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PHYLOGENETICS OF PRESCOTTIINAE DRESSLER AND SYSTEMATICS OF *GOMPHICHIS* LINDL. (ORCHIDACEAE)

By

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DEDICATION

In loving memory of my mother and sister

ABSTRACT

PHYLOGENETICS OF PRESCOTTIINAE DRESSLER AND SYSTEMATICS OF *GOMPHICHIS* LINDL. (ORCHIDACEAE)

by

Aída Alvarez

Adviser: Dr. Kenneth M. Cameron

The phylogenetics of the subtribe Prescottiinae (tribe Cranichideae, family Orchidaceae) and the systematics of the genus *Gomphichis* were investigated.

Cladistic analyses of nucleotide sequences from *psa*B, *atp*B, *rbc*L, *trn*L intron, *trn*L-F spacer, and ITS, found that the Prescottiinae as delimited by Dressler (1990, 1993) and Szlachetko (1995) are paraphyletic and consist of two highly supported clades: "the high elevation Prescottiinae" (*Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, and *Stenoptera*) and "the low elevation Prescottiinae" (*Prescottia* and *Pseudocranichis*). The recovered clades of the Prescottiinae show an affinity to Spiranthinae rather than to Cranichidinae. *Prescottia* is paraphyletic because *Pseudocranichis* is nested within it. These results support the transfer of *Pseudocranichis* to *Prescottia* and the re-classification of the subtribe Prescottiinae.

Gomphichis, as monographed here, consists of at least 17 species ranging from Costa Rica to Bolivia with disjunct populations in the Guayana Highlands. Three unnamed taxa may represent novelties in *Gomphichis*, but additional material and analyses are needed before formal descriptions are proposed. *Gomphichis* is distinguished by its unusual strongly reflexed flower, held at a right angle with the ovary, its sigmoid column, and saccate fleshy labellum. Phylogenetic analyses using DNA sequence data from *trn*L intron, *trn*L-F spacer, and ITS, found *Gomphichis* to be monophyletic and nested within a clade comprising "the high elevation Prescottiinae". Within this clade, *Gomphichis* is resolved as sister to *Porphyrostachys*, *Myrosmodes*, and *Aa*; *Altensteinia* is sister to these genera and *Stenoptera* is sister to all of them. The morphological resemblance of *Gomphichis* to *Stenoptera* is due to symplesiomorphic characters rather than common ancestry. Most species of *Gomphichis* fall into one of three clades characterized by either weakly- or distinctly 3-lobed labellum.

Demographic studies indicate that populations of *Gomphichis crassilabia* in three selected habitats of the Estación Biológica Guandera of Ecuador (primary forest with open and closed canopy and secondary forest) follow the reverse J-curve since there are more seedlings and juveniles present than adult plants. As a result the studied populations are reproducing well. Furthermore, field experiments show that *G. crassilabia* reproduce by facultative out-breeding, in which, the flowers self-fertilize in the absence of pollinators late in the season.

RESUMEN

FILOGENETICA DE PRESCOTTIINAE DRESSLER Y SISTEMATICA DE *GOMPHICHIS* LINDL. (ORCHIDACEAE)

Por

Aída Alvarez

Profesor tutor: Dr. Kenneth M. Cameron

La filogénia de la subtribu Prescottiinae (tribu Cranichideae, familia Orchidaceae) y la sistemática del género *Gomphichis* fueron investigadas.

Análisis cladísticos con secuencias del nucleótido de *psa*B, *atp*B, *rbc*L, *trn*L intron, *trn*L-F spacer, e ITS, muestran que Prescottiinae conforme a la delimitación de Dressler (1990, 1993) y Szlachetko (1995) es parafilética y consiste de dos clados distintos, altamente apoyados: "las Prescottiinae de elevaciones altas" (*Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, y *Stenoptera*) y "las Prescottiinae de elevaciones bajas" (*Prescottia* y *Pseudocranichis*). Los clados recuperados de las Prescottiinae muestran una afinidad a Spiranthinae antes que a Cranichidinae. El género *Prescottia* es parafilético puesto que *Pseudocranichis* está anidado dentro del mencionado género. Los resultados de este estudio apoyan la transferencia de *Pseudocranichis* a *Prescottia* y la reclasificación de la subtribu Prescottiinae.

Gomphichis, según la monografía aquí presentada, consiste de al menos 17 especies distribuídas desde Costa Rica hasta Bolivia con poblaciones disjuntas en las tierras altas de la Guayana. Tres táxones podrían representar especies nuevas de *Gomphichis*, sin embargo material adicional y otros análisis son necesarios antes de que descripciones formales se propongan. *Gomphichis* se distingue por sus flores inusuales, fuertemente reflexas que forman un ángulo recto con el ovario, su columna sigmoide, y el labelo carnoso en forma de saco. Análisis filogenéticos utilizando secuencias de ADN del *trn*L intron, *trn*L-F spacer, e ITS, muestran que *Gomphichis* es monofilético y está anidado en un clado conformado por "las Prescottiinae de elevaciones altas". Dentro de este clado, *Gomphichis*, es el grupo hermano de *Porphyrostachys*, *Myrosmodes* y *Aa*; *Altensteinia* es hermano de estos géneros y *Stenoptera* es hermano de todos los demás géneros. La similitud morfológica de *Gomphichis* y *Stenoptera* es debida a caracteres simplesiomórficos antes que a ancestría común. La especies muestreadas de *Gomphichis* se hallan en uno de tres clados caracterizados por labelo distintivamente o ligeramente tri-lobado.

Estudios demográficos indican que las poblaciones de *Gomphichis crassilabia* en tres hábitats de la Estación Biológica Guandera en Ecuador (bosque primario con dosel abierto o dosel cerrado y bosque secundario) siguen la curva J-revertida puesto que hay más plántulas y juveniles presentes que adultos. Como resultado las poblaciones estudiadas se está reproduciendo bien. Además, experimentos de campo muestran que *G. crassilabia* se reproduce por cruzamiento facultativo externo, mecanismo por el cual, las flores se autofertilizan ante la ausencia de polinizadores a fines de la estación reproductiva.

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CHAPTER 1

OVERVIEW OF SUBTRIBE PRESCOTTIINAE (ORCHIDACEAE)

1.1. INTRODUCTION

Orchidaceae are probably the largest and most diverse flowering plant family with more than 25,000 species in 725 genera and a worldwide distribution (Atwood, 1986). Orchids show an overwhelming floral and vegetative diversity that may have evolved in close association with insect pollinators (van der Pijl & Dodson, 1966) and symbiotic fungi (Benzing, 1987). They can be diagnosed by a collection of features including the fusion of the pistil and stamen into a column, the aggregation of the pollen grains into pollinia, and the differentiation of one petal into a lip or labellum (Dressler, 1961, 1981). Orchids are monophyletic and positioned as sister to members of the order Asparagales (Dahlgren & Rasmussen, 1983; Fay et al., 2000). Despite the absence of a positive fossil record for Orchidaceae, molecular clock estimates suggest an ancient origin of the family (Cameron & Chase, 1999).

The most widely used system of orchid classification (Dressler, 1993) divides the subfamily Spiranthoideae into tribes Dicerastoteleae, Tropidieae, and Cranichideae. In this system the tribe Cranichideae is the largest of that subfamily and includes six subtribes. These are Spiranthinae, Prescottiinae, Cranichidinae, Goodyerionae, Manniellinae, and Pachyplectroninae. The terrestrial orchids of tropical America that inhabit higher altitudes are classified within the subtribe Prescottiinae. The subtribe, as defined by Dressler (1990), is united by the *Spiranthes* type of velamen, non-resupinate flowers (labellum held uppermost), a laminar rostellum, and soft-pollinia lacking a hamulus. The Prescottiinae include approximately 100 species in seven genera: *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, and *Stenoptera* (Dressler, 1990, 1993). Szlachetko (1995) proposed including the morphologically distinctive genus *Pseudocranichis* in the Prescottiinae as well. The subtribe is most abundant in Andean South America, where over two-thirds of the species are found.

Most recently, Chase et al. (2003) proposed a new classification of the Orchidaceae to reflect phylogenetic patterns within the family as suggested by a variety of published molecular studies. In this system subtribe Prescottiinae was not recognized, but rather included in an expanded concept of subtribe Cranichidinae (*sensu* Dressler, 1981). This decision was mainly based on molecular studies of the tribe Cranichideae by Salazar et al. (2003), in which the Prescottiinae were shown to be paraphyletic. Sampling of the Prescottiinae in that work was incomplete (not all genera were sampled) and the relationships among Prescottiinae, Cranichidinae, and Spiranthinae were not clearly determined, especially the placement of the genus *Prescottia*. Due to these uncertainties and the lack of support for the monophyly of an expanded Cranichidinae, further studies are needed to resolve these issues, especially the circumscription of subtribes Prescottiinae and Cranichidinae, and to elucidate their phylogenetic relationships (see Chase et al., 2003; Pridgeon et al., 2003; Salazar et al., 2003).

As summarized above, the monophyly of subtribe Prescottiinae requires further testing and its placement in the most recently published classification of the orchid family (Chase et al., 2003) is problematic. The first chapter of this dissertation will provide a synthesis of the available data about subtribe Prescottiinae, and herein I adopt Dressler's 1993 classification system.

TAXONOMIC HISTORY

In 1840, Lindley, the father of orchid taxonomy, placed some of the currently recognized genera of the subtribe Prescottiinae (*Altensteinia*, *Gomphichis*, *Prescottia*, and *Stenoptera*) along with other distantly related orchid genera in the tribe Neotteae division Cranichidae. This division was characterized by non-resupinate flowers, a concave labellum, an erect or incumbent column, and a truncated rostellum. Division Spiranthidae was also proposed to accommodate genera with resupinate flowers.

Bentham (1881) and subsequently Bentham and Hooker (1883) modified the tribal and subtribal system of Lindley and merged the resupinate and non-resupinate orchids in the subtribe Spirantheae. This subtribe was composed of *Aa*, *Altensteinia*, *Gomphichis*, *Prescottia*, and *Stenoptera* together with other spiranthoid taxa.

Almost simultaneously, Reichenbach (1881) described the genus *Manniella* from west tropical Africa and hypothesized its close relationship to the prescottioid genus *Stenoptera* of the Neotropics. The suggested affinities between *Manniella* and *Stenoptera* were based on shared floral features including the connation of the sepals, the adnation of the petals to the labellum, and the sigmoid column.

On the basis of vegetative features, Pfitzer (1887) proposed the subfamily Neottiinae consisting of several subtribes. Two of these included "subtribe Cranichideae" comprising genera such as *Gomphichis*, *Prescottia*, *Altensteinia* (including *A*a and *Myrosmodes*), and *Stenoptera*, as well as subtribe Spirantheae consisting of nine genera. This scheme, with minor modifications, was used in *Die Natürlichen Pflanzenfamilien* of Engler and Prantl (1889).

Schlechter (1915), in his "System der Orchideen", placed the Cranichidinae within the monandrous orchids that possess acrotonae pollinia and polychondreae anthers (having pollen grains arranged in tetrads inside the pollinia). In this system, *Aa* (including *Myrosmodes*), *Altensteinia*, *Porphyrostachys*, *Prescottia*, and *Stenoptera* (including *Gomphichis*) were included in the same group with *Cranichis*, *Pterichis*, and *Fuertesiella*.

Five years later, Schlechter (1920) published a synthesis of the Spiranthinae placing in it genera characterized by a reduced and notched rostellum. In this group the notch is membranaceous with a terminal viscidium. Subtribe Cranichidinae differs from subtribe Spiranthinae by the position of the labellum, held uppermost in the former.

In 1926, Schlechter's previously proposed classification system was refined, expanded to include keys for subtribal identification, and posthumously published. In the new scheme presented as a dichotomous key, subtribe Cranichideae was subdivided into two major groups: "obtusirostellata" and "productirostellata" based on the shape of the rostellum. In the former, *Aa*, *Altensteinia*, *Gomphichis*, *Pophyrostachys*, and *Stenoptera* were placed close to *Wullschlaegelia* (now considered a member of subfamily Epidendroideae).

In 1937, Mansfeld proposed a revision of Schlechter's system of classification. One of the major modifications of this classification was the introduction of a new division among the monandrous orchids, the “Tribengrouppe”. Two major groups were recognized: the “Thrauosphaereae tribengrouppe” consisting of tribes Neottieae and Ophrydeae and the “Kerosphaereae tribengrouppe”. Subsequently, Mansfeld (1955) provided a more detailed description of the characters used in his classification scheme. The tribe Neottieae in Mansfeld's system was characterized by a combination of free anthers and non sectile pollinia. The tribe included 17 subtribes, of which one (subtribe

Cranichidinae) included genera with herbaceous leaves, roots in tufts and non-resupinate flowers.

In the classification of the Orchidaceae by Dressler and Dodson (1960), subtribe Spiranthinae was expanded to include the previously recognized Cranichidinae. They justified this decision on the many floral characters shared by these groups. The newly defined Spiranthinae consisted of two alliances. The *Cranichis* alliance included genera with non-resupinate flowers such as *Altensteinia*, *Porphyrostachys*, *Prescottia*, and *Stenoptera*. The *Spiranthes* alliance contained genera with resupinate flowers.

During the early 1970's in the series Die Orchideen (Schlechter) the genera belonging to subtribes Cranichidinae and Spiranthinae were placed in tribe Spirantheae of subfamily Neottioideae (Brieger, 1971, 1974, 1975). Within Cranichidinae they proposed two informal groups: "acolumnata" and "columnata". Acolumnata members were characterized by not having a true column but possessing a style separated from the stamens, whereas the columnata group consisted of taxa containing a well-developed column. These authors included *Gomphichis*, *Stenoptera*, and *Porphyrostachys* in the columnata group; and *Altensteinia* and *Prescottia* along with *Baskervillea*, *Pterichis*, *Cranichis*, *Ponthieva* and additional genera in the acolumnata group. Within the Spiranthinae (subdivided into four groups), they accommodated taxa such as *Brachystele*, *Manniella*, *Pelexia*, *Spiranthes* and others.

Within the Cranichidinae, Dressler (1981; 1990) recognized 15 genera in two alliances. The *Altensteinia* alliance characterized by a blunt column, soft pollinia without caudicles, and a simple labellum free from the column, included *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, and *Stenoptera*. The *Cranichis* alliance incorporated genera having a pointed column, firm pollinia with caudicles, and a labellum usually fused to the column. These alliances essentially followed Schlechter's 1926 divisions.

In a published generic revision of the Spiranthinae, Garay (1982) recognized 390 species in 44 genera. In this revision he proposed the monotypic genus *Pseudocranichis* for *Cranichis thysanochila*. This taxon has peculiar morphological features that resemble those of *Altensteinia*. Burns-Balogh (1986), assigned *Pseudocranichis* to Cranichidinae rather than to Spiranthinae based on the following characters present in *Pseudocranichis*: lateral dehiscence of the anthers, circular pollinia in cross section, and non-resupinate flowers.

Rasmussen (1985), in his treatment of the Orchidaceae, placed *Prescottia* and its allies in the *Spiranthes* group. This group was included in the tribe Neottieae, subfamily Neottioideae. Rasmussen's *Spiranthes* group was defined by a rosette of basal leaves and thick clustered storage organs. The *Spiranthes* group as defined by Rasmussen is comparable to the Cranichideae of Dressler.

Burns-Balogh and Funk (1986) characterized the subtribe Cranichidinae primarily by non-resupinate flowers, hamular stipe, and round pollinia in cross section. They incorporated 15 genera and about 200 species, including the genera of Prescottiinae as members of an expanded Cranichidinae. These authors, in agreement with Schlechter's classification of 1926, also recognized the monotypic subtribes Manniellinae and Plachyplectroninae within the tribe Cranichideae.

The Prescottiinae were formally proposed as a subtribe of the Cranichideae by Dressler (1990) to accommodate the non-resupinate terrestrial orchids of the Neotropics. The newly erected subtribe included *Aa*, *Altensteinia*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, and *Stenoptera*. A sister relationship between Prescottiinae and Spiranthinae was suggested (Dressler, 1990). The same circumscription of the subtribe was followed by Dressler in his later classification system of the family published in 1993.

In his classification of Orchidales, Szlachetko (1995) recognized the tribe Spirantheae as a monophyletic group containing six subtribes. One of them was subtribe Prescottiinae, which included *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, *Pseudocranichis*, and *Stenoptera*. Szlachetko hypothesized a close relationship of Prescottiinae to Spiranthinae.

González-Tamayo (1996) discussed the inappropriate placement of many non-resupinate taxa under the genus *Cranichis*. He suggested the inclusion of *Pterichis*, *Nothostele*, and *Fuertesiella* in the Prescottiinae rather than in Cranichidinae based on the adnation of petals to the dorsal sepal.

More recently, using cladistic methods in a morphology-based analyses of Cranichideae and Prescottiinae, Vargas (1997) recovered a monophyletic Prescottiinae, supporting Dressler's (1990; 1993) and Szlachetko's (1995) circumscription of the subtribe, but its sister relationship to the Spiranthinae was only weakly supported. The following three synapomorphies support the monophyly of the Prescottiinae: non-resupinate flowers, absence of a galea, and a glabrous perianth. These characters, however, are not uniquely derived synapomorphies for the subtribe, since they have evolved independently in other closely related groups. In addition, the African genus *Manniella* and the Neotropical Prescottiinae were found to be sister to each other on the basis of having a labellum free from the column, despite their distinctive distributions.

In contrast, molecular systematic studies of the nuclear ribosomal DNA internal transcribed spacer (ITS) region and three chloroplast DNA regions of taxa in the Cranichideae (Salazar et al., 2003) have recovered a paraphyletic group of Prescottioids divided into two lineages, *Prescottia* and a monophyletic group comprising the remaining sampled genera of the subtribe (*Aa*, *Gomphichis*, *Porphyrostachys*, and *Stenoptera*).

In 2003, Chase et al. proposed a phylogenetic classification of the Orchidaceae in which subtribe Prescottiinae did not receive taxonomic recognition and was instead merged into subtribe Cranichidinae *sensu* Dressler (1981). This classification has been adopted in the series *Genera Orchidacearum* that provides the most up-to-date information about orchids at the generic level (Pridgeon et al., 1999, 2001, 2003).

MORPHOLOGY

Habit. Plants of the Prescottiinae *s.l.* (*Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, *Pseudocranichis*, and *Stenoptera*) are primarily terrestrial herbs or facultative epiphytic herbs. They are quite diverse in height. Some (e.g., *Myrosmodes*) are no taller than 5-10 cm, a few (e.g., *Aa*) are small plants up to 20 cm, many (e.g., *Altensteinia*, *Stenoptera*, and *Porphyrostachys*) are medium sized plants reaching 50 cm; whereas others are nearly 2 m tall (e.g., a few *Gomphichis* species).

Habitat. Most of these orchids are confined to the middle and upper altitudes of Neotropical mountains, with the exception of *Prescottia* which flourishes in the lowlands. Plants of the subtribe inhabit the extreme points of elevation of the Neotropics since they can be found growing near sea level (e.g., *Prescottia plantaginea*) or reaching the highest altitude attained by any orchid, at 4900 m in the Andes of Bolivia (e.g., *Myrosmodes chiogena*). Species of the genus *Prescottia* are chiefly adapted to the warm, rainy, and humid conditions of tropical rainforests, although a very few species have been reported growing at high elevations. In contrast, those members of the subtribe growing at high elevations are exposed to extreme climatic (i.e., low temperature, high humidity, high insolation, and strong wind) and physical conditions (e.g., acidic soils, low nutrients, and reduced soil layers). They withstand extreme humidity and temperature fluctuations in the same day, especially those found in the *tepuis* and *páramos*. It is likely that these plants as a result may have evolved specific adaptations to cope with these harsh environments.

These orchids may grow in primary forests and have also diversified in montane cloud forests, páramos, puna, and jalca dominated by grassy, boggy and marshy areas, see Huber and Riina (1997),. They are also found in lowland tropical and subtropical rain forests (mainly species of *Prescottia*). Some species also occur in secondary zones including landslides and roadsides, and rocky places near the summit of mountains.

Roots. The roots of Prescottiinae are fasciculate, fusiform, elongate, extremely thick and fleshy, and pale-brown in color. All roots possess an indument of persistent root hairs and are usually described as pubescent, pilose, or villose.

Rhizome. The rhizome is very short and located below or on the substrate surface. The first internodes are horizontal and thickened. The terminal and lateral inflorescences of the Prescottiinae arise from the rhizome.

Leaves. The foliage leaves of Prescottiinae are green, darker and glossier on the adaxial surface than the abaxial surface, spirally arranged, and sheathing at their base. They are either basal or cauline. The basal leaves usually form a rosette, and are soft, herbacaeous, and glabrous. The leaves are exceedingly variable in length. Some species have linear leaves over 30 cm long, which are sessile or pseudopetiolate (*Altensteinia*, *Stenoptera*, and *Gomphichis*); others are elliptic and mainly with distinctive short or long petioles (*Prescottia* and *Pseudocranichis*); and a few are lanceolate, small, about 3 cm long, and pseudopetiolate or sessile (*Myrosmodes*).

In some genera, such as *Aa*, *Myrosmodes*, and *Porphyrostachys*, the leaves are absent or withered at flowering, whereas in others (e.g., *Altensteinia*) flowering starts only after the full development of the leaves.

Inflorescence. The inflorescence is terminal or lateral, long- or short-pedunculate, and arranged in a spike with sessile axillary flowers. The inflorescence can be densely many-flowered or laxly few-flowered, short or long.

Peduncle. The peduncle is simple, erect or slender (*Pseudocranichis*), and densely or sparsely covered by foliaceous sheaths. The majority of genera of Prescottiinae are completely glabrous. However, in *Stenoptera*, *Altensteinia*, and *Gomphichis* the portion just below the inflorescence is glandular-pubescent, pubescent, villose, or hirsute and covered by small sheaths.

Sheaths. These are leaf-like structures that surround the peduncle. The basal portion of these structures is mostly tubular in shape and tightly or loosely clasp the peduncle. The leaf sheaths are usually green, but in some genera such as *Aa* and *Myrosmodes* they are transparent. The sheaths are ovate or linear in shape and apiculate or acute at the apex. The basal ones are almost similar in shape and length to the rosette leaves but they become smaller and narrower upwards. In some genera, the laminar portion may bear a small amount of indumentum.

Flowers. The flowers are small or medium in size, between 1-5 cm long; some are slightly colored and whitish (*Aa*, *Pseudocranichis*, *Gomphichis* and *Stenoptera*), yellowish-brownish (*Myrosmodes*), or greenish (*Altensteinia*), while others are colorful and red (*Porphyrostachys*), yellow (*Gomphichis*) or green (*Prescottia*). They are hermaphroditic, and protandrous in *Prescottia*, andromonoecious in *Myrosmodes*; non-resupinate; spirally arranged and subtended by a bract. For the most part flower opening starts from the base to the apex (acropetal) with the exception of *Myrosmodes* which is basipetal.

The *floral bracts* are ovate or lanceolate, and sharply acuminate or acute. They clasp the base of the ovary, are shorter or longer than the flowers, suberect or reflexed in the middle, usually ciliate, glandular-pubescent, pubescent, or rarely glabrous. The bracts are green in most genera, but are hyaline and diaphanous in *Aa*, or scarious in *Myrosmodes*.

The *sepals* are commonly free or basally connate and form a short cup (*Prescottia*) or an elongated tube (*Stenoptera*). They are glabrous to variously glandular-pubescent on the abaxial surface only. The sepals are adpressed (*Gomphichis*), spreading (*Altensteinia*) or reflexed (*Aa* and *Prescottia*).

The *petals* are variable in shape, but are usually ovate or elliptic and taper to both ends. They are free, sometimes basally adnate to the labellum base, or connate to form a tube as in *Stenoptera*. Some species bear glabrous petals but others sometimes scattered trichomes on the abaxial surface only. The margins are often with ciliate or fringed. In general, the petals are spreading (*Altensteinia*), curved (*Prescottia*), reflexed (*Aa*) or circinnate (*Porphyrostachys*).

The *labellum* (*lip*) is highly modified, simple, or three-lobed. The apical lobe is mostly unilobolate or bilobed (*Pseudocranichis*). Some genera bear 2-3 calli on the upper surface (*Stenoptera* and *Pseudocranichis*) or on both the upper and lower surfaces (*Aa*, *Myrosmodes* and *Altensteinia*). In some genera such as *Pseudocranichis*, the upper portion of the labellum is adorned with well marked veins covered by short trichomes. The outer surface of the labellum is smooth in most genera, but papillose in *Gomphichis*. The margin is flat, rarely undulate (Stenoptera), usually entire, rarely fimbriate (*Altensteinia*), eciliate (*Porphyrostachys*), or variously ciliate (*Aa*, *Gomphichis*) with either simple or moniliform hairs (*Myrosmodes*). The labellum shape is also diverse being hood-shaped (*Prescottia*), snail-shaped (*Porphyrostachys*), tubular (*Myrosmodes*), or calceolate (*Aa*). All species of the Prescottiinae *s.s.* have nectariferous glands at the base of the labellum, and thus offer nectar as reward to pollinators. In addition to producing nectar, some species emit fragrances; some of these can be sweet and spicy (*P. plantaginea*) or musky and unpleasant (*Myrosmodes*, *P. densiflora*).

The *column (gynostemium)* is blunt, erect, slightly curved or sigmoid, short or elongate. The ventral surface of the column is glabrous, pubescent or pilose, and the dorsal surface is mostly puberulent or occasionally pubescent. The stigma is on the ventral surface and may be elongated or reduced. The rostellum is absent in the majority of genera but it is laminar and thin in *Prescottia*. The hamulus, a hook like structure developed from the apex of the rostellum (Dressler, 1993), is absent in all genera.

The *pollina* are four (two-bipartite), club-shaped or linear, soft, without caudicles except in *Porphyrostachys*, and yellow in color. They are adnate to a terminal, small, brown viscidium, which is globular or elongated, and very sticky. The *pollen* grains are arranged in tetrads and have a reticulate exine.

The *anther* is oblong-ovate, erect, opening towards the center of the flower or laterally in *Prescottia*, and two-locular. Each anther locule further subdivides into two longitudinal partitions which are evident in all Prescottioid genera. The anther is parallel to the axis of the column, firmly or slightly attached to a short, thick filament; and, the anther base is at or near the stigma base (*Gomphichis*, *Myrosmodes*), or may be below the stigma base (*Aa*, *Altensteinia*, *Porphyrostachys*, *Prescottia*, and *Pseudocranichis*).

Ovary. The ovary is unilocular, usually ovoid, and has three longitudinal ridges externally. The single locule contains numerous small ovules and the placentation is parietal. The outer surface of the ovary ranges from densely pubescent or villose to glabrous or nearly so.

Fruits. The fruits are capsules, suberect, and accompanied by the persistent remnants of the floral segments. They are usually glandular-pubescent to pubescent, glabrous or glabrate, unilocular, and with prominent ridges. Dehiscence occurs while the fruits are still attached to the rachis of the infrutescence. The three valves of the fruit are widely spreading which allows the dry seeds to be easily released and wind-dispersed. Young fruits are light green, whereas mature fruits are medium to dark brown.

Seeds. The seeds are very small, and dust-like in appearance. They are usually fusiform, golden brown, range from 0.1-1.0 x 0.1-0.3 mm, are approximately five to eight cells wide, and are covered by a thin-ornamented seed coat that surrounds a minute embryo.

ANATOMY

Root. All prescottioid genera have stout roots that are circular in transverse section. The roots are surrounded by a velamen, a spongy outer layer of cells (no longer alive), of the *Spiranthes* type (Porembski & Barthlott, 1988). In *Altensteinia* and *Prescottia*, the velamen consists of three-layers of slightly thickened cells without differentiation into an epi- or endovelamen; the cells show fine helical thickenings and unthickened wall portions containing small pores. Immediately below the velamen is the epidermis which consists of uniseriate rectangular cells with lignified walls, but without tilosomes (Pridgeon, 1987), followed by the cortex made of living parenchyma cells bordered internally by a uniseriate endodermis. The endodermis in turn surrounds the vascular cylinder which is occupied externally by the pericycle and is followed by conductive tissue and a central portion of pith that contains thin-walled parenchyma cells (Arditti, 1992). Starch cells are absent, in the cortical cells of Prescottiinae, but abundant spiranthosomes (specialized amyloplasts) are present (Stern et al., 1993a). Fungal hyphae and pelotons are abundant in the cortical cells as well.

Peduncle. According to the studies of Stern et al. (1993b) the sampled species of *Altensteinia* and *Prescottia* have no trichomes on their peduncles. The stomata are located superficially and subtended by small substomatal chambers. The cuticle is thin; the epidermal cells are square to rectangular, elliptical to ovate, spherical to domed; the outer epidermal cell walls are usually thicker than the other walls; and the cortex cells are rounded to polygonal, thin-walled, parenchymatous with chloroplasts, but thick-walled in *Prescottia stachyodes*. In this last species small intercellular spaces as well as spiranthosomes are present. Cortical parenchyma cells are poorly developed with ground tissue surrounding the vascular elements; a true endodermis (a layer of tangentially flattened cells with casparian strips) separates the cortex from the internal ground tissue. Ground tissue cells bordering conductive elements are parenchymatous, thin-walled, and rounded to polygonal without starch but with intercellular spaces present. Vascular bundles are collateral with xylem adaxial and phloem abaxial and schlerenchyma and stegmata absent. The vascular bundles are variable in number and generally in two series, especially in *P. stachyodes*; the outer bundles are arranged in a discrete ring while the inner bundles are scattered. Spiranthosomes occur in thick-walled ground tissue cells of *P. stachyodes.*

Leaf surface. Trichomes are absent on both leaf surfaces. In the abaxial and adaxial surfaces, the epidermal cells are polygonal, isodiametric with straight anticlinal walls. The cuticle is thin and smooth with the outer tangential walls thicker than the other walls. The adaxial epidermal cells are larger than the abaxial ones which appear radial in *Prescottia stachyodes*. The stomata are superficial, abaxial, and predominantly anisocytic or disocytic, rarely tetracytic. Among the spiranthoid orchids, *Altensteinia* shows the largest mean guard cells and moderately large to large substomatal chambers (Stern et al., 1993b).

Stegmata. Longitudinal series of silica cells adjacent to vascular or nonvascular fibers (stegmata) have not been found in the roots or the leaves of *P. plantaginea* or in other representatives of the Cranichidinae and Spiranthinae (Møller & Rasmussen, 1984).

Column. A common finding of anatomical studies that included the Prescottiinae *s.s.* and *s.l.* was that the hamulus (pollinium stalk developed from the apex of the rostellum) is absent in the Prescottiinae, unlike its relatives of the subtribe Cranichidinae (Rasmussen, 1982; Szlachetko & Rutkowski, 2000). These independent results confirm that the lack of a hamulus is one of the diagnostic features of Prescottiinae as indicated by Dressler's original circumscription of the subtribe (1990). Salazar et al. (2003), however, stated that *Gomphichis* possesses a hamulus suggesting the possibility of its presence in other members of the subtribe. These contradictory observations indicate that a more careful scrutiny of this character is required (see Chapter 2 and 3 of this work).

In 1988, Kurzweil provided detailed description of the floral development of *Prescottia plantaginea* with special emphasis on the early differentiation of the column. This study found a delayed development of the inner lateral staminodes in this species, which is a distinctive feature of the neottioid orchids *sensu* Rasmussen (1985).

Anther endothecium. An examination of the endothecial structure of the anther wall (the innermost layers) revealed that two types (IIIa and IVc) are present in the sampled Prescottiinae (except *Pseudocranichis* not included) (Freudenstein, 1991). Most Prescottioid genera (*Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, and *Porphyrostachys*) possess indistinct individual thickenings, which are closely spaced, thick and short (type IVc). In contrast, *Prescottia* shows closed thickenings with long and very distinct anticlinal bars (type IIIa). The heterogeneity of the distribution of endothecial thickenings within Prescottiinae does not support the monophyly of the subtribe.

PALYNOLOGY

Pollen and pollinaria. Pollen tetrads with net-like exines were documented by Schill and Pfeiffer (1977) in *Altensteinia*, *Gomphichis*, and *Prescottia.* Burns-Balogh (1991) published a series of micrographs of orchid pollen and pollinaria that were generated as part of a large-scale phylogenetic analysis of the Orchidaceae (Burns-Balogh & Funk, 1986). An examination of these scanning electron micrographs show that the sampled members of the Prescottiinae (*Altensteinia*, *Gomphichis*, *Porphyrostachys* [as *Stenoptera*], and *Prescottia*) have pollen grains arranged in tetrads with reticulate exine, and round pollinia in cross section (Burns-Balogh & Funk, 1986; Burns-Balogh, 1991). Non-sectile pollinia (non-differentiated caudicles) and uniform massulae were reported by Freudenstein and Rasmussen (1997) in *Prescottia stachyodes* and *Porphyrostachys pilifera* (as *Stenoptera pilifera*). Similar characteristics were found in the Cranichidinae and Spiranthinae.

A detailed study of the structure and development of the pollen and anther structure of *Aa achalensis* indicates a proximalipolar aperture of the pollen grains and the reduction of the anther wall to form 4 layers. This type of aperture has been previously described in bryophytes and pteridophytes only and therefore it may represent an unusual feature of the genus.

EMBRYOLOGY

Little information is available about the embryology of the Prescottiinae. The only specific study was published by Coccuci (1964), in which the major embryological events of *Aa achalensis*, a species from Argentina, were described. In this species, the development of the ovules, which are anatropous, occur just before pollination. The inner integument differentiates first into 2-layers of cells, followed by the outer integument that also contains 2-layers. The mycropile originates in the inner integument and it is wider when fertilization takes place and becomes narrower after it. During megasporogenesis, the archesporial cell elongates into the megaspore mother cell. In the first meiotic division, the micropylar dyad cell rarely divides and the chalazal cell completes the second division. In total, three rows of cells are formed in which one is the chalazal megaspore and the others are degenerating cells. During mitotic division, the nuclear epidermis of the megaspore disintegrates leaving the embryo sac in direct contact with the inner integument. The 2-nucleate embryo sac gives rise to an 8-nucleate sac with the antipodal nuclei reduced. The mature embryo is composed of two eggs and two synergids. The synergids show a conspicuous filiform apparatus in the upper end, while the remaining part is occupied by a vacuole. Starch grains are absent in the mature embryo sac. After the germination of the pollen grains on the stigma, the spermiogenic nucleus partitions into two male gametes in the pollen tube. The latter in turn reaches the embryo sac allowing contact of the sperms into one synergid. The male gametes enlarge and break the synergid membrane releasing the sperm. These enter the egg and the central cell. One sperm and the egg fuse apparently after post-mitosis, while the other sperm and the secondary nucleous fuses only after the embryo reaches the three or four-celled stage. The zygote undergoes several divisions forming an undifferentiated mass of cells. The embryo does not develop suspensors in contrast to other orchids. This pattern of development of the embryo is known as the Aster type in the system of Swamy (1949).

More general information about the embryology of orchids was summarized by Clements (1999). In this work 15 major embryological developmental patterns (including the development of the embryo and the major accessory structures) were found within Orchidaceae. According to this system, the Spiranthinae embryological type is present in *Prescottia* and other spiranthoid genera. In the Spiranthinae type, all cells of the embryo are similar in appearance and contain storage bodies. The external surface of the contact zone of the proembryo is autoflorescent, whereas the cells of the inner and outer integuments have numerous vacuoles and fewer storage bodies. In this embryological type, as in the entire family, endosperm is lacking.

SEED MORPHOLOGY

Seed coats. Based on the publications of Beer (1863) and other workers (Barthlott, 1976; Barthlott & Ziegler, 1981), Dressler (1993), commented that the seeds of Prescottiinae belong to the *Goodyera* type and are thus characterized by isodiametric and slightly elongated cells of the same size throughout, and prominent intercellular spaces particularly at the cell corners. More recent work on seed morphology in spiranthoid orchids by Molvray and Kores (1995) has found that representatives of the Prescottiinae (*Myrosmodes*, *Stenoptera* and *Pseudocranichis* were not evaluated) have seed coats of the *Spiranthes* type, with high anticlinal walls that roll outward, elongate medial cells between 20-60 in number, intercellular gaps and beading.

CYTOGENETICS

Chromosomes. A preliminary literature search reveals no reports of chromosome counts in Prescottiinae. However, in members of the subtribe Cranichidinae, a haploid chromosome number of 23 has been reported (Martínez, 1985), and within other orchidoid taxa, variable chromosome numbers between n=15 to n=24 have been documented. Additionally, numerous cases of chromosome number variation within the same taxa have been found in other terrestrial orchids such as *Spiranthes*.

1.2. SYNOPSIS OF SUBTRIBE PRESCOTTIINAE

DESCRIPTION OF THE SUBTRIBE

PRESCOTTIINAE Dressler

Prescottiinae Dressler, Lindleyana 5(2): 115. 1990; Szlachetko, Fragm. Flor. Geobot. Supp. 3: 42. 1995.

Type Genus: *Prescottia* Lindl. (Fig. 1.1).

Description: Small to medium-sized terrestrial herbs. *Roots* clustered, fleshy with velamen of the *Spiranthes* type. *Rhizome* short. *Leaves* few to many, basal or spiral, clustered, subpetiolate, rarely petiolate, non-articulate, soft-herbaceous, glabrous. *Inflorescence* terminal or lateral. *Flowers* small to medium-sized, non-resupinate; labellum concave, often with fimbriate margin and lobes; column blunt, short, erect or bent; hamulus lacking; anther dorsal, erect, subequal to rostellum; pollinia 2, bipartite, soft; viscidium small, terminal; anther oblong to ovate with thick connective; ovary sessile, ovoid to ellipsoid; stigma entire with lateral lobes rudimentary. *Fruit* an ovoid capsule with 3 prominent ridges, glabrous or pubescent. *Pollen* reticulate, heterobrochate. *Seeds* numerous, very small, dust-like, with high anticlinal walls, intercellular gaps, and rudimentary embryo (Fig. 1.2).

Genera: *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottiia*, *Stenoptera* and (possibly) *Pseudocranichis*.

Number of species: About 100.

Distribution: A Neotropical and subtropical subtribe ranging from southern Florida throughout Mexico, Central America, and South America into northern Chile, northern Argentina, Paraguay and Uruguay (Fig. 1.3).

Ecology: The Prescottiinae are mostly found above 1200 m in specialized high elevation ecosystems (cloud forests, páramos, jalca, puna, and tepuis), with the exception of species of the genus *Prescottia* that inhabit subtropical and tropical forests. Flowering and fruiting mainly occurs throughout the year.

DESCRIPTIONS OF THE GENERA OF PRESCOTTIINAE *s.l.*

AA REICHB. F.

Xenia Orchid. 1: 18. 1854.

Type: *Aa paleacea* (Kunth) Rchb. f., Xenia Orchid. 1: 18. 1854.

(Basyonym: *Ophrys paleacea* Kunth, Nov. Gen. Sp. Pl. 1: 334. 1816.)

Etymology: The exact derivation of the name is unknown. It has been suggested that is an artificially contrived name by Reichenbach so as to always be at the beginning of any botanical list, or from the first and last letters of *Altensteinia*, the genus from which *Aa* was segregated (Schultes & Pease, 1963).

Distinguishing features: Characterized by basal leaves, absent or withering at anthesis; hyaline, tubular sheaths completely covering the peduncle; lateral inflorescence; small glabrous flowers, white in color; papery bracts shorter or longer than the flowers; calceolate labellum, with a fimbriate, involute margin and two small calli at the base; and, a short, glabrous column. (Fig. 1.4).

Distribution: The genus ranges in a continuum from Venezuela to northern Chile and Argentina with disjunct populations of only one species in Costa Rica (Barringer, 1984). It has not been reported from Panama perhaps due to the absence of suitable habitats (Fig. 1.5.A).

Number of Species: 25.

Ecology: Species of the genus are found on the summits of mountains, mainly above tree line in the páramo, puna and jalca ecosystems between 2700 to 4600 m of elevation. A few species have been documented below 2700 m in Argentina and Ecuador. Flowering specimens have been collected throughout the year, especially in the months of July and January. Fruiting collections have been recorded more commonly in the months of April, July and December (Fig 1.5.B).

Common names and uses: Some species of *Aa* are referred to as "cacho de venado", "curiquingue" in Ecuador; or, "sara-sara", "llantencillo", "pampa-liripa" in Peru. The roots are used medicinally to help overcome difficulties in giving birth in some Andean communities of Ecuador.

Notes: The first species of the genus *Aa* was initially described as *Ophrys paleacea* from type material collected by Humboldt and Bonpland in the early 1800's near Quito, Ecuador during their trip to tropical America. This species was later included in the genus *Altensteinia* (Kunth, 1822) from which *Aa* was separated by Reichenbach in 1854.

ALTENSTEINIA KUNTH

Nov. Gen. Sp. Pl. 1: 332. 1816.

Lectotype: *Altensteinia fimbriata* (Kunth) Rchb. f., Xenia Orchid. 1: 18. 1854.

Etymology: Dedicated to Baron Karl von Stein zum Altenstein, a Prussian minister interested in Brazilian botany (Schultes & Pease, 1963).

Distinguishing features: Characterized by cauline leaves, completely developed before anthesis; terminal inflorescence; petals and labellum free from the column; dorsal sepal free from the lateral sepals; column erect, pubescent with a truncate rostellum (Fig. 1.6).

Number of species: 9.

Distribution: *Altensteinia* occurs from Venezuela to Bolivia along the Andes (Fig. 1.7.A).

Ecology: All species are terrestrial and found in the wet montane forests at elevations of 1800-3000 meters. A few species occur in disturbed habitats such as road banks, pasture borders, and stream and river edges, where they proliferate quite successfully. Flowering occurs throughout the year but is most pronounced in May and from June to July, with fruiting known in April, September and December (Fig. 1.7.B).

One of the showiest and widespread species of the genus is *Altensteinia fimbriata*. Plants of this species appear to respond quite well in cultivation to bright light, cool temperatures, and soils with high moisture retention (Christenson, 2003).

Common names and uses: *Altensteinia fimbriata* is commonly known as “llubu-llubu” in the region of Cusco, Peru.

Notes: *Altensteinia* was originally defined in a broad sense and included some heterogeneous taxa (Kunth, 1816). Reichenbach in 1854 redefined *Altensteinia* segregating from it the currently recognized genera *Aa* and *Porphyrostachys*.

GOMPHICHIS LINDL.

Gen. and Sp. Orch. Pl. 446. 1840.

Type species: *Gomphichis goodyeroides* Lindl.

Etymology: From the greek *gomphos*= (nail, club) referring either to the glandular hairs that cover the flowers or to the club-shaped column (Schultes & Pease, 1963).

Distinguishing features: Leaves basal, pseudopetiolate; dorsal sepal free from lateral sepals; labellum strongly fleshy, parallel to and covering the column; column sigmoid, sharply bent at a right angle to the ovary, pubescent to puberulent (Fig. 1.8).

Number of species: 17.

Distribution: This genus is distributed from Costa Rica to Bolivia along the Andean region and the Guayana Highlands in Venezuela, but expected in Brazil and Guyana (Fig. 1.9.A).

Ecology: Terrestrial plants rarely epiphytic in wet cloud forest, elfin forest, subpáramo and páramos at elevations from 1000 to 4800 meters. Flowering and fruiting occur throughout the year, but most frequently between May to July and December (Fig. 1.9.B).

Common names and uses: *Gomphichis goodyeroides* is known as “inquil” in Peru.

Notes: Since the recognition of *Gomphichis* by Lindley in 1840, the circumscription of the genus has been problematic due to its morphological similarity to *Stenoptera*.

MYROSMODES RCHB. F.

Xenia Orchid. 1: 19. 1854.

Type species: *Myrosmodes nubigenum* Rchb. f.

Etymology: From the greek *myron* (perfume) and *osmodes* (fragrant), alluding to the strong fragrance of the flowers (Schultes & Pease, 1963).

Distinguishing features: Plants very small; leaves absent or withering at anthesis; peduncle with imbricate, infundibuliform, scarious sheaths; lateral inflorescence; sepals connate at the base to form an elongate tube; dorsal sepal and petals adnate to the column; labellum erect, tubular or flared with fimbriolate margin, never involute, with two spherical calli at the base; column erect , glabrous, with a large stigma; rostellum truncate (Fig. 1.10).

Number of species: 12.

Distribution: The genus is distributed from Venezuela to northern Argentina (Fig.1.11.A).

Ecology: Species of *Myrosmodes* grow at the highest elevations between 3500 to 4800 m in the boggy zones of the páramo, puna, and jalca ecosystems of the Andean region. *Myrosmodes chiogena* found at 4900 m in Bolivia, reaches the highest elevation range of any orchid ("*Jordán 31*, NY"). Flowering and fruiting occur throughout the year but is most frequent in January, March, and April (Fig. 1.11.B). Studies of the reproductive biology of *M. cochleare* by Berry and Calvo (1991) indicate that this species is wasp and fly pollinated, and self-compatible but not autogamous.

Common name and uses: Species of the genus are known as "ruarlito del cerro" in Argentina and "chinankak-koriwakăk" in the surroundings of the Huascarán National Park, Peru.

Notes: After the description of *Myrosmodes* by Reichenbach in 1854, the genus was treated as a synonym of either *Altensteinia* (Reichenbach, 1878) or *Aa* (Schlechter, 1922) until Garay resurrected it in 1978. Vargas (1995) recognized two subgenera within the genus (subgenus *Myrosmodes* and subgenus *Rynchospora*) based on perianth morphology and arrangement.

PORPHYROSTACHYS RCHB. F.

Xenia Orchid. 1: 18. 1854.

Type species: *Altensteinia pilifera* Kunth, Nov. Gen. et Sp. Pl. 1: 333. 1816.

Etymology: From the greek *porphyra* (purple), and *stachys* (spike) in reference to the architecture and appearance of the dense red inflorescence.

Distinguishing features: Leaves basal, usually absent during flowering; sepals with recurved apices; lateral sepals decurrent on the ovary; petals linear circinate; labellum concave, clawed, adnate to the column foot and together with the lateral sepals, forming a tube; column erect, with a long decurrent foot (Fig. 1.12).

Number of species: 2.

Distribution: *Porphyrostachys* is restricted to Ecuador and Peru (Fig. 1.13.A).

Ecology: Species of *Porphyrostachys* are terrestrial and grow in primary or disturbed premontane cloud forests at intermediate elevations from 1200-2800 meters. Flowering and fruiting specimens have been collected throughout the year but more often in the months of April, May and July (Fig. 1.13.B).

Dressler (1993) suggested the possibility of hummingbird pollination of the reddish-flowered *Porphyrostachys pilifera*. On the other hand, the color, size and shape of the flowers of *P. parviflora* is congruent with insect pollination.

Common name and uses: *Porphyrostachys pilifera* is known as "flor de Jesucristo" in Ecuador.

Notes: Reichenbach (1854) noted several discordant taxa of Kunth's *Altensteinia* and proposed the genus *Porphyrostachys* to accommodate some of these.

PRESCOTTIA Lindl.

Exot. Fl. 2, t. 115. 1824.

Type species: *Prescottia plantaginea* Lindl.

Etymology: The generic name honors the British botanist John D. Prescott, who resided in St. Petersburg during the 1800's (Schultes & Pease, 1963).

Distinguishing features: Leaves petiolate or sessile; sepals basally connate, forming a short cup, spreading or reflexed; petals adnate to the sepaline cup; labellum attached to the column foot, clawed, basally auriculate above claw, deeply concave, galeate or cochleate, enclosing the column; column adnate to the sepaline cup (Fig. 1.14).

Species: 25.

Distribution: *Prescottia* has a widespread distribution throughout lowland tropical America including the Caribbean and South Florida (Fig. 1.15.A). It is especially diverse in Brazil.

Ecology: Species of the genus are remarkable for their broad ecological tolerance and phenotypic plasticity (Ackerman, 2000). The genus has been noted as growing in the understory of moist and wet montane forests at low to high elevations between 100 to 3800 meters. Flowering and fruiting specimens have been collected all year, but most often in February and March (Fig. 1.15.B).

Ackerman (1995) suggested autogamy as the breeding system of *Prescottia oligantha*, *P. pellucida* and *P. stachyodes* growing in Puerto Rico and the Virgin islands. A few years later, *P. stachyodes* was reported as self-pollinated and facultatively autogamous (Ackerman, 2000). Singer and Cocucci (1999) reported pollination by halictid bees for *P. densiflora*. More recently, *P. plantaginea* and *P. stachyodes* were found to be moth pollinated (Singer & Sazima, 2001).

Common names and uses: This genus is referred as "lengua de vaca" in Venezuela.

Notes: In the original publication of the genus the epithet was spelled as *Prescotia*, but subsequent works of Lindley spelled it with two t's. Ackerman (2000) commented that modern orchid taxonomists agree that the original epithet of this genus should be treated as an orthographic error and that its spelling with two t's should prevail.

Vargas (1997) based on the morphological resemblance of *Prescottia tubulosa* to species of *Porphyrostachys* (i.e., the hysteranthus habit, sessile leaves, and involute labellum which is rhomboidal in shape when spread), suggested that this species be transferred to *Porphyrostachys*. Evidence presented in chapter two of this dissertation and a recent molecular study (Salazar et al., 2003), have shown that the morphological similarities found in *Prescottia tubulosa* and *Porphyrostachys* are the result of convergent evolution, thereby supporting the placement of this species in *Prescottia*.

PSEUDOCRANICHIS (ROB. & GREENM.) GARAY

Bot. Mus. Leafl. 28(4): 347. 1982.

Type species: *Pseudocranichis thysanochila* (Rob. & Greenm.) Garay. *Cranichis thysanochila* Rob. & Greenm., Proc. Amer. Acad. Arts 32(1): 34-51. 1896.

Etymology: From the greek *pseudes* (false) and *Cranichis* (an orchid genus) alluding to the original assignment of the type species to the genus *Cranichis* (Schultes & Pease, 1963).

Distinguishing features: Leaves petiolate; dorsal sepal adnate at base to back of the column; lateral sepals connate at base, adnate to the labellum claw; petals free, with erose apex; labellum apically bilobed, the 3 callose-thickened veins of the disc with distinctly pubescent and thin margins; column with an obliquely extended base (Fig. 1.16).

Number of species: A monotypic genus.

Distribution: Restricted to Oaxaca, Mexico (Fig. 1.17.A).

Ecology: This species grows in calcareous soils at 1350 meters. Flowering specimens have been collected in October and November (based on two specimens).

Notes: This species was initially described in the genus *Cranichis* mainly because of its non-resupinate flowers. In 1982 Garay established the genus *Pseudocranichis* to accommodate *Cranichis thysanochila* and included it in subtribe Spiranthinae. Szlachetko (1995) placed *Pseudocranichis* in subtribe Prescottiinae due to the peculiar morphological features of this genus that sometimes resemble selected members of the Prescottiinae. In a more recent publication, Salazar et al. (2003) pointed out the similarities of the column and labellum of *P. thysanochyla* to the Mexican *Prescottia tubulosa*. The molecular studies presented in Chapter 2 of this work found *P. thysanochyla* sister to *Prescottia tubulosa*. This result strongly supports the transfer of *Pseudocranichis* to *Prescottia*, confirming in part Szlachetko's (1995) hypothesis of affinities.

STENOPTERA PRESL

Rel. Haenk. 1:95. 1827.

Type species: *Stenoptera peruviana* Presl

Etymology: From the Greek *stenos* (narrow) and *pteron* (wing) in reference to the narrow petals of the type species of the genus (Schultes & Pease, 1963).

Distinguishing features: Leaves basal, more or less distichous; sepals basally connate, forming a slender tube, erect, appressed, with spreading apices; petals free, linear and spreading; labellum galeate-fornicate, slightly fleshy, with membranaceous margin, long-unguiculate; column more or less arcuate; stigma large (Fig. 1.18).

Distribution: *Stenoptera* is an Andean genus distributed from Colombia to Bolivia with a few species growing in mid-elevation Brazilian forests (Fig. 1.19.A).

Number of species: 8.

Common names and uses: Some species of the genus are known as “tarckoy” in Peru.

Ecology: Species of *Stenoptera* are found in cloud forests with abundant epiphytes, open woodlands and rocky areas from 1200 to 3200 m of elevation. Flowering specimens have been gathered throughout the year, especially in the months of April, May and July. Fruiting specimens have been recorded in March, May, June, August and November (Fig. 1.19.B).

Notes: *Stenoptera* has been closely allied with *Gomphichis*, and the taxonomic distinctions between both genera have been unclear in the past. Recent molecular evidence (see chapters 2 and 5) shows *Stenoptera* as the most basal member of the Andean terrestrial orchids, distantly related to *Gomphichis.*

ARTIFICIAL KEY TO THE GENERA OF PRESCOTTIINAE *s.l.*

1. Inflorescence terminal.
  2. Petals and labellum adnate to or fused with sepaline cup.
    3. Labellum calceolate, unilobed, not constricted at apex ... *Prescottia*
    3. Labellum cochleate, bilobed, distinctly constricted at apex .... *Pseudocranichis*
  2. Petals and labellum free from sepals.
    4. Column with a long decurrent foot; ovary glabrous .... *Porphyrostachys*
    4. Column footless; ovary glandular-pubescent.
      5. Sepals basally connate into a slender tube; labellum long-clawed .... *Stenoptera*
      5. Sepals free; labellum sessile or shortly clawed 6
        6. Column erect, straight to the ovary; labellum erect, enclosing column, membranaceous .... *Altensteinia*

6. Column sigmoid, sharply bent at right angle to the ovary; labellum incumbent upon column, not enclosing column, fleshy .... *Gomphichis*

1. Inflorescence lateral.
    7. Sheaths infundibuliform, scarious not completely enclosing the peduncle; flower opening from the top to the bottom of the inflorescence; dorsal sepal and petals adnate to column; labellum tubular or flared, without involute margin .... *Myrosmodes*
    7. Sheaths spreading, hyaline-diaphanous, completely enclosing the peduncle; flower opening from the bottom to the top of the inflorescence; dorsal sepal and petals free from column; labellum calceolate, with involute margin .... *Aa*

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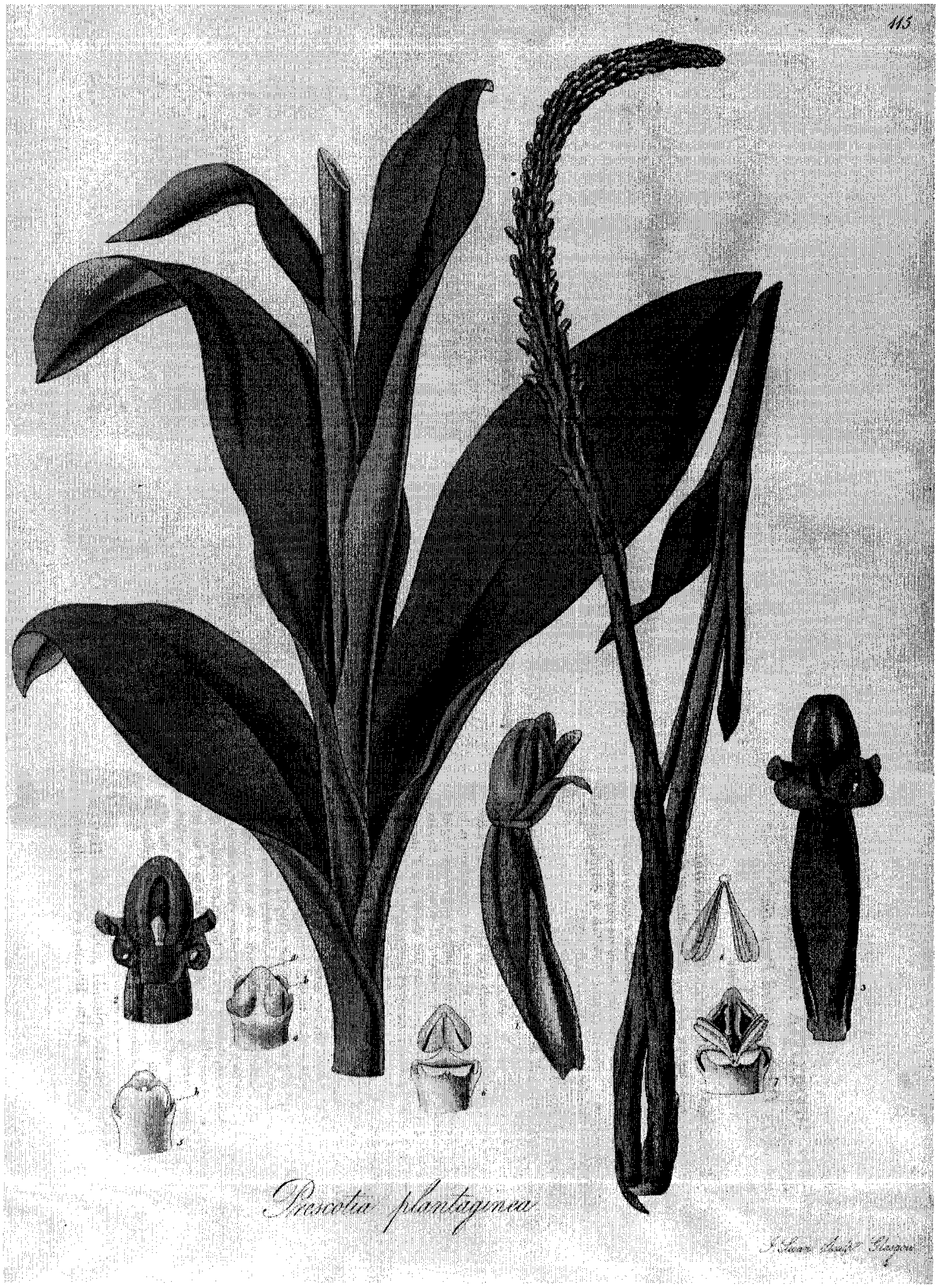

Fig. 1.1. Type genus of Prescottiinae, *Prescottia plantaginea*, Exot. Fl. 2, t. 115. 1824 (Library of the New York Botanical Garden).

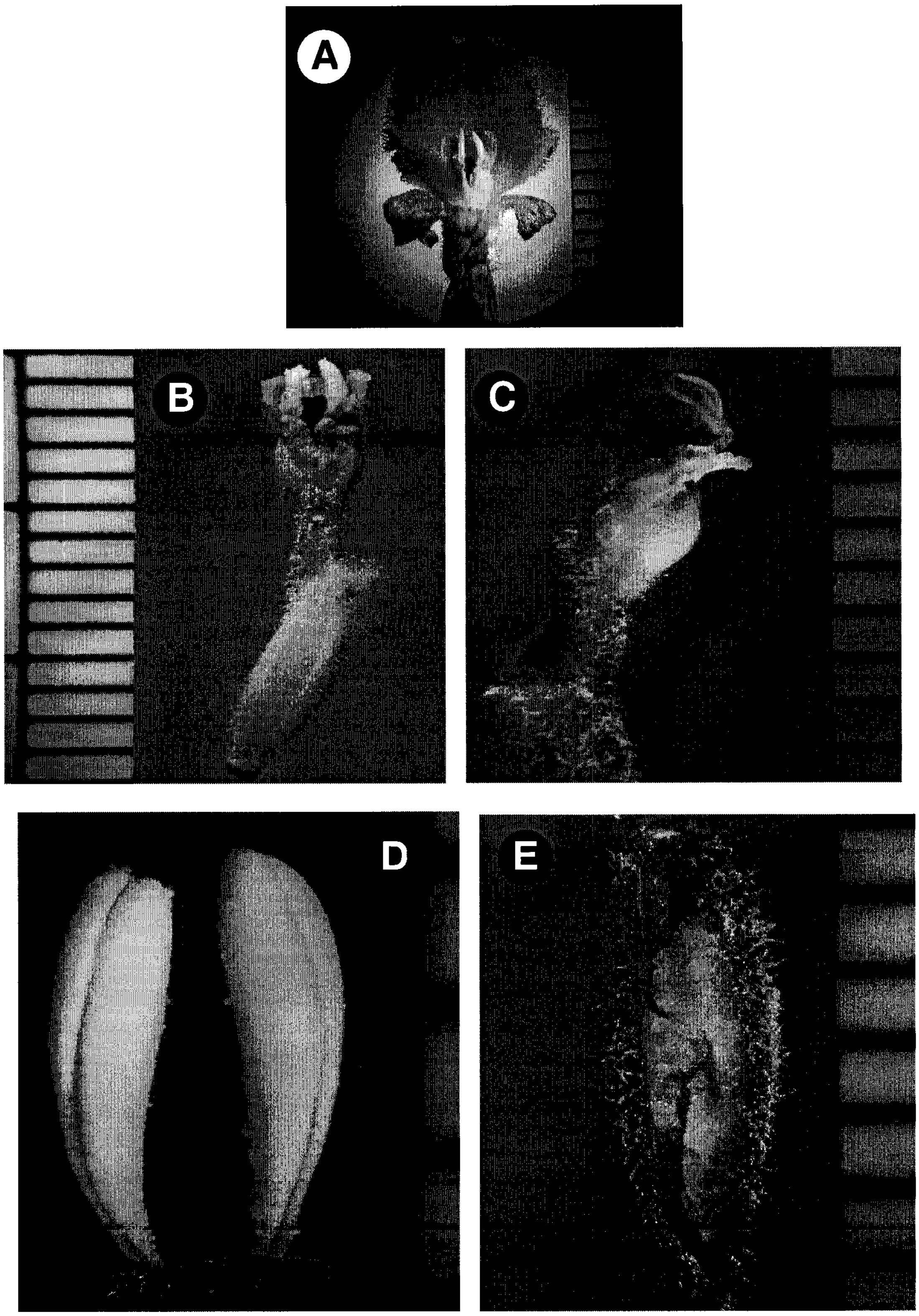

Fig. 1.2. Morphological characteristics of the Prescottiinae based on *Altensteinia fimbriata*. A, labellum. B-C, column, frontal view and lateral view. D, pollinia. E, ovary opened to show ovules.

Fig. 1.3. Generalized distribution of Prescottiinae; limits of distribution represented by red lines.

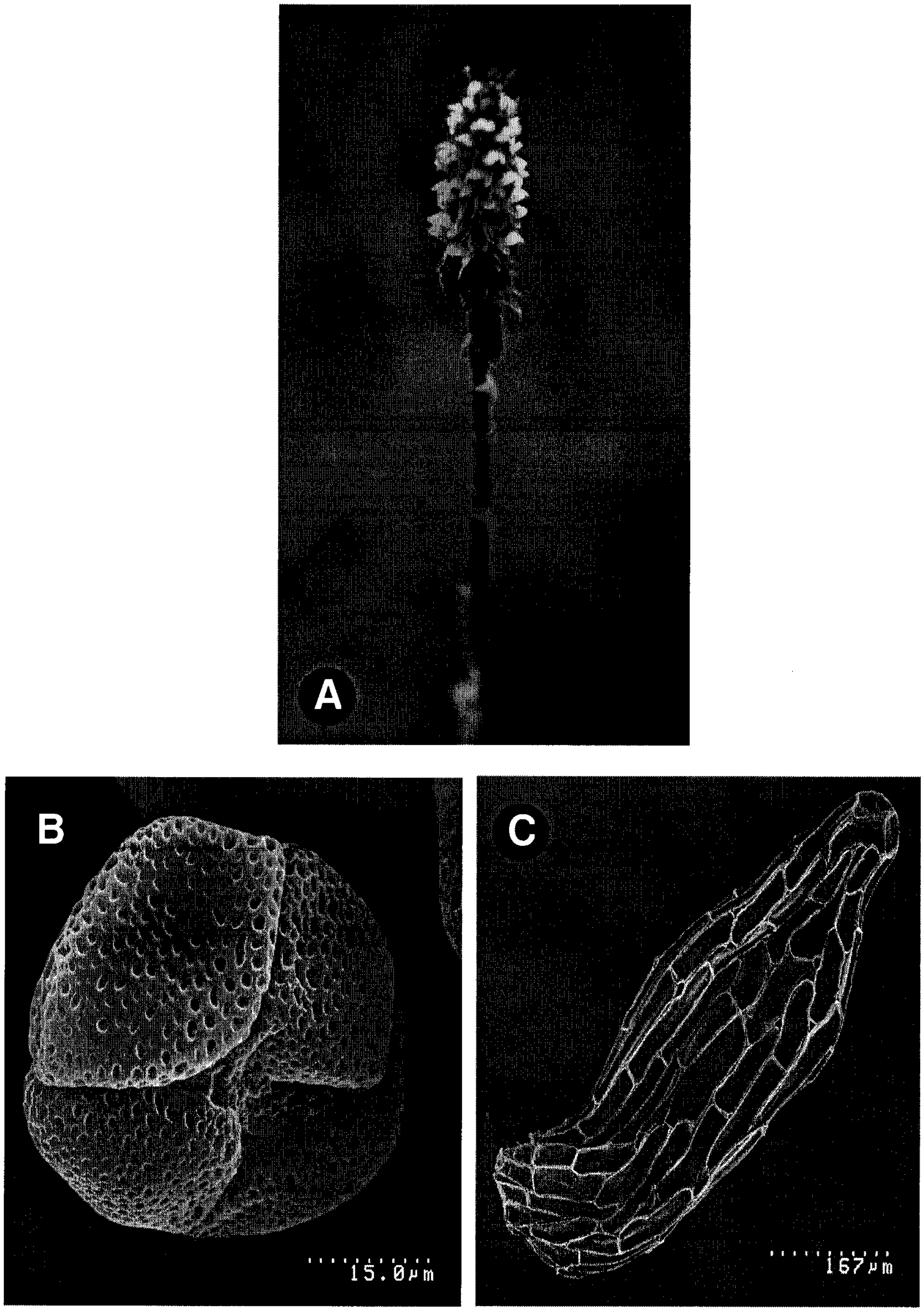

Fig. 1.4. Morphological features of *Aa* species. A, *Aa paleacea*, Cajamarca, Peru. B, *Aa maderoi*, tetrads of pollen (*Alvarez 2962*, NY). C, *Aa maderoi*, seeds (*Alvarez 2902*, NY).

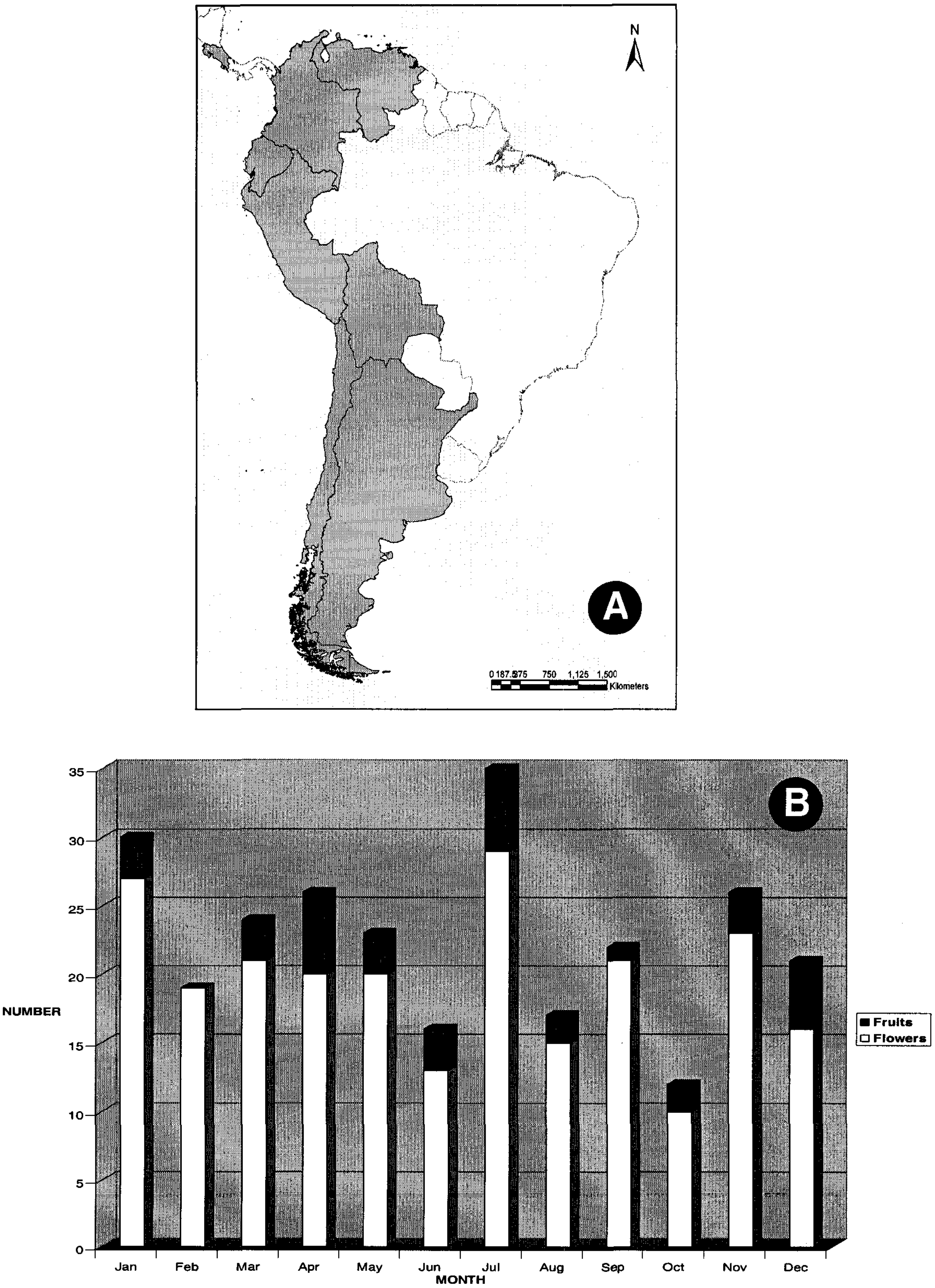

Fig. 1.5. Geography and phenology of the genus *Aa*. A, Distribution map of *Aa*. B, Flowering and fruiting of *Aa* taken from herbarium specimens.

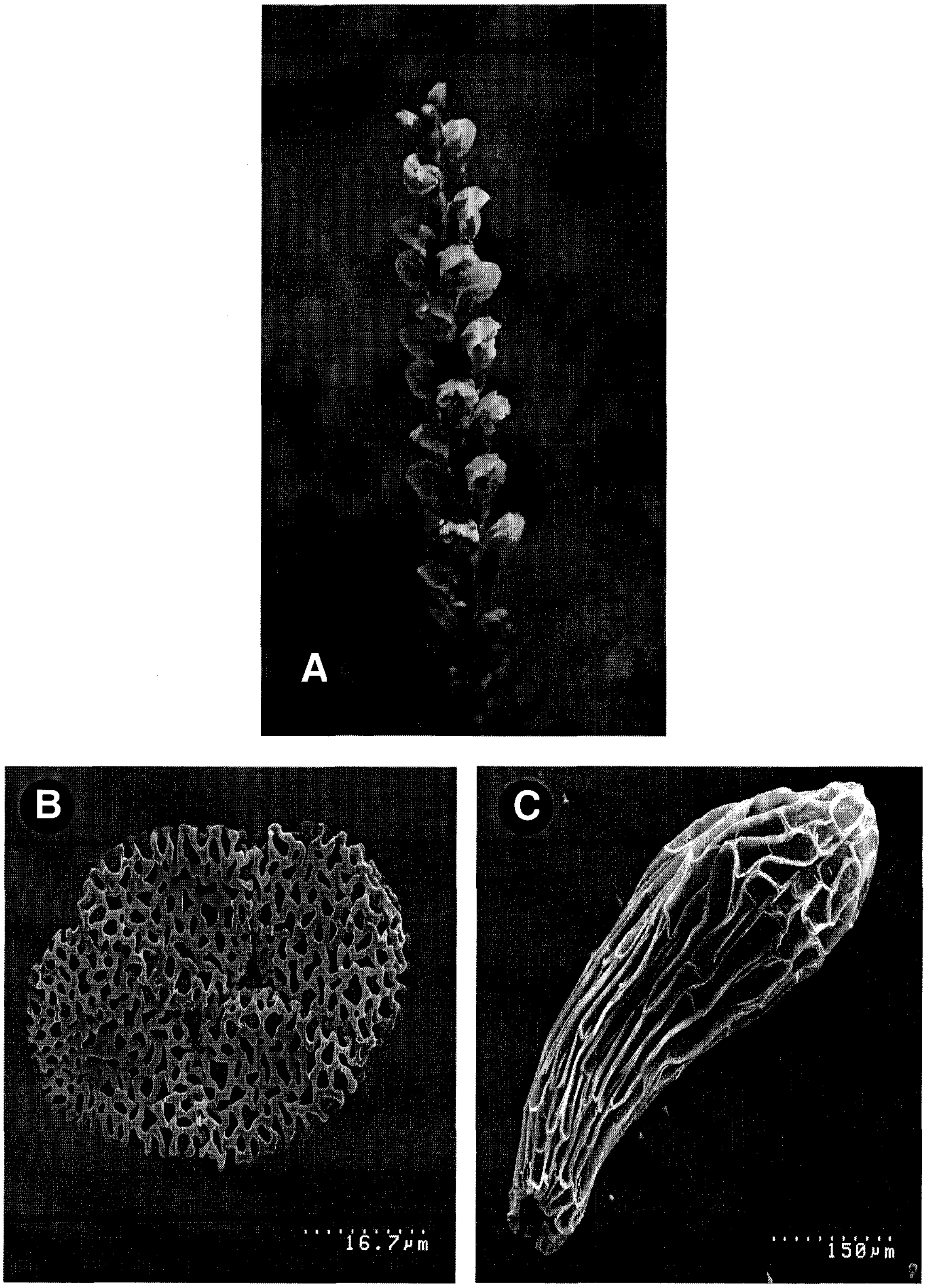

Fig 1.6. Morphological features of *Altensteinia* species. A, *A. fimbriata*, flowers, Cotopaxi, Ecuador. B, *A. fimbriata*, tetrads of pollen (*Alvarez 3016*, NY). C. *A. boliviensis*, seeds (*Alvarez 2902*, NY).

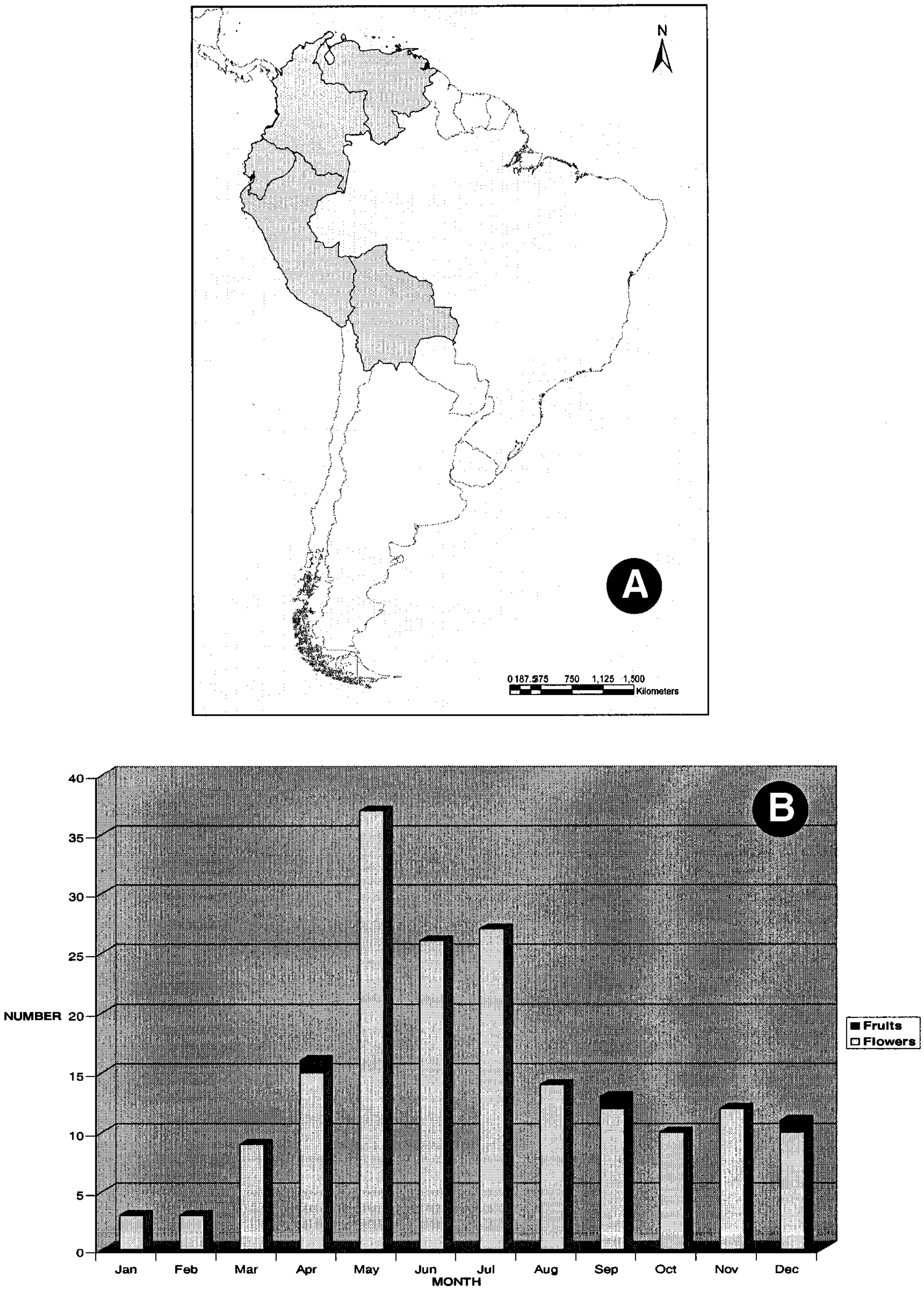

Fig. 1.7. Geography and phenology of the genus *Altensteinia*. A, Distribution map of *Altensteinia*. B, Flowering and fruiting of *Altensteinia* based on herbarium specimens.

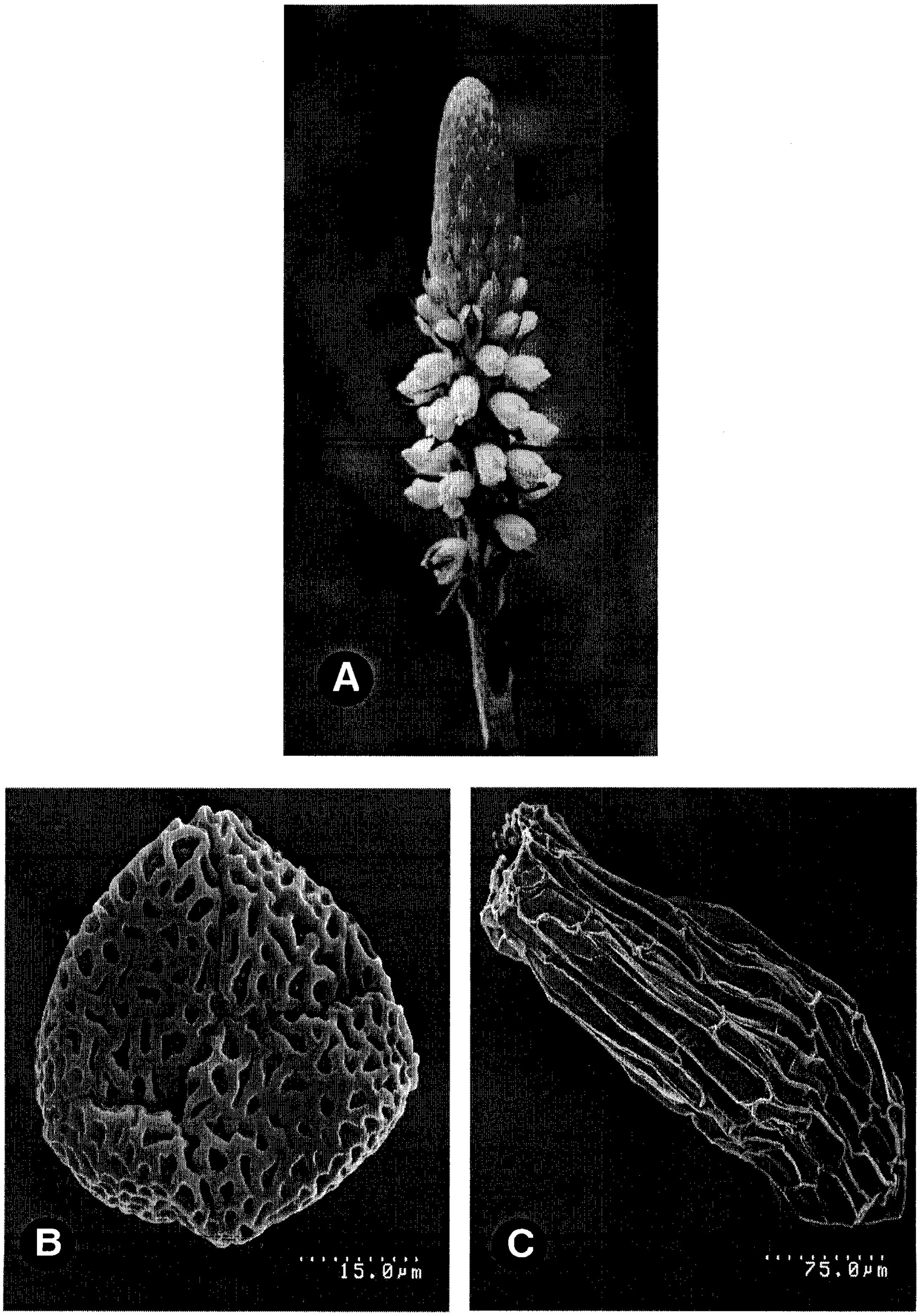

Fig. 1.8. Morphological features of *Gomphichis* species. A, *G. crassilabia*, flower, Ecuador, Carchi. B, *G. crassilabia*, tetrads of pollen (*Alvarez 2935*, NY). C, *G. bogotensis* (*Alvarez 3000*, NY).

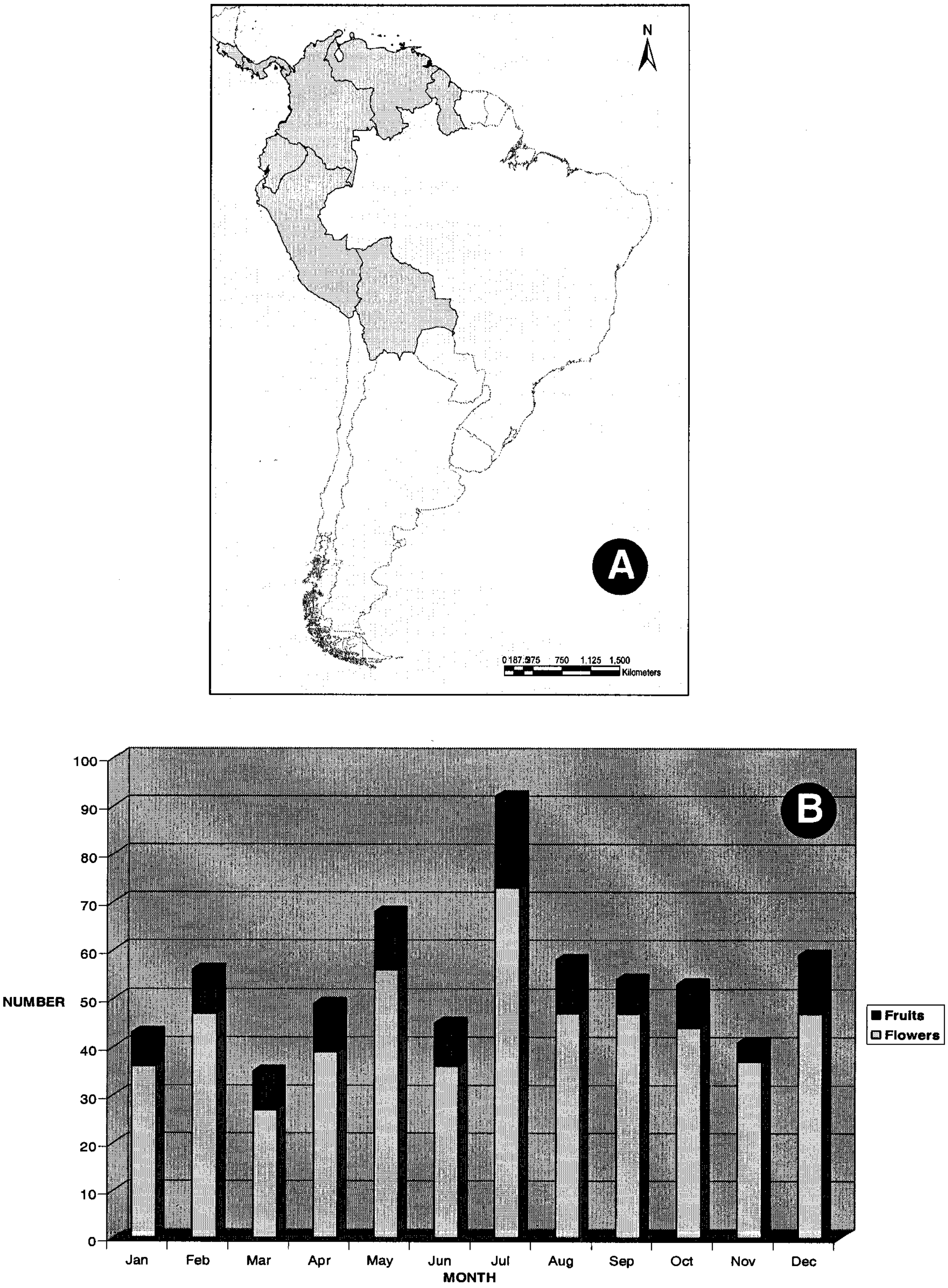

Fig 1.9. Geography and phenology of the genus *Gomphichis*. A, Distribution map of *Gomphichis*. B, Flowering and fruiting of *Gomphichis* based on herbarium specimens.

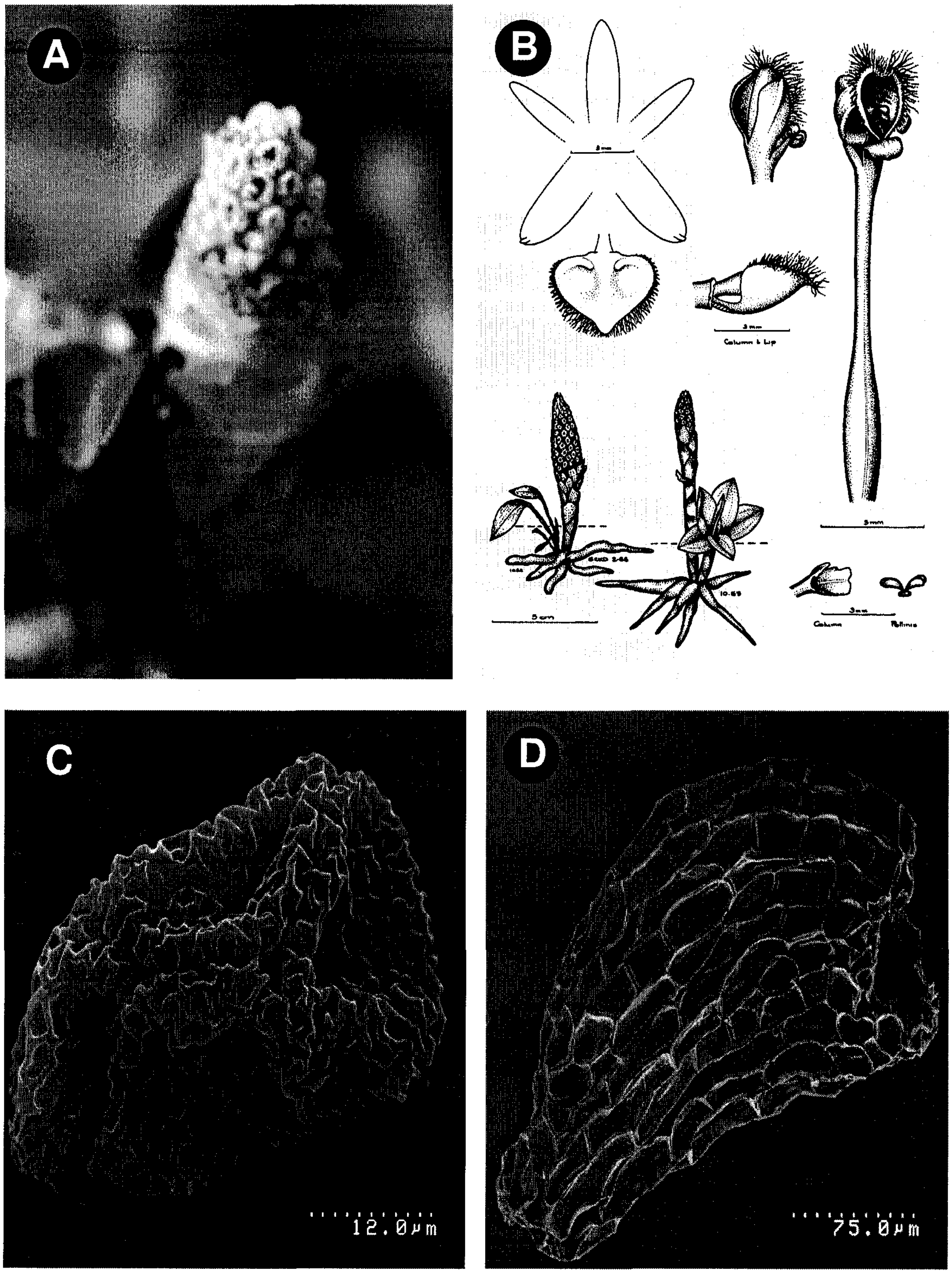

Fig. 1.10. Morphological features of *Myrosmodes* species. A, *M. nubigenum*, flowers, Cotopaxi, Ecuador. B, *M. cochleare*, reproduced from Romero-González and Carnevali Fernández-Concha (2000) with permission of the authors. C, *M. cochleare*, tetrads of pollen (*Alvarez 2955*, NY). D, *M. nubigenum*, seeds (*Alvarez 2822*, NY).

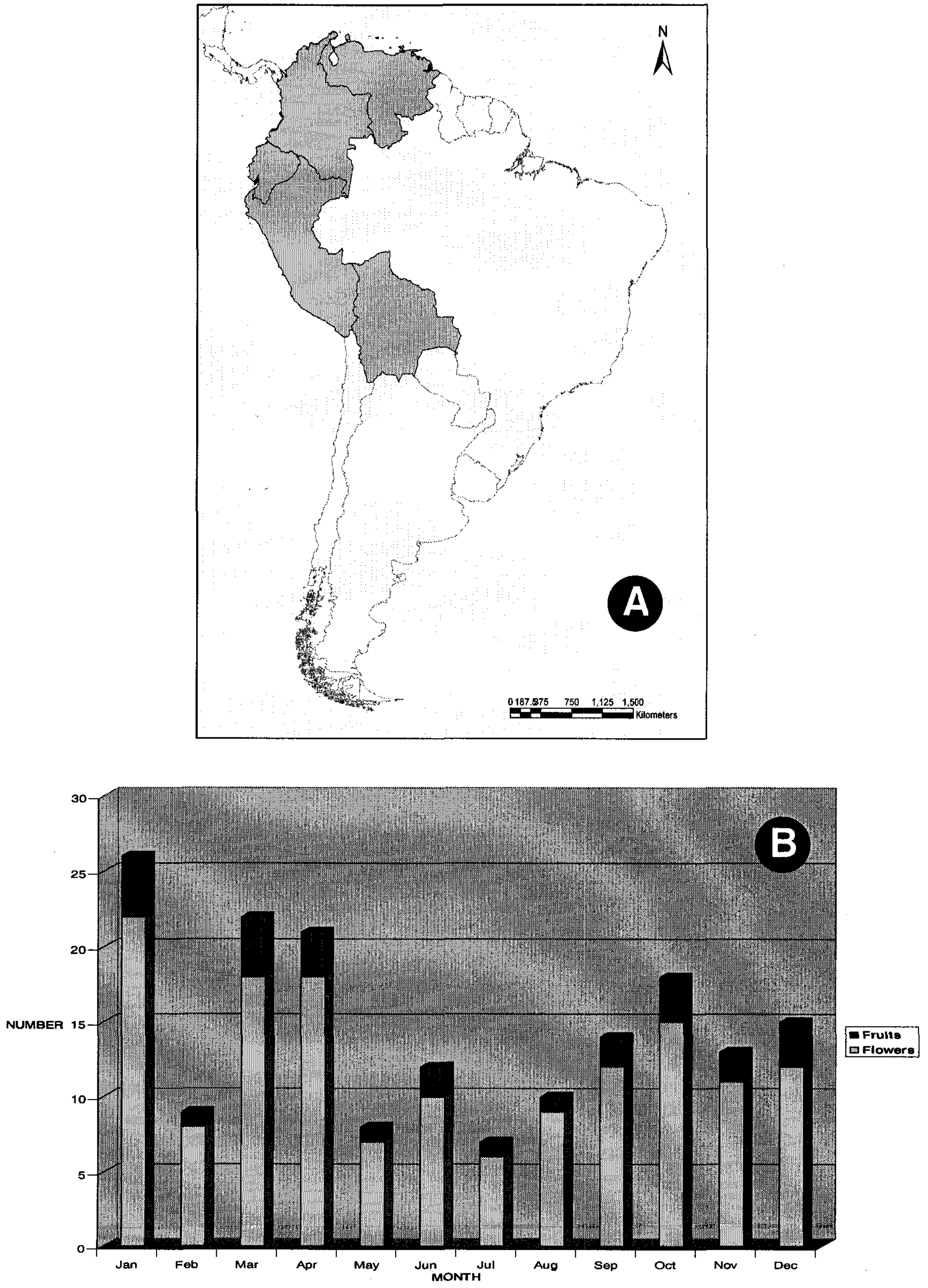

Fig 1.11. Geography and phenology of the genus *Myrosmodes*. A, Distribution map of *Myrosmodes*. B, Flowering and fruiting of *Myrosmodes* species based on herbarium specimens.

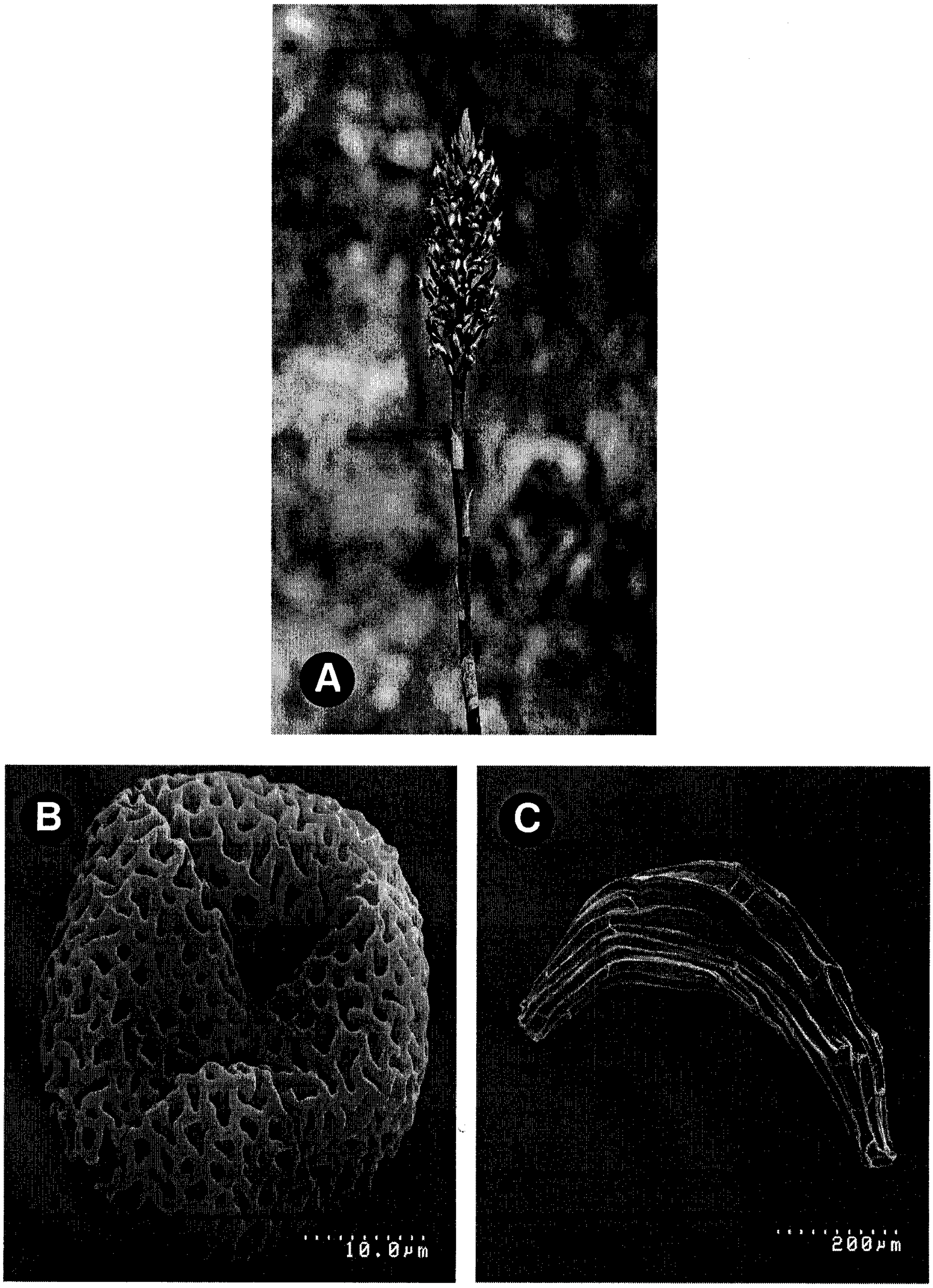

Fig 1.12. Morphological features of *Porphyrostachys* species. A, *P. pilifera*, flowers, Chimborazo, Ecuador. B, *P. parviflora*, tetrads of pollen (*López 8060*, MO). C, *P. parviflora*, seeds (*López 8060*, SEL).

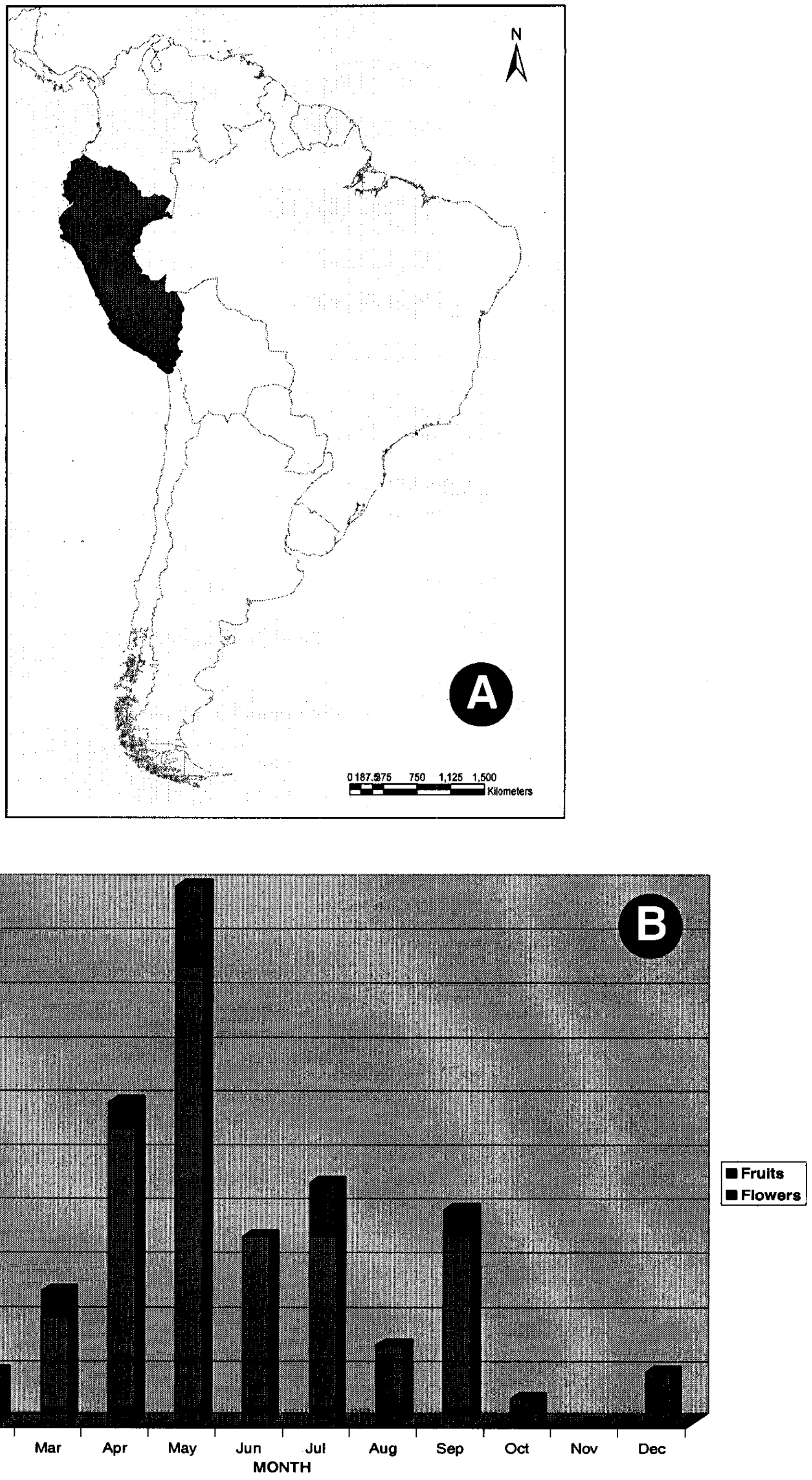

Fig 1.13. Geography and phenology of the genus *Porphyrostachys*. A, Distribution map of *Porphyrostachys*. B, Flowering and fruiting of *Porphyrostachys* species based on herbarium specimens.

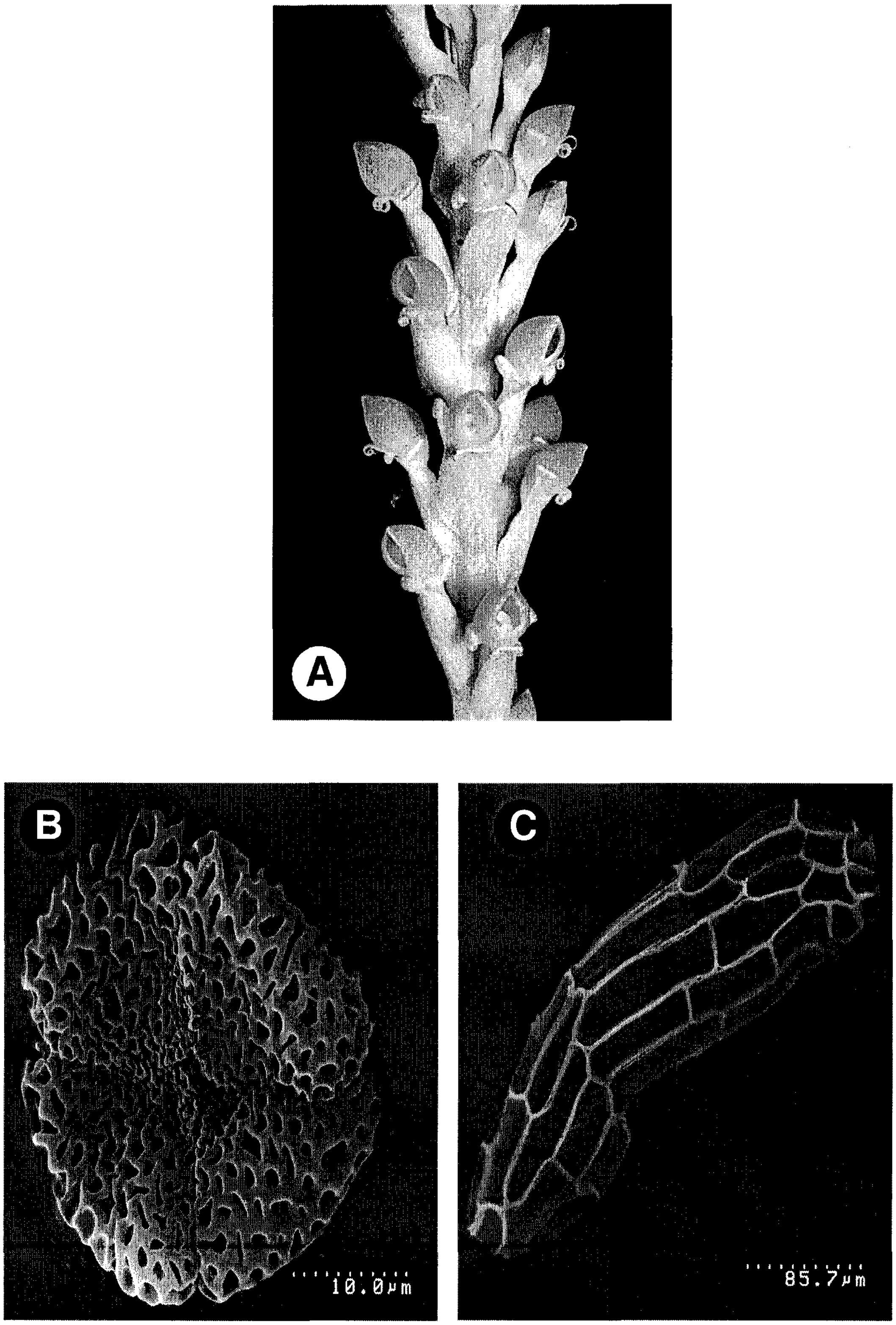

Fig. 1.14. Morphological features of *Prescottia* species. A, *P. stachyodes*, flowers, Costa Rica. B, *P. stachyodes*, tetrads of pollen (*Liogier 14434*, NY). C, *P. lojana*, seeds (*Madsen 75723*, AAU).

