

©2009

Katherine Burke Lepis

ALL RIGHTS RESERVED

EVOLUTION AND SYSTEMATICS OF CHELONANTHUS (GENTIANACEAE)

by

Katherine Burke Lepis

A dissertation submitted to the

Graduate School-New Brunswick

Rutgers, The State University of New Jersey

In partial fulfillment of the requirements

For the degree of

Doctor of Philosophy

Graduate Program in Plant Biology

Written under the direction of

Dr. Lena Struwe

And approved by

New Brunswick, New Jersey

January 2009

ABSTRACT OF THE DISSERTATION
EVOLUTION AND SYSTEMATICS OF CHELONANTHUS (GENTIANACEAE)

By KATHERINE BURKE LEPIS

Dissertation Director:

Dr. Lena Struwe

Chelonanthus is a widespread and common neotropical angiosperm genus in the tribe Helieae (Gentianaceae), a group known for its high morphological and ethnobotanical diversity. This genus has been riddled with taxonomic confusion for the last 150 years, and this is the first detailed study ever published on its morphology, evolution, and speciation. Molecular and morphology-based phylogenies of the tribe Helieae reveal a polyphyletic condition with *Chelonanthus* divided into two strongly separated lineages, one containing the purple-flowered type species *Chelonanthus purpurascens* and the other containing all other species, which have green to white corollas. This green-white corolla clade contains the most common and widespread species, *Chelonanthus alatus*, a polyphyletic species complex composed of six morphological variants. This dissertation sampled all recognized species of *Chelonanthus* as well as all morphological variation found in *Chelonanthus alatus*. The analytical tools of phylogenetics (Parsimony and Bayesian Analyses) and morphometrics (Principle Component Analysis) were combined to resolve inter- and intra-generic relationships between *Chelonanthus* and closely related genera of Helieae as well as define species boundaries within the species complex of *Chelonanthus alatus*. The presented

phylogeny, based on 5S-NTS and ITS data, together with a Principle Component Analysis of morphological characters, supports the need to recircumscribe and rename this polyphyletic genus and segregate four of the six morphotypes of *Chelonanthus alatus* as four distinct species. Two new species will be described, *Chelonanthus hamatus* found in the Guayana Highlands of French Guiana and Venezuela and *Chelonanthus pterocaulis* found in Central America, Trinidad and northeastern South America from Costa Rica to French Guiana. Two typified names associated with the *Chelonanthus alatus* species complex, *Chelonanthus acutangulus* and *Chelonanthus grandiflorus* also will be resurrected. In addition, a new species of the previously monotypic genus *Sipapoantha* (Helieae) will be described from northeastern Brazil. The new knowledge of this group was included in the floristic treatments of *Chelonanthus* for the Flora of the Guianas and the Catalogue of Vascular Plants of Bolivia.

ACKNOWLEDGEMENT

Funding for this project was provided by the National Science Foundation (grant no. 317612), The New World Consortium, and Rutgers Research Council to LS. Latin names were chosen with the help of Jason R. Grant, University of Neuchâtel. The illustration of *Sipapoantha obtusisepala* was provided by Mr. Hendrik Rypkema and the illustration of *Chelonanthus hamatus* and *Chelonanthus pterocaulis* was drawn by Bobbie Angell. The maps were created with the assistance of Phillip Miarmi. I gratefully thank the following people: Maria Fernanda Calió and José Pirani, University of São Paulo, for all their help in locating specimens and helping me with my Portuguese; Paul and Hiltje Maas, Utrecht University, for advice on *Chelonanthus*, providing silica dried plant material, and welcoming me into their home; Michael May, Rutgers University, for the generous use of his scanning electron microscope and Ricarda Riina, University of Wisconsin, for sending silica dried material. In addition, I would like to thank the helpful staff and curators of the following herbaria that helped during visits or provided loans and information regarding scientific materials: AAU, COL, F, G, IAN, INPA, K, MG, MO, NY, S, SP, U, UPS, and US. Chapter four of this dissertation is an excerpt from: Lepis, K. B., L. Cobb & M. I. Palmer. in press. Gentianaceae (*Chelonanthus* treatment) In: Flora of the Guianas, Marion Jansen-Jacobs ed. Amsterdam: J. H. De Bussy Ltd. Chapter five is an excerpt from: Lepis, K. B. in press. Gentianaceae (*Chelonanthus* treatment) In: Catálogo de las Plantas Vasculares de Bolivia, Jørgensen et al. eds. St. Louis: Missouri Botanical Garden Press. Chapter five

was translated from Spanish to English and further altered from the published text by the inclusion of an identification key and list of specimens observed.

DEDICATION

I want to thank my advisor, Lena Struwe, for her guidance and for providing me with meaningful scientific opportunities. I also must thank my mom, Sandra Burke, and both of my mothers-in-law, JoAnn Peck and Marie Lepis, without their help in watching my daughter Adrienne, I would never have completed this. My entire family has been very supportive, thank you. Of course I want to thank my husband, Mathew, a true friend who has always been there for me. I dedicate this work to Matt and Azy.

TABLE OF CONTENTS

COPYRIGHT	
TITLE PAGE	
ABSTRACT	ii - iii
ACKNOWLEDGEMENT	iv - v
DEDICATION	vi
LIST OF TABLES	viii - ix
LIST OF ILLUSTRATIONS	x - xii
INTRODUCTION	1 - 7
CHAPTER 1 - Phylogenetic and Species Structure in the Widespread Neotropical Genus <i>Chelonanthus</i> (Gentianaceae)	8 - 57
CHAPTER 2 - A Monograph of the Neotropical Genus <i>Chelonanthus</i> Gilg (Gentianaceae: Helieae)	58 - 100
CHAPTER 3 - Two New Species of <i>Sipapoantha</i> and <i>Chelonanthus</i> from the Guayana Highlands (Gentianaceae: Helieae)	101 - 124
CHAPTER 4 - <i>Chelonanthus</i> Treatment for the Flora of Guianas	125 - 143
CHAPTER 5 - <i>Chelonanthus</i> Treatment for Catálogo de las Plantas Vasculares de Bolivia	144 - 157
APPENDICES	158 - 160
LITERATURE CITED	161 - 166
CURRICULUM VITA	167

LIST OF TABLES

Table 1, Page 12 - 14: A list of names associated with the genus *Chelonanthus*. The names in bold are those recognized by Struwe et al., 1999. The names listed below each bolded name are taxa considered to be synonyms by Maas (1985), Pringle (1995) and/or Struwe et al. (1999). The names in each corresponding row are synonyms of the names listed in the first column. * Struwe et al. (1999) tentatively recognized *C. schomburgkii* has a distinct species, but remarks it may be a synonym of *C. alatus*. This paper considers it part of the *C. alatus* species complex.

Table 2, Page 16: A list of type specimens and names associated with the *Chelonanthus alatus* species complex.

Table 3, Page 20 - 26: A list of species used in the phylogenetic analyses along with voucher location, collector and collector number, Genbank reference number (if ITS was downloaded from Genbank), collection location, indication of data type included, and if included in the Principle Component Analysis.

Table 4, Page 39: Percent variance explained by the first four principle components and expected Broken Stick values (Frontier, 1976) indicating the first two axes worthy of inspection.

Table 5, Page 41: Eigenvector loadings of each character onto the first three principle components. Values in bold represent loadings > 0.3.

Table 6, Page 63: A list of herbarium specimens from which seed characters were collected using scanning electron microscopy.

Table 7, Page 115: Table comparing five taxa with *Sipapoantha obtusisepala* using ten morphological characters. Characters in bold are those shared with the new *Sipapoantha* species. Numbers in parentheses below each taxon name represent the number of characters shared with *S. obtusisepala*. Note: *Rogersonanthus* in this circumscription does not include *R. coccineus*, which has been moved to *Roraimaea* (Struwe et al., 2008).

Table 8, Page 124: Table comparing morphology and habitat data for *Chelonanthus*

hamatus with the specimens considered hybrids and the three species representing the most probable parental stock: *C. albus*, *C. angustifolius*, and *C. grandiflorus*.

LIST OF ILLUSTRATIONS

Figure 1, Page 34: 5S-NTS and ITS strict consensus tree of 10,000 most parsimonious trees, length = 1245 steps, CI = 0.66, RI = 0.86. Numbers to the right of each node represent jackknife values. Branches in bold, are those leading to clades or terminals currently classified as *Chelonanthus alatus*.

Figure 2, Page 35: 5S-NTS and ITS Bayesian inference, 50% majority consensus phylogram of 6000 trees. Bold posterior probabilities represent support for monophyletic taxa of *Chelonanthus*.

Figure 3, Page 38: A simplified topology of one of the most parsimonious fully bifurcating trees. Monophyletic groups composed of one taxonomic group were reduced to a single terminal for use in the DIVA analysis. Branches in bold indicate the green-white lineage of *Chelonanthus* including *Helia*. Current distributions are indicated at the terminals and ancestral distributions are along the branches. Ab = Amazon Basin, An = Andes, Bh = Brazilian Highlands, Ca = Central America and Mexico, Car = Caribbean, Gh = Guayana Highlands.

Figure 4, Page 40: Scatter plot of the first and second principle components resulting from a Principle Component Analysis of 191 observation and 10 characters. Numbers next to each axis represent the percent variance explained by that axis.

Figure 5, Page 42: Scatter plot of the first and third principle components resulting from a Principle Component Analysis of 191 observation and 10 characters. Numbers next to each axis represent the percent variance explained by that axis.

Figure 6, Page 48: Map illustrating the distribution of the green-white corolla species of *Chelonanthus* and the morphotypes currently included in *C. alatus* (based on 480 collections).

Figure 7, Page 55: a) Scatter plot of the first and second principle components, as seen in Figure 5, but only the *Chelonanthus alatus* - grandiflorus points are shown. Different symbols indicating petiolate and sessile specimens are used to illustrate the lack of separation between the two. b) Same as in a), but based on the first and third principle components.

Figure 8, Page 70: Map illustrating the distribution of *Chelonanthus purpurascens* (based on 158 collection sites).

Figure 9, Page 78: *Chelonanthus pterocaulis* **sp. nov.** A, unbranched, quadrangular 4-winged stem bearing elliptical leaves that are decurrent onto the stem. B, apical portion of the inflorescence with fruits and a narrowly tubular flower. C, complete inflorescence with horizontally positioned, medially dehiscent capsules and persistent corollas. D, close up of tubular corolla and erect corolla lobes. E, dissected flower revealing the gynoecium, the position of sexual structures within the corolla tube, and the insertion of filaments near the base of the corolla. F, anthers with sterile apical appendage. G, angular seeds. A-G from *Prance et al.* 4008. Illustrator: Bobbi Angell.

Figure 10, Page 100: Map illustrating the distribution of specimens determined as *Chelonanthus candidus* and *C. viridiflorus* (based on 94 collection sites).

Figure 11, Page 107: *Sipapoantha obtusisepala* **sp. nov.** A, flowering stem in the fruiting stage, with leaves evenly spread out along stem. B, leaves with prominent midvein and one pair of prominent, arcuate secondary veins. C, young capsule with persistent calyx, style, and stigma and an older capsule with apical portions of style and stigma missing, note the short and obtuse calyx lobes. D, angular seeds with sunken sides and ridges. A-D from *Ribeiro* 369. Illustrator: Hendrik Rypkema.

Figure 12, Page 112: *Chelonanthus hamatus* **sp. nov.** A, strongly quadrangular 4-winged stem bearing large strap-like leaves. B, part of the inflorescence. C, close-up of flower showing the minutely winged calyx lobes that terminate in an upward facing hook at the apex of each glandular area. D, dissected corolla showing the corona at the insertion point of the filaments. E, front and side view of anther. F, close-up of corona. G, gynoecium with nectary disc at base. H, mature medially dehiscent capsule with persistent corolla. I, SEM of pollen at 800X magnification, showing the exine with fine reticulum interspersed with thickened, knob-like muri. A-I from *de Granville et al.* 9713. Illustrator: Bobbie Angell.

Figure 13, Page 116: Map of Brazil, Guyana, and Venezuela illustrating the disjunct distribution of the genus *Sipapoantha*. The smaller map inserted in the upper left corner illustrates, the type species, *S. ostrina* (symbol ■) found on the tepuis in the western part of the Guayana Highlands in Venezuela. The location of the newly described species, *S. obtusisepala*, is believed to have been collected in the gray area near the town of Anauá, on the border of Brazil and Guyana. The larger map shows the proposed collection area in greater detail (see discussion for details). The area in gray represents the RADAM Project quadrat NA-21-YA. The area outlined by ---- represents a 200 km distance from the town of Anauá. The ▲ symbol represents mountain peaks.

Figure 14, Page 121: Map illustrating the collection points of *Chelonanthus hamatus* in French Guiana and Venezuela (symbol ■) and twelve of the thirteen intermediate specimens collected along the Rio Orinoco (symbol ▲). See discussion for details.

INTRODUCTION

Chelonanthus Gilg (Gentianaceae: tribe Helieae) is a common, widespread genus of herbs and subshrubs with terminal cymes that produce green, white to yellow or purple to blue, ampliate, slightly zygomorphic flowers. The ten species (Lepis et al., in progress; Chapter 2) that make up this genus can be found throughout much of the Neotropics and commonly grow in open, disturbed habitats such as forest edges or forest gaps, cerrado-type vegetation, savannas, river edges and roadsides, and most often these species are associated with white-sand, nutrient-poor soils.

As is common for much of Gentianaceae, five of the ten species have been documented in the ethnobotanical literature (Robison & López, 1999; Bertani et al., 2005) or in herbarium collections (Lepis et al., in progress; Chapter 2) to be medicinally usefully to native people from Ecuador, Guyana, Mexico, Peru, Suriname and Venezuela. Ailments that have been treated by these plants include relief from itching, stomachaches, parasitic worm infections, gonorrhea, kidney disease, smallpox and malaria. Veterinary uses have also been documented from Peru, where leaves of *C. acutangulus* (Ruiz & Pav.) Gilg are used to line chicken coops to combat chicken lice and as a remedy for worm-infested wounds in cattle (Lepis et al., in progress; Chapter 2).

Ecologically speaking, this genus is noteworthy by the bat-pollination of *Chelonanthus grandiflorus* (Aubl.) Chodat. & Hassl., one of few herbaceous angiosperms to be pollinated by bats (Machado et al., 1998). The study by Machado et al. (1998) determined the species to be *Irlbachia alata* (Aubl.) Maas, but an extensive

review of herbarium material revealed a Machado s.n. collection noting bat pollination that was determined here as *C. grandiflorus* (Lepis et al., in progress; Chapter 2). Several floral characters of *C. grandiflorus* observed in the Machado et al. study can be found in other bat-pollinated species. A terminal inflorescence with flowers horizontally positioned and bent to one side as well as reproductive organs grouped to the lower end of the corolla opening with anthers that deposit pollen on the chin of the bat are characters that have also been documented in chiropterophilous species of Bromeliaceae (Sazima & Sazima, 1995; Vogel, 1969). Additionally, flowers that are greenish in color and bell-shaped have also been determined as key floral characters for detecting chiropterophily by Dobat & Peikert-Holle (1985). The characters mentioned above can be found throughout *Chelonanthus* and it is likely that more pollination studies on this group would reveal additional chiropterophilous species. Dobat & Peikert-Holle (1985) list fourteen species of Gentianaceae as being bat-pollinated, but direct evidence exists for only two species, *C. grandiflorus* discussed here, and the shrub *Symbolanthus latifolius* Gilg (Vogel, 1958). The field study of Machado et al. (1998) also observed hawkmoth pollination and nectar robbing by hummingbirds in *C. grandiflorus*. Other organisms observed in association with species of *Chelonanthus* include the presence of ants on the dorsal glandular area of the calyx lobes in *C. grandiflorus* and *C. acutangulus* (Lepis et al., in progress; Chapter 2) and black flies on unopened flower buds of *C. grandiflorus* (Lepis et al., in progress; Chapter 2).

A stable taxonomy is crucial for the implementation of accurate ethnobotanical and ecological studies and the taxonomic status of *Chelonanthus* has been in continuous flux for more than 150 years. The species of *Chelonanthus* have also been

circumscribed under the generic names of *Lisyanthus*, *Lisianthus*, *Helia* and *Irlbachia*. *Chelonanthus* was first used to denote a section of the genus *Lisyanthus* Aubl. (Grisebach, 1839), a predominantly South American genus with a synonym that is homonymous with *Lisianthus*, a name used by Linnaeus (1767) to convert P. Browne's Caribbean-Central American genus *Lisianthus* (Gentianaceae: Potalieae) into his binomial naming system (Struwe & Albert, 1998). For an in-depth explanation on these homonymous generic names see Lepis et al. (in progress; Chapter 1), Nilsson (1970) and Struwe & Albert (1998). In an effort to clarify the confusion associated with these homonyms, Kuntze (1891), combined all of Aublet's *Lisyanthus*/*Lisianthus* (including *Chelonanthus* and excluding Linnaeus' *Lisianthus* = P. Browne's *Lisianthus*) with the species of *Irlbachia* Mart. into the genus *Helia* Mart., but this move was largely ignored. Based primarily on palynological characters, Gilg (1895) segregated the Caribbean-Central American *Lisianthus* L. from *Lisyanthus* Aubl., and elevated Grisebach's sections of the former genus (including *Chelonanthus*) to generic status. A more recent effort, based on gross morphology, anatomy and pollen microstructure, sorted out the taxonomic issues associated with *Chelonanthus* and closely related genera in the tribe Helieae and concluded that *Chelonanthus*, *Adenolisianthus* (Progel) Gilg, *Calolisianthus* (Griseb.) Gilg, and *Helia* be circumscribed under *Irlbachia* (Maas, 1985). Due to Kuntze's work in 1891, the name *Helia* has priority over *Irlbachia*, rendering the move by Maas taxonomically invalid (Struwe & Albert, 1998). In addition, subsequent molecular phylogenetic studies on the tribe Helieae (Struwe et al., 2002; in press), determined Maas' broad definition of *Irlbachia* to be systematically inaccurate.

Based on phylogenetic analyses of molecular (*trnL*, *matK*, ITS, 5S-NTS) and morphological characters, *Chelonanthus*, as currently defined, is evolutionarily circumscribed inaccurately (Lepis et al. in progress; Chapter 1; Struwe et al., 2002; in press). All species of this genus are positioned in the derived *Symbolanthus* subclade of *Helieae*, albeit strongly polyphyletic (Struwe et al., 2002; in press; Lepis et al. in progress; Chapter 1). The type species, *C. purpurascens* (Aubl.) Struwe, S. Nilsson & V.A. Albert, is positioned as sister to *Irlbachia pratensis* (Kunth) L. Cobb & Maas in a clade also containing several monotypic genera (Struwe et al., in press). These sister species can be identified by purple corollas and pollen shed as polyads. The rest of the species of *Chelonanthus* have green to white corollas, shed their pollen as tetrads, and are positioned in a clade with *Adenolisianthus*, *Helia* and two *Rogersonanthus* Maguire & B.M. Boom species (Struwe et al., in press). A molecular phylogenetic analysis including multiple samples of nine of the ten species of *Chelonanthus* (Lepis et al., in progress; Chapter 1) is in agreement with the findings and conclusions of the *Helieae* study (Struwe et al., in press). In particular, the need to revise *Chelonanthus* to consist of *C. purpurascens* and *I. pratensis* and include the green to white corolla species within the genus *Helia* was also supported in the Lepis et al. study. These revisions have not been implemented within this dissertation because several relationships remain unclear. As mentioned above, the Lepis et al. (in progress; Chapter 1) study and that of Struwe et al. (in press) are, for the most part, in agreement, but where they diverge is the placement of the species *Calolisianthus amplissimus* (Mart.) Gilg. In the Lepis et al. analysis this taxon was intimately positioned within *Chelonanthus purpurascens*, separate from the other *Calolisianthus* sampled, and in Struwe et al. *Ca. amplissimus*

was positioned with the rest of *Calolisianthus* in a clade well separated from *Ch. purpurascens*. The revision of the genera *Calolisianthus* and *Helia* is near completion by Maria Fernanda Calió at the University of São Paulo and it is our wish to hold off on the revision of *Chelonanthus*, as suggested above, until all the data on these closely related genera can be combined. Therefore, the revision of *Chelonanthus* in the following chapters deals with accurately delineating its species as the genus is currently defined but does not provide a recircumscription of the genus at this time.

The systematic issues that surround *Chelonanthus* can also be observed for several of its species. The work explained in the following pages deals, in particular, with the highly variable and widely distributed *C. alatus* (Aubl.) Pulle species complex. Through the use of molecular phylogenetics and a Principle Component Analysis (PCA) of morphological characters, four hidden species have been identified within the species complex of *Chelonanthus alatus* (Lepis et al., in progress; Chapter 1; Chapter 2). Those species include: *C. alatus sensu stricto* (which is synonymous with *C. longistylus* (J.M.G. Pers. & Maas) Struwe & V.A. Albert), *C. acutangulus* (Ruiz & Pav.) Gilg and *C. grandiflorus* (Aubl.) Chodat & Hassl., names resurrected in Chapter 2, and a new species, *C. pterocaulis* Lepis (in progress; Chapter 2), has been described¹ from Central America and the Guayana Highlands. Additionally, the research resulted in the identification and description¹ of another new species of *Chelonanthus* from the Guayana Highlands, *C. hamatus* Lepis (in progress; Chapter 3).

The extensive review of herbarium material resulted in the addition of a third new species¹ to the botanical record, *Sipapoantha obtusisepala* Lepis, Maas & Struwe

¹ The new names included here are not accepted by the author as validly published in this dissertation (Botanical Code, Article 34.1[a]).

(in progress; Chapter 3). Known from a single herbarium specimen, this new species from the Brazilian state of Roraima, on the border of Brazil and Guyana, changes the generic description to include woody plants and depicts this previously monotypic genus as highly disjunct. The type species, *S. ostrina* Maguire & B.M. Boom, occurs only in the Amazonas State of Venezuela, on the tepui mountains (flat-topped mesas) of Cerro Sipapo, Cerro Cuao, and Cerro Autana, about 1000 km from the collection site of *S. obtusisepala* (Lepis et al., in progress; Chapter 3). The placement of this new species was determined to be most appropriate in the genus *Sipapoantha* Maguire & B.M. Boom, but a lack of floral characters present on the specimen makes this placement tentative. A second genus, *Rogersonanthus*, was also a likely candidate, sharing as many characters with the new species as *Sipapoantha*. It was determined, though, that the characters that unite *S. obtusisepala* and *Rogersonanthus* (habit and leaf placement) are variable within other related genera and therefore not as stable as the characters that unite the new species and *Sipapoantha*.

The genus *Sipapoantha* is also part of the Helieae tribe, but is not positioned with *Chelonanthus* within the derived Symbolanthus subclade (Struwe et al., in press). Rather, it is tentatively placed as one of the basal branches of the Helieae tribe. The placement is tentative due to its inclusion into the Struwe et al. study based solely on morphological characters. This genus is quite rare and a lack of suitable herbarium material prevented the acquisition of molecular data.

This primarily herbarium-based, systematic study of *Chelonanthus* has led to a better understanding of the inter-specific relationships within the genus and added evidence and clarity to the inter-generic relationships within the Symbolanthus subclade

of Helieae established by Struwe et al. (2002; in press). A collaborative effort is underway to combine the evidence presented here with information gathered on the genera of *Calolisianthus* and *Helia*, which will further justify recircumscription of *Chelonanthus* into two genera. Field characters have been identified for distinguishing the species of *Chelonanthus* and in particular, to provide identification tools for the previously hidden species teased from the species complex of *Ch. alatus*. As a result of this revision, treatments for *Chelonanthus* have been provided to the Flora of the Guianas (Chapter 4) and Catálogo de las Plantas Vasculares de Bolivia (Chapter 5).

CHAPTER 1

**Phylogenetic and Species Structure in the Widespread Neotropical Genus
Chelonanthus (Gentianaceae)**

ABSTRACT

Chelonanthus, a neotropical angiosperm genus in tribe Helieae (Gentianaceae), has been plagued with taxonomic confusion for more than 150 years. The phylogeny presented here, based on 5S-NTS and ITS data, is congruent with previous studies depicting *Chelonanthus* as polyphyletic and supports the need to recircumscribe the genus to a smaller *Chelonanthus* that would include the type species *C. purpurascens* and *Irlbachia pratensis*. Additionally, *Calolisianthus amplissimus*, the type species of *Calolisianthus*, was also positioned in *Chelonanthus sensu stricto* for the first time, but this needs to be verified with additional sequencing. This placement raises concerns about the monophyly of *Calolisianthus*, as well as what generic name is most appropriate, considering the names *Chelonanthus* and *Calolisianthus* were published simultaneously. The placement of *Helia* within the clade containing all species of *Chelonanthus* with green to white corollas also supports the separation of this group from *Chelonanthus sensu stricto* and its inclusion in the genus *Helia*. This clade also contains the most common and widespread species in the genus, *Ch. alatus*, a polyphyletic species complex composed of six morphotypes. The molecular-based phylogeny and a Principle Component Analysis of morphological characters support the segregation of four morphological variants as separate species. The evidence presented in this paper is congruent with previous studies, forming the basis for the first revision of *Chelonanthus* and closely related genera.

INTRODUCTION

Often found in open habitats, the genus *Chelonanthus* is distributed across the Neotropics, from southern Mexico to northern Argentina and from the eastern portion of the Andes to the Atlantic and Gulf Coasts, with the center of species diversity in the Guayana Highlands. The most recent floristic treatment to reference the entire genus recognized 7-8 species (Struwe et al., 1999). *Chelonanthus* is characterized as herbs or subshrubs with terminal cymose inflorescences that bear green, yellow to white or purple ampliate flowers that are slightly zygomorphic, due to the sexual structures grouping to lower side of the corolla opening.

The taxonomic history of *Chelonanthus* Gilg is riddled with confusion. The name was first used to denote a section of the genus *Lisyanthus* Aubl. (Grisebach, 1839), a genus originally composed of four species from the Guianas and predominantly South American. Aublet's generic spelling was extremely close to *Lisianthus*, a name used by Linnaeus (1767) to convert P. Browne's Caribbean-Central American genus *Lisianthus* (Gentianaceae: Potalieae) into his binomial naming system (Struwe & Albert, 1998). The species of *Lisyanthus* Aubl. and those of *Lisianthus* L. are not closely related, but Linnaeus' son, Linnaeus f. (1781), fused the two names when he added two species of *Lisyanthus* Aubl. to *Lisianthus* L. (Nilsson, 1970). The confusion created by these nearly identical names can be exemplified by Grisebach, who spelled Aublet's genus correctly (1839) when he established his generic sections, but in subsequent papers dealing with the species of Aublet's *Lisyanthus*, choose Linnaeus' spelling (*Lisianthus*; 1845; 1862). Additionally, in the floristic treatment of Brazil, Martius (1827) cites the authors of the name *Lisianthus* as, "(P. Browne.) Aubl.

Ruiz et Pav.," but only describes South American species. In an effort to overcome the confusion of homonyms, Kuntze (1891) combined Aublet's *Lisyanthus/Lisianthus* (including *Chelonanthus*, but excluding all of P. Browne's *Lisianthus* species) and *Irlbachia* Mart. into the genus *Helia* Mart., but this transfer was largely ignored. In 1895, Gilg elevated *Chelonanthus* to generic status using narrow circumscriptions of Helieae genera, based on pollen characters (i.e., *Adenolisianthus* Gilg, *Calolisianthus* Gilg, *Helia*, *Irlbachia* and *Symbolanthus* Don). There has been a continuing debate in the literature on how broadly or strictly defined the genera of Helieae should be. Authors invoking more narrow circumscriptions of genera include Malme (1904), Gilg (1906), Gleason (1931, 1939), Nilsson (1970), Maguire & Boom (1989) and Struwe et al. (1999, 2002). Other authorities have maintained the view that *Chelonanthus* and closely related genera are part of the broad circumscription of *Lisyanthus/Lisianthus*, a name which has been interpreted either as different combinations of the genus in Aublet's sense (mainly South American taxa) or in Linnaeus' sense (including Caribbean and Central American taxa; Bentham, 1854; Jonker 1936; Lemée, 1950; MacBride, 1959; Steyermark, 1953). As already noted above, *Lisyanthus/Lisianthus* Aublet and Linnaeus' *Lisianthus* (= *Lisianthus* P. Browne, the name in current use) are classified in the tribes Helieae and Potalieae, respectively, and are therefore not closely related (Struwe et al., 2002). An effort to sort out the taxonomy of Helieae genera, based on gross morphology, anatomy and pollen microstructure concluded that *Chelonanthus* and closely related genera (excluding *Symbolanthus*) should be circumscribed as the genus *Irlbachia* (Maas, 1985). Although *Irlbachia* and *Helia* were described simultaneously (Martius, 1827), Kuntze's inclusion of *Irlbachia* in *Helia* in

1891 gave *Helia* priority over *Irlbachia* and, thereby, rendered Maas' move taxonomically invalid (Struwe & Albert, 1998). A broadly circumscribed *Irlbachia* sensu Maas (1985) also fails to reflect evolutionary relationships, based on phylogenetic analyses of molecular and morphological data (see below; Struwe et al., 2002; in press). The cumbersome list of synonyms associated with the various species of *Chelonanthus* (Table 1) is the product of this long history of nomenclatural and classification changes. Please see Nilsson (1970) and Struwe & Albert (1998) for additional information about the taxonomic history of the genera in the tribe Helieae.

The genus *Chelonanthus* has not only been beset by taxonomic confusion, but has also been determined to be polyphyletic. Helieae phylogenies, based on *trnL*, *matK*, ITS and morphology, identified two lineages (Struwe et al., 2002; in press). One lineage consists of the type species, *C. purpurascens* (Aubl.) Struwe, S. Nilsson & V.A. Albert, as closely related to non-*Chelonanthus* taxa with purple corollas and pollen shed as polyads, and the second clade includes species with green, yellow to white corollas and pollen shed as tetrads. The two *Chelonanthus* clades are part of a larger *Symbolanthus* clade. The phylogenies in Struwe et al. (in press) consistently show *C. purpurascens* as sister to *Irlbachia pratensis*, with the authors suggesting a future reclassification to include *I. pratensis* as part of a smaller, recircumscribed *Chelonanthus*. Other, mostly monotypic genera included in the clade with *C. purpurascens* are *Aripuana* Struwe, Maas & V.A. Albert, *Lagenanthus* Gilg, *Lehmanniella* Gilg, *Purdieanthus* Gilg and *Roraimaea* Struwe, S. Nilsson & V.A. Albert. The second *Chelonanthus* lineage, now referred to as the green-white lineage, contains all other species sampled along with

Table 1: A list of names associated with the genus *Chelonanthus*. The names in bold are those recognized by Struwe et al., 1999. The names listed below each bolded name are taxa considered to be synonyms by Maas (1985), Pringle (1995) and/or Struwe et al. (1999). The names in each corresponding row are synonyms of the names listed in the first column. * Struwe et al. (1999) tentatively recognized *C. schomburgkii* has a distinct species, but remarks it may be a synonym of *C. alatus*. This paper considers it part of the *C. alatus* species complex

Bold names recognized by Struwe et al. 1999	Classification of Kuntze, 1891	Classification of Maas, 1985	Names of Aublet (1775) Gilg (1895) and Grisebach (1839)	Additional names
<i>Chelonanthus alatus</i> (Aubl.) Pulle	<i>Helia alata</i> (Aubl.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i> (Aubl.) Maas	<i>Lisyanthus alatus</i> Aubl.	
<i>Chelonanthus acutangulus</i> (Ruiz & Pav.) Gilg	<i>Helia acutangula</i> (Ruiz & Pav.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i>		<i>Lisianthus acutangulus</i> Ruiz & Pav.
	<i>Helia auriculata</i> (Benth.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i>		<i>Lisianthus auriculatus</i> Benth.
	<i>Helia campanulacea</i> (Desr.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i>	<i>Lisyanthus campanulaceus</i> (Desr.) Griseb.	<i>Lisianthus campanulaceus</i> Desr. in Lam.
<i>Chelonanthus chelonoides</i> (L.) Gilg	<i>Helia chelonoides</i> (L.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i>	<i>Lisyanthus chelonoides</i> (L.) Griseb.	<i>Pentstemon chelonoides</i> L. <i>Lisianthus chelonoides</i> (L.) Linn. f.
	<i>Helia crassicaulis</i> (M. Martens & Gelotti)	<i>Irlbachia alata</i> ssp. <i>alata</i>		<i>Lisianthus crassicaulis</i> M. Martens & Gelotti
<i>Chelonanthus fistulosus</i> (Poir.) Gilg	<i>Helia fistulosus</i> (Poir.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i>	<i>Lisyanthus fistulosus</i> (Poir.) Griseb.	<i>Lisianthus fistulosus</i> Poir. in Lam.
<i>Chelonanthus grandiflorus</i> (Aubl.) Chodat & Hassl.	<i>Helia grandiflora</i> (Aubl.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i>	<i>Lisyanthus grandiflorus</i> Aubl.	
<i>Chelonanthus leucanthus</i> Gilg				
	<i>Helia oerstedii</i> (Griseb.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i>		<i>Lisianthus oerstedii</i> Griseb.

Table 1: Continued.

Bold names recognized by Struwe et al. 1999	Classification of Kuntze, 1891	Classification of Maas, 1985	Names of Aublet (1775) Gilg (1895) and Grisebach (1839)	Additional names
<i>Chelonanthus schomburgkii</i> (Griseb.) Gilg*	<i>Helia schomburgkii</i> (Griseb.) Kuntze	<i>Irlbachia alata</i> ssp. <i>alata</i>		<i>Lisianthus schomburgkii</i> Griseb. in Prod. (DC.)
<i>Chelonanthus albus</i> (Spruce ex Progel) V.M. Badillo	<i>Helia alba</i> (Spruce ex Progel) Kuntze	<i>Irlbachia alata</i> (Aubl.) Maas ssp. <i>alba</i> (Spruce ex. Progel) J.M.G. Pers. & Maas		<i>Lisianthus albus</i> Spruce ex Progel
<i>Chelonanthus angustifolius</i> (Kunth) Gilg	<i>Helia angustifolius</i> (Kunth) Kuntze	<i>Irlbachia alata</i> (Aubl.) Maas ssp. <i>angustifolius</i> (Kunth) J.M.G. Pers. & Maas	<i>Lisyanthus angustifolius</i> (Kunth) Griseb.	<i>Lisianthus angustifolius</i> Kunth
<i>Chelonanthus bifidus</i> (Kunth) Gilg	<i>Helia bifida</i> (Kunth) Kuntze	<i>Irlbachia alata</i> ssp. <i>angustifolius</i>	<i>Lisyanthus bifidus</i> (Kunth) Griseb.	<i>Lisianthus bifidus</i> Kunth
<i>Chelonanthus camporum</i> Gilg		<i>Irlbachia alata</i> ssp. <i>angustifolius</i>		
<i>Chelonanthus pyriformis</i> Gleason				<i>Lisianthus pyriformis</i> (Gleason) Steyerl.
<i>Chelonanthus longistylus</i> (J.M.G. Pers. & Maas) Struwe & V.A. Albert		<i>Irlbachia alata</i> (Aubl.) Maas ssp. <i>longistyla</i> J.M.G. Pers. & Maas		
<i>Chelonanthus matogrossensis</i> (J.M.G. Pers. & Maas) Struwe & V.A. Albert		<i>Irlbachia alata</i> (Aubl.) Maas ssp. <i>matogrossensis</i> J.M.G. Pers. & Maas		
<i>Chelonanthus purpurascens</i> (Aubl.) Struwe, S. Nilsson, & V.A. Albert	<i>Helia purpurascens</i> (Aubl.) Kuntze	<i>Irlbachia purpurascens</i> (Aubl.) Maas	<i>Lisyanthus purpurascens</i> Aubl.	<i>Lisianthus purpurascens</i> Kunth (not Aubl.)
	<i>Helia amoena</i> (Miq.) Kuntze	<i>Irlbachia purpurascens</i>		<i>Lisianthus amoenus</i> Miq.

Table 1: Continued.

Bold names recognized by Struwe et al. 1999	Classification of Kuntze, 1891	Classification of Maas, 1985	Names of Aublet (1775) Gilg (1895) and Grisebach (1839)	Additional names
	<i>Helia gracilis</i> (Griseb.) Kuntze	<i>Irlbachia purpurascens</i>	<i>Lisyanthus gracilis</i> Griseb.	
<i>Chelonanthus spruceanus</i> (Benth.) Gilg	<i>Helia spruceanus</i> (Benth.) Kuntze	<i>Irlbachia purpurascens</i>		<i>Lisianthus spruceanus</i> Benth.
<i>Chelonanthus uliginosus</i> (Griseb.) Gilg	<i>Helia uliginosus</i> (Griseb.) Kuntze	<i>Irlbachia purpurascens</i>	<i>Lisyanthus uliginosus</i> Griseb.	
<i>Chelonanthus viridiflorus</i> (Mart.) Gilg	<i>Helia viridiflora</i> (Mart.) Kuntze	<i>Irlbachia alata</i> (Aubl.) Maas ssp. <i>viridiflora</i> J.M.G. Pers. & Maas	<i>Lisyanthus viridiflorus</i> (Mart.) Griseb.	<i>Lisianthus viridiflorus</i> Mart.
<i>Chelonanthus candidus</i> Malme		<i>Irlbachia alata</i> ssp. <i>viridiflora</i>		

Adenolisianthus, *Helia* and two species of *Rogersonanthus* Maguire & B.M. Boom.

This green-white lineage forms a polytomy with a *Calolisianthus* subclade, a *Symbolanthus* subclade and *Tetrapollinia* Maguire & B.M. Boom. In addition to the suggestion above, Struwe et al. (in press) recommended that the green-white lineage of *Chelonanthus*, along with *Adenolisianthus*, *Rogersonanthus arboreus* (Britton) Maguire & B.M. Boom and *R. quelchii* (N.E. Br.) Maguire & B.M. Boom be renamed, with a change in generic circumscription under *Helia*, the oldest name in this subclade.

The taxonomic confusion surrounding *Chelonanthus* is not only present at the generic level, but penetrates into the circumscriptions of several of its species. *Chelonanthus alatus* (Aubl.) Pulle serves as a prime example of a species complex whose boundaries have been continually redefined. As many as fourteen typified names and thirty-five synonyms have been included within *C. alatus sensu lato* (Table 2). The broadest circumscription of this species was that proposed by Maas (1985), who considered all

other species of *Chelonanthus* except *C. purpurascens* to be subspecies under *Irlbachia alata* (Table 2). As was the case with *Irlbachia sensu* Maas, the far-reaching circumscription of *I. alata* (*C. alatus*) was also taxonomically incorrect, with the synonyms corresponding to *C. alatus*, *C. albus* (Spruce ex Progel) Badillo, *C. angustifolius* (Kunth) Gilg and *C. viridiflorus* (Mart.) Gilg being superfluous as combinations under *Helia* had priority (Struwe & Albert, 1998). Since *C. longistylus* (J.M.G. Pers. & Maas) Struwe & V.A. Albert and *C. matogrossensis* (J.M.G. Pers. & Maas) Struwe & V.A. Albert were first described by Maas (1985) [as subspecies of *C. alatus* = *Irlbachia alata*] they were not indicated as superfluous names in Struwe & Albert (1998). This paper utilizes the *Chelonanthus* classification presented in Struwe et al. (1999) and supports the notion that *C. alatus sensu* Maas is not a valid taxon, based on taxonomic and phylogenetic investigations. The validity of *C. alatus sensu lato* was further tested by the inclusion of *C. longistylus* in the analysis, as a potential morphotype of *C. alatus*. Specimens of *C. longistylus* have similar morphological characters portrayed in the first description and plate for *C. alatus* (= *Lisyanthus alatus*; Aublet, 1775), it will therefore be tentatively treated in this study as a morphotype of *C. alatus*.

Chelonanthus alatus sensu lato is a weedy, widespread plant whose morphology is highly variable. This species is notable as one of the few herbaceous angiosperms to be pollinated by bats (Machado et al., 1998). In addition, multiple herbarium specimens labeled as *C. alatus* refer to medicinal use by native people from Ecuador, Guyana, Mexico, Peru, Suriname and Venezuela for treating ailments such as stomachaches, parasitic worm infections, gonorrhea, smallpox and malaria. Bioprospecting activities

Table 2: A list of type specimens and names associated with the *Chelonanthus alatus* species complex.

Type	Synonym with <i>C. alatus</i> by Maas (1985)	Synonym with <i>C. alatus</i> by Pringle (1995)	Synonym with <i>C. alatus</i> by Struwe et al. (1999)	List of synonyms associated with typified names
<i>Lisianthus acutangulus</i> Ruiz & Pav.	x	x	x	<i>Chelonanthus acutangulus</i> (Ruiz & Pav.) Gilg <i>Helia acutangula</i> (Ruiz & Pav.) Kuntze
<i>Lisianthus auriculatus</i> Benth.	x	x		<i>Helia auriculata</i> (Benth.) Kuntze
<i>Lisianthus campanulaceus</i> Desr. in Lam.	x	x		<i>Lisyanthus campanulaceus</i> (Desr.) Griseb. <i>Helia campanulacea</i> (Desr.) Kuntze
<i>Pentstemon chelonoides</i> L.	x	x	x	<i>Lisianthus chelonoides</i> (L.) Linn.f. <i>Chelonanthus chelonoides</i> (L.) Gilg <i>Helia chelonoides</i> (L.) Kuntze
<i>Lisianthus crassicaulis</i> M. Martens & Gelotti		x		<i>Helia crassicaulis</i> (M. Martens & Gelotti) Kuntze
<i>Lisianthus fistulosus</i> Poir. in Lam.	x	x		<i>Chelonanthus fistulosus</i> (Poir.) Gilg <i>Helia fistulosa</i> (Poir.) Kuntze <i>Lisyanthus fistulosus</i> (Poir.) Griseb.
<i>Lisyanthus grandiflorus</i> Aubl.	x	x		<i>Chelonanthus grandiflorus</i> (Aubl.) Chodat & Hassl. <i>Helia grandiflora</i> (Aubl.) Kuntze
<i>Chelonanthus leucanthus</i> Gilg		x	x	
<i>Lisianthus oerstedii</i> Griseb.		x		<i>Helia oerstedii</i> (Griseb.) Kuntze
<i>Lisianthus schomburgkii</i> Griseb.		x		<i>Chelonanthus schomburgkii</i> (Griseb.) Gilg <i>Helia schomburgkii</i> (Griseb.) Kuntze
<i>Lisianthus tetragonus</i> Benth.		x		<i>Helia tetragona</i> (Benth.) Kuntze
<i>Lisianthus trifidus</i> Kunth	x	x	x	<i>Helia trifidus</i> (Kunth) Kuntze <i>Lisyanthus trifidus</i> (Kunth) Griseb.
<i>Lisianthus virgatus</i> Progel in Mart.			x	<i>Adenolisianthus virgatus</i> Gilg
<i>Chelonanthus whitei</i> Rusby		x		

and ecological studies that would investigate these topics further would be undoubtedly hindered by the current, uncertain taxonomic status. One goal of this study is to provide evidence that can be applied to developing a circumscription that accurately reflects the evolutionary history of *Chelonanthus alatus*.

