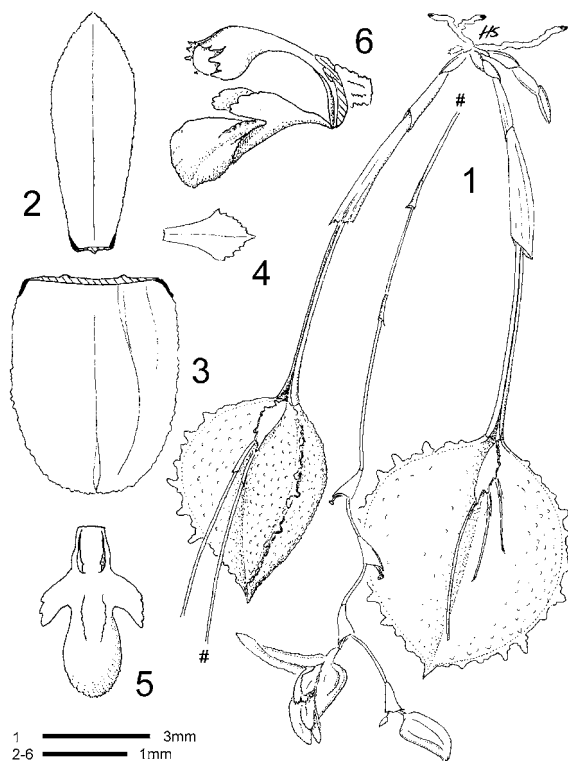


Fig. 23: *Pleurothallis murex* Rchb. f.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

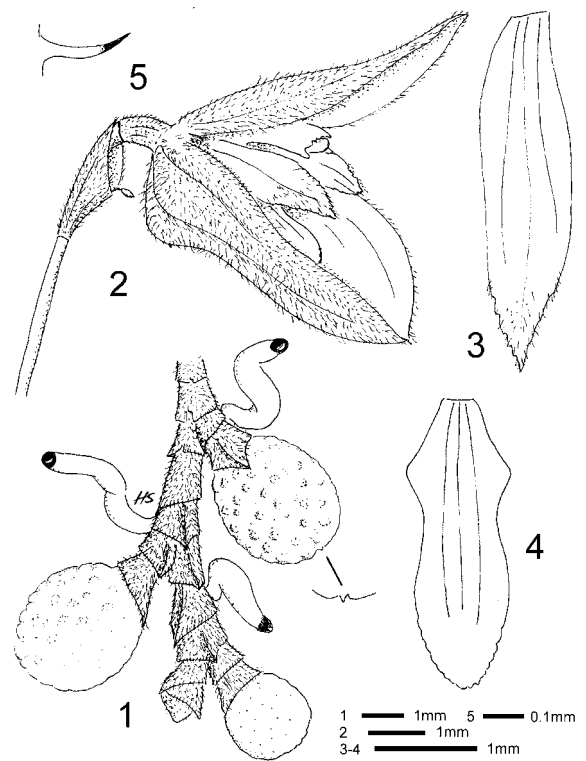


Fig. 24: *Pleurothallis nummularia* Rchb. f.  
1 – Plant. 2 – Flower. 3 – Petal. 4 – Lip.  
5 – Hair.

***Pleurothallis obliquipetala* Acuña & C. Schweinf.** in Bot. Mus. Leaf. 6(1): 3. 1938. = *Trichosalpinx acunae* Luer in Phytologia 54: 394. 1983. Holotype: "Cuba, Oriente, Estribo del Este, Pico Turquino", 1650 msm, 01-VIII-1935, Acuña 9540 (HAC!; isotypes: AMES No. 46830!, HAC ex herb Roig. No. 6644!, NY No. 59686 ex herb Roig. No. 6644!). – Fig. 25.

**Herbs**, caespitose, 0,8-1,7 cm high. **Rhizome** reduced. **Ramicauls** very short, 1-1,5 mm long, basally 3-articulated, entirely covered by three membranous sheaths; annulus

present. **Leaves** thickened, narrow elliptic to oblanceolate, acute to subobtusate, short apiculate,  $0,7-1,4(-1,6) \times 0,2-0,3$  cm, green on the upper side, green-purple on the lower side, glabrous; base narrow attenuate; margin minutely denticulate. **Inflorescence** a terminal, solitary raceme, erect, 2(-3) flowers, subtended at the base by an ovate sheath of 0,8 mm in length; peduncle glabrous, 1,5-2,5 mm long, with a bract; axis glabrous, 1-2 mm long. **Pedicels** 1-1,6 mm long, barely basally fused with the axis; bract membranous, tubular to infundibuliform, 0,9-1,1 mm long. **Flowers** resupinate, anthesis successive. **Sepals** membranous and slightly thickened along the nerves, whitish with purple stripes and yellow tips, carinate; **dorsal** sepal connate basally with the lateral ones, lanceolate, apically attenuate to slightly caudate, 3-veined,  $3,9-4,1 \times 1,1$  mm; margin entire; the **lateral** ones connate up to the middle, ovate, falcate, caudate, 2-veined,  $4,2-4,3 \times 1,6$  mm; margin minutely denticulate in the middle. **Petals** membranous, hyaline and purple, oblique rhombic, acute, 1-veined,  $2 \times 1$  mm; margin denticulate in the upper part. **Labellum** slightly thickened, purple, oblong, trilobate, obtuse,  $3-3,1 \times 1,3$  mm when expanded, midlobe oblong, carinate and papillose, the lateral ones  $\pm$  straight, papillose, antrorse; upper side with two elongated verrucate calli; base truncate; margin papillose or crenulate. **Column** whitish and purple, slender, curved inwards, 1,8-1,9 mm long; foot 0,7 mm long, with an elongated cavity; clinandrium distinctly winged and apically denticulate. **Anther** apical; pollinia 2, elongated, claviform, sculpture psilate. Stigma ventral. **Ovary** 0,6 mm long, glabrous, red. **Capsule** 3-3,5 mm long, glabrous, ribbed. – Fl.: VIII-I, Fr.: VIII-II.

**Distribution:** Endemic in East Cuba: Gr (Sierra Maestra: falda norte of the Pico Turquino), SC (Sierra Maestra: Pico Turquino; Sierra del Cobre: Loma del Gato; Gran Piedra). Epiphytic or lithophytic on base of trunks or on rocks; prefers shady and humid places in montane rainforests and cloud forests from 1100 to 1700 m, in vegetation on soils derived from volcanic rock. Rare.

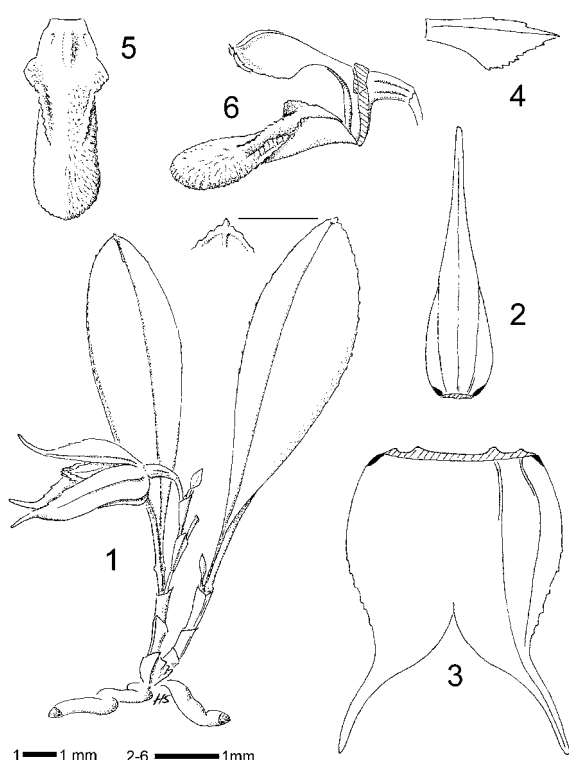


Fig. 25: *Pleurothallis obliquipetala* Acuña & C. Schweinf.

1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip. 6 – Lip, ovary and column in natural position.

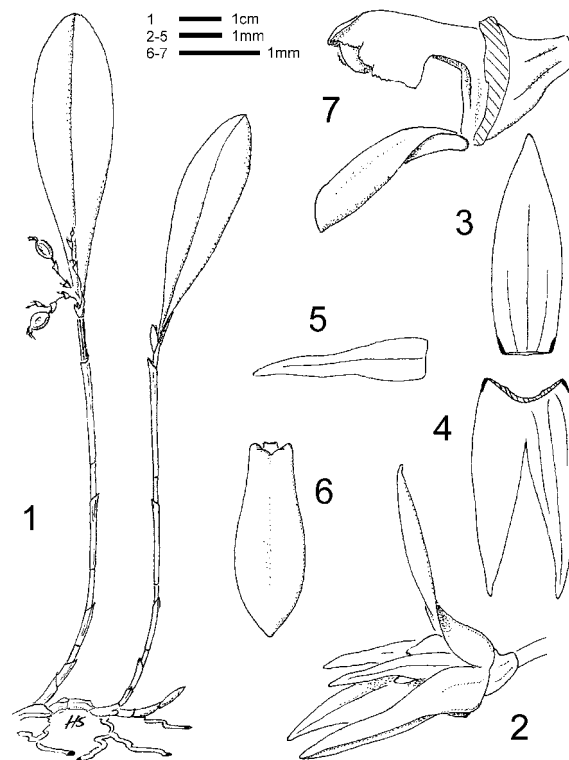


Fig. 26: *Pleurothallis obovata* (Lindl.) Lindl.

1 – Plant. 2 – Flower. 3+4 – Sepals. 5 – Petal. 6 – Lip. 7 – Lip, ovary and column in natural position.

***Pleurothallis obovata* (Lindl.) Lindl.** in Bot. Reg. 28: misc. 75, no. 51. 1842.  $\equiv$  *Specklinia obovata* Lindl. in Bot. Reg. 25: misc. 86, no. 137. 1839.  $\equiv$  *Anathallis obovata* (Lindl.) Pridgeon & M. W. Chase in Lindleyana 16: 250. 2001. Lectotype (Luer 1999: 115):

"*Specklinia obovata*" [Brasil], anón. (K-L!). – Fig. 26.

= *Pleurothallis albida* Lindl. in Ann. Mag. Nat. Hist., ser. 3, 1: 327. 1858. Holotype: "in Cuba Orientali, 1856-7" [blue label], Wright 655 (K-L!; isotypes?: G ex herb. Barbey-Boissier!, K!).

**Herbs**, repent, 7-20 cm high. **Rhizome** elongated, separating the ramicauls by 4-15 mm, covered by three membranous sheaths of light brown. **Ramicauls** erect or ascending, lengthwise surcate (in sicco), 2,5-12 cm long, 4-5-articulated, partially covered by 4-5 sheaths; annulus present. **Leaves** coriaceous, narrow obovate, oblanceolate or subspathulate (rarely narrow elliptic), obtuse to rounded, rarely subacute, minutely tridentate, 4,5-9 × 1,7-2,8 cm, green, glabrous; base narrow attenuate; margin entire, slightly revolute. **Inflorescence** a terminal few-flowered raceme, 2-8 per stem, subtended at the base by an ovate and laterally compressed sheath of 0,5 cm in length; peduncle filiforme, 2 mm long, with a bract; axis fine, flexuosus, 3-13(-18) mm long. **Pedicels** up to 4 mm long, fused below the middle with the axis; bract membranous, infundibuliform or triangular, up to 3 mm long. **Flowers** resupinate, anthesis successive or simultaneous. Segments membranous, whitish to yellowish, acute; margin entire. **Sepals** 3-veined; **dorsal** sepal connate barely basally connate with the lateral ones, narrow ovate, 4,8-5,4 × 1,7-1,8 mm; the **lateral** ones connate basally by 1 mm, lanceolate to triangular, slightly falcate, 4,7-5,2 × 1,2-1,3 mm. **Petals** subulate, 1-veined, 4-4,2 × 1 mm. **Labellum** slightly thickened, yellowish, simple, narrow obovate to oblong, acute, 2,2-2,4 × 0,9 mm when expanded; base slightly papillose, truncate with two small lateral lobes; margin entire, apically revolute. **Column** whitish, 2 mm long; foot 0,7 mm long, with a cavity elongated; clinandrium distinctly winged and serrate. **Anther** apical; pollinia 2, pyriform, sculpture gemmate. Stigma ventral. **Ovary** 0,5-1 mm long, glabrous. **Capsule** 0,5 cm long, globose, glabrous, ribbed. – Fl.: VI-XII, Fr.: VI-I.

**Distribution**: Central America, Venezuela, Colombia (Luer 1999), Brasil, Greater Antilles (except Jamaica). Present in East Cuba: Gr, Ho, SC, Gu. Epiphytic or lithophytic; prefers open or shady places like rocks or the canopies of the trees in vegetation of the mogotes, mesophyllous evergreen rainforests, gallery forests and secondary forests (cupeyales) from 500 to 900 m, indifferente to the type of the soil. Scattered.

*Pleurothallis odontotepala* Rchb. f. in Flora 48: 275. 1865. Holotype: "Cuba, 1860-1864", Wright 3349 (K!; isotypes?: AMES No. 72381 [photo!], K ex herb. Prior!). – Fig. 27.

= *Pleurothallis brachypetala* Griseb., Cat. Pl. Cub.: 257. 1866. Holotype: "721, Cuba occ. Wr. 3349b, 1863" [handwritten label], Wright "3349b" (GOET!).

**Herbs**, subcaespitose, 3-7(-9) cm high. **Rhizome** reduced. **Ramicauls** erect or ascending, laterally compressed, lengthwise surcate, carinate, 1-4 cm long, basally 3-articulated, covered by three tubular, conduplicate sheath to beyond the middle; without an annulus. **Leaves** coriaceous, narrow ovate to elliptic, acute, tridentate, 2-5 × 0,8-1,8 cm, green, glabrous, carinate; base short attenuate to obtuse; margin entire, slightly revolute. **Inflorescence** a terminal raceme, ascending or prostradas on the foliar limb, 1-4(-7) per stem, 2-7 flowers, glabrous, subtended at the base by a conduplicate and acute sheath of 0,3-0,5 cm in length; peduncle rigid, 0,3-0,8 cm long, with a bract; axis rigid, 0,5-1 cm long. **Pedicels** 1,6-1,8 mm long, fused by 4/5 su longitud with the axis; bract slightly thickened, tubular, acute, carinate, 1,8-2 mm long. **Flowers** thickened, resupinate, anthesis successive or subsimultaneous. **Sepals** green with purple stripes, 3-veined, carinate, connate basally; margin papillose in the upper part; **dorsal** sepal pandurate, apically papillose on the inner side, obtuse or acute, 5,2-5,3 × 1,7-1,8 mm; the **lateral** ones free but adnate to 3 mm, ovate, falcate, acute, 4,9-5,1 × 2,1-2,5 mm. **Petals** light reddish, oblanceolate to spathulate, acute to short acuminate, 1-veined, 2-2,1 × 0,7-1 mm; margin minutely serrate in the upper part. **Labellum** purple, oblong to narrow obovate, trilobate, obtuse or acute, 2,9-3,1 × 1,8-1,9 mm when expanded, midlobe broadly ovate, papillose, the lateral ones rounded, antrorse; upper side lengthwise with two crenulate papillose calli, bordering a central verrucate disc; base cordate and short clawed; margin

crenulate or papillose beyond the middle. **Column** light reddish to purple, curved inwards, 1,9-2 mm long; foot 0,9-1 mm long, with an elongated depression; clinandrium winged. **Anther** apical; pollinia 2, obtusely triangular to suborbicular, sculpture granulate. Stigma ventral. **Ovary** 1-1,2 mm long, glabrous, surcate. **Capsule** 10-12 mm long, glabrous, ribbed. – Fl.: II-X, Fr.: II-XI.

**Distribution**: Greater Antilles (Jamaica and Cuba; Hispaniola fide Dod 1984: 105). Present in East Cuba: Gr (Sierra Maestra, Turquino, Buey Arriba, Pico Verde), SC (Gran Piedra). Epiphytic; prefers shady and humid places in montane rainforests from 600 to 1300 m, in vegetation on soils derived from volcanic rock. Locally common.

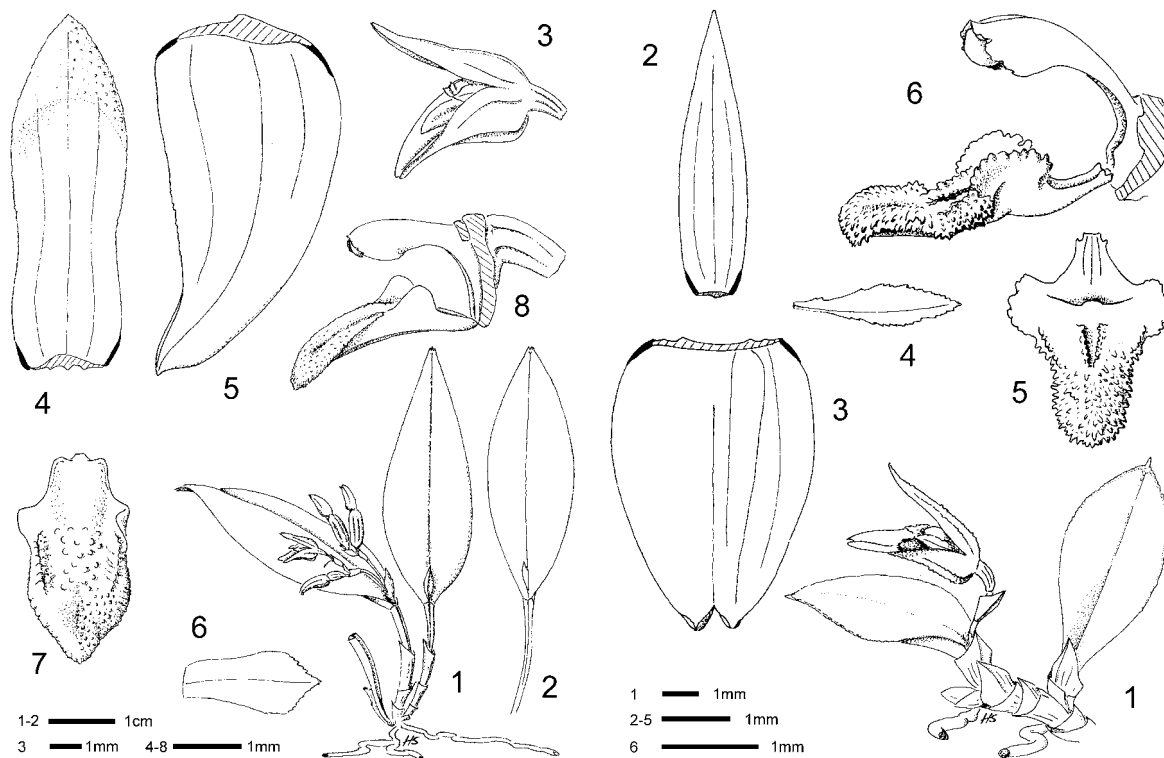


Fig. 27: *Pleurothallis odontotepala* Rchb. f.  
1 – Plant. 2 – Leaf shape variant. 3 – Flower.  
4+5 – Sepals. 6 – Petal. 7 – Lip. 8 – Lip, ovary  
and column in natural position.

Fig. 28: *Pleurothallis oricola* H. Stenzel  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

***Pleurothallis oricola* H. Stenzel** in Willdenowia 32(1): 101. 2002. Holotype: “Cuba: Pinar del Río, Peninsula de Corrientes, en el camino de María la Gorda a Cabo Corrientes, bosque siempreverde micrófilo sobre diente de perro, sobre *Vitex guanahacabibensis* Borhidi”, Urquiola & al. (HAJB!; isotype: B!, HPPR!). – Fig. 28.

**Herbs**, repent, 0,6-1,2 cm high. **Rhizome** short, separating the ramicauls by 1-2 mm long and covered by three scarious, somewhat conduplicate sheaths. **Ramicauls** very short, up to 0,5 mm long, 2-articulated, entirely covered by two scarious and hyaline sheaths; without an annulus. **Leaves** thickened, elliptic or slightly oblanceolate, prostrate, acute, short mucronate or apiculate, 0,5-0,8 × 0,2-0,4 cm, green to greyish green, verrucate on the upper side, glabrous on the lower side; base (short) attenuate; margin crenulate to erose. **Inflorescence** terminal, two per stem, single-flowered; peduncle 2 mm long, basally with an ovate bract 1 mm long. **Pedicels** and bract up to 1 mm long; bract membranous, oblique, slightly conduplicate. **Flowers** resupinate. **Sepals** membranous and slightly thickened along the nerves, greenish, mottled with purple, carinate; margin entire or papillose; **dorsal** sepal connate basally with the lateral ones, lanceolate, acute, 3-veined, 4-4,5 × 1 mm; the **lateral** ones connate basally but adnate almost up to the tip, the base forming a mentum with the ovary, synsepal ovate, bifid, 6-veined, 4-4,5 × 3 mm. **Petals** membranous, whitish, nerves and base purple, oblique oblanceolate, acute, 1-veined, 2,5 × 1 mm; margin dentate. **Labellum** thickened in the middle and membranous

in the marginal parts, yellowish, mottled with purple, ovate, trilobate, obtuse,  $3,2 \times 2,5$  mm when expanded, midlobe oblong, densely covered by dentiform calli, the lateral ones antrorse; upper side with a cavity basal and two calli lengthwise verrucate in the middle; base clawed, biauriculate; margin crenulate to erose in central part, serrate to denticulate above. **Column** yellow, mottled with purple, slightly curved inwards, 2 mm long; foot 0,6 mm long, with two calli; clinandrium slightly winged, serrate or dentate in el margen. **Anther** apical; pollinia 2. Stigma ventral. **Ovary** 1 mm long, somewhat papillose or verrucate. **Capsule** up to 0,5 cm long, with ribs slightly verrucate. – Fl.: IV-V, Fr.: V.

**Distribution:** Endemic in West Cuba: PR (Guanahacabibes: between Cabo Corrientes and Maria La Gorda). Epiphytic; prefers open to shady places in mesophyllous evergreen rainforests in low elevations, exclusively in vegetation on limestone. Known from only one locality.

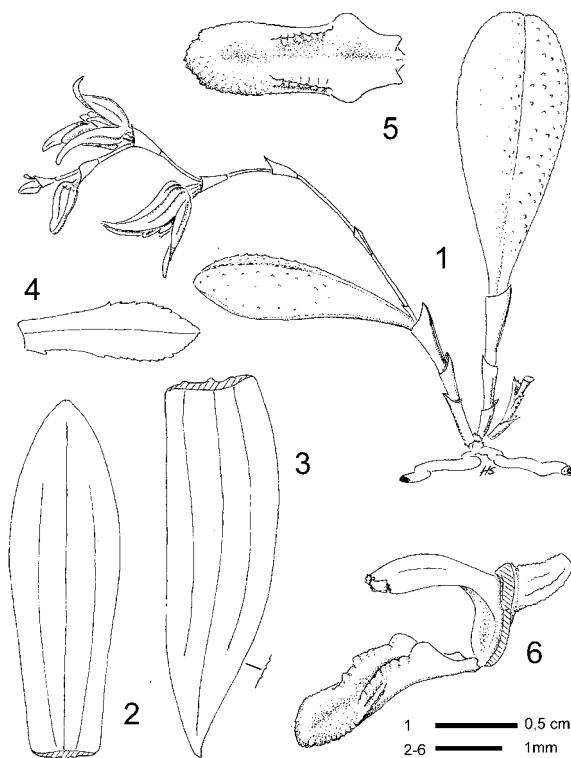


Fig. 29: *Pleurothallis papulifolia* Luer  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

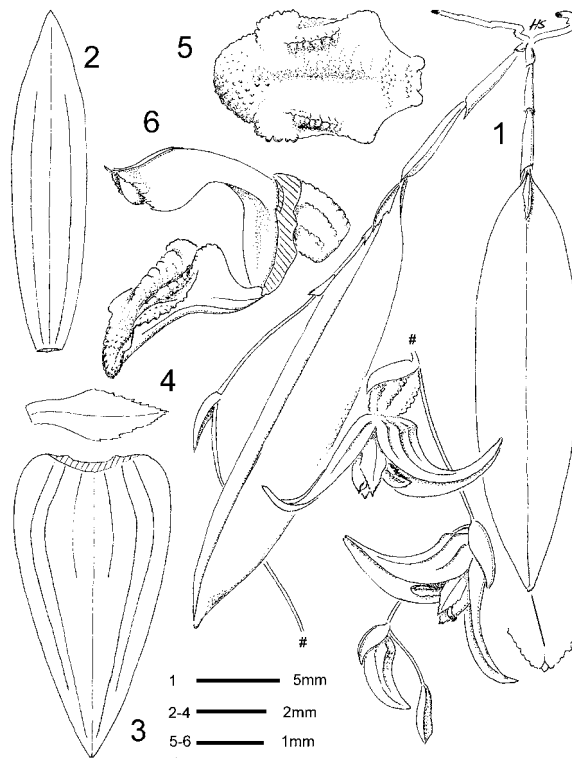


Fig. 30: *Pleurothallis prostrata* Lindl.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

***Pleurothallis papulifolia* Luer** in Lindleyana 14: 116. 1999. Holotype: "Cuba, Moa, entre Alto de la Calinga y el Toldo, suelo serpentina", 21-IV-1985, Panfet & Silva (HAJB!). – Fig. 29.

**Herbs**, subcaespitose, 1,5-4 cm high (excluding the inflorescence). **Rhizome** very short, separating the ramicauls by 0,5-1 mm and covered by two tubular sheath. **Ramicauls** erect or ascending, 0,5-2 cm long, 3-articulated, completely covered by three infundibuliform, conduplicate and acute sheaths; without an annulus. **Leaves** thickened, oblanceolate or obovate to spatulate, rounded to retuse,  $1-3,2 \times 0,4-0,7$  cm, green, verrucate on the upper side, glabrous and carinate on the lower side; base attenuate; margin entire. **Inflorescence** a terminal raceme, ascending, 1-3 per stem, 2-6 flowers, subtended at the base by an ovate sheath of 1,8-2,2 mm in length; peduncle glabrous or with minute warts, 0,8-1,5(-2,5) cm long, with two bracts; axis slightly flexuosus, glabrous or with papillae, 0,7-2,0 cm long. **Pedicels** 1-1,3 mm long, fused below the middle with the axis; bract membranous, triangular, often minutely papillose, 1,6-1,8 mm long. **Flowers** resupinate or not, anthesis successive. **Sepals** slightly thickened, yellowish or greenish, the nerves red, 3-veined, acute, papillose-carinate; margin entire or minutely papillose;



**dorsal** sepal free, oblong-ob lanceolate, 5-5,2 × 1,5-1,7 mm; the **lateral** ones adnate to  $\frac{3}{4}$ , lanceolate, 5,4-5,5 × 1,6-1,7 mm. **Petals** membranous, hyaline, light purple, oblong-spathulate, acute, 1-veined, 2,5-2,6 × 0,7-0,8 mm; margin minutely denticulate in the upper part. **Labellum** thickened, purple, oblong, slightly trilobate, obtuse, 3,1-3,2 × 1,4 mm when expanded, midlobe oblong, papillose to granulate, the lateral ones glabrous, antrorse; upper side lengthwise with two calli, granulate in the middle; base abruptly attenuate, minutely biauriculate; margin thickened, verrucate to crenulate in the central and apical porción. **Column** pale green, curved inwards, 1,9-2 mm long; foot 0,7-0,8 mm long; clinandrium winged and apically denticulate, purple. **Anther** apical; pollinia 2, obovate, sculpture punctate to fossulate. Stigma ventral. **Ovary** 0,8 mm long, papillose. **Capsule** 6-7 mm long, papillose-ribbed. – Fl.: II-V, Fr.: II-VI.

**Distribution**: Endemic in East Cuba: Ho, Gu. Lithophytic or epiphytic; prefers open and humid places like the banks of rivulets in gallery forests, charrascales and pine-forests from 100 to 700 m, restricted to the vegetation on serpentine rock. Rare.

**Ecology**: Plants growing on river banks stand temporal inundations during the rainy season.

***Pleurothallis prostrata* Lindl.** in Ann. Mag. Nat. Hist., ser. 3, 1: 327. 1858. Lectotype (Luer 2000: 47, specified here): “in Cuba Orientali, 1856-7” [blue label], [Monte Verde, according to Wright in Lindley (1858)], Wright 629 (K-L!; isolectotypes?: AMES No. 72383 [photo!], BR No. 843509!, G!, G ex herb. Barbey-Boissier!, G ex herb. de Candolle!, GOET!, K!, W ex herb. Reichenbach Orch. No. 42708!). – Fig. 30.

**Herbs**, caespitose, pendent, 2-5(-6) cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** elongated, straight, surcate and carinate, 0,4-1,4 cm long, 3-articulated, entirely covered by three conduplicate sheaths; without an annulus. **Leaves** coriaceous and rigid, (linear) elliptic, acute, tridentate, 1,6-4,5 × 0,4-0,8 cm, green, glabrous, carinate; base acute to cuneate; margin minutely serrate. **Inflorescence** a terminal raceme, pendent, 1-3 per stem, 1-5 flowers, subtended at the base by a conduplicate and acute sheath of 2-3 mm in length; peduncle rough, 1-2 cm long, with two bracts; axis rough, flexuosus, 1-5 cm long. **Pedicels** 0,5 mm long, fused with the axis; bract slightly rigid, falcate, conduplicate, papillose along the keel, 2,8-3,2 mm long. **Flowers** resupinate because of the pendent inflorescence, anthesis successive. **Sepals** thickened and rigid, greenish, mottled with purple, papillose-carinate, acute, apically slightly recurved; margin entire or minutely papillose; **dorsal** sepal free, narrow elliptic, 3-veined, 9,8-10 × 2-2,2 mm; the **lateral** ones connate basally but adnate up to the tip, the base forming a mentum with the ovary, synsepal ovate, 6-veined, 8,7-9,2 × 4,5-5,0 mm. **Petals** membranous, hyaline, purple, elliptic, acute, 1-veined, 4,3-4,5 × 1,6 mm; margin apically serrate. **Labellum** thickened, whitish and purple, oblong, lengthwise plicate, slightly trilobate, obtuse to rounded, 3,2-3,3 × 2 mm when expanded, midlobe broad, verrucate, basally with two curled lobes, the lateral ones less distinct, obtuse, antrorse; upper side with two lengthwise granulate calli; base minutely auriculate; margin thickened, papillose to crenulate in el  $\frac{3}{4}$  superior. **Column** greenish and purple, curved inwards, 2,5 mm long; foot 1,2 mm long, with a elongated, shallow cavity; clinandrium distinctly winged, apically denticulate. **Anther** apical; pollinia 2, obtusely triangular, sculpture punctate to granulate. Stigma ventral. **Ovary** 0,9-1,2 mm long, papillose. **Capsule** 6-7 mm long, verrucate, ribbed. – Fl.: II-V, Fr.: II-VI.

**Distribution**: Endemic in East Cuba: Ho (Sierra del Cristal; Río Cabonico; Sierra Moa), Gu (Yateras: Pico Galán). Epiphytic; prefers humid and shady places in gallery forests, montane rainforests, charrascales from 600 to 800 m, exclusively in the vegetation on serpentine rock. Very rare.

**Ecology**: Apparently restricted to an arborescent species of the genus *Senecio* as phorophyte (Wright in herb. and pers. observ. in the field).

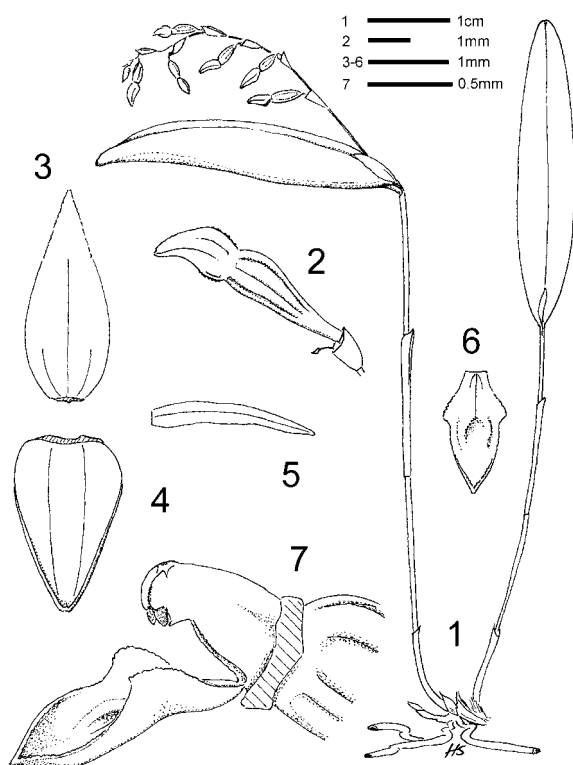


Fig. 31: *Pleurothallis pruinosa* Lindl.  
**1** – Plant. **2** – Fruit with persistent flower.  
**3+4** – Sepals. **5** – Petal. **6** – Lip. **7** – Lip, column and ovary in natural position.

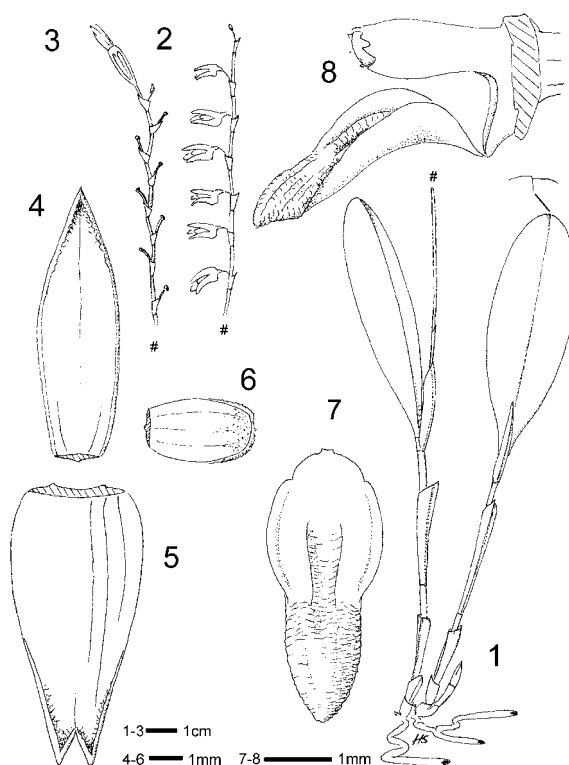


Fig. 32: *Pleurothallis racemiflora* (Sw.) Lindl.  
**1+2** – Plant. **3** – Rhachis with fruit.  
**4+5** – Sepals. **6** – Petal. **7** – Lip. **8** – Lip, column and ovary in natural position.

***Pleurothallis pruinosa* Lindl.** in Bot. Reg. 28: misc. 75, no. 55. 1842. Holotype: "Surinami, ad ramos Crescentiae, flores flavescentes", I-1838, Splitgerber 527 (K-L!; isotype: W ex herb. Reichenbach Orch. No. 17554!). – Fig. 31.

= *Pleurothallis brachyglottis* Rchb. f. in Flora 48: 275, 1865. Holotype: "Cuba, 1860-1864", [Monte Verde, 28-VIII, according to Wright in AMES], Wright 3344 (K!; isotypes?: AMES No. 72361 [photo!], GOET [n.v.]).

**Herbs**, subcaespitose to slightly repent, 4-9(-11) cm high (excluding the inflorescence). **Rhizome** very short, separating the ramicauls by 0,5-1 mm, covered by two sheaths. **Ramicauls** slender, erect or ascending, with base decumbente, 1,5-5(-7) cm long, 3-articulated, partially covered by three carinate sheaths of light brown color; without? an annulus. **Leaves** fleshy, narrow oblong-ovate or elliptic, acute to obtuse, minutely tridentate, 2,7-4 × 0,4-0,7 cm, green, glabrous; base acute to obtuse; margin entire. **Inflorescence** a terminal raceme, ascending or prostrate on the foliar limb, 1-4 per stem, 2-10 flowers, subtended at the base by a lanceolate, conduplicate, acute sheath of 0,5-0,7 cm in length; peduncle capillary, ascending, 0,5-1,5 cm long, with a bract; axis capillary, slightly flexuosus, 0,3-3 cm long. **Pedicels** 1-2 mm long, fused below the middle with the axis; bract membranous, tubular, obtuse, 1-2,5 mm long. **Flowers** resupinate. **Sepals** slightly thickened, whitish to yellowish; margin entire; **dorsal** sepal free, narrow ovate, acute, 3-veined, 2,5-2,6 × 0,9-1 mm; the **lateral** ones connate to the tip, synsepal ovate, subobtuse, 2-veined, 2-2,1 × 1,2-1,7 mm. **Petals** membranous, whitish, subulate, slightly falcate, acute, 1-veined, 1,9-2 × 0,25-0,3 mm; margin glabrous. **Labellum** thickened, whitish, narrow elliptic, slightly trilobate, acute, 1,4 × 0,8 mm when expanded, midlobe ovate, the lateral ones ± rectangular; upper side with two calli in the middle, bordering a shallow, suborbicular cavity; base truncate; margin minutely crenulate, antrorse. **Column** whitish, straight, thick, 0,8 mm long; foot reduced; clinandrium reduced. **Anther** apical with a reduced cap; pollinia 2, obovate or amorphous, sculpture psilate to lepanthiform (s.

Stenzel 2000). Stigma ventral. **Ovary** 2,5-3 mm long, glabrous, surcate. **Capsule** 7-8 mm long, glabrous. – Fl.: III-VI, Fr.: III-VII.

**Distribution**: Central America (Luer 1999), North of South America to Peru and the Guyanas, Antilles. Present in Central Cuba: SS (Trinidad); East Cuba: Ho (Sierra del Cristal: Río Lebisa), SC (Sierra del Cristal: headwaters of the Río Lebisa; Sierra Maestra: Loma del Gato), Gu. Epiphytic or lithophytic; prefers humid and shady places in mesophyllous evergreen rainforests, gallery forests and vegetation of the mogotes from 200 to 600 m, on limestone. Rare.

**Reproduction biology**: Some characteristics, like the generally closed flowers (Wright in herb. and pers. observ.) and the amorphous pollinia with a reduced and fragile exinous layer, suggest autogamy and probably cleistogamy in most of the Greater Antillean plants.

***Pleurothallis racemiflora* (Sw.) Lindl.** in Exot. Fl. 2: t. 123 [excl. fig. & descr.]. 1824. = *Epidendrum racemiflorum* Sw., Prodr.: 125. 1788. = *Dendrobium racemiflorum* (Sw.) Sw. in Nova Acta Regiae Soc. Sci. Upsal. 6: 83. 1799. Lectotype (Fawcett & Rendle 1910: 55, specified here): “*Epidendrum racemiflorum* Swartz”, Jamaica, Swartz (BM No. 82214!; isoelectotypes?: B ex herb. Willdenow No. 16896, G [n.v.], M [n.v.], S [photo!], S ex herb. Alstroemer [photo!], S ex herb. Swartz [photo!], W ex herb. Reichenbach Orch. No. 26616!). – Fig. 32.

= *Pleurothallis oblongifolia* Lindl. in Comp. Bot. Mag. 2: 355. 1837. = *Stelis oblongifolia* (Lindl.) Pridgeon & M. W. Chase in Lindleyana 16: 265. 2001. Holotype: “Jamaica, Loddiges”, 12-XI-1836 [cultivated], Loddiges (K-L!).

= *Pleurothallis multirostris* Rchb. f. in Linnaea 41: 49. 1877. Holotype: “E Jamaica allata. H.K. 9/73” [collected 1871 at Thompson Gap, flowered in Kew 8-IX-1873 according to Reichenbach in W], 8-IX-1873, anon. (K!).

= *Pleurothallis tricostata* Cogn. in Urban, Symb. Antill. 7: 175. 1912. Lectotype (designated here): [unedited drawing] “H. v. Türkheim no. 3481” [drawing by Cogniaux based on the holotype] (BR No. 843536!). Epitype (designated here): “República Dominicana: Prov. Azua, Las Lagunas”, 750 msm, 12-VI-1926, Ekman 6343 (K!; isoeotype: S [n.v.]).

– “*Pleurothallis racemiflora*” sensu Luer (2000: 80) and Pridgeon & Chase (2001: 250,266) (non “*Pleurothallis racemiflora* Lindl. ex Lodd.”, nom. inval.).

**Herbs**, subcaespitose, 10-20 cm high (excluding the inflorescence). **Rhizome** very short, separating the ramicauls by 1-2 mm, covered by two scarious sheaths. **Ramicauls** erect or ascending, 6-11 cm long, 2- articulated, partially covered by three scarious, conduplicate and carinate sheaths; annulus present. **Leaves** coriaceous, elliptic to obovate, obtuse to rounded-retuse, 4-9 × 1-2,5 cm, green, glabrous; base attenuate; margin entire. **Inflorescence** a terminal raceme, erect, solitary, multi-flowered, subtended at the base by a narrow oblong, falcate, laterally compressed sheath of 1-3,5 cm in length; peduncle straight, rigid, 3-10 cm long, with two bracts; axis 2-9 cm long, often flexuosus when fruit-bearing. **Pedicels** 4-5(-8) mm long, fused by 1-2 mm with the axis; bract membranous, infundibuliform, 2-4 mm long. **Flowers** resupinate, anthesis subsimultaneous. **Sepals** membranous and slightly thickened along the nerves, green-purple; margin involute, ciliate in the upper part; **dorsal** sepal free, lanceolate, acuminate, 3-veined, 8,5-9 × 2,3-2,6 mm; the **lateral** ones connate almost up to the tip, synsepal narrow ovate, acute, bifid, 6-veined, 8,5-9 × 4 mm. **Petals** slightly thickened, light reddish and purple, oblong, rounded to emarginate, 3-veined, internally along the nerves and in the upper part on the outside verrucate, 2,9-3,2 × 2-2,2 mm; margin papillose or erose. **Labellum** thickened and membranous, reddish, simple, oblong, acute, 3,7-3,9 × 1,8-2 mm when expanded; upper side in the middle with two less distinct calli and above the middle with two transverse calli; base abruptamente attenuate; margin entire and antrorse in the basal portion, apically crenulate, verrucate and revolute. **Column** light reddish, straight,

2,2 mm long; foot 0,8 mm long; clinandrum slightly winged. **Anther** apical; pollinia 2, obovate, sculpture octomeriaeform. Stigma ventral. **Ovary** 2-2,4 mm long, glabrous or verrucate, greenish purple. **Capsule** 1 cm long, ribbed. – Fl.: VI-X, Fr.: VI-XI.

**Distribution:** Greater Antilles. Present in West Cuba: PR (La Palma: Río San Marcos, Mil Cumbres); Central Cuba: Ci (Sierra de Escambray: Pico San Juan); East Cuba: Gr, SC, Gu (Sierra Imías: Alto la Yamagua and Tres Piedras). Epiphytic; prefers shady places in montane rainforests and cloud forests from 900 to 1500 m, usually in vegetation on soils derived from volcanic rock. Scattered.

**Variability:** The collection *Stenzel 888* is from vegetation on serpentine. These plants show a slightly different habitus, with the otherwise conspicuous spathe being reduced, dark purple colored flowers and other minor differences. However, unless more material from this area has been examined to evaluate the stability of these characteristics, it is not advisable to treat those populations as a separate subspecies.

***Pleurothallis rubroviridis* Lindl.** in Ann. Mag. Nat. Hist., ser. 3, 1: 327. 1858. = *Acianthera rubroviridis* (Lindl.) Pridgeon & M. W. Chase in Lindleyana 16: 246. 2001. Holotype: “in Cuba Orientali, 1856-7” [blue label], [Monte Verde, according to Wright in Lindley (1858)], Wright (K-L!). – Fig. 33.

= *Pleurothallis cubensis* Lindl. in Ann. Mag. Nat. Hist., ser. 3, 1: 328. 1858. = *Acianthera cubensis* (Lindl.) Pridgeon & M. W. Chase in Lindleyana 16: 243. 2001. Lectotype (designated here): “in Cuba Orientali, 1856-7” [blue label], [Monte Verde, 28-IV, according to Wright in K-L], Wright 653 (K-L!; isolectotypes?: AMES No. 72363 [photo!], K!).

**Herbs**, subcaespitose, 6-20 cm high. **Rhizome** very short, separating the ramicauls by 2-3 mm, covered by three tubular sheaths. **Ramicauls** elongated, erect or ascending, rigid, laterally compressed, surcate, 4-14 cm long, basally 2-articulated, to ¼ covered by two conduplicate sheaths; without an annulus. **Leaves** coriaceous and rigid, narrow elliptic to oblanceolate, acute, minutely tridentate, 2-6 × 1-2 cm, yellowish green, glabrous; base cuneate; margin erose. **Inflorescence** a terminal raceme very short, 1-3(-4) per stem, 2-3 flowers, subtended at the base by a falcate sheath of 0,6-0,8 cm in length; peduncle erect, 0,3 cm long, with two bracts; axis 0,2-0,5 cm long. **Pedicels** 1 mm long, entirely fused with the axis; bract membranous, infundibuliform, often papillose, 2-3 mm long. **Flowers** resupinate or not, anthesis successive. **Sepals** thickened, yellowish green, basally mottled with purple, verrucate on the inner side and papillose externally; margin entire; **dorsal** sepal free, pandurate, obtuse to subacute, 3-veined, 6,2-6,6 × 1,2-1,4 mm; the **lateral** ones connate almost up to the tip, synsepal ovate, lengthwise folded, obtuse, bifid, 6-veined, 5,9-6,2 × 2,1-2,3 mm. **Petals** thickened, purple, narrow obovate, slightly falcate, obtuse to rounded, 1-veined, 2,5 × 1,1 mm; margin slightly crenulate in the upper part. **Labellum** slightly thickened, greenish, simple, oblong to narrow ovate, obtuse to rounded, 2,5 × 1,5 mm when expanded; upper side lengthwise surcate from base almost up to the tip, with two elongated calli in the middle, verrucate in the ¼ apical; base biauriculate, short clawed; margin slightly crenulate or serrate. **Column** yellowish, slightly curved inwards, 2 mm long; foot 0,5 mm long; clinandrum winged. **Anther** apical; pollinia 2, suborbicular, sculpture punctate. Stigma ventral. **Ovary** 1 mm long, papillose. **Capsule** 0,5 cm long, verrucate. – Fl.: III-VI, Fr.: III-VII.

**Distribution:** Venezuela (Foldats 1970), Cuba. Present in East Cuba: SC (Sierra de Cobre: Loma del Gato; Gran Piedra), Gu. Epiphytic; prefers humid and shady or open places in montane rainforests and secondary formations, mesophyllous evergreen rainforests from 800 to 1200 m, in vegetation on lateritic soil derived from limestone. Rare.

**Variability:** Regarding the overall plant size *Pleurothallis rubroviridis* varies considerably. These differences prompted Lindley to describe the species a second time within the same paper. Both descriptions are based on material collected by Charles Wright.

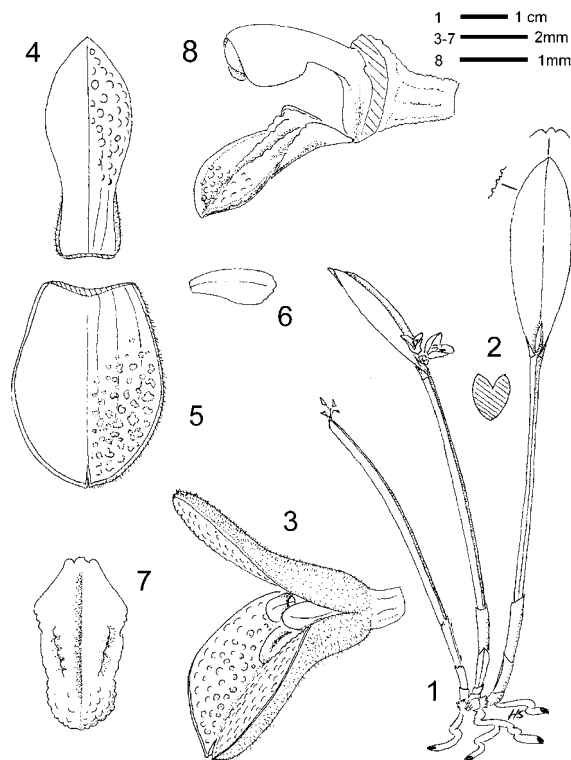


Fig. 33: *Pleurothallis rubroviridis* Lindl.  
1 – Plant. 2 – Leaf, cross section. 3 – Flower.  
4+5 – Sepals. 6 – Petal. 7 – Lip. 8 – Lip, ovary  
and column in natural position.

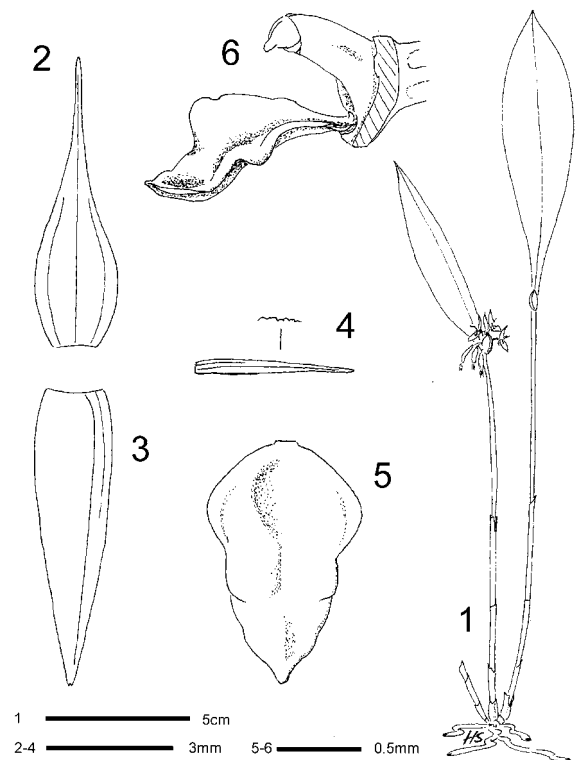


Fig. 34: *Pleurothallis ruscifolia* (Jacq.) R. Br.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

***Pleurothallis ruscifolia* (Jacq.) R. Br.** in Aiton, Hortus Kew. 2. 5: 211. 1813.  $\equiv$  *Epidendrum ruscifolium* Jacq., Enum. Syst. Pl. 29. 1760.  $\equiv$  *Dendrobium ruscifolium* (Jacq.) Sw. in Nova Acta Regiae Soc. Sci. Upsal. 6: 84. 1799. Holotype: [drawing] “*Ruscus? foliis solitariis lanceolato-ovatis*” [based on material from Martinica?] in Burman, Pl. Amer. t. 176, f. 2. 1758. – Fig. 34.

**Herbs**, subcaespitose, 15-35 cm high. **Rhizome** very short, separating the ramicauls by 2-3 mm, covered by three tubular sheaths. **Ramicauls** elongated, 11-21 cm long, 2-articulated, below the middle partially covered by two tubular sheaths; without? an annulus. **Leaves** oblanceolate to narrow elliptic, acute to subacuminate, tridentate, 4-14  $\times$  1-3,5 cm, green, glabrous; base attenuate; margin entire. **Inflorescence** a terminal multi-flowered fasciculus, subtended at the base by a suborbicular to broadly ovate and laterally compressed sheath of 0,4-0,6 cm in length. **Pedicels** up to 6 mm long, free; bract membranous, infundibuliform, up to 4 mm long. **Flowers** resupinate, anthesis successive or simultaneous. **Sepals** membranous, yellowish, carinate; margin entire; **dorsal** sepal free, lanceolate, slightly caudate, 3-veined, 6,5-7,5  $\times$  2-2,1 mm; the **lateral** ones entirely connate, synsepal lanceolate, acute, 4-veined, 6,5-7,5  $\times$  1,7-1,9 mm. **Petals** slightly thickened, yellowish, subulate, acute, 2-veined, 3,7-3,9  $\times$  0,3-0,4 mm; margin minutely serrate. **Labellum** slightly thickened, whitish, ovate, apiculate, 1,5-1,6  $\times$  0,9 mm when expanded; upper side basally with an orbicular papillose depression; base obtuse; margin membranous and antrorse below the middle, slightly sinuate in the upper portion. **Column** whitish, stout, slightly curved inwards, 0,8 mm long; foot reduced; clinandrium truncate; base with two calli. **Anther** apical; pollinia 2, oblong to claviform, sculpture psilate and lepanthiform. Stigma ventral. **Ovary** 1 mm long, glabrous. **Capsule** 5-8 mm long, ribbed. – Fl.: III-VIII, Fr.: VI-X.