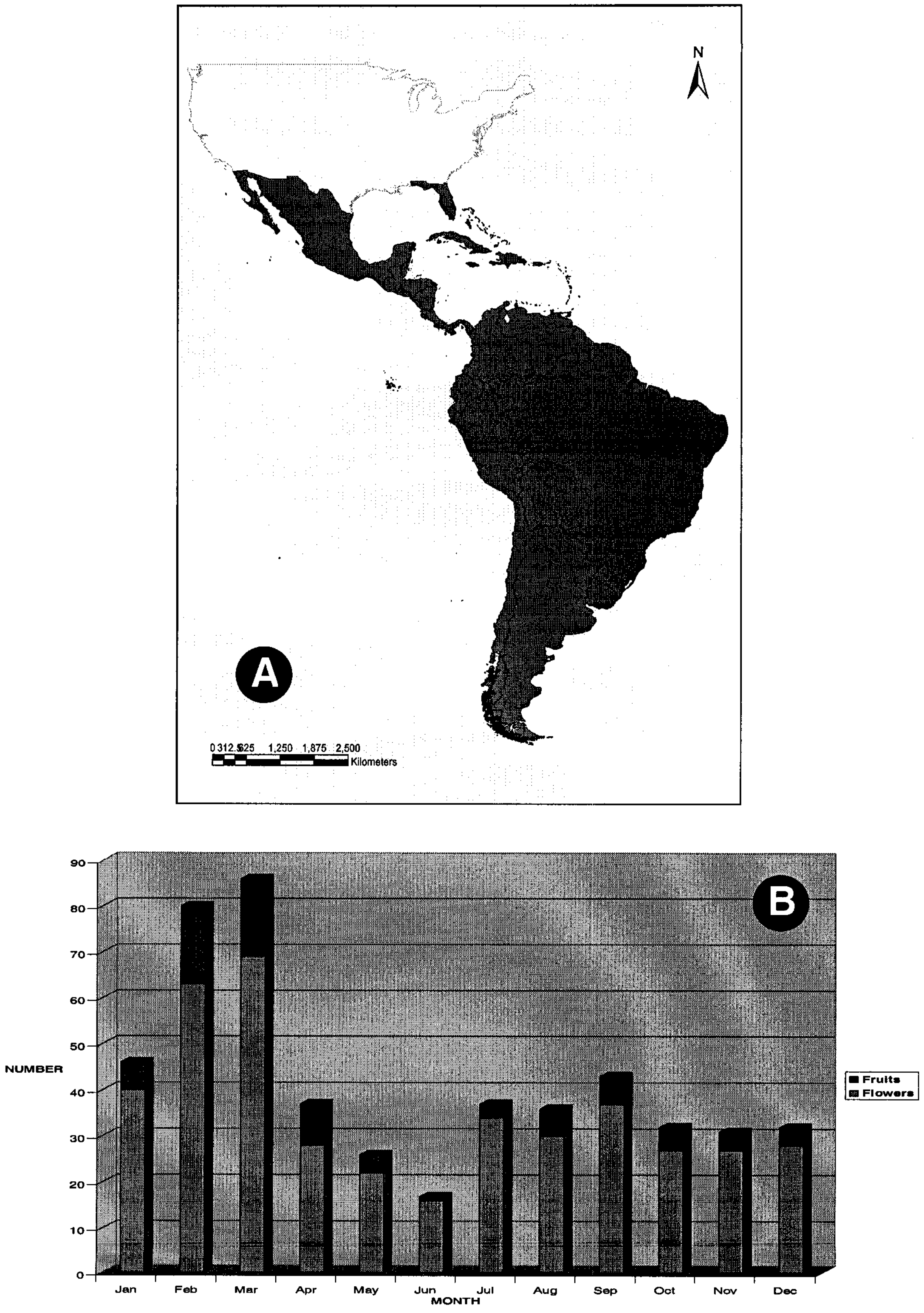

Fig 1.15. Geography and phenology of the genus *Prescottia*. A, Distribution map of *Prescottia*. B, Flowering and fruiting of *Prescottia* based on herbarium specimens.

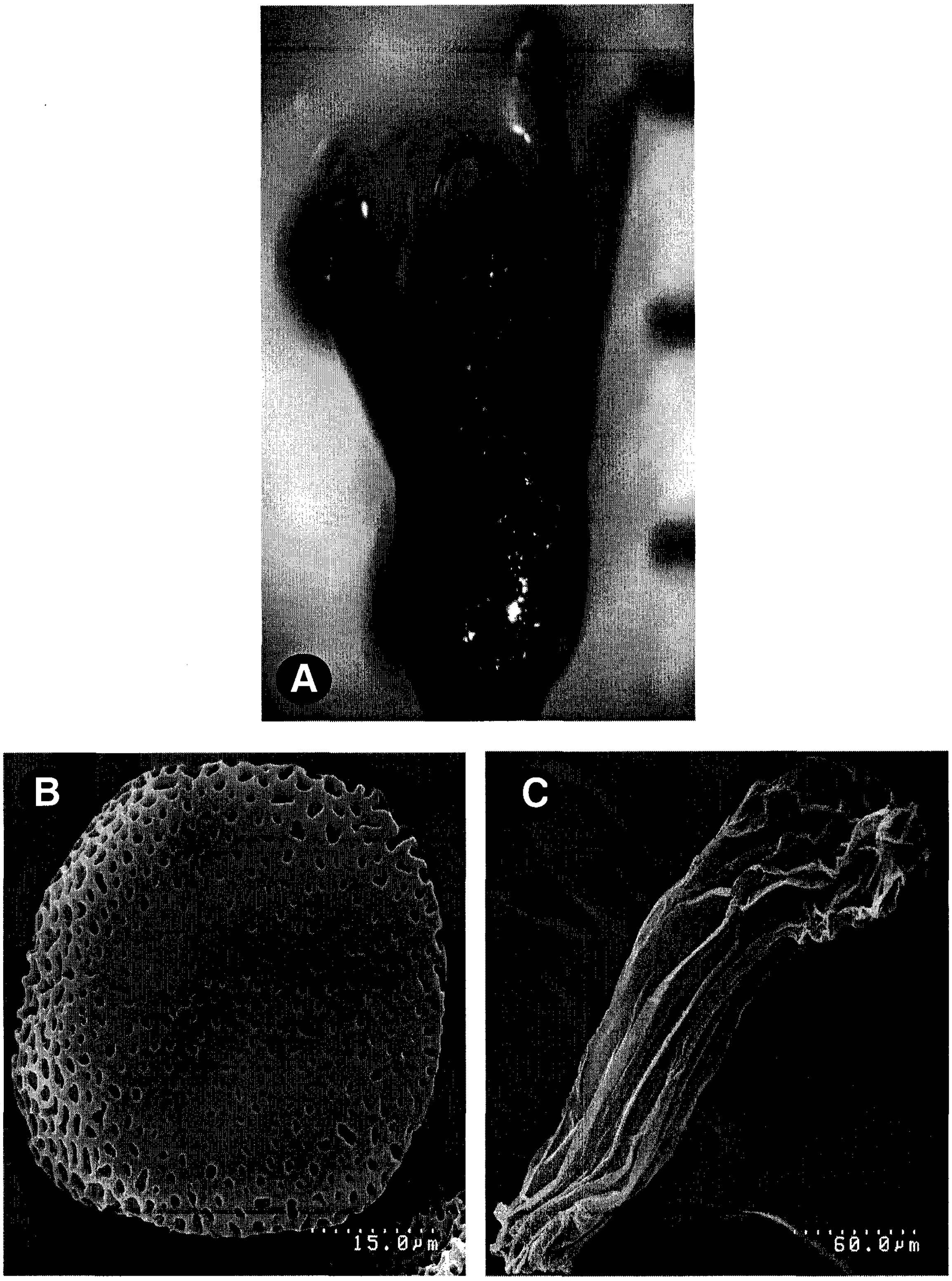

Fig. 1.16. Morphological features of *Pseudocranichis* species. A, *P. thysanochila*, flower, Oaxaca, Mexico (*MacDougall s.n.*, E). B, *P. thysanochila*, a pollen grain, (*Tenorio 17900*, AMES). C, *P. thysanochila*, seeds, (*Seler 1409*, AMES).

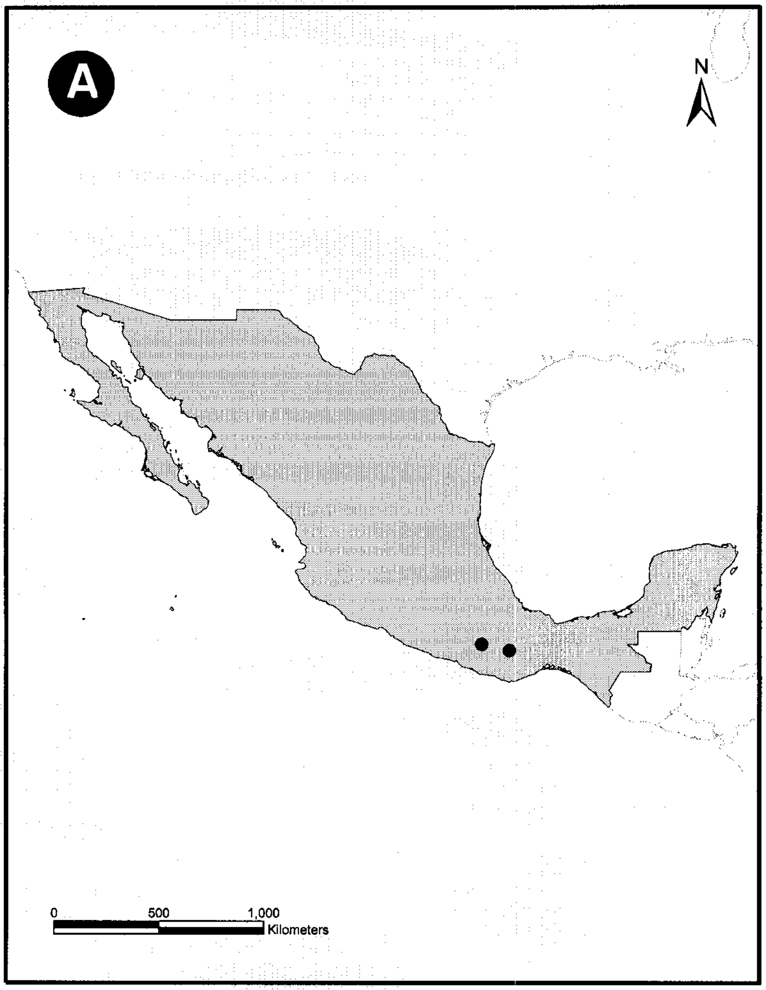

Fig. 1.17. Distribution map of *Pseudocranichis thysanochila*.

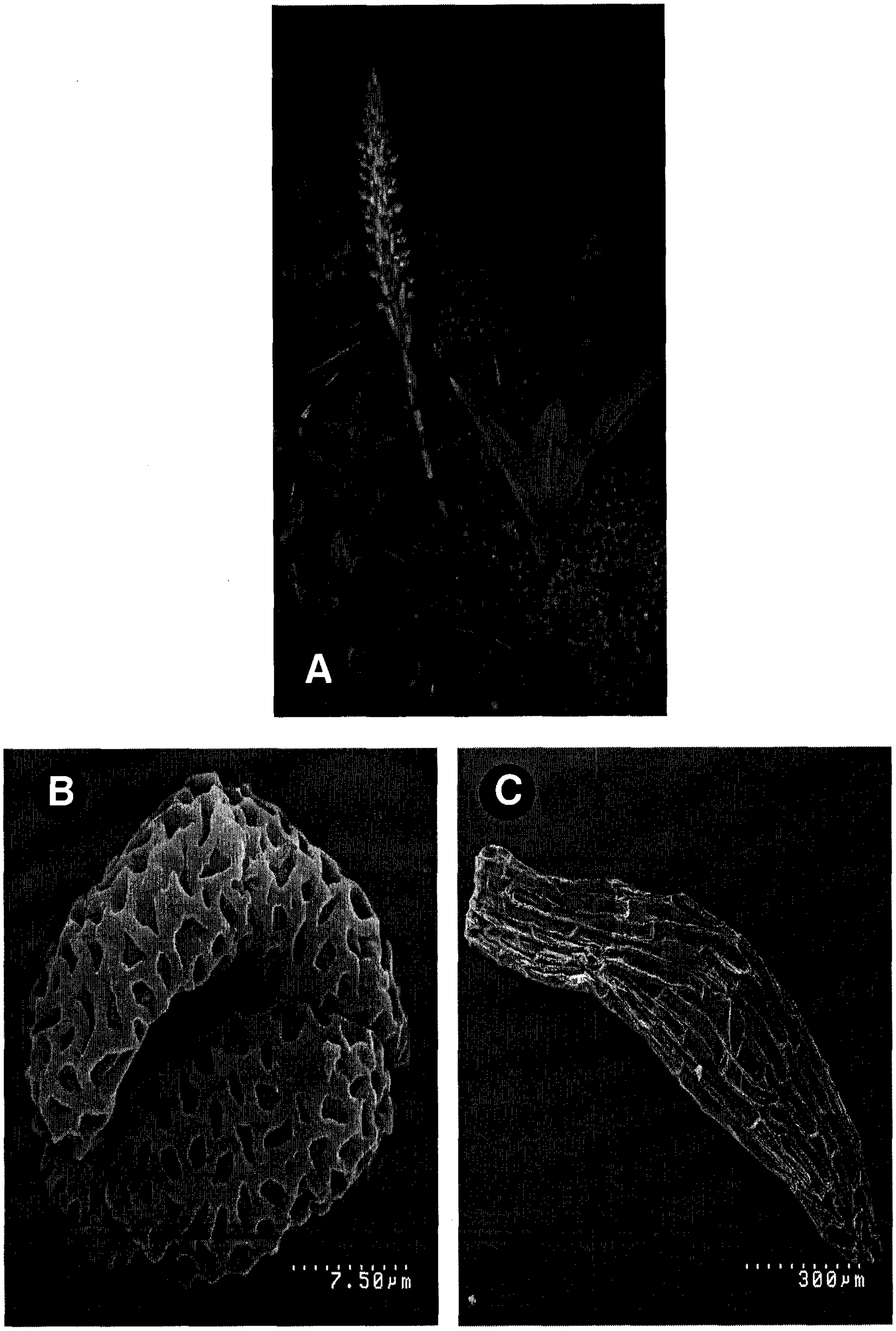

Fig. 1.18. Morphological features of *Stenoptera* species. A, *S. acuta*, Santa Cruz, Bolivia (photo by R. Vásquez). B, *S. acuta*, tetrads of pollen (*Macedo 2332*, NY). C, *S. acuta*, seeds (*Metcalf 30438*, AMES).

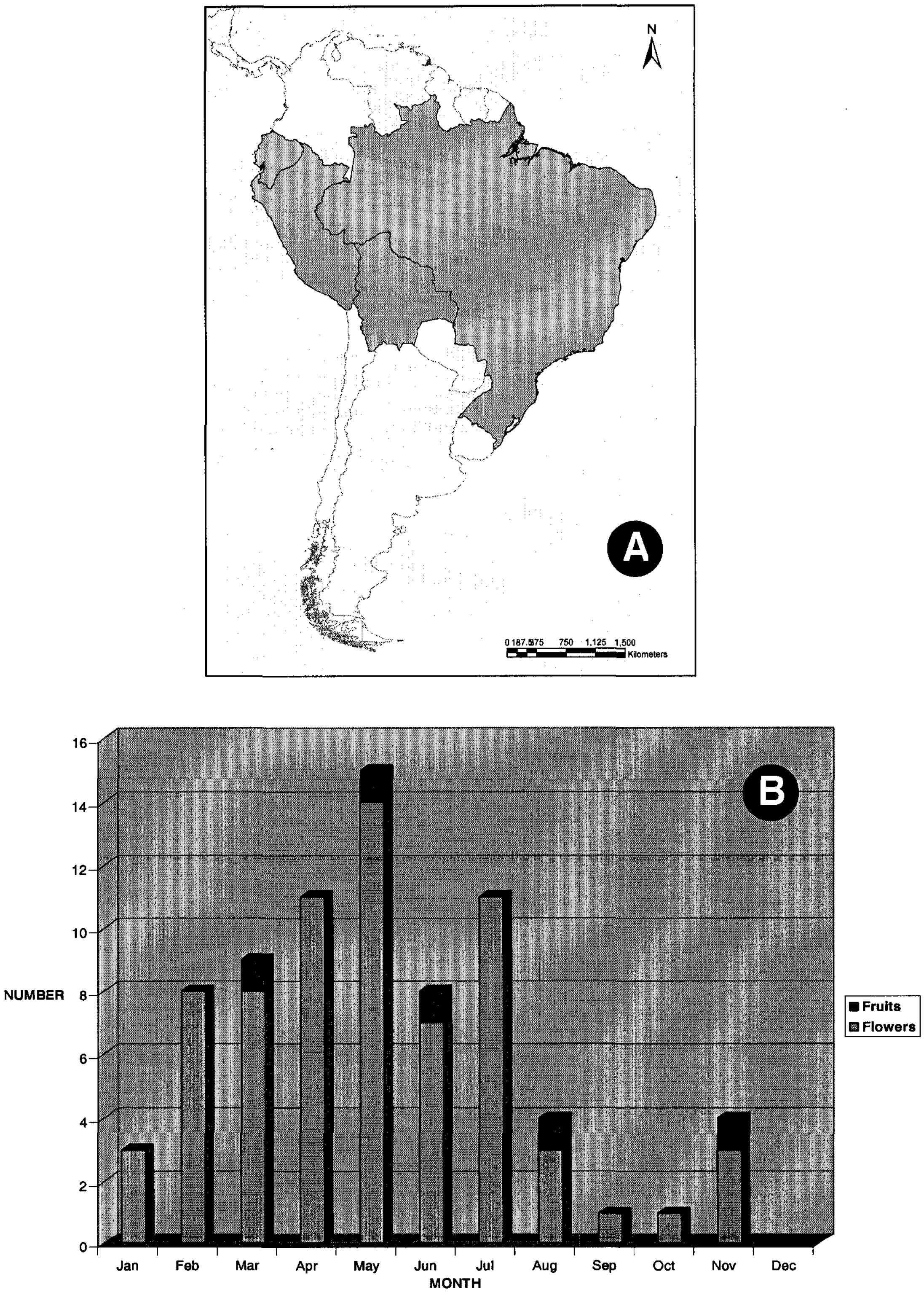

Fig. 1.19. Geography and phenology of the genus *Stenoptera*. A, Distribution map of *Stenoptera*. B, Flowering and fruiting of *Stenoptera* based on herbarium specimens.

CHAPTER 2

MOLECULAR SYSTEMATICS OF PRESCOTTIINAE (ORCHIDACEAE) BASED ON CHLOROPLAST AND NUCLEAR RIBOSOMAL DNA SEQUENCES: INSIGHTS INTO THE PHYLOGENY OF CRANICHIDEAE

2.1. INTRODUCTION

Prescottiinae are one of the six subtribes along with Spiranthinae, Cranichidinae, Goodyerinae, Manniellinae, and Pachyplectroninae into which Dressler (1993) divided the tribe Cranichideae within subfamily Spiranthoideae.

Prescottiinae are diagnosed by non-resupinate flowers, *Spiranthes* type velamen, laminar rostellum, soft pollinia, and lack of hamulus (Dressler, 1990). These plants are primarily terrestrial and may be dwarf rosette herbs only 5 cm in stature or large vigorous plants up to 2 m tall. Their roots are fasciculate, stout, and fusiform. The leaves are basal, subpetiolate or petiolate, extremely variable in length, fleshy, completely glabrous, green, shiny on the upper surface, and often fully developed only after anthesis is completed. The inflorescences are sparsely or densely many-flowered, terminal or lateral spikes and the peduncle is covered by green hyaline sheaths. The flowers are non-resupinate, yellow, white, green or red in color, vary in size from 0.25 to 3.5 cm long, and are always subtended by a glandular-pubescent or glabrous bract shorter or longer than the flowers. The labellum is uppermost, variable in fleshines and shape, glabrous or pubescent, bears 2-4 calli, and posseses multi-cellular, uniseriate, branched or unbranched, nonglandular or moniliform cilia on the margins. The column is short or elongated, erect, arcuate or sigmoid, often club-shaped, footless or with a long decurrent foot. The anther is dorsal, erect, usually ovate, or ovate-lanceolate to oblong. The pollinia are 4, soft, pale yellow, asymmetrically ovate to linear-oblong and attached to a small viscidium, which is brown (when fresh) and circular or transversally linear. The pollen grains are arranged in tetrads and the exine is reticulate. The fruits are sessile, fleshy, unilocular, and usually pubescent. The seeds are very small, ranging from 0.1-0.5 mm, and are usually fusiform and numerous.

Prescottiinae *s.s.* comprise about 100 species in the following seven genera: *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, and *Stenoptera* (Dressler, 1990, 1993). Recently, the genus *Pseudocranichis* was proposed as a member of the Prescottiinae (Szlachetko, 1995) due to the resemblance of this species to other genera of this subtribe. The subtribe is found from Mexico, southern Florida and the Caribbean to northern Argentina, Uruguay and Brazil. A few genera of the subtribe have restricted geographic distributions (e.g. *Porphyrostachys* in Ecuador and Peru and *Pseudocranichis* in Mexico), whereas the genus *Prescottia* is widespread throughout the Neotropics and even extends to southern Florida. The Prescottiinae are most diverse in the South American Andes, occurring in a diversity of habitats. The great majority of genera inhabit montane cloud forests from 2300-3500 m but some are restricted to the páramo or tropical alpine zone above 3500 m. The genus *Prescottia* generally occurs in tropical rain forest and the transition between rain forest and cloud forest. Most members of the

Prescottiinae are highly dependent on humidity and have diversified in wet, moist, temperate environments, but a few of them are found in moderately dry habitats (e.g., *Porphyrostachys* and *Pseudocranichis*).

Taxonomic history of Prescottiinae

The genera of Prescottiinae have been variously arranged in the different classification systems of the Orchidaceae based on pollen and anther features (e.g. Lindley, 1840; Bentham, 1881) and nonresupination of their flowers (e.g. Schlechter, 1926; Dressler & Dodson, 1960; Dressler, 1981; Burns-Balogh & Funk, 1986). In most systems of classification, members of the Prescottiinae have been included within the subtribe Cranichidinae (see Table 2.1 for a summary).

Schlechter (1926) first divided the Cranichidinae into two major groups based on rostellum shape. He placed the Prescottioid genera, along with *Wullschlaegella* (a genus belonging to the Epidendroid subfamily), in his Obtusirostellata division.

In 1981, Dressler divided the subtribe Cranichidinae into two alliances. The *Altensteinia* alliance with seven genera was distinguished by a blunt column, soft pollinia, lack of caudicles, simple labellum, and a column free from the labellum. The *Cranichis* alliance with eight genera was characterized by a pointed column, solid pollinia, and caudicles and labellum usually adnate to the column.

Almost a decade later, members of the *Altensteinia* alliance *sensu* Dressler 1981 were segregated from the Cranichidinae and accommodated in the new subtribe Prescottiinae (Dressler, 1990). The newly erected subtribe was classified within the tribe Cranichideae (Dressler, 1990, 1993) which, along with the tribes Diceratosteleae and Tropidieae, encompassed the subfamily Spiranthoideae, collectively known as spiranthoids or lady's tresses (Dressler, 1979, 1993). The majority of spiranthoid orchids are found in the subtribes Spiranthinae, Cranichidinae and Prescottiinae which together form a strongly supported clade, referred to as the "core spiranthoids" (Kores et al., 1997). Recent molecular evidence supports the inclusion of subfamily Spiranthoideae in the Orchidoideae (Kores et al., 1997; Cameron et al., 1999; Freudenstein et al., 2000).

Szlachetko (1995) placed an expanded Prescottiinae (including *Pseudocranichis*) along with other five subtribes, in a redefined tribe Spirantheae. The Prescottiinae *s.l.* was characterized by non-resupinate flowers, a concave and often fringed labellum, an erect to bent, slender to stout column with an obscure column foot, a large and bi-winged clinandrum, an entire to separately bilobed stigma, a shelf-like rostellum bearing a small viscidium, and an oblong to ovate anther with a thick connective.

The taxonomic position of the Prescottiinae was challenged in the most recent classification system of the Orchidaceae by Chase et al. (2003). In this system, the Prescottiinae were not recognized and rather included in an expanded concept of subtribe Cranichidinae as proposed by Dressler in 1981.

Morphological and molecular cladistic analyses have not yet succeeded in clarifying the phylogenetic placement and circumscription of subtribe Prescottiinae within the Cranichideae, and its hypothesized sister relationship to Spiranthinae (Dressler, 1990, 1993; Szlachetko, 1995). For example, the morphological cladistic analyses by Vargas (1997) found Prescottiinae sister to Spiranthinae with weak statistical support in a fifty-percent majority rule consensus tree. These relationships, however, collapsed into a polytomy comprising Prescottiinae, Spiranthinae and Manniellinae in the strict consensus tree. The higher level molecular studies of Kores et al. (1997; 2001), Cameron et. al. (1999), Freudenstein and Chase (2001), and Freudenstein et al. (2004) found that the Cranichidinae was monophyletic and sister to the Spiranthinae. The sole species of Prescottiinae included in their analyses, *Aa paleacea* (listed as *Altensteinia paleacea*), was sister to Cranichidinae and Spiranthinae which supports Dressler's (1990) segregation of the subtribe. Clements et al. (2002), inferring phylogenetic relationships in the Diurideae, found that *Stenoptera peruviana* was sister to the Cranichidinae and Spiranthinae subtribes. In a recent study, Salazar et al. (2003) assessed the monophyly and circumscription of the tribe Cranichideae *sensu* Dressler (1993) using a combination of plastid and nuclear markers. This study sampled all subtribes recognized within the Cranichideae, but only a few representatives of the Prescottiinae. Among the sampled Prescottiinae two clades were recovered: one clade containing species of *Prescottia* sister to the Cranichidinae (with no statistical support) and these in turn sister to the Spiranthinae, and a second one comprising the remaining sampled Prescottioid genera sister to all of them (with moderate statistical support). The placement of *Prescottia* and the boundaries of Prescottiinae and Cranichidinae are not clear (Fig. 2.1). Results from this study were the basis for the inclusion of the Prescottiinae within the Cranichidinae in the most updated classification of the Orchidaceae by Chase et al. (2003). However, recognizing a broadly defined Cranichidinae, including the Prescottiinae, renders the former paraphyletic (see Fig. 2.1). As a result this taxonomic reinterpretation is controversial and inconsistent with phylogenetic evidence.

Thus, it became apparent that additional characters and sampling were needed to further test the monophyly of the Prescottiinae, their circumscription, relationships, and placement within the tribe Cranichideae. The study presented here concentrates on generic relationships within the subtribe Prescottiinae and its close allies by using sequence data from the plastid and nuclear genome.

Molecular markers

A combination of three plastid loci: *trn*L-F, *rbc*L, *atp*B, and *psa*B, and the nuclear locus ITS, were used in this study. Different genes and gene regions from the chloroplast and nuclear genomes were selected for phylogenetic reconstruction because they may provide a clearer picture of evolutionary relationships thereby avoiding potential pitfalls associated with estimating organismal phylogenies based on a single organelle or nuclear genome (e.g., chloroplast capture, lineage sorting, hybridization, introgression, concerted evolution, etc.) (Wendell & Doyle, 1998). Furthermore, regions from the plastid and nuclear genomes with different levels of variation are desirable because combining them improves the resolution and support in different areas of the cladogram as suggested by Chase and Cox (1998) and Soltis et al. (1998). A brief description and usefulness of each of the molecular markers follows.

The *psa*B chloroplast gene is about 2,202 bp in length, comprises 734 codons, and it is located between *psa*A and *rps*14. This gene along with five other genes, codes for the large and small subunits of the protein P700, a major component of photosystem I which is involved during light reactions of photosynthesis (Shimada & Sugiura, 1991). A recent study that evaluated the evolutionary rates of the major genes encoding Photosystem I showed that sequence divergence in *psa*B is higher than expected and that there were very few conserved areas (van der Staay et al., 2000). The *psa*B gene has been little explored in phylogenetic reconstruction, and studies using this gene are relatively few in number within the plant kingdom. This gene was first used to evaluate relationships among distantly related plant lineages such as bryophytes and tracheophytes (Nishiyama & Kato, 1999); reconstruct phylogenies within the green algal order Volvocales (Nozaki et al., 2000); and study branching patterns in prokaryotes (van der Staay et al., 2000). These studies found useful levels of variation in this gene to address evolutionary questions at the family and infrafamilial taxonomic ranks within plants. The utility of the *psa*B gene sequences in resolving phylogenetic relationships has been recently evaluated in the Orchidaceae (Cameron, 2004b). This work found that, in general, *psa*B and *rbc*L have comparable levels of variation and phylogenetic signal to elucidate relationships at the family level and below, suggesting that *psa*B may provide additional useful information needed to resolve inter-clade relationships at the subfamily, tribe, and subtribe taxonomic ranks.

The *atp*B gene encodes the ß subunit of the ubiquitous metabolic enzyme ATP synthase. The ß subunit contains catalytic as well as allosteric sites that take part in the inter-conversion of ADP and ATP. In the chloroplast genome *atp*B is present as a single-copy and it is located downstream from *rbc*L. The two genes are separated by a 900 bp intergenic spacer. Although *atp*B is easily amplified, there have been fewer phylogenetic studies published for this gene compared with *rbc*L, and its performance at different taxonomic levels has not been clearly evaluated. Among ferns, *atp*B sequences have been successfully utilized to infer phylogenies at lower taxonomic levels (Wolf et al., 1998). Hoot et al. (1995) were the first authors to use *atp*B to study phylogenetic relationships in angiosperms. They compared the performance of *atp*B to *rbc*L and 18S reporting that *atp*B does not contain introns and indels and that *atp*B and *rbc*L have almost similar nucleotide substitution rates (Hoot et al., 1995). These conclusions were further confirmed by Savolainen et al. (2000) in a large phylogenetic study among angiosperm families. This study also suggested that combining *atp*B and *rbc*L improves clade support in different parts of the topology (Savolainen et al., 2000). More recently, Cameron (2004a, subm.) evaluated phylogenetic relationships within the orchid family using combined analyses of *atp*B and *rbc*L data sets. Higher resolution and bootstrap values were found when both genes were combined over the topology obtained from either data set alone. Overall the results of this analysis showed that *atp*B contains a higher number of phylogenetically informative sites and has less homoplasy than *rbc*L. Insertion/deletions were found in few orchid taxa belonging to the Vanilloideae subfamily, but were interpreted as isolated events.

The *rbc*L gene encodes the large subunit of ribulose-1,5-biphosphate carboxylase/oxygenase (RUBISCO), an essential photosynthetic enzyme. The gene is located in the large single-copy region of the plastid genome and has been employed extensively to evaluate relationships at different taxonomic levels (Olmstead & Palmer, 1994; Soltis & Soltis, 1998). At the highest ranks of the taxonomic hierarchy *rbc*L has been used to infer plant phylogenies among families of angiosperms (Chase et al., 1993), pteridophytes (Hasebe et al., 1993; Hasebe et al., 1995), and algae (Freshwater & Ruenes, 1994; Chapman et al., 1998). Phylogenies based on *rbc*L sequences have been especially useful to elucidate relationships at the family level in the Orchidaceae (Cameron et al., 1999), Saxifragaceae (Soltis et al., 1990), Asteraceae (Jansen et al., 1991), and Poaceae (Doebley et al., 1990), among others. At lower taxonomic levels, the utility of the *rbc*L varies. In ferns the gene has been valuable to assess generic and specific relationships (Crane et al., 1995; Gastony & Rollo, 1995). Other workers have successfully applied *rbc*L in certain angiosperm genera to clarify relationships at the species level; for example in *Cornus*, *Saxifraga* and *Drosera* as discussed by Soltis and Soltis (1998). Chase and Albert (1998), examining the variation patterns in *rbc*L, suggested that the number of informative characters of this gene when applied below the family level may equal or even exceed that of chloroplast introns and spacers.

A number of noncoding regions of the plastid genome have been proven useful for analyses of generic and specific relationships (Gielly & Taberlet, 1994; Olmstead & Palmer, 1994). Among them are the noncoding sequences from the *trn*L intron and *trn*L-F intergenic spacer (Taberlet et al., 1991; Gielly & Taberlet, 1994), which evolve as much as three times faster than *rbc*L in the Orchidaceae (Whitten et al., 2000) and other plant families.

The internal transcribed spacer (ITS) of the nuclear rDNA (Baldwin et al., 1995) consisting of two noncoding spacer regions (ITS1 and ITS2) flanking the 5.8S gene, is relatively short (500-600 base pairs) and has been used extensively in phylogenetic analyses of species and genera. The degree of variability in ITS sequences appears to be as high as the plastid *trn*L-F region (Gielly et al., 1996). Numerous studies have shown that ITS sequences are G+C rich and that some parts of these regions are conserved among angiosperms (Hershkovitz & Lewis, 1996; Hershkovitz & Zimmer, 1996). Nevertheless, previous cladistic analyses of ITS sequence data have found that this gene region provides useful phylogenetic information in other groups of orchids at the tribal and subtribal taxonomic levels (Whitten et al., 2000; Clements et al., 2002).

Rationale and objectives

To test the conclusions from previous molecular phylogenies, this study expanded the sampling of Prescottiinae to include all the genera recognized in the subtribe, included additional genera of Cranichidinae, as well as representatives of each of the subtribes classified in the Cranichideae by Dressler (1993). The molecular phylogenetic hypotheses resulting from the analysis of the combined data sets were discussed and compared to available data. Diagnostic characters used traditionally to define Prescottiinae and their members were examined and assessed in light of the new findings. This phylogeny will also be used to reconstruct the biogeography of the subtribe Prescottiinae and its close allies belonging to tribe Cranichideae.

Objectives

The specific objectives of this study are to:

1) Test the monophyly and circumscription of the Prescottiinae *s.s.* and *s.l.*
2) Determine the phylogenetic position of the subtribe Prescottiinae.
3) Test the monophyly of the Cranichidinae *sensu* Chase et al. (2003).
4) Investigate character evolution and biogeographic patterns within the tribe Cranichideae.

This study complements a published investigation of Cranichideae phylogeny (Salazar et al., 2003) by using a different set of accessions, a thorough sampling, and a composite of five loci from the plastid and nuclear genomes.

2.2. MATERIALS AND METHODS

Taxon Sampling

In order to reconstruct a robust phylogeny for the Prescottiinae and their close relatives, the sampling strategy was to include as many taxa as possible from all subtribes recognized within the Cranichideae by Dressler (1993) and Chase et al. (2003). This strategy is not only important for examining relationships within the Prescottiinae and among the major subtribes of Cranichideae but inclusion of DNA sequence data from both nuclear and chloroplast regions will allow examination of previous phylogenetic hypotheses that have included some of these genomes (Kores et al., 1997; Clements et al., 2002; Salazar et al., 2003). Table 2.2. lists all species examined and sampled in this study with voucher information. A total of 31 genera and 56 species representing all genera of Prescottiinae *s.l.* (Dressler, 1990, 1993; Szlachetko, 1995), each of the subtribes recognized within the Cranichideae by Dressler (1993), the newly described subtribe Galeottiellinae (Salazar et al., 2002a), and two representatives of tribe Diurideae as defined by Dressler (1993) but currently included within Cranichideae (Chase et al., 2003) were sampled for this study. Ingroup and putative outgroup taxa were selected on the basis of previous classifications of the family (Dressler, 1981, 1993; Chase et al., 2003), phylogenetic studies of Spiranthoideae (currently included in Orchidoideae) (Kores et al., 1997), cladistic analyses within the Diurideae (Kores et al., 2000; Kores et al., 2001), phylogenetic analyses of Cranichideae (Vargas, 1997; Salazar et al., 2003), and molecular and morphological phylogenetic family level studies (Cameron et al., 1999; Freudenstein & Rasmussen, 1999; Freudenstein et al., 2004). Two of the most distantly related members of the Cranichideae, *Chloraea* and *Pterostylis*, were selected as outgroups. The same individual DNA samples were utilized to sequence each target locus.

Selection of molecular markers

In the present study a composite of quickly and slowly evolving genes and gene regions were utilized to infer phylogenetic relationships at the tribal and subtribal levels. The selected loci included three coding genes (*rbc*L, *atp*B, and *psa*B) and two noncoding regions (*trn*L-F, and ITS) that have been extensively sequenced from angiosperms, ferns, and algae at both higher and lower taxonomic levels. These loci previously have been found to be phylogenetically informative and complement each other in the kind and quality of information they provide at different hierarchical levels.

DNA extraction

DNA was extracted using a slightly modified CTAB (acetyl-trimethyl-ammonium bromide) method (Struwe et al., 1998) from 0.5-1 cm^2 of dried leaf tissue. Leaf material was ground in a lysing matrix tube containing one zirconia bead and garnet sand (Bio 101, Carlsbad, CA) and pulverized for 15 seconds in a Bio 101 /Savant Fastprep tissue disrupter at speed 5. Tissue was bathed in 500 µl of Carlson Lysis Buffer (2 g CTAB, 8.18 g NaCl, 0.745 g EDTA, 10 ml 1M Tris/HCl, nanopure water to 100 ml, verified to pH 9.5, autoclaved, then added 1 g PEG 4000 when cool) to which 75 μl of ß-mercaptoethanol was added. Next, tubes were incubated at 74ºC with occasional shaking for 60-90 minutes. Following this, 575 μl of SEVAG (24:1 chloroform:iso-amylalcohol) were added to each tube which were then placed on a tipping board for 30 minutes at room temperature. Tubes were then centrifuged at 14,000 rpm for 1 minute, and 350 μl of supernatant were added to new tubes containing 1050 μl of NaI solution, 20 μl glassmilk and 4 μl TBE modifier (Bio 101). These tubes were placed on a tipping board for 30 minutes at room temperature. Subsequently, tubes were centrifuged at 14,000 rpm for one minute and all of the supernatant was discarded. Glassmilk pellets containing DNA were washed three times with 800 μl and once with 150 μl of ice cold New Wash solution (Bio 101). After the last wash, the solution was pipetted off keeping the glassmilk pellet and 50 μl of 10 mM Tris were added to resuspend the DNA. Tubes were incubated at 55ºC for 10 minutes and then centrifuged at 14,000 rpm for one minute. The supernatant containing the DNA was transferred to sterile tubes.

A few extractions were made using the Dneasy Plant Mini kit (Qiagen Inc., Valencia, CA). The Dneasy kit uses a SDS-potassium acetate method followed by chaotropic DNA binding to a silica membrane mini-column. Difficult to extract DNA and herbarium material followed the Dneasy manufacturer's protocol with the modification of the buffer AP1 lysis conditions by the addition of 570 μg of PCR grade proteinase K (Roche, Indianapolis, IN), 6.5% ß-mercaptoethanol and incubation at 42°C for 24 hours on a rocking platform. This mini-prep method proved to be useful to minimize sample loss and contamination risks from herbarium material.

A few DNA aliquots corresponding to three-taxa were provided by the RBG KEW DNA bank as indicated in Table 2.2.

DNA amplification

Amplifications of DNA were performed using the polymerase chain reaction (PCR) in 25 μl reactions consisting of 10x buffer with 15mM $MgCl_2$ (Qiagen, Maryland), 9.3 μl autoclaved nanopure water, 2.5 μl BSA (bovine serum albumin), 2.5 μl dNTP (Roche, Indianapolis, IN), 1μl each of two 20 μM primers, 5μl betaine (Q solution), 0.2 μl Taq polymerase (Qiagen, Valencia, CA) and 1 μl of genomic DNA. Primers used to amplify each gene region are listed in Table 2.3.

Weak PCR's were improved with a second round of PCR using 1 μl of a 1:50 dilution of the first PCR. Some samples that failed to amplify under standard conditions were successfully amplified using 5% DMSO as an additive instead of betaine in the PCR mix. Difficult to amplify samples were also successfully amplified in two separate reactions using 4 primers (amplification and sequencing primers) in two pairs that yielded two non-overlapping fragments. Other PCR products that produced multiple bands (mainly the *trn*L-F locus) were easily isolated by electrophoresis from a 2% agarose 1X TBE gel and purified using the QIAquick Gel Extraction Kit (QIAGEN Inc., Valencia, CA). Degraded DNA's extracted from herbarium specimens were amplified using the

TaKara Taq™ PCR core (TaKara Bio Inc., Japan) including 10x buffer, dNTP mixture and enzyme following the manufacture's protocol for the cool start method.

To detect successfully amplified products and the possible contamination of negative controls, PCR product were examined on 1% agarose gels stained with ethidium bromide, quantified using 1 Kb Plus DNA ladder (Invitrogen/Life Technologies/GibcoBRL, USA), and visualized under ultraviolet light. Amplified products were purified with spin columns from the QIAquick PCR purification kit (QIAGEN Inc., Valencia, CA) following the manufacturer's instructions.

The PCR conditions for amplification of each of the gene regions utilized in this study are detailed in Table 2.4 and were performed in either a 9600 Perkin Elmer GeneAmp PCR system or a Peltier Thermal Cycler DNA engine (DYAD™).

Sequencing

Purified PCR products were cycle sequenced using 2.75 μl water, 0.5 μl DMSO (dimethyl sulfoxide), 1.25 μl dilution buffer (400mM Tris pH 9 and 10mM magnesium chloride), 1.25 μl Big Dye Terminator v.3. (ABI PRISM, Applied Biosystems, Foster City, CA), 1 μl of 10 mM primer, and 3-5 μl purified amplified PCR template. Typically four primers were used for cycle sequencing reactions two of which were the same as in the PCR reactions. The cycle sequencing profile conditions are detailed in Table 2.4. These reactions resulted in complete forward and reverse strands of the target loci. Cycle sequencing products were cleaned with Centri-Sep sephadex spin columns (Princeton Separations, Inc., Adelphia, NJ) using G-50 Fine DNA Grade (Amersham Biosciences, Uppsala, Sweden). Reaction products were subsequently vacuum evaporated under low heat for 45 minutes. The purified products were resuspended in 2 μl of formamide (83.5%) and EDTA (16.5%), heated at 95°c for 2 minutes and immediately placed on ice slurry. Samples were loaded onto polyacrylamide gels containing ACRYL/BIS Solution (Amresco Inc., Solon, OH), poured on 36 cm plates and run on an ABI Prism^{TM} 377 XL DNA automated sequencer (Applied Biosystems, Foster City, CA). Raw data files were analyzed with the ABI Prism^{TM} 377 Software Collection 2.1 package (Perkin Elmer, Applied Biosystems, Foster City, CA).

Sequence editing and alignment

Sequence fragments were subjected to BLAST searches to verify their identity. Next, the sequences were assembled, primer regions trimmed, and edited in Sequencher version 4.0.2 for Windows (Gene Codes Corporation, 1998). Sequences were aligned using ClustalX version 1.81 (Higgins & Sharp, 1988, 1989; Thompson et al., 1997) using the default parameters except for the delay divergent sequences set to 25%. The created alignment was examined and optimized by eye using Bioedit version 5.09 (Hall, 2001).

The alignments of the two non-coding loci utilized in this study, ITS and *trn*L-F, were inspected for the presence of ambiguously aligned regions caused by the insertion of gaps and these were delimited using the criteria described by

Lutzoni et al. (2000). In a second step, the identified ambiguous regions were recoded with a weighting scheme in which transitions, transversions, and gaps all weighted as 1 throughout the generation of symmetric step matrices using the program INAASE 2.3b for Macintosh (Lutzoni et al., 2000). The final output of this process consisted of a code for each ambiguous region with its own step matrix. These coded characters were appended at the end of the data matrix.

Phylogenetic analyses

Parsimony analyses.- The ITS, *trn*L-F, *rbc*L, *atp*B, and *psa*B data were analyzed independently and in combination using the parsimony criterion in PAUP* version 4.0b10 (Swofford, 2002). Characters were equally weighted, with gaps treated as missing data, and with DELTRAN optimization of characters onto resulting trees. All equally parsimonious trees were found by executing a heuristic search of 1,000 random addition replicates using TBR branch swapping, but holding 10 trees per replicate in order to find possible islands of maximum parsimony (Maddison, 1991). The resulting trees were then used as starting trees for a second heuristic search using the same parameters, except this time saving all shortest trees (MULTREES option in effect) until a pre-set maximum limit of 50,000 trees was reached.

A matrix consisting of 56 taxa was assembled. In addition, for the noncoding gene regions (ITS and *trn*L-F) two alternative matrices were constructed: one consisting of unambiguously aligned characters and recoded ambiguous regions, this last step accomplished with the program INAASE

(Lutzoni et al., 2000) and a second one including only unambiguously aligned regions (ambiguous aligned characters were excluded). Each locus was analyzed independently and in combination.

To facilitate the summary and discussion of results the phrase "spiranthoid orchids" or "spiranthoids" follows the definition of Dressler (1979) and includes all the subtribes of Cranichideae represented in the analysis except (*Pterostylis* and *Chloraea*). The term "core spiranthoids" refers to members of the subtribes Prescottiinae, Cranichidinae and Spiranthinae as defined by Kores et al. (1997).

Bayesian analyses.- Bayesian analyses were conducted on the combined data sets containing only unambiguously aligned regions (without ambiguous and recoded characters). The appropriate model and starting parameters for Bayesian analyses were chosen for each of the data sets using the likelihood ratio test implemented in Modeltest 3.06 (Posada & Crandall, 1998, 2001) with the default settings. Bayesian analyses were performed using MrBayes version 3.0B4 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) for each data set under the general time reversible model (GTR+I+G) that best fit the data sets. The Bayesian analyses started from random trees sampling one tree every 100th generation with four incrementally heated chains, and a uniform prior for branch lengths and the gamma shape parameter. Invariant sites frequency was estimated using the "invgamma" setting with a uniform (0, 1) prior for proportion of invariant sites. Uniform priors were used because they are less likely to bias the estimated values. The Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) (Larget & Simon,

1999) was used to estimate posterior probabilities as implemented in MrBayes. The MCMCMC algorithm was run for 4,000,000 generations for each data set and the number of trees to be discarded (burn-in period) was determined graphically (typically about 10% of the total number of generations= 400,000 generations = 400 trees). The first 400 trees corresponding to the "burn-in" period were excluded to avoid random trees that might have been sampled prior to convergence of the Markov chains and do not contain useful parameter estimates. A majority rule consensus tree was constructed from the retained 3,600 trees. The resulting posterior probability values (pp) are interpreted as true probabilities for each clade under the assumed model (Rannala & Yang, 1996). As a result clades with probabilities of 0.9 or greater were considered significantly supported to avoid overestimation of this parameter (Cummings et al., 2003).

Branch support.- Relative levels of branch support were assessed by bootstrap analyses of 1000 pseudoreplicates, each with ten random addition sequences followed by TBR branch swapping and saving only one tree per pseudoreplicate. Bootstrap robustness was interpreted using three categories: bootstrap values (bts) between 50-69% (weak); between 70-79% (moderate); and between 80-100% (strong).

Support for each clade within phylogenies was also evaluated using decay analysis (Bremer, 1988). Decay indices (di) or "Bremer support" were estimated with the software TreeRoot version 2.0 (Sorenson, 1999). The settings used to generate the indices were identical to those utilized in finding the strict consensus tree in PAUP* and default values of TreeRoot (20 heuristic searches with random addition of taxa for each constrain statement per node).

Congruence test.- The significance of character incongruence among partitions of the total matrices was assessed using the Incongruence Length Difference Test (ILD) (Farris et al., 1995) implemented in PAUP*4.0b10 as the Partition Homogeneity Test. Partitions corresponded to various pairwise 2-way, 3-way and 4-way combinations of character sets using 1,000 replicates with 10 random addition sequences per replicate holding 10 trees at each step, and saving only one tree per replicate. Interpretation of the incongruency among data partitions using the ILD test followed suggestions by Cunningham (1997).

Congruence of the separate molecular data sets was also evaluated by visual inspection of the individual bootstrap consensus trees. Cladograms were compared to assess instances of strongly-supported alternative topologies. Different topologies with bootstrap values of 70-100% were considered as "hard incongruence" (incongruent) and values with < 70% bootstrap support were taken as "soft incongruence" following Mason-Gamer and Kellog (1996).

Character evolution.- To reconstruct historical shifts in morphology and biogeography, key morphological characters were optimized and traced onto one of the strict consensus trees resulting from the combined analyses. Using MacClade 4.06 (Maddison & Maddison, 2003) ambiguities in character tracing were solved assuming accelerated transformation (ACCTRAN), which maximizes reversals.

2.3. RESULTS

Parsimony analyses

***psa*B sequence analysis.-** The *psa*B matrix consisted of 1684 characters, 224 (13.3%) variable characters, and 130 (7.72%) potentially parsimony informative characters (Table 2.5). A total of 50,000 equally parsimonious trees were saved. They have a length of 377 steps, a CI of 0.66, and a RI of 0.74. The strict consensus tree is presented in Fig. 2.2 with bootstrap percentages indicated above branches. Twelve clades received bootstrap support of 80% or greater (Table 2.5). The strict consensus tree shows little resolution. Pachyplectroninae and Goodyerinae form a monophyletic moderately supported clade (79% bts). This pair plus a clade encompassing the remaining spiranthoids (79% bts) along with *Pterostylis oliveri* (one outgroup) form a polytomy without statistical support of 50% or greater indicating that Cranichideae may not be monophyletic. Following this is positioned *Manniellinae* sister to all other spiranthoids including *Galeottiella*, relationship that is moderately supported (79% bts). Within the remaining spiranthoids only a monophyletic Cranichidinae was recovered with a moderate bootstrap support (66% bts) and a number of intergeneric relationships were supported as well such as *Brachystele* and *Spiranthes* (96% bts), and *Pelexia* and *Sauroglossum* (77% bts).

***atp*B sequence analysis.-** The aligned sequences of *atp*B were 1468 base pairs long, with 234 (15.94%) variable sites of which 134 (9.13%) were potentially phylogenetically informative (Tables 2.5). Using parsimony analyses a preset limit of 50,000 equally parsimonious trees were generated. These trees have a length of 380 steps, a CI of 0.69, and a RI of 0.78 (Table 2.5). The consensus tree with bootstrap percentages is shown in Fig. 2.3. This tree overall is poorly resolved and does not provide evidence for the monophyly of the Cranichideae. *Pachyplectron*, *Goodyerinae* (88% bts) and the remaining spiranthoids (81% bts) are not resolved from *Pterostylis oliveri* (outgroup). Manniellinae is sister to the remaining spiranthoids and this relationship received high support (81% bts). Also recovered was a weakly supported clade (53% bts) including the core spiranthoids plus *Galeottiella*, within which few assemblages received bootstrap support of 50% or greater and only the monophyly of Spiranthinae was moderately supported (76% bts).

***rbc*L sequence analysis.-** The *rbc*L matrix included a total of 1331 characters, 169 (12.7%) variable characters, 91 (6.84%) potentially parsimony informative characters (Table 2.5). This analysis resulted in 1884 most parsimonious trees with 277 steps, a CI of 0.68, and a RI of 0.82. The strict consensus is not equally resolved and it is depicted in Fig. 2.4. Interclade relationships are reasonably resolved at the base of the tree, but there is little resolution within the groups of the core spiranthoids. Starting at the base of the tree Pachyplectroninae and Goodyerinae are sister to each other with a moderate support (72%), this pair and the remaining spiranthoids (79% bts) are not resolved from *Pterostylis oliveri*, one of the outgroups. This outcome does not provide support for the monophyly of Cranichideae and is congruent with the results reported in Salazar et al. (2003) for the *rbc*L analysis alone. In the clade containing the remaining spiranthoids, the sister relationship of *Galeottiella* to the remaning spiranthoids received a moderate support (79% bts). *Manniella* (82% bts) branch next and is sister to a moderately supported grade (75%) containing the core spiranthoids. Resolution among the core spiranthoid is poor resulting in low bootstrap support for most clades. The only notable exception is the monophyletic Spiranthinae supported by a moderate bootstrap value (78% bts).

***trn*L-F sequence analysis.-** In the *trn*L-F matrix four long A-T rich regions totaling 79 base pairs were excluded from the analyses because they could not be aligned readily due to repeated motifs and numerous indels. Over the entire alignment six short ambiguously aligned regions adding up 98 base pairs were identified, scored and appended to the matrix. After exclusion of the hypervariable regions and addition of the recoded ambiguous characters the aligned matrix was 1,422 base pairs in length. This matrix included 588 variable sites (41.35%), and 333 parsimony informative nucleotide positions. The analysis of the *trn*L-F resulted in 108 trees of 1299 steps, a CI of 0.64, and a RI of 0.73 (Table 2.5). The strict consensus of these 108 trees is presented in Fig. 2.5. The tree is fully resolved and relationships for the most part are supported. Fourty-four clades received bootstrap support of 50% or greater, of these, 31 were 80% or greater. The topology of the strict consensus tree is resolved but a number of clades did not receive bootstrap support greater than 50%. There is strong support for the monophyly of the Cranichideae (94% bts) *sensu* Dressler (1993). The monophyly of Goodyerinae is highly supported (100% bts) but there is no complete resolution within this subtribe. The sister relationship of *Pachyplectron* and Goodyerinae is moderately supported (79% bts). This clade is sister to a well supported (100% bts) polytomy comprising Galeottiellinae, Manniellinae and the core spiranthoids. Within the weakly supported core spiranthoids (56% bts) relationships are resolved but not fully supported. Cranichidinae is sister to the remaining core spiranthoids, and Spiranthinae and Prescottiinae are united in a clade without statistical support. The monophyly of Cranichidinae (84% bts) and Spiranthinae (99% bts) are strongly supported, but Prescottiinae are paraphyletic comprising two distantly related assemblages. One lineage includes six predominantly Andean genera (*Stenoptera*, *Altensteinia*, *Gomphichis*, *Porphyrostachys*, *Myrosmodes*, and *Aa*) hereafter informally referred as to the *Altensteinia* clade (70% bts), and the second one consists of the predominantly low-elevation genera, *Prescottia* and *Pseudocranichis* (74% bts), that will be identified as the *Prescottia* clade. Relationships within the *Altensteinia* and *Prescottia* clades are resolved with few exceptions. Within the *Altensteinia* assemblage the sister relationship of *Aa* and *Myrosmodes* is not resolved, but the clade containing these taxa is highly supported (100% bts). A surprising finding of this analysis is the placement of the monotypic *Pseudocranichis thysanochila* in the *Prescottia* assemblage and its highly supported (84% bts) sister relationship to *Prescottia tubulosa*.

ITS sequence analysis.- The raw aligned matrix of the ITS region consisted of 781 characters. In this matrix a total of 130 base pairs in eight ambiguously aligned regions were found. After the inclusion of the INAASE characters, the ITS aligned matrix consisted of 659 total characters, 329 variable characters (49.9%) and 252 (38.54%) parsimony informative characters (Table 2.5). Parsimony analysis employing this data matrix yielded 16 equally parsimonious trees of 1,219 steps, a CI of 0.57, and a RI of 0.75. Relationships in the strict consensus tree for the most part are resolved and well supported with only three clades receiving less than 50% bootstrap (bts) (Fig. 2.6). Cranichideae is highly supported as monophyletic (76% bts) and the recovered clades correspond well to most of the subtribes that have been recognized previously. These results differ from the ITS tree of Salazar et al. (2003) in that the levels of clade support in that study were generally lower and the monophyly of Cranichideae was not supported. In the current analysis the first clade to diverge at the base of the tree corresponds to a moderately supported clade (71% bts) containing *Pachyplectron* and Goodyerinae (100% bts) sister to the remaining spiranthoids. This clade is followed by Galeottiellinae which is highly supported (98% bts) as sister to all remaining Cranichideae corroborating its segregation from Spiranthinae as proposed by Salazar et al. (2002a). The West African genus *Manniella* is strongly supported (99% bts) as sister to the core spiranthoids. The core spiranthoid clade is highly supported (94% bts) and comprises four lineages, three of them are moderately to strongly supported, but their relationships to each other received bootstrap support of less than 50%. Prescottiinae are polyphyletic comprising once again two clades: the *Altensteinia* and *Prescottia* clades. The *Altensteinia* clade is monophyletic and strongly supported (84% bts) as sister to the Cranichidinae, Spiranthinae, and *Prescottia*-

Pseudocranichis clades. The monophyly of Cranichidinae is moderately supported (76% bts), the relationships within this lineage are well resolved, but its sister relationship to the Spiranthinae and *Prescottia-Pseudocranichis* clades is not statistically supported. Spiranthinae is strongly supported as monophyletic (100% bts), but its placement as sister to *Prescottia-Pseudocranichis* is not supported. The *Prescottia* assemblage did not receive bootstrap support as monophyletic although the internal relationships are well resolved and strongly supported. Within this assemblage the sister relationship of *Pseudocranichis thysanochila* to *Prescottia tubulosa* is highly supported (99% bts).

Incongruence tests.- A comparison of the bootstrap percentages for each of the recovered clades across the independent analyses revealed a single case of “soft incongruence” (Mason-Gamer & Kellogg, 1996). This topological incongruence was found in the ITS phylogeny where the *Altensteinia* clade was placed sister to the rest of the core spiranthoids (Cranichidinae, Spiranthinae and *Prescottia-Pseudocranichis*) with a low bootstrap value (<50%) (Fig. 2.6) unlike the *trn*L-F parsimony based analyses in which the position of the Cranichidinae has shifted, but again with no statistical support (<50% bts) (Figs. 2.5).

The results of various pairwise 2-way, 3-way and 4-way tests employing the ILD test to determine the significance of the incongruence observed between the different data partitions are summarized in Table 2.6. These tests revealed that the partitions (nuclear locus vs plastid loci, noncoding vs coding loci and ITS vs each plastid locus) are not significantly incongruent ($p > 0.01$). As a result, all data sets were combined and analyzed.

Combined analyses of ITS+*trn*L-F+*rbc*L+*atp*B+*psa*B.- The combined data matrix with recoded ambiguous regions consisted of 6564 total characters, 1,544 (23.54%) of which are variable and 942 (14.35%) parsimony-informative characters (Table 2.5). Analysis of this data matrix found a single most parsimonious tree of 3,572 steps with a CI of 0.62 and a RI of 0.75 (Fig. 2.7). The tree is fully resolved and the majority of the recovered clades are highly supported as monophyletic. Only two major clades within the core spiranthoids received low bootstrap values. Highly supported clades include a monophyletic Goodyerinae (100% bts) and *Pachyplectron* (100% bts) as sister to all remaining Cranichideae, followed by *Galeottiella sarcoglossa* (100% bts), and then *Manniella cypripedioides* (100% bts) as sister to the core spiranthoids (100% bts). The weakly supported clades involve the sister relationship of Cranichidinae to a poorly supported clade (53% bts) comprising the *Altensteinia* (95% bts), the Spiranthinae (100% bts) plus and *Prescottia-Pseudocranichis* (93% bts) clades. The sister relationship between Spiranthinae and *Prescottia* is also supported by a low bootstrap percentage (69% bts). Inter-generic relationships within the monophyletic *Altensteinia* clade are completely resolved. In this last clade, *Myrosmodes* is embedded within *Aa*, but the paraphyly of *Aa* is weakly supported (65% bts). *Prescottia*, including *Pseudocranichis*, forms a strongly supported monophyletic clade (93% bts). Within it, *Pseudocranichis thysanochila* is allied to *Prescottia tubulosa* with a high support (100% bts).

A parsimony analysis with the same data set and composite loci but without ambiguous regions or recoded characters (see Table 2.5 for statistics) was included. In this case the data matrix consisted of 6,550 base pairs in length with 1,530 (23.36%) variable characters, and 928 (14.1 7%) parsimony informative characters. Analyses with this matrix yielded three most parsimonious trees with a length of 3,270 steps, a CI of 0.60, and a RI of 0.75. The topology of this strict consensus tree is almost identical to the tree that resulted from the analysis including recoded ambiguous regions with the only differences being that relationships within *Myrosmodes* are not resolved and the embedding of *Myrosmodes* in *Aa* is moderately supported (78%bts) (Fig. 2.8).

Bayesian analyses

Bayesian analysis ITS+*trn*L-F+*rbc*L+*atp*B+*psa*B.- Overall, the Bayesian analysis using the combined data set of five loci without recoded and ambiguous regions resulted in a less resolved majority-rule consensus tree (Fig. 2.9) than the parsimony consensus tree with the same dataset (Fig. 2.8). A comparison of the two trees reveals a single major topological difference within the core spiranthoids. Parsimony shows Cranichidinae sister to the other core spiranthoids (only 51% bts), but the Bayesian analysis puts the *Altensteinia clade* in this position (only 0.74 pp). A few additional topological changes occur within the Spiranthinae mainly regarding the placement of *Stenorrhynchos*.

2.4. DISCUSSION

The contribution of the molecular loci used in this study

Some authors have shown that non-coding and non-transcribed gene regions, unlike coding genes, experience more rapid evolutionary rates most likely due to their more limited constraints (Li, 1997). Consequently, noncoding or nontrascribed regions are generally used in phylogenetic studies at lower taxonomic levels (Hillis et al., 1996). This study uses a combination of both noncoding regions (ITS and *trn*L-F) and protein-coding genes (*rbc*L, *atp*B and *psa*B) to infer phylogenetical relationships among closely related genera. Even though the variation observed in all the conducted analyses at each loci is in agreement with the expectation that non-coding gene regions (intron and spacer regions) are more variable than coding genes, it is worth noting that the more conserved coding genes (*rbc*L, *atp*B and *psa*B) contribute informative characters to the combined analysis since their exclusion changes the structure of the resulting trees (analyses not shown).

Phylogeny inferred from the combined analyses

Because the matrix with recoded characters integrate information from ambiguously aligned regions from ITS and the *trn*L-F non-coding loci, I favor the results from these analyses over the complete exclusion of them. Analyses performed using maximum parsimony with the combined data set including recoded ambiguous regions resulted in a single most parsimonious tree. Since this tree is fully resolved, and for the most part well supported, as inferred by bootstrap percentages and decay indices, it is taken as the best hypothesis of relationships for this study. Thus, unless otherwise stated, the discussion refers to the phylogenetic hypothesis from parsimony analyses with recoded treatments (Figs. 2.7) and the Bayesian analysis excluding recoded regions (Fig. 2.9).

Phylogenetic relationships in the Cranichideae. The phylogeny presented here supports a monophyletic origin for members of the Cranichideae (100% bts) as circumscribed by Dressler (1993), unlike previous published studies (Clements et al., 2002; Salazar et al., 2003). However, this study included only a small outgroup sampling because it was not specifically designed to be a rigorous test of the monophyly of Cranichideae. As such, the strong support for the monophyly of the Cranichideae *sensu* Dressler (1993) revealed by this analysis should be tentatively accepted.

Goodyerinae and Pachyplectroninae clade. The sister relationship between Pachyplectroninae and Goodyerinae seen in almost all independent or combined analyses are consistent with morphology as members of these lineages share a labellar spur (Dressler, 1993; Szlachetko, 1995). This result is consistent with other phylogenetic studies (Kores et al., 2000; Kores et al., 2001; Salazar et al., 2003) and supports either the placement of *Pachyplectron* within Goodyerinae in the most updated classification of the family (Chase et al., 2003) or its recognition as a separate subtribe *sensu* Schlechter (1926) followed by Dressler (1981; 1993) and Szlachetko (1995).

Galeottiellinae clade. In analyses where this taxon was included, *Galeottiella sarcoglossa* is sister to the Manniellinae and all remaining spiranthoids. The placement of *Galeottiella* is strongly supported (bts=100%, di=20, pp=1.00), corroborates the findings of previous molecular studies (Salazar et al., 2003), and supports its segregation from the Spiranthinae.

As a subtribe, Galeottiellinae was recently proposed by Salazar et al. (2002a) to accommodate the morphologically distinctive *G. sarcoglossa* previously included in subtribe Spiranthinae. According to Salazar and others (2002a), *Galeottiella* can be readily characterized by the leaf veins sunken on the adaxial surface and prominent on the abaxial surface, the labellum free from the column, the connate lateral sepals for one third their length, the fleshy concave labellum, the blunt and bilobed rostellum, and the thick and short viscidium.

Manniellinae clade. According to all analyses Manniellinae occupies an isolated position as sister to the core spiranthoids with the exception of *Galeottiella*, and its placement is strongly supported (bts= 100%, di= 14, pp= 1.00). *Manniella*, the only genus of this subtribe, contains two species and is characterized by a column strongly bent inwards (at anthesis), conspicuous staminodia and a tubular nectary (Salazar et al., 2002b). *Manniella* had been allied in the past with the genus *Stenoptera* (Reichenbach, 1881) and with the Spiranthinae (Dressler, 1981; Garay, 1982; Dressler, 1993). The twice bent column of *Manniella* (at least in recently opened flowers) superficially resembles the column of *Gomphichis* and *Stenoptera*, but its straightening later in development makes this feature a unique autapomorphy for *Manniella.* The genus has been variously classified within Cranichidinae (Schlechter, 1911), Spiranthinae (Garay, 1982) and within its own subtribe (Schlechter, 1926; Dressier, 1993; Szlachetko, 1995; Szlachetko & Rutkowski, 2000; Chase et al., 2003). The results presented here strongly support the recognition of subtribe Manniellinae.

Cranichidinae clade. Data from this study found Cranichidinae strongly supported as monophyletic (bts=100%, di=12, pp=1.00), but its exact sister relationship to the rest of the core spiranthoids is not completely certain. The resulting tree from parsimony analyses weakly supports the sister relationship of Cranichidinae to the other core spiranthoids (bts=53%, di=1). These results are corroborated by Bayesian analysis that places Cranichidinae in an unresolved, weakly supported polytomy (pp= 0.74) along with Spiranthinae and *Prescottia-Pseudocranichis*.

Since the establishment of Cranichidinae by Lindley (1840) its taxonomic history has been linked to the currently recognized prescottioid taxa on the basis of non-resupinate flowers. This is an example of how early classifications relied on few morphological characters because very few collections of tropical taxa were available for study. As more material and information became available at least two distinctive groups were found to be included in the Cranichidinae *s.l.* The segregation of Prescottiinae from the Cranichidinae better defined the latter as a monophyletic assemblage (Dressler, 1990). Cranichidinae *s.s.* (Dressler, 1990, 1993) is well differentiated by the *Calanthe* type velamen, a labellum united with the column, a straight column, a long rostellum with a pointed hamulus, and clavate, compact and hard pollinia. The monotypic genera *Fuertesiella* and *Nothostele*, and the small genus *Solenocentrum* were not available for study, and neither had been included in previous published works.

Based on herbarium specimens, however, their morphology (especially the pollinia and pointed rostellum) indicate these taxa are best classified in Cranichidinae. These observations are in agreement with Dressler's definition of the Cranichidinae (1993), but do not support the transfer of *Fuertesiella* and *Nothostele* to the Prescottiinae as suggested by González-Tamayo (1996). In addition, parsimony analyses consistently place *Pterichis* in Cranichidinae, and on morphological grounds (especially features of the column) the suggested morphological resemblance of *Pterichis* to other prescottioid genera by González-Tamayo (1996) is not supported.

Spiranthinae clade. The clade comprising genera belonging to subtribe Spiranthinae emerged as a well supported monophyletic group (bts=100%, di=37, pp=1.00) in all analyses. The subtribe includes the greatest number of species in the Cranichideae with over 400. Modern treatments of the Spiranthinae have been built on Schlechter's (1926) delimitation of Spiranthinae and varies greatly according to broad (Balogh, 1982) or narrow concepts (Garay, 1982) employed for the generic circumscriptions. Most current taxonomists agree that further attention is sorely needed to understand the complexity of this group, and most follow Garay's circumscription of the subtribe and genera (Dressler, 1993; Salazar, 2003). Other workers such as Szlachetko (1995) have treated the Spiranthinae in the sense of Garay (1982) as tribe Spirantheae subdivided into subtribes Prescottiinae, Spiranthinae, Stenorrhynchidinae, Cyclopogoninae, Manniellinae and Pachyplectroninae on the basis of column structure, especially rostellum and viscidum morphology. Szlachetko's spiranthoid subtribes render Spiranthinae as currently understood polyphyletic (Fig. 2.20). Some advanced features of the Spiranthinae include the adherence of the labellum to the sides of the column and the presence of dimorphic tetrads, even though these are not synapomorphies found exclusively in the subtribe (Salazar, 2003; Salazar et al., 2003). Additional characteristics of the Spiranthinae include the fascicled roots, resupinate flowers, and saccate labellum with basal nectar glands (Dressler, 1993).

The combined parsimony analysis shows that the Spiranthinae are sister to the *Prescottia* group, but this relationship is only weakly supported (bts=69%, di=2). The Bayesian analysis did not resolve the position of Spiranthinae. Common morphological features shared by *Prescottia* and Spiranthinae are the spiranthoid retrorse glands at the base of the labellum and the *Spiranthes* type velamen.

Phylogenetic relationships in the Prescottiinae. The analyses presented here indicate that Prescottiinae are not monophyletic as circumscribed by Dressler (1990; 1993) or Szlachetko (1995), but rather that the subtribe consists of two highly supported clades informally referred to as the *Altensteinia* clade and the *Prescottia* clade. The *Altensteinia* clade comprises genera that are mostly Andean in distribution (*Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, and *Stenoptera*), whereas the *Prescottia* clade includes all sampled species of *Prescottia* plus the monotypic genus *Pseudocranichis*. Although *Pseudocranichis thysanochila* has a restricted distribution in Mexico, *Prescottia* is broadly distributed in the Neotropical lowlands. As indicated before, a paraphyletic Prescottiinae was also reported by Salazar et al. (2003).

***Altensteinia* clade.** The independent and combined parsimony analyses support the monophyly of the *Altensteinia* clade (bts=95%, di=7, pp=1.00). All parsimony analyses based on chloroplast independent sequences place the *Altensteinia* clade sister to a clade with two inclusive subclades: Spiranthinae and the sampled species of *Prescottia* and *Pseudocranichis*, or in an unresolved clade with these taxa. In contrast, the nuclear phylogeny from parsimony analysis (Fig. 2.6) and the Bayesian tree (Fig. 2.9) place the *Altensteinia* clade sister to the rest of the core spiranthoids (i.e., subtribe Cranichidinae, Spiranthinae and *Prescottia* plus *Pseudocranichis*). These relationships, however, in all instances were only low or moderately supported by bootstrap percentages ("soft incongruence"). In fact, the ILD test did not find significant incongruence ($p<0.01$) among the different combinations of nuclear and chloroplast data sets.

Inter-generic relationships within the *Altensteinia* clade are well resolved and supported (Fig. 2.7). The clade comprising both *Aa* and *Myrosmodes* is highly supported (bts=100%, di=21, pp=1.00). The monophyly of *Aa*, however, is rejected by the placement of *Myrosmodes* within it but usually with low to moderate statistical support (bts=65-78%, di=1, pp=0.77). On morphological grounds, both genera display a suit of adaptations that have helped them to cope with the harsh and cold environments of the highest ecosystems of the Neotropical mountain chains (páramos). These characters include dwarf stature, lateral inflorescences, small, glabrous, creamy or whitish flowers, a glabrous column, and a large stigma. *Aa* is a highly variable genus of considerable size (about 25 species), distinguished from *Myrosmodes* by possessing hyaline bracts and sheaths and a calceolate labellum with an involute margin. Garay (1978) and Dodson (1994) recognize two informal groups within the genus: one comprises those species with small bracts and the other one contains species with long bracts. Additional sampling, however, is needed to test whether or not the proposed sectional rank is supported. *Myrosmodes* as currently circumscribed comprises nearly 12 species and is diagnosed by the imbricate, infundibuliform, scarious sheaths and bracts, the accrescent peduncle after anthesis, the basipetal inflorescences (flowers opening from the top to the bottom), and the tubular labellum with moniliform hairs. Vargas (1997) identified three synapomorphies supporting the sister relationship of *Aa* and *Myrosmodes*: the lateral inflorescences, spherical labellum glands, and a reniform viscidium. Both genera have been treated in the past under the genus *Altensteinia* until Garay (1978) restored *Myrosmodes*. Most current orchid taxonomists follow Garay (Dodson, 1994; Vargas, 1995) by recognizing both *Aa* and *Myrosmodes*.

Sister to *Aa* and *Myrosmodes* is the small genus *Porphyrostachys* (bts=100%, di=18, pp=1.00). The two currently recognized species of the genus are included in this phylogeny. On molecular grounds, the genus is uniquely characterized by a 3-base pair insertion at position 227 of the nuclear ITS alignment. Some morphological features distinguishing the genus include the presence of a long column foot, a tubular nectary, and a cochleate labellum.

They appear to be morphologically and geographically intermediate between the middle and high elevation allies of the *Altensteinia* group. For instance, *P. parviflora* possess small, whitish flowers, and hyaline sheaths and bracts like *Aa* and *Myrosmodes*, whereas *P. pilifera* has medium-sized red flowers and the sheaths and bracts are greenish and herbaceous as the remaining members of the *Altensteinia* group. *Porphyrostachys parviflora* was initially recognized as a variety of *P. pilifera* (under *Stenoptera*). However, its peculiar morphology, character differences, and placement in this phylogeny supports it recognition as a separate species of *Porphyrostachys*.

Gomphichis diverges next and its sister relationship to *Porphyrostachys*, *Aa*, and *Myrosmodes* is strongly supported (bts=100%, di=7, pp=1.00). The genus is characterized by a one base pair deletion at position 685 of the ITS alignment and by an eight base pair insertion/deletion at position 833 of the *trn*L-F alignment. The morphological features that distinguish *Gomphichis* from its allies are the sigmoid column, fleshy labellum, and the hairy and sharply bent flowers that form a right angle with the ovary.

Sister to these four genera is *Altensteinia* (bts=98%, di=4, pp=1.00). This genus was the first described among the members of the clade (Kunth, 1816) and has been variously interpreted until Reichenbach (1854) redefined *Altensteinia* by segregating from it the currently recognized *Aa* and *Porphyrostachys*. *Altensteinia* is easily distinguished from its close relatives by an erect and hairy column, an erect, flaring to galeate labellum, a lobulate clinandrium, and a small stigma.

Finally, the genus *Stenoptera* is the most basal member of this assemblage, and is sister to all the remaining elements of the clade (bts=95, di=1, pp=1.00). Its placement in a position distant from *Gomphichis* was unexpected, particularly because of the superficial morphological resemblance of their flowers which has resulted in taxonomic confusion (Lindley, 1840). In the past, *Gomphichis* was usually treated under the genus *Stenoptera*, although a number of characters delimit these genera. *Stenoptera* can be diagnosed by fused sepals that form a long tube or nectary, a footless column, and a galeate-fornicate slightly fleshy labellum. The morphological resemblance between *Gomphichis* and *Stenoptera* may be the result of shared plesiomorphies, which are also revealed by the placement of *Stenoptera* in the cladogram.

In summary, the *Altensteinia* clade is monophyletic and comprises at least five genera (*Aa*, *Altensteinia*, *Gomphichis*, *Porphyrostachys*, and *Stenoptera*) and approximately 80 species that are of mainly terrestrial, but also facultative epiphytes inhabiting the middle and high elevation montane forests and páramos of southern Central America, the Andean region and the Guayana highlands in South America. The recognition of a sixth genus, *Myrosmodes*, is tenuous, and may ultimately prove to be better accommodated in *Aa* with more taxon sampling. All these genera have basal pseudo-petiolate leaves, an elongate, prominent, glabrous or pubescent column and petals and labellum free from the sepals in common.

***Prescottia* and *Pseudocranichis*.** One of the most surprising results uncovered by these phylogeny reconstructions is the placement of *Prescottia* outside of the *Altensteinia* clade, and the association of *Pseudocranichis* with *Prescottia tubulosa*. This strongly supported outcome was unexpected, mainly because of the radically different floral morphologies of these species. The genus *Prescottia* as currently recognized consists of about 25 species and it is easily diagnosed by glabrous small flowers, an erect, calceiform and spurless labellum with spiranthoid glands at the base, petals and labellum free from the column, connate sepals forming a sepaline cup, and a short and glabrous column. On the other hand, the monotypic genus *Pseudocranichis* can be recognized by a lax inflorescence, small, glabrous flowers; a bi-lobed labellum with a fringed apex; a disc with three-callose thickened and pubescent veins; a long-pubescent column; and a bi-lobed, large, saddle-shaped stigma. The genus was proposed by Garay (1982) for a species described in *Cranichis* and included in subtribe Spiranthinae. This is a poorly studied taxon known only from few collections. It is endemic to Oaxaca, Mexico. Szlachetko (1995) first noticed the morphological similarity of *Pseudocranichis* to members of the Prescottiinae (e.g., the stigma shape similar to the genus *Altensteinia*, reduced hamulus, simple column, and soft-pollinia), and placed the genus in this subtribe. A relationship of *Pseudocranichis* to *Altensteinia* was shown by Vargas (1997) in his morphology-based cladistic analysis of the Cranichideae and Prescottiinae. However, the molecular phylogenetic tree presented here shows *Pseudocranichis* embedded in *Prescottia* and strongly supports its position as sister to *Prescottia tubulosa* (bts=100%, di=11, pp=1.00). This finding confirms hypothesized affinities of *Pseudocranichis* to the Prescottiinae *s.l.* (i.e., to *Prescottia*) and not to the *Altensteinia* group (Szlachetko, 1995; Vargas, 1997).

The *Prescottia-Pseudocranichis* clade includes terrestrial, rarely epiphytic, orchids inhabiting the lowlands of the Neotropics. They have in common basal leaves and glabrous sepals and petals that there are free from the column. Although the center of diversity of *Prescottia* is Brazil, and some species have broad distribution ranges, it appears that the two endemic species of the Mexican-Guatemalan regions (i.e., *Prescottia tubulosa* and *Pseudocranichis thysanochila*) have undergone differentiation possibly in response to relatively dry environments and calcareous soils.

Evolution of selected characters

Three major morphological features and their states proposed by Dressler (1990) to define the Prescottiinae were optimized onto the tree resulting from molecular reconstruction (Fig. 2.14). These characters are presented in Figs. 2.21-2.23 and discussed in light of the available information.

Evolution of flower position. The position of the flowers, i.e. resupinate vs nonresupinate, has long been a major criterion for placing the Prescottiinae in the Cranichidinae in early classification schemes (see taxonomic history above). The resulting consensus tree shows that nonresupinate flowers evolved once from an ancestral resupinate condition and were retained in the *Altensteinia*, *Prescottia-Pseudocranichis*, and Cranichidinae clades (Fig. 2.10). Resupination in the Spiranthinae is interpreted as a reversal as has been suggested previously by Dressler (1990; 1993).

Evolution of pollinia. It is evident that most clades of the core spiranthoids (*Altensteinia*, Spiranthinae, and *Prescottia-Pseudocranichis* clades) have retained the plesiomorphic condition of the tribe in which pollen grains are soft, granular, and loosely held together by small amounts of elastoviscin separating easily as they are shed out of the anther (Fig. 2.11). In contrast, the Cranichidinae show hard, solid and coherent pollinia, a character that constitutes a unique synapomorphy for this subtribe. It is interesting to note that sectile pollinia (pollen grains aggregated into packets or massulae) characterize the Goodyerinae, but this pollinium type is absent in *Pachyplectron*, classified as a member of the Goodyerinae in the system of Chase et al. (2003).

Evolution of hamulus. A hamulus, as defined by Rasmussen (1982) and Dressler (1993), is a pollinium stalk of rostellar origin which is present in subtribe Cranichidinae, but absent in all the remaining spiranthoid orchids (Fig. 2.12). Although this character has been examined in detail by Rasmussen (1982) and Szlachetko and Rutkowski (2000), there is still a great deal of misunderstanding in its interpretation. In fact Salazar et al. (2003, p. 789) stated that "a hamulus is present in the genus *Gomphichis* and likely in other prescottioid genera besides the Cranichidinae *s.s.*" and labeled this character as a putative synapomorphy linking the mainly Andean members of the Prescottiinae (his *Stenoptera* clade) to the Cranichidinae. Nonetheless, a careful examination of the column of the Prescottiinae *s.l.* and Cranichidinae *s.s.* from living plants, liquid preserved material, and herbarium specimens (more than 2000 specimens of *Gomphichis*, ca. 2500 specimens of other prescottioid genera, and a number of Cranichidinae specimens), leads me to conclude that a hamulus is absent in the Prescottiinae *s.l.* (Fig. 2.13) and present only in the Cranichidinae *s.s.* (Fig. 2.14). These observations are largely in agreement with previous morpho-anatomical data published on this subject in which all prescottioid and cranichioid genera were included (Rasmussen, 1982; Szlachetko & Rutkowski, 2000).

Velamen. Another feature proposed by Dressler (1990; 1993) to characterize the Prescottiinae is the velamen type. It may be that a velamen of the *Spiranthes* type is indeed a synapomorphy shared by the Prescottiinae *s.l.* and Spiranthinae. This character, however, has not yet been studied in enough taxa to test whether it is a reliable synapomorphy for these groups in an unbiased phylogenetic context.

Rostellum. The rostellum (tissue that separates the anther from the fertile stigma) is laminar and almost undifferentiated in all Prescottiinae, but conspicuous and well-developed in the remaining spiranthoids. When this character is considered alone, there is a clear split in the Cranichideae between taxa possessing a conspicuous rostellum and those with a laminar one.

Biogeography. The extant genera of the Cranichideae are mostly neotropical, with only a few exceptions. These exceptions include some members of the Goodyerinae found in North America, Europe, Asia and Oceania (Australia, New Zealand and the Pacific Islands); the Pterostylidinae centered in Australia, New Zealand and the Pacific Islands (Oceania); and the Manniellinae with two species native to Africa. The greatest diversity of the tribe is found in the Neotropics and these genera fall into at least five major clades. The plotted distribution depicted in Fig. 2.15 demonstrates that the ancestral areas of the Cranichideae are found in Oceania and the Old World. Although in this study only taxa from South America have been sampled, when the current global distribution of the Cranichideae is considered, it becomes apparent that the Cranichideae may have evolved from an ancient, widespread ancestor at a time when all the continents formed a large land mass called Pangaea (Scotese, 1997). This ancestor may have given rise to the extant species of *Galeottiella* that possibly had a northern boreal distribution or to ancient Gondwanaland relics before the breakup of Africa from South America around 80 million years ago (Raven & Axelrod, 1974). After the split of Gondwana the African precursor of *Manniella* and the New World spiranthoids may have continued to evolve in isolation. It seems that the ancestor of the extant New World spiranthoids was once part of a widespread flora common to South America and North America and speciation was promoted by long-distance dispersal to novel habitats.

The modern Cranichidinae exhibit a mainly South American distribution with few endemic genera (not included in this study) (Dressler, 2004). The subtribe mainly inhabits the foothills of montane forests, and only the genus *Pterichis* reaches high elevations. Nonetheless, due to the paucity of sampling in the Cranichidinae, no conclusive ideas about the plesiomorphic area for the subtribe can be attained.

The Spiranthinae is the major tropical New World group of the Cranichideae, with the exception of species of *Spiranthes* and *Cyclopogon obliquus* (Pridgeon et al., 2003) which are broadly distributed and largely inhabitants of the northern temperate zones of North America, Europe and Asia, and tropical Oceania. Although sampling of this subtribe in the present study is limited and biased towards South American centered species, present-day distribution patterns of the Spiranthinae suggest that they may be remnants of a widely distributed ancestor that may have had a continuous distribution rapidly expanded by long distance dispersal and vicariance at various stages in its phylogeny. Further detailed ongoing studies of this subtribe by Salazar and collaborators (Salazar et al., 2003) may help to clarify biogeographic patterns within the Spiranthinae.

The ancestral geographic range of Prescottiinae *s.l.* (including the *Altensteinia* and *Prescottia-Pseudocranichis* clades) is South America with possible dispersals to Central America, the Caribbean and Florida.

The clade comprising *Prescottia* and *Pseudocranichis* shows a broad distribution range and ecological tolerance across the Neotropics with south America as the major center of diversification and speciation. Given that most species of this clade occur in the South American lowlands, it seems quite likely that their common ancestor was adapted to warmer, humid, and wet climates before they reached Central America, the Caribbean and South Florida via long distance dispersal. In these new environments, they found suitable habitats and opportunities to colonize and spread. This hypothesis is supported by the presence of three wide ranging South and Central American species (*Prescottia oligantha*, *Prescottia pellucida*, and *Prescottia stachyodes*) that also reach the Caribbean (Ackerman, 1995) and Florida (*Prescottia stachyodes*).

Contrary to most *Prescottia* species, the position of *Pseudocranichis thysanochila* as sister to *Prescottia tubulosa* suggests that this species pair may have evolved from an ancestor growing under moist and humid conditions that gradually adapted to relatively dry environments.

The *Altensteinia* clade is restricted primarily to the upper mountain chains of South America and southern Central America (Fig. 2.17), which have undergone many geological and climatic changes during the Cretaceous, Tertiary and Quaternary. These include the separation from Africa, the uplift of the Andes, the formation of the Isthmus of Panama and the Amazon basin, and the marine incursion from the Caribbean (Gentry, 1982; Rich & Rich, 1983). Furthermore, climatic changes, especially glacial-age cooling and drying during the Quaternary and the historical events of Andean orogeny, undoubtedly had significant implications for the distribution and evolution of the plant taxa of high tropical mountains (Raven & Axelrod, 1974) including orchids of the *Altensteinia* clade. Considering these geological and climatic events, three important remarks can be made about the present distribution of species of *Altensteinia*. First, because the Andean Cordillera is approximately five million years old and was recently uplifted (Simpson, 1975), members of the *Altensteinia* clade may be regarded as recently evolving genera still in the process of evolution and differentiation. The short branch leading to this clade supports the idea of a recent origin for these genera, probably in an early or middle period of the Pleistocene when highly dynamic changes were taking place throughout the Andes. Second, the climatic history of the Andes influenced the horizontal and vertical migration of many taxa by range expansion across the low Andean montane forests (van der Hammen & Cleef, 1986) and gradually to higher altitudinal habitats, resulting in changes in the composition of plant communities due to competition and displacement of populations (Colinvaux, 1996). The resulting phylogeny suggests that taxa of the *Altensteinia* clade may have originated from a South American lowland ancestor, like other elements of the flora of the Adean region (Simpson, 1975). Influenced by both the humid and dry glacial periods of the Pleistocene, this ancestor may have expanded its horizontal range by spreading over short distances. Likewise, the slow migration of taxa into higher-altitudinal habitats (van der Hammen & Cleef, 1986), led them to gradually adapt to temperate environments (i.e., cool, cold, and freezing temperatures and moist and humid climates). Thirdly, migration of floristic elements from distant areas into novel and isolated habitats might have been possible by long distance dispersal. Range expansion of new populations of the composite taxa of the *Altensteinia* clade leading ultimately to speciation may have been facilitated by the numerous and dust-like seeds easily dispersed by wind. Their establishment and long-time survival, however, may have depended on their reproductive success assured by flower and fruit availability and self-fertilization. Flowering and fruiting is almost continuous throughout the year in most if not all genera of the *Altensteinia* clade due to successive flower opening.

This strategy, in conjunction with facultative out-crossing and self-fertilization, may have played a significant role in the radiation and speciation of these genera in the upper Andes by providing greater opportunities for pollination to occur in places where pollinators are scarce (van der Pijl & Dodson, 1966; Catling, 1990) thereby resulting in a greater number of seeds for dispersal. Self-fertilization has been documented in geographically widespread orchid groups and suggested as a major factor in promoting the exploitation of higher latitudinal habitats (Catling, 1990; van der Cingel, 2001). Although there are some differences between latitudinal and tropical high elevation habitats, these mechanisms may explain the disjunct distribution of the predominantly Andean genus *Gomphichis*, in the summits of the Guayana highlands (Steyermark, 1986), and *Aa* in the Costa Rican páramos (Barringer, 1984).

Altitudinal distribution. A close examination of the elevation ranges within the Cranichideae reveals that the evolutionary history of the Neotropical terrestrial orchids matches a progressive elevational gradient from low to high (Fig. 2.16). The cladogram indicates a single origin for the genera restricted to the high elevations from an ancestor centered in the low and mid-elevations. A marked preference for high altitudes is shared by all members of the *Altensteinia* group. Both *Aa* and *Myrosmodes* are found almost exclusively at the highest elevations in the Andes (above 3500 m) and in disjunct populations in the mountains of Costa Rica. Some species of *Myrosmodes* grow at the highest elevations of any orchid on Earth. Many species of *Porphyrostachys* and *Gomphichis* are distributed above 2500 m, although a number of species also occur at middle elevations. *Altensteinia* is found in the high altitudinal belt between 2500 to 3500 m. The most basal genus, *Stenoptera*, occurs principally below 2500 m. The radiation and speciation of the genera of this clade into the high altitudinal zone of the Neotropics is certainly the result of the evolution of a tremendous degree of specialization in response to environmental extremes, especially diurnal and nocturnal shifts in temperature that may reach the freezing point (Rundel, 1994). As a result, members of this clade are humid dependent and cool, cold and freezing tolerant. These characteristics are evidenced by the presence of a few species below 2500 m (mid-elevations). Within this clade, *Aa* and *Myrosmodes*, can be considered high elevation specialists due to their restricted distribution in the highest zone of the Andes and the high mountain ranges of Central America. These plants have developed numerous morphological traits that are likely genetically fixed and allow them to cope with the moist, freezing, and windy environments of the páramos and jalca and the arid conditions of the puna (Rundel, 1994). Some of the specialized features found in plants of these zones (Miller, 1994; Leuschesner, 2000) and observed in *Aa* and *Myrosmodes* include: small stature; coriaceous leaves with thick walls, thick cuticles, and a shiny upper surface; stomata restricted to the lower surface; sheaths completely covering the peduncle; compact and cylindric, inflorescences; and numerous, small flowers, subtended by bracts. In addition, species of these genera have succeeded in this demanding environment by maximizing resources that contribute to survival and reproduction (fitness). Some examples involve an acaulescent rosette habit (> photosynthetic/thermal capacity) (Cabrera et al., 1998), development of leaves only after anthesis is completed (> resources towards reproductive organs), successive opening of the flowers (> availability of flowers over time), self-fertilization (> reproductive assurance in the absence of external pollinators), facultative out-crossing (> genetic variability and gene flow), and vegetative reproduction (> fecundity).

The other members of the clade (*Porphyrostachys*, *Gomphichis*, *Altensteinia* and *Stenoptera*) are common at much lower elevations, reaching their elevation limit at tree line (about 3500 m) and therefore showing fewer adaptations to high altitudes. These plants have in common the following characteristics: medium size, facultative epiphytism, distant sheaths covering the peduncle, compact or loose many-flowered inflorescences; dense or sparse floral indumentum; and medium-size flowers.

The Spiranthinae exhibit a wide elevational range with their members occurring from sea level to near 3500 m. In the *Prescottia-Pseudocranichis* clade there is a remarkable preference for those habitats of low and middle elevations. Most species of *Prescottia* are found at elevations below 1000 m, a few grow in the mid-elevation belt up to 2500 m, and only two species attain high elevations. The other taxon of this clade, *Pseudocranichis thysanochila*, has only been reported growing at mid-elevations. Most genera of the Cranichidinae are found at middle elevations with the exception of *Pterichis* that flourishes in the upper montane forests below 3500 m. The remaining taxa of the Cranichideae occupy the lowlands and foothills of the mountains. For instance, species of Manniellinae and Goodyerinae are primarily lowland elements of the paleotropics, and the monotypic *Galeottiella* is found mainly at middle altitudes in the montane and upper montane forests of Mexico and Guatemala.

Phylogenetic status of the Prescottiinae. The reconstructed phylogeny using parsimomy and Bayesian inferences summarized in Fig. 2.18 shows that Prescottiinae consist of two strongly supported clades: the *Altensteinia* and *Prescottia* clades. It also demonstrates the following: first, that Prescottiinae are polyphyletic; second, both clades of the Prescottiinae show an affinity to Spiranthinae rather than Cranichidinae as suggested by Dressler (1990, 1993) and Szlachetko (1995); and, third, that *Prescottia* is paraphyletic because *Pseudocranichis* is nested within it. Consequently, these results indicate that no current or previous system of classification for these taxa is correct. For example, Dressler's delimitation of the Prescottiinae (1990; 1993) is not monophyletic (Fig. 2.19); the expanded Prescottiinae proposed by Szlachetko's (1995) is paraphyletic (Fig. 2.20); and, Chase et al.'s (2003) revised classification to include Prescottiinae in Cranichidinae in the sense of Dressler (1981) (Fig. 2.21) renders the latter polyphyletic.

In previous classifications, members of the Prescottiinae *s.l.* (*Altensteinia* and *Prescottia* clades) have been diagnosed by the following suit of characters: nonresupinate flowers, simple labellum, soft-pollinia, laminar rostellum, and *Spiranthes* type velamen (Dressler, 1990, 1993; Szlachetko, 1995). Because the *Altensteinia* and *Prescottia* clades appear not to be closely related to one another, their morphologies may be the result of shared plesiomorphies rather than shared ancestry. However, no distinctive morphological synapomorphies have yet been found for each of the monophyletic clades recovered and supported in this study. The lack of morphological characters supporting the monophyly of the separate *Altensteinia* and *Prescottia-Pseudocranichis* clades may reflect the paucity of knowledge about these terrestrial orchids. For example, very little is known about micromorphological and anatomical features of these orchids. Overall, the characteristic morphologies, habitat, and discrete geographic distributions exhibited by members of the *Altensteinia* and *Prescottia* clades suggest that they may be distinctive lineages. Factors that may have played a significant role during the evolution of the *Altensteinia* clade include the high altitude they inhabit, the low number of pollinators at such altitudes, and a shift to a predominantly autogamous breeding system.

In summary, results from the phylogeny indicate that the classification of the Prescottiinae and closely related groups of the core spiranthoids needs to be re-examined. These are the suggested options: 1) erect a new subtribe for the *Altensteinia* clade (Altensteininae) and include *Prescottia* and *Pseudocranichis* in the Spiranthinae; 2) place *Prescottia* and *Pseudocranichis* in their own subtribe (Prescottiinae) and establish a new subtribe for the *Altensteinia* clade; or, 3) recognize Prescottiinae *s.l.* as part of the Spiranthinae. In addition, since recognizing *Pseudocranichis* as a different genus renders *Prescottia* paraphyletic, it seems more logical to classify it within the genus *Prescottia* by transferring *Pseudocranichis thysanochila* to *Prescottia*. Finally, within the *Altensteinia* clade, although resolution and bootstrap support are only moderate for the sampled species of *Aa* and *Myrosmodes*, the evidence suggests that these genera may not be monophyletic. Additional sampling is needed within their full geographic ranges before any reclassification is considered.

2.5. CONCLUSIONS

The trees reconstructed from a composite of five plastid and nuclear loci: ITS, *trn*L-F, *rbc*L, *atp*B, and *psa*B suggest that the Prescottiinae as circumscribed by Dressler (1993) or Szlachetko (1995) are not monophyletic, but that the subtribe comprises two distinctive evolutionary lineages. These lineages (the *Altensteinia* clade and the *Prescottia* clade) are monophyletic and strongly supported as such, but the total evidence parsimony tree, although fully resolved, provides only moderate statistical support for their exact arrangement in the Cranichideae (see Fig. 2.18). Some gene trees place the *Altensteinia* clade sister to the remaining spiranthoids, whereas other gene trees place it as sister to the Cranichidinae. However, both outcomes are weakly supported. Furthermore, Bayesian analyses consistently place the *Altensteinia* clade sister to a clade containing the remaining core spiranthoids, but this is also only weakly supported (pp=0.74). Results from maximum parsimony and Bayesian analyses also suggest that all genera of the *Altensteinia* clade are monophyletic, with the possible exception of *Aa* within which *Myrosmodes* is embedded. As such, additional sampling of characters and species of these genera are needed to make conclusive decisions about their taxonomic status. The gene trees also strongly show that *Prescottia* is monophyletic only if *Pseudocranichis* is classified within it. Therefore, the taxonomic transfer of *Pseudocranichis* to *Prescottia* is strongly suggested.

Although it is clear from the reconstructed phylogenies that there are four major monophyletic assemblages within the core spiranthoids (the Cranichidinae, *Prescottia*, Spiranthinae, and *Altensteinia* clades) their relationships are not yet fully resolved. Short branches on the back bone of the tree comprising these lineages may be an additional indication of their recent origin and rapid radiation. This is not surprising given the fact that these spiranthoid groups are found primarily in the New World (the continent of most recent formation), especially Central and South America. Furthermore, members of the *Altensteinia* clade that inhabit the high Andes, which is a young geological area available for colonization only since the end of the Pliocene (Berry et al., 1995), may be the most recently evolved members of the spiranthoid orchids. It is likely that phylogenies constructed with more variable gene regions and greater sampling of species will help resolve inter-generic and inter-clade relationships among these rapidly evolving orchids.

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Table 2.1. Classification history of the genera of Prescottiinae in different systems of Orchidaceae

AUTHOR	MAIN DIVISIONS OF SYSTEM & GENERA
LINDLEY 1840	Tribe Neotteae Division Cranichidae (12 genera) *Prescottia, Altensteinia, Gomphichis, Stenoptera*
BENTHAM 1881	Tribe Neottieae Subtribus Spirantheae (82 genera) *Altensteinia, Prescottia, Gomphichis, Stenoptera*
PFITZER 1887; ENGLER & PRANTL 1889	Monandrae Acrotonae Subfamily Neottiinae Tribe Cranichideae (10 genera) *Altensteinia, Gomphichis, Stenoptera, Prescottia*
SCHLECHTER 1915	Subfamily Monandrae Disivion Acrotonae Tribe Polychondreae Group Cranichidinae (12 genera) *Aa* (*Myrosmodes*), *Altensteinia, Porphyrostachys, Prescottia, Stenoptera* (*Gomphichis*)
SCHLECHTER 1926	Subfamily Monandrae Division Acrotonae Tribe Polychondreae Subtribe Cranichideae Obtusirostellata (7 genera) *Gomphichis, Stenoptera, Altensteinia, Aa, Porphyrostachys, Prescottia*
MANSFELD 1937	Tribal Group Thrauosphaereae Tribe Neottieae Subtribe Cranichidinae
DRESSLER & DODSON 1960	Subfamily Orchidoideae Tribe Neottieae Subtribe Spiranthinae Cranichis alliance (12 genera) *Altensteinia, Porphyrostachys, Prescottia, Stenoptera*
VERMEULEN 1966	Family Orchidaceae Subfamily Epidendroideae Contribe Neottianthe Tribe Neottieae
BRIEGER 1974-1975	Tribe Spirantheae Subtribe Cranichidinae Acolumnata (11 genera) *Altensteinia* (including *Aa*), *Prescottia* Columnata (3 genera) *Gomphichis, Stenoptera, Porphyrostachys*

Dressler 1981	Subfamily Spiranthoideae Tribe Cranichideae Subtribe Cranichidinae (15 genera) **Altensteinia alliance** (7 genera) *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, *Stenoptera* Cranichis alliance (8 genera) *Baskervilla*, *Coilostylis*, *Cranichis*, *Fuertesiella*, *Ponthieva*, *Pseudocentrum*, *Pterichis*, *Solenocentrum*
Rasmussen 1985	Subfamily Neottioideae Tribe Neottieae Spiranthes group (46 genera)
Burns-Balogh & Funk 1986	Monandrous orchids Subfamily Spiranthoideae Tribe Cranichideae Subtribe Cranichidinae (15 genera) [Same as Dressler, 1981]
Dressler 1990	Subfamily Spiranthoideae Tribe Cranichideae Subtribe Prescottiinae (7 genera) *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, *Stenoptera*
Dressler 1993	Subfamily Spiranthoideae Tribe Cranichideae Subtribe Prescottiinae (7 genera) *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, *Stenoptera*
Szlachetko 1995	Monandrous orchids Subfamily Spiranthoideae Tribe Spirantheae Subtribe Prescottiinae (8 genera) *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, *Pseudocranichis*, *Stenoptera*
Chase *et al.* 2003; Pridgeon et al. 2003	Subfamily Orchidoideae Tribe Cranichideae Subtribe Cranichidinae (17 genera) *Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, *Prescottia*, *Pseudocranichis*, *Stenoptera, Nothostele, Solenocentrum, Baskervilla, Pseudocentrum, Ponthieva, Pterichis, Fuertesiella, Cranichis, Exalaria*

Table 2.2. List of species sequenced.

Genus	Species	Author	Collector	Number	Voucher
Aa	*leucantha*	(Rchb. f.) Schltr.	M. Weigend	2000-413	NY
Aa	*paleacea*	(Kunth) Rchb. f.	A. Alvarez	2845	NY
Aa	*calceata*	(Rchb. f.) Schltr.	A. Alvarez	2899	NY
Altensteinia	*virescens*	Lindl.	A. Alvarez	2685	NY
Altensteinia	*fimbriata*	Schltr.	A. Alvarez	2726	NY
Baskervilla	*colombiana*	Garay	E. A. Christenson	s.n. 4	QCNE
Brachystele	*polyantha*	(Rchb. f.) Burns-Bal.	G. Salazar	6007	NY
Chloraea	*reticulata*	Schltr.	M. Weigend	2000-361	NY
Cranichis	*longipetiolata*	C. Schweinf.	A. Alvarez	2672	NY
Cranichis	*engelii*	Rchb. f.	A. Alvarez	2693	NY
Cranichis	*ciliata*	(HBK) Kunth	A. Alvarez	2974	NY
Cyclopogon	*sp.*		A. Alvarez	2920	NY
Cyclopogon	*peruvianus*	(C. Presl.) Schltr.	A. Alvarez	2959	NY
Exalaria	*parviflora*	(Presl) Garay & Romero	L. Suin	1034	NY
Erythrodes	*arietina*	(Rchb.f. & Warm.) Ames	A. Alvarez	2924	NY
Galeottiella	*sarcoglossa*	(A. Rich. & Galeotti.) Schltr.	G. Salazar		MEXU
Gomphichis	*crassilabia*	Garay	A. Alvarez	2878	NY
Gomphichis	*valida*	Rchb. f.	A. Alvarez	2759	NY
Gomphichis	*traceyae*	Rolfe	A. Alvarez	2712	NY
Gonatostylis	*vieillardii*	(Rchb. f.) Schltr.	K. M. Cameron	985	NY
Goodyera	*pubescens*	(Willd.) R. Br.	K. M. Cameron	1064	NY
Goodyera	*repens*	(L.) R. Br.	K. M. Cameron	1112	NY
Kreodanthus	*simplex*	(C. Schweinf.) comb. nov. ined.	M. Weigend	2000-429	NY
Manniella	*cypripedioides*	Salazar, T. Franke, Zapfack & Beenken	G. Salazar	6323	K
Myrosmodes	*nubigenum*	Rchb. f.	A. Alvarez	2822	NY
Myrosmodes	*paludosum*	(Rchb. f.) C. Vargas	A. Alvarez	2894	NY
Myrosmodes	*cochleare*	Garay	A. Alvarez	2955	NY
Myrosmodes	*cochleare*	Garay	A. Alvarez	2961	NY

Genus	Species	Author	Collector	Number	Voucher
Pachyplectron	*arifolium*	Schltr.	T. J. Motley	1171	NY
Pelexia	*maculata*	Rolfe	D. Bennett	5590	NY
Platythelys	*querceticola*	(Lindl.) Garay	Kew-DNA	O-378	NY
Ponthieva	*sp.*		M. Leon	3041	NY
Ponthieva	*villosa*	Lindl.	A. Alvarez	2914	NY
Porphyrostachys	*parvifolia*	(C. Schweinf.) Garay	A. Alvarez	2891	NY
Porphyrostachys	*pilifera*	(Kunth) Rchb. f.	A. Alvarez	2699	NY
Prescottia	*stachyodes*	(Sw.) Lindl.	E. A. Christenson	s.n. 1	NY
Prescottia	*stachyodes*	(Sw.) Lindl.	A. Alvarez	2862	NY
Prescottia	*sp.*		C. Hajeckt	s.n. 1	NY
Prescottia	*oligantha*	(Sw.) Lindl.	A. Alvarez	2989	NY
Prescottia	*tubulosa*	(Lindl.) L. O. Williams	G. Salazar	6054	MEXU
Pristiglottis	*montana*	(Schltr.) Cretz. & J. J. Sm.	T. J. Motley	2151	NY
Pseudocranichis	*thysanochila*	(Rob. & Greenm.) Garay	P. Tenorio	17900	NY
Pterichis	*triloba*	(Lindl.) Schltr.	M. Weigend	244	NY
Pterichis	*acuminata*	Schltr.	A. Alvarez	2832	NY
Pterostylis	*oliveri*	Petrie	K. M. Cameron	1102	NY
Sarcoglottis	*acaulis*	(J. E. Sm.) Schltr.	A. Alvarez	2933	NY
Sarcoglottis	*grandiflora*	(Lindl.) Klotzsch.	A. Alvarez	2791	NY
Sauroglossum	*corymbosum*	(Lindl.) Garay	M. Weigend	2000-272	NY
Sauroglossum	*aurantiacum*	(C. Schweinf.) Garay	M. Weigend	2000-430	NY
Spiranthes	*romanzoffiana*	Cham.	J. Grant	3757	NEU
Spiranthes	*spiralis*	(L.) Chevall.	A. Alvarez	3015	QCNE
Stenoptera	*ecuadorana*	Dodson & C. Vargas	A. Alvarez	2913	NY, QCNE
Stenoptera	*acuta*	Lindl.	M. Weigend	2000-431	NY
Stenorrhynchos	*vaginatum*	Cogn.	A. Alvarez	2969	NY, PORT
Stenorrhynchos	*sp. nov.*		A. Alvarez	2915	NY
Stenorrhynchos	*speciosum*	(Jacq.) Rich.	NYBG-living	NY293-82E	NY-living

Table 2.3. Primers used for PCR and/or sequencing.