The present study utilizes two ribosomal nuclear gene regions, the 5S non-transcribed spacer (5S-NTS) and the internal transcribed spacer (ITS). Maximum parsimony and Bayesian inference will be used to deduce the inter- and intra-generic relations of *Chelonanthus*. This is the first phylogenetic analysis to include all currently recognized species of *Chelonanthus*, and with all species represented with multiple accessions, with the exception of *C. matogrossensis*. Based on the relationships revealed by Struwe et al. (in press), species in the closely related genera *Calolisianthus*, *Helia*, *Irlbachia*, *Symbolanthus* and *Tetrapollinia* were also included. The goals of the phylogenetic analyses are two-fold: 1) to achieve a resolved phylogeny, thereby increasing support for the generic relationships involving *Chelonanthus* and other closely related taxa, 2) testing the phylogenetic accuracy of *Chelonanthus alatus sensu lato*.

MATERIALS AND METHODS

Taxon Sampling

A total of fifty-five taxa were included in the phylogenetic analysis. Forty-four of those samples represented *Chelonanthus*, with seven samples representing *C. purpurascens*. Two specimens from the genus *Helia* were included, but efforts to amplify DNA from *Adenolisianthus* and *Rogersonanthus* were fruitless and prevented

inclusion. To resolve the Helieae polytomy involving the green-white lineage, eight samples from the genera *Calolisianthus*, *Symbolanthus* and *Tetrapollinia* were included. Due to the previously suggested sister relationship between *C. purpurascens* and *Irlbachia pratensis* (Struwe et al., 2002, in press), a sample of *I. pratensis* was included. A strategy to sample across *Chelonanthus* species' distributions as well as to include all morphological variation was implemented, but without complete success. All seven species recognized by Struwe et al. (1999) were included in the analysis, with two or more accessions representing each. The rare species *C. matogrossensis* was the exception, with only one sample present. The most widespread species, *C. alatus*, was represented by twenty-two samples, yet not all morphological variation observed in this species complex was sampled. Of the six morphotypes identified, four were included in the phylogenetic analyses, with no successful DNA amplification obtained from the other two. All fifty-five samples were represented in the 5S-NTS data matrix, but I was not able to amplify total ITS for some specimens and fifteen others were completely lacking for ITS. Even though there is missing data in the ITS matrix, all genera, species and morphotypes have at least one ITS representative (Table 3).

Molecular Analysis

Eleven samples of ITS were downloaded from Genbank, including species of *Calolisianthus*, *Chelonanthus*, *Irlbachia*, *Symbolanthus* and *Tetrapollinia* (Table 3). All remaining sequences were obtained using the protocols outlined below.

Total DNA was extracted with a DNeasy kit (Qiagen) using ca. 1 cm² of leaf tissue.

Mainly leaf material from herbarium specimens was used, or when available, from silica dried material. The DNeasy protocol was modified slightly in step 2 by adding 30

μl of β -mercaptoethanol instead of 4 μl of RNase A stock solution. The optional centrifuge in step 4 was always performed. These modifications follow the protocols developed at The New York Botanical Garden. Amplification of both genes was accomplished by polymerase chain reaction (PCR) in a GeneAmp® PCR System 9700 (Applied Biosystems) on 25 μl of solution containing 2.5 μl of bovine serum albumin (BSA 0.025 $\mu\text{g}/\mu\text{l}$). When amplifying 5S-NTS 5 μl of betaine (5M) was also used. The primers for 5S-NTS (forward: TGGGAAGTCCTYGTG-TTGCA and reverse: KTMGYGCTGGTATGATCGCA) were taken from Cox et al. (1992). The program ran an initial incubation of 2 min. at 94°C, then 27 cycles of 94°C for 1 min., 60°C for 1 min., and 72°C for 1 min. with the last cycle followed by 72°C for 4 minutes. ITS total (ITS1-5.8S-ITS2) was amplified when possible, but for problematic samples ITS1 and ITS2 were amplified separately with the use of internal primers. The ITS1 primers used were forward external: TATGCTTAAAYTCAGCGGGT and reverse internal: GCATCGAT-GAAGAACGTAGC and for ITS2 the primers used were forward internal: CGTACGTTCTTCATCGATGC and reverse external: AACAAGGTTTCCGTAGG-TGA. The external primers are described in Nickrent et al. (1994) and the internal primers are those developed by White et al. (1990). Other ITS primers (ITS5 & ITS2) described in White et al. (1990) and those described in Thiv et al. (1999) were attempted without success.

PCR products were run on 1% agarose gel to determine quality and quantity of product and then cleaned using QIAquick spin columns (Qiagen). Once purified, the PCR product was cycle sequenced using the same PCR primers and Big Dye terminator reaction mix (Applied Biosystems). The cycle sequencing program for 5S-NTS had an

Table 3: A list of species used in the phylogenetic analyses along with voucher location, collector and collector number, Genbank reference number (if ITS was downloaded from Genbank), collection location, indication of data type included, and if included in the Principle Component Analysis.

Taxon	Herb. voucher at	Collector #/Genbank accession number	Country, State	Location	5S NTS	ITS 1	ITS 2	PCA
<i>Calolisianthus amplissimus</i>	NY	Irwin et al. 26303	Brazil, Minas Gerais	Campo. Steep slopes, cerrado and campo, ca. 4km NW of Paracatu. Elev. 700 m.	x			
<i>Ca. speciosus</i>	NY	Anderson 10265	Brazil, Goias	Ca. 15 km (straight line) North of Corumba de Goias. Wooded hill of blocky quartzite outcrops and sandy, rocky cerrado at its base. Elev. 1250-1300 m.	x		x	
<i>Ca. speciosus</i>	NY	Reeves et al. 239	Brazil, Goias	Niquelandia. Southernmost ultramafic hill of Tocantine complex. Herb field in gully and lower part of hill slope. Rocky serpentine slope. Elev. 800 m.	x		x	
<i>Chelonanthus alatus</i> – <i>acutangulus</i>	US	Barclay et al. 3464	Colombia, Cundi-namarca	South of Silvania on toll road to Fusagasuga, near kilometer marker 37 turn W and proceed for 1 km on road to Tibacuy. Corillera Oriental. Elev. 1400 m.	x			x
<i>Ch. alatus</i> – <i>acutangulus</i>	MO	Gomez et al. 837	Colombia, Antioquia	Municipio de Tamesis, Antioquia. Vereda el Tabor, quebrada cerca a Rio Frio. Elev. 900-1000 msnm. 5°25' N, 75°30'30" W.	x	x	x	
<i>Ch. alatus</i> – <i>acutangulus</i>	US	Molina 13455	Honduras	Frecuente a orillas del bosque mixto y humedo de Montaña La Bellota 20 km al N.W. de Campamento.	x			
<i>Ch. alatus</i> – <i>acutangulus</i>	US	Bell & Wiser 88-36	Peru	Tambopata Reserve Zone. Bank of Rio La Torre near La Torre Trail. Sandy Soil. Full sun. 12°50' N, 69°17' W.	x	x	x	
<i>Ch. alatus</i> – <i>acutangulus</i>	US	Fosberg 56174	Peru	La Merced, on Rio Chanchamayo. Rare on very weedy brushy slopes.	x	x		
<i>Ch. alatus</i> – <i>acutangulus</i>	US	Pittier 12786	Venezuela, Merida	In bushes near Tovar.	x			

Table 3: Continued.

Taxon	Herb. voucher at	Collector #/Genbank accession number	Country, State	Location	5S NTS	ITS 1	ITS 2	PCA
<i>Ch. alatus</i> – <i>acutangulus</i>	NY	Grant & Struwe 01-4011	Ecuador	5 km S of Zamora towards PN Podocarpus (Bombuscara entrance). Disturbed overgrown roadside vegetation.	x	x	x	x
<i>Ch. alatus</i> – <i>acutangulus</i>	MO	Hawkes et al. 5048	Bolivia	North Yungas. 6 km from Coroico on road to Caranavi. On grassy banks by roadside.	x	x		
<i>Ch. alatus</i> – <i>acutangulus</i>	NY	Rimachi 320	Peru	Maynas: Dtto. Iquitos. Quebrada Aucaya, in periodically inundated or never inundated forest.	x			
<i>Ch. alatus</i> – <i>acutangulus</i>	US	Brummitt et al. 19339	Peru	Prov. Carrasco. Cerro el Salvador above Bula Bula; evergreen forest margin on low hills just above plain.	x	x	x	
<i>Ch. alatus</i> – <i>acutangulus</i>	CHRB	Riina 1397	Ecuador	25 km al NE de El Puyo en la via a Tena. Vegetacion secundaria herbacea a lo largo de la carretera. Elev. 900 m. 1°21'30" S, 77°56'10" W.	x	x	x	
<i>Ch. alatus</i> – <i>acutangulus</i>	CHRB	Riina 1427	Ecuador	Carretera Zamora-Jamboe, a 10 km de Zamora a las orillas del Rio Jamboe. Vegetacion secundaria herbacea. Elev. 960 msnm. 4°5'59" S, 78°56'43" W.	x			
<i>Ch. alatus</i> – <i>acutangulus</i>	CHRB	Riina 1446	Peru	500 m de CCNN Yullcunmax, 12 km de Cacazu, ca del Rio Yullcunmax. Vegetacion secundaria herbacea al lado de la carretera. Elev. 740 msnm. 10°34'12" S, 75°5'31" W.	x	x	x	
<i>Ch. alatus</i> – <i>acutangulus</i>	CHRB	Riina 1480	Peru	Paucartambo. Carretera Paucartambo-Pilcopata, ca. de la Reserva San Pedro. Bosque montano. Elev. 1800 msnm. 13°3'10" S, 71°32'20" W.	x	x		
<i>Ch. alatus</i> – <i>acutangulus</i>	MO	D'Arcy 9570	Panama	Cerro Campana.	x			x
<i>Ch. alatus</i> – <i>grandiflorus</i> - <i>petiolate</i>	NY	Maguire, B. et al. 60128	Brazil, Amazonas	Along Rio Cauaburi between Cachoeira Manãus and river camp.	x			x

Table 3: Continued.

Taxon	Herb. voucher at	Collector #/Genbank accession number	Country, State	Location	5S NTS	ITS 1	ITS 2	PCA
<i>Ch. alatus</i> – <i>grandiflorus</i>	US	Kelloff et al. 598	Guyana	Soesdyke-Linden Hwy, S. of Timehri Int'l Airport. White sand savana-sclerophyllous forest. Elev. 0-25 m. 6°16' N, 58°15' W.	x	x	x	x
<i>Ch. alatus</i> – <i>grandiflorus</i>	NY	Fonseca 177	Brazil, Pará	Belém, Maguaré, dentro da mata.	x			
<i>Ch. alatus</i> – <i>grandiflorus</i>	NY	Mori et al. 24076	French Guiana	Saül and vicinity, on road to airport. 3°37' N, 53°12' W.	x			
<i>Ch. alatus</i> – <i>grandiflorus</i>	NY	Mori et al. 25561	French Guiana	Nouragues Field Station and vicinity. Vicinity of Crique Cascade, c.a. 1.2 km S of Camp Inselberg. Open area by helicopter pad near hydroelectric dam. Elev. 200 m. 4°5' N, 52°40' W.	x	x	x	x
<i>Ch. alatus</i> – leafy-wing	NY	Vargas 454	Costa Rica	Canton de Turrubares. Valle del Tarcoles. Cabinas Vina del Mar. 200 m de la playa. 9°46'40" N, 84°32'10" W.	x	x		
<i>Ch. albus</i>	NY	Poole 2049/ EU709789	Brazil, Amazonas	Manaus-Pôrto Velho Highway: BR319, Manaus-Porto Velho Road, Km. 245, 3 km south of Igapó Açu, forest on terra firme.	x		x	
<i>Ch. albus</i>	NY	Alencar 686	Brazil, Amazonas	Morro dos Seis Lagos, ca. 80 km N. of Sao Gabriel. terre firme with many streams. 0°20' N, 66°45' W.	x			
<i>Ch. angustifolius</i>	US	Alencar 621	Brazil, Amazonas	Along Rio Curicuriari and Igarape Cariua to Cachoeira Piraiauara; igapo and caatinga. 0°20' S, 66°55' W.	x		x	
<i>Ch. angustifolius</i>	US	Molina 18S364	Colombia, Santander	En los alrededores de Lebrija en suelos secos y pedregosos. Elev. ca. 300 m.	x	x	x	
<i>Ch. alatus angustifolius</i>	MO	Wurdack & Adderley 43659	Venezuela, Amazonas	Cerro Cariche, sandstone hill near left bank of Rio Orinoco, halfway between Tama-Tama and San Antonio. Rio Orinoco. Elev. 125-150 m.	x		x	

Table 3: Continued.

Taxon	Herb. voucher at	Collector #/Genbank accession number	Country, State	Location	5S NTS	ITS 1	ITS 2	PCA
<i>Ch. alatus angustifolius</i>	MO	43552	Venezuela, Amazonas	Dome on the right bank of Rio Siapa just below Raudal Gallineta, open laja. Elev 130-900 m.	x			
<i>Ch. alatus - longistylus</i>	U	Maas 9316	French Guiana	Bagne des Annamites, km 15 on Route Departementale 5. Old secondary forest along white sand dike on poorly drained laterite clay.	x	x	x	
<i>Ch. alatus - longistylus</i>	NY	Berry 5541/ EU709790	Venezuela, Bolívar	La Escalera, km 119 S of El Dorado, pullover off road for Salto El Danto. Tall, moist forest. Elev. 1200 m.	x	x	x	
<i>Ch. alatus - longistylus</i>	US	Cowan 38834	French Guiana	Occasional along roadside. Montagne de Kaw. Elev. 250-270 m.	x			x
<i>Ch. matogrossensis</i>	NY	Solomon 7880	Bolivia	Prov. of Vaca Diez: 37 km E of Riberalta on Road to Guayaramerin. Grassy savanna with many shrubs and scattered gnarled trees 4-6 m tall. Elev. 230. 11°5 S, 65°45 W.	x		x	
<i>Ch. purpurascens</i>	US	Granville 11913	Suriname	Talouakem - Inselberg - Monts Tumuc-Humac. Isolated thickets within rocky savanna. Summit. In the thickets it's more significant.	x	x	x	
<i>Ch. purpurascens</i>	US	Jansen-Jacobs et al. 1388	Guyana	Gunn's, Essequibo River. Savanna. 1°39' N, 58°38' W.	x	x	x	
<i>Ch. purpurascens</i>	MO	Berry & Brako 5533	Venezuela, Bolívar	Gran Sabana, 11 km East of Kavanayen. 5°38'07" N, 61°41'35" W.	x	x	x	
<i>Ch. purpurascens</i>	US	Archer 2826	Suriname	From near Zanderij I in shaded places under bushes.	x	x	x	
<i>Ch. purpurascens</i>	US	Maas 7456	Guyana	Summit of Mt Makarapan. Thin gravely soil overlying granite rock covered with dense Clusia-dominated scrub, with patches of exposed bare rock.	x	x		

Table 3: Continued.

Taxon	Herb. voucher at	Collector #/Genbank accession number	Country, State	Location	5S NTS	ITS 1	ITS 2	PCA
<i>Ch. purpurascens</i>	US	Harley 15889	Brazil, Bahia	Serra do Sincorá. By Rio Cumbuca, ca. 3 km S. of Mucugé, near site of small dam on road to Cascavel. Riverside, damp sandy soil, sandstone rocks and partially burnt over vegetation.	x	x	x	
<i>Ch. purpurascens</i>	MO	Croat 74296	French Guiana	Along road between Cayenna and Regina Route de l'Est, N. 2, south of Cayenne P.K. 85, virgin forest near highway and secondary vegetation on road banks. Swampy area.	x	x	x	
<i>Ch. viridiflorus</i>	CHRB	Calió 83	Brazil, Minas Gerais	Gouveia: Rodovia Diamantina-Gouveia (BR 259), 300 m sul do entrocamento para Datas, a oeste da Rodovia. Capoa de mata com brejo circundante.	x		x	
<i>Ch. viridiflorus</i>	NY	Herringer et al. 4284	Brazil, Distrito Federal	Brasilia, Bacio do Rio São Bartolomeu. Mata ciliar umida e rala. Erva. Burmannia.	x			
<i>Ch. viridiflorus</i>	U	Chatrou 321	Bolivia	Prov. Velasco, Parque Nacional Noel Kempff Mercado, surroundings of Camp Los Fierros, road to El Reugio. Open savanna with clusters of shrubs, inundated during the rainy season.	x	x	x	
<i>Ch. viridiflorus</i>	US	Eiten & Eiten 1923	Brazil, São Paulo	Município de Moji-Guaçu: "Campos das Sete Lagoas." Fazenda Campininha, just north of Rio Moji-Guaçu. 3.7 km NNW of Padua Sales. About 27 Km NW of city of Moji-Mirim. General vegetation: camp cerrado on upland or very rarely forest. Open marsh field or dense secondary forest along the streams. The habitat: open, marshy field long west side of brook.	x			

Table 3: Continued.

Taxon	Herb. voucher at	Collector #/Genbank accession number	Country, State	Location	5S NTS	ITS 1	ITS 2	PCA
<i>Ch. viridiflorus</i>	NY	Anderson 9743	Brazil, Matto Grosso	Eastern base of mountain ca. 9 km NE of Barra do Garcas; gallery forest along stream and brejo (sedge meadow) and cerrado on slopes above; sandy soil and sandstone rocks. Elev. 450-500 m.	x	x	x	
<i>Ch. viridiflorus</i>	CHRB	Calió 84	Brazil, Minas Gerais	Joaquim Felicio: Serra do Cabral. Estrada Joaquim Felicio-Varzea da Palma, 15.5 km alem da ponte sobre o Corrego da Onca. Capao de mata com brejo circundante. Elev. 1132 msnm. 17°42'4"S, 44°15'50" W.	x		x	
<i>Irlbachia pratensis</i>	NY	Berry 7579/ EU709797	Venezuela, Amazonas	Sabaneta de Chiricoa, lower Rio Pacimoni, seasonally flooded shrubland on white sand. Elev. 120 m. 1°52'33"N, 66°35'35"W.	x	x	x	
<i>Helia oblongifolia</i>	NY	H. Irwin 21805	Brazil, Minas Gerais	Serra do Espinhaço, ca. 27 km SW of Diamantina on road to Gouveia; grassy meadow bordering gallery forest. Elev. 1300 m.	x	x	x	
<i>Helia oblongifolia</i>	NY	R. M. Harley 25924	Brazil, Bahia	Pico das Almas, vertente leste. 9-11 km ao NW da cidade. Brejo e área cultivada, solo arenoso. Elev. 1120 m. 13°32'S, 41°53'W.	x	x		
<i>Symbolanthus australis</i>	NY	Dorr et al. 6691/ EU709801	Bolivia, La Paz	Prov. Sud Yungas, 9 km from Huancané, on the road to San Isidro, "Bosque de alta montaña con Podocarpus", disturbed by logging. Elev. 2540 m. 16° 22' S, 67° 32' W.	x	x	x	
<i>S. frigidus</i>	NY	Cooley 8211/ AY143370	St. Vincent	Charlotte Parish, on the west slope of Soufriere Mountain among scrub vegetation.	x	x	x	

Table 3: Continued.

Taxon	Herb. voucher at	Collector #/Genbank accession number	Country, State	Location	5S NTS	ITS 1	ITS 2	PCA
<i>S. nerioides</i>	NY	Sobel & Strudwick 2164/AY143377	Venezuela, Mérida	Estanques - Paramis de los Colorados Road. Cloud forest in sheltered valley. Elev. ca. 2300 m.	x	x	x	
<i>S. pulcherrimus</i>	NY	J. F. Morales 16008/AY143379	Costa Rica, Cartago	Cantón del Guarco, Distrito de San Isidro, bosque secundario y robledales alterados en las cercanías de El Empalme. Elev. 2300 m. 9°43'04" N, 84°03'01" W.	x	x	x	
<i>Tetrapollinia caerulescens</i>	NY	H. Irwin 34170	Brazil, Goiás	Serra dos Pireneus, ca. 10 km. East of Pirenópolis. Wet campo slopes. Elev. 1000 m.	x		x	

initial incubation of 95°C for 1 min., then 32 cycles of 96°C for 10 sec., 50°C for 5 sec., and 60°C for 3 minutes. The cycle sequencing program for ITS had an initial incubation of 97°C for 1 min., then 30 cycles of 94°C for 1 min., 55°C for 1 min., and 72°C for 2 min., with the last cycle followed by 72°C for 4 minutes.

Sequencing reactions were then cleaned using Sephadex column purification and sequencing gels were run at the Rutgers University's sequencing facility at the Center for Biotechnology. Sequences were initially aligned using ClustalW2 (Chenna et al., 2003), with subsequent minor manual adjustments.

Phylogenetic Analysis

Phylogenetic analyses were performed with 5S-NTS and ITS in a combined matrix with insertions/deletions (indels) coded as present/absent. Inserted, consecutive base pairs, shared by two or more taxa, were considered a character and coded as present or absent. Indel coding provided an additional twenty-four characters of 5S-NTS and

seven characters of ITS to the combined matrix. Two analytical approaches were used to explore the data, maximum parsimony (MP) and Bayesian inference (BI).

The MP analysis was run in PAUP* 4.0b10 (Swofford, 2002), using the heuristic search option and TBR branch swapping. Searches employed 1000 random addition-sequence replicates. MaxTrees was set to 10,000. The number of rearrangements for each addition-sequence replicate was set to 1 million. The steepest descent option was not in effect. Zero length branches were collapsed and MulTree option was in effect. Multistate characters were interpreted as uncertain, characters were unordered and given equal weight and character optimization used Accelerated Transformation (ACCTRAN). Branch support was calculated with a jackknife analysis, using 1 million replicates employing the step-wise addition search option with a removal of 36.79% characters for each replicate (Farris et al., 1996).

MrModelTest ver. 2.2 (Nylander, 2004.) was used to determine the appropriate model parameter for 5S-NTS and ITS separately, using Akaike Information Criteria, a method determined to outperform the hierarchical likelihood ratio test for model selection (Posada & Buckley, 2004). The Bayesian inference (BI) analysis was run using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003, 2005). Separate data partitions were set-up for 5S-NTS, ITS and coded indels with the appropriate models of evolution applied to each. The model used for the indel partition was the MrBayes ver. 3.1.2 default for standard data. The analysis performed two runs of two million generations, with every 500 generations sampled. Four Markov Monte Carlo chains (3 cold and 1 warm) were run in the analysis. As suggested by the MrBayes 3.1 manual (Ronquist et al. 2005), the first 25% was discarded as "burn-in", with the remaining 6000 trees used

to construct a 50 % majority rule consensus tree with branch support represented as posterior probabilities. The consensus tree with posterior probabilities was constructed using TreeView ver.1.6.6 (Page, 1996).

Biogeography

The historical biogeography of the green-white lineage of *Chelonanthus* (including *Helia*) was estimated using the dispersal-vicariance analysis, which employs a set of algorithms that minimize dispersal and extinction events, while allowing for multiple and reticulate relationships between areas (Ronquist, 1997). The software DIVA ver. 1.1 (Ronquist, 1996) was used to reconstruct the ancestral distributions based on this model. The tree on which the ancestral history was estimated was chosen arbitrarily from one of the most parsimonious, fully bifurcating trees. The topology was reduced in such a way that each monophyletic group representing one species or morphotype was reduced to a single terminal. Taxa distributions were divided into six major plant regions, Amazon Basin (Ab), Andes (An), Brazilian Highlands (Bh), Caribbean (Car), Central America and Mexico (Ca), and Guayana Highlands (Gh).

Morphology and Principle Component Analysis

Over 1500 herbarium collections from AAU, COL, F, G, IAN, INPA, K, MG, MO, NY, S, SP, U, UPS, and US were surveyed to identify all morphological variants of *Chelonanthus alatus*. The abbreviations for herbaria follow *Index Herbariorum* (Holmgren & Holmgren, 1998). The terminology used to describe morphological structures follows Stearn (1983,1999) and was collected using a ruler, a caliper, or an ocular scale of an Olympus dissecting scope at 10X or 50X magnification. Ten characters were collected from 191 specimens, representing six morphotypes of *C.*

alatus and three of the fourteen type specimens treated as synonymous with *C. alatus* in previous literature (Table 2). Principle Component Analysis (PCA) is intolerant of missing data, therefore the remaining ten type specimens listed in Table 2 were excluded from the analysis due to missing characters.

Four of the morphotypes were similar in morphology and distribution to previously described taxa and were designated by the appropriate typified names. The morphotypes named in such a manner include *C. alatus* - *acutangulus*, *C. alatus* - *grandiflorus*, *C. alatus* - *longistylus* and *C. alatus* - *virgatus*. The two remaining morphotypes were not similar in morphology to any of the previously described names and were therefore given purely descriptive names. *Chelonanthus alatus* - "leafy-wing" was named to describe specimens with large stem wings that were visibly extensions of the leaf blade decurrent onto the stem. *Chelonanthus alatus* - "neoschomburgkii" specimens were unbranched herbs with leaves that had an obtuse apex. That name was chosen because the morphology follows the description of *C. schomburgkii* (Griseb.) Gilg found in the Flora of the Venezuelan Guayana (Struwe et al., 1999), but that description is not congruent with the type material for *C. schomburgkii*.

It is uncertain if *C. alatus* - *virgatus* is really part of this species complex. Maas (1985) and Pringle (1995) treated this name as part of *Adenolisianthus arboreus* (Progel) Gilg, which Maas considered a subspecies of *Irlbachia alata* (*C. alatus*). It is included here as part of *C. alatus*, because Struwe et al., (1999) listed *Lisianthus virgatus* Progel as a synonym after observing the type material. It is uncertain whether *Lisianthus virgatus* has closer affinities to the *C. alatus* species complex or to *Adenolisianthus*.

Ten morphological characters, composed of two qualitative characters coded as present/absent and eight continuous quantitative characters, are described as follows:

1. *Stem shape below inflorescence* (ssb). This character refers to the shape of the internode below the most apical leaf pair that subtends the inflorescence; it has two states, quadrangular with 4-wings/4-ridges or terete. To avoid redundancy, only one state was included in the analysis since a 0 for 'quadrangular' implied the stem was terete.
2. *Wing width below inflorescence* (wing_width_a). This was a measurement of the wings or ridges present on the internodes referred to above. Measurements were taken at 50X magnification.
3. *Length of inflorescence* (lg_infl). If more than one inflorescence was present, then the longest was measured in mm. The measurement was from the node of the most apical leaf pair to the bract of the most apical flower or flower bud.
4. *Length of 1st internode of inflorescence* (lg_1infl). Also measured in mm, this internode was found between the most apical leaf pair and the first dichotomous branching point in the inflorescence. If the inflorescence was monochasial, then the measurement was to the bract subtending the most basal flower or fruit.
5. *Length of 2nd internode of inflorescence* (lg_2infl). This internode was just above the one described previously; if more than one secondary internode was present, the longest was measured in mm.
6. *Apex shape of the bracts*. This character describes the apex of the bracts that subtend each flower and consists of three states, acute (bra_acut), acuminate (bra_acum), or

obtuse (bra_ob). To avoid redundancy, only the states bra_acut and bra_ob were include, since a code of (0) for both would imply the bract was acuminate.

7. *Length of calyx in fruit* (fr_cal_l). The calyx of mature capsules was measured at 10X magnification. Up to five calyces were measured and the average was taken for input into PCA.

8. *Length of calyx lobe in fruit* (fr_lob_l). A calyx lobe of each calyx described above was measured at 10X magnification and the average used in the PCA.

9. *Length of calyx in flower* (fl_cal_l). The calyx of mature flowers was measured at 10X magnification. Up to two calyces were measured and the average was taken for input into the PCA.

10. *Distance of sexual structures relative to base of corolla lobe* (dist_sex). The tip of the tallest sexual structure, stigma or anther, was measured at 10X relative to the point where the corolla lobes are no longer connate. The point at which the lobes were no longer fused was zero. If the tallest structure was below the base of the lobes, the value was negative. When two flowers were present, both were measured and the average of the two was used in the analysis.

Prior to analysis, continuous quantitative data was standardized by computing z-scores (Shaw, 2003). Since the characters used in the PCA were collected from separate morphotypes or populations, the assumption of normality was not met, but PCA has demonstrated to be robust to deviations from normality (Tabachnik & Fidell, 2001). A typical consequence of using highly skewed data is that the separation of points in the first two components is that of objects (species in this case) with extreme values from the rest, instead of based on the variation present in all objects of the study (Legendre,

1998). Since these data knowingly push PCA to its limits, the results should be viewed with some caution. The software SAS 9.1.3 (SAS Institute Inc.) was used to perform the PCA.

The Broken Stick Model, as described by Shaw (2003), was used as a measure of meaningful signal produced by each principle axis and therefore estimated the number of axes worth examining. Jackson (1993) examined many methods for determining how many useful components exist and concluded the Broken Stick Model (Frontier, 1976) performed the best. This method determines whether there is a signal or whether the distribution of points is due to random noise by comparing observed % variance to the expected Broken Stick value (calculated from the eigenvalues) for each axis. If the observed % variance is greater than the Broken Stick value, then the axis may contain useful information.

RESULTS

Phylogenetic Analysis

The alignment of 5S-NTS and ITS resulted in a data matrix totaling 1106 characters. Indels were coded from each matrix, adding 24 and 7 characters respectively, for a total of 1139 characters in the combined matrix. Of that total, 554 (49%) were variable and 391 (34%) were parsimony-informative. In the MP analysis, MaxTrees limit was met with 10,000 most parsimonious trees, each having a tree length of 1245, with a consistency index of 0.66 and a retention index of 0.86 (Figure 1). The BI 50% majority rule consensus tree (Figure 2) of 6,000 trees (after discarding 2000 as burn-in) was highly congruent with respect to the major species clades identified in the MP strict consensus tree. Differences in the topologies can be found in the position of terminals

within the species clades, as well as the placement of *C. alatus* "leafy-wing" and a petiolate form of *C. alatus* - *grandiflorus*. There is also a conflicting sister relationships involving the *Symbolanthus* clade and the *Calolisianthus*/*Tetrapollinia* clade.

The phylogenetic analyses strongly supported the polyphyly of *Chelonanthus*. The type species, *C. purpurascens*, was positioned in a clade with *Irlbachia pratensis* and *Calolisianthus amplissimus* (JK (jackknife value) = 100%; PP (posterior probability) = 1.0) and separate from the green-white flowered species. The inclusion of those three species together in a clade also indicates the polyphyly of *Irlbachia* and *Calolisianthus*. The clade containing the green-white lineage of *Chelonanthus* including *Helia* was strongly supported as monophyletic (JK = 86%; PP = 1.0).

The monophyly of *Chelonanthus albus*, *C. angustifolius* and *C. viridiflorus* was strongly supported by JKs of 100, 96, and 98, respectively, and with PPs of 1.00. All three species form a clade supported by 100% of the JK replicates and a PP of 1.0.

The four morphotypes of *C. alatus* were also strongly supported as separate lineages. *Chelonanthus alatus* - *acutangulus* (henceforth referred to as *acutangulus*) was placed in the most derived subclade and received strong monophyletic support (JK = 91%; PP = 1.0). Sister to the *acutangulus* clade was *C. matogrossensis* (JK = 96%; PP = 0.96). This most derived subclade, composed of *acutangulus* and *C. matogrossensis* was sister to *Helia oblongifolia*, receiving 98% JK support and a PP of 1.0. The morphotype *C. alatus* - *longistylus* (henceforth referred to as *longistylus*) was also strongly monophyletic (JK = 100%; PP = 1.0), but *C. alatus* - *grandiflorus* (henceforth referred to as *grandiflorus*) was polyphyletic with four of the five samples placed in one clade (JK = 100%; PP = 1.0) and uncertain placement of the fifth *grandiflorus* specimen.

Figure 1: 5S-NTS and ITS strict consensus tree of 10,000 most parsimonious trees, length = 1245 steps, CI = 0.66, RI = 0.86. Numbers to the right of each node represent jackknife values. Branches in bold, are those leading to clades or terminals currently classified as *Chelonanthus alatus*.

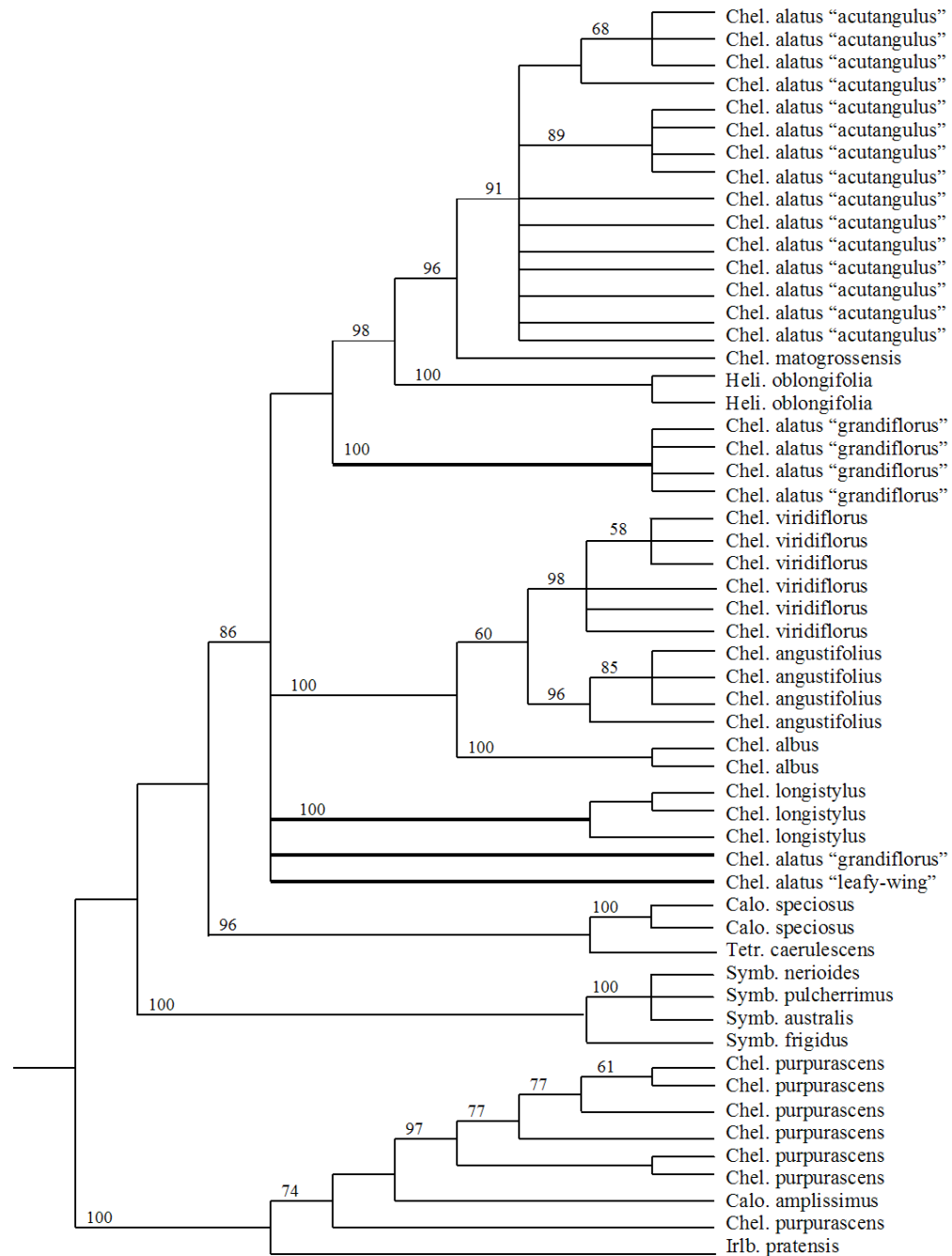
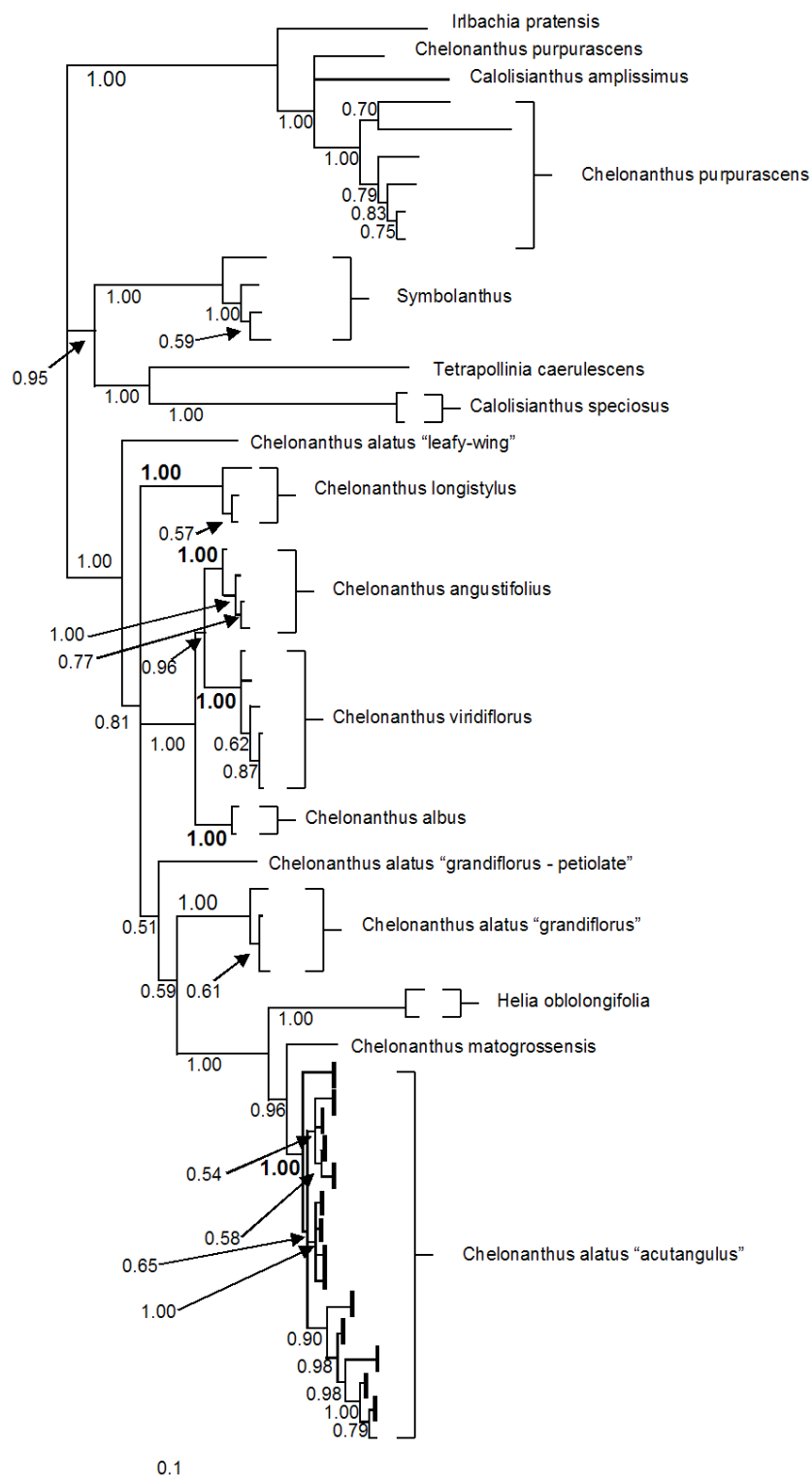


Figure 2: 5S-NTS and ITS Bayesian inference, 50% majority consensus phylogram of 6000 trees. Bold posterior probabilities represent support for monophyletic taxa of *Chelonanthus*.



The sister placement of the grandiflorus clade to acutangulus, *C. matogrossensis* and *H. oblongifolia* was found in both consensus trees but, with low support (JK > 50%; PP = 0.59). The MP analysis resulted in a polytomy involving the three major clades of the green-white lineage, the fifth grandiflorus specimen (henceforth referred to as petiolate grandiflorus) and the one specimen of *C. alatus* "leafy-wing" (hence forth referred to as "leafy-wing"). In contrast, the BI tree placed petiolate grandiflorus sister to the other grandiflorus, *Helia*, *C. matogrossensis* and acutangulus (PP = 0.51). In either case, grandiflorus was not monophyletic. The BI topology strongly placed the sample of "leafy-wing" as sister to the rest of the green-white lineage (PP = 1.0). The relationships between the major clades of the green-white lineage were not resolved in this study, with polytomies emerging in both trees.

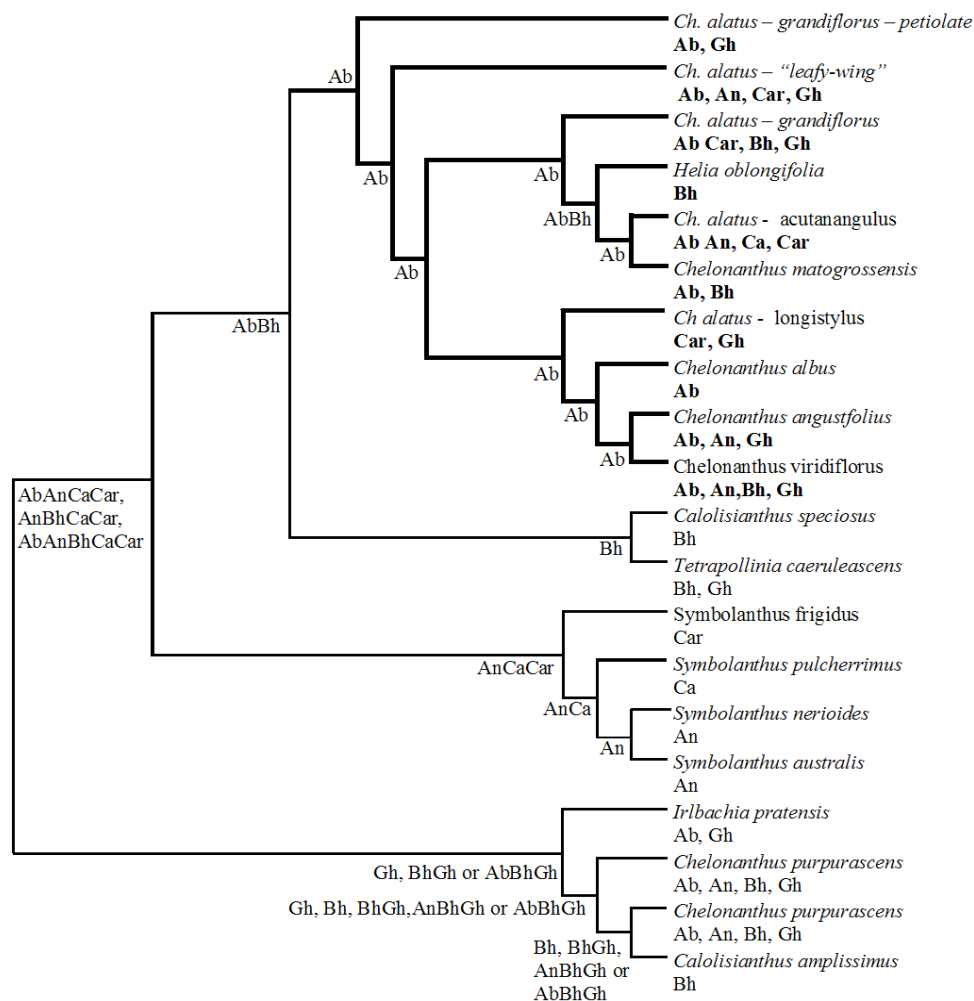
The clade containing *Calolisianthus speciosus* and *Tetrapollinia* (JK = 95%; PP = 1.0) was placed sister to the green-white lineage in the MP tree, although not well supported (JK > 50%). In contrast, the BI topology strongly supported (PP = 0.95) placement of this *Calolisianthus*/*Tetrapollinia* clade sister to the monophyletic *Symbolanthus* species (JK = 100%; PP = 1.0). The conflicting topologies suggest the relationship between these two groups and the green-white lineage including *Helia* need to be examined further. Based on both the MP and BI analyses, *Calolisianthus* is not monophyletic with the two *Calolisianthus speciosus* specimens sister to *Tetrapollinia* and *Calolisianthus amplissimus* nested within the *Chelonanthus purpurascens* (JK = 74%; BI = 1.0).