**Distribution**: Tropical America from Costa Rica to Brazil and Bolivia, Antilles. Present in East Cuba: Gr, SC, Gu (Sierra de Imías: Alto Clavellinas). Epi- or lithophytic; in partially open places of gallery forests, montane rainforests and cloud forests, 400-1500 m. Rare.

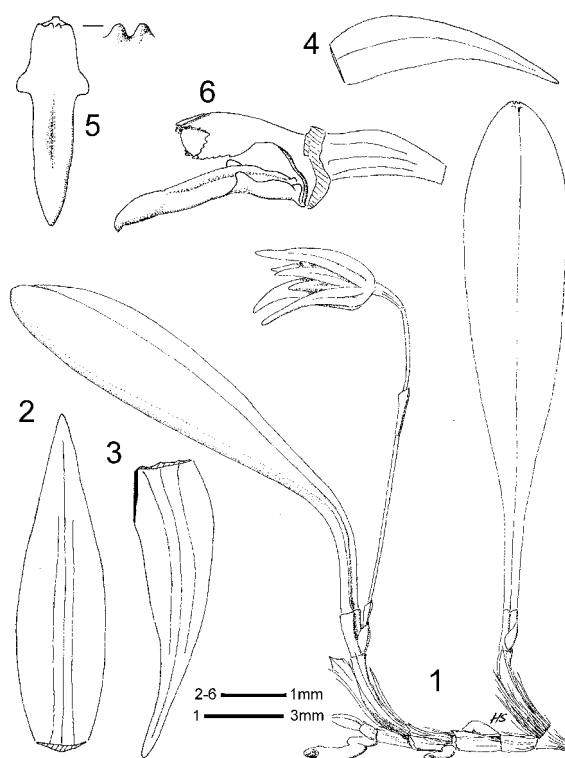


Fig. 35: *Pleurothallis sertularioides* (Sw.) Spreng.

1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip. 6 – Lip, ovary and column in natural position.

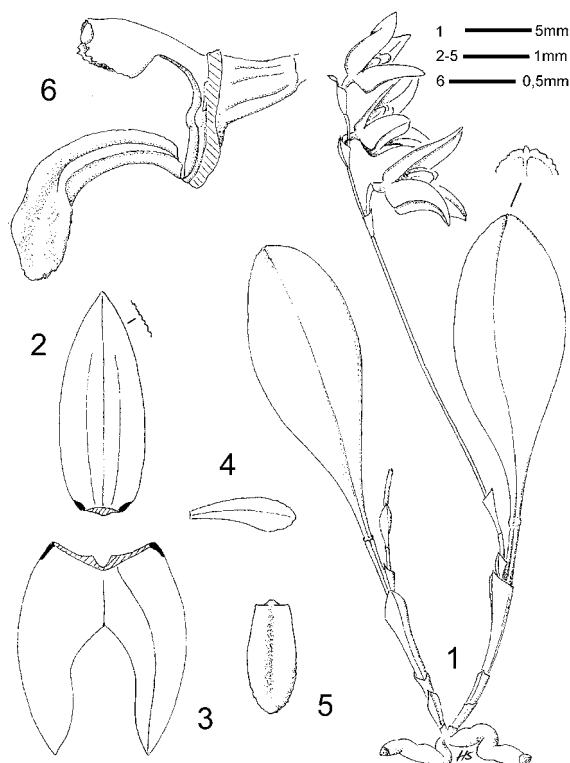


Fig. 36: *Pleurothallis shaferi* Ames

1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip. 6 – Lip, ovary and column in natural position.

***Pleurothallis sertularioides* (Sw.) Spreng.**, Syst. Veg. 3: 731. 1826.  $\equiv$  *Epidendrum sertularioides* Sw., Prodr.: 122. 1788.  $\equiv$  *Dendrobium sertularioides* (Sw.) Sw. in Nova Acta Regiae Soc. Sci. Upsal. 6: 83. 1799.  $\equiv$  *Specklinia sertularioides* (Sw.) Lindl., Gen. Sp. Orchid. Pl.: 8. 1830.  $\equiv$  *Anathallis sertularioides* (Sw.) Pridgeon & M. W. Chase in Lindleyana 16: 250. 2001. Lectotype (Fawcett & Rendle 1910: 65, specified here): “*Epidendrum sertularioides* Swartz, Jamaica”, Swartz (BM No. 82293!; isoelectotypes?: B ex herb. Willdenow 16895 [photo!], C [n.v.], G [n.v.], S [photo!], S ex herb. Alstroemer [photo!], W ex herb. Reichenbach Orch. No. 26610!). – Fig. 35.

**Herbs**, repent, 1,2-4,5 cm high. **Rhizome** elongated, separating the ramicauls by 0,2-0,5 cm, covered by three tubular sheath. **Ramicauls** very short, ascending, 0,2-0,4 cm long, basally articulated, entirely covered by a scarious sheath; annulus present. **Leaves** fleshy, oblanceolate to subspathulate, obtuse, minutely tridentate, 1-4  $\times$  0,3-0,4 cm, yellowish green, glabrous; base narrow attenuate; margin entire. **Inflorescence** a terminal raceme, erect, solitary (rarely two) per stem, 1(-2) flowers, subtended at the base by an ovate sheath of  $\pm$  1 mm in length; peduncle capillary, erect, 0,8-1,5 cm long, basally with a bract; axis (in two-flowered inflorescences) capillary, straight, 0,5 cm long. **Pedicels** 3-5 mm long, free; bract membranous, infundibuliform, acute, 1,5-2 mm long. **Flowers** resupinate, anthesis successive, segments whitish and apically yellow. **Sepals** membranous and slightly rigid, carinate, 3-veined, acute; margin entire; **dorsal** sepal free, lanceolate, 4,9-5  $\times$  1,1-1,2 mm; the **lateral** ones connate to 1 mm, sometimes adnate up to the middle, lanceolate to triangular, falcate, apically attenuate, 4,6-4,7  $\times$  1,1-1,2 mm. **Petals** membranous, lanceolate or subulate, falcate, acute, 1-veined, 3,4-3,5  $\times$  0,9-1 mm; margin entire. **Labellum** slightly thickened, simple, oblong to lanceolate, acute, 3  $\times$  1 mm when expanded; upper side with an elongated depression in the middle; base abruptly attenuate, with two minute dentiform calli; margin antrorse-auriculate below the middle, apically minutely papillose and revolute. **Column** whitish, slightly curved inwards,

± 2 mm long; foot 0,5 mm long, with a shallow and ovate cavity; clinandrium winged with a serrate margin. **Anther** apical; pollinia 2, pyriform, laterally compressed, sculpture gemmate. Stigma ventral. **Ovary** 1,7-1,8 mm long, glabrous, surcate. **Capsule** 3-5 mm long, glabrous. – Fl.: V-X, Fr.: V-XI.

**Distribution:** Central America from México to Nicaragua (Luer 1975a), Greater Antilles (Jamaica and Cuba) and Trinidad[?]. Present in West Cuba: PR; Central Cuba: Ci (Sierra de Escambray; Matagua de la Vega), SS (Trinidad: Pico Potrerillo, Mogote Mi Retiro, Trinidad Mts. Habanilla Falls); East Cuba: Gr, Ho, SC, Gu. Epiphytic or lithophytic; prefers shady to open places in montane rainforests, mesophyllous evergreen rainforests, gallery forests and vegetation of the mogotes (occasionally in secondary forests too) from 200 to 1400 m. Common. Most frequent species of the genus in Cuba.

***Pleurothallis shaferi* Ames** in *Orchidaceae* 7: 119. 1922 [as “schaferi”]. Lectotype (Nir 2000: 302): “Cuba, Sierra Nipe, near Woodfred”, 450-550 m, 05-I-1910, Shafer 3441 (AMES No. 21122!; islectotype: NY No. 9214!). – Fig. 36.

**Herbs**, caespitose, 0,5-1,7 cm high. **Rhizome** reduced. **Ramicauls** very short, erect or ascending, 1-4 mm long, 3-articulated, entirely covered by three scarious, tubular or infundibuliform sheaths; annulus present. **Leaves** spatulate to oblanceolate, obtuse, minutely tridentate, 0,4-1,3 × 0,2-0,4 cm, thickened, green, glabrous; base attenuate; margin entire or minutely crenulate. **Inflorescence** a terminal raceme, erect, capillary, solitary (rarely two per stem), 3(or very rarely 4-5) flowers, subtended at the base by an ovate sheath of 0,9-1,2 mm in length; peduncle 0,3-1 cm long, with a basal bract; axis 0,2-0,8 cm long. **Pedicel** 1-1,8 mm long, fused basally with the axis; bract membranous, acute, 1 mm long. **Flowers** with simultaneous anthesis, segments membranous, whitish or greenish, apically yellowish. **Sepals** papillose-carinate; margin entire or minutely papillose; **dorsal** sepal basally connate with the lateral ones, narrow elliptic-ovate, acute, 3-veined, 2,5-3,2 × 1,1-1,2 mm; the **lateral** ones connate to 1 mm, the base forming a mentum with the ovary, lanceolate, falcate, acute, 1-veined, 2,4-3 × 0,9-1,1 mm. **Petals** spatulate, slightly falcate, obtuse to rounded, 1-veined, 1,4-1,6 × 0,6 mm; margin glabrous or slightly serrate in the upper part. **Labellum** simple, oblong, obtuse, 1,6-1,7 × 1,1 mm when expanded; upper side with an elongated depression in the central portion; base abruptly clawed; margin apically crenulate and revolute. **Column** whitish, slightly curved inwards, ± 1 mm long; foot 0,7-0,8 mm long, with an elongated cavity and two orbicular calli; clinandrium winged with a serrate margin. **Anther** apical; pollinia 2, obovate, sculpture psilate. Stigma ventral. **Ovary** 0,6 mm long, glabrous, surcate. **Capsule** 3-4 mm long, glabrous. – Fl.: III-VII, Fr.: III-VIII.

**Distribution:** Endemic in East Cuba: Ho, SC (Sierra del Cristal: headwaters of the Río Lebisa; Sierra Maestra: Pico Turquino; Sierra Cobre: Loma del Gato), Gu. Epiphytic; prefers humid places in montane rainforests and charrascales from 300 to 800 m, usually in vegetation on soils derived from serpentine. Scattered.

**Variability:** Populations in Guantánamo, which marks the eastern limit of its distribution, have larger flowers and inflorescences with 4(-5) flowers instead 3. This morphology shows similarities to *Pleurothallis simpliciflora* D.D.Dod from Hispaniola.

***Pleurothallis testaefolia* (Sw.) Lindl.** in *Ann. Mag. Nat. Hist.*, ser. 3, 1: 328. 1858. ≡ *Epidendrum testaefolium* Sw., *Prodr.*: 122. 1788. ≡ *Cymbidium testaefolium* (Sw.) Sw. in *Nova Acta Regiae Soc. Sci. Upsal.* 6: 71. 1799. Lectotype (Nir 2000: 304, specified here): “*Cymbidium testaefolium* Swartz, *Herb. Swartzii*, Jamaica”, Swartz (S ex herb. Swartz [photo!]; islectotypes?: B ex herb. Willdenow 16984 [photo!], BM No. 82277!, SBT [n.v.], W ex herb. Reichenbach Orch. No. 16036!). – Fig. 37.

**Herbs**, repent, prostrate. **Rhizome** elongated, separating the ramicauls by 0,5-1,5 cm long and covered by three conduplicate and carinate sheath. **Ramicauls** 3-7 mm long, basally 2-articulated, entirely covered by two scarious sheath, conduplicate and carinate; without an annulus. **Leaves** rigid, elliptic to suborbicular, prostrate, limb usually turned

upside down, obtuse, short acuminate, minutely tridentate, 1-3 × 0,7-1,5 cm, green, dotted with purple, glabrous, carinate; base short attenuate; margin entire. **Inflorescence** a terminal raceme, solitary, single flowered, subtended at the base by a conduplicate and serrate sheath of 3-6 mm in length; peduncle 2 mm long, with two or three bracts. **Pedicels** 1 mm long; bract membranous, tubular, up to 1 mm long. **Sepals** slightly thickened, purple, whitish-pubescent, convex, carinate; margin entire; **dorsal** sepal free, oblong, obtuse, 3-veined, 5-5,2 × 2,2-2,3 mm; the **lateral** ones connate almost up to the tip, synsepal broadly ovate, obtuse, apically bidentate, 6-veined, 5,9-6 × 5-5,4 mm. **Petals** membranous, hyaline, spatulate, obtuse to rounded, 1-veined, 2,4-2,6 × 1 mm; margin denticulate in the tip. **Labellum** slightly thickened and membranous, light reddish to purple, oblong, rounded, 4-4,2 × 2-2,3 mm when expanded; upper side with two verrucate calli in the middle, apically covered with minute, dentiform calli; base short cuneate-attenuate, biauriculate; margin serrate to fimbriate or lacerate. **Column** whitish, slender and curved inwards, 2,2 mm long; foot 0,6 mm long, with a elongated and shallow cavity; clinandrium distinctly winged, apically serrate. **Anther** apical; pollinia 2, obovate, sculpture rugulate to granulate. Stigma ventral. **Ovary** 1,5 mm long, papillose-pubescent. **Capsule** pubescent. – Fl.: II-IX, Fr.: II-X.

**Distribution:** (Sub)Tropical America from Honduras to Venezuela and Surinam (Foldats 1970), Greater Antilles (except Puerto Rico), Martinica. Present in East Cuba: Gr (Sierra Maestra: macizo of the Turquino, La Aguada de Joaquín), SC (Sierra Cobre: Loma del Gato). Epiphytic on trunks of trees; prefers shady places in montane rainforests or secondary forests, sometimes on cultivated fruit trees (*Mangifera indica*), from 1000 to 1400 m, in vegetation on soils derived from volcanic rock. Rare.

**Reproduction biology:** In the natural position the prostrate leaf exposes the lower side, while the upper one with the flowers are hidden on the substrate.

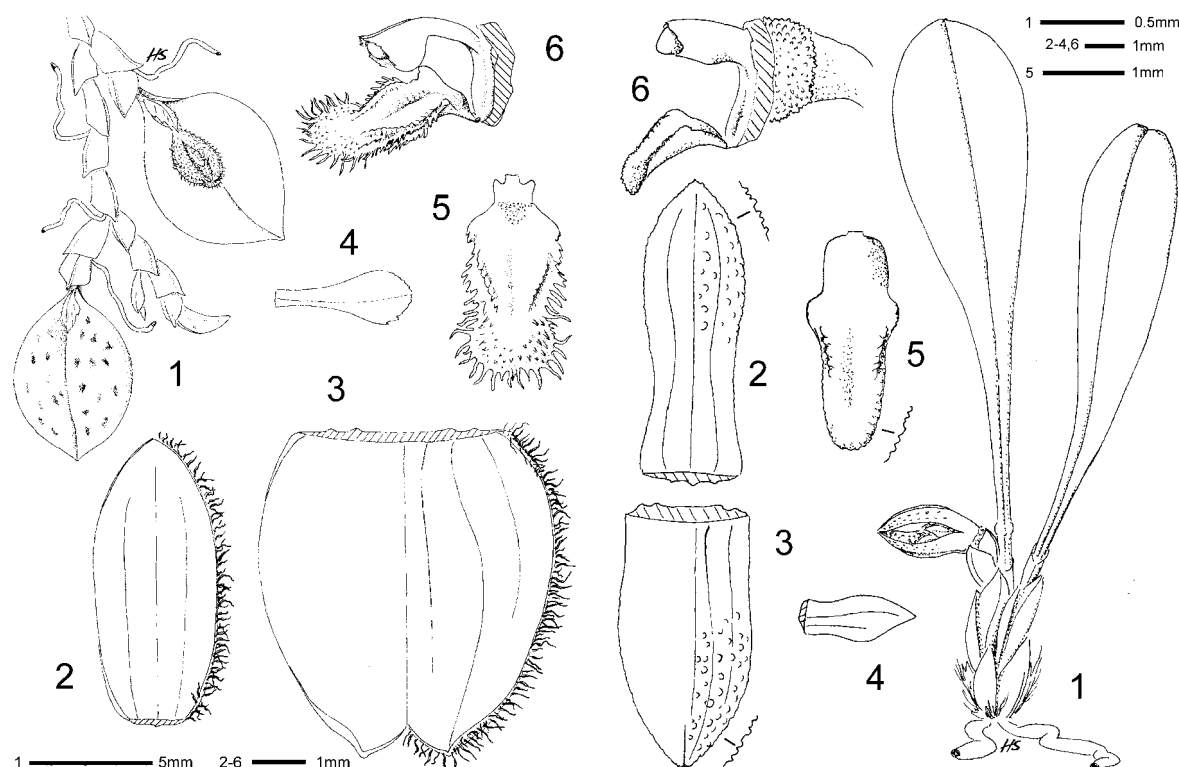


Fig. 37: *Pleurothallis testaeifolia* (Sw.) Lindl.  
1 – Plant with flower. 2+3 – Sepals. 4 – Petal.  
5 – Lip. 6 – Lip, ovary and column in natural position.

Fig. 38: *Pleurothallis tribuloides* (Sw.) Lindl.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

***Pleurothallis tribuloides* (Sw.) Lindl.**, Gen. Sp. Orchid. Pl.: 6. 1830. ≡ *Epidendrum tribuloides* Sw., Prodr.: 123. 1788. ≡ *Dendrobium tribuloides* (Sw.) Sw., Nova Acta Regiae Soc. Sci. Upsal. 6: 83. 1799. ≡ *Cryptophoranthus tribuloides* (Sw.) H. Dietrich in Revista



Jard. Bot. Nac. Univ. Habana 5: 48. 1984. = *Specklinia tribuloides* (Sw.) Pridgeon & M. W. Chase in Lindleyana 16: 259. 2001. Lectotype (Fawcett & Rendle 1910: 62, specified here): "Epidendrum tribuloides Swartz, Jamaica", Swartz (BM No. 82281!; isolectotypes?: B ex herb. Willdenow 16893 [photo!], G!, S [photo!], S ex herb. Alstroemer [photo!], W ex herb. Reichenbach Orch. No. 26480!). – Fig. 38.

= *Pleurothallis spathulata* A. Rich. & Galeotti in Ann. Sci. Nat., Bot., ser. 3, 3: 17. 1845. Lectotype (designated here): "Mexico, près Jalapa, 4000 [pies?]", XI-IV-1840, Galeotti 5181 (W ex herb. Reichenbach Orch. No. 12730!).

= *Pleurothallis fallax* Rchb. f. in Bonplandia (Hannover) 3: 224. 1855. Lectotype (designated here): "México", Leibold 615 (W ex herb. Reichenbach Orch. No. 24905!).

**Herbs**, caespitose, 3-5 cm high. **Rhizome** very short, ascending, separating the ramicauls by 0,5-1 mm, covered by two or three conduplicate and carinate sheaths. **Ramicauls** very short, 0,2-0,5 cm long, basally 1-articulated, entirely covered by a scarious and conduplicate sheath; annulus present. **Leaves** slightly coriaceous and fleshy, spathulate, obtuse to emarginate, tridentate, 3-4,5 × 0,5-1 cm, green, glabrous; base narrow attenuate; margin entire. **Inflorescence** a terminal raceme, solitary, with 1-3 flowers, basally covered by various sheaths; peduncle straight, 1-2 mm long, with two or three bracts; axis 1 mm long. **Pedicels** up to 4 mm long, free; bract scarious, conduplicate, acute, 5-7 mm long. **Flowers** resupinate, brick-colored, anthesis successive. **Sepals** thickened and rigid, carinate; margin papillose, covered in the upper part on both sides with minute warts (0,2 mm in diameter); **dorsal** sepal free but adnate to the lateral ones, panduriforme to (narrow) oblong, acute, 3-veined, 6,5-7,2 × 2,2-2,6 mm; the **lateral** ones connate almost up to the tip, the base forming a mentum with the ovary, synsepal oblong, slightly attenuate below the middle, acute to subobtuse, 6-veined, with minute papillae on the keels, 5,7-6,2 × 3-3,2 mm. **Petals** slightly thickened, spathulate, oblique in the upper part, acute, 2-veined, 2,6-2,7 × 1,1 mm; margin entire. **Labellum** slightly thickened, oblong, obtuse to rounded, 2,5 × 1,1 mm when expanded; upper side in the middle with two less distinct calli, apically papillose; base truncate; margin apically crenulate or papillose. **Column** thick, slightly curved inwards, 2 mm long; foot 1,5 mm long, with a elongated cavity; clinandrium winged and bidentate. **Anther** apical; pollinia 2, pyriform, laterally compressed, sculpture granulate. Stigma ventral. **Ovary** 1 mm long, densely papillose. **Capsule** 0,5 cm long, echinate. – Fl.: III-X, Fr.: III-XI.

**Distribution**: Tropical America from México to Panamá and Surinam (Luer 1975b), Greater Antilles (Cuba, Jamaica). Present in West Cuba: PR; Central Cuba: SS, (Trinidad Mts. Habanilla Falls, S.Clara, Pitajones to Ciegos Ponciano; Banao, Yayabo River); East Cuba: Gr, Ho, SC, Gu. Epiphytic or lithophytic; prefers shady or partially open places in vegetation of the mogotes, mesophyllous evergreen rainforests, montane rainforests, gallery forests; in secondary forests (cupeyales) too, from 200 to 1000 m, usually on limestone. Common.

**Ecology**: Frequently in association with *Pleurothallis sertularioides*, *Pleurothallis tribuloides* and *Pleurothallis wilsonii*.

*Pleurothallis trichophora* Lindl. in Ann. Mag. Nat. Hist., ser. 3, 1: 326. 1858. Lectotype (Luer 2000: 48, specified here): "in Cuba Orientali, 1856-7" [blue label], [summit of Loma del Gato, according to Wright in Lindley (1858)], Wright 659 (K-L!; isolectotypes?: AMES No. 72414 [photo!], BR No. 843534!, G ex herb. Barbey-Boissier!, K!). – Fig. 39.

**Herbs**, caespitose, 3-8 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** ascending to pendent, 1,5-3,5 cm long, up to the middle 4-articulated, surcate, to 2/3 covered by 4 scarious, conduplicate and carinate sheaths; without an annulus. **Leaves** coriaceous, narrow elliptic-lanceolate, acute, 1,5-4,5 × 0,8-1 cm, green to greyish green and slightly rough on the upper side, green on the lower side; base acute; margin denticulate and erose. **Inflorescence** a terminal raceme, slightly pendent,

(1-)2-5(-8) per stem, 2-15-flowered, subtended at the base by a conduplicate sheath of 2-9 mm in length; peduncle 1-6 cm long, with a bract; axis 2-14 long. **Pedicels** (3-)4 mm long, free; bract membranous, conduplicate, acute to apiculate, 2(-3) mm long. **Flowers** resupinate, but in pendent inflorescences apparently not, anthesis successive. **Sepals** membranous, slightly thickened along the nerves, purple with yellow tips, 3-veined, carinate; **dorsal** sepal connate basally up to 0,8 mm with the lateral ones, lanceolate, acute,  $6 \times 1,8$  mm; margin entire or slightly crenulate in the upper part; the **lateral** ones adnate up to the middle, the base forming a mentum with the ovary, narrow ovate, falcate, slightly caudate,  $6 \times 2$  mm; margin entire. **Petals** membranous, hyaline, narrow spatulate, apically subulate or subcaudate, 1-veined,  $5 \times 1$  mm; margin entire. **Labellum** membranous, purple, suborbicular to obtuse-cordiforme, rounded,  $3 \times 2$  mm when expanded; upper side with two lengthwise calli bordering a central depression; base clawed; margin in the middle with two small antrorse lobes, apically denticulate. **Column** whitish or light reddish, slender and curved inwards, 3 mm long; foot 1 mm long; clinandrium winged and denticulate. **Anther** apical; pollinia 2, triangular, sculpture punctate to vermicular-fossulate. Stigma ventral. **Ovary** 2 mm long, papillose and verrucate. **Capsule** verrucate. – Fl. and Fr.: II-IV?.

**Distribution**: Endemic in Central Cuba: Ci (Sierra de Escambray), SS (Trinidad: Pico Potrerillo, Finca El Avi6n); East Cuba: Gr (Victorino: Loma El Gigante), SC (Sierra Cobre: Loma del Gato; Loma Redonda, Sevilla). Epiphytic; prefers shady or partially open places in montane rainforests from 900 to 1200 m. Very rare.

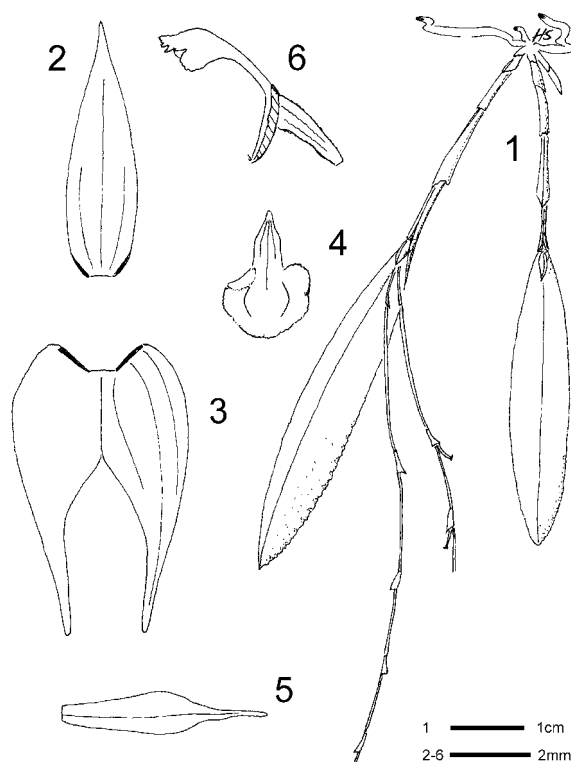


Fig. 39: *Pleurothallis trichophora* Lindl.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

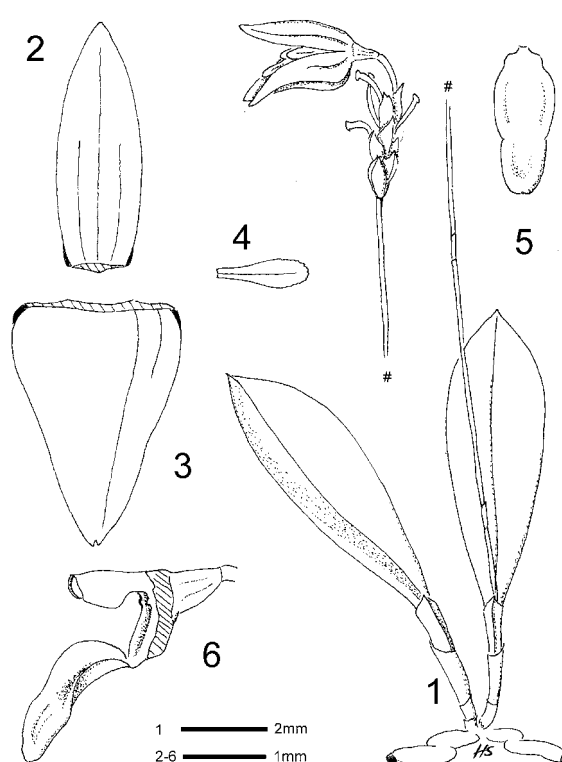


Fig. 40: *Pleurothallis trichyphysis* Rchb. f.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

***Pleurothallis trichyphysis* Rchb. f.** in Flora 48: 276. 1865. Lectotype (designated here): “Cuba, 1860-1864”, Wright 3345 p.p. (K!; isolectotypes?: AMES No. 72415 [photo!], BM No. 82343!, G ex herb. Barbey-Boissier!, G ex herb. de Candolle!, GOET!). – Fig. 40.

**Herbs**, caespitose, 0,8-1,5 cm high (excluding the inflorescence). **Rhizome** reduced. **Ramicauls** very short, 0,5-1,5 mm long, 3-articulated, entirely covered by three scarious and tubular sheaths; annulus present. **Leaves** slightly thickened, oblanceolate to subspathulate, acute and short apiculate,  $0,4-1,3 \times 1,5-3$  mm, green, glabrous; base

attenuate; margin entire or minutely erose above. **Inflorescence** a terminal raceme, solitary, few-flowered, subtended at the base by a tubular sheath of 0,5 mm in length; peduncle erect, 0,8-2,6(-3,5) cm long, with two bracts; axis congested, 0,2-0,5 cm long. **Pedicels** 1-3,5 mm long, free; bract membranous, acute, 1-2 mm long. **Flowers** resupinate, anthesis successive. **Sepals** membranous, yellow, slightly carinate, acute; margin entire; **dorsal** sepal connate to 0,5 mm with the lateral ones, lanceolate to narrow elliptic, 3-veined, 2,6-3,8 × 1,1-1,2 mm; the **lateral** ones connate almost up to the tip, the base forming a mentum with the ovary, synsepal ovate to triangular, bifid, 4-veined, 2,6-3,8 × 2-2,2 mm. **Petals** membranous, hyaline, spatulate, obtuse to rounded, 1-veined, 1-1,2 × 0,4 mm; margin apically denticulate. **Labellum** membranous, yellowish, oblong, obtuse to emarginate, 1,6-1,8 × 0,7 mm when expanded; base truncate; margin antrorse below the middle. **Column** whitish, slightly curved inwards, 1 mm long; foot 0,7 mm long, with an elongated cavity and two orbicular calli; clinandrium winged, glabrous. **Anther** apical; pollinia 2, triangular, sculpture psilate to slightly rugulate. Stigma ventral. **Ovary** 0,6 mm long, glabrous. **Capsule** 2 mm long, glabrous. – Fl.: VIII, Fr.: VIII-IX.

**Distribution**: Endemic in East Cuba: Gr (Guisa: Victorino), Gu (Sierra Imías: Loma Maestra la Yamagua). Epiphytic; prefers partially shaded places in humid mogote vegetation and mesophyllous evergreen rainforests from 400 to 800 m, in vegetation on limestone. Very rare.

***Pleurothallis wilsonii* Lindl.** in Ann. Mag. Nat. Hist., ser. 3, 1: 326. 1858. ≡ *Acianthera wilsonii* (Lindl.) Pridgeon & M. W. Chase in Lindleyana 16: 247. 2001. Lectotype (Fawcett & Rendle 1909b: 129): “*Pleurothallis wilsonii* m.; Jamaica”, Wilson ex herb. Hooker (K!). – Fig. 41.

= *Pleurothallis confusa* Fawc. & Rendle in J. Bot. 47: 129. 1909. Lectotype (designated here): “in Cuba Orientali, 1856-7” [blue label], [Sta. Isabel, according to Wright in Lindley (1858)], Wright 668 (K-L!).

**Herbs**, repent, 4-9 cm high. **Rhizome** elongated, separating the ramicauls by up to 1,3 cm, covered by three scarious and brown sheaths. **Ramicauls** elongated, slender, ascending, 2-5 cm long, basally 2-articulated, up to the middle covered by two scarious, carinate sheaths; without an annulus. **Leaves** coriaceous, lanceolate to (narrow) elliptic, acute, tridentate, 2-4 × 0,8-1 cm, green, glabrous; base obtuse to subacute; margin entire. **Inflorescence** a terminal raceme, 1-5 per stem, 1(-2) flowers, subtended at the base by a conduplicate sheath of 2-4 mm in length; peduncle ascending, 2-5 mm long, without a bract; axis (in two-flowered inflorescences) 2 mm long. **Pedicels** 0,6 mm long, fused up to  $\frac{3}{4}$  with the axis; bract membranous, infundibuliform, 1,3-1,5 mm long. **Flowers** resupinate, anthesis successive. **Sepals** membranous or slightly thickened, yellowish and reddish, carinate; margin entire; **dorsal** sepal free, narrow oblong, acute to subobtuse, 3-veined, 4-4,3 × 1,4-1,5 mm; the **lateral** ones entirely connate, the base forming a mentum with the ovary, synsepal ovate, obtuse to subacute, 6-veined, 3,9-4,1 × 2,8-3,2 mm. **Petals** slightly thickened, whitish, spatulate, acute, 1-veined, 2,5 × 0,9 mm; margin apically serrate. **Labellum** slightly thickened, oblong, narrow ovate or slightly trilobate, obtuse to rounded, 2,6-2,9 × 1,5-1,6 mm when expanded; upper side in the central portion with two elongated calli; base broadly cuneate, auriculate; margin basally antrorse, serrate and denticulate. **Column** whitish, slightly curved inwards and winged, 1,7-1,9 mm long; foot 0,8 mm long, with an elongated, shallow cavity; clinandrium dentate. **Anther** apical; pollinia 2, amorphous, sculpture irregular. Stigma ventral. **Ovary** 1,5-1,8 mm long, glabrous. **Capsule** 8-10 mm long, ribbed. – Fl.: IV-VIII, Fr.: IV-IX.

**Distribution**: Venezuela (Foldats 1970); Greater Antilles, Domínica and Guadalupe. Present in Central Cuba: SS (Cordillera Banao); East Cuba: Gr, Ho, SC, Gu. Epiphytic or Lithophytic; prefers partially open places in vegetation of the mogotes and mesophyllous evergreen rainforests from 300 to 600 m, usually on limestone. Scattered.

**Reproduction biology**: Probably this species shows auto- or cleistogamy, since the majority of the flowers set fruit without opening. The pollen morphology

(amorphous pollinia with no defined surface) backs this suggestion.

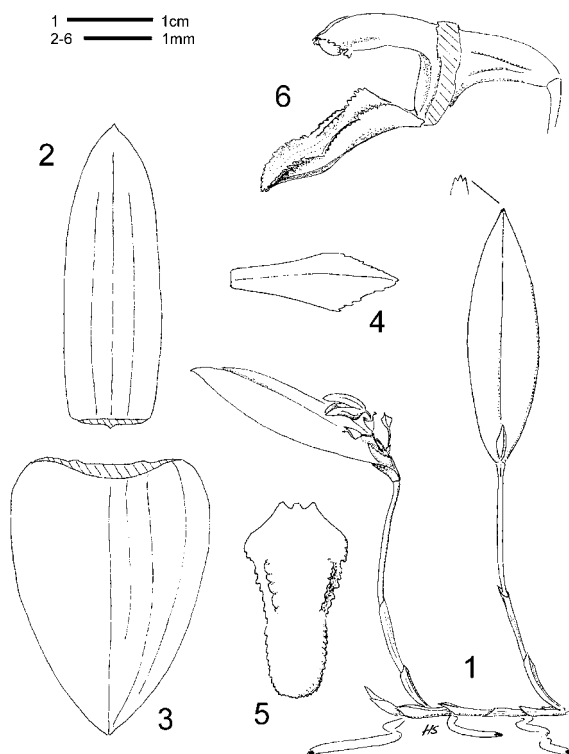


Fig. 41: *Pleurothallis wilsonii* Lindl.  
1 – Plant. 2+3 – Sepals. 4 – Petal. 5 – Lip.  
6 – Lip, ovary and column in natural position.

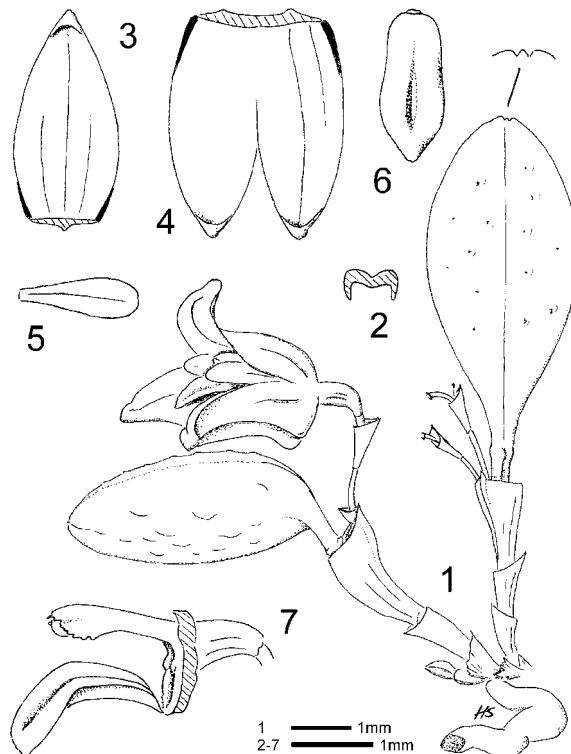


Fig. 42: *Pleurothallis wrightii* Rchb. f.  
1 – Plant. 2 – Leaf, cross section. 3+4 – Sepals.  
5 – Petal. 6 – Lip. 7 – Lip, ovary and column in natural position.

***Pleurothallis wrightii* Rchb. f.** in Flora 48: 276. 1865. Lectotype (designated here): “Cuba, Wright 1509”, Wright “1509” (W ex herb. Reichenbach Orch. No. 13015!). – Fig. 42.

= *Pleurothallis lichenicola* Griseb., Cat. Pl. Cub.: 259. 1866. ≡ *Specklinia lichenicola* (Griseb.) Pridgeon & M. W. Chase in Lindleyana 16: 258. 2001. Lectotype (designated here): “prope villam Monte Verde dictam, Cuba Orientali, Jan.-Jul. 1959”, [Monte Verde, 3-XII, according to Wright in AMES], Wright 1507 (GOET!; isolectotypes?: AMES No. 72371 [photo!], K!, K-L!).

= *Pleurothallis richteri* H. Dietr. in Orchidee (Hamburg) 35: 223. 1984. Holotype: “Cuba, Guantánamo, Baracoa, Vega de la Palma, alrededores del Río Duaba”, Bisse & al. (HAJB No. 39729!).

**Herbs**, subrepent, 0,5-1,3 cm high. **Rhizome** very short, separating the ramicauls by < 0,5 mm, covered by two membranous sheaths. **Ramicauls** very short, ascending, 1-2,5 mm long, 3-articulated, entirely covered by three membranous and tubular sheaths; annulus present. **Leaves** thickened, elliptic to obovate or suborbicular, obtuse to rounded, minutely tridentate, 4-10 × 1,5-3 mm, green to greenish purple, usually laxamente diminutely verrucate on both sides; base short attenuate; margin entire. **Inflorescence** a terminal raceme, (1-)2-3 per stem, generally single flowered, subtended at the base by a tubular sheath of 0,5 mm in length; peduncle capilar, erect, glabrous, 2-3 mm long, with a bract. **Pedicels** up to 1 mm long, free; bract membranous, infundibuliform, up to 0,8 mm long. **Flowers** resupinate. **Sepals** slightly thickened, light reddish purple, somewhat carinate, narrow ovate to elliptic, apically thickened, cucullate and slightly recurved; margin entire; **dorsal** sepal connate to 0,8 mm with the lateral ones, narrow ovate, 3-veined, 2,4-3 × 1,1-1,3 mm; the **lateral** ones connate basally up to 1 mm, forming a mentum with the tip of the ovary, 2-veined, 2,5-3 × 1-1,2 mm. **Petals** membranous, white or slightly light reddish, spatulate, obtuse to rounded, 1-veined, 1,4-1,7 × 0,5 mm; margin entire. **Labellum** slightly thickened, dark purple, simple, oblong to panduriforme, slightly

recurved, acute to obtuse, 1,6-1,9 × 0,5-0,8 mm when expanded; upper side with a central depression; base obtuse, abruptly clawed; margin basally papillose, apically revolute. **Column** whitish, slender, almost erect, 1,4 mm long; foot 0,6 mm long, with an elongated cavity, two orbicular calli and a papillose base; clinandrium serrate. **Anther** apical; pollinia 2, lentiform to obtuse triangular, sculpture psilate. Stigma ventral. **Ovary** 0,8 mm long, glabrous, purple. **Capsule** 2,5-3,5 mm long, glabrous. – Fl.: III-VI, Fr.: III-VII.

**Distribution:** Endemic in East Cuba: Ho, SC (Sierra del Cristal; Sierra de Cobre: Loma del Gato; Turquino massif: Pico Cardero), Gu (Vega la Palma: banks of the Río Duaba; Maisí: banks of the Arroyo Yarey). Epiphytic; prefers humid and shady places in montane rainforests, mesophyllous evergreen rainforests, gallery forests and charrascales from 300 to 900 m, usually in vegetation on soils derived from serpentine. Scattered.

**Variability:** The plants from the South of Oriente (Sierra Maestra) have smooth instead of verrucate leaves.

### 3.2 Reproductive biology

There was only one observation of potentially pollinating insects during the whole field work. A specimen of the dipterian genus *Drosophila* was observed visiting *Pleurothallis* 'flabelliformis'. The insect entered the flower several times, but no pollinia were removed (Stenzel 2001).

Empirical data from observations in the field concerning anthesis and fruit set is presented in Tab. 5. The taxa included in this list comprise the whole subtribe in Cuba.

Tab. 5: Observations on anthesis and fruit set in pleurothallid genera.

x – no observations; \* – information was obtained from material elsewhere in the Antilles; ? – information questionable because of limited data). The Cuban species of *Lepanthes* were entirely uniform regarding the open flowers and irregular fruit set.

Taxon	Amorphous pollinia with degenerated surface	Irregular fruit set after anthesis	Complete fruit set after anthesis	Complete fruit set without anthesis
<i>Barbosella dussii</i> (Cogn.) Dod	x	+	+	
<i>Brachionidium parvum</i> Cogn.	+			+
<i>Lepanthes</i> spp.		+		
<i>Lepanthopsis anthoctenium</i> (Rchb. f.) Ames	x			
<i>Lepanthopsis melanantha</i> (Rchb. f.) Ames			+	
<i>Lepanthopsis microlepanthes</i> (Griseb.) Ames		+		
<i>Lepanthopsis pygmaea</i> C. Schweinf.		+		
<i>Octomeria ventii</i> H. Dietrich	x	+		
<i>Platystele ovalifolia</i> (Focke) Garay & Dunsterv.	+			+
<i>Platystele hyalina</i> H. Stenzel		+		
<i>Pleurothallis appendiculata</i> Cogn.	x	+		
<i>Pleurothallis aristata</i> Hooker		+		
<i>Pleurothallis bissei</i> Luer		+		
<i>Pleurothallis brighamii</i> S. Wats.	+/-	+		
<i>Pleurothallis caymanensis</i> C.D.Adams	x	+		
<i>Pleurothallis corniculata</i> (Sw.) Lindl.	+		+	+
<i>Pleurothallis denticulata</i> Cogn.		+		
<i>Pleurothallis domingensis</i> Cogn.	+/-		+	+
<i>Pleurothallis ekmanii</i> Schltr.		+		
<i>Pleurothallis excentrica</i> (Luer) Luer		+		
<i>Pleurothallis</i> 'flabelliformis' H. Stenzel		+		
<i>Pleurothallis gelida</i> Lindl.		+		
<i>Pleurothallis gemina</i> H. Stenzel		+		
<i>Pleurothallis ghiesbreghtiana</i> A. Rich. & Galeotti		+	+	
<i>Pleurothallis grisebachiana</i> Cogn.		+		
<i>Pleurothallis helenae</i> Fawc. & Rendle	+			+
<i>Pleurothallis llamachoi</i> Luer		+		
<i>Pleurothallis longilabris</i> Lindl.		+		
<i>Pleurothallis mucronata</i> Lindl. ex. Cogn.		+		
<i>Pleurothallis murex</i> Rchb. f.		+		
<i>Pleurothallis nummularia</i> Rchb. f.	?	+		
<i>Pleurothallis obliquipetala</i> Acuña & C. Schweinf.		+		
<i>Pleurothallis obovata</i> (Lindl.) Lindl.		+		
<i>Pleurothallis odontotepala</i> Rchb. f.			+	
<i>Pleurothallis oricola</i> H. Stenzel	x			
<i>Pleurothallis papulifolia</i> Luer		+		

<sup>1</sup> Confirmed by Wright (in herb.) and Dod (1986b: 188)

<sup>2</sup> Plants (Stenzel 1298) in cultivation showed self-pollinization: after 7-10 days the rostellar tissue began to produce mucus that connected the anther with the stigma. Ovaries began to swell and the perianth wilted rapidly.

<i>Pleurothallis prostrata</i> Lindl.		+		
<i>Pleurothallis pruinosa</i> Lindl.	+			+
<i>Pleurothallis racemiflora</i> (Sw.) Lindl.		+		
<i>Pleurothallis rubroviridis</i> Lindl.		+		
<i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.	+		+	
<i>Pleurothallis sertularioides</i> (Sw.) Spreng.		+		
<i>Pleurothallis shaferi</i> Ames		+		
<i>Pleurothallis testaeifolia</i> (Sw.) Lindl.		+		
<i>Pleurothallis tribuloides</i> (Sw.) Lindl.		+		
<i>Pleurothallis trichophora</i> Lindl.		+		
<i>Pleurothallis trichyphis</i> Rchb. f.		+		
<i>Pleurothallis wilsonii</i> Lindl.	+/-	+	+	
<i>Pleurothallis wrightii</i> Rchb. f.		+		
<i>Trichosalpinx dura</i> (Lindl.) Luer		x		
<i>Zootrophion atropurpureum</i> (Lindl.) Luer		+		

### 3.3 Palynology

#### *Description of pollen morphology*

Details of the pollen morphology of each taxon examined are given in the following. Figures are included in the CD-ROM attached to the back cover of this thesis. They can be viewed with the program REMview.exe on the CD. Comparative results are presented subsequently.

*Arpophyllum giganteum* Hartw. ex Lindl.: Eight pollinia, 500x220 µm, asymmetrically claviform, caudicles distinct, tetrads with a tendency to level off, sculpture irregularly punctate granulate.

*Brachionidium parvum* Cogn.: Four pollinia, ca. 300x250 µm, pyriform to clavate (?), fused with the tapetum, sculpture irregular. Pollinia could not be removed entirely from the anther tissue.

*Dilomilis elata* (Benth. & Hook.) Summerhayes: Eight pollinia, 300-500x300 µm, irregularly lenti- to pyriform, caudicles of tetrads loosely attached to each other, surface aciantheroid, sculpture psilate.

*Lepanthes diaziae* Luer: Two pollinia, 310x100 µm, elongate clavate, caudicles elaborate elongate, firm, surface lepanthoid, sculpture psilate.

*Lepanthes dorsalis* Schltr.: Two pollinia, 400-500x100-150 µm, elongate clavate, caudicles elaborate elongate, firm, surface lepanthoid, sculpture granulate to punctate.

*Lepanthes dressleri* Hesp.: Two pollinia, 400-500x100-150 µm, claviform, caudicles elongate, firm, surface lepanthoid, sculpture punctate to granulate

*Lepanthes fulva* Lindl.: Two pollinia, 350x80 µm, caudicles elongate, firm, surface lepanthoid, sculpture punctate.

*Lepanthes melanocaulon* Schltr.: Two pollinia, 400-450x100-120 µm, caudicles elongate, firm, surface lepanthoid, sculpture psilate.

*Lepanthes obliquilobia* Hesp.: Two pollinia, 420-500x100-120 µm, caudicles elongate, firm, surface lepanthoid, sculpture psilate to punctate.

*Lepanthes silvae* H. Dietrich: Four pollinia, a normally sized and shaped pair (350-400x70 µm, caudicles elongate, surface lepanthoid, sculpture psilate to punctate) and a reduced pair (150-200x50-90 µm, claviform, no caudicles, sporoderm collapsed, sculpture irregular).

*Lepanthes trichodactyla* Lindl.: Two pollinia, 400-500x200 µm, claviform, caudicles

capillary, short, surface lepanthoid (Stenzel 072) or less levelled (Stenzel 447), sculpture psilate.

*Lepanthes turquinoensis* Schltr.: Two pollinia, 500-550x100 µm, claviform, caudicles elongate, capillary, surface lepanthoid, sculpture perfectly psilate.

*Lepanthopsis microLepanthes* (Griseb.) Ames: Two pollinia, 220x100 µm, claviform, caudicles elaborate, elongate, surface lepanthoid, sculpture psilate (Stenzel 2000).

*Lepanthopsis pygmaea* C. Schweinf.: Two pollinia, 60-80 µm in diameter, sublentiform to hemispherical, caudicles absent, sculpture octomerioid with gemmate flanks.

*Platystele hyalina* H. Stenzel: Two pollinia, 350-400 µm, elongate clavate, caudicles long, firm, surface lepanthoid, sculpture punctate.

*Platystele ovalifolia* (Focke) Garay & Dunsterv.: Pollinia not removable.

*Pleurothallis alpestris* (Sw.) Lindl.: Two pollinia, 150 µm in diameter, angular lentiform, caudicles absent, sculpture punctate.

*Pleurothallis appendiculata* Cogn.: Two pollinia, 400x300 µm, obtuse-triangular to suborbicular, caudicles absent, sculpture granulate.

*Pleurothallis aristata* Hooker: Two pollinia, 250x180 µm, obliquely pyriform, laterally flattened, caudicles present, outer tetrads well separated (Puerto Rico) or with partially levelled edges (Suriname), sculpture punctate (Puerto Rico) or psilate (Suriname).

*Pleurothallis bissei* Luer: Two pollinia, ±300 µm in diameter, lentiform to obtusely triangular, caudicles absent, sculpture granulate.

*Pleurothallis brighamii* S. Wats.: Two pollinia, 350x200 µm, obovate to pyriform in outline, laterally flattened, caudicles elaborately ribbon-shaped, sculpture punctate to granulate.

*Pleurothallis claudii* D.D.Dod: Two pollinia, 400-450x200 µm, asymmetrically pyriform with indistinct caudicles, surface with levelled tetrads, sculpture psilate to punctate.

*Pleurothallis cordatifolia* D.D.Dod: Two pollinia, 400x280 µm, broadly triangular to subreniform, caudicles indistinct, sculpture psilate.

*Pleurothallis corniculata* (Sw.) Lindl.: Two pollinia, a) in presumably cleistogamous flowers amorphous, 700 µm long, exinous layer fragile and collapsed, sculpture reduced and irregular 4031, 4131-32; b) in open flowers (presumably xenogamous), oblong to obovate, 400x150 µm, caudicles distinctly ribbon-shaped, sculpture granular.

*Pleurothallis curtisii* D.D.Dod: Two pollinia, 450x190 µm, pyriform with elongate ribbon-like caudicles, sculpture psilate with a tendency to octomerioid patterns.

*Pleurothallis delicatula* Lindl.: Two pollinia, 200-250x100 µm, piri- to claviform, caudicles the tapering ends of the pollinia, indistinct, sculpture psilate.

*Pleurothallis denticulata* Cogn.: Two pollinia, 200-250 µm in diameter, obtusely triangular, caudicles rudimentary of loose tetrads, sculpture punctate to granulate.

*Pleurothallis domingensis* Cogn.: Two pollinia, 150-200 µm in diameter, suborbicular to triangular or amorphous (Stenzel 662), caudicles rudimentary, sculpture psilate octomerioid or indistinct (Stenzel 662).

*Pleurothallis ekmanii* Schltr.: Pollinia 8, 130-180 µm long, short claviform, caudicles of loose tetrads at the tapering end, sculpture perforate, punctate to fossulate.

*Pleurothallis excentrica* (Luer) Luer: Pollinia 8, 160-200x80-100 µm, cone-shaped, caudicles of loose tetrads at the tapering end of the pollinium, sculpture psilate.

*Pleurothallis 'flabelliformis'* H. Stenzel: Pollinia 8, 200-250x80-110 µm long, conical to



claviform, caudicles of loose tetrads at the tapering end of the pollinium, sculpture psilate.

*Pleurothallis formondii* D.D.Dod: Two pollinia, 250x150 µm, angular lentiform with short distinct caudicles, sculpture psilate with the edges of the tetrads partially fused or covered by an unknown layer.

*Pleurothallis gelida* Lindl.: Two pollinia, 200-250 µm in diameter, broadly ovate to sublentiform, caudicles very short, sculpture granulate to pregemmate.

*Pleurothallis gemina* H. Stenzel: Two pollinia, 170-200x100 µm, obliquely reni- to lentiform, sculpture psilate to punctate with a tendency to level tetrads.

*Pleurothallis ghiesbreghtiana* A. Rich. & Galeotti: Two pollinia, 350-400x250-260 µm, pyriform to obtusely triangular, laterally flattened, caudicles of loosely attached tetrads at the tapering end of the pollinium, sometimes with distinct threads of elastoviscin (fig. 6751), surface aciantheroid, sculpture varying psilate (*Loddiges*, Jamaica), punctate (*Stenzel* 967 from Puerto Rico, *Stenzel* 1298 from Cuba, *Sandoval* from El Salvador) to reticulate (Hort. Kew. 1999-2869 from Ecuador) or octomerioid (*Hinton* from Mexico, *Marshal* from Nicaragua, Hort Kew. 1968-22804 from Nicaragua).

*Pleurothallis grisebachiana* Cogn.: Two pollinia, 280-320x130-200 µm, claviform, laterally flattened, caudicles usually ribbon-like (fig. 6983) sculpture variably psilate, granulate or subgemmate.