Primer Name	Direction	PCR/ Sequencing	Primer sequence (5' to 3')	Source
ITS				
ITS5A [NY183]	Forward	PCR, Seq	CCTTATCATTTAGAGGAAGGAG	(Standford et al., 2000)
26S-25R [NY43]	Reverse	PCR, Seq	TATGCTTAAAYTCAGCGGGT	Hill, R.
ITS3 [NY17]	Forward	Seq	GCATCGATGAAGAACGCAGC	(White et al., 1990)
ITS2 [NY16]	Reverse	Seq	GCTGCGTTCTTCATCGATGC	(White et al., 1990)
***trn*L-F**				
c (B49317) [NY55]	Forward	PCR, Seq	CGAAATCGGTAGACGCTA	(Taberlet et al., 1991)
f (A50272) [NY57]	Reverse	PCR, Seq	ATTTGAACTGGTGACACGAG	(Taberlet et al., 1991)
e (B49873) [NY66]	Forward	Seq	GGTTCAAGTCCCTCTATCCC	(Taberlet et al., 1991)
d (A49855) [NY56]	Reverse	Seq	GGGGATAGAGGGACTTGAAC	(Taberlet et al., 1991)
***rbc*L**				
nt636 [NY23]	Forward	PCR, Seq	GCGTTGGAGAGATCGTTTCT	Unknown
Not I [NY3]	Reverse	PCR, Seq	TGTGTTGCGGCCGCCTTCACAAGCAGCAGCTAGTTCAGGACTCC	(Albert et al., 1992)
1F-short [NY149]	Forward	Seq	ATGTCACCACAAACAGAAACTA	(Zurawski and Clegg, 1987); modified by M. W. Chase
nt724 [NY28]	Reverse	Seq	TCGCATGTACCYGCAGTTGCAGCAAGT	Unknown
***atp*B**				
S2 [NY172]	Forward	PCR, Seq	TATGAGAATCAATCCTACTACTTCT	(Hoot et al., 1995)
S1494R [NY173]	Reverse	PCR, Seq	TCAGTACACAAAGATTTAAGGTCAT	(Hoot et al., 1995)
S611 [NY174]	Forward	Seq	AACGTACTCGTGAAGGAAATGATCT	(Hoot et al., 1995)
S766R [NY175]	Reverse	Seq	TAACATCTCGGAAATATTCCGCCAT	(Hoot et al., 1995)
***psa*B**				
*psa*B-F [NY159]	Forward	PCR, Seq	ACGCGTCGTATTTGGTTTGGTATTGC	(Nishiyama and Kato, 1999)
*psa*B-R [NY160]	Reverse	PCR, Seq	CAATGCCAATAAAAAGTAACCCATCC	(Nishiyama and Kato, 1999)
[NY178]	Forward	Seq	CCGATATKGCTCATCATCAYTTAGC	(Cameron, 2004b)
[NY229]	Reverse	Seq	GCTAAATGATGATGAGCAATATCGG	(Cameron, 2004b)

Table 2.4. Thermal profiles for DNA amplification and sequencing.

Genes	Thermal Profiles
Amplification	
ITS	Initial denaturation of 94°C for 4 minutes followed by 30 cycles of 94°C denaturation for 1 minute, 55°C annealing for 1 minute and 72°C for 2 minutes and 30 seconds per cycle, with a final extension at 72°C for 10 minutes.
*trn*L-F, *rbc*L, *atp*B	Initial denaturation of 97°C for 2 minutes, followed by 30 cycles of 94°C denaturation for 1 minute, 48°C annealing for 2 minutes and 72°C extension for 2 minutes, with a final extension at 72°C for 16 minutes.
*psa*B	Initial denaturation of 95°C for 50 seconds, followed by 30 cycles of 60°C denaturation for 50 seconds, with a final extension at 72°C for 1.5 minutes.
Sequencing	
ITS	Hold at 95°C for 1 minute; 32 cycles of 96°C for 10 seconds, 55°C for 5 seconds and 60°C for 3 minutes.
*trn*L-F, *rbc*L, *atp*B, *psa*B	Hold at 95°C for 1 minute; 32 cycles of 96°C for 10 seconds, 50°C for 5 seconds and 60°C for 3 minutes.

Table 2.5. Values and statistics from parsimony analyses of the expanded data matrix containing 56 taxa (with missing data).

	***psa*B**	***atp*B**	***rbc*L**	***trn*L-F including nonambiguous & recoded INAASE**	**ITS including nonambiguous & recoded INAASE**	**5 loci[1] including nonambiguous & recoded INAASE**	**5 loci excluding ambiguous &recoded INAASE**
Total characters	1684	1468	1331	1422	659	6564	6550
No. of parsimony uninformative characters	94	100	78	255	75	602	602
No. of parsimony informative characters	130	134	91	333	254	942	928
Variable characters	224	234	169	588	329	1544	1530
% of parsimony informative characters	7.72	9.13	6.8	23.4	38.5	14.35	14.17
% of variable characters	13.30	15.94	12.7	41.35	49.9	23.52	23.36
No. of most parsimonious trees	50000	50000	1884	108	16	1	3
Tree length	377	380	277	1299	1219	3572	3270
CI	0.66	0.69	0.68	0.64	0.57	0.62	0.60
RI	0.74	0.78	0.82	0.73	0.75	0.75	0.75
No. of clades w/ bootstrap =>80%	8	23	12	30	34	47	43

[1]= 5 loci (ITS, *trn*L-F, *rbc*L, *atp*B and *psa*B)

Table 2.6. Incongruence Length Difference (ILD) test summary.

Combined data sets	**nuclear-plastid (p values)**	**noncoding-coding (p values)**	**ITS-*trn*L-F (p values)**	**ITS-*rbc*L (p values)**	**ITS-*atp*B (p values)**	**ITS-*psa*B (p values)**
5 genes expanded dataset (56 taxa)						
excluding ambiguously aligned & recoded regions	0.263	0.373	0.121	0.370	0.622	0.775
including recoded ambiguous regions	0.276	0.301	0.184	0.891	0.86	0.974

$p > 0.01$ (data sets are congruent)

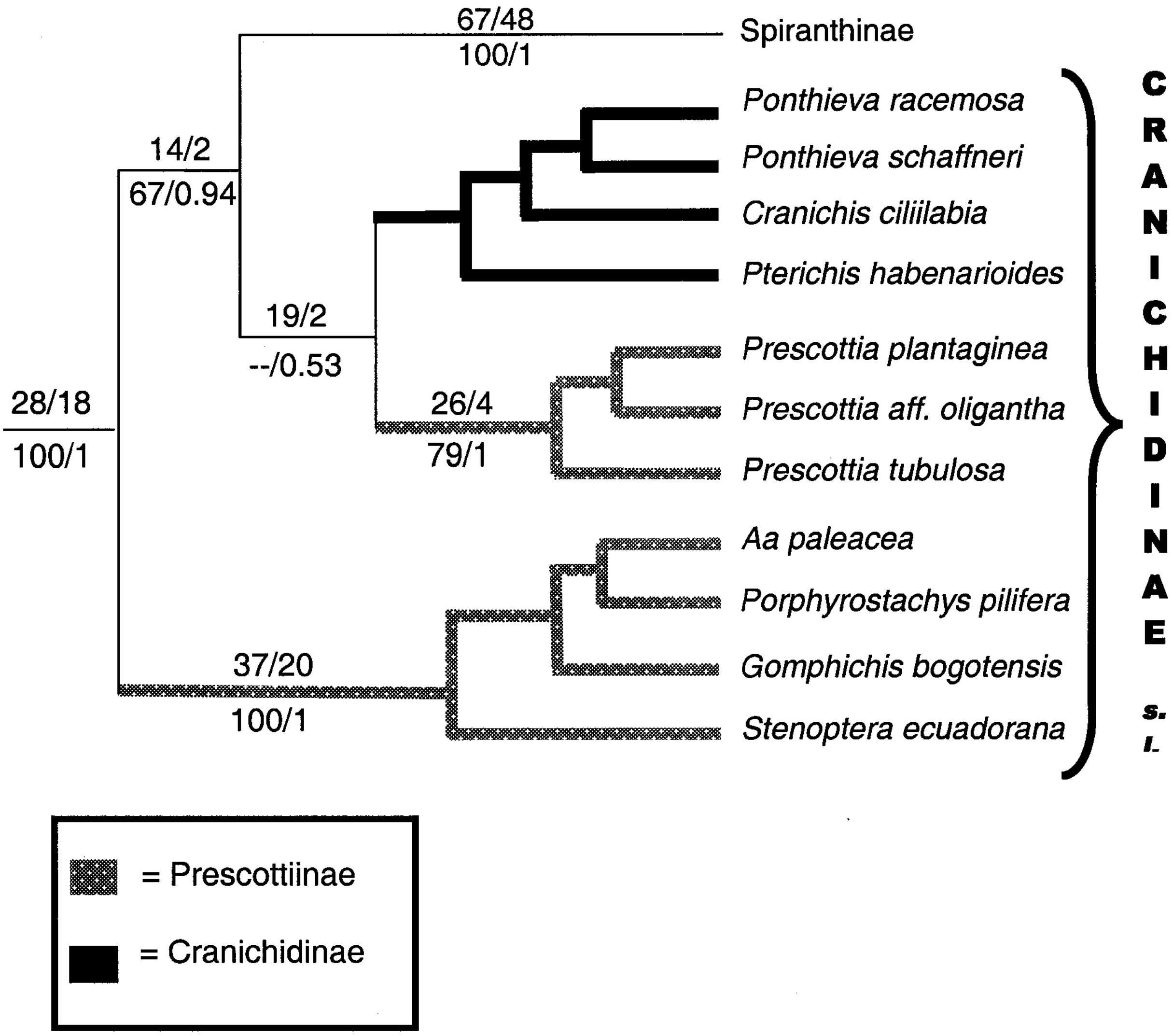

Fig. 2.1. Pruned tree from the phylogenetic analysis published by Salazar et al. (2003) showing placement of Cranichidinae *s.l.* (Prescottiinae, Cranichidinae *s.s.*) and Spiranthinae as adopted by Chase et al. (2003). Branch length/Bremer support (above branches) and bootstrap percentage (>50%)/posterior probability (below branches).

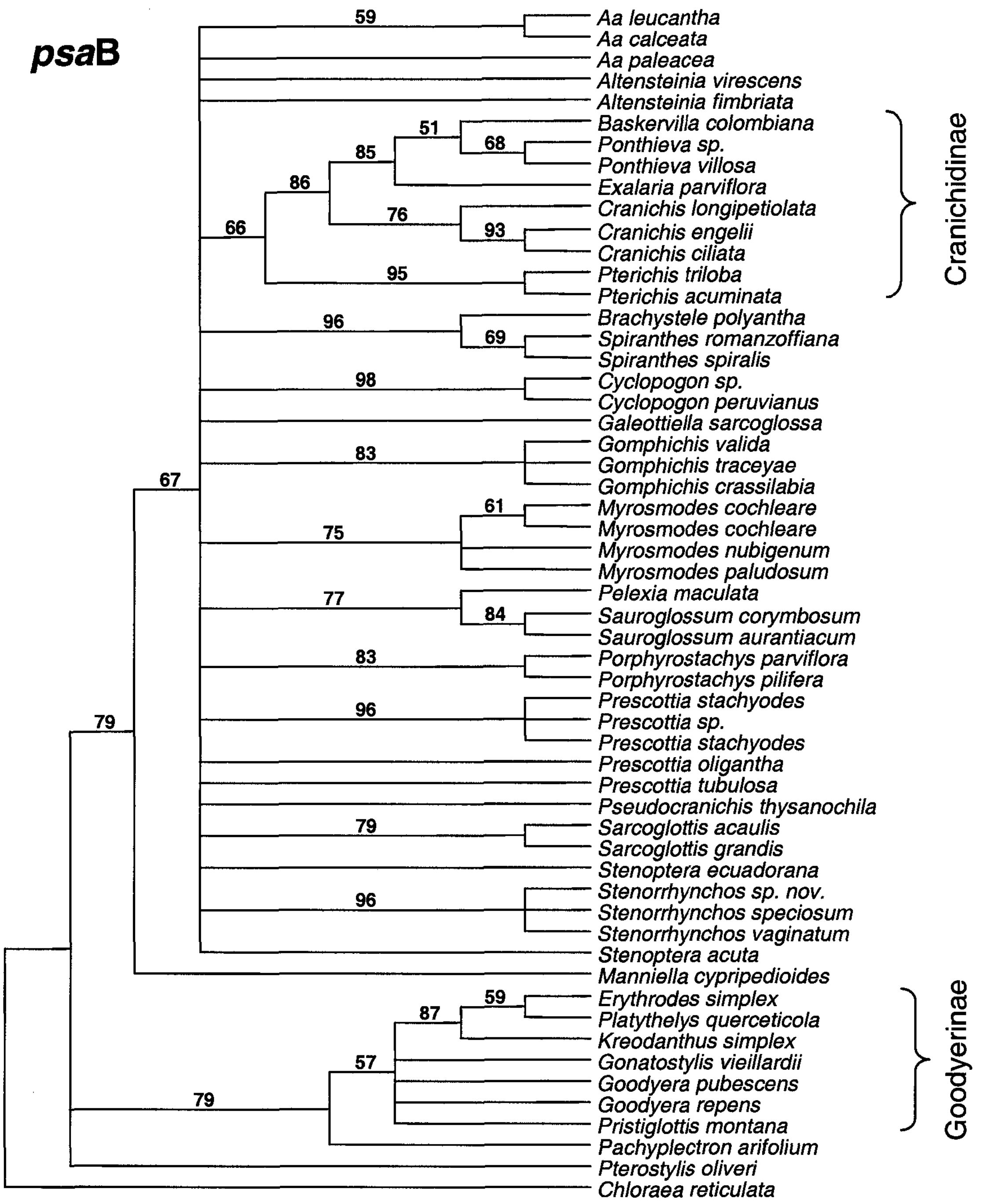

Fig. 2.2. Strict consensus of 50,000 equally parsimonious trees based on *psa*B sequence data. Bootstrap values above branches. L= 377, CI= 0.66, and RI= 0.74.

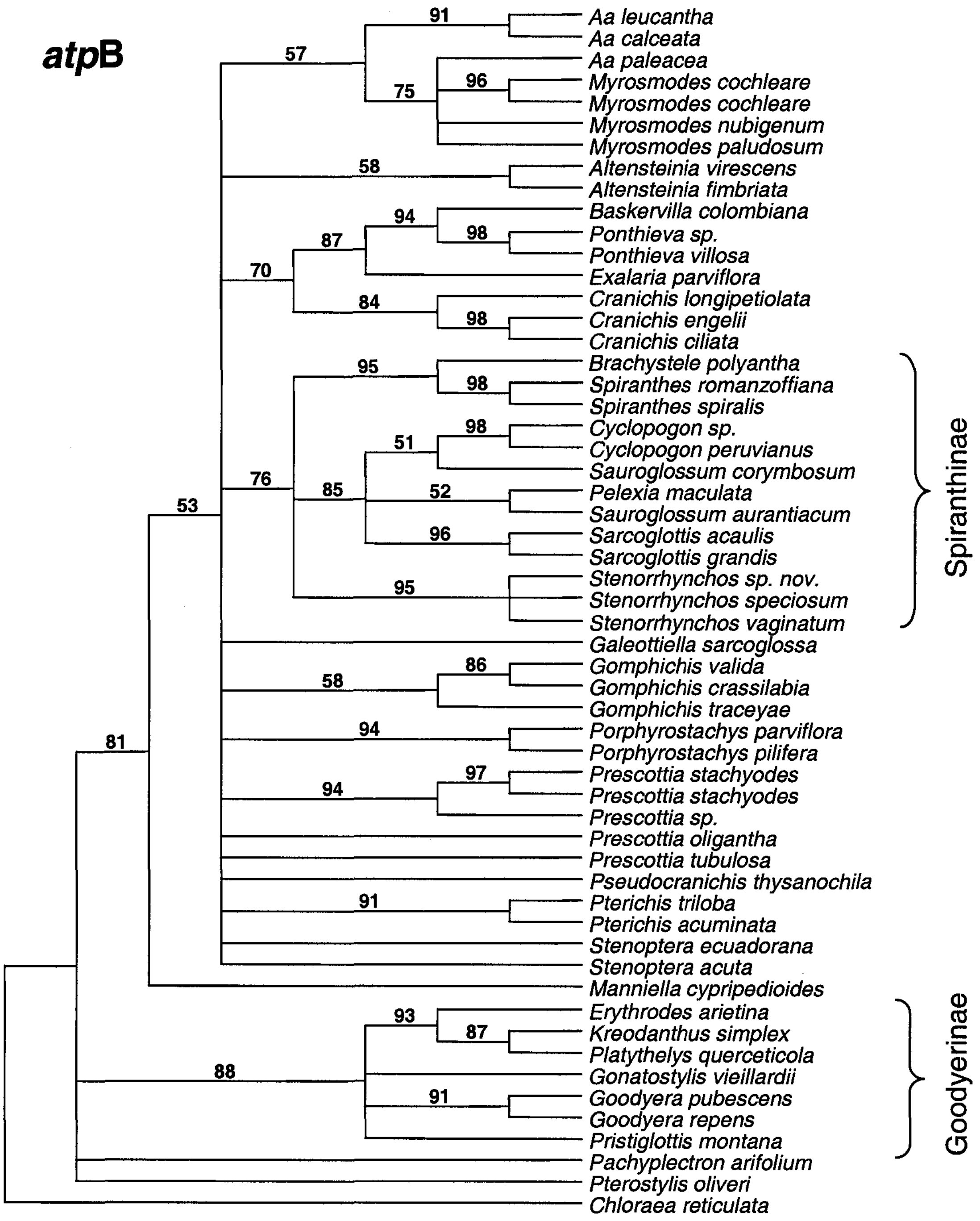

Fig. 2.3. Strict consensus of 50000 equally parsimonious trees based on *atp*B sequence data. Bootstrap values above branches. L= 380, CI= 0.69, and RI= 0.78.

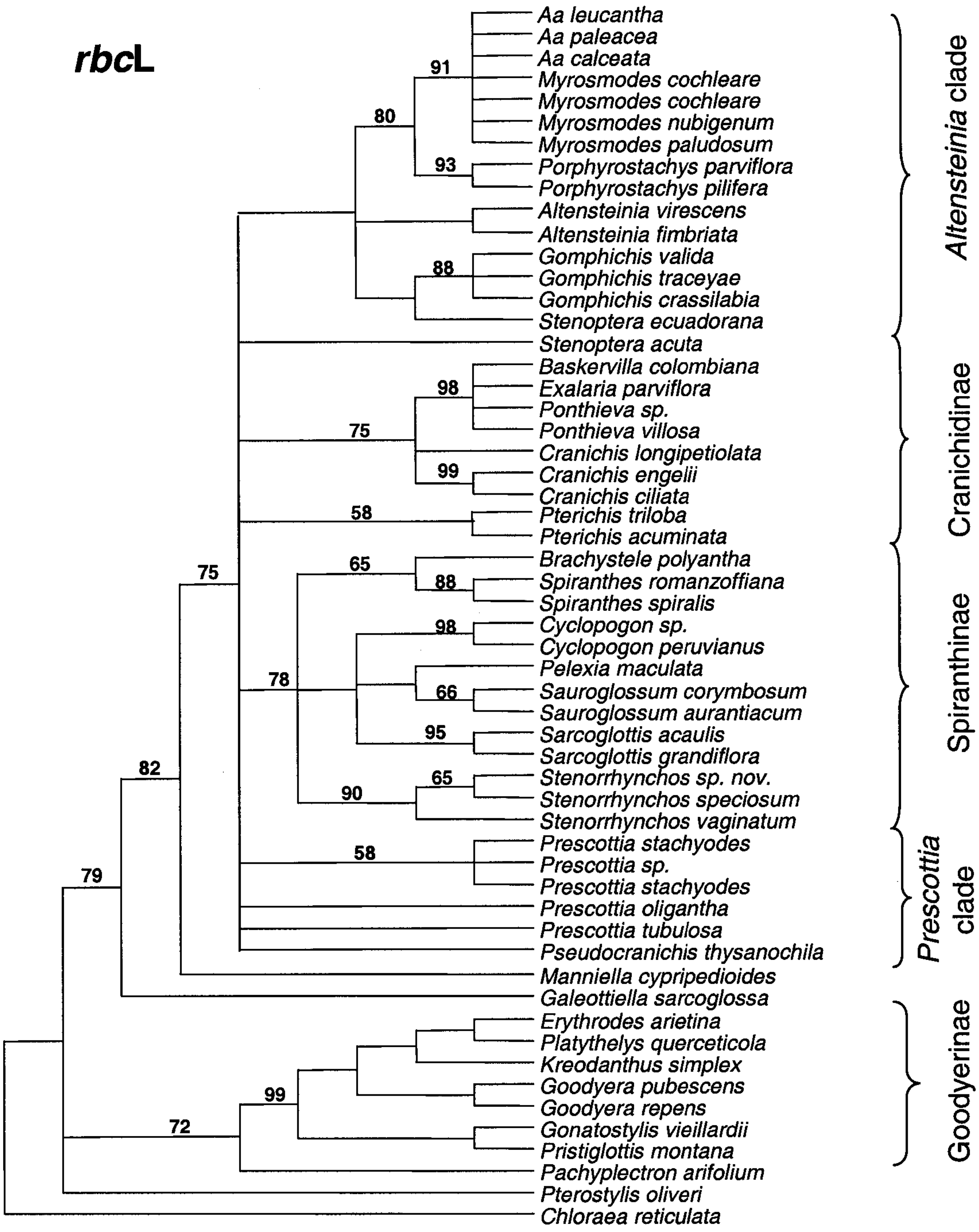

Fig. 2.4. Strict consensus of 1884 most parsimonious trees based on *rbc*L sequence data. Bootstrap percentages above branches. L= 277, CI= 0.68, and RI= 0.82.

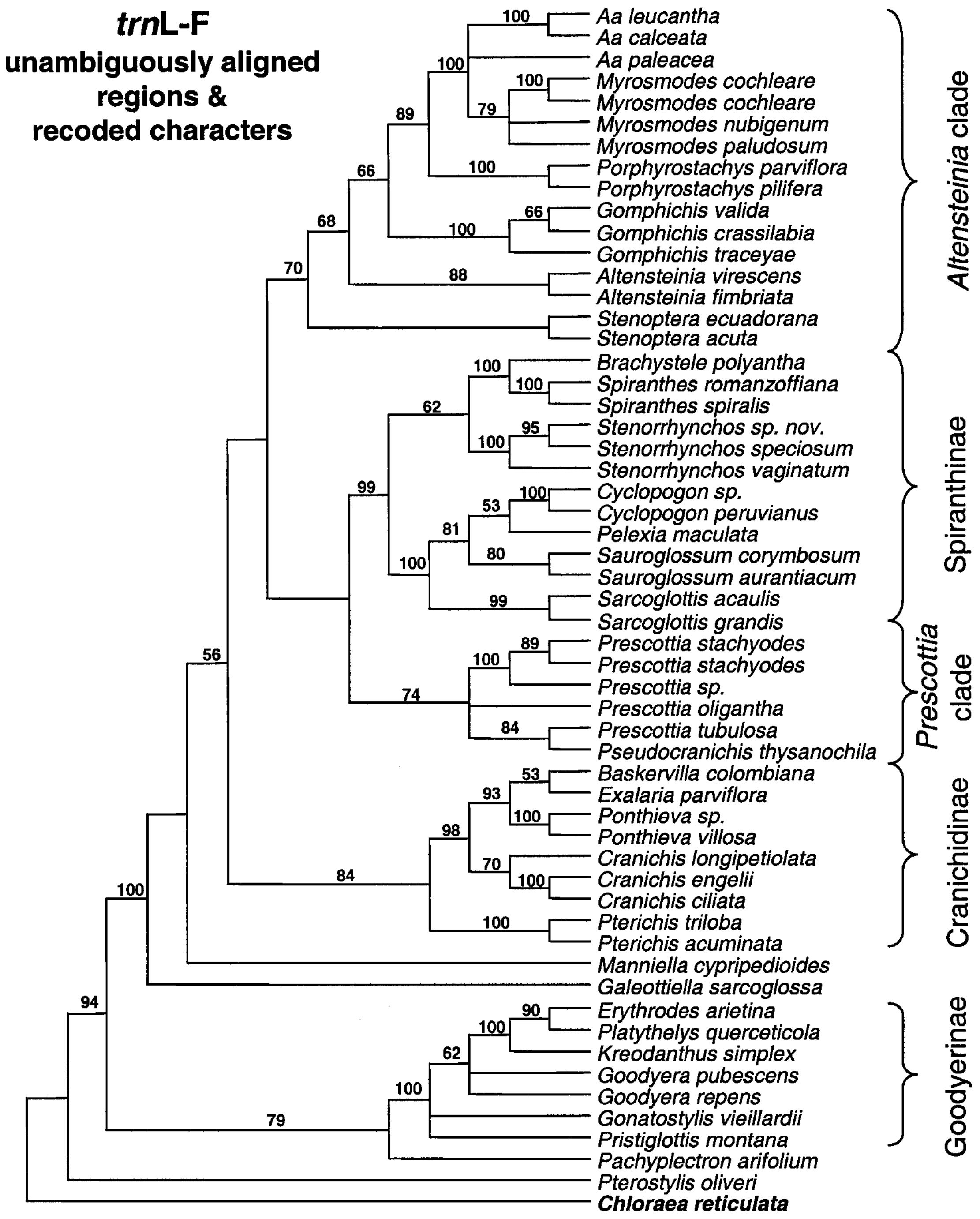

Fig. 2.5. Strict consensus of 108 equally parsimonious trees based on *trn*L-F sequence data with unambiguously aligned characters plus recoded ambiguous regions. Bootstrap values above branches. L=1299, CI=0.6390, and RI=0.7337.

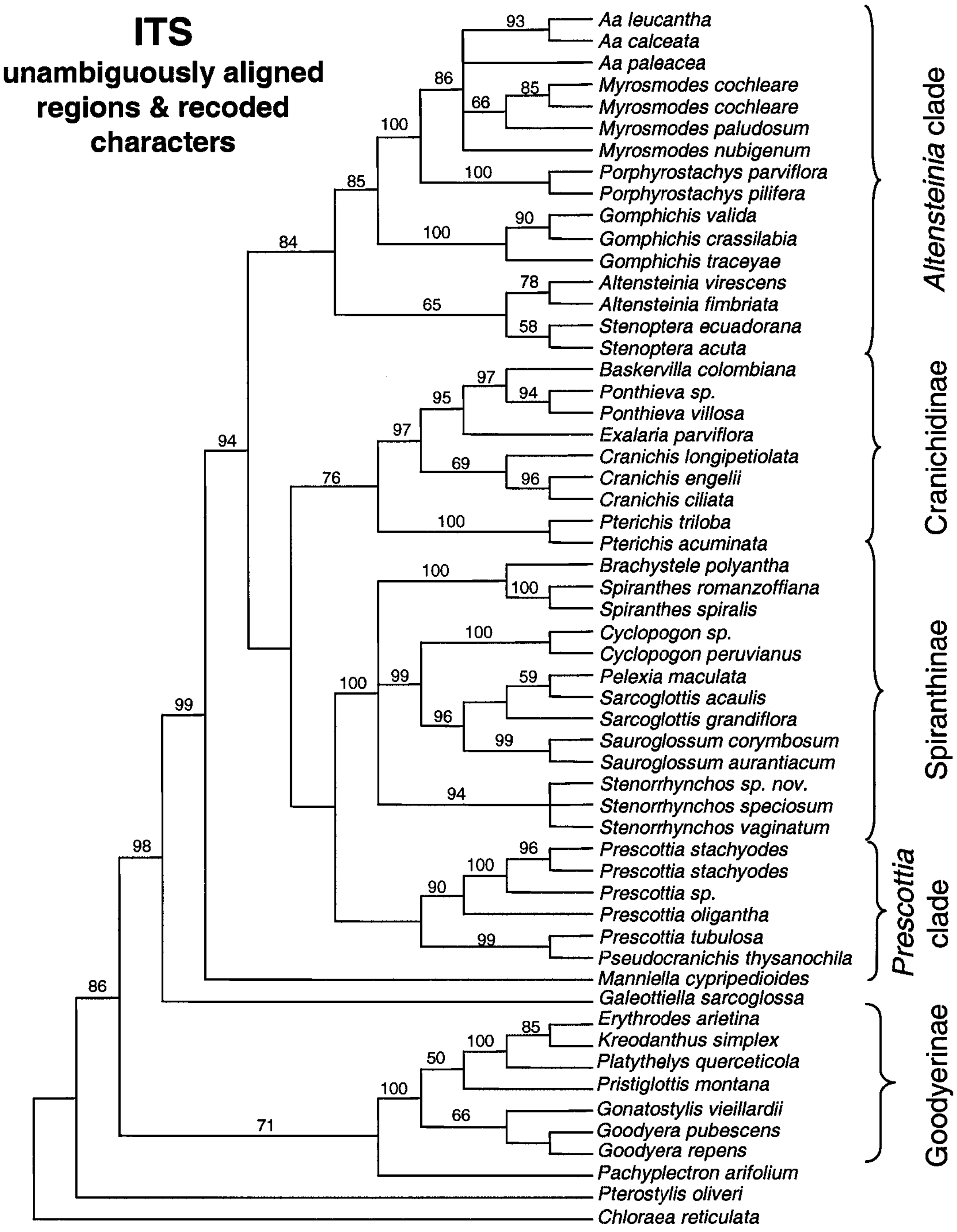

Fig 2.6. Strict consensus of 16 most parsimonious trees based on ITS sequence data with unambiguously aligned characters plus recoded ambiguous regions. Bootstrap values above branches. L=1219, CI=0.57, and RI=0.75.

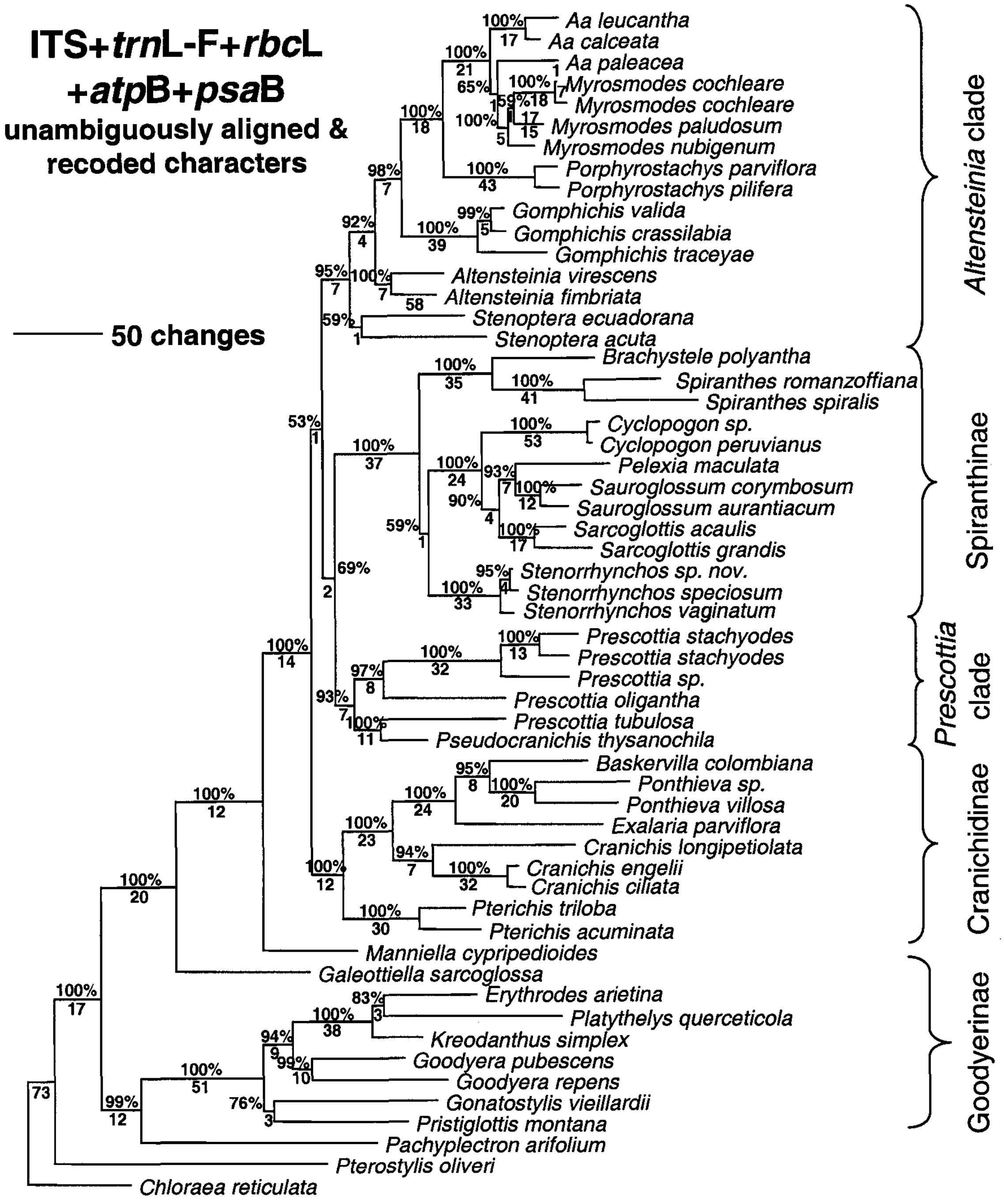

Fig. 2.7. Single most parsimonious tree from combined analysis of ITS, *trn*L-F, *rbc*L, *atp*B and *psa*B sequence data including unambiguously aligned regions plus recoded ambiguous characters. Bootstrap values above branches; decay indices below branches. L=3572, CI=0.62, and RI=0.75.

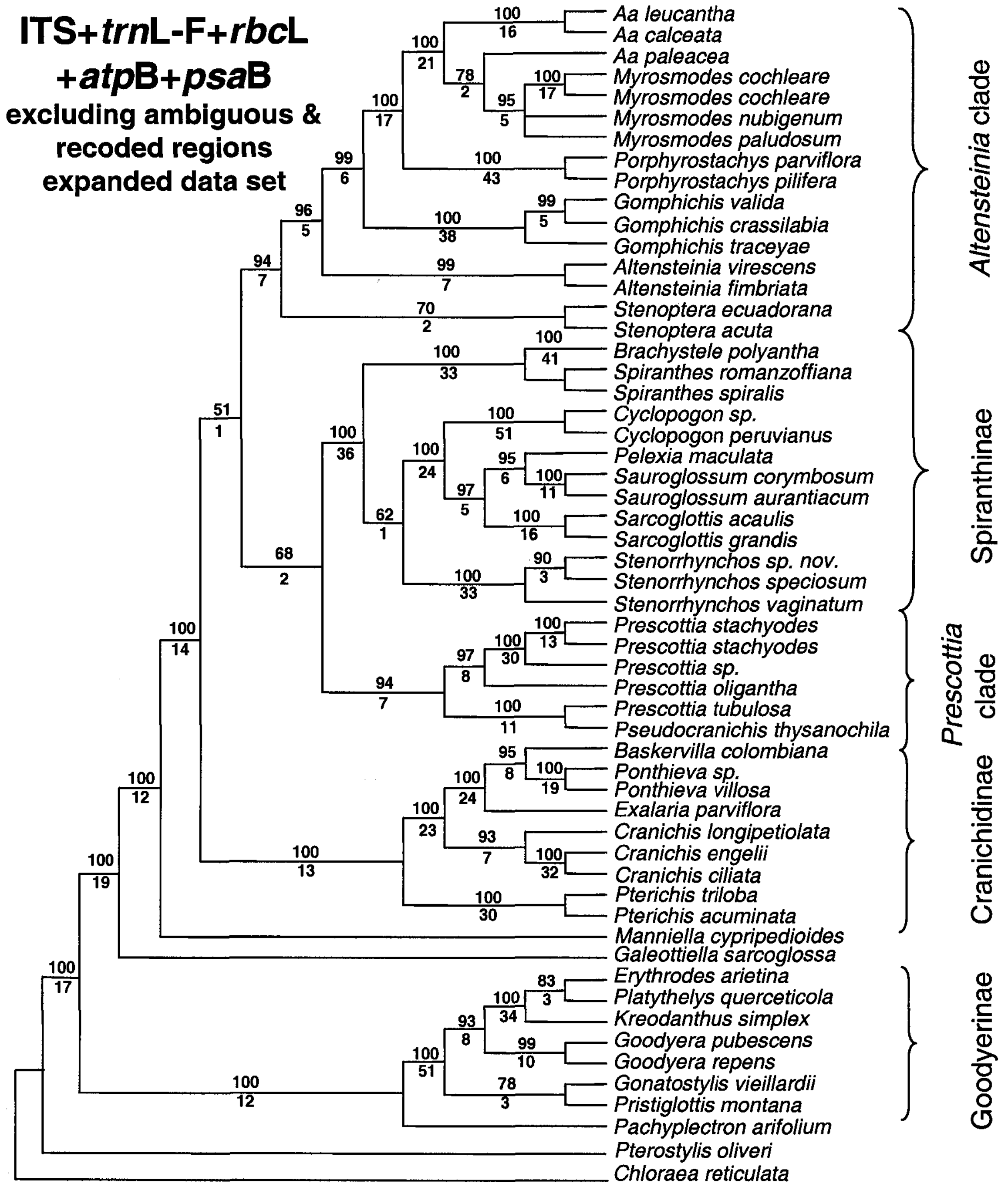

Fig. 2.8. Strict consensus of 3 trees from parsimony analyses of *psa*B, *atp*B, *rbc*L, *trn*L-F, and ITS sequence data, excluding ambiguous or recoded regions. Bootstrap values above branches; decay values below branches. L=3270, CI=0.60, and RI=0.75.

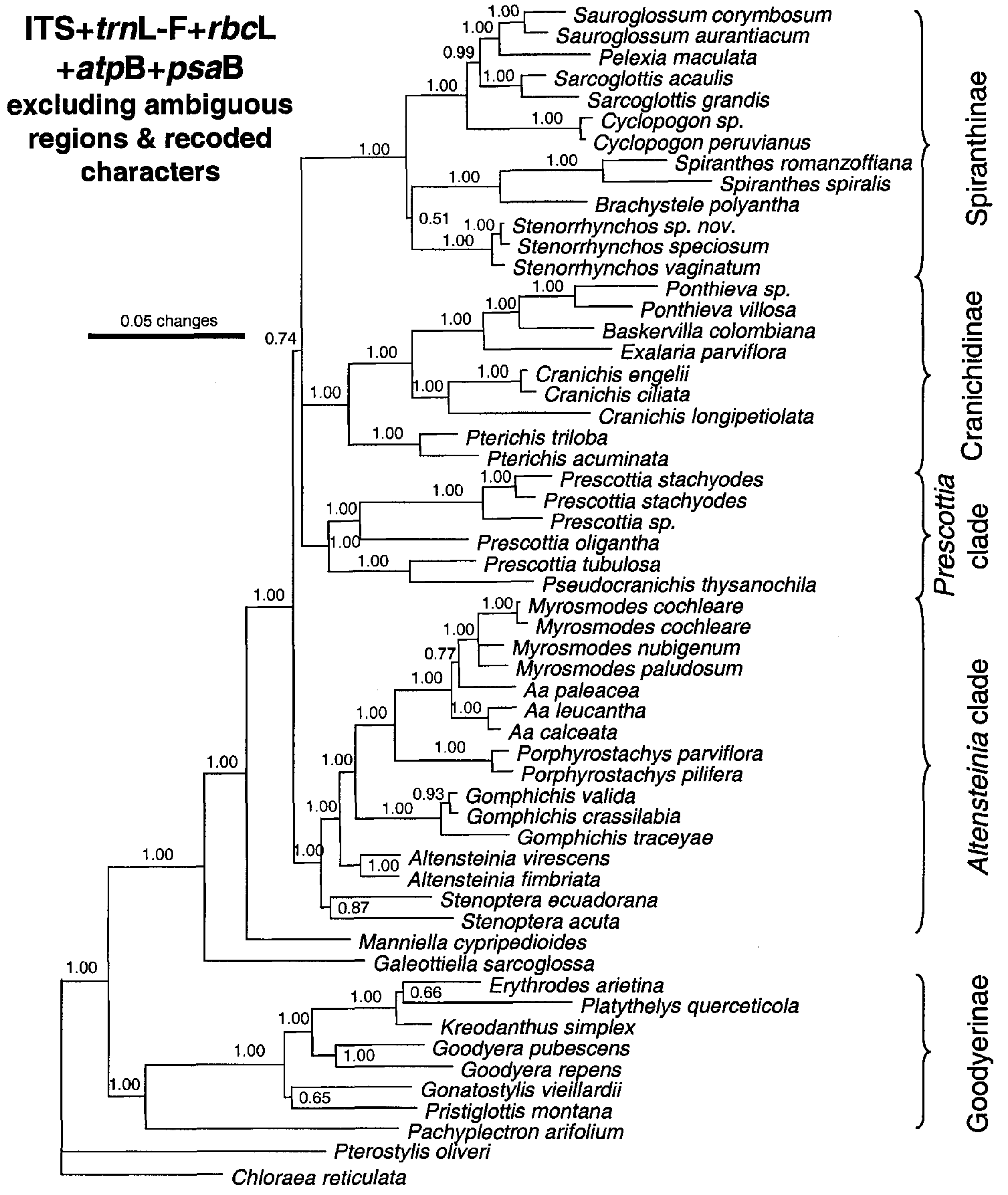

Fig. 2.9. Majority rule consensus of 3,600 trees from the Bayesian analysis under the GTR+I+G model. Posterior probabilities are indicated above branches.

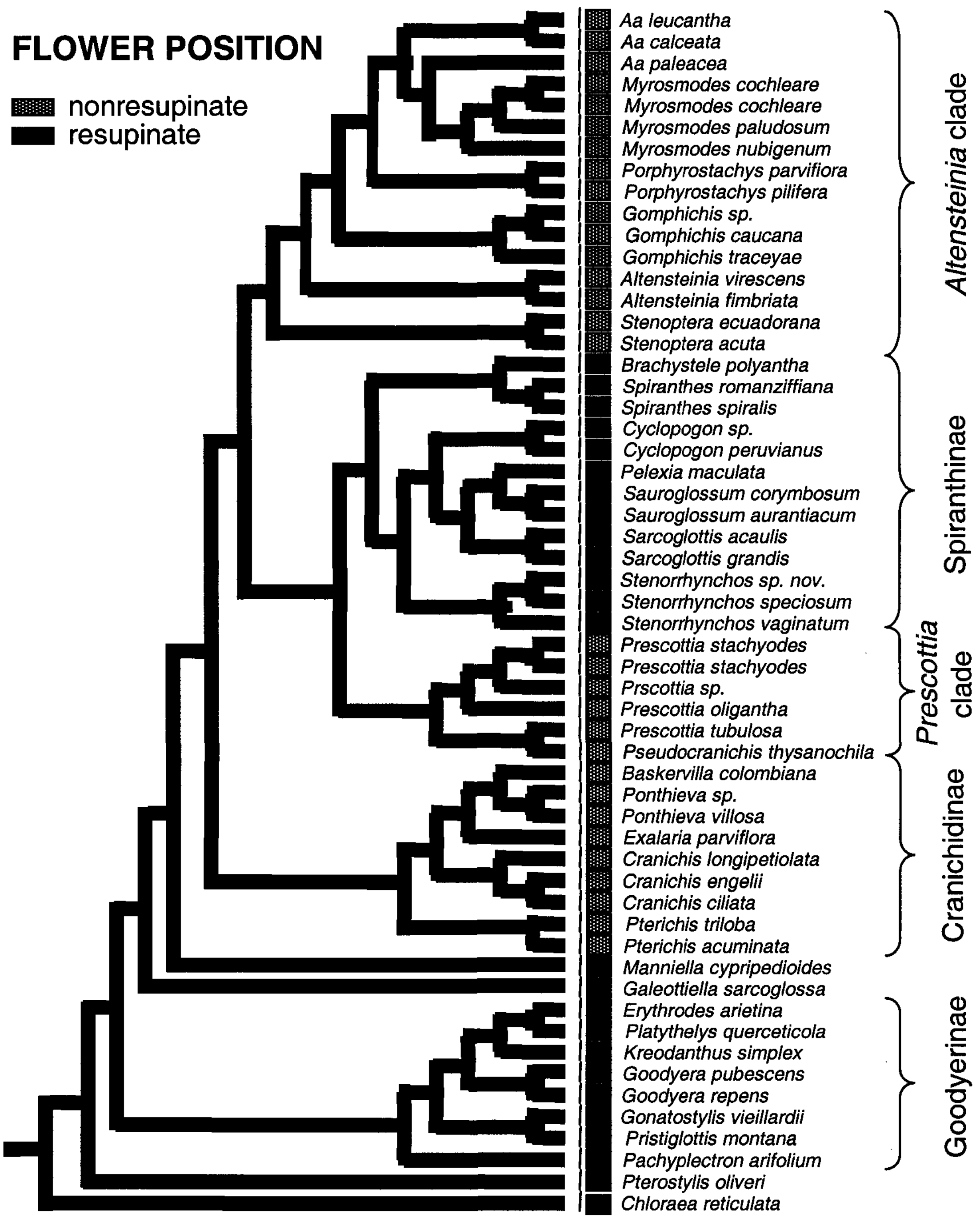

Fig. 2.10. Optimization of flower position onto the strict consensus tree from the combined analysis depicted in Fig. 2.7.

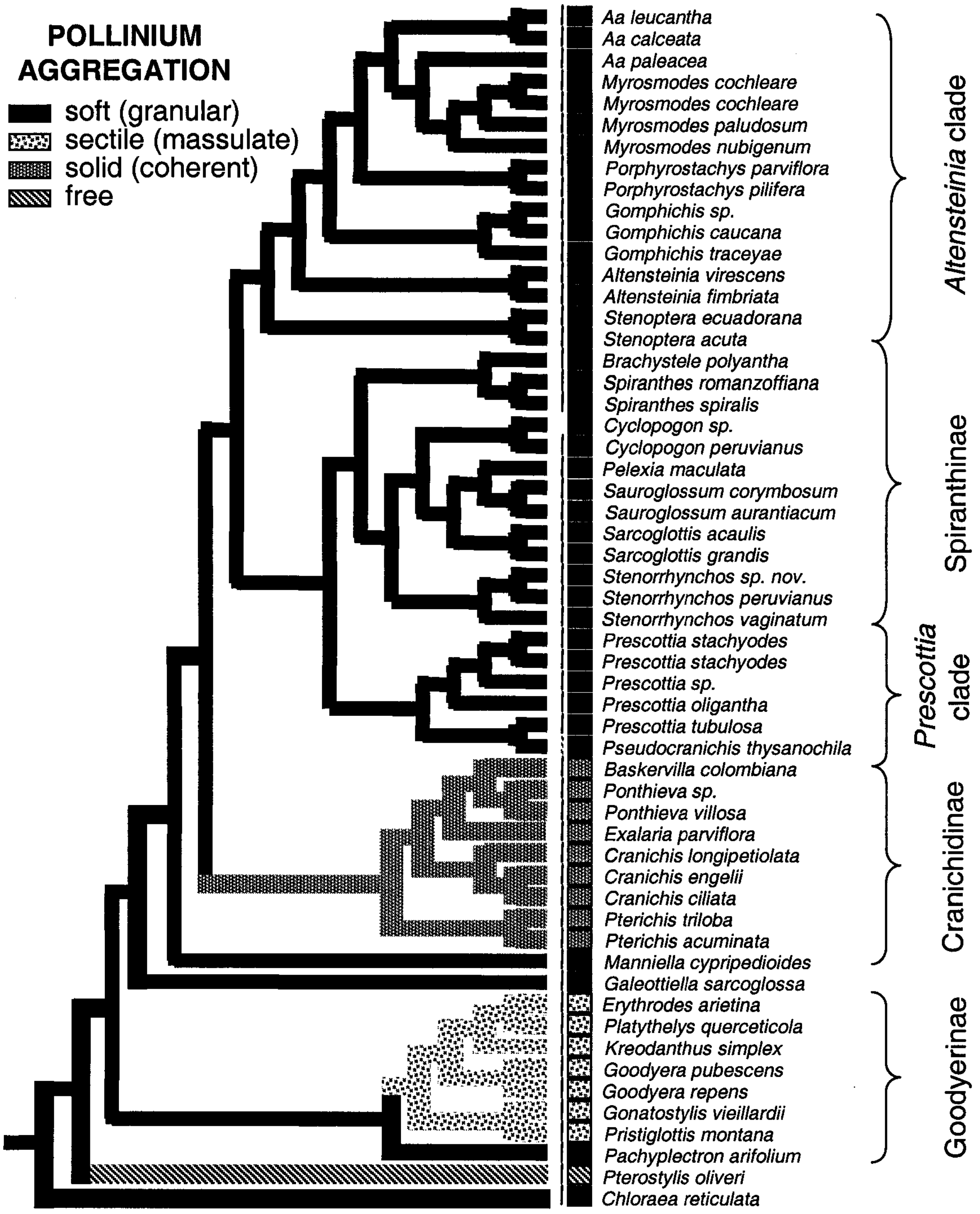

Fig. 2.11. Optimization of pollinium aggregation onto the strict consensus tree from the combined analysis depicted in Fig. 2.7.

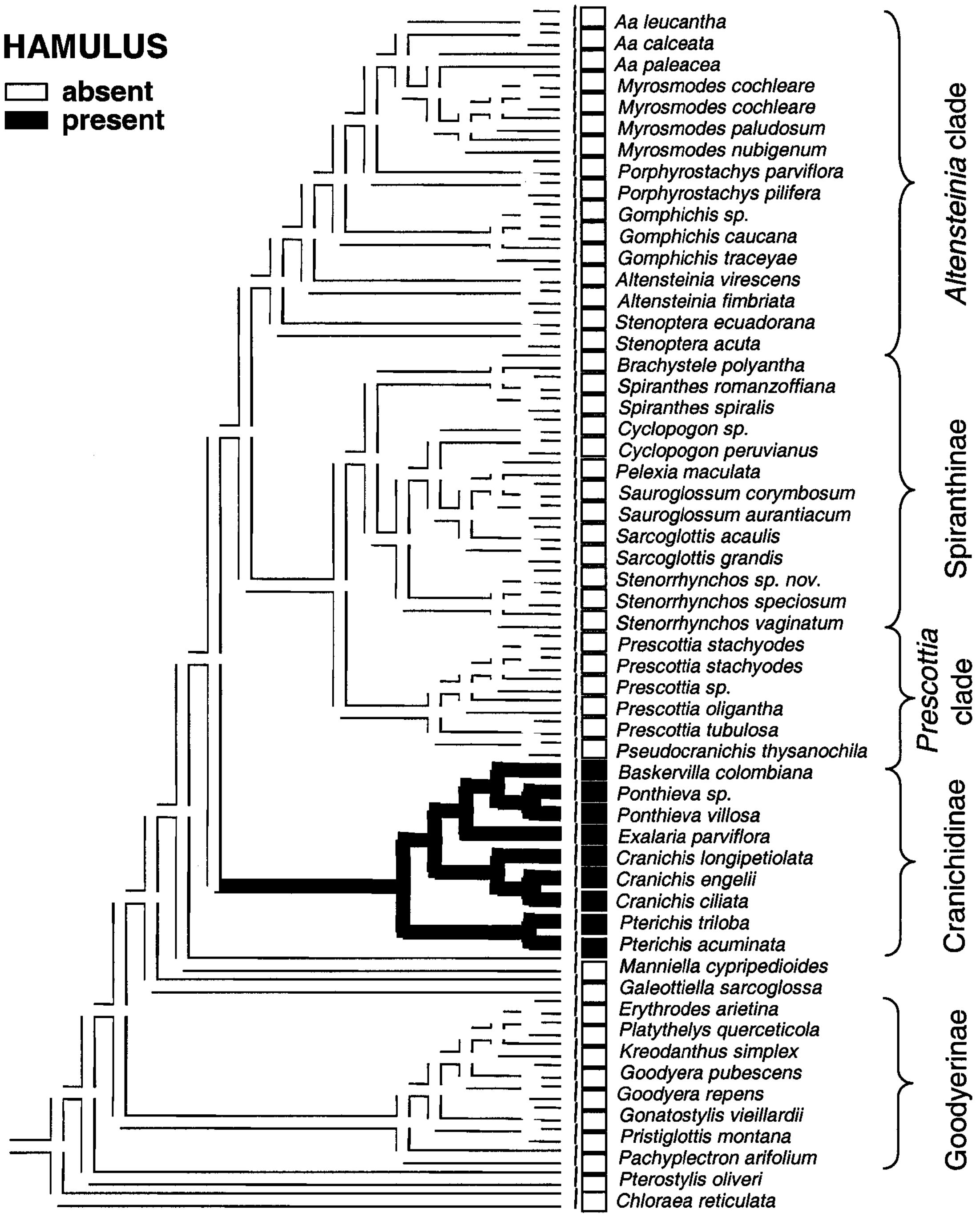

Fig. 2.12. Optimization of the presence/absence of hamulus onto the strict consensus tree from the combined analysis depicted in Fig. 2.7.

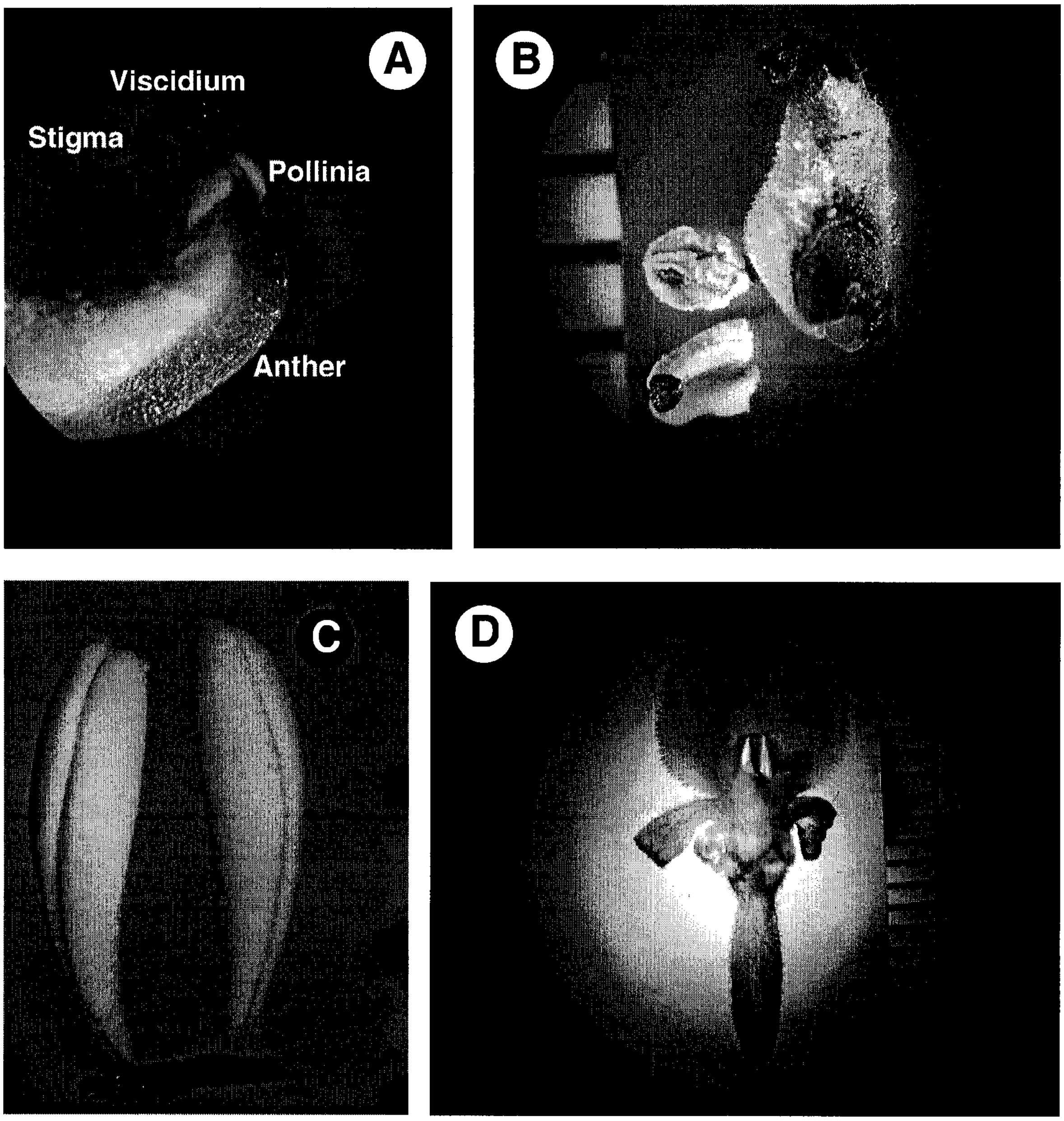

Fig. 2.13. Column of the Prescottiinae. A, *Gomphichis crassilabia*: viscidium, anther and stigma. B, *Gomphichis crassilabia*: column, anther and pollinia. C, *Altensteinia fimbriata*: pollinia and viscidium. D, *Altensteinia fimbriata*: column, labellum and lateral sepals.

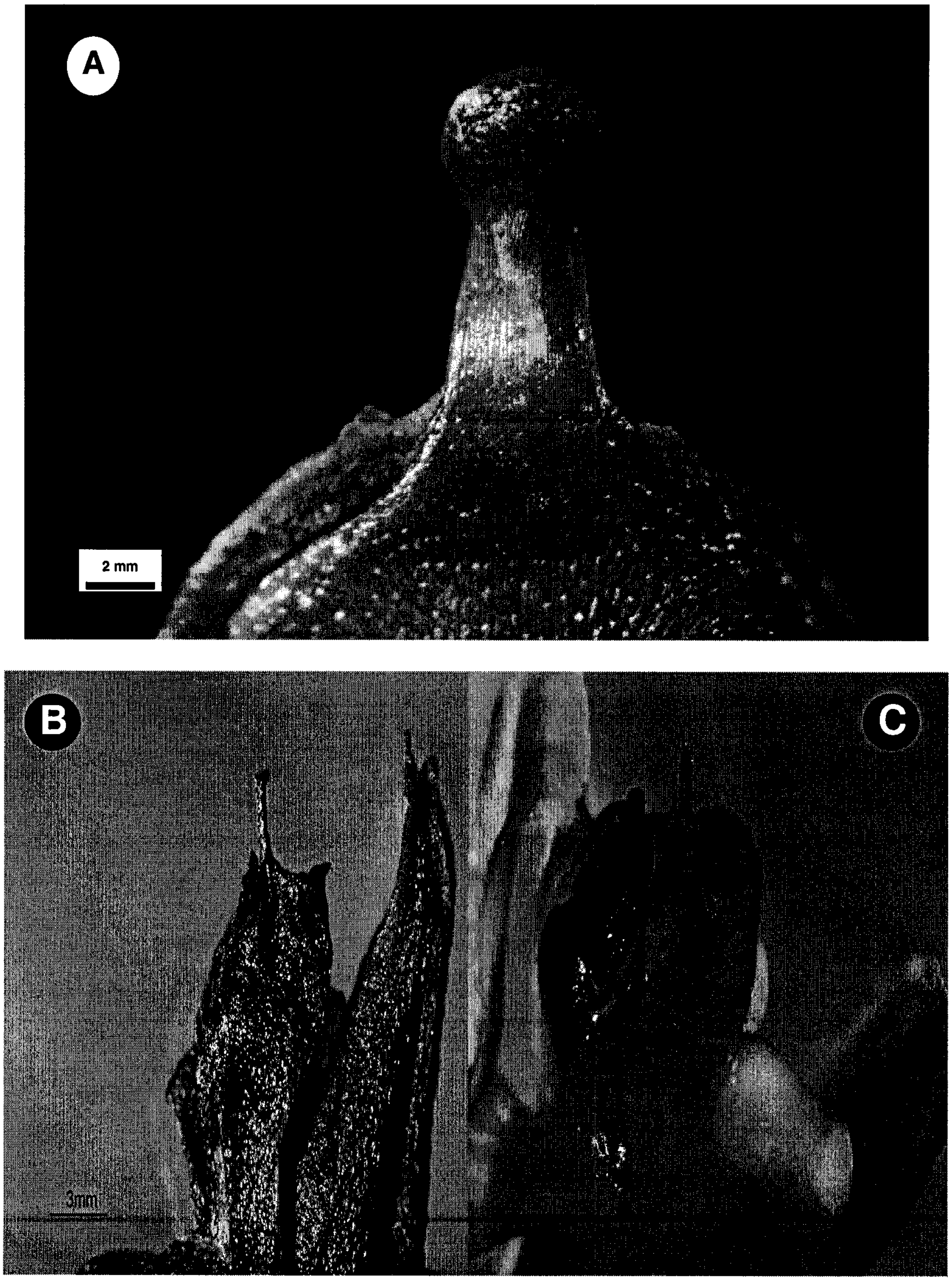

Fig. 2.14. Pointed hamulus of the Cranichidinae: A, *Pterichis acuminata* (*Alvarez 2832*, NY). B, *Baskervilla colombiana* (*Christenson s.n.*, QCNE*)*; C, *Ponthieva diptera* (*Alvarez 2929*, NY).

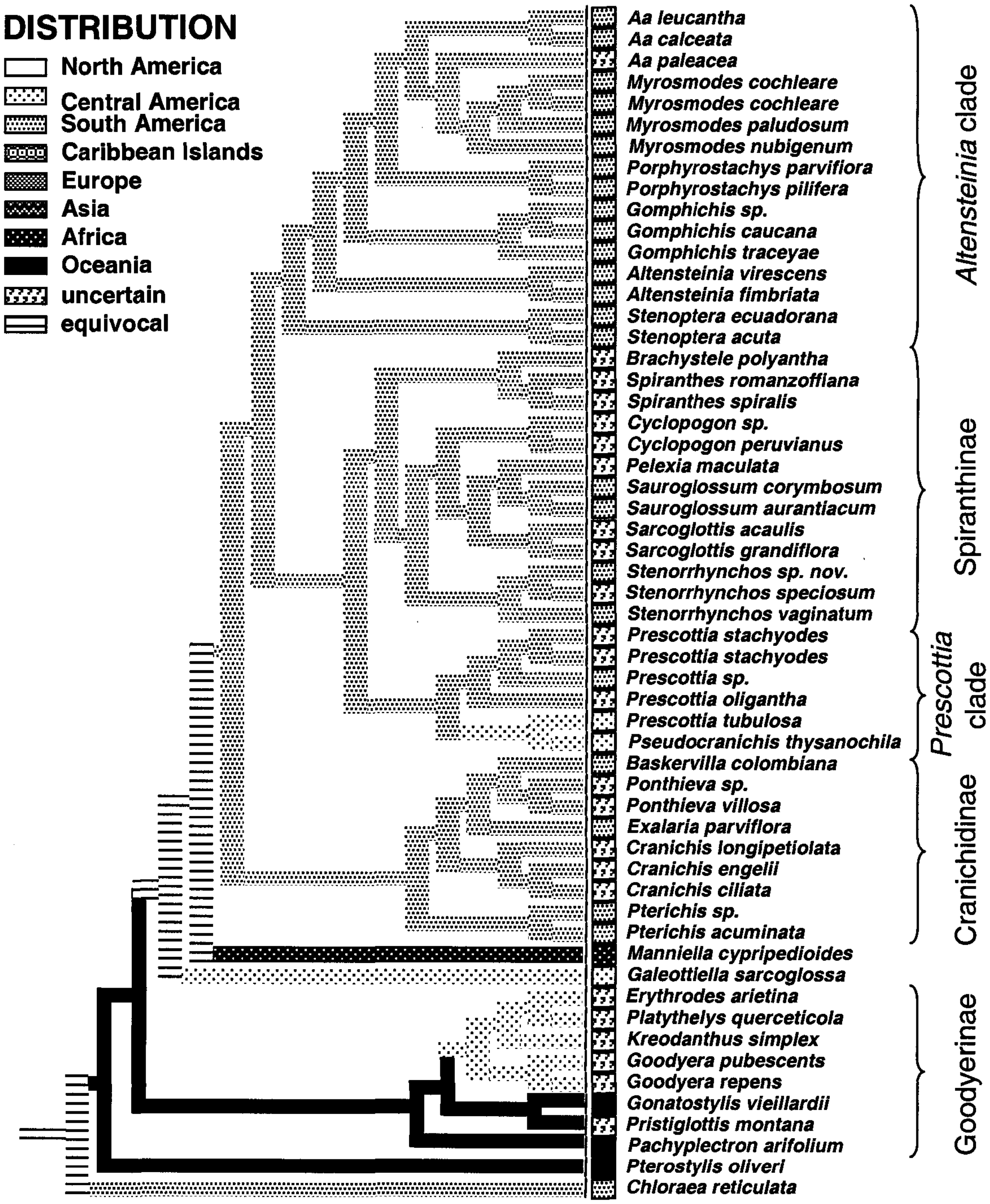

Fig. 2.15. Optimization of geographic distributions onto the single most parsimonious tree from the combined analysis of five loci depicted in Fig. 2.7.

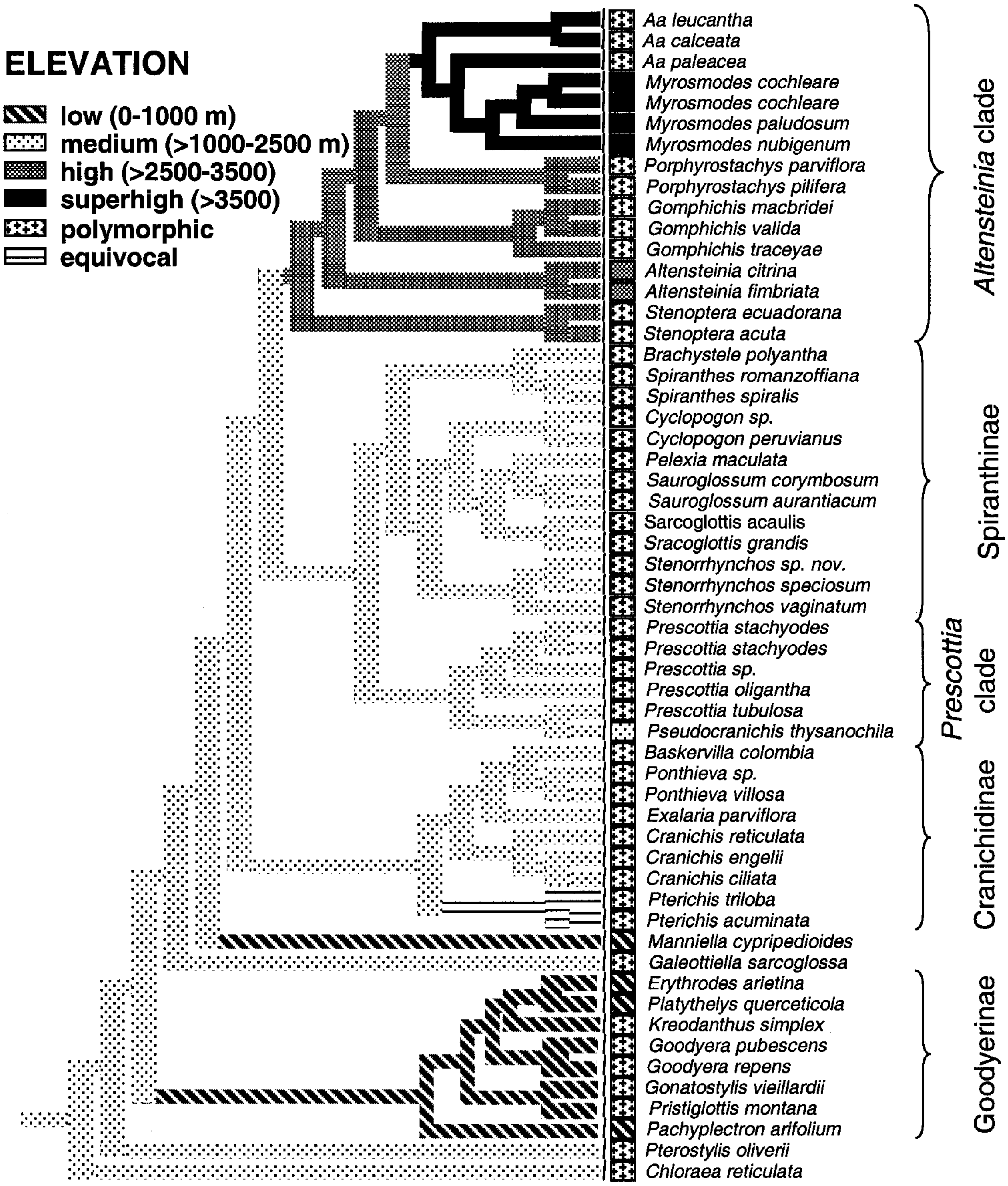

Fig. 2.16. Optimization of elevation onto the single most parsimonious tree from the combined analysis of five loci depicted in Fig. 2.7.

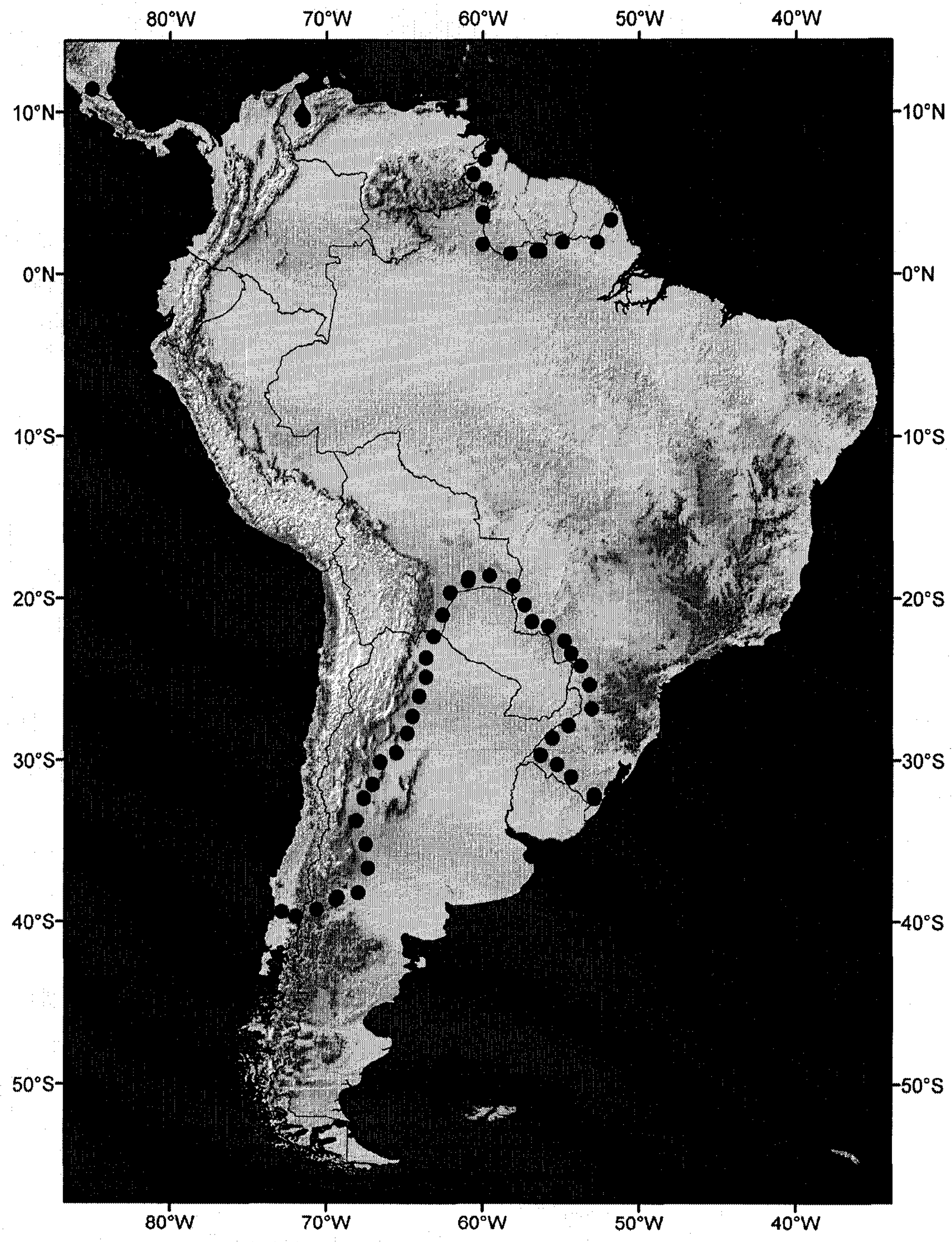

Fig. 2.17. Geographic range of members of the *Altensteinia* clade (*Aa*, *Altensteinia*, *Gomphichis*, *Myrosmodes*, *Porphyrostachys*, and *Stenoptera*) from Costa Rica in the north down to Chile, Argentina and Bolivia in the south and from Costa Rica and Chile in the west to Venezuela and Guyana in the east.

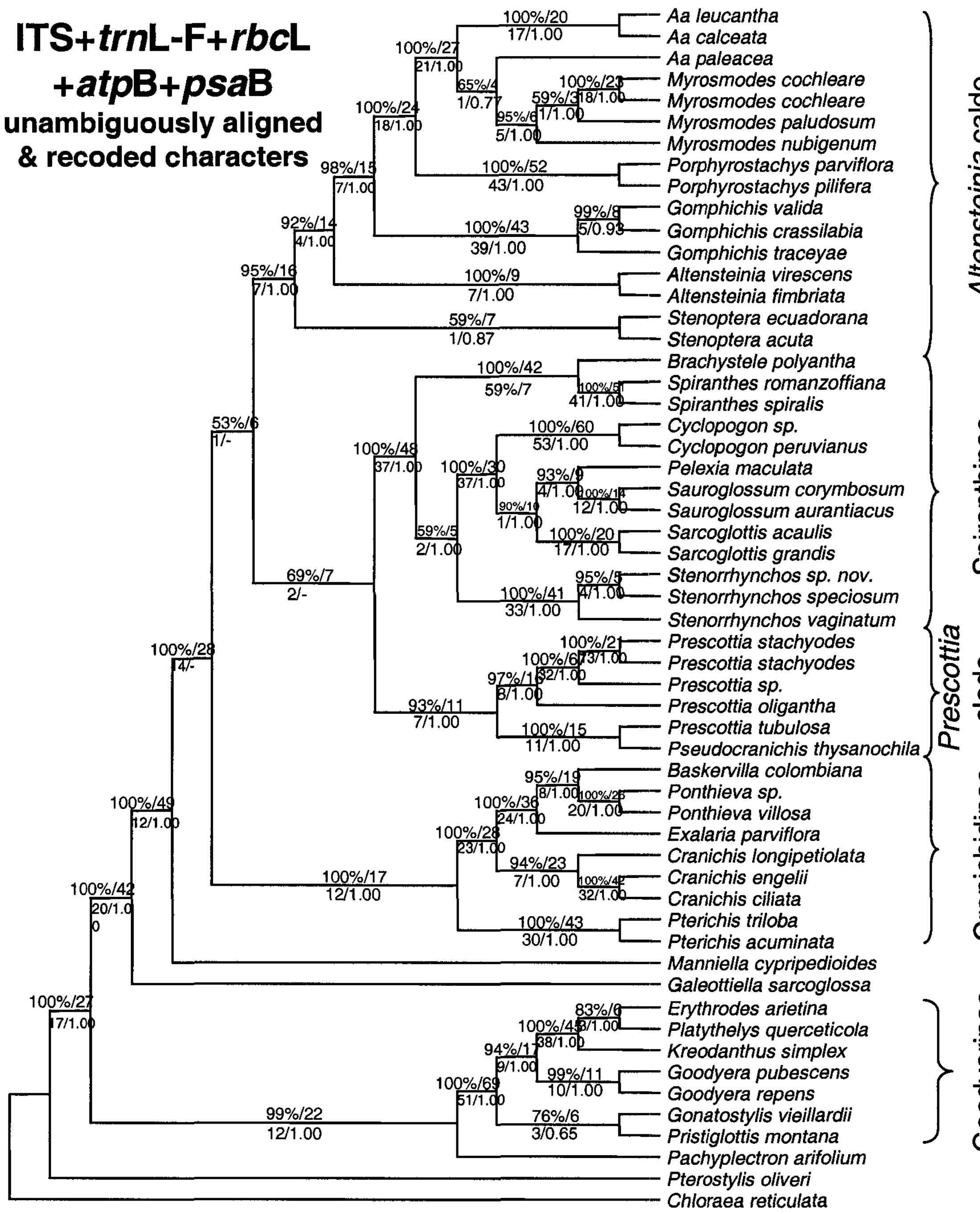

Fig. 2.18. Single most parsimonious tree from combined analysis of ITS, *trn*L-F, *rbc*L, *atp*B and *psa*B sequence data with unambiguously aligned regions plus recoded ambiguous characters. Bootstrap values/character changes above branches; decay indices/posterior probabilities below branches. L=3572, CI=0.62, and RI=0.75.

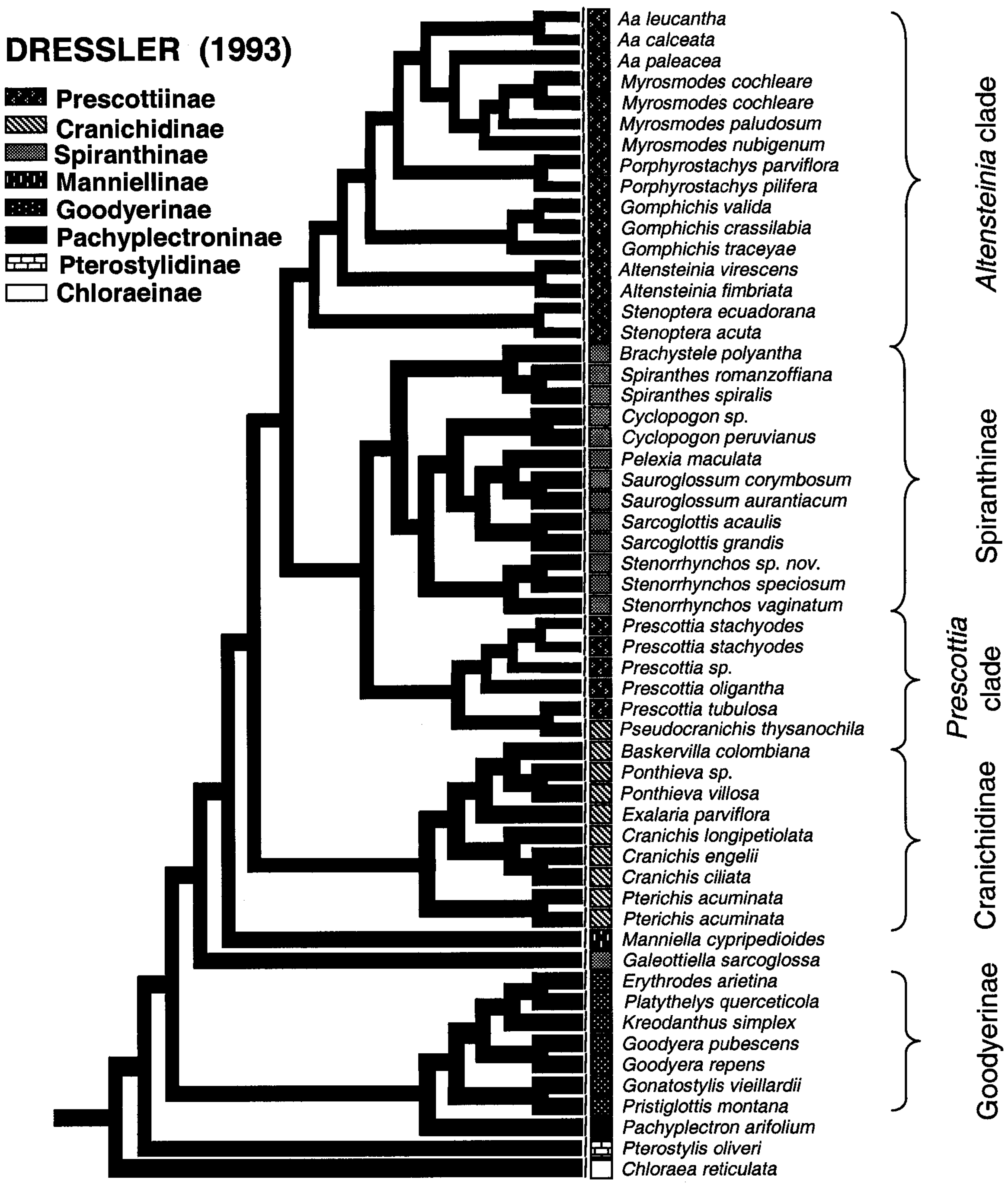

Fig 2.19: Dressler's (1993) subtribes of Cranichideae and Diurideae plotted onto the single most parsimonious tree depicted in Fig. 2.7.

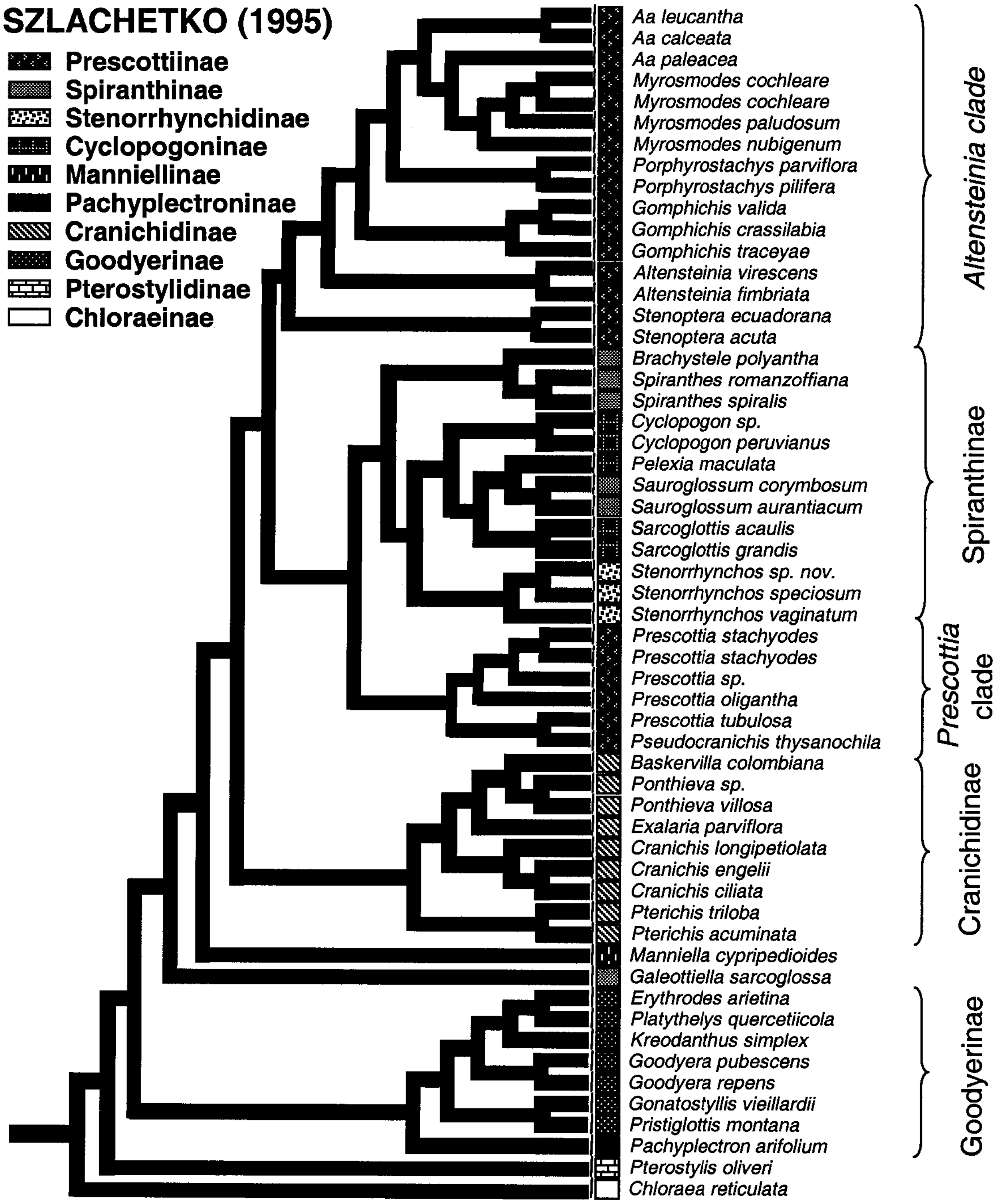

Fig. 2.20. Szlachetko's (1995) subtribes of Cranichideae plotted onto the strict consensus tree depicted in Fig. 2.7.

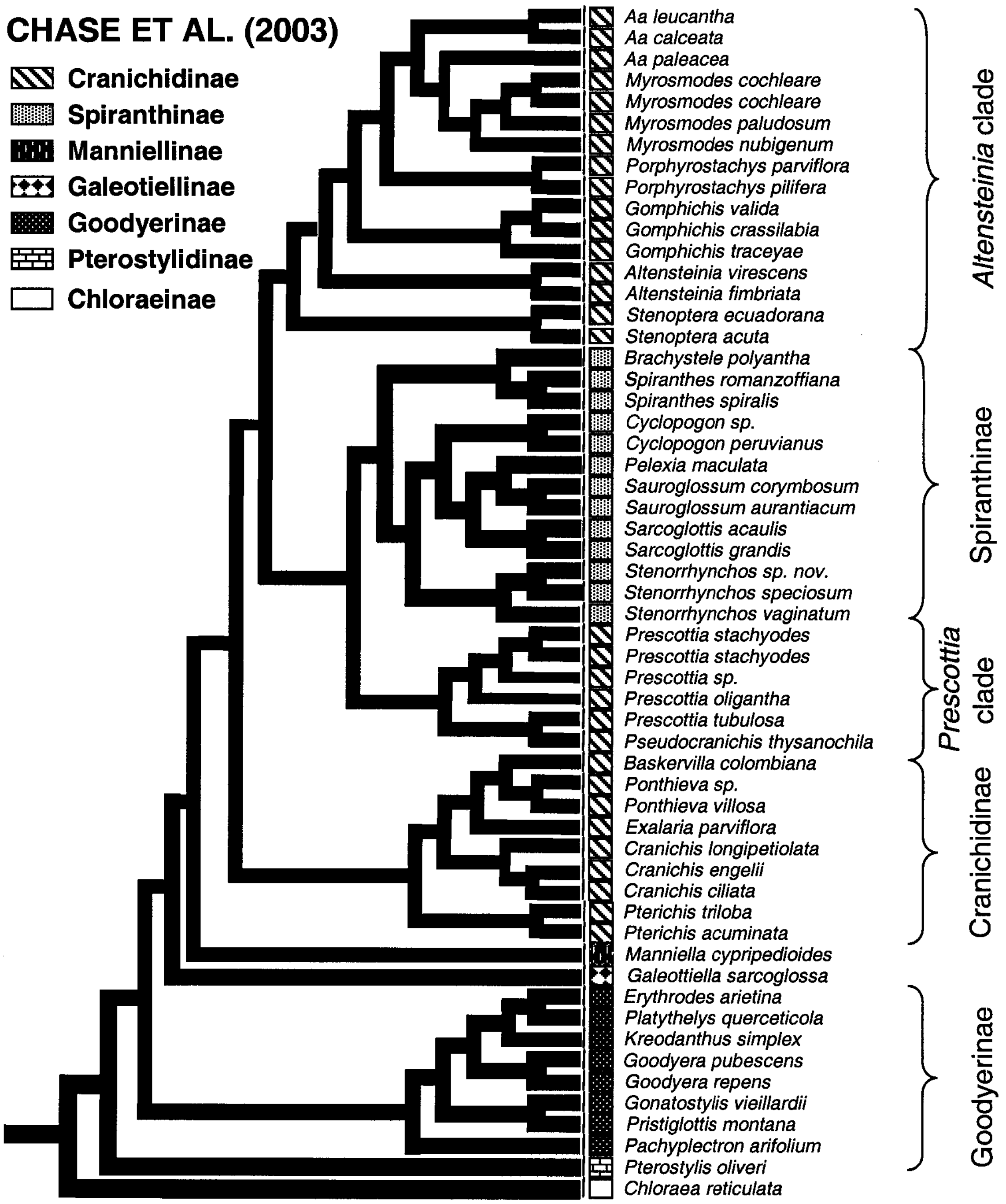

Fig. 2.21. Chase et al.'s (2003) subtribes of Cranichideae plotted onto the single most parsimonious tree depicted in Fig. 2.7.

CHAPTER 3

MORPHOLOGY, ANATOMY AND SYSTEMATICS OF *GOMPHICHIS* LINDL. (ORCHIDACEAE)

3.1. INTRODUCTION

Gomphichis Lindl., as here circumscribed, is a Neotropical genus comprising at least 17 species of delicate or robust herbaceous, terrestrial or facultative epiphytic plants. Species of *Gomphichis* are found primarily in the moist and wet uplands of the mountain ranges of southern Central America and South America from Costa Rica to Bolivia. Its species are characterized by a basal rosette of leaves; glandular pubescent flowers incumbent on the ovaries; free petals, a dorsal sepal from the column, an extremely fleshy, tri-lobed, and papillose labellum, and a sigmoid column.

Taxonomic confusion has persisted at both generic and specific levels since the proposition of *Gomphichis* by Lindley in 1840. Species of *Gomphichis* have been referred to *Stenoptera* because of the superficial morphological similarity of these genera. Difficulties in the identification of specimens of *Gomphichis* stem from the few morphological characters used to circumscribe species, the morphological variation within the genus, and the lack of a taxonomic revision of the genus. *Gomphichis* has never been monographed nor have its morphological variation and phylogenetic relationships been assessed.

This study clarifies the circumscription of *Gomphichis* and delineates the species on the bases of morphology, anatomy and ecology. Particular features of the genus and each of the recognized species will be discussed, its geographic distribution assessed throughout its range and its elevational preferences examined.

3.2. MATERIALS AND METHODS

3.2.1. Herbarium studies

Approximately 2,100 herbarium specimens representing 735 different collection numbers from 57 herbaria were examined (herbarium acronyms with asterisk were visited). These included specimens from the following herbaria: AAU, AMES*, BH, BM*, BR*, C, CAS, CGE, COL, CPUN*, CR, DAV, E, F, FI (photos only), FLAS, G, GB, GOET, HBG, HAO, HEID*, HUA, K*,LIL, LOJA, LPB, M*, MA, MICH, MO, MSB, NY*, OXF, P*, PA, PH, PORT, PR, QCA*, QAP*, QCNE*, QPLS*, RENZ*, S, SEL, SP, TEX, TI, U, UC, US, VEN, VT, W*,WIS, and Z.

Databases. Voucher specimen information was managed using an Access database. A total of 180 quantitative and discrete characters were examined, measured, and scored for each species. Taxonomic descriptions were generated from the scored characters using the DELTA software package (Description Language for Taxonomy) (Dallwitz, 1980; Dallwitz et al., 1999).

Maps. Latitude and longitude attributes in decimal degrees were gathered from the labels of herbarium vouchers examined. Missing coordinate data from voucher specimens were assigned after consulting geographic gazetteers available on line (Luteyn, 2002; Falling Rain Genomics (FRG), 2004; Geonet

Names Server (GNS), 2004) or maps from the country of origin. A data source of 735 plant collections of *Gomphichis* containing coordinate data was the foundation for generating the distribution maps. Distribution maps for each taxon were prepared by creating a layer of points that were placed on top of a digital map utilizing Arc Catalog and Arc Map, which are two of the major applications of ArcGis8.3 (Environmental Systems Research Institute (ESRI), 2003).

Interpretation of descriptions. The dichotomous key is artificial and therefore does not reflect evolutionary relationships. Species are listed alphabetically by specific epithet. All specimens studied are cited in the list of exsiccatae and were examined unless indicated as not seen (n.v.).

Numeric values are given in their statistical normal ranges, with extreme values enclosed in parentheses. Descriptions of growth habit, color and information shown in the section on distribution, ecology and common names have been derived from herbarium specimen labels, and from field observations.

Typification. All type specimens of *Gomphichis* deposited at the Berlin herbarium (B) were destroyed during World War II. Lectotypes were designated from among the extant isotypes whenever appropriate. For a number of species no extant types were available for study but published line drawings based on these specimens were consulted. In such cases, following the International Code of Botanical Nomenclature (Greuter et al., 2000) under the article 9.2, these illustrations were selected as lectotypes.

Notes on terms and abbreviations. Descriptive terminology followed Dressler (1981; 1993a), Harris and Harris (1994), Kiger and Porter (2001), Lawrence (1951), Quer (1979), Stearn (1983), and van der Pijl and Dodson (1966). Standard abbreviations were used for authors of Latin names (Brummitt & Powell, 1992) and herbarium acronyms (Holmgren et al., 1990). Abbreviations for book citations follow Taxonomic Literature, 2do. ed. (Stafleu & Cowan, 1976-1988; Stafleu & Mennega, 1992-2000) and for periodicals Botanico-Periodicum-Huntianum (Lawrence et al., 1968; Bridson & Smith, 1991; Bridson, 2004).

Phylogenetic relationships. Throughout the systematic treatment, the discussion of species relationships in *Gomphichis* is primarily based on the cladogram depicted in Fig. 5.5. (chapter 5).

Species concept. Species delimitations were made by applying the Phylogenetic Species Concept *sensu* Cracraft (1983) as modified by Nixon and Wheeler (1990). In accordance with this criterion, a species was defined as a population or populations of individuals that shared at least one qualitative character accompanied by other qualitative or quantitative reproductive and/or vegetative traits that allowed it to be consistently separated from other populations.

3.2.2. Field studies

Plant collecting. Many individuals of *Gomphichis* were observed in Ecuador, Peru and Venezuela in their natural habitats, and specimens were fixed in a solution of formalin-acetic acid-alcohol (FAA), and transferred to 70% ethanol. Climatic, ecological and topographic conditions were noted during field work. These observations and the preserved specimens gathered were important for expanding information on character variation within and among populations of the genus.

3.2.3. Laboratory studies

A combination of light microscopy (LM) and scanning electron microscopy (SEM) studies were conducted to investigate and document both vegetative and reproductive features of *Gomphichis*. Representative species of *Gomphichis* for which material was available were studied. Variation found in *Gomphichis* species will be summarized, and the findings discussed in light of published studies of spiranthoid orchids.

Anatomy

Root and foliar anatomy. Anatomical observations on the blade, midrib and pseudopetiole were conducted on selected mature leaves. Leaves fixed in FAA were transferred to 70% ethanol. Transverse sections of leaves and petioles were made from the middle portions of these structures. Pieces of leaf and petiole to be cut were placed on a flat, plastic surface, held down with the blunt side of a single-edged razor blade and freehand sectioned with another sharp single-edged razor blade. The thinner cross sections (ca. 50-100 μm) were rinsed in 15% ethanol for 5 minutes and stained metachromatically for 1-3 minutes using either cresyl violet acetate (CVA 1/100% dye into 15% ethanol) or iodine-potassium iodide (I_2KI: 0.2 g I_2 to 2.0 g KI per 100 ml 15% ethanol) (O'Brien & McCully, 1981) until the sections changed color to dark violet or dark yellow respectively. After a brief rinse in 15% ethanol (except those stained in I_2KI), the sections were wet mounted on a microscope slide using a few drops of 2% calcium chloride ($CaCl_2$) solution as mounting medium as described by Herr (1992) and Keating (1996). The cross sections were observed under a light microscope and photographed at different magnifications. The solution of iodine-potassium iodide (I_2KI) was also used to test for the presence of spiranthosomes (stored starch cells) in cortical root cells. Spiranthosomes treated with I_2KI stain orange at first and then change to deep red or dark blue (Stern et al., 1993a).

Leaf clearings. Methods for clearing leaves were adapted from Arnott (1959), Payne (1969), and Radford et al. (1974). Entire leaves or small leaf pieces fixed in FAA and stored in 70% alcohol were submerged in a 5% NaOH solution and placed in an oven at 37°C for 24-72 hours. Extremely fleshy leaves were bleached in 2% commercial solution of bleach until white. After almost all pigment was removed from the leaves they were washed briefly in clean water and then dehydrated in a 30% and 50% ethanol series for 15 minutes each. The leaf tissue was stained in 0.2% safranin in 50% ethanol for a few minutes under gentle agitation. The stained tissue was dehydrated further in a 70% and 95% alcohol series for 5-10 minutes followed by two or more changes in 100% ethanol, each for 30 minutes. The dehydrated tissue was placed in a solution of 1 part absolute ethanol and 1 part HemoDe for several minutes followed by another solution of 1 part absolute ethanol and 2 parts of HemoDe. Clearing was completed by flooding the tissue with HemoDe. The cleared tissue was stored in HemoDe and studied and photographed under the dissecting scope. The description and terminology follow the recommendations of the Leaf Architecture Working Group (1999).

Macromorphology

Vegetative and inflorescence features were studied on dry material under a dissecting microscope at magnifications up to 50x. Flowers, fruits, and seeds were examined either from material preserved in a modified FAA (53% ethanol of 70%, 37% water, 5% formaldehyde and 5% glycerol) solution or from dried material was rehydrated in concentrated ammonia for 24 hours or until reconstitution after which it was rinsed in regular water (Taylor, 1976; Toscano de Brito, 1996). Measurements of flowers at anthesis, mature fruits, and seeds were taken only from material re-hydrated in ammonia to avoid differences in the measurements caused by different rehydration methods.

Measurements. Measurements of vegetative parts were taken with an ordinary ruler in centimeters and rounded to the nearest half-centimeter; whereas, measurements from reproductive structures were made in millimeters with the aid of an ocular micrometer and rounded to the nearest tenth of the millimeter. The measurements included maximum length or width of the respective organ as well as the diameter of the roots, peduncle, and fruits in their natural positions. The width of the labellum was taken after it had been spread out. The lowermost foliaceous sheath was discerned from the neighboring leaves when it was completely visible in its entire length (Fig. 3.1.).

Micromorphology

Images of the structures obtained under the SEM and light microscopes were recorded digitally at different magnifications. Measurements were taken directly from the digital images or from the ocular scale of the compound or dissecting microscopes.

Trichomes. Different floral segments from specimens preserved in FAA were dehydrated in several changes of alcohol for 30 minutes each and critical point dried. Small pieces (3 x 3 mm) of different floral parts were mounted on stubs and sputter coated for SEM study. Some preserved wet samples were directly observed and photographed under the dissecting microscope.

Pollen and pollinaria. SEM studies on pollen and pollinaria were studied using a non-acetolytic method to avoid destruction of the exine and other delicate tissue as suggested by Webster and Carpenter (2002), Burns-Balogh (1979), and Toscano de Brito (1996). Dried flowers from herbarium specimens were pre-treated in concentrated ammonia for at least 24 hours or until the reconstitution was completed. Then, pollinaria and pollen from both alcohol-preserved specimens and pre-treated samples were extracted from the anthers under a dissecting scope and pipetted into plastic 1500 μL microcentrifuge tubes. The tubes were centrifuged for 1 minute at 1000 rpm to concentrate pollen. The ammonia was removed and the samples rinsed with 3 changes of nanopure water after centrifuging the samples before each change. The nanopure water was pipetted off and 70% alcohol was added. Alcohol-preserved samples were only changed once in 70% alcohol. The tubes were then placed in a water bath sonicator for 4 minutes to remove pollenkit. The samples and liquid preserved samples were dehydrated in an alcohol series, filtered, immersed in amyl acetate, and subsequently dried to the critical point in a TOUSIMIS SAMDRI-790 drier. Dried specimens were mounted onto double-sided adhesive tape attached to aluminium stubs. Specimens were gold sputter coated and examined in a Hitachi S-2700 SEM microscope. Pollen terminology follows Nilsson and Muller (1978).

Seeds. Methods were adapted from Chase and Pippen (1988) and Molvray and Kores (1995). Seeds from naturally dehiscing capsules taken from spirit preserved collections and dried specimens were examined under both light and SEM microscopes. Seeds from dried specimens and pickled material were dehydrated through a graded series of alcohol. Specimens were critical point dried using CO_2, affixed to stubs with double-faced tape, sputter coated and examined.

3.3. TAXONOMIC HISTORY

Gomphichis was established by Lindley (1840) in *The Genera and Species of Orchidaceous Plants* with the description of *G. goodyeroides* from specimens collected by the English botanist Mathews in Peru. In his circumscription of the genus, Lindley discussed the diagnostic differences between *Gomphichis* and *Stenoptera*. According to Lindley (1840), *Stenoptera* differs from *Gomphichis* in its adnate sepals and petals that form a long tube; a fornicate lip; long, narrow, flexuose and spreading petals; and a long and curved column. Since the establishment of *Gomphichis*, its circumscription has been debated. This has resulted in the treatment of *Gomphichis* either as an independent genus or under the concept of *Stenoptera*.

Reichenbach *filius* (1856), based on material collected by Ruiz and Pavón in Peru, included *Gomphichis* in *Stenoptera*, transferred *Gomphichis goodyeroides* to *Stenoptera*, and described *S. viscosa*. A few years later, this worker described *Gomphichis valida* from Bolivian material brought to Europe by Mandon (Reichenbach, 1878).

Lehmann and Kränzlin (1899) proposed the new species *Gomphichis alba*, based on specimens Lehmann collected in Colombia. Two syntypes were included in the protologue (*Lehmann 6034* and *7112*). Subsequent workers found these specimens to represent two distinctive species, *G. alba* and *G. traceyae*.

Kränzlin (1906) described *Cranichis longiscapa*, but this species was later transferred to *Gomphichis* by Schlechter. The following year, Rusby, in a series of publications describing plants Miguel Bang collected in Bolivia, proposed *Stenoptera longifolia*, which is here excluded from *Gomphichis*.

Schlechter (1912) described *Stenoptera plantaginea* from Bolivia stressing its differences from *Gomphichis plantaginea*. The proposed species was later found to be better treated under *Gomphichis*. A few years later, Schlechter (1915) provided an account of the genera of Orchidaceae treating *Gomphichis* as a synonym of *Stenoptera*.

Rolfe (1916) clarified the taxonomic status of *Gomphichis alba* and described *G. traceyae* from specimens collected in the páramos of Colombia.

In his critical review of the Central American Orchidaceae, Schlechter (1918) described several new species in different genera including *Stenoptera costaricensis*. In this publication, on the basis of floral morphology, he also suggested the close relationship of this species to *S. viscosa* Lindl.

Subsequently, Schlechter re-established the genus *Gomphichis*, transferred a few species of *Stenoptera* to it, and described numerous new species of the genus from Central and South America (Schlechter, 1919, 1920; 1921b, 1921a, 1922). All Schlechter's types were destroyed during World War II in the Berlin Herbarium, which has caused taxonomic and nomenclatural difficulties in the understanding and circumscription of *Gomphichis*.

In 1922, Ames described *Gomphichis foliosa* from Colombia based on specimens collected by Pittier.

Mansfeld (1929; 1930), compiled and published illustrations of the species of *Gomphichis* described and prepared by Schlechter based on the holotypes deposited in the Berlin herbarium just before their destruction during wartime. These line drawings are the only documented records of those species and many serve as types.

In 1934, Ames et al. as part of the preparation of a checklist of the orchids of Costa Rica transferred *Stenoptera costaricensis* to *Gomphichis* without further discussion.

A few years later, in the first article of a series devoted to Peruvian Orchids, Schweinfurth (1941) described and illustrated *Gomphichis macbridei*. The same year, Williams published *Gomphichis montana* from material collected in Venezuela and discussed its affinities with *G. plantaginea*. A year later, Williams (1942) briefly summarized the major morphological characters of *Gomphichis* and *Stenoptera* and reduced the species of *Gomphichis* known to him to *Stenoptera* because of the few distinctive characters separating the genera.

In a later publication, Schweinfurth (1944) proposed the new *name Gomphichis plantaginifolia* to accommodate *Stenoptera plantaginea* since the specific epithet was already used for an earlier species of *Gomphichis*.

Renz (1948) described five new species of *Gomphichis* (*G. psilosepala*, *G. bogotensis*, *G. cundinamarcae*, *G. altissima*, and *G. cladotricha*) and reported the occurrence of some others in Colombia. Besides illustrating the newly described species, Renz presented a figure summarizing the variability in shape and trichome density of the sepals and petals.

In 1953, Garay followed the generic concepts of Williams by transferring *Gomphichis lancipetala* to *Stenoptera*. He also described *S. huilaensis*. In the same year, Schweinfurth (1953) proposed *G. koehleri* var. *minor* based on material from Cuzco, Peru. The major criteria for the recognition of this variety were plant size, flower color, and lack of pubescence.

Schneider (1955) provided a synthesis of the Colombian species of *Gomphichis*, discussed the taxonomic problems encountered within the genus and pointed out the difficulties to delimit species in *Gomphichis*. In this publication Schneider also commented that ".... One of the least showy [genera among terrestrial orchids] is *Gomphichis*.... It is one of the most difficult genera among orchids."

In his treatment of the *Orchidaceae of Peru*, Schweinfurth (1958) ignored the earlier suggestions of Schlechter, Williams, and Garay, and kept *Gomphichis* and *Stenoptera* separate without citing, the transfers by the other authors.

Foldats (1968) described *Gomphichis steyermarkii* from Venezuela based on a collection made by Steyermak and Dunsterville. This species in the current treatment is considered a synonym of *G. adnata*.

The most recently described species in the genus is *Gomphichis merzii* (Senghas, 1994). Some pictures and detailed line drawings followed the diagnosis of the species. A general overview of the genus and a discussion of the major distinctive features with respect to *Stenoptera* were also provided.

In summary, most recent workers have recognized *Gomphichis* and *Stenoptera* as different genera (Renz, 1948; Schneider, 1955; Schweinfurth, 1958; Garay, 1978; Dressler, 1993b, a; Senghas, 1994). Currently, 31 binomials have been published under *Gomphichis*, and five additional names have been transferred to the genus, mainly from *Stenoptera*. During the 19th century only five species were published, while in the last century the remaining names were proposed. Schlechter described the greatest number of species in *Gomphichis* with a total of 15. The most recently described species is *G. merzii* based on collections made in Costa Rica (Senghas, 1994).

In recent years, *Gomphichis* has been treated in the context of regional floras, without any attempt to evaluate previous taxonomic views (Schweinfurth, 1958; Garay, 1978; Dressler, 1993a). Partial accounts of the number of species have been provided in the format of checklists for Panama (Dressler, 1980; D'Arcy, 1987), Ecuador (Dodson, 1999), and Peru (Brako et al., 1993). Among the illustrated orchid works depicting the genus can be mentioned: Escobar (1994) for Colombia (genus only); Bennett and Christenson (1993; 1995) for Peru (2 species); and Dunsterville and Garay (1979), 1st ed., and Romero-González and Carnevali Fernández-Concha (2000), 2do ed. for Venezuela (3 species). Available treatments of *Gomphichis* within country boundaries are the following: Colombia (Schneider, 1955), Peru (Schweinfurth, 1958), Ecuador (Garay, 1978), Venezuela (Foldats, 1969), Panama (Williams & Allen, 1980), Costa Rica and, Panama (Dressler, 1993a).

3.4. VEGETATIVE ANATOMY

This section presents information on the root and foliar anatomy of *Gomphichis* and discusses the results in light of available information in closely related genera.