The outgroup included *Chelonanthus purpurascens* and *Irlbachia pratensis*. *Calolisianthus amplissimus* was also positioned in the outgroup in the rooted strict

consensus tree. The MP tree depicted a well-supported clade (JK = 97%), containing six of the seven *Ch. purpurascens* sampled. The relationship between *Ch. purpurascens* and *Ca. amplissimus* was not predicted. *Calolisianthus amplissimus* was nested within *Ch. purpurascens* in the MP topology (JK > 50%) and was represented as a polytomy in the BI tree (Figure 1 & 2). Sister to this *Ch. purpurascens*/*Ca. amplissimus* clade (JK = 74% and PP = 1.0) was *Irlbachia pratensis*, with 100% JK and 1.0 PP support.

Biogeography

The DIVA analysis was run with all taxonomic groups included in this study, but because a number of taxa were missing from the *Symbolanthus* subclade and DIVA's ability to reliably estimate centers of origin decreases as one approaches the root node (Ronquist, 1996), the results (Figure 3) will focus only on the ancestors pertaining to the green-white lineage of *Chelonanthus* and *Helia*. The hypothesized location of the ancestor to the green-white lineage was the Amazon Basin. The pattern of an Amazonian ancestor radiating outward and dispersing into the surrounding regions is repeated several times within this clade, with at least four separate dispersal events into the Guayana Highlands. The oldest movements into the Guayana Highlands involved an increase in the distribution of the ancestors to petiolate grandiflorus and "leafy-wing" to include that region. The ancestor to "leafy-wing" then spread to the Andes, Central America and the Caribbean. Similarly, the ancestor to the morphotype longistylus appears to have dispersed to the Guayana Highlands and from there to the Caribbean. A separate dispersal event involved the ancestor of *C. angustifolius* and *C. viridiflorus*, with a subsequent speciation. The derivative species dispersed in opposite directions, *C. angustifolius* to the north and *C. viridiflorus* to the south. The dispersal involving the



ancestor of *grandiflorus* could have been into the Guayana Highlands, but considering the ancestor to *Helia*, *C. matogrossensis* and *acutangulus*, from which it split, also occurred in the Brazilian Highlands, it seems more likely that the first dispersal was from the Amazon to the Brazilian Highlands. Once in the Brazilian Highlands, the ancestral population split and the lineage leading to *grandiflorus* spread into the Guayana Highlands and from there to Trinidad. A vicariance event involving the most recent common ancestor to *Helia*, *C. matogrossensis* and *acutangulus* appears to have occurred, with the decedents occupying more narrow ranges. The lineage leading to *Helia*, occupied the Brazilian Highlands, and the lineage leading to *C. matogrossensis* and *acutangulus* occupied the Amazon Basin. A speciation event occurred and the *C. matogrossensis* lineage colonized the Brazilian Highlands, an area previously occupied by its ancestors. The *acutangulus* lineage spread to the Andes, with subsequent dispersals into Central America and Mexico and to Grenada.

Morphology and Principle Component Analysis

The expected values from the Broken Stick Model (Frontier, 1976) indicated the first two components as worthy of inspection (Table 4). The first two components

Table 4: Percent variance explained by the first four principle components and expected Broken Stick values (Frontier, 1976) indicating the first two axes worthy of inspection.

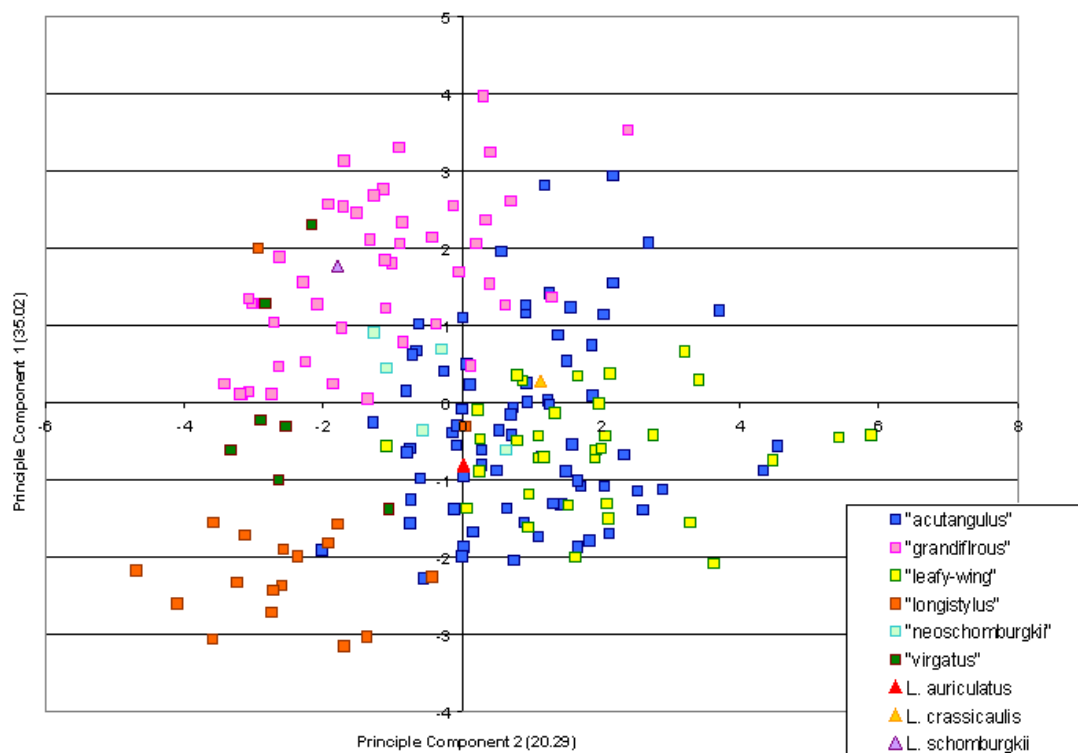
Principle Component	Percent Variance	Broken Stick Value
1	35.02	27.45
2	20.29	18.36
3	12.42	13.82
4	10.18	10.76

explain ca. 55 % of the variation present in the data. Although the third axis failed the Broken Stick Test, it will be considered here because of the strong eigenvector loading

(> 0.3; Table 5) observed for the character of sexual parts relative to the corolla lobe base. This is a crucial field character used in the identification of the "leafy-wing" morphotype, and this character has the weakest influence on segregating morphotypes of any character tested along the second component (eigenvector loading = 0.030502; Table 5). Therefore, it is the opinion of this author, that the risk of information lost by excluding component three from this paper is greater than the risk of false relationships conveyed by its inclusion. Considering the third axis in this discussion increases the variation explained by the data to ca. 68 %.

Plotting the first two components (Figure 4), one sees a separation of longistylus from most of the other points along the second axis. Segregation of the morphotype

Figure 4: Scatter plot of the first and second principle components resulting from a Principle Component Analysis of 191 observation and 10 characters. Numbers next to each axis represent the percent variance explained by that axis.



grandiflorus from acutangulus and "leafy-wing" also occurred along the second PCA axis. The eigenvector loadings for stem shape, and the three calyx measurements (calyx length in fruit and in flower and calyx lobe length in fruit) were largest for that axis (Table 5). There was a lack of clear separation of points along the first axis, but longistylus did separate from acutangulus, "leafy-wing" and *C. alatus* "neoschomburgkii" (henceforth referred to as "neoschomburgkii"). The characters with strong loadings on the first PCA axis include wing width, inflorescence measurements, and bract apex shape (Table 5). There was virtually no separation of acutangulus and "leafy-wing" based on the first two components. The squares representing the

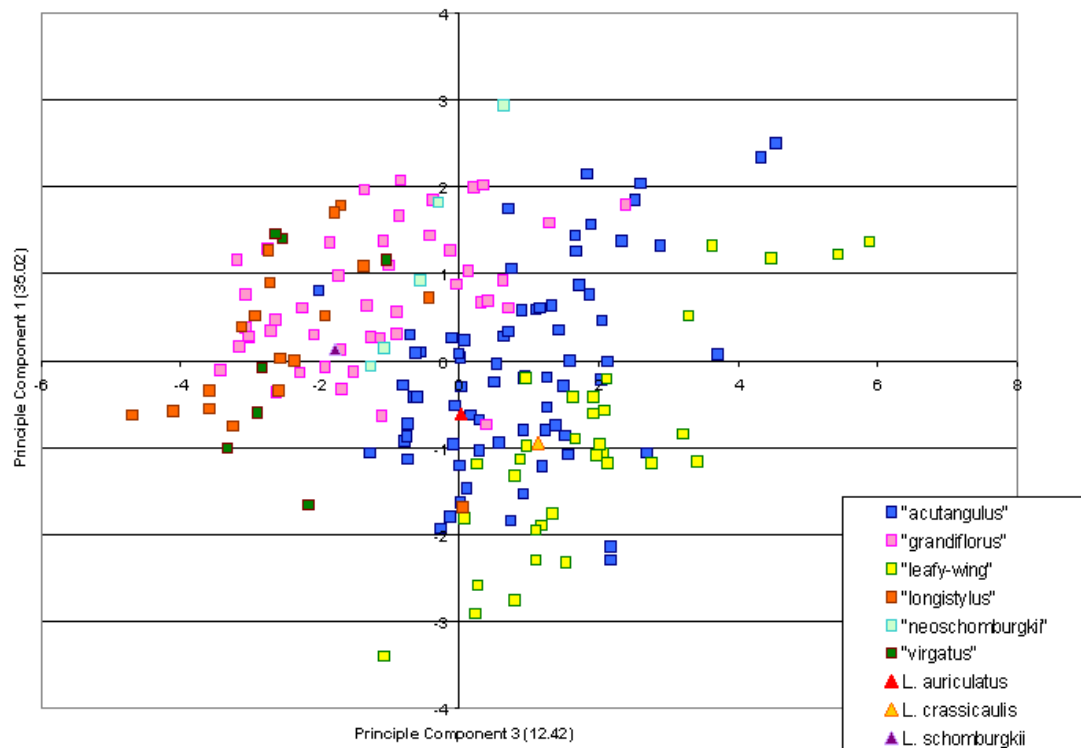
Table 5: Eigenvector loadings of each character onto the first three principle components. Values in bold represent loadings > 0.3.

Character Description	Principle Component 1	Principle Component 2	Principle Component 3
Stem shape below inflorescence	0.213719	-0.389386	-0.376447
Wing width below inflorescence	0.311454	-0.279076	-0.295053
Length of inflorescence	0.344749	-0.074358	0.561035
Length of 1 st internode of inflorescence	0.404837	-0.170493	0.261395
Length of 2 nd internode of inflorescence	0.364661	-0.117463	0.390357
Bracteole apex acute	0.376855	-0.119663	-0.238646
Bracteole apex obtuse	-0.303382	-0.168215	0.08436
Length of calyx in fruit	0.238649	0.512992	-0.080912
Length of calyx lobe in fruit	0.194332	0.467754	-0.019678
Length of calyx in flower	0.216937	0.443396	-0.161926
Distance of sexual structures relative to base of corolla lobes	-0.256432	0.030502	0.372214

morphotype "neoschomburgkii" are not at all segregated from grandiflorus, acutangulus or "leafy-wing" as those points cluster in an area where there is the greatest overlap

among the three later morphotypes. With the exception of two outliers, *C. alatus* virgatus (henceforth referred to as virgatus) forms a cloud of points separate from longistylus and grandiflorus along the second axis and from acutangulus and "leafy-wing" along the first axis. A comparison of PCA-1 and PCA-3 (Figure 5) shows a tightening of clusters along the third axis, providing better separation of acutangulus

Figure 5: Scatter plot of the first and third principle components resulting from a Principle Component Analysis of 191 observation and 10 characters. Numbers next to each axis represent the percent variance explained by that axis.



and "leafy-wing". The characters with the largest vector loadings on axis three are stem shape, length of total inflorescence and the second internode, and distance of sexual parts relative to the corolla lobe base (Table 5). The separation of longistylus observed on the second axis is completely void along axis three with no distinction between

grandiflorus and virgatus. The plot of PCA-2 and PCA-3 provided no additional information, and it is not included here.

DISCUSSION

Phylogenetic Analysis

THE OUTGROUP. The paraphyletic state of *Chelonanthus* presented by Struwe et al. (2002; in press) was supported by the results of this study. In addition, the close relationship between *Ch. purpurascens* and *Irlbachia pratensis* was well supported and congruent with earlier findings (Struwe et al., 2002; in press). It is clear that a recircumscription of the genus *Chelonanthus* is greatly needed. The inclusion here of *Calolisianthus amplissimus* within the *Ch. purpurascens* clade is the first to suggest that *Calolisianthus* is not monophyletic (Figure 1 & 2). *Ca. amplissimus* shares the trait of shedding pollen as polyads with *Ch. purpurascens* and *I. pratensis* (Nilsson, 1970; 2002). The Helieae phylogeny included *Ca. amplissimus*, *Ca. pendulus*, *Ca. pulcherrimus* and *Ca. speciosus* and determined the genus to be monophyletic with moderate support (Struwe et al., in press). The three latter species listed above shed pollen as tetrads. The conflicting results could be an artifact of missing data. In the Helieae paper *Ca. amplissimus* was included based only on morphological characters and in the current study was represented only by 5S-NTS. The evidence presented here is not conclusive, but reveals the need for further sampling. Should future studies support the inclusion of *Ca. amplissimus* within *Ch. purpurascens*, it will further support an evolutionary split between species shedding pollen as polyads vs. tetrads. In addition, it will have a taxonomic effect on the suggestion of Struwe et al. (in press) to recircumscribe a smaller *Chelonanthus* including *Ch. purpurascens* and *I. pratensis*.

Pringle (1995) designated *Ca. amplissimus* as the type species and *Chelonanthus* and *Calolisianthus* were first published simultaneously (Grisebach, 1839). Therefore, the question of what generic name to use for the new genus will have to be decided.

Ongoing revisionary work of *Calolisianthus* at the University of São Paulo should provide the evidence needed to better discern the inter- and intra-generic relationships of *Calolisianthus*.

CALOLISIANTHUS, TETRAPOLLINIA AND SYMBOLANTHUS. The relationships involving *Calolisianthus speciosus*, *Tetrapollinia*, *Symbolanthus* and the green-white lineage were not conclusive. The sister relationship between *Calolisianthus speciosus* and *Tetrapollinia caerulescens* was well supported in this study and congruent with the Struwe et al. (in press) topology based on ITS data. However, their combined analysis of only the taxa with molecular characters resulted in a trichotomy of *Calolisianthus*, *Symbolanthus* and *Tetrapollinia* (Struwe et al., in press). Morphological characters supporting a closer relationship between *Calolisianthus* and *Tetrapollinia* than to *Symbolanthus* include habit: unbranched herbs in *Calolisianthus* and *Tetrapollinia* vs. trees/shrubs or branched suffrutescent herbs of *Symbolanthus*, the presence of a corona at stamen insertion point in *Symbolanthus*, a characteristic that does not exist in the other genera and capsule type: woody vs. leathery or near berry-like, respectively (Struwe et al., 1999; 2002). The goal of this study was not focused on these genera and further sampling is needed before firm conclusions can be drawn.

The inclusion of *Symbolanthus* within *Chelonanthus* in phylogenies based solely on ITS data (Struwe et al., 2002; in press) was not supported here. In fact, the present study strongly supports *Symbolanthus* and the green-white *Chelonanthus* (including *Helia*) as

separate lineages, and is congruent with the small combined analysis from Struwe et al. (in press), which analyzed only the taxa represented by every data type. As mentioned by those authors, the majority of the taxa making up the *Symbolanthus* subclade can be divided into two groups: One group containing the green-white lineage of *Chelonanthus*, characterized by green-yellow-white flowers and flower buds with round apices, and another group containing *Symbolanthus*, *Calolisianthus* and *Tetrapollinia* characterized by blue-purple-pink-red flowers and flower buds with an acute apex. These morphological characters provide support for *Symbolanthus* and the green-white flowered *Chelonanthus* as separate lineages.

THE GREEN-WHITE LINEAGE. The well-supported monophyletic clade including *Helia* and the green-white lineage of *Chelonanthus* was in agreement with the relationship suggested by the Helieae study (Struwe et al., in press). However, the placement of *Helia* well within the green-white lineage was not suggested previously and is probably due to increased sampling in the current analysis. The Helieae paper of Struwe et al. (in press) included the species *C. alatus* morphotypes *grandiflorus* and *longistylus*, *C. albus*, and *C. viridiflorus*. Therefore, the relationship suggested by both studies between *Helia* and the four species sampled by Struwe et al. (in press) is not contradictory. The phylogenies presented here propose *Helia* as sister to the clade of *C. matogrossensis* and *acutangulus*, two taxa not included in the tribal study. The evidence presented here supports the suggestion of Struwe et al. (in press) to include the green-white lineage within the genus *Helia*. A morphology matrix needs to be included in a combined analysis so that *Adenolisianthus* and *Rogersonanthus arboreus* and *R. quelchii* can be included in a more complete study of the green-white lineage.

ALBUS, ANGUSTIFOLIUS AND VIRIDIFLORUS. All of the MP and BI trees contained a clade composed of *C. albus*, *C. angustifolius* and *C. viridiflorus*, and these three species have been consistently placed together in the past (Struwe et al., 2002; in press). Even though all three species are similar in appearance, it is difficult to find morphological characters unique to this clade. One character, stigma lobes that are round in shape, is a potential synapomorphy, but the shape of the stigma can change with maturity and the validity of this character, at this point, is uncertain. Most of the green-white lineage of *Chelonanthus* has quadrangular stems to varying extents and the three species here share predominantly terete stems, but this character is also found in *Helia* and *C. matogrossensis*.

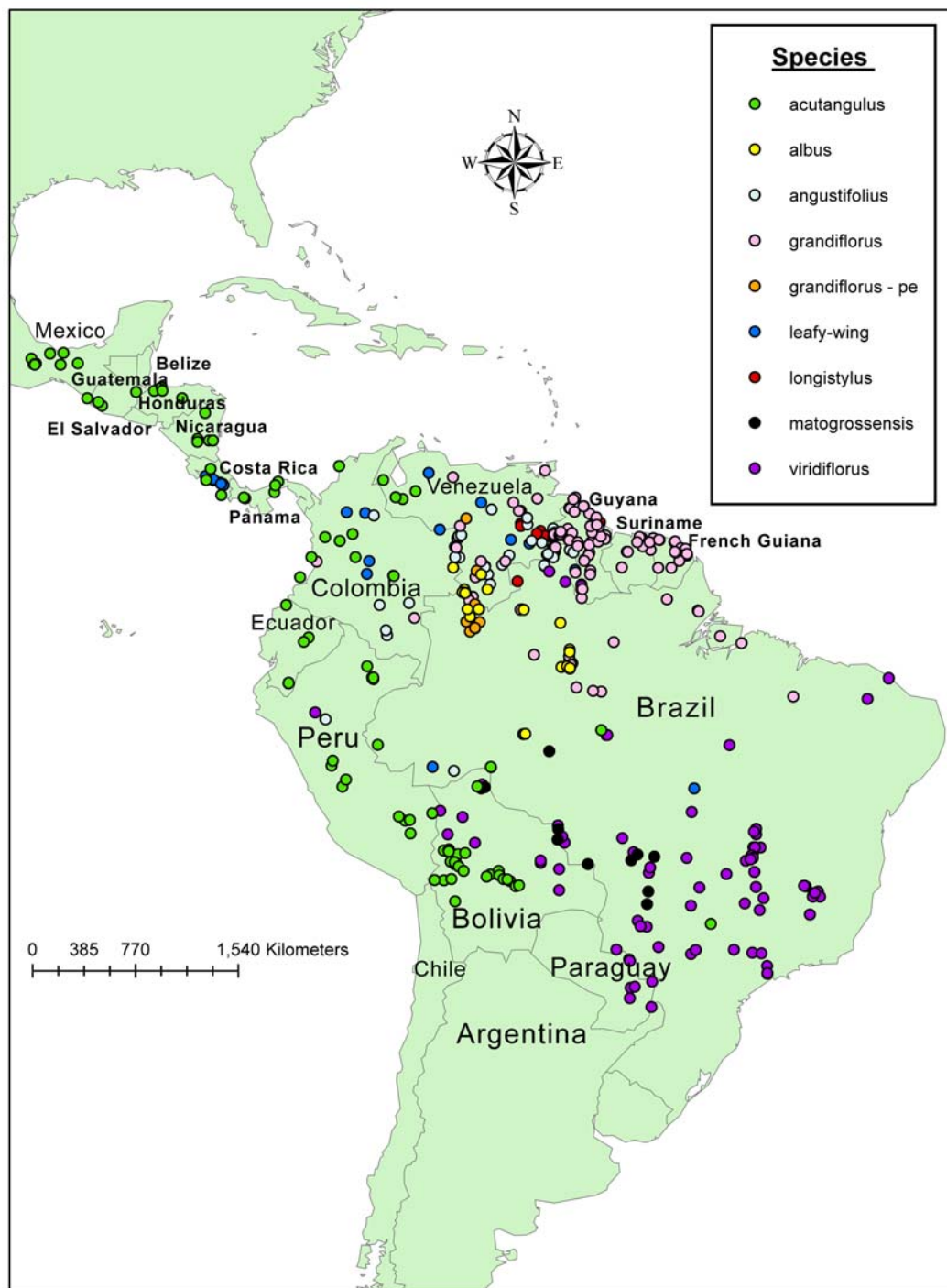
CHELONANTHUS ALATUS SPECIES COMPLEX. For the first time the taxonomic accuracy of *Chelonanthus alatus sensu lato* was tested using molecular phylogenetic methods. Four of the six morphotypes identified from a survey of more than 1500 herbarium specimens were included. The paraphyly of this species complex was strongly supported by the presence of three separate clades, the acutangulus clade, the longistylus clade and the grandiflorus clade (Figures 1 & 2). The fourth morphotype, "leafy-wing", was represented by a single specimen and its position was unclear, but it was not nested within the three well-supported clades.

The four *C. alatus* morphotypes included in the phylogenetic analysis are morphologically distinct and have separate yet overlapping distributions (Figure 6). The morphological characters distinguishing these morphotypes will be treated in detail in the PCA section of the discussion. The morphotype acutangulus was named for the type specimen *Lisianthus acutangulus* Ruiz & Pav., collected in Peru. The morphology

of that type and the specimens of *acutangulus* are clearly similar. The distribution of *acutangulus* is predominantly Andean, extending from Bolivia to Venezuela and north to southern Mexico as well as to the Caribbean Island of Grenada. The only other *C. alatus* morphotype found in the Andes and Central America is "leafy-wing", whose distribution covers the northern Andes of Colombia and Venezuela and extending as north as Costa Rica. These two morphotypes are also found in overlapping altitudes and habitats, but the reliable characters of plant girth, stem wing width, corolla shape, and position of sexual structures within the flower can be used to distinguish them.

From southern Central America and the northern Andes of Colombia and Venezuela, the distribution of the "leafy-wing" morphotype extends across the Guayana Highlands and the northeastern portion of the Amazon Basin, as well as to the Caribbean Island of Trinidad. The *C. alatus* morphotypes of *grandiflorus* and *longistylus* overlap in distribution with "leafy-wing" in the Guayana Highlands and Trinidad, with *grandiflorus* also overlapping in the Amazon Basin. As was the case with *acutangulus* and "leafy-wing", the three morphotypes compared here are found in similar habitats and altitudes, but differ in identifiable morphological characters. Again, these characters are discussed in detail below. The morphotype *grandiflorus* was not monophyletic with four specimens placed in a strongly supported clade and the fifth, a petiolate specimen, positioned in various places. The uncertain placement of the petiolate specimen is likely due to missing data, as ITS was completely lacking for this sample. Multiple shortest trees, unresolved consensus trees and uncertain placement of incomplete taxa are problems associated with missing data, but as Weins (2003) points out, the problem with incomplete taxa is not the number of missing characters; it is

Figure 6: Map illustrating the distribution of the green-white corolla species of *Chelonanthus* and the morphotypes currently included in *C. alatus* (based on 480 collections).



rather the dearth of characters used. Perhaps the addition of morphology and chloroplast markers will solidify the placement of the petiolate specimen as well as the "leafy-wing" specimen.

The phylogenies presented here (Figures 1 & 2) are based solely on rDNA markers; they are, in fact, gene trees. Funk & Omland (2003) provide several reasons or evolutionary mechanisms that could be the source of the apparent polyphyly described for *grandiflorus*. Misidentified specimens, inaccurate species limits, and inadequate phylogenetic information can potentially result in artifactual polyphyly. It is possible that the first two sources listed are at play, if the petiolate form of *grandiflorus* is a species in its own right. I do not believe this to be the case, as the PCA of morphological characters completely fails to segregate these samples from the rest of the *grandiflorus* points (Figure 7; see more detail below). Inadequate phylogenetic information is a potential problem, considering the petiolate specimen was included in the analysis, based only on the rapidly evolving 5S-NTS marker. As explained by Funk & Omland (2003), this can lead to "artifact" polyphyly if the gene evolves too rapidly, relative to speciation rates, resulting in a saturation of site changes and homoplasy. The inclusion of the more conservative ITS region could offset this problem, but efforts to include that marker were unsuccessful.

A potential problem with the ribosomal nuclear data is unrecognized paralogs resulting from gene duplication events (Funk & Omland, 2003). The tandemly repeated arrays of 5S-NTS and ITS are advantageous with respect to ease in amplification, but can also be a detriment to phylogenetic estimation if concerted evolution is incomplete, resulting in intra-individual paralogous polymorphisms (Cronn et al., 1996; Bailey et

al., 2003; Mort et al., 2007). At this point, the validity of the scenarios described is unknown, but they highlight some potential problems with this data set and the need to include additional character types (i.e. morphological, chloroplast DNA) in future analyses.

Biogeography

The fossil record for neotropical Gentianaceae is represented by a single pollen record of *Lisianthus* (Potalieae) from mid to late Eocene of Panama (Graham, 1984). The lack of fossil evidence prevents a direct estimation of the ancestral origin and divergence times. Therefore, the program DIVA was employed.

All of the internal ancestors are inferred to have had a distribution that includes the Amazon Basin supporting the hypothesis of an Amazonian origin for the green-white lineage of *Chelonanthus* and *Helia* (Figure 3). The inference concerning the ancestral distribution can be no better than the phylogeny on which it is based. Considering the uncertain placement of the two most basal taxa, "leafy-wing" and petiolate grandiflorus, along with the failure to include *Adenolisianthus* and the two *Rogersonanthus* species in the analysis, these results must be viewed with caution. The addition of *Adenolisianthus* to the phylogeny would probably not change the inferred ancestral distribution much given that *Adenolisianthus* occurs in the Amazon Basin and Guayana Highlands. Depending on their position in the phylogeny, the *Rogersonanthus* species could have an influence, since *R. quelchii* is an endemic to the Guayana Highlands and *R. arboreus* is found in the Guayana Highlands and Trinidad. It has been suggested that the areas with the highest diversity are the oldest (Stephens & Weins, 2003), based on the idea that the longer a clade is present in an area, the more time there is for speciation to take

place. If that were the case for the green-white lineage, then the Guayana Highlands would have the highest probability as a center of origin. If we consider the current distribution of all identified clades in the green-white lineage (including *Adenolisianthus* and the *Rogersonanthus* clade from Struwe et al., in press), nearly 75% of those clades are found in the Guayana Highlands. The observed diversity could very well be a function of the variety of altitudes and environments in that region. The large range in altitude (0-3000 m) found in the Guayana Highlands was described by Rull (2004) as an altitudinal succession of life zones, each with a characteristic plant community.

Morphology and Principle Component Analysis

The PCA provided morphological evidence for the segregation of several of the morphotypes within the *Chelonanthus alatus* species complex. In the scatter plot of PC-1 and PC-2, the separation of all but one longistylus point is clear (Figure 4). Stem shape was one of four characters with an absolute vector loading > 0.3 (Table 5). This morphotype has a strongly quadrangular stem and tends to retain that shape in the apical portions of the stem. The points representing grandiflorus, virgatus and "neoschomburgkii" all have terete stems (grandiflorus is quadrangular at the base) explaining the clear separation along PC-2. The stems of acutangulus and "leafy-wing" are also strongly quadrangular and account for the lack of separation between longistylus, acutangulus and "leafy-wing" along this principle axis. The measurements relating to the calyx in fruit and flower also explained much of the variation observed along PC-2. A useful field character for identifying the longistylus morphotype is calyx size in flower, relative to calyx size in fruit. In longistylus one often sees a calyx in

flower that is visibly smaller than the calyx in fruit. The flower calyx hugs the base of the corolla, with more tightly overlapping calyx lobes. While the calyx lobes in fruit are not flaring, the calyx lacks the restricted nature seen in flower. This character is not observed in the other morphotypes and therefore contributes to the separation of the longistylus specimens. While the measurements of calyx length in flower and in fruit, along with the length of fruit calyx lobes help to capture this difference, the inclusion of calyx width in flower and fruit would probably have been more useful measurements.

PC-1 explained much of the variation in wing/ridge width below the inflorescence. Study-wide, the range in wing width was between 0 and 1.0 mm. This character was not as helpful in distinguishing morphotypes as initially expected. All of the "neoschomburgkii" and most of the grandiflorus and virgatus specimens lacked wings or ridges and therefore occupied the 0 end of the spectrum. The lack of separation apparently results from specimens of the latter two morphotypes measuring in the lower (0.1 mm) range of this character. While most acutangulus and longistylus have larger stem wings, it was within their morphological range to have ridges as small as 0.1 mm wide below the inflorescence. Wing/ridge width of at least 0.2 mm and greater was only observed in acutangulus, longistylus and "leafy-wing", but the overlap explained above prevented better separation, based on this character. A better performing character could have been wing width of the stem base or a ratio explaining the difference between wing size at the base and the apex. The character of wing width at the base was not used, because too many herbarium specimens were missing this portion of the plant. The variation in measurements pertaining to the inflorescence also had large loadings on the first axis, but the variation in these characters was continuous and did not help to

designate discrete groups. The third character to have larger loadings on PC-1 was apex shape of the bracts. The apex shape of the bracts has some identifying merit, but it is not a totally reliable character. The morphotypes of *acutangulus* and "leafy-wing" have bracts with acute apices and in the latter group, appears to always be the character state present. This is also the case in *acutangulus*, except for populations from Mexico, which have obtuse apices. The character state observed in *longistylus* is largely obtuse, but acute has been observed. The *longistylus* specimen that fell well within the *acutangulus* cloud had an acute apex. In the majority of *grandiflorus* specimens the apex shape is acuminate, but acute and obtuse are also present. In the morphotype "neoschomburgkii", only obtuse apices have been found, but in *virgatus*, obtuse and acute are equally likely.

The most notable difference between the plots of PC-1 vs. PC-2 (Figure 4) and PC-1 vs. PC-3 (Figure 5) is a better separation of the *acutangulus* and "leafy-wing" points. The characters with strong loadings onto PC-3 include total length of inflorescence, length of second internode of inflorescence, and position of sexual structures relative to corolla lobes. As discussed above, inflorescence measurements are not helpful in discerning morphotypes. The position of sexual structures deep within the corolla tube is the "signature" character for the "leafy-wing" morphotype. All other morphotypes and species of *Chelonanthus* have sexual structures that are positioned around the corolla lobe area. Some taxa have structures that are exerted slightly beyond the lobes and others have sexual structures that are near the lobe base, but "leafy-wing" is the only taxon in *Chelonanthus* to have these structures deeply placed within the corolla tube.

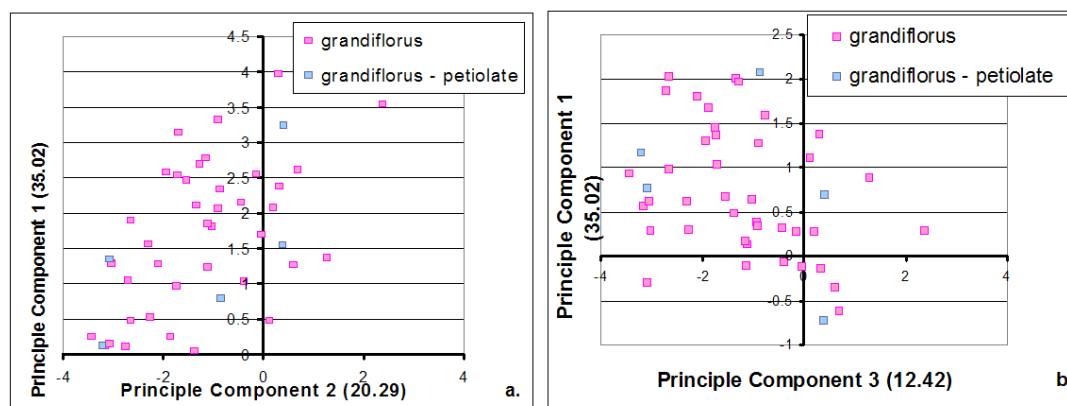
The PCA analysis does not support "neoschomburgkii" as a distinct morphotype and based on the plot of PC-1 vs. PC-2 (Figure 4), the placement of this taxon is unclear. On the other hand, PC-1 vs. PC-3 (Figure 5) and PC-3 vs. PC-2 (not shown) suggest the best placement within grandiflorus. The status of virgatus also remains unclear. A plot of PC-1 vs. PC-2 shows a nice separation of five specimens, but the other two fell well into the grandiflorus cloud and in PC-1 vs. PC-3 there was virtually no separation of the virgatus points from grandiflorus and longistylus. Considering that "neoschomburgkii" and virgatus were not included in the phylogenetic analysis, decisions on how to treat these troublesome specimens must await future studies.

In the phylogenetic analysis, the one petiolate grandiflorus specimen was not part of the monophyletic clade containing the rest of grandiflorus. Based on the morphological characters analyzed using PCA, petiolate and sessile grandiflorus specimens were not distinct (Figure 7). The only macro-morphological character differentiating these two taxa is petiolate vs. sessile leaves, a trait that is polymorphic in other (and undisputed) species of *Chelonanthus*.

The plots in Figure 4 and 5 place the type specimen of *Lisianthus schomburgkii* well within the cloud of grandiflorus specimens. The type specimens of *L. auriculatus* and *L. crassicaulis* are consistently placed in the PCA area where acutangulus and "leafy-wing" overlap. The type of *L. auriculatus* was collected in Colombia, so based on location, could be of either morphotype, but the sexual structures are not included within the corolla throat. Therefore it must be included as part of acutangulus. The type of *L. crassicaulis* was collected in Mexico, so it cannot be included in "leafy-wing",

based on range limits. When dealing with a species complex, the ability to place type material objectively into one group or another using PCA can be a valuable tool,

Figure 7: a) Scatter plot of the first and second principle components, as seen in Figure 5, but only the *Chelonanthus alatus* - grandiflorus points are shown. Different symbols indicating petiolate and sessile specimens are used to illustrate the lack of separation between the two. b) Same as in a), but based on the first and third principle components.



especially when you consider destructive sampling for inclusion in molecular studies is not permitted with obvious reason. The draw back to PCA is its inability to deal with missing values, a characteristic which prevented the inclusion of more type material into the PCA analysis.

In addition to the phylogenetic analysis, the morphological characters discussed above support *Chelonanthus alatus* - acutangulus, - grandiflorus, - longistylus, and - "leafy-wing" as distinct taxa. A residual question remains: "What is 'true alatus'?" The first description of *C. alatus* was vague (Aublet, 1775) and the condition of the type

specimen of *C. alatus* (at BM) is poor, with an inflorescence including only a portion of one calyx. Based on the first description and only vegetative characters observed in the type specimen, *C. alatus* could be one of several morphotypes. Once that question is answered, these distinct morphological variants can be dealt with. That work will be left for the revision of *Chelonanthus*.

CONCLUSION

This paper provides additional molecular evidence supporting the split of *Chelonanthus* between the purple-flowered type species, *Ch. purpurascens*, and the other green- to white-corolla species. The evidence presented here also supports a previous suggestion to revise *Chelonanthus* to include *Ch. purpurascens* and *Irlbachia pratensis*, but new evidence supporting the inclusion of *Calolisianthus amplissimus* in this group raises the question of what to name this new generic combination, *Chelonanthus* or *Calolisianthus*. This placement of *Ca. amplissimus* with *Ch. purpurascens* and *I. pratensis* in our phylogeny provides additional support of an evolutionary split between polyad and tetrad bearing plants. This evidence is also the first to suggest that *Calolisianthus* is not a natural group and highlights the need for further study. The placement of *Helia* well within the green-white *Chelonanthus* clade supports previous suggestions of a new generic circumscription of *Helia* to include the green-white lineage of *Chelonanthus*. The DIVA estimation of ancestral distribution for this group suggests the Amazon Basin as the point of origin, with multiple dispersals into the Guayana and Brazilian Highlands. This conclusion is tentative, as the inclusion of *Adenolisianthus* and *Rogersonanthus* in the analysis is necessary. Phylogenetic

analysis, combined with morphometric analysis, supports the split of the wide-ranging (and internally heterogeneous) species, *C. alatus*, into four separate taxa, but dealing with the taxonomic issues of doing so will be left to a future paper.

CHAPTER 2

A Monograph of the Neotropical Genus***Chelonanthus* Gilg (Gentianaceae: Helieae)²**

ABSTRACT

The first revision of the neotropical genus *Chelonanthus* (Gentianaceae: Helieae) is presented. This genus formerly encompassed seven species, but as a result of recent molecular and morphological studies, ten species are now recognized. Two names, *Chelonanthus acutangulus* and *C. grandiflorus*, are resurrected from the large species complex of *C. alatus*. A third hidden species, *C. pterocaulis*, from Central America and northeastern South America is identified from this complex and described here for the first time. A fourth species treated in Chapter 3, is *C. hamatus* from the Guayana Highlands of French Guiana and Venezuela. The name *C. longistylus*, previously considered a separate species, was found to be a synonym of *C. alatus sensu stricto*. The distribution of *C. alatus sensu stricto* includes only the Guayana Highlands and the Caribbean island of Trinidad. A new generic description is included to encompass characters not previously observed in this group. A taxonomic key to species using field-based characters has been developed, as well as ethnobotanical information and common names, when known, are listed. Morphological comparisons of species are discussed and historically confounding taxonomic issues are resolved.

² The new name included within this chapter is not accepted by the author as validly published in this dissertation (Botanical Code, Article 34.1[a]).

INTRODUCTION

The genus *Chelonanthus* Gilg is characterized by herbaceous annuals or perennials with slightly zygomorphic corollas that are green, white to yellow or blue to purple in color. They occupy mostly open, disturbed habitats in southern Mexico, through Central America and throughout most of South America. Like many of their gentian relatives, species of *Chelonanthus* are used medicinally by native people in the Neotropics for the treatment of a variety of ailments (Robinson & López, 1999; Bertani et al., 2005).

The current taxonomic status of *Chelonanthus* is in a state of chaos (Lepis et al. in progress; Chapter 1; Struwe & Albert, 1998; Nilsson, 1970) and fails to accurately reflect evolutionary relationships at the generic and species levels. Previous investigations focusing at the tribe Helieae (Struwe et al., 2002, in press) and on the subclade *Symbolanthus* (of Helieae; Lepis et al. in progress; Chapter 1) strongly support *Chelonanthus* as two separate lineages with the type species, *Chelonanthus purpurascens* (Aubl.) Struwe, S. Nilsson & V.A. Albert, closely related to *Irlbachia pratensis* (Kunth) L. Cobb & Maas (and possibly *Calolisianthus amplissimus*) and rest of the genus more closely related to the genera *Adenolisianthus* (Progel) Gilg, *Helia* Mart. and *Rogersonanthus* Maguire & Boom. Both studies strongly support the need to recircumscribe a narrow *Chelonanthus* to include *Ch. purpurascens* and *Irlbachia pratensis* with the evidence for the inclusion of *Calolisianthus amplissimus* inconclusive. As suggested by Struwe et al., (in press) the remaining species of *Chelonanthus* should be placed within *Helia*, the generic name with priority in that clade. In addition, Lepis et al. (in progress; Chapter 1) identified at least three hidden species within the highly variable species complex of *Ch. alatus* Aubl. (Pulle).

The evidence presented by Struwe et al. (in press) and Lepis et al. (in progress; Chapter 1) for redefining *Chelonanthus* and *Helia* is well supported, but incomplete. The Helieae study of Struwe et al. (in press) included all but one rare, recently identified genus (*Yanomamua* J. R. Grant, Maas, & Struwe; Grant et al., 2006) and was based on multiple gene markers as well as morphological data, providing a good estimate of the inter-generic relationships for the tribe, but inter-specific estimates are needed to accurately redefine *Chelonanthus* and *Helia*. The Lepis et al. (in progress; Chapter 1) paper focused on the genus *Chelonanthus*, sampling all species recognized in the Flora of the Venezuelan Guayana (Struwe et al., 1999) as well as morphotypes within the *C. alatus* species complex. Due to the intertwined nature of the polyphyly of *Chelonanthus* with other genera, *Calolisianthus*, *Helia*, *Irlbachia*, *Symbolanthus* and *Tetrapollinia* were also included, but *Adenolisianthus* and *Rogersonanthus* were not. In addition, M. F. Calió is currently investigating the species of *Calolisianthus* and *Helia*. When her studies are complete our work will be merged, resulting in a complete inclusion of taxa into the new circumscriptions of *Chelonanthus* and *Helia*. In the meantime, this revision is restricted to *Chelonanthus* in the traditional sense.