*Pleurothallis grobyi* Batem. ex. Lindl.: Two pollinia, 250x140µm, sublentiform with short distinct stalky caudicles, sculpture octomerioid to gemmate.

*Pleurothallis haitiensis* D.D.Dod: Two pollinia, 300x120 µm, elliptical to slightly pyriform, caudicles indistinctly formed by the tapering ends of the pollinia, sculpture psilate or partially irregular. 8121-22. Two pollinia 220x150 µm, lentiform with short distinct caudicles, sculpture psilate to slightly punctate or granulate.

*Pleurothallis helenae* Fawc. & Rendle: Pollinia could not be removed, since they were in all stadiums neatly fused with the anther tissue (tapetum).

*Pleurothallis hirsutula* Fawc. & Rendle: Two pollinia, 250 µm in diameter, caudicles absent or consisting of a few tetrads loosely attached to each other, sculpture psilate to punctate or subgranulate.

*Pleurothallis lanceola* (Sw.) Lindl.: Two pollinia, 350-400x150-200 µm, caudicles in form of the tapering ends of the clavi- to coniform, laterally flattened pollinia, surface ± lepanthoid, sculpture punctate.

*Pleurothallis laxa* (Sw.) Lindl.: Two pollinia, ±200 µm in diameter, angular lentiform, caudicles absent, sculpture punctate to fossulato-granulate.

*Pleurothallis llamachoi* Luer: Two pollinia, 300x100 µm, claviform to coniform, caudicles indistinctly consisting of loose tetrads at the tapering end of the pollinium, sculpture psilate

*Pleurothallis longilabris* Lindl.: Two pollinia, 350x100 µm, slender, claviform, caudicles elongate, sculpture psilate.

*Pleurothallis miguelii* Schltr.: Two pollinia, 200-220 µm in diameter, angular lentiform, caudicles absent or of loosely grouped tetrads, sculpture punctate (fossulate).

*Pleurothallis mitchellii* D.D.Dod: Two pollinia, 320x120 µm, clavi- to pyriform, laterally flattened, caudicles formed by the tapering ends of the pollinia, sculpture psilate to slightly octomerioid.

*Pleurothallis mucronata* Lindl. ex. Cogn.: Two pollinia, 150x120 µm, obtusely triangular in outline, laterally flattened, sculpture psilate to granulate.

*Pleurothallis murex* Rchb. f.: Two pollinia, 110-150 µm in diameter, suborbicular

(hemispherical), caudicles absent, sculpture vermiculato-fossulate to granulate

*Pleurothallis obliquipetala* Acuña & C. Schweinf.: Two pollinia, 300x90 µm, claviform, caudicles elongate, sculpture psilate.

*Pleurothallis obovata* (Lindl.) Lindl.: Two pollinia, 350x200 µm, pyriform, caudicles distinct, sculpture gemmate.

*Pleurothallis odontotepala* Rchb. f.: Two pollinia, 80-100 µm in diameter, obtusely triangular to suborbicular (hemispherical), laterally flattened, caudicles extremely reduced, sculpture granulate. .

*Pleurothallis papulifolia* Luer: Two pollinia, 280x180 µm, obovate, caudicles indistinct, sculpture punctate to fossulate. .

*Pleurothallis prostrata* Lindl.: Two pollinia, 300x220 µm, obtusely triangular to broadly reniform, caudicles indistinct, sculpture punctate to granulate. .

*Pleurothallis pruinosa* Lindl.: Pollinia of Cuban material could not be removed, since they were neatly fused with the anther tissue (tapetum) regardless which stage of development they were in. Type material from Surinam (*Splitgerber* 527): Two pollinia, 200-220x150-170 µm, pyriform, laterally flattened, caudicles distinct, surface lepanthoid, sculpture psilate. Material from Costa Rica was slightly longer (250x120 µm) with a perfectly lepanthiform surface. .

*Pleurothallis pubescens* Lindl.: Two pollinia, ±280 µm in diameter, angular lentiform, caudicles absent, sculpture vermiculato-fossulate .

*Pleurothallis quisqueana* D.D.Dod: Two pollinia, obtusely triangular in outline to angular lentiform, caudicles absent or indistinct, sculpture punctate.

*Pleurothallis racemiflora* (Sw.) Lindl.: *Stenzel* 643: two pollinia, 250x180 µm, obovate in outline, laterally flattened, caudicles indistinctly short, sculpture octomerioid. *Stenzel* 888: two pollinia, 300x210 µm, obovate in outline, laterally flattened, caudicles a loose agglomeration of tetrads, sculpture granulate.

*Pleurothallis rubroviridis* Lindl.: Two pollinia, 280x220 µm, suborbicular (hemispherical) to broadly ellipsoid in outline, laterally flattened, caudicles absent, sculpture punctate. .

*Pleurothallis ruscifolia* (Jacq.) R. Br.: No material from Cuba could be examined. Horich s.n. (Costa Rica) and an unvouchered specimen: two pollinia, 300x180 µm, conical to claviform, surface lepanthoid, sculpture psilate. Material from the Antillean resisted preparation. The residues showed at best remnants of the typical lepanthoid sculpture type (Stenzel 2004b).

*Pleurothallis shaferi* Ames: Two pollinia, 200x110 µm, pyriform, laterally flattened, caudicles small and slender, sculpture psilate.

*Pleurothallis sertularioides* (Sw.) Spreng.: Two pollinia, 300x140 µm, pyriform, laterally compressed, caudicle a distinct flat stalky structure, sculpture gemmate.

*Pleurothallis simpliciflora* D.D.Dod: Two pollinia, 230x150 µm, lentiform with one end abruptly tapering into the short but distinct caudicle, sculpture ± psilate.

*Pleurothallis testaefolia* (Sw.) Lindl.: Two pollinia, 240x180 µm, broadly reniform, caudicles reduced, sculpture rugulate to granulate

*Pleurothallis tribuloides* (Sw.) Lindl.: Two pollinia, 350x190 µm, pyriform, laterally compressed, caudicle a short but distinct ribbon-shaped structure, sculpture granulate

*Pleurothallis trichophora* Lindl.: Two pollinia, 210x150 µm, triangular to broadly reniform, laterally flattened, caudicles absent or few loosely packed tetrads, sculpture punctate to vermicular-fossulate.

*Pleurothallis trichyphus* Rchb. f.: Two pollinia, 140x90 µm, obliquely pyriform to triangular, laterally flattened, caudicles indistinct tapering ends of the pollinia, sculpture psilate to slightly asper.

*Pleurothallis velaticaulis* Rchb. f.: Two pollinia, 140-200 µm in diameter, obtusely triangular to angular lentiform, caudicles absent, sculpture octomerioid.

*Pleurothallis wilsonii* Lindl.: Two pollinia, 220x140 µm, asymmetrically elliptical, caudicles reduced, sculpture punctate or fossulate to rugulate.

*Pleurothallis wrightii* Rchb. f.: Two pollinia, 110x80 µm, sublentiform to pyriform, laterally flattened, sculpture psilate to punctate with a tendency to smooth and level tetrad edges.

*Stelis pygmaea* Cogn.: Two pollinia, 210x100 µm, claviform, caudicles elongate, sculpture gemmate octomerioid.

*Trichosalpinx dura* (Lindl.) Luer: Two pollinia, 200x100 µm, coniform, caudicular end tapering, sculpture reticulate octomerioid.

*Zootrophion atropurpureum* (Lindl.) Luer: Two pollinia, 350x220 µm, lentiform with the caudicular end slightly elongate, sculpture psilate octomerioid (reticulate edge).

#### *Atypical pollinia*

The following species of Cuban pleurothallids did not render any examinable pollen material:

- *Brachionidium parvum* Cogn.
- *Platystele ovalifolia* (Focke) Garay & Dunst.
- *Pleurothallis corniculata* (Sw.) Lindl. p.p.
- *Pleurothallis domingensis* Cogn. p.p.
- *Pleurothallis helenae* Fawc. & Rendle
- *Pleurothallis pruinosa* Lindl. p.p.
- *Pleurothallis ruscifolia* (Jacq.) R. Br.

The pollinia of these species were often firmly attached to the tapetum and were of amorphous texture. The surface, if accessible, showed an irregularly collapsed sculpture.

#### *General types of pollen characteristics*

Antillean species of *Pleurothallis* shows the whole set of pollen morphological patterns found elsewhere in the subtribe, as was found already by Stenzel (2000). Antillean material of the other pleurothallid genera show the the palynological traits, that had been found to be characteristic for the respective genus in earlier studies (Schill & Pfeiffer 1977, Zavada 1990, Stenzel 2000). Fig. 43 and Fig. 44 provide a survey of the palynological variety found.

Most pollinia are laterally flattened on one side, i.e. they are  $\pm$  circular in cross-section as unit (Fig. 43b). Caudicles may be absent (Fig. 43a), consist of loose tetrads (Fig. 43d), held together by threads of elastoviscin (Fig. 43h), or may be firm structures (Fig. 43e,f,g), usually forming the tapering end of a pollinium.

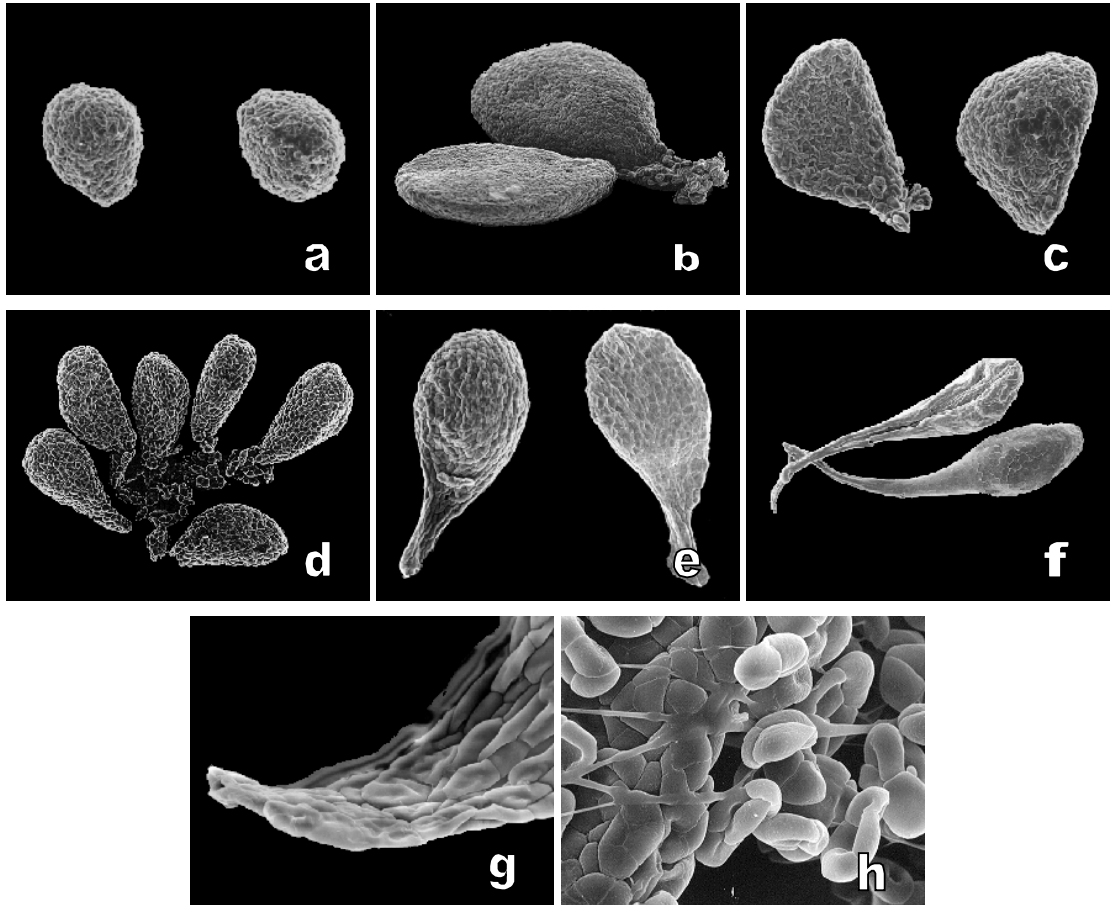


Fig. 43: Types of shape of pollinia in Cuban pleurothallids.  
**a** – hemispherical, no caudicles (*Pleurothallis murex*); **b** – lentiform, caudicles of loosely aggregated tetrads (*Zootrophion atropurpureum*); **c** – obtusely triangular, reduced caudicles (*Pleurothallis trichophora*); **d** – irregular subpyriform, caudicles of loosely attached tetrads (*Pleurothallis ekmanii*, only 6 of the 8 tetrads shown); **e** – coniform, caudicles tapering (*Pleurothallis grisebachiana*); **f** – elongate claviform, caudicles stalky (*Lepanthes dressleri* Hesp.); **g** – ribbon-like caudicle (*Pleurothallis grisebachiana*); **h** – elastoviscin threads unifying caudicular tetrads (*Pleurothallis pubescens*).

There is a strong tendency towards a levelled surface (Fig. 44b: lepanthoid) and a highly reduced sculpture. The exinous layer may be reduced to a thin coating (Fig. 44b: *Lepanthes*) or may disintegrate via the following evolutionary sequence: punctate  $\rightarrow$  fossulate  $\rightarrow$  (reticulate)/gemmate/ octomerioid (Fig. 44c-f). A classic reticulate pattern, rare anywhere in *Pleurothallidinae* (Stenzel 2000), was observed in this study only in non-Antillean material of *Pleurothallis ghiesbreghtiana* (Fig. 44d).

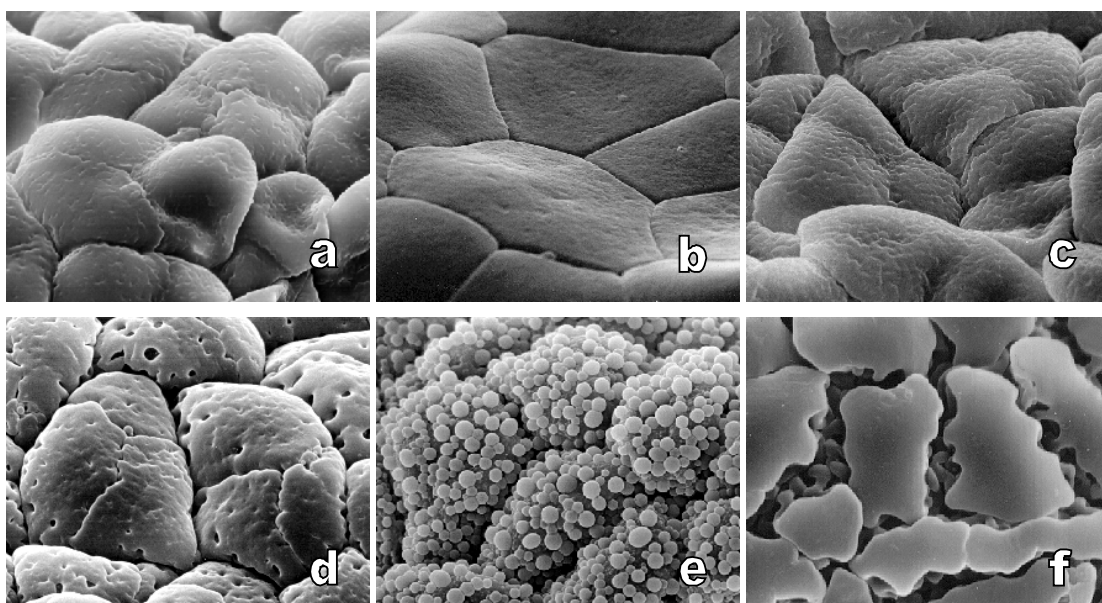


Fig. 44: Types of surface and sculpture of the exinous layer in Cuban pleurothallids. **a** – aciantheroid surface (*Pleurothallis wilsonii*); **b** – lepanthoid surface (*Lepanthes diaziae*); **c** – punctate fossulate sculpture (*Pleurothallis papulifolia*); **d** – punctate reticulate sculpture (*Pleurothallis ghiesbreghtiana*); **e** – gemmate sculpture (*Pleurothallis sertularioides*). **f** – octomerioid sculpture (*Lepanthopsis pygmaea*).

#### *Intraspecific variability of pollen characteristics*

Eight specimens of ***Pleurothallis ghiesbreghtiana* A. Rich. & Galeotti**, spanning the whole area of distribution (Greater Antilles, Central and northern South America), were examined. Plants from the Caribbean generally have pollinia with a psilate to punctate pattern, whereas those of Central America show a tendency towards octomerioid conditions. Finally, the sample from EC showed the most advanced sculpture with a reticulate pattern. Thus, the further north, the more ancestral conditions we find in the pollen morphology of this species.

Within Cuba several species were represented by multiple samples. ***Pleurothallis grisebachiana* Cogn.**, a relatively common and morphologically variable endemic, showed the greatest variety in pollen morphology. Samples had been chosen to reflect the species' phytogeography as accurate as possible (Fig. 45). They include samples from both limestone and serpentine bound vegetation. As a result, the set of sculptures found reflects a presumably natural evolutionary line. Fig. 45 illustrates the distribution of the sculpture types: starting with a psilate surface (4,8), via a punctate and fossulate sculpture (1,9,3,10) with beginning formation of gemmae in larger fossulae and foveolae (1,2,6,7,10) to almost gemmate conditions (4). Some of the populations are represented by more than one plant and in this case different sculpture types can be found even within one population. Perhaps the most striking example is *Stenzel 489* from the Sierra de Nipe. Pollinia of this collection show either a psilate or gemmate sculpture. Thus, there is no

phytogeographical or ecological correlation with the sculpture pattern. The most distant populations from the centre of distribution in Oriente show neither an exclusively advanced nor a primitive morphology.

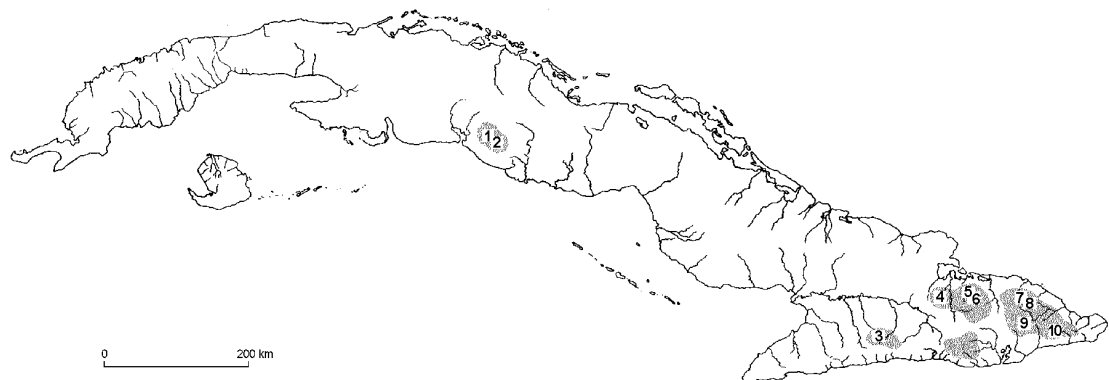


Fig. 45: Distribution of the 10 samples of *Pleurothallis grisebachiana* for palynological studies (dotted – area of distribution; 1-10 – localities of samples).

***Pleurothallis mucronata* Lindl. ex. Cogn.**, a serpentine bound endemic in Holguín, was represented by 3 samples (Sierra de Nipe, Sierra del Cristal, Sierra de Moa) spanning all three mountains the species is currently known to occur in (Fig. 46). All specimens show the same pollen morphology.

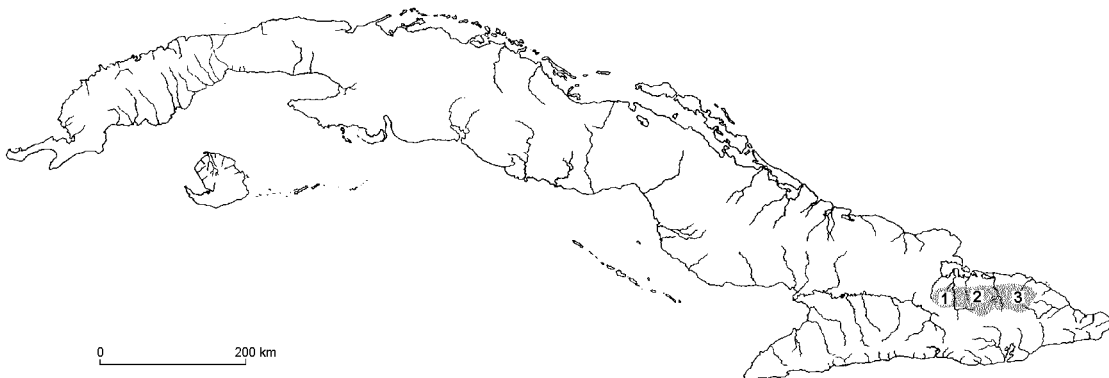


Fig. 46: Distribution of the 3 samples of *Pleurothallis mucronata* for palynological studies (dotted – area of distribution; 1-3 – localities of samples).

***Pleurothallis ekmanii* Schltr.**, with a distribution similar to that of *Pleurothallis mucronata*, was sampled also 3 times (Fig. 47: Sierra del Cristal, Yateras). Again, no differences in pollen morphology was found.



Fig. 47: Distribution of the 3 samples of *Pleurothallis ekmanii* for palynological studies (dotted – area of distribution; 1-3 – localities of samples).

***Pleurothallis* subgenus *Antilla* Luer** is endemic in the Greater Antilles with ~10 species (Luer 2000), 7 of which were included in this study. All species show a rather homogenous pollen morphology: suborbicular to obtusely triangular, reduced caudicles, sculpture punctate to granulate. The surface shows often an aciantheroid organisation of the tetrads (Fig. 44c), which suggests a closer relationship with that subgenus (*Acianthera* sensu Pridgeon & Chase 2001).

### 3.4 Taxonomy

The nomenclatural results as applied in this study with complete synonymy are part of the MS presented earlier (p. 27). There are 39 species referable to *Pleurothallis* (sensu Luer 1986b) in Cuba. Species with 8 pollinia (*P. ekmanii* Schltr., *P. excentrica* (Luer) Luer, *P. 'flabelliformis'* nom prov.) are included.

The following list enumerates all epithets that have been referred to Cuban *Pleurothallis* (left column). If different, the correct name is given on the right. Valid names are printed in bold type. Homotypic synonyms as well as Grisebach's names published *pro syn.* (Grisebach 1866) are not included.

Tab. 6: Epithets of *Pleurothallis* referred in literature to the Cuban taxa. Valid names, if necessary, are given at the right side.

<i>Pleurothallis albida</i> Lindl.	<i>Pleurothallis obovata</i> (Lindl.) Lindl.
<b><i>Pleurothallis appendiculata</i> Cogn.</b>	
<b><i>Pleurothallis aristata</i> Hooker</b>	
<i>Pleurothallis atropurpurea</i> (Lindl.) Lindl.	<i>Zootrophion atropurpureum</i> (Lindl.) Luer
<b><i>Pleurothallis bissei</i> Luer</b>	
<i>Pleurothallis blepharoglossa</i> Luer	<i>Pleurothallis grisebachiana</i> Cogn.
<i>Pleurothallis blepharophylla</i> Griseb.	<i>Lepanthes blepharophylla</i> (Griseb.) Hespenh.
<i>Pleurothallis bovilabia</i> C. Schweinf.	<i>Pleurothallis ekmanii</i> Schltr.
<i>Pleurothallis brachyglottis</i> Rchb. f.	<i>Pleurothallis pruinosa</i> Lindl.
<i>Pleurothallis brachypetala</i> Griseb.	<i>Pleurothallis odontotepala</i> Rchb. f.
<b><i>Pleurothallis brighamii</i> S. Wats.</b>	
<i>Pleurothallis broadwayi</i> Ames	<i>Trichosalpinx dura</i> (Lindl.) Luer
<b><i>Pleurothallis caymanensis</i> Adams</b>	
<i>Pleurothallis confusa</i> Fawc. & Rendle	<i>Pleurothallis wilsonii</i> Lindl.
<b><i>Pleurothallis corniculata</i> (Sw.) Lindl.</b>	

<i>Pleurothallis crassipes</i> Lindl.	wrong classification, mostly <i>Pleurothallis domingensis</i> Cogn.
<i>Pleurothallis cubensis</i> Lindl.	<i>Pleurothallis rubroviridis</i> Lindl.
<b><i>Pleurothallis denticulata</i> Cogn.</b>	
<b><i>Pleurothallis domingensis</i> Cogn.</b>	
<b><i>Pleurothallis ekmanii</i> Schlechter</b>	
<b><i>Pleurothallis excentrica</i> (Luer) Luer</b>	
<b><i>Pleurothallis</i> 'flabelliformis'</b>	nom. prov. in this study for <i>Octomeria prostrata</i> H. Stenzel
<i>Pleurothallis foliata</i> Griseb.	<i>Trichosalpinx dura</i> (Lindl.) Luer
<b><i>Pleurothallis gelida</i> Lindl.</b>	
<b><i>Pleurothallis gemina</i> H. Stenzel</b>	
<b><i>Pleurothallis ghiesbreghtiana</i> A. Rich. &amp; Galeotti</b>	
<b><i>Pleurothallis grisebachiana</i> Cogn.</b>	wrong classification, mostly <i>Pleurothallis grisebachiana</i> Cogn.
<i>Pleurothallis grobyi</i> Batem. ex. Lindl.	
<b><i>Pleurothallis helenae</i> Fawc. &amp; Rendle</b>	wrong classification; <i>Pleurothallis corniculata</i> (Sw.) Lindl. and
<i>Pleurothallis hymenantha</i> Lindl.	<i>Barbosella dussii</i> (Cogn.) Dod (Stenzel & Llamacho 2002)
	<i>Pleurothallis wrightii</i> Rchb. f.
<i>Pleurothallis lichenicola</i> Griseb.	
<b><i>Pleurothallis llamachoi</i> Luer</b>	
<b><i>Pleurothallis longilabris</i> Lindl.</b>	
<i>Pleurothallis longissima</i> Lindl.	<i>Pleurothallis ghiesbreghtiana</i> A. Rich. & Galeotti
<i>Pleurothallis maestrensis</i>	nom. nud.
<b><i>Pleurothallis mucronata</i> Lindl. ex Cogn.</b>	
<i>Pleurothallis multirostris</i> Rchb. f.	<i>Pleurothallis racemiflora</i> (Sw.) Lindl.
<b><i>Pleurothallis murex</i> Reichb. f.</b>	
<i>Pleurothallis nubigena</i> Lindl.	<i>Pleurothallis corniculata</i> (Sw.) Lindl.
<b><i>Pleurothallis nummularia</i> Reichb. f.</b>	
<b><i>Pleurothallis obliquipetala</i> Acuña &amp; C. Schweinf.</b>	
<i>Pleurothallis oblongifolia</i> Lindl.	<i>Pleurothallis racemiflora</i> (Sw.) Lindl.
<b><i>Pleurothallis obovata</i> (Lindl.) Lindl.</b>	
<b><i>Pleurothallis odontotepala</i> Reichb. f.</b>	
<b><i>Pleurothallis oricola</i> H. Stenzel</b>	
<i>Pleurothallis pachyrhachis</i> A. Rich.	<i>Bulbophyllum pachyrhachis</i> (A. Rich.) Griseb.
<b><i>Pleurothallis papulifolia</i> Luer</b>	
<i>Pleurothallis parvula</i> Ames & C. Schweinf.	<i>Pleurothallis denticulata</i> Cogn.
<i>Pleurothallis platyglottis</i> L. O. Williams	<i>Pleurothallis denticulata</i> Cogn.
<b><i>Pleurothallis prostrata</i> Lindl.</b>	
<b><i>Pleurothallis pruinosa</i> Lindl.</b>	possibly conspecific with <i>P. ghiesbreghtiana</i> A. Rich. & Galeotti;
<i>Pleurothallis quadrifida</i> (Llave & Lex.) Lindl.	<i>quadrifida</i> would be the valid epithet then, due to priority
<b><i>Pleurothallis racemiflora</i> (Sw.) Lindl.</b>	
<i>Pleurothallis racemiflora</i> Lindl. ex Lodd.	nom. illeg.
<i>Pleurothallis richteri</i> H. Dietr.	<i>Pleurothallis wrightii</i> Rchb. f.
<b><i>Pleurothallis rubroviridis</i> Lindl.</b>	
<b><i>Pleurothallis ruscifolia</i> (Jacq.) R. Br.</b>	
<b><i>Pleurothallis sertularioides</i> (Sw.) Spreng.</b>	
<b><i>Pleurothallis shaferi</i> Ames</b>	
<b><i>Pleurothallis testaefolia</i> (Sw.) Lindl.</b>	
<i>Pleurothallis toaensis</i>	nom. nud.
<b><i>Pleurothallis tribuloides</i> (Sw.) Lindl.</b>	
<b><i>Pleurothallis trichophora</i> Lindl.</b>	
<b><i>Pleurothallis trichyphus</i> Reichb. f.</b>	
<i>Pleurothallis tricostrata</i> Cogn.	<i>Pleurothallis racemiflora</i> (Sw.) Lindl.
<i>Pleurothallis trigonifolia</i>	nom. nud.
<i>Pleurothallis tuberculata</i>	nom. nud.
<i>Pleurothallis univaginata</i> Lindl.	<i>Pleurothallis gelida</i> Lindl.
<i>Pleurothallis urbaniana</i> Rchb. f.	<i>Pleurothallis aristata</i> Hooker
<i>Pleurothallis velaticaulis</i> Rchb. f.	wrong classification, mostly <i>Pleurothallis domingensis</i> Cogn.
<i>Pleurothallis verruculosa</i>	nom. nud.
<b><i>Pleurothallis wilsonii</i> Lindl.</b>	
<b><i>Pleurothallis wrightii</i> Reichb. f.</b>	
<i>Pleurothallis yamanigüeyensis</i>	nom. nud.

All recent studies on the orchid flora of Cuba (Acuña Galé 1939, León & Schweinfurth 1946, Hawkes 1951, Dietrich 1984b) enumerate a total of ~40 taxa in *Pleurothallis*. Ironically, this work comes to almost the same conclusion. Until the start of this study in 1998, 55 heterotypic epithets that were referred to the Cuban *Pleurothallis* flora had been validly published. 5 of these are currently treated in different genera, 17 are synonymous with those herein accepted, 4 are based on wrong classifications, and 1 could not be evaluated because of the missing type material (*Pleurothallis quadrifida* (Llave & Lex.) Lindl.). 5 species new for Cuba have been detected in material from herbaria and field



work (Stenzel & Llamacho 2002). 6 new epithets have been published (Luer 1998c, 1999a; Stenzel 2001, 2002) since 1998, one of which is treated here as a synonym of *Pleurothallis grisebachiana*.

In the Cuban herbaria, *Pleurothallidinae* are notoriously misdetermined. Even if not considering synonymous names, 25% of the material in HAC, HAJB and HPPR had to be revised. The overall portion of wrong classifications, including synonyms, was 40%. Closely associated with this phenomenon is the low quality of Cuban standard works as Acuña's Catálogo (1939) and the Flora de Cuba treatment by León and Schweinfurth (1946). There are not only taxonomic errors passed on from one work to the next, but plenty of phytogeographical misconcepts, too. León lists 21 of 38 taxa as confined to Oriente. Among these there are species that are not found at all in the Greater Antilles (*Pleurothallis hymenantha*). In turn, taxa of allegedly Greater Antilles distribution are actually local endemics in Moa-Baracoa (*P. longilabris*).

### 3.5 Phytogeography

In the following, Cuban species of *Pleurothallis* were analysed as to their chorological affinities with certain variables, e.g. islands, vegetation types, geographic and climatological parameters.

#### 3.5.1 Phytogeographic relationships of the Greater Antilles with other neotropical areas

There are ~ 70 species of *Pleurothallis* in the Greater Antilles, 68% of which are endemic to one of the islands and ~80% are confined to the Archipelago. Endemism within island boundaries does not reach that rate. Yet, *Pleurothallis* shows a higher endemism than orchids in general. Comparing recent rough estimates of Cuban orchidaceous endemism (Dietrich 1984b, 1989b; Trejo-Torres & Ackerman 2001) which rate ~1/3 as endemic, Cuban *Pleurothallis* shows a much higher geographical restriction on the island level. Fig. 48 shows species totals and the endemic portion of the Greater Antilles islands. Hispaniola and Cuba have rather similar values, with the former being slightly richer in the endemic portion (but see p. 142 for objections) whereas in Jamaica the level drops sharply. Puerto Rico, finally, has no endemic *Pleurothallis* at all.

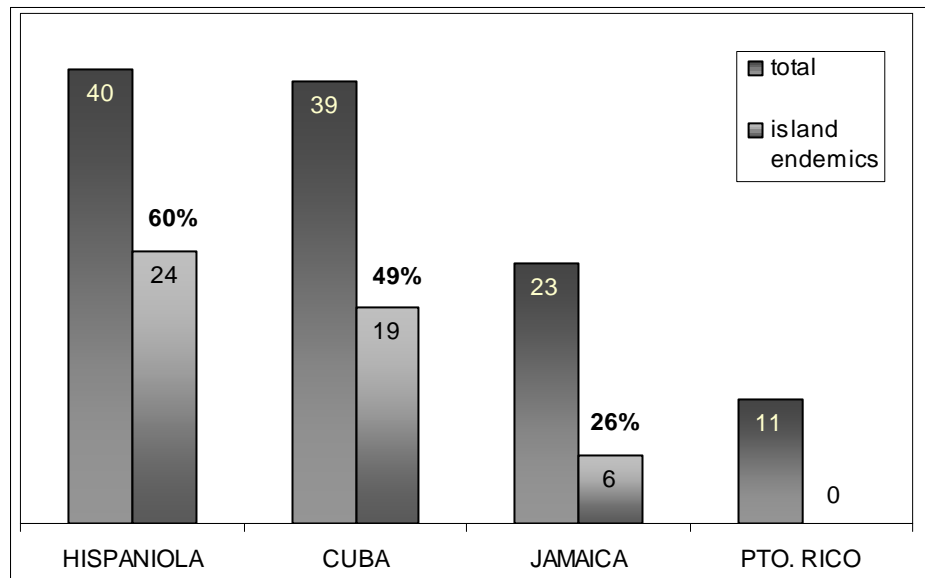


Fig. 48: *Pleurothallis*: absolute number of species occurring on the Greater Antilles islands and the endemic portion (absolute and percentage).

Species that are not confined to a single island show the following distribution pattern (Fig. 49). 8 species are endemic in the Greater Antilles. Of the 15 taxa that reach beyond the island arc, 4 are confined to Central America and another 4 to Central America-South America. 6 are Pan-Caribbean elements (West Indies, Central America, South America) with one species occurring in Florida too. Only one taxon is found in the Lesser Antilles and South America. There is no indication for the disjunction Greater Antilles-South America! All islands reflect more or less the Greater Antillean proportions of the respective elements; however, Cuba comes closest to absolute numbers.

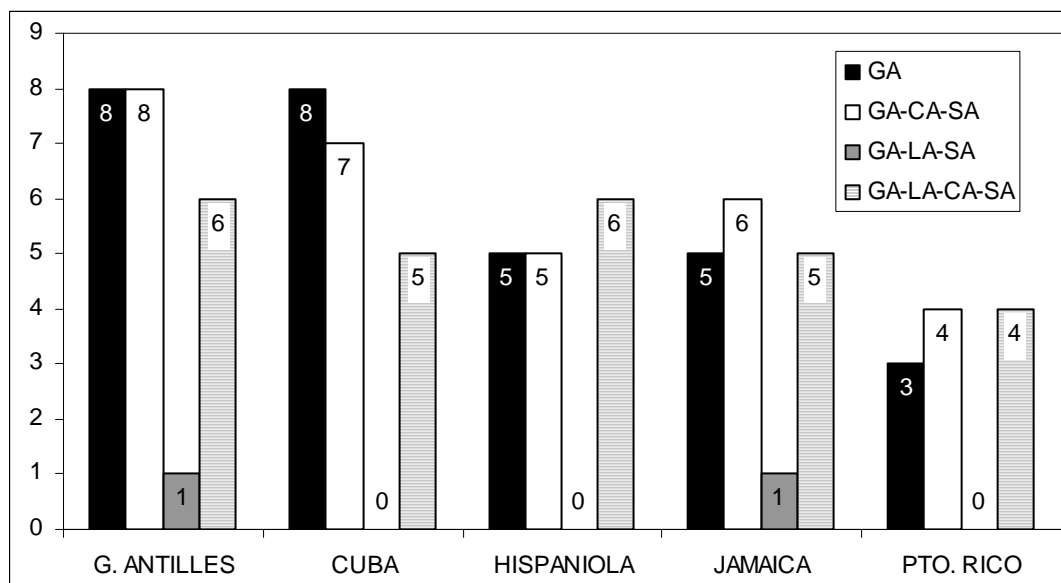


Fig. 49: *Pleurothallis*: distribution of species that are not endemic on the island level. GA - Greater Antilles, LA - Lesser Antilles, CA - Central America, SA - South America). Bars show the absolute number of species of a given distribution (e.g. 3 Puerto Rican species are endemic in the Greater Antilles).

There is a chorological bipolarity in the Greater Antilles in that most species are either endemic on one island (49 spp.) or are widespread in the West Indies, Central America or/and South America (15 spp.). By way of contrast, there are only a few Greater Antillean endemics (8 spp.) which are confined to more than one island within the archipelago (Fig. 50).

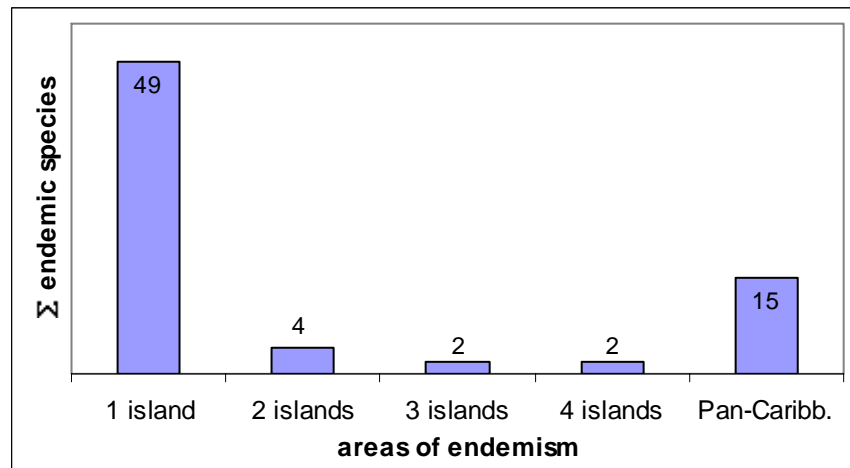


Fig. 50: Greater Antillean *Pleurothallis*: levels of endemism. Bars show the number of species confined to a certain area.

The set of those 23 species which are not confined to only one island was used to find phytogeographical relationships among the West Indies, adjacent Central America and South America. It turned out that the topologies obtained by MP analyses depended heavily on the areas included and how these areas were defined. MP trees reflect relationships not only based on shared species (coded 1), but on absent species too (0). Since MP algorithms do not weight character states, the absence of a species will group areas just as will do the presence. Hence, areas poor in diversity will a priori be clustered regardless which species they share. To give an example, Grand Cayman shares its only species with West Cuba. Analysing the Greater Antilles islands and adjacent continental areas, Grand Cayman came out as sister to the Lesser Antilles in all MP trees. However, it does not share a single *Pleurothallis* with that archipelago. The grouping came out only by the general poorness of the local floras. When Cuba was split into 3 subareas (West, Centre, East), 4 MP trees resulted from that matrix with Grand Cayman falling sister to the Lesser Antilles still in 3 trees. Finally, after the exclusion of the outgroup, one most parsimonious tree was found with Grand Cayman forming a clade with West Cuba! Thus, the presence of a 0-coded outgroup can have strong influence on the topology, affecting especially those areas with low diversity. The same effect is apparent in several phytogeographic studies using MP analysis. (Trejo-Torres & Ackerman 2001) examined phytogeographical relationships in the Antilles based on MP analysis of orchid distributions. The trees were Lundberg rooted. A closer look at the distribution within trees

shows that basal branches of the majority tree are generally poor in species numbers. Diversity rises with growing distance from the outgroup, hence, basal units may have been grouped above all by the shared absence of taxa which is not necessarily a reflection of true relationship. If using MP in this context, one should be aware that those clades with the greatest distance from the outgroup or units with low diversity, reflect the information in the matrix best. Although the authors discuss the influence of species numbers (Trejo-Torres & Ackerman 2001: 781), they do not return to the original phytogeographical matrix, to detect the influence of species absence on the topology among island that are poor in taxa. MP related pitfalls and their avoidance have been described in the original papers on PAE already (Rosen & Smith 1988, Rosen 1992). Yet, to date one can find misconcepts of MP analysis (Judd 2001: half of matrix including regional endemics, i.e. parsimony uninformative)

As a consequence, outgroups were excluded from the following analyses. The general floristic affinities between the Greater Antilles and continental areas as inferred from chorological patterns in *Pleurothallis* are illustrated in Fig. 51. This tree is based on 15 taxa of Caribbean and continental distribution and clearly shows the closer relationships between the Greater Antilles and Central America. South America, and even more the Lesser Antilles, are floristically less tied to the islands. In the case of South America, which does not border the Greater Antilles, this does not automatically mean a disjunction, since all but one species occurring in South America can be found in Central America, too. Likewise, all but one taxa in the Lesser Antilles can be found in South America and/or Central America, too. The descending order reflects actually more the arithmetic similarity of the Greater Antilles with Central America (14 of 15 taxa), South America (11 taxa) and the Lesser Antilles (7 taxa).

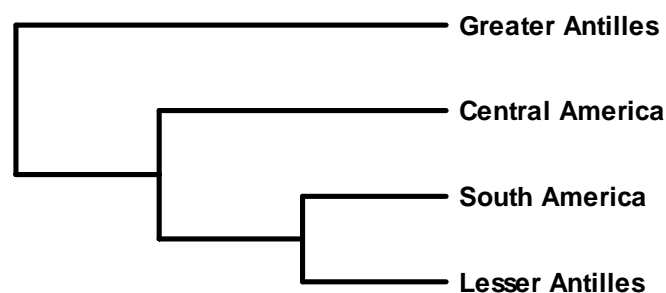


Fig. 51: Floristic affinities between the Greater Antilles and adjacent neotropical areas. MP tree based on the distribution of the 15 Greater Antillean species that occur outside the archipelago.

However, the relationships of the Greater Antillean islands with adjacent continental areas and among each other are not equally developed. A complete analysis of the islands, the Lesser Antilles, Central, and South America left some branches unresolved in the strict consensus tree, which is due to the small number of species shared by the areas. As a consequence, in order to compare affinities of the individual Greater Antilles islands with

adjacent areas, the relationships with South, Central America and the Lesser Antilles was analysed independently. In the case of South America and the Lesser Antilles, these areas fell sister to the Greater Antilles (trees not presented) with Puerto Rico as the nearest branch, i.e. both areas had closest affinities to the smallest and easternmost island of the Greater Antilles. Central America, however, formed a group with Cuba-Jamaica, stressing the closer affinities between nearby continental areas and the western Greater Antilles islands (tree not shown). The underlying chorological pattern is represented by two species that are endemic to Cuba-Jamaica and three confined to Cuba-Jamaica-Central America. Hispaniola is tied to that group only by sharing one taxon with Cuba and another with Cuba-Jamaica-Central America. Summing up, the relationships of the islands with each other as well as with adjacent neotropical areas are not strongly developed, i.e. in most of the cases they are represented only by weak chorological imbalances.

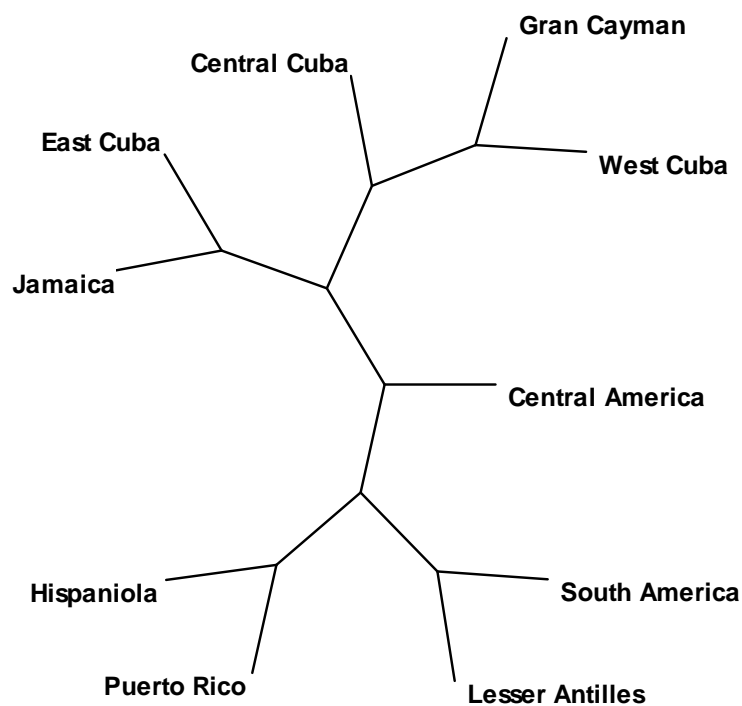


Fig. 52: Floristic affinities between Cuba's three mountainous areas, the Greater Antilles and adjacent continental areas. Only most parsimonious tree found.

The irregular distribution continues as one zooms further into the Antilles. Within Cuba, *Pleurothallis* is found in all three major mountainous areas, as reflected by the principal collecting areas (Fig. 2). However, species diversity is highly skewed among the three areas (Fig. 53). Fig. 52 shows the relationships among Cuba's subregions and with respect to other islands and neighbouring areas. Cuba's central part shows more affinities with the East, due to three Cuban endemics shared. The eastern part of Cuba in turn is closer allied with Jamaica (two species endemic in these areas). Again, Cuba and Jamaica fell sister to Central America. This region shares a number of taxa, which are not

found in Hispaniola, Puerto Rico, South America and the Lesser Antilles. As mentioned before, the number of those taxa which would distinguish areas is too small and their distribution often contradicting. Thus minor relationships between Hispaniola and East Cuba (one species), as well as Hispaniola, Puerto Rico and East Cuba blur the topologies.

### 3.5.2 Distribution patterns on the island of Cuba

Generally, pleurothallid species are confined to the mountainous western, central and eastern end of the island. Extrazonal locations comprise the coastal lowlands of Guanahacabibes (*Pleurothallis caymanensis*, *Pleurothallis oricola*) and Canasí (*Pleurothallis corniculata*).

#### *East vs. Central vs. West Cuba*

As mentioned above, species of *Pleurothallis* are not evenly distributed among the three main areas. On the contrary, there is an overwhelming floristic richness in Oriente (36 taxa), whereas the central (11) and western (9) areas are poor both in species diversity and endemism (Fig. 53).

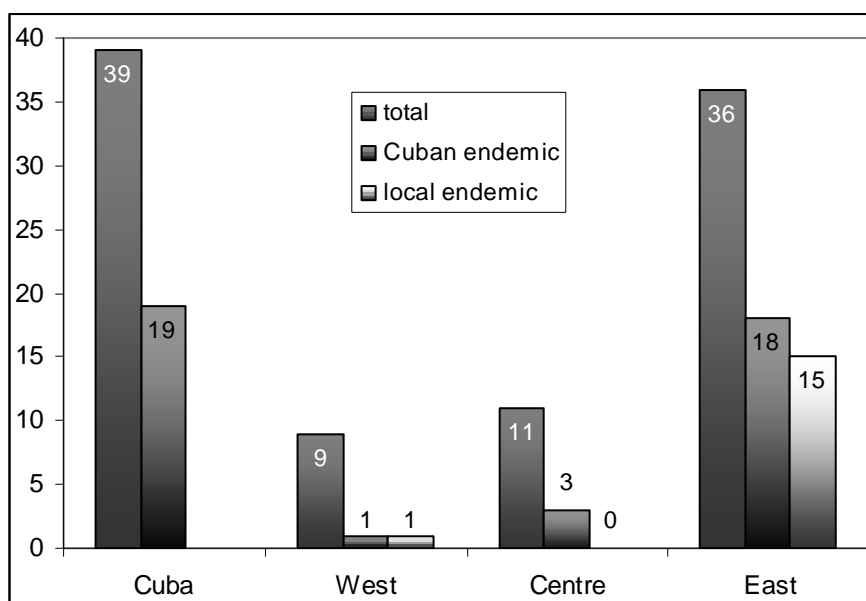


Fig. 53: *Pleurothallis*: number of species in East, Central and West Cuba. Island totals are given again for comparison.

Floristic affinities of the three subregions with neighbouring areas have been presented earlier (Fig. 52). East Cuba shows closest relationships with Jamaica (*Pleurothallis odontotepala*, *P. nummularia*) and Hispaniola (*P. denticulata*). Moreover, eastern Cuba shares three endemics with Central Cuba, *P. grisebachiana*, *P. murex* and *P. trichophora*, as well as two taxa of wider distribution, *P. pruinosa* and *P. wilsonii*, none of which is

found in West Cuba. The latter, in turn, accommodates one species not found in the other subregions that tie it with Central America and the other Greater Antilles (*P. ghiesbreghtiana*) and one with the distribution West Cuba – Grand Cayman (*P. caymanensis*).

#### *Distribution ~ ecology: elevation*

Pleurothallid orchids were found to inhabitate the whole vertical range from sea level to the summit of Pico Turquino (Fig. 54). The maximum species diversity is found between 300 and 900 m with the peak at 600-700 m elevation. Remarkable are the relatively poor higher elevations. Ranges above 1300 m refer exclusively to the Turquino massif (**a**), which is especially poor in species diversity in the 300 m cloudforest belt [!] above 1400m. The small peak below 1200 m (**b**) is brought about by the enriched summit floras of several mountain tops reaching just this height (Pico Cristal, Gran Piedra, Loma El Gigante). The massive concentration of taxa around 600 m (**c**) is due to the accumulation of endemics from the Nipe-Cristal-Moa-Toa and Sierra de Imías range along with the *flora* of the mogote summits. Finally, two species from Guanahacabibes and one from Moa (**d**), show a coastal distribution which is very unusual for the typically mountain bound genus *Pleurothallis*.

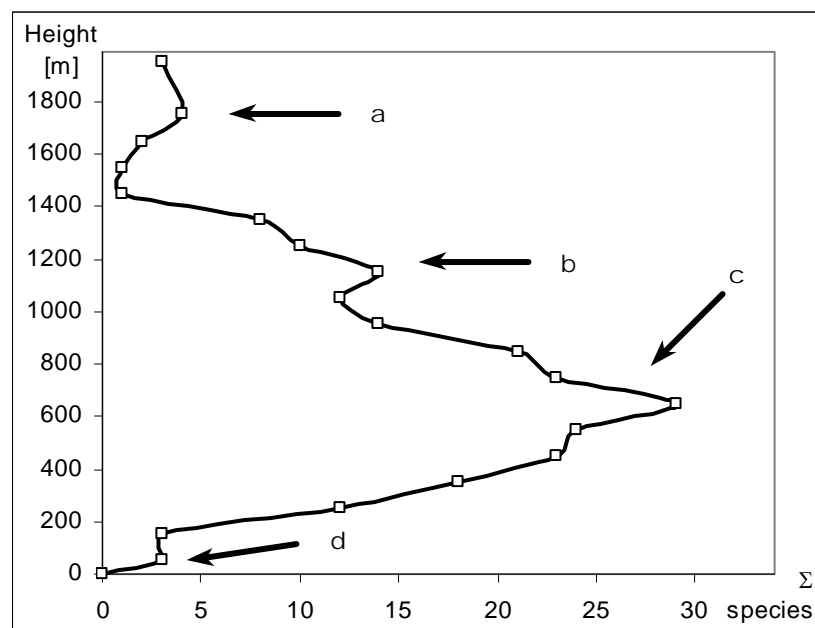


Fig. 54: *Pleurothallis*: vertical distribution of species at different elevations. Numbers show the total of species that have been collected in the respective vertical section of 100 m. Arrows (a-d) are explained in the text.

Concerning the altitudinal amplitude, most species occur in an elevation belt of 300-1000 m in height (Fig. 55). Of course, these belts may differ regarding the absolute height they are inserted in. Thus, *P. prostrata* and *P. denticulata* occur both within a belt of about 400 m, the former between 600-1000 m, the latter from 1100-1500 m.