Root anatomy. The rhizodermis consists of 1 layer of velamen. The cortex is uniform, homogeneous, and composed of nearly isodiametric cells. The cortex consists of a uniseriate exodermis which is situated internal to the rhizodermis. The body of the cortex consists of 12-15 layers of cells and a uniseriate endodermis at its internal margin. The vascular cylinder is located internally to the endodermis, and comprises a uniseriate parenchymatous pericycle, conductive tissue consisting of strands of xylem and phloem, and a central portion made of thin-walled parenchyma cells (Fig. 3.2). Spiranthosomes (specialized amyloplasts) are abundant in the cortical cells of *Gomphichis* (they stain blue when exposed to iodine potassium-iodide). The presence of spiranthosomes in many cortical cells of *Gomphichis* confirm the observations of Stern and collaborators (1993a; 1993b) in other closely related spiranthoid orchids such as *Altensteinia* and *Prescottia*.

Leaf anatomy. The midrib is narrowly rounded adaxially and broadly rounded-convex abaxially. The epidermis consists of 1-layer of polygonal cells which are roughly isodiametric with thick cuticles in both the adaxial and abaxial surfaces. The epidermal abaxial cells are smaller and slightly more roundish than the ones located in the adaxial surface. The mesophyll is homogeneous, consists of 5-6 layers of cells that are circular or nearly circular in outline, and possesses few intercellular spaces (Fig. 3.3).

The blade consists of adaxial epidermal cells mostly polygonal with a thick cuticle and cell that are larger than the abaxial epidermal cells. The epidermal cells of the lower surface tend to be roundish in shape. The secondary vascular bundles are equally dispersed throughout the blade (Fig. 3.3).

Stomata. The stomata are superficial, randomly distributed and restricted to the abaxial leaf surfaces. They are also found sporadically over all epidermal surfaces such as sheaths and bracts, but are not found in roots. The guard cells of the stomata have the typical kidney shape. The subsidiary cells in some cases are not well defined. At least three different types of stomata can be distinguished in a single leaf: tetracytic, anisocytic and diacytic (Fig. 3.4). Similar observations were reported by Stern et al. (1993b) in *Altensteinia* and *Prescottia* and other terrestrial orchids of the Cranichideae.

Peduncle. The epidermal cells are isodiametric, compact, and arranged in 9-10 layers. The tissue of the peduncle has no discernable intercellular spaces. The epidermis is followed by a 9-10 multilayered sheath compose of dense, small, and thick-walled lignified cells (stained blue with CVA). Internal to this sheath are two series of vascular bundles embedded in ground tissue; the outer series is arranged in a discrete ring and is composed of small vascular bundles, whereas the inner bundles are scattered, larger, and more parenchymatous than those of the outer ring (Fig. 3.5.).

Leaf venation pattern. Two different venation patterns were found in the leaves of *Gomphichis*: parallelodromous and reticulate.

The parallel venation pattern, typical of most monocots, was found in those species of the genus with primarily thick-coriaceous and narrowly oblong leaves. In *Gomphichis crassilabia*, there are approximately 10-12 primary veins that originate beside each other at the base leaf, run parallel the length of the leaf, and converge at the apex. The secondary veins are straight to slightly curved and connect adjacent primary veins in a regular pattern. The secondary veins depart the primary veins perpendicularly and completely traverse the intercostals spaces (Fig. 3.6, A).

The reticulate venation pattern was observed in *Gomphichis adnata*, a species with thin-coriaceous and primarily elliptic to obovate leaves. Its secondary veins are thin and regularly distributed, and run parallel to the primary vein. The tertiary veins are also thin, sinuous, and irregularly branched, to form a reticulate pattern. Only a few free unbranched vein endings were observed (Fig. 3.6, B-C). There are very few studies of the patterns of leaf venation in orchids and no published studies for terrestrial orchids were found. Cameron (1998) reported reticulate-veined leaves in some genera of the Vanilloideae and suggested that reticulate leaf venation has evolved several times independently in unrelated monocot groups.

3.5. MACROMORPHOLOGY

Habit. *Gomphichis* species are terrestrial, occasionally epiphytic, perennial herbs that attain between 16.5 cm to 180 cm tall. Some of the smallest species such as *G. bogotensis* and *G. traceyae* rarely exceed 50 cm in height. In contrast, the tallest representatives, such as *G. altissima*, *G. valida*, and *G. crassilabia*, are usually over 60 cm tall.

Roots. The roots are fusiform, fasciculate, elongate, fleshy, thick, and 0.2-0.9 cm diam. They are pubescent to villose or rarely glabrous.

Rhizome. The rhizome is usually very short, rarely elongated, and slender. The roots develop from the rhizome.

Leaves. The foliage leaves of *Gomphichis* are basal or cauline with overlapping and sheathing leaf bases. They are glabrous, thick or thin coriaceous, and vary in number from 2-14. The blades are lanceolate, elliptic, oblong, or linear to obovate with an entire margin and an acute to acuminate or rarely obtuse apex. The petiole, hereafter referred to as subpetiole, is often not clearly delimited because the blade is decurrent into it. The base of the subpetiole is wider and clasps the peduncle. The leaves (including the subpetiole) may attain lengths of over 47.5 cm and widths of 0.55-5.9 cm. However, there is great variation in the length and width of leaves throughout the genus, and in many cases there is extensive overlap. When fresh, leaves of *Gomphichis* are usually shiny green adaxially and pale green abaxially. Dried leaves are usually tan to dark brown and light to olive or dark green.

Sheaths. The leaf sheaths are closed or nearly so basally and thus form a tube around the main axis. The sheaths are glabrous, glandular-pubescent to glandular-villose, with eciliate or glandular-ciliate margins, loose-fitting or tight-fitting around the peduncle and acute to acuminate. The sheaths become shorter as they approach the apex, the lower sheaths are 2.60-38 cm long by 0.20-3 cm wide, and the upper ones are 0.50-3.50 cm long by 0.1-1.80 cm wide.

Inflorescence. The inflorescence is a terminal, pedunculate, many-flowered, loose or congested spike that is cylindrical in shape. It varies in length from 2.2-34 cm long and in width from 0.8-3.7 cm. *Gomphichis viscosa* exhibits the longest inflorescences, whereas *G. valida* produces the widest and densest inflorescences in the genus.

Peduncle. The inflorescence is subtended by a long peduncle. The peduncle is either sparsely or densely sheathed and varies in length from 11.5-

158 cm. The lower portion is usually glabrous, but is glandular-villose in *Gomphichis altissima*. The upper portion is moderately to densely glandular-villose or glandular-pubescent.

Rachis. The rachis is obscure or clearly visible, densely glandular-villose exhibiting a ferrugineous color.

Bracts. A single floral bract subtends each flower. The floral bracts range in shape from ovate to oblong, are ca. 0.9-28 mm long by 0.5-12 mm wide, and are shorter, as long as, or longer than the ovaries. The bracts are membranous, persistent, with 1-5 noticeable nerves, and vary from glabrous to glandular-pubescent, glandular-pilose or glandular-hirsute. The bract bases are always truncate and the apices acuminate. The bract margin is glandular-ciliate.

Flowers. The flowers of *Gomphichis* are non-resupinate, hermaphroditic, zygomorphic, 3-merous, pendent, sessile, and vary in length from 2.2-15 mm. The sepals and petals are appresed to the labellum to form a galea.

The *dorsal sepal* is free, basically oblong to oblong-obovate in shape, often 3-nerved, extremely to slightly concave, and 2-12 mm long by 1.5-5.2 mm wide. The dorsal sepal is abaxially commonly pubescent in the lower half.

The *lateral sepals* are basally adnate to the labellum, mostly oblong in shape, mostly 3-nerved or 1-2-nerved, symmetrical or asymmetrical, and ranging from 2.2-15 mm long by 0.29-5.2 mm wide.

The *petals* are free, often asymmetrical, narrowly elliptic to broadly elliptic, obovate to spatulate, shortly or long-decurrent, as long as or longer than the sepals, and ranging from 3.5-13 mm long by 1.1-56 mm wide. The petals are white, yellow, yellowish to greenish in color. The lamina of the petals is usually 3-nerved but varies from 1-2-nerved, and is often glandular-pubescent, glandular-pilose, or glandular-hirsute abaxially. The petals are usually glabrous adaxially or puberulent in *Gomphichis goodyeroides* and *G. altissima.* The margins of the petals is entire, glandular-ciliate, or glandular-ciliolate. The cilia consist of multicellular, branched or unbranched trichomes.

The *labellum* is uppermost, conduplicate, incumbent upon the column, conspicuously or obscurely three-lobed, shortly clawed, and ranges from 3-15 mm long by 2.2-9.8 mm wide. The lateral lobes are slightly fleshy and involute giving a tubular or obpyriform shape to the labellum in the natural position. The abaxial and adaxial surfaces of the lateral lobes are pubescent to puberulent in the middle, and possess a pair of small reniform to ovate, glabrous calli at the base and near the edges. The midlobe is extremely fleshy with a fleshy or nearly so entire margin. The abaxial surface of the midlobe is covered densely by papillae except apically. The adaxial surface of the midlobe exhibits two fleshy calli that are covered by non-glandular puberulent to non-glandular tomentose trichomes. The apex of the midlobe is generally covered by non-glandular pubescent or non-glandular hirsute trichomes.

The *column* is elongate, geniculate, broadly ellipsoidal, clavate, or sigmoidal. The total length of the column varies from 3-9.5 mm and the column stalk ranges in length from 0.5-4 mm. The abaxial surface of the column is mostly sparsely non-glandular puberulent to non-glandular pubescent. With the exception of *Gomphichis valida*, the column bears sparsely to densely non-glandular trichomes adaxially.

The *anther* is erect, oblong to ovate, dorsi-ventrally flattened, proportionally large and wide (0.9-3.5 mm long by 0.5-2.6 mm wide) in comparison to the size of the column. The anther is fleshy, motile with 2 parallel locules dehiscing longitudinally.

The *pollinia* are non-sectile, linear to narrowly-ovoid, 4 in number, soft, and pale yellow in color. The pollen grains are united by elastoviscin.

The *viscidium* is single, detachable, rounded, 0.1-1.2 mm in diameter, and dark brown in color. The pollinia are directly connected to the viscidium.

Nectary. The exact location of the nectary is unclear since no evident histological differentiation has been observed. The nectary may well be located at the base of the labellum and column. It is also possible that the lateral calli may be the functional nectaries.

Ovary. The ovary is sessile, inferior, 3-carpellate, 1-locular with parietal placentation, usually ovoid, elliptic or fusiform, and 1.7-15 mm long by 0.5-7.4 mm wide. The ovary ranges from glabrous in unnamed taxon 3 to densely glandular-pubescent, glandular-villose or glandular-hirsute. Dissected ovaries show three distinctive placental arms. Most of the unilocular ovary is occupied by numerous ovules.

The *stigma* is ventral to subventral, 3-lobed, generally concave, rarely flat, transverselly elliptic to elliptic, with slightly revolute margins, and varying in length from 0.2-2.5 mm. The apex of the stigma is foveolate to slightly notched after the removal of the pollinia. The receptive stigma is covered by a wet transparent and sticky substance.

Fruit. The fruits are 1-loculicidal capsules, ovoid, ellipsoidal to fusiform, and 6-14 mm long by 0.7-10 mm wide. The fruits are displayed upright on the rachis and accompanied by persistent floral segments. Young fruits are light green and mature fruits are medium to dark brown. Mature fruits are erect, thin-walled, and dehisce by splitting along the mid-line of each carpel.

3.6. MICROMORPHOLOGY

A combination of light and electron microscope studies were conducted to document the characters of *Gomphichis*, assess character variation occurring within species, summarize the patterns observed, and discuss the findings in light of other studies within the Orchidaceae.

Trichomes. In this treatment, trichomes are any cellular structure arising from the epidermis. The indumentum of *Gomphichis* is composed of four different types of trichomes (Fig. 3.7). These, according to the scheme of Hewson (1988) are the following:

1) Papillae are confined to the abaxial surface of the labellum.

2) Simple, non-glandular trichomes are often found on the column and adaxial surface of the labellum. These trichomes are variable in length.

3) Multicellular, glandular, unbranched trichomes are the most common type found mainly on the abaxial surface of the sepals, petals, bracts, sheaths, and

young axes. These trichomes are variable in density, range in length from 0.1-0.8 mm, and may be straight or twisted.

4) Multicellular, glandular, branched trichomes are generally sparingly branched, usually forked, and occur on the petal margins or more frequently on the abaxial surface of the petals of few species in the genus.

The terms used to describe pubescence are based on the length, rigidity, orientation, and form of the trichomes and are defined below:

Pubescent.- Short, downy, soft, straight trichomes, 0.2-0.5 mm long.

Puberulent.- Very short, downy, soft, straight trichomes, less than 0.2 mm long.

Tomentose.- Short, more or less appressed, matted or tangled, rigid, soft, dense trichomes less than 0.5 mm long.

Villose.- Long, soft, weak, shaggy, curly, unmatted , sparse trichomes.

Pilose.- Long, weak, thin, slender, more or less erect, sparse trichomes more than 0.5 mm long.

Hirsute.- Long, more or less erect, rough, coarse, stiff, unmatted trichomes more than 0.5 mm long.

Papillose.- Simple, unicellular trichomes less than 0.1 mm long.

Ciliate.- Margin bordered with fine multicellular hairs more than 0.5 mm long.

Ciliolate.- Margin with very short fine unicellular hairs less than 0.2 mm long.

Although in a couple of species (*G. altissima*, *G. goodyeroides*, and *G. caucana*) the type and placement of the indumentum is a useful taxonomic character, they are too variable to be employed alone in distinguishing species of *Gomphichis*.

Pollen and pollinaria. *Gomphichis* has four non-sectile pollinia containing pollen grains arranged in tetrads and held together by elastoviscin (Fig. 3.8). Some workers have reported the number of pollinia in *Gomphichis* as two (Foldats, 1969; Garay, 1978), whereas others describe it as two and bipartite (Szlachetko & Rutkowski, 2000). Observations under LM and SEM of the pollinia of species of *Gomphichis* in different developmental stages show that each pollinium originates independently even though they are very close at the apex to the point of attachment of the viscidium. The exine of the pollen grains is reticulate and heterobrochate (Fig. 3.9). This type of exine sculpturing in *Gomphichis* was also noted by early workers (Schill & Pfeiffer, 1977; Burns-Balogh, 1991). Pollen morphology is not very useful as a species marker in *Gomphichis* because it is homogeneous and uniform for most of the characters and there is overlap, especially in size and shape among species.

Seeds. The seeds are roughly fusiform, spatulate, between 0.44-1.70 mm long by 0.12-0.26 mm wide, and light brown in color. The shape of the ends of the seeds varies from rounded to squarish due to the tight packaging of adjacent seeds in the locule during development. The testa is thin walled, ridged-reticulate, with high anticlinall walls, and cell openings along the cell-to cell adhesions which are usually located at the cell vertices. Adjoining anticlinal cell-walls roll inward at their edges to form more or less straight sided cells. The number of cells that form the testa in *Gomphichis* range from 10-18 in length and 10-12 in width (Fig. 3.10). The individual cells vary in shape from oblong, subquadrate, elliptical, or irregular in outline. The shape and size of the cells is variable depending on their position, with cells occupying central positions generally longer than ones at the edges. The embryo is often located towards the center and rarely near the micropylar end. The characteristics of the seeds observed in *Gomphichis* are in agreement with the Spiranthoid type seeds described by Molvray and Kores (1995).

The seeds of species of *Gomphichis* examined here are rather uniform with no apparent differences in testa structure. No discernable pattern of cell openings was found among species of the genus, and, thus, the suggestions of Molvray and Chase (1999) on the utility of this feature at lower-taxonomic levels are not applicable for *Gomphichis.* The differences in surface patterns tend to be quantitative rather than qualitative and have limited utility in species delimitation in *Gomphichis.*

3.7. CYTOGENETICS

A literature search reveals no reports of chromosome counts in *Gomphichis* and any of its allies. In members of the subtribes Cranichidinae and Spiranthinae the chromosomes are small and homogeneous in size, little differentiated morphologically, variable in number even within the same taxon (n=15 to n= 24), and, display different levels of polyploidy (Martínez, 1985). Chromosome variation among terrestrial orchids has been attributed to polyploidy (Brandham, 1999) rather than aneuploidy (Chase & Olmstead, 1988). As suggested by the published information, it is likely that the chromosomes of the species of *Gomphichis* will show a combination of the characteristics described for their close allies.

3.8. ECOLOGY

Habitats. The majority of species inhabit montane cloud forests and some reach the subpáramos and páramos. They are most frequently found in light gaps in primary forests. A number of species are also located in disturbed sites such as secondary forests, forest margins, stream borders, road banks, pastures, and clearings. About a third of the species occur in open páramos, boggy zones, and rocky places near the permanent snow line. Plants of *Gomphichis* are scattered or clustered in a given area, but usually rare in primary forests. Individual species most often occupy broad geographic ranges.

Soils. Species of the genus are known to occur on volcanic, sandy, and rocky soils. Species of *Gomphichis* appear to tolerate a wide range of acidic pH, soil nutrients, and drainage. Nonetheless, dense populations are usually found in places where the nutrient level is high and there are several layers of humus.

Phenology. Fertile collections of species of *Gomphichis* have been made throughout the year, but flowers and fruits have been found most frequently in July.

Elevational range. The greatest number of species occurs from 1500 to 3000 m (Fig. 3.11). The only exceptions are the narrow endemics, *Gomphichis crassilabia* and *G. koehleri* which never occur below 3000 m. Moreover, three primarily epiphytic species, *G. adnata*, *G. costaricensis*, and *G. hetaerioides* show high degree of altitudinal tolerance by extending their altitudinal ranges below 1500 m. Among all species of *Gomphichis*, *G. traceyae* and *G. adnata* exhibit the highest degree of variability in their altitudinal preferences. In contrast, *G. merzii* and those species with restricted distributional ranges, *G. crassilabia* and *G. koehleri*, show also narrower altitudinal preferences.

3.9. DISTRIBUTION

Geographical range. All species of *Gomphichis* are native to the high mountains of the Neotropics, including the cordilleras of southern Central America, the Andes and the Guayana Highlands. *Gomphichis* has a continuous range from Costa Rica, Panama, and Colombia south through Bolivia, between latitudes of approximately 10°N and 17°S. It ranges from Costa Rica in the west to the Guayana Highlands at the border of Venezuela, Guyana and Brazil in the east, between longitudes of approximately 84°W to 60°W from east to west, respectively (Fig 3.12, Table 3.1). The center of diversity is in the northern Andes with the greatest concentration of species in Venezuela and Colombia where 10 species are presently recognized in each country.

Most species have a relatively broad distribution with only two being local endemics. The most widely distributed species is *Gomphichis viscosa* which ranges from Colombia through Ecuador, Peru, and Bolivia. The relatively large range of *G. viscosa* could be caused by the different environmental conditions found throughout its distribution. In contrast, *G. crassilabia* and *G. koehleri* are found only in restricted localities of the Ecuadorian and Peruvian Andes, respectively. A few species grow sympatrically in a number of localities. For instance, *G. crassilabia* and *G. caucana* occur within the limits of the Parque Nacional Podocarpus in Ecuador.

The restriction of species of *Gomphichis* to the neotropical montane regions suggests a recent origin of the genus. Only three species of *Gomphichis* are found in Central America. These species, *G. costaricensis*, *G. merzii* and *G. hetaerioides*, also extend into northern South America. Given that *Gomphichis* is highly diverse in the Andean region, it is likely that it moved into Central America from South America either via long distant dispersal and/or direct migration after a land connection was established between Central and South America in the late Pliocene (Raven & Axelrod, 1974). Long distance dispersal may have also occurred in the case of *G. adnata* which is found in the Andes of Venezuela and Colombia into the Guayana Highlands (Berry et al., 1995).

3.10. SYSTEMATIC TREATMENT

GENERIC DESCRIPTION

Gomphichis Lindl., Gen. Sp. Orchid. Pl. 446. 1840; Schweinfurth, Fl. Peru, Fieldiana, Bot. 30(1): 78-84. 1958; Foldats, Fl. Venez. 15: 381-396. 1969; Garay, Fl. Ecuador 9:146-153. 1978; Williams, Fl. Panama, Monogr. Syst. Bot. Missouri Bot. Gard. 4: 145-146. 1980; Dressler, Field Guide to the Orchids of Costa Rica and Panama 304. 1993. Type species. *Gomphichis goodyeroides* Lindl.

Gomphiches Lindl., nom. illegit. orth. var. used by Schlechter in Repert. Spec. Nov. Regni Veg. Beih. 6: 51. 1919; 9: 50. 1921; 10: 60. 1922.

Etymology. Derived from the Greek word (*gomphos* = nail) in reference either to the glandular hairs that cover the flowers of the genus, or to the club-shaped column (Schultes & Pease, 1963).

Terrestrial, occasionally epiphytic, small to large-sized, perennial ***herbs***. ***Roots*** fascicled, fleshy, thick, elongate, pubescent, lanate, or villose, rarely glabrous. ***Rhizome*** short, the first few internodes somewhat thickened. ***Leaves*** basal and/or cauline, rosulate or clustered, ascending or spreading, glabrous, shiny green adaxially and paler green abaxially when fresh; subpetiole weakly-to well-differentiated, the base expanded; blade elliptic, lanceolate, oblong, linear, or obovate, thin- to thick-coriaceous, light green, dark to olive green, tan to medium brown or dark brown to black when dry, the base not attenuate, or short- to long-attenuate, the apex acute, subacuminate, acuminate, or obtuse, the margin entire. ***Peduncle*** erect, usually glabrous, rarely sparsely glandular-villose in lower portion, moderately to densely glandular-villose or glandular-pubescent in upper portion. ***Sheaths*** foliaceous, tubular, sparse to congested and imbricate, tight- to loose-fitting, decreasing in size and thickness upwards, the lower sheaths glabrous to glabrate, acute to acuminate, usually eciliate, rarely glandular-ciliate, acute to acuminate, the upper ones usually sparsely to moderately pubescent or hirsute, sometimes glabrous, usually acuminate, eciliate or glandular-ciliate. ***Inflorescence*** terminal, erect, spicate, narrowly to broadly cylindrical, slightly obtuse to obtuse, loose or congested, many-flowered. ***Rachis*** visible or obscure, moderately to densely glandular-pubescent or glandular-villose with ferruginous glandular trichomes. ***Bracts*** persistent, subtending each flower, ovate, ovate-oblong, lanceolate, ovate-elliptic, ovate-lanceolate, or oblanceolate, 1-3-nerved, the proximal bracts longer and broader than the distal bracts, densely to sparsely glandular-pubescent, glandular-pilose to glandular-hirsute, occasionally glabrous often basally, the base truncate, the apex acute to acuminate, glandular-ciliate throughout. ***Flowers*** acropetal, nonresupinate, strongly reflexed, corolla and ovary forming a right angle, whitish, yellowish to greenish, and glandular-pubescent to glandular-hirsute, rarely glabrous, few to many, small to medium-size. ***Dorsal sepal*** free, usually symmetrical, elliptic, ovate, obovate or oblong, usually concave to deeply concave, sparsely glandular-pubescent to glandular-hirsute, rarely glabrous, the base truncate, the apex acute or obtuse, rarely acuminate, the margin entire, eciliate. ***Lateral sepals*** basally adnate to the labellum, ovate, obovate, elliptic or oblong, usually slightly concave, rarely plane or deeply concave, 1-2(-3)-nerved, usually asymmetrical, usually sparsely to densely glandular-pubescent to glandular-hirsute basally or throughout, rarely glabrous, the base truncate, the apex usually obtuse, occasionally acute and rarely subacuminate, the margin entire, eciliate. ***Petals*** free, elliptic to broadly elliptic, obovate to obovate-oblong, slightly concave or plane, 1- or 3-nerved, occasionally 2-nerved, sometimes asymmetrical, pubescent to hirsute, rarely glabrous abaxially, usually glabrous, occasionally puberulent adaxially, the margin, entire, glandular-ciliate, rarely glandular-ciliolate, mostly medially. ***Labellum*** tubular, oblong-ligulate or obpyriform in natural position, often ovate or rhombic when spread out, longer than broad or broader than long, obscurely or distinctly 3-lobed, fleshy; claw quadrate or rectangular, 3-nerved; lateral lobes usually subrotund, 5-9- nerved, concave, usually densely puberulent or sometimes densely pubescent abaxially, densely pubescent, puberulent or tomentose adaxially, the base usually subcordate, occasionally cordate, rarely cuneate, the calli usually reniform, occasionally ovate, usually fleshy, horizontal or inclined; midlobe oblong to narrowly oblong, broadly to narrowly triangular, erect, rarely curved outwards, very fleshy to slightly fleshy, rarely with prominent reticulate marks, the apex usually obtuse or acute, rarely constricted at apex, usually slightly fleshy, glabrous abaxially, often hirsute, rarely pubescent or glabrous adaxially, the margin often flat, rarely involute or undulate, slightly fleshy, entire, usually eciliate, rarely ciliolate, the calli usually oblong, rarely obovate or roundish, fleshy to slightly fleshy, mostly occupying two thirds of the midlobe, often deeply sulcate, puberulent adaxially, rarely tomentose or pubescent over the entire length. ***Column*** geniculate, clavate, often sigmoid, rarely subglobose, short to elongate, usually puberulent or pubescent, rarely papillose on abaxially and along margins, mostly pubescent, tomentose or villose or rarely glabrous adaxially, hardly to distinctly stalked. ***Anther*** ovate, rarely oblong, dorsal, obtuse, and basally thickened on the outer side, glabrous. ***Pollinia*** 4, soft, non-sectile, usually asymmetrical, linear to oblong-ovoid, pale yellow. ***Viscidium*** small, rounded, brown. ***Stigma*** large, transverse, 3-lobed, the median lobe (rostellum) thin, transverse, obtuse to truncate, the lateral lobes rudimentary, usually slightly convex. ***Ovary*** ovate, fusiform or elliptic, sessile, with 3 longitudinal ridges, densely pubescent, villose to hirsute, rarely glabrous. ***Fruit*** ovoid, ellipsoidal to fusiform, capsules dehiscing longitudinally by 3-slits, subtended by persistent bracts and remnants of the perianth, green when immature, brown when mature, moderately to densely pubescent, villose or hirsute, rarely glabrous. ***Seeds*** pale brown, minute, numerous, fusiform, occasionally spathulate or broadly elliptic.

Distribution. A montane, neotropical genus of 17 species ranging from southern Costa Rica through Central America, south to Bolivia, and from Costa Rica in the west to Venezuela in the east.

Key to the Species of *Gomphichis*

1. Labellum weakly 3-lobed, tubular, oblong-ligulate, lanceolate, ovate to cordate in outline, the lateral lobes as long as broad when spread out.
    2. Margin of petals ciliate throughout; margin of labellum undulate with well marked nervation .... 12. *G. macbridei.*
    2. Margin of petals ciliate in middle portion and proximally; margin of labellum flat, without noticeable nervation.
        3. Column broadly ellipsoidal (subglobose); sheaths imbricate .... 7. *G. crassilabia.*

3. Column elongate, narrowly ellipsoidal; sheaths laxly arranged along peduncle to congested, usually not imbricate.
    4. Petals sparsely puberulent adaxially along midrib; calli of labellum midlobe occupying distal 1/2 the total length, tomentose adaxially .... 9. *G. goodyeroides*.
    4. Petals glabrous adaxially; calli of labellum midlobe occupying almost completely the total length, puberulent-papillose adaxially.
        5. Labellum midlobe obovate-oblong, the apex truncate; petals obovate-oblong .... 14. *G. plantaginifolia*.
        5. Labellum midlobe broadly oblong, the apex obtuse; petals elliptic.
            6. Flowers pubescent (trichomes 0.2-0.5 mm long).
                7. Leaves linear, linear-oblong to oblanceolate-ligulate; flowers yellow to yellowish, rarely white; lateral sepals asymmetrical .... 5. *G. caucana*.
                7. Leaves narrowly elliptic; flowers white; lateral sepals symmetrical .... 18. Unnamed taxon 1.

6. Flowers hirsute (trichomes > 0.5 mm long).
    8. Inflorescence narrowly cylindrical (up to 2.5 cm width); dorsal sepal asymmetrical; labellum width up to 4.6 mm; column slightly villose .... 11. *G. koehleri.*
    8. Inflorescence broadly cylindrical (> 2.5 cm width); dorsal sepal symmetrical; labellum width > 6 mm; column glabrous to glabrate .... 16. *G. valida.*

1. Labellum distinctly 3-lobed, obpyriform in outline, the lateral lobes twice as long as broad when spread out.
    9. Terrestrial herbs; leaves shortly subpetiolate (very nearly sessile); plants of páramos, mostly above 3000 m elevation.
        10. Petals symmetrical, the apex acute to slightly obtuse, entire, the margin ciliolate (trichomes < 0.3-0.5 mm long); labellum midlobe truncate, the midlobe calli with membranaceous margin; flowers yellow .... 4. *G. bogotensis.*
        10. Petals asymmetrical, the apex round, erose-denticulate, the margin ciliate (trichomes > 0.5 mm long); labellum midlobe obtuse with slightly fleshy margin; flowers greenish-white or yellowish .... 15. *G. traceyae.*

9. Terrestrial or epiphytic herbs; leaves evidently subpetiolate; plants of montane cloud forests, usually below 3000 m elevation.
    11. Inflorescence congested, the rachis obscure; petals densely glandular-ciliate.
        12. Sepals apically obtuse; labellum midlobe with roundish calli; petals asymmetrical, broadly elliptic with simple and branched cilia, the margin retrorsely glandular-ciliate, the apex obtuse .... 6. *G. costaricensis*.
        12. Sepals apically acute to apiculate; labellum midlobe with oblong calli; petals symmetrical, narrowly elliptic with only simple cilia, the margin spreading glandular-ciliate, the apex acute to slightly obtuse .... 8. *G. cundinamarcae*.
    11. Inflorescence lax to subdense, the rachis evident; petals sparsely glandular-ciliate.
        13. Bracts glabrous to pubescent; petals with spreading glandular-cilia.
            14. Ovary elliptic, glabrous; sepals and petals glabrous .... 20. Unnamed taxon 3.
            14. Ovary fusiform, pubescent; sepals sparsely pubescent, petals glabrous 19. Unnamed taxon 2.
                15. Labellum acute, ciliolate .... 13. *G. merzii*.
                15. Labellum obtuse, eciliate.

16. Bracts oblong, shorter than or as long as ovaries; flowers small, up to 5.5 cm long; lateral sepals symmetrical; petals obtuse .... 2. *G. alba.*

16. Bracts ovate, longer than ovaries; flowers medium size, greater than 5.5 cm long; lateral sepals asymmetrical; petals acute .... 1. *G. adnata.*

13. Bracts pilose; petals with retrorse glandular cilia.

17. Peduncle moderately to densely villose throughout; labellum with apex puberulent adaxially; petals pubescent abaxially, often puberulent adaxially .... 3. *G. altissima.*

17. Peduncle glabrous; labellum with apex hirsute adaxially; petals glabrous on both surfaces.

18. Labellum as long as broad when expanded, 5-7.2 x 5-7 mm; column strongly sigmoid .... 17. *G. viscosa.*

18. Labellum longer than broad when expanded, 5.6-6.8 x 4.4-6.4 mm; column geniculate, clavate ...... 10. *G. hetaerioides.*

1. ***Gomphichis adnata*** (Ridl.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 6: 51. 1919. *Stenoptera adnata* Ridl., Timehri 5: 205. 1886. Type. Venezuela. Bolívar: Roraima, upper slope, Oct-Jan 1884–1885 (fl, fr), *E. F. im Thurn 173* (holotype, K). (Fig. 3.13.A).

Gomphichis gracilis Schltr., Repert. Spec. Nov. Regni Veg. Beih., 6: 29. 1919. Type. Venezuela. Distrito Federal: Caracas, 1896 (fl), *A. Ernst s.n.* (holotype, B, destroyed; lectotype, here designated, illustration AMES).

Gomphichis steyermarkii Foldats, Acta Bot. Venez. 3: 331, fig. 8A. 1968. Type. Venezuela. Táchira: Headwaters of Río Quinimarí, along Quebrada de Las Copas, below Páramo de Judío, 20 km S of San Vicente de la Revancha, 35 km S of Alquitrana, SW of Santa Ana, 13 Jan 1968 (fl, fr), *J. A. Steyermark et al. 100883* (holotype, VEN; isotypes, AMES-2 sheets).

Terrestrial or rarely epiphytic *herbs*, 50–91(–120) cm tall; roots (0.3–)0.4–0.5 cm diam., lanate. *Leaves* basal, clustered, (4–)5–7(–8), ascending, (11.5–)16.7–24(–26) x (2–)2.4–3.5(–4.8) cm; subpetiole well-differentiated; blade elliptic or oblanceolate, thin-coriaceous, tan to medium brown or dark brown to black when dry, the base attenuate, the apex acuminate. *Peduncle* (34–)42–78.5(–96.5) x (0.4–)0.5–0.6(–0.8) cm, glabrous in lower half, sparsely glandular-villose in upper half; sheaths (5–)6–7(–9), sparsely arranged along peduncle, tight-fitting, the lower sheaths (7–)9–12.3(–16.5) x (0.8–)1–2(–2.6) cm, glabrous with acuminate apex and eciliate margin, the upper sheaths (1–)1.1–1.6(–2.5) x (0.3–)0.4–0.45(–0.5) cm, glabrous with acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, subdensely many-flowered, (6.5–)10.5–19(–23) x (0.8–)1.7–2.5(–3.1) cm; rachis visible, densely glandular-villose; bracts ovate, (1–)3-nerved, (6–)8–10(–11) x (1.5–)2.7–4.1(–4.4) mm, glabrous, sparsely glandular-pubescent at base, the apex acute or acuminate, the margin glandular-ciliate. *Flowers* white, (4.2–)5.5–6.7(–7.5) mm long. *Dorsal sepal* elliptic-obovate, deeply concave, 1(–2)-nerved, (4.5–)5–6.3(–8) x (2–)2.2–2.8(–3.2) mm, abaxially glabrous to sparsely glandular-pubescent basally, the apex acute. *Lateral sepals* oblong, slightly concave, 1(–2)-nerved, (4.2–)5.1–6.6(–7) x (2–)2.2–3.1(–3.3) mm, asymmetrical, abaxially sparsely glandular-pubescent basally, the apex acute. *Petals* elliptic, slightly concave, (1–)2–3-nerved, (4.1–)5–6.1(–7) x (1.6–)2–2.8(–2.9) mm, the blade abaxially and adaxially glabrous, the base attenuate, the apex acute, the margin entire, sparsely glandular-ciliate medially, glandular-ciliolate apically with simple hairs. *Labellum* obpyriform in outline, rhombic when spread, (4.2–)5.4–6.9(–7) x (4–)4.5–5.5(–6.5) mm, distinctly 3-lobed; claw oblong, 3-nerved, (0.3–)0.7–1.3(–1.6) x (0.7–)0.9–1.3(–1.6) mm; lateral lobes subrotund, 5(–7)-nerved, abaxially densely puberulent, adaxially sparsely pubescent in middle, the base subcordate, the calli reniform, very fleshy, inclined; midlobe broadly triangular, slightly curved outwards, fleshy, the apex obtuse, slightly fleshy, adaxially densely pubescent, the margin flat, fleshy, entire, eciliate, the calli oblong, fleshy, occupying two thirds of the midlobe, adaxially slightly sulcate, sparsely puberulent over entire length with few glandular hairs at base. *Column* slightly sigmoid, (3.9–)4.4–5.5(–6.8) x (1.2–)1.4–1.8(–1.9) mm, sparsely pubescent on abaxial surface, densely pubescent on adaxial surface, the stalk (0.6–)0.9–1.5 mm long; anther oblong, (1.1–)1.5–2.2(–3) x (0.7–)0.9–1.4(–2) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.2–)0.3–0.4(–0.5) mm diam.; stigma transversely ovate, slightly convex, (0.4–)0.5–0.7(–1) x (1–)1.1–1.4(–1.5) mm. *Ovary* ellipsoidal, (4.5–)6–9.3(–12) x (1.6–)3–4.5(–5.7) mm, densely glandular-pubescent. *Fruits* ellipsoidal, 7.8–10.5(–14) x (3.3–)4–6(–6.5) mm, densely glandular-pubescent; seeds fusiform, 0.6–0.7(–0.9) x (0.15–)0.18–0.21 mm.

Distribution. (Fig. 3.13.B). Venezuela and Colombia. This species was described from material collected on the summit of the Mount Roraima in the Guayana Highland of southeastern Venezuela. Since this formation extends also into western Guyana and northern Brazil, this species eventually may be found in the latter countries as well. This species is found in primary and disturbed areas in cloud forests reaching the subpáramos, at 1000–3300 m elevation, in rich and sandy soils. All epiphytic specimens have been collected below elevations of 2650 m. Flowering occurs throughout the year except in April, more conspicuously in December. Fruiting is mainly from October to January and May.

Specimens examined. COLOMBIA. Antioquia: E of Sonsón, 2800 m, 30 Oct 1948 (fl), *Araque & Barkley 327* (US); Mpio. Medellín, Santa Elena, 1500-2000 m, 1 Jan 1931 (fl), *Archer 1283* (AMES, US); Mpio. Medellín, La Sierra, 18 km N of Medellín, 2000 m, 29 Jan 1931 (fl), *Archer 1509* (AMES, NY, US); Mpio. Jardín, Jardín-Alto de Ventanas rd., 2350-2550 m, 25 May 1983 (im fl), *Escobar 2683* (SEL); Mpio. Medellín, Vereda Santa Elena, 12 km E of Medellín, 2400 m, 18 Dec 1980 (fl), *Galeano et al. 304* (COL); San Pedro, 9 Feb 1939 (fl), *Tomás*

379 (US). **Cauca:** Mpio. Tambo, La Romelia, Parque Natural Nacional Munchique, 2600-2800 m, 5 Aug 1980 (fl, fr), *Lozano 3648* (COL); Cordillera Occidental, Mount El Derrumbo, 2700-3000 m, 29 Jun 1922 (fl), *Pennell 7506* (AMES). **Huila:** Cordillera Oriental, headwaters of Río Neiva, Cerro Neiva-Cerro del Diablo, 35 km ESE of Neiva, 2300-2360 m, 6 Dec 1942 (fl), *Fosberg 19272* (US). **Nariño:** Reserva La Planada, 7 km from Chucunes, 7 Jan 1988 (fl), *Gentry et al. 60549* (MO). **Santander:** Cordillera Oriental, mountains E of Las Vegas, 3000-3300, 20-21 Dec 1926 (fl, fr), *Killip & Smith 15857* (AMES, NY, US); Cordillera Oriental, vic. Las Vegas, 2600-3000 m, 21-23 Dec 1926 (fl), *Killip & Smith 15955* (AMES). **Valle del Cauca:** Cordillera Occidental, E slopes, Hoya del Río Cali, left slopes of Río Pichindé, 2250-2260 m, 22 Jul 1946 (fl), *Cuatrecasas 21602* (F).

VENEZUELA. Anzoátegui: Fila Grande, headwaters of Quebrada La Tigra, Cerro San José, Bergantín-Cerro Peonía (Cerro Los Pajaritos), 1800-1850 m, 19 Mar 1945 (fr, st-NY), *Steyermark 61543* (AMES, F, NY). **Barinas:** Páramo de Calderas, Calderas-Las Mesitas, 2900 m, 19 Sep 1951 (fl), *Renz 7392* (RENZ). **Bolívar:** Mount Roraima, Oct-Jan 1884-1885 (fl), *im Thurn 131* (K); N-facing slope, Soropopán-Tepuí, 1800 m, 18 Dec 1952 (fl), *Maguire & Wurdack 33943* (NY, RENZ-photocopy); Mount Roraima, on SW-facing sandstone ledge, 2100-2620 m, 28 Sep 1944 (im fl), *Steyermark 58922a* (F). **Lara:** Dtto. Andrés Eloy Blanco, 14 km SE of Sanare rd. to Parque Nacional Yacambú, 1000-1500 m, 13 Nov 1982 (im fl), *Aymard et al.* 1500 (PORT); Páramo de Las Rosas, Humucaro Alto-Carache, 2300 m, 25 Oct 1952 (im fl), *Renz 7867* (RENZ); Dtto.

Jiménez, Sanare-El Volcán new rd., 5.5 km WSW of Sanare, 1700 m, 14 Feb 1959 (fr), *Renz 9351* (RENZ); El Volcán, nr. Sanare, *Unknown 535* (K). **Lara-Trujillo border:** Páramo de los Ñepes, slopes above La Peña, 2500 m, 24-25 Dec 1959 (fl), *Barclay & Juajibioy 10319* (AMES, MO). **Mérida:** vic. Mérida, 15 Feb 1957 (fl), *Bernardi s.n.* (NY); Tabay, 2500-3200 m, 18 Sep 1930 (fl), *Gehriger 467a* (NY), *467b* (US); La Montaña study area, ca. 5 km S of La Montaña teleférico station, 2450-2650 m, 28 Oct 1987 (fr), *Kelly 9195* (K); La Carbonera-Páramo de Los Conejos, 2700 m, 27 Mar 1949 (fr), *Renz 5321* (RENZ); Canalejos, Egido-Valle de La[s] Gonzales, 3000 m, 2 May 1949 (fl), *Renz 5538* (RENZ); Tovar-Guaraque, slopes of Tovar, 2000 m, 26 Jul 1949 (fl), *Renz 5870* (RENZ); La Cruz de Mora-El Molino, 2500 m, 12 Nov 1949 (fl, fr), *Renz 6091* (RENZ). **Sucre:** Cerro Turumuquire [Turimiquire], N-facing slopes La Trinidad, zone of cloud forest, 1700-2000 m, 5 May 1945 (fl, fr), *Steyermark 62517* (AMES, F). **Táchira:** nr. Boca de Monte, Bailadores-Pregonero, 2000 m, 13 Aug 1949 (fl), *Renz 5803 & 5899* (both RENZ); La Revancha in the Valley of Río Quinamarí, 1700 m, 18 May 1951 (fr), *Renz 7035* (RENZ). **Trujillo:** Mpio. Boconó, Parque Nacional Guaramacal, SE part, 1.7 km beyond the entrance, 2839 m, 6 Dec 2002 (fl, fr), *Alvarez & León 2981* (NY-2 sheets, PORT); Mpio. Boconó, 14.3 km from the town of Guaramacal to antennas of communication, 2794 m, 6 Dec 2002 (fl), *Alvarez & León 2984* (NY, PORT); Mpio. Trujillo, Km 23.6 of the old rd. San Rafael-Trujillo, 2263 m, 7 Dec 2002 (fl), *Alvarez & León 2986* (NY-2 sheets, PORT); Mpio. Boconó, Parque Nacional Guaramacal, Boconó-Guaramacal rd., SE of Boconó, below the television antennas, 3000 m, 14 Jul 1995 (fl), *Dorr & Barnett 8105* (PORT); Mpio. Boconó, Parque Nacional Guaramacal, Boconó-Guaramacal rd., SE of Boconó, S slope of mountain, 2770 m, 22 Jul 1995 (fl), *Dorr & Barnett 8238* (PORT); Mpio. Boconó, Arbol Redondo, 12-13 Dec 1994 (fl), *Licata & Niño 793* (PORT); Trujillo-Boconó rd., Km 48, 2300 m, 13 Sep 1947 (fl), *Renz 4339* (RENZ), 2200 m, 24 Feb 1950 (fl), *Renz 6260* (RENZ); Trujillo-Boconó rd., 2500 m, 26 Nov 1947 (fl), *Renz 4514* (RENZ), 1800 m, Oct 1947 (fl), *Renz 4521* (RENZ), 2700 m, 12 Nov 1948 (fl), *Renz 5019* (RENZ), 2400 m, 24 Dec 1948 (fl), *Renz 5042* (RENZ), 2450 m, 21 Nov 1951 (fl), *Renz 7569* (RENZ); Alto del Tomón, NW of Páramo de los Torres, 2300 m, 8 Dec 1948 (im fl), *Renz 5006* (RENZ); mountain range S of Boconó, 2700 m, 3 Nov 1951 (fl), *Renz 7510* (RENZ); Trujillo-Boconó, nr. Trujillo, 2000 m, 21 Nov 1951 (fl), *Renz 7563*, (RENZ), 2300 m, 21 Nov 1951 (fl), *Renz 7567* (RENZ); La Puerta-Timotes, 1800 m, 17 Dec 1953 (fl), *Renz 8163* (RENZ); Dtto. Carache, Páramo Los Ñepes, Carache-Humocaro Bajo, 2300 m, 6 Sep 1959 (fl), *Renz 9683* (RENZ); Parque Nacional Guaramacal, Fila de Agua Fria, 2700-2800 m, Jan-Feb 1996 (fl, fr), *Stergios & Zambrano 17695* (PORT); Mpio. Boconó, Parque Nacional Guaramacal, Quebrada Jirajara, S slope, 2200-2900 m, Jun 2001 (im fl), *Stergios et al. 19268* (PORT); La Quebrada Cortijo, by boundary line Lara-Trujillo, above Humocaro Bajo, Quebrada de Morro, 2600-2800 m, 6 Feb 1944 (fl), *Steyermark 55331* (F).

Gomphichis adnata is distinguished from its closest relative, *G. alba*, by larger flowers, ovate, glabrous to basally pubescent bracts, and acute petals with a ciliolate apex. *Gomphichis adnata* and *G. alba* inhabit the middle and upper cloud forest zone of the Andean region, although the former is also found on the summits of tepuis in the Guayana Highlands. They have in common basal and cauline leaves, which are essentially lanceolate in shape with long-decurrent pseudopetioles, elliptic and glabrous petals, and basally pubescent sepals. Both species can be differentiated easily by the size of the flowers and bracts, these being longer and broader in *G. adnata*.

Specimens of *Gomphichis adnata* have been reported in the literature erroneously as *G. viscosa*. Almost all descriptions of new taxa of *Gomphichis* published after about 1900 include comparisons with specimens assigned to *G. adnata* (incorrectly refered to as *G. viscosa*).

The type specimens of *Gomphichis steyermarkii* are in late fruit and bear some flower remains and very few late flowers. The available floral elements show sepals and petals slightly narrow and apiculate. Thus, *G. steyermarkii* is treated under *G. adnata*.

This species has been recorded in the extreme distributional range of the genus in the east.

2. *Gomphichis alba* F. Lehm. & Kraenzl., Bot. Jahrb. Syst. 26: 500. 1898. Type. Colombia. Vall del Cauca: Cali, 1700–2000 m, Jun-Aug (fl, fr), *F. C. Lehmann 7112* (lectotype, here designated, K; isolectotypes, LE, n.v., frag. HBG (probably from LE), photo NY, RENZ). (Fig. 3.14.A).

Gomphichis psilosepala Renz, Candollea 11: 245, Fig. 5. Type. Venezuela. Aragua: Colonia Tovar, 1854–1855 (fl, fr), *A. Fendler 1402* (holotype, G; isotypes, AMES, K, MO, P, PH).

Terrestrial or rarely epiphytic *herbs*, (60–)67–96(–118) cm tall; roots (0.2–)0.3–0.5 cm diam., lanate. *Leaves* basal, clustered, (3–)4–5(–7), ascending, (12.5–)16.5–20.5(–22) x (2–)2.5–3.5(–4.2) cm; subpetiole well-differentiated; blade ovate, thin-coriaceous, tan to medium brown when dry, the base long-attenuate, the apex acuminate. *Peduncle* (46–)56.9–81.5(–96.5) x (0.4–)0.5–0.6(–0.7) cm, glabrous in lower half, sparsely glandular-pubescent in upper half; sheaths (4–)5–8(–12), sparsely arranged along peduncle, tight-fitting, the lower sheaths (4.5–)7–11.2(–13.5) x (0.5–)0.9–1.4(–2.3) cm, glabrous with acuminate apex and eciliate margin, the upper sheaths (0.9–)1–1.2(–3) x (0.2–)0.3(–0.4) cm, glabrous with acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, loosely or subdensely many-flowered, (8.8–)13–21(–26.5) x (1–)1.3–2(–3) cm; rachis visible, sparsely glandular-villose; bracts ovate-oblong, (1–)3-nerved, (4.5–)5.5–9(–9.8) x (1.9–)2.5–3.2(–3.8) mm, glabrous or glabrate, the apex acuminate, the margin glandular-ciliate. *Flowers* white, (3.6–)4–5.1(–5.5) mm long. *Dorsal sepal* obovate, concave, 1(–3)-nerved, (4–)4.2–4.8(–5.2) x (1.6–)1.9–2.5(–2.6) mm, abaxially glabrous to sparsely glandular-pubescent basally, the apex acute. *Lateral sepals* obovate, slightly concave, 1(–2)-nerved, (3.7–)4–4.5(–5.1) x (1.8–)2–2.4 mm, abaxially glabrous to sparsely glandular-pubescent basally, the apex acute. *Petals* elliptic, slightly concave, (1–)3-nerved, (3.5–)3.8–4.5(–5.2) x 1.9–2.3(–2.5) mm, the blade abaxially and adaxially glabrous, the base attenuate, the apex obtuse or rounded, the margin entire, sparsely glandular-ciliate medially, glandular-ciliolate apically with simple hairs. *Labellum* obpyriform in outline, rhombic when spread, (3–)4–5(–6.2) x (2.2–)3.5–5.6(–7.5) mm, distinctly 3-lobed; claw oblong, 3-nerved, (0.5–)0.6–0.9(–1) x (0.6–)0.7–1(–1.1) mm; lateral lobes subrotund, 5(–7)-nerved, abaxially densely puberulent, adaxially sparsely puberulent in middle, the base subcordate, the calli reniform, slightly fleshy, horizontal; midlobe broadly triangular, erect, very fleshy, the apex acute or obtuse, slightly fleshy, adaxially densely pubescent, the margin flat, slightly fleshy, entire, eciliate, the calli obovate, strongly fleshy, occupying two thirds of the midlobe, adaxially deeply sulcate, sparsely puberulent at base. *Column* slightly sigmoid, (3.7–)3.8–4.6(–5.5) x (1–)1.3–1.5(–1.7) mm, moderately pubescent on abaxial surface, densely pubescent on adaxial surface, the stalk (1–)1.1–1.5 mm long; anther ovate, (1.1–)1.2–1.6(–1.8) x (0.5–)0.7–1.1(–1.2) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.2–)0.3–0.4 mm diam.; stigma transversely ovate, slightly convex, (0.3–)0.4–0.6(–0.8) x (0.7–)1–1.3(–1.6) mm. *Ovary* ellipsoidal or fusiform, (3.5–)5–7(–8) x 1.8–3.2(–3.9) mm, glabrous, moderately glandular-pubescent. *Fruits* ellipsoidal, (7–)8.5(–9.3) x 3–3.2(–4.3) mm, glabrous or glabrate; seeds fusiform or broadly elliptic, 0.74–0.83 x 0.12–0.2 mm.

Distribution. (Fig. 3.14.B). Known from Colombia and Venezuela. It grows in humid soils, of dense cloud forests, at elevations between 1500 and 3200 m. Flowering specimens have been collected throughout the year except in

August and October. Fruiting specimens have been collected in January, April to June, August and November.

Specimens examined. COLOMBIA. Antioquia: mountains W of Sonsón, 2700 m, 20 Aug 1948 (fr), *Johnson & Barkley 18C814* (US). **Cundinamarca:** Facatativá, 29 Jan 1883 (fl, fr), *Lehmann 2607* (G-2 sheets, RENZ-frag=Renz 11614). **Tolima:** Tolima, 2400-3200 m, 10 Jan 1883 (fl), *Lehmann 2414* (G).

VENEZUELA. Caracas, Dtto. Federal: Caracas, *Buschel s.n.* (K). **Mérida:** Sierra Nevada, above Mérida, 2700 m, 2 Feb 1939 (fl), *Alston 6778* (BM); Monte Zerpa, 2500-2600 m, 25 Jun 1953 (fl), *Bernardi 695* (NY); vic. Mérida, El Valle in the Cordillera del Norte, 2300 m, 13 Jan 1952 (fl), *Renz & García 7675* (RENZ); W side of La Azulita, 1700 m, 2 Apr 1949 (fl), *Renz 5213* (RENZ); La Carbonera, Egido-La Azulita, 2300 m, 4 Mar 1949 (fl), *Renz 5287* (RENZ); Capaz-Gebét, El Trigal, 2600 m, 30 Mar 1949 (fr), *Renz 5303* (RENZ), 2500 m, 30 Mar 1949 (fl), *Renz 5365* (RENZ); Cordillera de Mérida, Mérida-Los Nevados, site in Mérida above Casa Blanca, 2200 m, 21 May 1949 (fl, fr), *Renz 5389* (RENZ); La Carbonera-Chorotal, 2300 m, 14 Sep 1949 (fl), *Renz 5910* (RENZ); vic. Mérida, W slopes of Valle Mucujún, 2300 m, 20 Mar 1951 (fl), *Renz 6711* (RENZ), El Valle in the Cordillera del Norte, 2000 m, 19 Jul 1951 (im fl), *Renz 7259* (RENZ), El Valle-Cordillera del Norte, 2500 m, 18 Nov 1951 (fl, fr), *Renz 7544* (RENZ). **Monagas:** Cerro Negro, above La Sabana de las Piedras, NW of Caripe, around summit, 1500-2180 m, 15 Apr 1945 (fl, fr), *Steyermark 62112* (F). **Táchira:** vic. La Fundación, Río Quinimarí, 2600 m, 16 May 1951 (fr), *Renz 7017* (RENZ); Páramo Zumbador-Queniquea, 1800 m, 5 Sep 1951 (fl), *Renz 7616* (RENZ). **Trujillo:** La Puerta-Timotes rd., 1800 m, 24 Dec 1948 (fl), *Renz 4932* (RENZ).

Gomphichis alba is characterized by very small flowers that are 4–5.1 mm long, as well as lanceolate, glabrous, short and narrow bracts, which are as long as or shorter than the ovaries, and elliptic, obtuse petals with spreading cilia.

Gomphichis alba is probably closely related to *G. adnata*; the differences between these two species are discussed under the latter.

3. ***Gomphichis altissima*** Renz, Candollea 11: 253, figs. 5, 7A a-g. Type. Colombia. Cundinamarca: N of San Miguel, 2700–2800 m, 16 Feb 1941 (fl), *O. Renz 4152*, (lectotype, here designated, RENZ). (Fig. 3.15.A).

Gomphichis cladotricha Renz, Candollea 11: 256, figs. 7B, h-n. Type. Colombia. Cundinamarca: E of Usaquén, 2800 m, 23 Aug 1941 (fl), *O. Renz 4167* (holotype, RENZ).

Terrestrial *herbs*, (58–)74–134(–180) cm tall; roots (0.3–)0.4–0.6(–0.9) cm diam., villose. *Leaves* basal, clustered, 6–9(–13), ascending, (17–)21–36(–47.5) x (1.5–)2.3–3.5(–4) cm; subpetiole well-differentiated; blade oblong-lanceolate, thin-coriaceous, light green when dry, the base attenuate, the apex acuminate. *Peduncle* (44–)71–124(–158) x (0.5–)0.6–0.9(–1.3) cm, sparsely glandular-villose in lower half, densely glandular-villose in upper half; sheaths (5–)7–11(–13), sparsely arranged along peduncle, tight-fitting, the lower sheaths (8–)9–22(–

34.3) x (0.7–)0.9–1.8(–3) cm, glabrate with acuminate apex and eciliate margin, the upper sheaths 0.8–1.8(–3.2) x (0.2–)0.3–0.5(–0.8) cm, sparsely glandular-villose with acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, loosely many-flowered, (10–)15.5–24.1(–27) x (1.3–)2–2.7(–3.2) cm; rachis visible, densely glandular-villose; bracts lanceolate, 3-nerved, (8.5–)9.8–13(–15) x (2.2–)3–4(–4.7) mm, sparsely or moderately glandular-pilose, the apex acuminate, the margin glandular-ciliate. *Flowers* white or greenish, (6.3–)7–8.2(–9.5) mm long. *Dorsal sepal* obovate, concave, 1(–3)-nerved, (5.9–)6.3–7.1(–8) x (2.5–)2.7–3.2(–3.5) mm, abaxially sparsely glandular-pubescent, the apex acute. *Lateral sepals* oblong or obovate-oblong, slightly concave, 1–2(–3)-nerved, 6–7(–8.5) x (2.2–)2.8–3.5(–3.9) mm, asymmetrical, abaxially sparsely glandular-pubescent, the apex acute. *Petals* elliptic, slightly concave, (1–)3-nerved, (5.7–)6–7.1(–8) x (2.5–)2.9–3.3(–3.7) mm, asymmetrical, abaxially sparsely glandular-pilose with simple and branched trichomes, adaxially glabrous to sparsely puberulent along midrib, the base attenuate, the apex acute or obtuse, the margin entire, sparsely glandular-ciliate medially, glandular-ciliolate apically with simple and branched retrorse hairs. *Labellum* obpyriform in outline, rhombic when spread, (5.6–)6.7–8.5(–10) x (4.1–)5.7–7.5(–8.5) mm, distinctly 3-lobed; claw oblong, 3-nerved, (0.6–)0.8–1.2(–1.5) x (0.9–)1–1.4(–1.5) mm; lateral lobes subrotund, 5–7(–9)-nerved, abaxially densely puberulent, adaxially moderately pubescent in middle, the base subcordate, the calli reniform, slightly fleshy, horizontal; midlobe broadly triangular, slightly curved outwards, very fleshy, the apex acute or obtuse, fleshy, adaxially densely puberulent, the margin flat, fleshy, entire, eciliate, the calli oblong, strongly fleshy, occupying two thirds of the midlobe, adaxially deeply sulcate, sparsely papillose or pubescent at base. *Column* clavate or geniculate, (4.8–)5.5–6.6(–7) x (1.2–)1.6–2.3(–2.5) mm, sparsely puberulent on abaxial surface, densely tomentose on adaxial surface, the stalk (1–)1.3–2(–2.6) mm long; anther oblong, (1.5–)1.8–2.2(–2.3) x (0.8–)1–1.5(–1.7) mm; pollinia symmetrical, linear; viscidium circular, (0.2–)0.3–0.5(–0.6) mm diam.; stigma transversely ovate, slightly convex, (0.5–)0.7–1(–1.2) x (1–)1.3–1.8(–2) mm. *Ovary* fusiform, (5–)6.4–10(–12) x (2.1–)2.9–5.2(–6.5) mm, densely glandular-pilose. *Fruits* ellipsoidal or ovoid, 14 x 5.3 mm, densely glandular-pilose; seeds spatulate or fusiform, 1.1 x 0.26 mm.

Distribution. (Fig. 3.15.B). Venezuela, Colombia, Ecuador, and Peru. The species is found in montane cloud and elfin forests, at elevations of 1600–3150 m. Flowering and fruiting occurs mainly from August to December, but especially in September.

Specimens examined. COLOMBIA. Cauca: W slopes of Cerro Munchique, 2300 m, 2 Mar 1884 (fl), *Lehmann 3723* (BM, G, RENZ-frag); Cordillera Occidental, Mount Santa Ana, 2700-3000 m, 29-30 Jun 1922 (fl), *Pennell 7466a* (US). **Cundinamarca:** Cordillera Oriental, Dtto. Ferrolarada, Correg. de Carinto, 10 km NE of Choachí, crest of Cerro de Fonté, 2600 m, 24 Nov 1943 (fl), *Fosberg 21384* (US).

VENEZUELA. Mérida: Tabay, 2500-3200 m, 18 Sep 1930 (fl, fr), *Gehriger 467* (F, NY); Piñango-Torondoy, 2300 m, 15 Mar 1949 (fl), *Renz 5126* (RENZ); Los Canalejos, Egido-Valle de Gonzales, 2700 m, 2 May 1949 (im fl), *Renz 5801* (RENZ); La Carbonera-Chorotal, 2300 m, 14 Sep 1949 (im fl), *Renz 5923* (RENZ); Egido-La Azulita, Páramo de La Carbonera, 2400 m, 7 Nov 1949 (fl), *Renz 6084* (RENZ); Las Cruces-Páramo Capaz, Las Quebraditas, 2300 m, 23 Nov 1949 (fl), *Renz 6187* (RENZ); vic. Mérida, El Valle to Cordillera del Norte, 2400-2500 m, 23 Nov 1951 (fl), *Renz 7583* (RENZ); Egido-La Azulita, Chorotal, 2400 m, 25 Nov 1951 (fl), *Renz 7597* (RENZ); nr. La Trampa, around Lagunillas, 2000 m, 6 Nov 1953 (fl), *Renz 8095* (RENZ). **Portuguesa:** Mpio. Sucre, Parque Nacional Guaramacal, Divisoria de la Concepción, 1600-1850 m, Jan 2000 (fl), *Stergios 19142* (PORT). **Táchira:** Boca de Monte, 2200 m, 22 Oct 1949 (fl), *Renz 5991* (RENZ). **Trujillo:** Mpio. Boconó, Parque Nacional Guaramacal, N slope, plot number 16, 2530-2580 m, 3-4 Feb 2000 (fl, fr), *Cuello et al. 1946* (PORT); Trujillo-Boconó rd., 2500 m, 13 Sep 1947 (fl), *Renz 4363* (RENZ); Alto del Tomón-NW of Páramo de Los Torres, 2300 m, 8 Dec 1948 (fl), *Renz 5021* (RENZ). **Zulia:** Dtto. Perijá, Campamento Frontera VI, on tepuí-like sandstone ridge 4 x 0.5-1 km running E-W, E of the International border, headwaters of Río del Norte-southernmost branch of Río Aricuaisa, 2400 m, 23-28 Jul 1974 (fl), *Berry 168* (MO, NY).

ECUADOR. Loja: S of Yangana above Cachaco, 2440 m, 12 May 1981 (fl), *Kuhn et al. 108* (SEL). **Napo:** slopes of Guagra Urcu, on the loma above upper Río Borja, 2720 m, 25 Sep 1980 (fl), *Hølm-Nielsen et al. 26965* (AAU);

upper slopes of Guagra Urcu, 2840 m, 26 Sep 1980 (fl), *Hølm-Nielsen et al. 27228* (AAU); Guagra Urcu, Loma Jaramillo, SW of the pass Río Borja-Río Suno, 2800 m, 27 Sep 1980 (fl), *Hølm-Nielsen et al. 27318B*, *27327* (both AAU); Guagra Urcu, lomita SE of summit Jaramillo, 2900 m, 29 Sep 1980 (fl), *Hølm-Nielsen et al. 27621, 27646* (both AAU).

PERU. Amazonas: Prov. Chachapoyas, middle E Calla-Calla slopes, nr. kms 415-418 of Leimebamba-Balsas rd., 2900-3150 m, 20 Aug 1962 (fl, st), *Wurdack 1734* (US-2 sheets).

Gomphichis altissima is a poorly known species that is morphologically similar to *G. viscosa* and *G. hetaerioides*, but differing in its peduncle, which is covered by dense, villose trichomes along its entire length, petals that are acute or apically obtuse, and elliptic in outline, bearing branched and simple trichomes and slightly retrorse cilia, and a labellum with a recurved apex that is longer than the sepals and petals.

I have expanded the concept of *Gomphichis altissima* to include *G. cladotricha* due to the lack of discrete characters separating these taxa. A careful examination of the type specimens shows only two minor morphological differences between these two taxa: the shape of the apex of the petal, which is acute in *G. altissima* and subtruncate to slightly obtuse in *G. cladotricha*, and the presence of trichomes on the adaxial surface of the petals of *G. altissima* (absent in *G. cladotricha*). The majority of the specimens examined show mostly obtuse petals bearing branched and simple trichomes and cilia. In stature and morphological architecture they match closely with *G. altissima*. A number of specimens, however, are intermediate, possessing morphological features described for both taxa. Moreover, in contrast to Renz's descriptions, all specimens studied have a combination of glandular, branched and simple cilia. It should be noted also that the inflorescences of the types are in different developmental stages. Perhaps this explains the unfixed phenotypic variation observed in the type specimens as described by Renz. Given that both taxa were published in the same article by the same author, and that the type of *G. cladotricha* is incomplete, I am designating *G. altissima* as the name for this species.

4. *Gomphichis bogotensis* Renz, Candollea 11: 249. 1948. Type. Colombia. Cundinamarca: Mountain range N of Monserrate in Bogotá, 3000–3300 m, 9 Jan 1937 (fl), *O. Renz 4144* (holotype, RENZ). (Fig. 3.16.A).

Terrestrial *herbs*, (21–)29–40(–50) cm tall; roots (0.2–)0.25–0.3(–0.4) cm diam., glabrous. *Leaves* basal, rosulate, (4–)5–6(–7), spreading, (4–)7–10.5(–18) x (0.6–)1–1.5(–2.2) cm; subpetiole weakly differentiated; blade oblong, thin-coriaceous, dark brown to black when dry, the base short-attenuate, the apex acute. *Peduncle* (18.5–)25.2–35(–43.7) x (0.2–)0.3–0.6(–0.9) cm, glabrous in lower half, densely glandular-villose in upper half; sheaths (4–)5–6(–7), sparsely arranged along peduncle, tight-fitting, the lower sheaths (3.7–)5–8.3(–11.8) x (0.2–)0.4–0.8(–1) cm, glabrous with acute apex and eciliate margin, the upper sheaths (0.5–)0.7–1.1(–1.5) x (0.2–)0.3–0.4(–0.5) cm, sparsely glandular-pubescent at base with acute apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, congested many-flowered, (2.2–)3.5–5.9(–7.1) x (0.8–)1.2–1.6(–1.8) cm; rachis obscure, densely glandular-villose; bracts ovate, (1–)3-nerved, (0.9–)5.8–8.2(–9.7) x (2–)2.5–4(–5.6) mm, sparsely glandular-pubescent in the lower half, the apex acuminate, the margin glandular-ciliate. *Flowers* yellow, (4–)4.9–6.2(–6.7) mm long. *Dorsal sepal* asymmetrically, elliptic or obovate, concave, 1–2(–3)-nerved, (4–)4.2–5.3(–7) x (1.6–)1.9–2.6(–3.5) mm, abaxially sparsely glandular-pubescent basally, the apex acute. *Lateral sepals* elliptic, plane, 1(–3)-nerved, (2.2–)4.2–5.7(–6.6) x 1.9–3(–5.2) mm, asymmetrical, abaxially sparsely glandular-pubescent, the apex acute. *Petals* oblong, slightly concave, 1(–3)-nerved, (4–)4.5–5.2(–5.6) x (1.4–)1.5–2(–2.4) mm, asymmetrical, abaxially sparsely glandular-pubescent in distal half, adaxially glabrous, the base attenuate, the apex slightly obtuse, the margin entire, sparsely glandular-ciliolate except at base and apex with simple hairs. *Labellum* obpyriform in outline, rhombic when spread, (4.2–)5.2–6.5(–6.9) x (3.5–)4–5.2(–5.8) mm, distinctly 3-lobed; claw oblong, 3(–4)-nerved, (0.2–)0.6–1.2(–1.5) x (0.2–)0.5–1 mm; lateral lobes subrotund, (3–)5–6(–7)-nerved, abaxially densely puberulent, adaxially moderately puberulent in lower portion, the base subcordate, the calli ovate, very fleshy, erect or inclined; midlobe triangular, erect, fleshy, the apex truncate, membranaceous, adaxially densely puberulent, the margin flat, membranaceous, entire, ciliolate at apex only, the calli oblong, fleshy, completely occupying the midlobe, adaxially slightly sulcate, sparsely papillose over the entire length. *Column* geniculate or strongly sigmoid, (3.3–)4–

5.4(–6) x (0.6–)0.9–1.6(–1.9) mm, sparsely pubescent on both surfaces, the stalk (0.6–)1.2–2(–2.1) mm long; anther ovate, (1.3–)1.4–1.7(–2) x (0.7–)0.9–1.1(–1.3) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.2–)0.3–0.7(–1.2) mm diam.; stigma transversely elliptic, applanate, 0.6–0.9(–1.5) x (0.7–)1–1.4(–1.5) mm. *Ovary* ovoid, (1.7–)4–5.3(–7.3) x (1.2–)1.9–3.7(–5) mm, densely glandular-pubescent. *Fruits* ovoid, 6–7.5 x 4.5–5.5 mm, densely glandular-pubescent; seeds spatulate, 0.44–0.57 x 0.18–0.2 mm.

Distribution. (Fig. 3.16.B). Venezuela and Colombia. *Gomphichis bogotensis* occurs in subpáramos and *Espeletia* páramos, and also in disturbed habitats such as road banks and pasture borders at elevations of 2000–3500 m. Flowering occurs throughout the year except in the months of March and June with a peak flowering in October. Fruiting specimens have been collected in November and December.

Specimens examined. COLOMBIA. Cundinamarca: Bogotá, El Chicó, Dec 1946 (fl), *Black, G. A. 46-570* (AMES); Mpio. Chía, nr. the house of the Cabildo Indígena, 2690 m, 17 May 1996 (fr), *Cortés 555* (COL); Bogotá, 13 Oct 1852 (fl), *Holton 201* (NY, PH); NE of Bogotá, Buenavista, Río Teusaca, 2900-3000 m, 6 Oct 1917 (fl), *Pennell 2362* (NY); Sibaté, 2700-2800 m, 13-15 Oct 1917 (fl), *Pennell 2505* (AMES, NY); Usme, 2700-2800 m, 26 Sep 1951 (fl), *Schneider 245* (S); Cota, 2800 m, 16 Jul 1953 (fl), *Schneider 245/2* (COL); Bogotá, Páramo de Monserrate, 3200 m, 22 Aug 1948 (fl), *Schneider 245/3* (RENZ). **Magdalena:** Santa Marta, Sierra Nevada, *Simons s.n.* (BM).

Santander: E of Bucaramanga toward Berlín, 3250 m, 3-5 Nov 1981 (fl), *Luer & Escobar 6567* (SEL), 3050 m, 3-5 Nov 1981 (fl), *Luer & Escobar 6585* (SEL).

VENEZUELA. Lara: Páramo de Las Rosas, Humucaro Alto-Carache, 3000 m, 25 Oct 1952 (fl), *Renz 7858* (RENZ); Dtto. Morán, trail Buenos Aires-Páramo de las Rosas, 2300-2600 m, 15 Nov 1984 (fl), *van der Werff & Rivero 7955* (PORT). **Mérida:** Campo Elías, 2.6 km from San José del Sur towards Mucutuy, 2497 m, 2 Dec 2002 (fl), *Alvarez & León 2965* (NY, PORT), 5.3 km from San José del Sur towards Mucutuy, 2830 m, 2 Dec 2002 (fl), *Alvarez & León 2966* (NY, PORT), ca. 10 km from San José del Sur towards Mucutuy, 2989 m, 2 Dec 2002 (fl, fr), *Alvarez & León 2968, 2968a* (both NY, PORT); nr. Estación Alto de la Aguada, 3300-3500 m, 4 Nov 1976 (fl, fr), *Bernardi 17113a, Bernardi et al. 17108* (G); Dtto. Campo Elías, 4.5 km from San José de Acequias on the way to Mucutuy, 2900 m, 14 Oct 1984 (fl), *Berry & Calvo 4381* (MO-2 sheets); Parque Nacional Sierra Nevada, Páramo de Mucubají, 10 km SW of Los Frailejones, 3500 m, 17 Sep 1994 (fl), *Merz 740, 749* (both NY); Piñango-Timotes rd., 2500 m, 17 Dec 1948 (fl, fr), *Renz 4929* (RENZ); Mucutuy-Puente de Gonzales, Páramo de San José, 3000-3200 m, 5 Nov 1949 (fl), *Renz 6048* (RENZ); Caraguá-Pueblo Nuevo, Piedras Blancas-Pueblo Nuevo, NW side of Páramo San José, 2300 m, 20 Nov 1949 (fl, fr), *Renz 6170* (RENZ); Las Cruces-Páramo Capaz, 2700 m, 23 Nov 1949 (fl), *Renz 6180* (RENZ); Páramo de Santo Domingo, 2900 m, 30 Sep 1951 (fl), *Renz 7422* (RENZ); Dtto. Rangel, Parque Nacional Sierra Nevada, Mucubají, Laguna Negra, 19 Sep 1978 (fl), *Stergios 1384* (PORT). **Táchira:** Dtto. Sucre, Páramos El Batallón and La Negra, rd. to

Queniquea, 2800 m, 11 Dec 2002 (fl, fr), *Alvarez et al. 3000* (NY, PORT); Llano San Antonio, surroundings above Boca del Monte, Bailadores-Pregonero, 2000 m, 13 Aug 1949 (fl), *Renz 5693* (RENZ); Páramo Zumbador, 2700 m, 15 Sep 1949 (fl), *Renz 5921* (RENZ); Páramo La Negra, 3000 m, 22 Oct 1949 (fl), *Renz 5999* (RENZ); Páramo Zumbador, 2200 m, 8 Oct 1950 (fl), *Renz 6538* (RENZ). **Trujillo:** Páramo de Los Torres, 3000 m, 16 Oct 1947 (fl), *Renz 4324* (RENZ); Carache-Humucaro Bajo, Las Palmas, 2500 m, 8 Feb 1948 (fl), *Renz 4585* (RENZ); above Niquitao, nr. Páramo Calderas, 2500 m, 24 Oct 1951 (fl), *Renz 7478* (RENZ).

Gomphichis bogotensis has been confused in the past with *G. traceyae*, but can be distinguished from the latter by the very short inflorescences ranging from 3.5 to 5.9 mm, deeply yellow flowers, acute to slightly obtuse and ciliolate petals, a labellum consisting of a pair of fleshy calli surrounded by a membranaceous margin, and short ovaries 4–5.3 mm long.

According to cladistic studies this species is sister to a clade containing *Gomphichis viscosa*, *G. traceyae*, *G. adnata*, *G. costaricensis*, *G. cundinamarcae*, and an unnamed taxon. All have in common small flowers with a broadly three-lobed labellum.

Although Renz (1948) characterizes the labellum apex of *Gomphichis bogotensis* as acute, the type specimen and additional material examined shows it is truncate. The apex of the labellum in young flowers, however, is usually folded given the appearance of acute instead of a labellum with a truncate apex.

5. ***Gomphichis caucana*** Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 53. 1920. Type. Colombia. Cauca, 3500 m, *M. Madero* [*163*] (holotype, B, destroyed; lectotype, here designated, illustration AMES). (Fig. 3.17.A).

Gomphichis lancipetala Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 54. 1920. Type. Colombia. Cauca and Antioquia, 3500 m, *M. Madero* [*39*] (holotype, B, destroyed; lectotype, here designated, illustration AMES).

Gomphichis foliosa Ames, Sched. Orchid. 1: 1. 1922. Type. Colombia. Cauca: Páramo de Moras, entre Mozoco and Pitayó, tierra o[a]dentro, 3000–3500 m, Feb 1906 (fl), *H. F. Pittier 1397* (holotype, US; isotypes, frag. AMES).

Stenoptera huilaensis Garay, Svensk Bot. Tidskr. 47(2): 195. 1953. Type. Colombia. Huila: La Plata, "in selva primaera", 2600 m, 11 Feb 1939 (fl), *K. von Sneidern 2028* (holotype, S).

Terrestrial h*erbs*, (35–)52–98(–132) cm tall; roots (0.2–)0.3–0.4(–0.5) cm diam., villose. *Leaves* basal, clustered, (2–)5–7(–10), ascending, (7–)11–29(–47) x (0.7–)1–1.6(–2) cm; subpetiole weakly differentiated; blade linear-oblong or oblanceolate-ligulate or linear, thick-coriaceous, light green when dry, the base attenuate, the apex acute or subacuminate. *Peduncle* (30–)44.7–91.5(–123.5) x (0.3–)0.6–1.1(–1.5) cm, glabrous in lower half, moderately glandular-villose in upper half; sheaths (5–)9–13(–17), congested along peduncle, loose-fitting, the lower sheaths (6.5–)9.5–19(–38) x (0.4–)1–1.8(–2.4) cm, glabrous with acute apex and eciliate margin, the upper sheaths (0.8–)1.2–2(–3.2) x (0.2–)0.3–0.7(–1.8) cm, glabrous with acute apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse to obtuse at apex, congested many-flowered, (3.2–)5–10.5(–15.5) x (1.5–)2.1–2.9(–3.6) cm; rachis obscure, densely glandular-villose; bracts ovate, (1–)3(–4)-nerved, (9–)11–15(–21) x (3.5–)4.5–7(–9) mm, glabrous, sparsely glandular-pubescent at base, the apex acute, the margin glandular-ciliate. *Flowers* white or yellow, (6.5–)7.9–10.5(–15) mm long. *Dorsal sepal* obovate-elliptic, concave, (1–)2–3-nerved, (4.5–)6.5–8.7(–12) x (1.5–)2.8–3.9(–5) mm, abaxially sparsely glandular-pubescent, the apex acute or obtuse. *Lateral sepals* elliptic or elliptic-oblong, plane, (1–)2–3-nerved, (6–)7.5–9.5(–12) x (2.3–)2.9–4.1(–5.2) mm, asymmetrical, abaxially sparsely glandular-pubescent, the apex obtuse. *Petals* oblong-elliptic or narrowly-ovate, slightly concave, (1–)2–3-nerved, (6.1–)6.9–8.5(–10) x (1.6–)2.3–3.1(–3.9) mm, asymmetrical, abaxially sparsely glandular-pubescent in distal half, adaxially glabrous, the base attenuate, the apex acute or obtuse, the margin entire, sparsely glandular-ciliate medially, except at base and apex with simple hairs. *Labellum* tubular in outline, ovate when spread, (6–)8–10.8(–15) x (3.3–)5–7.2(–9) mm, obscurely 3-lobed; claw square, 3-nerved, (0.2–)0.8–1.5(–2) x (0.4–)0.8–1.4(–2) mm; lateral lobes subrotund, (3–)5–7(–9)-nerved, abaxially densely pubescent, adaxially sparsely puberulent in lower portion, the base subcordate, the calli reniform, slightly fleshy, inclined or horizontal; midlobe oblong, erect, very fleshy, the apex obtuse, membranaceous, adaxially glabrous, the margin involute, membranaceous, entire, eciliate, the calli oblong, strongly fleshy, completely occupying the midlobe, adaxially deeply sulcate, sparsely puberulent at base. *Column* clavate or geniculate, (4.1–)4.7–6(–7.5) x (1.2–)1.7–2.4(–3) mm, sparsely pubescent or villose on abaxial surface with a dense tuft of hairs on adaxial surface, the stalk

(0.8–)1.4–2.3(–3) mm long; anther ovate, (1–)1.7–2.3(–3) x (0.8–)1–1.5(–2) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.3–)0.4–0.9(–1) mm diam.; stigma transversely elliptic, slightly convex, (0.7–)1–1.5(–2) x (0.8–)1.3–1.9(–2.5) mm. *Ovary* cylindric, (2.8–)6–10(–13) x (0.5–)2.5–4.5(–5.9) mm, densely glandular-pubescent. *Fruits* ellipsoidal, (11–)12–14(–15) x (4.6–)5.9–8.1(–9.2) mm, moderately glandular-puberulent; seeds spatulate or fusiform, (0.9–)1.2–1.55 x (0.13–)0.18–0.23(–0.26) mm.

Distribution. (Fig. 3.17.B). Southern Venezuela to southern Ecuador. The plants inhabit montane cloud forests, elfin forests, scrub-páramos, treeless ridge-top cloud forests, and disturbed areas between 2100–3850 m of elevation. This species has a marked preference for moist and very humid places. It is often found on soils with thick layers of moss. Flowering collections have been made throughout the year, but mainly in April and May. Fruiting specimens have been collected from March to August, and in October, and December.

Specimens examined. COLOMBIA. Antioquia: Mpio. Urrao, Inspección Jaiperá, Vereda El Chuscal, Páramo de Frontino, Llanogrande, 3000-3390 m, 4 Apr 1989 (fl), *Callejas et al. 7510* (HUA). **Boyacá:** Peña de Arnical, N of Vado Hondo, SE slopes of Lajas de Arenisca, 3470 m, 6 Apr 1973 (fl), *Cleef 9423* (AAU, SEL, U); Mpio. Duitama, Vereda El Carmen, El Rosal, nr. La Recebera, 17 Mar 1994 (fl, fr), *Rangel et al. 11669* (COL). **Cauca:** transepto cabaña INDERENA, Páramo de Letreros, Laguna de Santiago, Mirador, 3200-3640 m, 15 Feb 1987 (im fl, fl), *Cristancho 95* (COL); Cordillera Central, Páramo de

Puracé, S of Volcán en el filo de la cordillera, San Francisco, 3400-3450 m, 23 Jul 1943 (fl), *Cuatrecasas 14620* (AMES); Cordillera Central, W slopes, headwaters of Río Palo, Quebrada del Río López, Quebrada del Duende,3400-3450 m, 2 Dec 1944 (fl), *Cuatrecasas 18926* (AMES, MO, NY); Macizo Central Colombiano, Alto del Buey, Farallones, Lagunas Teta de Bruja, 3600-3800 m, 22 Feb 1979 (fl), *Downer 104* (COL); Páramo de Guanacas, 3000-3300, Mar-Jul (fl), *Lehmann, C. B. 5383* (AMES, K); Cordillera Central, Mount Pan de Azúcar, 3300-3600 m, 16 Jun 1922 (fl, fr), *Pennell 7021* (AMES-3 sheets, K, NY, US); Dtto. Cauca, Cordillera Central, Puracé, 3450 m, Feb 1938 (fl), *von Sneidern 1752* (S). **Chocó:** Macizo del Tamaná, down the pass towards Valle de las Mirlas, 3700 m, 10 Feb 1983 (fl), *Torres et al. 1824* (COL). **Cundinamarca:** Nemocón, Cerro del Mortiño, 2780 m, 30 Dec 1962 (fl), *García-Barriga 17715* (AMES); rd. E from Guasca, 3100 m, 23 May 1947 (fl), *Haught 5758* (US). **Huila:** Huila, 15 Mar 1939 (fl), *von Sneidern 2146* (S). **Huila-Cauca border:** Macizo Colombiano, Páramo de Las Papas, hills SE of Laguna La Magdalena above Cerro La Carona and El Boquerón, slope of the Magdalena river, 3330-3520 m, 8 Sep 1958 (fl), *Idrobo et al. 3105* (COL). **Nariño:** Pasto-Sibundoy rd., 2600-2800 m, 5 Jan 1952 (fl), *Fernández & Knoth 1025* (COL); Cordillera de Pasto, mountains of Bordoncillo, 3000-3500 m, 12 Feb 1881 (fl), *Lehmann 265* (BM, G, frag. RENZ, illustration W); crater lake on the E slope of Volcán Galeras, 3200 m, 21 Jan 1979 (fl), *Luer & Luer 3741* (SEL); Mpio. Túquerres, Volcán Azufral, E slopes, ca. 9-13 km W of Túquerres, 3500-3800 m, 12 May 1989 (fl), *Luteyn et al. 12845* (NY). **Putumayo:** Cuenca alta del Río Putumayo, filo de la Cordillera

El Encano-Sibundoy, Páramo de San Antonio del Bordoncillo, 3250 m, 4 Jan 1941 (fl), *Cuatrecasas 11729* (F, US); high mountain páramos, pueblo-La Laguna de Pasto, 3353 m, 8 Nov 1878 (fl), *Lehmann 2907* (RENZ); La Cocha-Sibundoy, 3200 m, 20 Jan 1979 (fl), *Luer & Luer 3728* (SEL); Mpio. Santiago, Páramo del Bordoncillo, Vereda San Antonio de Bellavista, 3200-3400 m, 17 Apr 1993 (fl), *Muñoz & Ramírez 312* (COL). **Tolima:** Cordillera Central, La Línea, Cerro El Campanario, 3600-3700 m, 4 Mar 1969 (fl), *Cuatrecasas & Echeverry 27657* (MA, US). **Valle del Cauca:** "Tambo, LaNavilla?" [illegible], [probably "cuchilla del Tambo"], 1876 (fl), *André s.n.* (K); Cordillera Occidental, Los Farallones de Cali, filo de la cordillera, Páramo Cerro la Torre, 3750 m, 10 Oct 1944 (fl), *Cuatrecasas 17860* (AMES). **Without locality:** *Lehmann 1233* (K).

VENEZUELA. Táchira: La Fundación-Las Cruces, headwaters of Río Quinamarí, 3100 m, 15 May 1951 (fl), *Renz 7000* (RENZ); Páramo de Tamá, nr. Colombia-Venezuela boundary, 3045-3475 m, 15 Jul 1944 (fl, fr), *Steyermark 57385* (F); Pata de Judío, between Alto de Cruces, above Quebrada Teleférica, nr. the Colombia-Venezuela frontier, 28 km S of San Vicente de la Revancha; 30 km S of Alquitrana, SE of Páramo de Tamá, SW of Santa Ana, 2900-3100 m, 20 Jan 1968 (fl), *Steyermark et al. 101153* (AMES-2 sheets).

ECUADOR. Azuay: Cordillera Oriental, E of El Pan, [rocas de Galápagos], 3300 m, 21 Jul 1943 (fl), *Acosta-Solís 5123* (F); Gualaceo-Loma de la Virgen-Limón Indanza rd., Km 17, 3100 m, 19 Jul 2000 (fl), *Alvarez et al. 2734* (NY, QCNE), Km 27, 3300 m, 19 Jul 2000 (fl), *Alvarez et al. 2738* (NY, QCNE); Jima-Moriré rd., Km 21, Páramo de Matanga, 3350 m, 20 Jul 2000 (fl), *Alvarez et* *al. 2746* (NY, QCNE); eastern Cordillera, 4-6 km N of the village of Sevilla de Oro, 2743-3048 m, 14 Aug 1945 (fl), *Camp E-4705* (AMES, MO, NY, QCNE); 23.4 km SE of Gualaceo, nr. summit of pass, Páramo de Culebrillas, 3450 m, 28 Oct 1988 (fl, fr), *Dorr & Barnett 5931* (AMES, MO, NY, QCNE); El Cajas, nr. 20 km W of Sayausid, 3300 m, 11 Apr 1982 (im fl), *Harling et al. 20202* (AMES); Sigsig-Gualaquiza rd., campamento Molón, 1 km below Molón, 2800-3000 m, 11-12 Apr 1968 (fl, fr), *Harling et al. 8275* (GB, QCA); Páramo de Matanga, km 30 on rd. Sigsig-Gualaquiza (old muletrack), W of the pass, 3350, 14 Dec 1980 (fl), *Hølm-Nielsen et al. 29495* (AAU); about km 74 S of Cuenca, 2800 m, 24 Feb 1978 (fl), *Luer & Luer 2500* (SEL). **Imbabura:** Cordillera Oriental, nr. Camp Equator, due E of Volcan Cayambe, 3170 m, 15 Jul 1944 (fl), *Drew E-327* (AMES); Ibarra-Mariano Acosta rd., W of the pass, on Hacienda Yura Cruz, 3500-3600 m, 9-10 Aug 1976 (fl), *Øllgaard & Balslev 8636* (AAU). **Loja:** Parque Nacional Podocarpus, Nudo de Sabanilla, trail nr. the refuge, 3350 m, 29 Jul 2000 (fl), *Alvarez et al. 2780* (NY, QCNE); km 10 of the rd. to Fierro Urco, entrance from Km 54 of the Loja-Saraguro rd., 3500 m, 3 Aug 2000 (fl, fr), *Alvarez et al. 2819* (NY, QCNE); Loja-Saraguro rd., 5 km N of San Lucas, 2800 m, 17 Jul 1983 (fl, fr), *Bohlin & Bohlin 1037* (AMES); Nudo de Guagrauma, S of Saraguro, 19 Mar 1958 (fl, fr), *Correll E-420* (COL, TEX); Loja-Saraguro rd., Km 12 turn off to Fierro-Urco, 3500 m, 12 Mar 1989 (fl, fr), *Freire-Fierro 1301* (QCA); Loma El Loro, 6 km S of Saraguro on rd. to Loja, 3200 m, 11 Feb 1985 (fl), *Harling & Andersson 21885* (AMES, GB, QCA); Yangana-Toledo rd., 3420 m, 28 Dec 1988 (fl), *Jaramillo 10594* (NY); recently burned area in "Loma del Oro", just

S of Saraguro, 3100-3200 m, 4 Aug 1986 (fl), *Jørgensen 61398* (AAU); Fierro Urco, Saraguro-Loja, km 12.4 turnoff towards Fierro Urco, Km 23.8, 3840 m, 6 Dec 1994 (fl, fr), *Jørgensen et al. 1204* (LOJA, QCNE); Cerro Toledo, 3050 m, 12 Dec 1995 (fl), *Merino et al. 4685* (LOJA); Parque Nacional Podocarpus, S of Loja, above "Centro de Información", E of Nudo de Cajanuma, 3000-3200 m, 22 Feb 1985 (fl), *Øllgaard et al. 57986* (AAU, LOJA, QCA, QCNE); Parque Nacional Podocarpus, above Nudo de Cajanuma, Mirador, away from "Centro de Información", 3000-3050 m, 15 May 1988 (fl, fr), *Øllgaard et al. 74166* (AAU, LOJA); **Loja-Zamora Chinchipe border:** Parque Nacional Podocarpus, around pass on the Loja-Zamora rd., 2750-2950 m, 23 May 1988 (fl), *Øllgaard et al. 74347* (LOJA); withouth locality, 2500 m,1 Dec 1876 (fl), *André s.n.* (K). **Morona Santiago:** Cantón Gualaquiza, Cuenca-Sigsig-Chigüinda rd., km 85, 2700 m, 27 Jul 2000 (fl), *Alvarez et al. 2775* (NY, QCNE); Cantón Gualaquiza, Campamento Achupalla, Cordillera del Cóndor, 15 km E of Gualaquiza, 2090 m, 21 Jul 1993 (fl), *Gentry 80290* (QCNE); path Campamento San Miguel (on rd. in construction Sigsíg-Gualaquiza)-Gualaquiza, 9 Apr 1968 (fl), *Harling et al. 8135* (GB); Cordillera de Matanga, nr. border with Azuay, rd. in construction Sigsig-Gualaquiza, 3200 m, 10 Apr 1968 (fl), *Harling et al. 8159* (QCA); Cantón Gualaquiza, Tambillo Protected Forest and Vegetation, 2710 m, 26 Jun 2001 (fl), *Suin & Guartán 1030* (NY-2 sheets). **Napo:** Cantón Archidona, Sumaco Napo-Galeras National Park, Sumaco, summit crater, 3732 m, 16 Mar 1996 (fl, fr), *Clark 2222* (QCNE, SEL); N side of Cerro Sumaco, upper part of the loma, NW of campsite, 3750 m, 25 Apr 1979 (fl), *Hølm-Nielsen et al. 17236* (AAU); N side of Cerro Sumaco, loma NW of campsite, 3100-3150 m, 28 Apr 1979 (fl), *Hølm-Nielsen et al. 17370, 17371* (both AAU, NY); Cerro Sumaco, upper 100 m of cone, 3700-3800 m, 1 May 1979 (fl), *Hølm-Nielsen et al. 17591* (AAU); Cerro Sumaco, loma "315 degrees of summit", 3200 m, 2 May 1979 (fl), *Hølm-Nielsen et al. 17680, 17684* (both AAU), 3100-3300 m, 3 May 1979 (fl), *Hølm-Nielsen et al. 17759* (AAU, NY); N side of Cerro Sumaco, quebrada NW of campsite, 3450 m, 4 May 1979 (fl), *Hølm-Nielsen et al. 17795* (AAU-2 sheets), *17805*, 17807 (AAU); N side of Cerro Sumaco, quebrada N of campsite, 3350 m, 5 May 1979 (fl), *Hølm-Nielsen et al. 17944* (AAU), *17958* (AAU, NY); NE-facing ridge on the N side of Cerro Sumaco, 3600-3700 m, 24 Apr 1979 (fl, fr), *Løjtnant & Molau 12706* (AAU, QCA); E-facing ridge on the N side of Cerro Sumaco, 3300-3400 m, 25 Apr 1979 (fl), *Løjtnant & Molau 12766* (AAU); S side of Cerro Sumaco, 100-200 S of the main crater, 3700-3800 m, 29 Apr 1979 (fl), *Løjtnant & Molau 12916* (AAU); N-facing ridge on the N side of Cerro Sumaco, 3650 m, 4-6 May 1979 (fl), *Løjtnant & Molau 13178* (AAU); Cerro Sumaco, base camp, 3700 m, 24 Apr 1979 (fl), *Madison 6801* (AMES, SEL); Cerro Sumaco, SE slope, 3600 m, 29 Apr 1979 (fl, fr), *Madison 6880* (F, K, SEL). **Pichincha:** Cordillera Oriental, surroundings of the Laguna de Chiqui, NE of Cayambe, 3800 m, 4 Jun 1944 (fl), *Acosta-Solís 8156* (F).

Gomphichis caucana is recognized by its oblanceolate-ligulate to almost linear and thin-coriaceous leaves, ovate and acuminate bracts, compact inflorescences that are small to medium in size, and a shortly stalked, geniculate column that bears a heavy tuft of hairs. The petals of this species are variable in shape, ranging from narrowly ovate to oblong-elliptic; the petal apices may be acute to obtuse. Flower color is also variable from shades of white to yellow.

Gomphichis caucana is a member of an unresolved clade containing *G. valida*, *G. crassilabia*, *G. goodyeroides*, *G. macbridei*, and an apparently undescribed species. *Gomphichis caucana* seems to be more closely related to *G. crassilabia* than to the remaining species of the clade. It differs from *G. crassilabia* by having pubescent flowers, smaller bracts that are up to 15 cm long, a clavate and geniculate column, oblong-elliptic to narrowly-ovate petals, and fusiform ovaries.

6. *Gomphichis costaricensis* (Schltr.) Ames, F. T. Hubb & C. Schweinf., Bot. Mus. Leafl. 3: 37. 1934. *Stenoptera costaricensis* Schltr., Beih. Bot. Centralbl. 36(2): 375. 1918. Type. Costa Rica. Cartago: Turrialba, ca. 800 m, *A. Tonduz s.n.* (holotype, B, destroyed; lectotype, here designated, illustration AMES). (Fig. 3.18.A).

Terrestrial or rarely epiphytic *herbs*, (21–)28–52(–106) cm tall; roots (0.4–)0.5–0.6(–0.7) cm diam., villose. Leaves basal, rosulate, (3–)5–8(–10), spreading, (14–)15.5–30.5(–39.5) x (2.2–)3.2–4.5(–5.9) cm; subpetiole well-differentiated; blade elliptic, thin-coriaceous, tan to medium brown or dark brown to black when dry, the base attenuate, the apex acute or acuminate. *Peduncle* (11.5–)15–38.5(–85) x (0.5–)0.6–1 cm, glabrous in lower half, densely glandular-villose in upper half; sheaths (3–)4–8(–13), sparsely arranged along peduncle, loose-fitting, the lower sheaths (4.8–)8–15(–20) x 1–2.1(–2.9) cm, the upper sheaths (1–)1.1–1.9(–2.2) x (0.1–)0.3–0.5(–0.8) cm, the lower and upper sheaths glabrous with acuminate apex and glandular-ciliate margin. *Inflorescence* broadly cylindric, obtuse at apex, congested many-flowered, (4–)9.5–15(–20.5) x (1.8–)2–2.6(–3) cm; rachis obscure, densely glandular-villose; bracts ovate-elliptic, 1–3-nerved, (7.2–)8–13(–15) x (2.1–)3–5.2(–8) mm, sparsely glandular-pubescent in the lower half, the apex acuminate, the margin glandular-ciliate. *Flowers* white or greenish, (4.3–)5–6(–6.8) mm long. *Dorsal sepal* obovate, concave, 1(–3)-nerved, (4.7–)5–6.1(–6.5) x (2.4–)2.6–3.2(–3.6) mm, abaxially sparsely glandular-pubescent basally, the apex obtuse. *Lateral sepals* obovate-oblong or elliptic-oblong, slightly concave, 1(–2)-nerved, (4–)5–5.8(–6.2) x 0.29–3.4 mm, abaxially sparsely glandular-pubescent basally, the apex obtuse. *Petals* broadly elliptic, slightly concave, 3-nerved, (3.7–)4.5–5(–6.5) x 2–3.3(–5.6) mm, asymmetrical, the blade abaxially glabrous or sparsely glandular-pubescent in distal half, adaxially glabrous, the base shortly attenuate, the apex obtuse, the margin entire, densely glandular-ciliate medially, glandular-ciliolate apically with simple retrorse hairs. *Labellum* obpyriform in outline, rhombic when spread, (4–)4.7–6(–6.5) x (4–)4.5–5.6(–6) mm, distinctly 3-lobed; claw oblong, 3-nerved, (0.5–)1(–1.5) x (0.8–)1–1.5 mm; lateral lobes rotund, 5(–7)-nerved, abaxially sparsely puberulent, adaxially sparsely pubescent in middle, the base subcordate, the calli reniform, slightly fleshy, horizontal; midlobe broadly triangular, erect, very fleshy, the apex obtuse, slightly fleshy, adaxially densely hirsute, the margin flat, fleshy, entire, eciliate, the calli roundish, strongly fleshy, occupying two thirds of the midlobe, adaxially deeply sulcate, moderately puberulent over the entire length. *Column* strongly sigmoid, (3–)4–5.5(–6.5) x (1.3–)1.6–2(–2.2) mm, densely pilose on both surfaces, the stalk (0.5–)1–1.5(–2) mm long; anther ovate, (1.1–)1.29–1.6(–2) x (0.8–)0.9–1.2(–1.4) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.2–)0.3–0.4(–0.5) mm diam.; stigma transversely elliptic, slightly convex, (0.2–)0.4–0.6(–0.7) x (1.1–)1.4–1.7(–1.8) mm. *Ovary* cylindric, (5.8–)6.1–9.2(–11) x (3–)3.2–4.5(–6) mm, densely glandular-pubescent. *Fruits* cylindric, 8.8–14 x 5.4–7 mm, sparsely glandular-pubescent; seeds fusiform or broadly elliptic, 0.8–1 x 0.2–0.25 mm.

Distribution. (Fig. 3.18.B). Costa Rica, Panama, and Venezuela. This species is found in cloud forests at elevations between 1000 to 2600 m. Flowering specimens have been collected from December to March, July, and October. Fruiting collections have been made in February, May, and December. Flowering and fruiting are most frequent in February.

Specimens examined. COSTA RICA. Alajuela: Volcán Poas, La Lechería, 1922 (im fl), *Jiménez 2082* (AMES); Poas Lake, 2591 m, 6 May 1928 (fr), *Stork 2453* (AMES). **Cartago:** crest of Carpintera Mountains, nr. Tres Ríos, 1700-1800 m, 22 Mar 1961 (fl), *Horich s.n.*, (K, UC, US). **Heredia:** El Gallito, 1900 m, 30 Oct 1938 (fl), *Valerio 2666* (AMES). **San José:** Rd. to Providencia de Dota about 1-2 km from "Tr. 2" on Sierra de la Muerte, 7 Mar 1986 (im fl), *Atwood 86-55* (SEL); Providencia de Dota rd. from Rt. 2 (Km 78), 12 Jul 1986 (im fl), *Atwood 86-77* (SEL); nr. Finca La Cima, above Los Lotes, N of El Copey, 2100-2400 m, 21-22 Dec 1925 (fl), *Standley 42663* (AMES, US), *Standley 42728* (AMES). **Without locality:** 1931-1932 (fl, fr), *Kupper s.n.* (M).

PANAMA. Bocas del Toro: headwaters of Río Colubre (Colubre camp), 2400-2550 m, 3 Mar 1984 (fl), *Gómez et al. 22383* (MO). **Chiriquí:** Slopes of Las Cumbres, nr. Cerro Punta, 20 Feb 1971 (fl, fr), *Croat 13703* (MO-2 sheets, NY); Dtto. Boquete, Bajo Chorro, 18 Feb 1938 (fl, fr), *Davidson 163* (AMES, F, US), 1829 m, *Davidson 309* (F); San Ramón, headwaters of Río Caldera, 2000 m, 22 Oct 1967 (fl), *Dressler 3101* (FLAS); Cerro Hornito, NNE of Gualaca, 1750-2000 m, 27 Dec 1977 (im fl), *Dressler 5768* (FLAS); NW of Boquete, Cerro Horqueta, 1524-1768 m, 13 Dec 1966 (fl, fr), *Dwyer et al. 527* (MO); Dtto. Boquete, from Boquete 3 miles N, 1006-1280, 12-13 Dec 1966 (fl, fr), *Lewis et al. 527* (AMES); vic. Las Nubes, 2.7 miles NW of Río Chiriquí Viejo, W of Cerro Punta, 2200 m, 27 Feb 1973 (fl), *Liesner 306* (MO); Dtto. Bugaba, Cerro Punta, from STRI house to edge of mountain across the river, 2200 m, 24 Jan 1985 (fl), *van der Werff & Herrera 6302* (MO).

VENEZUELA. Aragua: Henri Pittier National Park, Pico Guacamaya, ridge extending NW from peak, 1750 m, 13 Feb 1990 (fl), *Edwards 205* (K). **Bolívar:** Chimantá Massif, along Río Tírica above upper falls, 1965 m, 7 Feb 1955 (fl, fr), *Steyermark & Wurdack 543* (NY).

Gomphichis costaricensis can be distinguished by its compact inflorescences, flowers with obtuse, broadly elliptic and glabrous, rarely pubescent petals with retrorsely glandular-ciliate margins, strongly sigmoid column, erect labellum with obtuse apex, and basal, obovate and acuminate leaves.

In the molecular-based phylogeny, *Gomphichis costaricensis* is placed in the clade that unites *G. viscosa*, *G. adnata*, *G. cundinamarcae*, and an unamed taxon. Morphologically, this species most closely resembles *G. merzii*, but differs conspicuously in the density and size of its inflorescence, the shape of the leaves, the apex and symmetry of the lateral sepals, and the absence or presence of trichomes on the adaxial surface of the petals. *Gomphichis costaricensis* has dense and compact inflorescences, elliptic leaves, obtuse and asymmetrical lateral sepals and adaxially glabrous petals, whereas *G. merzii* possesses subdense and long inflorescences, oblanceolate leaves, symmetrical acute lateral sepals and adaxially puberulent petals. *Gomphichis costaricensis* also shows some morphological similarities with *G. cundinamarcae* of Colombia and Venezuela, but differs from that species especially in the shape of the petals and labellum. *Gomphichis costaricensis* possesses broadly elliptic, obtuse petals with densely retrorse cilia and an obtuse labellum with roundish calli, whereas *G. cundinamarcae* exhibits narrowly elliptic, acute petals with densely spreading cilia and oblong calli.

Gomphichis costaricensis has been often seen growing as epiphyte. Some specimens of *G. costaricensis* reported as terrestrial exhibit some morphological differentiation. For example, a specimen from the Chimantá Massif in Venezuela shows remarkably large leaves and inflorescence. Other specimens found growing as epiphytes are very short but the inflorescence fall into the average for this species.

Gomphichis costaricensis occurs in the westernmost distribution of the genus.

7. ***Gomphichis crassilabia*** Garay, Fl. Ecuador 9: 147, fig. 47A. 1978. Type. Ecuador. Napo: nr. Lag. Porjuantag [Puruanta] region, *G. W. Prescott 548* (holotype, NY). (Fig. 3.19.A).

Terrestrial *herbs*, (42–)51–110(–144) cm tall; roots (0.2–)0.4–0.5 cm diam., pubescent. *Leaves* basal and cauline, clustered, (4–)6–8(–9), ascending, (10.8–)16.3–30(–37.5) x (0.8–)1.1–1.9(–2.8) cm; subpetiole weakly differentiated; blade lanceolate-oblong, thick-coriaceous, light green or dark to olive green when dry, the base not attenuate, the apex acute. *Peduncle* (35.4–)44–83(–125) x (0.6–)0.7–1.1(–1.2) cm, glabrous in lower half, glabrous, glabrate to sparsely glandular-villose in upper half; sheaths (6–)8–12(–17), imbricate, loose-fitting, the lower sheaths (10.5–)14–24(–35.5) x (1.2–)1.5–2.1(–2.4) cm, glabrous with acute apex and eciliate margin, the upper sheaths (1.5–)1.8–2.8(–3.5) x (0.3–)0.5–0.8(–1) cm, glabrous with acute apex and glandular-ciliate margin. *Inflorescence* broadly cylindric, obtuse at apex, congested many-flowered, (3.9–)6.1–11.1(–19) x (1.9–)2.4–3.2(–3.5) cm; rachis obscure, densely glandular-villose; bracts ovate or ovate-oblong, 3(–5)-nerved, (10–)11–20(–28) x (5–)6–8(–10) mm, glabrous, sparsely glandular-pubescent at base, the apex acuminate, the margin glandular-ciliate. *Flowers* yellow or yellowish, (6.5–)8.9–11(–12) mm long. *Dorsal sepal* elliptic, concave, (1–)2–3-nerved, (6–)7.1–8.8(–10) x (2.4–)3.2–4.2(–4.8) mm, abaxially sparsely glandular-villose, the apex acute or obtuse. *Lateral sepals* elliptic, slightly concave, (1–)2–3-nerved, (7–)8.1–10(–12) x (3–)3.7–4.4(–5.1) mm, asymmetrical, abaxially sparsely glandular-villose, the apex acute or obtuse. *Petals* elliptic, concave, (1–)2–3-nerved, (7–)7.4–9.3(–13) x (2–)2.5–3.1(–3.3) mm, asymmetrical, abaxially moderately glandular-hirsute in distal half, adaxially glabrous, the base attenuate, the apex acute or slightly obtuse, the margin entire, densely glandular-ciliate medially, glandular-ciliolate apically with simple hairs. *Labellum* oblong-ligulate in outline, lanceolate when spread, (6.5–)8.9–11(–12) x (5–)6.4–8.2(–9.8) mm, obscurely 3-lobed; claw oblong, 3(–5)-nerved, (0.5–)0.8–1.8(–2.2) x (1–)1.2–1.7(–2) mm; lateral lobes subrotund, (5–)7(–9)-nerved, abaxially densely puberulent, adaxially moderately puberulent in middle, the base subcordate, the calli reniform, slightly fleshy, inclined; midlobe oblong, erect or slightly curved outwards, very fleshy, the apex obtuse, fleshy, adaxially glabrous, the margin involute, slightly fleshy or fleshy, entire, eciliate, the calli oblong, strongly fleshy, completely occupying the midlobe, adaxially deeply sulcate, moderately papillose over the entire length. *Column* broadly ellipsoidal, (4.8–)5–6(–8) x (1.6–)1.8–2.7(–3.1) mm, sparsely puberulent on abaxial surface, densely pubescent on adaxial surface, the stalk (0.6–)1.2–2.1(–3) mm long; anther ovate, (1.5–)1.8–2.5(–3.5) x (0.9–)1.1–1.7(–2.5) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.1–)0.4–0.8(–1) mm diam.; stigma transversely ovate, applanate, (0.5–)1–1.5(–1.7) x (1.5–)1.6–2.1(–2.5) mm. *Ovary* broadly ellipsoidal, (3.5–)7.7–12(–15) x (1.2–)3–5.3(–7.4) mm, densely glandular-hirsute. *Fruits* broadly ellipsoidal, 11–13 x 7.2–8 mm, moderately glandular-hirsute; seeds fusiform, 1.42–1.44 x 0.15–0.25 mm.