The three hidden species within the *Chelonanthus alatus* species complex include two resurrected species, *C. acutangulus* and *C. grandiflorus* and a new species described here for the first time, *C. pterocaulis* Lepis. In addition, a second new species from the Guayana Highlands, *C. hamatus* Lepis, was treated in chapter 3. The addition of these four taxa to *Chelonanthus* presents the need to recharacterize the genus. This paper is therefore a revision of the genus *Chelonanthus* as it is currently defined.

TAXONOMIC HISTORY

The genus *Chelonanthus* is one of the most taxonomically complex genera within the order Gentianales, although it is composed of only ten species. The name was first used by Grisebach (1839) as a section of the genus *Lisyanthus* Aublet (renamed *Lisianthus* in Grisebach, 1845), and was elevated to the status of genus by Gilg (1895). Throughout the literature, species and generic boundaries have constantly been debated with members of the genus alternatively being included within *Helia* Mart. (Kuntze, 1891), *Irlbachia* Mart. (Maas, 1985; Pringle 1995) and *Lisyanthus*/*Lisianthus* (Bentham 1839, 1854; Grisebach 1839, 1845, 1862; Jonker 1963; Kunth 1818; Lamarck 1792; Lemée 1950; Linné f. 1781; Martens & Gelotti 1844; Martius 1827; Progel 1865; Ruiz & Pavon 1799; Steyermark 1953). It must be noted that many of the references listed above cite Linnaeus (L.) as the author of *Lisianthus*. This is due to the creation of a homonym in Grisebach (1845) between *Lisyanthus*/*Lisianthus* in Aublet's sense and *Lisianthus* in Linnaeus' sense. Look to Lepis et al. (Chapter 1), Nilsson (1970) and Struwe & Albert (1998) for a more detailed discussion of this homonymic relationship. This history of name changing has also led to a long list of synonyms associated with the species of *Chelonanthus* (Table 1 & 2).

MATERIALS AND METHODS

The morphological characters presented here were collected from pressed material. More than 1500 collections (many of these duplicates) were examined from the following herbaria: AAU, COL, F, G, IAN, INPA, K, MG, MO, NY, S, SP, U, UPS, and US. For rehydration, pressed flowers were soaked in a solution of 70% ethanol and

glycerol for several days before observation. All measurements were observed using a ruler, caliper or ocular scale of an Olympus dissecting scope at 10X or 50X magnification. The terminology used to describe structures follows Stearn (1983, 1999). Abbreviations for herbaria follow *Index Herbariorum* (Holmgren & Holmgren, 1998).

With the exception of the new species described here, *Chelonanthus pterocaulis*, data for pollen characters were taken from Haquet (2007), Lepis et al. (in progress; Chapter 3), Maguire & Boom (1989) and Nilsson (1970, 2002). Since the taxonomic status of species in this genus has been in continuous flux, characters were only taken from the above references when pollen data was collected from vouchers that were determined as part of this study. Voucher information for *C. pterocaulis* as well as the vouchers used in the references listed above with a comparison of species identification between those references and this treatment can be found in Appendix A. *Chelonanthus matogrossensis* is lacking pollen data due to its rarity and the lack of appropriate herbarium material. Pollen grains were coated using a Hummer X Sputter System by Anatech LTD for two minutes. Characters were observed using a Hitachi S-510 scanning electron microscope at 800X magnification.

Seed testa characters were taken from Bouman et al. (2002) for the species *C. alatus* (determined as *C. longistylus* by Bouman et al., 2002), *C. albus*, *C. angustifolius*, *C. matogrossensis*, *C. purpurascens* and *C. viridiflorus* and from Lepis et al. (in progress; Chapter 3) for *C. hamatus*. The determination of specimens used in Bouman et al. (2002) was reviewed and in agreement with this treatment for all seed data used. Testa cell characters for *C. acutangulus*, *C. grandiflorus* and *C. pterocaulis* were collected using methodologies similar to those outlined for pollen above, with the exceptions of

seeds coated for three minutes and characters observed at 80X magnification. Voucher information can be found in Table 6.

Table 6: A list of herbarium specimens from which seed characters were collected using scanning electron microscopy.

Species	Collector, coll. number	Herbarium	Country of origin
<i>Chelonanthus acutangulus</i>	Barclay, 3464	US	Colombia
<i>C. acutangulus</i>	Simpson & Schunke, 651		Peru
<i>C. grandiflorus</i>	Irwin et al., 55510	NY	Suriname
<i>C. grandiflorus</i>	Pipoly and Lall, 8388	MO	Guyana
<i>C. pterocaulis</i>	Goodland, 256	US	Guyana

TAXONOMIC TREATMENT

Chelonanthus Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 98. 1895. TYPE: *Chelonanthus purpurascens* (Aubl.) Struwe, S. Nilsson, & V.A. Albert.

Plants erect herbs (rarely prostrate in *C. purpurascens*) to subshrubs (rarely vines in *C. albus*), 0.2-3.0 m high, glabrous. *Stems* usually unbranched to sparsely branched or less often distinctly branched, quadrangular and 4-winged to terete, smooth (foveate in *C. matogrossensis*). *Leaves* cauline, evenly spaced (except the internode between the two most apical set of leaves visibly longer), sessile to shortly petiolate, ovate, elliptic, obovate, lanceolate, oblanceolate, linear, rarely orbicular, glabrous, sometimes glaucous in *C. albus*; petiole 0-2.0 cm long; base of lower leaves most often attenuate (cuneate in *C. angustifolius* and *C. matogrossensis*, rarely perfoliate in *C. pterocaulis*); base of upper leaves obtuse, acute to truncate (often connate to perfoliate in *C. pterocaulis*); margins entire, membranaceous (rarely coriaceous in *C. angustifolius* and *C. purpurascens*), flat; venation arcuate, raised on underside of leaf, with 1-2(-3) pairs of

well developed secondary veins; apex acute, acuminate to obtuse. *Inflorescence* a terminal cyme, monochasial or with 1-3(-4) dichasial branches basally diverging into 2 or more monochasial branches; bracts scale-like (sometimes leaf-like when subtending most basal flower). *Flowers* pedicellate, 5-merous, sexual parts zygomorphic with stamens and style bent toward bottom of corolla mouth (clustered together in corolla throat in *C. pterocaulis*). *Calyx* campanulate, green, basally fused for 1/6-4/5 of total length, coriaceous, persistent in fruit; lobes circular, ovate, elliptic to obovate, not winged or keeled (small wings present in *C. hamatus*); apex obtuse (acute apex present in *C. purpurascens* and *C. viridiflorus*); margin hyaline, papillose, dorsal glandular area present (in *C. hamatus* hook present at apex of each dorsal glandular area). *Corolla* campanulate, funnelform, tubular, to salverform, when campanulate often ventricose, green, yellow to white or purple to blue, 18-87 mm long, fused for 3/5-6/7 of total length, thin membranaceous; bud apex rounded (sometimes acute in *C. purpurascens*); lobes erect to reflexed in mature flowers; lobes ovate to circular; lobe apex mostly obtuse (may be acute or acuminate in *C. angustifolius* and acute in *C. viridiflorus*), often with a darker apical spot (not observed in *C. purpurascens*); margins papillose. *Stamens* zygomorphic inserted in corolla tube at 1/6-5/8 of total corolla length from the base (near midpoint in *C. grandiflorus* and *C. matogrossensis*); filaments unequal to subequal (within 2 mm) in length, winged or filiform, after anthesis straight to curved downward apically, base usually without specialized structures, staminal gaps present or absent in *C. acutangulus* and *C. grandiflorus*, corona present in *C. hamatus*; anthers elliptic to slightly ovate, obovate, or oblong, with apical sterile appendage, after anthesis straight to curved; pollen in tetrads (polyads in *C. purpurascens*). *Gynoecium* with nectary disk at base; ovary

ellipsoid, bicarpellate, with inrolled placentas; style long, slender, filiform, when dry often flattened and twisted, persistent or deciduous in fruit; stigma bilamellate, with elliptic, obovate, linear to orbicular lobes. *Fruit* capsular, dehiscence medially septicidal; calyx persistent in fruit; corolla persistent, partially persistent or deciduous in fruit. *Seeds* many, angular-cuboidal, 0.1-0.6 mm in diameter; testa cells dome-like and/or concave with or without band-like thickenings.

Habitat and Distribution. Guayana Highlands, Brazilian Highlands (with one species, *C. viridiflorus*, reaching Paraguay and northeastern Argentina), Caribbean islands of Trinidad and Grenada, Amazon Basin, Andes from Bolivia to Venezuela and Central America (with one species, *C. acutangulus*, through Nicaragua to southern Mexico). Moist forests, forest openings and edge, wet to dry savannas, riversides and roadsides, sometimes in caatinga and cerrado type vegetation. Most often found in low nutrient, white sand soils, but may also be found in clay, lateritic or rocky soils. Altitude range: 0-3500 m.

Number of species. Ten species.

Etymology. The name *Chelonanthus* was first used by Grisebach (1839) to represent a section of the genus *Lisyanthus* Aubl. In that publication Grisebach did not explain the origin of the name, but in Greek "chelone" or "Khelone" means tortoise and may have been chosen to reflect the ventricose shape of the corolla found in several species. Linnaeus used the name *Pentstemon chelonoides* in 1775 to describe a specimen (Dalhberg 141 - LINN) considered a synonym of *Chelonanthus grandiflorus*. On that herbarium sheet the genus *Chelone* L. was also noted. Perhaps Grisebach studied this

specimen and was influenced by the note or choose *Chelonanthus* to reflect the similarities in corolla shape with the genus *Chelone*.

KEY TO THE SPECIES OF CHELONANTHUS

- 1 Corolla blue, purple to lavender, sometimes with white throat, without any markings on the tips of lobes; pollen shed as polyads *purpurascens*
Corolla green, yellow to white with darker spots on the tip of each lobe; pollen shed as tetrads 2
- 2 Stems foveate *matogrossensis*
Stems smooth 3
- 3 Stems terete to weakly quadrangular, or with only 3-4 of the most basal internodes quadrangular and 4-winged 4
Stem strongly quadrangular, 4-angled to 4-winged along entire length 6
- 4 Stem quadrangular for 3-4 of the most basal internodes then abruptly becoming terete (Colombian populations with terete, 4-ridged stem for 3-4 of the most basal internodes); stamens inserted into corolla above midpoint, staminal gaps present/absent *grandiflorus*
Stem terete to weakly quadrangular along entire length; stamens inserted near base of corolla; staminal gaps absent 5
- 5 Stem usually branched with 2 or more branching nodes below the inflorescence; mature capsule horizontal to nodding; corolla deciduous in fruit *albus*
Stem usually unbranched or with 1 branching node below the inflorescence; mature capsule horizontal to erect; corolla persistent to partially persistent in fruit 7
- 6 Sexual structures positioned within corolla tube; corolla tubular to salverform; mature capsule erect to horizontal; calyx lobes orbicular *pteroaulis*
Sexual structures positioned in corolla mouth or protruding from it; corolla funnelform to campanulate; mature capsule nodding; calyx lobes ovate 8
- 7 Leaves elliptic to ovate; calyx lobes fused for 1/6-1/5 of total length *viridiflorus*
Leaves linear, sometimes narrowly lanceolate to narrowly elliptic; calyx lobes fused for c. 4/5 of total length *angustifolius*
- 8 Calyx lobes dorsally winged with upward facing hook near lobe apex; corona present at insertion point of stamens into corolla *hamatus*

- Calyx lobes without dorsal wings or hooks; corona absent, sometimes with staminal pockets 9
- 9 Corolla usually with reflexed lobes in mature flowers; stigma not exerted beyond corolla; stamens unequal in length; corolla constrained below insertion point of stamens and inflated above *acutangulus*
 Corolla with erect lobes; stigma often exerted beyond the corolla; stamens subequal in length (within a 2 mm length difference); corolla constrained well above insertion point of stamens *alatus*

1. ***Chelonanthus purpurascens*** (Aubl.) Struwe, S. Nilsson, & V.A. Albert, Harvard

Papers in Botany 3: 70. 1998. -*Lisyanthus purpurascens* Aubl., Hist. Pl. Guiane 1: 201-202, t. 79. 1775. -*Helia purpurascens* (Aubl.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Irlbachia purpurascens* (Aubl.) Maas, Proc. Kon. Ned. Akad. Wetensch., Ser. C., 88 (4): 408. 1985. TYPE: French Guiana, Aublet s.n. (holotype BM [n.v.]; isotype P [n.v.]

- *Lisianthus amoenus* Miq., Linnaea, ser. 1, 19: 139. 1846. -*Helia amoena* (Miq.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: Suriname, Para, Focke 999 (holotype U [photo U]).
- *Lisyanthus gracilis* Griseb., Gen. Sp. Gent.: 182-183. 1839. -*Helia gracilis* (Griseb.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: St. Vincent, Guilding 356 (holotype K [photo U]).
- *Lisianthus spruceanus* Benth., Hooker's J. Bot. Kew Gard. Misc. 6: 202. 1854. - *Helia spruceana* (Benth.) Kuntze, Rev. Gen. Pl. 2: 427. 1891. -*Chelonanthus spruceanus* (Benth.) Gilg in Koch-Grünberg, Zwei Jahre den Indianern 2: 31. 1910. TYPE: Brazil, Amazonas, São Gabriel, Rio Negro, Spruce 2304 (holotype K; isotype W [photo U]).
- *Lisyanthus uliginosus* Griseb., Gen. Sp. Gent.: 181-182. 1839. -*Helia uliginosa* (Griseb.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Chelonanthus uliginosus* (Griseb.) Gilg, Nat. Pflanzenfam. 4(2): 98. 1895. TYPE: Brazil, Bahia, Salzmann s.n. (lectotype G [photo U]; lectoisotype K [lectotype designated by Pringle 1995]).

Plants erect (rarely prostrate), herbs to subshrubs, up to 2.7 m high. *Stems* sparsely to distinctly branched, terete to weakly quadrangular 4-angled to 4-winged; branches up to 5 mm in diameter; internodes 0.5-15.1 cm long; wings 0.1-0.4(-1.0) mm wide.

Leaves membranaceous (rarely coriaceous), sessile to shortly petiolate; petiole 0-20 mm long; blade elliptic, ovate to lanceolate (rarely orbicular), 1.0-13.3 x 0.4-5.1 cm; base of lower leaves attenuate, base of upper leaves attenuate, acute or obtuse; apex acute to acuminate, rarely obtuse. *Inflorescence* dichasial or monochasial, 1-39-flowered; bracts ovate or oblong, 0.1-3.2(-5.7) mm long; apex acute if ovate or obtuse if oblong. *Flowers* horizontal to nodding, pedicels 4-20 mm long. *Calyx* campanulate, 4-10 x 3-6 mm, fused 1/2 of total calyx length; lobes ovate to orbicular, 2-5 x 2-3 mm; lobe apex acute to obtuse. *Corolla* funnelform to tubular, sometimes nearly campanulate, 18-72(-87) mm long, 9-36 mm wide at mouth, blue, purple to lavender, inner side of throat sometimes white, deciduous in fruit; lobes ovate to orbicular, 5-17 x 3-14 mm, erect in mature flowers; lobe apex obtuse to acute. *Stamens* inserted in corolla tube near base at 1/5-1/4 of total corolla length, not exserted, or sometimes the longest stamen exceeds the corolla mouth slightly; filaments filiform or winged, unequal, 16-45 mm long, after anthesis strongly curved apically; anthers oblong, 2.6-6.7 mm long, white, yellow or orange, after anthesis recurved; pollen exine differentially reticulated with polar loops (fide Maguire & Boom, 1989; Nilsson, 1970, 2002). *Gynoecium* 27-44 mm long; ovary narrowly ellipsoid, 4.0-5.4 x 1.2-1.3 mm; style 20-50 mm long; stigma lobes elliptic, 1.9-5.4 x 0.7-2.1 mm. *Capsule* ellipsoid, 6-20 x 3-9 mm, brown, horizontal to nodding. *Seeds* angular-cuboidal, 0.1-0.4 mm in diameter, brown; testa cells dome-like and/or concave with band-like thickenings (fide Bouman et al., 2002).

Phenology. Flowers and fruits collected year-round.

Habitat and Distribution. Guayana Highlands of Brazil (Pará and Roraima), Colombia, French Guiana, Guyana, Suriname and Venezuela, Brazilian Highlands (Brazil: Bahia, Espírito Santo, Maranhão, Mato Grosso, Minas Gerais, Paraíba, Paraná, Pernambuco, Rio Grande do Norte, Rio de Janeiro and São Paulo), Amazon Basin of Bolivia, Brazil (Acre, Amapá, Amazonas, and Pará), Colombia, Peru, and Venezuela, Andes of Bolivia, Colombia, Ecuador, and Peru, and Caribbean island of Trinidad (Figure 8). Commonly found in moist forests, forest edges, gallery forests, savannas and along rivers. Rarely found in cloud forests, campo rupestre, scrub type vegetation, and along roadsides. Most commonly found in white sand, low nutrient soils and rocky soils and rarely found on clay or lateritic soil. Altitude range: 0-3500 m.

Vernacular names. Pemón: Wakauyek (Venezuela, Bolívar); Papai-nicolau (Brazil, Bahia); Wild tobacco (Guyana).

Ethnobotany. In Guyana an infusion of the leaves was used by the Arawaks for smallpox (teste Harrison 1345), and has been used against fungal infections (teste Hoffman & Patterson 878).

2. **Chelonanthus matogrossensis** (J.M.G. Pers. & Maas) Struwe & V.A. Albert, Harvard Papers in Botany 3: 70. 1998. -*Irlbachia alata* (Aubl.) Maas ssp. *matogrossensis* J.M.G. Pers. & Maas in Maas, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 88(4): 410. 1985. TYPE: Brazil, Mato Grosso, Barra do Arica, near Cuiaba. In sandy semi-humid cerrado, Malme 3254 (holotype S [photo U; photo published in Maas, 1985]).

Figure 8: Map illustrating the distribution of *Chelonanthus purpurascens* (based on 158 collection sites).



Plants erect herbs to subshrubs, up to 2.0 m high. *Stems* sparsely branched to distinctly branched, terete; branches up to 9.3 mm in diameter; internodes 2.1-22.8 cm long; wings absent. *Leaves* membranaceous, sessile; blade ovate, elliptic to orbicular, 2.0-12.3 x 1.8-7.8 cm; base obtuse to cuneate; apex obtuse. *Inflorescence* dichasial or monochasial, 9-25(-46)-flowered; bracts ovate, 1.6-3.5(-6.2) mm long; apex acute. *Flowers* horizontal, pedicels 4-8 mm long. *Calyx* campanulate, 6-10 x 4-8 mm, fused 1/3-2/3 of calyx length; lobes ovate, 3-6 x 3-5 mm; apex obtuse. *Corolla* funnelform, 18-31 mm long, 13-23 mm wide at mouth, green to cream, persistent in fruit; lobes ovate, 5-7 x 6-9 mm, erect to reflexed in mature flowers; lobe apex obtuse. *Stamens* inserted in corolla tube just below midpoint at 3/8-2/5 of total corolla length, only longest stamen slightly exserted from corolla mouth; filaments winged, unequal to subequal, 8-13 mm long, after anthesis straight; anthers ovate to elliptic, 2.2-4.3 mm long, white, after anthesis straight to slightly curved; no pollen data. *Gynoecium* 15-20 mm long; ovary ellipsoid, 2.6-3.0 x 1.5-2.6 mm; style 9-14 mm long; stigma lobes obovate, 1.8-3.1 x 0.9-1.5 mm. *Capsule* ellipsoid, 8-19 x 4-8 mm, brown, nodding. *Seeds* angular-cuboidal, 0.1-0.4 mm in diameter, brown; testa cells concave with band-like thickenings (fide Bouman et al., 2002).

Phenology. Flowers and fruits collected from January to June and October with no records for the remaining months.

Habitat and Distribution. Brazilian Highlands (Brazil: Goiás, Mato Grosso, Mato Grosso do Sul), Amazon Basin and Andes of Bolivia (El Beni, La Paz, Santa Cruz; Figure 6). Commonly found in savannas and cerrado type vegetation, sometimes in open forests. Almost always found in rocky or sandy soil. Altitude range: 10-1100 m.

3. ***Chelonanthus grandiflorus*** (Aubl.) Chodat & Hassl. Addenda Pl. Hassl. 5. 1917. - *Lisyanthus grandiflorus* Aubl., Hist. Pl. Guiane 1: 205, t. 81, 1775. - *Helia grandiflora* (Aubl.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: French Guiana, Aublet s.n. (holotype BM; isotypes LINN [n.v.], P [n.v.]).
- *Chelonanthus chelonoides* (L.) Gilg in Engler & Prantl., Nat. Pflanzenfam. 4(2): 98. 1895. - *Pentstemon chelonoides* L., Plantæ Surinamenses: 6. 1775. - *Lisianthus chelonoides* (L.) Linn.f., Suppl. Pl. 134. 1781. - *Lisyanthus chelonoides* (L.) Griseb., Gen. Sp. Gent.: 184-185. 1839. - *Helia chelonoides* (L.) Kuntze, Rev. Gen. Pl. 2: 427. 1891. TYPE: Suriname, in high sands, Dalhberg 141 (holotype LINN).
- *Chelonanthus fistulosus* (Poir.) Gilg, Nat. Pflanzenfam. 4(2): 98. 1895. - *Lisianthus fistulosus* Poir. in Lam., Encycl., t. 11: 564. 1814. - *Lisyanthus fistulosus* (Poir.) Griseb., Gen. Sp. Gent.: 180-181. 1839. - *Helia fistulosa* (Poir.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: French Guiana, Martin s.n. (holotype P [n.v.; photo F, U]).
- *Chelonanthus schomburgkii* (Griseb.) Gilg, Nat. Pflanzenfam. 4(2): 98. 1895. - *Lisianthus schomburgkii* Griseb. in Prodr. (DC.), 9: 75. 1845. - *Helia schomburgkii* (Griseb.) Kuntze, Rev. Gen. Sp.: 428. 1891. TYPE: British Guiana, Berbice, Schomburgk 298 (holotype B [destroyed]; isotypes BM [n.v.], CGE [n.v.], F [n.v.], G [photo U, K, & L], US).

Plants erect herbs to subshrubs, up to 2.5 m high. *Stems* unbranched, sometimes sparsely branched, quadrangular and 4-winged on the 3-4 most basal internodes, then abruptly becoming terete (Colombian specimens with the lowest 3-4 internodes terete and 4-ridged); branches up to 11 mm in diameter; internodes 2.3-27.2 cm long; wings 0.1-1.8 mm wide. *Leaves* membranaceous, sessile or sometimes petiolate; petiole 0-0.5 cm long; blade ovate to elliptic, 2.0-23.9 x 0.9-11.7 mm; base of lower leaves attenuate, base of upper leaves obtuse; apex acute. *Inflorescence* dichasial, sometimes

monochasial, 5-45-flowered; bracts ovate, 1.3-9.3 mm long; apex usually acuminate, sometimes obtuse or acute. *Flowers* horizontal, pedicels 4-11 mm long. *Calyx* campanulate, 5-11 x 5-9 mm, fused 2/5-2/3 of calyx length; lobes ovate, 3-6 x 3-5 mm; apex obtuse. *Corolla* funnelform, 21-44 mm long, 13-27 mm wide at mouth, pale green, cream to yellow, persistent to partially persistent in fruit; lobes ovate, 5-10 x 6-8 mm, erect in mature flowers; lobe apex obtuse. *Stamens* inserted in corolla tube just above midpoint of corolla at 5/8 of total corolla length, at insertion point staminal pockets +/- present, not exerted; filaments winged, unequal, 12-18 mm long, after anthesis curved downward apically; anthers elliptic to ovate, 2.4-3.6 mm long, white, after anthesis straight; pollen exine differentially reticulated with muri thickened at the poles (fide Nilsson, 1970, 2002). *Gynoecium* 21-27 mm long; ovary ellipsoid, 5.9-7.9 x 2.7-3.1 mm; style (9-)14-20 mm long; stigma lobes elliptic, 2.5-5.4 x 1.5-2.4 mm. *Capsule* ellipsoid, 9-20 x 4-9 mm, brown, nodding. *Seeds* angular-cuboidal, 0.1-0.4 mm in diameter, brown; testa cells subcircular to polygonal, concave with band-like thickenings.

Phenology. Flowers and fruits collected year-round.

Habitat and Distribution. Guayana Highlands of Brazil (Amapá and Roraima), French Guiana, Guyana, Suriname and Venezuela, Caribbean islands of Trinidad and Grenada, Amazon Basin of Brazil (Amapá, Amazonas and Pará), Venezuela, and Colombia, Brazilian Highlands (Brazil: Maranhão, Paraíba, Pernambuco, Rio de Janeiro and São Paulo) and Andes of Colombia (Figure 6). Often found in forest openings, forest edges, along streams or roads, or in secondary growth. Sometimes found in grassy savannas and cerrado or caatinga type vegetation. Most often found in moist

white sand, low nutrient soils, sometimes in rocky soil and in clay or lateritic soil.

Altitude range: 0-1900 m.

Vernacular names. Aha (Guyana), Amerindian tobacco (Guyana), Dia tabaka (Suriname), Dankuna tabaka (French Guiana), Fumo do brejo (Brazil, Maranhão), Joelieballi (Suriname), Kawai-banada-yek (Venezuela, Bolívar), Koeraja (Suriname), Kwasi-bitá (Suriname), Sabana-tabacca (Suriname), Sabana tabak (Suriname), Salidore (Guyana), Tabaco do igapó (Brazil, Pará), Tabaco de veado (Brazil, Amazonas), Tabaco de veado (Venezuela, Amazonas), Tobaco-rana (Brazil, Pará), Tabaquilla (Venezuela, Amazonas), Wild tobacco (Guyana), Yuriballi (Guyana).

Ethnobotany. In Guyana, the uses for this species include boiling the leaves for ‘bowels’ (teste Gorts-van Rijn et al. 434), and to “clean out of dirty tummy”, and malaria (teste Reinders & Torres 29).

Pollination and Ecology. The presence of ants and possible myrmecophily has been noted by several collectors (teste Maas & Westra 3992, Ramsammy 81 & Steege et al. 466). The nectaries on the bases of the calyces and pedicel bases appear to be especially attractive to ants. Black flies have also been noted as visitors to the young flower buds (teste Steege et al. 466). Bat-pollination has also been observed (teste Machado s.n.; Machade et al., 1998).

4. **Chelonanthus albus** (Spruce ex Progel) V.M. Badillo in Pittier et al., Cat. Fl. Venez. 2: 293. 1947. -*Lisianthus albus* Spruce ex Progel, Fl. Bras. 6(1): 237. 1865. -*Helia alba* (Spruce ex Progel) Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Irlbachia alata* (Aubl.) Maas ssp. *alba* (Spruce ex Progel) J.M.G. Pers. & Maas in Maas, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 88(4): 409. 1985. TYPE: Brazil, Amazonas: in vicinia Barra [Manaus], Spruce s.n. (holotype K [photo NY]; isotype G).

Plants erect herbs (rarely vines), up to 2.5 m high. *Stems* sparsely branched to distinctly branched, terete; branches up to 5.4 mm in diameter; internodes 2.2-12.0 cm long; wings absent. *Leaves* membranaceous, sessile to petiolate; petiole 0-8 mm long; blade elliptic or lanceolate, 2.5-15.7 x 1.0-6.9 cm; base attenuate; apex acute to acuminate. *Inflorescence* dichasial, sometimes monochasial, 8-32-flowered; bracts orbicular, 1.1-1.9(-2.8) mm long; bract apex obtuse, sometimes weakly acute. *Flowers* horizontal, pedicels 2-8 mm long. *Calyx* campanulate, 3-9 x 3-8 mm, fused 1/4-3/5 of total calyx length; lobes ovate, 2-5 x 2-4 mm; apex obtuse. *Corolla* funnelform to campanulate, 23-39 mm long, 8-23 mm wide at mouth, white, deciduous in fruit; lobes ovate, 5-7 x 5-11 mm, erect to spreading in mature flowers; lobe apex obtuse. *Stamens* inserted in corolla tube near base at 1/6-1/4 of total corolla length, not exserted; filaments winged, unequal, 19-31 mm long, after anthesis curved downward apically; anthers oblong, 1.6-2.6 mm long, white, after anthesis straight to slightly curved; pollen exine differentially reticulated with pila and elongated processes (fide Maguire & Boom 1989; Nilsson, 1970, 2002). *Gynoecium* 30-35 mm long; ovary ellipsoid, 3.8-5.0 x 2.1-2.6 mm; style 21-50 mm long; stigma lobes orbicular, elliptic to obovate, 1.8-2.8(-4.5) x 1.2-1.5(-2.1) mm. *Capsule* ellipsoid, 7-17 x 4-8 mm, brown, horizontal to nodding. *Seeds* angular-cuboidal, 0.1-0.4 mm in diameter, brown; testa cells dome-like and concave with band-like thickenings (fide Bouman et al., 2002).

Phenology. Flowers and fruits collected year-round.

Habitat and Distribution. Amazon Basin of Brazil (Amazonas), Colombia and Venezuela, Guayana Highlands of Brazil (Roraima) and Venezuela, one collection in Andes of Colombia (Figure 6). Predominantly found in riverine habitats associated with

forests, or along forest edges, in clearcut forests and rarely in open fields, campina or scrub type vegetation. Most commonly found in low nutrient sandy, terra firme soils and rarely in clay or lateritic soils. Altitude range: 60-450; 990-1670 m.

Vernacular names. Tabaco bravo (Brazil, Amazonas), Tabaco de venado lyurimabare (Venezuela, Amazonas), Sarusa (Venezuela, Amazonas), Tabaco picure (Venezuela, Amazonas).

5. ***Chelonanthus pterocaulis* Lepis, sp. nov.**

TYPE: Brazil. Roraima. Igarape Agua Boa, Rio Mucajaí between Pratinha and Rio Apiaú, sandy high savanna at riverbank, 22 January 1967, Prance, G. T. et al. 4008 (holotype INPA; isotypes F, NY, S [x2], U, US) Figure 9.

Plants erect herbs, up to 1.5 m high. *Stems* unbranched to sparsely branched, quadrangular, 4-winged; branches up to 6(-10) mm in diameter; internodes 0.7-15.0 cm long; wings 0.6-3.7 mm wide. *Leaves* sessile, membranaceous; blade ovate, obovate or elliptic, 1.3-13.8(-20.2) x 0.5-4.7(-8.5) cm; base cuneate, attenuate, often the two most apical leaf pairs connate to perfoliate (rarely all leaves perfoliate); apex acute or obtuse. *Inflorescence* dichasial, sometimes monochasial, 2-33-flowered; bracts ovate, 1.6-6.5 mm long; apex acute. *Flowers* erect, pedicels 2-7 mm long. *Calyx* campanulate, 6-10 x 4-7 mm, fused 2/5-5/8 of total calyx length; lobes circular, 3-5 x 3-5 mm; apex obtuse. *Corolla* tubular to salverform, 19-40 mm long, 8-20 mm wide at mouth, greenish white, cream to pale yellow, persistent to partially persistent in fruit; lobes ovate, 3-6 x 3-7 mm, erect to spreading in mature flowers; lobe apex obtuse. *Stamens* inserted in corolla tube near base of corolla at 1/4-1/3 of total corolla length, not exserted, positioned deep within the corolla tube; filaments winged, subequal (within 2 mm), 8-15 mm long, after

anthesis straight; anthers elliptic to slightly ovate, 1.6-3.0 mm long, white, after anthesis straight or curved; pollen exine differentially reticulated. *Gynoecium* 17-26 mm long; ovary ellipsoid, 4.1-6.6 x 2.2-4.3 mm; style 8-14 mm long; stigma lobes ovate, obovate to oblong, 2.5-5.1 x 1.8-2.0 mm. *Capsule* ellipsoid, 11-20 x 4-10 mm, brown, erect to horizontal. *Seeds* angular-cuboidal, 0.1-0.4 mm in diameter, brown; testa cells subcircular, dome-like and concave with band-like thickenings.

Phenology. Flowers and fruits collected year-round.

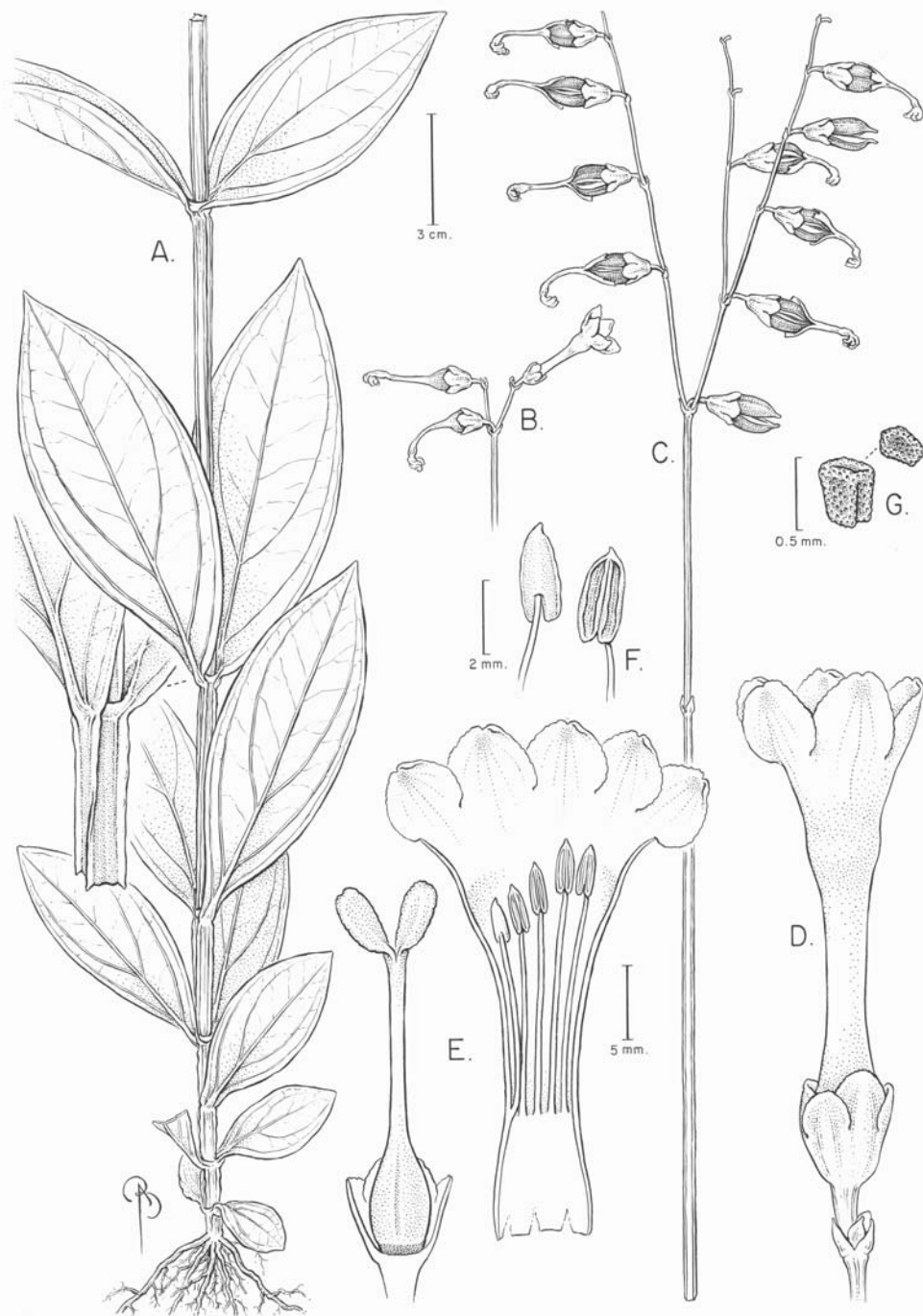
Habitat and Distribution. Guayana Highlands of Brazil (Roraima), French Guiana, Guyana, Suriname and Venezuela, Caribbean islands of Trinidad and Grenada, Amazon Basin of Brazil (Amazonas and Pará), Colombia and Venezuela, Andes of Colombia and Venezuela and Central America (Costa Rica, presumably Panama; Figure 6 - listed as leafy-wing). This species occurs in secondary growth forests, scrub, savannas, riverbanks, roadsides, and often in sandy or rocky, moist soils and sometimes on lateritic soil. Altitude range: 0-1820 m.

Vernacular names. Wild tobacco (Guyana) and Tabaco bravo (Brazil, Amazonas).

Ethnobotany. This species has been listed in Guyana for "for removing worms and "dirt" in the body," in Guyana (teste Riley 8).

Etymology. The name *pteroaulis* comes from the Greek meaning 'winged stem' and was chosen to reflect the presence of a strongly quadrangular, 4-winged stem.

Figure 9: *Chelonanthus pterocaulis* sp. nov. A, unbranched, quadrangular 4-winged stem bearing elliptical leaves that are decurrent onto the stem. B, apical portion of the inflorescence with fruits and a narrowly tubular flower. C, complete inflorescence with horizontally positioned, medially dehiscent capsules and persistent corollas. D, close up of tubular corolla and erect corolla lobes. E, dissected flower revealing the gynoecium, the position of sexual structures within the corolla tube, and the insertion of filaments near the base of the corolla. F, anthers with sterile apical appendage. G, angular seeds. A-G from *Prance et al.* 4008. Illustrator: Bobbie Angell.



6. **Chelonanthus viridiflorus** (Mart.) Gilg. Nat. Pflanzenfam. 4(2): 98. 1895. -

Lisianthus viridiflorus Mart., Nov. Gen. Sp. Pl.: 94-95, fig. 173. 1827. -*Lisyanthus*

viridiflorus (Mart.) Griseb., Gen. Sp. Gent.: 192-193. 1839. -*Helia viridiflora* (Mart.)

Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Irlbachia alata* (Aubl.) Maas ssp. *viridiflora*

(Mart.) J.M.G. Pers. & Maas in Maas, Proc. Kon. Ned. Akad. Wetensch., ser. C. 88(4):

410. 1985. TYPE: Brazil, Minas Gerais: near Villa Rica, Sabará, Martius 772 (holotype

M).

— *Chelonanthus candidus* Malme, Arkiv. Bot. 3(12): 13, fig. 2, #3. 1904. TYPE:

Brazil, Mato Grosso: Serra da Chapada, Santa Anna da Chapad, Malme 3293

(holotype S; isotypes B [n.v.; photo F, U], F [n.v.], G [n.v.], K [n.v.], MO).

Plants erect, herbs, up to 1.2 m high. *Stems* unbranched or sparsely branched, terete; branches up to 7 mm in diameter; internodes 1.1-14.3 cm long. *Leaves* membranaceous, sessile, petiole 0-4 mm long; blade elliptic, ovate towards apex, 1.3-15.5 x 0.3-7.9 cm; base of lower leaves attenuate, base of upper leaves obtuse; apex acute. *Inflorescence* dichasial, sometimes monochasial, 1-34-flowered; bracts ovate to oblong, 0.4-4.1 mm long; apex acute to obtuse. *Flowers* erect to horizontal, pedicels 4-13 mm long. *Calyx* campanulate, 6-14 x 5-10 mm, fused 1/6-1/5 of total calyx length; lobes ovate to oblong, 4-11 x 3-8 mm; apex acute. *Corolla* funnelform, 28-80 mm long, 15-28 mm wide at mouth, greenish-white, greenish-yellow, whitish-yellow to white, deciduous as capsules dehisce; lobes ovate, 4-11 x 3-12 mm, spreading in mature flowers; lobe apex obtuse. *Stamens* inserted in corolla tube near base at 1/6-3/8 of total corolla length, not exserted; filaments winged, unequal, 13-38 mm long, after anthesis straight; anthers oblong, 1.5-3.2 mm long, white, after anthesis straight; pollen exine differentially

reticulated with complete muri or sometimes fragmented into globules and elongated processes (fide Nilsson, 1970, 2002). *Gynoecium* 23-54 mm long; ovary ellipsoid, 5.0-6.0 x 3.0-5.0 mm; style 16-41 mm long; stigma lobes orbicular, 1.7-4.2 x 1.7-3.6 mm. *Capsule* ellipsoid, 6-22 x 5-11 mm, brown, erect. *Seeds* angular-cuboidal, 0.1-0.6 mm in diameter, brown; testa cells dome-like and/or concave with band-like thickenings (fide Bouman et al., 2002).

Phenology. Flowers and fruits collected year-round.

Habitat and Distribution. Guayana Highlands of Brazil (Roraima), Guyana and Suriname, Brazilian Highlands (Brazil: Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Paraná and São Paulo) and Paraguay, Amazon Basin of Bolivia, Brazil (Amazonas and Pará) and Peru, and Andes of Bolivia and Peru (Figure 6). This species is commonly found along headwater streams, in wet savannas and forest edges, but rarely along roadsides, in scrub, cerrado or campo rupestre type vegetation. It is most commonly found in white-sand, low-nutrient soils, and rarely in clay, lateritic, or rocky soils. Altitude range: 30-1346 m.

Vernacular names. Nicotiana (Colombia).

7. ***Chelonanthus angustifolius*** (Kunth) Gilg, Nat. Pflanzenfam. 4(2): 98. 1895. - *Lisianthus angustifolius* Kunth, Nov. Gen. Sp. 7: 181. 1818. - *Lisyanthus angustifolius* (Kunth) Griseb., Gen. Sp. Gent.: 186. 1839. - *Helia angustifolia* (Kunth) Kuntze, Rev. Gen. Pl. 2: 428. 1891. - *Irlbachia alata* (Aubl.) Maas ssp. *angustifolia* (Kunth) J.G.M. Pers. & Maas in Maas, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 88(4): 409-410. 1985. TYPE: Venezuela, Amazonas: Near Esmeralda in a grassy place (Orinoco), Humboldt & Bonpland 1004 (holotype P [n.v.]; isotypes W [n.v.], B [n.v.; photo MO & U]).

- *Lisianthus bifidus* Kunth, Nov. Gen. Sp. 7: 181. 1818. -*Lisyanthus bifidus* (Kunth) Griseb., Gen. Sp. Gent.: 186. 1839. -*Helia bifida* (Kunth) Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Chelonanthus bifidus* (Kunth) Gilg in Engler & Prantl, Naturl. Pflanzenf. 4(2): 98. 1895. TYPE: Colombia, Tolima: near Sta. Anna, alt. 400 m, Humboldt & Bonpland 1731 (holotype P [n.v.]; isotype W [n.v.], B [n.v.; photos F, MO & U]).
- *Chelonanthus camporum* Gilg in Feddes Repert. Spec. Nov. Regni Veg. 2: 54. 1906. TYPE: Peru, Loreto: near Moyobamba, alt. 1000 m., Weberbauer 4546 (holotype B [destroyed; photos F, U, & US]; isotypes G, P [n.v.]).
- *Chelonanthus leucanthus* Gilg in Feddes Repert. Spec. Nov. Regni Veg. 2: 55. 1906. TYPE: Peru, Puno, Weberbauer 1094 (holotype B [n.v.; photos F & U]).
- *Chelonanthus pyriformis* Gleason, Bull. Torrey Bot. Club 58: 450. 1931. -*Lisianthus pyriformis* (Gleason) Steyerl., Fieldiana. Bot. 28: 498. 1953. TYPE: Venezuela, Amazonas: summit of Mount Duida, dry crests of savanna hills, alt. 4400 ft., Tate 747 (holotype NY [photo U]; isotype US [photo F]).