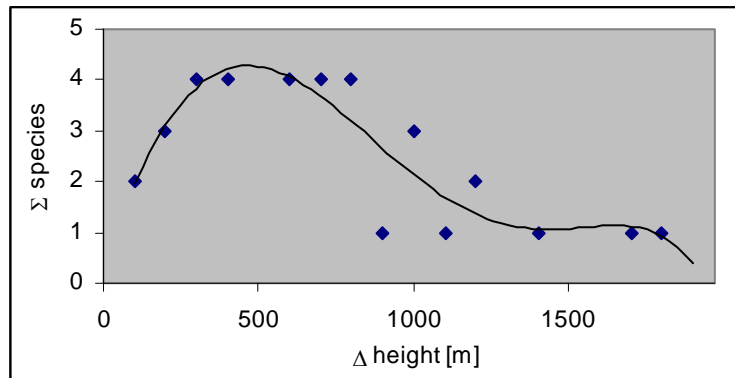


Fig. 55: Altitudinal amplitude of Cuban *Pleurothallis*. Values indicate the number of species that share the respective altitudinal range, e.g. 3 species occur within an altitudinal belt of 1000 m in height. A polymorph trend curve (5<sup>th</sup> order) is added.

The greatest altitudinal amplitude can be observed in *Pleurothallis domingensis* ( $\Delta 1800$  m) and *P. racemiflora* ( $\Delta 1700$  m), two Greater Antillean endemics, but with very close relatives in Central (Luer 1998b) and South America (Luer 1998a). Other species of likewise ample altitudinal distribution comprise rather widespread taxa like *Pleurothallis corniculata*, *P. gelida*, *P. obovata*, *P. ruscifolia*, *P. sertularioides*, *P. tribuloides*. On the other hand, Cuban endemics tend to be restricted to a narrower altitudinal belt (Fig. 56).

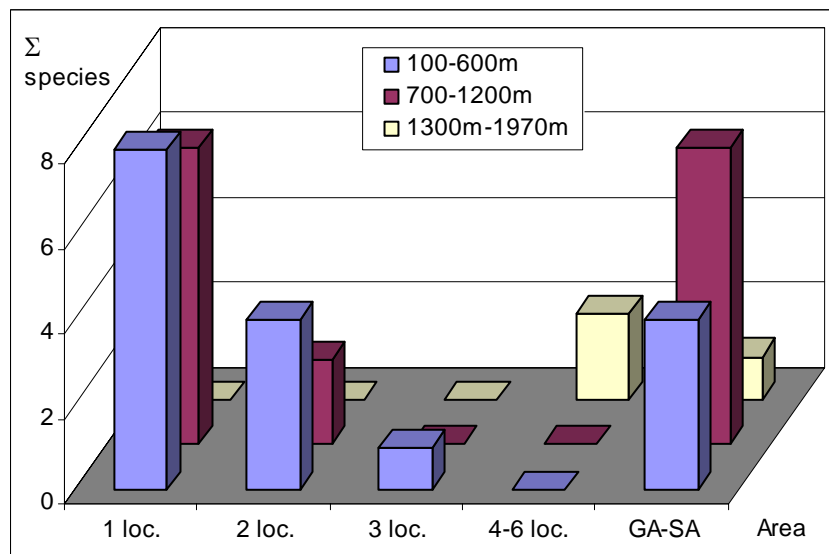


Fig. 56: *Pleurothallis*: Correlation between general distribution of Cuban species and their altitudinal amplitude. Note that the altitudinal classification does not represent the range but the width of the elevation belt the species occur in! Horizontal distribution (area) is growing on the x-axis from left to right, ecological amplitude from the foreground towards the background. Given are the totals of species. See p. 18 for further methodical details.



Although Borhidi's (1996) climate map of Cuba, based on data from 217 stations, is the best available, it often provides too low spatial resolution yet, to assess climatic affinities in detail. In the following, a list is presented of those climate types where pleurothallid orchids occur. It has to be stressed, however, that habitat preferences depend often on microclimatic features that are not reflected in Borhidi's system. These empirical data, gathered during extensive field work, are given where necessary.

Only 3-6 of the 15 types listed for Cuba by Borhidi (1996) seem to be too hostile for pleurothallids. These comprise types with extended arid periods and/or a combination of high temperatures and low amounts of precipitation. The remaining types are suitable for *Pleurothallidinae* to various degrees. Although the evaluation is empirical, those types that appear to host the greatest number of pleurothallids are marked in bold type.

1. Summer dry tropical climate: 3 (b-)c-d T. 1000(?) -1500 mm/a. (5-)4-1 dry months.

This special type prevails only at the NE coast of Oriente and is brought about by the contact of bixeric climates in the lowlands with neighbouring wet climates in the mountains. The type can be included only tentatively, since it is hard to distinguish from the bixeric type on Borhidi's map (Borhidi 1996). If at all, habitats are restricted to gallery forests which provide a suitable microclimate especially in localities with an extended arid season (see p. 91 #3).

2. Winter dry tropical climate: 4 (b-)c-**d Th**. 1300-2400 mm/a. (5-)4-1 dry months.

This is the most common type in Cuba (Borhidi 1996). Areas that accommodate *Pleurothallis* comprise lowlands (Guanahacabibes), colline (Pinar del Río, Escambray, Sierra Maestra: -800 m) to submontane belts (as colline, but 800-1440 m). Localities with a strong to moderate dry period (Guanahacabibes: 5 months) show secondary microclimatic traits with a higher level of air humidity (see p. 91 #2) that moderates the impact of drought. The same applies to habitats at lower and middle elevations close to waterways (see p. 91 #3). A third microclimatic trait related to relief is found at lower altitudes in the Sierra de los Órganos (see p. 91 #1). Mesoclimatic features as condensation belts provide an additional source of shade, humidity, and precipitation at higher elevations (see p. 91 #4).

3. Bixeric tropical climate: 5 **d Th**. 1400-1800 mm/a. 1-2 dry months. This type occurs only in NE Oriente in Moa, Toa, and Baracoa at lower elevations. Special microclimatic features provide favourable conditions for microphytic orchids (see p. 91 #3). Several collections of pleurothallid orchids (*P. obovata*, *P. sertularioides*) around Siboney (S of Gran Piedra) would fall in the category 5 b or 5 a even. Unfortunately, no further information, concerning the specific climatic features of

this peculiar locality could be obtained. Considering the strong influence of meso- and microclimatic traits that have been observed to blur macroclimatic patterns in Cuba, it is safe to assume that this area must have a strong secondary climatic impact either from the nearby shore or from altitude.

4. Axeric tropical climate: **6 a-b**. 1400-3200(-5000) mm/a. No dry period. Restricted to E Sierra de los Órganos, Sierra del Rosario (Taco Taco, Rangel?) and above all the Moa-Toa-Baracoa range at middle elevations (6 a), as well as in (sub-)mountainous belts (600-1400m) in Central and East Cuba (6 b). Again, macro- and mesoclimatically drier habitats show sources of additional humidity and precipitation (see p. 91 #3-4).
5. Tropical montane climate: **7 a-b**. >2000 mm/a. No dry period. Restricted to the central Sierra Maestra (7 a) and the Pico Turquino massif (7 b). The latter type seems to host much less *Pleurothallis* species. The high ridges above 1800 m fall under its influence. Local meso- and microclimatic phenomena smooth the harsh impact of insolation and drought in exposed epiphytic and epilithic habitats (see p. 91 #4).

#### *Distribution ~ ecology: vegetation types*

It is essential to bear in mind the definition of the vegetation types as employed here (p. 16). Despite the adoption of many formations sensu Borhidi (1996) there are differences which should be considered. Distribution data of the individual species in natural and secondary vegetation types are listed in the second part of this thesis. Fig. 57 shows the totals of species that have been found in the different vegetation types.

Concerning the importance of natural habitats, it is interesting that 12 of the 39 species could be found in areas disturbed by man or even in **cultivations**. The latter, however, has to be considered with caution, since the relevant data is drawn from rather indifferent collecting information, e.g. "en montes y cafetales". The data for **secondary shrubwoods** is almost completely obtained from a destroyed montane rainforest in the Sierra de Imías (Los Calderos), a low vegetation termed tree-fern-*Dicranopteris*-shrubwood (matorral seminatural con helechos arborescentes y *Dicranopteris* spp. according to Borhidi, 1996). This is the only case where an endemic *Pleurothallis* (*P. rubroviridis*) has been found in secondary formations. All other species that were collected in vegetation types affected by man represent widespread taxa of Antillean or Pan-Caribbean distribution.

Of the natural formations defined by Borhidi (1996) which were partially adopted here, *Pleurothallis* is

1. present in all non-coniferous **forest** types except semideciduous xerophytic forests. Seasonal rainforests, were excluded from the screening since “undisturbed stands are hard to find anywhere in Cuba” (Borhidi 1996).
2. absent in most **shrubwood** communities. The major exception from that rule are charrascal formations, which accommodate a great number of species.
3. strongly under-represented in all types of **pine** forests.
4. entirely absent in **savannahs** and grasslands, **mangroves**, **coastal** vegetation on both sandy and rock ground.

*Species diversity* – With the exception of species poor cuabales, dry, and semi-deciduous forests, species of *Pleurothallis* are generally not found in lowland formations. All other types are bound more or less to the colline, submontane and montane belt. Unexpectedly, **elfin formations**, the hallmark of which is epiphytism, are relatively poor in pleurothallids. In fact, on the summits of the Turquino massif there are relatively extended areas, that seem to be almost free of them. This is especially striking when ascending the traditional trail to the Turquino peak. Below La Aguada de Joaquín along the crest a very rich epiphytic layer with no less than 10 species of *Pleurothallis* can be observed. The second steep part between La Aguada and Pico Joaquín hosts almost no plants of this genus. There are still specimens of *Lepanthes* growing on the trunks, but the impression of a highly reduced phanerogamous epiphytic layer is striking. The summit crests again are characterised by numerous epiphytes that grow in and on the dwarf forests and shrubwoods. The discontinuity of the distribution even within small distances seems to be the result of unfavourable light conditions: the steep part between La Aguada and the summit crests is exposed to the West, i.e. least insolated. Furthermore it is dominated by dense forests with rather closed canopy. The crests below La Aguada and on the summit ridges receive more light due to their exposition and a broken and partially open vegetation. It is here that the greatest number of orchids can be found in epilithic, pseudo-terrestrial and epiphytic habitats.

Among the simple formations, not surprisingly, **montane and submontane rainforests** are the ones with the richest pleurothallid *floras*.

Among vegetation complexes, **gallery forests** show the greatest diversity. Gallery forests, as defined by Capote & Berazaín (1984) include smaller rivers and creeks, the banks of which are generally rich in epiphytes. These stands were difficult to score, since it is almost impossible to draw the line between the bank vegetation and the adjacent forests or shrubwoods. Therefore, high species numbers in (sub)montane rainforests and evergreen forests are partially brought about by scoring the species double, both under

“gallery forest” and an adjacent vegetation type. Further from the waterway, the adjoining forests or shrubwoods were, in fact, often free of the respective species. One of the most illustrative examples can be found in Sierra del Cristal following the lower (N→S) and upper (SW→NE) course of Río Levisa.

**Pine forests** have been found to be very poor in orchid diversity. During the field work for this study only drought-resistant bromeliads and mesophytic orchids with developed storage organs (e.g. *Epidendrum* s.l., *Oncidium*) were found in these formations. However, closeby waterways may change the picture. Thus, some pleurothallid orchid have been found and reported for this vegetation type too. In the Sierra del Cristal the large **pine-charrascal** of the SW slope below the summit is virtually free of pleurothallids. Only *P. ekmanii* has been found, growing pseudo-terrestic or epilithic among and on rocks. The N section of Río Levisa occasionally touches stands of **pine forests**. Pleurothallid species growing on conifers have been found only here. Under normal conditions, i. e. away from additional water sources like rivers, pine forests seem to be generally free of *Pleurothallis* species.

Semi-dry serpentine shrubwoods (**charrascal**) receive their high score partially due to the spatial closeness to the riverside vegetation. However, on high mountain plateaus (e.g. Toldo), there do exist extended charrascal areas with many species of *Pleurothallis*.

**Karstic forests** (mogotes) are the other complex that receives relatively high scores. It is potentially composed of at least 3 forest types, montane rainforest (summit of Pico Potrerillo), seasonal evergreen rainforest (most mogotes of Oriente), semideciduous forests (predominating on and around western mogotes). Karstic forests are included as a separate unit for traditional and conservation reasons.

*Endemic portion* – Concerning the endemic portion (island endemics) of the species present in each type (Fig. 57, in red), four formations show values of at least 50%: (sub)montane rainforest on serpentine, charrascal formations, pine forest on serpentine and gallery forests. The first three appear exclusively on serpentine rock. Gallery forests, too, receive high scores from the serpentine-bound endemics (9 of 13). The close affinities among these formations (pine forests excluded) is illustrated in Fig. 58. In montane rainforests and karstic forests, still 25-35% are represented by island endemics.

Most of the endemic taxa occur in more than one vegetation type, i.e. formations are poorly defined by pleurothallid orchids! Only three species are currently known to be restricted to just one type: *Pleurothallis murex*, *P. oricola*, *P. trichyphus*. However, even in the case of these three taxa conclusions have to be drawn with care. Experience from the distribution patterns of other taxa has shown that presumably local endemism often turned out to be a collection artefact.

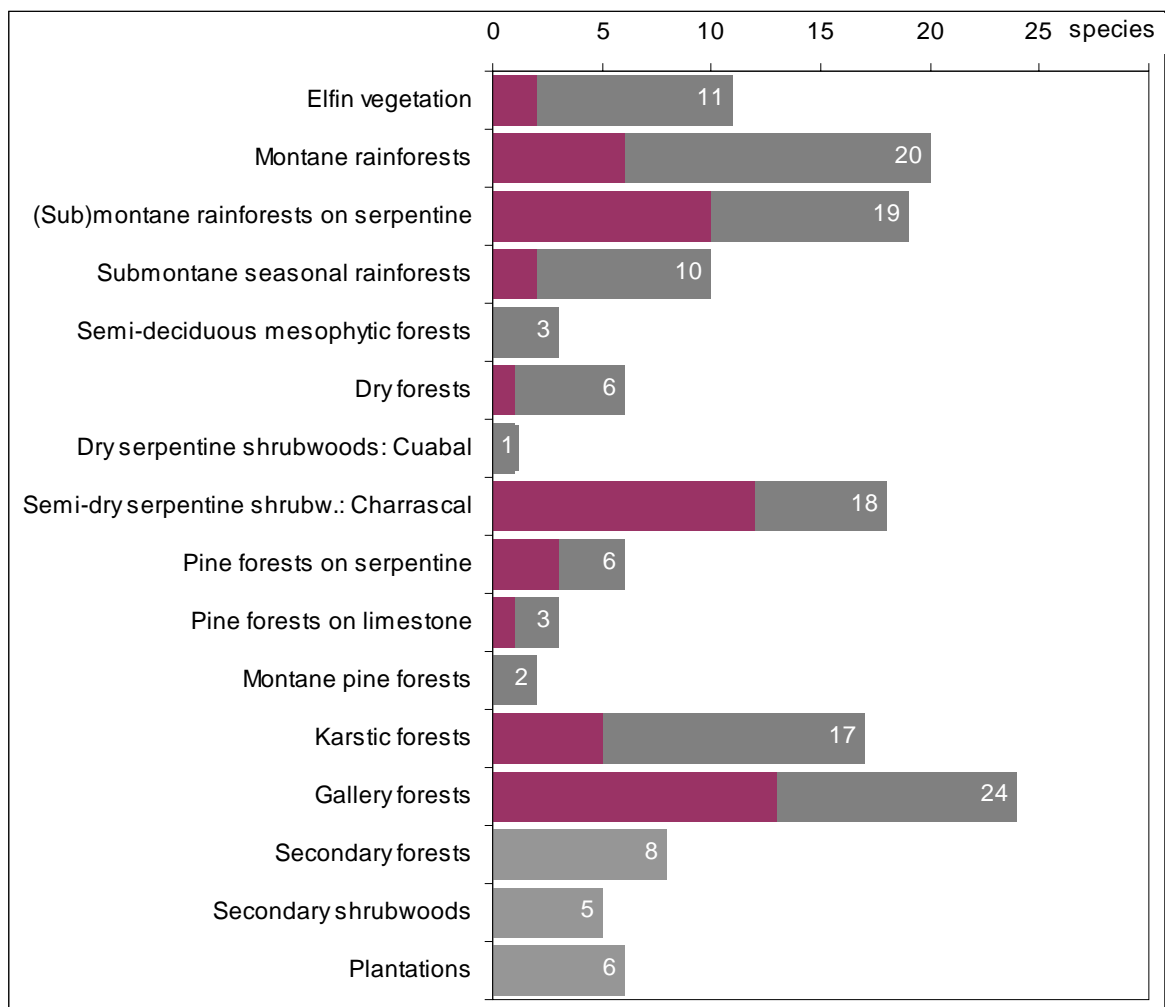


Fig. 57: *Pleurothallis*: Occurrence of Cuban species in different vegetation types. Given are the totals of the species found in the respective formation along with the portion of Cuban endemics (in red; not shown in secondary formations).

As mentioned before, in many cases only special microclimatic situations allow the colonisation by microphytic orchids. For these in general and the non-pseudobulbous<sup>3</sup> pleurothallids in particular, even moderate climates would probably prevent a successful establishment. During field work empirical data on climatic conditions was collected to characterise habitats. Drawn from these observations, the following list will summarise special meso- and microclimatically defined habitats that may explain the occurrence of *Pleurothallis* under otherwise unfavourable macroclimatic conditions

1. Hoyos. – The haystack mountains (mogotes) in West Cuba show a mosaic of microclimatic niches, that are mainly influenced by the relief. The so called hoyos, sagged plateaus, that develop a seasonal evergreen forest on the ground, are characterised by a higher humidity and are less insolated. *Pleurothallis*

<sup>3</sup> However, pleurothallid orchids possess various substitutes for the lack of pseudobulbs: succulent leaves are the most common way to store water.

*caymanensis*, *P. corniculata*, *P. tribuloides* and *P. sertularioides* can be found just on the border to adjacent stands of drier and more open stands of mogote forests. A special microclimatic phenomenon occurs where the hoyos are open to one side. These areas are especially suited for epiphytes, since they benefit from the humid air of the inner hoyo, that flows out during the morning hours (R. Novo Carbó, Pinar del Río, pers. commun.).

2. Partially inundated areas (swamp vegetation). – On Guanahacabibes peninsula, there are two types of forests, dry forest (microphyllous evergreen forest) and semi-deciduous forest. In some areas underground channels lead seawater through the karstic rock. Open ponds along with the nearby shore produce a high humidity that attracts several species of orchids and bromeliads (Poza Redonda, María La Gorda, Barra de La Sorda). Among these are *Pleurothallis caymanensis* and *P. oricola*.
3. Small creeks and rivers. – As mentioned before, gallery vegetation accommodates the majority of the Cuban species of *Pleurothallis* and even *Pleurothallidinae*. In these formations, species are able to colonise low elevations and unfavourable habitats as rocks, pine forests, cuabales, charrascales and semi-deciduous forests. To give an example: the S slope of the Cajálbana mountains is generally free of microphytic epiphytes. Yet, along creeks, a few meters away from sun-torched cuabal vegetation, species of *Lepanthes* can be found.
4. Crests. – While the previous type plays a major role at lower elevations, crests are more important above the condensation belt (900 m, sometimes lower). These habitats accommodate the small species of the Pan de Guajaibón, Sierra de Escambray, Sierra de Nipe, Sierra de Cristal, Sierra Maestra, Yateras and Sierra de Imías. The cloud-enveloped summits and crests of the Sierra Maestra chain often show the same set of species (*Pleurothallis denticulata*, *P. helenae*, *P. obliquipetala*, *P. odontotepala*, *P. racemiflora*, *P. trichophora* and *Lepanthes microlepanthes*).
5. Ground proximity – *Pleurothallis* usually occur on trunks or rocks close to the ground, i.e. in < 3 m height. Specimens have been found only exceptionally as high as 5 m above the ground. In these cases, plants grew either on foggy ridges or specimens belonged to the hardier taxa (*P. obovata*, *P. gelida*) with a high ecological amplitude. This spatial proximity to the ground may be connected to the substrate bound pollinator set, at any rate it benefits from the increased humidity of the terrestrial strata.

Observations in the field had suggested, that some of the vegetation types are more similar to each other concerning the set of pleurothallids that they accommodate. These

floristic relationships of the different natural vegetation types are illustrated by a MP analysis based on the distribution of *Pleurothallis* species.

When analysing all formations, 23 [!] trees were computed. Bearing in mind the limited applicability of the MP algorithm discussed earlier (p. 80), all formations with less than 6 taxa present were excluded from the matrix in the next run. The resulting tree (strict consensus of two trees computed) is shown in Fig. 58. There seems to be a striking dissimilarity within groups, e.g. the combination of shrubwoods and rainforests. The underlying pattern is apparently based on geology, which forms two major groups: 1) formations on serpentine and 2) formations on volcanic rock and limestone. The grouping of elfin and montane rainforests does not surprise, since these two types are often found as a neighbouring vertical succession (Sierra Maestra) and both share a number of taxa not present in other types (*Pleurothallis denticulata*, *P. obliquipetala*, *P. odontotepala*, *P. trichophora*). Another 4 species (*Pleurothallis rubroviridis* Lindl., *P. domingensis*, *P. ruscifolia*, *P. wilsonii*) tie this group with karstic and dry forests. The latter has, despite the topology found, more affinities with Karstic forests (*P. caymanensis*, *P. wilsonii*) than with seasonal forests or pine forests on serpentine. The alliance is probably an artefact caused by the low number of species present (see p.80).

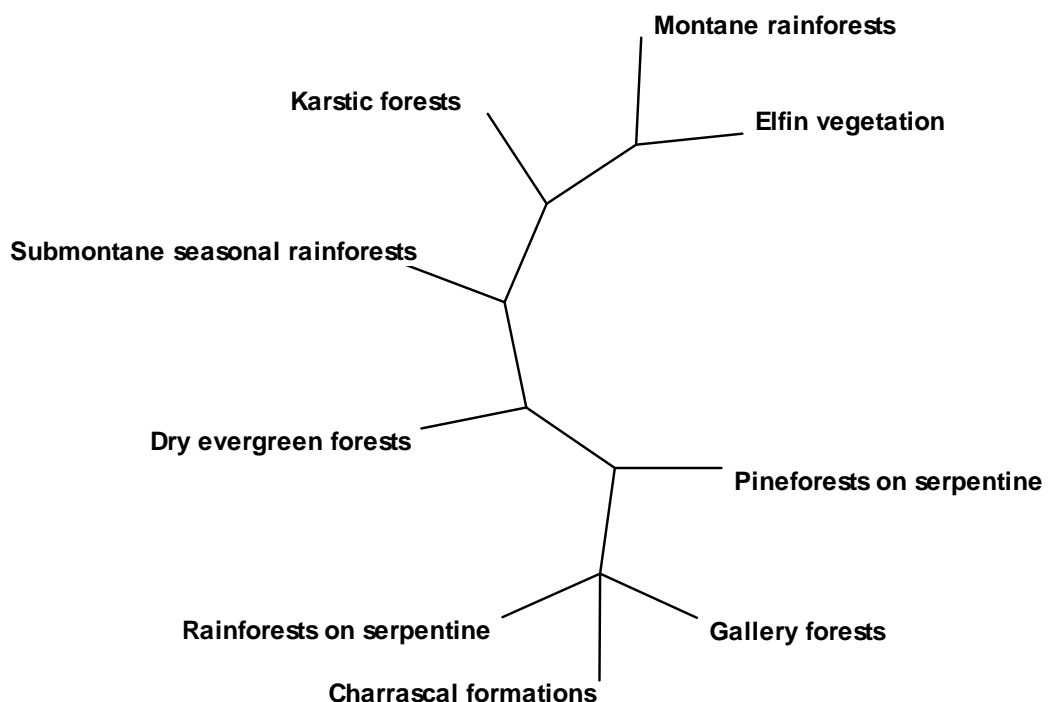


Fig. 58: Floristic relationships between major vegetation types inhabited by *Pleurothallis* (>5 species present). Strict consensus tree of two most parsimonious trees found.

At first sight, the other group is not as clearly defined as the first one. The three formations pine forests, rainforests and charrascales are associated with ultrabasic rock. Surprisingly, gallery forests fell just in this group, a topology that is 100% supported by bootstrap tests. Gallery forests seem to play a major role in areas with serpentine.

As with other variables, species are not evenly distributed among the natural Cuban vegetation types. The most widespread taxa are *Pleurothallis corniculata*, *P. gelida*, *P. obovata*, *P. sertularioides*, and *Pleurothallis tribuloides* occurring in at least 8 of the 13 natural types. They are all of major general distribution. On the other hand, empirical data show that endemics might be restricted to only a small number of formations. Fig. 59 shows that there is indeed a correlation between the two variables, in that the most widespread taxa occur in the greatest number of formations and vice versa. The only exception from that rule is the endemic *P. grisebachiana* which occurs in 6 natural types, an unusually high number among endemic taxa.

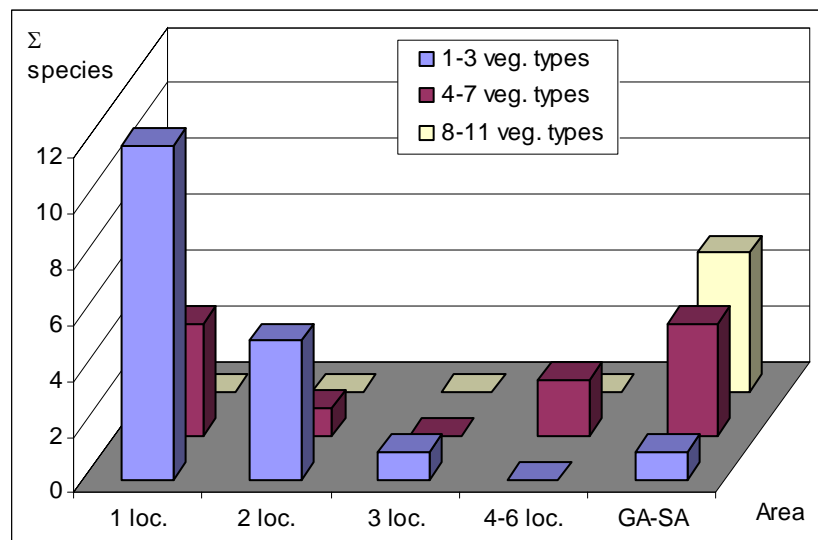


Fig. 59: *Pleurothallis*: Correlation between general distribution of Cuban species and their occurrence in different vegetation types. Horizontal distribution (area) is growing on the x-axis from left to right, ecological amplitude from the foreground towards the background. Given are the totals of species.

#### *Distribution ~ ecology: geology*

Fig. 60 shows the geological affinities of Cuban endemics. The association with a single type of rock is striking. The rate of petrologic endemism would still be higher if Greater Antillean endemics of restricted distribution (two islands) would have been included. *P. caymanensis* (West Cuba – Grand Cayman) is known only from karstic forests. *P. odontotepala* (East Cuba – Jamaica) has been found so far only on volcanic rock. The correlation between overall distribution and the level of petrologic restriction, is shown in Fig. 61.



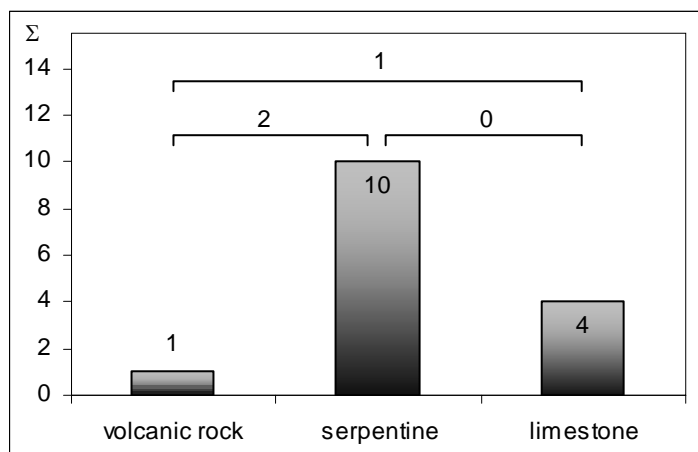


Fig. 60: *Pleurothallis*: distribution of Cuban endemics among different petrologic types. Given are the absolute numbers of species. *P. murex* was excluded because of unreliable data.

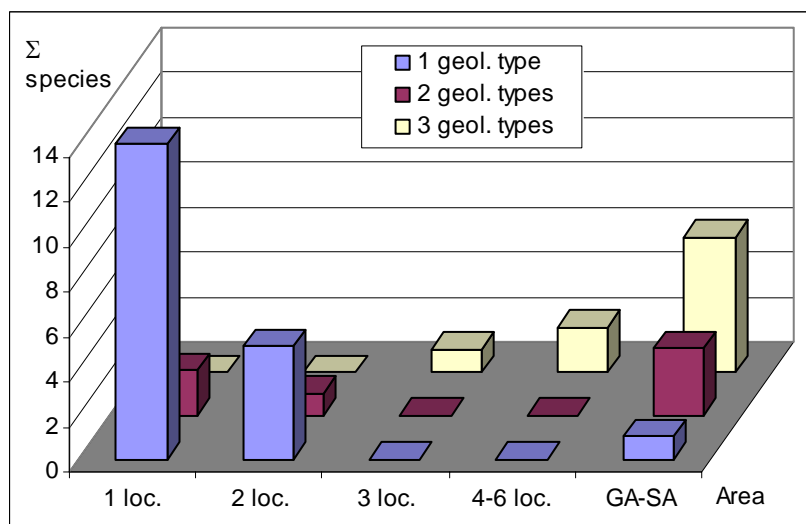


Fig. 61: *Pleurothallis*: Correlation between general distribution and the occurrence on a different number of petrologic types (ecological amplitude). Horizontal distribution (area) is growing on the x-axis from left to right, ecological amplitude from the foreground towards the background. Given are the totals of species.

According to Cuban data, widespread species occur mainly on all types of rock distinguished here. Endemics, on the contrary, are restricted mainly to one type of rock, which reflects the strict geological bonding of most of the Cuban endemics shown in Fig. 60.

#### *Distribution ~ ecological amplitude*

Preliminary studies and field observations had indicated a correlation between the general distribution of *Pleurothallis* species and their ecological amplitude.

The following diagrams (Fig. 62) show the relationships between the horizontal distribution (area) and other ecological variables, i.e. altitudinal amplitude, number of vegetation types and number of petrologic types. It should be emphasised that these variables are always

of quantitative nature, i.e. the aim is to find if there is a correlation between the overall area of distribution and the level [!] of ecological restriction. To give an example, species are not classified regarding their distribution in different vegetation types (quality) but the number of formations they occur in (quantity), e.g. the species that occur in all 7 localities (Pan-Caribbean elements) grow in 6 vegetation types on average (Fig. 62 – b).

Concerning the analysis of vegetation types, phytosociological classifications are largely based on priorities employed by the author (see p.16). In order to compare data, both the classification adapted from Borhidi (1996) which was used in this work (Fig. 62 - c) and the system proposed by Capote & Berazaín (1984) (Fig. 62 - b) were analysed, too.

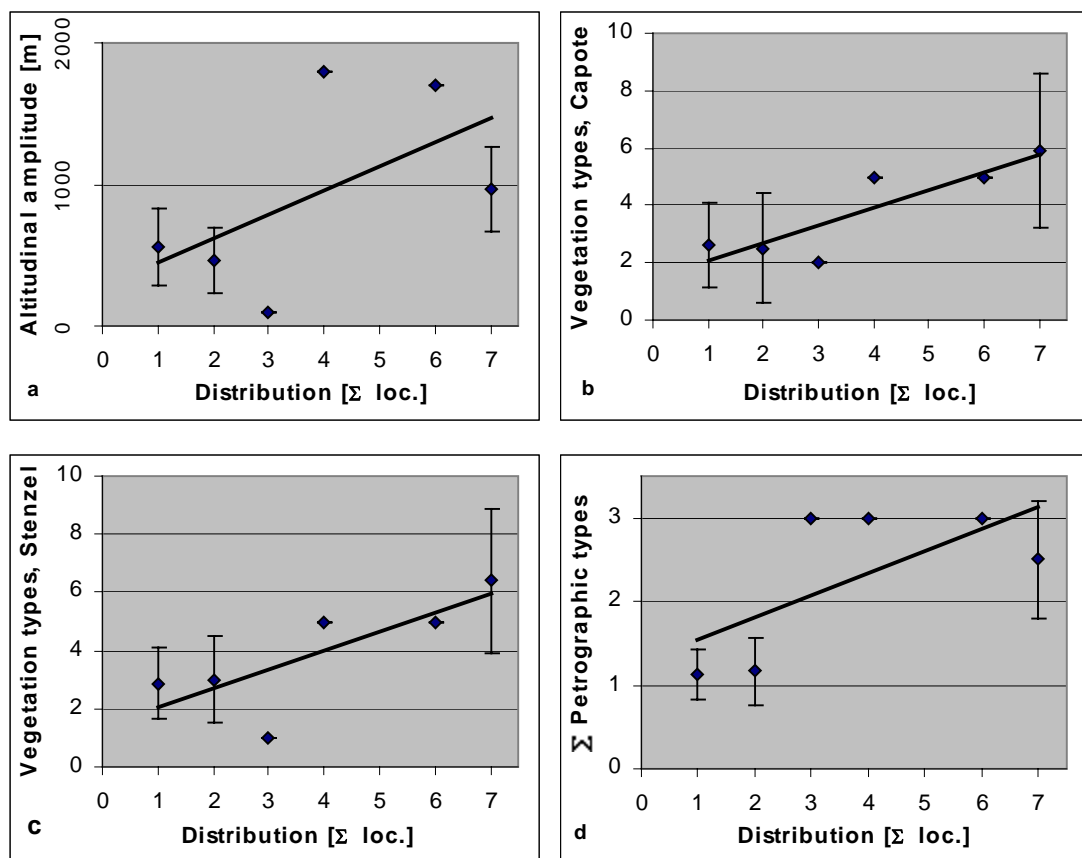


Fig. 62: *Pleurothallis*: Correlation between horizontal distribution and different ecological variables. Species are classified by the overall area of distribution expressed by the number of localities they are found in. Localities 1-6 are Greater Antillean areas, #7 represents the adjacent areas, Lesser Antilles, Central and South America (see p. 18). Analyses are based on mean values (standard deviation given in the graph) except for species occurring in 3,4 and 6 localities, which are single entries.

Spearman correlation, N= 35; **a** –  $r_s = 0.473$ ,  $P = 0.004$ ; **b** –  $r_s = 0.506$ ,  $P = 0.002$ ; **c** –  $r_s = 0.531$ ,  $P = 0.001$ ; **d** –  $r_s = 0.728$ ,  $P < 0.001$ ).

There is a significant correlation between the overall area of distribution and the ecological amplitude of the Cuban species in all tests, i.e. the most wide-spread taxa are the most euryoecious ones.

### 3.6 GENETICS

#### *DNA extraction*

DNA isolation results from material collected in 1998 which had not been stored in a deep freeze immediately showed a quick deterioration process depending on the time they had been exposed to (subtropical) room temperature (Fig. 63).

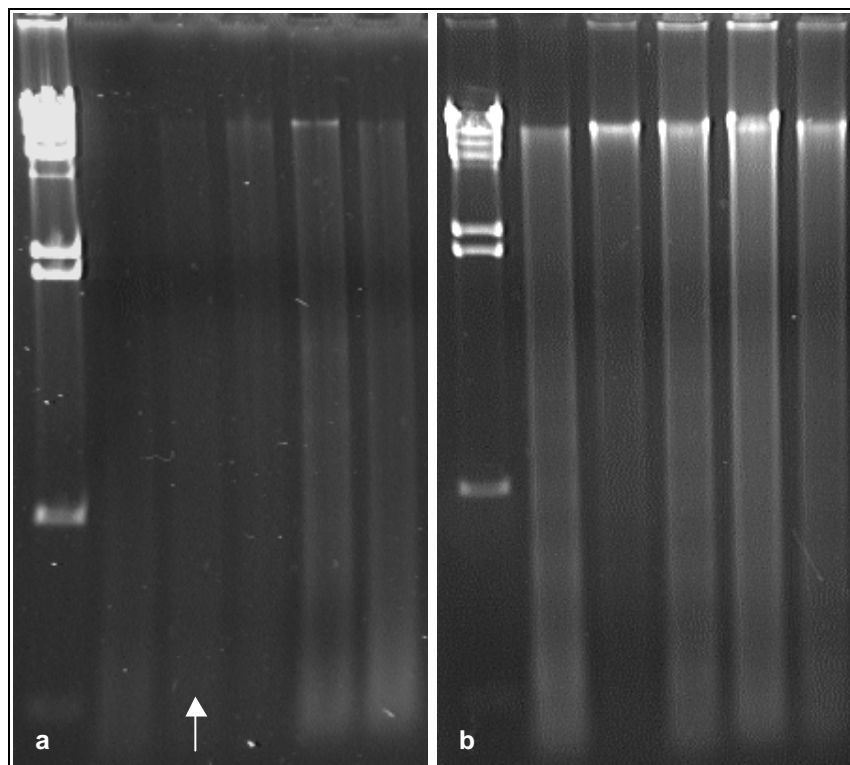


Fig. 63: Agarose gel pictures of DNA extractions from material collected in 1998 (a) and 1999/2000 (b). The arrow marks sample Stenzel 634, which apparently did not contain exploitable DNA material.

On the contrary, material gathered in 1999 and 2000, which had been maintained right after desiccation at least at a temperature of  $\sim 4^{\circ}\text{C}$ , gave excellent results (Fig. 63b). Negative agarose gel analysis not always meant complete failure of the extraction. In some cases (Fig. 63a: arrow), PCR did work, though gel analysis had indicated absence of any DNA in the extract. Extractions from herbarium material, obtained from traditional herbarium collections failed in *P. appendiculata*.

#### *Alignments*

Unaligned ITS sequences differ only slightly in length. The shortest sequence was found in *Pleurothallis pruinosa* (542 bp) due to a gap of 84 bp in the 5.8S gene. *Pleurothallis flabelliformis* has a major deletion close to the *pruinosa* gap too (32 bp, total length of sequence: 609 bp). The rest of the species yielded sequences between 622 bp (*Pleurothallis domingensis*) and 640 bp (*Pleurothallis rubroviridis*).

The following table summarises the length variability of the sequences.

Tab. 7: Length variability (bp) of the unaligned sequences of Cuban *Pleurothallis* species. Two major deletions in 5.8S (*Pleurothallis pruinosa* and *P. 'flabelliformis'*) were ignored in the table.

ITS1		5.8S	ITS2		ITSges	
min.	max.		min.	max.	min.	max.
213	227	164	244	254	622	640

CLUSTAL was run with different options. Different delay values (5%, 30%, 50%), i.e. the amount of bp differences by which a sequence's addition is postponed, did not alter the output alignment. Gap open penalties of 10 and 15 produced identical alignments. Lower values extended insertions as follows: 5: +3 bases, 4: 17 bases, 3: 29 bases.

The five matrices (Tab. 8) used in this study differ mainly in the way how gaps were treated. Of the two initial CLUSTAL alignments received with gap costs 4 (hereafter ITS4C) and 15 (ITS15C) another two were derived by deleting ambiguous gaps (ITS4CR and ITS15CR resp.). A fifth set originating from ITS4C was achieved by eliminating all gaps (ITS4D). All alignments were manually adjusted and gaps presumably caused by single events (duplications) were coded as one base. Thus, the treatment of gaps as a fifth base seemed to be reasonable.

Tab. 8: Characteristics of the five alignments used in this study: gap tolerance, length and informative sites.

\* – two major gap segments in *Pleurothallis 'flabelliformis'* and *P. ruscifolia* were neither deleted nor counted.

matrix	initial gap cost (CLUSTAL)	manual adjust.	indel coding	deletion of ambiguous indels	complete deletion of indels*	$\Sigma$ loci with gaps*	$\Sigma$ bases: total, variable, parsimony-informative
ITS4C	4	yes	yes	no	no	150	704, 552, 318 (45%)
ITS4CR	4	yes	yes	yes	no	118	672, 520, 291 (43%)
ITS15C	15	yes	yes	no	no	116	686, 537, 316 (46%)
ITS15CR	15	yes	yes	yes	no	80	647, 499, 282 (43%)
ITS4D	4	yes	yes	yes	yes	0	553, 193 (35%)

The next table shows the alignment ITS15C.

Tab. 9: Matrix ITS15C. Names of the sequences follow species' epithets. Given are the two sequences of *Pleurothallis pruinosa* as well as those of the different accessions of *P. ghiesbreghtiana* and *P. trichophora*. *Dilomilis montana* represents the sequence used by Pridgeon & al. (2001) as one outgroup (AF262915).

	.... ....	.... ....	.... ....	.... ....	.... ....	.... ....
	5	15	25	35	45	55
aristata	TCGAGATCA-	AAATATAT--	-CGAGCGATT	TGAA-AA-CC	TGTGA---AT	GAGCGG-CGG
bissei	TCGAGACCG-	AAATATAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AC	GAGCGG-CGG
brighamii	TCGAGACCG-	AAATATAT--	-CAAGCGATT	CGGAGAA-CC	CATGA---AC	GAGCTG-TGG
corniculata	TCGAGACCG-	AAATATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AT	GAGTGA-CGG
domingensis	TCGAGACCG-	AA-TATAT--	-CGAGCGATT	CAGAGAA-CC	TGTGA---AC	GAACGA-TGG
ekmanii	ATGAGACCG-	AAAAATAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AT	GAGCGG-CGG
excentrica	ATGAGNCCG-	AAATATAT--	-CGAGCGATT	TGGAGAA-CC	CNTGA---AT	GAGCGG-CGG
'flabellif.'	ATGAGACCA-	AAATATAT--	-CGAGCGATT	TGGAAAAACC	CGTGA---AT	GAGCGG-CGG
gemina	TCGAGACCG-	AA-TATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AT	GAATGAGCGG
ghiesb.#1298	TCGAGACCG-	AAATGTAC--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AC	GAGCGA-CGG
ghiesb.#967	TCGAGACCG-	AAATGTAC--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AC	GAGCGA-CGG
grisebachian	TCGAGACCG-	AA-TATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AT	GAATGAGCGG
helenae	TCGAGATCA-	AAAAATAT--	-CAAGCGATT	TGGATAA-CA	TGTGA---AT	GAGCAG-CGG
llamachoi	TCGAGATCG-	AAATATAT--	-CGAACGATT	TGAAAAA-CC	TGTTA---AT	GAGTGG-TGG
longilabris	TCGAGATCG-	AAATATAT-A	TCGAACGATT	TGAAAAA-CC	TGTTAATAAT	GAGTGG-TGG
mucronata	TCGAGATCG-	AAACATAT--	-CGAGCGATT	TGAAAAA-CC	TGTGA---AT	GAGCGG-TGG
nummularia	TCGAGACCG-	AAACATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AA	GAGCGG-CGG
obliquipetal	TCGAGATCG-	AAATATGT-A	TCGAACGATT	TGAAAAA-CC	TGTTAATAAT	GAGTGG-TGG
obovata	TCGAGATCG-	AAATATAT--	-CGAGCCATC	CGGAGAA-CC	TGTGA---AT	GTGCGG-TGG
odontotepala	TCGAGACCG-	AAACATAT--	-CGAGCGATT	CGGAGAA-CC	TGTTA---AC	AAGCGG-CGG
papulifolia	TCGAGACCG-	AAAAGTAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AC	AGGCGG-CGG
prostrata	TCGAGACCG-	AAAAGTAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AC	ATGCGG-CGG
pruino_long	TCGAGACCG-	AAATATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AT	GAGCGA-TGG
pruino_short	TCGAGACTG-	AAATATAT--	-CGAGCGATT	CAGAGAA-CC	TGTGA---AT	GACCGA-TGA
racemiflora	TCGAGACCG-	AAATATAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AC	GAGCGA-TGG
rubroviridis	TCGAGACCG-	AAACATAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AC	GAGCGG-CGG
ruscifolia	TCGAGACCG-	AAATATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AT	GAGCGA-TGA
sertulario	TCGAGATCG-	AAATATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AT	GAGCGG-TGG
shaferi	TCGAGACCG-	AA-TATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AT	GAATGAGCGG
testaefolia	TCGAGACCG-	AAACATAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AC	GAGCGG-CGG
tribuloidis	TCGAGACCG-	AAATATAT-A	TCGAGCGATT	TGGAGAA-CC	TGTGA---AC	GAGCGG-CGG
trichop.#606	TCGAGACCG-	AAAAGTAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AA	AGGCGG-CGG
trichop.#630	TCGAGACCG-	AAAAGTAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AA	ATGCGG-CGG
trichyphus	TCGAGACCG-	AA-TATAT--	-CGAGCGATT	CGGAGAA-CC	CGTGA---AC	GAATGAGCGG
wilsonii	TCGAGACCCC	AAGCATTA--	-CGAGCGATT	TGGAGAA-CC	CGTGA---AC	GAGCGG-CGG
wrightii	TCGAGACCG-	AA-TATAT--	-CGAGCGATT	CGGAGAA-CC	TGTGA---AT	GAATGAGCGG
Dil. mont.	TCGAGACCG-	AAATATTTCA	TTGAGCGATT	CAGAGAA-CC	CGTGA---AC	AAGCGG-CAG
	.... ....	.... ....	.... ....	.... ....	.... ....	.... ....
	65	75	85	95	105	115
aristata	CACT-----	--TGCCGTGG	CGTAACCT--	GCCGTCTC-C	AATGCTGGCC	TCATAAA---
bissei	CGCC-----	--CGCCGTGC	CGCAACT---	GCCGTCCCCG	GTCGTGCACC	TC-----
brighamii	CACA-----	--CGCCGTGG	CGCAACT---	GCCGTCTC-C	ATCGTCAGCC	TCATCAA---
corniculata	CACC-----	--CGCCGTGC	CGTGACT---	GCTGTCTT-C	TTTGTGCGCC	TCATAAA---
domingensis	CACT-----	--CGCCGTGC	CGTAACA---	GCCGTCCC-T	GTTGTGCGCC	TCAT-----
ekmanii	CGGT-----	--CGCCGTGC	CGCGAAAACA	TTCGCCCC-C	GTCGC-GGGC	TCGTCTGC-A
excentrica	CGGC-----	--TGCCATCG	CGTAACACCA	GCCGTCCC-G	GTCGT-GGCA	TCGTGTCC-G
'flabellif.'	CGGC-----	--TGCCGTGC	CGTAACACCA	GCCATCCC-G	GTCAT-GGCA	TCGTGTCC-G
gemina	CGGC---AT-	--CGTCGTGC	CGCAAAAT---	GCCGCCTC-C	ATCGCCGGCC	TTGTTAA---
ghiesb.#1298	CGCC-----	--CGCCGTGC	CGTAAAT---	GCCATCCC-G	GTCGACGGCC	TCAC-----
ghiesb.#967	CGCC-----	--CGCCGTGC	CGTAAAT---	GCCATCCC-G	GTCGACGGCC	TCCC-----
grisebachian	CGGC---AT-	--CGTCGTGC	CTTTAAT---	GCCGCCTC-C	ATCTTCGGCC	TTGTTAA---
helenae	CACA-----	--TGCCGTG-	CGTTAATC-	ACCATCTC-C	AATGTTGGCA	TCGTAA---
llamachoi	CACT-----	--TGCCGTGC	CGTAATTT--	ACCGTCTC-C	AATGCTGGCT	TTATAAA---
longilabris	CACT-----	--TGCCGTGC	CGTAATTT--	ACCGCCTC-C	AATGTTGGCC	TTATAAA---
mucronata	CACT-----	--TGCCGTGC	CGTAACCT---	GCCGTCTC-C	AACATTGGAC	TTCTAA---
nummularia	CGCT-----	--CGCCGTGC	CGTGATG---	GCCGTCCC-G	GTCGTGCGCC	CCGA-----
obliquipetal	CACT-----	--TGCCGTGC	CGTAATTT--	ACCGCCTC-C	AATGTTGGCC	TTATAAA---
obovata	CACC-----	--AGCCGTGC	CGTAACA---	CTCGTCCT-G	GTTGTTGGCC	CCGTCACCTG

odontotepala	CACA-----	--TGTCGTCG	CGTAACA---	GCCGTCCC-G	ATCGTCGGCC	TCACCTCG-A
papulifolia	CGCC-----	--TGCCGCCG	CGTGATA---	GCCGCCTT-G	GTCGTCGGCC	TCGCTC----
prostrata	CGCC-----	--TGCCGCCG	CGCGGTA---	GCCGCCCC-G	GTCGTCGGCC	TC-----
pruino_long	CACT-----	--CGCCGTCG	CGTAACA---	GCCATCCC-G	GTCGTCGGCC	TCAC-----
pruino_short	CACT-----	--CGCCGTCA	TATAATA---	GCCATCCC-G	GTCGTTGGCC	TCAG-----
racemiflora	CACCCGCCAG	GGTGCCATCG	CGTAACA---	GCCGTCCC-T	GTTGTGCGCC	TCAT-----
rubroviridis	CACC-----	--TGTCGTCG	TGTAACA---	GCCGTCCC-G	GTCGTCGACC	TCGCCTCA-A
ruscifolia	CACT-----	--TGCCGTCG	CGTAACA---	GCCATCCC-G	GTCGTTGGCC	TCAC-----
sertulario	CACC-----	--TGCCGTCG	CGTAACA---	GTCGTCCCT-G	GTTGTGCGCC	CCGCACCTG
shaferi	CGAC---AT-	--CGTCGTCG	CGCAAAT---	GCCGCCTC-C	ATCTTCGGCC	TTGTTAA---
testaefolia	CAAC-----	--TGTCATCG	CGTAACA---	GCCGTCCC-G	GTCGTCATCC	TCGCCTCG-A
tribuloidis	CGCA-----	--AGCCGTCG	CGCAACT---	GCCGTCTC-C	ATCGCCGGCC	TCATAAAA--
trichop.#606	CGCG-----	--AGCCGCCG	CGCGATA---	GCCGCCCC-G	GTCGTCGGCC	TC-----
trichop.#630	CGCG-----	--AGCCGCTG	CGTGATA---	GCCGCCCC-G	GTCGTCGGCC	TC-----
trichyphis	CGACGATAT-	--CGTCGTCG	CGCAAAT---	GCCGTCTT-C	ATCGTCGGCC	TTGTAAA---
wilsonii	CTTC-----	--GGCCGTCG	CGTGACA---	GCCGTCCC-G	GTCGTCGGCC	TCGCCTGC-G
wrightii	CGGC---AT-	--CGTCGTCG	CGCAAAT---	GCCGCCTC-C	ATCGCCGGCC	TTGTTAA---
Dil. mont.	CGGCGG----	--TTGCTGCTG	CATAACA---	GCCGCCTC-G	GCCGT-GGCC	TCATCTCCCA