Distribution. (Fig. 3.19.B). Endemic to Ecuador. This species grows in subpáramos, páramos, and humid upper montane cloud forests dominated by *Polylepis.* It is found in primary forest and disturbed areas above 3000 m. Flowering occurs throughout the year with a peak on November. Fruiting takes place from May to July, and in November, January, and February.

Specimens examined. ECUADOR. Carchi: Parroquia La Libertad, Comunidad de Moraspungo, sitio Cobos, buffer zone of the Reserva Ecológica El Angel, 3300-3450 m, 1 Jul 2000 (fl, fr), *Alvarez & Alvarez 2620* (NY, QCNE); Cantón Huaca, Parroquia Mariscal Sucre, Estación Biológica Guandera, 3575 m, 10 Jan 2001 (fl), *Alvarez & Narváez 2844* (NY, QCNE), nr. the Osos trail, 3412 m, 2 Sep 2001 (fl), *Alvarez & Caranqui 2883* (NY, QCNE), 3433 m, 4 Sep 2001 (fl), *Alvarez & Caranqui 2890* (NY, QCNE), 3400-3500 m, 12 Jan 2001 (fl), *Alvarez & Narváez 2860* (NY, QCNE), 3438 m, 30 May 2002 (fl), *Alvarez & Padilla 2945* (NY, QCNE), nr. the Clusia trail, 3550 m, 13 Jan 2001 (fl), *Alvarez & Narváez 2861* (NY-2 sheets), 3600 m, 14 Apr 2003 (fl), *Alvarez & Padilla 3014* (NY-2 sheets, QCNE), nr. the Islas de Páramo, 3421 m, 24 May 2002 (fl), *Alvarez & Padilla 2935* (NY, QCNE), 3575 m, 29 May 2002 (fl), *Alvarez & Padilla 2941* (NY, QCNE), 3575 m, 30 May 2002 (fl, fr), *Alvarez & Padilla 2947* (NY-2 sheets, QCNE), *2951* (NY, QCNE), 3555 m, 13 Apr 2003 (fl), *Alvarez & Padilla 3010* (NY, QCNE); E zone, on SE direction, trail to Río Bretaña, 300 m away from the river margin, transect # 10, 3520-3530 m, 13 Feb 2000 (fl), *Mites et al. 415* (NY); E of Colonia Huaqueña, sector Bretaña, Loma Corazón, 3200-3450 m, 20 Feb 1989 (fl, fr), *Palacios & van der Werff 3949, 3962* (QCNE); Cantón Tulcán, Tufiño rd., Aguas Hediondas at the base of Volcán Chiles, border with Colombia, 3500-3650 m, 8 Nov 1993 (fl), *Palacios 11830* (QCNE). **Carchi-Napo border:** Nr. 12 km N of El Playón de San Francisco, Mirador, 3300-3500 m, 27 nov 1983 (fl), *Eriksen & Larsen 45799* (AAU). **Loja:** Yangana-Cerro Toledo rd., nr. the antennas, Km 19, 3250-3300 m, 31 Jul 2000 (fl, fr), *Alvarez et al. 2799* (NY, QCNE); Parque Nacional Podocarpus, trail Cajanuma-Laguna del Compadre, páramo around the first pond, half way to Laguna de Compadres, 3200-3340 m, 26 Dec 1988 (fl), *Jørgensen et al. 65631* (QCNE); Cordillera de Las Lagunitas, Amaluza-Jimbura-Zumba, km 37, 3390 m, 24 Nov 1994 (fl), *Jørgensen et al. 898* (QCNE), above the Refugio of Cajanuma (Centro de Información), 3200-3400 m, 15 Dec 1991 (fl), *Keating 2* (QCA), vic. Lagunas del Compadre ca. 6 hours walking from Centro de Información, 3000-3400 m, 21-24 Nov 1989 (fl), *Madsen & Pedersen 86443* (AAU, MO); off rd. Yangana-Valladolid Km 1.1, track to Sierra Toledo, Km 18.7, 3350 m, 14 Nov 1997 (fl), *Klitgaard & Lewis 718* (LOJA), Cerro Toledo, 3200 m, 27 Nov 1988 (fl), *Madsen 75620a* (AAU, LOJA), 3350 m, 1 Dec 1988 (fl), *Madsen et al. 75679* (AAU, LOJA, QCA), 3000-3400 m, 21 Jul 1989 (fl), *Madsen et al. 86090* (AAU), 3150 m, Jan 1995 (fl), *Palacios 12905* (QCNE, SEL), E of Yangana, 3300-3450 m, 23 Feb 1985 (fl), *Øllgaard et al. 58063* (AAU), around radio station, 3400-3450 m, 26 Feb 1985 (fl, st-QCA), *Øllgaard et al. 58146* (AAU, LOJA, MO, NY, QCA, QCNE); Amaluza, 10-12 km ENE of the village, nr. Laguna Negra, 3000-3400 m, 23 Sep 1976 (fl), *Øllgaard & Balslev 9768* (AAU). **Morona Santiago:** Cantón Gualaquiza, Cuenca-Sigsig-Chigüinda rd., Km 79, 3200 m, 27 Jul 2000 (fl, fr), *Alvarez et al. 2771* (NY, QCNE); trail Alao-Huamboya, E slopes above and around La Magdalena, 3550-3700 m, 7 May 1982 (fl), *Øllgaard et al. 38316* (AAU), nr. La Magdalena, 3450-3600 m, 8 May 1982 (fl), *Øllgaard et al. 38362* (AAU-2 sheets). **Napo:** Cantón Quijos, Papallacta site, trail to Lagunas de Cojunco y Verde, 3350-3450 m, 5 Jan 2000 (fl, fr), *Alvarez & Alvarez 2550* (NY, QCNE), 3400 m, 6 Jan 2000 (fl), *Alvarez & Alvarez 2565* (NY, QCNE), 3487 m, 18 Jan 2001 (fl), *Alvarez & Alvarez 2878* (NY, QCNE), 6 Jun 2002 (fl, fr), *Alvarez & Alvarez 2953* (NY, QCNE), 3350-3450 m, 4 Apr 2003 (fl), *Alvarez & Alvarez 3009* (NY, QCNE), 3350-3450 m, 25 Jun 2000 (fl), *Alvarez et al. 2612* (NY, QCNE); Cantón Quijos, volcanic lava flow of Papallacta, 3600 m, 27 Dec 1984 (fl), *Huttel 525* (QCNE); Cantón Quijos, Laguna de Papallacta, 3400 m, 22 Jan 1991 (fl), *Palacios 6858* (QCNE); Cordillera de los Llanganates, SW Laguna Encantada, 3410 m, 14 Mar 1983 (fl), *Hølm-Nielsen et al. 41704* (AAU); ca. 6 km NE of Km 45 on the rd. Salcedo-Napo, 3600 m, 16-18 Nov 1984 (fl), *Lægaard 53348* (AAU); ca. 60 km E of Salcedo, 3100 m, 12 Nov 1979 (fl, fr), *Luer et al. 4770* (SEL); E-facing ridge on the N side of Cerro Sumaco, 3400-3600 m, 25 Apr 1979 (fl), *Løjtnant & Molau 12742* (AAU). **Sucumbíos:** Playón de San Francisco, El Mirador, 16 Aug 1978 (fr), *Boeke & Jaramillo 2675* (NY); S of El Playón de San Francisco on the slopes of Cerro Mirador, 3600-3800 m, 29 Dec 1980 (fl), *Hølm-Nielsen et al. 29970* (AAU), 16 Aug 1978 (fl, st-AAU), *Jaramillo & Boeke 564* (AAU, QCA), 3600-3800 m, 29 Dec 1980 (fl), *Jaramillo & Coello 3911* (AAU). **Tungurahua:** Cordillera de los Llanganates, at Río Verde Grande at base of Cerro Hermoso, 2 km WSW of the summit, 3800 m, 11 Nov 1980 (fl), *Hølm-Nielsen & Jaramillo 28395* (AAU), 2.5 km SW of the summit, 3700 m, 12 Nov 1980 (fl), *Hølm-Nielsen & Jaramillo 28604* (AAU), Loma 2.5 km W of Cerro Hermoso, 3800 m, 12 Nov 1980 (im fl), *Hølm-Nielsen & Jaramillo 28627* (AAU); Cantón Patate, Cordillera de Los Llanganates, 12 km from El Triunfo, trail to the lakes, 3100-3600 m, 3 Mar 1995 (fl), *Vargas & Sandoval 321* (QCNE); Cantón Baños, Parque Nacional Llanganates, Páramo de Soguillas, Valle de Los Frailejones, 3660 m, 12 Oct 1998 (fl), *Vargas et al. 2773* (QCNE).

The main distinguishing characteristics of *Gomphichis crassilabia* are its imbricate and conspicuously long sheaths, very long and broad ovate to ovate-oblong bracts, very fleshy, oblong-ligulate labellum, and a subglobose, broadly ellipsoidal column which has dense hairs on the upper surface.

This species has affinities with *Gomphichis caucana*, *G. valida* and an unnamed species. It appears to be most closely related to *G. caucana* and their relationships are discussed under that species' description.

The specimens that most closely fit the description of *Gomphichis crassilabia* show variation in the size of the column stalk and the fleshiness of the labellum margin. These characters, therefore, appear to represent normal variation within this species. Nonetheless, a combination of all the diagnostic features places this species apart from its close allies.

8. *Gomphichis cundinamarcae* Renz, Candollea 11: 252, figs. 5, 6B. 1948. Type. Colombia. Cundinamarca: Retiro-Calera, N of Bogotá, 2700 m, 18 Nov 1938 (fl), *O. Renz 4053* (lectotype, here designated, RENZ). (Fig. 3.20.A).

Terrestrial *herbs*, (40–)57–92(–105) cm tall; roots (0.3–)0.4–0.5(–0.6) cm diam., villose. *Leaves* basal, clustered, (3–)4–7(–10), ascending, (7–)15.8–25(–27) x (0.9–)1.5–2.6(–3) cm; subpetiole weakly differentiated; blade oblanceolate-ligulate or oblong-ligulate, thin-coriaceous, dark brown to black when dry, the base attenuate, the apex acute or acuminate. *Peduncle* (28.5–)48.5–77(–87) x (0.5–)0.6–1(–1.5) cm, glabrous in lower half, glabrous to sparsely glandular-pubescent in upper half; sheaths (6–)7–10(–15), sparsely arranged along peduncle, loose-fitting, the lower sheaths (8–)9–21(–29.5) x (0.6–)1–1.8(–2.3) cm, glabrous with acuminate apex and eciliate margin, the upper sheaths (0.8–)1.1–1.8(–2.5) x 0.2–0.6(–1.4) cm, glabrate with acute or acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, obtuse at apex, congested many-flowered, (4.5–)6.1–12(–16.5) x (1.2–)1.8–2.6(–3.2) cm; rachis obscure, densely glandular-villose; bracts ovate or oblong-ovate, (1–)3(–4)-nerved, (7.5–)8.5–11(–12) x (2.7–)3–4.1(–5.5) mm, sparsely glandular-pubescent at base, the apex acuminate, the margin glandular-ciliate. *Flowers* white or greenish or greenish-white, (5–)6–7.5(–8.5) mm long. *Dorsal sepal* obovate or elliptic-obovate, deeply concave, 1(–2)-nerved, (4.6–)5.5–7.1(–8) x (2.2–)2.6–3.2(–3.5) mm, abaxially sparsely glandular-pubescent basally, the apex acute. *Lateral sepals* oblong, slightly concave, 1(–2)-nerved, (4.5–)5.6–7.1(–8.5) x (2.5–)2.7–3.4(–3.5) mm, asymmetrical, abaxially sparsely glandular-pubescent basally, the apex acute. *Petals* narrowly elliptic, slightly concave, 1–3-nerved, (4.2–)5.5–6.7(–8) x 2.1–3(–3.8) mm, asymmetrical, the blade abaxially glabrous to sparsely glandular-pubescent in proximal half, adaxially glabrous, the base attenuate, the apex acute or slightly obtuse, the margin entire, densely glandular-ciliate medially, except at base and apex with simple hairs. *Labellum* obpyriform in outline, rhombic when spread, (5–)6–8(–9.2) x (2.8–)5.2–7(–7.8) mm, distinctly 3-lobed; claw oblong, 3-nerved, (0.3–)0.9–1.1(–1.5) x (0.5–)0.8–1.3(–1.5) mm; lateral lobes subrotund, (3–)5(–7)-nerved, abaxially densely puberulent, adaxially densely pubescent in upper portion, the base subcordate, the calli reniform, very fleshy, inclined; midlobe triangular, erect, very fleshy, the apex acute, slightly fleshy, adaxially densely puberulent, the margin flat, fleshy, entire, eciliate, the calli oblong, strongly fleshy, occupying two thirds of the midlobe, adaxially deeply sulcate, sparsely pubescent over the entire length. *Column* strongly sigmoid, (3.5–)4.8–6.5(–7) x (1.5–)1.8–2.2(–2.5) mm, sparsely pubescent on abaxial surface, moderately pubescent on adaxial surface, the stalk (0.5–)1.2–2.1(–2.4) mm long; anther ovate, (1–)1.3–2(–2.5) x (0.8–)0.89–1.5(–2.1) mm; pollinia symmetrical, linear; viscidium circular, (0.2–)0.3–0.6(–0.7) mm diam.; stigma transversely ovate, slightly convex, (0.4–)0.6–1(–1.2) x (1–)1.29–1.8(–2) mm. *Ovary* ellipsoidal, (4.2–)5.2–7(–9.1) x (2.1–)2.6–4.3(–6) mm, densely glandular-pubescent. *Fruits* ellipsoidal, 7.5–14 x (4.5–)5.3–6.4(–7.4) mm, sparsely glandular-pubescent; seeds spatulate or fusiform, (0.52–)0.81–1(–1.35) x 0.19–0.22 mm.

Distribution. (Fig. 3.20.B). Colombia and Venezuela. *Gomphichis cundinamarcae* is found growing in primary forests especially upper montane wet forests, cloud forests and subpáramos, sometimes on rich, sandy soils, at elevations between 1500–3700 m. Flowering specimens have been collected throughout the year except in the months of January and May. Fruiting specimens have been collected most frequently from June to September.

Specimens examined. COLOMBIA. Antioquia: Mpio. Medellín, Boquerón, military base at Cerro del Padre Amaya, 5 Aug 1986 (fl), *Albert de Escobar & Giraldo 6852* (HUA); Morro Pelado, Anocosca-Abriaqui trail, 3190 m, 15 Mar 1944 (fl), *Core 452* (US); nr. televisora San Pedro, Cerro Padre Amaya, W of Medellín, 2800-3000 m, 3 Oct 1971 (fl), *Dressler 4111* (FLAS); Boquerón, Cerro del Padre Amaya, 2860 m, 4 Aug 1979 (fl, fr), *Palacios et al. 67* (HUA); Cordillera Occidental, below Páramo de Chaquiro, 2800-3100 m, 24 Feb 1918 (fr), *Pennell 4294* (NY). **Caldas:** Cordillera Occidental, Cerro Tatamá, 3400-3700 m, 8-10 Sep 1922 (fl), *Pennell 10558* (AMES). **Cauca:** Cordillera Occidental, Mount Santa Ana, 2700-3000 m, 29-30 Jun 1922 (fl, fr), *Pennell 7451* (AMES-3 sheets, K, NY, US). **Cundinamarca:** region of Bogotá, 1919 (fl), *Ariste-Joseph s.n.* (US); Cordillera Oriental, Bogotá-La Calera, 2650-3000 m, 27 Nov 1947 (fl), *Barkley 17C768* (US); Mpio. Chía, summit of Cerro Manjuy, 2910 m, Aug 1996 (im fl), *Cortés 816* (COL); Cordillera Oriental, Sabana de Bogotá SE extreme at San Miguel, 2800-3000 m, 10 Sep 1941 (fl), *Cuatrecasas 12035* (US); Cordillera Oriental, above Cogua, 2850-2900 m, 4 Jul 1942 (fl), *Cuatrecasas 13619* (US);

Suesca, 2621, 9 Oct 1946 (fl), *Foster & Foster 1815* (AMES-2 sheets); Sasaima, Vereda La Victoria, Hacienda Gualivá, Peñas del Aserradero, N of Facatativá, 2300-2900 m, 18-19 Oct 1957 (fl), *García-Barriga 15726* (AMES); vic. Guasca, Páramo de Guasca, 2800 m,19 Nov 1971 (fl), *García-Barriga 20219* (AMES, COL); Une-Fosca rd., 2800 m, 5 Sep 1960 (fl), *Hatheway & Smith-Mumm 1145* (MO); Boyacá, shore of Laguna de Tota, 7 Sep 1960 (fl), *Hatheway 1148* (MO); Serranía Chía-Tenjo, 9 Nov 1985 (fl), *Ospina-Hernández 1153* (COL); hill slopes of Zipaquirá, 2800-2900 m, 20-24 Oct 1917 (fl), *Pennell 2629* (AMES, NY); mountains E of Bogotá, 3000 m, 9 Aug 1941 (fl), *Renz 4189* (RENZ); vic. Bogotá, El Retiro-La Calera, 2800 m, 6 Mar 1955 (fl, fr), *Renz 8321, 8325* (both RENZ); vic. Bogotá, El Retiro, upper Chicó Valley, 6 Aug 1955 (fl), *Renz 8488* (RENZ); Suba Hill, Sabana of Bogotá, 11 Oct 1945 (fl), *Schiefer 964* (AMES); Mpio. Usaquén, 2800 m, 6 Mar 1948 (fl), *Schneider 297/2* (RENZ); El Retiro, 2950 m, 27 Sep 1953 (fl, fr), *Schneider 692* (COL); Bogotá, Quebrada del Chicó, 2800 m, 15 Feb 1944 (fl), *Schneider 9/3* (RENZ); 2591-2896 m, 30 Nov 1952 (fl), *Schultes 18595* (AMES); Bogotá, *Schultze 120* (US); nr. Zipaquirá, 2700 m, 1939 (fl), *Uribe 330* (US). **Magdalena:** Mpio. Santa Marta, Cerro Quemado-Cerro San Lorenzo, 2600-2800 m, 16 Apr 1959 (fr), *Romero-Castañeda 7751* (COL). **Nariño:** La Cocha-Santiago, 2500-2700 m, 4 Aug 1961 (fl), *Garay 487a* (AMES-3 sheets). **Norte de Santander-Cesar border:** Cordillera Oriental, Jurisdicciones, Cerro de Oroque, 3000-3900 m, 22-27 Jul 1974 (fl), *García-Barriga & Jaramillo 20686* (AMES). **Risaralda:** Mpio. Santuario, Vereda Las Colonias, 2910 m, 2 Feb 1983 (fr), *Torres et al. 1624* (COL), border of the Río

San Rafael, 2500 m, 25 Feb 1983 (fr), *Torres et al. 2286* (COL). **Tolima:** path to Nevado del Tolima, above El Rancho (termales), 3700 m, 17 Jul 1969 (fl), *Echeverry 1990* (COL); Manizales-Fresno, Letras-Fresno rd., 3300 m, 9 Apr 1956 (fl), *Renz 8612* (RENZ).

VENEZUELA. Mérida: Sierra Nevada, Valley of Río Loro, forestry station-Laguna Coromoto, 3125 m, 2 Dec 1959 (fl), *Barclay & Juajibioy 9935* (AMES, MO); Mucutuy-Puente de Gonzales, Páramo de San José, 2700 m, 5 Nov 1949 (fl), *Renz 6045* (RENZ); Santa Cruz de Mora-El Molino, 2700 m, 12 Nov 1949 (fl), *Renz 6096* (RENZ). **Táchira:** Jauregui, Páramos El Batallón-La Negra, nr. turn-off to Bailadores, 2900 m, 13 Dec 2002 (fl, fr), *Alvarez & Yustiz 3005* (NY, PORT); Páramo La Negra, 1500-3000 m, 17 Nov 1976 (fl), *Charpin et al. AC13528* (G), SW slopes around Sabana Larga, 2200 m, 22 Oct 1949 (fl), *Renz 5992* (RENZ), Sabana Larga-Pueblo Londo [Hondo], 2400 m, 22 Oct 1949 (fl), *Renz 5994* (RENZ), SW slopes above La Cañada, 2500 m, 22 Oct 1949 (im fl), *Renz 5995* (RENZ), NE slopes, 2800 m, 21 Oct 1949 (fl) *Renz 5996* (RENZ), nr. Pregonero, 2600 m, 22 Oct 1949 (fl), *Renz 6003* (RENZ), SW slopes, 2600 m, 2 Dec 1949 (fl), *Renz 6250* (RENZ), NE slopes, 2700 m, 17 Jul 1951 (fl, fr), *Renz 7245* (RENZ); Páramo Zumbador, nr. Michilena, 2300 m, 3 Sep 1951 (fl), *Renz 7453* (RENZ).

Gomphichis cundinamarcae can be diagnosed by its peduncle with sparsely glandular-pubescent distal surface, large leaves, congested inflorescence of medium size, distinctively 3-lobed labellum with an acute apex, and obtuse to subtruncate petals which have glabrous to sparsely pubescent laminas bordered by dense and spreading cilia. Fresh flowers of this species have white or greenish sepals and petals, and the midlobe of the labellum is bright yellowish, whereas the lateral lobes and claw are greenish.

Gomphichis cundinamarcae bears an initial morphological similarity to *G. costaricensis*, which occurs from Costa Rica to Venezuela, and also to *G. goodyeroides*, which ranges from Ecuador to Peru. These species have in common dense to subdense inflorescences with white flowers and elliptic petals. However, *G. cundinamarcae* has a distinctive 3-lobed labellum without any constriction at the apex, which is not observed in *G. goodyeroides*; its petals are acute to truncate with conspicuous and dense cilia, and its petals are never puberulent adaxially (as in *G. goodyeroides*), nor broadly elliptic and retrorsely ciliate (as in *G. costaricensis*). Moreover, *G. cundinamarcae* and *G. goodyeroides* are almost exclusively terrestrial plants, whereas *G. costaricensis* is often reported as being epiphytic.

In 1948 Renz published the name and description for *Gomphichis cundinamarcae* citing three collections from Colombia, but he selected none as the type. The lectotype of this species is here designated as *Renz 4053* (RENZ), the herbarium specimen of which has attached to it the original detailed drawing used in the publication of this name. Although Renz indicated that the diagnostic features of this species include the glabrate peduncle and the absence of glandular hairs on bracts or flowers, all collections referable to *G. cundinamarcae* have the upper half of the peduncle covered by glandular villose indument, whereas the bracts and sepals are glandular-pubescent and the petals are often pubescent.

I have annotated the specimen *Albert de Escobar 6852* from Antioquia, Colombia as *Gomphichis adnata*, but it is atypical in comparison to the remaining specimens examined. It has much larger leaves and an elongated narrow inflorescence. These features most likely are the result of the plant growing in a garbage dump, which may be unusually nutrient rich.

This species reaches the northermost limit of the distributional range of the genus.

9. *Gomphichis goodyeroides* Lindl., Gen. Sp. Orchid. Pl. 445. 1840. *Stenoptera goodyeroides* (Lindl.) Rchb.f., Bonpl. 4: 211. 1856. Type. Peru. Amazonas: Prov. Chachapoyas, 1836 (fl), *A. Mathews s.n.* (holotype, K, frag. of holotype W, illustration K, photo of illustration AMES). (Fig. 3.21.A).

Terrestrial or rarely epiphytic *herbs*, (31.7–)49–96(–151) cm tall; roots (0.2–)0.3–0.4(–0.5) cm diam., pubescent or villose. *Leaves* basal and cauline, clustered, (2–)4–7(–9), ascending, (8.5–)13.5–24.5(–36.6) x (1.5–)1.79–2.7(–3.8) cm; subpetiole well-differentiated; blade lanceolate, thick-coriaceous, dark to olive green when dry, the base attenuate, the apex acute. *Peduncle* (24.5–)44.5–86(–143.9) x (0.5–)0.6–1(–1.1) cm, glabrous in lower half, moderately glandular-tomentose in upper half; sheaths (5–)7–13(–18), sparsely arranged along peduncle or imbricate, tight-fitting, the lower sheaths (9.3–)11.7–21(–29.5) x (0.8–)1.4–2.1(–2.8) cm, glabrous with acuminate apex and eciliate margin, the upper sheaths (0.9–)1.29–1.9(–3.3) x (0.3–)0.4–0.6(–0.8) cm, glabrous, sparsely glandular-pubescent at base with acuminate apex and glandular-ciliate margin. *Inflorescence* broadly cylindric, obtuse at apex, subdensely many-flowered, (5.2–)6.5–12(–16) x (1.5–)1.8–2.8(–3.1) cm; rachis obscure, densely glandular-tomentose; bracts ovate or ovate-lanceolate, (1–)3(–4)-nerved, (5.8–)10–12(–15) x (0.5–)2.5–5.1(–7.5) mm, sparsely glandular-pubescent at base, the apex acuminate, the margin glandular-ciliate. *Flowers* white or greenish, (4.5–)7–9.6(–11) mm long. *Dorsal sepal* oblong-elliptic, deeply concave, 1–2(–3)-nerved, (5.5–)6.5–8.5(–9) x (2.6–)2.8–3.6(–4.2) mm, abaxially sparsely glandular-pubescent basally, the apex obtuse. *Lateral sepals* ovate-oblong, slightly concave, (1–)2(–3)-nerved, (6–)7–8.5(–9.5) x (2.1–)2.5–3.5(–3.7) mm, asymmetrical, abaxially sparsely glandular-pubescent basally, the apex acute. *Petals* obovate or obovate-elliptic, concave, (1–)2–3-nerved, (5.2–)7–8.5(–9) x (1.7–)2.5–3.3(–3.5) mm, the blade abaxially glabrous, adaxially sparsely puberulent along midrib, the base shortly attenuate, the apex slightly apiculate or obtuse, the margin entire, sparsely glandular-ciliate medially and proximally with simple hairs. *Labellum* tubular in outline, ovate when spread, (5.7–)7.8–10(–11) x (4.2–)5.5–7(–9) mm, obscurely 3-lobed; claw oblong, 3(–5)-nerved, 1–2(–5) x (0.7–)1–1.8(–2.5) mm; lateral lobes subrotund, (5–)7(–9)-nerved, abaxially densely pubescent, adaxially sparsely tomentose in upper portion, the base cordate, the calli ovate, slightly fleshy, inclined; midlobe broadly triangular, erect, fleshy, the apex constricted, acute, membranaceous, adaxially glabrous, the margin flat, fleshy, entire, eciliate, the calli oblong, fleshy, occupying the upper half of the midlobe, adaxially slightly sulcate, densely tomentose over the entire length. *Column* slightly sigmoid, (4.1–)5–6.5(–6.8) x (1.4–)1.5–2.2(–3) mm, sparsely puberulent on abaxial surface, densely villose on adaxial surface, the stalk (1.1–)1.5–2.3(–2.7) mm long; anther ovate, (1.6–)1.9–2.3(–2.5) x (0.7–)0.9–1.4(–1.7) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular or transversely obovate, (0.3–)0.4–0.7(–1) mm diam.; stigma transversely elliptic or transversely ovate, slightly convex, (0.7–)0.9–1.3(–1.5) x (1–)1.39–1.9(–2.2) mm. *Ovary* ovoid, (4.2–)6–10(–14) x (1.6–)2.2–5.2(–7) mm, moderately or densely glandular-tomentose. *Fruits* ovoid, 13 x 6.7 mm, glabrate; seeds spatulate or fusiform, 1.18 x 0.18 mm.

Distribution. (Fig. 3.21.B). Ecuador to Peru. This species is found in primary and secondary montane cloud forests and elfin forests, at 2200–3400 m elevation. Flowering specimens have been collected in all months of the year. Fruiting specimens are known from July through September.

Specimens examined. ECUADOR. Azuay: Cuenca, Parroquia Baños, Hacienda Yanasacha, 3000-3200 m, 24 Jul 1978 (fl), *Boeke & Jaramillo 2519* (NY); 1 km from the control in the route to Loja, rd. to the right towards Yanasacha, 26 Jul 1978 (fl), *Jaramillo & Boeke 408* (QCA); Gualaceo-Culebrillas rd., 2500 m, 12 May 1983 (im fl), *Lawesson et al. 43841* (AAU); nr. Km 80 S of Cuenca, 3000 m, 17 Jul 1977 (fl), *Luer et al. 1722* (SEL); vic. Tablón de Oña, 27 Sep 1918 (fl, fr), *Rose et al. 23123* (US); slopes bordering Río Collay, known as Huagrarancha, S of El Pan, 2650-3290 m, 6 Jul 1943 (fl), *Steyermark 53345* (F). **Cañar:** Parroquia Zhoray, Azogues-Taday-Pindilig-Rivera rd., Km 48, 3100 m, 17

Jul 2000 (fl, fr), *Alvarez et al. 2722* (NY, QCNE); at pass on Pindilig-Rivera (La Virgen) rd., 3200 m, 9 Mar 1985 (fl), *Harling & Andersson 22979* (AMES, GB); Rivera, NE of Pindilig, 2900 m, 13 Dec 1980 (fl), *Hølm-Nielsen et al. 29217* (AAU); Cerro Yanguán, NE of Pindilig, 3200 m, 13 Dec 1980 (im fl), *Hølm-Nielsen et al. 29287* (AAU); Loja, Jardín Botánico Reinaldo Espinosa of the Universidad de Loja, 2300 m, 24 Feb 2000 (fl), *Cerón et al. 40080* (QAP); Loma Santiago, 3 km S of Santiago and 14 km S of San Lucas, 2900 m, 18 Feb 1993 (fl), *Harling & Ståhl 26478* (GB); San Lucas-Oña, 2200-3100 m, 7 Sep 1923 (fl), *Hitchcock 21511* (US); ca. 8 km E of Yangana on footpath to Numbala, 3100 m, 31 Jan 1966 (fl), *Knight 31* (WIS-2 sheets); Andes of Loja, 3000-3400 m, Oct 1888 (fl), *Lehmann 7109* (HBG, K); Saraguro-Loja rd., 6-8 km from Saraguro, 2900-3100 m, 16 Jun 1079 (fl), *Løjtnant et al. 14985* (AAU); Loja-Zamora rd., 2-7 km W of the pass, 2400-2700 m, Jun 17 1979 (fl), *Løjtnant et al. 15031* (AAU); Parque Nacional Podocarpus, above Nudo de Cajanuma, trail to Mirador, 3000-3150 m, 6 Sep 1988 (fl), *Madsen & Elleman 75292* (AAU, LOJA); Loja: Parque Nacional Podocarpus, Cerro Toledo, 3200 m, 27 Nov 1988 (fl), *Madsen 75620b* (MO, QCA, QCNE); Nudo de Sabanilla, 0-500 m W of (above) the pass on the Yangana-Valladolid rd., 2800-2900 m, 24 Feb 1988 (fl, fr), *Molau & Eriksen 3213* (AAU, QCNE); Parque Nacional Podocarpus, Páramo of Cerro Toledo, 3150 m, Jan 1995 (fl), *Palacios 12905* (SEL); Villonaco, ca. 15 W of Loja, 2500-2900 m, 24 Oct 1987 (fl), *van der Werff & Palacios 8944* (QCNE); Parque Nacional Podocarpus, Yangana-radio towers-Cerro Toledo rd., 2900-3200 m, 29 Apr 1987 (fl), *van der Werff & Palacios 9188* (MO). **Loja-Zamora Chinchipe border:**

Yangana-Valladolid rd., at entrance of Parque Nacional Podocarpus, 2500-3000 m, 10 Dec 1989 (fl), *Madsen 86676* (AAU-2 sheets, LOJA, MO). **Morona Santiago:** Cuenca-Gualaquiza rd., Km 31, 2900 m, 16 Feb 1986 (fl), *Embree 16* (QCNE); Muletrack Sevilla de Oro-Méndez, E slope, at Cerro Negro, El Castillo, 3000-3250 m, 16 Sep 1976 (fl), *Øllgaard & Balslev 9518* (AAU). **Zamora Chinchipe:** Nudo de Sabanilla, pass on Yangana-Valladolid rd., 2800-2900 m, 5 Apr 1985 (fl), *Harling & Andersson 23718* (AMES, GB, QCA).

PERU. Amazonas: Prov. Chachapoyas, Leimebamba-Lajasbamba trail, 28 Jun 1977 (fl), *Boeke 2035* (NY); Prov. Chachapoyas, Kuelap Fortress and surrounding, 3000 m, 16 May 2001 (fl), *Henning & Schneider 256* (M); Cerros Calla Calla, 18 km above Leimebamba on rd. to Balsas, 3100 m, 7 Jun 1964 (fl), *Hutchison & Wright 5594* (AMES, UC); middle eastern Calla-Challa slopes, 3-5 km SE of Km 422, Leimebamba-Balsas rd., 3000-3200 m, 22 Aug 1962 (fl), *Wurdack 1767* (AMES, F, K, NY, US). **Cajamarca:** Prov. Jaén, Sallique, Lanchal, 2400-2550 m, 4 Jul 1998 (fl), *Campos et al. 5230* (SEL). **Huánuco:** Pachitea, 5 km WNW of Panao, 2 km SW of La Punta, 2950 m, 21 Aug 1965 (fl, fr), *Bird 1363* (MO); W of Panao, 7 Aug 1980 (fl), *Luer et al. 5306* (SEL); Panao, 2743 m, 10 May 1923 (fl), *Macbride 3605* (AMES, F); Km 451 on Lima-Tingo María rd., Carpish, 2450 m, 2 Jun 1981 (fl), *Young & Sullivan 515* (MO). **Without locality:** from the living collection of David E. Bennett, 26 Jul 1965 (fl), *Bennett 1880* (UC); *Mathews s.n.* (BM), *Pavón & Ruiz s.n.* (W).

WITHOUT COUNTRY. Without locality: *Unknown s.n.* (W)

Gomphichis goodyeroides is characterized by its congested inflorescence, a weakly 3-lobed labellum which has glabrous, membranaceous, constricted and narrow apex and tomentose calli, and obovate to obovate-elliptic petals which are abaxially glabrous, adaxially puberulent, and marginally ciliate along the lower half.

Based on DNA sequence data, *Gomphichis goodyeroides* is sister to *G. macbridei*, but this relationship is not supported. Both species in turn are closely related to the remaning species possessing an obscurely 3-lobed labellum including *G. valida*, *G. crassilabia*, *G. caucana* and a cluster of accessions that may represent an unnamed taxon.

This mostly terrestrial species has been reported as an epiphyte in Chachapoyas, Peru. Specimens from Cerro Toledo (Loja, Ecuador) above 3200 m of elevation have glabrous to slightly glandular-pubescent sheaths. The sheaths of these collections are imbricate and the petals are ciliate throughout.

The collection *Macbride 3605* from Peru (AMES) is characterized by a labellum with broad lateral lobes, but the remaining features fit *G. goodyeroides.* The only known duplicate of this collection (F) has a weakly-3 lobed labellum typical of *G. goodyeroides.*

10. ***Gomphichis hetaerioides*** Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 54. 1920. Type. Colombia. Cauca: Cauca, 2400 m, *M. Madero s.n.* (holotype, B, destroyed; lectotype, here designated, Mansf., Repert. Spec. Nov. Regni Veg. Beih. 57, t. 16, nr. 58. 1929). (Fig. 3.22.A).

Gomphichis cranichoides Schltr., Repert. Spec. Nov. Regni Veg. Beih. 8: 40. 1921. *Stenoptera cranichoides* (Schltr.) L. O. Williams, Caldasia 5: 12. 1942. Type. Ecuador. Pichincha: Nanegal-Gualea, Mart. 1900, *L. Sodiro s.n.* (holotype, B, destroyed; lectotype, here designated, Mansf., Repert. Spec. Nov. Regni Veg. Beih. 57, t. 75, nr. 292. 1929.).

Gomphichis sodiroi Schltr., Repert. Spec. Nov. Regni Veg. Beih. 8: 41. 1921. Type. Ecuador. Pichincha: Nanegal, Mart. 1900, *L. Sodiro s.n.* (holotype, B, destroyed; lectotype, here designated, Mansf., Repert. Spec. Nov. Regni Veg. Beih. 75, t. 75, nr. 293. 1929).

Gomphichis plantaginea Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9: 50. 1921. Type: Peru. Junín: Chanchamayo Valley, *E. Köhler s.n.* (holotype, B, destroyed; lectotype, here designated, Mansf., Repert. Spec. Nov. Regni Veg. Beih. 57, t. 104, nr. 409. 1929).

Terrestrial or rarely epiphytic *herbs*, (35–)48–86(–128) cm tall; roots (0.3–)0.4–0.6(–0.8) cm diam., villose. *Leaves* basal, clustered, (3–)4–6(–7), ascending, (12.5–)16–30(–40.5) x (1.6–)1.9–3.5(–4.3) cm; subpetiole well-differentiated; blade lanceolate-elliptic, thick-coriaceous, dark to olive green when dry, the base long-attenuate, the apex acute or acuminate. *Peduncle* (29–)30.5–59.5(–112.5) x (0.3–)0.4–0.7(–0.8) cm, glabrous in lower half, moderately glandular-pubescent in upper half; sheaths (4–)5–7(–8), sparsely arranged along peduncle, loose-fitting, the lower sheaths 7–16(–33) x (0.5–)0.6–1.4(–2) cm, glabrous with acuminate apex and eciliate margin, the upper sheaths 1–2.01(–3.3) x (0.2–)0.3–0.4(–0.8) cm, sparsely glandular-pubescent with acuminate apex and eciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, loosely many-flowered, (5.7–)6.4–20.5(–31) x (1–)1.3–2.1(–2.8) cm; rachis visible, densely glandular-villose; bracts ovate-lanceolate, (1–)3-nerved, (6.5–)7.5–9.6(–11) x (2.2–)2.7–3.5(–4.2) mm, sparsely glandular-pilose at base, the apex acute or acuminate, the margin glandular-ciliate. *Flowers* white, (4.2–)5.2–6.8(–7.6) mm long. *Dorsal sepal* ovate or ovate-elliptic, deeply concave, 1-nerved, (4.5–)5–6.2(–7) x (2.1–)2.2–2.9(–3.3) mm, abaxially sparsely glandular-pubescent basally, the apex acute. *Lateral sepals* oblong or obovate-oblong, slightly concave, 1-nerved, (4.3–)4.9–6.2(–7) x (2.1–)2.2–2.6(–3.1) mm, asymmetrical, abaxially sparsely glandular-pubescent basally, the apex acute. *Petals* elliptic, slightly concave, (1–)3-nerved, (4.5–)4.8–5.8(–6.4) x (1.4–)2.2-3.1(–3.4), asymmetrical, the blade abaxially and adaxially glabrous, the base shortly attenuate, the apex slightly apiculate, the margin entire, sparsely glandular-ciliate medially, glandular-ciliolate apically with simple and branched hairs. *Labellum* obpyriform in outline, rhombic when spread, (4.5–)5.6–6.8(–7.5) x (2.2–)4.4–6.4(–7.1) mm, distinctly 3-lobed; claw oblong, 3(–5)-nerved, (0.5–)0.9–1.5(–2) x (0.6–)0.8–1.4(–2) mm; lateral lobes subrotund, 5(–7)-nerved, abaxially densely puberulent, adaxially sparsely puberulent in lower portion, the base subcordate, the calli reniform, very fleshy, inclined or horizontal; midlobe broadly triangular, erect, very fleshy, the apex acute or obtuse, membranaceous, adaxially densely hirsute, the margin flat, slightly fleshy, entire, eciliate, the calli oblong, strongly fleshy, occupying two thirds of the midlobe, adaxially slightly sulcate, densely papillose or puberulent over the entire length. *Column* geniculate, (4–)5–6.3(–7.4) x (1.2–)1.4–1.9(–2) mm, densely villose-tomentose on abaxial surface, densely pubescent or villose-tomentose on adaxial surface, the stalk (1–)1.3–1.9(–2.5) mm long; anther oblong, (1.4–)1.5–1.7(–1.9) x (0.6–)0.8–1.1(–1.3) mm; pollinia asymmetrical, linear; viscidium circular, (0.2–)0.3–0.4(–0.5) mm diam.; stigma transversely ovate, slightly convex, 0.4–0.9(–1.4) x (0.5–)1.1–1.5(–1.6) mm. *Ovary* fusiform, (4–)5.6–8(–8.5) x (2.1–)2.3–3.3(–4.6) mm, densely glandular-pilose. *Fruits* ovoid, 8.5–11 x 5.8–6.2 mm, densely glandular-pilose; seeds fusiform, 0.6–0.7 x 0.19–0.2 mm.

Distribution. (Fig. 3.22.B). Panama, Colombia, and Ecuador. This species occurs in montane cloud forests, disturbed oak forests, and steep road embankments, on gravel soils, at elevations of 1200–3100 m. This species is known to flower throughout the year, except in March and July. Fruits have been collected in August, September, and December.

Specimens examined. PANAMA. Chiriquí: above Guadalupe, 2300 m, 8 Dec 1983 (fl), *Luer 9287* (SEL). **Darién:** trail from Río Pucuro base camp up W ridge of Cerro Mali, Cerro Tacarcuna Expedition to the Serrania del Darién, Panamá-Colombia frontier, 640-1000 m, 6 Feb 1975 (fl), *Gentry & Mori 14175* (MO).

COLOMBIA. Antioquia: Mpio. El Retiro, Hacienda Normandía, Cordillera Central, 2500 m, 2-3 Dec 1956 (fl), *Ospina-Hernández 89* (AMES). **Chocó:** Cordillera Occidental, Radio station La Sirena, 3 km W of La Mansa on top of Cordillera Occidental, 2300-2400 m, 16 Jan 1979 (fl), *Gentry & Rentería 24184*

(MO). **Cundinamarca:** Mpio. Quetame, Monte Redondo, 1650 m, 18 Dec 1950 (fl, fr), *Schneider 447/5, 447/6* (both RENZ). **Santander:** Santa Bárbara-Guaca, 2400 m, 6 Nov 1981 (fl), *Luer & Escobar 6596* (SEL).

ECUADOR. Carchi: Cantón Espejo, Cerro Golondrina Hembra foothills, 2300-2400 m, 20 Aug 1994 (fr), *Palacios 12732* (QCNE). **Loja:** Loja, 1 Apr 1961 (fl), Dodson 394 (SEL). **Loja-Zamora Chinchipe border:** Loja-Zamora rd., Km 44, 1 May 1963 (fl), *Dodson s.n.* (SEL). **Napo:** Cordillera de los Guacamayos, E-facing slope beyond pass on Baeza-Tena rd., 1850 m, 21 Sep 1987 (fl), *Dodson et al. 17284* (QCNE). **Pastaza:** Río Blanco-Río Pastaza, 1500 m, 14 Dec 1880 (fl), *Lehmann 218* (RENZ, W). **Pichincha:** below San Juan towards Chiriboga, 3100 m, 5 May 1955 (fl), *Asplund 16205* (S); Cantón Quito, Parroquia Calacalí, Reserva Geobotánica Pululahua, path surrounding El Pondoña, 1800-3356 m, 8 Aug 1987 (fl, fr), *Cerón et al. 1853* (MO, QCNE); Nono-Tandayapa rd., Km 17, big boulder on left side of rd. along Río Alambí, 2160 m, 14 May 1981 (fl), *Dodson et al. 10776* (SEL); Dos Ríos, old rd. Quito-Santo Domingo, Km 82, 1200 m, 6 Oct 1979 (fl), *Dodson et al. 8861* (SEL); Volcán Pululahua, 35 km NW of Quito, beyond the Monument to the center of the earth, 2300 m, May 1985 (fl), *Hirtz 2619* (QCNE); Cantón Quito, Parroquia Nanegal, along Río Umachaca, ca. 6 km airline SE of Nanegal, 1400 m, 6 Sep 1993 (fl, fr), *Webster et al. 30336* (QCNE). **Tungurahua:** Mount Tungurahua, 2200 m, 4 Aug 1977 (fl), *Brenner 127* (SEL), Jun 1983 (fl), *Hirtz 994* (SEL), nr. Baños, 28 Oct 1979 (fl), *Luer 4420* (SEL). **Without locality:** *Sodiro s.n.* (QPLS).

Gomphichis hetaeridoides is distinguished from the related *G. viscosa* and *G. altissima* by its sparsely flowered inflorescence, longer than broad labellum with subrotund lateral lobes, glabrous, elliptic, 3-nerved, rarely 1-nerved petals with obtuse apex and sparsely retrorse glandular-cilia consisting of branched and simple trichomes, a geniculate and clavate column, and lanceolate-elliptic acuminate leaves.

Gomphichis hetaerioides appears to be more common in its southernmost distribution (Ecuador), but rarely documented in Colombia and Panama. This species has not yet been reported in Venezuela and it is possible that its disjunct distribution may only be a collecting artifact.

Three names considered under this species present problems of typification although the correct application of the names is clear. The holotype of *G. hetaeroides* was destroyed at B, but the line illustration in Mansfeld (1929) was likely taken from it and agrees with the description and the specimens cited. There is a single specimen of this species in the Sodiro Herbarium in Quito (QPLS). However, there is no indication whether this *Sodiro s.n.* specimen is the type of *G. cranichoides* or of *G. sodiroi*, although it is certainly an isotype of one of these names. The drawings in Mansfeld (1929) were undoubtedly based on the holotypes at B and they leave little doubt as to the application of the names *G. cranichoides* and *G. sodiroi.*

I am placing *Gomphichis plantaginea* Schltr. in the synonym of *G. hetaerioides.* The holotype of this species, deposited at B, was also destroyed, but Mansfeld (1929) published a drawing based on the type collection and the diagnosis of this species closely resembles that of *G. hetaerioides*. The former differs slightly from *G. hetaerioides* in plant stature, number of petal nerves, and column indument type. These characters, however, are variable within this species.

11. *Gomphichis koehleri* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9: 50. 1921; Mansf., Repert. Spec. Nov. Regni Veg. Beih. 57, t. 104, nr. 408. 1929. Types. Peru. Junín: Chanchamayo, *E. Koehler s.n.* (syntype B, destroyed); Junín: W of Huacapistana, 3000–3100 m, *A. Weberbauer 2062* (syntype B, destroyed). (Fig. 3.23.A).

Gomphichis goodyeroides Kranzl. ex Weber., Pflanzw. Peruv. And. 251. 1911., non Lindl.

Gomphichis koehleri Schltr. var. *minor* C. Schweinf., Bot. Mus. Leafl. 16(1):1. 1953. Type. Peru: Cuzco: Prov. Paucartambo, Tres Cruces, 3600 m, Oct 1941 (fl), *J. C. Vargas C. 2257* (holotype, AMES).

Terrestrial *herbs*, 66–66.5 cm tall; roots 0.3–0.5 cm diam., villose. *Leaves* basal, clustered, 5–6, ascending, 12.5–17 x 1.39–2 cm; subpetiole weakly differentiated; blade oblong, thick-coriaceous, dark to olive green or tan to medium brown when dry, the base not attenuate, the apex acute. *Peduncle* 55.8–58.5 x 0.9–1 cm, glabrous in lower half, moderately glandular-villose in upper half; sheaths 8–11, congested along peduncle, loose-fitting, the lower sheaths 11–12.5 x 2 cm, the upper sheaths 1.3–2.5 x 0.4–0.9 cm, the lower and upper sheaths glabrous with acute apex and eciliate margin. *Inflorescence* narrowly cylindric, obtuse at apex, congested many-flowered, 7.5–10.7 x 2.3–2.5 cm; rachis obscure, densely glandular-villose; bracts ovate-oblong, 3-nerved, 11–15 x 5.7–7 mm, sparsely glandular-hirsute at base, the apex acute, the margin glandular-ciliate. *Flowers* yellow or yellowish, 7.5–8.2 mm long. *Dorsal sepal* asymmetrically, oblong, concave, 3-nerved, 6.1–6.5 x 2–3.6 mm, abaxially moderately glandular-hirsute, the apex obtuse. *Lateral sepals* narrowly oblong, slightly concave, 3-nerved, 7.2–8 x 3.4–3.5 mm, asymmetrical, abaxially moderately glandular-hirsute, the apex obtuse. *Petals* oblong-obovate, slightly concave, 1–3-nerved, 6.5–7.5 x 2.3–2.7 mm, asymmetrical, abaxially sparsely glandular-hirsute in distal half, adaxially glabrous, the base attenuate, the apex obtuse, the margin entire, sparsely glandular-ciliate medially, except at base and apex with simple hairs. *Labellum* tubular in outline, ovate when spread, 7–7.7 x 6 mm, obscurely 3-lobed; claw oblong, 3-nerved, 0.5–1.2 x 0.4–1 mm; lateral lobes subrotund, 5–7-nerved, abaxially densely puberulent, adaxially moderately pubescent in upper portion, the base subcordate, the calli reniform, slightly fleshy, inclined; midlobe oblong, erect, fleshy, the apex obtuse, slightly fleshy, adaxially glabrous, the margin flat, slightly fleshy, entire, eciliate, the calli oblong, fleshy, completely occupying the midlobe, adaxially slightly sulcate, sparsely puberulent over the entire length. *Column* clavate or geniculate, 4.5–5 x 1.7–1.9 mm, sparsely pubescent on abaxial surface, moderately villose on adaxial surface, the stalk 1.5–2 mm long; anther ovate, 1.5–2 x 1–1.4 mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, 0.6–0.7 mm diam.; stigma transversely ovate, slightly convex, 1.1–1.2 x 1.2–1.4 mm. *Ovary* ellipsoidal, 6–

7.3 x 2.7–3.4 mm, densely glandular-hirsute. *Fruits* ellipsoidal, 11 x 5.7 mm, moderately glandular-hirsute; seeds fusiform or broadly elliptic, 1.01 x 0.2 mm.

Distribution. (Fig. 3.23.B). Endemic to Peru. *Gomphichis koehleri* has been found in humid elfin forests and open páramos, growing on humus-rich soils, at elevations of 3100–3600 m. Flowering specimens have been collected in August and October. Fruiting material has been collected in August.

Specimens examined. PERU. Amazonas: Prov. Bagua, Cordillera Colán, E of La Peca, 3139 m, 25 Aug 1978 (fl, fr), *Barbour 3184* (MO, SEL).

Gomphichis koehleri can be diagnosed by its approximate, inflated sheaths that almost completely cover the peduncle, ovate-oblong bracts, narrowly cylindric inflorescence, oblong-obovate, obtuse and hirsute petals, densely villose column and cream to yellow colored flowers.

Gomphichis koehleri is poorly known, rarely collected and was not available for molecular studies. It most closely resembles *G. caucana*, a widespread species that reaches southern Ecuador; both species have a similar labellum, sepals, and flower color. However, *G. koehleri* differs from *G. caucana*, especially in the shape and vestiture of the petals, which are oblong-obovate and hirsute in the former (*G. koehleri*) and narrowly ovate to oblong-elliptic and pubescent in the latter.

I have not seen the syntypes of this species, which were deposited at Berlin (B) and were destroyed. The possibility remains that duplicates of the syntype *Weberbauer 2062* are preserved in the herbarium La Molina (MOL) in Lima, Peru where most of his collections were deposited.

Schweinfurth (1953) published a variety within this species: *Gomphichis koehleri* var. *minor*. A few years later, the typical and the newly published variety were recognized and keyed in Schweinfurth's treatment of the Orchidaceae in the Flora of Peru (1958). My concept of this species, therefore, was derived from the published line drawing of *G. koehleri* (Mansfeld, 1929), the holotype of *G. koehleri* var. *minor*, and the original diagnoses of these taxa. Among the Peruvian collections available for study, only one recently collected specimen, *Barbour 3184*, from the Department of Amazonas appears to represent this species. Due to these considerations, I am not confident in recognizing varieties within this species until additional material can be examined. It would be especially valuable to study any extant specimens that were seen by Schlechter. Therefore, the published varieties of *G. koehleri* are herein included as synonyms.

12. *Gomphichis macbridei* C. Schweinf., Bot. Mus. Leafl. 9: 58. 1941. *Stenoptera macbridei* (C. Schweinf.) L. O. Williams, Caldasia 5: 13. 1942. Type. Peru. Huánuco: Yanano [24 km NE of Panao], 1830 m, 13–16 May 1923 (fl), *J. F. Macbride 3839* (holotype, F; isotype, AMES, frag. RENZ). (Fig. 3.24.A).

Terrestrial *herbs*, (69–)73–92 cm tall; roots 0.2–0.4(–0.6) cm diam., villose. *Leaves* basal, rosulate, 4–8, ascending, (18–)19.5–23(–25.3) x 1.2–1.8 cm; subpetiole weakly differentiated; blade linear-oblong, thick-coriaceous, light green when dry, the base attenuate, the apex acute. *Peduncle* (54.5–)58.5–61(–76) x (0.7–)0.8–1(–1.1) cm, glabrous in lower half, densely glandular-tomentose in upper half; sheaths (6–)7–9(–10), sparsely arranged along peduncle or congested along peduncle, tight-fitting, the lower sheaths (12.1–)12.7–16.5(–18.5) x 1.4–2(–2.4) cm, glabrous with acuminate apex and eciliate margin, the upper sheaths (1.4–)1.7–2(–2.5) x (0.3–)0.4–0.5 cm, moderately glandular-pubescent with acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, loosely many-flowered, 13.5–26.6(–33) x (2.5–)2.7–2.9(–3.5) cm; rachis visible, densely glandular-tomentose; bracts lanceolate, 3(–4)-nerved, (12–)13–17(–20) x (3–)3.5–4(–5.2) mm, sparsely glandular-pubescent, the apex acuminate, the margin glandular-ciliate. *Flowers* greenish-white, (8–)10–13(–15) mm long. *Dorsal sepal* oblong-oblanceolate or elliptic-lanceolate, concave, 1–3-nerved, 7.5–10(–12) x (2.5–)3–3.4 mm, abaxially sparsely or moderately glandular-pubescent, the apex acute or obtuse. *Lateral sepals* elliptic or elliptic-lanceolate, deeply concave at base, 1–3(–4)-nerved, (7.2–)9.5–14(–15) x 2.4–3.5(–4) mm, asymmetrical, abaxially sparsely or moderately glandular-pubescent, the apex acute. *Petals* rhombic-lanceolate or obovate-oblanceolate, slightly concave, 3-nerved, (6.8–)8.2–10(–12) x (1.5–)1.8–2.3(–3) mm, abaxially densely glandular-pubescent in distal half, adaxially glabrous, the base attenuate, the apex acute, the margin entire, densely glandular-ciliate throughout with simple hairs. *Labellum* tubular in outline, lanceolate when spread, (7–)9.5–12 x (4.5–)5.5–6.2(–6.6) mm, obscurely 3-lobed; claw oblong, 3-nerved, (1–)1.2–2.7(–3) x 0.9–1.3(–1.4) mm; lateral lobes subrotund, 5–7 -nerved, abaxially densely puberulent, adaxially sparsely pubescent in middle, the base subcordate, the calli reniform, very fleshy, inclined; midlobe narrowly oblong, slightly curved outwards, slightly fleshy to fleshy with prominent reticulate marks, the apex acute or subtruncate, slightly fleshy, adaxially glabrous, the margin undulate, fleshy, entire, eciliate, the calli oblong, slightly fleshy, completely occupying the midlobe, adaxially slightly sulcate, moderately puberulent at base. *Column* geniculate, (6.5–)7.5–9(–9.5) x 1.8–2(–2.2) mm, moderately puberulent on abaxial surface, sparsely pubescent or tomentose on adaxial surface, the stalk (2–)2.5–3.5 mm long; anther ovate, (2.9–)3–3.2(–3.4) x (1.5–)1.9–2.2(–2.4) mm; pollinia asymmetrical, narrowly ovoid; viscidium transversely broadly elliptic, 0.2–0.9(–1) mm diam.; stigma transversely ovate, applanate, (1.1–)1.2–1.4(–1.5) x (1.5–)1.6–1.8(–1.9) mm. *Ovary* fusiform, (6–)7–10(–11) x (2–)2.6–3.5(–3.8) mm, densely glandular-villose. *Fruits* ellipsoidal, 11–13 x 5.7–6 mm, densely glandular-villose; seeds fusiform, 0.57–0.77 x 0.19–0.22 mm.

Distribution. (Fig. 3.24.B). Southern Ecuador to central Peru, on the eastern slopes of the Eastern Cordillera. This species occurs mainly in undisturbed habitats, such as wet and humid montane forests, and less frequently in pioneer and secondary vegetation zones, on gravel soils, at elevations of 1800–3000 m. Most flowering specimens have been gathered from April to August, peaking in early August. Fruiting specimens have been collected in August.

Specimens examined. ECUADOR. Loja: old rd. Loja-La Toma, Km 2, nr. Monte Villonaco, 2520 m, 31 Jul 2000 (fl), *Alvarez et al. 2802* (NY, QCNE); old rd. Loja-La Toma, Km 5, nr. Monte Villonaco, 2650 m, 1 Aug 2000 (fr), *Alvarez et al. 2803b* (NY, QCNE); Loma El Loro, Km 9, entrance from Km 54 of the Loja-Saraguro rd., 2800 m, 1 Aug 2000 (fl, fr), *Alvarez et al. 2806* (NY, QCNE); terrace 3-4 km W of Loja, 2400-2450 m, 10 Feb 1945 (fl), *Fosberg & Giler 22918* (US); summit and upper slopes of Cerro Villonaco, 2600-2750 m, 12 Apr 1974 (fl), *Harling & Andersson 13474* (AMES); pass S of Loja, 2640 m, 9 May 1981 (fl), *Kuhn et al. 75* (SEL); Loja-Zamora, Km 9.5, 2575 m, 28 Feb 1997 (fl), *Lewis 3017* (LOJA, QCNE); Loja, track from Universidad Nacional to Uritusinga, km 8, 2750 m, 1 Apr 1997 (fl), *Lewis 3139* (LOJA). **Without locality:** 26 Aug 1987 (fl), *Unknown, s.n.* (K-spirit coll., no voucher, ex Götenberg BG).

PERU. Amazonas: Prov. Chachapoyas, Kuelap Fortress and surrounding, 3000 m, 16 May 2001 (fl), *Henning & Schneider 249* (M); Prov. Chachapoyas, vic. Chachapoyas, 1840 (fl), *Mathews 3194* (BM, G).

Gomphichis macbridei is one of the most distinctive species in the genus, and is easily differentiated by its large flowers that are 10–11 mm long, narrowly oblong labellum with obvious nervation and an undulate margin, rhomboidal and densely glandular-ciliate petals with acute apices, lateral sepals that are larger than the dorsal sepal, as well as a long column and claw. In the field it is easily recognized by the deep green nerves of the labellum.

In the molecular phylogeny, *Gomphichis macbridei* is sister to *G. goodyeroides* from which it differs by its many-flowered, loose inflorescences, a narrowly oblong and marginally undulate labellum possessing reticulate venation, a large claw up to 2.7 mm and large flowers (greater than 9.6 cm).

13. *Gomphichis merzii* Senghas, Orchidee (Hamburg) 2: 26. 1994. Type. Costa Rica. Cartago: Cordillera de Talamanca, Cerro de la Muerte, Villa Mills, 2700 m (fl), *S. Merz s.n.* (holotype, HEID 0–21464). (Fig. 3.25.A).

Terrestrial or rarely epiphytic *herbs*, 105 cm tall; roots 0.5 cm diam., villose. *Leaves* basal, rosulate, 4–5, ascending, 23.5–31.5 x 2.1–3.6 cm; subpetiole well-differentiated; blade oblanceolate, thin-coriaceous, dark to olive green when dry, the base short-attenuate, the apex acute. *Peduncle* 44–82.5 x 0.5–0.7 cm, glabrous in lower half, densely glandular-villose in upper half; sheaths 7, sparsely arranged along peduncle, tight-fitting, the lower sheaths 15.5 x 1.4 cm, glabrous with acute apex and eciliate margin, the upper sheaths 12 x 0.4 cm, sparsely glandular-pubescent with acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, subdensely many-flowered, 22.5 x 2.8 cm; rachis visible, densely glandular-villose; bracts oblanceolate, 3-nerved, 9.1–18 x 3.4–6 mm, moderately glandular-villose, the apex acuminate, the margin glandular-ciliate. *Flowers* white, 5.5–7.6 mm long. *Dorsal sepal* oblong-elliptic, concave, 1–3-nerved, 6–6.1 x 2.7–3.2 mm, abaxially sparsely glandular-pubescent, the apex acute. *Lateral sepals* oblong, slightly concave, 1–3-nerved, 6.5 x 3.2–4 mm, asymmetrical, abaxially sparsely glandular-pubescent, the apex acute. *Petals* broadly elliptic, concave, 3-nerved, 5.2–6 x 2.5–2.8 mm, asymmetrical, the blade abaxially glabrous to sparsely glandular-pubescent in proximal half, adaxially sparsely puberulent along midrib, the base shortly attenuate, the apex slightly obtuse, the margin entire, sparsely glandular-ciliate medially, glandular-ciliolate apically with simple hairs. *Labellum* obpyriform in outline, rhombic when spread, 4.9–7.2 x 5.2–6 mm, distinctly 3-lobed; claw oblong, 3-nerved, 0.6–1 x 1–1.1 mm; lateral lobes subrotund, 5–7 -nerved, abaxially densely pubescent, adaxially sparsely pubescent in upper portion, the base subcordate, the calli reniform, slightly fleshy, horizontal; midlobe broadly triangular, erect, very fleshy, the apex acute, membranaceous, adaxially densely hirsute, the margin flat, slightly fleshy, entire, eciliate, the calli roundish, strongly fleshy, occupying two thirds of the midlobe, adaxially slightly sulcate, sparsely pubescent at base. *Column* strongly sigmoid, 5–5.8 x 1.5 mm, sparsely pubescent on abaxial surface, moderately pubescent on adaxial surface, the stalk 1.5–1.8 mm long; anther ovate, 1–1.5 x 0.9 mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, 0.2–0.3 mm diam.; stigma transversely elliptic, slightly convex, 0.5 x 1.1–1.3 mm. *Ovary* ellipsoidal, 5.5–8 x 1.9–2.5 mm, densely glandular-villose. *Fruits* ellipsoidal, 11 x 0.7 mm, sparsely glandular-villose; seeds fusiform, 1.33 x 0.23 mm.

Distribution. (Fig. 3.25.B). Costa Rica and Venezuela. *Gomphichis merzii* is found in cloud forests, where it grows in association with *Quercus* and dense thickets of *Chusquea* species. It occurs at elevations of 2400–2700 m. Flowering specimens have been collected in December and January. Fruiting specimens have been collected in December.

Specimens examined. COSTA RICA. San José: Cordillera de Talamanca, nr. Villa Mills, 2700 m, 12 Jan 1990 (fl), *Merz 624* (SEL).

VENEZUELA. Mérida: Campo Elías, rd. to La Azulita, 500 m before Finca La Bravera, 2379 m, 3 Dec 2002 (fl, fr), *Alvarez & León 2977* (NY, PORT).

Gomphichis merzii may be distinguished from *G. costaricensis* by its obovate and acute leaves, subdense inflorescence, long bracts that are larger than the flowers, asymmetrical lateral sepals, elliptic petals which have acute apices and spreading cilia, and acute labellum bearing very fleshy, puberulent calli and a hirsute apex.

Although in the molecular phylogeny *Gomphichis merzii* is sister to the major clades of *Gomphichis* species, it shares some morphological similarities with *G. costaricensis*. Both species have broadly elliptic, 3-nerved petals, which are pubescent adaxially and puberulent abaxially, and a labellum with broad lateral lobes of which the midlobe possesses a pair of roundish calli.

Gomphichis merzii is the most recently described species in the genus and one of the three species that occur in Central America. This species was collected by Dr. Stephan Merz in Costa Rica. It is kept in cultivation at the University of Heidelberg Botanical Garden. The cultivated material unlike other specimens examined shows pubescence on the abaxial surface of the petals.

14. *Gomphichis plantaginifolia* C. Schweinf., Bot. Mus. Leafl. 11(8): 217. 1944. *Stenoptera plantaginea* Schltr., Repert. Spec. Nov. Regni Veg. 10(27–29): 446. 1912; Mansf., Repert. Spec. Nov. Regni Veg. Beih 58, t. 13, nr. 50. 1930. *Gomphichis plantaginea* (Schltr.) Schltr., Repert. Spec. Nov. Regni Veg. 10: 60. 1922. non *Gomphichis plantaginea* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9: 50. 1921; Mansf., Repert. Spec. Nov. Regni Veg. Beih. 57, t. 104, nr. 409. 1929. Type. Bolivia. La Paz: Unduavi, 3200 m, Nov 1900 (fl), *O. Buchtien 2623* (lectotype, here designated, US; isolectotypes, AMES-2 sheets). (Fig. 3.26.A).

Terrestrial *herbs*, (44–)53–82(–90) cm tall; roots (0.3–)0.4–0.5(–0.6) cm diam., villose. *Leaves* basal, clustered, (2–)3–8(–14), spreading, (8–)11.8–19.1(–29) x (1.1–)1.5–2.1(–2.4) cm; subpetiole well-differentiated; blade elliptic-oblanceolate, thick-coriaceous, dark to olive green when dry, the base attenuate, the apex acute or acuminate. *Peduncle* (33–)44.7–75(–82) x (0.4–)0.5–0.7(–1) cm, glabrous in lower half, densely glandular-villose or glandular-pubescent in upper half; sheaths (7–)8–10(–13), sparsely arranged along peduncle, loose-fitting, the lower sheaths (7.3–)9–20(–33) x (0.5–)1.1–1.8(–2.4) cm, the upper sheaths (1–)1.4–1.8(–2) x (0.2–)0.3–0.4(–0.5) cm, the lower and upper sheaths glabrous with acuminate apex and eciliate margin. *Inflorescence* broadly cylindric, obtuse at apex, subdensely many-flowered, (5.7–)6.9–9.8(–12.8) x (1.8–)1.9–2.5(–3) cm; rachis obscure, densely glandular-villose; bracts lanceolate, 1–2(–3)-nerved, 3–15(–16) x (1.3–)3–4.4(–5.5) mm, densely glandular-pubescent, the apex acute or acuminate, the margin glandular-ciliate. *Flowers* white or green, (6.5–)7.3–9(–11) mm long. *Dorsal sepal* obovate-oblong, deeply concave, (1–)2–3-nerved, 6.5–7.7(–8.8) x (2–)2.4–3(–3.5) mm, abaxially sparsely glandular-hirsute, the apex acute or obtuse. *Lateral sepals* oblong, slightly concave, (1–)2(–3)-nerved, (6.5–)7–8.5(–9.5) x (2–)2.2–3(–3.9) mm, asymmetrical, abaxially sparsely glandular-hirsute, the apex acute or obtuse. *Petals* obovate-oblong, slightly concave, 1–2(–3)-nerved, (6–)6.5–7.7(–8.5) x (1.1–)2.1–2.7(–3.2) mm, the blade abaxially glabrous, sparsely glandular-puberulent or glandular-pubescent in distal half, adaxially glabrous, the base attenuate, the apex acute or slightly obtuse, the margin entire, sparsely glandular-ciliate medially, except at base and apex with simple hairs. *Labellum* oblong-ligulate in outline, lanceolate when spread, (6.5–)7–9(–11) x (3.2–)4.5–6(–6.5) mm, obscurely 3-lobed; claw square, 3(–5)-nerved, (0.3–)0.7–1(–1.5) x (0.5–)0.9–1.2(–1.5) mm; lateral lobes subrotund, (3–)5–6(–7)-nerved, abaxially densely puberulent, adaxially sparsely puberulent in middle, the base subcordate, the calli reniform, very fleshy, horizontal; midlobe obovate-oblong, slightly curved outwards, fleshy, the apex truncate, membranaceous, adaxially glabrous, the margin flat, membranaceous, entire, eciliate, the calli oblong, slightly fleshy, completely occupying the midlobe, adaxially slightly sulcate, sparsely puberulent over the entire length. *Column* geniculate, elongate, narrowly elliptic, (5–)5.5–6.7(–8.5) x (0.9–)1.4–1.9(–2.1) mm, sparsely puberulent on abaxial surface, sparsely pubescent on adaxial surface, the stalk (0.5–)1.4–2.5(–3) mm long; anther ovate, (1–)1.8–2.5(–3) x (0.7–)0.8–1.2(–1.6) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.3–)0.5(–0.6) mm diam.; stigma transversely ovate, applanate, (0.5–)0.8–1.1(–1.2) x (1–)1.2–1.8(–2) mm.

Ovary cylindric, (6–)6.5–9.2(–12) x (2–)2.2–4.7(–6.7) mm, densely glandular-pubescent or glandular-hirsute. *Fruits* ovoid, 10–13 x 4.2–7 mm, densely glandular-pubescent; seeds fusiform, 0.93 x 0.2 mm.

Distribution. (Fig. 3.26.B). Peru to Bolivia. *Gomphichis plantaginifolia* occurs in montane forests, cloud forests, and subpáramos, at elevations of 2300–3900 m. Flowering specimens have been collected throughout the year, except in September, December, and January. Fruiting collections are known from February, June, October, and November.

Common names. Peru (Huancavelica): inquill.

Specimens examined. PERU. Ayacucho: Prov. Huanta, Choimacota Valley, 2900-3000 m, 28 Feb-10 Mar 1926 (fl), *Weberbauer 7569* (AMES-2 sheets, F, US). **Cusco:** Prov. Urubamba, nr. Wenner Gren ruins [Winay Wayna ruins], 3400-3600 m, 5-6 Aug 1942 (fr), *Metcalf 30772* (AMES, UC); Pillahuata, Cerro de Cusilluyoc, 2800-2900 m, 3-6 May 1925 (fl), *Pennell 14097* (AMES, NY, PH); Prov. Urubamba, Phuyupatamarca area [ruins], 3200 m, 29 Mar 1942 (fl), *Vargas J. C., C. 2770* (AMES); Prov. Paucartambo, Laderas de Ajcapacu, 3500 m, 12 Oct 1943 (fl), *Vargas 3680* (AMES); Prov. La Convención, Cusco-Quillabamba rd., after Abra Malaga pass and before Ipal, 3200 m, 23 Feb 2000 (fl), *Weigend & Weigend 2000/415* (NY). **Huancavelica:** Prov. Tayacaja, Dtto. Huachocolpa, above Marcavalle, 3100 m, 21 Apr 1964 (fl), *Tovar 4772* (UC). **Puno:** Prov. Carabaya, Ollachea, above falls, 14 Aug 1980 (fr), *Boeke & Boeke*

3009 (NY); Prov. Sandia, nr. Limbani, 3200-3450 m, 14-16 May 1942 (fl), *Metcalf 30520* (UC). **Without locality:** Jul 1954, (fl), *Lechler 2223* (K).

BOLIVIA. La Paz: Prov. Nor Yungas, Unduavi, at junction of rd. La Paz-Coroico-Chulumani, 3048 m, 1 Jul 1950 (fl), *Brooke 6592* (BM), in the open at the edge of the path to the station, 3170 m, 13 Oct 1950 (fl), *Brooke 6843* (BM, F, NY), 3100 m, Oct 1931 (fl, fr), *Buchtien 8929* (HBG, NY, Z); Prov. Nor Yungas, Chuspipata, 10 Jun 1957 (fl), *Cañigueral 672* (LPB); Prov. Nor Yungas, Fundam 3 rd., ca. 29.6 km SW of Yolosa junction, toward Unduavi, site is a narrow saddle at which the abandoned railroad track is very close to the rd. but not visible from it, ca. 1/2 mile away is the old station, 2911 m, 10 Nov 1976 (fl, fr), *Davidson 4928* (F); Prov. Sur Yungas, trail to Chuspipata, 2939 m, 17 may 1991 (fl), *Feuillet 15037* (LPB); Prov. Nor Yungas, La Paz-Coroico rd., between Chuspipata and Sacramento, 3000 m, 11 Aug 1991 (fl), *García 1962 (*NY, SEL); Prov. Nor Yungas, 2 km NE of Chuspipata on rd. to Yolosa, 2900 m, 8 Jun 1985 (fl, fr), *McCook & Solomon 1159* (LPB); Prov. Nor Yungas, Unduavi-Coroico rd., above Sacramento, 2804 m, 22 Feb 1975 (fl), *Plowman & Davis 5143* (AMES); Prov. Nor Yungas, 1.6 km below Chuspipata on old rd., abandoned railroad cut and surrounding area, 3100 m, 10 Aug 1981 (fl), *Solomon 5994* (LPB, MO, NY, SEL); Prov. Nor Yungas, 1.6 km NW of Chuspipata, 3100 m, 26 Aug 1983 (fl), *Solomon 10662* (G, LPB, MO, NY); Prov. Murillo, 20.8 km N of the summit of Río Zongo Valley, 3200 m, 20 Feb 1987 (fl, fr), *Solomon 16095* (LPB, MO, SEL), Zongo-Cahua, 2300 m, 25 Aug 1991 (fl), *Vásquez et al. 1506* (LPB).

Gomphichis plantaginifolia may be distinguished from *G. goodyeroides* by its much smaller, congested inflorescence, very long bracts, elongated, oblong-quadrate, and retuse labellum which has a wide membranaceous margin and apex, and elongated, somewhat fleshy calli. Moreover, the apical constriction of the labellum is absent in *G. plantaginifolia.*

Gomphichis plantaginifolia is the most basal species of the genus according to DNA studies. This species is sister to all the remaining species of *Gomphichis.*

Although in the original description of *Stenoptera plantaginea* the petals are characterized as glabrous, an examination of duplicates of *Buchtien 2623* (AMES, US) as well as additional material, show that the petals are usually pubescent abaxially. Moreover, the shape of the petals varies from elliptic-spathulate to elliptic. Neither an extant specimen, nor a photograph of *Buchtien 2623* was found in Berlin (B), where Schlechter worked.

Gomphichis plantaginifolia was proposed by Schweinfurth (1944) because the epithet *plantaginea* was already in use in another species of *Gomphichis* when *Stenoptera plantaginea* was found to be better treated under *Gomphichis.*

15. *Gomphichis traceyae* Rolfe, Kew Bull. 78. 1916. Type. Colombia. Cundinamarca: nr. Bogotá, 3505 m, 21 Oct 1915 (fl), *J. A. Tracey 107* (lectotype, here designated, K; frag. of isolectotype RENZ). (Fig. 3.27.A).

Gomphichis brachystachys Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 52. 1920. *Stenoptera brachystachys* (Schltr.) L. O. Williams. Caldasia 5: 12.

1942. Type. Colombia. Cauca: Cauca, *M. Madero* [*94*] (holotype, B, destroyed; lectotype, here designated, illustration AMES).

Gomphichis montana L. O. Williams, Lilloa 6: 242. 1941. Type. Venezuela. Táchira: Páramo de Tamá, 3100–3300 m, Jul 1939 (fl), *F. Cardona 336* (holotype, VEN, n.v., photo AMES neg. 2029; isotype, US).

Terrestrial *herbs*, (22–)37–59(–77) cm tall; roots (0.2–)0.4 cm diam., villose. *Leaves* basal, rosulate, (3–)5–6(–9), spreading, (2.2–)4.2–11.5(–21.8) x (0.55–)1–2(–2.6) cm; subpetiole weakly differentiated; blade oblong-obovate, thin-coriaceous, dark brown to black when dry, the base short-attenuate, the apex acute or acuminate. *Peduncle* (14.1–)31.8–49.8(–68.5) x (0.2–)0.4–0.6(–0.8) cm, glabrous in lower half, densely glandular-villose in upper half; sheaths (4–)5–8(–10), sparsely arranged along peduncle, loose-fitting, the lower sheaths (4.2–)6–10.5(–13.5) x (0.5–)0.6–1(–1.6) cm, glabrous with acute apex and eciliate margin, the upper sheaths (0.6–)0.8–1.5(–2.1) x (0.2–)0.3–0.5(–1) cm, glabrous with acute apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, obtuse at apex, congested many-flowered, (2.4–)3–7.5(–9.8) x (1–)1.2–1.6(–2.1) cm; rachis obscure, densely glandular-villose; bracts ovate or ovate-lanceolate, (1–)3(–5)-nerved, (6–)7–10.3(–14) x (2.5–)3.4–4.2(–4.8) mm, sparsely glandular-pubescent at base, the apex acute, the margin glandular-ciliate. *Flowers* yellowish or greenish-white, (3.6–)4.2–6.2(–8) mm long. *Dorsal sepal* ovate, deeply concave, 1–2(–3)-nerved, (4–)4.2–5.6(–6.6) x (1.5–)2–2.5(–2.8) mm, abaxially sparsely glandular-pubescent, the apex obtuse. *Lateral sepals* ovate, slightly concave, 1–2(–3)-nerved, 4.5–6.2(–7.6) x (1.5–)2–2.6(–3) mm, asymmetrical, abaxially sparsely glandular-pubescent, the apex acute or obtuse. *Petals* obovate-elliptic or obovate-oblong, slightly concave, 1(–3)-nerved, (3.9–)4–5.3(–7.5) x (1.2–)1.5–1.8(–2.4) mm, asymmetrical, abaxially sparsely glandular-pubescent in proximal half, adaxially glabrous, the base attenuate, the apex rounded, the margin erose-denticulate at apex, sparsely glandular-ciliate medially, except at base and apex with simple hairs. *Labellum* obpyriform in outline, rhombic when spread, (4.2–)4.8–6.2(–8) x (3.1–)4–5.5(–6.5) mm, distinctly 3-lobed; claw oblong, 3-nerved, (0.3–)0.6–1.2(–2) x (0.5–)0.8–1.2(–1.7) mm; lateral lobes rotund, (3–)5–7(–10)-nerved, abaxially densely pubescent, adaxially sparsely pubescent in middle, the base subcordate, the calli reniform, very fleshy, inclined or horizontal; midlobe obovate-oblong, erect, very fleshy, the apex obtuse, membranaceous, adaxially glabrous or densely puberulent, the margin flat, slightly fleshy, entire, ciliolate at apex only, the calli oblong, strongly fleshy, completely occupying the midlobe, adaxially deeply sulcate, sparsely papillose over the entire length with few glandular hairs at base. *Column* geniculate or slightly sigmoid, (3.4–)3.9–5.2(–6) x (0.9–)1–1.9(–3.5) mm, sparsely pubescent on both surfaces, the stalk (0.6–)1–1.7(–2.1) mm long; anther ovate, (1–)1.2–2(–3.1) x (0.7–)0.9–1.4(–1.6) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.3–)0.4–0.5(–0.6) mm diam.; stigma transversely elliptic, slightly convex, 0.4–0.7(–1.7) x (0.5–)0.9–1.7(–2) mm. *Ovary* ovoid or obovoid, (4–)4.9–7(–10) x (2.1–)2.8–4(–6) mm, densely glandular-pubescent. *Fruits* ovoid or obovoid, 6.5 x 5 mm, densely glandular-pubescent; seeds spatulate or fusiform, 0.67 x 0.22 mm.

Distribution. (Fig. 3.27.B). Venezuela to Ecuador. *Gomphichis traceyae* is found in montane cloud forests, subpáramos, páramos, and secondary vegetation such as scrub, forest edges, cleared slopes, and disturbed roadsides between 1200 and 4500 m of elevation. Flowering specimens have been collected throughout the year but more frequently from July to October. Fruting has been reported in all months except June.

Specimens examined. COLOMBIA. Antioquia: Páramo Frontino, Cerro de Campanas, 3650-4290 m, 28 Oct 1976 (fl, fr), *Boeke & McElroy 285* (NY, SEL); San José de Cuerquia, trail to páramo, 31 Jul 1958 (fl), *Garganta 2164* (US); Mpio. Urrao, Páramo de Frontino, Llano Grande, border of trail from la casa del Morro to Sitio Campanas, 3450 m, 10 Sep 1986 (fl, fr), *Roldán et al. 347* (HUA, MO). **Boyacá:** Mpio. Duitama, Páramo de la Rusia, 3400-3500 m, 28 Nov 1978 (fl), *Díaz 1226* (COL); Cordillera Oriental, Sierra Nevada del Cocuy, Laguna Seca-Bachiva., 2750 m, 19 Aug 1957 (fl), *Grubb 609* (K, US); nr. El Playón, 10 Sep 1957 (fl), *Grubb 773* (K, US); W slopes of Nevado del Cocuy, 4400-4500 m, 5 Jan 1939 (fl), *Renz 4133* (RENZ); Mpio. Chinavita, Cerro Mamapacha, 2900 m, 11 Dec 1998 (fl), *Stancik 1590* (COL); Mpio. Arabuco, Santuario Iguaque, on slope above Laguna Ojo de Agua, cuchilla Laguna Ojo de Agua-Laguna Iguaque, 3600 m, 15 Oct 1998 (fl), *Stancik et al. 929* (COL). **Caldas:** Cordillera Central, W slopes, headwaters of Río Otún, páramo of Laguna del Mosquito-Plan del Villar, 3650-3750 m, 26 Nov 1946 (fl), *Cuatrecasas 23253* (F). **Cauca:** Macizo Colombiano, Valle de las Papas, nr. Hacienda Los Andes, sta. 4., 2-2.5

km from houses, 3150 m, 4 Oct 1958 (fl), *Barclay & Juajibioy 5910* (AMES, MO-2 sheets); Volcán Puracé, 23 Jul 1956 (fl), *Barclay & Schultes 144* (AMES), Páramo de San Rafael, 3048 m, 23 Jul 1960 (im fl), *Garay 8* (AMES); Páramo de Guanacas, 3300 m, 8 Nov 1882 (fl), *Lehmann 2183* (BM, G), 3000-3500 m, Jan 1886 (fl), *Lehmann 6034* (HBG, K-2 sheets); Cordillera Central, Paletara, "Llano de Paletara", 2950-3100 m, 15-17 Jun 1922 (fl), *Pennell 6915* (AMES), nr. Río Cauca, 2950-3000 m, 15-17 Jun 1922 (fl), *Pennell 7080* (AMES); Puracé, in matorrales de Chiquín, 2700-3100 m, 11 Jul 1939 (fl), *Pérez-Arbeláez 5941* (US); Totoro-Inza rd., km 32 E of Cali-Popayán hwy., 2743 m, 13 Aug 1974 (fl), *Plowman & Davis 4120* (AMES). **Cauca-Huila border:** Cordillera Central, Mpio. Coconuco-San Agustín, 4-10 km Paletará-Pitalito, Páramo del Buey, Parque Nacional Natural del Puracé, 2975-3200 m, 12 May 1991 (fl), *Betancur & Churchill 2500* (HUA). **Cundinamarca:** Quebrada Chicó, hills above Bogotá, 3353 m, 11 Jul 1943 (fl), *Allen 3008* (MO, US); valley E of Pacho, 2896 m, 7 Jul 1968 (fl), *Barkley & Mullen 38951* (AMES); Cordillera Oriental, Monserrate, nr. Bogotá, 3210 m, 20 Aug 1938 (fl), *Cuatrecasas 20* (F, US); Cordillera Oriental, W slopes of Páramo de Cruz Verde, 3150 m, 7 oct 1938 (fl), *Cuatrecasas 389* (US); Cerro de Monserrate, Bogotá, 3200 m, 8 Oct 1944, (fl), *Fassett 25872* (US), 3048 m, 8 Oct 1944 (fl), *Fassett 25883* (US); Mpio. Subachoque, Páramo El Tablazo, 3450 m, 1 Sep 1983 (fl), *García 6* (COL); Cordillera Oriental, Chinga Valley, 3 km E of Gutiérrez, 50 km S of Bogotá, 2350 m, 22 Jul 1944 (fl), *Grant 9640* (US); Mpio. Santafé de Bogotá, Bogotá, Guadalupe, 2900 m, 29 Sep 1946 (fl), *Haught 5042* (US), 3300 m, 17 Jul 1949 (fl), *Haught 6492* (US); Cordillera

Oriental, Cordillera de Tunjaque, divortium aquarum, between headwaters of rivers Guavio and Siecha or Tominé, 3700 m, 12 Oct 1956 (fl), *Idrobo & Jaramillo-Mejia 2257* (COL, NY); Zipaquirá, El Carrizal, 3200-3400 m, 14 Oct 1961 (fl), *Murillo 400* (NY); Páramo Boquerón de Chipaque, 3300 m, 17 Nov 1956 (fl), *Ospina-Hernández & Idrobo 33* (AMES, COL); Mpio. Santafé de Bogotá, above Bogotá, Mt. Guadalupe, 2800-3300 m, 12 Sep 1917 (fl, fr), *Pennell 1918* (AMES, NY, US); vic. Monserrate, E of Bogotá, 3200 m, 2 Oct 1936 (fl), *Renz 4134* (RENZ); Retiro-La Calera, N of Bogotá, 3000 m, 9 Dec 1937 (fl), *Renz 4135* (RENZ); Boquerón de Chipaque, E of Bogotá, 3300 m, 26 Nov 1938 (fl), *Renz 4136* (RENZ); Monserrate, E of Bogotá, 3200 m, 28 Nov 1936 (fl, fr), *Renz 4143* (RENZ); Retiro-Calera pass, 3100 m, 13 Jul 1941 (fl), *Renz 4154* (RENZ); E slopes of Bogotá, 3000 m, 9 Aug 1941 (fl), *Renz 4166* (RENZ); vic. Bogotá, Monserrate-chain, N of the church, 27 Aug 1955 (fl), *Renz 8451* (RENZ-2 sheets); S Usne-Gutiérrez, vic. Pueblo Viejo, 8 Jul 1955 (fl), *Renz 8466* (RENZ); Páramo de Choachí, Bogotá-Choachí, 5 Aug 1955 (fl), *Renz 8486* (RENZ); vic. Bogotá, Monserrate-chain, N of the church, 27 Aug 1955 (fl), *Renz 8492* (RENZ-2 sheets); Zipaquirá-Pacho, N of Cerro de los Buitres, 30 Aug 1955 (fl), *Renz 8514* (RENZ); Suba Hill nr. Bogotá, N end of hill, 7 Sep 1945 (fl), *Schiefer 907* (AMES-2 sheets); Bogotá, mountains back of Calle 75, 12 Oct 1945 (fr),*Schiefer 927* (AMES); Bogotá, Monserrate, 2 Jul 1950 (fl), *Schneider 242/12* (RENZ), 22 Aug 1950 (fl), *Schneider 288/6* (RENZ), 2 Jul 1950 (fl, fr), *Schneider s.n.* (COL); Bogotá-Choachí rd., 31 Aug 1956 (fl), *Schultes et al. 22513* (AMES); Cordillera Oriental, ca. 15 km NW of Zipaquirá, "Alto del Páramo", 3200 m, 6 Aug

1950 (fl), *Smith 1385* (COL, UC); Mpio. Villapinzón, Páramo La Calavera, 3350 m, 22 Jul 1998 (fl), *Stancik 477* (COL); Mpio. Santafé de Bogotá, Guadalupe Mountain summit, Sep 1917 (fl), *Tracey 173* (K); Páramo Cruz Verde, nr. Bogotá, Oct 1921 (fl), *Tracey s.n.* (K); Bogotá, La Mesa, 1200 m, 1828-1890 (fl), *Triana 623* (BM). **Magdalena:** Sierra de Perijá, Cerro Pintado, 3100 m, 5-6 Jul 1942 (fl), *Carriker 36* (US), E of Manaure, Sabana Rubia, 3000-3100 m, 7 Nov 1959 (fl), *Cuatrecasas & Romero Castañeda 25060* (US). **Meta:** Páramo de Sumapaz, Hoya de la Quebrada Sitiales, 1.5 km NW from Laguna La Guitarra, 3450 m, 26 Jan 1972 (fl, fr), *Cleef 1080* (COL, U); Cordillera Oriental, above confluence of Río del Nevado and Río Arroz, 3385 m, 2 Sep 1943 (fl), *Fosberg 20973* (US); Páramo Cruz Verde, 3500 m, 6 Sep 1967 (fl), *Kirkbride & Idrobo 344* (MO). **Nariño:** Nariño: Mpio Túquerres, Azufral, 18 May 1876 (fl), *André 3241* (K); Mpio. Pasto, forest of the Botana Farm, 2900-3100 m, 3 Mar 1963 (fr), *Mora 2567* (AMES). **Putumayo:** Laguna La Cocha-Páramo de Tábano rd., 2800-3000 m, 1 Jun 1946 (fl), *Schultes & Villarreal 7834* (AMES). **Santander:** Páramo de Santurbán, 3600 m, 27 Aug 1948 (fl), *Araque & Barkley 185022* (US); Cordillera Oriental, E slope of Páramo de Las Coloradas, above La Baja, 3900 m, 27 Jun 1927 (fr), *Killip & Smith 18385* (AMES); Cordillera Oriental, Páramo de Romeral, "Norte de Santander", 3800-4200 m, 30 Jan 1927 (fl, fr), *Killip & Smith 18686* (AMES); nr. Vélez, *Purdie s.n.* (W). **Valle del Cauca:** Cordillera Central, Mpio. Cerrito, W slopes, Páramo de Pan de Azúcar, 3625 m, 5 May 1983 (fl), *Silverstone-Sopkin 1467* (MO).

VENEZUELA. Barinas: Páramo Calderas, Calderas-Las Mesitas, 3400 m, 19 Sep 1951 (fl), *Renz 7385* (RENZ), 2800-3100 m, 19 Sep 1951 (fl), *Renz 7390* (RENZ). **Lara:** Páramo de las Rosas, Humucaro Alto-Carache, 3000 m, 25 Oct 1952 (fl), *Renz 7864* (RENZ). **Mérida:** Miranda, 22.2 km above Timotes towards Pico El Aguila, 3318 m, 1 Dec 2002 (fl, fr), *Alvarez & León 2963* (NY, PORT); Laguna Coromoto, 3200 m, Sep 1956 (fl), *Aristeguieta 2588* (AMES); Páramo de Timotes, Timotes-Laguna Huacha, W-facing, dry, rocky slope of cerro (hill) La Ventana-Laguna Huacha, 3700 m, 21-26 1959 (fl), *Barclay & Juajibioy 9838* (AMES); Sierra Nevada, Mérida, 19 Jul 1958 (fl), *Dennis 2110* (K); Páramo de Mucuchíes, *Dec 1927* (fl), *Gutzwiller 35* (VEN); Páramo del Tambor, 2865 m, 26 Aug 1938 (fl, fr), *Hanbury-Tracey 43a* (K); N slopes of the sierra, 2900-3000 m, 6-8 Oct 1952 (fl), *Humbert 26778* (RENZ); Páramo de los Conejos, 3000 m, Dec 1942 (fl), *Lasser 499* (VEN); Parque Nacional Sierra Nevada, Páramo de Mucubají, 10 km SW of Los Frailejones, 3500 m, 17 Sep 1994 (fl), *Merz 741, 748* (NY); Páramo las Gonzales, 1 Mar 1949 (fr), *Renz 5270* (RENZ-2 sheets); Serranía Negra, Santa Cruz de Mora-El Molino, 3000 m, 4 Jun 1949 (im fl), *Renz 5619* (RENZ); Tovar-Guaraque, nr. Guaraque, 2000 m, 26 Jul 1949 (fl), *Renz 5872* (RENZ); beyond Pregonero, old rd. around Bailadores-La Grita, 3000 m, 1 Oct 1951 (fl), *Renz 7423* (RENZ); Las Piedras-Niquitao and Llano Corredor-Cerro Guirigay, 3400-3700 m, 20 Oct 1951 (fl), *Renz 7463* (RENZ-2 sheets); Las Piedras-Mucubají, kms 37-14, Apartaderos-Barinas rd., 13 Aug 1980 (fl), *Stergios & Taphorn 2108* (PORT); between la Cumbre, San José and Mucutuy, 1820-2590 m, 3 May 1944 (fr), *Steyermark 56245* (AMES); Dtto. Rangel, Santo

Domingo-Apartaderos rd., 27 Oct 1985 (fl), *van der Werff 7684* (MO, PORT, SEL). **Merida-Trujillo border:** Las Piedras-Niquitao, Llano Corredor, 3300-3500 m, 20 Oct 1951 (fl, fr), *Renz 7461* (RENZ-2 sheets). **Táchira:** Páramo de Taimá [Tamá], 2500-3000 m, 12 Nov 1976 (fl), *Charpin et al. AC13229* (G); Páramo Zumbador, 2800 m, 20 Aug 1949 (fl), *Renz 5800* (RENZ); San José-Páramo de La Grita, above Los Ranchos, 2800 m, 20 Sep 1949 (fl), *Renz 5915* (RENZ); Páramo Zumbador, 2300 m, 3 Sep 1951 (fl), *Renz 7322* (RENZ); 25 Jul 1976 (fl), *Stergios 609a* (PORT); Boca de Monte-Zumbador, 3000 m, 28 Aug 1966 (fl), *Steyermark & Rabe 96833* (AMES). **Trujillo:** Guirigay, towards Laguna la Parida, 3400 m, Aug 1958 (fl), *Aristeguieta & Medina 3580* (VEN); Las Piedras-Niquitao, Llano Corredor, 23 Nov 1951 (fl), *Renz 7581* (RENZ-2 sheets). **Trujillo-Lara border:** Mpio. Carache, Parque Nacional Dinira, trail Páramo de Jabón-Pico Cendé, 3000 m, 30 Dec 1999 (fl, fr), *Duno et al. 1117* (PORT); Parque Nacional Dinira, path Páramo de Jabón entry to Los Altos, 3100 m, 16 Aug 1999 (fl), *Riina et al. 812* (PORT).

ECUADOR. Azuay: Jima-Moriré rd., Km 19, Páramo de Matanga, 3250 m, 20 Jul 2000 (fl, fr), *Alvarez et al. 2745* (NY, QCNE); Cuenca-Loja rd., ca. 20 km S of Cumbe, 3000-3200 m, 19 Mar 1974 (fl), *Harling & Andersson 12636* (GB); Cuenca-Loja rd., upper northern slopes of Valle del Río León and S Páramo de Tinajillas, 2800-3200 m, 9 May 1974 (fl), *Harling & Andersson 14491* (AMES, GB); S of Cumbe, high rd. slope, 3000 m, 22-24 Apr 1968 (fl), *Harling et al. 8726* (GB); Oña-Cuenca, 2700-3300 m, 9-10 Sep 1923 (fl), *Hitchcock 21657* (US); Km 85, Pan American Hwy. N of Loja, 2850-2950 m, 3 May 1973 (fl), *Hølm-Nielsen et al. 4829* (AAU); Km 67 S of Cuenca, Pan American Hwy., 3250 m, 4 May 1973 (fl, fr), *Hølm-Nielsen et al. 4933* (AAU, AMES, SEL); above Sigsig, 2800 m, 6 May 1981 (fr), *Kuhn et al. 49a, 49b* (both SEL); S of Cuenca towards Saraguro, 3000 m, 17 Mar 1984 (fl, fr), *Luer et al. 9539* (SEL); Páramo de Tinajillas, kms 23-28 Cumbe-Loja rd., 3200-3300 m, 16 Jun 1979 (fl), *Løjtnant et al. 14953* (AAU), 21-23 kms S of Cumbe along rd. to Loja,. 0-1 km E of the rd., 3300-3400 m, 27 Feb 1985 (fl), *Molau & Öhman 1417* (GB); 10 km S of Cumbe on rd. to Oña, 3150-3200 m, 28 Jan 1988 (fl), *Molau et al. 2688* (GB); Cuenca-Loja rd., 68 km S of Cuenca, 3350 m, 19 Feb 1985 (fl), *Øllgaard et al. 57774* (AAU). **Cañar:** Azogues-Taday-Pindilig rd., Km 17, 3150 m, 17 Jul 2000 (fr), *Alvarez et al. 2712* (NY, QCNE). **Carchi:** Tufiño-Maldonado rd., vic. Comuna La Esperanza, 3200 m, 8 Jan 2000 (fl), *Alvarez & Alvarez 2569* (NY, QCNE); Tulcán-Tufiño-Maldonado rd., Km 16, 3200 m, 2 Jul 2000 (fl), *Alvarez & Alvarez 2626* (NY, QCNE); Reserva Ecológica El Angel, buffer zone, rd. to Laguna El Voladero, 3300 m, 2 Jul 2000 (fl, fr), *Alvarez & Alvarez 2632* (NY, QCNE); Tulcán-El Carmelo rd., Km 18, 3300 m, 27 May 1980 (fl), *Balslev & Quintana 23860* (AAU); Páramo El Angel, 30 km SW of Tulcán, 4000 m, 20 Apr 1983 (fl, fr), *Bohlin & Bohlin 574* (GB); Tulcán-El Carmelo, Km 18, 3200 m, 7 Jul 1990 (fl), *Dodson et al. 18415* (QCNE); Tulcán-Maldonado, Km 20, 3215 m, 29 Apr 1993 (fl), *Dodson et al. 19037* (QCNE); Tulcán-San Gabriel rd., ca. 20 km S of Tulcán, nr. El Voladero, 3000-3100 m, 22 Feb 1974 (fl, fr), *Harling 12044* (GB); El Angel, 3750 m, 15 Jul-15 Oct 1983 (fr), *Hirtz 1163* (SEL); Tulcán, *Karsten s.n.* (W); Cantón Espejo, Páramo del Azufral, E of El Angel, 3500 m, 27 Jul 1935 (fl), *Mexia 7530* (US); Las Juntas-El Angel rd., Páramo El Angel, 3300-3400 m, 21 Feb 1989 (fl), *Palacios & van der Werff 3975* (QCNE); 10-11 km NE of Páramo El Angel, 3353 m, 8 Aug 1978 (fl, fr), *Webster 23093* (DAV). **Cotopaxi:** Area Nacional de Recreación El Boliche, ca. 3 km from the entrance, Km 1 of the rd. to the "cascajo" mine, 3350 m, 13 Jun 2000 (fl), *Alvarez & Alvarez 2596* (NY, QCNE); Parque Nacional Cotopaxi, rd. to Laguna Limpiopungo, 3200-3350 m, 14 Jun 2000 (fl), *Alvarez & Alvarez 2598* (NY, QCNE); Parque Nacional Cotopaxi, rd. to Laguna Limpiopungo, 3200-3350 m, 14 Jun 2000 (fr), *Alvarez & Alvarez 2599* (NY, QCNE); railroad station Cotopaxi, 3500 m (fl, fr), *Asplund 6472* (S); Parque Nacional Cotopaxi, railroad station-southern entrance, 3400 m, 27 May 1988 (fl, fr), *Balslev & Paz y Miño 69220* (AAU); Parque Nacional Cotopaxi, 1-3 km before entrance, 3500 m, 30 May 1982 (fl), *Balslev 2639* (NY); Volcán Cotopaxi, along the rd. to and at Laguna Limpiopungo, 3500-3850 m, 23 Mar 1984 (fl), *Lægaard 51855* (AAU); Parque Nacional Cotopaxi, 3 km towards the entrance of park, 3200 m, 1 May 1982 (fr), *Sosa & Briones 48* (QCA); Pan American Hwy., about 6 km N of Lasso, ENE Pasto-Calle, 3400 m, 29 Apr 1967 (fl, fr), *Sparre 15818* (AAU, S, TEX, US); Parque Nacional Cotopaxi, slopes nr. pine plantation, 3550 m, 16 Apr 1983, (fr), *Zambrano 19* (QCA). **Imbabura:** slope of Mount Cotacachi, above Lake Cuicocha, 3300 m, 11 Apr 1956 (fl), *Asplund 20236* (S); Otavalo-Selva Alegre rd., Km 45, 3200 m, 28 May 1980 (fl), *Balslev & Quintana 24090* (AAU); route Lago Cuicocha entry from Pan American Hwy. Otavalo-Ibarra, Km 40, 3000 m, 20 Mar 1986 (fl, fr), *Dodson et al. 16398* (QCNE, SEL); above Laguna de Piñan, slope of Volcán Cotacachi, 3292 m, 3 Dec 1944 (fl, fr), *Drew E-101* (AMES); W rim of the Cuicocha crater, 3150 m, 4 May 1980 (fl), *Hølm-Nielsen 23248* (AAU); La Joya-Laguna de Mojanda Cajas rd., S the town of Otavalo, 3109-3659 m, 26 Jan 1980 (fl), *Jaramillo & Coello 2051* (QCA); Selva Alegre, W of Otavalo, 3150 m, 1-2 May 1981 (fl), *Kuhn et al. 22* (SEL); Cantón Cotacachi, Reserva Cotacahi-Cayapas, Laguna Cuicocha, at Quebrada Chumabí, 3300-3400 m, 1 Mar 1992 (fl), *Peñafiel et al. 1001* (QAP, QCNE); highlands de Cayachupa, ca. 5 km NW of Piñán, 3200 m, 16 Jun 1980 (fr), *Sperling & Bleiweiss 5107* (QCNE). **Loja:** Cantón Saraguro, Loja-Saraguro rd., Km 54, branch on rd. to Cerro Cacana, nr. military guard site, 3250 m, 1 Aug 2000 (fl), *Alvarez et al. 2805* (NY, QCNE); summit and upper slopes of Cerro Villonaco, 2600-2750 m, 12 Apr 1974 (fl, fr), *Harling & Andersson 13492* (GB); slopes of Cerro Villonaco, ca. 10 km W of Loja, 2800 m, 6 Mar 1966 (fl), *Knight 526* (WIS); Páramo de Oña, 3100 m, 16 Sep 1987 (fl, fr), *Ramsay & Merrow-Smith 563* (K, QCNE). **Pichincha:** below San Juan towards Chiriboga, 3250 m, 27 Apr 1955 (fl), *Asplund 16082* (S); Mojanda, 3300 m, *Hirtz 1022* (SEL); N slopes of Cerro Corazón, between Hacienda La Granja and Hacienda El Pongo on rd. from Aloag, 3300-3450 m, 13 May 1979 (fl), *Løjtnant & Molau 13243* (AAU); old rd. Quito-Santo Domingo, 3-4 km SW of (below) San Juan towards Chiriboga, 3300-3400 m, 12 Jan 1988 (fl), *Molau et al. 2430* (GB). **Tungurahua:** NW slopes of Volcán Tungurahua below the refuge, 2850-3150 m, 15 Jan 1988 (fl), *Molau et al. 2493* (QCA). **Without locality:** 23 Nov 1961 (fl), *Pennington 62* (K-spirit coll., no herbarium voucher).

WITHOUT COUNTRY. Mountain of Ullzhum [illegible], *Jameson s.n.* (W).

Gomphichis traceyae differs from *G. bogotensis* in having greenish-white or yellowish flowers; oblique, rounded, erose-denticulate and ciliate petals, and an obtuse, ciliolate and membranaceous labellum apically that bears two strongly fleshy calli.

This species in the molecular based phylogeny is included in a clade without resolution consisting of *Gomphichis adnata*, *G. viscosa*, *G. costaricensis*, and *G. cundinamarcae*. However, the sister species of *G. traceyae* is unclear. These species all have small flowers ranging from 4.2–6.2 mm long, a labellum with three-well defined lobes, and white flowers.

The collection *Pennell 7451*, from Colombia (Cauca, Monte Santa Ana) is unusual in having plants with larger inflorescences and leaves, as compared to other typical collections. This is the most heavily collected species of the genus and the best represented in the herbaria.

16. *Gomphichis valida* Rchb.f., Xenia Orchid. 3: 20. 1878. *Stenoptera valida* (Rchb.f.) Schltr., Orchideen (Schlechter) 109. 1914. Type. Bolivia. La Paz: nr. Sorata, Lancha de Cochipata, between Laripata and Pani, in rocky places, temperate region, Oct, 1859-Apr, 1860 (fl), 3100–3200 m, *G. Mandon 1166* (lectotype, here designated, BM; isotypes G, K, P, frag. RENZ, W). (Fig. 3.28.A).

Terrestrial *herbs*, (54–)64–105(–130) cm tall; roots 0.3–0.5(–0.6) cm diam., villose. *Leaves* basal, clustered, (4–)5–6(–9), ascending, (11.5–)16–30(–46) x (1.1–)1.6–2.5(–2.8) cm; subpetiole weakly differentiated; blade lanceolate-elliptic, thick-coriaceous, dark to olive green or dark brown to black when dry, the base not attenuate, the apex acute or obtuse. *Peduncle* (32.4–)50.5–91.6(–115) x (0.5–)0.8–1.1(–1.5) cm, glabrous in lower half, densely glandular-villose in upper half; sheaths (6–)9–12(–15), sparsely arranged along peduncle, loose-fitting, the lower sheaths (2.6–)9–20(–32) x (0.5–)1.6–2.2(–3) cm, glabrous with acute apex and eciliate margin, the upper sheaths (1.1–)1.2–2.2(–3) x (0.4–)0.5–0.8(–1.1) cm, glabrous, sparsely glandular-pubescent at base with acute apex and glandular-ciliate margin. *Inflorescence* broadly cylindric, obtuse at apex, congested many-flowered, (7–)8.7–14.5(–24.5) x (2.1–)2.5–3.2(–3.7) cm; rachis obscure, densely glandular-villose; bracts oblong-elliptic or obovate, 3-nerved, (1.4–)10–15(–25) x (0.7–)4–8.8(–12) mm, sparsely glandular-villose, the apex acute, the margin glandular-ciliate. *Flowers* white, yellowish or greenish, (2.2–)7.7–10(–12) mm long. *Dorsal sepal* obovate-oblong, concave, 3-nerved, (2–)6.3–9(–10) x (2.5–)2.7–4(–5.2) mm, abaxially densely glandular-hirsute, the apex acute or obtuse. *Lateral sepals* obovate-oblong, slightly concave, 3-nerved, (7.1–)7.7–9.5(–11.5) x (2–)2.8–4(–5.2) mm, asymmetrical, abaxially densely glandular-hirsute, the apex acute or subacuminate. *Petals* elliptic, concave, (1–)2–3-nerved, (6.3–)7–8.6(–10) x (2–)2.4–3.2(–3.5) mm, asymmetrical, abaxially densely glandular-hirsute in distal half, adaxially glabrous, the base cuneate, the apex subtruncate, the margin entire, sparsely glandular-ciliate medially, except at base and apex with simple hairs. *Labellum* tubular in outline, lanceolate when spread, (7–)8.5–10.1(–12) x (1.5–)2.8–4(–4.6) mm, obscurely 3-lobed; claw square, 3-nerved, (0.5–)1–1.9(–2.5) x (0.5–)1–1.6(–2) mm; lateral lobes subrotund, 3-nerved, abaxially densely puberulent, adaxially sparsely puberulent in middle, the base cuneate, the calli ovate or reniform, very fleshy, horizontal; midlobe oblong, erect, very fleshy, the apex obtuse or rounded, membranaceous, adaxially glabrous, the margin involute, slightly fleshy, entire, eciliate, the calli oblong, fleshy, completely occupying the midlobe, adaxially deeply sulcate, moderately papillose over the entire length. *Column* geniculate, (5.5–)5.7–7.6(–8.5) x (1.1–)1.5–3(–4.5) mm, sparsely papillose on abaxial surface, glabrous to glabrate on adaxial surface, the stalk (1.3–)1.6–2.6(–3.5) mm long; anther ovate, (1.6–)2.2–3(–3.5) x (0.5–)1.1–1.7(–2) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.4–)0.5–0.6(–0.7) mm diam.; stigma transversely elliptic, applanate, (0.5–)0.7–1.3(–1.6) x (1.1–)1.5–2(–2.2) mm. *Ovary* cylindric or fusiform, (5–)6.5–10.35(–14) x (2.4–)3.1–5.7(–6.9) mm, densely glandular-pubescent. *Fruits* cylindric or fusiform, (10–)11–12 x (0.9–)5.2–7.4(–10) mm, densely glandular-pubescent; seeds spatulate, (1–)1.15–1.27 x 0.19–0.22 mm.