Plants erect, herbs, up to 1.6 m high. *Stems* unbranched to sparsely branched, terete to weakly quadrangular, with or without small wings; branches up to 7 mm in diameter; internodes 0.5-17.4 cm long; wings, 0.1-0.3 mm wide. *Leaves* membranaceous (rarely coriaceous), sessile to shortly petiolate; petiole 0-4 mm; blade linear, elliptic or lanceolate, 1.0-21.0 x 0.2-3.7 cm; base attenuate to cuneate; apex acute to acuminate. *Inflorescence* dichasial, sometimes monochasial, 1-60-flowered; bracts ovate to oblong, 1.2-5.0 mm long; apex obtuse (rarely acute). *Flowers* erect to horizontal, pedicels 2-24 mm long. *Calyx* campanulate, 4-9 x 3-7 mm, fused 3/10-4/5 of total calyx length; lobes ovate to circular, 2-6 x 2-5 mm; apex obtuse. *Corolla* funnellform to tubular, 21-52 mm long, 10-32 mm wide at mouth, white, green, to greenish yellow, partially persistent in fruit; lobes ovate to orbicular, 3-9 x 3-15 mm, erect to spreading in mature flowers; lobe

apex obtuse (rarely acute). *Stamens* inserted in corolla tube near base at 1/6-1/4 of total corolla length, not exserted; filaments winged, unequal, 17-35 mm long, after anthesis usually straight or curved downward apically; anthers elliptic to slightly obovate, 2.3-3.5 mm long, white, after anthesis straight; pollen exine differentially reticulated with globules (fide Nilsson, 1970, 2002). *Gynoecium* 29-32 mm long; ovary ellipsoid, 3.2-4.3 x 1.9-2.4 mm; style 20-40 mm long; stigma lobes orbicular, 1.5-2.4 x 1.1-2.4 mm. *Capsule* ellipsoid, 5-14 x 1-8 mm, brown, erect to horizontal. *Seeds* angular-cuboidal, 0.1-0.5 mm in diameter, brown; testa cells dome-like and concave with band-like thickenings (fide Bouman et al., 2002).

Phenology. Flowers and fruits collected year-round.

Habitat and Distribution. Guayana Highlands of Brazil (Roraima), Guyana and Venezuela, Amazon Basin of Brazil (Acre and Amazonas), Venezuela, Colombia and Peru, and Andes of Colombia and Peru (Figure 6). This species grows in wet and dry savannas, sometimes along streams and forest edges, and is often found on white-sand, low-nutrient soils and sometimes in rocky soil. Altitude range: 37-1980 m.

8. ***Chelonanthus hamatus*** Lepis in Lepis, Maas & Struwe, in preparation. Chapter 3.

Plants erect, herbs to subshrubs, up to 1.2 m high. *Stems* branched, strongly quadrangular, 4-angled to 4-winged; branches up to 11 mm in diameter; internodes 2.5-13.5 cm long; wings 1.0-1.3 mm wide. *Leaves* membranaceous to subcoriaceous, sessile; blade oblanceolate (populations in French Guiana) to elliptic (populations in Venezuela), 4.3-20.7 x 2.9-6.2 cm; base of lower leaves attenuate, base of upper leaves obtuse; apex acute to obtuse. *Inflorescence* dichasial, terminating with two or more monochasial branches, 16-40-flowered; bracts ovate with acuminate to cuspidate apex, 2.2-3.8(-8.1) mm long. *Flowers* erect to horizontal, pedicels 6-9 mm long. *Calyx*

campanulate, 6-8 x 5-7 mm, fused 3/8-3/5 of total calyx length; lobes ovate, 3-4 x 3-4 mm, minutely winged, upward facing hook present near the apex of dorsal glandular area; wings c. 0.4 mm wide; hook 1.3-2.1 mm long; apex obtuse. *Corolla* campanulate to funnelform, 20-27 mm long, 10-18 mm wide at mouth, green, persistent; lobes ovate, 3-6 x 3-7 mm. *Stamens* inserted in corolla tube near base at 1/3 of total corolla length, corona present at insertion point, not exerted; corona 0.9 mm wide with free triangular flaps c. 0.8 x 0.7 mm; filaments winged, subequal (within 2 mm), 10-12 mm long, after anthesis straight to curved downward apically; anthers elliptic, 1.8-3.2 mm long, white to yellow, after anthesis straight; pollen exine with fine reticulum interspersed with thickened, knob-like muri (fide Lepis et al., in progress; Chapter 3). *Gynoecium* 18 mm long; ovary ellipsoid, 4.4 x 2.1 mm; style 11 mm long; stigma lobes elliptic, 2.4-2.8 x 1.8 mm (internal floral characters taken from a single flower due to rarity of material). *Capsule* ellipsoid, 9-17 x 4-8 mm, brown, nodding. *Seeds* angular-cuboidal, 0.1-0.6 mm in diameter, brown; testa cells subcircular, concave with band-like thickenings (fide Lepis et al., in progress; Chapter 3).

Phenology. Flowers and fruits collected in January, April and August with no record for the remaining months.

Habitat and Distribution. Guayana Highlands of southwestern French Guiana and eastern Venezuela, south of the Rio Orinoco (Bolívar; Figure 14). Mostly in rocky savannas, but also found in cloud forests on exposed rock. Altitude range: 160-600 m.

9. **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg in Engler & Prantl, *Naturl. Pflanzenf.* 4(2): 98. 1895. -*Lisianthus acutangulus* Ruiz & Pav., *Fl. Peruv.* 2: 14. Plate CXXII, a. 1799. -*Helia acutangula* (Ruiz & Pav.) Kuntze, *Rev. Gen. Pl.* 2: 428. 1891.

TYPE: Peru, Huanuco, Pavon s.n. (holotype MA [photo F, MO, NY, U]; isotype BM [n.v.], G).

- *Lisyanthus auriculatus* Benth., Pl. Hartw.: 226. 1846. -*Helia auriculata* (Benth.) Kuntze, Rev. Gen. 2: 428. 1891. TYPE: Colombia, Cauca, Popayan, El Tambo, Hartweg 1240 (holotype K; isotype K).
- *Lisianthus crassicaulis* M. Martens & Gelotti, Bull. Acad. Roy. Sci. Bruxelles 11(1): 374. 1844. -*Helia crassicaulis* (M. Martens & Gelotti) Kuntze, Rev. Gen. Pl. 2: 427. 1891. TYPE: Mexico, Oaxaca, 3000 ft., Galeotti 7176 (holotype BR [n.v.], isotypes BR [n.v.], G-DEL [n.v.; photo F, MO], F [n.v.], G, W).
- *Lisianthus oerstedtii* Griseb., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn: 54. 1853. -*Helia oerstedtii* (Griseb.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: Nicaragua, Segovia, between Matagalga and Muimui, Ørsted 22742 (holotype C [photo F]).
- *Lisyanthus tetragonus* Benth., Pl. Hartw.: 68. 1840. -*Helia tetragona* (Benth.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: Mexico, Oaxaca, Talea, Hartweg 496 (holotype K; isotype K).
- *Lisianthus trifidus* Kunth in HBK, Nov. Gen. Sp. Pl. 7: 182. 1818. -*Lisyanthus trifidus* (Kunth) Griseb., Gen. Sp. Gent.: 185-186. 1839. -*Helia trifidus* (Kunth) Kuntze, Rev. Gen. Pl. 2: 427. 1891. TYPE: Colombia, Tolima, between Mariquita and Santana, alt. 400 h. ø, Humboldt & Bonpland s.n. (holotype P [n.v.; photo U]).
- *Chelonanthus whitei* Rusby, Mem. New York Bot. Gard. 7: 322. 1927. TYPE: Bolivia, Ixiamas, alt. 245 m., White 1145 (holotype NY). Note: Protologue lists collection number as 1195, but this specimen is in agreement on all other accounts so this is believed to be a typographic error.

Plants erect, herbs or subshrubs, up to 3.0 m high. *Stems* unbranched to sparsely branched, quadrangular, 4-winged to 4-ridged; branches up to 15.2 mm in diameter; internodes 1.2-32.5 cm long; wings 0.4-1.5 mm wide. *Leaves* membranaceous, sessile; blade ovate to elliptic, 2.7-27.5 x 1.6-13.5 cm; base of lower leaves attenuate, base of

upper leaves obtuse; apex acute. *Inflorescence* dichasial or monochasial, 6-100-flowered; bracts ovate, 1.3-5.5 mm long; apex acute (obtuse in Mexican populations). *Flowers* horizontal to erect, pedicels 3-17 mm long. *Calyx* campanulate, 4-9 x 4-9 mm, fused $3/7-1/2$ of total calyx length; lobes ovate, 2-6 x 2-5 mm; apex obtuse. *Corolla* campanulate (sometimes funnelform in Amazonian and Mexican populations), 16-32 mm long, 11-26 mm wide at mouth, green to yellowish-green, deciduous in fruit (persistent to partially persistent in Mexican populations); lobes ovate, 2-8 x 5-10 mm, reflexed to erect in mature flowers, lobe apex obtuse. *Stamens* inserted in corolla tube near base at $1/5-2/5$ of total corolla length, not exserted; filaments filiform or winged, unequal, 10-20 mm long, after anthesis curved downward apically; anthers ovate, 1.9-4.9 mm long, cream, after anthesis straight to slightly curved; pollen exine differentially reticulated with pila or thickened muri at the distal poles (fide Nilsson, 1970, 2002). *Gynoecium* 23-28 mm long; ovary ellipsoid, 2.9-5.9 x 2.9-3.8 mm; style 12-16 mm long; stigma lobes obovate or ovate, 4.1-5.7 x 2.1-3.5 mm. *Capsule* ellipsoid, 9-20 x 4-9 mm, brown, pendulous. *Seeds* angular-cuboidal, 0.1-0.4 mm in diameter, brown; testa cells subcircular, concave without band-like thickenings.

Phenology. Flowers and fruits collected year-round.

Habitat and Distribution. Southern Mexico and Central America, Andes of Bolivia, Colombia, Ecuador, Peru and Venezuela, Caribbean island of Grenada, Amazon Basin of Bolivia, Brazil (Acre, Amazonas, Rondônia), Ecuador and Peru (Figure 6). This species is commonly found along roadsides and in open forests such as disturbed primary forests, secondary growth forests, forest remnants and forest edges. Less often, it is found along rivers and in savanna type vegetation. It is equally likely to be found in

nutrient poor sandy soils and clay soils, and sometimes also in rocky soils. Altitude range: 0-3000 m.

Vernacular names. Arbol de mal casada (Spanish: Panama), Campanita (Peru), Eshcacahui (Guatemala), Habas-habas (Spanish: Peru), Hai-bí-ki (Witoto: Peru), Hierba de Adam (Spanish: Ecuador), Oja manga (Spanish: Peru), Pichispan (Chunchu: Peru), Sachatabaco (Peru), Sasafras de loma (Venezuela, Merida), Tabacillo (Peru), Tabaco masha (Peru), Tres esquinas (Peru), Tsiutsimuhe (Bora: Peru), Zome gĩákaĩ (Witoto: Colombia).

Ethnobotany. This species has many recorded ethnobotanical uses in Peru. The leaves are crushed and applied to the skin to treat ‘chupas’ and screw worm (teste Macrae 23, Balick et al. 1008), as well as used for cuts (teste Killip & Smith 25402). A tea is made for regulating menstruation (teste Alexiades & Pesha 1102), and it is also said to be a medicine for kidney diseases (teste Dudley 11766). Leaves are rubbed on women’s breasts to wean children from breast feeding (likely because of its bitter taste; teste Balick et al. 1008). It also has veterinarian applications as a remedy against worm infested wounds in cattle (teste Mexia 4153) and chicken coops are lined with the leaves to combat chicken lice (teste Salick 7306). In Peru as well as Mexico this plant is used to alleviate stomach aches (teste Plowman 6956, Ramirez 747) and in Ecuador it is used for neck pain and snake bites (teste Rios 67).

Pollination and Ecology. This species is visited by ants (teste Maas et al. 4539); photographic evidence of plants from Ecuador document the presence of ants on the calyx.

10. **Chelonanthus alatus** (Aubl.) Pulle, Vasc. Pl. Surinam.: 376. 1906. -*Lisyanthus alatus* Aubl., Hist. Pl. Guiane 1: 204. t. 80. 1775. -*Helia alata* (Aubl.) Kuntze, Rev. Gen. Pl. 2: 427. 1891. -*Irlbachia alata* (Aubl.) Maas, Proc. Kon. Ned. Akad. Wetensch., Ser. C., 88: 408. 1985. TYPE: French Guiana, Aublet s.n. (holotype BM; isotypes LINN [n.v.], P [n.v.]).

— *Chelonanthus longistylus* (J.M.G Pers. & Maas) Struwe & V.A. Albert, Harvard Papers in Botany 3: 70. 1998. -*Irlbachia alata* (Aubl.) Maas ssp. *longistyla* J.M.G. Pers. & Maas in Maas, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 88(4): 410. 1985. TYPE: Venezuela, Bolivar: km 106 of road El Dorado - Sta. Elena de Uairén, forest margin, alt. 700 m., Maas & Steyermark 5344 (holotype U [3 sheets] & photo [photo published in Maas, 1985]; isotypes K, MO, COL [n.v.], NY, P [n.v.], US, VEN [n.v.].

Plants erect, herbs to subshrubs, up to 2.5 m high. *Stems* unbranched to sparsely branched, strongly quadrangular, 4-winged; branches up to 11 mm in diameter; internodes 0.5-30.3(-47.3) cm long; wings 0.1-1.3 mm wide. *Leaves* membranaceous, sessile; blade elliptic, 2.9-23.2 x 1.2-8.0(-12.0) cm; base attenuate, obtuse to truncate; apex acute to acuminate. *Inflorescence* dichasial, sometimes monochasial, 3-100-flowered; bracts ovate, 0.8-9.4 mm long; apex obtuse, rarely acute. *Flowers* erect to horizontal, pedicels 4-9 mm long. *Calyx* campanulate, 4-8 x 3-6 mm, fused 1/4-1/2 of total calyx length; lobes ovate, 2-6 x 2-4 mm; apex obtuse. *Corolla* campanulate to funnelform, 20-50 mm long, 8-21 mm wide at mouth, white to cream, sometimes pale green to yellow, deciduous in fruit; lobes ovate, 3-11 x 4-13 mm. *Stamens* inserted in corolla tube near base at 1/5-1/3 of total corolla length, exserted or not; filaments winged, subequal (within 2 mm), 14-40 mm long, after anthesis straight or curved downward apically; anthers oblong, 2.0-3.8 mm long, white or pale green, after anthesis

straight to curved; pollen exine strongly reticulate along the equatorial regions with muri fragmented into elongated to knob-like processes (fide Hequet, 2007; Maguire & Boom 1989; Nilsson, 1970, 2002). *Gynoecium* 24-34 mm long; ovary ellipsoid, 4.4-5.6 x 2.1-2.6 mm; style 14-23 mm long; stigma lobes elliptic to obovate, 2.8-4.4 x 1.1-2.3 mm. *Capsule* ellipsoid, 8-23 x 3-10 mm, brown, nodding. *Seeds* angular-cuboidal, 0.1-0.4 mm in diameter, brown; testa cells concave with band-like thickenings (fide Bouman et al., 2002).

Phenology. Flowers and fruits collected year-round.

Habitat and Distribution. Guayana Highlands of Brazil (Roraima), Guyana, French Guiana, Suriname and Venezuela, Caribbean island of Trinidad (Figure 6). This species occurs in moist areas of forests, savannas, and scrub vegetation, as well as along rivers and roadsides. It is most commonly found on white sand, low nutrient soils, but is also reported from clay and lateritic soils and rarely from rocky soil. Altitude range: 0-2255 m.

Vernacular names. Wild tobacco (Guyana), Pepiatamit [uncertain spelling] (Carib: Suriname), Todo Tabaka (Negro English: Suriname), Todo Tabalso (Dutch English: Suriname), Pipjataner (Suriname), Sabama tabaka (Suriname), Wakauyek (Pemon: Venezuela, Bolívar).

Ethnobotany. The leaves have been used to relieve itching in Suriname (teste Archer 2652) and as a bitter in Guyana (teste McDowell & Stobey 3831).

DISCUSSION

Vegetative morphology

HABIT. The species of *Chelonanthus* are all herbaceous, but range from slender plants as small as 2 cm to stout and basally suffrutescent plants as tall as 3 m. Even in the case of the larger herbs, unbranched or sparsely branched stems are most common. A consistent pattern of leaves evenly placed along the stem except for longer internodes between the two most apical leaf pairs is present throughout the genus.

STEMS. Stem shape is a helpful, initial character for use in the process of species identification. The full spectrum of strongly quadrangular, 4-winged stems to terete with no wings or ridges exists. A stem that is strongly quadrangular and 4-angled to 4-winged along the entire length can be found in four species, *C. acutangulus*, *C. alatus*, *C. hamatus* and *C. pterocaulis*. *Chelonanthus angustifolius* and *C. purpurascens* range from terete to weakly quadrangular with wings or ridges, but the largest wings observed in the two latter species are not wider than 0.3 and 0.4 mm, respectively. When this width is compared to the largest wings found in *C. acutangulus* (1.5 mm), *C. alatus* (1.3 mm), *C. hamatus* (1.3 mm) and *C. pterocaulis* (3.7 mm), the difference is obvious. The stem of *C. grandiflorus* is unique and useful in species identification. The overall shape is terete, but the 3-4 most basal internodes are quadrangular and 4-winged (population from Colombia have basal internodes that are terete with 4 ridges), with the next internode abruptly becoming terete. The remaining species, *C. albus*, *C. matogrossensis*, and *C. viridiflorus* all have terete stems without wings or ridges.

LEAVES. Leaf shape in *Chelonanthus* can be highly variable with ovate, elliptic, obovate, lanceolate, oblanceolate, linear and orbicular leaves, but because much intra-specific variation exists, this character is not useful in species identification. There are two exceptions to this statement: *C. angustifolius* with linear leaves, and *C. hamatus*

with large oblanceolate leaves. Even in these two instances there are variants of *C. angustifolius* with elliptic or lanceolate leaves, and populations of *C. hamatus* with elliptic leaves, so even in these cases leaf shape is not always helpful in field identification.

Reproductive morphology

INFLORESCENCE. A terminal cymose inflorescence that is dichasial and terminating with two or more monochasial branches is most commonly observed, but purely monochasial inflorescences are also present in several species. The inflorescence can contain from two to nearly 100 flowers with a wide range observed within each species. All flowers are pedicellate and subtended by two bracts. The bract apex can be acute, acuminate or obtuse, and can be used in species identification to a certain extent, although the variation that exists within species can make this difficult. In the species *Chelonanthus matogrossensis* and *C. pterocaulis* only bracts with acute apices have been observed. This is also largely the case with *C. acutangulus* and *C. viridiflorus*, but specimens with obtuse apices also exist in these two species. A potential geographical pattern has been identified in *C. acutangulus*. Specimens with obtuse apices have only been collected in Mexico. Those Mexican populations also vary in other character states, which will be discussed below. The species *C. alatus*, *C. albus*, and *C. angustifolius* predominantly have bracts with obtuse apices but acute has also been observed. An acuminate bract apex is commonly found in *C. grandiflorus* and *C. hamatus*, but the character states of acute and obtuse sometimes occur in the first species and cuspidate has been observed in the latter. *Chelonanthus purpurascens* has bracts that are either acute or obtuse, but because this species has a strong branching

pattern and is the only one to have purple corollas, this character is not needed in identification.

FLOWERS. All flowers of *Chelonanthus* are 5-merous and zygomorphic with sexual structures grouped towards the lower part of the corolla opening. The exception is the slightly less zygomorphic flowers of the newly described species, *C. pterocaulis*, which has sexual structures that are subequal in length and positioned deep within the narrow corolla tube (Figure 9).

CALYX. The calyx characters of most *Chelonanthus* species are largely invariable; having a green coriaceous calyx that is persistent in fruit and wingless calyx lobes that are dorsally thickened by a glandular area. The outlier in calyx characters is the species *C. hamatus* with minute wings on each calyx lobe and an upward facing hook near the apex of the glandular area.

The extent to which the calyx lobes are fused is a character useful in identifying *C. viridiflorus*. All other species of *Chelonanthus* have ovate to orbicular lobes that are fused for 1/4 to 4/5 of the total calyx length. The lobes of *C. viridiflorus* are oblong to ovate and fused for only 1/6 to 1/5 of the total length.

The general appearance of the calyx in flower is often a good indicator of the species *C. alatus* and *C. albus*. These species share a calyx with lobes that are more tightly overlapping in flower so they appear to ‘hug’ the base of the corolla. The calyx also appears small relative to the size of the corolla at anthesis, but as the calyx expands with capsule formation the calyx and fruit are more proportionally sized. The appearance of a small ‘hugging’ calyx has not been observed in other species.

COROLLA. Campanulate, funnelform, tubular and salverform corollas are observed in *Chelonanthus*. Although this character can be helpful in identifying species, the intra-specific variation makes it inadequate for use in a taxonomic key. The species *C. grandiflorus*, *C. matogrossensis*, and *C. viridiflorus* consistently have funnelform corollas that gradually and steadily amplify. This corolla shape is within the range of variability found in all other species except the newly described *C. pterocaulis*, which has narrowly tubular to salverform corollas (Figure 9). The only other species to have a narrowly tubular corolla is *C. angustifolius*, but stem and leaf characters, and the position of sexual structures relative to the corolla lobes can easily differentiate these two species. Most commonly found in *C. acutangulus* are campanulate corollas that emerge from the calyx only slightly more narrow than the width of the corolla mouth. There appears to be two geographical areas in which funnelform corollas are found in *C. acutangulus*, one is in the northernmost part of its range in Mexico (the same population with obtuse bracts as discussed above) and the easternmost part of its range in the Amazon Basin. The latter is an area where the distribution overlaps with several other species and this may be the result of hybridization. Campanulate corollas may also be found in *C. alatus*, *C. albus*, *C. hamatus* and *C. purpurascens*. When *C. alatus* corollas are campanulate, it can usually be distinguished from *C. acutangulus* by other corolla characters such as erect corolla lobes and exerted stigma in *C. alatus* vs. corolla lobes reflexed and stigma only reaching the base of the corolla lobes in *C. acutangulus*. When *C. albus* has a campanulate corolla, it is narrowly restricted for c. 1 mm at the very base and then abruptly expands to about the same width as the corolla mouth. In *C.*

hamatus and *C. purpurascens* other characters are used (mentioned above) for identify these species and corolla shape is not needed as an identification tool.

ANDROECIUM. All species of *Chelonanthus* have zygomorphic stamens that are isomeric with the corolla lobes. The positioning of the stamens is a helpful character in identifying *C. pterocaulis* which has anthers clustered within the corolla tube. Usually the filaments are inserted near the base of the corolla and only in *C. grandiflorus* and *C. matogrossensis* is the insertion closer to the corolla tube mid-point or above it.

Most species of *Chelonanthus* lack specialized structures at the insertion point of the stamens. *Chelonanthus hamatus* is unique in having a small corona present at the insertion point, a character otherwise found only in *Symbolanthus* (Molina & Struwe, 2008). In *C. acutangulus* and *C. grandiflorus* staminal pockets are sometimes present, a character also found in the Helieae genera of *Adenolisianthus* (Progel) Gilg, *Calolisianthus* Gilg, *Helia* Mart., *Lehmanniella* Gilg, *Rogersonanthus* Maguire & B. M. Boom and *Symbolanthus* G. Don (Struwe et al., in press).

Winged filaments are the most common state in *Chelonanthus*, but in several *C. acutangulus* specimens filiform filaments have been observed. After anthesis, the filaments remain straight in *C. matogrossensis*, *C. pterocaulis*, and *C. viridiflorus*. Filaments that are curved apically can be found in *C. acutangulus*, *C. albus*, *C. grandiflorus* and *C. purpurascens*. Both character states have been observed in *C. alatus*, *C. angustifolius* and *C. hamatus*. *Chelonanthus purpurascens* is the only species to have strongly recurved anthers after anthesis with the rest of the genus having anthers that remain straight or curved slightly.

GYNOECIUM. All species of *Chelonanthus* except the new species *C. pterocaulis* have a slightly bent style, resulting in a zygomorphic gynoecium. Other variations in gynoecium morphology in this genus (stigma, style and ovary dimensions) are overlapping between species and therefore not useful in species identification.

FRUITS. All *Chelonanthus* species have medially dehiscent capsules that are woody in texture with a persistent calyx. There is some variability in capsule orientation with a horizontal to nodding position observed in most species, except *C. angustifolius*, *C. pterocaulis*, and *C. viridiflorus* (with horizontal to erect capsules). Variability is also present in the presence or absence of a persistent corolla around the capsule. Portions of the corolla can be seen clinging to mature capsules in *C. angustifolius*, *C. grandiflorus*, *C. hamatus*, *C. matogrossensis* and *C. pterocaulis*; all other species have deciduous corollas.

SEEDS. There is virtually no variability present in seed characters of *Chelonanthus*; however, investigations have been limited in sampling within each species. All species have angular to cuboidal seeds that are brown in color and are all within the same size range.

Taxonomic issues

CHOOSING THE TRUE *CHELONANTHUS ALATUS*. As discussed in Lepis et al. (in progress; Chapter 1), *Chelonanthus alatus* had previously been considered a wide-ranging, highly variable species that was determined to be more accurately defined as four smaller species. Those species include *C. acutangulus*, *C. alatus sensu stricto* (referred to as *C. longistylus* or longistylus morphotype in Lepis et al., in progress; Chapter 1), *C. grandiflorus* and *C. pterocaulis*. The first description of *C. alatus* (=

Lisyanthus alatus) was based on a specimen collected by Aublet (s.n.) in French Guiana and was described as a suffrutescent annual with a quadrangular and winged stem, ovate-oblong leaves, and nodding pedicels (Aublet, 1775). The plate (pl. 80) that accompanies the description illustrates a plant with tubular flowers, exerted sexual structures and a persistent, pendulous style in fruit. The type specimen of *C. alatus* at BM has been consulted, but the condition of the specimen is poor, with an inflorescence only consisting of a portion of one calyx. Based on vegetative characters alone, this type specimen could have represented any of the hidden species mentioned above, except *C. grandiflorus*. The presence of pendulous styles in fruit, as well as a distribution that includes French Guiana, are parameters met only by specimens previously determined as *C. longistylus*. Therefore, the molecular and morphological evidence establishing the presence of at least four distinct species within the *C. alatus* species complex (Lepis et al., in progress; Chapter 1) and, *C. longistylus*, the only taxon to be congruent in morphology and distribution with the first description of *C. alatus*, results in the conclusion that the name *C. longistylus* is a later synonym of *C. alatus*. Most of what has previously been called *C. alatus* (or its synonym *Irlbachia alata*) will now be considered either *C. acutangulus* or *C. grandiflorus*.

IDENTIFYING THE HOLOTYPE OF *LISIANTHUS CHELONOIDES*. One of three typified names synonymous with *Chelonanthus grandiflorus* is *C. chelonoides*. In the reviewed literature, the author of the first description of *C. chelonoides* (= *Lisianthus chelonoides*) is consistently cited as Carl von Linnaeus filius [junior], 1781 (Gilg, 1895; Gleason, 1931; Grisebach, 1845; Jonker 1936; Lemée, 1953; MacBride, 1959; Maguire & Boom, 1989; Malme, 1904; Nilsson, 1970; Progel, 1865; Pringle 1995; Pulle, 1906;

Steyermark, 1953; Struwe et al. 1999). As was common practice at that time, Linnaeus f. (Linn.f., 1781) never cited the *L. chelonoides* description as *species novum*, nor did he make a reference to the type material used in the description. Linn.f. did refer to the location and habitat in which the species was collected, "Surinamo, Cayenna, altis arenosis," which translates to Cayenne, Suriname, high sands. The older Linnaeus described *Pentstemon chelonoides* in 1775 based on the collections Dahlberg 141, with a similar description of the collection site as high sands of Suriname. The morphology of the two descriptions is compatible, but Linnaeus (1775) was so brief that it doesn't provide much evidence: "Herb three feet tall. Flowers yellow in high sands". The collection that Linnaeus, the older, used for his description was identified at LINN with the help of Dr. Charles Jarvis and his work on the Linnaean Plant Name Typification Project at the Linnean Society of London. An image of this specimen can be viewed at <http://www.linnean-online.org/2288/>. The number 141 is cited in Linnaeus' description (1775) and written on the herbarium specimen linked above. The collector of specimen 141 was not designated on the sheet or within the description, but was determined to be Dahlberg based on information provided by Taxonomic Literature (1976-1998) for the publication, *Plantæ Surinamenses* (Linnaeus, 1775). The morphology of this specimen is congruent with the description published by Linn.f. (1781). Previously, Paul Maas designated three specimens from S as syntypes of *Lisianthus chelonoides* (Dahlberg s.n.). One of those specimens refers to Linn.f.'s description and was collected the same year as his publication, 1781. These specimens should no longer be considered syntypes since the collection, Dahlberg 141 (LINN), has been located and determined to be the holotype of *Pentstemon chelonoides* based on the evidence presented here.

Linnaeus and Aublet published their names *Pentstemon chelonoides* and *Lisyanthus grandiflorus* in 1775. Taxonomic Literature (Staflue & Cowan, 1981) cites the actual publication dates of *P. chelonoides* as the 23rd of June and *C. grandiflorus* as the 10th of June. Therefore, the name *grandiflorus* is older than *chelonoides* by thirteen days and has priority.

CHELONANTHUS FISTULOSUS, SYNONYM WITH *CHELONANTHUS GRANDIFLORUS*.

Another name synonymized here with *C. grandiflorus* is *C. fistulosus*. There has been some confusion in the literature about the possible affinity of *C. fistulosus* (= *Lisianthus fistulosus*) to *C. purpurascens*. The confusion began when Grisebach (1839) described *L. fistulosus* as purple-flowered, even though the first description by Poiret (1814) listed a yellow-flowered plant. This was not just an oversight on Grisebach's part, because in subsequent works (1845, 1862) he continued to argue that “the authentic” *L. fistulosus* was purple-flowered and a part of the *L. purpurascens* complex. The floristic treatments of Lemée (1953) and Progel (1865) followed Grisebach's illegitimate description of a purple-flowered *L. fistulosus*. Photos of the type material have been observed (F, U), but because blue corollas in *Chelonanthus* often fade into brownish yellow, the flower color can no longer be accurately assessed. Those photos depict a plant with a stout stem and large leaves, a morphology not similar to *C. purpurascens*. In consideration of the original description and the type material, the name *C. fistulosus* has been regarded here as a synonym with *C. grandiflorus*.

WHITE VARIETY OF *CHELONANTHUS PURPURASCENS*. It has been suggested in the literature (Struwe et al., 1999; Bentham 1854) that a white corolla form of *C. purpurascens* exists. It was suggested by Struwe et al. (1999) that the field character

distinguishing it from *C. albus* was the presence of recurved anthers after anthesis. A review of 56 *C. albus* and 330 *C. purpurascens* herbarium specimens has not revealed any plants with white corollas and recurved anthers. Several *C. albus* specimens with strongly curved filaments have been identified (Brazil, Amazonas, Manaus: Miranda 48061; Venezuela, Amazonas, Canyon Grande of Cerro de la Neblina: Funk & Liesner 6143; Venezuela, Amazonas, Dept. Rio Negro, lower part of Rio Baria: Davidse 27674), but as documented in the descriptions above, apically curved filaments are not uncommon in the green, white, to yellow-flowered species of *Chelonanthus*. It should also be noted that when Bentham (1854) described the white variety of *C. purpurascens* (= *Lisianthus uliginosus* var. *floribus amplis albis*) the material he based his description on was the type material for *C. albus* (Spruce s.n.) and he mentions that Spruce distributed the specimen as a new species, *L. albus*. Considering the lack of botanical evidence and the fact that Bentham (1854) described this white variety of *C. purpurascens* based on the type material of *C. albus*, it is concluded here that a white form of *C. purpurascens* does not exist.

CHELONANTHUS CANDIDUS, SYNONYM WITH *CHELONANTHUS VIRIDIFLORUS*. The name *C. viridiflorus* was first described by Martius (1827) from Minas Gerais, Brazil, as an herb with a terete stem, semi-petiolate leaves and a pale green corolla more than 2.7 cm long. About seventy-five years later, Malme (1904) described *C. candidus* from Mato Grosso, Brazil. The two descriptions are very similar and Malme notes that *C. candidus* has an affinity to *C. viridiflorus* with similar stems and leaves, but differs in corolla size (twice as large) and color (white vs. pale green). A survey of herbarium collections revealed that specimens determined as *C. candidus* with large corollas, ranging from 4.8

to 6.4 cm long and occurring in southeastern Brazil and adjacent Paraguay (a subset of the distribution observed for *C. viridiflorus*; Figure 10). A Principle Component Analysis of thirteen morphological characters and sixty-six samples (Gorczyca et al., 2005) failed to segregate specimens of *C. candidus* and *C. viridiflorus*. The difference in corolla length is apparent when observing the two extremes, but a number of intermediate specimens were observed that could not readily be placed within one of the two groups. In addition, the difference in corolla color mentioned by Malme (1904) did not withstand the consensus of 157 herbarium specimens determined as *C. candidus* or *C. viridiflorus*. Therefore the name *C. candidus* has been combined under *C. viridiflorus*, a decision that was also supported by Maas (1985).

Figure 10: Map illustrating the distribution of specimens determined as *Chelonanthus candidus* and *C. viridiflorus* (based on 94 collection sites).



CHAPTER 3

Two New Species of *Sipapoantha* and *Chelonanthus* from the Guayana Highlands (Gentianaceae: Helieae)³

ABSTRACT. Two new species from the gentian tribe Helieae are described from Brazil, French Guiana, and Venezuela. *Sipapoantha obtusisepala* sp. nov. is distinct from the previously described *Sipapoantha ostrina* in its woody and branched habit, sessile ovate leaves with an acute apex, and a smaller calyx with circular lobes. This new species is found in northeastern Brazil and represents the second species of this previously monotypic genus. It is tentatively placed in *Sipapoantha* based on the presence of key generic characters such as coriaceous leaves with strongly revolute margins and blue corollas. *Chelonanthus hamatus* sp. nov. is described from French Guiana and Venezuela. It is unique to the genus by the presence of minute wings on the calyx lobes that are also equipped with a hook at the apex of each glandular area. In addition, a corona is present at the insertion point of the filaments.

Key words: floristics, Gentianaceae, Helieae, morphology, Neotropics, South America, new taxa.

The rare genus *Sipapoantha* Maguire & B.M. Boom is known from only a handful of herbarium specimens and until now has been considered a monotypic genus (Struwe et al., 1999 [Flora of Venezuelan Guayana]). The type species, *Sipapoantha ostrina*

³ The new names included in this chapter are not accepted by the author as validly published in this dissertation (Botanical Code, Article 34.1[a]).

Maguire & B.M. Boom, is a perennial herb endemic to the Guayana Highlands region of Venezuela, and more specifically, only occurs in the state of Amazonas, on the tepui mountains (flat-topped mesas) of Cerro Sipapo, Cerro Cuao, and Cerro Autana.

Sipapoantha obtusisepala, described here for the first time, is a woody shrub known from only a single herbarium specimen collected on a mountain in the Brazilian-Guyana border area in the Brazilian state of Roraima. It differs from *Sipapoantha ostrina* in its woody and branched habit, sessile ovate leaves with an acute apex, and a smaller calyx with circular lobes, but the two taxa share coriaceous leaves with strongly revolute margins that are sulfur yellow in color when dry and blue corollas. A new generic description of *Sipapoantha* is provided here since the genus is no longer monotypic. A key to the two species is also included.

The name *Chelonanthus* Gilg was first used to denote a section of *Lisyanthus* Aubl. (Grisebach, 1839) and was elevated by Gilg (1891) to generic status. *Chelonanthus* has also been synonymized with *Helia* Mart. by Kuntze (1891) and with *Irlbachia* Mart. by Maas (1985). Much taxonomic confusion is associated with this genus, for more detailed discussions on the history of *Chelonanthus* and related genera of Helieae look to Lepis et al. (in progress; Chapter 1), Nilsson (1970) and Struwe & Albert (1998).

The genus *Chelonanthus* is neotropical in distribution, with the center of diversity in the Guayana Shield (seven of the ten species are found there), extending south across the Amazon Basin and over the Brazilian Shield into Paraguay and northern Argentina, and westward across the Amazon Basin into the eastern foothills of the Andes from Bolivia in the south, to Venezuela, Colombia and Central America in the north. One species, *C. acutangulus* (Ruiz. & Pav.) Gilg, is found as north as southern Mexico.

Chelonanthus herbs are often unbranched, but can also be branched and suffrutescent at the base with leaves somewhat evenly dispersed along the stem, except for the two internodes just below the inflorescence, which are visibly longer. The terminal inflorescence is many-flowered, with one or two dichotomous branching points resulting in two or more monochasial branches. Flower buds are obtuse and flowers are zygomorphic with the sexual structure clustering at the lower part of the corolla mouth. The new species described fits well into typical *Chelonanthus* morphology and all herbarium sheets of the new species examined were previously determined as *C. alatus* (Aubl.) Pulle or *C. angustifolius* (Mart.) Gilg. *Chelonanthus hamatus* is commonly found in rocky savannas of French Guiana and Venezuela and is unique in the presence of large, oblanceolate leaves (population from Venezuela has elliptic leaves), upward facing hook-like structures at the apex of each dorsal, glandular area of the calyx lobes, and the presence of a corona at the insertion point of the filaments. This new species is only known from four collections. *Chelonanthus* is currently under revision by KBL and a full generic description and key to all species will be published in this upcoming work (Lepis et al., in progress; Chapter 2). The inclusion of *C. hamatus* in the genus does not change the current general characteristics of the genus, which cannot be said of the inclusion of *Sipapoantha obtusifolia* in the genus *Sipapoantha*.

The taxa described here represent two new species in the neotropical tribe Helieae (Gentianaceae; Struwe et al., 2002; in press). The latest phylogeny based on 127 morphological characters and DNA sequences (*matK*, *trnL* intron, and ITS) places *Sipapoantha* one step above the most basally divergent clade of the tribe (note that this placement is tentative due to a lack of molecular data for *Sipapoantha*; Struwe et al., in

press). In the same paper, the result consistently places *Chelonanthus* in the most derived *Symbolanthus* subclade. Both new species share the typical Helieae characters of terminal compound cymes with a pair of scale-like bracts subtending each flower, calyx lobes rounded with a dorsal glandular area, medially dehiscing capsule with a woody pericarp, and numerous angular seeds (Struwe et al., 1999; 2002).

MATERIALS AND METHODS

Morphological characters were collected from herbarium specimens from AAU, COL, F, G, IAN, INPA, K, MG, MO, NY, S, SP, U, UPS, and US. All measurements and sketches were taken from dried, pressed material with flowers (when available) rehydrated in a solution of 70% ethanol and glycerol for several days. A ruler was used to measure peduncle length and leaf dimensions, while all other measurements were observed using an eyepiece scale of an Olympus dissecting scope at 10X or 50X magnification. The terminology used to describe structures follows Stearn (1983 & 1999). The abbreviations for herbaria follow *Index Herbariorum* (Holmgren & Holmgren, 1998).

Pollen characters were taken from the *Chelonanthus hamatus* isotype from US, but seeds were not available from any of the type material. Therefore, seed characters were collected from de Granville 11737 (US). Seed and pollen characters are lacking for *Sipapoantha obtusisepala* due to rarity of material. Seeds and pollen were coated using a Hummer X Sputter System by Anatech LTD for three minutes and two minutes respectively. Observations were made with a Hitachi S-510 scanning electron microscope at 80X magnification for seeds and 800X magnification for pollen. Pollen

characters are lacking for *Sipapoantha obtusisepala* due to the absence of flowers on that the only known specimen.

TAXONOMIC TREATMENT

Sipapoantha Maguire & B.M. Boom. 1989: Mem. New York Bot. Gard. 51: 23, 25, figs. 17, 18. *Type: Sipapoantha ostrina* Maguire & B.M. Boom.

Plants herbaceous or woody shrubs, glabrous. *Stems* quadrangular, unbranched when herbaceous or branched when woody, with or without 4 narrow wings; interpetiolar line present. *Leaves* aggregated at the base or evenly dispersed along stem, sessile or petiolate; blade elliptic, ovate, to obovate, 1.0-7.5 x 0.5-4.0 cm, yellow in color when dry, very thick and coriaceous; margin revolute; midvein prominent, sometimes with 1-2 visible pairs of lateral veins; base narrowly attenuate on basal leaves or obtuse on apical leaves; apex obtuse or acute. *Inflorescence* terminal, cymose, dichotomously branched at the basal node, then monochasial, 1-12-flowered; peduncle up to 14.5 cm; bracts either similar to leaves, up to 10 mm long, or scale-like, about 2 mm long. *Flowers* showy, erect to nodding at anthesis, 5-merous; pedicel 6-9 mm long (not known from *S. obtusisepala*). *Calyx* campanulate, 6-10 mm long, fused up to 2/3 of total calyx length, green, thick and coriaceous, persistent and spreading in fruit; lobes oblong or circular, with a thickened dorsal ridge, 3-6 mm long; apex acute or obtuse; margin hyaline. *Corolla* funnelform, 5-96 mm long, dark blue to purple, deciduous in fruit; lobes 25-32 x 25 mm, circular, overlapping slightly, mucronate; flower bud apex bluntly tapering. *Stamens* included in corolla mouth; filaments flattened (when dry), of unequal length, 28-39 mm long, inserted very close to base of corolla tube, widened and

winged at the base; anthers lanceolate sagittate, 7-8 mm long, straight after anthesis, versatile, with a sterile apex; pollen in tetrads with pilate to verrucose exine (fide Nilsson, 2002). *Ovary* sessile, with a glandular disk below ovary; style flattened in fruit (when dry, then also twisted), persistent or deciduous; stigma broadly bilamellate (corolla, stamen, and pistil characters not known from *S. obtusisepala*). *Capsule* ellipsoid, 10-18 mm long, green when immature, brown at maturity, woody, dehiscing medially, horizontal to nodding. *Seeds* angular, roughly cubical or conical, 0.5-0.8 mm in diameter, brown.