	.... ....	.... ....	.... ....	.... ....	.... ....	.... ....
	125	135	145	155	165	175
aristata	-TGGGGCCAT	GTTGA-GGGG	CAGATTAAA-	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
bissei	ATGGGGTCAC	GACGA-GGGG	CGGATGAAA-	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
brighamii	-CGAGGCCGC	GATGAGAAGG	TGGATGAAGA	CCCAAA--CC	GGCGCAGCCA	CGCGCCAAGG
corniculata	-TGGGGCCAC	GATGA-AAGG	CGGATGAAAA	C--AAA--CC	GGCGCAGCTA	TGCGCCAAGG
domingensis	-CGGGGCCAT	GAT--G-GGG	CGGAT-AAAA	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
ekmanii	TCGGGGCCGC	GGCGG-GGGG	CGGGTGAAA-	CCCAAA--CC	GGCGCAGCCA	CGCGCCAAGG
excentrica	ACGGGG----	-----GG	CGGATGAAA-	CCCAAA--CC	GGCGCAGCCA	CGCGCCAAGG
'flabellif.'	ACGGGGCCAC	GGCGG-GGGG	CGGATGAAA-	CCCAAA--CC	GGCGTAGCCA	CGCACCAAGG
gemina	-AGCGCCGTC	GATGA-GAGG	CGGATGAAAA	CTCAAA--CC	GGCGCAGCTG	CGCGCCAAGG
ghiesb.#1298	-CGGGGCCGC	GACGA-GGGG	CGGAT-AAAA	CT-AAAAACC	GGCGCAGCTA	CGCGCCAAGG
ghiesb.#967	-CGGGGCCGC	GACGA-GGGG	CGGAT-AAAA	CT-AAAAACC	GGCGCAGCTA	CGCGCCAAGG
grisebachian	-AGGGCCGTC	GATGA-GATG	CGGATGAAAA	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
helenae	-TGGGGCCAC	GTTGA-GGGT	TGGATTAAA-	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
llamachoi	-TGGGGTCAC	ATTGA-GGGG	CGGATGAAAA	CTCAAT--CC	GGCGCAGCAA	CGCGCCAAGG
longilabris	-TGGGGTCAC	ATTGA-GGGG	CGGATGAAAA	CTCAAT--CC	GGCGCAGCAA	CGCGCCAAGG
mucronata	-TGGGGCCAC	GTTGA-GGGG	CGGATGAAA-	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
nummularia	-CGGGGCCCG	GGCGA-GGGG	CGGACGAAA-	CCAAAA--CC	GGCGCAGCCA	CGCGCCAAGG
obliquipetal	-TGGGGTCAC	ATTGA-GGGG	CGGATGAAAA	CTCAAT--CC	GGCGCAGCAA	CGCGCCAAGG
obovata	TCGGGGCCAC	GACAA-GGGG	CGAATGAAA-	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
odontotepala	GCGGGGACAC	GATGA-GGGA	CGGATGAAA-	CTCAAAA-CC	GGCGCAGCTA	CGCGCCAAGG
papulifolia	ACGGGGACGC	GATGA-GGG-	CGGATGAAA-	CTCAAA--CC	GGCGCAGCCA	CGCGCCAAGG
prostrata	ACGGGGACGC	GATGA-GGGG	CGGATGAAA-	CTCAAA--CC	GGCGCAGCCA	CGCGCCAAGG
pruino_long	-CAGGGCCAC	GATGA-GGGG	CGGAT-AAAA	CT-AAAA-CC	GGCGCAGCTA	CGCGCCAAGG
pruino_short	-TGGGGCCAC	GATGA-GGGG	CGGAT-AAAA	CT-AAAA-TC	GGCGCAGCCA	CGCGTCAAGG
racemiflora	-CGGGGCGAT	GATCA-GGGG	CGGAA-AAAA	CTCAAA--CC	GGCGCAGCCA	CGCGCCAAGG
rubroviridis	GCGGGGGCAC	GATGA-GGGG	TGGATGAAA-	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
ruscifolia	-CGGGGCCAC	GATGA-GGGG	CGGAT-AAAA	CT-AAAA-CC	GGCGCAGCTA	CGCGCCAAGG
sertulario	TCGGGGCCAC	GACGA-GGTG	CGAATGAAA-	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
shaferi	-AGGGCCGTC	GATGA-TGGG	CGGATGAAAA	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
testaefolia	GCGGGGACAC	GATGA-GGGG	CGGATGAAA-	CTCAAAA-CC	GGCGCAGCCA	CGCGCCAAGG
tribuloidis	-CGGGTCCAC	GATGG-AAGG	CGGATGAAAA	C--AAA--CC	GGCGCAGCTT	CGCGCCAAGG
trichop.#606	ACGGGGACGC	GATGA-GGGG	CGGACGAAA-	CTCAAA--CC	GGCGCAGCCA	CGCGCCAAGG
trichop.#630	ACGGGGACGC	GATGA-GGGG	CGGACGAAA-	CT-AAAA-CC	GGCGCAGCCA	CGCGCCAAGG
trichyphis	-TGGGCCGCG	GATGA-ATGG	CGGATGAAAA	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
wilsonii	GCGGGGACGC	GATGA-GGGG	CGGATGAAA-	CTCAAA--CC	GGCGCAGCTA	CGCGCCAAGG
wrightii	-AGCGCCGTC	GATGA-GAGG	CGGATGAAAA	CTCAAA--CC	GGCGCAGCTG	CGCGCCAAGG
Dil. mont.	-TGAGGCGAC	GGTGA-GGGG	CGGATGAAA-	CTCAAA--CC	GGCGCAGTTA	CGCGCCAAGG

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	185	195	205	215	225	235
aristata	GAATAT--AA	ATAGACATGA	GCCC-GCTTT	GGGTTTCGGTT	TCGTGTAGTG	CGGT----CG
bissei	GAATAT----	AAAGAGACGA	GCCCTGCAAC	GGGTTTCGGTG	GCGTGGAGTG	CTGT----GG
brighamii	AAATAC--GA	ATAGACACGA	GCCT-GTATC	AGGCACGGTG	GCATGGAGTG	CAGT----CG
corniculata	GAATAC--AA	ATAGACACGA	GCCT-GTATC	GGGTTTGTGTG	GCGTGGAGTG	CAGA----GG
domingensis	TAATGC--AA	ATAGACACGA	GCCC-GCATC	GGGTTTCGGTG	GCGTGGAGTG	CTTT----TG
ekmanii	GAATAC--GG	AAAAACACGT	GCCCCTCACA	GGGCGCGGTG	GCGCGGGGTG	CTGT----CG
excentrica	GAATAT--CA	AAAAGCACGA	GCCCTGCATC	GGGCTCGGTG	GCGTGGGGTG	CTGT----CG
'flabellif.'	GAATAT--CG	AAAAGCACGA	GCCCTGCATT	GGGCTCGGTG	GCGCGGGGTG	CTGT----TG
gemina	AAATAC--AA	ATATACACGA	TCCT-GTATT	GGGTTTCGGTG	GCGTGGAGTG	CAGT----CG
ghiesb.#1298	GAACAC--GA	ATAGACACGA	GCCC-GCGTC	GGGCTCGGTG	GCGTGGAGTG	CTGC----GG

ghiesb.#967	GAACAC--GA	ATAGACACGA	GCCC-GCGTC	GGGCTCGGTG	GCGTGGAGTG	CTGC----GG
grisebachian	AAATAC--AA	ATATACACGA	TCCT-GTATT	GGGTTTCGTTG	GCGTGGAGTG	CAGT----CG
helenae	GAATAT--AA	ATAGACACGA	GCCT-GCATC	GGGTTTCGATG	GCGTGGAGTG	----TT---G
llamachoi	GAATAT--AA	ATAGACACGA	GCCC-GCATC	GGGTTTCGGTG	GTGTGGAGTG	CTGT----CG
longilabris	GAATATATAA	ATAGACACGA	GCCC-GCATC	GGGTTTCGGTG	GCGTGGAGTG	CTGT----CG
mucronata	AATAATATAA	ATGGACACGA	GCCC-GCATC	GGGTTTCGGTG	GCGTGGAGTG	CTGT----CG
nummularia	GAATGGAGAC	ATATACACGG	GCCC-GCATC	GGGCTCGGTG	GCGTGGGGCG	CTGT----CG
obliquipetal	GAATAT--AA	ATAGACACGA	GCCC-GCATC	GGGTTTGGTG	GCGTGGAGTG	CTGT----CG
obovata	GAATATA-AA	AGAGACACGA	GCTC-GGATG	GAGCTCGGTG	GCGTGGAGTG	CTAT----CG
odontotepala	GAATAT----	GAAGAGACGA	GCCCTGCACA	GGGCTCGGTG	GCGTGGAGTG	----TTGTTG
papulifolia	GAATAC----	GAAGAGACGA	GCCCCGCATC	GGGTTTCGATG	GCTTGGCGTG	CTGT----CG
prostrata	GAATAT----	GAAGAGATGA	GCCCCGCATG	GGGTTTCGATG	GCCTGGCGTG	CGGT----CG
pruino_long	GATTAA--AA	AAAGACACGA	GCCC-GCATC	GGGTTTCGGTG	GCGTGGAGTG	CTGT----GG
pruino_short	GAATAC--AA	ATAGACACGA	GCCA-GCAAC	GGGTTTCGTTG	GCGTGGAGTG	CTGT----CG
racemiflora	GAATGC--AA	ATAGA--CGA	GCCC-ACATC	GGGTTTGGTG	GCGTGGGGTG	CTTT----TG
rubroviridis	GAATAT----	GAAGAGACGA	GCCCTGCATA	GGGTTTCGGTG	GCGTGGAGTG	CTGTTTGTG
ruscifolia	GAATAA--AA	AA-GACACGA	GCTC-GCATT	GGGTTTCGGTG	GCGTGGAGTG	CTGT----GG
sertulario	GAATGCA-AA	AGAGACACGA	GCTC-GTA-A	GGGCTCGGTG	GCGTGGAGCG	CTAT----CG
shaferi	AAATAC--AA	ATATACACGA	TCCT-GTATT	GGGTTTCGGTG	GCGTGGAGTG	CAGT----CG
testaefolia	GAATAC----	GAAGAGACGA	GCCCTGCATA	GGGTTTCGGTG	TGCTGGAGTG	----TT--CG
tribuloidis	GAATAC--AA	ATAGACACGG	GCCT-GTATC	GGGTCCGTTT	GCGTGGAGTG	CGGT----GG
trichop.#606	AAATAT----	GAAGAGACGA	GCCCCGCATG	GGGTTTCGATG	GCCTGGCGTG	CTGT----CG
trichop.#630	GAATAT----	GATGAGACGA	GCCCCGCATG	GGGTTTCGATG	GCCCTGGCGTG	CTGT----CG
trichyphis	AAATAC--AA	ACATACACGA	TCCC-GTATT	GGGTTTCGGTG	GCGTGGAGTG	CAGT----CG
wilsonii	GAATAT----	GAAGAGACGA	GCCCTGCAAA	GGGTTTCGGTG	GCGTGGAGTG	CTGT----CG
wrightii	AAATAC--AA	ATATACACGA	TCCT-GTATT	GGGTTTCGGTG	GCGTGGAGTG	CAGT----CG
Dil. mont.	GAATATATGA	A-AGACACGA	GCCCCGTATC	GGGCTCAGTG	GCGTGGAGTG	CTGT----TG

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	245	255	265	275	285	295
aristata	CACCTCACAC	GG-ATCAAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTT	GCATCGATGA
bissei	CACACCACAC	AG-ATTGAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
brighamii	CACACCACAC	GG-TC--AAA	CGACTCTCGG	CAATGTATAT	CTCGGCTCTT	GCATCGATGA
corniculata	CACACCACAA	CG-ATATAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTT	GCATCGATGA
domingensis	CACACCACAC	GG-ATCAAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
ekmanii	CACGCCGCGC	GG-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
excentrica	CACGCCGCGC	GG-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GTATTGATGA
'flabellif.'	CACACCACAC	GG-ATCAAAA	AGACTCTCGG	CAATGGATAT	CTCAGCTCTC	-----
gemina	CACACCACAC	GG-ATAAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
ghiesb.#1298	CACACCACAC	GG-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
ghiesb.#967	CACACCACAC	GG-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
grisebachian	CACACCACAC	GG-ATAAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
helenae	CACCTCACAC	GG-ATCAAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTT	GCATCGATGA
llamachoi	CACATCACAC	GG-GTCAAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
longilabris	CACATCACAC	GG-ATCAAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
mucronata	CACATCACAC	GG-ATCAGAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
nummularia	CGCACCACAC	GG-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
obliquipetal	CACATCACAC	GG-ATCAAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
obovata	CGCACCACAC	GG-ATCAAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
odontotepala	CACACCACAT	GA-ATCGAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
papulifolia	CACGCCGCGC	GG-AATGAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
prostrata	CACGCCGCGC	GG-AATGAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
pruino_long	CACACCACTC	GG-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
pruino_short	CACACCACAC	GA-ATCAAAA	CGACTCTCGA	GAATGGATAT	CTCGGCTCTC	ACATCGATGA
racemiflora	CACACCACGC	GG-ATCGAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
rubroviridis	CACACCACAC	GA-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
ruscifolia	CACACCACAC	GG-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
sertulario	CGCACCACAC	GG-ATAAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
shaferi	CACACCACAC	GG-ATGAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
testaefolia	CACACCACAC	GA-ATCAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
tribuloidis	CACACCACAC	GG-ATAAAAA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
trichop.#606	CACGCCGCGC	GG-AATGAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
trichop.#630	CACGCCGCGC	GG-AATGAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
trichyphis	CACACCACGT	GG-AT-AAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
wilsonii	CACACCACAT	TTTATCGAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
wrightii	CACACCACAC	GG-ATAAAAA	CGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA
Dil. mont.	CACACCATAT	GG-ATCGACA	TGACTCTCGG	CAATGGATAT	CTCGGCTCTC	GCATCGATGA

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	305	315	325	335	345	355
aristata	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCCGCGAAC	CATCGAGAAT

bissei	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
brighamii	AGAGCGCAGC	AAAATGCGAT	ATGTGGTGCA	AATTGCAGAA	TCCC GTAAAC	CATCAAGAAT
corniculata	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
domingensis	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
ekmanii	AGAGCGCAGC	GAAATGTGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
excentrica	AGAGCGCAGC	TAAATGCGAT	ACATGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
'flabellif.'	-----	-----	--ATGGTGCA	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
gemina	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
ghiesb.#1298	AGAGCGCANN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
ghiesb.#967	AGAGCGCAGC	GAAANNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
grisebachian	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC GCNANC	CATCGAGAAT
helenae	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
llamachoi	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
longilabris	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
mucronata	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
nummularia	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
obliquipetal	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
obovata	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
odontotepala	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
papulifolia	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
prostrata	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
pruino_long	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
pruino_short	AAAGCGCAGC	AAAATGCCGT	ACGTGCTGCA	-----	-----	-----
racemiflora	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
rubroviridis	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
ruscifolia	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
sertulario	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
shaferi	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
testaefolia	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
tribuloidis	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
trichop.#606	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
trichop.#630	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
trichyphis	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
wilsonii	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
wrightii	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT
Dil. mont.	AGAGCGCAGC	GAAATGCGAT	ACGTGGTGCG	AATTGCAGAA	TCCC CGGAAC	CATCGAGAAT

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	365	375	385	395	405	415
aristata	TTGAACGCAA	GTTGCGCCCC	AGGCCACCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
bissei	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
brighamii	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCTCGCTG	GGCGTCAAGC
corniculata	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
domingensis	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
ekmanii	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCTGAGGGCA	CGTCCGCCTG	GGCGTCAAGC
excentrica	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCGAGGGCA	CGTCCGCCTG	GGCGTCAAGC
'flabellif.'	TTGAACGCAA	GTTGCACTCG	AGGCCAGCCN	GCCGAGGGCA	CGTTTGCTTG	GGCGTCAAGC
gemina	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
ghiesb.#1298	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
ghiesb.#967	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
grisebachian	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
helenae	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
llamachoi	TTGAACGCAA	GTTGCGCCCC	AGGCCAACCG	GCTAAGGGCA	CGCCCGCCTG	GGCGTCAAGC
longilabris	TTGAACGCAA	GTTGCGCCCC	AGGCCAACCG	GCTAAGGGCA	CGCCCGCCTG	GGCGTCAAGC
mucronata	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGCCCGCCTG	GGCGTCAAGC
nummularia	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCGAGGGCA	CGTCCGCCTG	GGCGTCAAGC
obliquipetal	TTGAACGCAA	GTTGCGCCCC	AGGCCAACCG	GCTAAGGGCA	CGCCCGCCTG	GGCGTCAAGC
obovata	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCTGAGGGCA	CGTCCGCCTG	GGCGTCAAGC
odontotepala	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCTGAGGGCA	CGTCCGCCTG	GGCGTCAAGC
papulifolia	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCGGGC
prostrata	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
pruino_long	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
pruino_short	-----	-----	-----	-----	-----	----TCAAGC
racemiflora	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
rubroviridis	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
ruscifolia	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCTTG	GGCGTCAAGC
sertulario	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCTGAGGGCA	CGTCTGCCTG	GGCGTCAAGC
shaferi	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
testaefolia	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCCGAGGGCA	CGTCCGCCTG	GGCGTCAAGC
tribuloidis	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
trichop.#606	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC



trichop.#630	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCTG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
trichyphis	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
wilsonii	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
wrightii	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC
Dil. mont.	TTGAACGCAA	GTTGCGCCCC	AGGCCAGCCG	GCCAAGGGCA	CGTCCGCCTG	GGCGTCAAGC

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	425	435	445	455	465	475
aristata	GTTACGTTGC	TCCGT-GCCA	ACTCC--ATC	CC-ACCTGAC	GGGTG----T	GCATGAGGGA
bissei	GTTGCGTNGC	TCCGT-GCCA	ACTCC--ATC	AC-ACCCGAA	GGGTGTGT--	--GTGCGGGA
brighamii	GTTGCGTTGC	TCTGT-GCCA	ACTTC--GCC	CC-ACCCGAA	GGGTGCGG-T	GTACGGGGGA
corniculata	GTTACATCGC	TCCGT-GCCA	GCTCC--CTC	CC-ACCCAAC	GGGTG----T	GTACGGGGGA
domingensis	GTTGCGTCGC	TCTGT-GCCA	GCTCC--ATC	CC-ACCCAAC	AGGTG----T	GCATGGGG-A
ekmanii	GTTGCGTCGC	TCCGC-GCCG	ACTCC--GTC	GT-GCCCCGAT	GGGTG----C	GTCGGCGGGA
excentrica	GTTGCGTCGC	TCCGT-GCCA	ACTCC--GTC	CC-ACCCGAT	GGGTG----C	GTCGGTGGGA
'flabellif.'	GTTGCGTCGC	TCCGT-GCCA	ACTCC--GTC	CC-ACCCGAT	GGGTG----C	GTCGGCGGGA
gemina	GTTACGTCGC	TCCGT-GCCA	GCTCC--ATG	CC-ACCCGAC	GGGTG----T	GTATGGGGAG
ghiesb.#1298	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
ghiesb.#967	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
grisebachian	GTTACGTCGC	TCCGT-GCCA	TCTCC--ATG	CC-ACCCGAC	GGGTG----T	GTGTGGGGAG
helenae	GTTACATTGC	TCCGT-GCCA	ACTCC--ATC	CC-ACCCGAC	GGGTG----T	GCATGCGGGA
llamachoi	GTTTTGTTCG	TCCGT-GCCA	GTTCC--ATC	CC-ACCTGAT	GGGTG----T	GAATGTGGGA
longilabris	GTTTTGTTCG	TCCGT-GCCA	GCTCC--ATC	CCACCTGATG	GGGTG----T	GAATGTGGGA
mucronata	GTTACGTTGC	TCCGT-GCCA	GCTCC--ATC	CC-ACCTGAC	GGGTG----T	GCATGCGGGA
nummularia	GTTGCGTCGC	TCCGC-GCCA	GCTCC--ATC	CC-ACCCGAC	GGGTG----C	GCATGCGGGA
obliquipetal	GTTTTGTTCG	TCCGT-GCCA	GCTCC--ATC	CC-ACCTGAC	GGGTG----T	GAATGTGGGA
obovata	GTTGCATCGC	TCCGT-GCCA	TCTCC--ATC	CC-ACCTAAT	AAGTG----C	GAATGCGAGA
odontotepala	GTTGCGTCGC	TCCGTTGCCG	AACTCCATCC	CA-ACCCGAA	GAGTGTGTGT	GGGTGCAGGA
papulifolia	GTTGCGTCGC	TCCGT-GCCA	GCTCC--AGC	AC-ACCCGAT	GGGTGTGC--	--CGGCGGTT
prostrata	GTTGCGTCGC	TCCGC-GCCC	CTCCCCGAAC	GC-ACCCGCA	GGGTGTGC--	--CGGCGGGA
pruino_long	GTTGCGTCGC	TCCGT-GCCA	GCTCC--ATC	CC-ACCTGAC	AGGTG----T	GCATGCGGGA
pruino_short	GTTGCGTCGC	TCTGT-GTCA	GCTCT--GTC	CC-ACCTTAC	GGGTG----T	GCATGCGGGA
racemiflora	GTTGCGTCGC	TCCGT-GCCA	GCTCC--ATC	CC-ACCCGAC	GGGTG----T	GCATGGGGGA
rubroviridis	GTTGCGTCGC	TCCGT-GCCG	AACTCCATCC	CCCACCCGAC	GGGTGCGT--	GGGTGCAGGA
ruscifolia	GTTGCGTCGC	TCCGT-GCCA	GCTCC--ATC	CC-ACCTGAC	AGGTG----T	GCATGCGGGA
sertulario	GTTGCATCGC	TCCGT-GCCA	TCTCC--ATC	CC-ACCCGAT	GGGTG----C	GAATGCGGGA
shaferi	GTTACGTCGC	TCCGT-GCCA	TCTCC--ATG	CC-ACCCGAC	GGGTG----T	GTACGAGGAG
testaefolia	ATTGCGTCGC	TCCGT-GCCG	AACTCCATCC	AACACCCCAA	GGGTGCGTGT	GGGTGCAGGA
tribuloidis	GCTACGTCGC	TCCGT-GCCA	GCTCC--CTC	CCCGCCCGAC	GGGTG----T	GTACGGGGGA
trichop.#606	GTTGCGTCGC	TCCGT-GCCC	CTGCCCCGAAC	GC-ACCCGAT	GGGCGTGA--	--CGGCGGGA
trichop.#630	GTTGCGTCGC	TCCGT-GCCC	CTTCCCCGAAC	GC-ACCCGAT	GGGCGTGA--	--CGGCGGGA
trichyphis	GTTACGTCGC	TCCGT-GCCA	GCTCC--ATG	CC-ACCCGAT	GGGTG----T	GTATGGGGAG
wilsonii	GTTGCGTCGC	TCCGT-GCCG	AGCTCCATCC	CCCACCCGAC	GGGTGCGT--	GGATGCGGGA
wrightii	GTTACGTCGC	TCCGT-GCCA	GCTCC--ATG	CC-ACCCGAC	GGGTG----T	GTATGGGGAG
Dil. mont.	GTTGCGTCGC	TCCGT-GCCA	ACTCC--GTG	CC-ACCTTGT	GGGTG----T	GCCGCGGGA

	.... ....	.... ....	.... ....	.... ....	.... ....	.... ....
	485	495	505	515	525	535
aristata	GGGT--CGGA	TGTGGAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGCGCCGGGC	TTAAGAGCGG
bissei	GGCT--CGGA	TGCGCAGAGT	GGCTTGTCTGT	GCCC-GTAGG	CGCGGCGGGC	TGAAGAGCGG
brighamii	GGGC--CAGA	TGTGCAGAGT	GGTTCGTCTGT	GCCC-GCGGG	CACGGTGGGC	TTAAGAGCGG
corniculata	GGGT--CGGA	TGTGCAGAGT	GGCTCGTCGT	TCTT-GCGGG	TGCGGCGGGC	TTAAGCGCGG
domingensis	CGGC--CGGA	TGTGCAGATT	GGCTCGTCGT	GCCC-ACGAG	TGCGACGGGC	TGAAGAGCGG
ekmanii	GGCT--CGGA	TGTGCAGGGT	GGCCCCCGGT	GCCGTGCCGG	CGCGGCGGGC	TGAAGAGCGG
excentrica	GGCT--CGGA	TGTGCAGAGT	GGCTCGTTGT	GCCGCGCCGG	TGCGGCGGGC	TGAAGAGCGG
'flabellif.'	GGCT--TGGA	TGTGTAGAGT	GGCTCGTCGT	GCCGCGCCGG	TGCGACAGGC	TGAAGAGCAG
gemina	GGGT--CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGTGCGGGGC	TTAAGATCGG
ghiesb.#1298	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
ghiesb.#967	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
grisebachian	GG-T--CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGTGCGGGGC	TTAAGATCGG
helenae	GGGT--CGGA	TGTGGAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGCGGCGGGC	TAAAGAGCGG
llamachoi	GGGA--CGGA	TGTAGAGAGT	GGCTCGTCGT	GCGC-TCGTG	CGCGGCGGGC	TTAAGAGCGG
longilabris	GGGA--CGGA	TGTAGAGAGT	GGCTCGTCGT	GCGC-TCGTG	CGCGGCGGGT	TTAAGAGCGG
mucronata	GGGT--CGGA	CGTGGAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGCGGCGGGC	TTAAGAGCGG
nummularia	GGGTTTCGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGCGGCGGGC	TGAAGAGCGG
obliquipetal	GGGA--CGGA	TGTAGAGAGT	GGCTCGTCGT	GCGC-TCGTG	CGCGGCGGGT	TTAAGAGCGG
obovata	GGGT--CGGA	TGTGGAGAGT	GGCTCGTCGT	GCCC-ACCGG	CGCGGCGGGC	TGAAGAGTGG
odontotepala	GGCCT-CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GTCGG	CGCGGCGGGT	TGAAGAGCGG
papulifolia	GGCT--CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GTCGG	TGCGGCGGGC	TGAAGAGCGG
prostrata	GGCT--CGGA	TGCGTAGAAT	GGCTCGTCGT	GCCC-GTCGG	CGCGGCGGGC	TGAAGAGCGG
pruino_long	GGGC--CGGA	TGTGTAGAGT	GGCCCCGTCGT	GCCC-GCGGG	CGTGCGGGGT	TGAAGAGAGG

pruino_short	TGTC--CGGA	TGTGTAGAGT	TGCTCATCGT	GCTC-GCAGG	CGTGGCGGAGC	TGAAAAGAGG
racemiflora	GGGT--CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-ACGGG	TGCGACGGGC	TGAAGAGCGG
rubroviridis	GGCCT-CGGA	CGTGCAGAGT	GGCTCGTCGT	GCCC-GTCGG	CGCGGCGGGC	TGAAGAGAGA
ruscifolia	GGGC--CGGA	TGTGTAGAGT	GGCTCGTCGT	GCCC-GCGGG	TGTGGCGGGT	TGAAGAGAGG
sertulario	GTGT--CGGA	TGCGGAGAGT	GGCTCGTCGT	GCCC-GCCGG	CGCGGCGGGC	TGAAGTGTGG
shaferi	GG-T--CGGA	CGTGCAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGTGGCGGGC	TTAAGATCGG
testaefolia	GGCCT-CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GTCGG	CGCGGCGGGC	TGAAGAGCGG
tribuloidis	GGGC--CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGCGGCGGGC	TAAAGAGCGG
trichop.#606	GGCC--CGGA	TGTGTAGAGT	GGCTCGTCGT	GCCC-GTCGG	CGCGGCGGGC	TGAAGAGCGG
trichop.#630	GGCC--CGGA	TGTGTAGAGT	GGCTCGTCGT	GCCC-GTCGG	CGCGGCGGGC	TGAAGAGCGG
trichyphis	GG-T--CGGA	TGTGGAAGT	GGCTCGTCGT	GCCC-GCGGG	CGTGGCGGGC	TTAAGATCGG
wilsonii	GGCCG-CGGA	TGCGGAGAGT	GGCTCGTCGT	GCCC-GTCGG	CGCGGCGGGT	TGAAGAGCGG
wrightii	GGGT--CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GCGGG	CGTGGCGGGC	TTAAGATCGG
Dil. mont.	GGCT--CGGA	TGTGCAGAGT	GGCTCGTCGT	GCCC-GTCGG	TGCGGCGGGC	TGAAGAGTGG

	.... ....	.... ....	.... ....	.... ....	.... ....	.... ....
	545	555	565	575	585	595
aristata	GTGATCATCT	CGTTGGCCAT	GAACAACAAG	GGGTGGATGA	AAATT--GTG	CCTATGTTGT
bissei	GTGATTGTCT	CATCGGCCAC	GAACAGCAAG	GGGTGGATGA	AAGTT--GTG	CCTGTGCTGG
brighamii	GTGATCTTCT	CGTTGGCCAC	GAACAACAGG	GGGTGGATGA	AAATT--GTG	CTTGTGTTGT
corniculata	GCGATCGTCT	CGTTGGCCAC	GAACAACAAG	GGGTGGATGT	AAATT--GTG	CCTGTGTTGT
domingensis	GTGATCGTCT	CGTTGGCCAC	GAACAACAAG	GGGTGGATGA	AAATT--GTG	CCTGTGTTGT
ekmanii	GTGATCGTCT	CGTCGGGCGC	GAGCGGCAAG	GGGTGGATGA	AAGTT--GTG	CCTGTGCCGC
excentrica	GCGATCGTCT	CGTGGGCGGC	GAGCAGCAAG	GGGTGGATGA	AAGTT--GTG	CCTGTGCTGC
'flabellif.'	GCAATCGTCT	CATGGGCGGC	GAGCAGCAAG	GGGTGGATGA	AAGTT--GTG	CCTGTGCTGC
gemina	GTGATCGTCT	CGTTTGCCAC	GAACGATAAG	GG-TGGATGA	AAATT--GTG	CCTGTGTTGT
ghiesb.#1298	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
ghiesb.#967	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
grisebachian	GTGATCGTCT	CGTTGCGCAC	GGACGATAAG	GG-TGGATGA	AAATT--GTG	CCTGTGTTGT
helenae	GTGATCGTCT	CGTTGGCCAC	GAACAACAAG	GGGTGGATGA	AATAT--GTG	CCTATGTTGT
llamachoi	GTGATCATCT	CGTTGGCCAT	GAATAACAAG	GG-TGGATGA	AAATTTTGTG	CCTGTGTTAT
longilabris	GTGATCGTCT	CGTTGGCCAC	GAATAACAAG	GGGTGGATGA	AAATT--GTG	CCTGTGTTAT
mucronata	GTGATCGTCT	CGTTGGCCAC	GAACAACAAG	GGGTGGATGA	AAACG--TTG	CCTGTGTTGT
nummularia	GTGATCGTCC	CGTCGGCCAC	GGGCAGCAAG	GGGTGGATGA	AAATT--GTG	CCTGTGCTGT
obliquipetal	GTGATCGTCT	CGTTGGCCAC	GAATAACAAG	GGGTGGATGA	AAATT--GTG	CCTGTGTTAT
obovata	GTGATCGTCT	CGTTGCGAAC	GAGCAGCAAG	GGGTGGATAA	AATTT--GTG	CCTGTGCTGT
odontotepala	ATGATCGTCT	CGTTGGCTAC	GAGCAGCAAG	AGGTGGATGA	AAGTT--GTG	CCTGTGTTGT
papulifolia	GCGATCGTCT	CGTTGGCCAC	GAGCGGCAAG	GGGTGGATGA	AAGTT--GTG	CCTGTGCTGT
prostrata	GCGATCGTCT	CGTTGGCCAC	GAGCAGCAAG	GGGTGGATGA	AAGTTT-GTG	CCTGTGCTGT
pruino_long	GTGATCGTCT	CGTTTGCCAC	GAACAACAAG	GGGTGGATGA	AAATT--GTG	CCTGTGTTGT
pruino_short	GTGAACGTCT	CGTTGGCCAC	GAACAACAAT	GGGTGGATGA	AAATT--GTG	CCTGTGTTGT
racemiflora	GTGATCGTCT	CGTTGGCCAC	GAACAACAAG	GGGTGGATGA	AAATT--GTG	CCTGCGTTGT
rubroviridis	GTGATCGTCT	CGTTGGCCAC	GAACGGCAAG	AGGTGGATGA	AAGTT--GTG	CCTGTGCTGT
ruscifolia	GTGATCGTCT	CGTTGGCCAC	GAACAACAAG	GGGTGGATGA	AAATT--GTG	CCTGTGTTGT
sertulario	GTGATCGTCT	CGTTGCGAAC	GAGCAGCAAG	GGGTGGATGA	AATTT--GTG	CCTGTGCTGT
shaferi	GTGATCGTCT	CGTTTTCCAC	GAACGATAAG	GG-TGGATGA	AAAAT--GTG	CCTGTGTTGT
testaefolia	GTGATCGTCT	CGTTGGCCAA	GAGCAGCAAG	AGGTGGATGA	AAATT--GTG	CCTGTGCTGT
tribuloidis	GTGATCGTCT	CGTTGGCCGC	GAACAACAGG	GGGTGGATGA	AAATT--GTG	CCTGTGTTGT
trichop.#606	GCGATCGTCT	CGTTGGCCAC	GAGCAGCAAG	GGGTGGATGA	AAGTTT-GTG	CCTGTGCTGT
trichop.#630	GCGATCGTCT	CGTTGGCCAC	GAGCAGCAAG	GGGTGGATGA	AAGTTT-GTG	CCTGTGCTGT
trichyphis	GTGATCGTCT	CGTTTGCCAC	GAACAATAAG	GG-TGGATGA	AAATT--GTG	CCTGTGTTGT
wilsonii	GCGATCGTGT	CGTTGTCCAC	GAGCAGCAAG	AGGTGGATGA	AAGTT--GTG	CCTGTGCTGT
wrightii	GTGATCGTCT	CGTTTGCCAC	GAACGATAAG	GG-TGGATGA	AAATT--GTG	CCTGTGTTGT
Dil. mont.	GTCATCGTCT	CGCCGGCTGC	GAATAACAAG	GGGTGGATGA	AAGTTGTGCG	CCTATGTTGT

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	605	615	625	635	645	655
aristata	A-CCGACCGG	CTTGAGAA--	GAGATTACAC	CCA-ACGGAT	GATCCCAGCC	CAAGCGT--C
bissei	ATCGTGTCGG	CCTGAGAA--	AAGATTAGAC	CTT-ACGGAT	GATCCCAGCC	CGAGCGT--C
brighamii	ATCGTTCCGG	CGTGAG----	GAGATTGTAC	CCA-GCGGAT	GATCCCAGCC	CAAGCGT--C
corniculata	ATCGTGCTGG	CATGAGAA--	GAGATTATAC	CCA-CCGGAT	GATCCCAGTC	TAAGCGT--C
domingensis	ATCGTGCCGG	CCTGAGAA--	GAGATCATAC	CCT-GCGGAT	AATCCCAACC	CAAGCGT--T
ekmanii	ATCGTGTCGG	CCCGGAAG--	GAGGACGGAA	CCCGCGAGTT	GATCCCAGCC	CAAGC---GC
excentrica	ATCGTGTCGG	CCCGGGAA--	AGGGACGGAA	GCGTCGAGTT	GATCCCAGCC	CGAGCGCCGC
'flabellif.'	ATCGTGTCAG	CCCGGGAA--	AGGGACGGAA	GCGTCGAGTT	GATCCCAGCC	CGAGCTTCGC
gemina	ATCGTGCGGA	CGTGAGAA--	GAGATTGTAC	CCA-GCAGAT	GATCCCAATC	TAAGCGT--C
ghiesb.#1298	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
ghiesb.#967	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN	NNNNNNNNNN
grisebachian	TCGTGGCGA	CGTGAGGA--	GAGATTGTGC	CCA-GCGGAT	GATCCCAGTC	TAAGCGT--C
helenae	A-CTGTTTGG	CTCGAGAA--	GAGATTAC--	-CA-CCGGAT	CATCCCAGCC	CAAGCGT--GC
llamachoi	AACCGGCCAG	CCTGAGAT--	GAGATTACAC	CCA-ACGGAT	GATCCCAACC	CAAGTAT--T

longilabris	AACCGGCCAG	CCTGAGAT--	GAGATTACAC	CCA-ACGGAT	GATCCCAACC	CAAGCAT--T
mucronata	A-CCGGCCGG	CCTGAGAGAA	GAGATTACAC	CCA-ACGGAT	GATCCCAGCC	CAAGCAT--C
nummularia	GTCGTGCCGG	CCGGGGAA--	GAGATTGTAC	CCT-GCGGAT	GATCCCGGCC	CGAGCGT--C
obliquipetal	AACCGGCCAG	CCTGAGAT--	GAGATTACAC	CCA-ACGGAT	GATCCCAACC	CAAGCAT--T
obovata	ATCGTGTCGG	CCTGAGAA--	GAGATTATAC	CCT-GCAGAT	GATCCCGGAC	CAAGCGT--T
odontotepala	ATCGTGTCGG	CCCGAG-A--	GAGATTATAC	CTC-ACGGAT	GATCCCGGCC	CAAGCGT--C
papulifolia	ATCGTGCCGG	CCCGAGGA--	GCGATCGTAC	CCC-ACGGAT	GATCCCGGCC	CAAGCGT--C
prostrata	GTCGTGCCGG	CCCGAGGA--	GCGATCGTAC	CCC-ACGGAT	GATCCCGGCC	CGAGCGT--C
pruino_long	ATCGTGCCGG	CATGAGAA--	GAGATCGTAC	CCT-GCGGAT	GATCCCAGCC	CAAGCGT--C
pruino_short	ATCGTGCCGG	CATGAGAA--	AAGATCATAC	CTC-GCGAAT	GATCCCTGCT	TACGCAT--C
racemiflora	ATCGTGCCGG	CCTGAGAA--	GAGATCGTAC	CCC-GCGGAT	GATCCCAGCC	CAAGCGT--T
rubroviridis	ATCGTGCCGG	CCTGAG-A--	GAGATTATGC	CTC-ACGGAA	GATCCCGGCC	CAAGCGT--C
ruscifolia	ATCGTGCTGG	CATGAGAA--	GAGATCATAC	CCT-ATGGAT	GATCCCAGCC	CAAGTGT--C
sertulario	CTCGTGTCGG	CCTGAGAA--	GAGATTATAC	CCT-GCAGAT	GATCCCGGAC	CAAGCGT--T
shaferi	GTCGTGGCGA	CGTGAGAA--	GAGATTGTAC	CCA-GCGGAT	GATCCCAATC	TAAGCGT--C
testaefolia	ATCGTGTTGG	CCCGAG-A--	GAGATTATAC	CTC-ACGGAA	GATCCCAGAC	CATGCGT--C
tribuloidis	ATCGTGCTGG	CGTGAGAG--	GAGATTACAC	CCG-GCGGAT	AATCCCAGTC	TAAGCGT--C
trichop.#606	ATCGTGCCGG	CCCGAGGA--	GCGATCGCAC	CCCCACGGAT	GATCCCGGCC	CAAGCGT--C
trichop.#630	ATCGCGGCGG	CTCAAGGA--	GCGATCGCAC	CCC-ACGGAT	GATCCCGGCC	CAAGCGT--C
trichyphis	ATCGTTCCGG	CGTGAGAA--	GAGATTGTGC	CCA-GCGGAT	GATCCCAGTC	CAAGCGT--C
wilsonii	ATCGTGCCGG	CCCGAG-A--	GAGATTATGC	CTC-ATGGAT	GATCCCGGCC	CAAGCGT--C
wrightii	ATCGTGGCGA	CGTGAGAA--	GAGATTGTAC	CCA-GCAGAT	GATCCCAATC	TAAGCGT--C
Dil. mont.	ATCGTGCCGG	C-TGAGAA--	AAGATTATAT	ACC-T----T	GATCCCAGCC	CATACGT--C

	.... ....	.... ....	.... .
	665	675	685
aristata	AAT--CCACG	GACGACGGCT	TGGAAT
bissei	GAT--CCACG	GATGGCGGCT	TGGAAT
brighamii	GTT--CCACG	GACGTCGGCT	TGGAAT
corniculata	GGT--CCACG	GACGTCGGCT	TGGAAT
domingensis	ATT--CCACG	GATGGCGGCT	TGGAAT
ekmanii	GGT--CCACC	GACGGCGGCT	TGGAAT
excentrica	GAT--CGAGC	GACGGCGGCT	CGGAAT
'flabellif.'	GAT--CGAGC	GACGGCGGCT	CGGAAT
gemina	GTT--CCACA	GACGTCGGCT	TGGAAT
ghiesb.#1298	NNNNNNNNNN	NNNNNNNNNN	NNNNNN
ghiesb.#967	NNNNNNNNNN	NNNNNNNNNN	NNNNNN
grisebachian	GTT--CCACG	GACGTCGGCT	TGGAAT
helenae	AAT--CCACG	GATATTGGCT	TGGAAT
llamachoi	AAT--CCACG	GACGATGGCT	TGGAAT
longilabris	GAT--CCACG	GACGATGGCT	TGGAAT
mucronata	GAT--CCACG	GACGACGGCT	TGGAAT
nummularia	GAT--CGACG	GACGGCGGCT	TGGAAT
obliquipetal	GAT--CCACG	GACGATGGCT	TGGAAT
obovata	GAT--CCACG	GACGGCGGCT	TGGAAT
odontotepala	GAT--CGAAC	GATGGCGGCT	TGGAAT
papulifolia	TATC-CCACC	GATGGCGGCT	TGGAAT
prostrata	CAT-TTTTTT	GATGGCGGCT	TGGAAT
pruino_long	TAT--CCGCG	GATGGCGGCT	TGGAAT
pruino_short	GAT--CCACG	GACGACGGCT	TGGAAT
racemiflora	GAT--CCACG	GACGGCGGCT	TGGAAT
rubroviridis	GAT--CCAAC	GATGGCGGCT	TGGAAT
ruscifolia	TAT--CCACG	GATGGCGGCT	TGGAAT
sertulario	GAT--CCACG	GACGGCGGCT	TGGAAT
shaferi	GTT--CCACG	GACGTCGGCT	TGGAAT
testaefolia	AAT--CGAAC	GATGGCGGCT	TGGAAT
tribuloidis	GGT--CCACG	GACGTCGGCT	TGGAAT
trichop.#606	CAT--CGACC	GATGGCGGCT	TGGAAT
trichop.#630	TGT--CGACC	GATGGCGGCT	TGGAAT
trichyphis	TGT--CCACG	GACGTCGGCT	TGGAAT
wilsonii	GAT--CCGAC	GATGGCGGCT	TGGAAT
wrightii	GTT--CCACA	GACGTCGGCT	TGGAAT
Dil. mont.	GAT--CCATT	--CGACGGCT	TGGAAT

ITS variability among accessions turned out to be very different. Within species boundaries, ITS differed up to 7% (*Pleurothallis brighamii*), being much higher than in pairs of closely related species (*Pleurothallis domingensis* ~ *Pleurothallis velaticaulis*: 3,5%). Perhaps the most striking case of stability is the species pair *Pleurothallis gemina*

and *Pleurothallis wrightii* which shares the same sequence!

Tab. 10: Sequence divergence (total of mismatches and indel bases) at species level and among species.

\* – incomplete ITS2 sequence (AF262925).

	ITS1	5.8S	ITS2
<i>Pleurothallis brighamii</i> *	17	11	17
<i>Pleurothallis ghiesbreghtiana</i>	1	?	?
<i>Pleurothallis ruscifolia</i>	12	2	4
<i>Pleurothallis sertularioides</i>	7	0	2
<i>Pleurothallis tribuloides</i>	6	0	3
<i>Pleurothallis trichophora</i>	8	1	7
<i>Pleurothallis domingensis</i> ~ <i>Pleurothallis velaticaulis</i>	8	1	15
<i>Pleurothallis gemina</i> ~ <i>Pleurothallis wrightii</i>	0	0	0

Mutation rate was found to be unequally distributed among loci. Fig. 64 shows the entropy along the whole alignment (ITS4C). 5.8 S gene (pos. 270-433) is marked by an abrupt drop in mutations. However, there are islands of increased polymorphism especially in those 20% of the gene which neighbours ITS2.

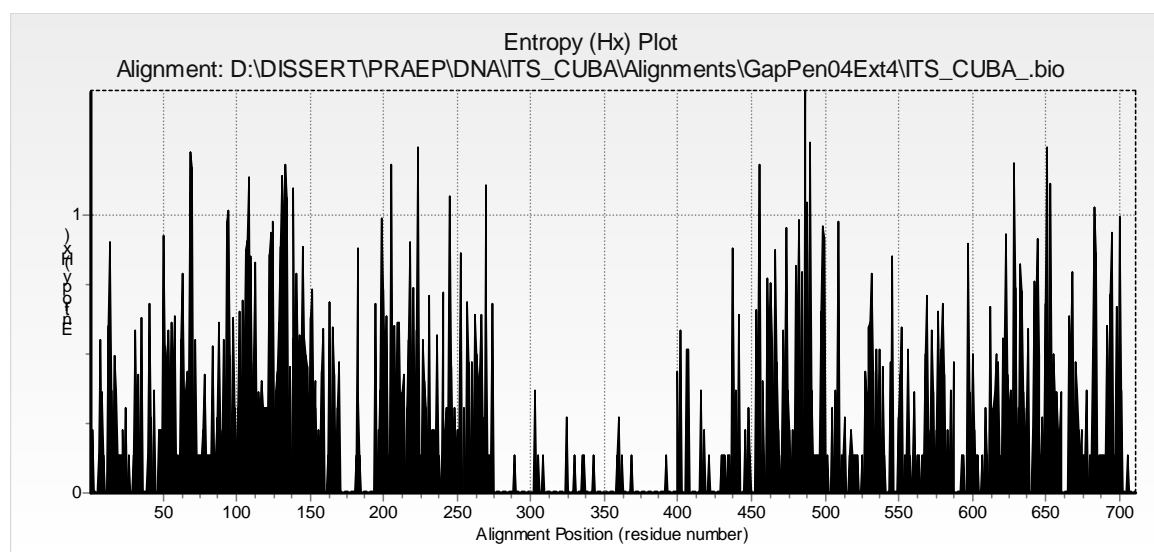


Fig. 64: Entropy (variability) along all loci of one sequence alignment (ITS4C). Given is the amount of variability in each column (base position). Species with larger deletions (>6 base pairs, *Pleurothallis flabelliformis*, *P. pruinosa* p.p.) and those with only incomplete sequences (ITS2 missing: *P. ghiesbreghtiana*) were excluded prior to analysis.

### Phylogenetic analyses

To test the substitution saturation of the sequences, transition and transversion portions were plotted against genetic distance (Fig. 65, Fig. 66). Transitions ( $A \leftrightarrow G$ ,  $C \leftrightarrow T$ ) are known to occur at higher rate than transversions ( $A \leftrightarrow C$ ,  $A \leftrightarrow T$ ,  $G \leftrightarrow T$ ). This is seen

in the diagrams presented here. Transversion are accumulating at a more or less linear rate, whereas transitions show an exponential growth and saturate much quicker. The saturation (a horizontal graph) however is not yet reached in the sequences employed.

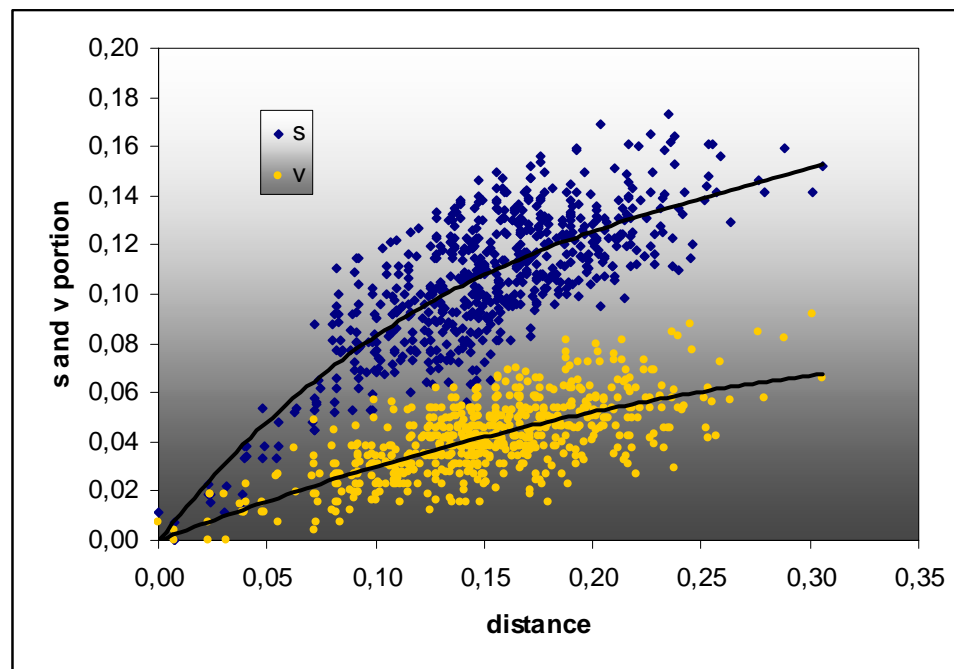


Fig. 65: Transition (s) and transversion (v) proportion versus distance (Tamura & Nei 1993) of the ITS4C matrix.

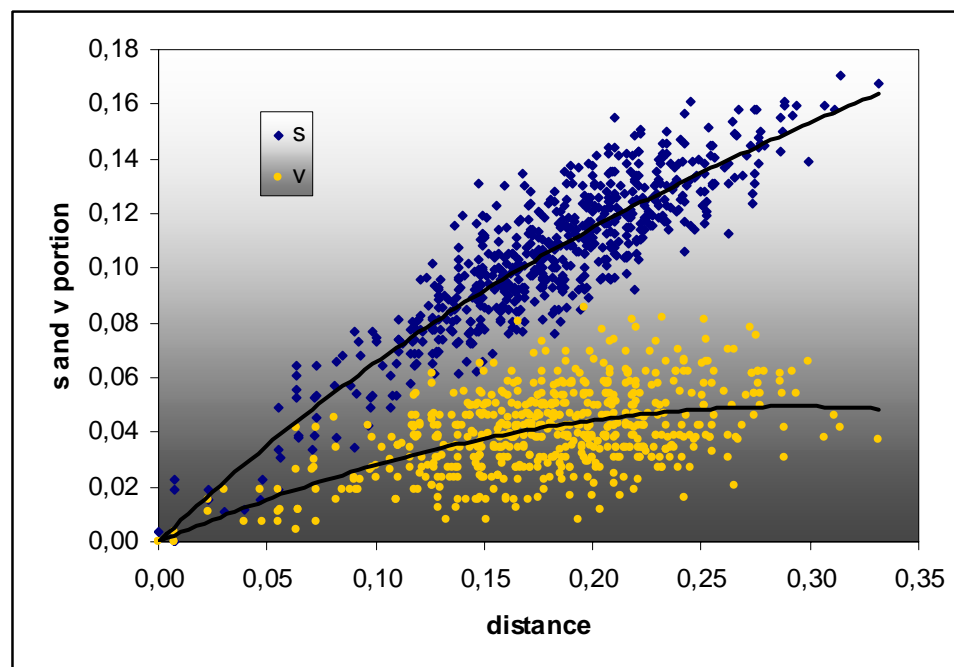


Fig. 66: Transition (s) and transversion (v) proportion versus distance (Tamura & Nei 1993) of the ITS4CR matrix.

Comparing the diagrams from the different matrices it turned out that the theoretical initial growth (exponential in transitions, linear in transversions) is blurred in sequences

containing indels. Since length mutations are rare events they are more apparent in distant taxa, i.e. their influence on the transitions/transversion ratio is much stronger towards the right part in the diagrams. In the initially homogenous segments s/v ratios should then be as divergent as in sequences of little distance ( $s \gg t$ ).

Thus, the exclusion of gap areas (Fig. 66) lowers the right portion of the s-graph and lifts that of the v-graph.

### *Cuban Analysis*

The term Cuban Analyses, hereafter, refers to those based on the Cuban taxa.

The following table shows statistical results of MP analyses. Gap tolerance thoroughly affected topologies. Best results, i.e. highest resolution of taxa, were achieved with a gap cost of 15 in the initial CLUSTAL alignment and very limited subsequent adjusting by eye.

Tab. 11: Statistical results of MP analyses.

<b>Matrix</b> (see Tab. 8)	<b><math>\Sigma</math> trees</b>	<b><math>\Sigma</math> steps</b>	<b><i>RI</i></b>	<b>Consensus tree: <math>\Sigma</math> unresolved nodes (and branches)</b>
ITS4C	8	1378	-	2 (10)
ITS4CR	3	1258	-	2 (6)
ITS15C	2	1369	0,70	1 (3)
ITS15CR	1	1234	0,68	0
ITSD	8	881	-	2 (11)

Deleting ambiguous indels increased the resolution of the tree (ITSxC→ITSxCR). However, a total omission of indels seems to be a loss of indispensable information (ITSD4), which resulted in the collapse of many branches. Generally, the topology of deeper splits, i.e. among distant taxa, is more affected by indel manipulation than relationships among lower ranks. Thus, the deletion of gaps (ITSxCR and ITSD alignments) affected only the relative position of subgeneric taxa (sensu Luer) to each other. Species complexes of lower ranks are rarely affected by any of the manipulations, i.e. relationships within subgenera were nearly the same in all topologies. Thus, the definition of homologies, which depends on gap costs and personal preferences of the author when adjusting the alignments by eye, influences major relationships in the first place!

Though ITS15C had two most parsimonious trees, its clades received stronger bootstrap support than those of the single tree drawn from the ITS15CR alignment. This may be in part due to the reduced number of parsimony informative sites in the latter. Moreover the two trees of ITS15C differed only slightly in having the relative position of *Pleurothallis*

*ghiesbreghtiana* and *P. pruinosa* (short sequence) exchanged. In a second run, with the sequences of *P. ghiesbreghtiana* being removed, as expected, only one most parsimonious tree was left. Naturally, bootstrap percentages rose substantially. One of the two trees of ITS15C shall be presented here (Fig. 67+Fig. 68).

In the following, clades A-G from Fig. 67 and Fig. 68 are described with reference to the system published by Luer (1986b), if not indicated otherwise.