Distribution. (Fig. 3.28.B). This species is widespread from Colombia to Bolivia. *Gomphichis valida* occurs in humid subpáramos, páramos, upper cloud forests, and in disturbed areas such as stream margins and road banks. It has been noted as growing with species of *Alnus* and *Polypepis* on granitic substrates. This species occurs at elevations of 2600–4800 m. Flowering has been reported from January through September, predominantly in July. Fruiting has been noted in January, and between March to April, and July to August.

Specimens examined. COLOMBIA. Cauca: Páramo de Barbillas, SE Popayán, 3070 m, 27 Jul 1978 (fl), *Luer et al. 3034* (SEL). **Nariño:** Pasto, Volcán

El Galeras, 3200-3500 m, 4 Jun 1946 (fl), *Schultes & Villarreal 8001* (AMES-2 sheets).

ECUADOR. Azuay: Cuenca-Molleturo-Naranjal rd., Km 37, 3600 m, 26 Jul 2000 (fl), *Alvarez et al. 2759* (NY, QCNE); Cuenca-Molleturo-Naranjal rd., branch to the margins of Río Mihüir at Km 37, 3520 m, 26 Jul 2000 (fl), *Alvarez et al. 2762* (NY, QCNE); Cuenca, Parroquia Baños, Hacienda Yanasacha, 3000-3200 m, 28 Jul 1978 (fl, fr), *Boeke & Jaramillo 2544* (NY); Cuenca-Molleturo rd., 45 km NW Cuenca, 26 Jul 1982 (fl, fr), *Clemants et al. 2174* (QCA, SEL); Río Mihuir, ca. 1 km below Mioir [Mihüir] on Cuenca-Molleturo rd., 3400 m, 8 Mar 1985 (fl), *Harling & Andersson 22918* (GB, QCA); Cerro Soldados, W of Sayausí, below Quinoas, 3500 m, 25 Apr 1968 (fl), *Harling et al. 8742* (AMES, GB); embankment rd. beyond Lago Zorrogucho, W of Cuenca, 3000 m, 7 Feb 1978 (fl), *Luer & Luer 2480a* (QCA). **Bolívar:** Guaranda-Salinas rd., Km 22, 2950-3150 m, 13 Jul 2000 (fr), *Alvarez et al. 2681* (NY, QCNE), Km 24, 3200 m, 13 Jul 2000 (fl), *Alvarez et al. 2687* (NY, QCNE); Guaranda-Caluma rd., Km 10, 3100 m, 15 Jul 2000 (fr), *Alvarez et al. 2688* (NY-2 sheets, QCNE); Guaranda region, 2600 m, Mar 1984 (fl), *Hirtz 1589* (QCNE); old rd. Guaranda-Caluma, 3100 m, 10-11 Mar 1982 (fl), *Luer & Dalström 7259* (SEL); Guaranda-Facundo Vela rd., ca. Km 45, 3200 m, 19 Feb 1991 (fl), *Whitten et al. 91069* (QCNE). **Cañar:** rd. to Lago Culebrillas, Km 6, 3350 m, 16 Jul 2000 (fr), *Alvarez et al. 2705* (NY, QCNE), Km 8, 3400-3600 m, 16 Jul 2000 (fr), *Alvarez et al. 2706* (NY, QCNE); Azogues-Taday-Pindilig rd., Km 17, 3150 m, 17 Jul 2000 (fl), *Alvarez et al. 2713* (NY, QCNE). **Carchi:** Reserva Ecológica El Angel, buffer zone, ca. 4 km before the control station El Salado, 3150 m, 1 Jul 2000 (fr), *Alvarez & Alvarez 2624* (NY, QCNE); Tulcán-Maldonado rd., km 34-71, 3500 m, 29 Apr 1993 (fl), *Dodson 19041* (QCNE); W slopes of Cordillera Occidental, Tulcán-Maldonado rd., 2900-3100 m, 2 Mar 1974 (fl, fr), *Harling & Andersson 12430* (GB); El Angel-Tulcán, route to El Voladero, Km 11, turn off towards the S, 3400 m, 8 Aug 1990 (fl, fr), *Jørgensen et al. 92295* (AAU); above San Gabriel, 3340 m, 16 May 1981 (fl), *Kuhn et al. 129* (SEL); El Angel, the "lagunas", 3500-3850 m, 21 May 1983 (fl, fr), *Lawesson et al. 43936* (AAU, QCA). **Imbabura:** Cordillera Occidental, Mina Chupa, Selva Alegre Region, W of Otavalo, 3200 m, 23 Apr 1944 (fl), *Drew E-141* (AMES); Páramo de Mojanda, Apr 1920 (fl, fr), *Sodiro s.n.* (QPLS-3 sheets).

PERU. Ancash: Prov. Yungay, Yungay-Llanganuco, 3950 m, 23 May 1970 (fl), *López & Sagástegui 7437* (NY); Prov. Carhuaz, Huascarán National Park, Quebrada Ishinca, N side of Valley, 3900-4000 m, 18 Jul 1985 (fl), *Smith & Buddensiek 11255* (F, LPB, MO, QCNE); Prov. Huari, Huascarán National Park, S side of Quebrada Carhuazcancha, 4000-4200 m, 6 May 1986 (fl), *Smith et al. 12247* (F), Quebrada Pachachaca, a lateral valley of Quebrada Rurichinchay, 3700-3860 m, 12 Jun 1986 (fl), *Smith et al. 12535* (MO); Prov. Huaylas, Huascarán National Park, Quebrada Santa Cruz, Punta Union-Taullipampa, 4300-4835 m, 15 Jan 1985 (fl, fr), *Smith et al. 9253* (F, MO); Prov. Yungas, Huascarán National Park, Llanganuco Sector, María Josefa trail, 3600-3700 m, 28 Jan 1985 (fl), *Smith et al. 9423* (MO); Prov. Carhuaz, Huascarán National Park, mouth of Quebrada Ishinca, 3880 m, 15 Feb 1985 (fl), *Smith et al. 9591* (MO). **Cajamarca:** Prov. Cajamarca, Dtto. La Encañada, Cajamarca-Shoclla-

Chanta Alta rd., 3700 m, 19 Sep 2001 (fl), *Alvarez et al. 2898* (HAO, NY); Prov. San Miguel, Las Lagunas, Cajamarca-Hualgayoc rd., 4000 m, 10 Jul 1995 (fl), *Sagástegui et al. 15733* (NY); Prov. Cajamarca, Cajamarca-Bambamarca rd., 55 km N of Cajamarca, 3750 m, 2 Jun 1984 (fl), *Smith & Sánchez 7453* (SEL). **Cusco:** Prov. Paucartambo, Tres Cruces, 3500-3600 m, 21 Jul 1990 (im fl), *Cano 3928* (MO); Río Umantuy [Umanui], 3600 m, 30 Jun 1954 (fl), *Hirsch 1470* (AMES); Prov. Paucartambo, Paucartambo-turn-off to Tres Cruces rd., shortly before turn-off, 3500 m, 9 Feb 2000 (fl), *Weigend & Weigend 2000/234* (NY). **La Libertad:** Prov. Huamachuco, Pallar-Huaguil, rd. to Tayabamba, 3300 m, 23 Jun 1974 (fl), *López & Sagástegui 8145* (NY, RENZ). **San Martín:** Prov. Huallaga, Valley of Río Apisoncho, 30 km above Jucusbamba, new rd. above river, 2600 m, 25 Aug 1965 (fl), *Hamilton & Holligan 1426* (K).

BOLIVIA. La Paz: Prov. Nor Yungas, new rd. above Unduavi toward Coroico, 3050 m, 22 Jan 1983 (fl), *Luer et al. 8539* (SEL); Prov. Larejaca, Mapiri, 762 m, May 1886 (fl), *Rusby 2783* (NY); Prov. Nor Yungas, 2 km E of Cotapata, 3100 m, 15 Feb 1983 (fl), *Solomon 9621* (MO).

WITHOUT COUNTRY. Without locality: *Unknown, s.n.* (W); ["Brazil: Minas Gerais"], *Claussen 390* (P).

Gomphichis valida is distinguished from its closely related allies by its combination of inflated sheaths, congested and cylindric inflorescences, large, hirsute flowers that are white, yellowish or greenish in color, oblong sepals, a fleshy labellum, and a glabrous to glabrate and elongated column with a long stalk. Most populations of *G. valida* are morphologically homogeneous and easy to recognize. Some localized variants occur, however, especially in the southern part of its range in Peru and Bolivia. Here, the flowers are yellowish and have a sparsely pubescent column.

Gomphichis valida is related to those species with large flowers and a weakly 3-lobed labellum including *G. caucana* and *G. crassilabia* among others. Due to the morphological resemblance of these species and the lack of resolution in this portion of the molecular tree, the sister species of *G. valida* cannot yet be determined.

There is a specimen of *Gomphichis valida* deposited at P labelled Minas Gerais, "*Claussen (390)*" and in another hand "Brésil"? annotated by A. Cogniaux as *Stenorrhynchos balanophorostachys*. However, no other collections of *Gomphichis* are known from Brazil, so that this disjunct record is dubious. It may well be a case of a labelling mistake similar to others recently found for collections of *Claussen* deposited at Florence (FI). In this particular example "a series of supposed Claussen specimens from Brazil are without a doubt actually Linden collections from Venezuela. A case of 'Herb. Claussen' being mistaken for 'leg. Claussen'" (Eric Christenson, in litt., 1 Dec 2003). *Gomphichis valida* as here interpreted, nonetheless, is not present in Venezuela, but in Colombia. As a result, it is likely that this specimen attributed to Claussen may have been collected by Linden in Colombia.

17. *Gomphichis viscosa* (Rchb.f.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 6: 51. 1919. *Stenoptera viscosa* Rchb. f., Bonplandia 4: 211. 1856. Type. Peru. Huánuco: Chinchao, (fl), *J. A. Pavón s.n.* (lectotype, here designated, G, n.v., photo F neg. 25528; isolectotypes, W, frag. BR, probable isolectotype BM). (Fig. 3.29.A).

Gomphichis scaposa Schltr., Repert. Spec. Nov. Regni Veg. 7: 55. 1920; Mansf. Repert. Spec. Nov. Regni Veg. Beih. 57, t. 17, nr. 60. 1929. Type. Colombia. Cauca-Antioquia, 2800 m, *M. Madero s.n.* (holotype, B, destroyed; lectotype, here designated, illustration AMES; isolectotypes frag. BR, W; probable isolectotype, BM).

Gomphichis longiscapa (Kraenzl.) Schltr., Repert. Spec. Nov. Regni. Veg. Beih. 9: 125. 1921. *Cranichis longiscapa* Bot. Jahbr. Syst. 37: 394. 1906. Type. Peru. Puno: Between Tambo Yunacoya and Ramospata, on the rd. from Sandia to Chunchusmayo, 2000–2400 m, *A. Weberbauer 1334* (holotype, B, destroyed, photo F neg. 18369).

Terrestrial or rarely epiphytic *herbs*, (56–)62–75(–89) cm tall; roots (0.3–)0.4–0.6(–0.7) cm diam., villose. *Leaves* basal, clustered, (3–)4–7(–9), ascending, (17.6–)22.5–32.5(–35) x (1.8–)2.5–4.1(–4.5) cm; subpetiole well-differentiated; blade linear-oblong or elliptic-oblanceolate, thin-coriaceous, tan to medium brown or dark brown to black when dry, the base long-attenuate, the apex acuminate. *Peduncle* (35.5–)38–57(–73.5) x 0.5–1(–1.4) cm, glabrous in lower half, densely glandular-villose in upper half; sheaths (3–)5–8(–11), sparsely arranged along peduncle, tight-fitting, the lower sheaths (5.2–)9–18.5(–25) x 1–

1.6(–2.2) cm, glabrous with acuminate apex and eciliate margin, the upper sheaths (0.8–)1–2.4(–3.5) x 0.2–0.7(–1) cm, sparsely glandular-pubescent with acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, loosely many-flowered, (14.8–)17–28(–34) x (1.1–)1.6–2.2(–2.4) cm; rachis visible, densely glandular-villose; bracts ovate-lanceolate, (1–)3(–4)-nerved, (1.6–)6–12(–15) x (2.4–)2.7–3.5(–4.7) mm, sparsely glandular-pilose, the apex acute or acuminate, the margin glandular-ciliate. *Flowers* white, (4.2–)5.8–7.2(–7.7) mm long. *Dorsal sepal* elliptic-obovate, concave, 1-nerved, (4.2–)6–7(–7.5) x (1.9–)2.4–3.5(–4.5) mm, abaxially sparsely glandular-pubescent basally, the apex acute or obtuse. *Lateral sepals* ovate-oblong, slightly concave, 1(–2)-nerved, (4.3–)4.7–6.7 x (2.2–)2.4–3.2(–3.5) mm, asymmetrical, abaxially sparsely glandular-pubescent basally, the apex acute or apiculate. *Petals* broadly elliptic, concave, 3-nerved, (4–)4.8–6.5(–7) x (2–)2.59–3.5(–4) mm, asymmetrical, the blade abaxially and adaxially glabrous, the base shortly attenuate, the apex obtuse or rounded, the margin entire, densely glandular-ciliate medially, glandular-ciliolate apically with simple hairs. *Labellum* obpyriform in outline, rhombic when spread, (4.5–)5–7.2(–8) x (4.2–)5–7(–8) mm, distinctly 3-lobed; claw oblong, 3-nerved, (0.5–)0.7–1.2(–1.5) x (0.7–)1–1.5(–1.7) mm; lateral lobes rotund, 5(–9)-nerved, abaxially densely pubescent, adaxially moderately pubescent in lower portion, the base cordate, the calli reniform, slightly fleshy, horizontal; midlobe broadly triangular, erect or slightly curved outwards, very fleshy, the apex obtuse, slightly fleshy, adaxially densely hirsute, the margin flat, fleshy, entire, eciliate, the calli obovate, strongly fleshy, occupying two thirds of the midlobe, adaxially deeply sulcate, sparsely papillose or pubescent over the entire length. *Column* strongly sigmoid, (3–)4.5–6(–7.5) x (1.1–)1.5–2(–2.1) mm, densely pubescent on abaxial surface, densely villose on adaxial surface, the stalk (0.7–)1.2–2(–2.5) mm long; anther oblong or ovate, (0.9–)1.4(–2.1) x (0.7–)0.8–1.5(–2.6) mm; pollinia asymmetrical, linear or narrowly ovoid; viscidium circular, (0.2–)0.3–0.4(–0.5) mm diam.; stigma transversely elliptic, slightly convex, 0.3–0.7(–2.5) x (0.9–)1.1–1.6(–1.8) mm. *Ovary* ellipsoidal or ovoid, (3.8–)5–7.3(–9.4) x (2–)2.6–4.2(–5.6) mm, densely glandular-villose. *Fruits* ellipsoidal or ovoid, 9.5–9.6 x 4.2–6.3 mm, densely glandular-villose; seeds fusiform, 0.9–1.18 x 0.12–0.15 mm.

Distribution. (Fig. 3.29.B). Venezuela to Bolivia. *Gomphichis viscosa* is found in montane cloud forests, subpáramos, and páramos, at elevations of 1400–3200 m. Flowering specimens have been collected from February to December, chiefly in July. Fruiting specimens have been recorded in June and July.

Specimens examined. COLOMBIA. Caldas: Cordillera Occidental, Río San Rafael, below Cerro Tatamá, 2600-2800 m, 7-11 Sep 1922 (fl), *Pennell 10359* (AMES). **Cauca:** Parque Nacional Munchique, El Tambo, Vereda Santa Ana, rd. from La Romelia to Cerro Santa Ana, 3000 m, 22 Jul 1993 (fl), *Barbosa et al. 8563* (MA), Vereda La Romelia, Quebrada Charco Azul-Quebrada El Tigrillo, 2500 m, 21 Jul 1993 (fl), *Barbosa et al. 8649* (COL, MA); Cordillera Occidental, La Gallera, Micay Valley, 2200-2600 m, 1 Jul 1922 (fl), *Killip 8006*

(AMES); Cordillera Central, Canaan, Mount Puracé, 3100-3300 m, 11-13 Jun 1922 (fl, fr), *Pennell & Killip 6633* (AMES, NY, US); Cordillera Occidental, San Antonio-Río Ortega, 2100-2300 m, 2 Jul 1922 (fl), *Pennell & Killip 8014* (AMES); Cordillera Occidental, Mount Santa Ana, 2700-3000 m, 29-30 Jun 1922 (fl), *Pennell 7466* (AMES, US). **Cundinamarca:** Boquerón, Bogotá-Caquetá, 2700 m, 1844 (fl), *Goudot s.n.* (P). **Nariño:** Pasto, Río San Pablo, 1400 m, 28 Jul 1879 (fl), *Lehmann 141* (W). **Norte de Santander:** Pica-Pica Valley, above Tapatá (N of Toledo), 2100-2400 m, 1-5 Mar 1927 (fl), *Killip & Smith 20247* (AMES). **Putumayo:** Pasto-Santiago-Sibundoy, 17 Feb 1881 (fr), *Lehmann 263* (RENZ-frag, W). **Risaralda:** Mpio. Pereira, Parque Regional Ucumarí, vic. La Pastora, left margin of Río Otún, trail to Los Chorros, sendero ecológico, 2470-2600 m, 12 Jun 1989 (fl), *Bernal et al. 1599* (COL). **Tolima:** 15.5 km from Las Juntas towards the Nevado del Tolima through Ibagué, 2760 m, 9 Apr 1984 (fl), *Albert de Escobar et al. 4230* (HUA, MO).

VENEZUELA. Trujillo: Trujillo-Boconó, 2700 m, 19 Sep 1948 (fl), *Renz 4779* (RENZ), Trujillo, 2300 m, 21 Nov 1951 (fl), *Renz 7561* (RENZ), Boconó, 2300 m, 21 Nov 1951 (fl), *Renz 7566* (RENZ). **Zulia:** Perijá, 2800-2908 m, 29 Dec 1950 (fl), *Gines 1983* (US).

ECUADOR. Carchi: Maldonado, Cultivated by Ecuagénera, Cuenca, Ecuador, 1700 m, 24 Sep 2001 (fl), *Alvarez et al. 2916* (NY); Valle de Maldonado, Km 67, Tulcán-Maldonado rd., 2600 m, 21 May 1973 (im fl), *Hølm-Nielsen et al. 6225* (AAU). **Loja:** Yangana-Cerro Toledo rd., nr. the antennas, Km 11, 2600 m, 31 Jul 2000 (fl), *Alvarez et al. 2797* (NY, QCNE); Estación Científica

San Francisco, 2800 m, 2 Aug 2000 (fl), *Alvarez et al. 2818* (NY, QCNE). **Morona Santiago:** Cantón Gualaquiza, Cuenca-Sigsig-Chigüinda rd., Km 83, 2850 m, 27 Jul 2000 (fl), *Alvarez et al. 2773* (NY, QCNE); Cantón Gualaquiza, Parroquia San Miguel de Cuyes, Bosque Protector Tambillo, lower slopes, 2400 m, 23 Sep 2001 (fl), *Alvarez et al. 2910* (NY, QCNE).

PERU. Cajamarca: Prov. Cutervo, El Suro-Playa Grande in the route to Santo Tomás, 2400 m, 4 Nov 1991 (im fl), *Sánchez-Vega et al. 6030* (CPUN). **Cusco:** Prov. Convención, Sapansachayaco, 2300 m, Sep 1961 (fl), *Vargas J. C., C. 13646* (AMES); Prov. La Convención, Hacienda Amaibamba, 29 Jul 1943 (fl, fr), *Vargas J. C., C. 3629* (AMES). **Huánuco:** Carpish hills, Huánuco-Tingo María, 2100 m, 10 Aug 1980 (fl), *Luer et al. 5363* (SEL); Carpish, 2590 m, 3 Nov 1945 (fl), *Sandeman 5267* (K). **Pasco:** Prov. Oxapampa, Cordillera Yanachaga, 12 km SE of Oxapampa, Cerro Pajonal, "chacos", 2700-2800 m, 7 Oct 1982 (fr), *Foster 9058* (MO). **Without locality:** *Pavón & Ruiz s.n.* (BM, BR).

BOLIVIA. Without locality: *Bang s.n.* (NY).

Gomphichis viscosa is distinguished by its linear-oblong to elliptic-oblanceolate leaves, a subdense inflorescence; a broader than long labellum with rotund lateral lobes, broadly elliptic, 3-nerved, always glabrous petals that show densely glandular retrorse cilia, and a strongly sigmoid column.

Although in the molecular cladogram there is poor resolution in the clade containing *Gomphichis viscosa*, based on shared morphological features, it appears that this species is closely related to *G. hetaerioides*. Both species grow in cloud forests, at middle elevations, either as terrestrial herbs or as epiphytes. They both have mostly triangular, and pilose bracts, peduncles which are densely villose apically and covered by sparsely distributed sheaths, inflorescences that are long, loose, narrowed, many-flowered, and the petals are concave, 3-nerved, glabrous, and always white.

Gomphichis viscosa has been largely confused with *G. adnata*. In fact all material from Roraima, Venezuela the type locality of *G. adnata*, has been wrongly assigned to *G. viscosa*. *Gomphichis viscosa* can be differentiated from *G. adnata* by its linear-oblong to elliptic-oblanceolate leaves, ovate-lanceolate, and pilose bracts, smaller flowers, and elliptic petals that are apically acute with retrorse cilia.

The specimen *Moritz 1103*, cited in the protologue by Reichenbach (1856), has not been found in any of the herbaria collections studied.

18. Unnamed taxon 1.

Terrestrial *herbs*, (85–)98–105(–142) cm tall; roots 0.3–0.4 cm diam., villose. *Leaves* basal, clustered, 5–8(–9), ascending, (15.2–)18–27(–30) x (1.4–)1.6–2(–2.4) cm; subpetiole weakly differentiated; blade narrowly elliptic, thick-coriaceous, tan to medium brown when dry, the base attenuate, the apex acute. *Peduncle* 77–93.9(–132.5) x (0.6–)0.7–1.3(–1.6) cm, glabrous in lower half, sparsely glandular-villose in upper half; sheaths 11–15(–23), congested along peduncle, tight-fitting, the lower sheaths 16–26.5(–32) x (1–)1.6–2.4(–2.6) cm, glabrous with acute apex or acuminate apex and eciliate margin, the upper sheaths (1–)1.1–2(–2.4) x 0.4–0.5(–0.6) cm, sparsely glandular-pubescent at base with acuminate apex and glandular-ciliate margin. *Inflorescence* broadly cylindric, slightly obtuse at apex, congested many-flowered, (6.7–)8–17(–21.7) x (2.2–)2.3–2.8(–3) cm; rachis obscure, densely glandular-villose; bracts ovate, 3(–4)-nerved, 12–17(–19) x (3.5–)5–6.2(–6.8) mm, sparsely glandular-pubescent at base, the apex acuminate, the margin glandular-ciliate. *Flowers* white, (8.2–)8.5–9.7(–9.8) mm long. *Dorsal sepal* obovate, concave, (1–)2–3-nerved, (7–)8–8.6(–9.5) x (3–)3.4–3.7(–4) mm, abaxially sparsely glandular-pubescent, the apex obtuse. *Lateral sepals* obovate, plane, (1–)2–3-nerved, (7–)8.5–9 x (2.5–)3–3.8(–4) mm, abaxially sparsely glandular-pubescent, the apex obtuse. *Petals* elliptic or obovate-oblong, plane or slightly concave, (1–)3-nerved, (6.8–)7.7–8.5(–9) x (2–)2.7–3.2(–3.5) mm, abaxially sparsely glandular-pubescent in distal half, adaxially glabrous, the base attenuate, the apex rounded, the margin entire, sparsely glandular-ciliate medially, except at base and apex with simple hairs. *Labellum* tubular in outline, lanceolate when spread, (8.2–)9.2–9.5(–10) x (6–)7–7.5(–8) mm, obscurely 3-lobed; claw square, 3(–5)-nerved, (0.7–)1.1–1.7(–2) x (0.5–)1–1.5(–1.8) mm; lateral lobes rotund, (5–)7 -nerved, abaxially densely puberulent, adaxially densely pubescent in middle, the base cordate, the calli reniform, slightly fleshy, horizontal; midlobe oblong, slightly curved outwards, fleshy, the apex obtuse, membranaceous or slightly fleshy, adaxially densely puberulent, the margin flat, slightly fleshy, entire, eciliate, the calli oblong, fleshy, occupying two thirds of the midlobe, adaxially slightly sulcate, sparsely papillose over the entire length. *Column* clavate, (5.5–)6–6.5(–6.9) x (1.5–)1.6–2.1(–2.5) mm, moderately puberulent on abaxial surface with a dense tuft of hairs on adaxial surface, the stalk (1.5–)1.7–2.5(–2.8) mm long; anther ovate, (1.5–)1.6–2.2(–2.5) x (1–)1.2–1.6(–1.7) mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, (0.3–)0.5–0.6(–0.8) mm diam.; stigma transversely ovate, slightly convex, (0.7–)1–1.2(–1.5) x (1–)1.5–1.8(–2) mm. *Ovary* ovoid, 8–10(–12) x (2.7–)3–3.7(–4) mm, moderately glandular-pubescent. *Fruits* ovoid, 12 x 7–9 mm, sparsely glandular-pubescent; seeds spatulate, 1.7 x 0.22 mm.

Distribution. (Fig. 3.30). Colombia to Peru. This taxon is found in the upper montane cloud forests, subpáramos, and open, humid páramos between 2800 to 4000 m of elevation. It grows in pristine habitas but it is often found in disturbed habitats. Flowering specimens have been collected in January, February, April, June, August, September, and November. Fruiting specimens have been collected in January, and April.

Specimens examined. COLOMBIA. Putumayo: Sibundoy-Pasto rd., La María-Páramo de San Antonio, 2900-3180 m, 1 Jun 1946 (fl), *Schultes & Villarreal 7806* (AMES).

ECUADOR. Carchi: Cantón Huaca, Parroquia Mariscal Sucre, Estación Biológica Guandera, just before the entrance to the Osos trail, 3412 m, 3 Sep 2001 (fl), *Alvarez & Caranqui 2888* (NY, QCNE), nr. the Clusia trail, 3550 m, 18 Jan 2002 (fl, fr), *Alvarez & Narváez 2863* (NY, QCNE), 3555 m, 14 Apr 2003 (fl, fr), *Alvarez & Padilla 3012* (NY, QCNE); Tulcán-El Carmelo rd., 3300 m, 8 Aug 1989 (fl), *van der Werff & Gudiño 11044* (MO). **Morona Santiago:** E of pass, Cuenca-El Limón rd., 2800 m, 20 Nov 1989 (fl), *Dodson et al. 17730* (K, QCNE); Cuenca-El Limón rd. through Gualaceo, 3000 m, 16 Feb 1986 (fl), *Hirtz 2762* (QCNE); Gualaceo-El Limon rd., from the pass towards El Limón, 3200-3400 m, 8 Feb 1989 (fl), *van der Werff & Palacios 10540* (QCNE-2 sheets). **Pichincha:** Cayambe, 4000 m, Jan 1981 (fl), *Hirtz s.n.* (SEL).

This taxon is characterized by narrowly elliptic leaves, white flowers with pubescent, ciliate petals showing a rounded apex, a geniculate column with a heavy tuft of hairs, and numerous sheaths near the base of the inflorescence. It is included in the clade containing those species with weakly differentiated lateral lobes, such as *Gomphichis caucana*, *G. crassilabia*, *G. valida*, *G. goodyeroides*, and *G. macbridei.* The DNA sequences of this taxon are unique among all sampled species of *Gomphichis*, however, its affinities cannot be determined due to the lack of resolution among subclades.

Plants in populations of this taxon are distinctive in having elongated and congested inflorescences, pubescent, white flowers, and a pubescent column. They grow sympatrically with *Gomphichis crassilabia* in Ecuador (Carchi).

19. Unnamed taxon 2.

Terrestrial *herbs*, 75–119(–163) cm tall; roots 0.5–0.7 cm diam., pubescent. *Leaves* basal, clustered, (4–)5–6, ascending, (33–)41.5–42 x 2.2–2.8(–3.7) cm; subpetiole well-differentiated; blade linear-oblong, thin-coriaceous, dark brown to black when dry, the base attenuate, the apex acuminate. *Peduncle*

61.5–100.2 x 0.7–0.8(–1) cm, glabrous in lower half, sparsely glandular-villose in upper half; sheaths 9(–10), sparsely arranged along peduncle, tight-fitting, the lower sheaths 13–17(–25.5) x 1(–1.2) cm, glabrous with acuminate apex and eciliate margin or glandular-ciliate margin, the upper sheaths 1(–2.5) x 0.2–0.3(–0.6) cm, moderately glandular-pubescent at base with acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, loosely many-flowered, (13–)16–17.7 x (1–)1.5–2.3 cm; rachis visible, moderately glandular-villose; bracts ovate, 3-nerved, (8–)8.5(–10) x 2.8–3.5(–3.9) mm, glabrous, sparsely glandular-pubescent at base, the apex acuminate, the margin glandular-ciliate. *Flowers* white, 4.2–8 mm long. *Dorsal sepal* obovate, concave, 1-nerved, (4.4–)7–7.3 x (2–)2.6–3 mm, abaxially sparsely glandular-pubescent basally, the apex acuminate. *Lateral sepals* obovate-oblong, slightly concave, 1-nerved, (4.5–)6.8–7.5 x (2.4–)2.5(–3) mm, asymmetrical, abaxially sparsely glandular-pubescent basally, the apex acuminate. *Petals* elliptic, slightly concave, 3-nerved, 4.1–6.5(–7) x 2.3–2.5(–2.8) mm, the blade abaxially and adaxially glabrous, the base attenuate, the apex slightly obtuse, the margin entire, sparsely glandular-ciliate medially, glandular-ciliolate apically with simple hairs. *Labellum* obpyriform in outline, ovate when spread, (4.5–)7.5–8 x (4.9–)5.5–6 mm, distinctly 3-lobed; claw oblong, 3-nerved, 1–1.5 x (0.8–)0.9(–1) mm; lateral lobes subrotund, 5(–9)-nerved, abaxially densely puberulent, adaxially moderately pubescent in upper portion, the base subcordate, the calli reniform, slightly fleshy, horizontal; midlobe broadly triangular, erect or slightly curved outwards, very fleshy, the apex obtuse, slightly fleshy, adaxially densely pubescent, the margin flat, fleshy, entire, eciliate, the calli obovate, strongly fleshy, completely occupying the midlobe, adaxially deeply sulcate, moderately puberulent over the entire length. *Column* slightly sigmoid, (3.5–)5.7–6.5 x (1.4–)1.8–2 mm, moderately pubescent on abaxial surface, densely pubescent on adaxial surface, the stalk (1–)1.5–2 mm long; anther oblong, (1.2–)1.5–1.7(–2) x 1–1.8 mm; pollinia symmetrical, linear; viscidium circular, 0.3–0.4(–0.5) mm diam.; stigma transversely ovate, slightly convex, 0.5–0.7(–0.9) x (1.1–)1.5–1.6(–1.9) mm. *Ovary* fusiform, 5–5.5(–7) x 1.8–2.7(–3.3) mm, densely glandular-pubescent. *Fruits* not seen.

Distribution. (Fig. 3.31). Venezuela and Colombia. This taxon occurs in primary and disturbed montane cloud forests, subpáramos, and páramos, on soils with abundant humus and organic matter, at elevations between 1700 and 3000 m. It flowers from October to December, but most commonly in November. It bears fruits in October.

Specimens examined. COLOMBIA. Caldas: Mpio. de Jardín, Km 20 of Jardín-Riosucio rd., ca. 15 km SSE of Jardín to Alto de Ventanas, 2700-2790 m, 29 Oct 1988 (fl), *Zarucchi et al. 6925* (HUA). **Norte de Santander:** Cordillera Oriental, Páramo de Tamá, Vertiente of Samaria, 2600-2900 m, 29 Oct 1941 (fl, fr), *Cuatrecasas et al. 12754* (AMES-4 sheets, F, US).

VENEZUELA. Táchira: Mpio. Rafael Urdaneta, Las Delicias-El Reposo rd., 1700 m, 10 Dec 2002 (fl), *Alvarez et al. 2996* (NY, PORT); Dtto. Junín, Villa Páez-Betania, nr. the frontier with Colombia, 2000-2400 m, 15 Nov 1975 (fl), *Bunting 4900* (NY); Páramo de Taimá [Tamá], 2500-3000 m, 12 Nov 1976 (fl), *Charpin et al. AC13252* (G-2 sheets, NY); vic. Las Delicias, Rubio-Regombalia old rd., 1900 m, 27 Nov 1951 (im fl), *Renz 7614* (RENZ).

This taxon is distinctive in its very long (greater than 41 cm), oblanceolate to linear-oblong, acuminate leaves with long-decurrent subpetioles, and by its acuminate sepals and petals.

Based on the molecular phylogenetic analysis this taxon is allied to *Gomphichis viscosa*, *G. adnata*, *G. traceyae*, *G. costaricensis*, and *G. cundinamarcae*. It is represented by few collections and the range of morphological variation is unknown. For this reason I am uncertain as to its exact affinities, although it is most similar morphologically to *G. adnata*, which has lanceolate leaves with long-decurrent bases, subdense inflorescences, and acute sepals and petals.

The unidentified specimen *Renz 7614*, collected in Venezuela at Las Delicias (Táchira), displays atypical, wider leaves with inflorescence and flowers that better fit this unnamed taxon.

20. Unnamed taxon 3.

Terrestrial *herbs*, 43–70 cm tall; roots 0.3 cm diam., lanate. *Leaves* basal, rosulate, 4–8, ascending, 17–25 x 1.4–2.9 cm; subpetiole well-differentiated; blade elliptic, thin-coriaceous, dark to olive green or tan to medium brown when dry, the base attenuate, the apex acuminate. *Peduncle* 35–58 x 0.5 cm, glabrous in lower half, sparsely glandular-villose in upper half; sheaths 4–8, sparsely arranged along peduncle, tight-fitting, the lower sheaths 12.5 x 1 cm, glabrous with acuminate apex and glandular-ciliate margin, the upper sheaths 0.8–1.4 x 0.3–0.4 cm, glabrous with acuminate apex and glandular-ciliate margin. *Inflorescence* narrowly cylindric, slightly obtuse at apex, subdensely many-flowered, 8–11.5 x 1.8–2 cm; rachis visible, moderately glandular-villose; bracts ovate, 3-nerved, 5.6–8.5 x 2.9–3.5 mm, glabrous, the apex acuminate, the margin glandular-ciliate. *Flowers* white, 6.3–6.5 mm long. *Dorsal sepal* oblong, plane, 1-nerved, 5.8–6 x 2.1–2.6 mm, abaxially glabrous, the apex acute. *Lateral sepals* obovate-oblong, slightly concave, 1-nerved, 5.9–6.2 x 3–3.2 mm, asymmetrical, abaxially glabrous, the apex acute. *Petals* obovate, slightly concave, 3-nerved, 5.5 x 2.7–2.9 mm, the blade abaxially and adaxially glabrous, the base cuneate, the apex acute, the margin entire, sparsely glandular-ciliate medially, except at base and apex with simple hairs. *Labellum* obpyriform in outline, rhombic when spread, 6.5 x 5.5–6.2 mm, distinctly 3-lobed; claw oblong, 3-nerved, 1–1.1 x 1.2–1.4 mm; lateral lobes rotund, 5 -nerved, abaxially sparsely puberulent, adaxially sparsely puberulent in upper portion, the base subcordate, the calli elliptic or reniform, slightly fleshy, inclined; midlobe broadly triangular, erect, very fleshy, the apex obtuse, fleshy, adaxially densely hirsute, the margin flat, fleshy, entire, eciliate, the calli obovate, fleshy, completely occupying the midlobe, adaxially slightly sulcate, sparsely puberulent over the entire length. *Column* geniculate, 4.2–4.5 x 1.5–1.8 mm, moderately pubescent on abaxial surface, moderately villose on adaxial surface, the stalk 1–1.5 mm long; anther ovate, 1.6–1.8 x 0.9–1.1 mm; pollinia asymmetrical, narrowly ovoid; viscidium circular, 0.2 mm diam.; stigma transversely ovate, slightly convex, 0.4–1 x 1.1–1.2 mm. *Ovary* ellipsoidal, 6.1–9.8 x 3.6–5.5 mm, glabrous. *Fruits* not seen.

Distribution. (Fig. 3.32). Bolivia. This unique taxon has been found growing in moist cloud forests and on the steep sides of a river valley, at elevations of 2100–2400 m. Flowering specimens have been collected in May and June. Fruiting is unknown.

Specimens examined. BOLIVIA. Cochabamba: Prov. Carrasco, Sehuencas, Km 18, 2100 m, 1 May 1993 (fl), *Ibisch & Ibisch 93.0153* (LPB), at end of rd., nr. 10 km below Sehuencas, 2400 m, 10 Jun 1995 (fl), *Wood 9892* (K).

This taxon is characterized by elliptic, acuminate, attenuate leaves and glabrous sheaths, bracts, and flowers.

The affinities of this unnamed orchid are unclear, although it exhibits some morphological similarity with *Gomphichis adnata*, a northern Andean species restricted to Venezuela and Colombia. The unnamed taxon can be easily distinguished from *G. adnata* by its glabrous flowers and bracts.

Populations of these orchids appear to have a very narrow distribution in the southernmost limit of the distribution of the genus in Cochabamba, Bolivia. Additional material from Bolivia is needed before the status of these collections can be certain, and the complete morphological variation and affinities understood.

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Gomphichis longifolia (Rolfe) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 10: 60. 1922. Type: Bolivia. *M. Bang 1920* (syntypes, US, MO).

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Table 3.1. Geographical distribution of *Gomphichis* species by country.

	COUNTRY						
	Costa Rica	**Panama**	**Colombia**	**Venezuela**	**Ecuador**	**Peru**	**Bolivia**
G. adnata			**X**	**X**			
G. alba			**X**	**X**			
G. altissima			**X**	**X**	**X**	**X**	
G. bogotensis			**X**	**X**			
G. caucana			**X**	**X**	**X**		
G. costaricensis	**X**	**X**		**X**			
G. crassilabia					**X**		
G. cundinamarcae			**X**	**X**			
G. goodyeroides					**X**	**X**	
G. hetaerioides		**X**	**X**		**X**		
G. koehleri						**X**	
G. macbridei					**X**	**X**	
G. merzii	**X**			**X**			
G. plantaginifolia						**X**	**X**
G. traceyae			**X**	**X**	**X**		
G. valida			**X**		**X**	**X**	**X**
G. viscosa			**X**	**X**	**X**	**X**	**X**
TOTAL spp.	**2**	**2**	**10**	**10**	**9**	**7**	**3**

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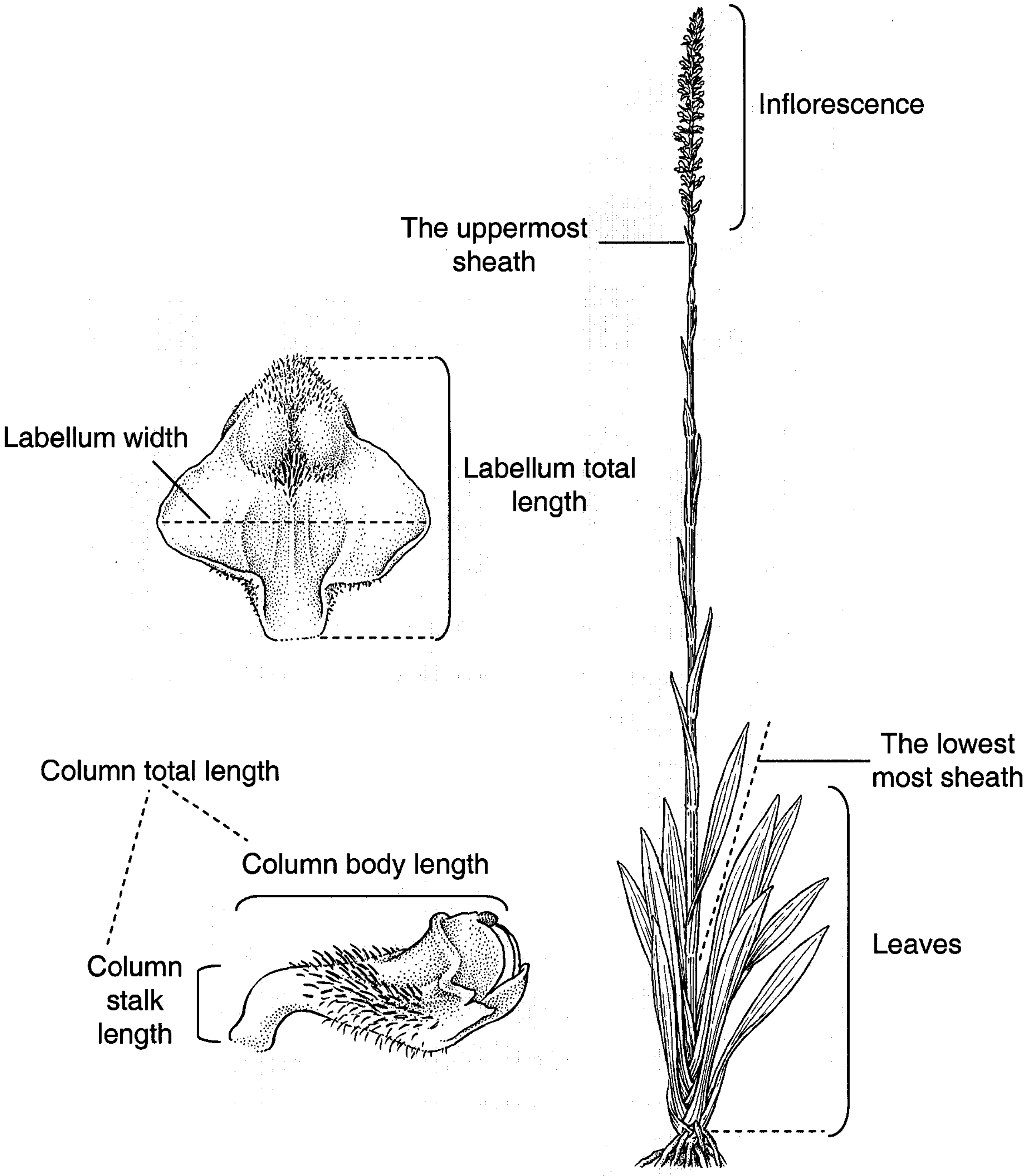


Fig. 3.1. Scheme of the measurements taken in *Gomphichis*.

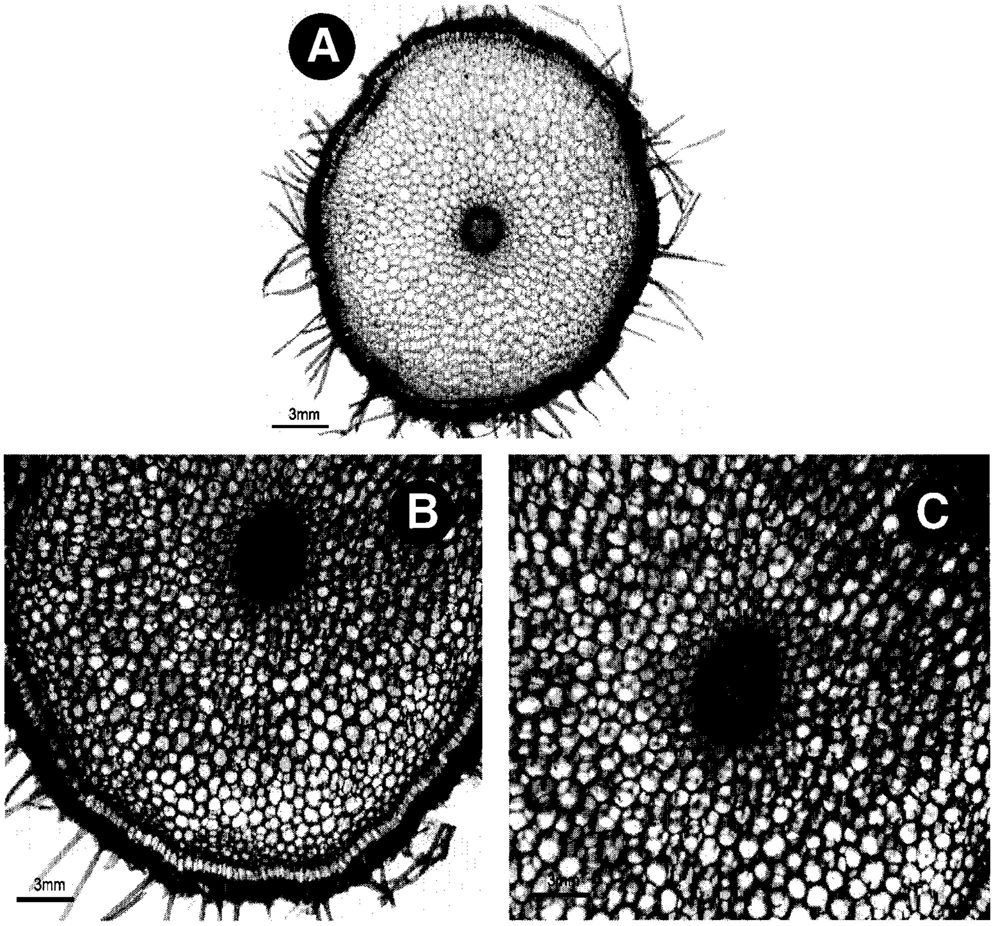


Fig. 3.2. Transverse sections of roots of *Gomphichis adnata*. A, Mature root (stained with safranine). B, Mature root (stained with CVA). C, Mature root, stele (stained with CVA). (All sections from *Alvarez & León 2986*, NY).

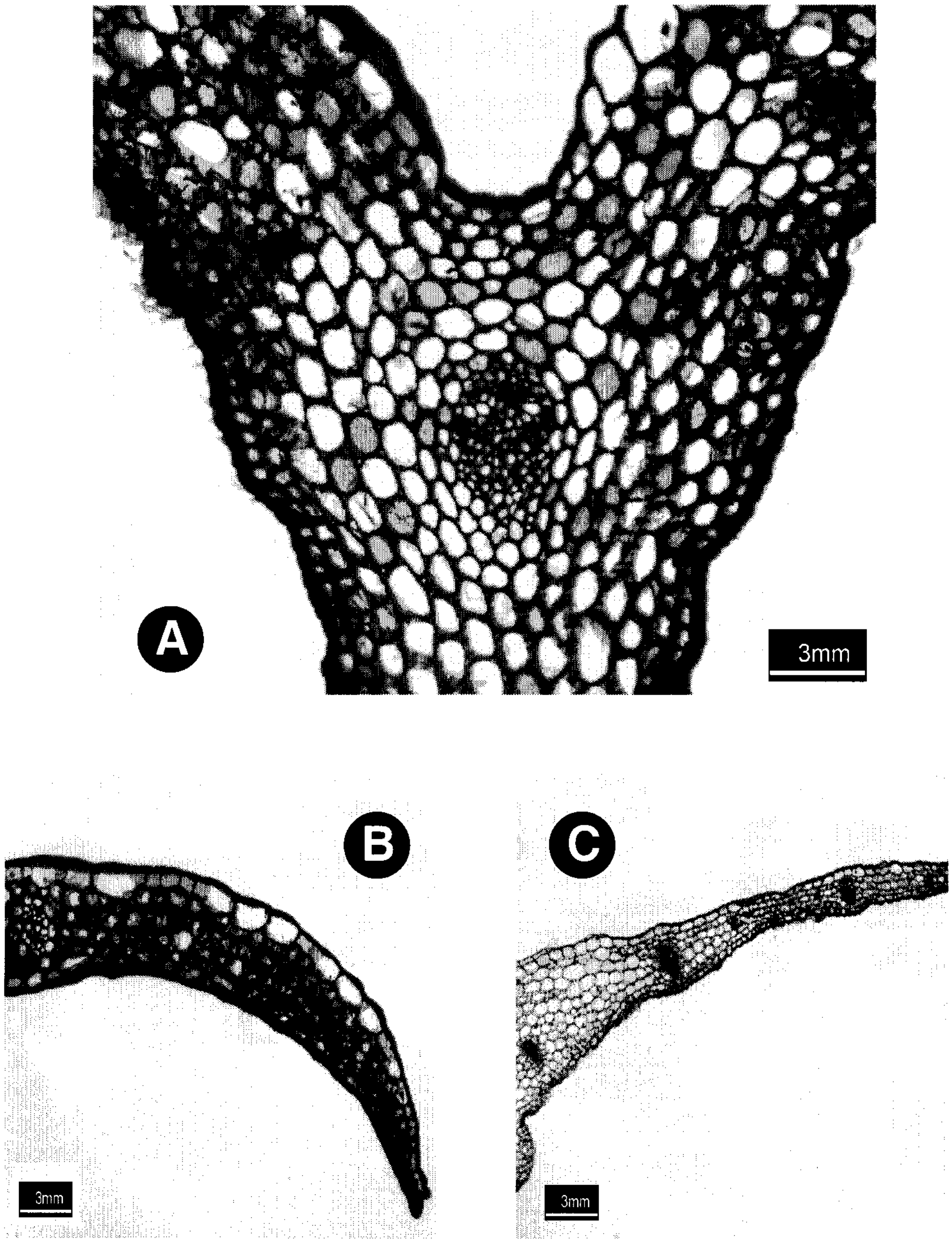


Fig. 3.3. Leaf anatomy of *Gomphichis.* A, Leaf midrib of *G. adnata* (*Alvarez & León 2981*, NY). B, Leaf blade of *G. adnata* stained with CVA (*Alvarez & León 2981*, NY). C, Leaf blade of *G. traceyae* stained with iodine potassium-iodide (*Alvarez & Alvarez 2599*, NY).

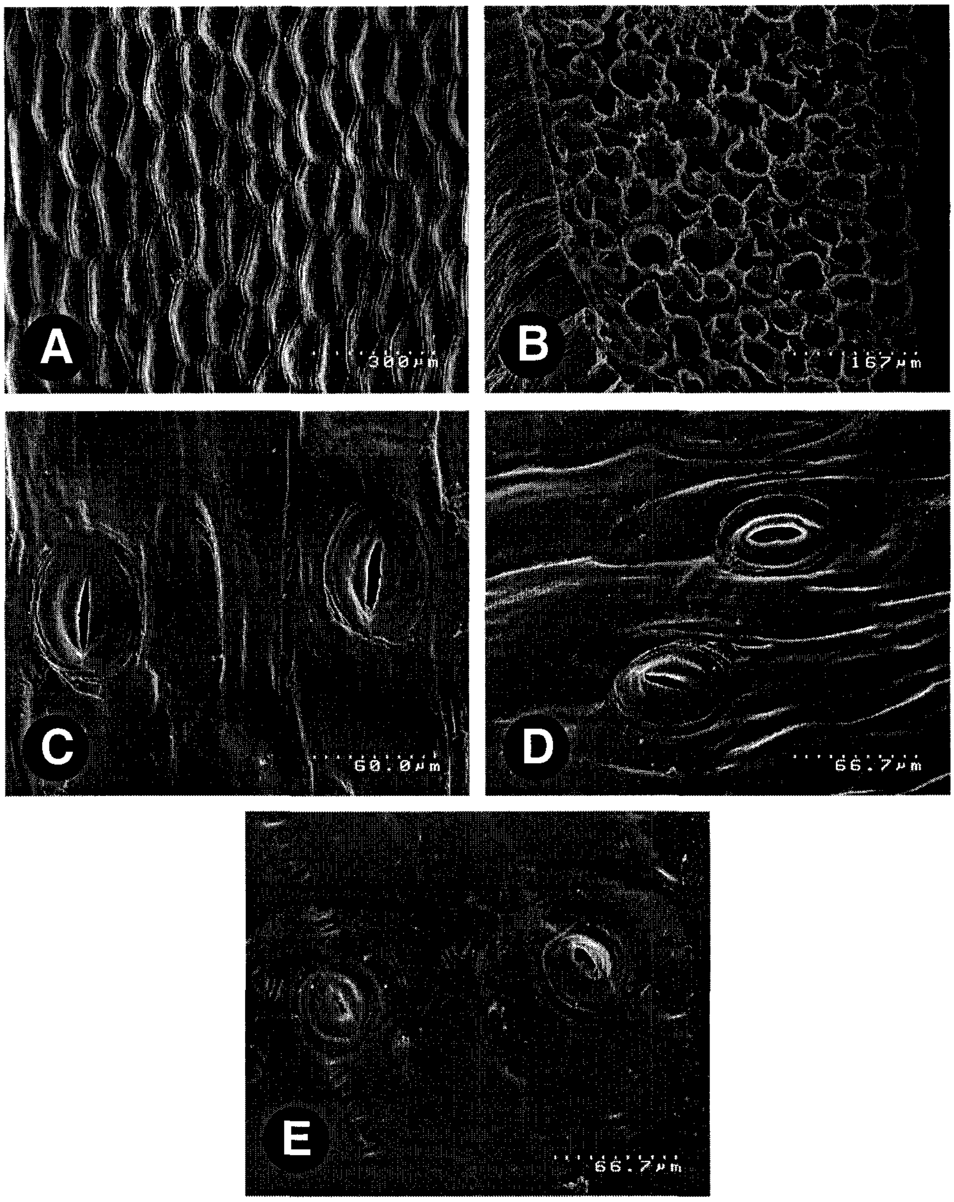


Fig. 3.4. Leaf surface and stomata of *Gomphichis crassilabia*. A, Adaxial surface (*Alvarez & Padilla 2953*, NY). B, Transverse section (*Alvarez & Padilla 3014*, NY). C-D, Abaxial surface, stomata (*Alvarez & Padilla 2935*, NY). E, Abaxial surface, stomata (*Alvarez & Padilla 3014*, NY).

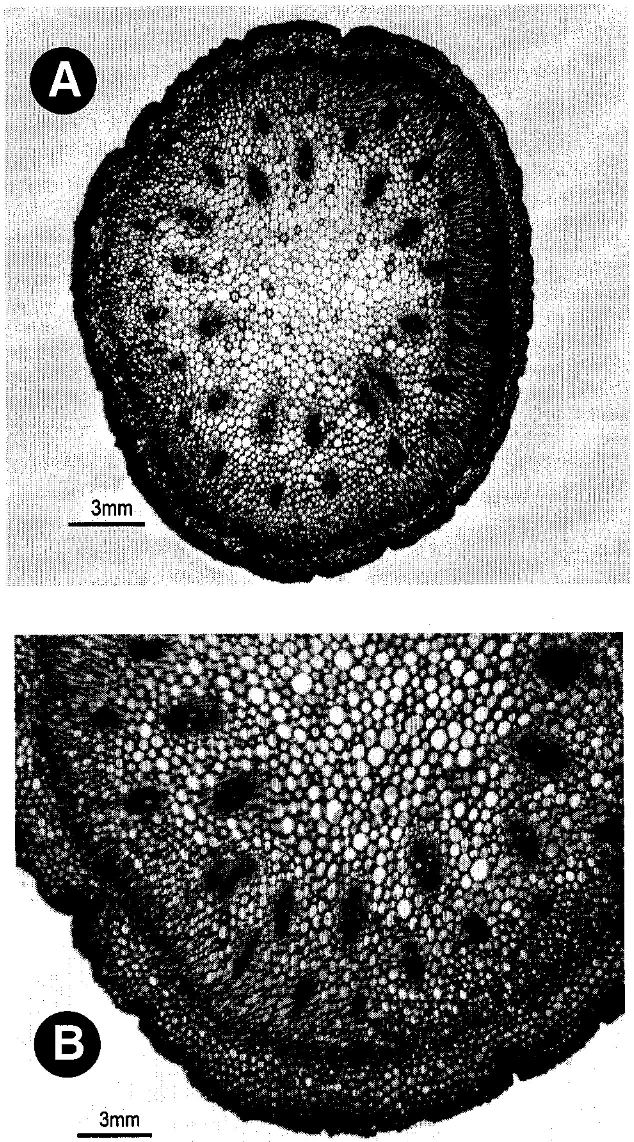


Fig. 3.5. A-B, Transverse sections of a peduncle of *Gomphichis crassilabia* (*Alvarez & Padilla 2935*, NY) .

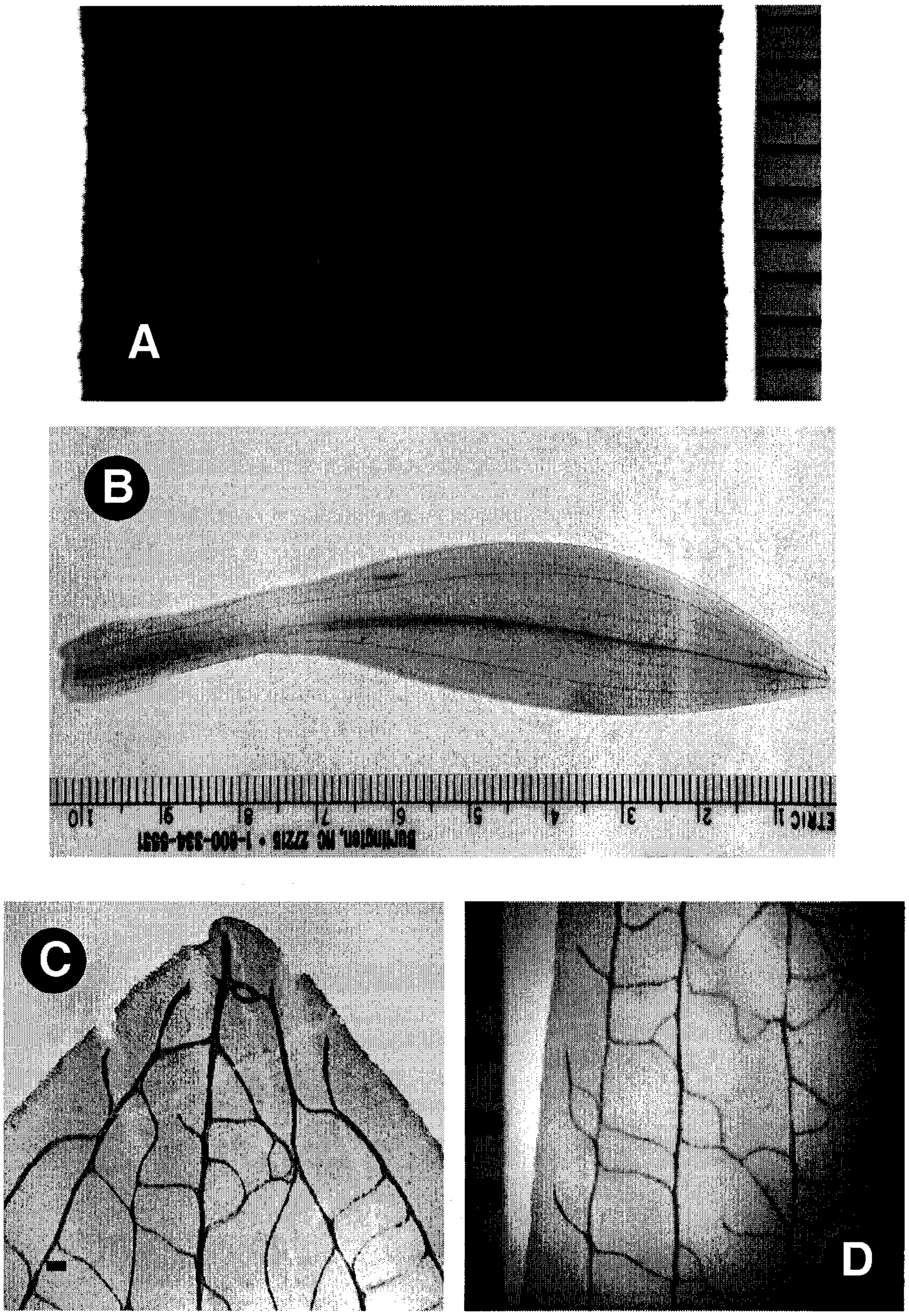


Fig. 3.6. Leaf venation pattern of *Gomphichis*. A, Parallel venation of *G. crassilabia* (*Alvarez & Padilla 2935*, NY). B, Parallel venation of G. caucana (*Alvarez et al. 2734*, NY). C-D, Reticulate venation of *G. adnata* (*Alvarez & León 2981*, NY).

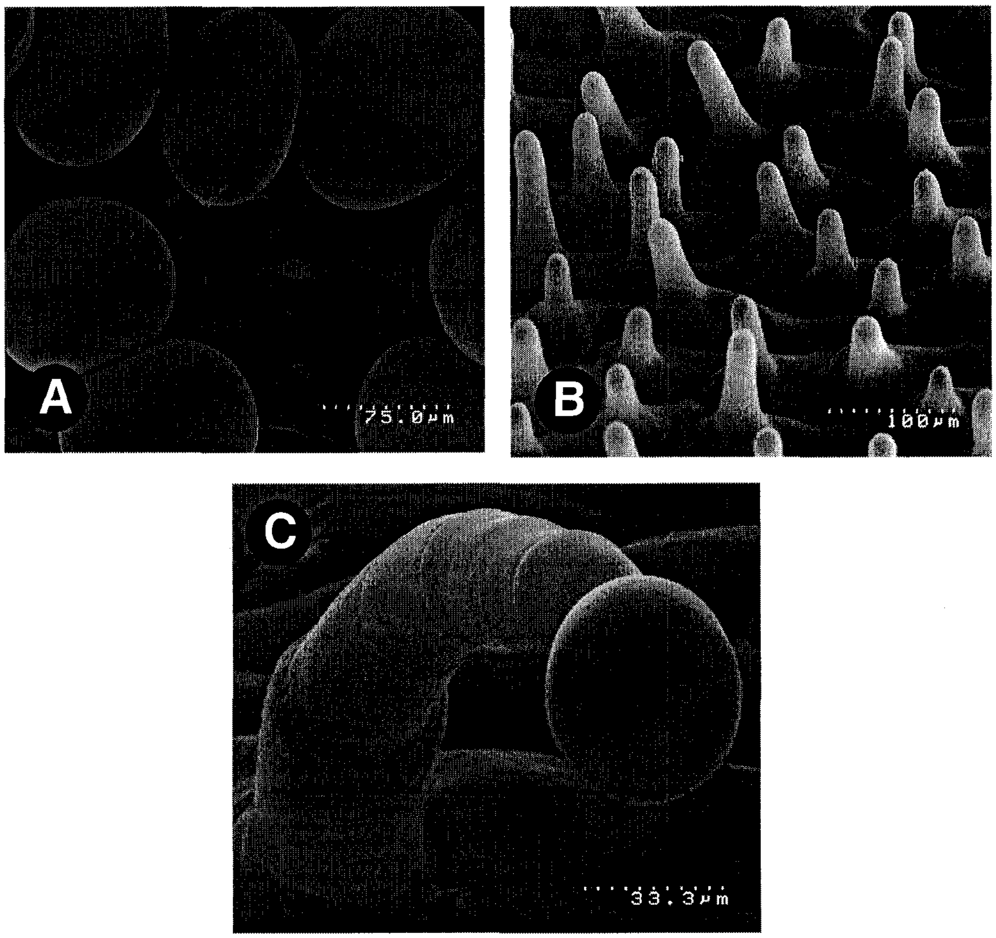


Fig. 3.7. Trichomes of *Gomphichis*. A, Papillae from the abaxial surface of the labellum (*Alvarez & Padilla 2935*, NY). B, Simple unbranched nonglandular trichomes from the adaxial surface of the labellum (*Alvarez & Padilla 2935*, NY). C, Multicellular unbranched glandular trichome from the ovary (*Alvarez & Alvarez 2878*, NY).

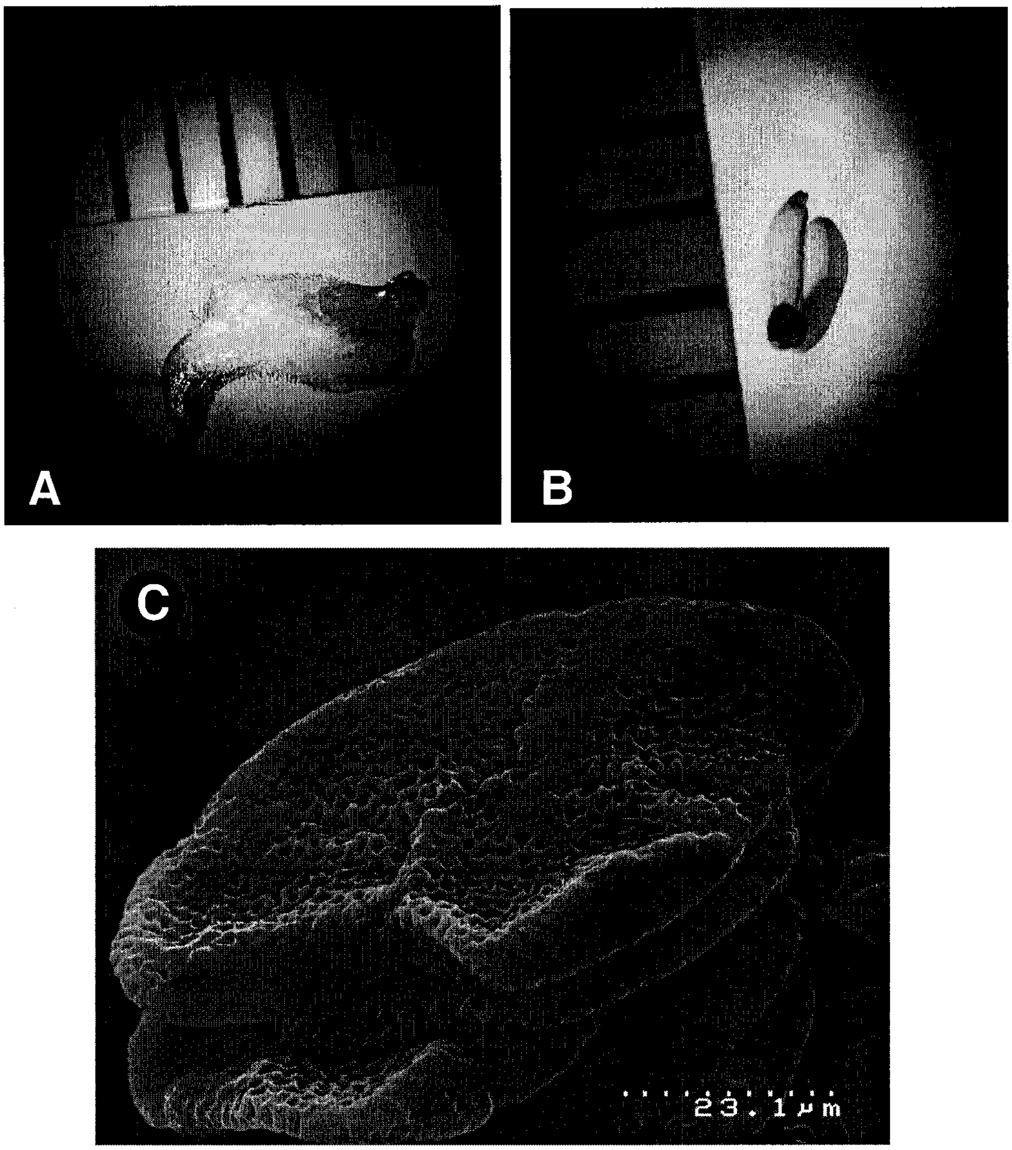


Fig. 3.8. Pollen and pollinaria of *Gomphichis*. A, Column of *G. crassilabia* (*Alvarez & Alvarez 3009*, NY). B, Pollinaria of *G. crassilabia* (*Alvarez & Alvarez 3009*, NY). C, Tetrads of pollen of *G. goodyeroides* (*Løjtnant 15031*, AAU).

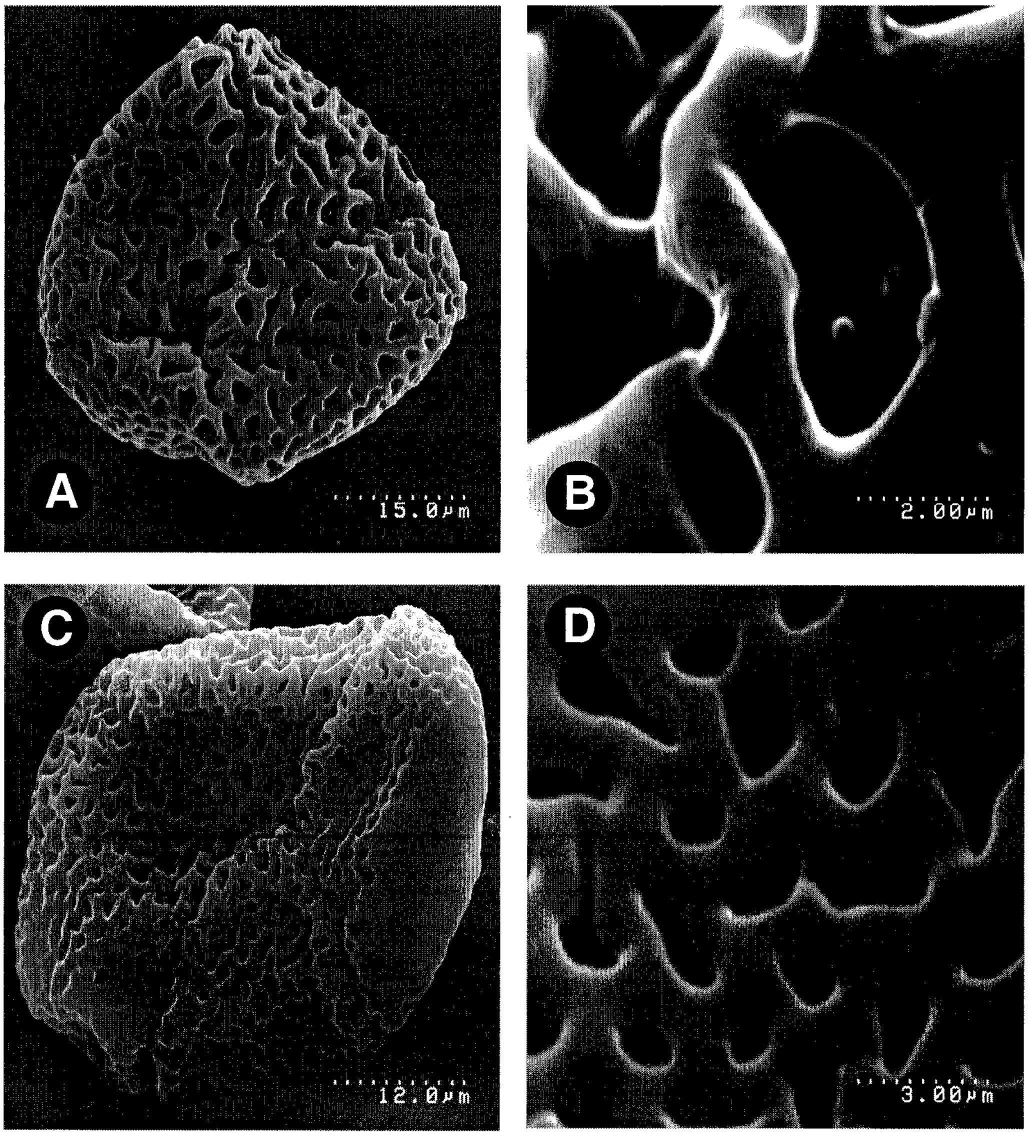


Fig. 3.9. *Gomphichis* pollen. A-B, *G. crassilabia* (*Alvarez & Padilla 2935*, NY). C-D, *G. goodyeroides* (*Løjtnant 15031*, AAU)

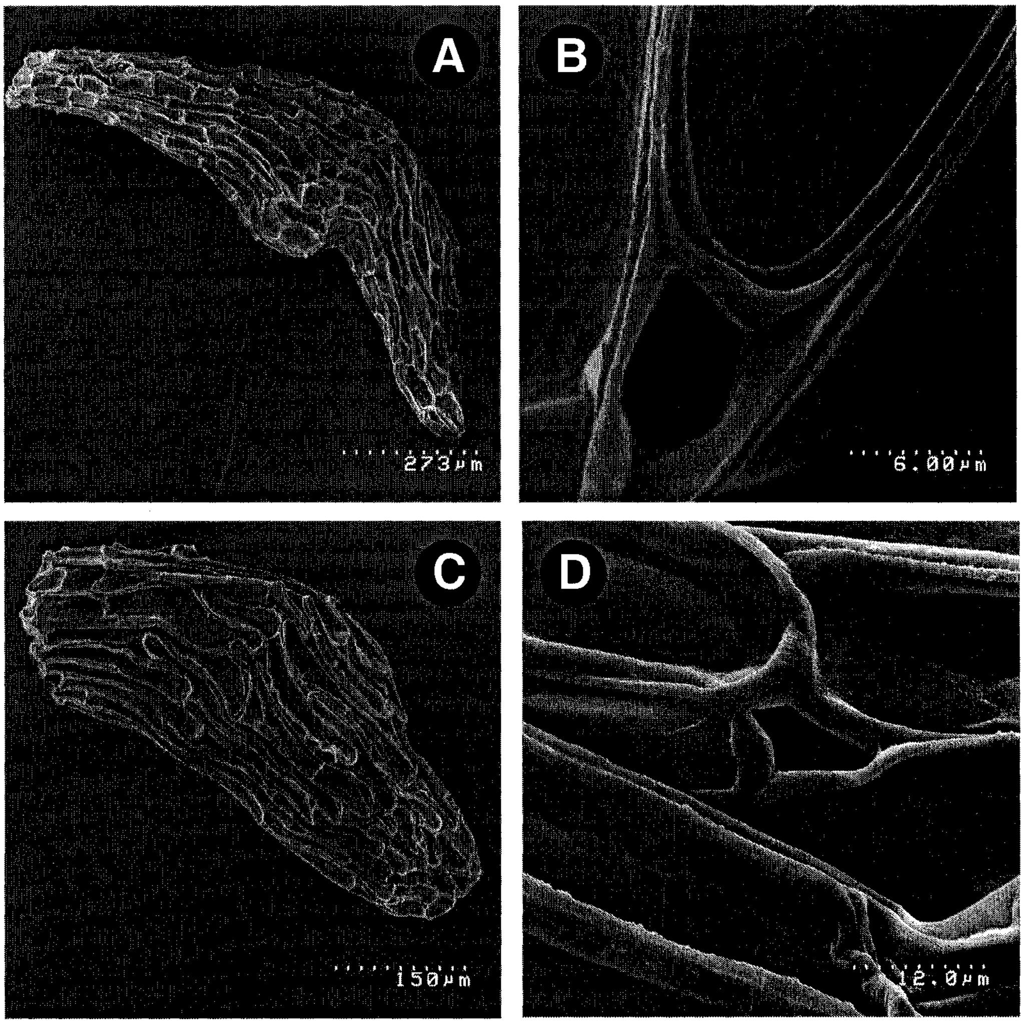
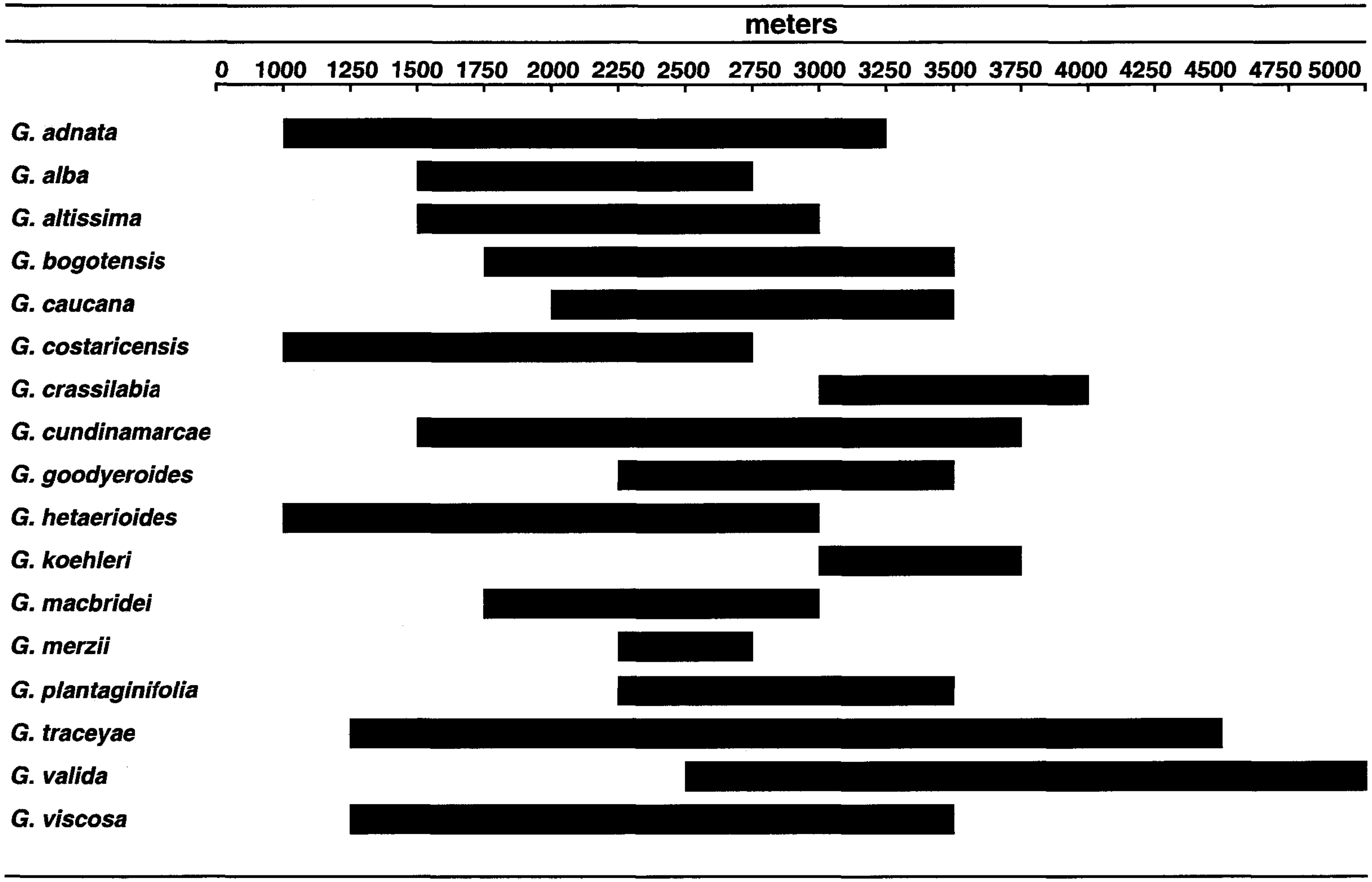


Fig. 3.10. *Gomphichis* seeds. A-B, *G. merzii* (*Alvarez & León 2977*, NY). C-D, *G. bogotensis* (*Alvarez & Yustiz 3000*, NY).

Fig. 3.11. Elevational range of species of *Gomphichis*.



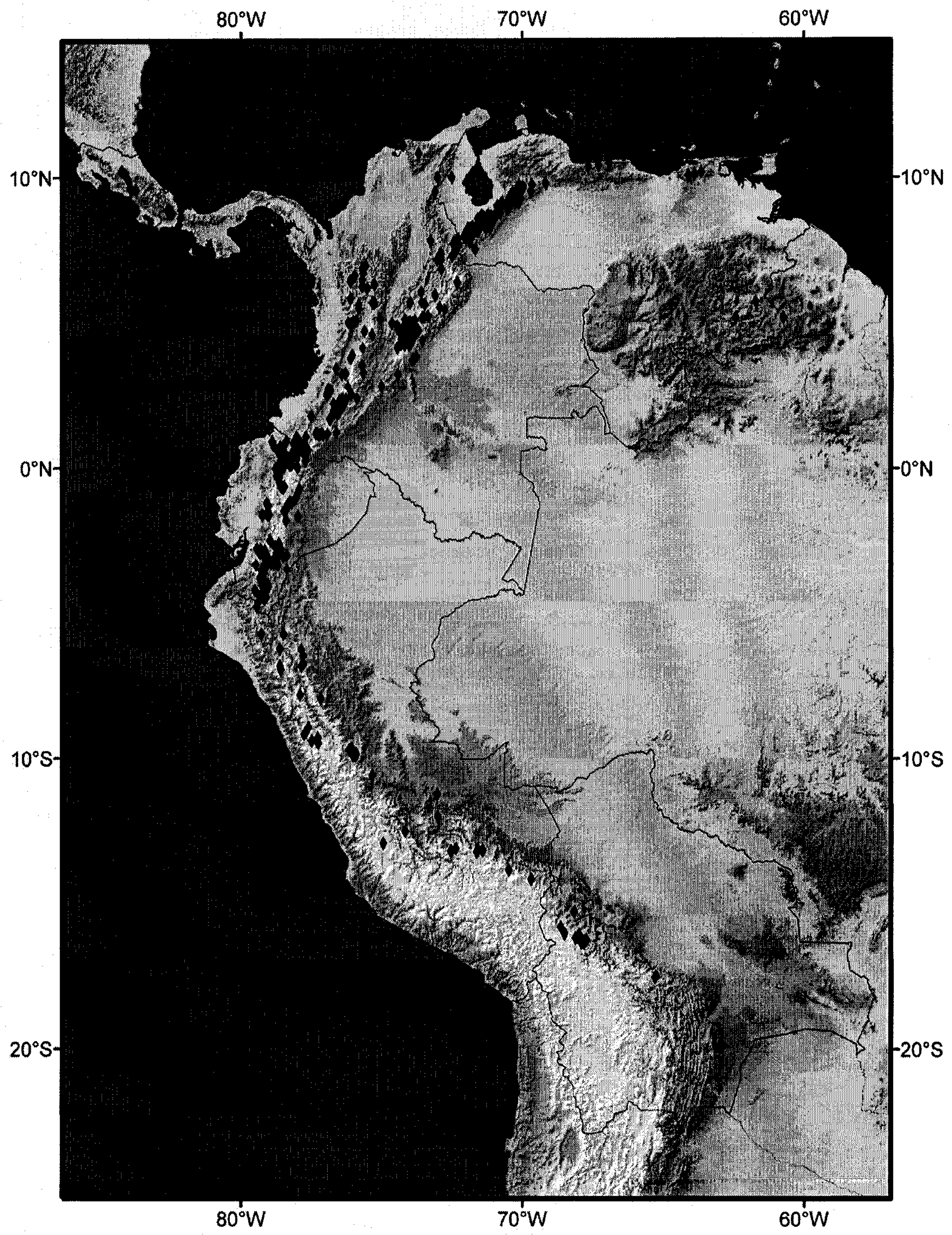


Fig. 3.12. Distribution map of species of *Gomphichis* based on herbarium specimens examined.

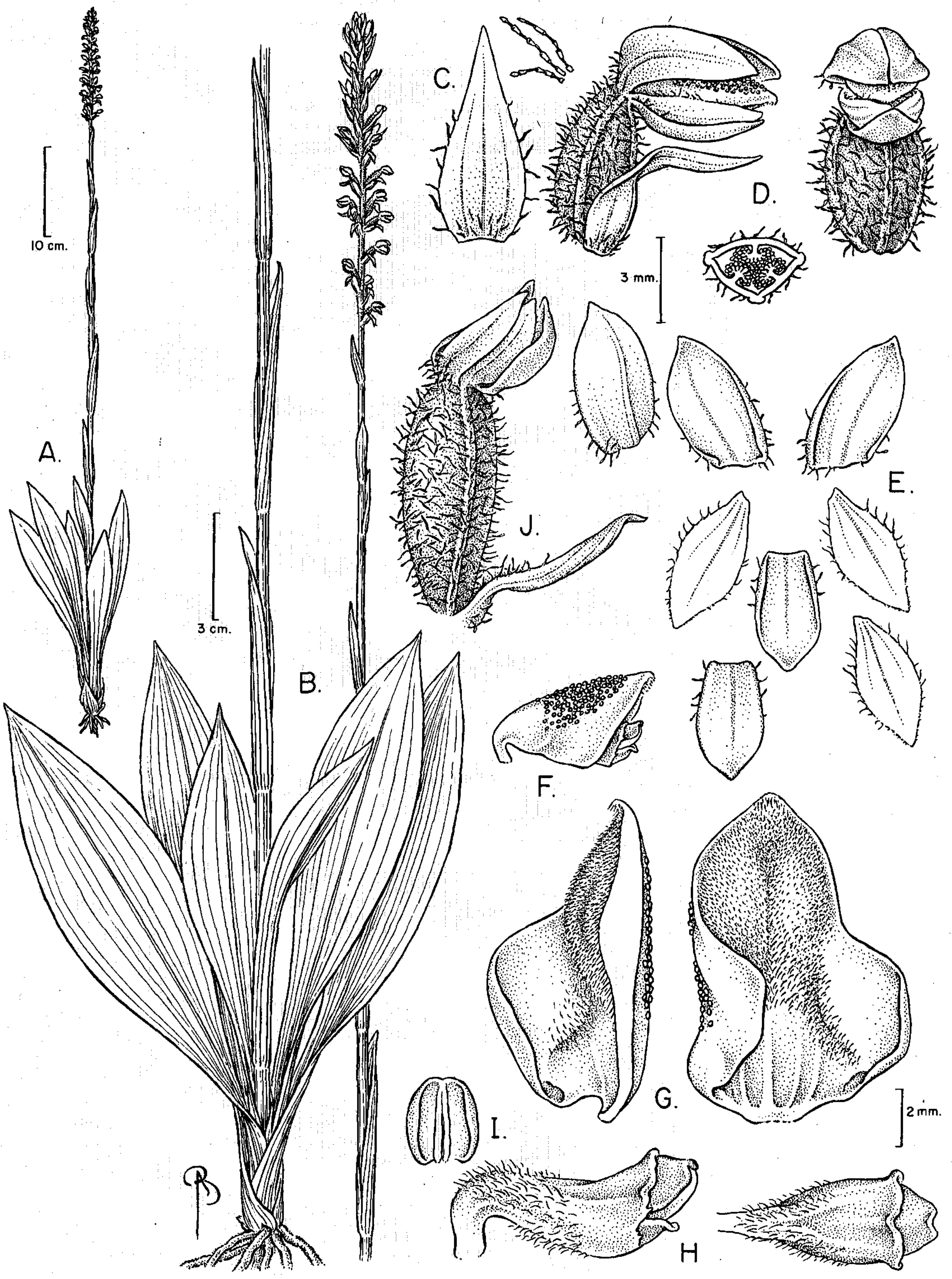


Fig. 3.13.A. *Gomphichis adnata*. A-B, habit. C, floral bract. D, lateral and frontal view of single flowers and ovary transverse section. E, sepals and petals. F, labellum abaxial surface and column. G, labellum section and adaxial surface. H, column and detail of the adaxial surface. I, anther. J, fruit. Based on *Alvarez 2986*, NY(A, C-I); *Alvarez 2981*, NY (B, J).

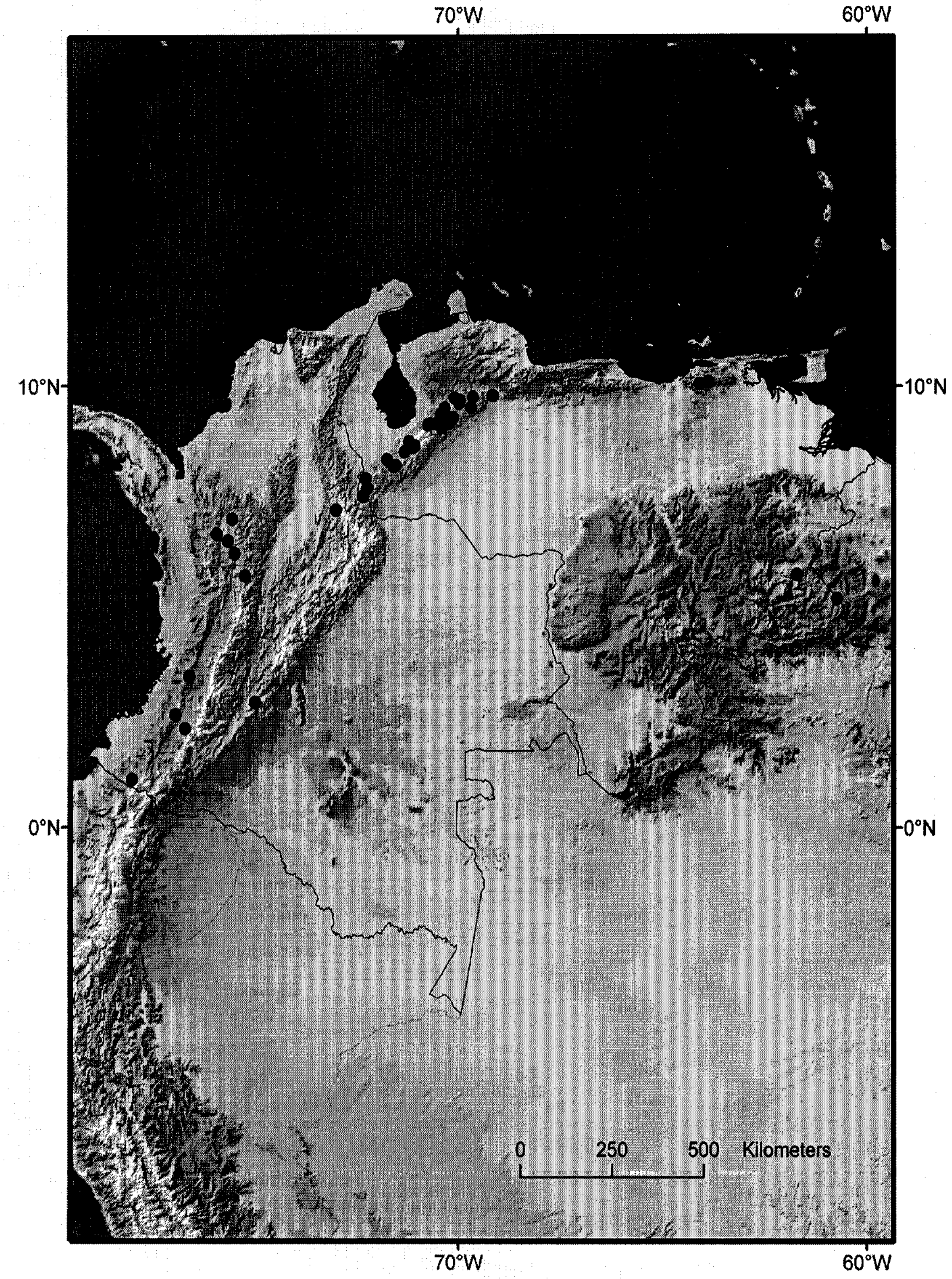


Fig. 3.13.B. Distribution of *Gomphichis adnata*.

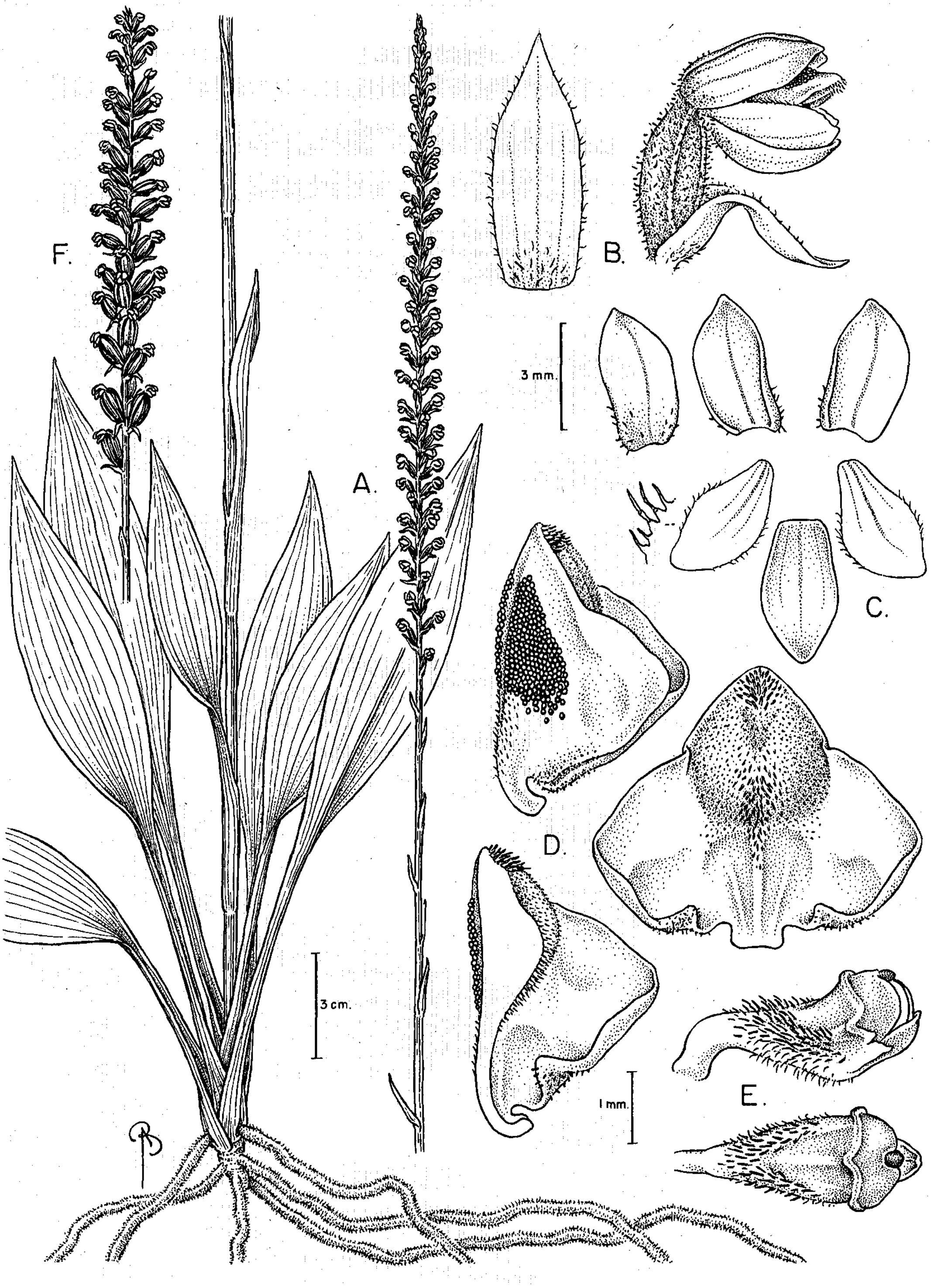


Fig. 3.14.A. *Gomphichis alba.* A, habit. B, floral bract and single flower. C, sepals and petals. D, labellum abaxial and adaxial surfaces and section. E, column and detail of the adaxial surface. F, infrutescence. Based on *Renz 5287*, RENZ (A-E); *Fendler 1402*, G (F).

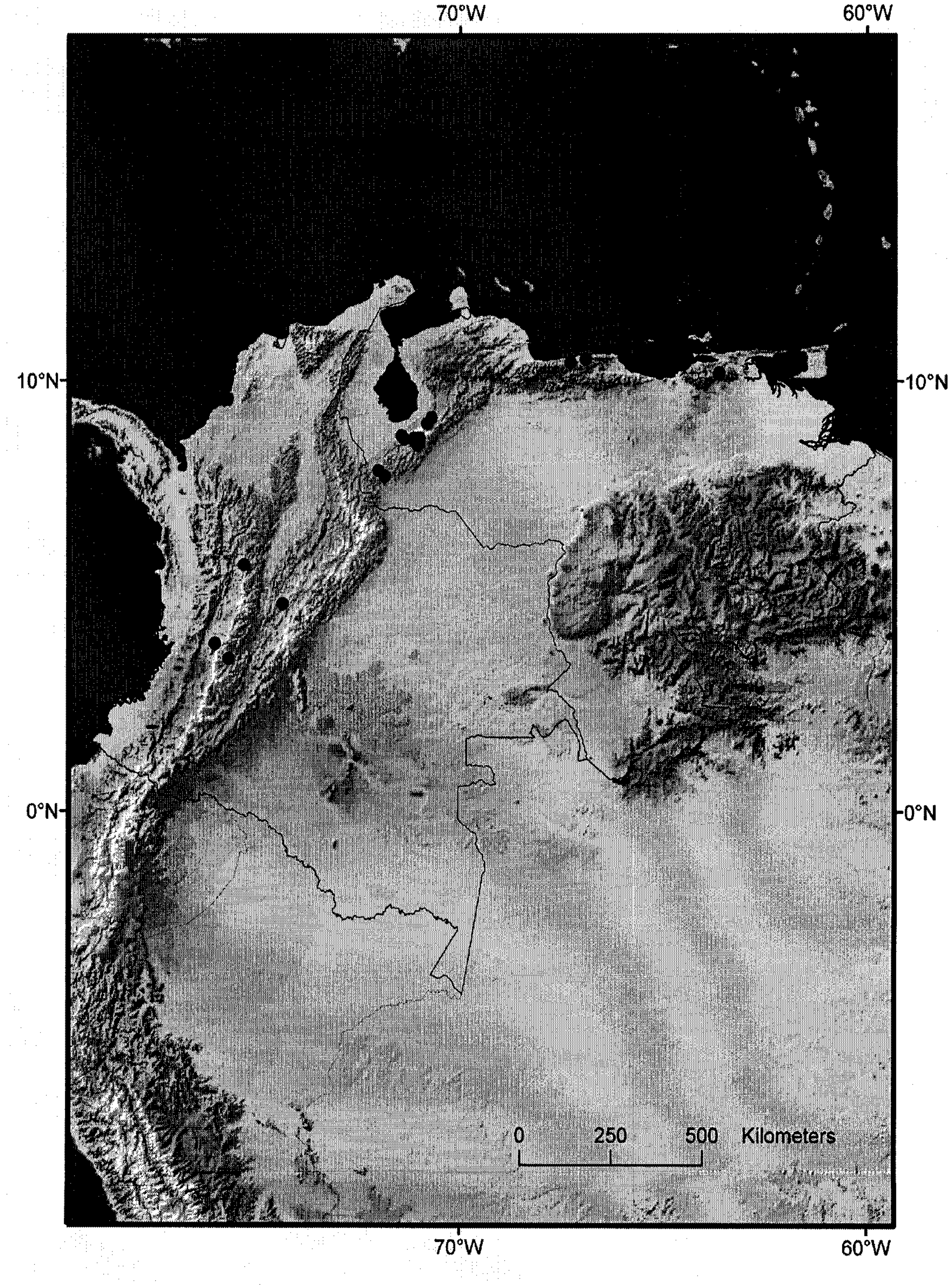


Fig. 3.14.B. Distribution of *Gomphichis alba.*

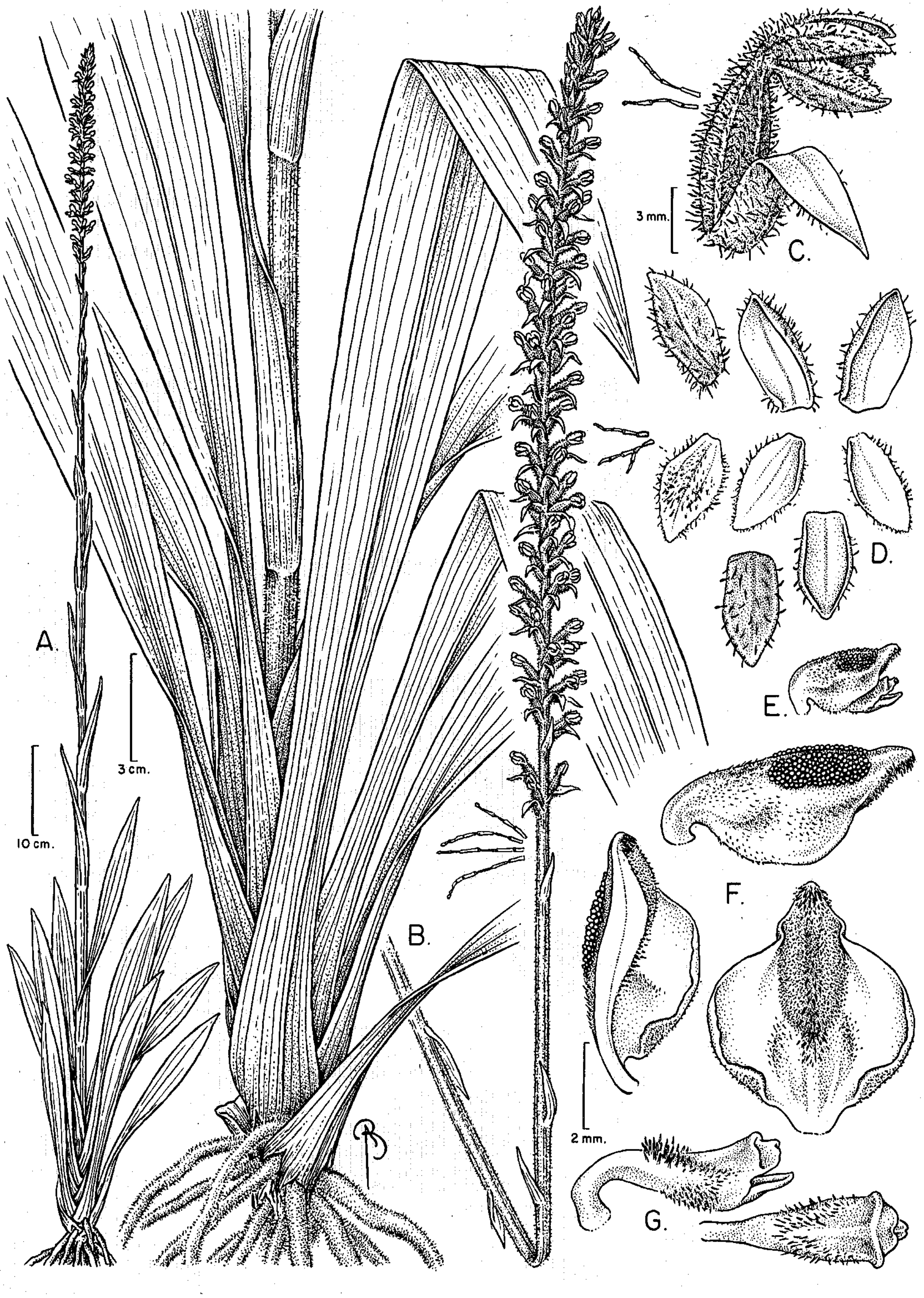


Fig. 3.15.A. *Gomphichis altissima*. A, habit. B, detail of the roots, leaves, basal and apical portions of the peduncle, and inflorescence. C, single flower. D, sepals and petals. E, labellum abaxial surface and column. F, detail of the labellum abaxial and adaxial surfaces and section. G, column and detail of the adaxial surface. Based on *Fosberg 21384*, US (A); *Wurdack 1734*, US (B-G).

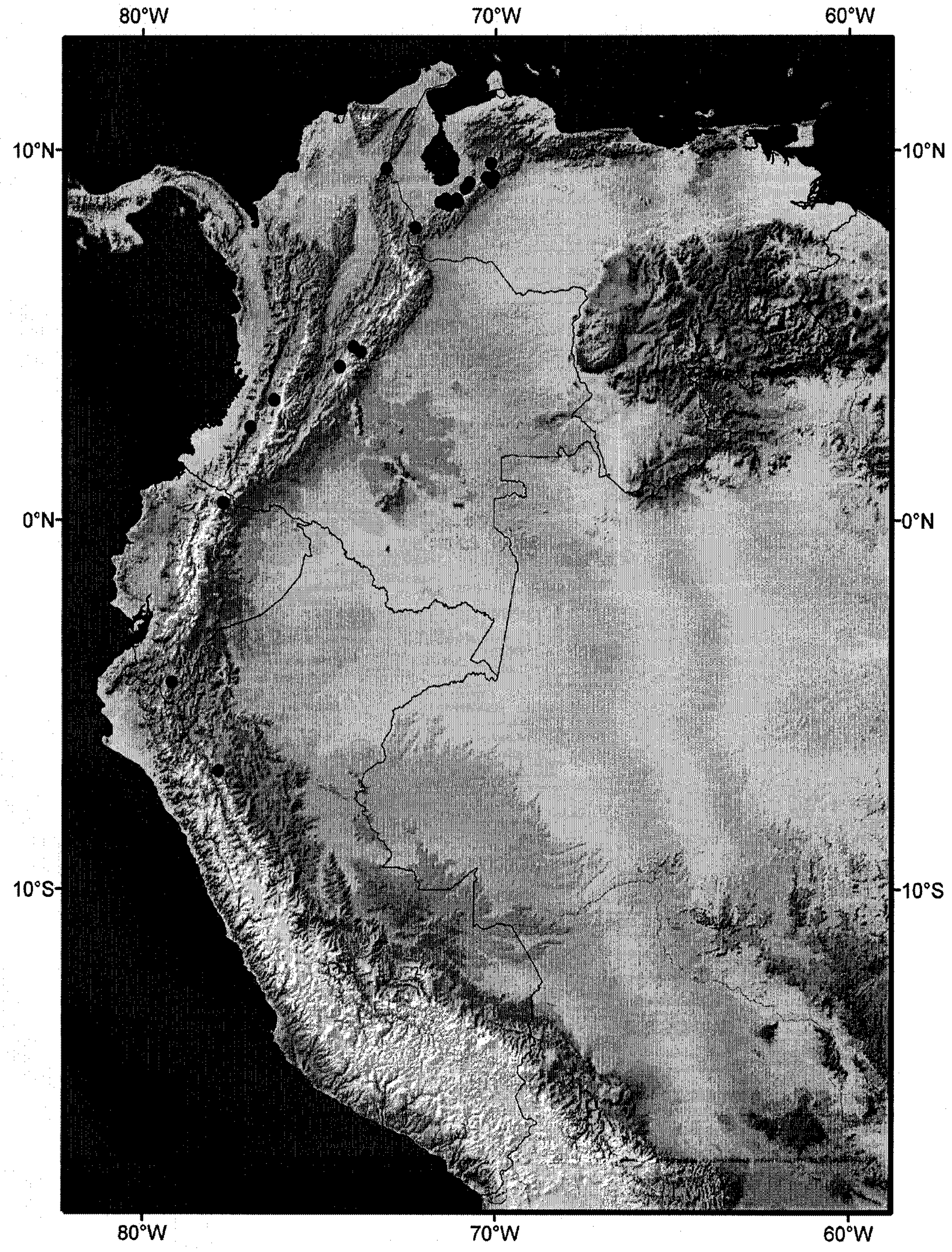


Fig. 3.15.B. Distribution of *Gomphichis altissima*.