KEY TO THE SPECIES OF *Sipapoantha*

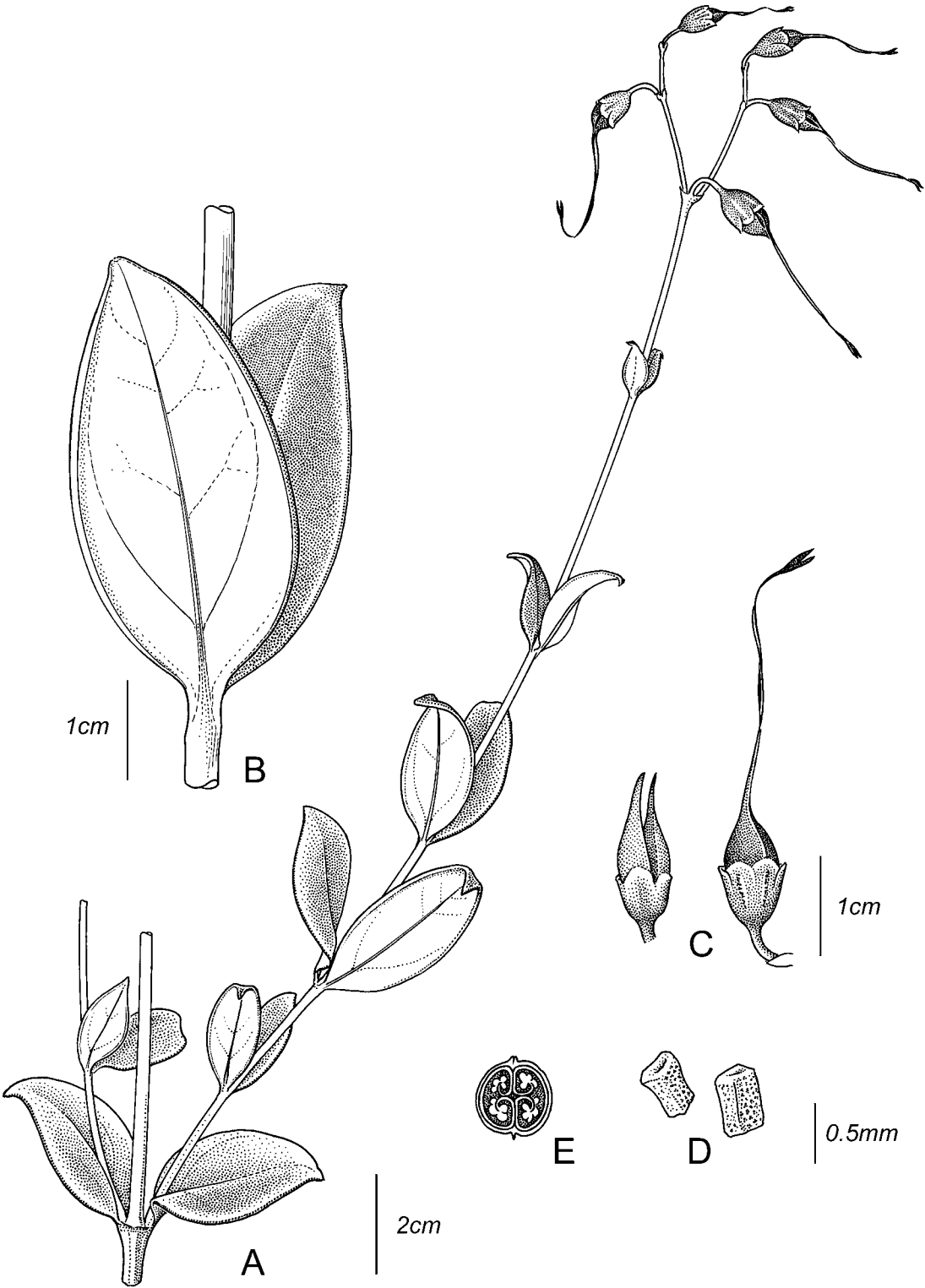
1. Woody, branching shrub; leaves evenly dispersed along stem, widest at the base or in the middle, apex acute; calyx 6-7 mm long; calyx lobes circular, 3-4 mm in diameter.....*S. obtusisepala*
1. Single-stemmed herb; leaves mainly aggregated on lower half of stem, widest above the middle, apex obtuse; calyx 8-10 mm long; calyx lobes oblong, 5-6 mm long.....*S. ostrina*

***Sipapoantha obtusisepala* Lepis, Maas, and Struwe, sp. nov.**

TYPE: Brazil, Roraima, Serra Baeta, perto de Suriname, 11 November 1973.

Arbusto sobre pedra; flôr azulada. *B. G. S. Ribeiro 396* (holotype: IAN). Figure 11.

Figure 11: *Sipapoantha obtusisepala* sp. nov. A, flowering stem in the fruiting stage, with leaves evenly spread out along stem. B, leaves with prominent midvein and one pair of prominent, arcuate secondary veins. C, young capsule with persistent calyx, style, and stigma and older capsule with apical portions of style and stigma missing, note the short and obtuse calyx lobes. D, angular seeds with sunken sides and ridges. A-D from *Ribeiro 369*. Illustrator: Hendrik Rypkema.



Shrub. Stems woody, branching, with four longitudinal ridges ca. 0.1 mm wide. *Leaves* evenly dispersed along stem, sessile; blade elliptic or ovate towards the apex of plant, 1.0-2.5 x 0.5-1.2 cm, upper side more lightly colored than lower side; base of lower leaves attenuate, base of upper leaves obtuse; apex acute. *Inflorescence* 5-12-flowered; peduncles 5.3-14.5 cm long; bracts scale-like with obtuse apex, 1.9-2.1 mm long; pedicels 6-9 mm long. *Calyx* campanulate, 6-7 mm long, fused 2/5-3/5 of total calyx length; lobes circular, 3-4 mm in diameter; apex obtuse. Corolla not seen, reported as blue (Ribeiro 396). Stamens not seen. Gynecium not seen in flower. *Capsule* medially dehiscent, ellipsoid, 10-12 mm long; calyx in fruit ca. 3/5 of capsule length, with a semi-persistent style, ca. 30 mm long with some apical portions broken off in older capsules. *Seeds* roughly cubical, ca. 0.2-0.5 mm in diameter.

Phenology. Fruiting specimen collected in November.

Habitat and Distribution. *Sipapoantha obtusisepala* is known from only one specimen growing among rocks on the Sierra Baeta mountain on the Brazilian-Guyana border in the Brazilian state of Roraima.

Etymology. The name *obtusisepala* derives from the Latin ‘*obtusus*’ meaning rounded and ‘*sepalum*’ meaning sepal. This name was chosen to reflect the obtuse apices of the calyx lobes.

Comparative specimens. *Sipapoantha ostrina* examined: VENEZUELA.

Amazonas: Dept. Atures, sandstones of Cerro Cuao, Caño Cabeza de Manteco, 73 km SE of Puerto Ayacucho, 1580 msnm, 05°06’N 67°24’W, Sept. 1989, *Fernandez 6236* (MO); Cerro Cuao, summit of the northern section, grasslands, shrubs and rock outcrops on south facing slope, 1600 m, 5°4’N 67°24’W, 11 Feb. 1993, *Huber 13541*

(U); Cerro Sipapo (Park), North mountain at 2000 m, 6 Dec. 1948, *Maguire & Politi* 27527 (holotype NY; isotypes GH [n.v.], S [n.v.], US, VEN [n.v.]); Cerro Sipapo (Park). North Mountain at 2000 m, 6 Dec. 1948, *Maguire & Politi* 27527A (NY); Cerro Sipapo (Park), lower Caño Negro, at 1400 m, 1 Jan. 1949, *Maguire & Politi* 28092 (K, NY); Cerro Sipapo (Park), Savanna Camp to Caño Profundo and East Terrace via Caño Negro, 1600 m, 8 Jan. 1949, *Maguire & Politi* 28219 (NY, P [n.v.], VEN); Cerro Sipapo, 1500 m, 15 Jan. 1981, *Maguire et al.* 65702 (NY [DNA voucher]); Cerro Autana, Summit of the Cerro Autana: savanna and dangerous outcrops, 1230-1240 m, 4°52'N 67°27'W, 20-22 Sept. 1971, *Steyermark* 105123 (NY, U); Cerro Sipapo, Dept. Atures, summit of northern section, savanna type vegetation along a small stream, 1500 m, 5°N 67°30'W, 17 Feb. 1981, *Steyermark et al.* 124554 (MO, NY).

Chelonanthus Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 98. 1895. TYPE: *Chelonanthus purpurascens* (Aubl.) Struwe, S. Nilsson, & V.A. Albert.

A generic description for *Chelonanthus* as well as a key to species can be found in the floristic treatments by Struwe et al. (1999) and Lepis et al. (in progress; Chapter 2). The new species described here does not drastically change how the genus is defined morphologically.

Chelonanthus hamatus Lepis, sp. nov.

TYPE: French Guiana. Cayenne. Camp # 3 - Roche n° 1 Akouba Booka goo Soula - Ha Basin 500 m to the southwest. Alt.: 160 m. Long.: 5° 41' Lat.: 2° 36'. Isolated thickets on rocks. Edge of rocky savanna, 26 August 1987, de Granville, J.J., L.

Allorge, W.H. Hahn, M. Hoff, & Weitzman 9713 (Holotype, CAY [n.v.]; isotypes, B [n.v.], G, MG, NY, P [n.v.], U, US) Figure 12.

Plants herbaceous, up to 1.2 m high. *Stems* branched, quadrangular, 4-winged; branches up to 11 mm in diameter; internodes 2.5-13.5 cm long; wings 1.0-1.3 mm wide. *Leaves* evenly attached along stem, sessile; blade oblanceolate to elliptic, 4.3-20.7 x 2.9-6.2 cm, subcoriaceous to membranaceous; base attenuate or obtuse near inflorescence; apex acute to obtuse. *Inflorescences* terminal, cymose, dichotomously branched at the basal node, then monochasial, 16-40-flowered; bracts ovate, 2.2-3.8(-8.1) mm long; apex acuminate to cuspidate. *Flowers* erect to horizontal at anthesis; pedicel 6-9 mm long. *Calyx* campanulate, 6-8 x 5-7 mm, fused 3/8-3/5 of calyx length; lobes ovate, 3-4 x 3-4 mm, minutely winged, with upward facing hook protruding from the apex of each glandular area; wings c. 0.4 mm wide; hooks 1.3-2.1 mm long; apex obtuse. *Corolla* campanulate to funnelform, 20-27 mm long, 10-18 mm wide at mouth, green, persistent in fruit; lobes ovate, 3-6 x 3-7 mm, with a dark green spot on each apex. *Stamens* inserted near base of corolla tube at 1/3 of total corolla length, corona present as a ring of tissue 0.9 mm wide with free triangular flaps in between each filament, flaps 0.8 x 0.7 mm; filaments winged, sub-equal in length (within 2 mm), 10-12 mm long, after anthesis straight to curved downward apically; anthers elliptic, 1.8-3.2 mm long, white-yellow, straight after anthesis; pollen exine with fine reticulum interspersed with thickend, knob-like muri. *Gynoecium* 18 mm long; ovary ellipsoid, 4.4 x 2.1 mm; style 11 mm long; stigma lobes elliptic, 2.4-2.8 x 1.8 mm (internal floral characters taken from a single flower due to rarity of material). *Capsule* ellipsoid, 9-17

x 4-8 mm, brown, nodding. *Seeds*, angular, 0.1-0.6 mm in diameter, brown; testa cells subcircular, concave with band-like thickenings.

Phenology. Flowering and fruiting specimens were collected in January, April and August, with no records for the remaining months.

Habitat and Distribution. Three of the four *Chelonanthus hamatus* specimens were found in rocky savannas of southwest French Guiana at an altitude of 160-450 m. The fourth specimen was collected in a cloud forest on exposed rock in Venezuela (Bolívar), at 500-600 m. altitude.

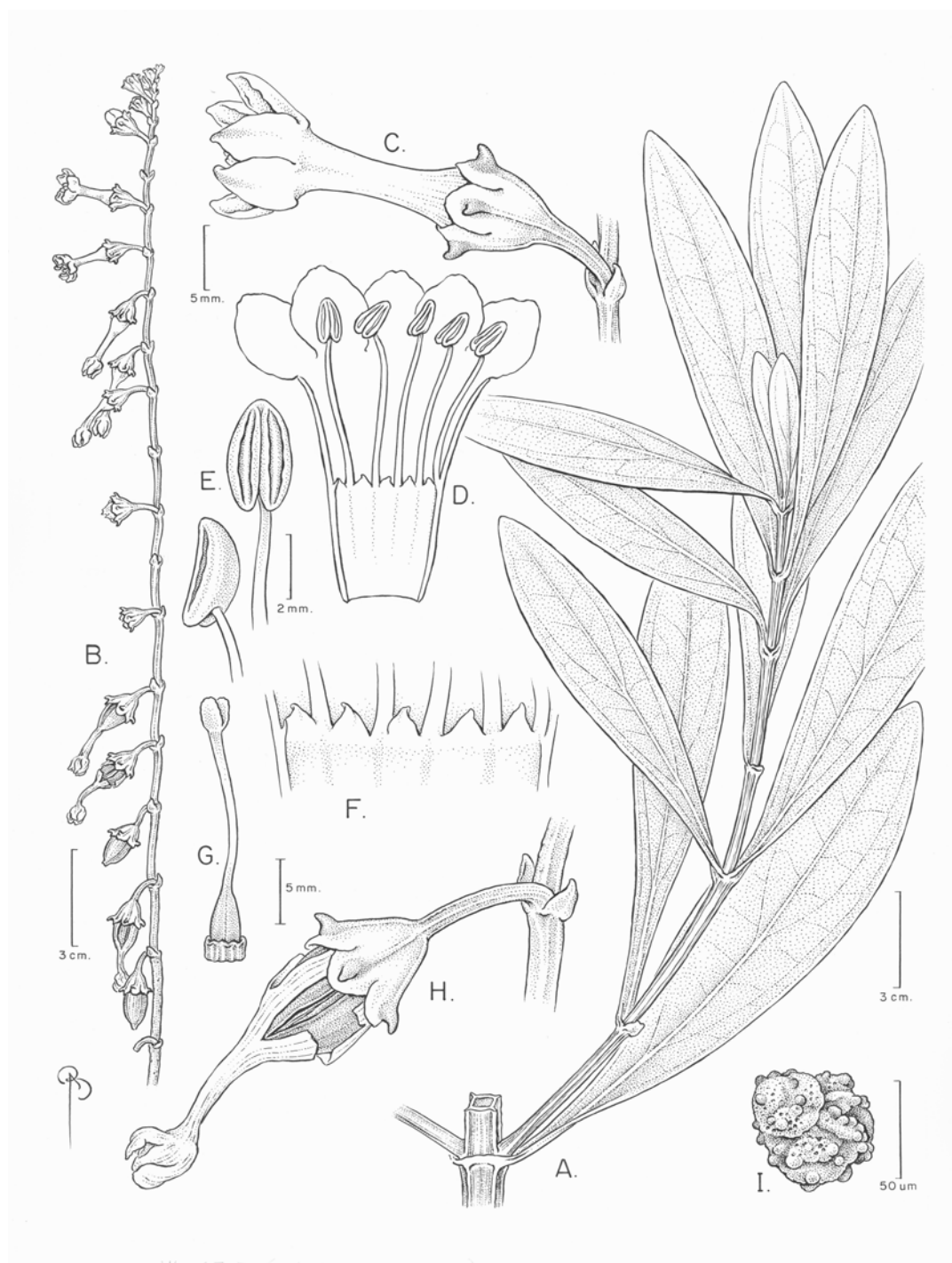
Etymology. The name *hamatus* derives from Latin meaning hooked. This name was chosen to reflect the hooks present at the apex of the glandular area of each calyx lobe.

Paratypes. FRENCH GUIANA. Borne Frontiere Numero 4 - Bassin du Marouini.

Vegetation herbacee de savane roche. Heliophile saxicole. A cote de la borne, 13 April 1993, *de Granville et al.* 11737 (B [n.v], K, NY, US, CAY [n.v], P [n.v.], U); Roche Koutou - Bassin du Haut-Marouini. Sommet de l'inselberg. Savane roche. En touffe sur rocher, 17 August 1987, *de Granville et al.* 9399 (CAY [n.v.], U, US).

VENEZUELA. **Bolívar:** E. of Miamo, Hato de Nuria. On large exposed boulder. Cloud forest. Summit of west-facing wooded escarpment. Elev. 500-600 m. 16 January 1961, *Steyermark* 88556 (G, NY).

Figure 12: *Chelonanthus hamatus* **sp. nov.** A, strongly quadrangular 4-winged stem bearing large strap-like leaves. B, part of the inflorescence. C, close-up of flower showing the minutely winged calyx lobes that terminate in an upward facing hook at the apex of each glandular area. D, dissected corolla showing the corona at the insertion point of the filaments. E, front and side view of anther. F, close-up of corona. G, gynecium with nectary disc at base. H, mature medially dehiscent capsule with persistent corolla. I, SEM of pollen at 800X magnification, showing the exine with fine reticulum interspersed with thickened, knob-like muri. A-I from *de Granville et al.* 9713. Illustrator: Bobbie Angell.



DISCUSSION

Sipapoantha

The species described here has been tentatively placed within *Sipapoantha* based on shared gross morphological characters. Table 7 provides a character comparison of *S. obtusisepala*, *S. ostrina* and other Helieae genera with which the newly described species share diagnostic characters. The coriaceous leaves of *S. obtusisepala* are similar to those of *S. ostrina*, *Prepusa* Mart., *Calolisianthus* Mart., and *Rogersonanthus* Maguire & B.M. Boom. The revolute leaf margin is also a character found in *Sipapoantha* and *Calolisianthus* as well as in one species of *Prepusa* and *Rogersonanthus* (*P. montana* and *R. quelchii*). Although there are similarities, it does not seem likely that the new species is part of *Prepusa* due to the 6-merous flowers and the chartaceous, showy and inflated calyx characteristic of that genus. *Calolisianthus* is another genus with vegetative similarities to *Sipapoantha obtusisepala*, but like *Prepusa*, are endemics to the Brazilian Highland, making the placement of the new species into these unlikely from a geographic standpoint.

Chelonanthus has many species found in the Guayana Highlands, but the vegetative morphology and habit fail to point to this genus as the best choice. When comparing the generic characters it is apparent that *Sipapoantha ostrina* and *Rogersonanthus* share the most characters with the new species *S. obtusifolia* (Table 7). All three taxa have coriaceous leaves, revolute leaf margins and 5-merous flowers with a coriaceous, green calyx. The characters that *Sipapoantha ostrina* shares with the new species, and which exclude it from *Rogersonanthus*, are the sulfur yellow color of the dried leaves and purple corollas. *Rogersonanthus*, on the other hand, shares a woody habit and leaves

that are evenly dispersed along the stem. Both genera occur in the Guayana Highlands region, making each a good candidate geographically. Considering that there are a number of genera in Helieae that are composed of woody and herbaceous species (*Macrocarpaea* (Griseb.) Gilg, *Neblinantha* Maguire, *Prepusa*, *Rogersonanthus*, and *Symbolanthus* G. Don, as well as genera with variable leaf placement along the stem (*Chelonanthus*, *Irlbachia* Mart., and *Prepusa*; Struwe et al., 2002), it seems more appropriate to place the new species in *Sipapoantha* based on the color and texture of its dried leaves and purple corollas.

In the circumscription presented here, *Sipapoantha* is a montane genus endemic to the Guayana Highlands, albeit strongly disjunct (Figure 13). *Sipapoantha ostrina* is known from only a few herbarium specimens from tepuis in the western part of the mountain range, and *S. obtusisepala* is found on a mountain outlier in the southeast, approximately 1000 km from *S. ostrina*.

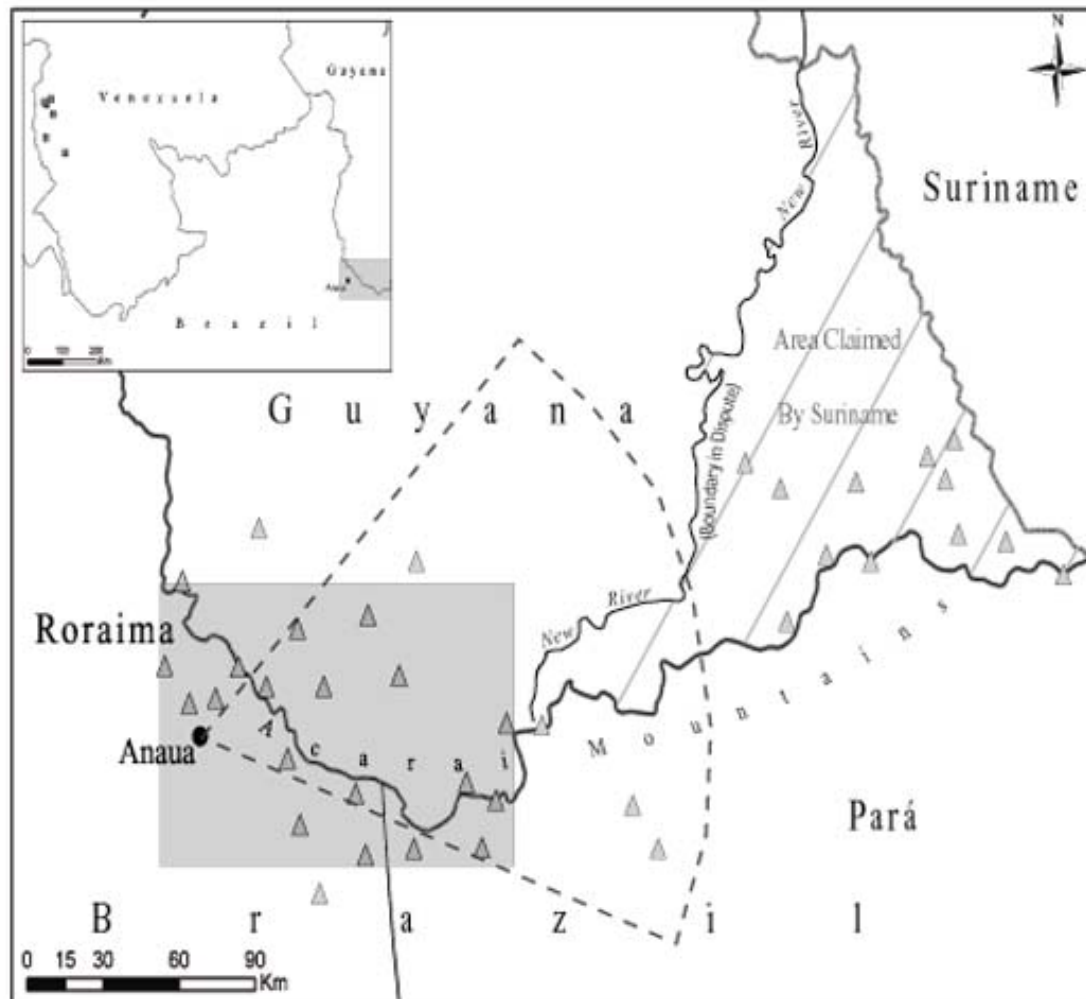
Sipapoantha obtusisepala is unique in the genus in its woody, branching habit. It also differs in having sessile leaves that are smaller in size with an acute apex, as opposed to *S. ostrina*'s petiolate leaves with an obtuse apex. The 6-7 mm long calyx of *S. obtusisepala* is smaller than the 8-10 mm long calyx of *S. ostrina*. Calyx lobe shape differs as well, with a circular shape found in *S. obtusisepala* and an ovate-oblong shape found in *S. ostrina*.

The collection site of the *Sipapoantha obtusisepala* type specimen is not clearly stated on the herbarium label. The label reads, "Serra Baeta, nearby Suriname, Roraima." It is not clear from the label if the location is referring to Roraima, the state in Brazil, or Mt. Roraima on the tri-border of Brazil, Guyana and Venezuela. In

Taxon (# of characters shared with new species)	Geographic distribution by region	Habit	Leaf position along stem	Leaf texture	Leaf color when dry	Leaf margin	Flower merosity	Calyx texture / Calyx color	Corolla color
<i>Sipapoantha obtusisepala</i>	Guayana Highlands	woody	evenly dispersed	coriaceous	yellow	revolute	5-merous	coriaceous / green	purple
<i>S. ostrina</i> (7)	Guayana Highlands	herbaceous	aggregated at the base	coriaceous	yellow	revolute	5-merous	coriaceous /green	purple-blue
<i>Rogersonanthus</i> (7)	Guayana Highlands	woody	evenly dispersed or aggregated at branch apex	coriaceous	green	flat (revolute - <i>R. quelchii</i>)	5-merous	coriaceous green	green, white, yellow
<i>Calolisianthus</i> (6)	Brazilian Highlands	herbaceous	evenly dispersed	coriaceous	green	revolute	5-merous	coriaceous green	purple, blue, red
<i>Chelonanthus</i> (5)	Central America, Guayana Highlands , Amazon, Andes, Brazilian Highlands	herbaceous (sometimes woody at the base)	evenly dispersed	chartaceous (rarely subcoriaceous)	green	flat	5-merous	coriaceous green	green, white, yellow (purple - Ch. purpurascens)
<i>Prepusa</i> (3)	Brazilian Highlands	herbaceous (woody - P. montana)	aggregated at base in herbs / aggregated at branch apex when woody	coriaceous	green	flat (revolute - P. montana)	6-merous	chartaceous red, purplish-red yellow, orange, or green	white, yellow

Table 7: Table comparing five taxa with *Sipapoantha obtusisepala* using ten morphological characters. Characters in bold are those shared with the new *Sipapoantha* species. Numbers in parentheses below taxon name represent the number of characters shared with *S. obtusisepala*. Note: *Rogersonanthus* in this circumscription does not include *R. coccineus*, which has been moved to *Roraimaea* (Struwe et al., 2008).

Figure 13: Map of Brazil, Guyana, and Venezuela illustrating the disjunct distribution of the genus *Sipapoantha*. The smaller map inserted in the upper left corner illustrates, the type species, *S. ostrina* (symbol ■) found on the tepuis in the western part of the Guayana Highlands in Venezuela. The location of the newly described species, *S. obtusisepala*, is believed to have been collected in the gray area near the town of Anauá, on the border of Brazil and Guyana. The larger map shows the proposed collection area in greater detail (see discussion for details). The area in gray represents the RADAM Project quadrat NA-21-YA. The area outlined by ---- represents a 200 km distance from the town of Anauá. The ▲ symbol represents mountain peaks.



addition, neither the state nor the mountain is located near the Suriname border. All efforts to locate Serra Baeta had been fruitless until a specimen of a different genus was found that was likely collected during the same expedition. This specimen of another gentian, *Aripuana cullmaniorum* Struwe, Maas, & V.A. Albert, was collected from the same mountain, on the same day, by B.S. Pena (*Pena 365*, IAN). This second (and remarkable, see below) collection of *A. cullmaniorum* provided enough information to narrow down the location to several peaks on the border of the Brazilian states of Roraima and Pará with Guyana. The *Aripuana* label reads, "On Serra Baieta 200 km from Anauá, quadrat NA-21-YA, RADAM Project, Federal Territory of Roraima." We located the mentioned quadrant on the RADAM website www.adimb.com.br/mapa.htm and were able to pinpoint the village Anauá on *A Traveller's Reference Map of Amazon Basin*, map # 421 (International Travel Maps, ITMB Publishing LTD., 1998). A second map, *The Guianas and Guyana* (International Travel Maps, ITMB Publishing LTD., 2004) shows multiple peaks within the area as well as the area east of the New River in Guyana as under dispute and claimed by Suriname. This would explain Ribeira's description of "...nearby Suriname..." The map in Figure 13 illustrates all of the location evidence we currently have from these two collections. Searches through databases of specimens at MO, NY, and US have not revealed any other collections from Serra Baeta (Baieta).

The collection of *Aripuana cullmaniorum* is also interesting because it reveals a highly disjunct population of this species. *Aripuana* was previously thought to be endemic to the lowland white sand areas of southeastern Amazonas in the border area of

the states Rondônia, Mato Grosso, and Pará (Struwe et al., 1997). The new genus *Roraimaea*, also in the tribe Helieae, was recently described from white sand areas of Roraima (Struwe et al., 2008). Gentianaceae are not heavily collected in this state and we expect new and interesting populations, and possibly species, to be added to the scientific record in the future.

Chelonanthus

Leaf morphology and winged calyx lobes are two distinguishing characters that set *Chelonanthus hamatus* apart from the rest of the genus and the presence of hooks on each calyx lobe is a characteristic unique to the family. Even though lack of floral material prevented sampling from specimens other than the type, the presence of a corona at the insertion point of the filaments is a remarkable character that has not been previously observed in the genus. Coronas are present in the closely related *Symbolanthus*, but this genus has large showy flowers, often pink, that are solitary or born in a few-flowered inflorescence and bears leathery, nearly berry-like fruits. The floral and fruit characteristics of *C. hamatus* (apart from the corona) clearly do not fit with *Symbolanthus* characteristics (Struwe et al., 2002). The latest phylogeny of Helieae strongly supports the placement of *Chelonanthus* and *Symbolanthus* together with several other genera in the most derived *Symbolanthus* subclade (Struwe et al., in press). It is possible that this character of corona presence is an evolutionary link between these two genera. All attempts to amplify DNA from *C. hamatus* have failed, but if a future phylogenetic study succeeds in including this new taxon, the role it will play in telling the evolutionary history of the *Symbolanthus* subclade should be interesting.

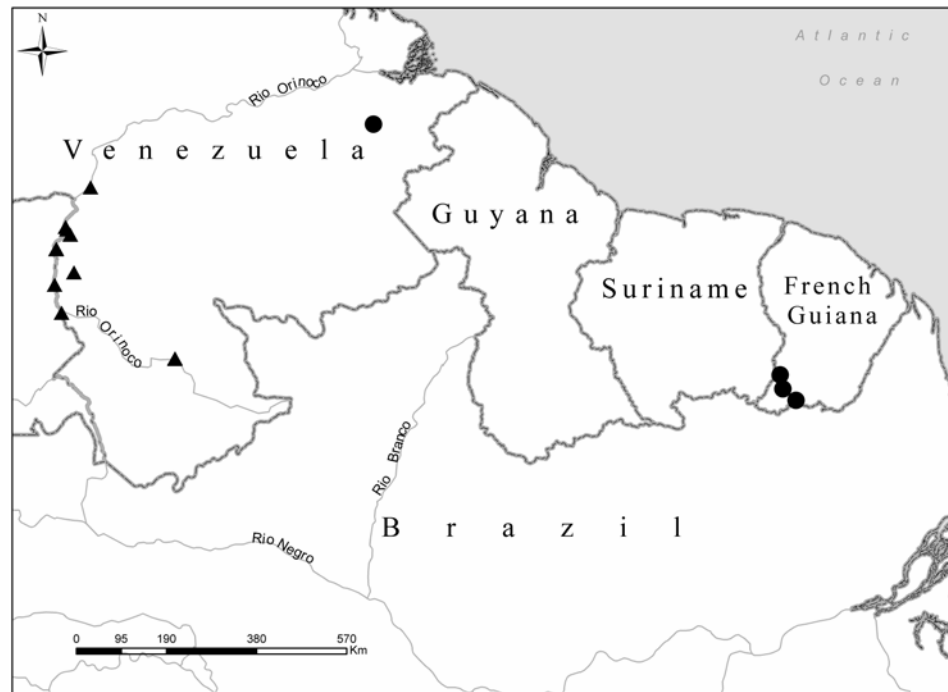
Specimens of *C. hamatus* are also unique in having quadrangular stems that are so strongly 4-winged, that the wings are noticeably continuous from base to pedicel and continue onto the calyx lobes. Three other species in *Chelonanthus* have strongly quadrangular stems, *C. alatus sensu stricto*, *C. acutangulus* (Ruiz & Pav.) Gilg, and *C. n. sp.* ('pterocaulis' Lepis, Chapter 2), but none of these have a continuous wing from base to plant apex.

It must be noted that several intermediate specimens have been identified. These specimens (look to Appendix B for a list of material observed) are considered intermediates because they have stems that are weakly quadrangular to terete instead of the notable quadrangular and 4-winged stems described above, examples of stem variation are present in the genus. *Chelonanthus acutangulus* specimens range from quadrangular and 4-winged to weakly quadrangular or terete with 4-ridges, and wings or ridges always present except for some of the smallest, most apical internodes. *Chelonanthus angustifolius* also has stem variability, ranging from terete to weakly quadrangular and 4-ridged. The variation in the specimens considered intermediates and those considered *C. hamatus* span the extremes and is greater than is seen in the rest of the genus. The presence of a well defined to highly reduced bump in the place of the calyx lobe hook, and staminal pockets or a reduced corona (ring of tissue 0.4 mm wide with free flaps 0.4 x 0.4 mm) instead of a more pronounced corona that is nearly twice as large (ring of tissue 0.9 mm wide with free triangular flaps in between each filament, flaps 0.8 x 0.7 mm) are additional characters that make these specimens possible intermediates. The variability seen in the characters above could, however, reflect intra-specific variation.

In addition, pollen characters for the type specimen of *C. hamatus* and four of the intermediates all have pollen exine characterized by fine reticulum interspersed with thickened, knob-like muri. In fact, the exine is so similar that the type and the intermediates are indiscernible (Figure 12 I; Figure 23 A-C & 28 D-F [Wurdack & Monachino 39764], Figure 28 A-C [Maguire et al. 36200], and Figure 29 [Wurdack & Adderley 42820] in Maguire & Boom, 1989). Pollen sampling for *Chelonanthus* has been quite extensive at the inter-generic level (Gilg, 1895; Köhler, 1905; Maguire & Boom, 1989; Nilsson, 1970 & 2002) and has demonstrated variability between species, but not until a survey of pollen at the species and intra-specific level is carried out can we say for sure how meaningful the similarities observed above really are. Considering the evidence presented the placement of the intermediate specimens within *C. hamatus* is highly likely, but it appears that the intermediates form a hybrid swarm along the Río Orinoco in Venezuela (states of Amazonas and Bolívar).

With the exception of leaf shape, oblanceolate leaves in French Guiana and elliptic leaves in Venezuela, the four specimens share a strongly quadrangular stem, winged and hooked calyx lobes and funnelform to tubular corollas. With a distance over 1000 km between the collections in French Guiana and Venezuela it would appear that this taxon with hooked calyx lobes has a relatively wide distribution, albeit rare. The collection pattern described above also suggests a disjunct distribution for *C. hamatus*. Disjunction of species, genera, and plant communities is not uncommon in South America. This paper alone documents three apparent disjunct taxa and the literature provides multiple examples (Mayle, 2004; Silva et al., 2006; Ulloa & Neill, 2006; Villagran, 2004).

Figure 14. Typical *Chelonanthus hamatus* is known from four collections, three from rocky savannas in southwestern French Guiana and one on an exposed boulder in a cloud Figure 14: Map illustrating the collection points of *Chelonanthus hamatus* in French Guiana and Venezuela (symbol ■) and twelve of the thirteen intermediate specimens collected along the Rio Orinoco (symbol ▲). See discussion for details.



The thirteen intermediates collections were found on the border of the Guayana Shield and Amazon Basin, in the Venezuelan states of Amazonas and Bolívar, within 400 km along the Río Orinoco or one of its smaller tributaries (Río Atabapo, Río Autana, Río Paraquaza, and Río Samariapo). These hybrids are also found at lower altitudes than *C. hamatus*, at an elevation of 75-150 m (*C. hamatus* is at 160-600 m). Habitat data is often incomplete on herbarium labels, but from the information provided it would appear the intermediates are found in overlapping, but more variable habitats. Rocky areas, rock slabs or exposed rock, savannas, and forests are mentioned for *C. hamatus* specimens and those designated here as intermediates. It is the consistent

association of the intermediates with a river that broadens the scope of their habitat information. There is no such mention of a riverine habitat for *C. hamatus*.

If these intermediate specimens are hybrids, what other species of *Chelonanthus* represent the potential parent stock? Six species, *C. alatus sensu stricto*, *C. albus* (Spruce ex Progel) Badillo, *C. angustifolius*, *C. grandiflorus* (Aubl.) Chodat & Hassl., *C. n. sp.* ('pterocaulis' Lepis, Chapter 2) and *C. purpurascens* (Aubl.) Struwe, S. Nilsson, & V.A. Albert have all been collected in the Venezuelan states of Amazonas and Bolívar where *C. hamatus* and the intermediates were found. When you consider pollen of the above species *C. alatus sensu stricto*, *C. albus*, *C. angustifolius*, *C. grandiflorus* and *C. n. sp.* ('pterocaulis' Lepis, Chapter 2), all are similar to *C. hamatus* in that they all shed pollen as tetrads and have pollen of the *Chelonanthus*-type (Nilsson 1970, 2002; Maguire & Boom, 1989). The purple-flowered outlier (and type of the genus), *Chelonanthus purpurascens*, sheds pollen as polyads and the exine sculpturing is of the *Uliginosus*-type (Nilsson 1970 & 2002). All species shedding *Chelonanthus*-type pollen are ecologically viable candidates with herbarium sheets found within altitude range and with habitat descriptors that overlap with *C. hamatus* and the intermediates specimens. When considering the 4-winged stem morphology of *C. alatus sensu stricto* and *C. n. sp.* (with wings up to 3.7 cm wide; 'pterocaulis' Lepis et al., in progress; Chapter 2), it seems unlikely that the product of two parents with strongly quadrangular, 4-winged stems would be progeny with stems that are terete. The three remaining species, *C. albus*, *C. angustifolius*, and *C. grandiflorus* have terete stems within their normal range of stem morphology. The dominating preference for a riverine habitat observed in *C. albus* could explain how this habitat type is prevailing in the

specimens considered intermediates. Two of the intermediate specimens have leaf shapes (long and linear) similar to *C. angustifolius* and were previously identified as such. *Chelonanthus grandiflorus* is the only species of *Chelonanthus* to have staminal pockets (but no corona) at the insertion point of the filaments, a trait shared with the intermediate specimens. An inflorescence of *C. grandiflorus* was found on a herbarium sheet of an intermediate specimen (Guanchez & Melgueiro 3357 [U]), providing strong evidence of the two taxa growing in sympatry. Table 8 presents a morphological character comparison of *Chelonanthus hamatus*, the intermediate specimens, and the three species most likely to be parental stock: *C. albus*, *C. angustifolius* and *C. grandiflorus*. Of course there is the possibility that other species hybridized with *C. hamatus* as well. A genetic study at the population level would be necessary to come to any real conclusions.

The generic placement of *Sipapoantha obtusisepala* as well as the status the *C. hamatus* intermediates is tentative, but we are confident that our study has revealed two new species. When working with rare specimens it is often difficult to come across herbarium material suitable for DNA extraction and additional data is needed to have greater confidence in some of the conclusions presented here. It is apparent, however, that these two new species are distinct. Considering the rarity of *Sipapoantha obtusisepala* and *Chelonanthus hamatus*, we believe their documentation crucial. Making others aware of these two unique taxa will aid in data collection and understanding.

Table 8: Table comparing morphology and habitat data for *Chelonanthus hamatus* with the specimens considered hybrids and the three species representing the most probable parental stock: *C. albus*, *C. angustifolius*, and *C. grandiflorus*.

Taxa	Habitat Descriptors	Elevation in meters	Stem morphology	Leaf morphology	Calyx morphology	Insertion point of filament
<i>Chelonanthus hamatus</i>	rocky savanna, on rock, exposed rock, cloud forest	160-600	strongly quadrangular, 4-winged	oblanceolate, acute apex or elliptic, obtuse apex; 4.3-20.7 x 2.9-6.2 cm	upward facing hook at the apex of the glandular area, hook 0.7-1.7 x 1.0	corona present
intermediate specimens	rocky savanna, on rock, laja (rock slab) margin, forest, river	75-150	weakly quadrangular to terete	elliptic to cuneate, obtuse apex or linear, acute apex; 3.3-16.8 x 1.4-6.5 cm	glandular area simple or with bump at apex, bump 0.4-0.6 x 1.0	reduced corona to staminal pockets present
<i>C. albus</i>	open rock, forest, river, swamp,	80-380; 990-1670	terete	elliptic to ovate, apex acute to acuminate; 2.5-17.0 x 0.8-6.5	glandular are simple	simple
<i>C. angustifolius</i>	dry sandy savanna, rocky savanna, laja (rock slab), forest	37-1980	weakly quadrangular to terete	elliptic, oblong to lanceolate, apex acute to acuminate; 1.0-17.0 x 0.2-3.7 cm	glandular are simple	simple
<i>C. grandiflorus</i>	savanna, rock outcrop, laja (rock slab), forest, river	80-1500	quadrangular, 4-winged at the base, abruptly becoming terete	elliptic to ovate, apex acute; 2.0-23.9 x 0.9-11.7 cm	glandular are simple	staminal pockets present or absent

Chapter 4

Chelonanthus Treatment for the Flora of Guianas

2. *Chelonanthus* Gilg in Engler & Prantl, Nat. Pflanzenfam. 4(2): 98. 1895. Type:

Chelonanthus purpurascens (Aubl.) L. Struwe, S. Nilsson, & V. A. Albert.

Erect herbs (rarely prostrate in *C. purpurascens*) to subshrubs. Leaves sessile to shortly petiolate, 0-2.0 cm; 2-4(-6) secondary veins. Inflorescence a terminal cyme, with 1-2 dichasial branching points terminating in 2 or more monochasial branches; bracts scale-like (sometimes leaf-like when subtending most basal flower). Flowers pedicellate, 5-merous, zygomorphic; calyx fused for 1/6-4/5 of total length, coriaceous, campanulate, lobes circular, ovate, elliptic to obovate, not winged or keeled (small wings present in species A), apex obtuse (acute apex present in *C. purpurascens* and *C. viridiflorus*); corolla bud apex rounded (sometimes acute in *C. purpurascens*); corolla fused for 3/5-6/7 of total length, thin, campanulate, funnelform, tubular, to salverform, 18-87 mm long; androecium zygomorphic with stamen and styles bent toward bottom of corolla mouth (in species B stamens and styles are clustered together in corolla throat); stamens inserted in corolla tube near base of corolla 1/6-5/8 of corolla tube length (just above midpoint in *C. grandiflorus*), of subequal to unequal length, filament base without specialized structures (in *C. grandiflorus* staminal gaps sometimes present and in species A corona present), anthers elliptic to slightly ovate, obovate, or oblong, with apical sterile

appendage; pollen in tetrads (polyads in *C. purpurascens*); pistil with nectary disk; stigma bilammellate. Fruit a capsule, with persistent calyx and persistent, partially persistent, or deciduous corolla; seeds angular-cuboidal, 0.1-0.6 mm in diameter; testa cells dome-like and/or concave with or without band-like thickenings.