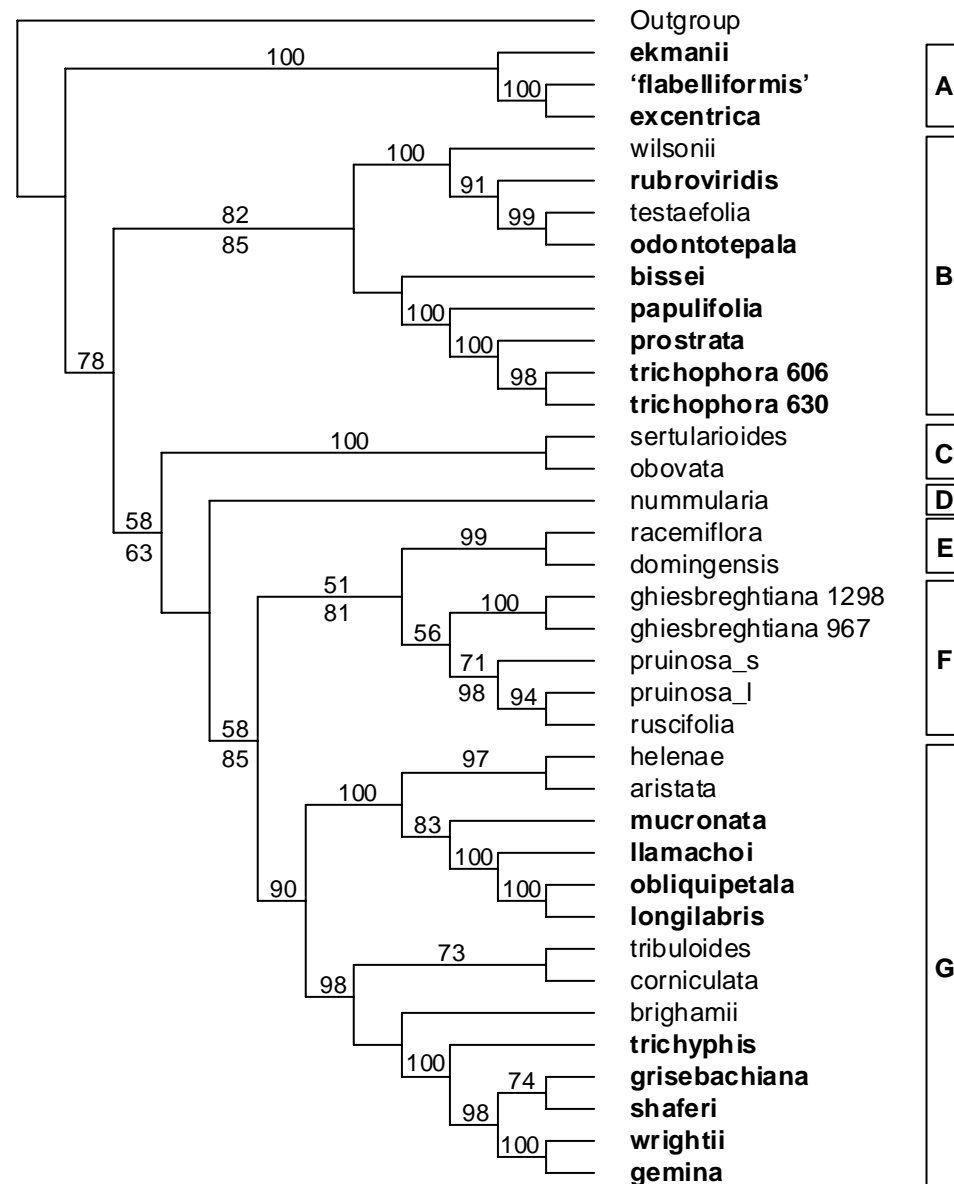


Fig. 67: One of the two most parsimonious trees from the ITS15C alignment. Numbers above the branches are bootstrap percentages >50%. Numbers below the branches represent bootstrap support when *Pleurothallis ghiesbreghtiana* had been removed from the alignment. Cuban endemics are in bold type. The second tree differed only in having the short sequence of *P. pruinosa*, *pruinosa\_s*, as the basal branch of clade E.

*Clade A* – This clade comprises three species with 8 pollinia which were published under the generic names *Octomeria* and *Pleurothallis*. All are Cuban endemics. The group came out as sister to the rest of the species in all most parsimonious trees from the 5

alignments. It received 98-100% bootstrap support in all bootstrap analyses, which is partially due to a considerably high branch length (100 steps).

*Clade B* – Three subgenera are assembled in this group: *Antilla* Luer, *Acianthera* (Scheid.) Luer and *Apodae-Proreperntia* Luer. The former is restricted to the islands of the Greater Antilles where it has 11 species (Luer 2000). Of the four Cuban taxa, two could be sequenced, *P. prostrata* and *P. trichophora*. The two accessions of the latter, one from Central Cuba (Stenzel 606), the other from Oriente (Stenzel 630), mark the limits of the geographic distribution of that taxon. The two samples show a relatively high branch length leading to their node and even within there is a fairly great number of steps (4 and 12 resp.)

Subgenus *Acianthera* was split by Luer into several sections, many of which are represented in Cuba: sect. *Brachystachyae* Lindl. (*Pleurothallis odontotepala*, *P. papulifolia*, *P. wilsonii*), sect. *Sicariae* Lindl. (*P. rubroviridis*), sect. *Tomentosae* Luer (*P. bissei*). Morphologically these species have a strong tendency towards succulence, including the flowers. The third subgenus, *Apodae-Proreperntia*, is represented by just one species, *P. testaefolia*.

All subclades receive strong bootstrap support, except for *P. bissei* which in the MP consensus trees ends up either in an unresolved position within clade B (ITS4C), as sister to *papulifolia-prostrata-trichophora* (ITS4CR, ITS15C: Fig. 67), or in a paraphyletic position to clade B as sister to clades C-G (ITS15CR).

*Clade C* comprises *P. obovata* and *P. sertularioides*, which belong to different subgenera in Luer's system, *Acuminatia* (Lindl.) Luer and *Specklinia* sect *Muscosae* Lindl. resp. This group is found in all bootstrap trees (100%).

*Clade D* represents *Pleurothallis nummularia*, which belongs to Luer's sect. *Phloeophilae* (Hoehne & Schltr.) Luer of subgen. *Acianthera*. Here it never fell within this group. The species' position is uncertain. In most of the consensus trees it is found as sister to clade C (ITS4CR, ITS15CR) or clades E-G (ITS15C). However, the branch which includes *P. nummularia*, always collapses in the majority bootstrap trees (<50%).

*Clade E* comprises only two taxa, *Pleurothallis domingensis* and *P. racemiflora*. The former belongs to subgen. *Crocodeilanthae*, the latter has been accommodated as subgen. *Dracontia* Luer. The group received 95-100% bootstrap support in all consensus trees.

*Clade F* consists of two taxa attributed to subgen. *Pleurothallis* sect. *Pleurothallis*, *P. ruscifolia* and *P. pruinosa*, and one classified under subgen. *Acuminatia* Luer (1999b), *P. ghiesbreghtiana*. Of the latter only ITS1 and 5.8S p.p. could be sequenced. All alignments (except ITSD) yielded a similar topology with *P. pruinosa* and *P. ruscifolia* as sister to *P. ghiesbreghtiana*, however, with low bootstrap support. The elimination of *P.*



*ghiesbreghtiana* from the matrices resulted in bootstrap values bouncing up (Fig. 67 – numbers below branches). A second MP run with only the partial sequence covered by *P. ghiesbreghtiana* (ITS1 and 5.8S p.p.) showed the same topology as Fig. 67. Bootstrap values from this stripped matrix, naturally, were much lower due to the limited data.

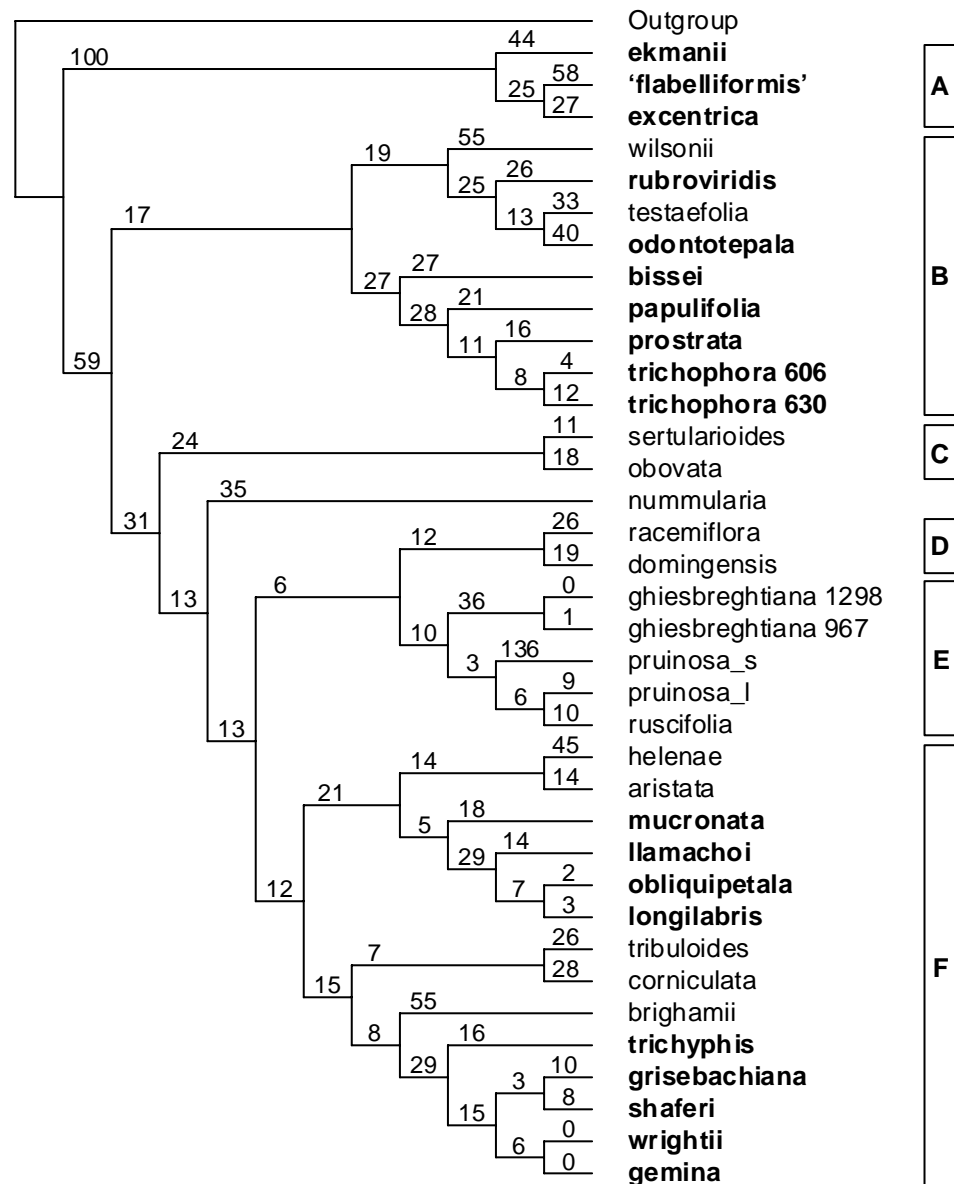


Fig. 68: One of the two most parsimonious trees from the ITS15C alignment (same tree as in Fig. 67).

Numbers above branches are branch lengths. Cuban endemics are in bold type.

The last *clade*, G, was found in all trees from the 5 matrices. It received high bootstrap support in the case of full ( $\geq 90\%$ ) but less in the case of stripped matrices (70-85%). The *clade* is subdivided into two groups which have been found again in all consensus trees, both with strong support ( $\geq 95\%$ ). The first one comprises taxa from subgen. *Specklinia* sect. *Muscariæ* Luer with *P. aristata* as the type species. The other group consists of taxa treated as subgen *Specklinia* sect. *tribuloides* Luer (*P. tribuloides*) and sect.

*Hymenodanthae* Barb. Rodr., the latter being divided into subsect. *Apodae-Caespitosae* (Lindl.) Luer (*P. corniculata*, *P. brighamii*, *P. trichyphus*) and subsect. *Longicaulae* (Barb. Rodr.) Luer (*P. gemina*, *P. grisebachiana*, *P. shaferi*, *P. wrightii*). Except for *P. brighamii* the relationships of all species received moderate to strong support by bootstrap tests.

### *Complete Analysis*

The term Complete Analysis, hereafter, refers to analyses comprising all taxa sequenced by both the author of this study and Pridgeon, Solano & Chase (2001). Similar to the findings in the Cuban Analysis, the incomplete sequence of the two accessions of *P. ghiesbreghtiana* had a great influence on the topology. Trees containing the *P. ghiesbreghtiana* data showed partially distorted clades with many groupings being in discordance of even highly preserved morphological features, e.g. number of pollinia. This may be due to the fact that PAUP ignores those loci that contain missing values in any of the sequences (A. Pridgeon, pers. comm.) which would reduce the amount of phylogenetically informative sites by > 50%. Since the presentation of the results should not be separated from discussion, the trees are shown in the next chapter (Fig. 69, Fig. 70) for convenience.

## 4 Discussion

### 4.1 General taxonomy

The subtribe *Pleurothallidinae*, despite the fact that it has been neglected scientifically for a long time, is now probably one of the scientifically best known orchidaceous groups. The morphological base was laid by Luer in his comprehensive *Icones Pleurothallidarum*, which, after more than a decade of thorough preparatory investigation, were started with a very detailed taxonomic system of this group (Luer 1986a). The complex genus *Pleurothallis* itself was reclassified in 1986 (Luer 1986b). In the following years this system was subject only to minor shifts or additions by the author. Luer delivered a detailed database of descriptions with morphological, chorological and taxonomic information on each taxon reviewed. Morphological data were complemented by anatomical characters examined by Pridgeon et al. (s. reference list on p. 5). Luer's classification is strictly morphological, focussing above all on shape, level of connation, and position of generative organs as well as inflorescence types, and number of pollinia. Traditionally, the latter plays an important role in pleurothallid classification. Being crucial in classifying genera meant not a classification according to the number, but to maintain a consistent number within generic boundaries. However, even this is not a general rule and so we find one genus having 6 and 8 pollinia (*Brachionidium* Lindl.) and another with two polymorphic pairs of pollinia (*Dresslerella* Luer). Moreover, according to Luer (2001), *Pleurothallis* would now comprise both species with 2 and with 8 pollinia, since he transferred the Cuban *Octomeria excentrica* Luer to *Pleurothallis*. Palynological data of pleurothallid orchids had been scarce and only sampled randomly (Schill & Pfeiffer 1977; Zavada 1983, 1990) until a broad survey on pleurothallid pollen morphology was prepared by (Stenzel 2000). Additional taxa, especially of the underrepresented genus *Pleurothallis* itself, were studied at the outset of the present work (Stenzel 2004b). Finally, Pridgeon & al. (2001) published a phylogenetic analysis based on a three-gene data set, which was the base for the most devastating "taxonomic storm" since Kuntze's time (Kuntze 1891), with more than 500 transfers and new creations (Pridgeon & Chase 2001). Not surprisingly, this radical reclassification of Luer's system provoked a sharp rebuttal (Luer 2002) of Pridgeon's and Chase's interpretations. However, despite Luer's reproach of nomenclatural inaccuracies, which in fact made 10% of Pridgeon & Chase's new combinations invalid (Barros 2002, Pridgeon & Chase 2002), he had little to offer against the new system. So, what could have been an interesting discussion of morphological vs. molecular views, ended up in a rather sulking "leave it as it is" (Luer 2002). Other than Luer's barren reply, who simply turned all taxonomical proposals by Pridgeon & Chase (2001) down, responses to the new system have been cautious (Hammel & al. 2002, Jost

& Endara 2002), principally acknowledging the main results and pointing out the various weaknesses in Pridgeon's and Chase's nomenclatural methodology. Thus, these authors doubt that the new system will be adopted in floristic works until the new generic concepts have been formalised and clearly articulated (Hammel & al. 2002). So far only one constructive approach has been published, resulting in a critical revision of the nomenclatural changes (Barros 2002). Ignoring the scattered nomenclatural awkwardnesses, the main weak points in Pridgeon & Chase's taxonomic methodology shall be discussed briefly.

1. *Morphology vs. DNA* – Pridgeon & al. (2001) see the great advantage of molecular data in avoiding the “homoplasy rife” when searching for relationships. However, translating phylogeny into taxonomy, they could not avoid to fall back upon Luer's system, which is based purely on morphological features. Ironically, they continue the classification that they are just criticising. It should be stressed that more than 3/5 of the taxonomic reclassifications were based indirectly on morphology, since they are made according to Luer's system! So, if the new classification is built on solid ground it is due to Luer's intuition and experience, too.

Unfortunately, morphological issues were discussed almost only if they were in concordance with molecular data, e.g. in the transfer of *Myoxanthus* subgen. *Satyria* Luer, which was not represented in the DNA matrix, but shares anatomical characters with subgenus *Silenia*, which was included in the molecular study. Direct morphological inconsistencies within DNA based clades were usually ignored.

2. *Absence of type material* – Of the genera sensu Luer, that were taxonomically altered in any way, only 2/3 were represented by their type taxon. The same applies to his subgeneric taxa of *Pleurothallis* that were validly<sup>4</sup> transferred to other genera. Section *Tomentosae* Luer of *Pleurothallis* subgen. *Acianthera* was reclassified without being sampled at all.

Likewise, 5 of the 7 resurrected or otherwise changed genera had not been represented by the respective type (*Acianthera*, *Anathallis*, *Andinia*, *Phloeophila*, *Stelis* / *Pleurothallopsis*, *Specklinia*). In some morphologically homogenous genera (*Stelis* s. Luer) this may not appear to be necessary. In groups that are polymorphous or, like *Phloeophila* Hoehne & Schltr. (*Pleurothallis* subgen. *Acianthera* sect. *Phloeophilae* sensu Luer (1986b), which even proved to be

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<sup>4</sup> Some taxa were tentatively included in *Pleurothallis* s.str., “pending DNA sequencing” (Pridgeon & Chase 2001).

polyphyletic in the same study [!] the inclusion of the type species ought to be a must.

3. *Sample size* – The addition of another 30+ taxa from Cuba has altered the general topology of the ITS tree presented in Pridgeon & al. (2001) only slightly. In some instances, the effect was stronger (p. 117), which illustrates the partially provisional status of the topology presented by Pridgeon & al. (2001). Cases of clear conflict between morphology and genetics should have been better excluded from the subsequent nomenclatural changes by Pridgeon & Chase.

Despite all deficiencies, neither Luer's works nor the results delivered by Pridgeon & al. can be underestimated, since each one provides the data that the other one lacks. Together with the palynological data (Stenzel 2000, 2004b) which are completed in the present work, they form an incomparable pleurothallid database. By combining these 3 sources of phylogenetically relevant information it should be possible to create a system much more natural than those published to date.

As indicated, palynological and molecular data of the material examined in this work yielded further insight into relationships and evolutionary processes. Prior to the present study another 40 taxa mainly from the underrepresented genus *Pleurothallis*, which had not been examined till then, were added to the palynological survey. Together with the data by Stenzel (2000) and the present work they represent a broad base for a discussion of taxonomic and phylogenetic issues. Concerning molecular data, this study adds another 33 taxa to the 70 species of *Pleurothallis* studied by Pridgeon & al. (2001). In the following, the impact of both palynological and molecular results on the systems proposed by Luer and Pridgeon & Chase will be discussed. The term "original tree/topology" hereafter refers to the tree from the large ITS matrix analysis by Pridgeon & al. (2001: 2296-2298), "Cuban Analysis" refers to the MP tree of the Cuban taxa alone and "Complete Analysis" describes the analysis of the mixed matrix (Cuban taxa and those from Pridgeon & al.). The latter resulted in several trees, the strict consensus of which is presented in the following figures. To facilitate easy orientation, clades containing Cuban taxa are marked with the same letter as in the Cuban Analysis (Fig. 67, Fig. 68).

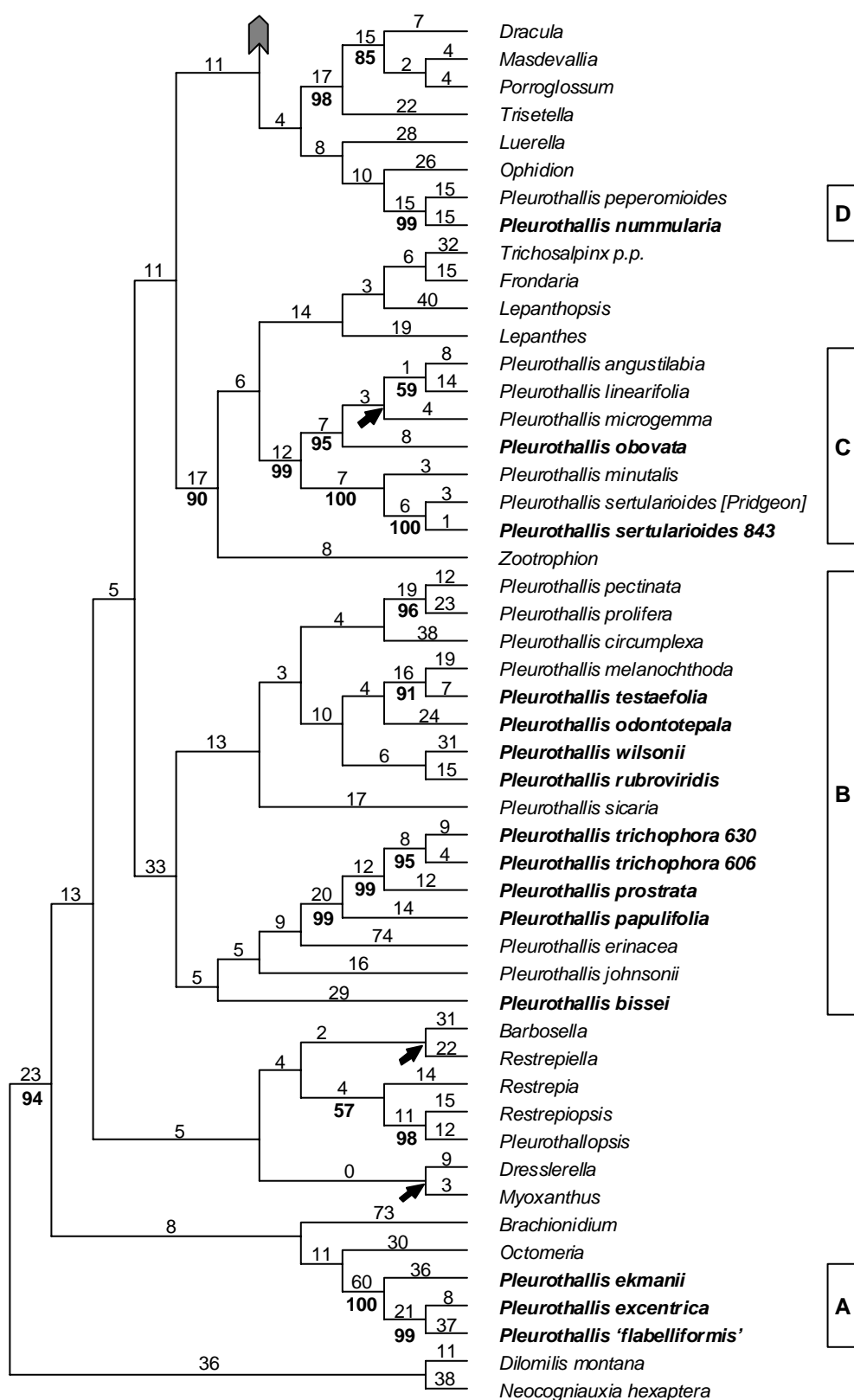


Fig. 69: Complete Analysis. First portion of one of the 10 MP trees.

(L=4326, RI=0.69, 452 parsimony-informative of 549 variable characters). Tree based on the ITS data set from the present study (in bold type) and the matrix by Pridgeon & al. (2001). Only those genera and species screened by Pridgeon & al. that neighbour Cuban taxa are shown in the tree. Branch lengths in normal type, bootstrap support percentages >50% in bold. Arrows indicate groups absent in the strict consensus tree. Numbers behind species names identify Cuban vouchers in multiple samples (e.g. *Stenzel* 606). Clade namings are in concordance with those in Fig. 67 and Fig. 68.

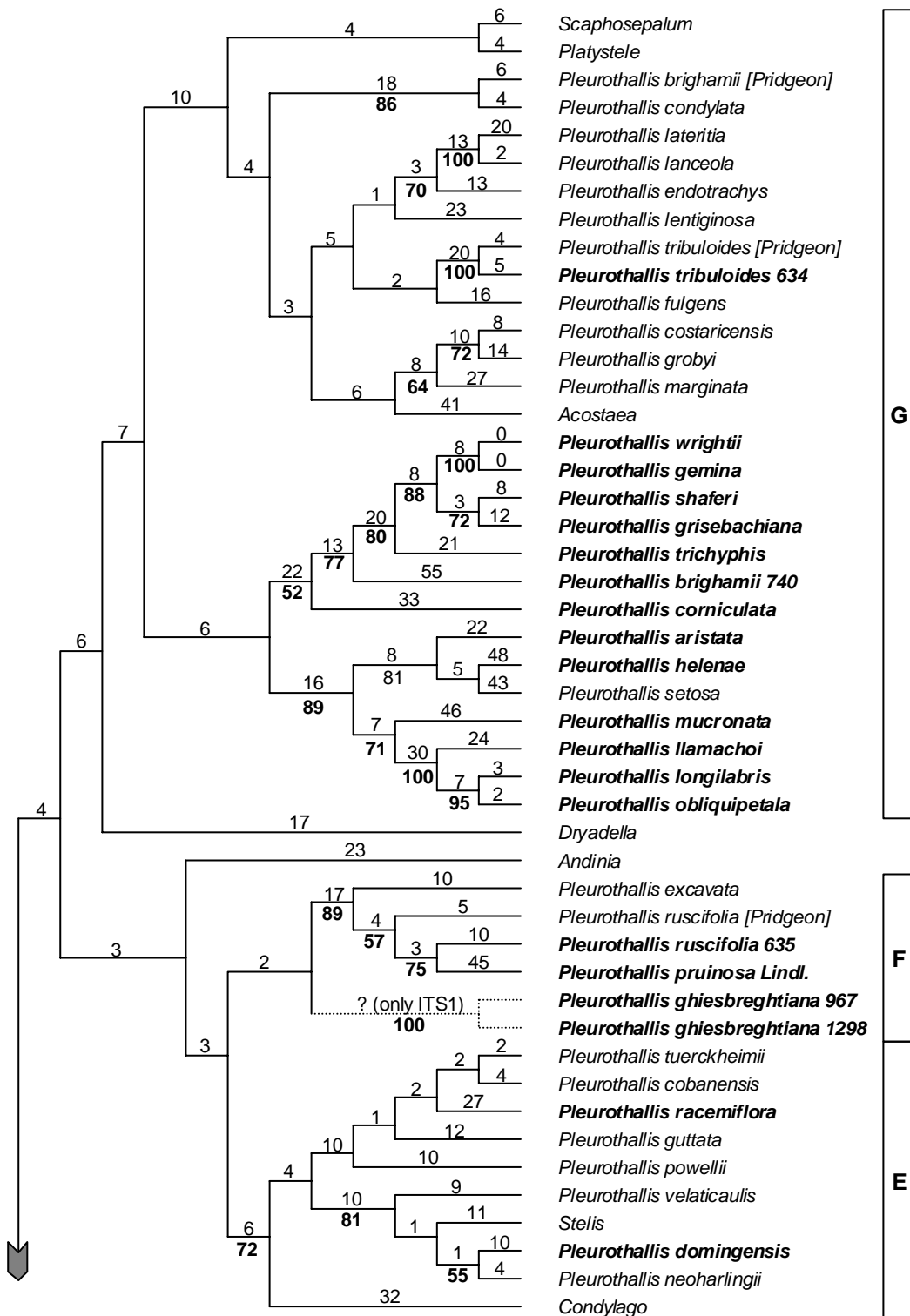


Fig. 70: Complete Analysis. Second portion of one of the 10 MP trees. (L=4326, RI=0.69, 452 parsimony-informative of 549 variable characters). Tree based on the ITS data set from the present study (in bold type) and the matrix by Pridgeon & al. (2001). Only those genera and species screened by Pridgeon & al. that neighbour Cuban taxa are shown in the tree. Branch length in normal type, bootstrap support percentages >50% in bold. Numbers behind species names identify Cuban vouchers in multiple samples (e.g. *Stenzel* 1298). Arrows indicate groups absent in the strict consensus tree. Clade namings are in concordance with those in Fig. 67 and Fig. 68. This tree was computed without the incomplete sequences of *P. ghiesbreghtiana*. The species was inserted in the tree, based on another analysis (see discussion in the text).

*Clade A* – The three Cuban endemics, *Pleurothallis ekmanii*, *P. excentrica*, and *P. 'flabelliformis'* had not been part of the study by Pridgeon & al. (2001). Their inclusion caused interesting changes in the topology. Originally, *Brachionidium* (6 and 8 pollinia) had fallen in the next higher subclade, along with all genera that have 4 pollinia and *Myoxanthus* with usually 2, rarely 4 (Stenzel 2000) pollinia. Together with the additional 33 taxa from Cuba, *Brachionidium* switched now to Clade A, a position already suggested by *matK* data (Pridgeon & al. 2001). Thus, all taxa with 8 pollinia are grouped in one and those with 4 pollinia in another clade. The second substantial change in the basal groups is the position of a member of *Pleurothallis* subgen. *Kraenzlinella* (Kuntze) Luer, *P. erinacea* Rchb. f., which fell sister to *Brachionidium* in the original tree. Besides striking differences in gross morphology, this species has only 2 pollinia, whereas the others, with the exception of *Myoxanthus* have 4 or even more. *P. erinacea* now ended up in Clade B (see next paragraph), the taxa of which share the feature of 2 pollinia.

*Clade B* – This group comprises what Pridgeon & Chase (2001) circumscribed as the resurrected *Acianthera* Scheidw. based on their molecular data. It combines *Pleurothallis* subgenera *Acianthera*, *Arthrosia* and *Sarracenella* of Luer's system.

Pollen morphology shows *Acianthera* as a homogenous entity (Stenzel 2004b). The aciantheroid surface of the pollinia together with a punctate or rarely fossulato-granulate and rugulate sculpture is characteristic for all species examined. However, these characteristics are not very specific and represent rather a plesiomorphic status. Thus, similar conditions can be found among the more "primitive" *Pleurothallidinae* with four or eight pollinia, e.g. *Restrepiella*. Among the genera with two pollinia it is unique, however. Molecular data of Cuban taxa reflect the natural classification of the genus as circumscribed by Pridgeon & Chase (2001). Though clade B receives weak to moderate bootstrap percentages in the Cuban Analysis and no support in the Complete Analysis, it is maintained in the strict consensus trees of both analyses. Moreover, Pridgeon, Solano & Chase (2001) found 100% bootstrap support for their set of taxa in plastid sequences which are evolutionary more stable than ITS regions. This should be related to the early split off of the group and subsequent accumulation of multiple mutations in variable sites (ITS) which lead to a low signal/noise ratio. Sect. *Tomentosae* Luer of subgen *Acianthera*, which could not be included by Pridgeon, Solano & Chase, was represented in the present study by *Pleurothallis bissei*, which fell within the *Acianthera* clade as sister to Luer's subgenus *Antilla* in the Cuban analysis. *Pleurothallis* subgen. *Antilla* Luer seems to be a natural group within *Acianthera*. However, it contains more taxa than actually assumed (Luer 2000). According to molecular data, *Pleurothallis papulifolia*, an endemic from Oriente, belongs to this subclade too. As pointed out before, *P. erinacea* came out in all trees as sister to the *Antilla* subclade while it had been placed as sister to *Brachionidium* in the original tree. This species belongs to subgen *Kraenzlinella* (Kuntze)



Luer, the affinities with subgen. *Acianthera* of which had been pointed out by Luer before (1994). Its position within *Acianthera* received no bootstrap support >50%. However, morphological and palynological data strongly suggest this alliance. Concerning Luer's subclassification of subgen. *Acianthera* (1986b), Pridgeon & Chase were loath to adopt his division, owing to the paraphyly of many of his sections. Data of the Cuban taxa yet increase the incompatibility of Luer's subgeneric system with molecular data.

Morphologically, *Acianthera* is difficult to describe. Though all species lack an annulus, this is found in other 'primitive' genera too and likely represents a plesiomorphism. Species of subclade *Antilla* Luer, along with *Pleurothallis papulifolia* and subgen. *Kraenzlinella* (*P. erinacea*), all of which form a clade in the Complete Analysis, have variably papillose, verrucate, or pubescent ovaries. Other tendencies within the group are leaf edges, which are decurrent to a variable degree on the ramicaul, which in turn may be surcate to strongly winged. Succulence is found in leaves and even flower parts, which are often papillose or pubescent. None of the characteristics is exclusively confined to this group, however.

Clade C – Pridgeon & Chase combined two of Luer's subgeneric taxa in the genus *Anathallis* Barb. Rodr. Both are represented by Cuban plants: subgen. *Acuminatia* (Lindl.) Luer (1999b) by *P. obovata* and subgen. *Specklinia* sect. *Muscosae* Lindl. by *P. sertularioides*. Palynological features back the molecular findings of a close alliance between *Acuminatia* and *Specklinia*, because of the advanced gemmate sculpture found in the Cuban plants and other species (Stenzel 2004b). Molecular data from *P. obovata*, which was not included by Pridgeon & al. (2001), reflect this relationship too.

Pridgeon & Chase found subgen. *Specklinia* polyphyletic and transferred sect. *Hymenodanthae* Barb. Rodr. and sect. *Muscosae* en bloc to the resurrected genus *Specklinia* Lindl. (see further down) and *Anathallis* resp. However, the monophyly of Luer's two sections is doubtful. His morphological distinction between sect. *Muscosae* and sect. *Hymenodanthae* is extremely blurred and virtually every characteristic of the one can be found in the other too. The mixed concept of the two sections is evident if we compare *P. sertularioides* (*Muscosae*) and *P. spiculifera* Lindl. (*Hymenodanthae*). The two species are not only morphologically similar but share the same highly advanced gemmate sculpture type with Luer's subgen. *Acuminatia*. The close relationship becomes clear when the two species are examined in detail. It turns out that they are merely miniature versions of many species in subgen. *Acuminatia*, among them *Pleurothallis obovata*! Ironically, this subgenus had been earlier treated as section of subgen. *Specklinia* (Luer 1986b). On the other hand, there are species treated under sect. *Muscosae* by Luer and transferred without molecular data by Pridgeon & Chase to *Anathallis*, which do not show the typical gemmate sculpture but a levelled surface which in turn can be found in species of sect. *Hymenodanthae* (Stenzel 2004b: *P. fuegii* Rchb. f.). In summary, the species

treated as *Pleurothallis* subgen. *Specklinia* sect. *Muscosae* by Luer and transferred to *Anathallis* sensu Pridgeon & Chase are not monophyletic.

Clade D – *P. nummularia* had been treated in section *Phloeophilae* (Hoehne & Schltr.) Luer of subgen. *Acianthera* by Luer (1986b). In the present study, it fell sister to the morphologically similar *P. peperomioides*. The two form a clade with the morphologically distinct genera *Ophidion* Luer and *Luerella* Braas, which led Pridgeon & Chase to raise sect. *Phloeophilae* to generic status. In the absence of palynological data the nomenclatural changes were drawn only on the base of molecular affinities. However, the grouping with *Luerella* is only supported by the *trnL* bootstrap test, and the inclusion of *Ophidion* is not backed by any of the bootstrap trees with values >50% (ITS, *matK*, *trnL*). Moreover, another member of sect. *Phloeophilae*, *P. raduliglossa*, ended up within clade B (*Acianthera*) in Pridgeon's study, indicating polyphyly in Luer's concept of *Phloeophilae*. Unfortunately, Pridgeon & al. do not indicate the source of their material. Thus, it was not possible to check for an erroneous determination. The genus *Phloeophila* sensu Pridgeon & Chase (2001) remains therefore a rather questionable taxon.

Clade E – One of the most radical taxonomic changes was the tremendous expansion of *Stelis* Sw. by Pridgeon & Chase. Several of Luer's subgenera of *Pleurothallis* (1986b) formed a clade with the genus *Stelis* s.str. itself in the study by Pridgeon & al. Two of these subgenera have representatives in Cuba, *Pleurothallis domingensis* (subgen. *Crocodeilanthæ* (Rchb. f. & Warsz.) Luer) and *Pleurothallis racemiflora* (Sw.) Lindl. (subgen. *Dracontia* Luer). Palynological examinations revealed a great uniformity within the broadened generic limits drawn by Pridgeon & Chase. The prevalent tendency is a reduction of the sporoderm towards octomerioid conditions (Stenzel 2004b), a pattern which can be found in the two Cuban species too. *P. domingensis* and *P. racemiflora* are situated in rather isolated positions. The latter forms a clade with other members of subgen. *Dracontia* (*P. cobanensis*, *P. powellii*, *P. tuerckheimii*), the inner structure of which is not supported by the bootstrap test, however. *P. domingensis* is found with other members of subgen. *Crocodeilanthæ* as sister to *Stelis*. The inner structure of this clade is not robust either, however the group itself is moderately supported by the bootstrap test (81%).

Clade F – This clade contains the type of genus *Pleurothallis*, *P. ruscifolia* (Jacq.) R. Br. The genus as circumscribed sensu Luer 1986b) comprises a great range of discordant palynological patterns suggesting the grouping of many unrelated taxa (Stenzel 2000). Those taxa assembled in *Pleurothallis* s.str. (Pridgeon & Chase 2001), on the contrary, show an uniform pollen morphology with a levelled surface and psilate to punctate sculptures (Stenzel 2004b). Palynological data was available for most of the subgenera proposed by Luer and sequenced by Pridgeon, Solano & Chase. The concordant pollen

morphology of those subsections of sect. *Pleurothallis* (sensu Luer) which could not be included by Pridgeon & al. backed the concept of a narrowed definition of *Pleurothallis*. Yet, subgenera *Pleurobotryum* (Barb. Rodr.) Luer and *Kraenzlinella*, which despite absent or insufficient molecular data, had been included in *Pleurothallis* by Pridgeon & Chase (2001) show a closer relationship with *Acianthera* instead. Representatives of both taxa have the typical combination of triangular pollinia without caudicles and with a punctate sculpture.

The two Cuban species, which had been classified in subgen. *Pleurothallis* sect. *Pleurothallis* by Luer (1986b), *P. ruscifolia* and *P. pruinosa*, were grouped with the two accessions of *P. ruscifolia* separated by *P. pruinosa*. Similar discordant topologies can be found in the next clade and will be discussed later (p. 125).

The third species that fell in the *Pleurothallis* s.str. clade, *P. ghiesbreghtiana*<sup>5</sup>, could be sequenced only partially (ITS1). The inclusion of the incomplete sequence had led to a number of distortions in the gene trees as well as substantial drops in bootstrap values, due to the loss of phylogenetic information of ITS2 and apparent insufficiencies in the MP algorithm (Pridgeon, pers. commun.). *P. ghiesbreghtiana* was analysed separately in the clade then and added to the tree afterwards. Yet, its position remains questionable for it doesn't match several autapomorphies of *Pleurothallis* s.str., e.g. apical anthers and a lepanthoid pollen surface and sculpture. Instead, palynological data strongly suggest an affiliation with the neighbouring clade E, i.e. *Stelis* s.l. This idea was recently confirmed by the work of R. Solano (pers. commun.). Moreover, a treatment of *P. ghiesbreghtiana* in *Anathallis* (Pridgeon & Chase 2001) is not only irrelevant as indicated by molecular data but is refuted by pollen morphology, too. Species of *Anathallis* show a distinct gemmate pattern, not found in any of the accessions of *P. ghiesbreghtiana*.

Clade G – This group comprises no less than 14 Cuban taxa, most of which, if treated at all, have been accommodated in the subgenus *Specklinia* in various sections (Luer 1986b). The addition of the Cuban species referable to this subgenus more than doubled the sample size that was employed by Pridgeon & al. (2001). However, compared with the number of species attributable it is still hopelessly underrepresented. This may account for the low bootstrap values received. For the respective sections of subgen. *Specklinia* alone, Luer enumerated more than 70 species, a list that still lacks many Antillean taxa and is probably completely outdated concerning its volume.

Still, the inclusion of the Cuban taxa had a striking effect on the original topology in some cases. Morphologically puzzling combinations in the original topology, as

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<sup>5</sup> All recent taxonomic publications in this connection (Luer 1986b, 2000; Pridgeon & Chase 2001; Pridgeon & Chase 2002) cite *Pleurothallis ghiesbreghtiana* A. Rich. & Galeotti under the invalid name *Pleurothallis racemiflora* Lindl. ex Lodd.

*Acostaea*–*Pleurothallis setosa*, were rearranged in a more natural pattern now. The tie of *Acostaea* to the *P.-grobyi*-subclade had been suggested by *matK* sequences (Pridgeon & al. 2001). The subdivision of sect. *Hymenodanthae*, based on the congested inflorescence, which was acknowledged even by Luer as a mere “key character”, is unlikely to reflect true relationships and a condensed rachis has apparently evolved several times in different lineages (*brighamii*, *condylata*, *corniculata*<sup>6</sup>, *fulgens*, *trichyphus*). It should be mentioned, however, that all examined taxa with condensed inflorescences except *P. trichyphus* show the same punctate to granulate sculpture, so that the ladderized appearance of this sculpture type along the distal spine of Clade G (*tribuloides* through *brighamii*) might still be a product of undersampling as shown by the inclusion of the Cuban taxa. Concerning the unexpected “unrelatedness” of different accessions of the same species as seen in *P. brighamii*, see the discussion on p. 126.

With the addition of pollen morphology, there are three groups of concordant elements. **1)** In the morphological homogenous *aristata*-clade (subgen. *Specklinia* sect. *Muscariae* Luer), relationships are neatly mirrored by pollen morphology. Two groups may be distinguished, one comprising *aristata*, *helenae* and *setosa* (not from Cuba) with obovate (flattened turbinate) pollinia and an almost aciantheroid pattern, the other unifying the endemic taxa *llamachoi*, *longilabris*, and *obliquipetala*, with clavate pollinia and psilate tetrads that show a tendency to fuse their edges. *P. mucronata* shows intermediate features which is reflected by a low bootstrap value. **2)** The *P.-grobyi*-subclade (including *Acostaea*) comprises typical representatives of sect. *Hymenodanthae* subsect. *Longicaulae* (Barb. Rodr.) Luer with elongate racemes and a reticulate to gemmate octomerioid pollen morphology. Even the shape of the pollinia is very stable (lentiform with abruptly narrowed caudicles). Consistency of pollen characteristics was found in other species of this group too (Stenzel 2004b). However, some taxa placed by Luer in this subsection are clearly related to Clade C (*Anathallis* s. Pridgeon & Chase 2001) with which they share the advanced gemmate sculpture (Stenzel 2004b: *P. spiculifera* Lindl.). **3)** The *P.-endotrachys*-subclade comprises morphologically inconsistent members, which share, however, a homogenous pollen morphology with levelled tetrads and a punctate sculpture. This is found nowhere else in the clade, except for the relatively closely positioned genus *Scaphosepalum*, which is habitually similar to *P. endotrachys* (Chase 1985) with which it shares distichous inflorescences and distinct conduplicate flower bracts.

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<sup>6</sup> *Pleurothallis corniculata*, though classified among those plants with a congested inflorescence (subsect. Apodae-Caespitosa) by Luer, must have evolved from a racemose ancestor by reducing the flower number rather than the rachis length. There is one collection with a racemose inflorescence (duplicate of HAJB 80113 in herb. Greuter) that shows the presumably ancestral state with racemose inflorescences.

The Cuban endemics *P. gemina*, *grisebachiana*, *shaferi*, *trichyphis*, and *wrightii* which form the most distant subclade, comprise (pollen-) morphologically discordant features. This may be the result of undersampling, which is indicated by long branches, especially among the deeper splits.

As a result, the addition of the Cuban data had the following effects on the original tree: the overall resolution in the strict consensus tree rose substantially and nearly all of the collapsed branches in the original consensus tree are resolved now. Puzzling combinations in the original ITS tree were rearranged in a more natural order, which had often been indicated before by data from more stable DNA regions like *matK* and *trnL-F* (Pridgeon & al. 2001), e.g. *Brachionidium-Octomeria*, *Acostaea-Pleurothallis grobyi*-alliance. In the following, some taxonomic suggestions drawn from the broadened insight in pleurothallid phylogeny shall be listed:

- The 3 Cuban taxa with 8 pollinia should be accommodated in a new genus, due to the (pollen) morphological incompatibility with *Octomeria* and *Brachionidium* as well as strong bootstrap support from ITS sequences. Most recent sequencing of cpDNA (*trnL-F*, data not included in this study) reflected the isolated phylogenetic position as sister to *Octomeria*.
- *Pleurothallis* subgen. *Apoda-Prorepentia* Luer should be placed in *Acianthera* Scheidw. and *Pleurothallis* subgen. *Specklinia* sect. *Muscosae* Lindl. must be excluded from the synonymy of *Acianthera*.
- *Pleurothallis* subgenera *Kraenzlinella* (Kuntze) Luer and *Pleurobotryum* (Barb. Rodr.) Luer should be included in *Acianthera* (Scheidw.). and not in *Pleurothallis* s.str. as tentatively suggested by Pridgeon & Chase (2001).
- *Pleurothallis* subgen. *Specklinia* sects. *Hymenodanthae* Barb. Rodr. and *Muscosae* as circumscribed by Luer (1986b) and uncritically adopted by Pridgeon & Chase (2001) must be checked for monophyly. Likewise, the generic circumscription of *Anathallis* and *Specklinia* sensu Pridgeon & Chase (2001) should be reconsidered.
- *Pleurothallis ghiesbreghtiana* should be excluded from *Anathallis* sensu Pridgeon & Chase 2001.

## 4.2 Relationships of the Cuban taxa – molecular evidence

Comparing the molecular results of this study, it becomes evident that the Cuban Flora of *Pleurothallis* does not represent a monophyletic group. Instead, it is nourished by different evolutionary lineages.

A great number of the Cuban species of *Pleurothallis* is not closely related with each other and many occupy even rather isolated positions in the system (*P. bissei*, *P. domingensis*, *P. nummularia*, *P. obovata*, *P. pruinosa*, *P. racemiflora*, *P. ruscifolia*, *P. sertularioides*). Other groups appear clustered in the molecular tree. However, morphological traits and long branch lengths indicate missing samples, i.e. they also represent independent lineages (*P. odontotepala*, *P. rubroviridis*, *P. testaeifolia*, *P. wilsonii*). Finally, there are tight clusters of species, cases in which molecular, morphological and palynological data indicates a close relationship (subgen. *Antilla*, i.e. lower branch of clade B; subgen. *Specklinia* sect. *Muscariae* and sect. *Hymenodanthae* subsect. *Longicaulae*).

Thus, the Cuban spectrum of *Pleurothallis*, comprises groups of closely related taxa as well as distantly related ones. This pattern is found in many of the Cuban genera, both orchidaceous and non-orchidaceous (Alain 1958, Borhidi 1996, Samek 1973) and coincides with the general notion of island biogeography as a product of immigration and radiation (MacArthur & Wilson 1963, 1967). A close examination of the groups reveals two unusual features: a) differences in rates of morphological (phenotype) and molecular (genotype) evolution, and b) differences in tree topologies inferred from morphological and molecular data, which, however, should not be confused with the overall discrepancies between morphology and genetics. These features will be discussed in the following

### *Molecular vs. morphological evolution: pace and branch lengths*

The first inconsistency concerns the unusual distribution of branch lengths. Rate heterogeneity among taxa is a widespread phenomenon (reviewed in Wendel & Doyle 1998) and is attributed to 1) variation in generation times, assuming a clocklike mutation rate, 2) non-hierarchical molecular evolution, e.g. recombination between paralogous or xenologous DNA, and 3) insufficient taxon sampling and/or extinction.

Since taxon sampling density is one of the major problems in this study, due to the limited number of Antillean taxa included, it is irrelevant to discuss substitution rate heterogeneity among deeper splits, since they are most probably brought about by just this methodical deficiency. However, even among the finest splits (Fig. 69, Fig. 70), which, on the base of additional gross and pollen morphological data, are assumed to be sister taxa, one can observe that branch lengths (genetic distance) often does not coincide with morphological differentiation (species concept based on morphological distance). On the one hand, we

find pairs of species which exhibit a low number of mutations (e.g. *P. gemina*–*wrightii*: 0 mutations; *P. longilabris*–*obliquipetala*: 5). On the other hand, there are instances, where substitution rates within specific boundaries strongly exceed even those between species (e.g. *P. sertularioides*: 4, *P. tribuloides*: 9; *P. trichophora*: 13; *P. ruscifolia*: 17). Since the Cuban pleurothallid species are usually well defined by morphology, these observations touch the underlying question if substitution rates are concordant with changes in morphological characters, i.e. if molecular evolution reflects morphological evolution and vice versa. In the species of *Pleurothallis* studied it is apparent that some taxa have maintained the original sequence while differentiating into morphologically distinct species, whereas others have undergone considerable molecular evolution while retaining a characteristic morphology. This is partially due to the fact that, when using ITS, we deal only with a small fragment of the pleurothallid nuclear genome, which, owing to the putatively non-coding character, is little exposed to environmental selection involved in speciation processes (reviewed in Baldwin & al. 1995). Differences between the molecular (ITS) and morphological pace of evolution should be therefore *a priori* no surprise. Moreover, even within the ITS region mutations do not occur randomly, partially because of the chemical behaviour of nucleotides (p. 105), partially because certain regions are more conserved than others (Fig. 64).

It is interesting, however, that one pair of species, despite the proneness of ITS to mutations, shares the same sequence. *P. gemina* and *P. wrightii* are abundant in Cuba's Oriente today, nevertheless, *P. gemina* had never been collected prior to the 1980ies. This and the common ITS sequence indicate a recent origin for the new species. Pairs of species exhibiting little genetic distance have been reported from other orchidaceous groups, too (Cox & al. 1997, Borba & al. 2002). ITS, despite its popularity in studies aimed at the species level, fails to reflect putatively recent phenotypic differentiation. This has been observed also in other orchidaceous (Borba & al. 2002, Van den Berg & al. 2000) and angiospermous taxa (Panero & al. 1999: in Macronesian *Asteraceae*). If we assume a clock-like rate in ITS evolution among lower taxonomic ranks at least, these results contradict the assumption (Soto Arenas 1996) that orchidaceous speciation processes are long-time events, although it may be the case in certain orchids (Ackerman & Ward 1999). In the case of the Cuban endemics *P. gemina* and *P. wrightii*, we possibly observe an example of what was coined “**evolutionary explosion**” by Gentry (1982), i.e. the genesis of new species within very short periods of time (Gentry & Dodson 1987). Gross morphology is quite similar with some synapomorphies shared by both taxa: similar creeping habit, verrucate leaves etc. Respective autapomorphies comprise single, two-flowered racemes with whitish flowers (*P. gemina*) and several single-flowered racemes with purple flowers (*P. wrightii*). Hybrids with a mixture of the paternal features were found on one occasion (Stenzel 2001). The speciation process was triggered perhaps by a

spontaneous mutation in one population, that met favourable environmental conditions and set up a reproductive barrier at once. The rest of the pool remained untouched. Except for leaf shape and overall plant size, herbarium specimens of *P. wrightii* do not show any morphological variation during the last 150 years. Thus, it was a process of splitting off rather than of parallel stepwise divergence which should be a requirement in sympatric speciation where back-crossing is an incidence easily imaginable.

Cox & al. (1997) present a much more complicate explanation for the divergence between morphological and molecular evolution rates. Certain special molecular evolution modes, e.g. reticulate inheritance, may explain inconsistencies between gene and species trees. However, in this particular case it ignores the simple fact, that ITS is not a coding region for morphological and physiological traits that are related with floral and ecological adaptations. Imbalances between the evolution of morphological, physiological and genetic characters seems to be a common trait in orchids (Cox & al. 1997; Borba & Semir 2001; Borba & al. 2000, 2001a, 2001b, 2001c, 2002). On condition that ITS represents a kind of a molecular clock among finer splits, the only but essential conclusion of different branch lengths among pairs of species is that speciation occurs at different rates of time. This hypothesis coincides with findings of different patterns and paces in orchidaceous evolution in this study and elsewhere (Gentry & Dodson 1987, Ackerman & Ward 1999, Tremblay & Ackerman 2001).

#### *Molecular vs. morphological evolution: topology*

Before going into detail, it has to be stressed, that most of the peculiar topologies that are subsequently discussed, did not receive bootstrap support above 50%. However, they are found in the strict consensus of the Complete Analysis without exception.