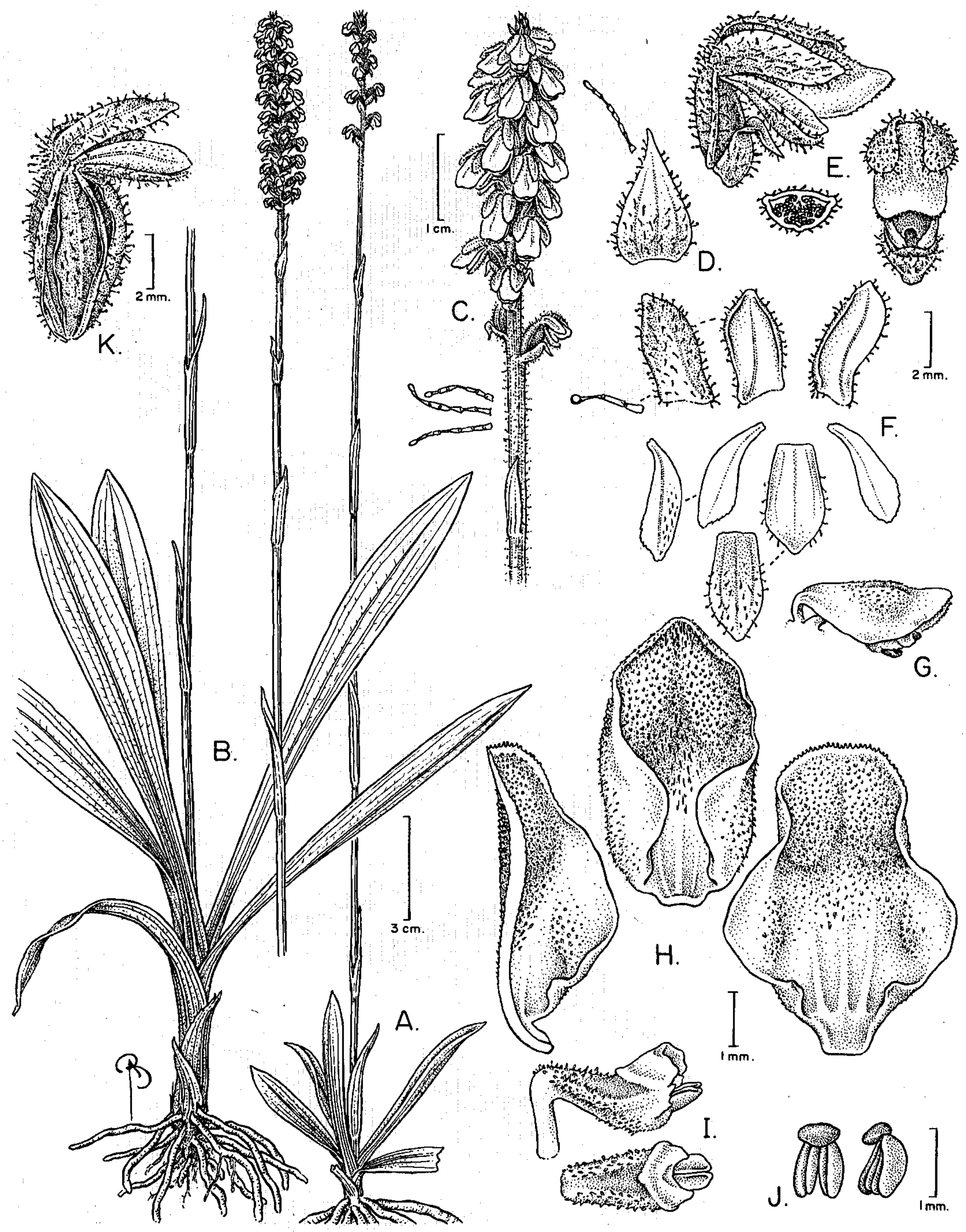


Fig. 3.16.A. *Gomphichis bogotensis.* A, habit. B, detail of roots, leaves, basal and apical portions of the peduncle, and inflorescence. C, detail of the inflorescence. D, floral bract. E, lateral and frontal view of a single flower and ovary transverse section. F, sepals and petals. G, labellum and column. H, labellum adaxial surface and section. I, column and detail of the adaxial surface. J, pollinaria. K, fruit. Based on *Renz 4144*, RENZ (A); *Alvarez 2966*, NY (B); *Alvarez 2965*, NY (C-J); *Alvarez 3000*, NY (K).

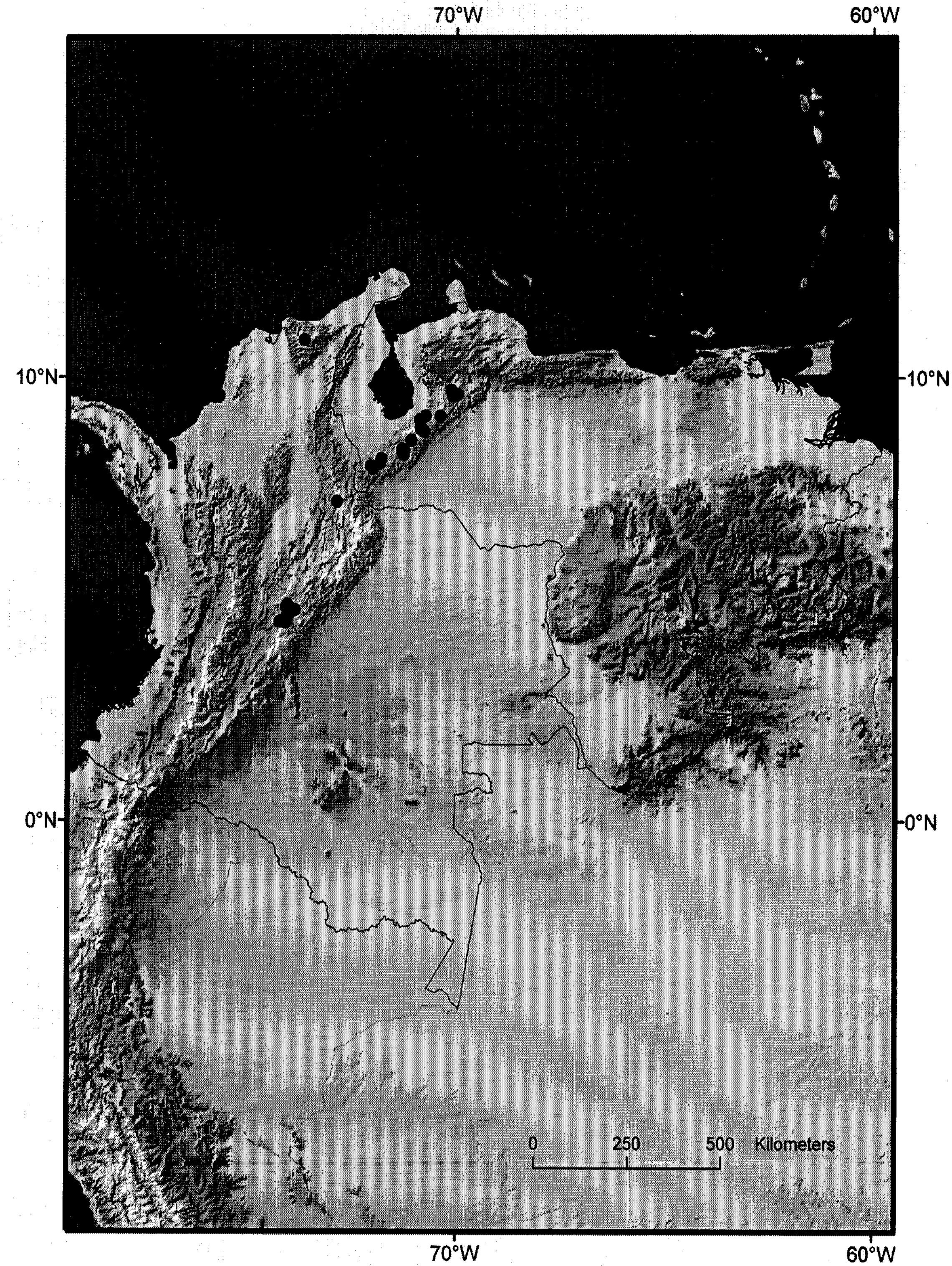


Fig. 3.16.B. Distribution of *Gomphichis bogotensis.*

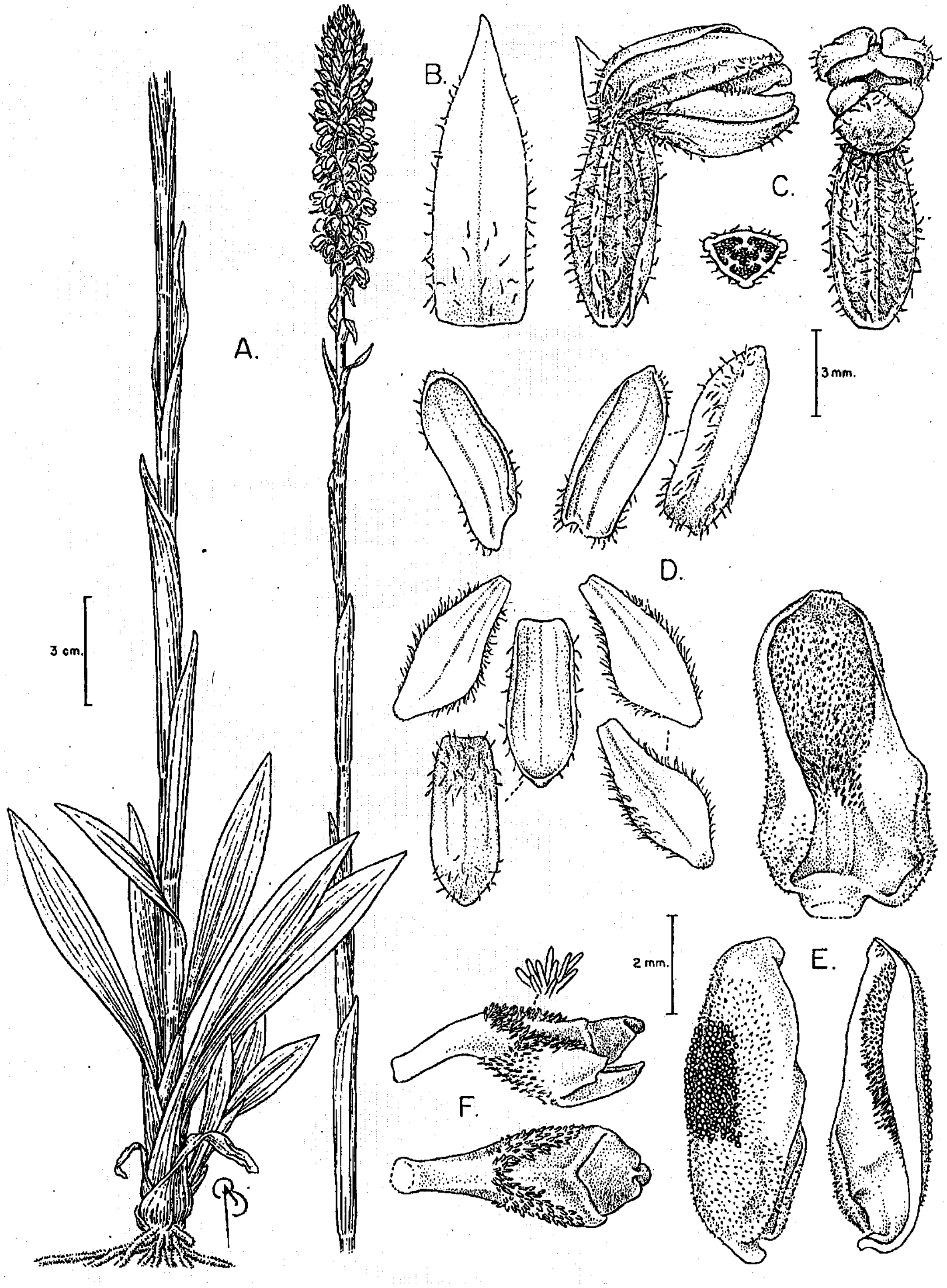


Fig. 3.17.A. *Gomphichis caucana*. A, habit. B. floral bract. C, lateral and frontal view of flowers and ovary transverse section. D, sepals and petals. E, labellum adaxial and abaxial surfaces and section. F, column adaxial and abaxial surfaces. Based on *Correll E-420*, AMES (A); *Alvarez 2775*, NY (B-F).

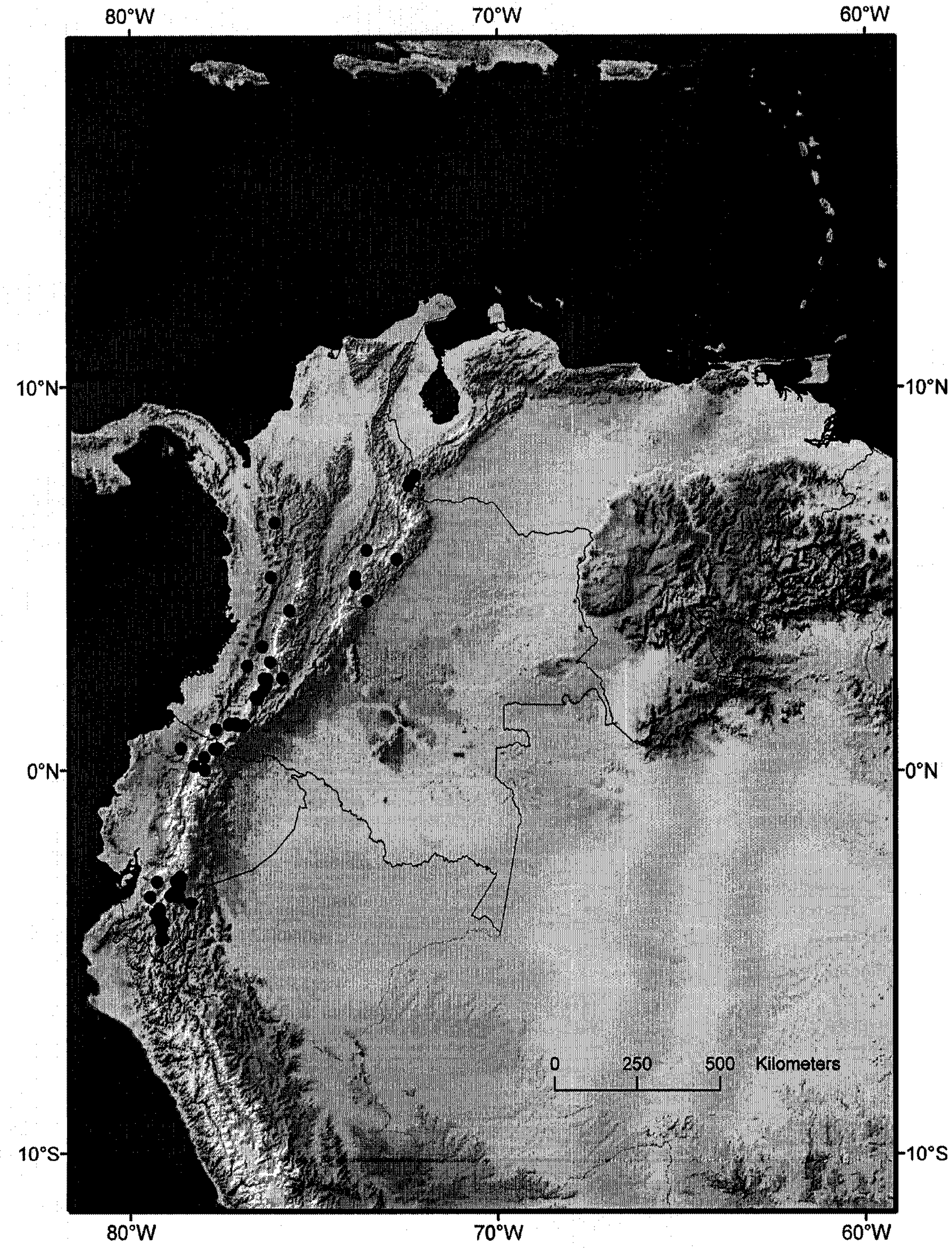


Fig. 3.17. Distribution of *Gomphichis caucana*.

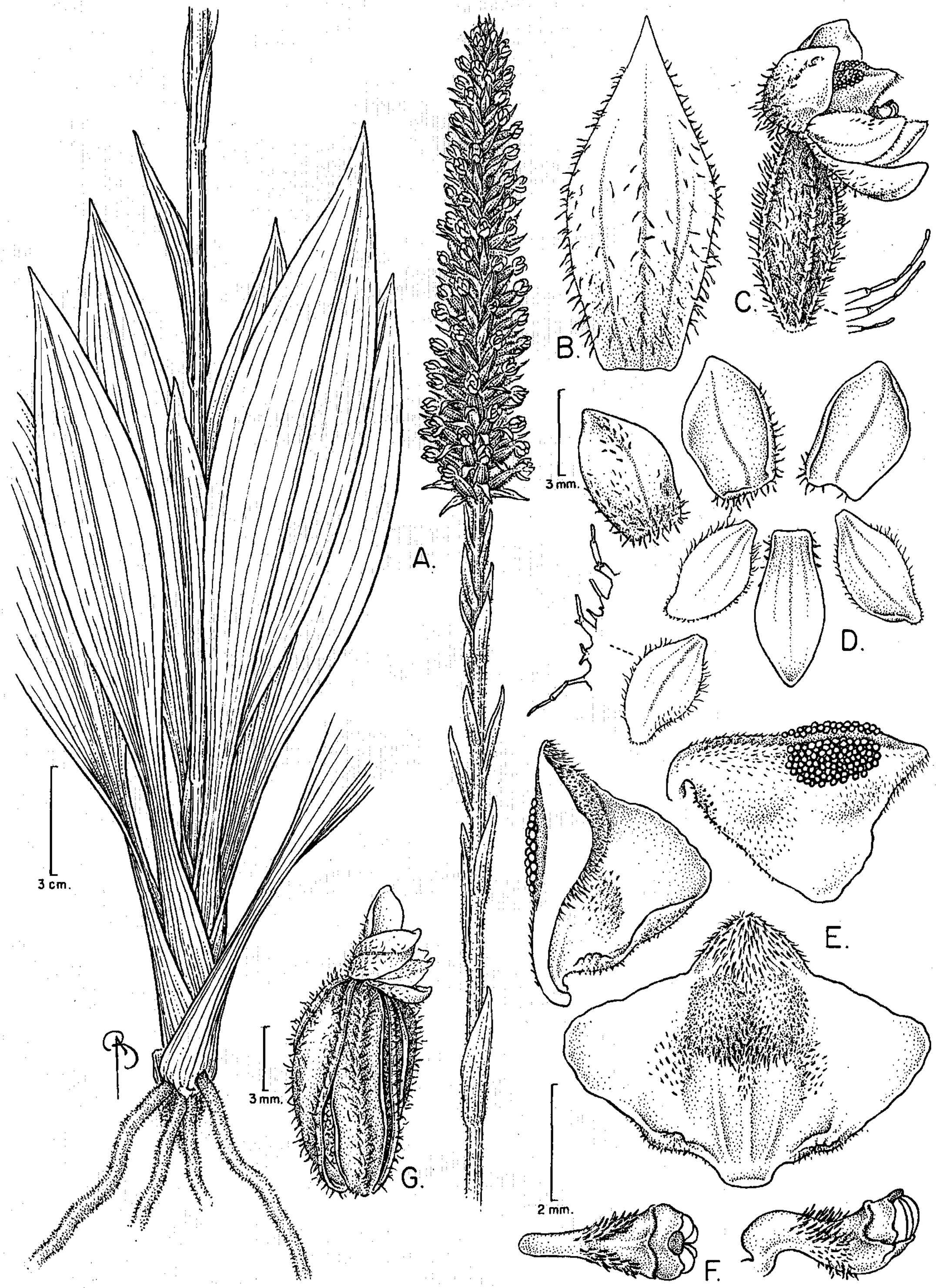


Fig. 3.18.A. *Gomphichis costaricensis.* A, habit. B, floral bract. C, lateral view of a single flower. D, sepals and petals. E, labellum abaxial and adaxial surfaces and section. F, column and detail of the adaxial surface. G, fruit. Based on *Standley 42728*, AMES (A-F), *Croat 13703*, MO (G).

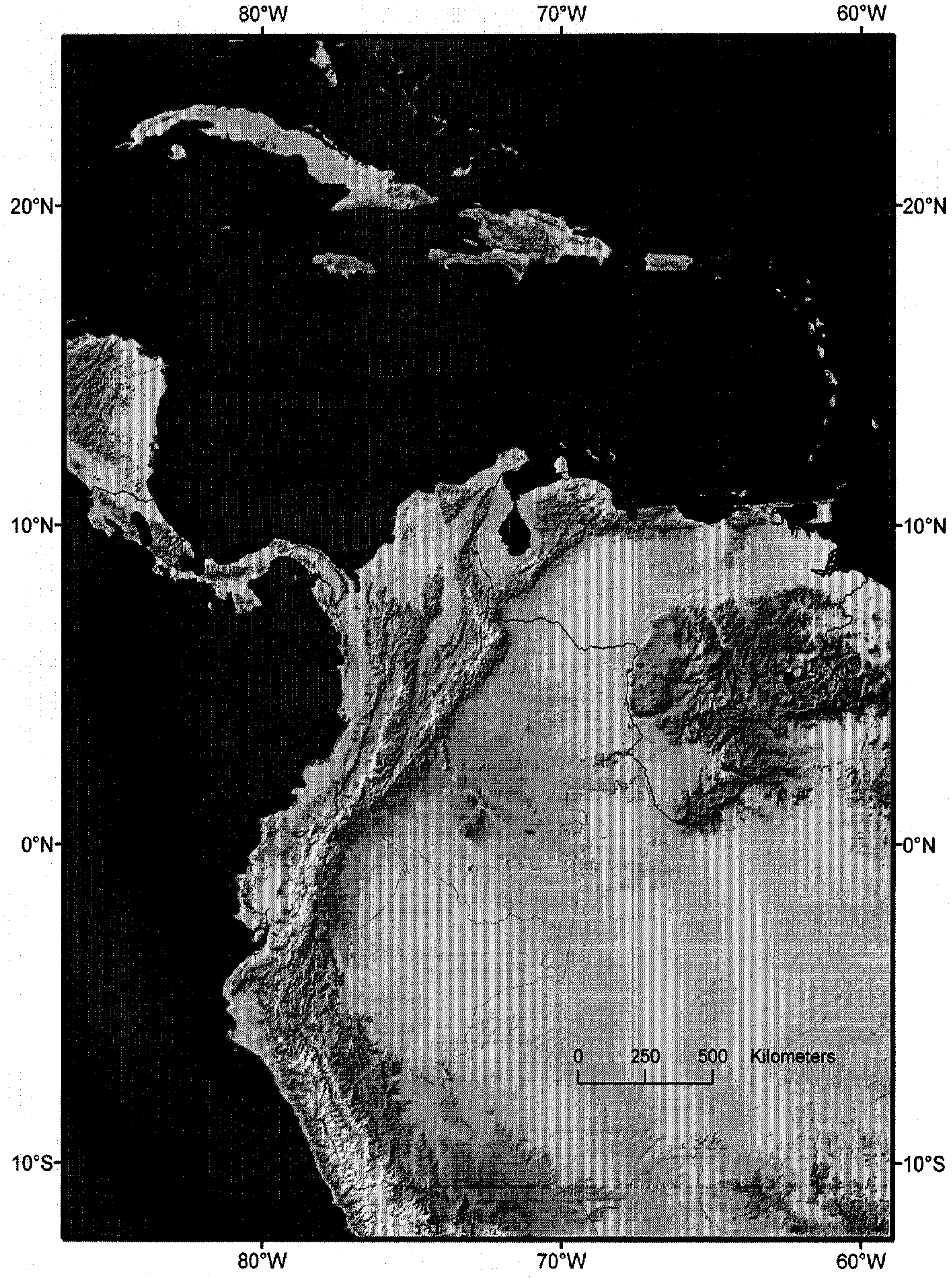


Fig. 3.18.B. Distribution of *Gomphichis costaricensis*.

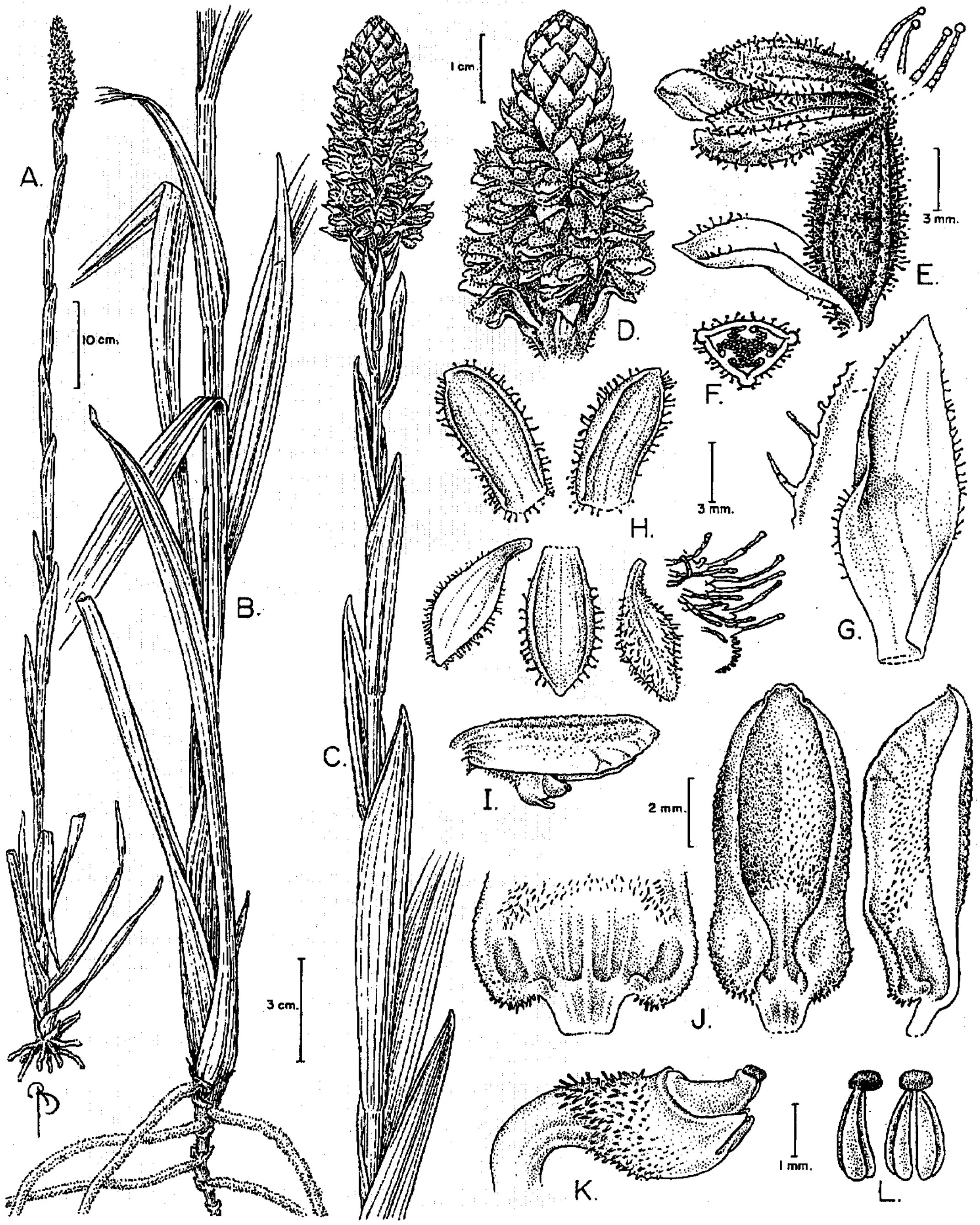


Fig. 3.19.A. *Gomphichis crassilabia.* A, habit. B, detail of the roots, leaves and the lower portion of the peduncle. C, detail of the peduncle upper portion. D, inflorescence. E, lateral view of a single flower. F, ovary transverse section. G, floral bract. H, sepals and petals. I, labellum abaxial surface and column. J, detail of the labellum adaxial surface and section. K, column. L, pollinaria. Based on *Alvarez & Narváez 2861*, NY (A); *Alvarez & Caranqui 2890*, NY (B); *Alvarez & Alvarez 2565*, NY (C-L).

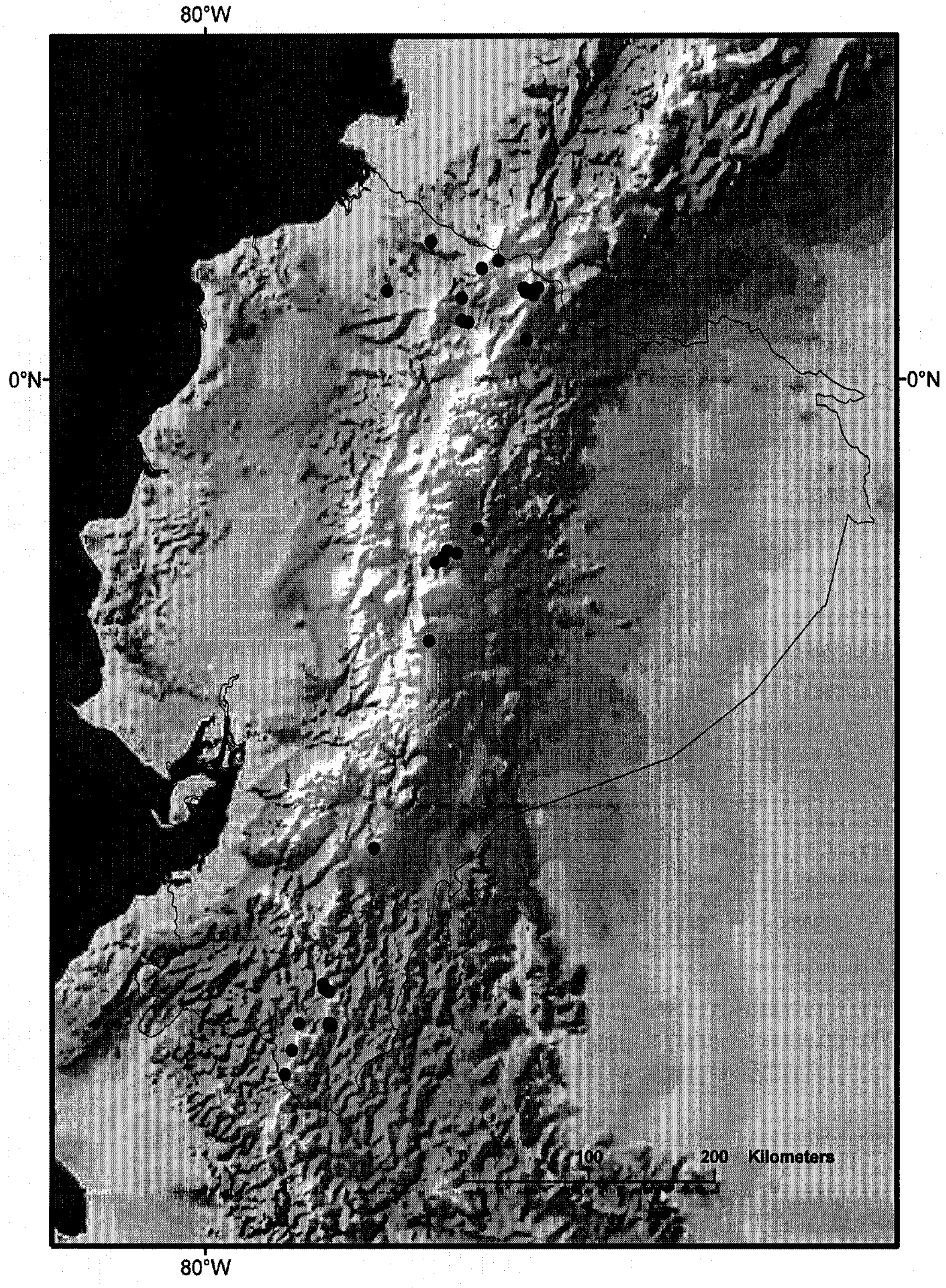


Fig. 3.19.B. Distribution of *Gomphichis crassilabia*.

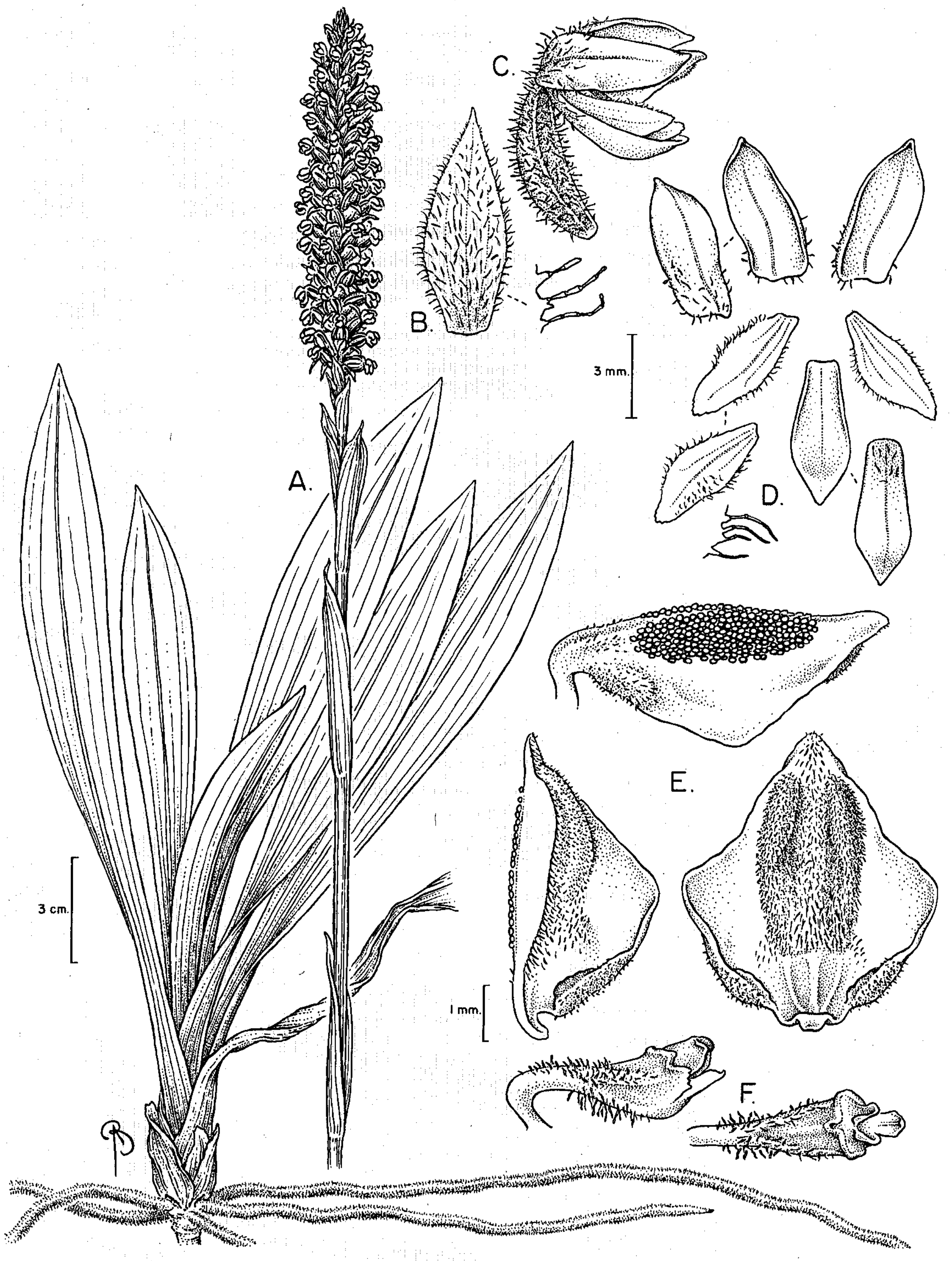


Fig. 3.20.A. *Gomphichis cundinamarcae*. A, habit. B, floral bract. C, lateral view of a single flower. D, sepals and petals. E, detail of the labellum abaxial and adaxial surfaces and section. F, column and detail of the adaxial surface. Based on *Renz 8325*, RENZ (A-F).

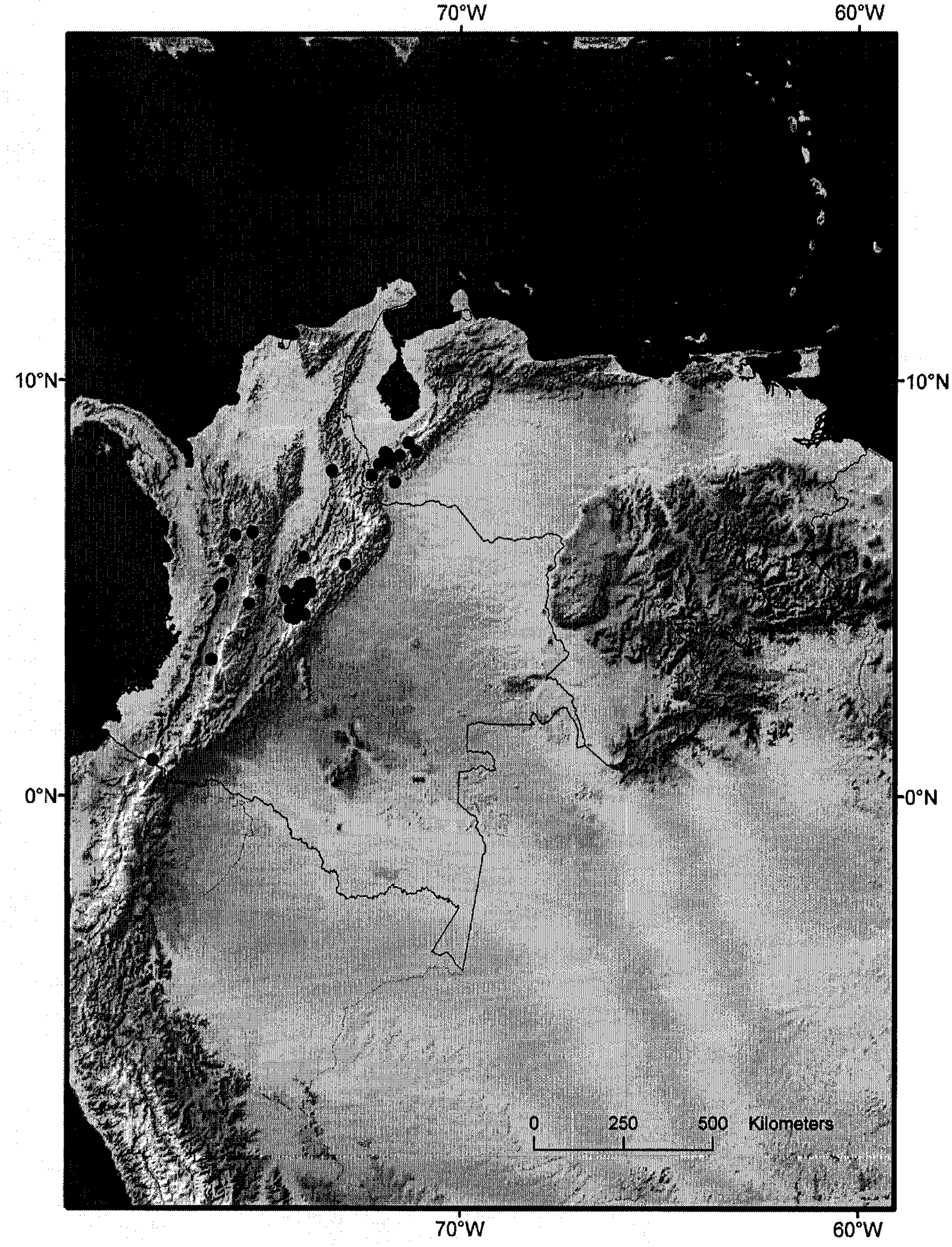


Fig. 3.20.B. Distribution of *Gomphichis cundinamarcae*.

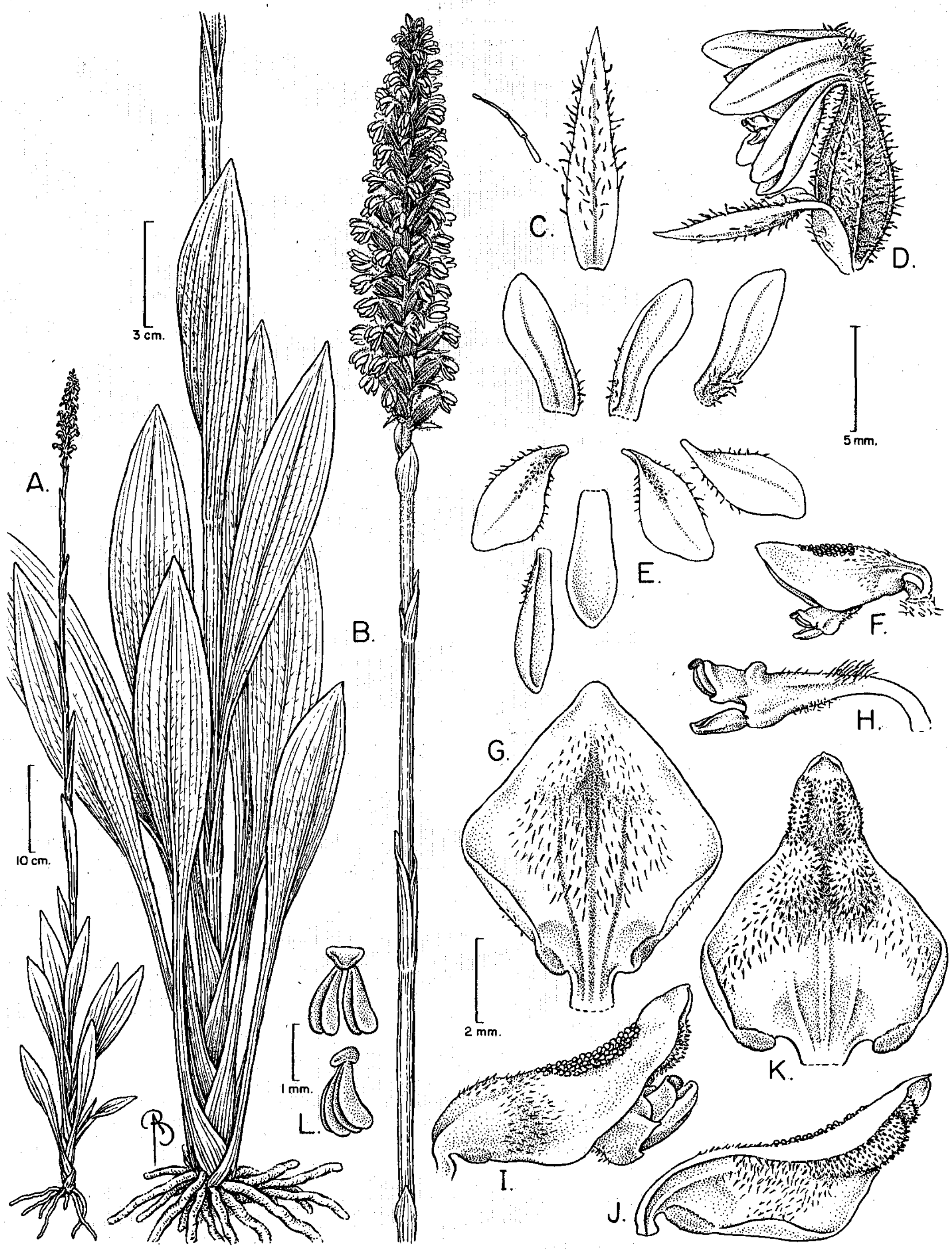


Fig. 3.21.A. *Gomphichis goodyeroides*. A, habit. B, roots, leaves, lower portion of the peduncle, and upper portion of the peduncle. C, floral bract. D, lateral view of a flower. E, sepals and petals. F, I, labellum abaxial surface and column. G, K, detail of the labellum adaxial surface. H. column. J, section of the labellum. Based on *Luer 5306*, SEL (A); *Campos 5230*, SEL (B); *Hutchison 5594*, UC (C-H, L); *Henning 256*, M (I-K).

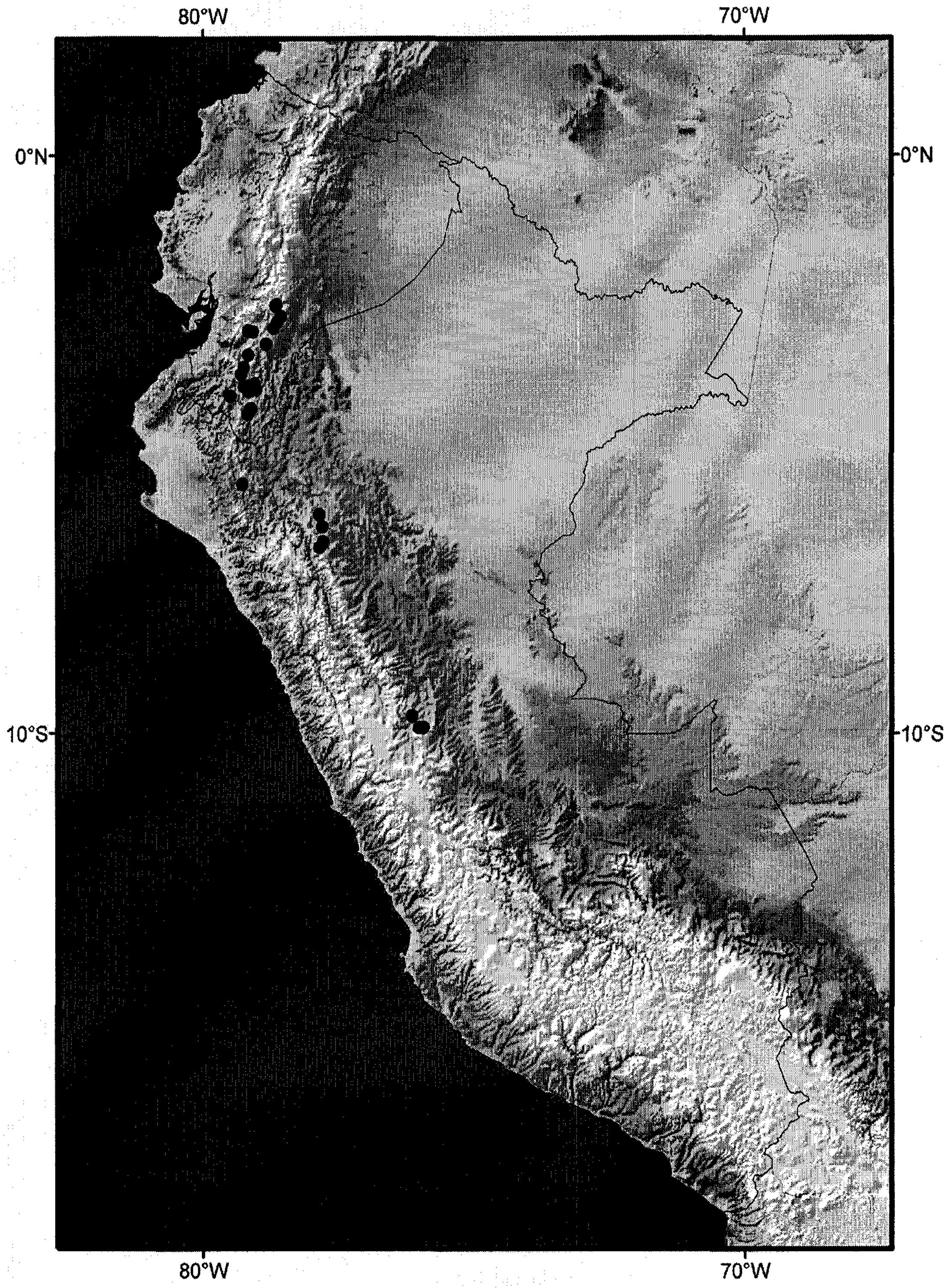


Fig. 3.21.B. Distribution of *Gomphichis goodyeroides*.

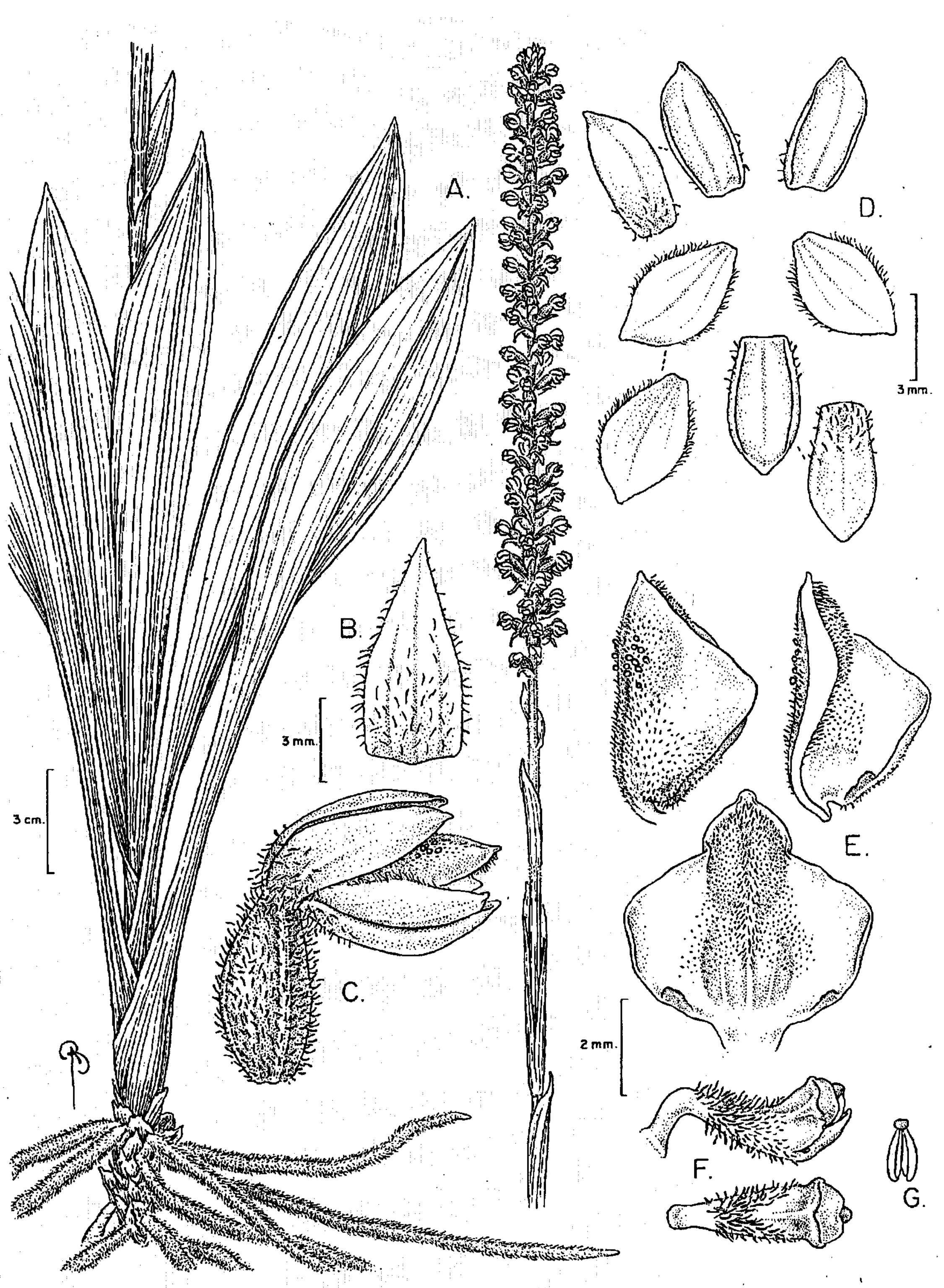


Fig. 3.22.A. *Gomphichis hetaerioides*. A, habit. B, floral bract. C, lateral view of a flower. D, sepals and petals. E, detail of the labellum abaxial and adaxial surfaces and section. F, column and detail of the adaxial surface. G. pollinaria. Based on *Cerón et al. 1853*, MO (A-G).

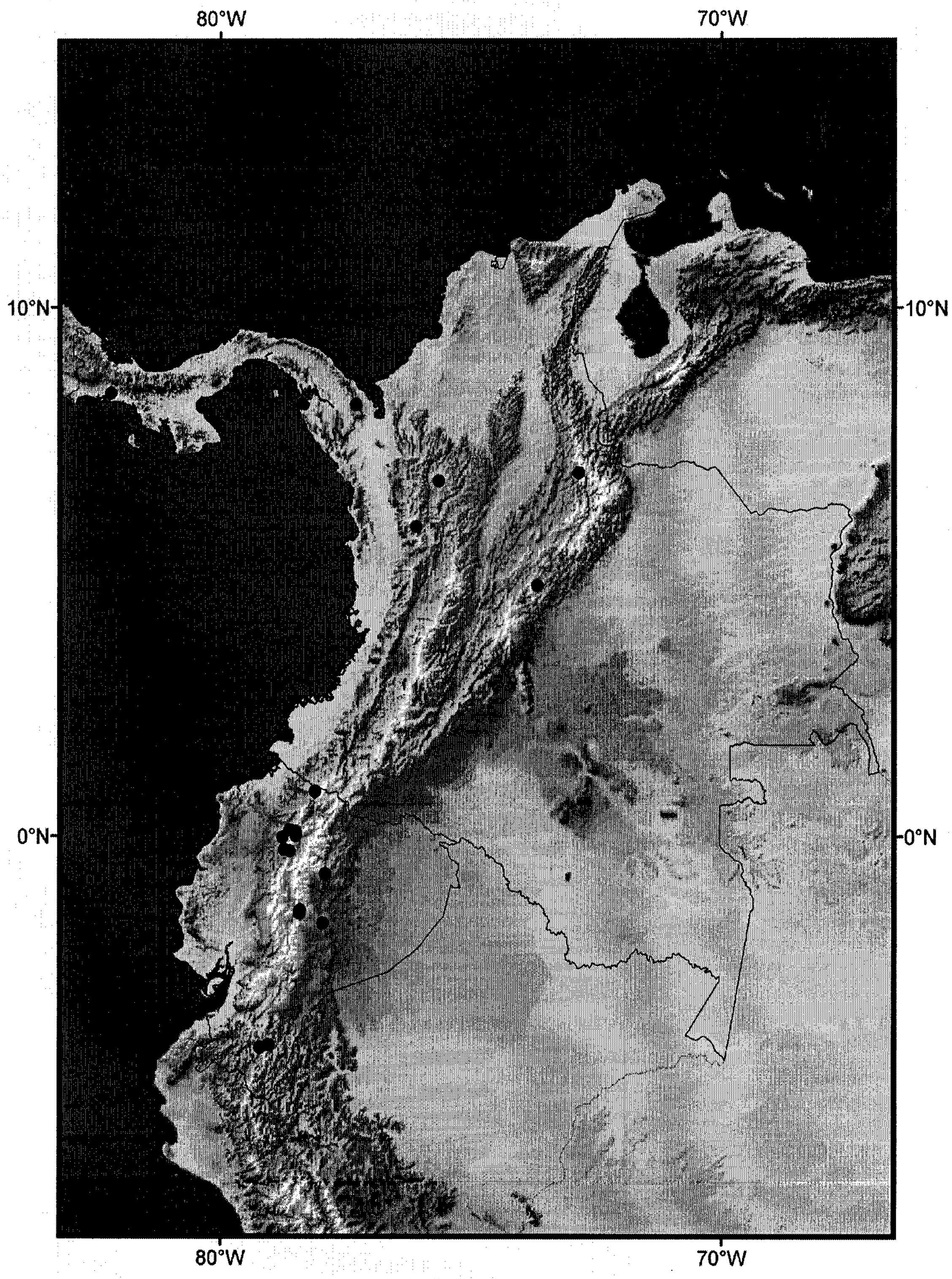


Fig. 3.22.B. Distribution of *Gomphichis hetaerioides.*

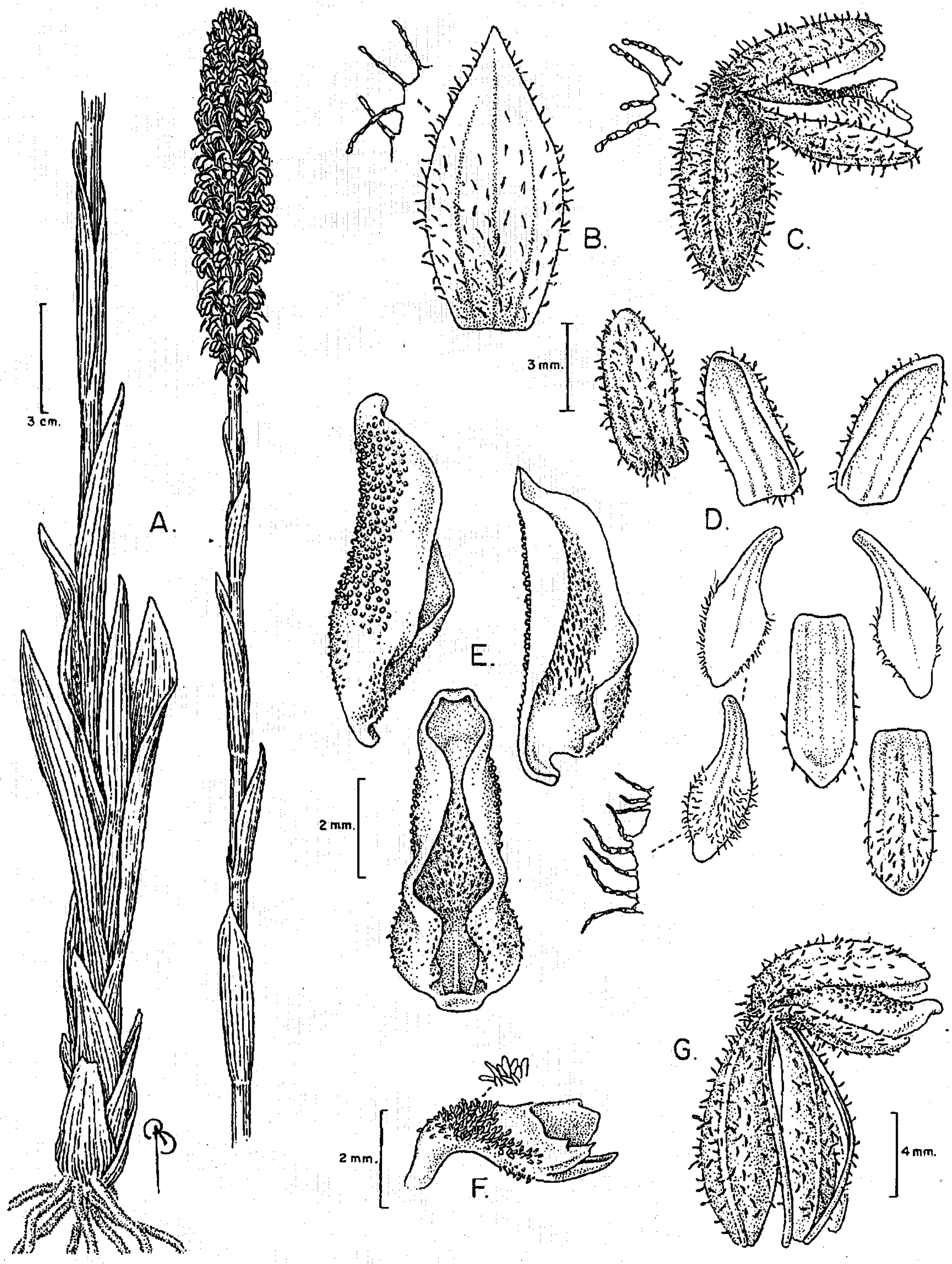


Fig. 3.23.A. *Gomphichis koehleri.* A, habit. B, floral bract. C, lateral view of a single flower. D, sepals and petals. E, labellum adaxial and abaxial surfaces and section. F, column. G, fruit. Based on *Barbour 3184*, SEL (A-G).

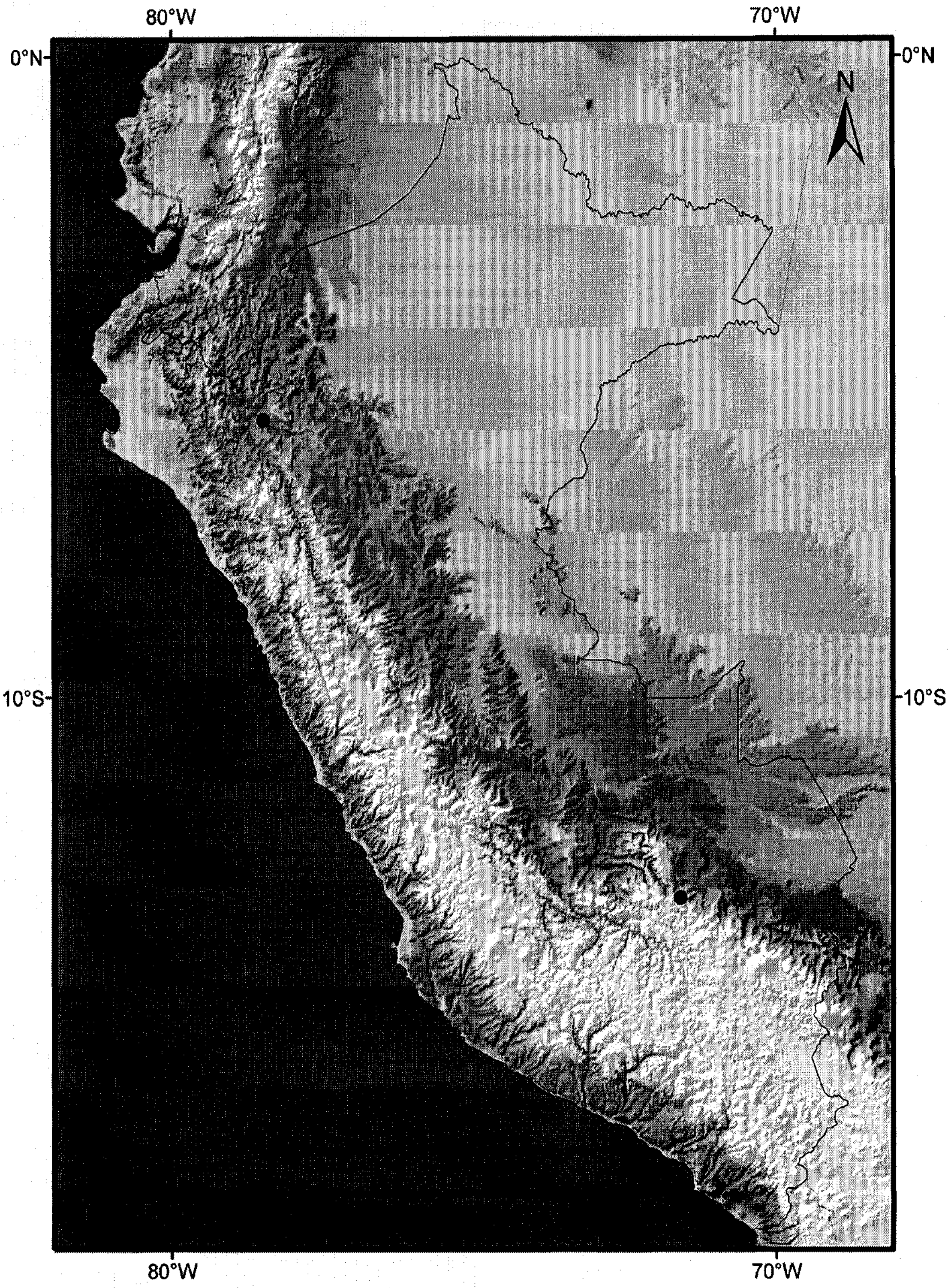


Fig. 3.23.B. Distribution of *Gomphichis koehleri*.

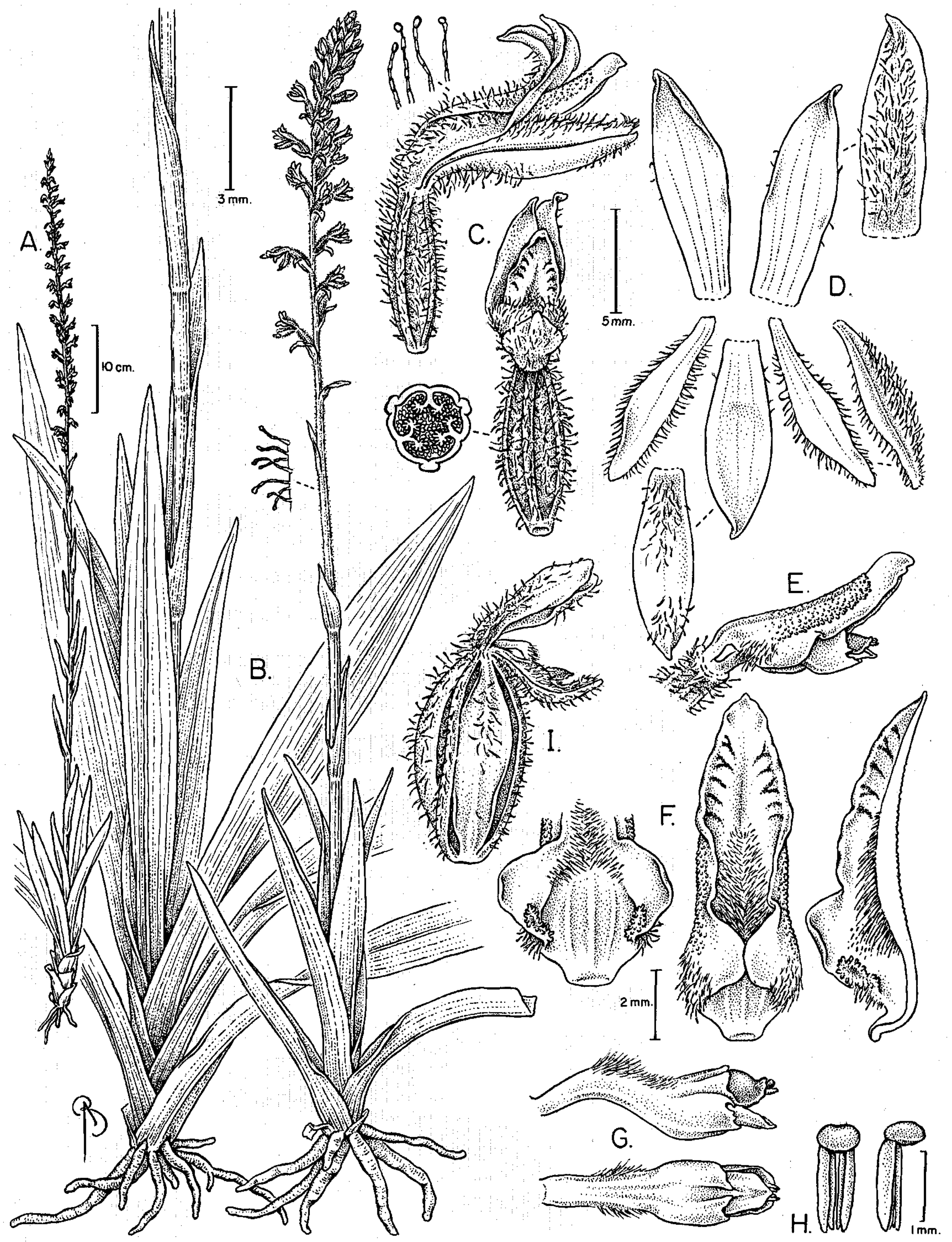


Fig.3.24.A. *Gomphichis macbridei.* A-B, habit. C, lateral and frontal view of a flower and ovary transverse section. D, sepals and petals. E, labellum and column. F, detail of the labellum adaxial surface and section. G, column and detail of the abaxial surface. H, pollinaria. I, fruit. Based on *Alvarez et al. 2806*, NY (A, C-I); *Lewis 3017*, QCNE (B).

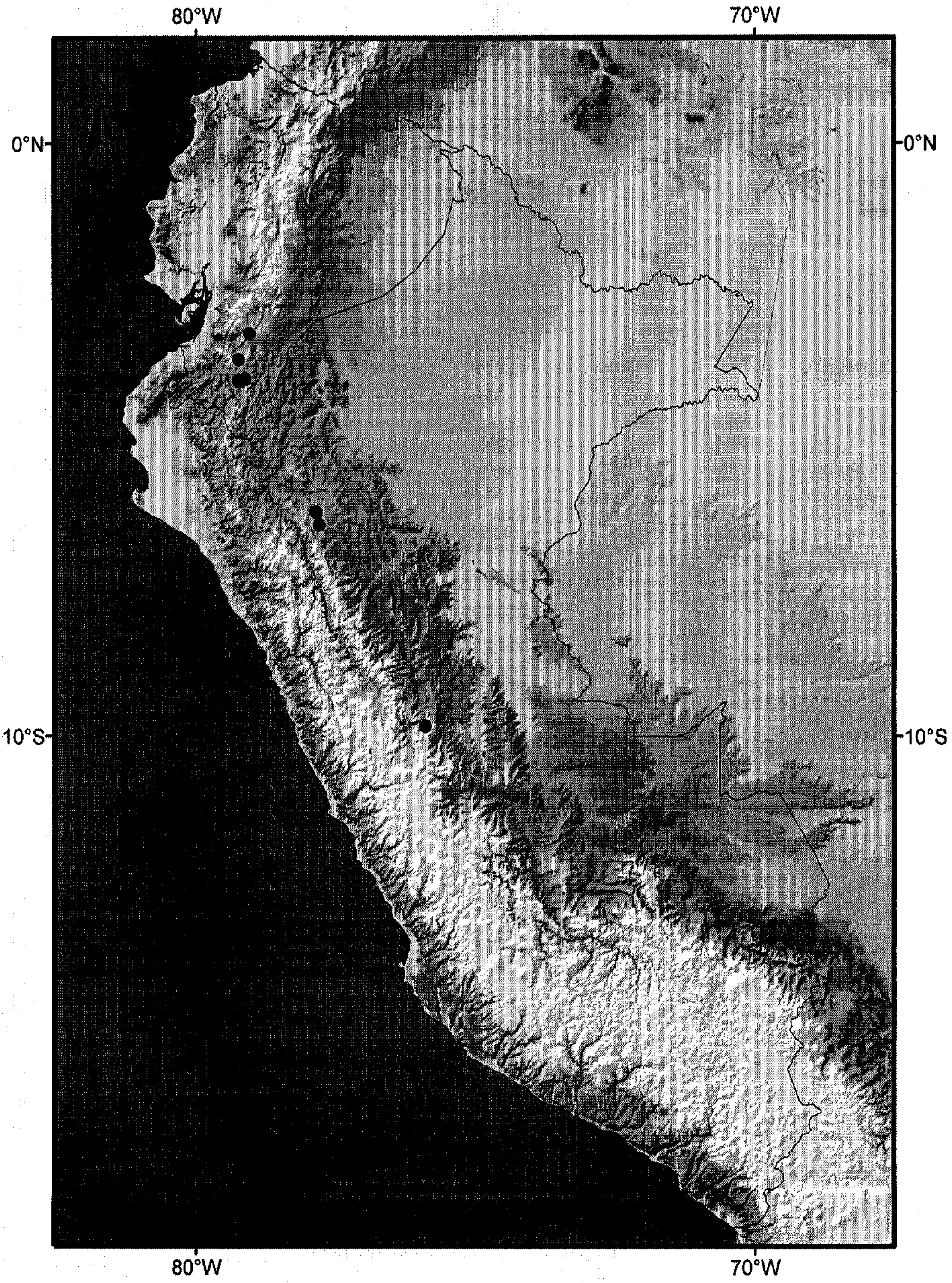


Fig. 3.24.B. Distribution of *Gomphichis macbridei.*

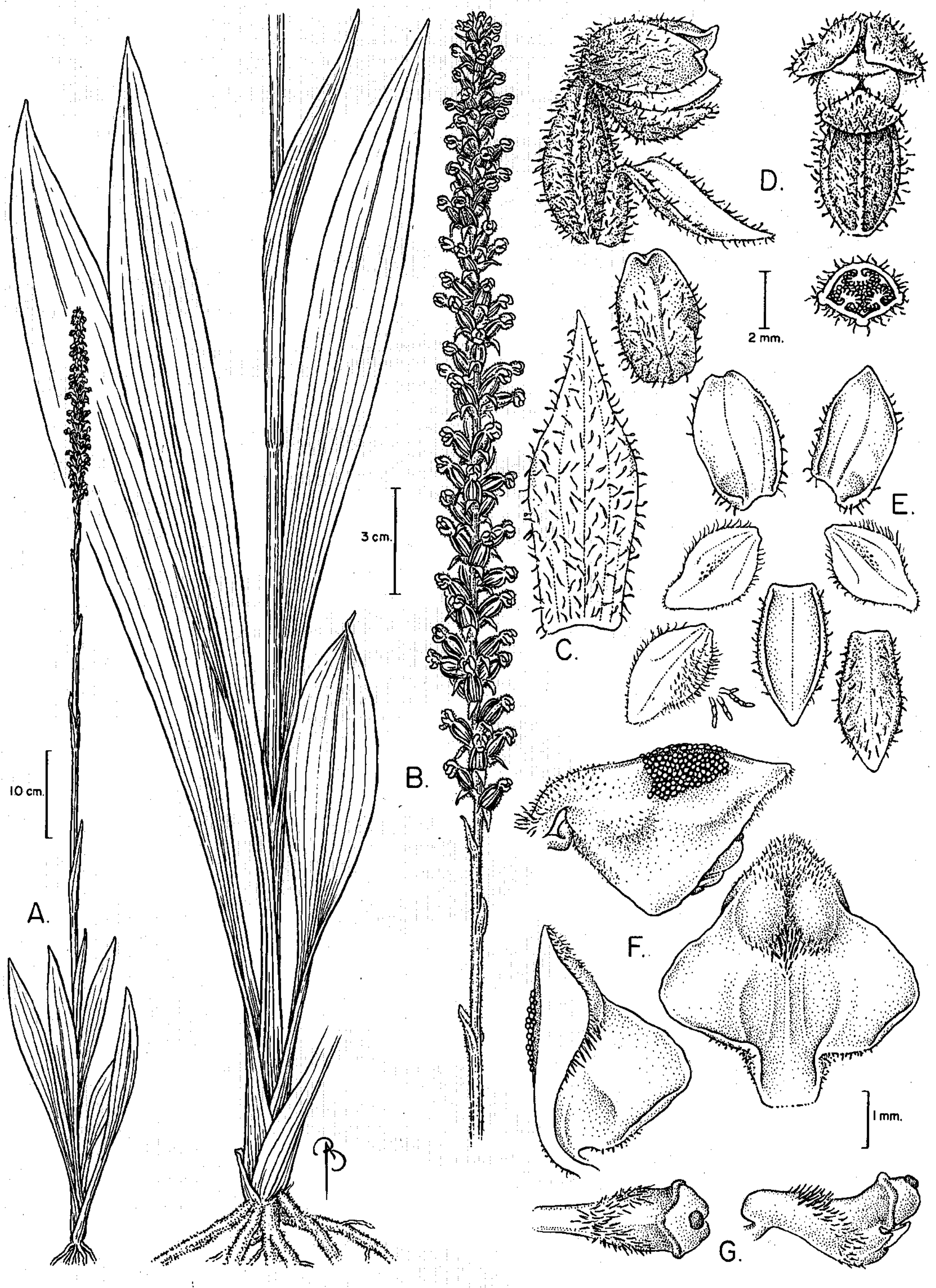


Fig. 3.25.A. *Gomphichis merzii.* A-B, habit. C, floral bract. D, lateral and frontal view of a single flower and ovary transverse section. E, sepals and petals. F, labellum adaxial and abaxial surfaces and section. G, column and detail of the adaxial surface. Based on *Alvarez & León 2977*, NY (A-B); *Merz s.n.*, NY (C-G).

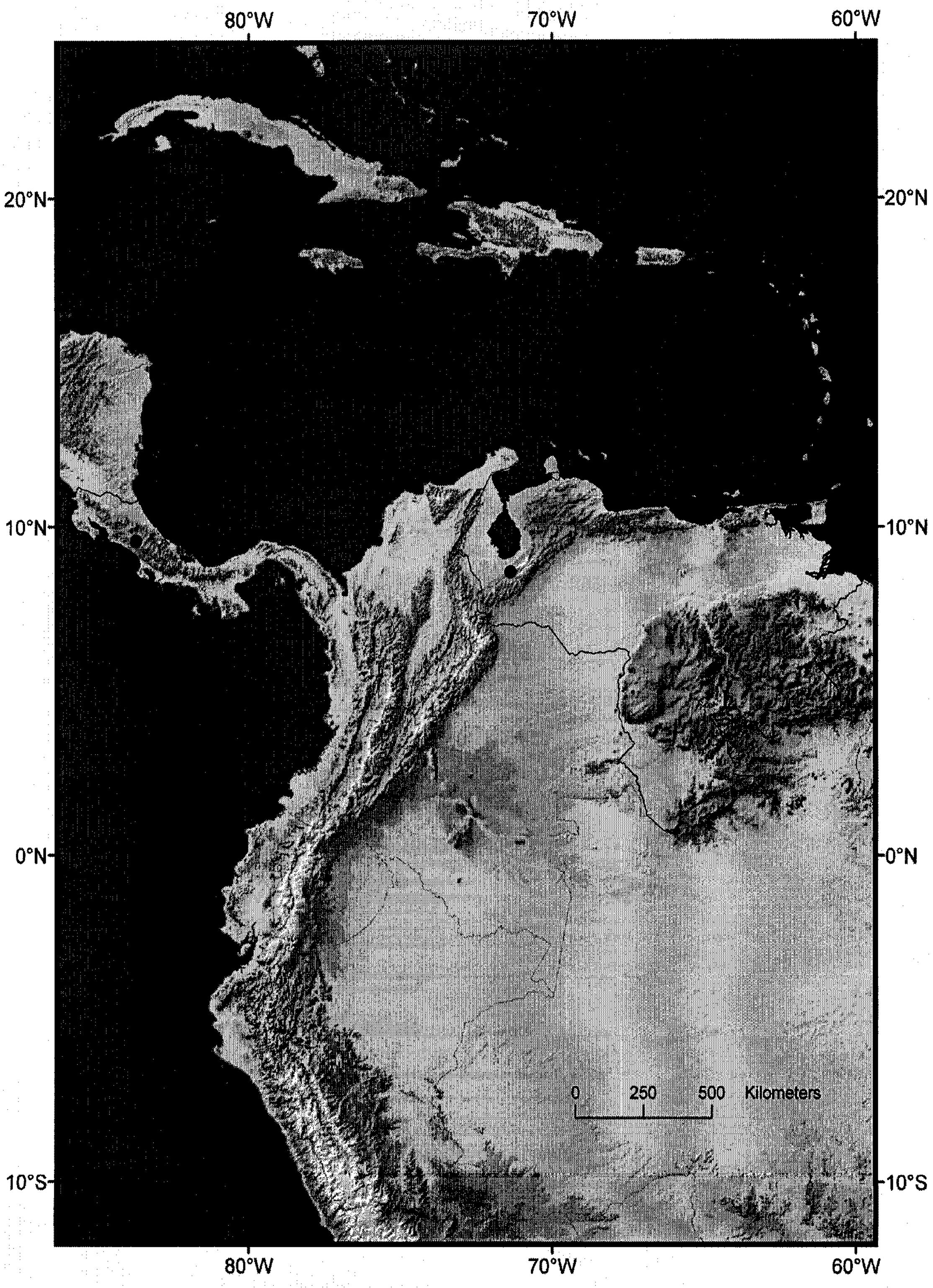


Fig. 3.25.B. Distribution of *Gomphichis merzii*.

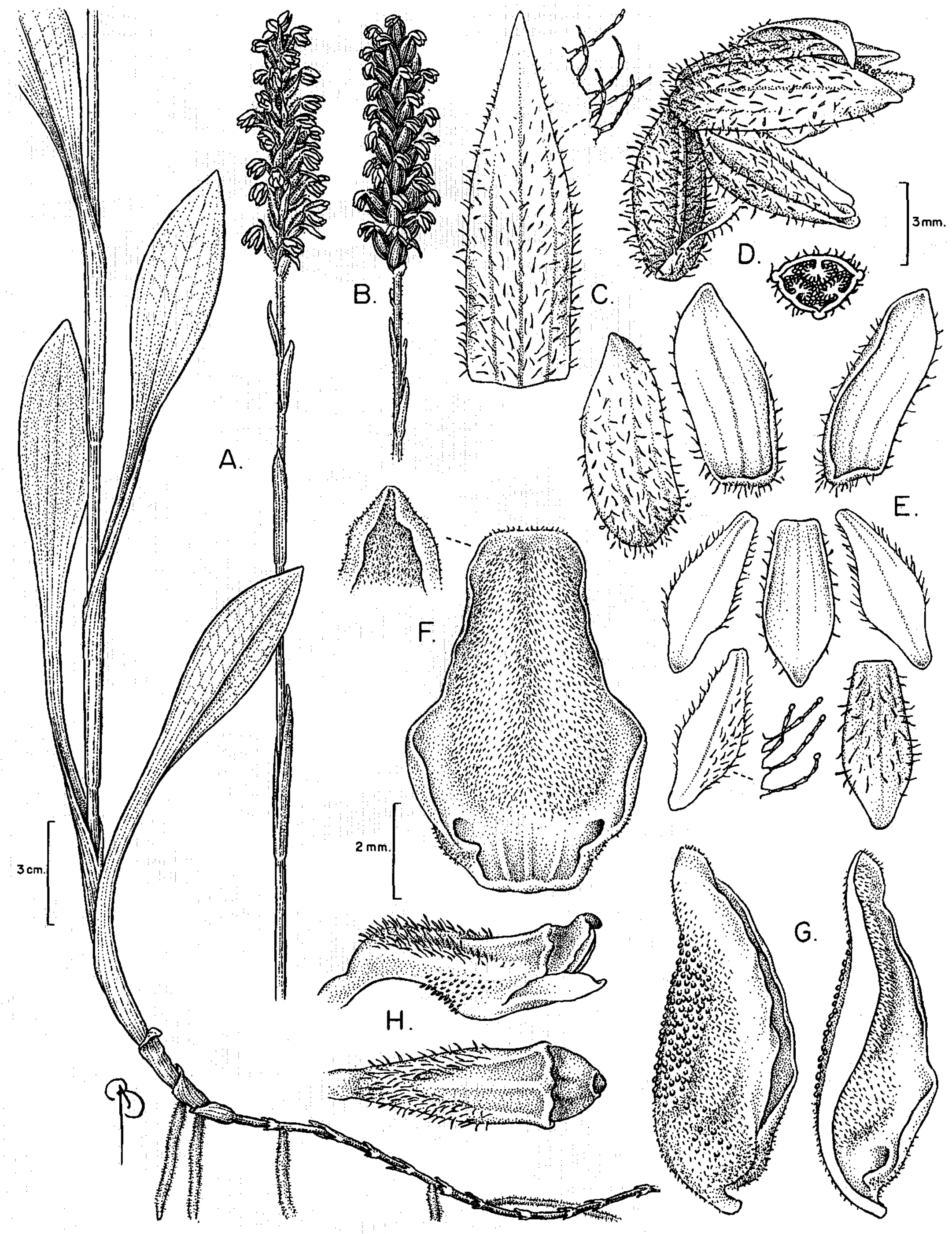


Fig. 3.26.A. *Gomphichis plantaginifolia*. A, habit. B, detail of an inflorescence. C, floral bract. D, lateral view of a single flower. E, sepals and petals. F, labellum adaxial surface and detail of the midlobe apex. G, labellum abaxial surface and section. H, column and detail of the adaxial surface. Based on *Solomon 10662*, LPBS (A); *Solomon 16095*, MO (B); *Weigend 2000/415*, NY (C-H).

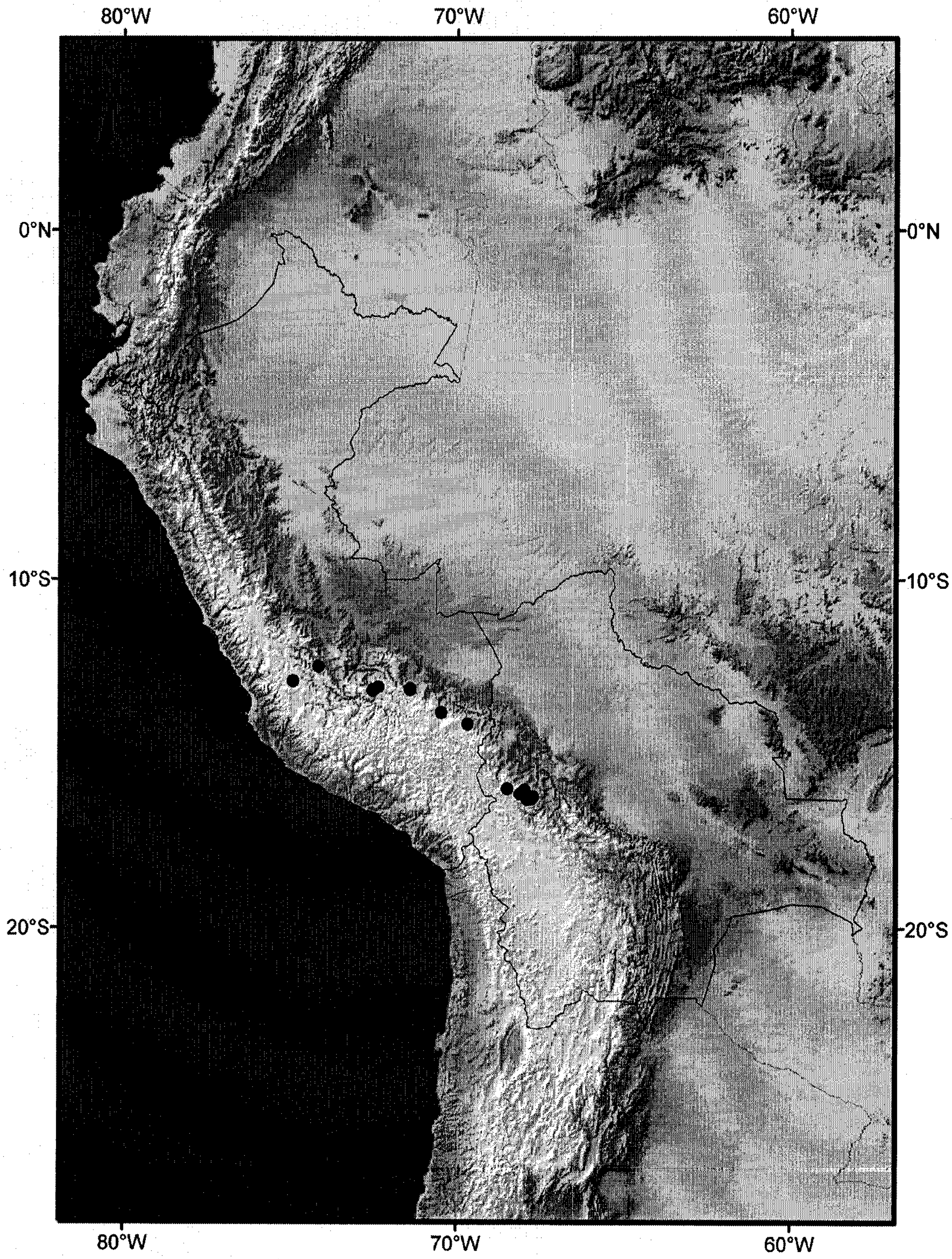


Fig. 3.26.B. Distribution of *Gomphichis plantaginifolia*.

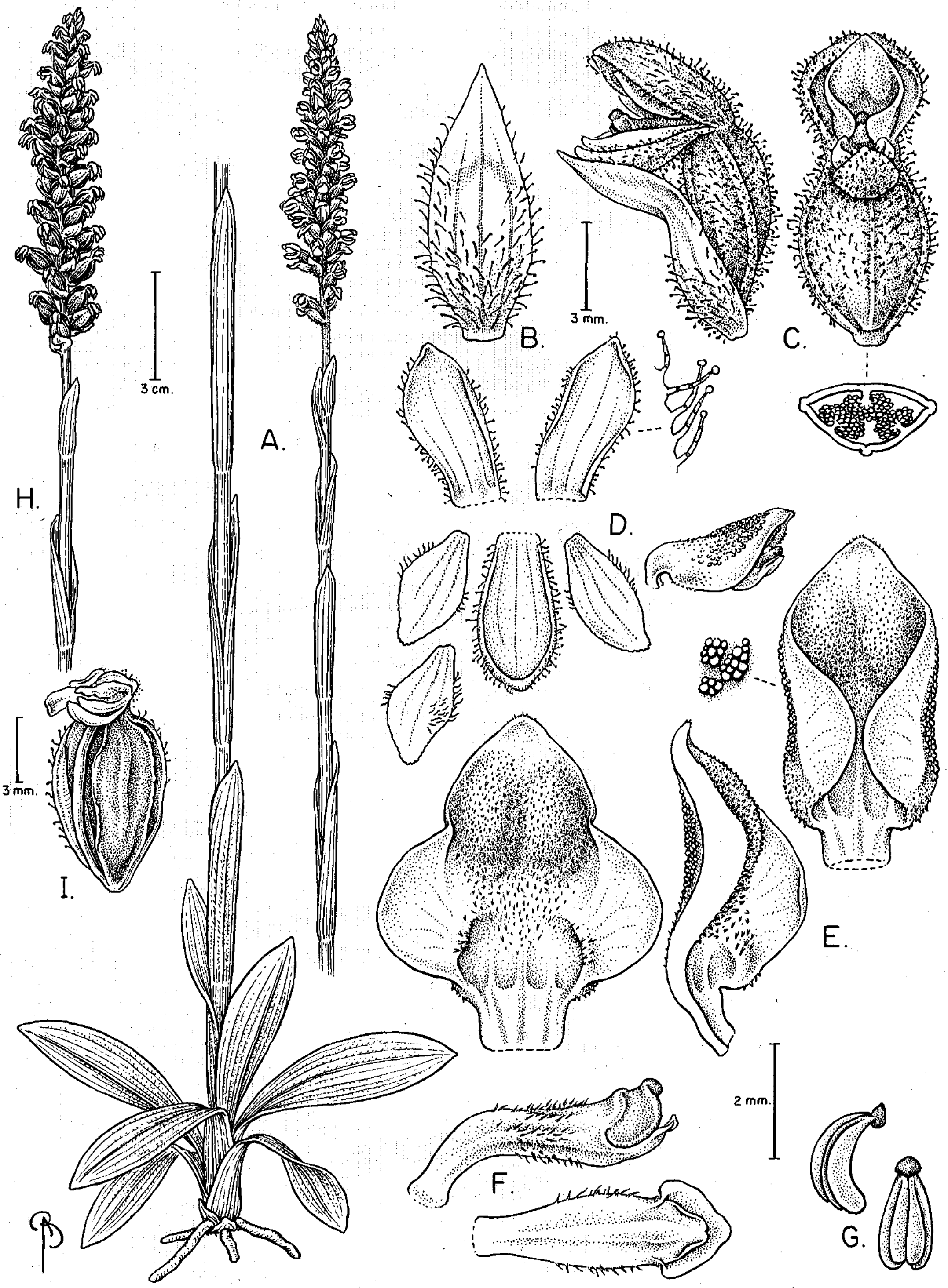


Fig. 3.27.A. *Gomphichis traceyae.* A, habit. B, floral bract. C, lateral and frontal view of a single flower. D, sepals and petals. E, labellum adaxial and abaxial surfaces and section. F, column and close up of abaxial surface. G, pollinaria, H, inflorescence. I, fruit. Based on *Sparre 15818*, US (A); *Alvarez 2632* & *Alvarez 2598*, both NY (B-G); *Alvarez 2712*, NY (H-I).

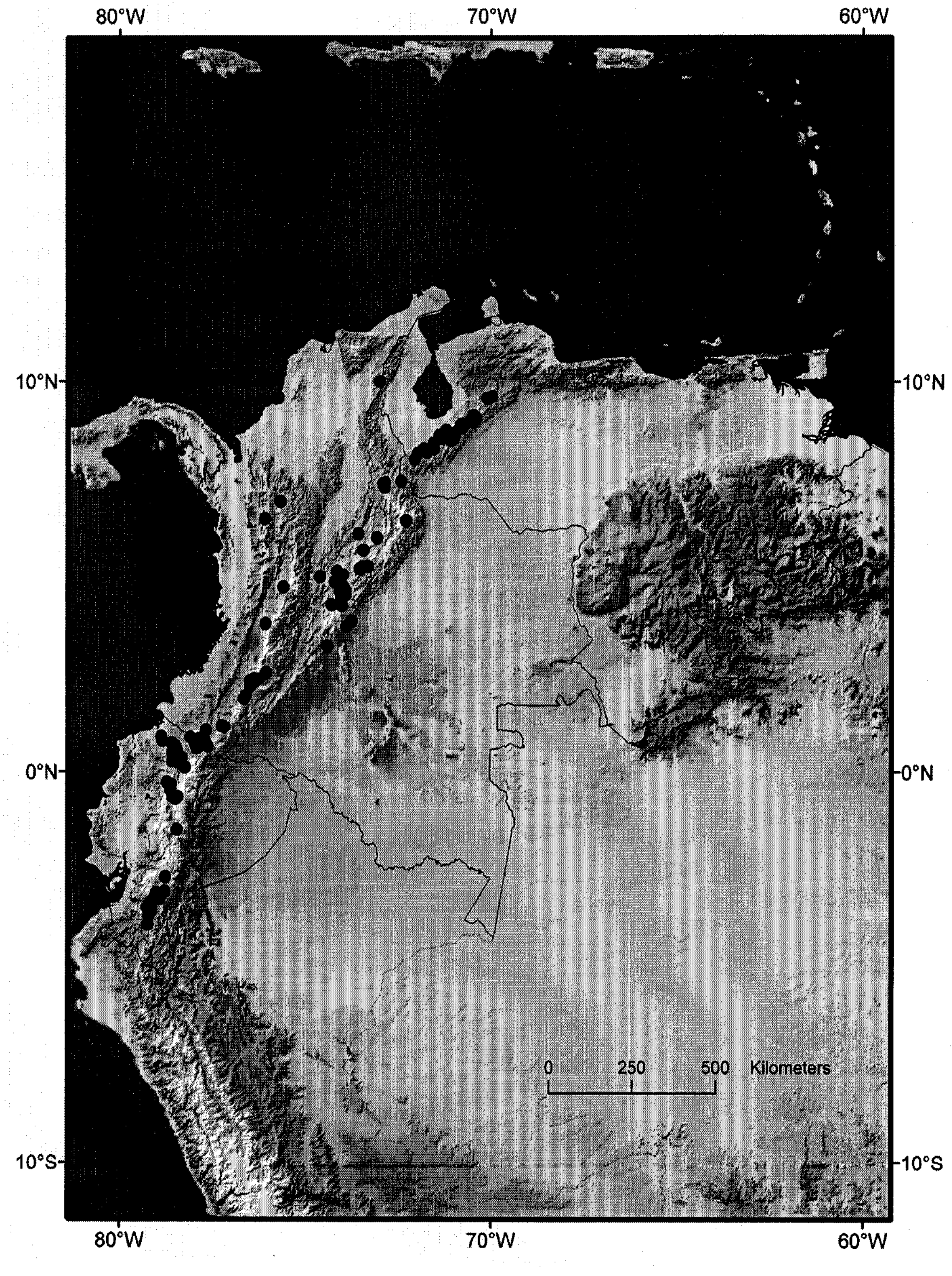


Fig. 3.27.B. Distribution of *Gomphichis traceyae*.

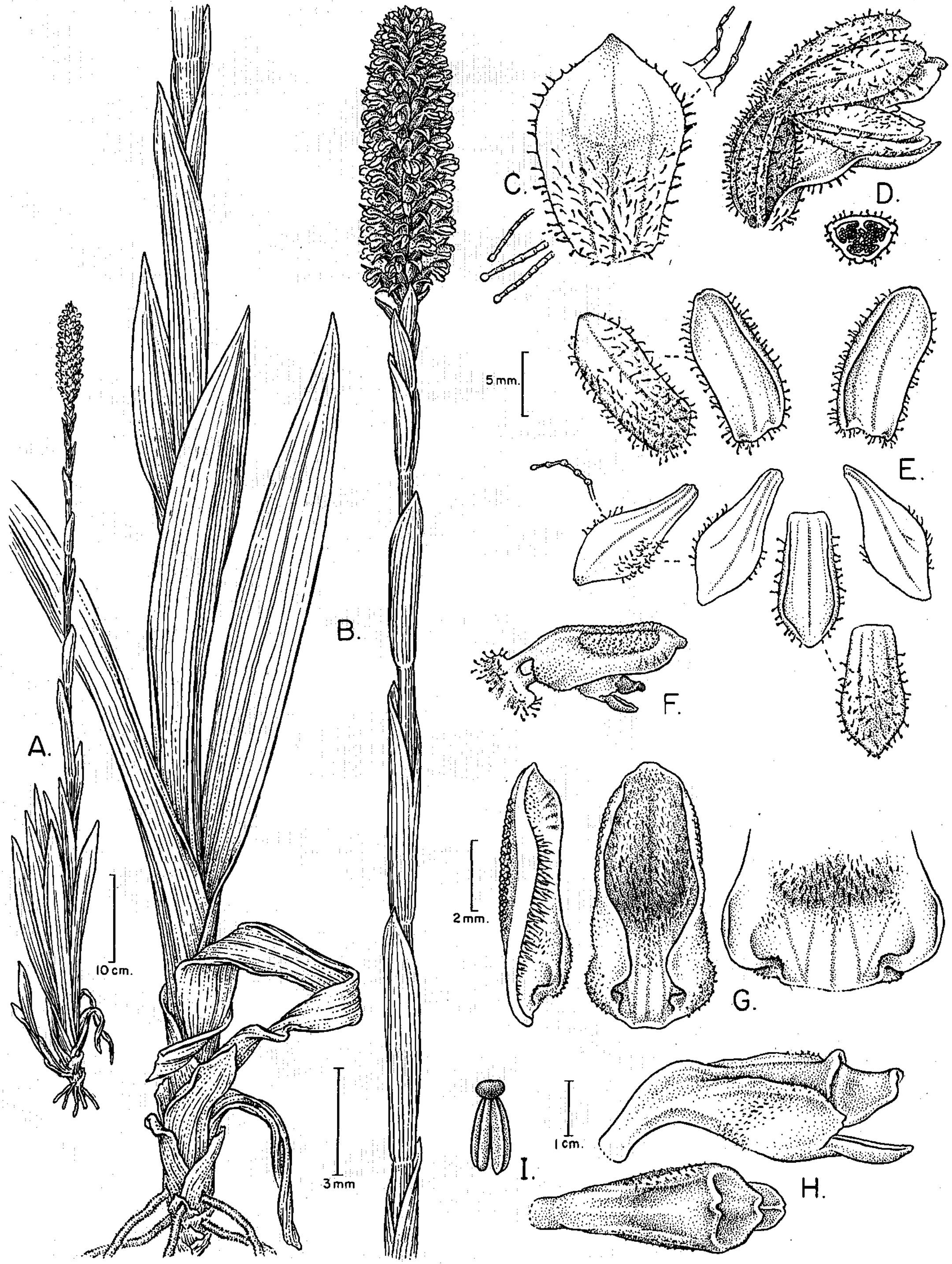


Fig. 3.28.A. *Gomphichis valida.* A-B, habit. C, floral bract. D, lateral view of a single flower. E, sepals and petals. F, labellum and column. G, detail of the adaxial and abaxial surfaces of the labellum. H, column and close up of the adaxial surface. I, pollinaria. Based on *Smith et al. 9591*, MO (A); *Smith et al. 9423*, MO (B); *Alvarez 2681*, NY (C-I).

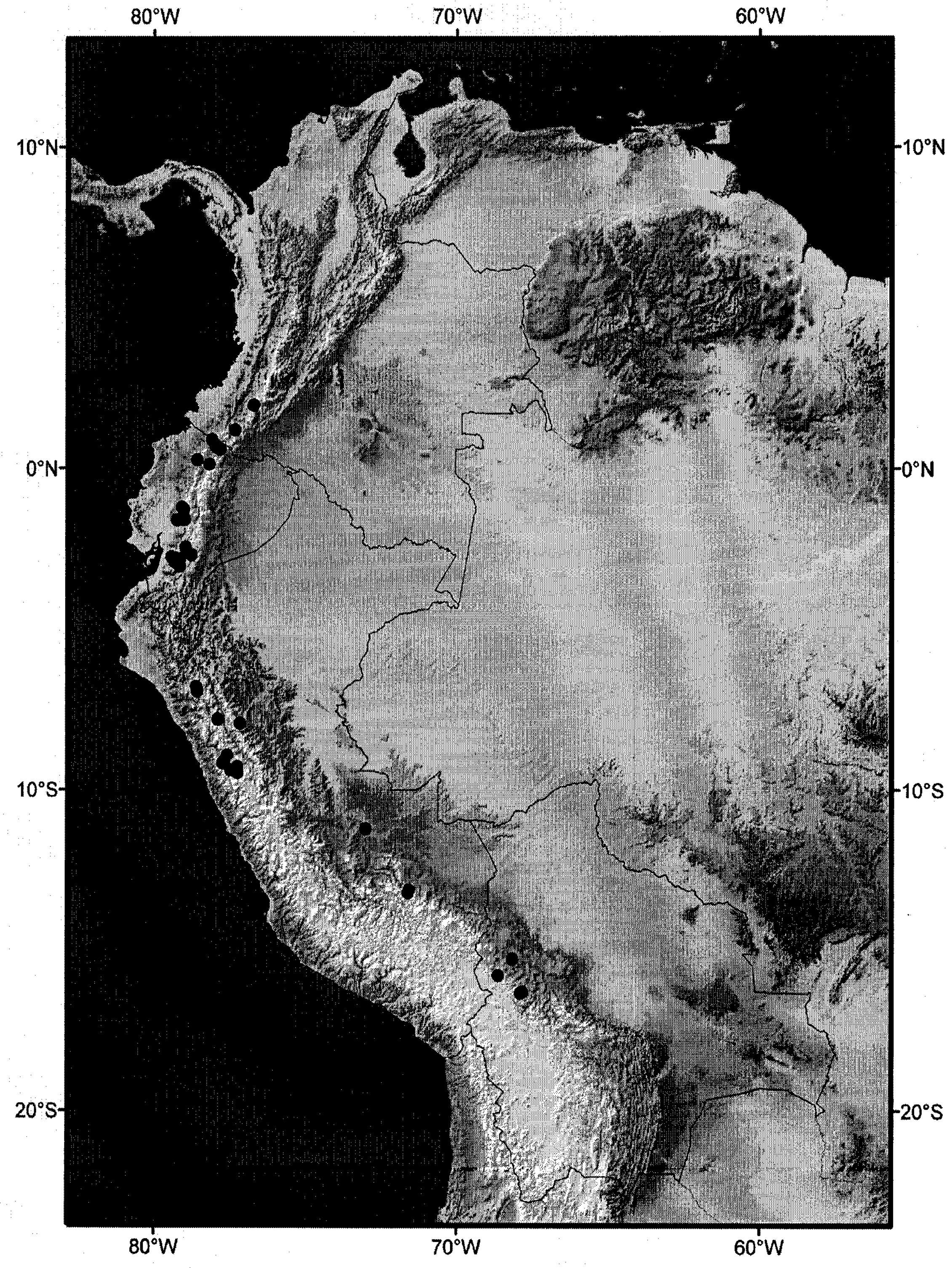


Fig. 3.28.B. Distribution of *Gomphichis valida*.