Habitat and Distribution. 10 species in Guayana Highlands, Brazilian Highlands (with one species to Paraguay and northeastern Argentina), Caribbean islands of Trinidad and Grenada, Amazon Basin, the Andes from Bolivia to Venezuela and Central America (with one species to southern Mexico); Moist forests, forest openings and edge, wet/dry savannas, riversides and roadsides, sometimes in caatinga and cerrado type vegetation; Most often found in low nutrient, white sand soils, but may also be found in clay, lateritic or rocky soil; 7 species in the Guianas.

KEY TO THE SPECIES

- 1 Stem strongly quadrangular, 4-angled to 4-winged along entire length 2
 Stem terete to weakly quadrangular, only 3-4 of the most basal internodes may
 be quadrangular and 4-winged 4
- 2 Upward facing hook present near the apex of the glandular dorsal area of each
 calyx; bracteole apex acuminate to cuspidate 1. species A
 Glandular dorsal area of calyx lacking an upward facing hook; bracteole apex
 acute to obtuse 3
- 3 Calyx lobe shape circular; corolla tubular to salverform; sexual structures
 positioned within corolla tube; mature capsule erect to
 horizontal 2. species B
 Calyx lobe shape ovate; corolla funnelform to campanulate; sexual structures
 positioned near corolla lobes or slightly exserted; capsule position
 nodding 3. *alatus*
- 4 Corolla blue to purple; anthers recurved after anthesis 4. *purpurascens*
 Corolla green, white, cream, or yellow; anthers straight or slightly curved after
 anthesis 5

- 5 Plant up to 2.5 m tall; stem quadrangular for 3-4 of the lower internodes then abruptly becoming terete, if wings present then 0.1-1.8 mm wide; stigma lobe shape elliptic; capsule position nodding 5. *grandiflorus*
 Plant up to 1.6 m tall; stem terete to weakly quadrangular along entire length, if wings or ridges present then 0.1-0.3 mm wide; stigma lobe shape orbicular; capsule position horizontal to erect 6
- 6 Leaves elliptic to ovate; calyx 6-14 x 5-10 mm, lobes fused for 1/6-1/5 of total length 6. *viridiflorus*
 Leaves linear, sometimes lanceolate to elliptic; calyx 4-9 x 3-7 mm, lobes fused for c. 4/5 of total length 7. *angustifolius*

1. *Chelonanthus* species A ('hamatus' Lepis et al., in prep.; Chapter 3).

Herbs to subshrubs, up to 1.2 m high, branched. Stems and branches up to 11 mm in diameter, quadrangular, winged; wings 1.0-1.3 mm wide; internodes 2.5-13.5 cm long. Leaves sessile, cauline, evenly positioned; blade membranaceous to subcoriaceous, oblanceolate (populations from French Guiana) to elliptic (population from Venezuela elliptic), 4.3-20.7 x 2.9-6.2 cm, margin not thickened, flat; apex acute to obtuse; base attenuate (to obtuse just below inflorescence). Inflorescences 16-40-flowered; bracts ovate with acuminate to cuspidate apex, 2.2-3.8(-8.1) mm long; pedicel 6-9 mm long. Flowers erect to horizontal; calyx green, 6-8 x 5-7 mm; lobes ovate, 3-4 x 3-4 mm, minutely winged, wings c. 0.4 mm, upward facing hook protruding from the apex of the glandular area, hook 1.3-2.1 long; margin membranaceous; apex obtuse; corolla green, with dark green spot on apex of each corolla lobe, funnelform to tubular, 20-27 mm long, 10-18 mm wide at mouth; lobes ovate, c. 6 x 7 mm; apex obtuse; stamens not exerted, filaments 10-12 mm long; corona present at insertion point, straight to curved downward close to

anther; anthers white-yellow, elliptic, 1.8-3.2 mm long, straight; pollen exine with fine reticulum interspersed with thickened, knob-like muri; gynoecium 18 mm long, ovary 4.4 x 2.1 mm; style 11 mm long; stigma lobes 2.4-2.8 x 1.8 mm, elliptic (internal floral characters taken from a single flower due to rarity). Fruit nodding, brown, ellipsoid, 9-17 x 4-8 mm; seeds brown, 0.1-0.6 mm in diameter.

Habitat and Distribution. Mostly in rocky savannas, but also found in cloud forests on exposed rock in the Guayana Highlands of southern French Guiana and eastern Venezuela; 160-600 m. alt.; 4 collections studied, 3 from the Guianas (GU:0; S:0; FG:3).

Selected Specimens. French Guiana. de Granville et al. 11737 (B [n.v.], K, NY, US, CAY [n.v.], P [n.v.], U), de Granville et al. 9399 (CAY [n.v.], U, US).

Phenology. Flowering and fruiting specimens collected in January, April and August with no record for the remaining months.

Note. Intermediate specimens have been collected in the Venezuelan states of Amazonas and Bolívar, along the Río Orinoco or one of its smaller tributaries. These specimens are considered intermediates due to a stem that is weakly quadrangular to terete vs. strongly quadrangular and 4-winged in species A, well defined to slight bumps on the calyx lobes vs. hooks in species A, and staminal pockets or reduced corona vs. a corona twice as large in species A. For a detailed discussion about the morphology and distribution of these intermediate specimens see Lepis et al. (in progress; Chapter 3).

2. *Chelonanthus* species B ('pterocaulis' Lepis, in prep.; Chapter 2).

Herbs, up to 1.5 m high, unbranched to sparsely branched. Stems and branches up to 6(-10) mm in diameter, quadrangular, winged; wings 0.6-3.7 mm wide; internodes 0.7-15.0 cm long. Leaves sessile, cauline evenly; blade membranaceous, ovate to elliptic, obovate, 1.3-13.8(-20.2) x 0.5-4.7(-8.5) cm, margin not thickened, flat, apex acute to obtuse, base cuneate or attenuate, often the two most apical leaf pairs are connate to fully perfoliate (rarely all leaves perfoliate). Inflorescences 2-33-flowered; bracts ovate with acute apex, 1.6-6.5 mm long; pedicel 2-7 mm long. Flowers erect; calyx green, 6-10 x 4-7 mm, lobes orbicular, 3-5 x 3-5 mm, margin membranaceous, apex obtuse; corolla greenish white, cream, to pale yellow, with dark green spot on apex of each corolla lobe, tubular to salverform, 19-40 mm long, 8-20 mm wide at mouth, lobes ovate, 3-6 x 3-7 mm, apex obtuse; stamens not exserted, positioned deep within corolla tube, filaments 8-15 mm long, straight; anthers white, elliptic to slightly ovate, 1.6-3.0 mm long, straight or curved after anthesis; pollen exine differentially reticulated; gynoecium 17-26 mm long, ovary 4.1-6.6 x 2.2-4.3 mm; style 8-14 mm long; stigma lobes 2.5-5.1 x 1.8-2.0 mm, ovate, obovate, oblong. Fruit erect to horizontal, brown, ellipsoid, 11-20 x 4-10 mm; seeds brown, 0.1-0.4 mm in diameter.

Habitat and Distribution. Secondary growth forests, scrub, savannas, riverbanks, roadsides, often in sandy, rocky, moist soil and sometimes in lateritic soil in Guayana Highlands of Brazil (Roraima), French Guiana, Guyana, Suriname and Venezuela, Caribbean island of Trinidad, Amazon Basin of Brazil (Amazonas and Pará), Colombia and Venezuela, Andes of Colombia and Central America (Costa Rica, presumably in Panama); 10-1820 m. alt.; 67 collections studied, 7 from the Guianas (GU:6; S:0; FG:1).

Selected Specimens. Guyana. Maas, P.J.M. & L. Westra 3759 (NY, S, U [3 sheets]); French Guiana. Sastre, C. 6424 (U).

Phenology. Flowering and fruiting specimens collected year round.

Common Names. Wild tobacco (Guyana) and Tabaco bravo (Brazil, Amazonas).

Ethnobotany. Herbarium label Riley 8 (U) cites, "for removing worms and 'dirt'."

Note. Two specimens, Grayum & Herrera 6063 from Costa Rica and Pirani 1276 from Mato Grosso, Brazil, follow floral characters of the species described above, as well as having leaves, which can be fully perfoliate. They are noted here, because of their large branching stems (up to 8 and 10 mm in diameter respectively) as well as the presence of large elliptic leaves (up to 20.2 x 8.5 cm) that are fully perfoliate along the entire length of the stem.

3. *Chelonanthus alatus* (Aubl.) Pulle, Vasc. Pl. Surinam: 376. 1906. — *Lisyanthus alatus* Aubl., Hist. Pl. Guiane 1: 204. t. 80. 1775. — *Helia alata* (Aubl.) Kuntze, Rev. Gen. Pl. 2: 427. 1891. — *Irlbachia alata* (Aubl.) Maas, Proc. Kon. Ned. Akad. Wetensch., Ser. C., 88: 408. 1985. TYPE: French Guiana: [without location], Aublet s.n. (holotype BM; isotypes LINN [n.v.], P [n.v.]).

— *Chelonanthus longistylus* (J.M.G. Pers. & Maas) L. Struwe & V.A. Albert, Harvard Papers in Botany 3: 70. 1998. — *Irlbachia alata* (Aubl.) Maas ssp. *longistyla* J.M.G. Pers. & Maas in Maas, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 88(4): 410. 1985. TYPE: Venezuela, Bolivar: km 106 of road El Dorado - Sta. Elena de Uairén, forest margin,

alt. 700 m., Maas & Steyermark 5344 (holotype U [3 sheets] & photo [photo published in Maas, 1985]; isotypes K, MO, COL [n.v.], NY, P [n.v.], US, VEN [n.v.]).

Herbs to subshrubs, up to 2.5 m high, unbranched to sparsely branched. Stems and branches up to 11 mm in diameter, strongly quadrangular, 4-winged; wings 0.1-1.3 mm wide; internodes 0.5-30.3(-47.3) cm long. Leaves sessile, cauline, evenly distributed along stem; blade membranaceous, elliptic, 2.9-23.2 x 1.2-8.0(-12.0) cm, margin not thickened, flat, apex acute to acuminate, base attenuate, obtuse to truncate. Inflorescences 3-100-flowered; bracts ovate with obtuse (acute) apex, 0.8-9.4 mm long; pedicel 4-9 mm long. Flowers erect to horizontal; calyx green 4-8 x 3-6 mm, lobes ovate 2-6 x 2-4 mm, margin membranaceous, apex obtuse; corolla white to cream (sometimes pale green to yellow), with dark green spot on apex of each corolla lobe, funnelform to tubular, 20-50 mm long, 8-21 mm wide at mouth, lobes ovate, 3-11 x 4-13 mm, apex obtuse or acuminate; stamens exerted or not, filaments 14-40 mm long, straight or, curved downward close to anther; anthers white to pale green, oblong, 2.0-3.8 mm long, straight to slightly curved; pollen exine with muri fragmented into elongated to knob-like processes that are thickened along the equatorial zone (fide Hequet, 2007; Maguire & Boom 1989; Nilsson, 1970, 2002⁴); gynoecium 24-34 mm long, ovary 4.4-5.6 x 2.1-2.6 mm; style 14-23 mm long; stigma lobe 2.8-4.4 x 1.1-2.3 mm, elliptic to obovate. Fruit nodding, brown, 8-23 x 3-10 mm; seeds brown, 0.1-0.4 mm in diameter.

Habitat and Distribution. Moist forests, savannas, and scrub, along rivers and roadsides. Most commonly found in white-sand, low-nutrient soils, but also in clay and

⁴ Look to Appendix A for a list of specimens used in pollen descriptions along with a comparison of species determination.

lateritic soils and rarely in rocky soil in Guayana Highlands of Brazil (Roraima), Guyana, French Guiana, Suriname and Venezuela, Caribbean island of Trinidad; 0-2255 m alt.; 84 collections studied, 52 from the Guianas (GU:11; S:12; FG:29).

Selected Specimens. Guyana. McDowell, T., et al. 4150 (COL, NY, U, US); French Guiana. Sagot, P. 358 (U, G, K, P [n.v.], S); Suriname. B.B.S. 231 (MO, U).

Phenology. Flowering and fruiting specimens collected year-round.

Common Names. Wild tobacco (Guyana), Pepiatamit [uncertain spelling] (Carib: Suriname), Todo Tabaka (Negro English: Suriname), Todo Tabalso (Dutch English: Suriname), Pipjataner (Suriname), Sabama tabaka (Suriname), Wakauyek (Pemon: Venezuela, Bolívar).

Ethnobotany. Herbarium label Archer 2652 (U, US) cites, "Leaves used in decoction for itch." Herbarium label McDowell & Stobey 3831 (U, US) cites, "Used medicinally for bitters."

Note. *Chelonanthus alatus* is defined here in a much stricter sense than has been employed in recent taxonomic treatments (Maas, 1985; Pringle, 1995; Struwe et al., 1999). This is the result of a phylogenetic analysis of nuclear markers, ITS and 5S-NTS, revealing *C. alatus sensu lato* as polyphyletic with the placement of specimens considered *C. alatus* in three separate clades. A principle component analysis analyzing morphological data also supports this division (Lepis et al., in progress; Chapter 1). As a result of additional taxonomic research, it was revealed that the type of *C. alatus* (*Lisyanthus alatus*) is conspecific with the type of *C. longistylus* and descriptions of their morphology and geography also agree (Lepis et al., in progress; Chapter 2). *Chelonanthus longistylus* is therefore included here as a synonym of *C. alatus*.

4. *Chelonanthus purpurascens* (Aubl.) Struwe, S. Nilsson, & V.A. Albert, Harvard

Papers in Botany 3: 70. 1998. -*Lisyanthus purpurascens* Aubl., Hist. Pl. Guiane 1: 201-202, t. 79. 1775. -*Helia purpurascens* (Aubl.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Irlbachia purpurascens* (Aubl.) Maas, Proc. Kon. Ned. Akad. Wetensch., Ser. C., 88 (4): 408. 1985. TYPE: French Guiana, Aublet s.n. (holotype BM [n.v.]; isotype P [n.v.]).

— *Lisyanthus amoenus* Miq., Linnaea, ser. 1, 19: 139. 1846. -*Helia amoena* (Miq.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: Suriname, Para, Focke 999 (holotype U [photo U]).

— *Lisyanthus gracilis* Griseb., Gen. Sp. Gent.: 182-183. 1839. -*Helia gracilis* (Griseb.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: St. Vincent, Guilding 356 (holotype K [photo U]).

— *Lisyanthus spruceanus* Benth., Hooker's J. Bot. Kew Gard. Misc. 6: 202. 1854. - *Helia spruceana* (Benth.) Kuntze, Rev. Gen. Pl. 2: 427. 1891. -*Chelonanthus spruceanus* (Benth.) Gilg. in Koch-Grünberg, Zwei Jahre den Indianern 2: 31. 1910. TYPE: Brazil, Amazonas: São Gabriel, Rio Negro, Spruce 2304 (holotype K; isotype W [photo U]).

— *Lisyanthus uliginosus* Griseb., Gen. Sp. Gent.: 181-182. 1839. -*Helia uliginosa* (Griseb.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Chelonanthus uliginosus* (Griseb.) Gilg, Nat. Pflanzenfam. 4(2): 98. 1895. TYPE: Brazil, Bahia, in humidis Salzmann s.n. (lectotype G [photo U]; lectoisotype K [lectotype designated by Pringle 1995]).

Erect (rarely prostrate) herbs to subshrubs, up to 2.7 m high, sparsely branched to branched. Stems and branches up to 5 mm in diameter, terete, slightly 4-angled to weakly quadrangular, 4-angled to 4-winged; wings 0.1-0.4 (-1.0) mm wide; internodes 0.5-15.1 cm long. Leaves sessile to shortly petiolate, cauline evenly; petiole 0-20 mm long; blade membranaceous (rarely coriaceous), elliptic, ovate to lanceolate (rarely orbicular), 1.0-13.3 x 0.4-5.1 cm, margin not thickened, flat, apex acute, acuminate (rarely obtuse), base attenuate, acute to obtuse; inflorescences 1-39-flowered; bracts ovate with acute apex or oblong with obtuse apex, 0.1-3.2(-5.7) mm long; pedicel 4-20 mm long. Flowers horizontal to nodding; calyx green, 4-10 x 3-6 mm, lobes ovate to circular, 2-5 x 2-3 mm, margin membranaceous, apex acute to obtuse; corolla blue, purple, lavender, inner side of throat sometimes white, funnelform to tubular, sometimes nearly campanulate, 18-72(-87) mm long, 9-36 mm wide at mouth, lobes ovate to circular, 5-17 x 3-14 mm, apex obtuse; stamens not exserted, sometimes the longest exceeds the corolla slightly, filaments 16-45 mm long, strongly curved close to anther; anthers white, yellow to orange, oblong, 2.6-6.7 mm long, recurved; pollen exine differentially reticulated with polar loops (fide Maguire & Boom 1989; Nilsson, 1970, 2002); gynoecium 27-44 mm long, ovary 4.0-5.4 x 1.2-1.3 mm, style 20-50 mm long, stigma lobe 1.9-5.4 x 0.7-2.1 mm, elliptic. Fruit horizontal to nodding, brown, ellipsoid, 6-20 x 3-9 mm; seeds brown, 0.1-0.4 mm in diameter.

Habitat and Distribution. Commonly found in moist forests, forest edges, gallery forests, savannas and along rivers. Rarely found in cloud forests, campo rupestre, scrub type vegetation and along roadsides. Most commonly found on white-sand, low-nutrient soils as well as on rocky soils and rarely in clay or lateritic soil in Guayana Highlands

of Brazil (Roraima and Pará), Colombia, French Guiana, Guyana, Suriname and Venezuela, Brazilian Highlands (Bahia, Espírito Santo, Maranhão, Mato Grosso, Minas Gerais, Paraíba, Paraná, Pernambuco, Rio Grande do Norte, Rio de Janeiro and São Paulo), Amazon Basin of Bolivia, Brazil (Acre, Amapá, Amazonas and Pará), Colombia, Peru, and Venezuela, and Andes of Bolivia, Colombia, Ecuador, and Peru; 0-3500 m. alt.; 325 collections studied, 143 from the Guianas (GU:87; S:31; FG:25).

Selected Specimens. Guyana. Jansen-Jacobs, M. J. et al. 2510 (K, MO, NY, U, US); Suriname. de Granville, J. J., et al. 11913 (CAY [n.v.], B [n.v.], BBS [n.v.], BR [n.v.], K, NY, P, U, US); French Guiana. Rova, J. H. E. et al. 1902 (UPS, NY, AAU, MO, S).

Phenology. Flowering and fruiting specimens collected year round.

Common Names. pemón: Wakauek (Venezuela, Bolívar); Papai-nicolau (Brazil, Bahia); Wild tobacco (Guyana).

Ethnobotany. Herbarium label Harrison 1345 (BRG (n.v.), K, NY) cites, "Infusion of leaves used by the Arawaks for smallpox." Herbarium label Hoffman & Patterson 878 (MA, NY, US) cites, "'lata' fungal infections."

Note. *Chelonanthus purpurascens* has had a confusing taxonomic history, with several misused or invalid names associated with this species. Kunth (1818) described *Lisianthus purpurascens* (note the change in spelling from Aublet's use) based on material he considered to be something other than the species Aublet described in 1775. Grisebach (1839) agreed that Aublet's *L. purpurascens* and Kunth's *L. purpurascens* were different taxa and therefore transferred Kunth's *L. purpurascens* to *L. uliginosus* as variety *guianensis*. This name is invalid since Grisebach did not specify any other varieties of *L. uliginosus*. In the same publication, Grisebach also described *Lisianthus*

fistulosus (Poir.) Griseb. as a purple-flowered plant, even though Poiret's (1814) first description cites a yellow-flowered *Lisianthus*. Grisebach continued to support that “the authentic” *L. fistulosus* was purple-flowered and part of the *L. purpurascens* complex (Grisebach, 1845, 1862). Other taxonomic treatments followed Grisebach's invalid description of *Lisianthus fistulosus* as a purple-flowered gentian (Lemée, 1953; Progel, 1865). The stout stem and large leaves of the type specimen of *L. fistulosus* is not similar to that of *C. purpurascens* and this name, in adhering to Poiret's original description of yellow flowers, has been placed in this treatment as a synonym to *C. grandiflorus* (Aubl.) Chodat & Hassl. In 1845, Grisebach classified the purple-flowered *Lisianthus* into section *Chelonanthus* where he combined *L. purpurascens* Kunth, *L. uliginosus* var. *guianensis* Griseb. and *L. grandiflorus* Willd. (based on an undescribed specimen with large purple flowers into *Lisianthus uliginosus* var. *grandiflorus*. Again Grisebach specified only one variety and therefore the name is invalid. This taxon should not be confused with *Lisianthus grandiflorus* Aubl., a synonym of *Chelonanthus grandiflorus* described below.

5. *Chelonanthus grandiflorus* (Aubl.) Chodat & Hassl. Addenda Pl. Hassl. 5. 1917. - *Lisianthus grandiflorus* Aubl., Hist. Pl. Guiane 1: 205, t. 81, 1775. - *Helia grandiflora* (Aubl.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: French Guiana, Aublet s.n. (holotype BM; isotypes LINN [n.v.], P-JJR [n.v.]).

— *Chelonanthus chelonoides* (L.) Gilg in Engler & Prantl., Nat. Pflanzenfam. 4(2): 98. 1895. - *Pentstemon chelonoides* L., Plantæ Surinamenses: 6. 1775. - *Lisianthus*

chelonoides (L.) Linn.f., Suppl. Pl. 134. 1781. -*Lisyanthus chelonoides* (L.) Griseb., Gen. Sp. Gent.: 184-185. 1839. -*Helia chelonoides* (L.) Kuntze, Rev. Gen. Pl. 2: 427. 1891. TYPE: Suriname, in high sands, Dalhberg 141 (holotype LINN).

— *Chelonanthus fistulosus* (Poir.) Gilg, Nat. Pflanzenfam. 4(2): 98. 1895. -*Lisianthus fistulosus* Poir. in Lam., Encycl., t. 11: 564. 1814. -*Lisyanthus fistulosus* (Poir.) Griseb., Gen. Sp. Gent.: 180-181. 1839. -*Helia fistulosa* (Poir.) Kuntze, Rev. Gen. Pl. 2: 428. 1891. TYPE: French Guiana, Martin s.n. (holotype P [n.v.; photo F & U]).

— *Chelonanthus schomburgkii* (Griseb.) Gilg, Nat. Pflanzenfam. 4(2): 98. 1895. -*Lisianthus schomburgkii* Griseb. in DC., Prodr. 9: 75. 1845. -*Helia schomburgkii* (Griseb.) Kuntze, Rev. Gen. Sp.: 428. 1891. TYPE: British Guiana, Berbice, Schomburgk 298 (holotype B [destroyed]; isotypes BM [n.v.], CGE [n.v.], F [n.v.], G [photo U, K, & L], US).

Herbs to subshrubs, up to 2.5 m high, unbranched, sometimes sparsely branched. Stems and branches up to 11 mm in diameter, quadrangular with wings on the lower 3-4 internodes then abruptly becoming terete without wings (Colombian populations with lowest 3-4 internodes terete and 4-ridged); wings 0.1-1.8 mm wide; internodes 2.3-27.2 cm long. Leaves sessile, sometimes petiolate, cauline evenly; petiole 0-0.5 cm long; blade membranaceous, ovate to elliptic, 2.0-23.9 x 0.9-11.7 cm, margin not thickened, flat, apex acute, base attenuate to obtuse just below inflorescence. Inflorescences 5-45-flowered; bracts ovate with acuminate or obtuse to acute apex, 1.3-9.3 mm long; pedicel 4-11 mm long. Flowers horizontal; calyx green, 5-11 x 5-9 mm, lobes ovate, 3-6 x 3-5 mm, margin membranaceous, apex obtuse; corolla cream, pale green, yellow-green to yellow, with dark

green spot on apex of each corolla lobe, funnellform, 21-44 mm long, 13-27 mm wide at mouth, lobes ovate, 5-10 x 6-8 mm, apex obtuse; stamens not exserted, filaments 12-18 mm long, staminal pockets +/- present at insertion point, curved downward close to anther; anthers white, elliptic to ovate, 2.4-3.6 mm long, straight after anthesis; pollen exine differentially reticulated with muri thickend at the poles (fide Nilsson, 1970 & 2002); gynoecium 21-27 mm long, ovary 5.9-7.9 x 2.7-3.1 mm; style (9-)14-20 mm long; stigma lobe 2.5-5.4 x 1.5-2.4 mm, elliptic. Fruit nodding, brown, ellipsoid, 9-20 x 4-9 mm; seeds brown, 0.1-0.4 mm in diameter.

Distribution. Often found in forest openings along streams or roads or in secondary growth, and sometimes found in grassy savannas and cerrado or caatinga type vegetation. Most often found on moist white-sand, low-nutrient soils, but sometimes in rocky soil or on clay or lateritic soil in Guayana Highlands of Brazil (Amapá and Roraima), French Guiana, Guyana, Suriname and Venezuela, Caribbean islands of Trinidad and Grenada, Amazon Basin of Brazil (Amapá, Amazonas and Pará), Venezuela, and Colombia, and Brazilian Highlands (Maranhão, Paraíba, Pernambuco, Rio de Janeiro and São Paulo); 80 - 1900 m. alt.; 298 collections studied, 138 from the Guianas (GU:76; S:27; FG:35).

Selected Specimens. Guyana. Pipoly, J. & H. Lall 8338 (NY, BRG [n.v.], MO, SP, U, US); Suriname. Daniels, A. & F. Jonker 832 (K, NY, U); French Guiana. Oldeman 2096 (NY, P, U, US) or Hoff, M. 7015 (CAY[n.v.], P, U, US).

Phenology. Flowering and fruiting specimens collected year round.

Common Names. Aha (Guyana), Amerindian tobacco (Guyana), Dia tabaka (Suriname), Dankuna tabaka (French Guiana), Fumo do brejo (Brazil, Maranhão),

Joeliballi (Suriname), Kawai-banada-yek (Venezuela, Bolívar), Koeraja (Suriname), Kwasi-bitá (Suriname), Sabana-tabacca (Suriname), Sabana tabak (Suriname), Salidore (Guyana), Tabaco do igapó (Brazil, Pará), Tabaco de veado (Brazil, Amazonas), Tabaco de veado (Venezuela, Amazonas), Tobaco-rana (Brazil, Pará), Tabaquilla (Venezuela, Amazonas), Wild tobacco (Guyana), Yuriballi (Guyana).

Ethnobotany. Herbarium label Gorts-van Rijn et al. 434 (U) cites "Boiled leaves used for 'bowels'." Herbarium label Reinders & Torres 29 (NY, U) cites "Clean out of dirty tummy, malaria."

Pollination and Ecology. Herbarium label Maas & Westra 3992 (K, MO, NY, U [x3]) cites, "...nectaries at pedicel base and on calyx attracting many ants." Herbarium label Ramsammy 81 (NY, US) cites, "myrmecophily." Herbarium label Steege, et al. 466 (U, US) cites, "...the buds with many little red and big black ants, and black flies." Herbarium label Machado s.n. (SP) cites, "bat pollinated."

Note. *Chelonanthus grandiflorus* is not a name recognized in recent taxonomic treatments (Maas, 1985; Pringle, 1995; Struwe et al., 1999). It is recognized here as a result of revisionary work on the genus (Lepis et al., in progress; Chapter 2). For details about the data supporting the resurrection of this name, see notes under *C. alatus*. For details on the inclusion of *C. fistulosus* as a synonym, see notes under *C. purpurascens*.

6. *Chelonanthus viridiflorus* (Mart.) Gilg. Nat. Pflanzenfam. 4(2): 98. 1895. -

Lisianthus viridiflorus Mart., Nov. Gen. Sp. Pl.: 94-95. Tab 173. 1827. -*Lisyanthus*

viridiflorus (Mart.) Griseb., Gen. Sp. Gent.: 192-193. 1839. -*Helia viridiflora* (Mart.)

Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Irlbachia alata* (Aubl.) Maas ssp. *viridiflora*

(Mart.) J.M.G. Pers. & Maas in Maas, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 88(4): 410. 1985. TYPE: Near Villa Rica, Sabará, and elsewhere in Province Minas Gerais, Martius 772 (holotype M).

— *Chelonanthus candidus* Malme, Arkiv. Bot. 3(12): 13. Tab. 2, #3. 1904. TYPE: Brazil, Mato Grosso: Serra da Chapada, Santa Anna da Chapad, Malme 3293 (holotype S; isotypes B [n.v.; photo U], F [n.v.], G [n.v.], K [n.v.], MO).

Herbs, up to 1.2 m high, unbranched or sparsely branched. Stems and branches up to 7 mm in diameter, terete, not winged; internodes 1.1-14.3 cm long. Leaves sessile, cauline evenly; blade membranaceous, elliptic to ovate towards branch apices, 1.3-15.5 x 0.3-7.9 cm, margin not thickened, flat, apex acute, base attenuate to obtuse just below inflorescence. Inflorescences 1-34-flowered; bracts ovate to oblong with acute to obtuse apex, 0.4-4.1 mm long; pedicel 4-13 mm long. Flowers erect to horizontal; calyx green, 6-14 x 5-10 mm, lobes ovate to oblong, 4-11 x 3-8 mm, margin membranaceous, apex acute; corolla white to greenish-white to pale yellow with dark green spot on apex of each corolla lobe, funnelform, 28-80 mm long, 15-28 mm wide at mouth, lobes ovate, 4-11 x 3-12 mm, apex acute to obtuse; stamens not exerted from corolla mouth, filaments 13-38 mm long, straight; anthers white, oblong, 1.5-3.2 mm long, straight; pollen exine differentially reticulated with complete muri or sometimes fragmented into globules and elongated processes (fide Nilsson, 1970, 2002); gynoecium 23-54 mm long, ovary 5.0-6.0 x 3.0-5.0 mm; style 16-41 mm long; stigma lobe 1.7-4.2 x 1.7-3.6 mm, orbicular. Fruit erect, brown, ovate to oblong, 6-22 x 5-11 mm; seeds brown, 0.1-0.6 mm in diameter.

Habitat and Distribution. Commonly found at headwater streams, wet savannas and forest edges, rarely along roadsides, in scrub, cerrado or campo rupestre type vegetation. Most commonly found in white sand, low nutrient soil and rarely in clay, lateritic or rocky soil in Guiana Highlands of Brazil (Roraima), Guyana and Suriname, Brazilian Highlands of Brazil (Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Paraná and São Paulo), Argentina and Paraguay, Amazon Basin of Bolivia, Brazil (Amazonas and Pará) and Peru, and Andes of Bolivia and Peru; 130-1346 m. alt.; 147 collections studied; 6 from the Guianas (GU:6; S:0; FG:0).

Selected Specimens. Guyana. Smith, A.C. 3064 (F, G, MO, NY, P, S, U, US); McDowell, T. & D. Gopaul 2726 (NY [x2], U, US).

Phenology. Flowering and fruiting specimens collected year-round.

Common Names. Nicotiana (Colombia).

7. *Chelonanthus angustifolius* (Kunth) Gilg, Nat. Pflanzenfam. 4(2): 98. 1895. -
Lisianthus angustifolius Kunth, Nov. Gen. Sp. [H.B.K.] 7: 181. 1818. -*Lisyanthus angustifolius* (Kunth) Griseb., Gen. Sp. Gent.: 186. 1839. -*Helia angustifolia* (Kunth) Kuntze, Rev. Gen. Pl. 2: 428. 1891. -*Irlbachia alata* (Aubl.) Maas ssp. *angustifolia* (Kunth) J.M.G. Pers. & Maas in Maas, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 88(4): 409-410. 1985. TYPE: Venezuela, Amazonas: Near Esmeralda in grass place (Orinoco), Humboldt & Bonpland 1004 (holotype P [n.v.]; isotypes B [n.v.]; photo MO & U), W [n.v.]).

- *Lisianthus bifidus* Kunth, Nov. Gen. Sp. 7: 181. 1818. - *Lisyanthus bifidus* (Kunth) Griseb., Gen. Sp. Gent.: 186. 1839. - *Helia bifida* (Kunth) Kuntze, Rev. Gen. Pl. 2: 428. 1891. - *Chelonanthus bifidus* (Kunth) Gilg, Engler & Prantl, Naturl. Pflanzenf. 4(2): 98. 1895. TYPE: Colombia, Tolima: near Sta. Anna, alt. 400 m, Humboldt & Bonpland 1731 (holotype P [n.v.]; isotype B [n.v.]; photo F, MO & U], W [n.v.]).
- *Chelonanthus camporum* Gilg, Feddes Repert. Spec. Nov. Regni Veg. 2: 54. 1906. TYPE: Peru, Loreto: near Moyobamba, alt. 1000 m., Weberbauer 4546 (holotype B [n.v.]; photo F, U, & US]; isotype G, P [n.v.]).
- *Chelonanthus leucanthus* Gilg, Feddes Repert. Spec. Nov. Regni Veg. 2: 55. 1906. TYPE: Peru, Puno, Weberbauer 1094 (holotype B [n.v.] - photos F, U, US [n.v.]).
- *Chelonanthus pyriformis* Gleason, Bull. Torrey Bot. Club 58: 450. 1931. - *Lisianthus pyriformis* (Gleason) Steyerf., Fieldiana. Bot. 28: 498. 1953. TYPE: Venezuela, Amazonas: summit of Mount Duida, dry crests of savanna hills, alt. 4400 ft., Tate 747 (holotype NY [photo U]; isotype US [photo F]).

Herbs, up to 1.6 m high, unbranched to sparsely branched. Stems and branches up to 7 mm in diameter, terete to weakly quadrangular with or without small wings; wings 0.1-0.3 mm wide; internodes 0.5-17.4 cm long. Leaves sessile to shortly petiolate, cauline evenly with the internode between the two most apical set of leaves visibly longer; petiole 0-0.4 cm long; blade membranaceous (rarely coriaceous), linear, lanceolate or elliptic, 1.0-21.0 x 0.2-3.7 cm, margin not thickened, flat, apex acute to acuminate, base attenuate or cuneate. Inflorescences 1-60-flowered; bracts ovate to oblong with obtuse (rarely acute) apex, 1.2-5.0 mm long; pedicel 2-24 mm long. Flowers erect to horizontal; calyx green, 4-9 x 3-7

mm, lobes ovate to circular, 2-6 x 2-5 mm, margin membranaceous, apex obtuse; corolla white, cream, green or greenish yellow, with dark green spot on apex of each corolla lobe, funnelform to tubular, 21-52 mm long, 10-32 mm wide at mouth, lobes ovate to circular, 3-9 x 3-15 mm, apex obtuse (rarely acute); stamens not exerted, filaments 17-35 mm long, mostly straight, curved downward close to anther; anthers white, elliptic to slightly obovate, 2.3-3.5 mm long, straight after anthesis; pollen exine differentially reticulated with globules (fide Nilsson, 1970, 2002); gynoecium 29-32 mm long, ovary 3.2-4.3 x 1.9-2.4 mm; style 20-40 mm long; stigma lobes 1.5-2.4 x 1.1-2.4 mm, orbicular. Fruit erect to horizontal, brown, ellipsoid, 5-14 x 1-8 mm; seeds brown, 0.1-0.5 mm in diameter.

Habitat and Distribution. Wet and dry savannas, sometimes along streams and forest edges often found on white-sand, low nutrient soils in Guayana Highlands of Brazil (Roraima), Guyana and Venezuela, Amazon Basin of Brazil (Acre, Amazonas), Venezuela, Colombia and Peru and Andes of Colombia and Peru; 37-1980 m alt.; 123 collections studied, 5 from the Guianas (GU:5; S:0; FG:0).

Selected Specimens. Guyana. Clarke, D. 937 (U, US); Henkle, T. & B. Hoffman 238 (U, US).

Phenology. Flowering and fruiting specimens collected year round.

CHAPTER 5

Chelonanthus Treatment for Catálogo de las Plantas Vasculares de Bolivia

Chelonanthus (Griseb.) Gilg in Engl. & Prantl Nat. Pflanzenfam. IV(2): 98. 1895.

4 species.

Chelonanthus acutangulus (Ruiz & Pav.) Gilg, in Engler & Prantl, Naturl. Pflanzenf. 4(2): 98. 1895.

Synonyms. *Lisianthus acutangulus* Ruiz & Pav., *Helia acutangula* (Ruiz & Pav.)

Kuntze, *Lisyanthus auriculatus* Benth., *Helia auriculatus* (Benth.) Kuntze,

Lisianthus crassicaulis M. Martens & Gelotti, *Helia crassicaulis* (M. Martens &

Gelotti) Kuntze, *Lisianthus oerstedtii* Griseb., *Helia oerstedtii* (Griseb.) Kuntze,

Lisyanthus tetragonus Benth., *Helia tetragona* (Benth.) Kuntze, *Lisianthus trifidus*

Kunth, *Lisyanthus trifidus* (Kunth) Griseb., *Helia trifidus* (Kunth) Kuntze,

Chelonanthus whitei Rusby.

References. Aublet, J. B. C. F. (1775), Foster, R. C. (1958), Maas, P. J. M. (1985),
Pringle, J. S. (1995).

Herb. Native. Low Lying Zone of Eastern Bolivia, Andes, Yungas, Dry Valleys, Humid
Forests, Amazonian Campos, Savannas of Southern Beni, Campos Cerrados,
Semideciduous Forests, Chiquitano Dry Forests, 0–3000 m.

Departments. BE, CO, LP, PA, SC.

Collections. *B.A. Krukoff 10301* (F, NY).

Chelonanthus matogrossensis (J.M.G. Pers. & Maas) Struwe & V.A. Albert, Harvard Pap. Bot. 3(1): 70. 1998.

Synonyms. *Irlbachia alata* (Aubl.) Maas subsp. *matogrossensis* J.M.G. Pers. & Maas.

References. Maas, P.J.M. (1985).

Subshrub. Native. Low Lying Zone of Eastern Bolivia, Humid Forests, Camp Cerrado, 0–500 m.

Departments. BE.

Collections. *W.R. Anderson 11988* (NY).

Chelonanthus purpurascens (Aubl.) Struwe & V.A. Albert, Harvard Pap. Bot. 3(1): 70. 1998.

Synonyms. *Lisianthus purpurascens* Aubl., *Helia purpurascens* (Aubl.) Kuntze,

Irlbachia purpurascens (Aubl.) Maas, *Lisianthus amoenus* Miq., Linnaea, *Helia amoena* (Miq.) Kuntze, *Lisyanthus gracilis* Griseb., Gen. Sp. Gent., *Helia gracilis* (Griseb.) Kuntze, *Lisianthus spruceanus* Benth., *Chelonanthus spruceanus* (Benth.) Gilg, *Lisianthus uliginosus* Griseb., *Chelonanthus uliginosus* (Griseb.) Gilg, *Helia uliginosa* (Griseb.) Kuntze,

References. Aublet, J. B. C. F. (1775), Killeen, T. J. & T. S. Schulenberg (1998), Struwe, L. & V. A. Albert (1998), Struwe et al. (1999).

Herb. Native. Low Lying Zone of Eastern Bolivia, Humid Forests, Campos Cerrados, 0–1000 m.

Departments. SC.

Collections. A. Jardim , M. Saldías & Surubí 536 (USZ).

Chelonanthus viridiflorus (Mart.) Gilg, Nat. Pflanzenfam. IV (2): 98. 1895.

Synonyms. *Lisianthus viridiflorus* Mart., *Helia viridiflora* (Mart.) Kuntze, *Irlbachia alata* (Aubl.) Maas subsp. *viridiflora* (Mart.) J.M.G. Pers. & Maas, *Chelonanthus candidus* Malme.

References. Martius, C. F. P. (1827), Maas, P. J. M. (1985), Parker, T. & B. Bailey (1991), Killeen, T. J. & T. S. Schulenberg (1998).

Herb. Native. Low Lying Zone of Eastern Bolivia, Savannas of Southern Beni, Campos Cerrados, 0–1000 m.

Departments. LP, SC.

Collections. Killeen 1791 (USZ).

KEY TO BOLIVIAN SPECIES OF *CHELONANTHUS*

1. Stems with a warty surface; leaves subcircular *C. matogrossensis*
 Stems lacking a warty surface; leaves ovate to ovate-oblong, elliptic, rarely obovate 2
2. Corolla purple to blue, sometimes with white corolla throat *C. purpurascens*
 Corolla white, yellow, green or a combination of the three 3
3. Stem terete; calyx lobes connate for 1/6 - 1/5 of total length; mature capsules erect *C. viridiflorus*
 Stem quadrangular, 4-winged; calyx lobes connate for 3/7 - 1/2 of total length; mature capsules pendulous *C. acutangulus*

LIST OF SYONYMS RELEVANT TO BOLIVIA (ACCEPTED NAMES IN BOLD)

Chelonanthus – Gentianaceae

alatus (Aubl.) Pulle = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

uliginosus (Griseb.) Gilg = **Chelonanthus purpurascens** (Aubl.) Struwe & V.A.

Albert

whitei Rusby = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

Helia – Gentianaceae

acutangula (Ruiz & Pav.) Kuntze = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

auriculata (Benth.) Kuntze = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

crassicaulis (M. Martens & Gelotti) Kuntze = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

oerstedtii (Griseb.) Kuntze = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

purpurascens (Aubl.) Kuntze = **Chelonanthus purpurascens** (Aubl.) Struwe & V.A. Albert

tetragona (Benth.) Kuntze = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

trifidus (Kunth) Kuntze = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

viridiflora (Mart.) Kuntze = **Chelonanthus viridiflorus** (Mart.) Gilg

Irlbachia – Gentianaceae

alata (Aubl.) Maas subsp. matogrossensis J.M.G. Pers. & Maas = **Chelonanthus matogrossensis** (J.M.G. Pers. & Maas) Struwe & V.A. Albert

alata (Aubl.) Maas subsp. viridiflora (Mart.) J.M.G. Pers. & Maas = **Chelonanthus viridiflorus** (Mart.) Gilg

purpurascens (Aubl.) Maas = **Chelonanthus purpurascens** (Aubl.) Struwe & V.A.