The second unusual pattern observed in the molecular tree should not be confused with the overall differences between relationships derived from morphological and molecular data. Rather it refers to those instances, where at low taxonomic ranks doubtless similar morphology is contradicted by differences in sequences and consecutively by topology. This can be observed in morphologically similar taxon pairs, however, it is most striking when comparing different samples from one and the same morphological well defined species. As one would expect, many of these pairs of species or samples reflect the close relationship by falling sister to each other (e.g. *P. ghiesbreghtiana*, *P. trichophora*; *P. nummularia*~*peperomioides*; *P. testaefolia*~*melanochthoda*; *P. racemiflora*~*powellii*; clade G: from *P. mucronata* onwards). However, in other cases they were, unexpectedly, separated by morphologically very different taxa. As an example, the Cuban endemic *P. rubroviridis* was separated from the morphological very similar *P. sicaria* by a number of (Cuban) taxa of comparably much less morphological affinities. Interestingly, the *P.-sicaria-rubroviridis* subclade consists almost exclusively of species that were



morphologically classified by Luer as section *Sicariae* in subgen. *Acianthera* which underlines the morphological affinities.

*P. grisebachiana*, a Cuban endemic, is morphologically very similar to the continental *Pleurothallis grobyi* Batem. ex. Lindl., sharing even such fragile features as lip coloration. Both species fell in a “disjunct” position comparable to that of *P. rubroviridis* and *P. sicaria*. Whilst considering species pairs may be often a matter of taste, classifying species should be less subjective. Yet, even within specific limits the described pattern can be observed. Perhaps the most striking instance is represented by *P. brighamii*. The Cuban sample fell within a group of other Cuban species. The accession of *P. brighamii* sequenced by Pridgeon & al. (2001), on the other hand, was separated from the Cuban plant by 7 nodes, which span even distinct genera, like *Scaphosepalum*. Theoretically, there are **three explanations**: unverified plant material, inadequate topology and reticulate evolution. As to the source of **material**, it was not possible to check for wrong determinations in the material used by Pridgeon & al. However, when those samples from this study that are represented by Cuban vouchers, too (*P. brighamii*, *P. tribuloides*, *P. ruscifolia*, *P. sertularioides*) were added to the Cuban matrix (ITS15C), all pairs came out as sisters! Considering the reliability of the **topology**, we have to face the limitations brought about by incomplete sampling. However, it is unlikely that sample pairs at such a low taxonomic rank which are so profoundly separated should become sisters by adding more taxa. On the contrary, species samples that had been pairs in the Cuban Analysis (33 taxa + Pridgeon’s accessions of taxa which are present in Cuba, too) became separated in the complete MP study (>200 taxa). Thus, the two accessions of *P. brighamii* fell sister to each other in the Cuban Analysis, and became separated only in the Complete one. Moreover, this “disjunct” topology was observed several times in clearly unrelated clades reducing the probability that we face an artefact due to an inappropriate molecular or data-processing methodology.

To explain these inconsistencies, special features in the evolution of ITS, resulting in differences between the gene tree and the species tree (Pamilo & Nei 1988; review in Soltis & Soltis 1998), might be the key. Distortions in the gene tree may have been brought about by “inadvertent analysis of paralogous ITS” copies, i.e. by additional ITS copies that originated within the branch of the species tree. This hypothesis was used to explain unusual molecular topologies among morphologically similar species in the subfamily *Cypripedioideae* (*Orchidaceae*) (Cox & al. 1997)]. In the Cuban Analysis, however, a second peculiar pattern was observed. It is striking that the “disjunct” positions of closely related taxa or infraspecific samples always involve other Cuban samples as a separating block (Fig. 71). In these instances the gene tree reflected more a phytogeographical pattern than the morphologically defined species tree, since it groups the Cubans on one side and the continentals on the other side.

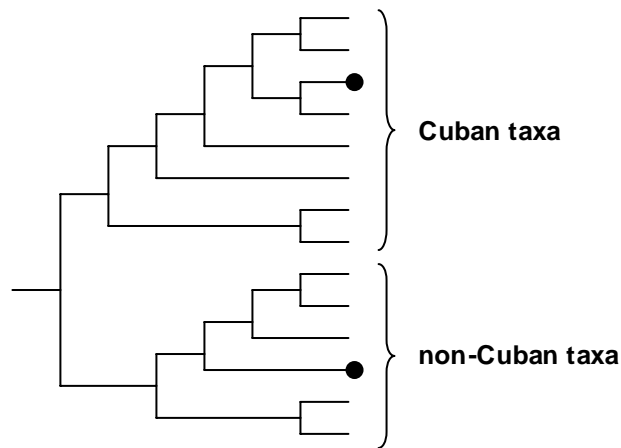


Fig. 71: Generalised example of a “disjunct” topology in the Complete Analysis involving either two closely related taxa or two accessions from one and the same taxon. Note the grouping of the Cuban samples. Positions of the Cuban and the non-Cuban sequence are marked with ●.

Thus, this distortion by phylogeographic patterns may be explained much easier by xenologous than by paralogous ITS sequences, i.e. **reticulate evolution**. It may be the result of hybridisation processes in sympatric, i.e. Antillean, populations of different taxa, which is supported by the well known proneness of orchids to hybridisation even at higher taxonomic ranks. What seems to be quite logical and compelling, becomes more complicated when we try to explain the creation of hybridogenous genetic information. Unfortunately, little is known how concerted evolution in the intergeneric spacers takes place (Soltis & Soltis 1998). Yet, a possible scenario would be both the homogenisation of hybridogenous ITS sequences towards either of the parental copies, as observed in *Gossypium* allopolyploids (Wendel & al. 1995) in combination with the positive selection of either of the ancestral phenotypes. A similar explanation has been offered by (Cox & al. 1997) concerning the polyphyly of two taxonomically synonymised species of *Paphiopedilum* (Orchidaceae). Although the return to one of the parental phenotypes might appear unlikely, it must be emphasised here that floral features might be under high pro-parental selective pressure due to the presence of the traditional pollinator sets.

To add even more to the complexity in the case of *P. brighamii*, however, both orthologous and xenologous information must be assembled in the same ITS copy, since voucher pairs like the two accession of *P. brighamii* came out as sisters in the Cuban Analysis, while the Complete Analysis placed them in separate positions. Theoretically this is quite possible, since manipulation of ITS subregions or loci must be an inherent feature in concerted evolution. Indeed, Buckler-IV & al. (1997) found evidence of recombinant ITS sequences that combine portion of two distinct copies in *Tripsacum* (Poaceae), *Bubbia* (Winteraceae) and *Nicotinia* (Solanaceae).

The role of hybridisation in the evolution of island floras has been demonstrated in other angiospermous families, too. Similar to the topology of *P. brighamii*, Francisco-Ortega & al. (1996) found subspecies and different accessions of *Argyranthemum* species

(*Asteraceae*) in a paraphyletic topology. The authors interpreted this phenomenon in the Macronesian flora by either introgression from other taxa as is suggested here, too.

(Pamilo & Nei 1988) recommend the employment of various markers with a different history, preferably both plastid and nuclear loci, to reduce the risk of irrelevant molecular information due to specific traits of ITS evolution. Results from Pridgeon & al. (2001: 2301), however, have shown that common plastid markers (*matK*, *trnL*) failed to resolve relationships among species of subgen. *Specklinia* (clade G). To test the hypothesis of local hybridisation as a cause for incongruence between gene and species trees, it will be essential to add other chloroplast markers which are evolutionary less stable. Similarly, cytological examinations of chromosomal features could help in identifying hybrids and additional PCRs using denaturing detergents (DMSO) should be conducted to check for functional vs. non-functional PCR products (Buckler-IV & al. 1997).

The observed pattern is rarely seen in genetic studies on orchids, since most of these projects deal either with phylogenetic issues at a larger scale or with population genetics in restricted areas (Borba & al. 2000, 2001a). The simultaneous study of sample sets defined by area (floras) and by systematics (phylogeny) including both distantly and closely related species or even multiple samples from different but well known localities is a requirement for the findings in the present study. Some studies are aimed at the phylogeny of distantly related taxa, thus, spanning a great array of species. Logically, sequencing of closely related taxa is usually avoided to guarantee an evenly spread sample set of the group under study. Multiple sampling of species is rare in molecular studies on *Orchidaceae* aimed at the phylogeny of large-scale taxa. Most studies include only one or two species with double accessions. Van den Berg & al. 2002 double sampled several taxa. In this study the two accessions of one species (*Cymbidium ensifolium* (L.) Sw.) were separated by an other (*C. kanran* Mak.), however, with bootstrap support < 50% and a collapsed branch in the strict consensus tree. Unfortunately, this interesting result was not discussed by the authors. Cox & al. (1997) reports a case where a taxonomically synonymised, hence morphologically very similar pair of species was separated by several other taxa in the ITS tree. This is exactly what was found here in *P. brighamii* and *P. grisebachiana*-*P. grobyi*. Again, the authors fail to further discuss these findings.

#### **4.3 Genesis of the Antillean *Pleurothallis* flora**

Reliable phylogenetic data along with distribution patterns are available for one of the major groups of Antillean orchids for the first time. This allows a detailed discussion of the genesis of Antillean orchid flora.

In order to assess the history of pleurothallid evolution in the Greater Antilles it is important to consider the **age of the orchid family** in general and that of *Pleurothallidinae* in particular. This issue has been discussed controversially in literature and personal communication (Arditti 1992). While some authors favour a relatively early origin of the family (Stebbins 1950: early Cretaceous), and the estimates differ considerably (Arditti (1992) citing from pers. comm.: Cretaceous to early Miocene), there is a widespread consensus now in that “most extant groups are probably very young” (Arditti 1992). Garay (1960), although supporting a Cretaceous origin, suggested a probable secondary “expansion” during the post-Pleistocene time. To my mind, a relatively late origin and/or radiation is quite comprehensible and is backed by the following traits: **1.** almost complete absence of fossil records (Doyle 1973; Schmid & Schmid 1977), although this may be in part due to the herbaceous growth and other physiological features (Wolter & Schill 1985); **2.** high diversity at the species level with an overwhelming specialists-generalists ratio, which should mark intensive adaptive radiation; **3.** relative genetic stability in contrast to the enormous morphological plasticity (Neyland & Urbatsch 1995) which characterises active speciation. Considering the presumable young age of the family it is quite safe to assume that advanced taxa like *Pleurothallidinae* were absent from the Antillean arc until the present island constellation was reached (Iturralde-Vinent & MacPhee 1999: late Eocene to middle Miocene, 35-14ma).

However, another factor may render the age of the family of secondary importance. Pleistocene climate fluctuations are known to have severely altered floral and faunal belts, not only in temperate zones but in (sub)tropical regions, too (Leyden 1994; cf. Curtis & al. 2001). Glaciation led to **temperature** depressions in the Circum-Caribbean, too, and there is even geomorphologic evidence for quaternary glaciation above 2200-2300 m in Hispaniola (Schubert & Medina 1982). As a result, mountainous **vegetation belts** were lowered, which was detected in several neotropical locations (Van der Hammen (1973): Colombian Andes; cited in Leyden (1984): Costa Rica and Panama, by 500-1000 m). A second effect is represented by a severe **aridization** in the Circum-Caribbean lowlands (Leyden 1984: N Guatemala; Grimm & al. 1993: Florida; Street-Perrott & al. 1993: Jamaica) with a parallel suppression of humid forests. Leyden (1984) and Leyden & al. (1994) found that mesic tropical forests were generally absent in the northern lowlands of Guatemala from 36-10000 years BP. Similarly, Köhler (pers. commun.) found evidence for striking anatomical adaptations to severe drought stress in Cuban *Buxus* even in those taxa that live under humid conditions at present. Climatic oscillation affected not only terrestrial habitats, but marine ones, too. Several studies (cf. Curtis & al. 2001) indicate that both air and sea surface temperatures decreased by 5°-8°C during the last glaciation compared with present conditions, hence, leading to a drastic drop in oceanic

evaporation.

A switch back to humid conditions between 10.000-8.500 BP is inferred from several Circum-Caribbean localities (Curtis & al. 2001).

Of course, without exact data that are gathered directly from the Antillean arc (only Street-Parrot 1993), generalising conclusions have to be drawn with extreme care. Specific local features, like the relief, may have altered the palaeoclimatic process regionally, as is seen in differing data for the onset of humid conditions in the Circum-Caribbean (cf. Curtis & al. 2001).

Nevertheless, the whole climatic turn-over must have had a severe impact on the pleurothallid flora. The specific impact on the distribution of microphytic orchids, like pleurothallids, must be due to changes in both biotic and abiotic environmental factors. **First**, despite general adaptations of orchids to drought, i.e. succulence, CAM, velamen, etc. (Arditti 1992), which is a temporal but prevalent climatic feature in all epiphytic habitats (Freiberg 1992, Gentry & Dodson 1987), many *Pleurothallidinae* show a higher affinity to even more humid habitats as is reflected in their ecological centre of diversity, the wet (sub)montane rain- and cloud forests. Data from this study reveal a demand of >1200-1400 mm/a precipitation. Yet, the predominantly occurrence in habitats with a specific microclimate (p. 90) even in areas with an increased annual rainfall, suggests that a high level of humidity is required. Together with absent pseudobulbs, the reduction and disintegration of the sporoderm (Stenzel 2000) may be interpreted along this line too. Consequently, these affinities should make them susceptible to drought stress, although, as a consequence of absent pseudobulbs, some members of *Pleurothallidinae* have shifted succulence to the leaves and/or flower tissues. Cuban species show these traits, above all in the *P.-ekmanii*-group and to a lesser extent in several taxa in *Acianthera* (clade B). However, other groups, e.g. *Pleurothallis* subgen. *Specklinia* (clade G), *Platystele* and *Lepanthopsis*, show little or no sign of succulence. Conclusively, certain groups of *Pleurothallidinae* must have suffered from Pleistocene aridity to a greater extent than macrophytic orchids. **Second**, aridity must have had an indirect double impact on pleurothallid habitats. While a general drop in atmospheric humidity led to the retreat of rainforests and seasonal forests, a subsequent dry-up of rivulets, affected the principal habitat of *Pleurothallis* in Cuba (p. 90). Another habitat favourable for *Pleurothallis* are the mountainous condensation belts, however, only where closed forests exist. In the high-mountainous open elfin-thickets and shrublands of the Turquino group almost no species of *Pleurothallis* occur. Thus, a humid yet generally more open vegetation even in cloudy ranges, would not have been a Pleistocene refuge for *Pleurothallis*. **Third**, it should not be neglected, that faunal fluctuations followed floral ones and, in the case of insect dependent orchids, floral distribution followed faunal in turn which must have even reinforced the impact of Pleistocene climate oscillations.

Although Holocene palynological data for Cuba is not available (Borhidi 1996) in order to draw at least a rough picture of how the **vegetation recovered** during the last 10.000 years, it is very likely that small epiphytic orchids, among them *Pleurothallidinae*, have re-[?]colonised the arc only after the last glaciation, when rising temperatures led to favourable levels of air humidity and temperature. Antillean *Pleurothallis* should range therefore among the youngest lineages within this mainly continental genus. This is considered a general trait of insular biotas with respect to their continental sister (Carlquist 1995).

This assumption puts aside all discussion concerning the existence of historical dry land extension, plate tectonics, and land bridges (Borhidi 1996, Iturralde-Vinent & MacPhee 1999, Hedge 2001). Closely connected with these palaeogeographic phenomena, is the, mainly zoogeographic driven, dispute, whether **dispersal or vicariance** accounts for the creation of the Caribbean biota (reviewed by Page & Lydeard 1994). However, the herein assumed post-glaciation evolution of *Pleurothallis* in the Caribbean is embedded in rather stable geological and climatic constellations, which yield no background for an application of the vicariance model. The two models have been developed and applied mainly in the zoogeographic field, where speciation dates are assumed to have paralleled the geological evolution of the Antillean arc (Hedges & al. 1992; Woods & Sergile (2001) with various papers; see refs. in Page & Lydeard 1994: 21-22), rather than the recent Holocenic era. In contrast, the debate was touched upon only marginally by botanists (cf. Prance's discussion of Haffer 1981). Although the dispersal-vicariance dispute seems to be irrelevant in this study, it should be mentioned here (cf. p.156).

*Characteristics of orchidaceous dispersal.* – The biogeographical assumption of a recent colonisation and radiation on the Antillean arc is admittedly unusual in a region where evolutionary processes have been traditionally discussed in the light of millions of years. Two major features connected with this issue, dispersal and speciation rates, will be briefly discussed now to provide further evidence for the hypothesis.

When comparing the studies on West Indian phytogeography it is frustrating how little attention is paid to the specific means of dispersal and chorologically relevant ecological traits to elucidate processes that led to the geographic patterns found (Dietrich 1989a; Judd 2001). This is mostly due to the fact that the present distribution in the West Indies is seen as a result of primarily Tertiary geological processes (revised in Iturralde-Vinent & MacPhee 1999; Borhidi 1996; Woods & Sergile 2001), which leaves little to discuss concerning the ecological influence on biogeography, i.e. migration in birds for avichory, air currents for anemochorous plants etc. When discussing the particular case of the genesis of Antillean *Orchidaceae*, dispersal observations made on the island of **Krakatau** are of crucial importance. The study of the re-colonisation of the entirely destroyed volcanic archipelago, 40-80 km off the Sumatra shore, showed the high **vagility** of

orchidaceous seeds. The first orchids were found after 13 years (Van der Leeuwen 1936). After another 40 years the number of species had risen to 25. Considering the low rate of growth and initial failure of successful colonisation, seeds must have reached Krakatau several years before 1896 even (Gandawijaja & Arditti 1983). Close & al. (1978) examined the probability of wind dispersal between Australia and New Zealand, separated by 2000 km, stating that seeds might reach the islands with the aid of prevailing W winds within 1-3 days. Their review of literature on orchidaceous Circum-Tasmanian phytogeography, revealed strong affinities between SE Australia and New Zealand, including a report of presumably recent migration in *Cryptostylis*. These findings, the Krakatau experience, in vitro studies of the floating capability of orchidaceous seeds by the same authors, as well as empirical studies of neophytic plant migration (Dod 1986a; Stern 1988) underline the strong potential for long distance dispersal in orchids within rather short periods of time.

*Speciation rate.* – While dispersal in orchids has been accepted as a probably frequent and fast phenomenon, **speciation** is traditionally considered a slow process even in this family (Soto Arenas 1996). Dietrich (1989a) cites subtribe *Angraecinae*, and the genera *Bulbophyllum* and *Polystachya* as examples for the West African / Madagascar – Caribbean disjunction in concordance with Wegener's theory on continental drift. On the other side, she doubts, *Orchidaceae* will be of any use in elucidating the Caribbean paleoclimatic and paleogeographic history, a statement which is not further discussed, unfortunately. Trejo-Torres & Ackerman (2001) found floristic similarities among Caribbean islands with a common geological history and related these affinities to existing or absent historical landbridges, among other causes. Dod (1984a) used the particular orchid flora of SW Hispaniola to show a separation of Massif de la Hotte from the rest of this mountain range until the Pliocene.

In contrast, the likelihood of explosive evolution has been discussed only sporadically in *Orchidaceae* (Gentry, 1982; Gentry & Dodson 1987). If any it has received mostly negative or at best ironic reception (Holm-Nielsen & al. 1989). Only recent studies in other plant groups, combining molecular and palaeogeographic data, seem to have cleared this issue of its speculative character. Richardson & al. (2001a) show the explosive speciation of *Phyllica* (*Rhamnaceae*) in the Cape region during the glacial epoch which they attribute to processes connected to aridization (ecological areal fragmentation, pollinator shift etc.). Likewise, Richardson (2001b) found evidence for explosive radiation in *Inga* (*Fabaceae*) since the bridging of the Panaman Isthmus (3.5 ma), stating that the intensely active speciation may be attributed to this event, later phases of Andean orogeny and Quaternary climatic oscillation. Long before speciation events have been dated with the help of molecular clocks, Gentry (1989) had proposed that close to ½ of the neotropical flora might have originated by explosive evolution. Interestingly these studies connect saltation with rather young epochs, usually not older than the Quaternary. Even younger,

i.e. post-glacial speciation, is widely ignored (Bateman & DiMichele 2003), however.

*Phytogeographic evidence for migration routes.* – Assuming an origin of *Pleurothallidinae* outside the Antilles and a colonisation of the islands at the earliest when most of the geographic conditions of both continents and the archipelago were fixed, the Greater Antilles may have been colonised directly via **two routes**. One starts in Central America and leaves the continent at the Yucatan shore passing Cuba and Jamaica, towards Hispaniola and Puerto Rico. The other would lead from the Guyanas via the Lesser towards the Greater Antilles.

As was shown, Antillean taxa of *Pleurothallis* are mainly island endemics (80%) or of neotropical distribution (9%). Based on present distribution, only 14% of the taxa are geographically informative with respect to the colonisation from continental areas. Present distribution patterns with 11% of the taxa being exclusively of Greater Antilles – Central America (–South America) distribution, strongly support the route **via Central America**. The MP analysis (Fig. 52) groups (East) Cuba and Jamaica together with Central America. Hispaniola and Puerto Rico have closer affinities to the Lesser Antilles and South America. The assumed floristic division of western and eastern Greater Antilles (Judd 2001) and respective affinities with Central America and the Lesser Antilles presents a tempting pattern, simply by the geographic neighbourhood of the respective source areas. A closer look at the species in concern reveals, however, that there are no taxa confined to the eastern Greater and the Lesser Antilles and/or South America. In fact, all but one taxa (*P. discoidea*) that occur in the Lesser Antilles (*P. aristata*, *P. discoidea*, *P. imraei*, *P. pruinosa*, *P. ruscifolia*, *P. wilsonii*) are Pan-Caribbean elements. They may or may not be absent on some of the islands, but are present in Central America and South America. Thus, the distribution of *P. discoidea*, if not a collection artefact, is the only example in *Pleurothallis* where colonisation may have taken place **via the Lesser Antilles**. All other taxa could have reached the Greater Antilles just as well via Central America. The topology of the tree is influenced by species absence too, which groups Puerto Rico, the Lesser Antilles and South America, although not a single taxon is confined to this area. Hispaniola, in spite of its high species diversity, is included in this group probably due to the scarcity of shared taxa with the Western Antilles and Central America.

The disjunction Cuba – South America has been often cited and apparently generally overestimated in Cuban literature on biogeography. *Pleurothallis* provides an illustrative example of how the growth of phytogeographic and taxonomic knowledge has improved our notion of Caribbean biogeography. Bearing the temporary character of floristic inventories in mind, it is astonishing that the general phytogeographical proportions of historical sources (Acuña Galé 1939, León & Schweinfurth 1946) are largely congruent with modern ones, despite the taxonomical and systematical problems of these works.



Tab. 12: *Pleurothallis* of Cuba: phytogeographical data of different sources in comparison with the present notion, drawn from this study.

	Acuña Galé 1939	León & Schweinfurth 1946	present study
total	39	38	39
island endemics	21	23	19
Greater Antilles endemics	6	5	8
+Central America endemics	1	1	4
+South America endemics	0	0	3
+Lesser Antilles endemics	3	3	0
+South America endemics	0	1	0
+South America endemics	2	3	0
neotropical elements	1	1	5

Differences are mainly to be found among finely resolved biogeographical relationships, especially those that include South America. Comparing these sources it is clear that many distributions originally thought to be disjunct (Greater Antilles-South America) or of restricted areal (island endemics, Greater Antilles-Lesser Antilles, Greater Antilles-Central America), have turned out to be collection artefacts or were based on wrong classifications (Stenzel & Llamacho 2002).

*Studies on orchidaceous phytogeography.* – The close floristic affinities of the orchid floras between Cuba, Jamaica and Central America have been stated already by Fawcett & Rendle (1910). On the contrary, Dietrich (1989a) and Trejo-Torres & Ackerman (2001) presented different views. Both studies used the whole orchidaceous spectrum of the Antillean. Dietrich found Cuba in closest floristic neighbourhood with the Bahamas and Puerto Rico [!], which is obviously due to methodical incompatibilities. In Dietrich's work the level of relationship is expressed by the percentage of the Cuban taxa in foreign floras. Thus, areas with indistinct floras, composed of wide spread species, showed the strongest affinities<sup>7</sup>. Trejo-Torres & Ackerman (2001) found that "the Guyanas form a sister group to the Greater Antilles" which is evidently a result of the exclusion of (sub)mountainous Central America from the study. According to their data, the Hispaniolian flora is more similar to the Cuban than to the Jamaican one. This, again, may be a methodical artefact, brought about either by different sample sizes, e.g. floras with different numbers of species, which may yield groupings by species number. It may be also due to the employment of a Lundberg outgroup (all species coded absent) which, as the present study shows, influences both tree number and topology. On the other hand, *Pleurothallis* may well show closer affinities with Jamaica, while other orchidaceous genera do not. There are numerous examples for both ties: *Homalopetalum*, a monotypic genus endemic to the Sierra Maestra massif and the Blue Mountains, and, on the other hand, *Domingoa*, a monotypic genus found in Cuba, Hispaniola, and a few other islands to the East but not in Jamaica. A third methodical difference makes data obtained in the

<sup>7</sup> According to this point of view, Grand Cayman would have had the strongest floristic affinities with Cuba, since it shares 100% of its *Pleurothallis* flora – *P. caymanensis* – with Cuba.

present study difficult to compare with those from Trejo-Torres & Ackerman. Pleurothallid affinities with Jamaica are brought about largely by a certain floristic similarity between Cuba, Jamaica and Central America, rather than by species exclusively shared by the two islands. Neither Dietrich nor Trejo-Torres & Ackerman included Central America except for some randomly picked isolated regions, e.g. Yucatan (Trejo-Torres & Ackerman), El Salvador or Nicaragua (Dietrich), which show but a portion of the Central American taxa. Finally, it should be stressed that the floristic exchange between the western Greater Antilles and Central America is still an active process, as can be seen in the most recent discovery of the Central American orchid *Catasetum integerrimum* Hook. in Guanahacabibes, Cuba's westernmost tip (Díaz & Cabrera 1985).

*Other large scale studies.* – It would go definitely beyond the scope of this discussion to compare the numerous studies that have dealt with floristic relationships of the Antilles that have been published within the scope of taxonomic treatments. However, some of the most comprehensive works and those in ecologically similar groups should be mentioned. **Alain** (1958), and especially **Borhidi's** (1996: 259) notion of the origin of the Antillean flora is strongly influenced by the geological history of the archipelago. Both stress the importance of Central America as a floristic source area for the Greater Antilles. Migration via the Lesser Antilles, in contrast, is granted less importance. So far, these general findings are congruent with pleurothallid data. Inconsistencies in other affinities are largely due to the specific ecological preferences of *Pleurothallis* and allies. Such incompatibility exists towards Florida/Bahamas, owing to the fact, that there are almost no pleurothallids N of Cuba. Other studies with a broader sample size (Trejo-Torres & Ackerman 2001) in contrast, do show that those relationships exist in orchids, too. **Samek** (1973), on the basis of the Antillean phanerogamous flora, detected closest affinities of Cuba with Hispaniola, Jamaica, and Puerto Rico in descending order, which is not backed by pleurothallid data. In return, Samek found less distinct, but equal similarities of Cuba with Central and South America. The phytogeographical disjunct tie between Cuba and South America has been stated in various works, and was, at least in pleurothallid data, an artefact due to the poorly reviewed orchid flora and a wrong notion of distribution patterns (s. Tab. 12 and accompanying text). **Howard** (1974), in contrast, found closer relationships between the Greater Antilles and Central America as well as the Lesser Antilles and South America. The latter, however, was qualified in a subsequent paper (cited in Borhidi 1996 as Howard 1982 [?]). Based on generic similarities he summarised the Greater Antilles – Central America – South America distribution as the 'Western Continental Range' (ibid. p.29) which he saw as an 'extension' [!] of Central American genera across the Greater Antilles. Similar to conditions found in *Pleurothallidinae*, he considered the Virgin Islands east of Puerto Rico as a phytogeographic terminus. Other relationships that he discussed are only poorly or not at all represented by *Pleurothallis*.

Concerning the taxonomic level to be chosen, Howard favoured a comparison between genera, although he stated, that similar results will be obtained at the species level (ibid. p.18). In the case of *Pleurothallis* this would be fatal and much of the chorological information would be lost treating the genus in Luer's (1986b) circumscription. However, even if taking the system proposed by Pridgeon & Chase (2001), many of relationships between the islands and continental areas would be drowned in genera like *Stelis* s.l. or *Acianthera*. In my view it is not advisable to restrict the study a priori to any particular taxonomic unit, since all taxonomic entities are man made (cf. Borhidi 1996: 285) and their taxonomic level does not necessarily reflect the evolutionary history. Phytogeographical studies should be done at all taxonomic levels instead, a goal that is finally envisaged by phylogeography, as will be shown next.

Since distribution patterns are heavily influenced by dispersal units, associated means of dispersal and other traits, it may be expected that other anemochorous plant groups should reflect to a certain degree a distribution paradigm similar to that found in *Pleurothallis*. Judd (2001: Sect. *Lyonia* of subgen. *Lyonia*, ***Ericaceae***) did not find any extant floristic affinities between the Greater Antilles and the Central American continent, but claimed such for phylogenetic relationships. This is interesting, since it shows that present-day distribution does not necessarily reflect historical migration routes. Like in *Pleurothallis*, there are only weak affinities with the Lesser Antilles. On the other hand, he found floristically well delimited island floras, i.e. with a high rate of endemism within island boundaries. As in *Pleurothallis* this applies above all to Hispaniola and E Cuba. The floristic affinities between *Lyonia* and *Pleurothallis* may be the result of analogous chorological patterns and a predominantly mountainous distribution. Quite in contrast, data of **Pteridophytes** presented by Borhidi (1996) show much lower island endemism (~11%) than *Pleurothallis* does (~50%). Furthermore, the Cuban pteridophytic flora has a predominantly Caribbean and Neotropical relationship. Unfortunately, Borhidi does not show the level of congruence with Central America. He lists a mere 6 taxa (~2%) that are of Central American – Cuban distribution. Interestingly, 4 of them are rainforest elements, an ecological proportion reflected by pleurothallid data. The specific geographical relationships should be mainly the result of the comparably great age of ferns, as stated by Borhidi. However, his second suggestion, fern vagility, is fairly qualified by conditions found in *Pleurothallis* and other *Orchidaceae*. Yet, it may hold in connection with the great age and an euryoecious characteristic of these plants.

*Molecular evidence for migration routes.* – Plotting horizontal distribution over phylogeny, it is possible to follow migration routes and study processes or features linked to speciation events. The main problem in **phylogeography** is, that for a reliable reconstruction of these routes and conditions, all taxa should be sampled, since each taxon absent from the matrix may represent a valuable link in dispersal and speciation

processes (Baldwin & al. 1998). Due to the limited number of continental and island taxa, only tentative conclusions concerning the closest continental relatives of Antillean taxa can be drawn in the present study (Fig. 69, Fig. 70).

Many of the Antillean endemics that occur on Cuba appear rather isolated in the phylogenetic tree, e.g. *P. nummularia*, *P. racemiflora*, *P. bissei* etc. This gives the impression of an Antillean flora largely dependent on the continental source area with a considerable frequency of colonisation events without further cladogenesis. Even where taxa came out as sisters in the molecular analysis (*P. ruscifolia* – *P. pruinosa*, *P. trichyphus* – *P. brighamii*), this does not automatically imply sisterhood, which is due to the limited sample size. Thus, even in tight clusters of several Cuban species (*P. corniculata* through *P. wrightii* in clade G), independent migration to the Antillean arc has to be assumed, where taxa show a distinct morphology, not found elsewhere in the Antillean set of species.

Consequently, **three groups** of species can be distinguished according to their evolutionary history (Tab. 13). Most of the Antillean endemics that are present in Cuba have their closest relatives inside the Greater Antilles (~17 spp = 44% of the Cuban species). Morphological data of the species that have evolved while reaching the island arc (~10 spp. = 26%), suggest that most have apparently not radiated into new taxa, however, this can be said with certainty only after the molecular study of the rest of the Antillean pleurothallid flora. The same applies to the 12 taxa (30%) that occur outside the archipelago, too.

Tab. 13: Origin of the Cuban taxa of *Pleurothallis* (endemics in bold).

The first row lists taxa that are widespread and do not show substantial anagenetic evolution. The two rows to the right show species that either originated while migrating to the Greater Antilles (centre) or evolved from plants already present on the islands (right).

Invasive species with no subsequent cladogenesis	Invasive species that evolved into new taxa during dispersal, but no further dichotomy of the lineage	Species that originated within the Greater Antilles
<i>P. aristata</i>	<b><i>P. bissei</i>?</b>	<i>P. appendiculata</i>
<i>P. brighamii</i>	<i>P. domingensis</i>	<i>P. caymanensis</i>
<i>P. corniculata</i>	<i>P. helenae</i>	<i>P. denticulata</i>
<i>P. gelida</i>	<i>P. nummularia</i>	<b><i>P. ekmanii</i>?</b>
<i>P. ghiesbreghtiana</i>	<i>P. odontotepala</i>	<b><i>P. excentrica</i>?</b>
<i>P. obovata</i>	<b><i>P. oricola</i></b>	<b><i>P. 'flabelliformis'</i>?</b>
<i>P. pruinosa</i>	<b><i>P. papulifolia</i></b>	<b><i>P. gemina</i></b>
<i>P. ruscifolia</i>	<i>P. racemiflora</i>	<b><i>P. grisebachiana</i></b>
<i>P. sertularioides</i>	<b><i>P. rubroviridis</i></b>	<b><i>P. llamachoi</i></b>
<i>P. testaeifolia</i>	<b><i>P. trichyphus</i></b>	<b><i>P. longilabris</i></b>
<i>P. tribuloides</i>		<b><i>P. mucronata</i></b>
<i>P. wilsonii</i>		<b><i>P. murex</i></b>
		<b><i>P. obliquipetala</i></b>
		<b><i>P. prostrata</i></b>
		<b><i>P. shaferi</i></b>
		<b><i>P. trichophora</i></b>
		<b><i>P. wrightii</i></b>

In the following, some clusters of Cuban *Pleurothallis* shall be shortly discussed, concerning their origin and migration to the island arc.

1. *P.-ekmanii*-group. This association comprises three morphologically “primitive” species with 8 pollinia (clade A). Backed by (pollen) morphology too, it is safe to claim that this group has no closer relatives among sequenced Cuban taxa (this study), other Antillean or continental taxa sequenced by Pridgeon & al. (2001). The clade fell sister to *Octomeria*, a genus with 8 pollinia too. The latter has a neotropical distribution, however, with a centre of diversity in S Brazil (Luer 1986a). In the Greater Antilles it is represented by just one species, *O. ventii* Dietrich (formerly treated as *Octomeria tridentata* Lindl.). Morphological and palynological traits clearly refute a possible relationship of this species with *ekmanii* & al., hence, *O. ventii* must have reached Cuba in an independent dispersal event. Consequently, two explanations exist for the present distribution of *ekmanii* and its allies. The high genetic distance to the sister group *Octomeria* (69 steps in Fig. 69) may indicate either loss of diversity by extinction, as observed in other plants of hot spot archipelagos (Baldwin & al. 1998: 412) or undersampling in *Octomeria*. In connection with the first, the distribution of *P. ekmanii* and its allies may therefore represent a **relict** of a formerly wide area of the common ancestor with *Octomeria*. Forest refuge theories (Prance 1973) based on vegetation fragmentation during the Pleistocene, although later qualified (Prance 1982), may serve to explain this pattern. Yet, the existence of such a basal pleurothallid clade in Cuba contradicts the assumption of a late colonisation of the Antilles by pleurothallid orchids. On the other hand, the reduced morphology with fused rhizome, ramicauls, sheaths and inflorescence along with succulence developed in virtually all organs of *P. flabelliformis* and *P. excentrica* may actually indicate adaptations to Pleistocene drought. The three species would therefore inhabit a palaeoendemic area. The post-Pleistocene colonisation of the archipelago, as proposed before may therefore represent a re-colonisation or secondary expansion in reality. Yet, it may appear difficult to explain why such a primitive group survived just in the northern Caribbean, while all other basal *Pleurothallidinae* have a primarily South American centre of diversity. Although the following suggestion provides no explanation and has often been exaggerated, it should be reminded that the disjunct biogeographical range between the archipelago and northern South America has been repeatedly reported from other groups of vascular plants (*Bonnetia*, *Burmannia* etc. according to Borhidi 1996).

Another explanation aims at a genetic background: **hybridisation**, i.e. the origin of this group from orchid species present on the same island. The comparatively high step number leading to the *ekmanii*-branch could then be interpreted freely by the

introgression of xenologous DNA. To search for the presumable parental taxa is considerably speculative, since we do not know how phenological traits are passed on to hybrid generations. Moreover, Rieseberg (1995) stated that most true hybrids do not show intermediate characters. In turn, Borba & al. (2000) found that intermediate features do not necessarily indicate hybridisation in *Pleurothallis fabiobarrosii*.

A relict status of *P. ekmanii*, *P. excentrica* and *P. 'flabelliformis'* seems to be the most compelling way to explain their history, despite the unusual distribution pattern far from the core area of *Pleurothallidinae*. After all, (presently extrazonal) relict areas are one of the commonly observed and discussed biogeographical issues.

2. *Pleurothallis* subgen. *Antilla*. – Perhaps the most clear phylogeographic picture can be found in one subclade of clade B, which hosts a number of Cuban endemics (*P. papulifolia* through *P. trichophora*), accommodated in the Antillean *Pleurothallis* subgen. ***Antilla*** Luer. This subgenus comprises  $\pm 10$  taxa in the Greater Antilles sensu Luer (2000), however, the present molecular and palynological analyses indicate the phylogenetic association with additional taxa, e.g. *P. papulifolia*, *P. murex* and perhaps *P. caymanensis* too.

The clade fell sister to the Central – South American *P. erinacea*. The latter belongs to *Pleurothallis* subgen. *Kraenzlinella*, a group which shows some morphological affinities to *Antilla* (verrucate, papillose or scaly ovaries and similarly ornamented capsules; the tendency to enlarged, conduplicate, and oblique flower bracts; unguiculate, basally biauriculate lip, often with two lateral lobules above the claw). The species of this subgenus are of South- and Central American distribution. The Mexican *P. hintonii* L.O Williams from seasonally dry forests (Luer 1994) shows succulent leaves, which in turn, can be found in the epilithic Cuban endemic *P. papulifolia*. It is apparently an adaptation to temporal drought (ibid.). Taking into consideration the geographical neighbourhood and morphological and molecular affinities, it is quite reasonable to assume a descent of *Antilla* via *P. papulifolia* from either a common ancestor with subgen. *Kraenzlinella* or from an extant member of that subgenus. In any way *Antilla* is clearly of Central American origin.

3. *Pleurothallis* subgen. *Specklinia* sect. *Muscariae*. – This large section was described by Luer to accommodate a number of species with rather similar habit and flower morphology. In the Antilles are at least 6 species, 4 of which are endemic to Oriente. *P. helenae* is a Greater Antillean endemic and *P. aristata* is of neotropical distribution. Both occur in Cuba. Although it is tempting to trace back the origin of the Cuban endemics to island populations of *P. aristata*, molecular data suggest rather an early split off from a common ancestor, which was most likely of continental distribution. This constellation is equal to that of many other *Pleurothallis*, which, although

occurring throughout the Caribbean, have apparently not brought about new species. *P. helenae* which, due to certain morphological similarities with *P. aristata*, was treated by some authors (Nir 2000) as a synonym of *P. aristata*, turned out to be closer related to other continental species. Relatively high numbers of mutations (Fig. 70) in both *P. helenae* and *P. setosa*, must be the result of the limited sample size.

How many continental lineages have turned into **radiation in the whole Greater Antillean arc** is difficult to ascertain, due to the limited sample size of the present molecular screening (1/2 of the Antillean taxa) and the probability of hybridisation, as shown in *P. brighamii*. A comparison of the Antillean taxa based on morphology (incl. palynology) shows that two of the discussed clusters comprise additional species on the other islands. Only the *aristata*-group (sect. *Muscariae*) seems to have radiated exclusively in E Cuba. Furthermore there are a few groups that consist of just two taxa: *P. bissei* – *P. hirsutula* and *P. miguelii* – *compressicaulis*. The rest of the Antillean endemics is morphologically very distinct, indicating that the closest relatives have to be back on the Central American mainland. Thus by comparing these three groups we receive the following portions. Even a conservative estimate would consider at least 50% of the Antillean flora as **autochthonous**, distributed mainly among three radiative subclades: *Pleurothallis* subgen. *Antilla* s.l. (15 taxa), subgen. *Specklinia* sect. *Muscariae* (4 taxa) and sect. *Hymenodanthae* subsect. *Longicaulae* (16 taxa). The dominance of autochthonous species is greater than in Cuba (44%), due to the frequency of successful migration from the continent which was observed to decrease with distance (MacArthur & Wilson 1963; Thornton 1996; see p. 147). Consequently, the rest of the Antillean species, i.e. up to 36, are the result of successful colonisation events of pleurothallid species. However, this number may increase, i.e. the level of infra-Antillean speciation may drop, if some of the radiative clades should turn out to be polyphyletic. Discounting two taxa that emerged from restricted cladogenesis (endemic species pairs) and 15 species (~20%) that have not morphologically changed during migration, ~20 taxa (~26%) are left that have undergone anagenetic speciation in the course of migration.

From the little that we know about the genesis of orchidaceous island floras it can be assumed that the level of pleurothallid radiation in the Greater Antilles is striking, compared with other oceanic archipelagos. Bateman & DiMichele (2003: 17) report only one autochthonous event among the 12 orchid species present in Macronesia. The other 11 taxa are the result of anagenetic allopatric speciation, i.e. they represent unrelated lineages originating from neighbouring continental areas. The fact that some lineages enter cladogenesis while others do not, can be observed in other Antillean orchids too. Among the ~10 genera of *Pleurothallidinae*, only a few have radiated, e.g. *Lepanthes* and *Pleurothallis*. Bateman & DiMichele stated a general imbalance in the evolutionary potential within clades, with only some groups entering adaptive radiation and saltation

evolution. According to the authors, absence of the appropriate set of pollinating insects as well as different mycorrhizal fungi for particular ontogenetic stages may account for the scarce post-immigration radiation on these islands. Similarly, an accumulation of pre-adaptations (genetic heritage) in successfully radiating groups may have been trigger for subsequent (Bateman & DiMichele 2003). On the other hand, migrated species that did not enter cladogenesis could represent stasigenetic lineages, which are genetically in a conservative phase that prevents active speciation. Which one of the features eventually triggers or prevents radiation cannot be judged here. However, the fact that these three Cuban lineages represent clades that have intensively radiated on the continent too (Luer 1986b), reflects the evolutionary potential inherent to these groups. Another, rather simple, explanation for the unequal rate of speciation in different clades would be the **time** of colonisation. Available time surely plays a role in evolution. However, two of the lineages that have actively radiated on the islands were presumably among the last colonisers of the arc. Members of these groups show almost no adaptations to drought. They are small, fragile plants, with a reduced sporoderm and delicate flowers. In contrast, it is just the more drought resistant taxa of subgen. *Acianthera*, with the exception of Luer's subgen. *Antilla*, that have 'failed' to radiate. These plants show a primitive sporoderm that provides full protection for the pollen masses and tend to have succulent organs including the flowers, features that indicate adaptation to drought stress. Hence, they should have been among the first *Pleurothallids* that were able to colonise the island arc after the Pleistocene drought.

Until now we have tacitly assumed that migration in the Caribbean is unidirectional. This is strongly suggested by molecular and phytogeographical data. On the other hand, considering the high vagility of orchids, an opposite migration cannot be ruled out completely. Theoretically, two patterns could exist: 1) the **re-migration** of species that had successfully colonised the islands without anagenetic evolution, i.e. continental mother-, island-, and secondary continental populations belong to the same species. This represents a likely process, since plants that re-migrate are faced with ecological features they are already adapted to and because species that have colonised the islands should have a high colonisation potential. 2) the migration of a new species that either originated from the islands or evolved in the process of dispersal towards the continent. This pattern is theoretically less likely, because it involves active adaptation to the new environment. Nevertheless, if we compare the number of island endemics (68%) to wide spread species in the Greater Antilles, it becomes clear that this process is by far more frequent than simple dispersal. Gathering from the Cuban species sampled, migration towards the island arc must be the predominant route since there is no occasion where continental plants came out in terminal position with island vouchers as basal branches.



The high level of both total species diversity and endemism in the Caribbean is well known and is reflected in the classification of this area as one of the 10 prime hotspots of biodiversity (Davis & al. 1997). Yet, rates tend to differ sharply, depending on the taxon as well as the area in concern.

Tab. 14: Numbers of species and regional endemics in the Greater Antilles.

References: Davis & al. (1997)<sup>1</sup>, Borhidi (1996: 284)<sup>2</sup>, Zanoni (1989)<sup>3</sup>, Adams (1972)<sup>4</sup>, Dietrich (1989a)<sup>5</sup>, Dod (1984b)<sup>6</sup>, Dietrich (1989b)<sup>7</sup>, Ackerman (1995)<sup>8</sup>, J. Ackerman (pers. commun.)<sup>10</sup> and unpublished data of the author.

	Phanerogamous plants	<i>Orchidaceae</i>	<i>Pleurothallis</i>
Greater Antilles	13000 / ~58% <sup>1</sup>	710 <sup>10</sup> / 44% <sup>10</sup>	72 / ~80 %
Cuba	6400 / ~50% <sup>2</sup>	310 <sup>7</sup> / 29% <sup>5</sup>	39 / ~50 %
Hispaniola	5300 / ~33 <sup>3</sup> -39% <sup>2</sup>	215 <sup>5</sup> -300 <sup>6</sup> / 40% <sup>10</sup>	40 / ~60 %
Jamaica	3250 / ~20 <sup>2</sup> -27% <sup>4</sup>	206 / 30 % <sup>4</sup>	23 / ~26 %
Puerto Rico	3000 / ~13 % <sup>2</sup>	150 / 11 % <sup>8</sup>	11 / 0 %

*Taxon.* – In almost all taxa we find the same unequal distribution of diversity and endemism among the next lower ranks. Endemism of Cuban *Orchidaceae*, although ranging among the most diverse families, is far outnumbered by other angiospermous families like *Myrtaceae* (88%), *Rubiaceae* (68%), or *Euphorbiaceae* (67%), let alone certain less diverse but highly endemic families like *Arecaceae* (90%) or *Ericaceae* (92%, all data from Capote & al. (1989). Similarly, there are diverse orchid genera with “only” low endemism, e.g. *Epidendrum* (27%), or with high endemism, as in *Lepanthes* (98%) on the Antillean level.

Diversity patterns of *Pleurothallis* come closer to phanerogamous than to orchidaceous conditions (Tab. 14) in some cases. On the greater islands, *Pleurothallis* shows a much higher level of endemism than the average orchid data, although some of the information may be positively or negatively exaggerated. The high figure in Hispaniola, e.g., has to be dealt with caution. Dod contributed almost 20 new epithets to *Pleurothallis* and 13 to *Lepanthopsis*, another pleurothallid genus. However, of the latter 1/3 are synonymous with older names according to Luer (1991). The number of *Pleurothallis* given for Hispaniola may be overestimated, too. Likewise, experience from the taxonomic and phytogeographical revision of *Pleurothallis* in Cuba has shown, that there is much left to be done in this family, hence overall orchid data for Cuba (Dietrich 1989b) may not exactly reflect real conditions either.

*Area.* – Although the absolute numbers may differ substantially among the three categories, the general proportions in the archipelago follow a similar pattern (Tab. 14). Diversity and endemism rate reflect the **size** of the respective island, a correlation that was considered by MacArthur & Wilson (1963) in the equilibrium theory of insular zoogeography. Hispaniola bears about the same number of taxa and endemics as Cuba, whereas the number drops abruptly in Jamaica and even more in Puerto Rico. Island size,

however, is not directly proportional to the rates of diversity. Jamaica has an area comparable to East Cuba, which accommodates the majority (36 of 39) of the Cuban taxa. However, Jamaica has a much lower diversity (23 spp.). Puerto Rico, finally, though not substantially smaller than Jamaica, hosts less than half the number of taxa. Plotting the horizontal distribution of *Pleurothallis* (Fig. 48) over geography (Fig. 72), the resulting chorological pattern is very uneven. The highest concentration both in total and endemics is found in a triangle that comprises E-Cuba, Jamaica and Hispaniola, specifically the mountainous W and middle Hispaniola. Species diversity abruptly drops towards the edges, i.e. W and middle Cuba, E Hispaniola, Puerto Rico and the Lesser Antilles.

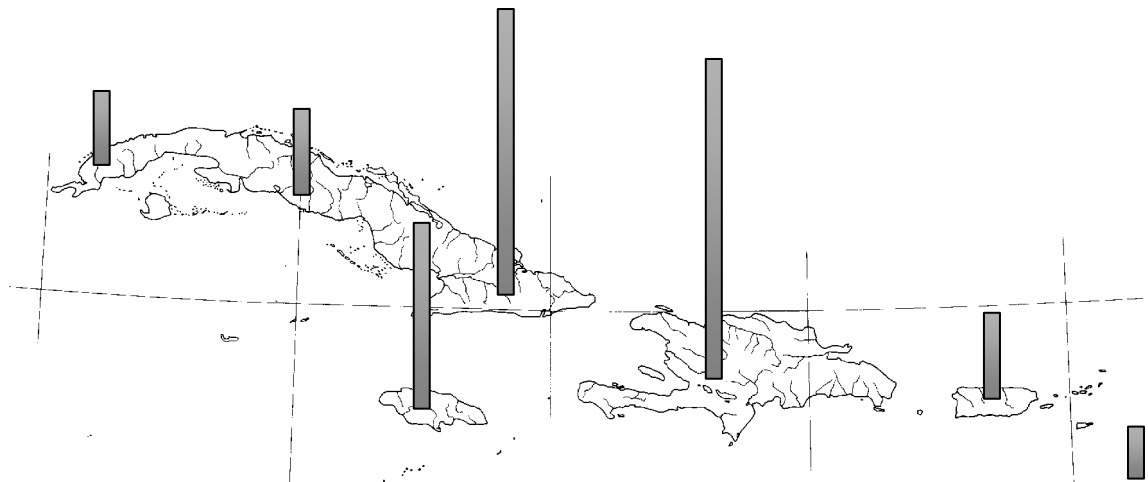


Fig. 72: *Pleurothallis*:  $\alpha$ -diversity in several locations of the Antilles: W-Cuba, middle Cuba, Jamaica, E-Cuba, Hispaniola, Puerto Rico, Lesser Antilles (islands not shown in the map sketch).

At least 50% of the Antillean species of *Pleurothallis* have reached the island arc from the Central American continent, hence, we have to deal with factors that influence dispersal at first to find out more about the Caribbean diversity.

*Means of dispersal.* – *Pleurothallis*, like most of the orchids, are wind dispersed, although other means have been repeatedly weighed (Garay 1964, Gandawijaja & Arditti 1983, Thornton 1996). Thus it would be only normal to touch upon meteorological issues when discussing orchidaceous phytogeography. Quite the contrary, these features have been, if mentioned at all (Trejo-Torres & Ackerman 2001: 779), only marginally considered (Borhidi 1996, Garay 1964). Only Cox & al. (1997:187) referred directly to major global air currents and their putative role in the realisation of trans-oceanic distribution of orchids. As mentioned before (p. 131), orchidaceous seeds possess strong long distance dispersal capabilities (Gandawijaja & Arditti 1983). The West Indies lay under direct influence of the **trade winds** with a main direction from the oceanic NE. These air currents are essentially counterproductive in the colonisation of the Caribbean. Coming from the Atlantic Ocean, they virtually prevent any floristic enrichment of the Antillean arc from both (sub)tropical continental joints. Only two areas benefit from this type of wind, Cuba from the Bahamas,

which, however, does not host any *Pleurothallis*, and Jamaica from E-Cuba and Hispaniola. Apart from these connections, trade winds can explain neither the floristic enrichment of the archipelago in general, nor the level of diversity in the E-Cuba-Jamaica-Hispaniola triangle, which accommodates 98% of the Greater Antillean *Pleurothallis*.