Albert

Lisyanthus/Lisianthus – **Gentianaceae**

acutangulus Ruiz & Pav. = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

auriculatus Benth. = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

crassicaulis M. Martens & Gelotti = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

oerstedtii Griseb. = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

purpurascens Aubl. = **Chelonanthus purpurascens** (Aubl.) Struwe & V.A. Albert

tetragonus Benth. = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

trifidus Kunth = **Chelonanthus acutangulus** (Ruiz & Pav.) Gilg

uliginosus Griseb. = **Chelonanthus purpurascens** (Aubl.) Struwe & V.A. Albert

viridiflorus Mart. = **Chelonanthus viridiflorus** (Mart.) Gilg

LIST OF EXAMINED BOLIVIAN *CHELONANTHUS* SPECIMENS

***Chelonanthus acutangulus* (41):**

-Bolivia, alt. 850 m. Collector: Otto Buchtien, 1189, May 14, 1927. (NY);

-Beni, Prov. Vaca Diez, 37 Km. E of Riberalta on road to Guayaramerin. Grassy

savanna with many shrubs and scattered gnarled trees, 11°05'S, 65°45'W, alt. 230

m. Collector: J.C. Solomon, 7880, June 1, 1982. (NY, U);

-Cochabamba, Chapare, cerca de Villa Tunari en dirección a Cochabamba, malezas y

bosque cerca de la carretera, alt. 500 m. Collector: Javier Fernández Casas, FC-

7979, December 31, 1982. (G, MA, MO, NY);

- Cochabamba, Antahuacana, Espiritu Santo, alt. 750 m. Collector: Otto Buchtien, 2320, June, 1909. (NY, US);
- Cochabamba, Prov. Carrasco. Cerro el Salvador above Bula Bula; evergreen forest margin on low hills just above plain, approx. 17°15'S, 64°30'W, alt. 350 m. Collector: R.K. Brummitt, J.R. Wood, D.C. Wasshausen & N. Ritter, 19339, May 29, 1996. (K, LBP, MO, US);
- Cochabamba, Road to Chimore on argilaceous soil on both sides of the car road, alt. 2500 m. Collector: M. Cardenas, 793, March 1940. (US);
- Cochabamba, Prov. Carrasco. Proyecto Valle del Sacta, km 240 en la carretera Santa Cruz-Villa Tunari. Bosque tropical humedo en bajio, intervenido. 17°00'S, 64°46'W, alt. 290 m. Collector: D.N. Smith, V. Garcia & M. Buddensiek, 13639, July 8-9, 1989. (MO);
- Cochabamba, Espiritu Santo, vicinity of Cochabamba. Collector: M. Bang, 1242, 1891. (F, G, NY, US);
- La Paz, Prov. Nor-Yungas, Sirupaya, on steep slope, in second growth on edge of corn field, rich soil, slate formation, partial shade, alt. 2600-3000 m. Collector: W.J. Eyerdam 25354, April 15, 1939. (F, K);
- La Paz, Prov. Nor-Yungas, 16.2 Km. NE (below) Chuspipata (13.5 Km. S of Yolosa), cloud forest with tree ferns. 16°15'S, 67°47'W, alt. 1900 m. Collector: J.C. Solomon 8030, July 19, 1982. (MO, NY);
- La Paz, near Yungas, growing along roadsides and in the borders of fields, alt. 1200 m. Collector: H.H. Rusby 1050 (same as Holton's 471), 1885. (NY, US);

- La Paz, Prov. S. Yungas,, basin of Rio Bopi, San Bartolome (near Calisaya), alt. 750-900 m. Collector: B.A. Krukoff 10301, July 1-22, 1939, (NY, F);
- La Paz, Road from Pararani to Mapiri, alt. 1600 m. Collector: G.H.H. Tate 394, March 30, 1926. (NY);
- La Paz, Mipiri region, S. Carlos, alt. 950 m. Collector: Otto Buchtien 1190, February, 1927. (F);
- La Paz, Mapiri, alt. 615 m. Collector: G.H.H. Tate 482, March 30 – April 9, 1926. (NY);
- La Paz, Hacienda Simaco sopra el camino a Tipuani, alt. 1400 m. Collector: Otto Buchtien 5524, March, 1920. (F, G, MO, US);
- La Paz, Chulumani, grassy slope, alt. 1800 m. Collector: W.M.A. Brooke 6523, June 21, 1950. (F);
- La Paz, Prov. de Larecaja, Copacabana, about 10 km south of Mipiri, alt. 850-950 m. Collector: Krukoff 11179, Oct. 8 - Nov. 15, 1939. (F, G, MO, S, UPS);
- La Paz, Coroico-Coripata; wet soil on hillside. Collector: Babcock 870, Nov. 11, 1967. (K);
- La Paz, Prov. Nor. Yungas, 6 km from Coroico on road to Caranavi. On grassy banks by roadside, alt. 1325. Collector: Hawkes et al. 5048, Jan. - April 1971. (C, MO);
- La Paz, Nord Yungas, Polo-Polo bei Coroico. Collector: Buchtien 5950, Oct.-Nov. 1912. (US);
- La Paz, Yungas, Puerto Villa, damp forest slopes. Collector: M. Cardenas 3554, Feb. 1946. (US);

- La Paz, Inquisiva: Along the Rancho Poqueloque-Cajuata Road between Huaritolo and Cajuata (7 km hike). Ca. 7-9 km N of Licoma Pampa. Semi-humid subtropical forest, grasslands, secondary habitats. Rare on deep shade bank. 16°42'S, 67°11'W, alt. 1800 m. Collector: M. Lewis 88860, June 16, 1988. (US);
- La Paz, Larecaja, 13.8 km al SO Guanay, por el camino a Tipuani. Bosque humido. 15°32'S, 67°58'W, alt. 1100 m. Collector: J. Solomon 17648, Jan. 23, 1988. (MO);
- La Paz, Prov. Nor Yungas, 1.8 km SW of Yolosa on road to Chuspipata; Old secondary growth forest, with some primary forest trees. Mixed moist and dry forest elements. 16°13'S, 67°45'W, alt. 1400 m. Collector: J. Solomon, B. Stein & M. Uehling 12041, March 22, 1984. (MO);
- La Paz, Prov. Nor Yungas. Serrania de Bella Vista. 16 km N of Carrasco (37 km N of Caravi) on road to Palos Blancos. Montane wet forest. Trees to 25 m, some buttressed trunks. 15°35'S, 67°34'W, alt. 1500 m. Collector: J. Solomon & M. Nee 12682, Oct. 31, 1984. (MO);
- La Paz, Prov. Larecaja, 6 km N (below) Consata. Moist forest with very little disturbance. Very steep slopes, sandstone with an abundance of tree ferns, epiphytes, Hymenophyllaceae. Exposed dry rocky roadcut. 15°20'S, 68°31'W, alt. 1300 m. Collector: J. Solomon, S. Beck, C. Sperling & S. King 6566, Dec. 15, 1981. (MO);
- La Paz, Prov. Murillo, Valley of the Rio Zongo, Cahua Hydro Electric Plant. Moist forest on very steep slopes. 11°02'S, 66°15'W, alt. 1400 m. Collector: J. Solomon 7476, April 21, 1982. (MO, NY);

- La Paz, Prov. Nor Yungas: 21.1 km al norestse del camino a Suapi. (ca. 2.5 km al oeste de Suapi, cerca del puente sobre el Rio Suapi). Bosque humedo muy tocado. Al borde del camino. 16°07'S, 67°47'W, alt. 1200 m. Collector: J. Solomon 18418, May 27, 1988. (LPB, MO);
- La Paz, Prov. Sud Yungas, 30 km al N de Palos Blancos hacia Quiquibey. Sabana edafica sobre suelos superficiales y rocosos. Dominado por *Trachypogon* sp. 15°30'S, 67°05'W, alt. 1500 m. Collector: T. Killeen 3698, Feb. 22, 1992. (G, LPB, MO);
- La Paz, Highway La Paz-Coroico, 7.3 km from Coroico. Roadside. Collector: J.D. Boeke 1425, March 31, 1977. (NY);
- Pando, Prov. Madres de Dios, Puerto Candelaria, along the Rio Madre de Dios, 21 Km. (by air) WSW of Riberalta, Clay slumps of high clay banks of river, the top with flat, non-inundated evergreen forest dominated by scattered emergent *Bertholletia excelsa*, alt. 125 m. 11°02'S, 66°15'W. Collector: M. Nee 31408, August 19, 1985. (NY);
- Pando, Nicolas Suarez: entre Porvenir y Cachuelita, a lo largo de la pista. Collector: F. Casas & S. Casas 8345, Jan. 19, 1983. (G, MO, NY).
- Santa Cruz, Prov. Sara, Buena Vista, campos humedos. Collector: José Steinbach 5392, March 5, 1921. (F, G, MO, NY);
- Santa Cruz, Prov. Ichilo, along dirt road, 2 Km. S of highway from Buena Vista to Río Ichilo, the turnoff 5.6 Km. E. of Villa San Germán. 17°23'S, 64°03'W, alt. 275 m. Collector: M. Nee 48424, February 22, 1998. (NY);

-Santa Cruz, Prov. Ichilo, floodplain of Rio Ichilo, downstream (N) of highway bridge.

Disturbed secondary brush and woods with *Cecropia*, *Gynerium*, *Sagittatum*, banana plantations. 17°16'S, 64°20'W, alt. 240 m. Collector: M. Nee & I. Vargas 43238, December 23, 1992. (NY);

-Santa Cruz, Prov. Ichilo, 3 Km. SW of El Hondo, "Potrerillo". Cerrado savanna vegetation south of the buildings, sandy soil. Rare scattered in pasture at edge. 17°40'20"S, 63°27'25"W, alt. 400 m. Collector: M. Nee 44893, February 12, 1994. (NY);

-Santa Cruz, Prov. Ichilo, along Rio Ichilo, 2.1 km by dirt road S from turnoff from main Buena Vista - Villa Tunari highway. Edge of floodplain, a narrow strip of secondary trees, but mostly in banana plantations. In grassy open area. 17°16'30"S, 64°14'W, alt. 240 m. Collector: M. Nee 50237, Oct. 20, 1999. (NY);

-Santa Cruz, Prov. Ichilo. Parque Nacional Amboro. Ca. 15 km (SE) up the Rio Pitasama from the rio Surutu. Moist tropical forest on lower montane slopes. sandstone. Riverbank. 17°44'S, 63°40'W, alt. 700 m. Collector: J. Solomon & S. Urcullo 14161, Aug. 30, 1985. (MO);

***Chelonanthus matogrossensis* (4):**

-Beni, 15-17 Km. SW of Guayaramerin on road to Riberalta. Brushy swamp with standing or gently flowing water now, probably seasonally dry (Pampa); and adjacent to open drainage ditch. 11°10'S, 66°00'W. Collector: William R. Anderson 11988, February 7, 1978. (INPA, NY);

- Santa Cruz, Velasco Prov. Parque Nacional Noel Kempff Mercado. Campamento Los Fierros. Bosque de cerrado con estrato graminiode bajo y con arboles de cobertura casi abierta de hasta 10 m. 14°35'13"S, 60°50'25"W. Collector: Sanchez et al. 281, May 14, 1997. (MO);
- Santa Cruz, Parque Nacional Noel Kempff Mercado. Los Fierros 1; parcela permanente. Campo cerrado, alt. 300 m. Collector: T. Killeen 6775, Oct. 14, 1994. (MO);
- Santa Cruz, Parque Nacional Noel Kempff Mercado colecta genderal de Huanchaca 1. Colectado en la pampa a 2km. de la pista (trail). 13°53'41" S 60°48'46"W. Collector: A. Soto et al. 377, Jan. 25, 1997. (MO).

***Chelonanthus purpurascens* (7):**

- Santa Cruz, Velasco province. Parque Noel Kempff Mercado, Campamento las Gamas, con ecotonos de bosque de galeria, cerrado y pampa. 14°48'17"S, 60°23'14"W, alt. 850 m. Collector: U. Guardia & Surubi 156, February 17, 1997. (MO);
- Santa Cruz, Velasco. Parque Nacional Noel Kempff M., Campamento Las Gamas. Mosaico de cerrado, campo rupestre, pampas humedas y bosque de galeria. 14°49'S, 60°23'W, alt. 900 m. Collector: P. Killeen & Arroyo 4764, March 26, 1993;
- Santa Cruz, Velasco Province. Parque Nacional Noel Kempff Mercado. Meseta de caparuch farallon; de regreso por Los Fierros. Bosque sobre arroyos cortando la pampa. 14°33'35"S, 60°45'50"W, alt. 800 m. Collector: S. Jimenez & E. Gutierrez 1382, March 10, 1997. (MO).

- Santa Cruz, Velasco Province. Parque Nacional Noel Kempff Mercado colectas
generales de Huanchaca 1. 13°53'41"S, 60°48'46"W, alt. 500 m. Collector: A. Soto
et al. 506, January 5, 1997. (MO).
- Santa Cruz, Velasco Province. Parque Nacional Noel Kempff M. Sector Sur.
Campamento Las Gamas. Bosque humedo con muchas epifitas. Arboles hasta 45 m
de alto. En cerrado. 14°48'S, 60°23'W, alt. 850 m. Collector: P. Killeen & Arroyo
5257, April 14, 1993. (MO).
- Santa Cruz, Velasco. Parque Nacional Noel Kempff M. Los Fierros. Cerrado con
Insertia, Rudgea cornifolia, Curatella, Caryocar, Keilmeyera, Ouratea, Roupala,
Waltheria, Himatanthus, Byrsonima, Pseudobombax. Substrato duricosta
ferruginosa y latosol. 14°36'17"S, 60°51'34"W, alt. 220 m. Collector: A. Jardim et
al. 536, April 10, 1994. (MO);
- Santa Cruz, Velasco. Parque Nacional Noel Kempff M; Campamento Huanchaca;
bosque de galeria, bosque humedo de 15 hasta 25 m altura con emergentes hasta 40
m; dominantes Erismia y Apuleia con abundante Phenakospermum. 13°54'S,
60°48'W, alt. 650 m. Collector: L. Arroyo et al. 679, May 17, 1994. (MO).

***Chelonanthus viridiflorus* (12):**

- Beni, 5-8 km SW of Guayaramerin on road to Riberalta; edge of secondary forest and
shrubby, cut over areas, at edge of pool. 10°54'S, 65°56'W. Collector: William R.
Anderson 12028, February 8, 1978. (NY);

- Beni, Prov. Ballivian. Estancia El Porvenir, 50 KM E of the Rio Maniqui (San Borja)
on the road to Trinidad. Forest islands and savannas. Savanna. 14°49'S, 66°25'W,
alt. 250 m. Collector: J. Solomon 14706A, Nov. 14, 1985. (MO);
- La Paz, Ixiamas, alt. 457 m. Collector: M. Cardenos, 1910, December 13, 1921. (NY,
F);
- La Paz, San Jose, alt. 488 m. Collector: R.S. Williams 235, February 2, 1902. (NY);
- La Paz, Prov. Iturralde, Luisita. Sabana humeda, W del Rio Beni. Sartenjal con
hormigueros de termites con agua estancada entre los monticulos pequenos. 13°5'S,
67°15'W. Collector: G. Beck & Hasse 10066, February 27, 1984. (U);
- La Paz, Ixamius, alt. 457 m. Collector: M. Cardenos 1910, Dec. 13, 1921. (F, NY);
- Santa Cruz, Nuflo de Chavez, Est. Las Madres, curiche near front gate, 9 Km. N of
Concepcion, Eroded tertiary plantation surface overlying Precambrian shield;
mosaic of semi-deciduous forest, wooded savanna and savanna marsh, common on
seasonally humid hillside seep. 16°00'S, 62°00'W, alt. 500 m. Collector: Tim
Killeen 1791, February 15, 1986. (F, NY);
- Santa Cruz, Prov. Velasco, c. 10-20 km N of Santa Ana on road to San Ignacio de
Velasco. Rolling lowland plain with areas of swampy grasslands, cerrado, and dry
forest. Uncommon in open swamp, alt. 400 m. Collector: J.R. Wood 14326, Dec.
31, 1998. (K);
- Santa Cruz, Prov. Velasco, Parque Nacional Noel Kempff M; Las Gamas; bosque de
galeria; borde de bosque. 14°48'41"S, 60°23'45"W, alt. 900 m. Collector: L. Arroyo
& K. Keil 153, March 26, 1993. (MO, U);

- Santa Cruz, Prov. Velasco, Parque Nacional Noel Kempff Mercado, Campamento Las Gamas, con ecotones de bosque de galeria, cerrado y pampa. 14°48'17"S, 60°23'W, alt. 850 m. Collector: Guardia, Uslar & Surubi 158, Feb. 17, 1997. (MO);
- Santa Cruz, Prov. Velasco, Parque Nacional Noel Kempff Mercado, Campamento La Torre. Sabana inundada y bosque de serrania, camino a la parcela. 13°39'14"S, 60°49'53"W, alt. 300 m. Collector: E. Gutierrez, R. Quevedo & F. Mamani 870, May 11, 1994. (MO, U);
- Santa Cruz, Prov. Velasco, Parque Nacional Noel Kempff Mercado, Campamento hunchaca II. Bosque cerrado a 5 km del huanchaca II. 14°31'27"S, 60°44'40"W, alt. 600 m. Collector: S. Jimenez, E. Gutierrez & J. Surubi 1254, March 8, 1997. (MO);
- Santa Cruz, Nuflo de Chavez, Est. Santa Maria, 7 Km. S of Concepcion. Eroded tertiary plantation surface overlying Precambrian shield; mosaic of semi-deciduous forest, wooded savanna and savanna wetland, rare, hillside seep. 16°10'S, 62°00'W, alt. 500 m. Collector: Tim Killeen 2435, April 5, 1987. (NY, F).

APPENDICES

Appendix A: Pollen exine characters of the voucher specimens listed were directly referred to in writing or in figures within the given references. Determinations of each are listed as they were considered in this treatment, as well as how they appeared in the references cited. Voucher information for the new species, *Chelonanthus pterocaulis*, is also included.

Determined by Lepis	Reference	Determined by reference	Collector, coll. number (Herbarium)
<i>Chelonanthus acutangulus</i>	Nilsson, 1970	<i>C. alatus</i>	Weaver & Foster, 1696 (S)
<i>C. acutangulus</i>	Nilsson, 2002	<i>C. alatus</i>	Prance <i>et al.</i> , 14378 (S)
<i>C. alatus</i>	Hequet, 2007	<i>C. longistylus</i>	Weitzman & Hahn, 266 (NY)
<i>C. alatus</i>	Nilsson, 1970	<i>C. alatus</i>	BBS, 231 (U)
<i>C. alatus</i>	Nilsson, 1970 & in Struwe <i>et al.</i> 2002	<i>C. alatus</i>	Steyermark, 88754 (U)
<i>C. alatus</i>	Nilsson, 1970 & in Struwe <i>et al.</i> 2002	<i>C. alatus</i>	LP, 475 (U)
<i>C. alatus</i>	Maguire & Boom 1989	<i>C. alatus</i>	Maguire <i>et al.</i> , 53522 (NY)
<i>C. albus</i>	Maguire & Boom 1998	<i>C. albus</i>	Wurdack & Adderley, 43593 (NY)
<i>C. angustifolius</i>	Nilsson in Struwe <i>et al.</i> 2002	<i>C. angustifolius</i>	Steyermark, 75290 (NY)
<i>C. angustifolius</i>	Nilsson in Struwe <i>et al.</i> 2002	<i>C. angustifolius</i>	Maguire, 33712 (NY)
<i>C. angustifolius</i>	Nilsson in Struwe <i>et al.</i> 2002	<i>C. angustifolius</i>	Killip & Smith, 14998 (BM)
<i>C. grandiflorus</i>	Nilsson, 1970 & in Struwe <i>et al.</i> 2002	<i>C. chelonoides</i>	Webster <i>et al.</i> , 9551 (US)
<i>C. grandiflorus</i>	Nilsson in Struwe <i>et al.</i> 2002	<i>C. chelonoides</i>	Maguire & Fanshawe, 22853 (U)
<i>C. grandiflorus</i>	Nilsson in Struwe <i>et al.</i> 2002	<i>C. alatus</i>	Smith, 10128 (NY)
<i>C. pterocaulis</i> sp. nov.			Prance <i>et al.</i> , 4008 (US), isotype
<i>C. pterocaulis</i> sp. nov.			Pittier, 10578 (US)
<i>C. purpurascens</i>	Nilsson in Struwe <i>et al.</i> 2002	<i>C. spruceanus</i>	Klug, 2345 (MO)
<i>C. purpurascens</i>	Nilsson, 1970 & in Struwe <i>et al.</i> 2002	<i>C. uliginosus</i>	Cox & Hubbard, 142 (NY)

Appendix A: Continued.

Determined by Lepis	Reference	Determined by reference	Collector, coll. number (Herbarium)
<i>C. purpurascens</i>	Maguire & Boom 1989	<i>C. uliginosus</i>	Wurdack & Adderley, 43554 (NY)
<i>C. purpurascens</i>	Nilsson in Struwe et al. 2002	<i>C. uliginosus</i>	Smith, 3639 (K, NY)
<i>C. purpurascens</i>	Nilsson in Struwe et al. 2002	<i>C. purpurascens</i>	Rova et al., 1902 (S)
<i>C. purpurascens</i>	Nilsson in Struwe et al. 2002	<i>C. uliginosus</i>	Pinkus, 287 (NY)
<i>C. purpurascens</i>	Nilsson in Struwe et al. 2002	<i>C. uliginosus</i>	Agostini, 394 (NY)
<i>C. viridiflorus</i>	Nilsson, 1970 & in Struwe et al. 2002	<i>C. candidus</i>	Malme, 3293a (S)
<i>C. viridiflorus</i>	Nilsson in Struwe et al. 2002	<i>C. candidus</i>	Dusén, 16538 (MO)
<i>C. viridiflorus</i>	Nilsson in Struwe et al. 2002	<i>C. grandiflorus</i>	Hassler, 9986 (NY)
<i>C. viridiflorus</i>	Nilsson in Struwe et al. 2002	<i>C. grandiflorus</i>	Hassler, 8324 (S)
<i>C. viridiflorus</i>	Nilsson in Struwe et al. 2002	<i>C. grandiflorus</i>	Hulk, 47a (U)
<i>C. viridiflorus</i>	Nilsson in Struwe et al. 2002	<i>C. bifidus</i>	Smith, 3064 (MO)

Appendix B: List of specimens examined that were determined to be potential intermediates between *Chelonanthus hamatus* and some unknown parent. For explanation of potential parental stock see discussion of Chapter three.

VENEZUELA. **Amazonas:** Samariapo. Bastante abundante en las lajas, 30 September 1960, *Foldats 3561* (NY); Samariapo, 7 November 1954, *Maguire et al 36200* (NY); La sabana que forma el aeropuerto de Esmeralda. 5 August 1971, *Foldats 312-A* (NY); An sanosis humidis decus Orinoci ripas, June 1854, *Spruce 3742* (K); Occasional in Laja margin. Caño Cupaven, right bank of Río Orinoco opposite mouth of Río Atabapo. Elevation 125-150 m, 5 June 1959, *Wurdack & Adderley 42820* (NY, US); Atures, near Estacion de Piscicultura de Puerto Ayacucho, laja. Very common at open sunny places on laja, 3 November 1980, *Maas & Huber 5156* (K, NY, U); Localmente frecuente

sobre laja granítica, ca. 100 m al oeste de sede de la Est. Exp. Amazonas, FONAIAP, 5 km al sur de Puerto Ayacucho, Alt. ca 55 m., October 1988, *Romero & Narbaize 1751* (NY, VEN); Dpto. Atures, afloramiento granítico de la margen derecha del Río Autana, en raudal Ceguera, 4°48'N, 67°28'W, alt. 100 m, 8 November 1984, *Guanchez & Melgueiro 3357* (U, VEN); In vicinity of Samariapo, near Río Samariapo, tributary of Orinoco River. On rocks at Samariapo, 8 September 1944, *Steyermark 58500* (F); Río Orinoco; San Pedro (entre Samariapo y San Fernando de Atabapo), en sabanita y bosque detras del pueblo, 6-19 July 1969, *Bunting et al 3589* (U); Puerto Samariapo. Sobre afloramientos rocosos característicos. Suelo negro y escaso. Cercanías del cerro Samariapo, 8 August 1982, *Parra 2* (NY); Muestras rupícolas colectadas en Laja, que se encuentra en la parte posterior de la estación de Piscicultura del MAC en Pto. Ayacucho, 31 August 1982, *Francisco & Ramos 56* (F, NY). **Bolívar**: Río Parguaza, crystalline laja 0.5 km above mouth of Río Parguaza, elevation 100-150 m., 10 December 1955, *Wurdack & Monachino 39764* (F, NY, S, U, US, UPS, VEN)

LITERATURE CITED

- Aublet, M.F. 1775. Histoire des plantes de la Guiane Françoise, vol. 1. London & Paris: P.F. Didot.
- Bailey, C.D., T.G. Carr, S.A. Harris & C.E. Hughes. 2003. Characterization of angiosperm nrDNA polymorphism, paralogy, and pseudogenes. *Molecular Phylogenetics and Evolution* 29: 435-455.
- Bentham, G. 1839. *Plantae Hartwegianae*. London: Gulielmus Pamplin.
- 1854. Notes on north Brazilian Gentianaceae, from the collections of Mr. Spruce and Sir Robert Schomburgk. *Hooker's Journal of Botany and Kew Gardens Miscellany* 6: 193-204.
- Bertani, S., G. Bourdy, I. Landau, J. Robinson, P. Esterre, & E. Deharo. 2005. Evaluation of French Guiana traditional antimalarial remedies. *Journal of Ethnopharmacology* 98: 45-54.
- Bouman, F., L. Cobb, N. Devente, V. Goethals, P.J.M. Maas & E. Smets. 2002. The seeds of Gentianaceae. Pages 498-572. In: L. Struwe & V.A. Albert, eds. *Gentianaceae systematics and natural history*. New York: Cambridge University Press.
- Browne, P. 1756. The civil and natural history of Jamaica in three parts, ed. 1. London: T. Osborne & J. Shipton.
- Chenna, Ramu, Sugawara, Hideaki, Koike, Tadashi, Lopez, Rodrigo, Gibson, Toby, Higgins, Desmond & Thompson. 2003. Multiple sequence alignment with the Clustal series of programs. *Nucleic Acids Research* 31(13): 3497-500.
- Cox, A.V., M.D. Bennett, & T.A. Dyer. 1992. Use of the polymerase chain reaction to detect spacer size heterogeneity in plant 5S – rRNA gene clusters and to locate such gene clusters in wheat (*Triticum aestivum* L.). *Theoretic Applied Genetics* 83: 684-690.
- Cronn, R.C., X. Zhao, A.H. Paterson & J.F. Wendel. 1996. Polymorphism and concerted evolution in a tandemly repeated gene family: 5S ribosomal DNA in diploid and allopolyploid cottons. *Journal of Molecular Evolution* 42: 685-705.
- Dobat, K. & T. Peikert-Holle. 1985. Blüten und Fledermäuse (Chiropterophilie). Frankfurt am Main: Kramer.
- Farris, J.S., V.A. Albert, M. Källersjö, D. Lipscomb and A.G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12: 99-124.
- Foster, R. C. 1958. A catalogue of the ferns and flowering plants of Bolivia. *Contr. Gray Herb.* 184: 1-223.
- Frontier, S. 1976. Étude de la décroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le modèle du bâton brisé. *Journal of Experimental Marine Biology and Ecology* 25: 67-75.
- Funk, D.J. & K.E. Omland. 2003. Species level paraphyly and polyphyly: frequency, Causes and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution & Systematics* 34: 397-423.
- Genbank website: <http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=Nucleotide>
- Gilg, E. 1895. Gentianaceae. Pages 50-108. In: A. Engler & K. Prantl, eds. *Die Natürlichen Pflanzenfamilien*, vol. 4(2). Verlag von Wilhelm Engelmann, Leipzig.

- 1906. Beiträge zur Kenntnis der Gentianaceae III. Gentianaceae andinae. In: F. Fedde, ed. *Repertorium novarum specierum regni vegetabilis*, No. 16/17.
- Gleason, H.A. 1931. Botanical results of the Tyler-Duida Expedition, *Bulletin of the Torrey Botanical Club* 58: 277-506.
- 1939. The Flora of Mount Auyan-tepui, Venezuela. *Brittonia* 3: 141-204.
- Graham, A. 1984. *Lisianthus* pollen from the Eocene of Panama. *Annals of the Missouri Botanical Garden* 71: 987-993.
- Grant, J.R., P.J.M. Maas & L. Struwe 2006. *Yanomamua araca* (Gentianaceae: Helieae), a new genus and species from outliers of the Guayana Shield on Serra Aracá in Amazonian Brazil. *Harvard Papers in Botany* 11(1): 33-41.
- Grisebach, A.H.R. 1839. *Genera et species Gentianearum*. Stuttgart and Tübingen: J.G. Cotta.
- 1845. Gentianaceae Pages 39-141. In: A. de Candolle, ed. *Prodromus systematis naturalis regni vegetabilis*, vol. 9. Paris: Fortin, Masson, et Sociorum.
- 1862. Notes on *Coutoubea volubilis*, Mart., and some other Gentianaceae from tropical America. *Journal of Proceedings of the Linnaean Society Botany* 6: 140-146.
- Gorczyca, A., K.B. Lepis & L. Struwe. 2005. Determining the boundaries of the species complex *Chelonanthus viridiflorus* (Gentianaceae). Northeast Ecology and Evolution Conference. March 18-20. The Pennsylvania State University, University Park, PA.
- Hequet, V. 2007. Pollen atlas of bat-pollinated plants of central French Guiana, New York Botanical Garden.
http://nybg.org/botany/tlobova/hequet/PollenAtlas_frameset.htm
- Holmgren, P.K. & N.H. Holmgren. 1998 onwards (continuously updated). Index Herbariorum. - New York Botanical Garden.
<http://sciweb.nybg.org/science2/IndexHerbariorum.asp>
- International Travel Maps. 1998. A traveler's reference map of Amazon Basin, 3rd edn., map 421. - Vancouver: ITMB Publishing LTD, scale 1:4,000,000.
- International Travel Maps. 2004. The Guianas and Guyana. - Vancouver: ITMB Publishing LTD, scale 1:1,200,000.
- Jackson, D.A. 1993. Stopping rules in principle components analysis: a comparison of heuristical and statistical approaches. *Ecology* 74(8): 2204-2214.
- Jonker, F.P. 1936. Gentianaceae. Pages 400-427 In: A. Pulle, ed. *Flora of Suriname (Netherlands Guyana)*, vol. 4. Amsterdam: J. H. de Bussy Ltd.
- Killeen, T.J. & T.S. Schulenberg. 1998. A biological assessment of Parque Nacional Noel Kempff Mercado, Bolivia. *RAP Working Papers* 10: 1-372.
- Köhler, A. 1905. Der Systematische Wert der Pollenbeschaffenheit bei den Gentianaceen. *Mitteil. Bot. Mus. Zürich* 25. (Dissertation)
- Kunth, C. 1818. Gentianaceae (*Lisianthus* treatment). Pages 180-185. In: Humboldt, Bonpland & Kunth, eds. *Nova Genera et Species Plantarum* vol. 3. Paris: Lutetiae Parisiorum.
- Kuntze, C.E.O. 1891. *Revisio generum plantarum* 2. Leipzig.
- Lamarck, J.B.P. De Monet, 1792. Sur quatre espèces d'hélices. *Journal d'Histoire Naturelle* 2:347-353, Pl. 42.
- Legendre, P. 1998. *Numerical Ecology*, 2nd edn. Amsterdam: Elsevier Science B.V.

- Lemée, A. 1950. Gentianaceae. Pages 277-288 In: Flore de Guyane Française, part 3
Paris: Lechevalier.
- Linnaeus, C. von. 1767. Mantissa plantarum. Stockholm.
- 1775. Plantæ Surinamenses, vol. 6. Upsala: Jacobus Alm.
- Linnaeus, C. von., filius. 1781. Supplementum Plantarum. Systema vegetabilium ed. 13,
Generum plantarum ed. 6, et Species plantarum ed. 2. Brunsvigae.
- Maas, P.J.M. 1985. Nomenclatural notes on neotropical Lisyantheae (Gentianaceae).
Proc. Kon. Ned. Akad. Wetensch. ser. C, 88: 405-412.
- MacBride, J.F. 1959. Flora of Peru. Botanical Series, vol. 13, part 5, number 1.
Chicago: Field Museum of Natural History.
- Machado I.C.S., I. Sazima & M. Sazima. 1998. Pollination of terrestrial herb *Irlbachia*
alata (Gentianaceae) in northeastern Brazil. *Plant Systematics & Evolution* 209:
231-237.
- Maguire, B. & B.M. Boom. 1989. Gentianaceae, part 3. Pages 2-56 In: B. Maguire &
collaborators, eds. The botany of the Guayana Highlands - Part XIII. *Memoirs of the*
New York Botanical Garden. 29.
- Malme, G.O.A.N. 1904. Die Gentianaceen der zweiten Regnell'schen Reise. *Arkiv för*
botanik 3(12).
- Martins, M. & H.G. Gelotti. 1844. *Bulletin of Academy of Royal Sciences Bruxelles* 11:
374.
- Martius, C.F.P., von. 1827. Nova genera et species plantarum quas in itinere per
Brasiliam, vol. 2. München: V. Wolf.
- Mayle, F. E. 2004. Assessment of the neotropical dry forest refugia hypothesis in the
light of palaeoecological data and vegetation model simulations. *Journal of*
Quaternary Science 19(7): 713-720.
- Molina, J. & L. Struwe. 2008. Revision of ring-gentians (*Symbolanthus*, Gentianaceae)
from Bolivia, Ecuador and Peru, with a first assessment of conservation status.
Systematics and Biodiversity (In Press).
- Mort, M.E., K.J. Archibald, C.P. Randle, N.D. Levens, T.R. O'Leary, K. Topalov, C.M.
Wiegand & D. J. Crawford. 2007. Inferring phylogeny at low taxonomic levels:
utility of rapidly evolving cpDNA and nuclear ITS loci. *American Journal of*
Botany 94(2): 173-183.
- Nickrent, D.L., K.P. Schuette, & E.M. Starr. 1994. A molecular phylogeny of
Arceuthobium (Viscaceae) based on nuclear ribosomal DNA internal transcribed
spacer sequences. *American Journal of Botany* 81(9): 1149-1160.
- Nilsson, S. 1970. Pollen morphological contributions to the taxonomy of *Lisianthus* L.
s. lat. (Gentianaceae). *Svensk Botanisk Tidskrift Utgifven af Svenska Botaniska*
Foreningen 64: 1-43.
- 2002. Gentianaceae: a review of palynology. Pages 377-497. In: L. Struwe &
V.A. Albert, eds. Gentianaceae: systematics and natural history. Cambridge:
Cambridge University Press.
- Nylander, J.A.A. 2004. MrModeltest v2. Program distributed by the author.
Evolutionary Biology Centre, Uppsala University.
- Page, R.D.M. 1996. TREEVIEW: An application to display phylogenetic trees on
personal computers. *Computer Applications in the Biosciences* 12: 357-358.

- Parker, T. & B. Bailey. 1991. A biological assessment of the Alto Madidi region and adjacent areas of Northwest Bolivia. RAP Working Papers 1: 1–108.
- Poiret, J.L.M. 1814. Lysianthe. Pages 562-564. In: J.B.P. Lamarck, ed. *Encyclopedie Methodique. Botanique, Supplement 3*. Paris: Chez. H. Agasse.
- Posada, D. & T.R. Buckley. 2004. Model selection and model averaging in phylogenetics: advantages of Akaike Information Criterion and Bayesian approaches over Likelihood Ratio Tests. *Systematic Biology* 53(5): 793-808.
- Pringle, J.S. 1995. 159A. Gentianaceae. Pages 3-31. In: G. Harling & L. Anderson, eds. *Flora of Ecuador*. No. 53. Copenhagen: Council for Nordic Publications in Botany.
- Progel, A. 1865. Gentianaceae. Pages 197-248 In: C.F.P. von Martius, ed. *Flora Brasiliensis*, vol. 6(1). Munich: Frid. Fleischer.
- Pulle, A.A. 1906. An enumeration of the vascular plants known from Surinam, together with their distribution and synonymy. Leiden: E.J. Brill LTD.
- Robinson, G.G. & B. López. 1999. Medicinal plant use patterns among the Amuzgos of Guerrero, Mexico. Instituto Lingüístico de Verano, A. C.
- Ronquist, F.R. 1996. DIVA version 1.1. Computer program and manual available by anonymous FTP from Uppsala University (<ftp.systbot.uu.se>).
- 1997. Dispersal-vicariance analysis: a new biogeographical approach to the quantification of historical biogeography. *Systematic Biology* 46: 195-203.
- Ronquist, F.R. & J.P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.
- 2005. Bayesian analysis of molecular evolution using MrBayes. Pages 183-232 In: R. Nielsen, ed. *Statistical Methods in Molecular Evolution*. New York: Springer.
- Ronquist, F.R., J.P. Huelsenbeck & P. van der Mark. 2005. MrBayes 3.1 Manual. <http://mrbayes.csit.fsu.edu/manual.php>.
- Ruiz, H. & J. Pavon. 1799. *Flora Peruviana et Chilensis*. Madrid: Gabrelis de Sancha.
- Rull, V. 2004. An evaluation of the lost world and vertical displacement hypotheses in the Chimantá Massif, Venezuelan Guayana. *Global Ecology and Biogeography* 13: 141-148.
- Rusby, H.H. 1927. Descriptions of new genera and species of plants collected on the Mulford Biological Exploration of the Amazon valley, 1921-1922. *Mem. New York Bot. Gard.* 7(3): 205–387.
- Sazima, M. & I. Sazima. 1995. Bat pollination of *Vriesea* in southeastern Brazil. *Bromélia* 2: 29-37.
- Shaw, P.J.A. 2003. *Multivariate Statistics for the Environmental Sciences*. London: Arnold.
- Silva, J. F., M. R. Farinas, J. M. Felfili & C. A. Klink. 2006. SPECIAL ISSUE: Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. *Journal of Biogeography* 33(3): 536-548.
- Staflue, F.A. & R.S. Cowan. 1981. *Taxonomic Literature. A selective guide to botanical publications and collections with dates, commentaries and types*, 2nd edn., vol. III. Utrecht: Bohn, Scheltema & Holkema.
- Stearn, W.T. 1983. *Botanical Latin*, 3rd edn. David & Charles Publishers plc.
- 1999. *Botanical Latin*, 4th edn. Portland: Timber Press.

- Stephens, P.R. & J.J. Weins. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *The American Naturalist* 161: 112-128.
- Steyermark, J.A. & collab. 1953. Contributions to the flora of Venezuela. Botanical exploration in Venezuela - III. *Fieldiana, Botany* 28: 496-1071.
- Struwe, L., P.J.M. Maas & V.A. Albert. 1997. *Aripuana cullmaniorum*, a new genus and species of Gentianaceae from white sands of southeastern Amazonas, Brazil. *Harvard Papers in Botany* 2: 235-253.
- Struwe, L. & V.A. Albert. 1998. *Lisianthus* (Gentianaceae), its probable homonym *Lisyanthus*, and the priority of *Helia* over *Irlbachia* as its substitute. *Harvard Papers in Botany* 3(1): 63-71.
- Struwe, L., P.J.M. Mass, O. Pihlar, & V.A. Albert. 1999. Gentianaceae. Pages 474-542. In: P.E. Berry, K. Yatskievych, & B.K. Holst, eds. *Flora of the Venezuelan Guayana*, vol. 5. St. Louis: Missouri Botanical Garden Press.
- Struwe, L., J.W. Kadereit, J. Klackenberg, S. Nilsson, M. Thiv, K.B. von Hagen & V.A. Albert. 2002. Systematics, character evolution, and biogeography of Gentianaceae, including a new tribal and subtribal classification. Pages 21-309. In: L. Struwe & V.A. Albert, eds. *Gentianaceae systematics and natural history*. New York: Cambridge University Press.
- Struwe, L., S. Nilsson & V.A. Albert. 2008. *Roraimaea* (Gentianaceae: Helieae) - a new gentian genus from white sands and tepuis of Brazil and Venezuela. *Harvard Papers in Botany* 13: 35-45.
- Struwe, L., V.A. Albert, M.F. Calió, C. Frasier, K.B. Lepis, K.G. Mathews & J.R. Grant. (In Press). Evolutionary patterns in neotropical Helieae (Gentianaceae): evidence from morphology, chloroplast and nuclear DNA sequences. *Taxon*.
- Swofford, D.L. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods). Sunderland: Sinauer Associates.
- Tabachnik, B. & L. Fidell. 2001 *Using multivariate statistics*. 4th edn. Boston: Allyn and Bacon.
- Thriv, M., L. Struwe, & J.W. Kadereit. 1999. The phylogenetic relationships and evolution of the Canarian laurel forest endemic *Ixanthus viscosus* (Aiton) Griseb. (Gentianaceae): evidence from matK and ITS sequences, and floral morphology and anatomy. *Plant Systematics and Evolution* 218: 299-317.
- Ulloa, C. U. & D. A. Neillb. 2006. *Phainantha Shuariorum* (Melastomataceae), una Especie Nueva de la Cordillera del Cóndor, Ecuador, Disyunta de un Género Guayanés. *Novon* 16(2): 281-285.
- Villagran, C., A. Leon & F. A. Roig. 2004. Paleodistribution of the alerce and cypres of the Guaitecas during the interstadial stages of the Llanquihue Glaciation; Llanquihue and Chiloe provinces, Los Lagos Region, Chile. *Revista Geologica de Chile* 31(1): 133-151.
- Vogel, S. 1969. Chiropterophilie in der neotropischen Flora. II. *Flora* 158: 185-222.
- 1958: Fledermausblumen in Südamerika. *Oesterreichische Botanische Zeitschrift. Gemeinnütziges Organ für Botanik* 104: 491-530.
- Weins, J.J. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Botany* 52(4): 528-538.

White, T.J., T. Burns, S. Lee & J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal DNA for phylogenetics. Pages 315-322. In: M.A. Innis, D.H. Gelfund, J.J. Sninsky & T.J. White, eds. PCR Protocols: A Guide to Methods and Applications. San Diego: Academic Press.

CURRICULUM VITA

Katherine Burke Lepis

EDUCATION

- Sept. 1999 - **Rutgers University**, New Brunswick, NJ
 Jan. 2009 Ph.D.: Plant Biology.
- Sept. 1990 - **University of Rhode Island**, Kingston, RI
 May 1995 B.S.: Natural Resource Management, Wildlife Biology: May, 1995.

PROFESSIONAL EXPERIENCE

- Fall Semester **Head Teaching Assistant**
 2002 - 2005 **Division of Life Sciences, Rutgers University**, New Brunswick, NJ
 and 2007
- Sept. 1999 - **Teaching Assistant**
 July 2002 General Biology I, General Biology II, Principles of Botany
- Field Seasons **Field Technician**
 2000 and 2002 **Center for Urban Restoration**, New Brunswick, NJ
- Field Season **Native Plant Propagator**
 2001 **Greenbelt Native Plant Nursery**, Staten Island, NY
- Jan. 1998 - **Horticultural Supervisor**
 2001 **Raimondi Horticultural Group**, Ho-Ho-Kus, NJ
- Jan. 1995 - **Assistant Ecologist, Intern**
 Nov. 1995 **The US Dept. of Agriculture, Div. of Animal Damage Control**, San
 Nicolas Island, CA

PUBLICATIONS

- In press **Catálogo de las Plantas Vasculares de Bolivia** – In press. *Chelonanthus*
 Treatment. Lepis. ed. Peter Møller Jørgensen (Missouri Botanical Garden).
- In press **Flora of the Guianas** – In press. *Chelonanthus* Treatment. Lepis, Cobb &
 Palmer. ed. Marion J. Jansen-Jacobs (Utrecht University).