These biogeographic traits are best explained with another climatic phenomenon of this area, cyclones. **Hurricanes** have been repeatedly cited in both zoo- and phytogeographic literature as putative means of dispersal, however, never with reference to particular features, like wind speed, tracks or structural traits. Hurricane-force winds can extend outward to about 40 km from the storm centre (eye) of a small hurricane and to more than 250 km for a large one (all data in this paragraph from the National Hurricane Center – <http://hurricanes.noaa.gov/prepare/structure.htm>). The area over which tropical storm-force winds occur is even greater, ranging as far out as almost 500 km from the eye of a large hurricane. A hurricane's forward speed averages around 25-35 (-100) km/h. Adding circular wind of the storm itself, the resulting speed ranges between 80-250 km/h. Flora (October 1963), one of the most devastating cyclones that hit Cuba, had wind speeds of 210 km/h. Thus, distances between East Cuba and Jamaica (140 km) or Haiti (77 km) are easily bridged within less than one hour. One crucial issue in discussing the translocation by cyclones is that of wind speed which is necessary for the transport for a specific item. Spectacular reports concerning the translocation of “complete huge trees... loaded by thousands of epiphytes” (Borhidi 1996: 50) are most probably a product of human fantasy. Such big items depend on a considerable wind speed. However, if the needed speed exceeds 75 mph then another problem appears. These strong winds “normally do not extend more than 25-50 nmi from the eye and any airborne material that close could very well wind up in the eyewall instead of being transported significant distances around the eye” (Dr. J. L. Beven, Tropical Prediction Center/National Hurricane Center, pers. comm.). Therefore, it is much more likely that seeds are the mean form of dispersal. For the transport of these vagile organisms, even weak storms would suffice, which increases the chance of successful transport.

Now that the potential for bridging the islands by air currents was shown to exist, the question remains if hurricane track directions are in concordance with floristic exchange routes as indicated by present distribution. In the Greater Antilles there are two main types of cyclones. One part forms in the southern Caribbean and passes Central America before hitting the islands (Fig. 73, Fig. 74). Those storms, rarely reach the eastern Greater Antilles. Instead, they pass over Cuba or Jamaica at best, before proceeding to the continental shelf of the southern USA or the Bahamas. Their route excellently explains the floristic connection **Central America–Cuba–Jamaica**. The only pleurothallid orchids N of the Tropic of Cancer, *Pleurothallis gelida* and *Lepanthopsis melanantha*, have reached Florida most probably via this route. The second type develops W of tropical Africa (Cape

Verde type) over the Atlantic Ocean (Fig. 73) These hurricanes frequently cross the Lesser Antilles and the eastern Greater Antilles before turning north. They should be mainly responsible for floristic exchange between the Lesser Antilles and **among the Greater Antilles**. *P. imraei*, which occurs on the continent, Hispaniola and Guadeloupe may have found its way with the help of a Cape Verde hurricane from South America rather than from Central America. In *P. discoidea* (Jamaica, Trinidad, South America) this is evidently the case, since the plant has not been known from Central America so far.

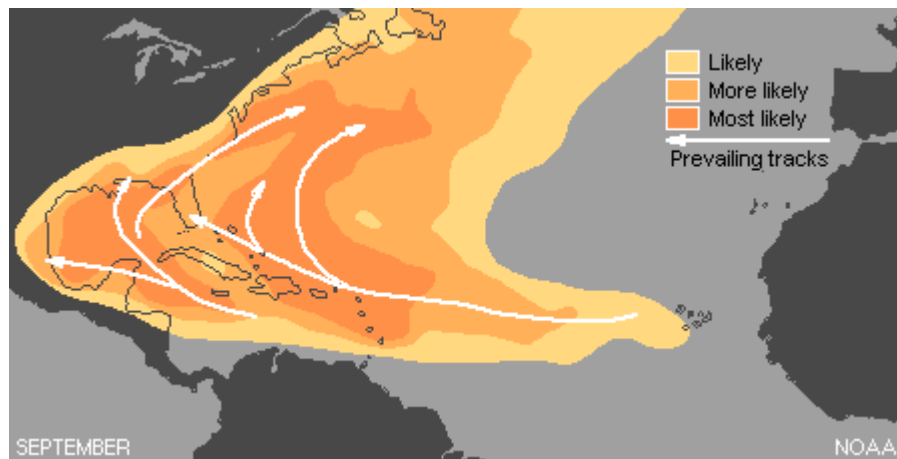


Fig. 73: Average zones of origin and tracks for hurricanes in September. Picture from the National Hurricane Center ([http://www.nhc.noaa.gov/HAW/basics/zones\\_origin.htm](http://www.nhc.noaa.gov/HAW/basics/zones_origin.htm)).

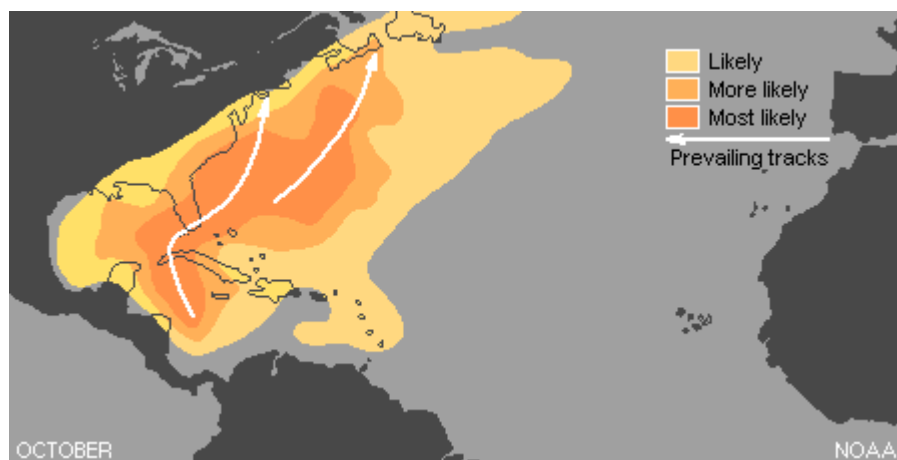


Fig. 74: Average zones of origin and tracks for hurricanes in October. Picture from the National Hurricane Center ([http://www.nhc.noaa.gov/HAW/basics/zones\\_origin.htm](http://www.nhc.noaa.gov/HAW/basics/zones_origin.htm)).

In this connection it should be stressed, that transport is possible in both directions (J. L. Beven, pers. comm.), a feature of hurricanes, that is essential in considering migration between the islands. Due to the circular construction of the storm, a hurricane moving from E to W along the Greater Antilles (Fig. 73), can transport items en route as well as in the opposite direction, e.g. from E Cuba to Haiti, e.g.. This represents an important means of transportation from W to the E in the otherwise trade winds influenced Caribbean region. Only cyclones that originate in the southern Caribbean and head NE across the Greater Antilles provide a similar transport (Fig. 74).

As Fig. 75 indicates, tracks of individual storms can differ substantially from average routes. Moreover, hurricanes should not be considered mere points on the map with linear tracks. They represent huge climatic complexes that affect vast areas, ranging 100-700 km in diameter.

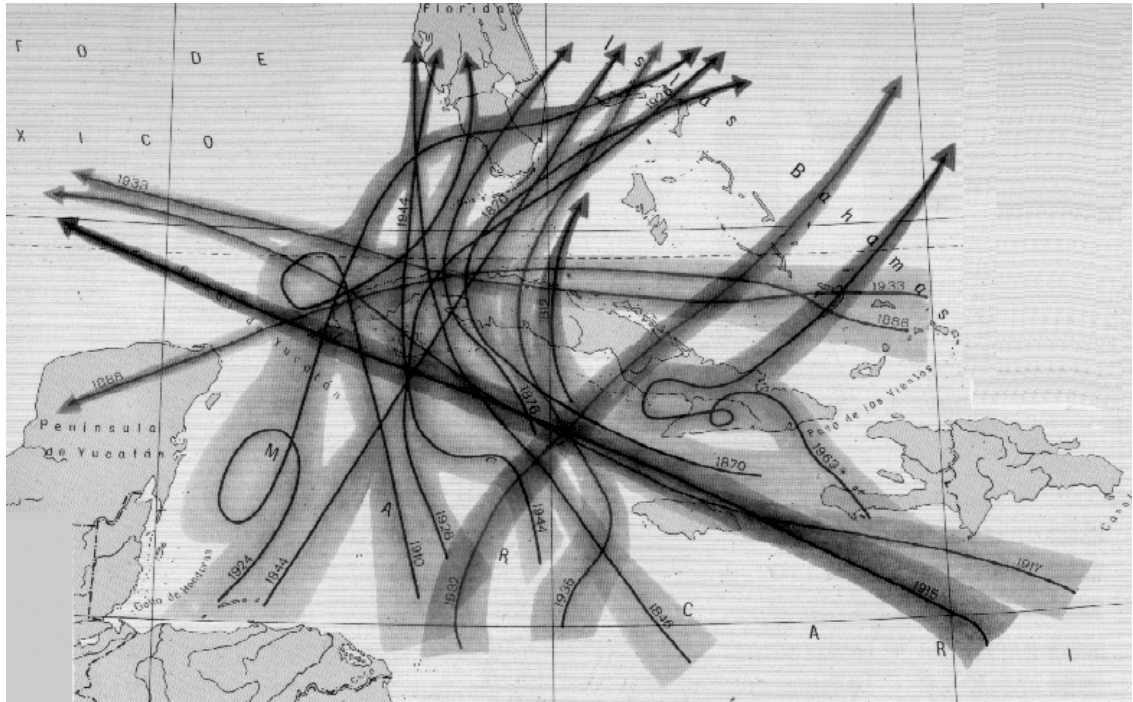


Fig. 75: Tracks of the main hurricanes in the last century 1900-1980 (Celeiro & Vásquez 1989).

Consequently, even if there are main tracks and directions, virtually every spot in the northern Caribbean can be affected by a hurricane, even more if we deal with such light items as orchidaceous seeds. Flotation time tests of orchid seeds showed an average of 0,72 km/h sink speed (Gandawijaja & Arditti 1983). Thus, these items do not depend on strong winds to be transported over significant distances. Below the line, the most important phytogeographical function of hurricanes is therefore that they break the ubiquitous trade winds from the NE, that would otherwise effectively counteract colonisation from the Central and South American continents. The role of hurricanes in long distance dispersal has been discussed in other anemochorous plant groups, too (*Pteridophyta*, L. Regalado, pers. commun.).

It should not be neglected that orchidaceous seeds represent **fragile** items simply by the small biomass that does not provide physical and physiological buffering. During long distance dispersal, seeds are likely to undergo physical stress like UV radiation, low temperatures and desiccation. Especially the latter was used when arguing against the likelihood of long distance dispersal (Garay 1964). Gandawijaja & Arditti (1983) and Arditti (1992: 611), however, state that the actual space of transport time may be rather short,

which seems to be a fact in the case of dispersal by hurricanes. Moreover, they report (unquoted) tests of freezing and desiccation that allegedly showed the hardness of orchidaceous seeds.

*Distance from the continental source area.* – This is a logical conclusion drawn from the probability of successful colonisation which should be negatively correlated with distance (MacArthur & Wilson 1963, Gandawijaja & Arditti 1983, Thornton 1996). This pattern is not only caused by the thinning of dispersal units with a growing distance from the source area. It does, moreover, reflect the growing probability of extinction, since remoter islands benefit less from the rescue effect (Thornton 1996). In the case of the Greater Antilles it should be therefore expected to find a decline in  $\alpha$ -diversity from West to East. This pattern should be polarised even more since hurricanes from Central America are less likely to reach the eastern islands (Fig. 73, Fig. 74) diminishing the frequency of direct colonisation. To assess the impact of distance from the mainland, we can only consider those 15 taxa that have colonised the arc without further speciation, since the frequency of successful colonisation in ana- or even cladogenetically active taxa cannot be determined with the present molecular and morphological data. Fig. 49 shows a shallow decline in species from Cuba and Jamaica (both each 12 taxa) over Hispaniola (11) to Puerto Rico (8). It is less contestable when considering only those taxa absent in the Lesser Antilles to exclude colonisation from the other direction. Here we find the islands in the same order with 7, 6, 5, and 4 taxa respectively.

Thus, the low diversity in species in **Puerto Rico** is partially caused by the great distance from the continent considering the present routes and means of dispersal, which accounts for the impoverished *Pleurothallis* flora of the Lesser Antilles too! This distribution, that was described as the “Western Continental” by Howard (1974) is found in numerous other anemochorous plant groups too (Howard 1974, Judd 2001). On the **other islands** of the Greater Antilles, anagenesis and especially cladogenesis accounts for the main part of the flora. The former is clearly dependable on migration frequencies from the continent. The close position of Cuba to the mainland is reflected by the fact that at least 56% of its taxa are directly related to continental ancestors. In contrast, Hispaniola, with a similar diversity, shows a greater portion of autochthonous species which is partially due to its greater distance from Central America. To elucidate the processes that have caused the Greater Antilles patterns of distribution in *Pleurothallis*, the subsequent discussion must therefore deal with features and processes that influence speciation on the Greater Antilles islands.

*Water supply.* – As was shown earlier (p. 130), Cuban *Pleurothallis* require a minimum of 1200-1400 mm with an additional water supply due to a favourable microclimate providing constant high humidity (p. 90) in most habitats. This strongly suggests that non-liquid water (humidity, fog and clouds) plays a major role in the pleurothallid water balance. Apart from the mentioned microclimatic exception, the Cuban climate is marked by two major sources of precipitation, macroclimatically from the NE (trade winds) and mesoclimatically from the mountainous condensation belts. The increased diversity in mountainous belts is easily explained by a positive water balance due to the reduced evaporation (lower temperatures) and additional water supply by clouds and fog. Furthermore, canopies of lowland forests, owing to a restricted water supply (rain) and little retention capacity, can suffer a severe drought in epiphytic habitats during extended periods of the day (Freiberg 1992). Thus, although Cuban species of *Pleurothallis* occur at virtually all altitudinal belts from sea level to the summits of the Turquino group, the greatest diversity can be found between 300 and 1300 m where at least 10 of the 39 Cuban taxa can be found in all 100 m belts (Fig. 54). The altitudinal concentration of orchids (pleurothallids) at middle to lower mountainous elevations with a substantial decline in both high montane rainforests and at lower altitudes, was reported for *Lepanthes* (Hespenheide & Dod, 1990) and orchids in general on the island of Puerto Rico (Woodbury 1974). Cuban *Pleurothallis*, in contrast, can be found in considerable numbers even at lower elevations (200-700 m). This is most probably related to the high species diversity in the submontane Nipe-Baracoa range. Descending vegetation belts in serpentine areas were reviewed by Borhidi (1996: 138) as a general phenomenon. This vertical anomaly is facilitated in part by the high precipitation rates (Borhidi 1996: >3000 mm/a) in this region and the subsequent existence of numerous creeks and rivulets that, almost exclusively, serve as habitats for a great number of *Pleurothallis* species even at lower altitudes (Fig. 57). The sudden drop in species diversity in high mountain rainforests, on the other hand, is unlikely a result of the high rainfall as suggested by (Woodbury 1974). As indicated, *Pleurothallis* occurs in a great variety under very wet conditions in Nipe-Baracoa. The observed imbalance is caused rather by an unequal orography in Oriente. Limestone and serpentine mountains do not reach beyond 1200 m. All species that are found above this limit are associated with the geologically more uniform Sierra Maestra range (Fig. 54). Thus, the decline above 1200 m reflects actually the general poorness in species diversity in the Sierra Maestra (17 taxa), compared with that of the diverse lower altitudes of NE Oriente (35 taxa). The imbalance in  $\alpha$ -diversity between serpentine and magmatic rock, has been observed in other plants groups, too (Borhidi 1996; E. Köhler pers. commun.: *Buxaceae*) and might be common. The relative

poorness in *Pleurothallis* found in the mountainous regions of W and middle Cuba, may be again associated with water supply. Here, instead of lacking precipitation, a petrologic feature may cause the decline in species diversity: habitats in these regions are almost exclusively found on limestone. This karstic rock is known to have little retention capacity for water. Water surplus is often directly drained by subterranean rivers and therefore immediately lost for the (epiphytic) vegetation, which strongly depends on favourable meso- and microclimatic situations. Localities where rivers prevail on the surface belong to classic collections sites for *Pleurothallis*: Taco Taco in Pinar del Río, Salto de Vegas Grandes in the Escambray mountains.

*Geological restriction.* – Apart from the secondary influence of the rock type on the water balance, petrologic features turned out to be closely associated with pleurothallid species diversity (Fig. 60). Especially striking is the level of ecological endemism ‘on’ serpentine. With 25% of the Cuban taxa, *Pleurothallis* surpasses the phanerogamous average by far (Reeves & al. 1996: 14%). The presence of the genera *Pleurothallis* and *Lepanthes* on serpentine in NE Cuba has been dramatically missed in favour of the putative dominance in the Turquino region (López Almirall 1994), which was seen as the centre of origin. López Almirall & al. (ibid. p.464) even denied the existence of *Lepanthes* in Moa, a region where at least 10 species were collected in the course of this study. The restriction of *Pleurothallis* to specific rock types was an unexpected result of the present study since epiphytism and edaphic issues are not considered necessarily interrelated issues. Moreover, in Cuban *Pleurothallis*, the relevance of rock types is not restricted to the (facultative) epilithic taxa, as may be assumed. By way of contrast, most of the lithophytic taxa belong to the euryoecious group of widespread taxa (*P. corniculata*, *P. gelida*, *P. obovata*, *P. sertularioides*, *P. tribuloides*), whereas petrologic restriction is most prevalent among endemic epiphytes from northern Oriente. Only two taxa are epilithic, *P. bissei* and *P. papulifolia*. Petrologic restriction of epiphytic orchids has been described only occasionally. Dietrich (pers. comm.) reported that *Oncidium undulatum* (Sw.) Salisbury is confined to limestone and Hespenheide & Dod (1990) reported a *Lepanthes* (‘kárstica’) being restricted to karstic zones. Trejo-Torres & Ackerman (2001) found evidence for a general floristic relationship of the geologically similar islands of the ‘calcareous group’ based on the entire orchidaceous flora, however. Another, though only empirically inferred, trait which is inherent to the ecological distribution of *Pleurothallis* in Cuba is the fact that the group of species which most frequently inhabits limestone niches is composed primarily of the widespread taxa mentioned above. This calciphilous character of the Pan-Caribbean species should be no surprise on the largely limestone dominated Caribbean Arc.



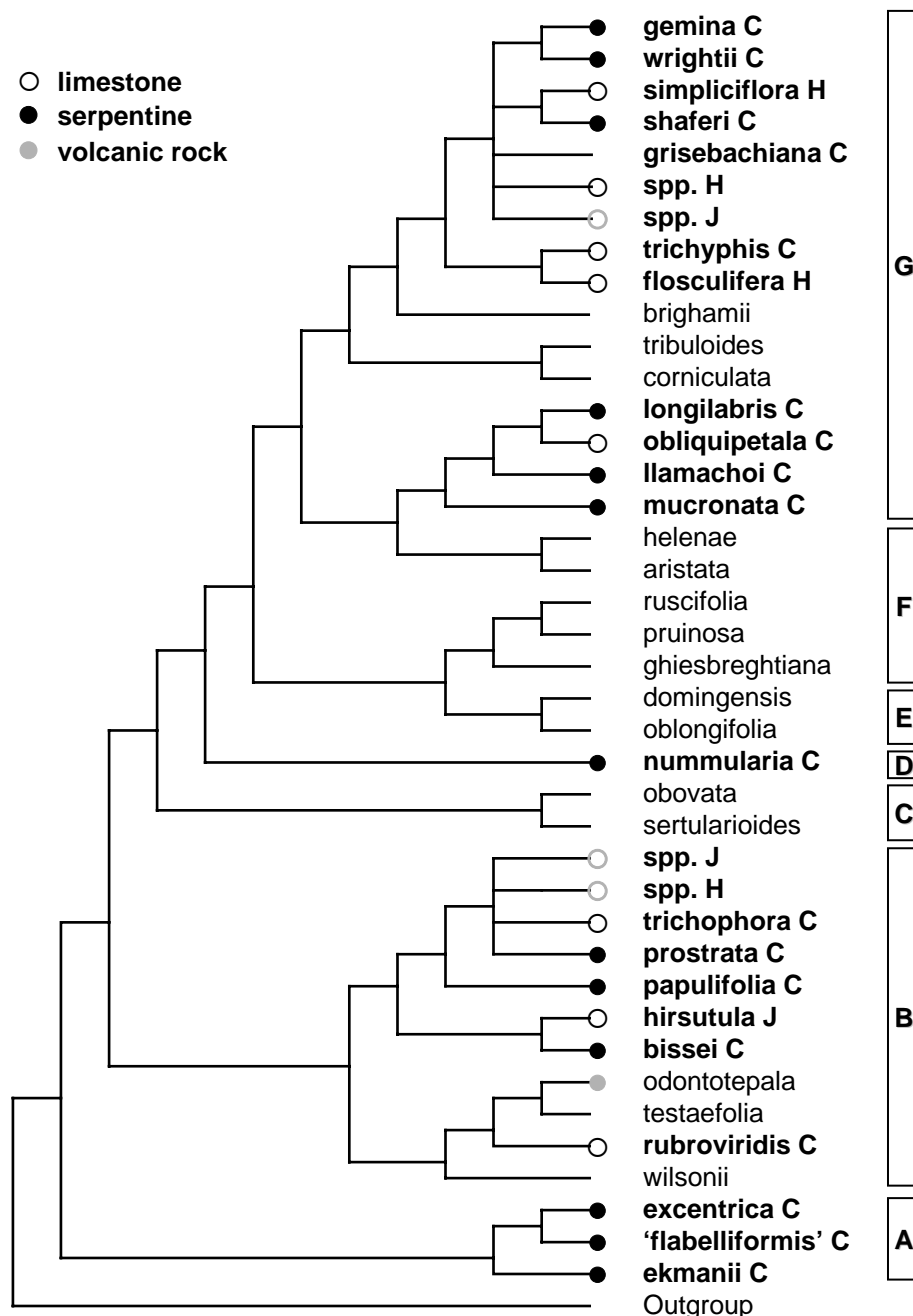


Fig. 76: Restriction of the Cuban taxa to certain types of rock. Included are distinct inter-island species pairs and indicators ('spp.') where multiple sister taxa on other islands would be placed according to morphological and palynological data. Since the latter comprise several taxa, geological classification is generalised.  
Letters after bold-typed endemics refer to the island (C – Cuba, J – Jamaica, H – Hispaniola).

Which **processes** precisely influence geological patterns of pleurothallid distribution remains a speculative matter. Theoretically, the limitation of epiphytic orchids to geologically defined areas could be the result of direct **physiological adaptation** to the chemistry of the respective rock. This mechanism is seen as an ubiquitous and irreversible phenomenon of the terrestrial vegetation on serpentine Borhidi 1996: 133). In epiphytes, however, this may not hold for several reasons. First, it is unknown how high the concentration of heavy metal ions on the bark is, i.e. to what degree, epiphytic plants

get in contact with them. Several *Buxus* and *Leucocroton* species which are restricted to ultramafic rock are known to hyperaccumulate Ni in their leaves (Reeves & al. 1996) and some of them do serve as phorophytes for species of *Pleurothallis*, e.g. *P. Ilamachoi* on hyperaccumulating species of *Buxus gonoclada* compl. and *P. ekmanii* on *Leucocroton* sp. It is likely that the bark, which serves often as a physiological waste disposal, reflects the geological traits just as the leaves do, although leaves should be a preferred place of storage for their ephemeral character and due to the fact, that many (sub)tropical trees do not build up a thick bark as do their temperate relatives (Vareschi 1980: 62). Nevertheless, even if we assume that the epiphytic plants come in contact with considerable amounts of serpentine bound heavy metals, a physiological, taxon specific tolerance is rather unlikely, since closest relatives of serpentine endemics are often restricted to non-ultrabasic rock (cf. further down). A post-Pleistocene origin of the Antillean endemics, as assumed in this study, would imply the physiological back- and forth adaptation to the chemistry of different rocks within 10000 years. Secondary ties by locally restricted **fungi** and/or pollinators are more likely, owing to the fact that both are probably in closer contact with the substrate. Due to the great age of these organisms, a physiological tie to the specific type of rock with a subsequent geologically defined area of distribution is likely. Unfortunately, little is known about both fungi-host and pollinator-plant specificity. Studies on the specificity of endophytic fungi (Currah 1997, Bayman & al. 1997) showed mixed infections in the same plants and a great heterogeneity in number and type of endophyte among species. The latter even presented evidence for shortcomings in widespread identifying methods that may have caused failure in extracting the whole set of fungi present in the root and/or other organs. Therefore, the fungal diversity may be even greater. Logically, co-evolution with a particular fungus of restricted ecological amplitude would narrow down the bottle neck of seed germination even more (Bayman & al. 1997). A widespread specialisation on yet another co-organism beside the pollinator is less likely and in fact, that is what the studies essentially show.

A **pollinator** dependent geographic restriction, on the other hand, would require a geologically confined biogeography of the insect. Interestingly, conservative estimates on the biogeography of Cuban insects, suggest a closer relationship between E Cuba and Hispaniola (Genaro & Tejuca 2001). Yet, in contrast to the vast number of species, profound studies on pollinator-plant interactions in pleurothallid orchids are by far under-represented (reviewed in Van der Cingel 2001; Chase 1985; Christensen 1992; Dod 1986c; Duque 1993; Mesler & al. 1980; Borba & Semir 2001; Blanco & Barboza 2001) and information on the distribution of pollinators are virtually absent. Borba & Semir found indications for a geologically defined biogeography in Brazilian species of *Pleurothallis*, which they interpreted implicitly by pollinator biogeography. In Cuba, pollinators of these presumably myophilous plants (Van der Pijl & Dodson 1966; Christensen 1994; Borba &

Semir 2001) should be basically substrate-bound, since most growing sites were found in 0-2.0(-3.0) m height above the ground. The ecology of the insects should therefore receive direct influence from the edaphic chemistry. Similar to the high level of endemism in Borhidi's Eu-Moanicum (Borhidi 1996, López Almirall & al. 1984) regional ecological restriction could be a zoogeographical phenomenon too. Moreover, dispersal in orchids could be very similar to that of pollinating insects, since Johnson (1969) found evidence for a correlation between meteorological pathways and insect migration "in many cases" (cited in Close & al. 1978). A switch from one to another edaphic type should be therefore associated with the loss of the traditional pollinator set or parts of it, which in turn should effectively prevent expansion when no adaptation to the new environment occurs. This is backed by the geographical structure of pleurothallid endemism in Cuba, which is different from many other plant families. In contrast to the predominantly local, not regional [!] phanerogamous endemism (>500 of ~1000 endemic taxa according to Borhidi (1996) in Nipe-Baracoa, which has been assumed for orchids, too (Dietrich 1989a), most of the serpentine endemics of *Pleurothallis* are found throughout the area from the Sierra de Nipe to the Jauco, i.e. along the whole spine of serpentine in Oriente. The notion that pleurothallid distribution in Cuba might often be confined to individual ridges and hills turned out to be rather a collection artefact.

### *Speciation*

Until now it was shown, that species distribution depends mostly on factors related to dispersal, (palaeo)climatic traits and ecological preferences. However, these features explain only in part why speciation has been so intense just in the triangle of Cuba's Oriente, Jamaica and western Hispaniola. To elucidate the underlying patterns, speciation processes would have to be analysed in detail. This is where the content of data gathered during this study limits further discussion. In the absence of data covering such important steps in the orchidaceous life circle as pollination, it is almost impossible to draw serious conclusions. Thus the following paragraph on speciation is aimed mainly on the development of some hypotheses on speciation, which are based on the present distribution and ecological preferences of the Cuban taxa.

*Allopatric speciation.* – Phylogeographic data of the Antillean species of *Pleurothallis* indicate that speciation has occurred both in allopatric and sympatric processes. The respective portion is difficult to ascertain owing to the limited molecular sample size. Allopatric events have led at least to ¼ of the Antillean *Pleurothallis* flora, i.e. those species which migrated from the continent. Among autochthonous taxa, allopatric speciation seems to be the rule too. **First**, there are many examples for groups of species with mutually exclusive distribution, e.g. in subgen. *Antilla*. **Second**, the ITS based phylogenetic tree shows often greater genetic distances between sympatric species of

Cuba than among those with no overlapping distribution (e.g. *P. mucronata-Ilamachoi-longilabris*, *P. shaferi-grisebachiana*) which is probably due to the omission of the closest relatives that occur on other islands. **Third**, there is much evidence for frequent geological vicariance in the three radiative lineages (Fig. 76). Although many cases of vicariance can be inferred only indirectly by unusual branch lengths, e.g. subgen. *Antilla*, some species pairs can be inferred directly from the tree. It turned out that vicariance occurs in three qualities.

1. Geographic and geological vicariance, i.e. species occur on both different islands and types of rock. This is apparently the most frequent case and occurs in the *grisebachiana*-group of clade G (subgen. *Specklinia* sect. *Hymenodanthae*) and the *papulifolia*-group of clade B (subgen. *Antilla*). Two examples: *P. shaferi* - *P. simpliciflora* (Hispaniola, limestone) and *P. bissei* (Cuba, serpentine) – *P. hirsutula* (Jamaica, limestone). In subgen. *Antilla*, the three Cuban endemics are restricted to limestone, serpentine and magmatic rock, while their sister taxa occur in Jamaica and most frequently in Hispaniola.
2. Petrologic vicariance within islands. This can be found in the *aristata*-group. All but one endemics are restricted to serpentine and are of sympatric distribution (Fig. 76). Genesis of this group may have been the result of several allopatric speciation events combined with a change of the geological background: *P. Ilamachoi* (serpentine) → *P. obliquipetala* (volcanic rock) → *P. longilabris* (serpentine). This type of vicariance is rather rare. It represents actually only a physiographic subtype of #1. Geological combined with island vicariance is much more frequent, which may be due to the extended areals of serpentine, volcanic rock and limestone in Cuba, Jamaica and Hispaniola respectively.
3. Geographic vicariance on the same petrologic ground. This can only be inferred indirectly from the molecular tree, however it is backed by morphological and palynological data. Among the Cuban taxa sampled no pair of species falls in this category. However, Hispaniola with its extended and numerous limestone areas may have species that show this type of vicariance, unless they form sympatric pairs.

**Sympatric** speciation, in turn, seems to be a rather rare event. It may have been the case in the *aristata*-group (Fig. 76), assuming that *P. longilabris* originated from *P. Ilamachoi* before it gave rise to *P. obliquipetala*. However, *P. obliquipetala* may be descended equally from *P. Ilamachoi*, as was just pointed out. Sympatry can be observed most clearly in *P. gemina* and *P. wrightii*, two endemics of the Nipe-Baracoa-range which share the same ITS sequence. Moreover, sympatric evolution may occur in Haiti more frequently, where a lot of taxa from the three radiative lineages have been described

uniformly from limestone habitats.

Thus, allopatric speciation accounts for the majority of infra-Antillean speciation in *Pleurothallis*, resulting frequently in inter-island and geological vicariance, i.e. ecological shift. Hence, pleurothallid evolution in the West Indies is based mainly on **founder events**, a common pattern of speciation in archipelagos (Crawford & al. 1987). Baldwin & al. (1998: 426ff) reviewed studies on the evolution on oceanic islands, finding examples for both inter- and infra-island radiation, depending on the taxon and the island group. Similarly, speciation events may or may not parallel environmental shifts (Francisco-Ortega & al. 1996). Unfortunately, little reference is made to chorological patterns and geographical features in the review (ibid. p.429). Judd (2001) found most radiation within Antillean island boundaries in *Lyonia*. Although the seeds are anemochorous this is most probably due to the lower vagility, compared with pleurothallid seeds.

Speciation triggering founder effects comprise the following traits.

1. Change of the genetic structure due to increased inbreeding and subsequent increase in homozygosity (Mayr 1954). In this context it should be pointed out that observations in the field suggest, that founder events in Cuban *Pleurothallis* are most probably launched by selfing. Species pairs are separated by 30-700 km. Considering the presumably low radius of pollinators, small dipters above all, selfing must be an inevitable result of this situation. In orchids, the impact on the genetic structure, like increased homozygosity, should be therefore even stronger.

Autogamy, suggested by degenerated pollinia, complete fruit set with or without anthesis, is widespread among the widespread Cuban taxa (Tab. 5), indicating that selfing is more common among *Pleurothallis* than assumed (Catling 1990). It has not been observed yet in Cuban endemics. Cross-pollination is ensured by a predominately subsequent anthesis at first sight. Yet, a closer look reveals that several traits have been developed to allow parallelly open flowers. Thus, *P. wrightii* has one-flowered inflorescences, which are produced in pairs on one stem. The recently from *P. wrightii* evolved *P. gemina*, by contrast, produces single two-flowered inflorescences, however, with a simultaneous anthesis! The same applies to *P. shaferi*. Plants of the endemic subgen. *Antilla* have many-flowered inflorescences with parallel anthesis. Even in species with subsequently multi-flowered inflorescences several secondary stems show synchronised flowering, thus ensuring multiple open flowers on one and the same plant. Borba & al (2001b) showed that in Brazilian *Pleurothallis* selfing results in dramatically low fruit set with decreased seed viability. However, intact

seeds remained in almost all tests. Selfing, though payed with a substantial drop in viable seeds, may be therefore a viable step in a colonisation event.

2. Random change of allele frequency due to genetic drift (Wright 1931).
3. Change of the environment resulting in new directions of selection (Wright 1931). This is one of the essentials of founder events, the role of which can be observed in Antillean *Pleurothallis* by the frequency of ecological vicariance (pollinator set distribution defined by geological traits).
4. Templeton (1980) added the feature of genetic variability in the founder population to his model of genetic transience. Genetic variability was found to be a common trait in pleurothallid (Borba & al. 2001a; Tremblay & Ackerman 2001) and other orchids (Ackerman & Ward 1999), based on isozyme data. Templeton (1980: 1013) pointed out that isozyme data, which is widely used to ascertain the genetic variability in populations and species may not reflect the genetic variability that is essential for adaptations of pollination and major traits at the life cycle level. Similarly, under certain conditions selfing is not necessarily accompanied by loss of adaptability (cf. Takebayashi & Morrell 2001: 1144). As founder events, as was hypothesized, may be based on single plants among pleurothallid orchids, genetic variability as inferred from isozyme allele variation, may be in fact of secondary importance for the adaptive potential in the new environment.

The prerequisite for a founder event, reproductive isolation, is most likely not induced by distance, although this parameter, as was shown, clearly influences dispersal, and therefore gene flow, too (Ackerman & Ward 1999). Although only indirectly inferred, most geologically restricted taxa in Cuba are apparently confined to their areal by pollinator distribution, which is illustrated by the fact that most of them occur exactly within the complete geologically defined area. These species are therefore obviously limited to an area that is much smaller than the potential extent based on dispersal traits (seed production, air currents etc.). This, in turn, is backed by the multiple speciation events that have occurred in *Pleurothallis* in the Caribbean, which per se represent extra-zonal migration. Moreover, the potential of pleurothallid dispersal can be seen in widespread taxa with obligate or facultative autogamy (Tab. 5), which are independent of pollinator distribution<sup>8</sup>. Based on this 'artificial' geographical restriction, it would be natural to assume that there is at least a moderate gene flow within populations of endemic taxa, which in turn would account for the scarcity of sympatric speciation and low probability of

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<sup>8</sup> Of course, there are more reasons that have added to the successful migration in these plants, e.g. high fruit set.

speciation due to genetic drift. However, several studies have shown, that even restricted gene flow does not inevitably result in genetic and morphological differentiation, leading to speciation (Ackerman & Ward 1999; Borba & al. 2001a; Tremblay & Ackerman 2001). As Ackerman points out, founder populations must be 'sufficiently geographically isolated' and, as indicated in this study, must be confronted with a new environment, i.e. potential pollinator sets. Interestingly there are indications, that the insect fauna of E Cuba is most similar to that of Hispaniola (Genaro & Tejuca 2001). As we have seen in *Pleurothallis*, biotic similarity may indicate congruent dispersal patterns, hence, there may be concordant patterns of distribution and speciation in *Diptera*. Unfortunately, little or none information is available concerning ecological patterns of distribution in flies, which in turn could coincide with pleurothallid phytogeography. A correlation between the ecogeography of the two organisms would elegantly demonstrate the evolutionary potential of co-evolution.

As a result, the pleurothallid floristic richness within the triangle E Cuba – Jamaica – Hispaniola can be traced back to the following features. **First**, geological diversity has apparently brought about a great variety of pollinators suitable for these orchids. The floristic richness of Cuba's serpentine flora has been related traditionally to the age of the region (Borhidi 1996: 129). López Almirall et al 1984: 447), in contrast, implicitly indicate that unfavourable conditions (physiological aridity, ion toxicity etc.) and consequently high selection pressure have led to accelerated speciation. This is essentially the pattern in *Pleurothallis*! This plant groups shows that intense speciation in this region is mainly due to the spatial proximity of limestone and serpentine and, to a lesser degree, volcanic rock. In fact, the pleurothallid endemism rate of W Hispaniola (Hespenheide & Dod 1990: *Lepanthes*; data from herbarium material of *Pleurothallis*), which is composed almost exclusively of limestone, may reflect that of serpentine areas in Cuba's N Oriente. **Second**, the triangle comprises the most extensive mountainous area in the Greater Antilles, providing optimal climatic conditions for microphytic epiphytes. **Third**, changes in the environment trigger speciation. In the Greater Antilles, this is enhanced by the mentioned hurricane activity, which 'increases' the instability of environmental characteristics directly by the mechanic impact on the habitat (Walker & al. 1980; Rodríguez-Robles & al. 1990) and indirectly by frequent translocation of plants and seeds.

Considering the **vicariance-dispersal** discussion mentioned before (s. p.131), the pleurothallid way of speciation provides a good example for the irrelevance of this dispute. In my mind, dispersal and vicariance processes depend simply on the point of view, whether an separating barrier is effective prior (dispersal) or after establishment of the ancestral areal (vicariance). The irrelevance of this classification becomes evident in the case of the South America – Africa disjunction (Wolfe 1981). Following the slow drift of the

two continents it is impossible to determine, when exactly dispersal stopped and vicariance set in, even more when completely ignoring specific dispersal traits. Both schools have the problem of static assumptions at a certain point of their train of thought: 'dispersalists' proceed along the idea of a stable geological constellation (Page & Lydeard 1994) and vicariance biogeography is based on the inalterability of distribution, i.e. ancestral and present distribution is the same (Bremer 1992). Consequently the former was most popular before plate tectonics was established, whereas the latter gained much benefit from Wegener's theory (Page & Lydeard 1994). However, both processes exist, and dispersal should be more prevalent in vagile taxa within a stable, not uniform!, environment, while vicariance in sedentary taxa within an inconstant area. Finally vicariance will not do without dispersal (Hedges & al. 1994), and dispersal results in vicariant taxa as well. Whether a barrier, oceanic gap, or mountains etc., effectively hinder gene flow right from the moment the ancestral areal has colonised or later due to secondary changes in the environment, can often assessed only after phenotype or genotype differentiation has started. Moreover, these processes are reversible, when gene flow is resumed due to changes in environmental factors. Given the present-day distribution is congruent with the historical, Caribbean data of pleurothallid phylogeography suggest a strict dispersal pattern, mainly due to orchidaceous vagility and the stable geographical environment. In contrast, if it was that part of the pleurothallid flora resulted from forest fragmentation due to climatic oscillations during the Holocene (Curtis & al. 2001), then the speciation events would be clearly referable to the vicariance model. This, however, is fairly unlikely, given the great vagility of orchidaceous seeds.



## 5 Conclusions

1. There are 39 species referable to *Pleurothallis* in Cuba, although 3 taxa with the atypical pollinium number of 8 should be removed to a separate genus. The endemic portion is ~50 %.
2. In Cuba, open and humid places like gallery forests and spatially diverse (sub-)montane rainforests are the habitats with the highest  $\alpha$ -diversity. Petrologic features play an important role, too, since almost all endemics are associated with one single rock type, of which the most important is serpentine. The highest altitudinal concentration of species can be found in the colline to submontane belt, i.e. 300-1200 m a.s.l., with the peak as low as 600 m a.s.l. Annual precipitation of more than 1200 mm/a is a prerequisite, but an additional high amount of unmeasured humidity and precipitation is provided in all habitats.
3. Horizontal distribution in Cuba correlates with the ecological amplitude, i.e. endemics are the most stenoecious taxa, while wide spread species are generally euryoecious. The latter correlation seems to be often extended into reproduction biology, since autogamy seems to be much more prevalent in wide spread than in an endemic taxa. Yet, endemic taxa are geographically not as restricted as assumed earlier.
4. Morphological, palynological and molecular data shows, that the Cuban taxa are not monophyletic.
5. There is much indication for a mainly post-Pleistocene colonisation and radiation in the Arc.
6. The Antillean flora of *Pleurothallis* has its origin almost exclusively in Central America. Floristic enrichment of the Greater Antilles can be explained best by late season hurricanes which originate in the S Caribbean Sea and pass frequently over Central America and the W Greater Antilles.
7. Besides mountainous Central America, the species of *Pleurothallis* have a secondary centre of diversity in the East Cuba – Jamaica – West Hispaniola triangle. This is probably based on: a) geological, hence, pollinator diversity; b) intensive hurricane activity in this area, causing frequent translocation; c) favourable climatic conditions due to the relief and high precipitation.
8. Classic dispersal, with subsequent anagenesis of the founder population is the principal way of speciation in these orchids in the Greater Antilles. Dispersal events can proceed from the mainland (25% of the Antillean species) or from within the archipelago (50%). In any case it results in allopatric distribution.

Besides, sympatric speciation and hybridisation occur, but seem to play a minor role. About 25% of the taxa did not enter speciation in the process of dispersal.

9. Only three lineages have further radiated, i.e. entered cladogenesis, in the West Indies. They represent ~50% of the Antillean taxa.
10. Speciation processes led to geographical and ecological vicariance in most cases. They were apparently triggered by founder events, i.e. the establishment of small extra-zonal populations under new environmental (pollinator?) conditions.

With the treatment of the genus from the Flora de Cuba, a substantial part of the Cuban orchid flora has been liberated of century-old errors and misconceptions. About 1/6 of the Cuban orchid species were revised orientated to the standard currently employed in modern Floras and revisions. Most of the Antillean endemics have been illustrated for the first time, providing easy visual access for the user. This is especially important in the case of the spatially shaped orchid flowers which are difficult to describe. Descriptions and illustrations have been completed with data on distribution and ecological preferences. With this information one of the most diverse neotropical plant groups on the largest Antillean island has been characterised in detail. The collected data form the base for the phytogeographical and evolutionary studies of the present thesis as well as for future research.

Phylogeographical aspects of an Antillean orchidaceous group have been studied for the first time now, tackling some of the most essential questions of Antillean biogeography, i.e. how the Arc was colonised and which conditions caused the intensive speciation in that region. While morphologically based phylogenetic trees have been used already earlier to discuss modes of migration and speciation in the Caribbean, the present paper combines molecular data with most recently collected information on horizontal, vertical and ecological distribution. Genetic methods had not been employed before to study the genesis of the Caribbean orchid floras. Thus, in the absence of reliable phylogenetic and high resolution phytogeographical data, studies on orchid speciation have focused especially on gene flow and other characteristics at the population level. The present results suggest a rather simple type of speciation in pleurothallid orchids, i.e. dispersal with subsequent exposure to new environmental conditions, combined with a specific genetic evolution like selfing. Founder events, i.e. allopatric speciation, account apparently for most speciation processes in Antillean *Pleurothallis* species.

Due to the limited sample size and the absence of material from other islands in the molecular study, **future research** should focus in the first line on the inclusion of more Antillean endemics in the molecular matrix. Moreover, more taxa should be added from the mainland, to sufficiently represent the source area of Caribbean *Pleurothallis*. Apart

from this fine-tuning of the present method some of the hypotheses established in this study should be studied in the future to provide further details of orchidaceous speciation on islands.

1. Is the geological restriction of *Pleurothallis* on the other Greater Antilles islands as widespread as on Cuba? Which petrologic types play a major role?
2. Does selfing represent the initial mode of propagation within new orchid populations? How does this process influence genetic variability?
3. Which are the pollinators of *Pleurothallis* in the Antilles? Do they show a similar pattern of distribution as their respective orchid species, i.e. can geological traits be synonymised with pollinator distribution?

It becomes clear from the questions suggested that genetics will play an important role in future research. In this context it should be emphasised that molecular tools should not be detached from other aspects, like morphology or ecology. It is frustrating to see the vast number of molecular papers compared with the small amount of information that has been drawn from them considering evolution of morphology, ecological adaptation etc. There is still a tremendous treasure of information that awaits recovery simply by linking the new phylogenetic trees with phytogeographical, ecological and many other patterns. Another important point is the importance of this non-molecular information to test the reliability of molecular data, i.e. the feedback of morphology, anatomy, distribution etc. to genetics. To check molecular trees with the help of other information is especially important where large taxa have been extremely undersampled in phylogenetic studies.

As was pointed out earlier in this study, for the *Pleurothallidinae* we have substantial data now, concerning macro- and micromorphology, anatomy as well as genetics. The subtribe should now be one of the most thoroughly studied orchid groups. Hopefully, these data will be merged into a new classification, providing a system that reflects phylogenetics and evolution much better than any of the former constructions that were based mainly on but one data set.

As a probably more topical issue, the results of this thesis which concern ecology, phytogeography and speciation of Antillean *Pleurothallis* represent important sources of information in conservation matters. Orchids are traditionally used as a political argument in this connection. In the Caribbean, which forms one of the 10 hot spots not only due to its biodiversity, but owing to the tremendous loss of prime forests, too, these biological data represent perhaps the most valuable result of this study.

## Appendix

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## Glossary and abbreviations

! – after the citation of type material: material seen.

**a.s.l.** – above sea level.

**aciantheroid** – pollen morphology, describes a surface that is marked by 1) irregularly protruding tetrads, 2) a tetraedic position of the sister pollen grains, and 3) borders of the sister grains recognisable by thin interruptions in the outer wall. The typical aciantheroid surface is seen in Fig. 43a+c: a domed tetrad with easily recognisable pollen grain walls.

**bp** – base pair(s).

**BP** – before present.

**C** – Centre, central.

**CA** – Central America.

**E** – east(ern).

**FCP** – Flora de Cuba Project.

**GA** – Greater Antilles.

**ma** – million years.

**LA** – Lesser Antilles.

**lepanthoid** – pollen morphology, describes a levelled surface with fused exinous layers of the outer tetrads. The sculpture may be psilate to punctate (Stenzel 2000).

**Lundberg rooting** – definition of a hypothetical outgroup with all characters (taxa) coded 0, i.e. absent.

**octomerioid** – pollen morphology, describes a psilate sculpture with a distal sporopollenin cap disintegrating into marginal ribbons, a reticulum, or gemmae (Stenzel 2000). This disintegration usually starts at the flanks of the exinous cap of a tetrad/pollen grain, however, in some cases it might affect the whole cap at once.

**MP** – maximum parsimony.

**N** – North(ern).

**punctate** – pollen morphology, the term as applied hereafter, does not automatically mean a tectal perforation (sensu Erdtman 1952) but refers to a small depression (< 1µm) on the surface of exposed pollen grains.

**PFC** – Proyecto Flora de Cuba. Herbarium material collected within this project received a special number, e.g. PFC 12345.

**ramicaul** – term coined by Stern & Pridgeon (1984) and adopted by Dod (1986b) for linguistic usage in Spanish. Refers to the non-pseudobulbous secondary stems in the subtribe *Pleurothallidinae*.

**s** – transition(s).

**S** – South(ern).

**SA** – South America.

**v** – transversion(s).

**W** – West(ern).

**WI** – West Indies.

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## Curriculum vitae

1967

Geboren am 05.10.1967; Eltern Rosemarie und Helge Stenzel; ein jüngerer Bruder.

1974-1986

Besuch der Polytechnischen Oberschule in Berlin-Buch.

Besuch der Erweiterten Oberschule Carl von Ossietzky in Berlin-Pankow.

1988-1990

Studium des Gartenbaus an der Humboldt-Universität zu Berlin, 4 Semester.

1990/1991

10-monatiger Aufenthalt in Nord- und Mittelamerika, Arbeit in einer Orchideengärtnerei in Guatemala.

1991-1997

Studium der Biologie an der Humboldt-Universität zu Berlin.

Mehrmalige Sammelreisen nach Venezuela, Kolumbien, Ecuador, Cuba und Hispaniola.

Betreuung mehrerer Studentenexkursionen nach West-Cuba.

Vordiplomarbeit über "Die Tafelberge im Südosten Venezuelas - floristische und ökologische Beobachtungen".

Diplomarbeit über "Pollenmorphologie und deren Bedeutung für die Systematik in der Subtribus *Pleurothallidinae* (*Orchidaceae*)". Betreuung Prof. Dr. E. Köhler (Berlin) und HD. Dr. H. Dietrich (Jena).

1998

Beginn der Doktorarbeit über die "Evolution und Systematik der Orchideengattung *Pleurothallis* auf Cuba und den Großen Antillen", gefördert über 5 ½ Jahre durch den DAAD, das Land Berlin (NaFöG), die Fazit-Stiftung (Frankfurt/M.) und die KKGS-Stiftung (Berlin). Betreuung durch Prof. Dr. E. Köhler (Berlin) und Doz. Dr. H. Dietrich (Jena). Genetischer Teil in Zusammenarbeit mit Dr. A. M. Pridgeon (Jodrell Lab, RBG Kew)

6-monatige Feldarbeit auf Cuba (gefördert durch den DAAD).

Teilnahme an einem CAMP-Seminar (Conservation Assessment Management Plan) über Artenschutz am Nationalen Botanischen Garten Havanna.

1999

3-monatige Feldarbeit auf Cuba (gefördert durch den DAAD und die Humboldt-Universität)

Betreuung einer Studentenexkursion nach Cuba.

Beginn der genetischen Arbeiten in Jena.

Teilnahme am 14. Internationalen Symposium der Sektion Biodiversität und Evolutionsbiologie in Jena, Vortrag.

2000

Beginn der Revision der Gattung *Pleurothallis* für Cuba.

Teilnahme an dem 6. Internationalen Botanikersymposium in Havanna, Vortrag.

Teilnahme an dem 5. Arbeitstreffen des Cuba-Flora-Projektes, Poster.

2-monatige Feldarbeit in Jamaica und Puerto Rico (gefördert durch den DAAD).

Teilnahme am Symposium Flora of the Greater Antilles 2000 im New York Botanical Garden, Poster.

Geburt meines Sohnes Jakob.

2001

1-monatige Feldarbeit in West-Cuba.

Arbeiten im Herbarium der Royal Botanical Gardens Kew und am Reichenbach-Herbarium im Naturhistorischen Museums Wien (gefördert durch die Humboldt-Universität zu Berlin).

2002

Fertigstellung des Flora-Manuskriptes.

Geburt meines zweiten Sohnes Julius.

Beendigung der genetischen Arbeiten.

2003

Niederschrift der Dissertation.

Berlin, den 01.10.03

## Publications

- Stenzel, H. 1998. Funktionalität der Pollinien einiger *Pleurothallidinae* Lindl.: Wasserhaushalt und Keimungsvermögen. *Orchidee* (Hamburg) 49(2):51-57.
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- Stenzel, H. 2000. Pollen morphology of the subtribe *Pleurothallidinae* Lindl. (Orchidaceae). *Grana* 39: 108-125.
- Stenzel, H. 2000. Patterns of distribution and speciation in the Cuban species of the genus *Pleurothallis* R. Br. (Orchidaceae). (Abstract 6<sup>th</sup> Symposium on Botany, La Habana, Cuba).
- Stenzel, H. 2000. Phytogeography of the Cuban species of the genus *Pleurothallis* R. Br. (Orchidaceae).
- Stenzel, H. 2001. New species of *Orchidaceae* subtribe *Pleurothallidinae* from Cuba. *Lindleyana* 16(1): 26-30.
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- Stenzel, H. 2003. *Pleurothallis ghiesbreghtiana* A. Rich. & Galeotti. *Orchidee* (Hamburg) 54(4): 985-986.
- Stenzel, H. 2003. *Pleurothallis racemiflora* (Sw.) Lindl. *Orchidee* (Hamburg) 54(4): 987-988.
- Stenzel, H. 2004. *Orchidaceae* I: *Pleurothallidinae* – Part 1 (*Barbosella*, *Brachionidium*, *Lepanthopsis*, *Platystele*, *Pleurothallis*, *Octomeria*, *Zootrophion*). – *Flora de Cuba*. Koeltz, Germany. In edition.
- Stenzel, H. 2004. Subtribe *Pleurothallidinae* Lindl.: pollen morphology. In: Pridgeon, A.M, Cribb, P.J., Chase, M.W. (eds.): *Genera Orchidacearum*. Vol. 4. Oxford University Press, Oxford. In edition.
- Stenzel, H. A new genus in the subtribe *Pleurothallidinae* R. Br. (Orchidaceae). In prep.
- Stenzel, H. & Dietrich, H. Genesis of the Antillean species of *Pleurothallis* (Orchidaceae). Evidence from molecular and ecological data. In prep.

## **Erklärung**

Hiermit erkläre ich, daß ich die vorliegende Arbeit selbst und nur unter Zuhilfenahme der angegebenen Mittel angefertigt habe.

Berlin, 01.10.2003

Hagen Stenzel