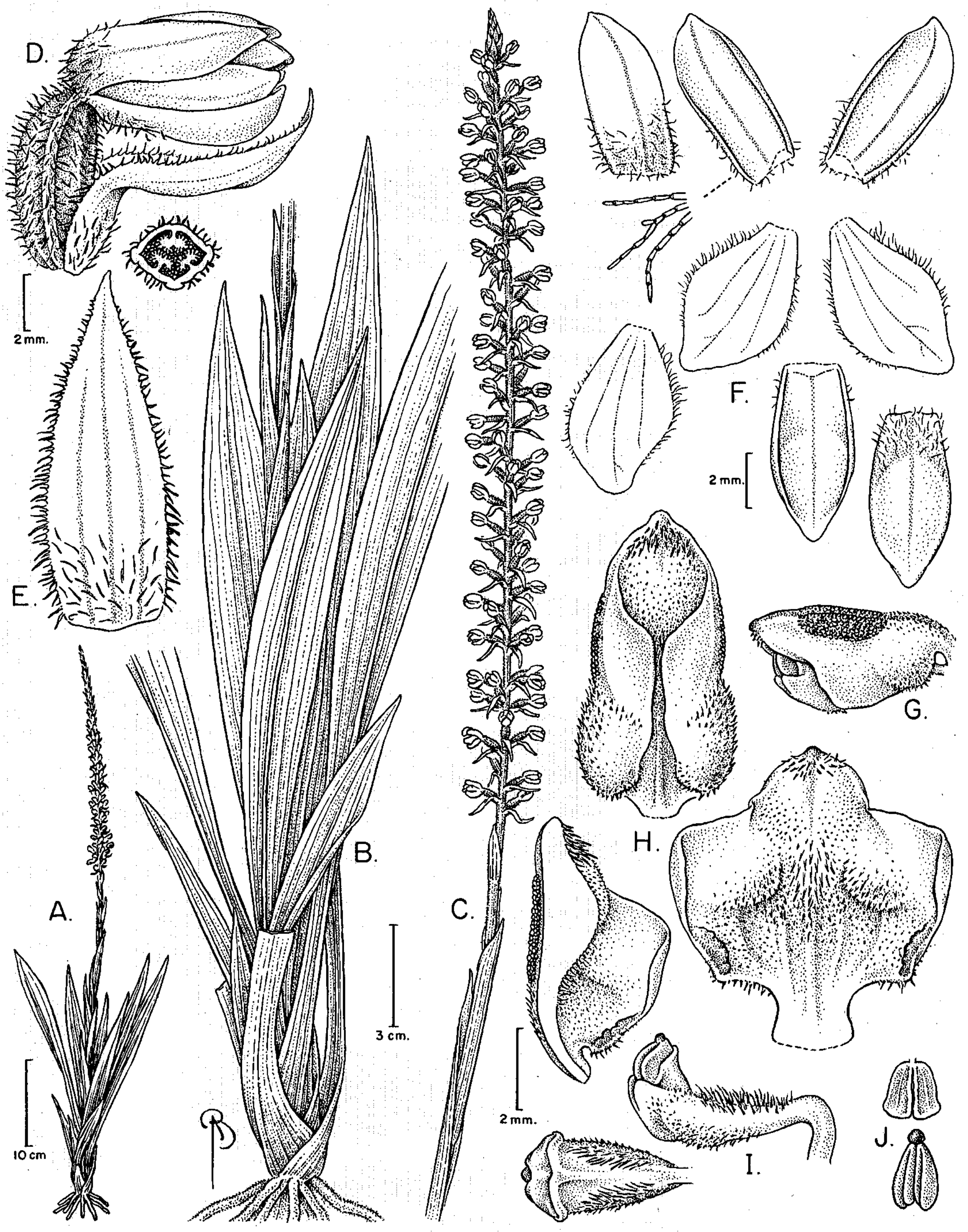


Fig. 3.29.A. *Gomphichis viscosa*. A, habit. B, roots, leaves and peduncle lower surface. C, peduncle upper surface. D, lateral view of a single flower and ovary transverse section. E, floral bract. F. sepals and petals. G, labellum abaxial surface and column. H, detail of the labellum abaxial and adaxial surfaces and section. I, column and close up of the adaxial surface. J. anther and pollinaria. Based on *Alvarez 2916*, NY (A-B); *Alvarez 2910*, NY (C); *Alvarez 2797*, NY (D-J).

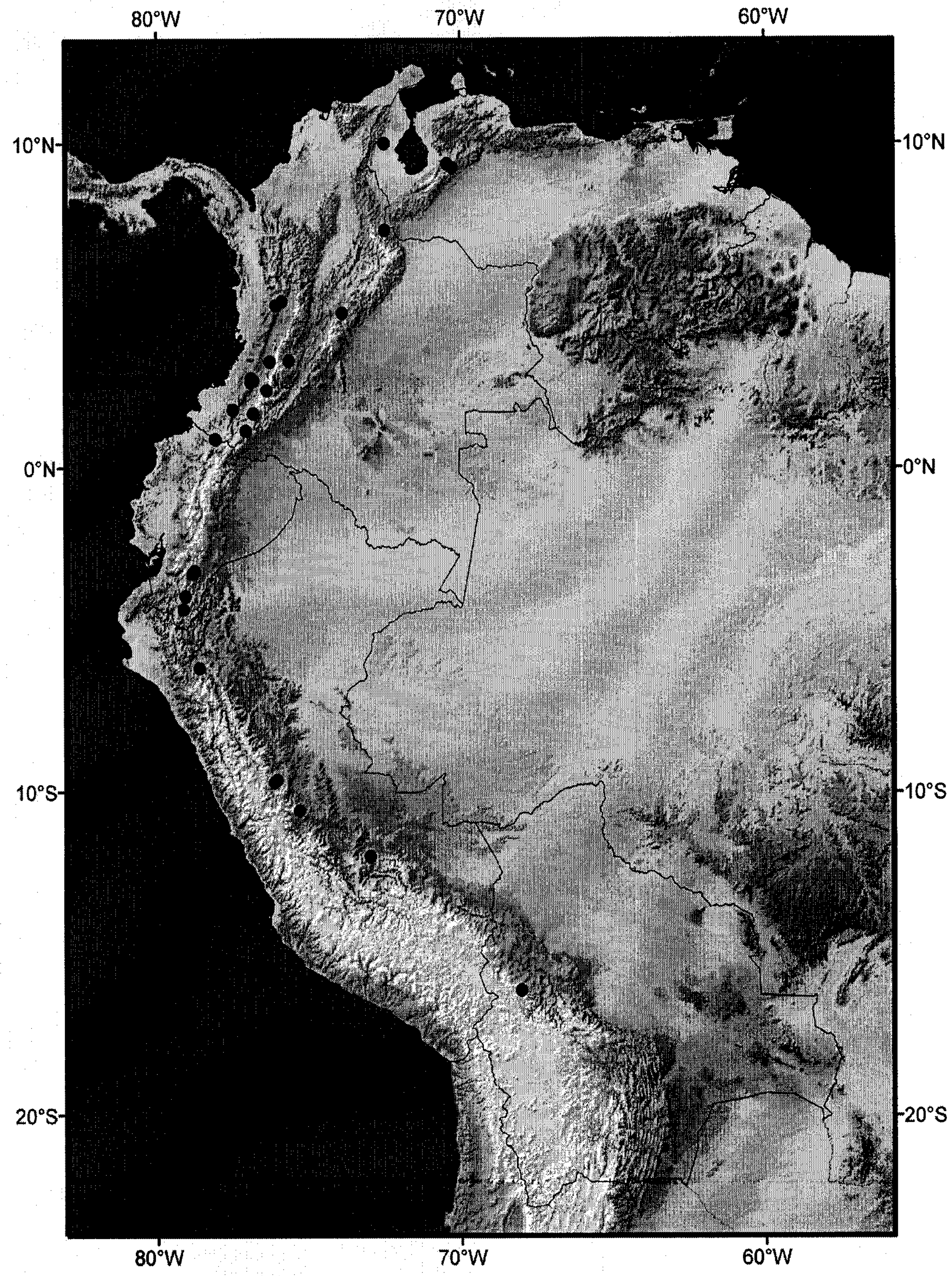


Fig. 3.29.B. Distribution of *Gomphichis viscosa*.

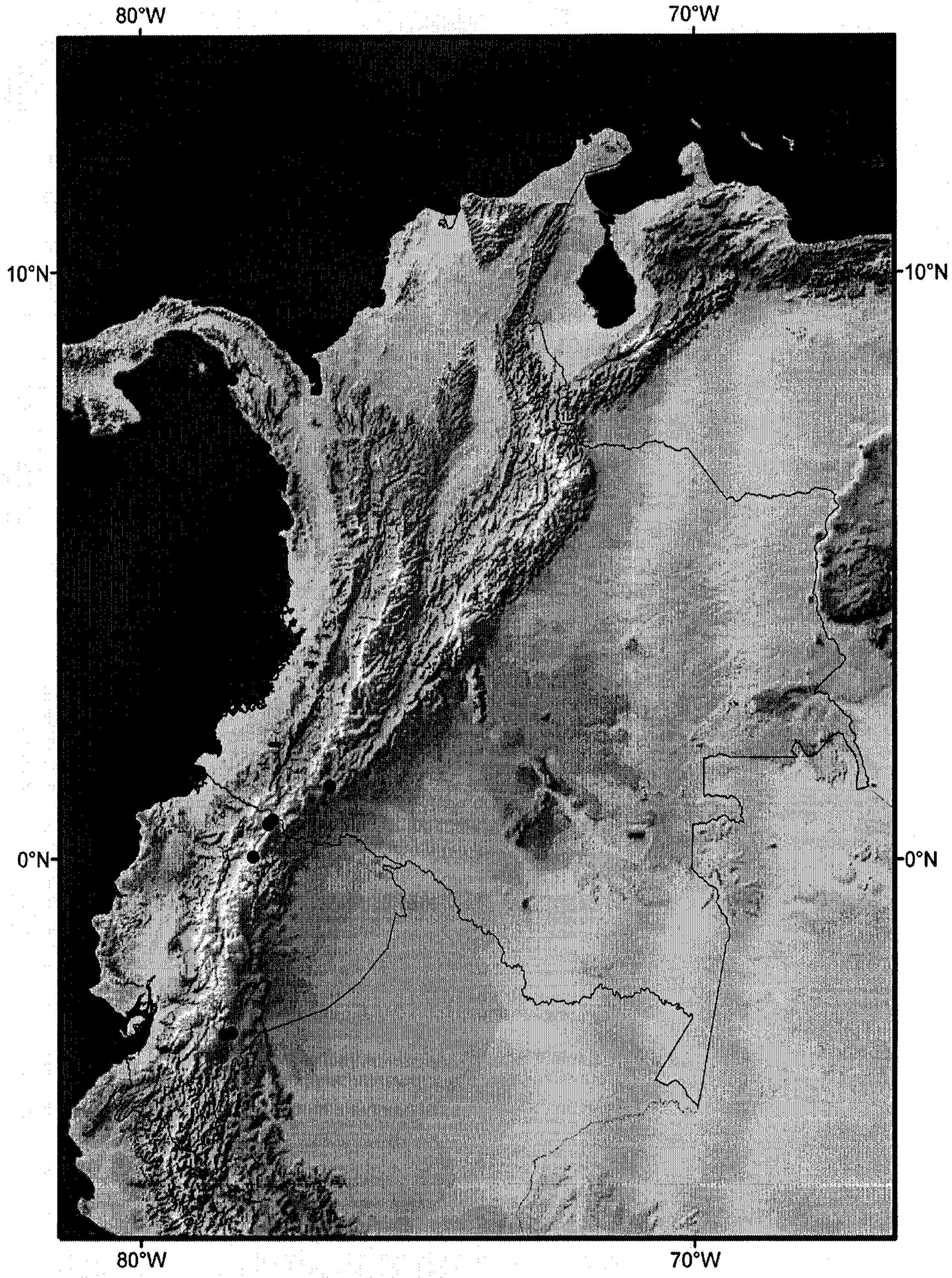


Fig. 3.30. Distribution of *Gomphichis* unnamed taxon 1.

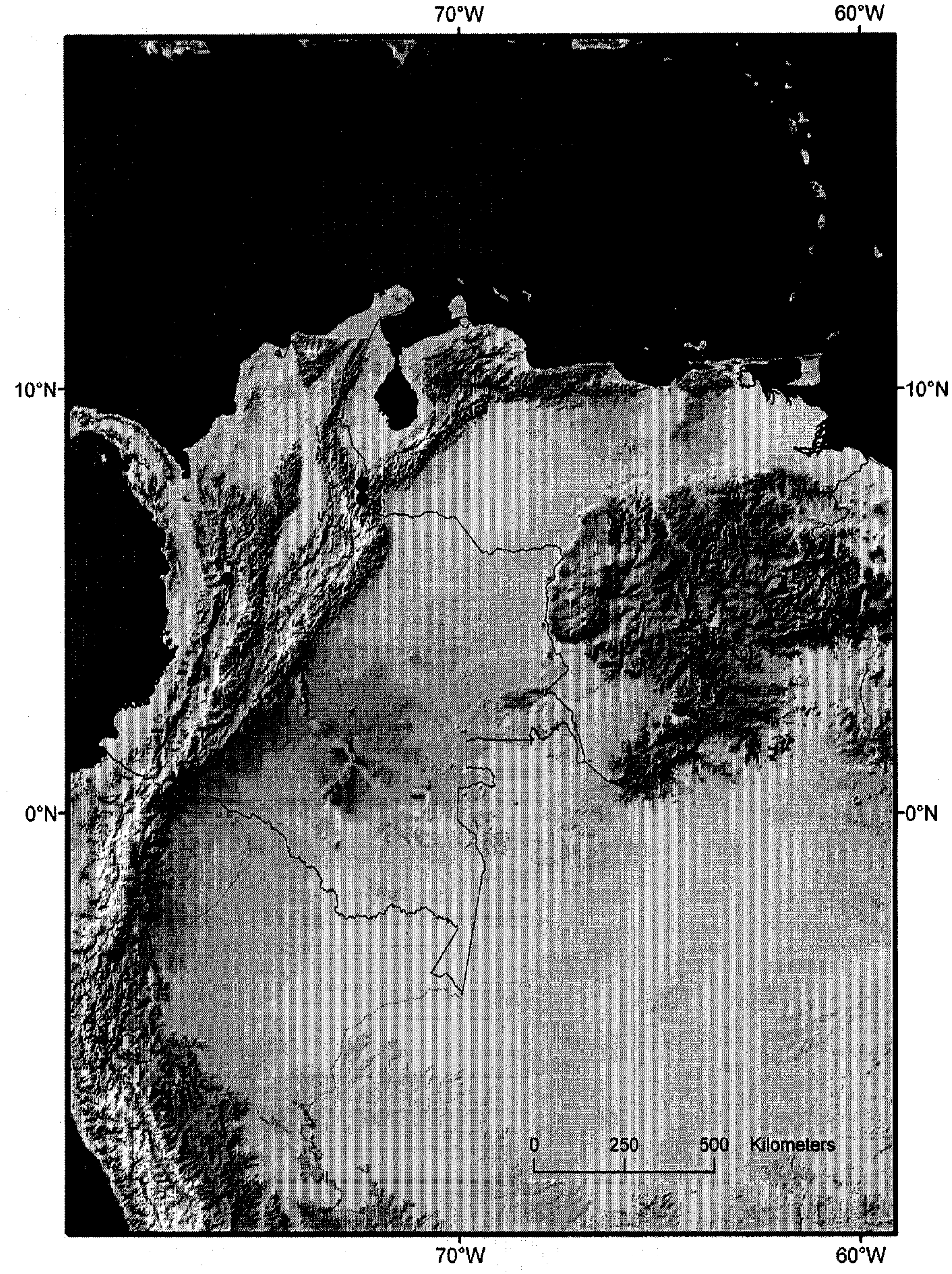


Fig. 3.31. Distribution of *Gomphichis* unnamed taxon 2.

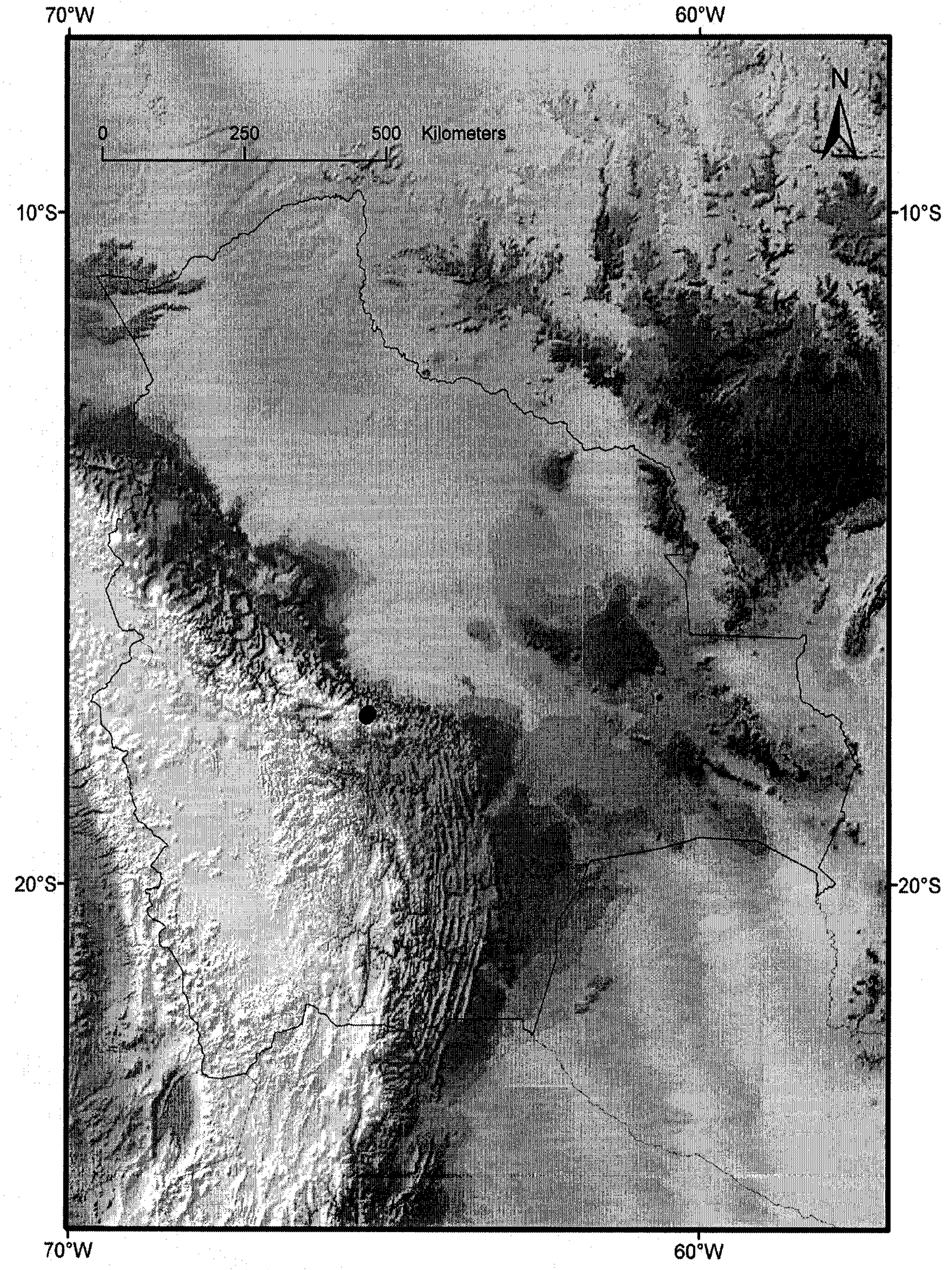


Fig. 3.32. Distribution of *Gomphichis* unnamed taxon 3.

NUMERICAL LIST OF TAXA

1. *G. adnata* (Ridl.) Schltr.
2. *G. alba* F. Lehm. & Kraenzl.
3. *G. altissima* Renz
4. *G. bogotensis* Renz
5. *G. caucana* Schltr.
6. *G. costaricensis* (Schltr.) Ames, F. T. Hubb & C. Schweinf.
7. *G. crassilabia* Garay
8. *G. cundinamarcae* Renz
9. *G. goodyeroides* Lindl.
10. *G. hetaerioides* Schltr.
11. *G. koehleri* Schltr.
12. *G. macbridei* C. Schweinf.
13. *G. merzii* Senghas
14. *G. plantaginifolia* C. Schweinf.
15. *G. traceyae* Rolfe
16. *G. valida* Rchb.f.
17. *G. viscosa* (Rchb.f.) Schltr.
18. *G.* unnamed 1
19. *G.* unnamed 2
20. *G.* unnamed 3

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CHAPTER 4

DEMOGRAPHY AND REPRODUCTIVE BIOLOGY OF *GOMPHICHIS CRASSILABIA* GARAY (ORCHIDACEAE)

4.1. INTRODUCTION

The Orchidaceae are one of the largest family of the plant kingdom (ca. 25,000 species), and as a result of their success in many different ecosystems on Earth they are of enormous interest from an ecological perspective. Their complex life cycle, involving a vast array of pollination mechanisms, reproductive strategies, spatial distribution, and population structure are yet poorly understood and little studied. Although most orchids occur in the tropics as epiphytes, terrestrial species are widespread from the lowlands to the highlands of the temperate and tropical regions. Terrestrial orchids make a higher percentage of the orchid flora with increasing elevation. The orchids of the Neotropical highlands are adapted to some of the most extreme climatic conditions but little is known about their strategies for survivorship and reproduction.

There are few data available on the pollinator behavior or breeding systems of high elevation Andean orchids. Although many orchid groups favor cross-pollination (out-crossing), self-pollination (pollination without the aid of a pollinator) and facultative out-crossing (self-pollination late in the reproductive season in the absence of pollination by an external agent) have been documented among many terrestrial orchids (Dressler, 1981; Catling, 1990). For example, Catling (1990) and Ackerman (1995) reported the Neotropical genus

Prescottia to be self-pollinated, whereas Berry and Calvo (1991) found that *Myrosmodes cochleare* was self-compatible, but not autogamous. Instead, this species is primarily pollinated by wasps and flies, and the success of fruit set is dependent on the position of the flowers within the inflorescence. For example, fruit set in open-pollinated flowers was high in the middle portion of the inflorescence, while in hand-pollinated flowers it was higher at the base. Observations of living plants and herbarium specimens of *Gomphichis* species (a close relative of *Myrosmodes*) indicate that fruit set is very high and may even approach 100%. This suggests that self-pollination is typical in the genus and this would not be surprising given the fact that a rostellum (the delicate layer of tissue between the stigma and the anther) is lacking in *Gomphichis* and its relatives. Nevertheless, shape, size, color and structure of the flowers of *Gomphichis* strongly suggest insect pollination. The role that the different floral organs play during pollination is unknown. For instance, the morphology of the reflexed column and its function during pollination of the nonresupinate flowers is especially intriguing. It would seem that the column could serve as a landing platform in the manner that the labellum normally does in other resupinate orchid flowers. An examination of pollinator behavior and reproductive strategies of *Gomphichis* in the field has the potential to provide fundamental information about the natural history of this enigmatic genus and terrestrial orchids of high elevations as a whole.

Demographic studies are necessary to understand the dynamics of populations and the vegetative and reproductive performance of individuals through time. Despite its explicit importance, there are no previous reports on the population structure and dynamics of the tropical terrestrial orchids of the Andes. Studies of the population ecology of terrestrial orchids from lowland tropical areas and temperate zones have revealed interesting life history traits, especially during the transition between vegetative and reproductive stages (Gill, 1989; Calvo, 1990). Given that species of high elevation montane areas are subject to unusually stressful conditions such as daily freezing temperatures, high insolation, and strong solifluction, it is likely that orchids in these places utilize different strategies at the population level to withstand these limiting factors.

This chapter will provide preliminary information gathered in the field on the pollination biology, mating systems, and demography of *Gomphichis crassilabia*, an endemic species of the Ecuadorian Andes with a restricted distribution (see Fig. 3.20).

OBJECTIVES

The objectives of this study are to:

1) Investigate the population structure of *Gomphichis crassilabia.*

2) Study the pollination biology and reproductive mechanisms of *Gomphichis crassilabia.*

4.2. MATERIALS AND METHODS

The ecological study was conducted over the course of four expeditions in January 2001, January 2002, June 2002 and April 2003.

Study site. Populations of *Gomphichis crassilabia* were observed at the Estación Biológica Guandera (00°35'N, 77°41'W, elevation 3420-3600 m) located in the Carchi province, near the village of San Gabriel (Fig. 4.1). The reserve encompasses a unique natural environment of upper mountain ecosystems with three major vegetation types: montane cloud forests, subpáramos and páramos in different stages of succession. The vegetation of the study site is classified as tropical montane wet forest, wet subalpine forest, and pluvial subalpine forest in the Holdridge life system (Cañadas, 1983) and receives around 1500 mm of annual rainfall. The climate is persistently humid, cold at night, chilly during the morning and slightly warm and sunny in the afternoon with extreme fluctuations of daily temperature (between 2-15°C). The topography is variable with moderate and steep slopes between 50-85%. Geologically, the reserve is situated on volcanic and metamorphic rocks originated during the Quaternary and Paleozoic as well as on sand formations derived of glacial erosion from the Pleistocene (Lützen, 1995).

Sampling localities. Three habitats were selected for this study: secondary forest, primary forest with closed canopy, and primary forest with open canopy. At each location, site characteristics such as soil type, elevation, associated vegetation, levels of disturbance, and geographic coordinates were recorded.

Study taxon. *Gomphichis crassilabia* was selected for study because it is represented in all the major habitats of the reserve. This species is a terrestrial herb up to 1.50 m tall occurring in primary and secondary forests as well as at the margins of subpáramos and open páramos. The leaves are basal, linear, and 4-9 in number. A many-flowered dense inflorescence is held on a long peduncle covered by many sheaths. The flowers open sequentially from bottom to top (acropetally), are yellow to cream colored, and covered by hirsute glandular hairs. Each flower is subtended by a very long, glandular-ciliate, hirsute bract. The labellum is slightly longer than the sepals and petals; the stigmatic surface is broad, bilobed and slightly convex; and the four pollinia are soft, pale yellow, and attached to a round, brown, sticky viscidium. The fruits are capsular, containing a large number of tiny wind-dispersed seeds.

Soil sampling. Soil samples for laboratory analyses were taken at a depth of 50 cm from the immediate proximity of the roots of a single *Gomphichis* individual in each of the three habitats. Elemental analyses of soil were carried out at the soil laboratory of the Ministerio de Agricultura y Ganadería in Quito, Ecuador.

Demographic studies. One permanent plot of 25 m^2 divided into smaller subplots of 5 m^2 was established in each of the three different habitats selected. The established plots were censused only once. This species is capable of both sexual and asexual reproduction and, because of the impossibility of knowing without destructive sampling whether aerial stems are from the same or different genet, the terms ramet and individuals will be used interchangeably. Every ramet or individual of *Gomphichis* within the plot was tagged and measured for height from the base of the rosette to the top of the inflorescence, inflorescence length, and longest leaf length. The reproductive stage was also recorded. All individuals were classified into three size-classes: 1-10 cm, 10.1-45 cm and >45.1 cm.

Flowering events. Flowering events were observed and noted when possible. Five accessible flower buds from five different plants were marked with numbered weather-resistant tags in order to study flowering progress. The observations were made following the methodology suggested by Dafni (1992) every day until the flower was senescent. For every observation the protocol involved recording: flowering stage (i.e., early bud, 1 day open flower, etc.), the wilting order of the flower organs, the position of the flower relative to the plant axis, the sepal/petal/labellum development (i.e., color changes, size changes), movements of the column, stigma changes (e.g., stickiness, diameter, receptivity), nectar production, odor presence or absence, and the direction of flowering within the inflorescence.

Nectar testing and sampling. Inflorescences from different habitats were covered with fine tulle exclusion bags for 12 hours. Nectar secretion was tested on flowers taken from these inflorescences by using glucose indicator paper strips (Chemstrip® 2 GP, Roche) following the protocol suggested by Kearns and Inouye (1993). The paper indicator was applied directly onto the nectar for about three seconds. In the presence of sugar the strips change from yellow to green (Fig. 4.2.A). Levels of glucose were obtained by direct visual comparison with the color scale provided in the directions for use of the test strips.

Nectar samples for subsequent high-performance liquid chromatography analyses were collected from five different flowers using small filter paper strips ("wicks") according to the technique outlined by McKenna and Thomson (1988) (Fig. 4.2.B). The "wicks" were cut from Whatman No. 1 filter paper into small triangles (2 x 8 mm) narrowed to one of the apices. These wicks were held with forceps to soak up the nectar. If the wicks became saturated with nectar additional ones were used as needed. The wicks were allowed to air dry at room temperature and stored in small labeled envelopes.

Pollination studies. The fixed sample method as delineated by Dafni (1992) was followed to carry out direct observations of visitors to inflorescences of the selected individuals. A total of 26 person-hours of observation were carried out. Observations took place on sunny days between 11:00 am and 3:00 pm when the temperature was relatively high (10-15°C) as suggested by Dodson (1962) and Berry and Calvo (1991). Nocturnal observations with the aid of a flashlight were conducted between 6:00 pm and 9:00 pm when the temperature varied between 3 and 5°C. The behavior of floral visitors was recorded and specimens were collected in separate vials for later identification.

Reproductive mechanisms. Breeding systems were investigated by adapting methods from Berry and Calvo (1991) and Kearns and Inouye (1993). A first trial to exclude potential pollinators from the flowers using bridal veil bags of fine mesh failed due to the excessive weight and humidity that the bags added to the plants after the daily rains typical of these ecosystems. After this learning experience, a second trial was designed to completely enclose the plants from the ground to the top without touching them by using cages made of fine nylon mesh, mosquito netting and pole wires (Fig. 4.3). To evaluate relative contribution of insects as pollination agents and to test for autogamy, 20 individuals of *Gomphichis* containing only flower buds were surrounded by cages. Four marked individuals were excluded because they died. As a control, 20 additional inflorescences were marked but not caged. The number of flowers in each inflorescence forming fruits was recorded after five months, and prior to fruit dehiscence. Seed fertility test were not carried out.

Data analyses. Demographic data was analyzed using univariate descriptive statistics, and frequency distributions using the statistical package JMP (SAS Institute, 2000). These tests provided statistical measurements of the population composition and distribution size patterns of the studied taxon. Significance statistical tests among size distributions were not carried out due to the uneven presence of this species in the selected habitats for study. The outcome of fruit set for experimental and control plants were analyzed using paired t-tests and chi-square tests. Data on fruit set was interpreted in light of the recent review on fruiting success of nectar and nectarless orchids by Neiland and Wilcock (1998) in which little information was available on autogamous taxa from the tropics.

4.3. RESULTS

Soil studies. The soils are of volcanic origin, dark black in color with abundant organic matter; high to medium levels of nitrogen and iron; low to medium levels of calcium, magnesium, manganese, phosphorous, copper, potassium and zinc; pH between 4.3-5.1; and medium fertility (Ministerio de Agricultura y Ganadería (MAG), 2001) (Table 4.1).

Demography. The population structure of *Gomphichis crassilabia* in the selected habitats tends towards the reverse-J curve (Fig. 4.4). Most of the individuals are less than 45 cm in length. The high quantity of regenerating individuals in the early developmental stages (seedlings and juveniles) suggests that the populations are replacing themselves.

Flowering events. The total length of the flowering period is about six months. Flower opening is sequential from the base towards the apex of the inflorescence (acropetal). The flowers exhibit a "fresh" appearance for up to 10-12 days after opening. Immature fruits attain maturity in about six months. During this period of time the ovules will fully develop into mature seeds ready for wind dispersal.

Nectar. Open flowers produce small amounts of nectar as evidenced by the positive results of tests conducted in the field. The glucose content in the nectar of *Gomphichis crassilabia* varies between 500 and 1000 μg/μL. However, the high-performance liquid chromatographic analysis failed to quantify the specific sugars of the nectar. This failure may be explained by the excessively high limit of detection (over 0.2% w/w) which, because of the low concentration of sugars in nectar, may make this methodology inappropriate for determining the types of sugar in *Gomphichis crassilabia*. An additional constraint is the very small amount of nectar available in each individual flower (each sample provided for analysis).

Pollination biology. Floral visitors to the flowers of *Gomphichis crassilabia* include flies (Diptera) and bumblebees. The primary visitors are bumblebees (*Bombus* spp.) on either cold or sunny days, especially during late morning and early afternoon hours (Fig. 4.5). After flower visitation, the bees were not observed carrying pollinaria. No floral visitors were seen during the nocturnal observations. I notice, however, that among the unbagged marked inflorescences, a few flowers did not have pollinaria.

Breeding systems. Data for fruit set in experimental and control plants are presented in Table 4.3. The number of fruits was slightly higher in bagged plants than in control (unbagged) plants, because the inflorescences of bagged-plants possessed a greater number of flowers. Nonetheless, reproductive success (measured as number of fruits/number of flowers) was higher in open-pollinated plants (87.5%) than in treated plants (86.8%). The exclusion of pollinators with plastic mesh bags reduced fruit success in comparison with untreated plants, but without statistical significance. For this reason, the null hypothesis that fruit set is the same in bagged and control plants cannot be rejected. Furthermore, a graphical test and statistical analysis for fruit set mean values of both bagged and control plants overlap, suggesting that fruit set means are not significantly different (Fig. 4.6).

4.4. DISCUSSION

Demography. The frequency distribution shows that this species is rarely found in primary forests but that it is abundant in disturbed habitats in the process of regeneration within the reserve (Fig. 4.4). Although little is known about the factors favoring orchid establishment, growth and reproduction in the high elevation of the Neotropics, it has been commonly accepted that seedling establishment is extremely dependant on suitably moist and shady substrates in which the appropriate fungal symbiont is present (Dixon, 1991). Seedlings, ramets, and juveniles of *G. crassilabia* in secondary zones were found growing often in association with individuals of the fern *Blechnum aurantum* and less commonly with species of the tree fern *Cyathea* (*C. straminea*, *C. pallescens*, and *C. frigida*). These tree-fern species seem to provide the appropriate microhabitat conditions for the establishment and growth of the studied species. In primary forest the few individuals of *Gomphichis* were growing under the most dominant trees of the forests, *Weinmannia* and *Clusia*. However, as plants attain maturity, light appears to be the most critical factor in favoring flowering and fruiting production. Once established in new environments, this terrestrial orchid seems to increase its population size because of the ability of its seedlings to become established directly around parental plants. In these sites, clusters of variously aged seedlings around a vigorous and flowering individual were frequently observed. These results (although preliminary in nature) do not support the common idea of a random spatial distribution of orchids as a result of their wind-dispersed dust-like seeds, and rather support a nonrandom (patchy) spatial distribution at a much smaller scale as suggested by mathematical models examining wind-dispersed orchid seeds and genetic based studies (Chung et al., 2004).

Although most individuals appear to reproduce by means of seed dispersal, exhibiting only a single aerial stem at a time (especially in the primary forest). A few were observed to have both clonal and seed reproductive capacity, producing vegetative derived plants adjacent or distant to the parental plant. Vegetative reproduction is achieved through extensions of the stem (rhizome) underground and, therefore, vegetative propagated plants are difficult to identify without digging up and destroying the plants. Clonal reproduction appears to be a common strategy documented in many terrestrial orchids of temperate regions (Gregg, 1991; Kull & Kull, 1991), but in fewer species of the tropics (Dod, 1989).

Flowering events. Receptive flowers were evidenced by the presence of a wet exudate on the stigma. In recently opened flowers, the labellum is very close to the column and the anther containing the pollinia is fully exposed and easily detached as the result of the brown colored, sticky viscidium sticking to pollinators. As the flowers age, the distance between the labellum and column expands leaving the stigmatic surface uncovered, thereby facilitating the deposition of pollen on the stigma. Similar flowering events have been noted and described, particularly for a number of species of *Spiranthes* and *Goodyera* (Catling, 1983b; Darwin, 1988; Catling & Catling, 1991). Movements of the column and labellum, sequential flowering, and protandry are listed among the features promoting cross pollination (Catling & Catling, 1991). These characteristics are found in *G. crassilabia* and were also found in *Prescottia stachyodes*, a close ally to *Gomphichis* (Singer & Sazima, 2001).

Nectar. Nectar appears to be secreted by a pair of calli located in the introrse lateral lobes of the labellum. Nectar secretion accumulates at the base of the lateral lobes of the labellum and on the ventral surface of the column. The nectar may be held in this position by the concave shape of the labellum and the dense non-glandular trichomes of the inner surface of the labellum and upper surface of the column.

Pollination biology. Bumblebees are the most active and important diurnal pollinators in cold and harsh environments due to their size, shape and special morphological features (e.g., longer and shaggier hairs), and physiological adaptations (e.g., muscular thermogenesis, insulating pile) (Kearns & Thomson, 2001). The bumblebees approach the flowers of *Gomphichis crassilabia* in flight and first explore the lowermost (old flowers) and then continue with the upper ones. Similar foraging behavior of bees of the genus *Bombus* have been reported in other spiranthoid orchids (Catling, 1983b). Additional studies are needed to confirm these initial observations and determine the true pollinator/s of this species. Furthermore, careful observations of living individuals throughout anthesis will be useful to determine possible movements of the labellum and column and changes in viscidium humidity, features correlated with protandry.

Breeding systems. The slightly lower percentage of fruit set in bagged flowers compared to unbagged flowers may be the result of experimental influences such as shading, lower air flow and higher humidity caused by the exclosures, or other uncontrollable factors inherent in field-based studies. The high fecundity of *Gomphichis crassilabia* here reported is in agreement with recent published data on the mating systems of species of the genus *Prescottia* from Brazil (Singer & Cocucci, 1999; Singer & Sazima, 2001). In contrast, the results of this study do not support suggestions of Neiland and Wilcock (1998) that tropical orchids are characterized by low fruit set of less than 50%. This study confirms that in *G. crassilabia* fruit-production takes place without pollinators –a phenomenon known as autogamy (self-pollination and self-fertilization). Autogamy is an effective way of dealing with pollinator scarcity, but not pollinator absence. However, agamospermy, a type of apomixis (seed production without male gametes), as a cause of fruit set cannot be ruled out, given that this breeding system has been found in other terrestrial orchids of the formerly known subfamily Spiranthoideae (currently placed in the Orchidoideae) (Catling & Catling, 1991). A combination of floral features such as pollinaria and stigma location in recently open flowers, soft and granular pollen grains, a large and convex stigma with copious exudate, the absence of a rostellum, and nectar secretion suggest that cross-pollination almost certainly occurs. This conclusion is supported by the observation of bumblebees and flies visiting the flowers. Other terrestrial orchids that produce nectar have been found to yield high fruit sets as well (Ackerman, 1975).

In summary, this experimental study supports the contention that the reproductive system of *Gomphichis crassilabia* is facultative out-breeding. It also suggests that in freshly opened flowers, cross-pollination is favored, but that if the flowers are not pollinated by external agents (due to their scarcity at high elevations) then the flowers can self-pollinate (although it is not clear yet whether self-pollination is accomplished only with pollen from the same flower or also from pollen of other flowers). This successful reproductive strategy has also been reported in terrestrial orchids of both temperate (Catling, 1983a, 1990) and Neotropical regions (Singer & Sazima, 2001).

4. 5. CONCLUSIONS

This preliminary study shows that the population structure of *Gomphichis crassilabia* follows the reverse-J curve indicating that there are more seedlings and juveniles than adults. In secondary forest the population studied is reproducing well. In secondary forest most individuals appear to be clustered near the parental plants. The low number of individuals and/or genets in primary forest (with open and closed canopy) prevented statistical analyses, and, thus the distribution of this species in primary forest is unclear.

Flowers of *Gomphichis crassilabia* offer nectar as reward. The primary visitors to the flowers of *G. crassilabia* were flies and large bees, and the most frequent visitors were bees of the genus *Bombus*. Nocturnal visitors were not observed. Nevertheless, further studies are needed to establish the identity of the most efficient pollinators.

In *Gomphichis crassilabia* overall fruiting success (% fruits/flowers) is very high (87.2%). This value was slightly higher in open-pollinated flowers (87.5%) than in bagged plants (86.8%). The high fruiting success of *G. crassilabia*, even when potential pollinators are excluded, suggests that this species is capable of self-pollination. Nectar production, as well as several floral features of *G. crassilabia* suggests that the breeding system of this taxon is facultative out-crossing.

Future monitoring of populations of *Gomphichis crassilabia* will certainly elucidate more aspects of the population and reproductive biology of this narrowly endemic species.

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Table 4.1. Characteristics of soil chemistry of three habitats of *Gomphichis crassilabia* in the Estación Biológica Guandera.

Habitat type (N= 2/per habitat)	**pH**	**Organic matter %**	**Total N %**	**(ppm)**							
				P	**K**	**Ca**	**Mg**	**Fe**	**Mn**	**Cu**	**Zn**
Secondary forest	5.1	17.31	0.86	5	30	32	4	111	0.4	0.5	0.1
Primary forest-open canopy	4.2	33.89	1.69	21.5	140	36	5	23	0.5	0.23	0.14
Primary forest-closed canopy	4.3	25.35	1.27	7	40	32	4	50	0.3	0.3	0.07

Interpretation of levels of content

MICROELEMENTS	**LEVELS**		
	LOW	**MEDIUM**	**HIGH**
Organic matter %	0-2%	2.1-4%	> 4%
Total N %	0.-0.15%	0.16-0.3%	> 0.31%
P	0.-10	10-20	> 21
K	0-75	76-150	> 151
Fe	0-20	21-40	> 41
Mn	0-5	6-15	> 15
Cu	0-1	1.1-4	> 4.1
Zn	0-3	3.1-7	> 7.1
Ca	0-150	151-300	> 300
Mg	0-25	25-50	> 50
pH LEVELS			
ACID	**SLIGHTLY ACID**	**NEUTRAL**	**ALKALINE**
< 5.5	5.6-6.4	6.5-7.5	> 7.6

Table 4.2. Number of individuals in three size classes per ¼ hectare of *Gomphichis crassilabia* in three habitats of the Estación Biológica Guandera.

Reproductive stage of ramets/individuals	**Size classes**	**Primary forest-gaps**	**Primary forest no-gaps**	**Secondary forest**
seedlings	0.10-10.00 cm	8	10	217
juveniles	10.10-45 cm	1	4	78
adults	=>45.10 cm	2	1	65
	Subtotal	**11**	**15**	**360**

Table 4.3. Fruit set of *Gomphichis crassilabia* following pollination treatments: bagged and control.

H_O: Fruit set is the same in bagged and control plants

H_A: Fruit set is not the same in bagged and control plants

	N	**Bagged**	**Control**	**Total**
No. flowers	20	1691	1617	3308
No. dehiscent fruits	20	1468	1415	2883
% Fruit success (fruits/flowers)	20	86.8%	87.5%	87.15%
Expected No. fruits		**1474**	**1409**	
$X^2_{cal}{}^*$ =		0.029	0.021	
TOTAL $X^2_{cal}{}^*$ =	**40**	**0.05**		

$X^2_{cal}{}^*$ formula with Yates correction.

$X^2_{cal} = 0.05 < X^2_{0.05,1} = 3.841$

Therefore, do not reject H_o.

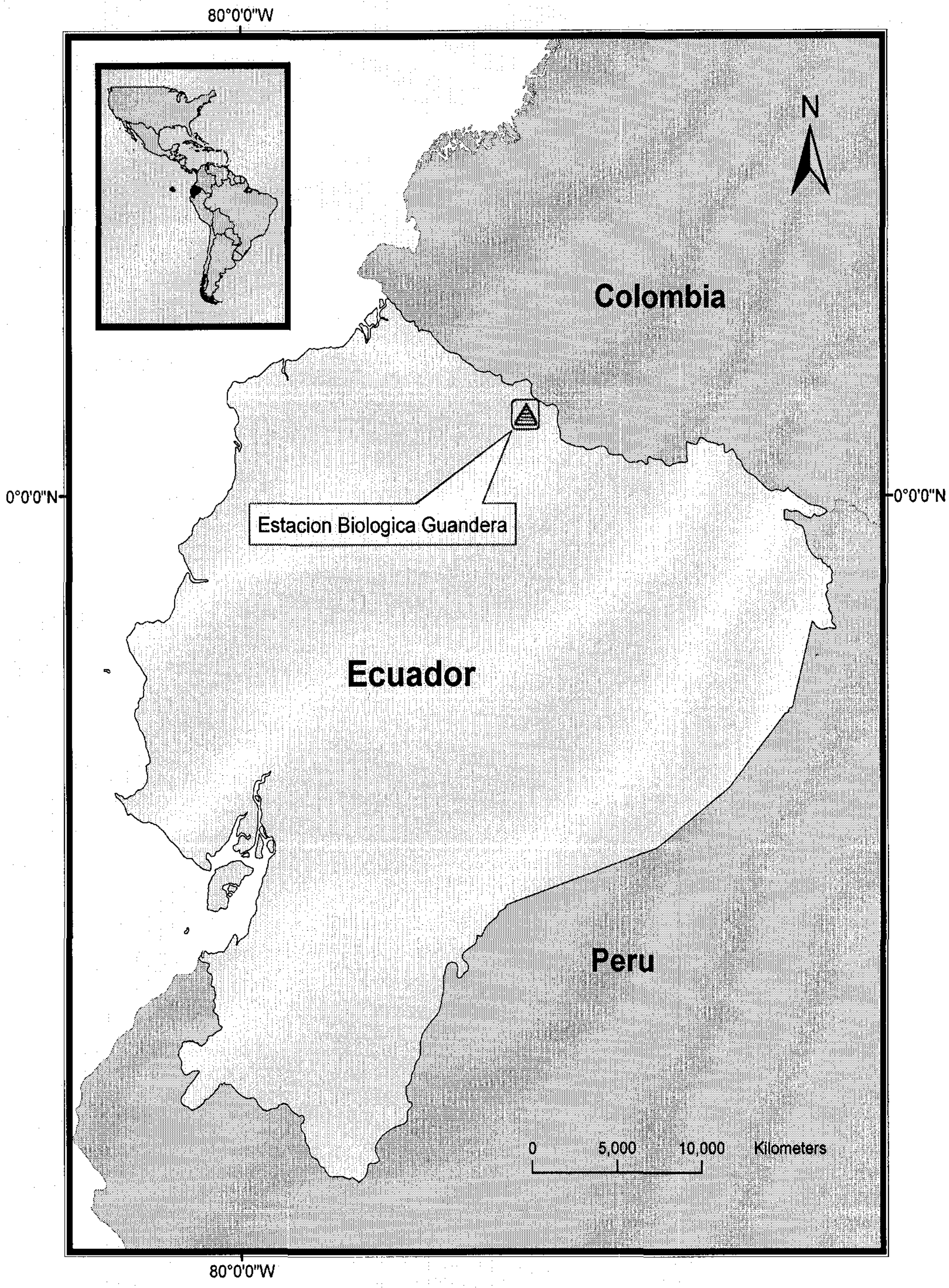


Fig. 4.1. Location of the study site, Estación Biológica Guandera, Carchi, Ecuador.

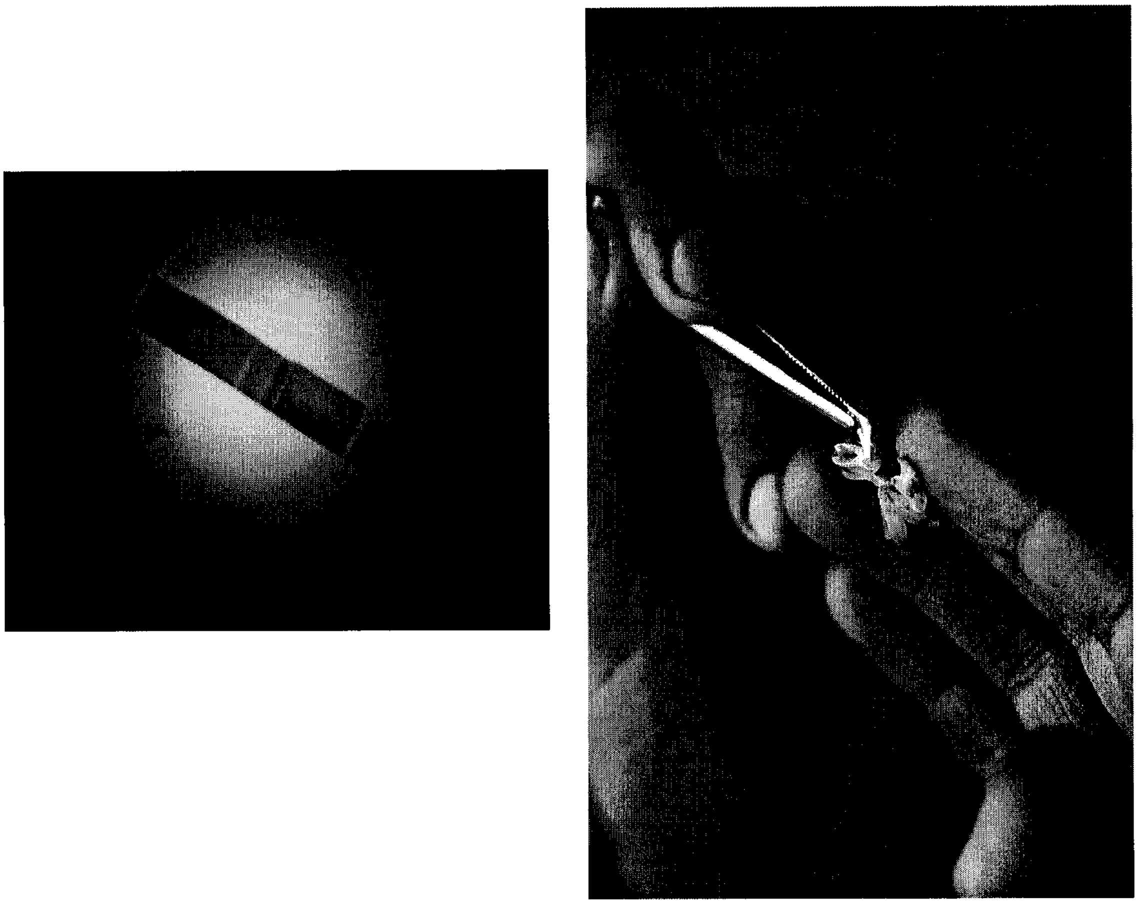


Fig. 4.2. Nectar. A, verification of nectar using paper test strips. B, nectar sampling.

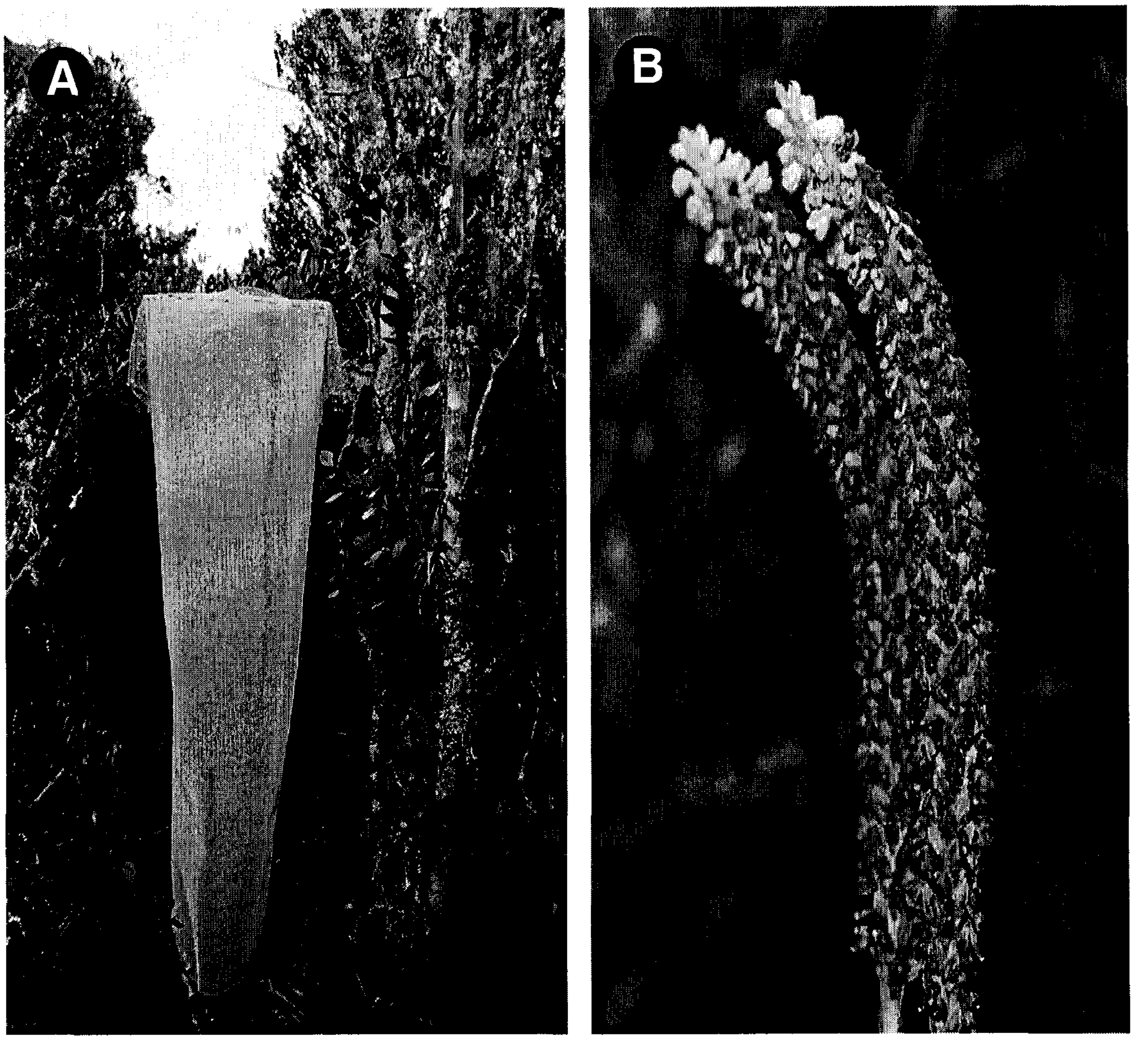


Fig. 4.3. Reproductive biology studies of *Gomphichis crassilabia*. A, bagged plants. B, unbagged plants.

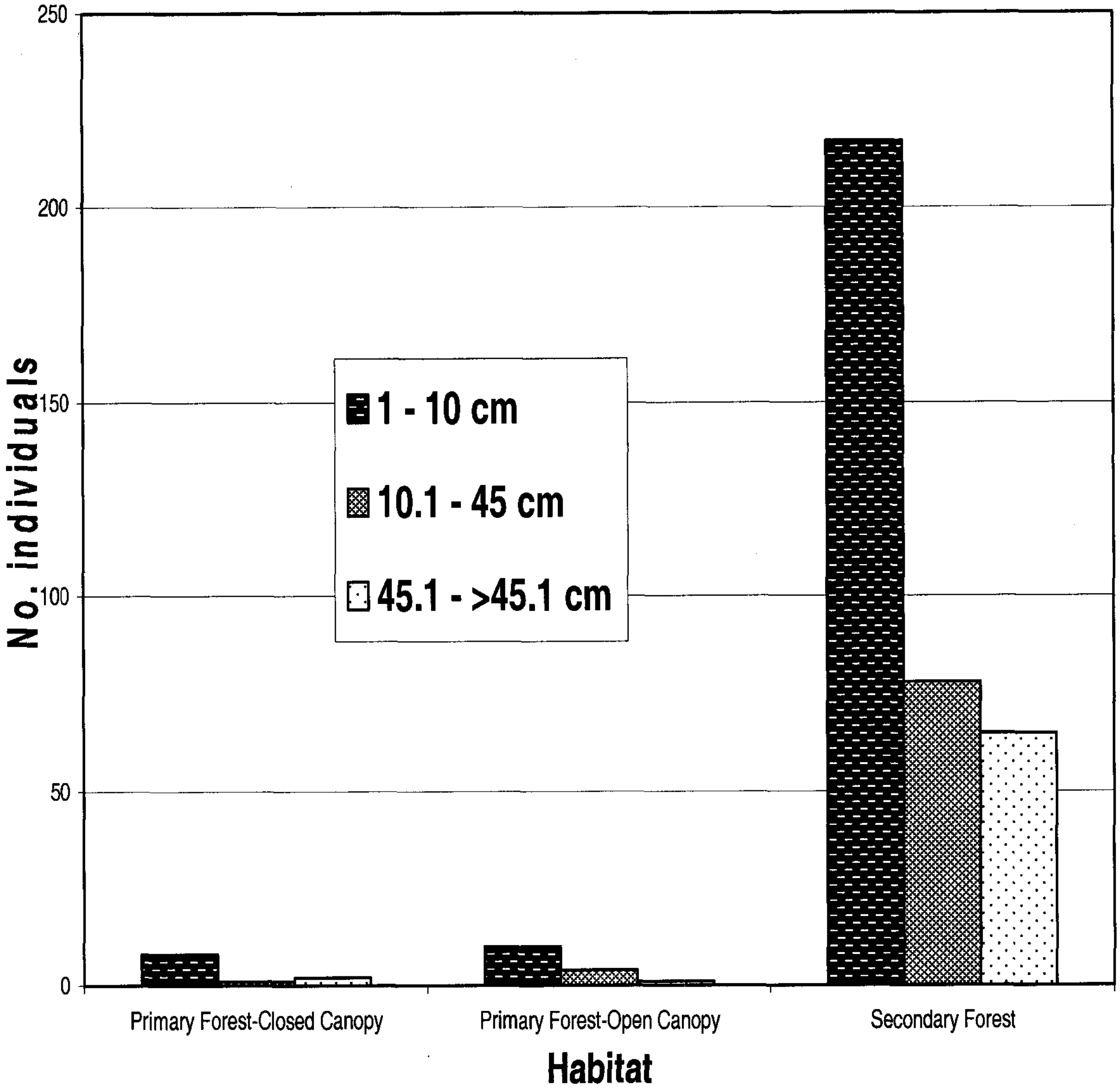


Fig. 4.4. Size class distribution of *Gomphichis crassilabia* in three habitats of the Estación Biológica Guandera

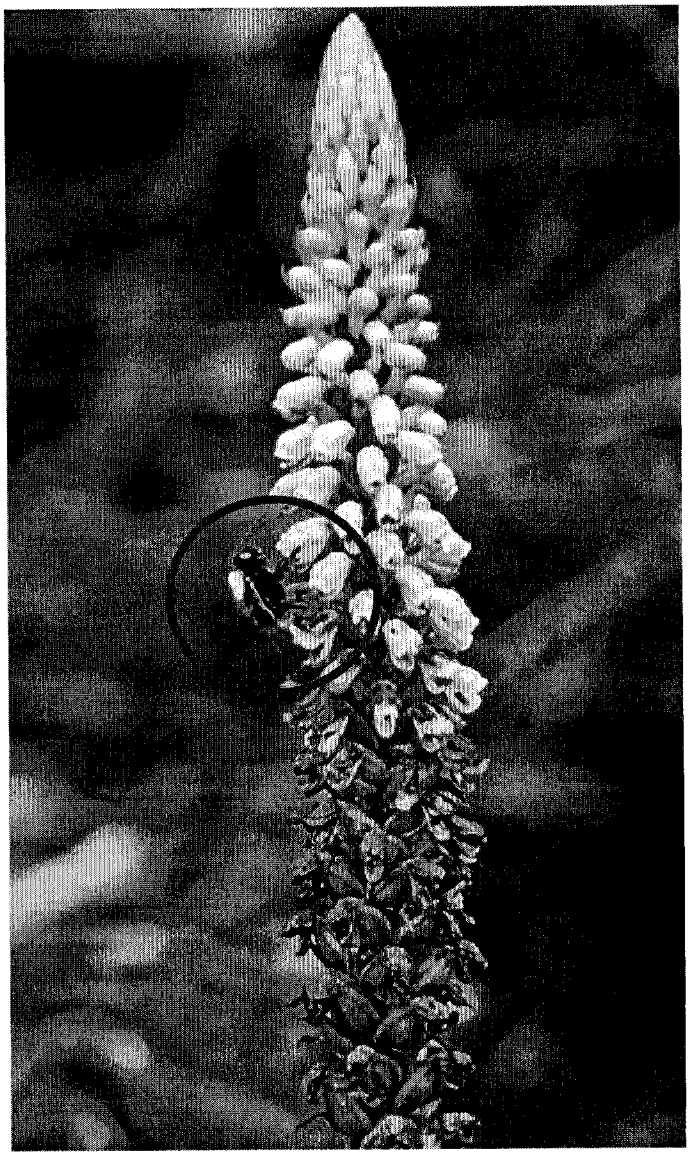
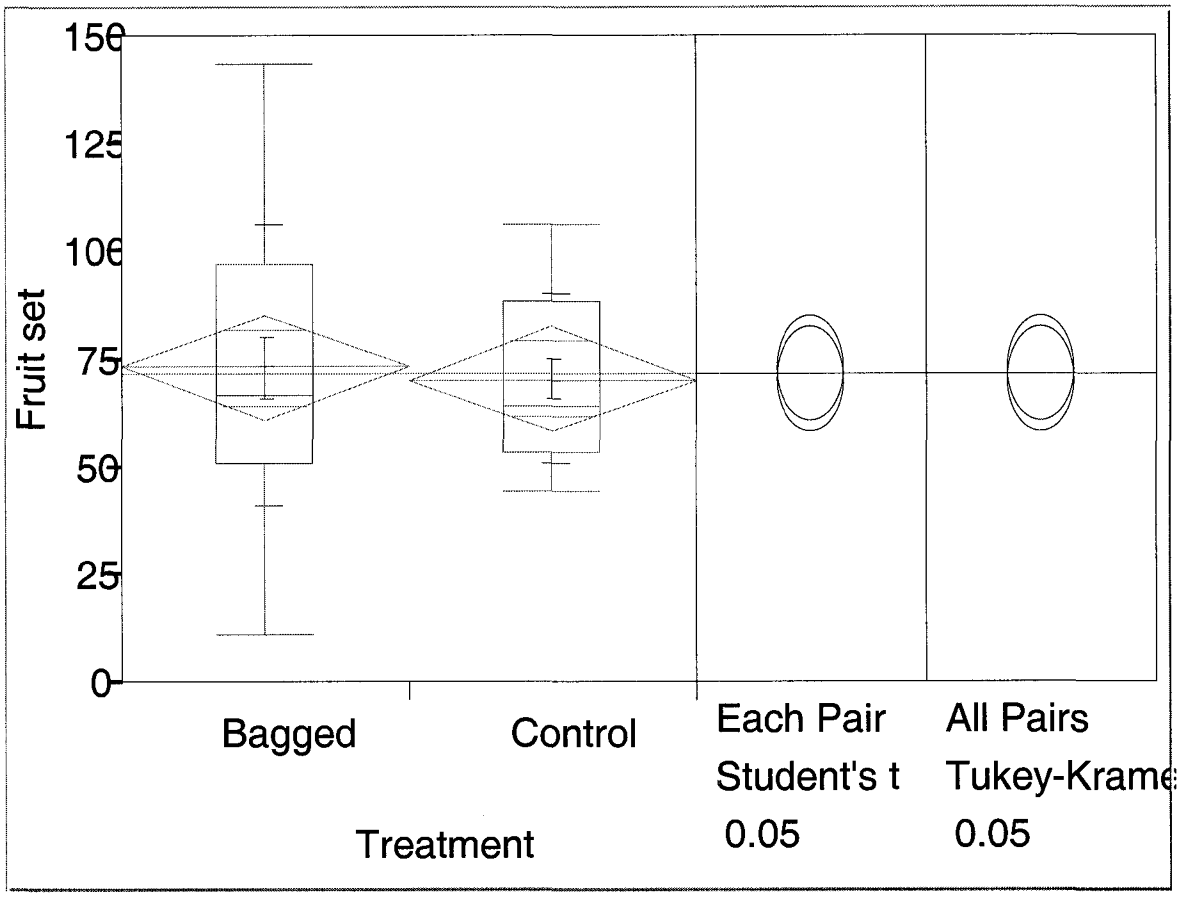


Fig. 4.5. Large bee (*Bombus* sp.) visiting flowers of *Gomphichis crassilabia*.



$t_{cal} = 0.76 < t_{0.05(2)38} = 2.021$

$H_O = H_A$

Fig. 4.6. Graphical test of fruit set mean values.

CHAPTER 5

MOLECULAR PHYLOGENY OF *GOMPHICHIS* LINDL. (ORCHIDACEAE) BASED ON NUCLEAR AND CHLOROPLAST DNA SEQUENCE DATA

5.1. INTRODUCTION

Gomphichis Lindl. as currently delimited is a genus comprising at least 17 species distributed in the New World tropics. It is a member of the subtribe Prescottiinae *sensu* Dressler (1993), which has been recently shown to be paraphyletic on the bases of molecular sequence data (Salazar et al., 2003) and Chapter 2 of this work. In the most recent classification of the Orchidaceae, *Gomphichis* is included in a broadly defined subtribe Cranichidinae *sensu* Dressler (1981), tribe Cranichideae, subfamily Orchidoideae (Chase et al., 2003). The majority of species of *Gomphichis* are delicate to robust terrestrial or facultative epiphytic plants up to 1.80 m tall. Most species are found in the wet and humid montane forests of the Andean region above 2500 m of elevation and some reach the highest elevations flourishing in the subpáramo and páramo ecosystem.

The genus is noted for its peculiar non-resupinate (labellum positioned uppermost) flowers consisting of a very fleshy labellum that along with the sepals, petals and column are displayed on top of the ovaries at a right angle. The flowers are of small to medium size yellow or yellowish, white or greenish in color and are covered with glandular simple or branched trichomes. The dorsal sepal is always free, but the lateral sepals and petals are adnate basally to the labellum and column. The petals are variously ciliate, occasionally erose, and often asymmetrical. The column is geniculate and sigmoid, ornamented by trichomes, or rarely glabrous. The pollinia are four in number, pale yellow, and attached to a circular, brown and wet viscidium. The ovary is ovoid, ellipsoidal to fusiform, ornamented with three well-pronounced ribs, and almost always densely covered by glandular hairs. The fruits are dehiscent capsules that retain the floral segments on top even during maturity. The seeds are numerous, very small, fusiform to spatulate in shape, and wind-dispersed.

The flowers have been observed to be visited primarily by large bees of the genus *Bombus* and can also self-pollinate and self-fertilize (Alvarez, pers. obs.). As a result fruit set is very high (> 85%). Most species of *Gomphichis* have broad distributional ranges while a few have fairly narrow distributions.

Objectives

The objectives of this study are to:

1) Investigate phylogenetic relationships within and among species of *Gomphichis*.
2) Explore evolutionary patterns within the genus.

5.2. MATERIALS AND METHODS

Taxon Sampling. Forty samples representing 13 species of *Gomphichis* were included in this study. Species names follow the revised classification presented in chapter 3 of this work. In addition, *Aa*, *Myrosmodes*, *Porphyrostachys*, *Altensteinia*, and *Stenoptera*, each represented by one species were included in the analysis as outgroups. Voucher data is shown in Table 5.1.

DNA extraction. Total genomic DNA was extracted mainly from silica gel-dried leaf material collected in the field and a few samples taken from herbarium specimens. Approximately 0.2 gm of leaf material was ground in a Lysing Matrix Tube (Bio 101, Carlsbad, CA) and pulverized for 15 seconds in a Bio 101 Fastprep machine at speed 5. The samples were then processed using the QIAGEN DNEasy Plant Mini-Kit (QIAGEN Corp., Valencia, CA) or a modified CTAB (cetyltrimethylammonium bromide) method (Struwe et al., 1998).

PCR. DNA was amplified using the polymerase chain reaction (PCR). All PCR reactions were run on a 9600 GeneAmp PCR system (Applied Byosistems, Foster City, CA) or a Peltier Thermal Cycler DNA engine (DYAD™). Reactions were performed in a 25 μl reaction mixture containing 2.5 μl of 10X PCR buffer which includes 15 mM $MgCl_2$ (Qiagen, Maryland), 9.3 μl autoclaves nanopure water, 2.5 μl BSA (bovine serum albumin), 2.5 μl dnTP (Roche, Indianapolis, IN), 1 μl each of two 20 μM primers, 5 μl betaine (Q solution), 0.2 μl Taq polymerase (Qiagen, Valencia, CA) and 1 μl of genomic DNA. The internal transcribed spacer (ITS) region of nuclear ribosomal DNA, composed of ITS1, the 5.8S gene, and ITS2 was amplified as a single unit using the external forward primer (5'-CCTTATCATTTAGAGGAAGGAG-3') and the reverse primer (5'-TATGCTTAAAYTCAGCGGGT-3') (Standford et al., 2000). Amplification of degraded DNA extracted from herbarium specimens was achieved using the internal forward primer (5'-GCATCGATGAAGAACGCAAGC-3') and the reverse primer (5'-GCTGCGTTCTTCATCGATGC-3') (White et al., 1990). The PCR conditions for amplification of the ITS region consisted of a preheating at 94°C for 4 minutes followed by 30 cycles of denaturation at 94°C for 1 minute, annealing at 55°C for 1 minute and 72°C for 2 minutes and 30 seconds per cycle, and a final extension at 72°C for 10 minutes. Amplification of the *trn*L intron and *trn*L-F spacer utilized the external forward primer "c" (5'CGAAATCGGTAGACGCTACG-3') and the reverse primer "f" (5'-ATTTGAACTGGTGACACGAG-3'). DNA extracted from herbarium specimens was amplified in two separate reactions using in addition to the external primer the internal forward primer "e" (5-GGTTCAAGTCCCTCTATCCC-3') and the internal reverse primer "d" (5'-GGGGATAGAGGGACTTGAAC-3') (Taberlet et al., 1991). The PCR conditions for amplification of the *trn*L-F region included an initial denaturation of 97°C for 2 minutes, followed by 30 cycles consisting of denaturation at 94°C for 1 minute, annealing at 48°C for 2 minutes and extension at 72°C for 2 minutes, with a final extension period at 72°C for 16 minutes.

To detect successful amplification, PCR products were electrophoresed in 1% agarose gels using a DNA ladder as indicator. Successful PCR products were cleaned using the PCR purification kit (QIAGEN, Inc., Valencia, CA). Some amplified *trn*L-F samples produced occasionally multiples bands that were easily separated by electrophoresis in 2% agarose gels using 1xTBE buffer containing 0.05 μl of ethidium bromide as a staining agent. Bands of the appropriate size were identified using a low-mass DNA ladder as a reference, excised and purified using the standard procedure.

Sequencing. Sequencing reactions were performed using Big Dye® Terminator v 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA) and cleaned using Sephadex® G-50 Fine DNA Grade (Amersham Biosciences, Uppsala, Sweden) in Centri-Sep Spin Columns (Princeton Separations, Inc., Adelphia, NJ), then subsequently dried in a vacuum centrifuge. Cycle sequencing fragments were re-suspended and separated as labeled fragments on polyacrylamide gels on an ABI Prism™ 377 automated sequencer (Perkin Elmer Applied Biosystems, Foster City, CA).

Sequence editing and alignment. Sequence chromatograms were assembled and edited using Sequencher v. 4.0.2 for Windows (Gene Codes Corporation, 1998). Sequence alignments were initially made in ClustalX v. 1.81 (Higgins & Sharp, 1988, 1989; Thompson et al., 1997) using the default parameters with the exception of the delayed divergent sequences set to 25% and edited manually using Bioedit v. 5.09 (Hall, 2001).

5.2.6. Phylogenetic analyses. Maximum parsimony analyses were performed, using PAUP* 4.0b10 (Swofford et al., 2001). All characters were equally weighted and gaps were treated as missing data. Heuristic searches to find out the most parsimonious trees were conducted in two steps following suggestions by Maddison (1991). In the first step, islands of most parsimonious trees were found using 1000 random taxon addition sequences, holding 10 trees at each step, with TBR branch swapping. In the second step, the resulting trees were used as starting trees for a heuristic search but this time saving only the shortest trees (MULTREES option in effect) until a maximum limit of 50000 was reached.

Bayesian analyses. To investigate the effects that a non-parsimony approach would have on the final topology, a Bayesian analysis was carried out. The Bayes analysis was used to calculate the posterior probability for each node as implemented in MrBayes v. 3.0B4 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) in the combined ITS and *trn*L-F data set under the general time reversible model (GTR+I+G). One out of every 100 trees was sampled for 5,000,000 generations with four incrementally heated chains, a uniform prior and the gamma shape parameter. Frequency of invariant sites was estimating using the invgamma setting with a uniform prior. The first 500 trees representing the "burn in" period were discarded. A majority rule consensus tree was constructed from the 4500 trees retained. Only posterior probability values of 0.9 or greater were considered significant.

Branch support. To ascertain the relative degree of support for branches, bootstrap support was evaluated using 1000 bootstrap replicates (Felsenstein, 1985), with ten random addition sequences per replicate, holding and saving one tree per replicate. Bootstrap values (bts) were interpreted using three categories: values between 60-69% (weak), between 70-79% (moderate), and between 80-100% (strong). Using the software TreeRot v. 2.0 (Sorenson, 1999) and the same setting with which the strict consensus tree of the combined analyses was generated "Bremer support" or "decay indices" (di) were also estimated.

Character evolution. Optimization of selected morphological characters onto the gene tree resulting form the combined analysis were performed using MacClade v. 4.06 (Maddison & Maddison, 2003).

5.3. RESULTS

Abbreviations and figures. In the resulting trees from parsimony and Bayesian inference, bootstrap values (bts) and posterior probabilities (pp) are shown above branches (Fig. 5.1-5.4). A summary gene tree from the combined parsimony analysis in which bootstrap values are indicated above branches and decay indices/posterior probabilities are printed below branches will be also used for discussion and it is shown in Figure 5.5. The following abbreviations are used in the text and figure captions: L= tree length in number of steps, CI= consistency index, and RI= retention index. The species groups referred to as distinctly three-lobed labellum (*G. viscosa*, *G. traceyae*, *G. adnata*, *G.* unnamed 1, *G. costaricensis*, *G. cundinamarcae*, *G. bogotensis* and *G. merzii*) and weakly three-lobed labellum (*G. caucana*, *G. crassilabia*, *G. valida*, *G. goodyeroides*, *G. macbridei*, and *G. plantaginifolia*) are labeled on all trees. Within the former group, the "*G. viscosa* complex" (consisting of *G. viscosa*, *G. traceyae*, *G. adnata*, *G.* unnamed 1, *G. costaricensis*, and *G. cundinamarcae*), and within the latter group, the "*G. valida* complex" (containing *G. caucana*, *G.* unnamed 2, *G. crassilabia* and *G. valida*) are discussed in the text.

***trn*L-F.** The *trn*L-F matrix contains 1228 characters of which 174 (14.17%) are variable and 102 (8.31%) are parsimony informative (Table 5.2).

Analysis of these data resulted in 1005 trees of maximum parsimony (L of 234 steps, CI of 0.8162, and RI of 0.888). Figure 5.1 shows the strict consensus tree of 1005 parsimonious trees. The trees differed in their arrangements within the obscurely three-lobed labellum clade.

The *trn*L-F tree unlike previously thought provides a strong evidence for the monophyly of *Gomphichis* (100% bts). In this analysis, *Gomphichis* is distantly related to *Stenoptera* and rather sister to a highly supported clade consisting of *Porphyrostachys*, *Myrosmdoes* and *Aa*. In the *trn*L-F matrix *Gomphichis* is characterized by an 8 bp deletion at position 361 of the aligned matrix.

The *trn*L-F phylogeny provided little resolution within *Gomphichis*. A single highly supported clade (83% bts) comprising species of the genus with a distinctive three-lobed labellum was recovered. All species of this clade share an 11 bp deletion at position 774 of the matrix. Within this clade, a moderately supported grade (63% bts), hereafter referred to as the "*Gomphichis viscosa complex*" and composed of at least 6 taxa (*G. viscosa*, *G. traceyae*, *G. adnata*, *G. costaricensis*, *G. cundinamarcae* and *G.* unnamed 1), emerged. This complex is sister to *G. merzii* and *G. bogotensis*, species of Central America and the Northern Andes.

The accessions of the remaining species of *Gomphichis* received low to high bootstrap support values. Although these species do not form a highly supported clade, they have in common a 29 bp deletion at position 1042 of the aligned matrix. Only one accession of *G. crassilabia* did not associate with the remaining accessions that form a monophyletic and highly supported clade (86% bts). *Gomphichis plantaginifolia* as here circumscribed is strongly supported (93% bts). Two accessions of *G. plantaginifolia* from Bolivia have in common a 17 bp deletion at position 774 of the matrix and its relationship is well-supported (91% bts). This deletion, however, is lacking in the third accession from central Peru.

ITS. The ITS data set provided a total of 738 characters of which 140 (18.97%) are variable and 77 (10.43%) are potentially informative (Table 5.2.). The five-most parsimonious trees have 170 steps, a CI of 0.8882, and a RI of 0.9488. The strict consensus of these trees is shown in Fig. 5.2. Most of the differences among the most parsimonious trees were the arrangements of the weakly three-lobed labellum species, and the accessions of *G. valida*, and unnamed taxon 1.

All sampled species of *Gomphichis* share a 1 bp deletion at position 684 of the aligned matrix. Once again, the monophyly of *Gomphichis* is highly supported (100% bts). Three monophyletic clades were recovered. The most basal clade consists of accessions of *G. plantaginifolia*, a species with an obscurely three-lobed labellum and southern distribution, which is highly supported (83% bts). *Gomphichis plantaginifolia* is sister to a weakly supported clade (59% bts) comprising two clades: one containing those species exhibiting weakly differentiated labellum lobes (61% bts), and a second clade strongly supported (89% bts) comprising species with distinctive labellum lobes. In the former clade, a moderately supported node (65% bts) without resolution comprises species of the *valida* complex and *G. macbridei.* These taxa in turn are sister to *G. goodyeroides*.

Combined ITS and *trn*L-F. The partition homogeneity test of the ITS and *trn*L-F sequence data resulted in a P value of (0.068) indicating that the data sets are congruent and have similar phylogenetic structure (Cunningham, 1997). Furthermore, as there were no conflicts in the separate analyses, the two data sets were combined, providing 179 parsimony informative characters out of 1243 characters. The parsimony analysis resulted in 168 most parsimonious trees with a length of 410 steps, a CI of 0.8341, and a RI of 0.9099. The strict consensus tree is shown in Fig. 5.3.

The resulting topology in the combined analysis is highly congruent with the independent analyses, and bootstrap support for all branches is increased. The resulting tree from the Bayesian analysis of the combined ITS and *trn*L-F data sets is generally identical to the parsimony tree obtained for the same data set, but fully resolved (Fig. 5.4).

In the combined parsimony and Bayesian analyses, the placement of *Gomphichis plantaginifolia* as sister to the remaining sampled species of the genus is highly supported (bts= 98%, pp= 1.00, di= 6). The clade containing species of *Gomphichis* with slightly three-lobed labellum is only weakly supported (bts= 53%, pp= 0.88, di= 1), but it segregates into one monophyletic clade (bts= 76%, pp= 0.99, di= 1) in which species with a tubular labellum (in natural position) and basically linear and thick-fleshy leaves cluster, and a second clade of two species (*G. goodyeroides* to *G. macbridei*) for which the sister relationship is not supported (bts= <50%, pp= 0.79, di= 1). The second major clade of *Gomphichis* with distinctly 3-lobed labellum is strongly supported (bts= 99%, pp= 1.00, di= 8) and is composed of three lineages: a clade comprising at least six taxa including *Gomphichis viscosa*, *G. traceyae*, *G. costaricensis*, *G. cundinamarcae*, *G. adnata*, and unnamed taxon 2. *Gomphichis merzii* and *G. bogotensis*, are the basal-most species of the second major clade.

Population sampling. Nine of the 13 sampled species of *Gomphichis* (11 out of the 15 taxa represented including the unnamed ones) were represented by more than one sample in each data set. None of the analyses rejected the monophyly of any of the species, although not all accessions of *G. crassilabia* and *G. valida* in the *trn*L-F and ITS phylogenies respectively completely cluster together, apparently due to little phylogenetic signal.

5.4 DISCUSSION

A summary tree that combines the results from parsimony and Bayesian inferences is depicted in Figure 5.5. This cladogram will be used in the discussion.

Monophyly of *Gomphichis*. Chloroplast and nuclear DNA sequences demonstrate that *Gomphichis* is a monophyletic genus. All sampled species of *Gomphichis* belong to a single strongly supported clade (bts=100%, di=32, pp=1.00). This result is therefore consistent with the most recent treatments of *Gomphichis* as an independent genus (Schweinfurth, 1958; Foldats, 1969; Garay, 1978). This analysis further suggests that *Gomphichis* is more closely allied with *Porphyrostachys*, *Myrosmodes* and *Aa* than with *Stenoptera* or *Altensteinia*. *Stenoptera* is distantly related to *Gomphichis* and is the most basal species of the clade that contains the orchids of high altitudes of the Neotropics.

Vargas (1997) identified two morphological synapomorphies supporting the monophyly of *Gomphichis*: an extremely fleshy labellum, and saccate labellum base. Optimization of these characters onto the recovered phylogeny (not shown) concurs with Vargas's findings.

Phylogenetic relationships among *Gomphichis* species. The groupings based on the distinctiveness of the labellum lobes show differing patterns of phylogenetic status. The species with wide and well defined lateral lobes form a clade in all parsimony and Bayesian analyses with strong bootstrap support and posterior probability. Although the monophyly of species of this clade is clear, the relationships within it are not fully resolved. On the other hand, the obscurely three-lobed labellum group is paraphyletic in the nuclear and combined analyses, with *G. plantaginifolia* well-supported as the sister species to the rest of the sampled taxa of the genus. The other clade of species with weakly 3-lobed labellum contains the majority of species but their relationships are not completely determined. This clade is sister to the species with distinctive labellum lobes, but this relationship is weakly supported.

There are two species of *Gomphichis*, *G. crassilabia* and *G. plantaginifolia*, that appear to include two assemblages, each based on molecular sequence data. In the current taxonomic treatment (chapter 3 of this work) these accessions have shown to be morphologically cohesive entities.

Moreover, no qualitative characters were found to characterize these accessions as different taxa.

Phylogeny, distribution, and habitat preferences of *Gomphichis*. The clades containing species of *Gomphichis* with a weakly 3-lobed labellum are restricted to the Andean region and are more diverse in the northern Andes (Venezuela to southern Ecuador). One species of this clade, *G. crassilabia* has been reported in the isolated Cordillera de Los Llanganates in eastern Ecuador. The members of this clade prefer the humid and cold environments and the highest elevations of the Andes above 1750 m some of them reaching nearly 5000 m. Moreover, with the sole exception of *G. goodyeroides*, the species of this clade are exclusively terrestrial plants. Some morphological features that appear to be correlated with the habitat preferences of the members of this clade include: thick-coriaceous leaves, a large number of sheaths covering the peduncle, compact and wide inflorescences, dense pubescence of the flowers, and a labellum longer than wide.

The species comprising the clade with distinct labellum lobes have more widespread distributions. For example, *Gomphichis cundinamarcae, G. costaricensis* and *G. adnata* occur in the northern, eastern and western extreme points of the distribution of the genus, and *G. viscosa* exhibits the largest distributional range among *Gomphichis* species. Furthermore, the species of the genus reported in Central America (e.g., *G. hetaerioides* not included in the molecular phylogeny) most likely belong to this clade. The great majority of species possessing a labellum with conspicuous lobes seem to prefer those habitats below 3500 m and some of them even grow in the lowest altitudinal limits found within the genus (1,000 m). *Gomphichis traceyae*, the species that displays the largest ecological plasticity within *Gomphichis* is also included in this clade. The morphological characters shared by the species of this clade include: thin-coriaceous leaves, loose and narrow inflorescences, few sheaths along the peduncle, sparse pubescent flowers, wider than long labellum.

Evolution of selected characters in *Gomphichis*. When groupings based on the degree of distinctiveness of the lobes of the labellum are superimposed on the phylogeny, the species with distinctive labellum lobes are monophyletic and highly supported, and those species with weak labellum lobes appear paraphyletic and only moderately supported (Fig. 5.6). In contrast the species groups delimited by habit preferences, terrestrial or epiphytic, are not fully congruent with the major groupings recovered in phylogenetic reconstruction (Fig. 5.7). Facultative epiphytism has evolved several times within *Gomphichis*. A similar result was obtained when inflorescence density was plotted onto the strict consensus tree (Fig. 5.8). The arrangement of the flowers into loose and compact inflorescences has evolved more than once within the genus. Species of *Gomphichis* with compact inflorescences show the plesiomorphic condition.

5.5. CONCLUSIONS

Results from the parsimony and Bayesian analyses strongly support the monophyly of *Gomphichis*. The genus is split into three major lineages: two clades consist of species with a weakly 3-lobed labellum and a third clade comprises species with a distinctly 3-lobed labellum. The character states related to labellum morphology appear to reflect the evolutionary history of species of the genus. This resulting phylogeny shows that labellum with distinctly 3-lobed labellum has evolved once in the genus and is the synapomorphyc condition among those species of *Gomphichis*.

Although there is no doubt as to the monophyly of *Gomphichis*, further work is necessary to resolve relationships within the genus. One obvious approach would be to obtain a better estimate of phylogenetic relationships using quickly evolving molecular markers. Possible candidates include three noncoding cpDNA regions (*trnD*^{GUC}-*trnT*^{GGU}, *rpoB*-*trnC*^{GCA}, and *trnS*^{GCU}-*trnG*^{UUC}) that among several phylogenetic lineages provided the greatest number of phylogenetically informative characters (Shaw et al., 2005). These noncoding regions were shown by Shaw et al. to be more variable than the ITS and *trn*L-F molecular markers used in his study. In addition coding for informative gaps will be important because these regions may provide additional informative characters useful for resolving phylogenetic relationships among *Gomphichis* species.

The molecular based phylogeny has been useful in helping to clarify the circumscription of species of *Gomphichis*, the nomenclature of the genus and to identify infertile material. The resulting phylogeny from the combined analysis was also used as the bases for discussion in the individual species descriptions presented in chapter 3.

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Table 5.1. Species of *Gomphichis* and outgroups sequenced.

Genus	**Species**	**Author**	**Collector**	**Number**	**Voucher**	**Country**
Aa	*calceata*	(Rchb. f.) Schltr.	A. Alvarez	2899	NY, QCNE	Ecuador
Altensteinia	*fimbriata*	Schltr.	A. Alvarez	2726	NY, QCNE	Ecuador
Gomphichis	*adnata*	(Ridl.) SChltr.	A. Alvarez	2981	NY, PORT	Venezuela
Gomphichis	*adnata*	(Ridl.) SChltr.	A. Alvarez	2986	NY, PORT	Venezuela
Gomphichis	*bogotensis*	Renz	A. Alvarez	2965	NY, QCNE	Ecuador
Gomphichis	*bogotensis*	Renz	A. Alvarez	3000	NY, PORT	Venezuela
Gomphichis	*bogotensis**	Renz	Bello	86	COL	Colombia
Gomphichis	*caucana*	Schltr.	A. Alvarez	2780	NY, QCNE	Ecuador
Gomphichis	*caucana*	Schltr.	A. Alvarez	2734	NY, QCNE	Ecuador
Gomphichis	*caucana*	Schltr.	A. Alvarez	2775	NY, QCNE	Ecuador
Gomphichis	*caucana*	Schltr.	B. Merino	4685	AAU	Ecuador
Gomphichis	*caucana*	Schltr.	L. Suin	1030	NY, QCNE	Ecuador
Gomphichis	*costaricensis*	(Schltr.) Ames, F. T. Hubb & C. Schweinf.	C. K. Horich	sn	US	Costa Rica
Gomphichis	*crassilabia*	Garay	A. Alvarez	2844	NY, QCNE	Ecuador
Gomphichis	*crassilabia*	Garay	A. Alvarez	2878	NY, QCNE	Ecuador
Gomphichis	*crassilabia*	Garay	A. Alvarez	2861	NY, QCNE	Ecuador
Gomphichis	*crassilabia*	Garay	A. Alvarez	3014	NY, QCNE	Ecuador
Gomphichis	*crassilabia*	Garay	A. Alvarez	2799	NY	Ecuador
Gomphichis	*crassilabia*	Garay	L. Hølm-Nielsen	28604	AAU	Ecuador
Gomphichis	*cundinamarcae*	Renz	A. Alvarez	3005	NY, PORT	Venezuela
Gomphichis	*goodyeroides*	Lindl.	T. Henning	256	M	Peru
Gomphichis	*macbridei*	C. Schweinf.	A. Alvarez	2806	NY, QCNE	Ecuador
Gomphichis	*merzii*	Senghas	A. Alvarez	2977	NY, QCNE	Costa Rica
Gomphichis	*merzii*	Senghas	S. Merz	sn	HEID-cultivated	Costa Rica
Gomphichis	*plantaginifolia*	C. Schweinf.	C. Feuillet	15037	LPB	Bolivia
Gomphichis	*plantaginifolia*	C. Schweinf.	L. McCook	1159	LPB	Bolivia

Genus	Species	Author	Collector	Number	Voucher	Country
Gomphichis	*plantaginifolia*	C. Schweinf.	M. Weigend	2000-415	NY	Peru
Gomphichis	*traceyae*	Rolfe	A. Alvarez	2569	NY, QCNE	Ecuador
Gomphichis	*traceyae*	Rolfe	A. Alvarez	2632	NY, QCNE	Ecuador
Gomphichis	*traceyae*	Rolfe	A. Alvarez	2569	NY, QCNE	Ecuador
Gomphichis	*traceyae*	Rolfe	A. Alvarez	2712	NY, QCNE	Ecuador
Gomphichis	*traceyae*	Rolfe	H. Balslev	24090	AAU	Ecuador
Gomphichis	*traceyae*	Rolfe	S. Merz	sn	NY	Venezuela
Gomphichis	unnamed taxon 1		A. Alvarez	2888	NY, QCNE	Ecuador
Gomphichis	unnamed taxon 1		A. Alvarez	3012	NY, QCNE	Ecuador
Gomphichis	unnamed taxon 2		A. Alvarez	2996	NY, PORT	Venezuela
Gomphichis	*valida*	Rchb. f.	A. Alvarez	2759	NY, QCNE	Ecuador
Gomphichis	*valida*	Rchb. f.	A. Alvarez	2705	NY, QCNE	Ecuador
Gomphichis	*valida*	Rchb. f.	A. Alvarez	2687	NY, QCNE	Ecuador
Gomphichis	*valida*	Rchb. f.	A. Alvarez	2688	NY, QCNE	Ecuador
Gomphichis	*valida*	Rchb. f.	M. Weigend	2000-234	NY	Peru
Gomphichis	*viscosa*	(Rchb. f.) Schltr.	A. Alvarez	2910	NY, QCNE	Ecuador
Gomphichis	*viscosa*	(Rchb. f.) Schltr.	A. Alvarez	2773	NY, QCNE	Ecuador
Porphyrostachys	*pilifera*	(Kunth) Rchb. f.	A. Alvarez	2699	NY, QCNE	Ecuador
Stenoptera	*ecuadorana*	Dodson & C. Vargas	A. Alvarez	2913	NY	Ecuador

* genbank accession number= GB0544495

Table 5.2. Comparison of results from *trn*L-F, ITS, and combined data matrices for *Gomphichis*.

	***trn*L-F**	**ITS**	***trn*L-F and ITS**
Total characters included	1228	738	1966
Variable characters (% of total)	174 (14.17%)	140 (18.97%)	314 (15.97%)
Potential informative characters (% of variable, % of total)	102 (8.31%/58.62%)	77 (55%/10.43%)	179 (57%/9.1%)
No. of equally parsimonious trees	1005	5	168
Tree length	234	170	410
CI	0.8162	0.8882	0.8341
RI	0.8880	0.9488	0.9099
No. of clades supported by bootstrap (=> 80%)	9	9	12

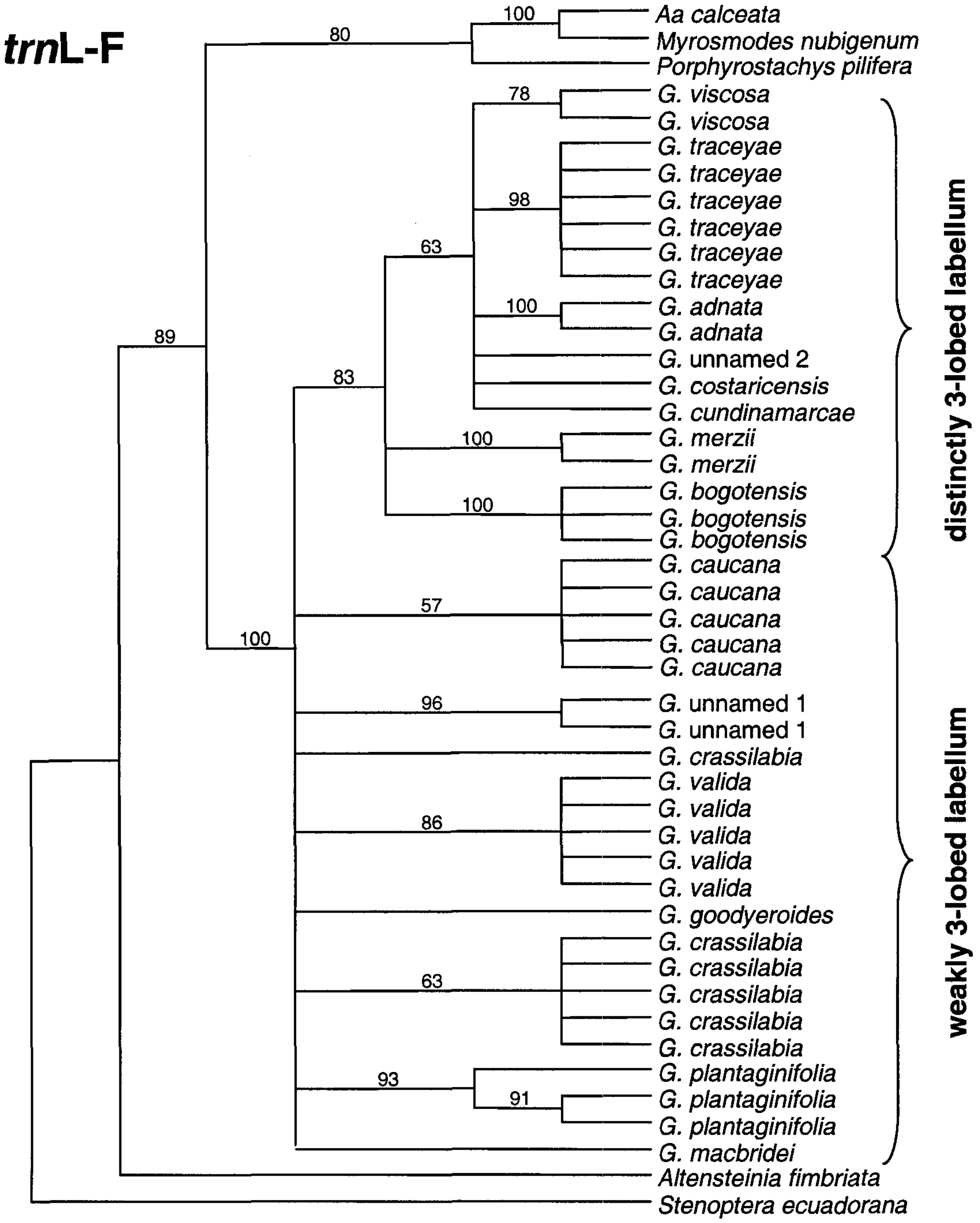

Fig. 5.1. Strict consensus of 1,005 trees from the parsimony analysis of *trn*L-F sequence data. L= 234, CI= 0.8162, and RI= 0.888. Bootstrap values are indicated above branches.

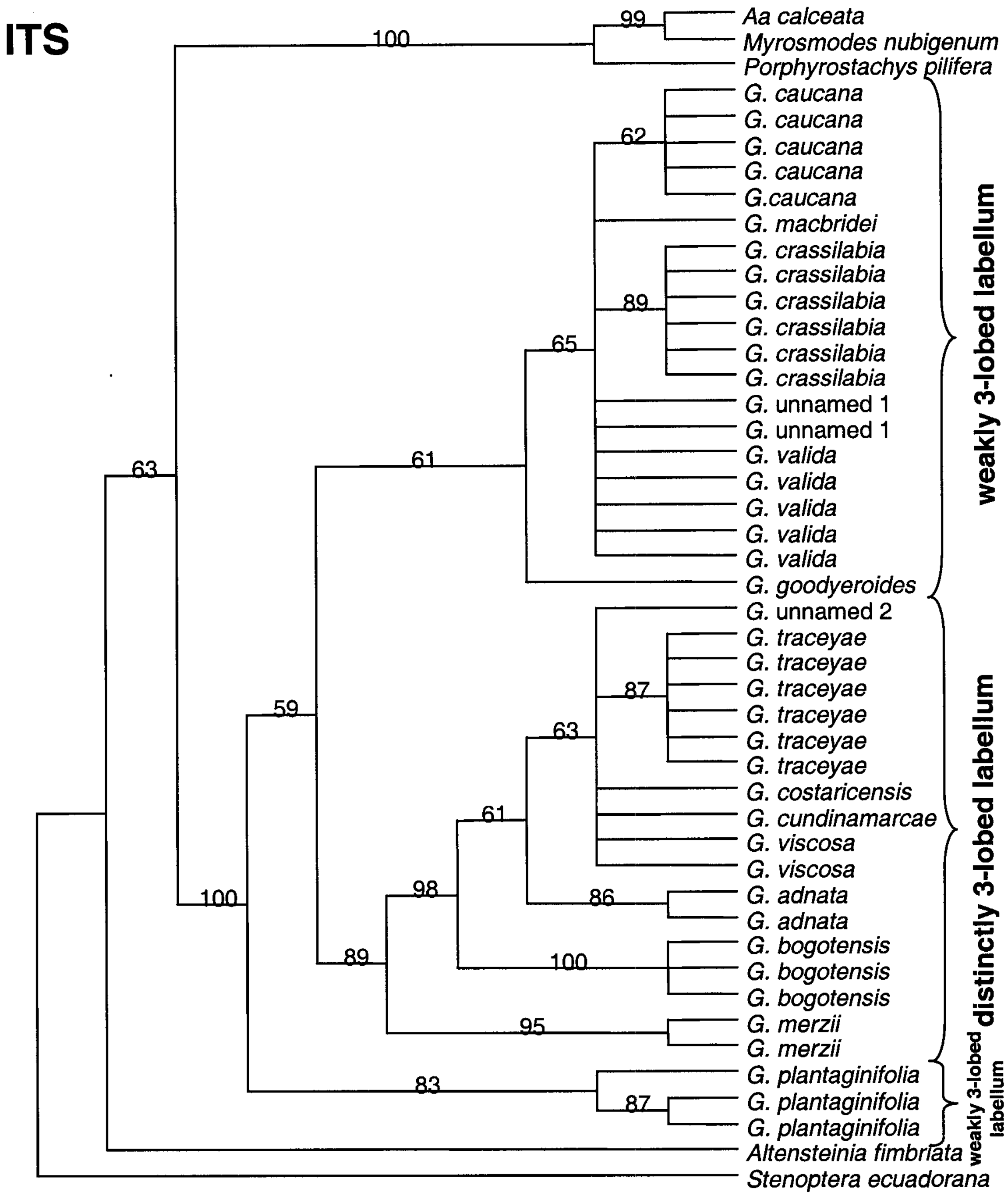

Fig. 5.2. Strict consensus of 5 trees from the parsimony analysis of ITS sequence data. L= 170, CI= 0.8882, and RI= 0.9488. Bootstrap values are indicated above branches.

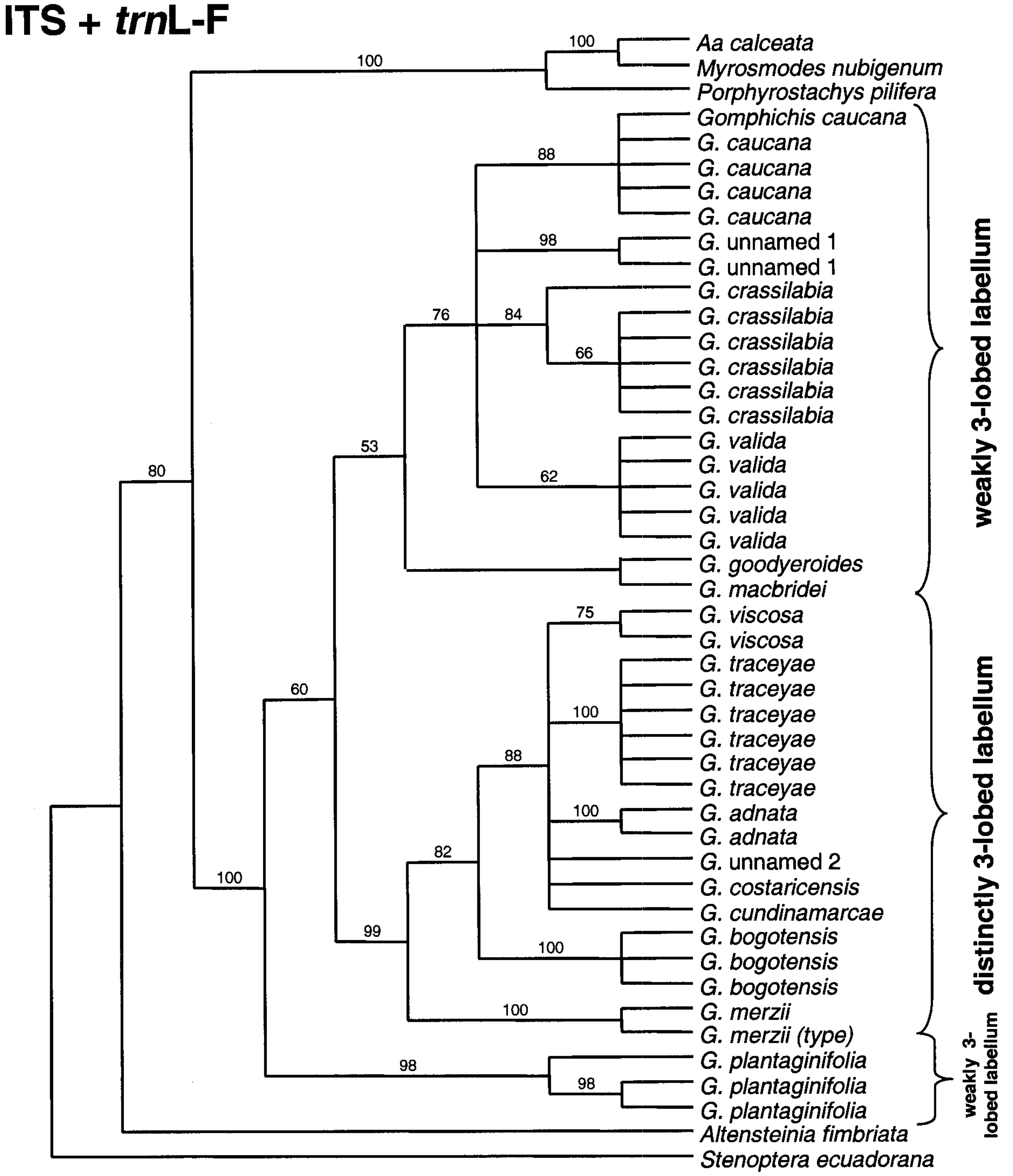

Fig. 5.3. Strict consensus of 168 trees from the parsimony analysis of ITS and *trn*L-F sequence data. L= 410, CI= 0.8341, and RI= 0.9099. Bootstrap values => 50% are indicated above branches.

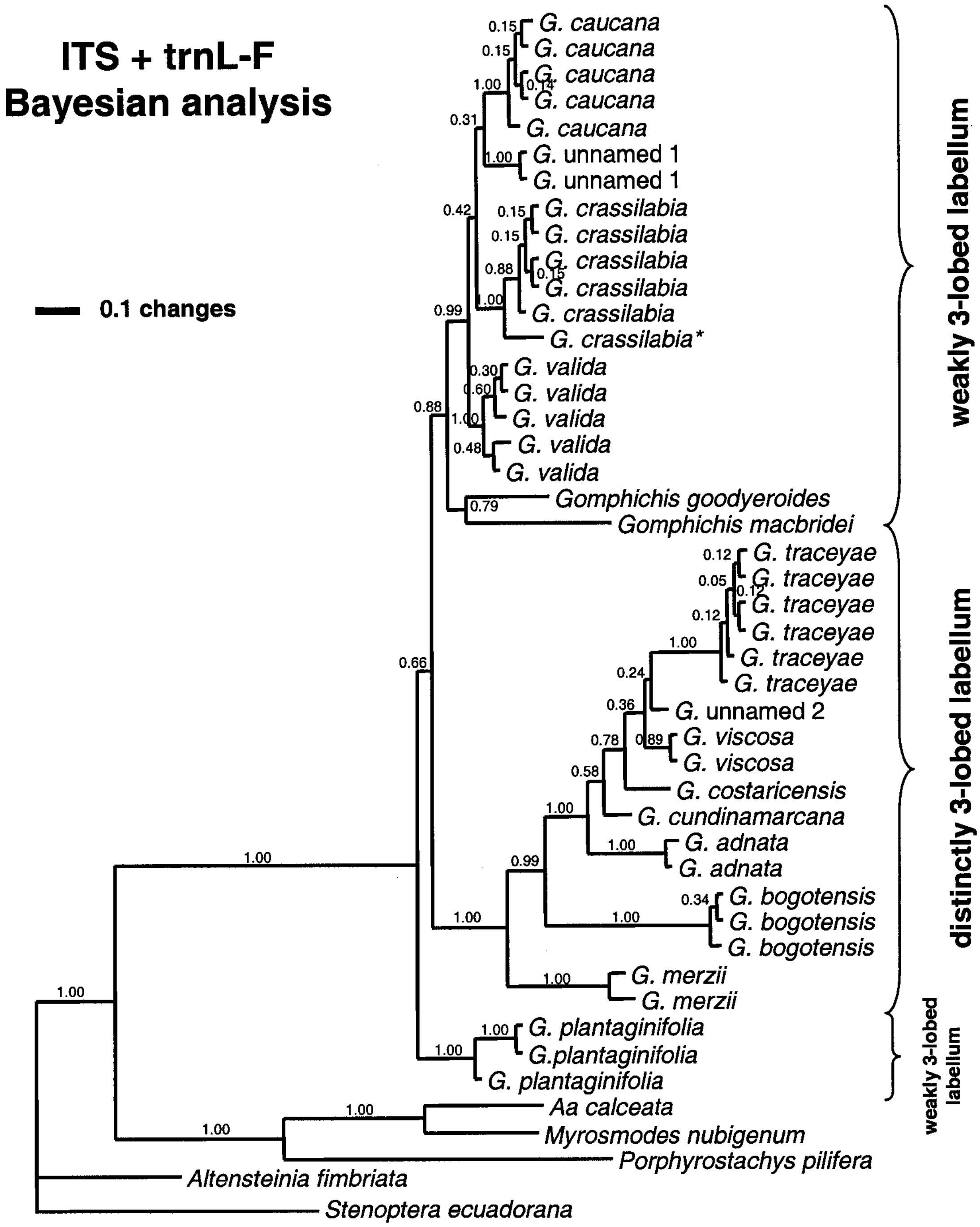

Fig. 5.4. Majority rule consensus of 4,500 trees (500,000 generations) from the Bayesian analysis under the GTR+I+G model. Posterior probabilities are shown above branches.

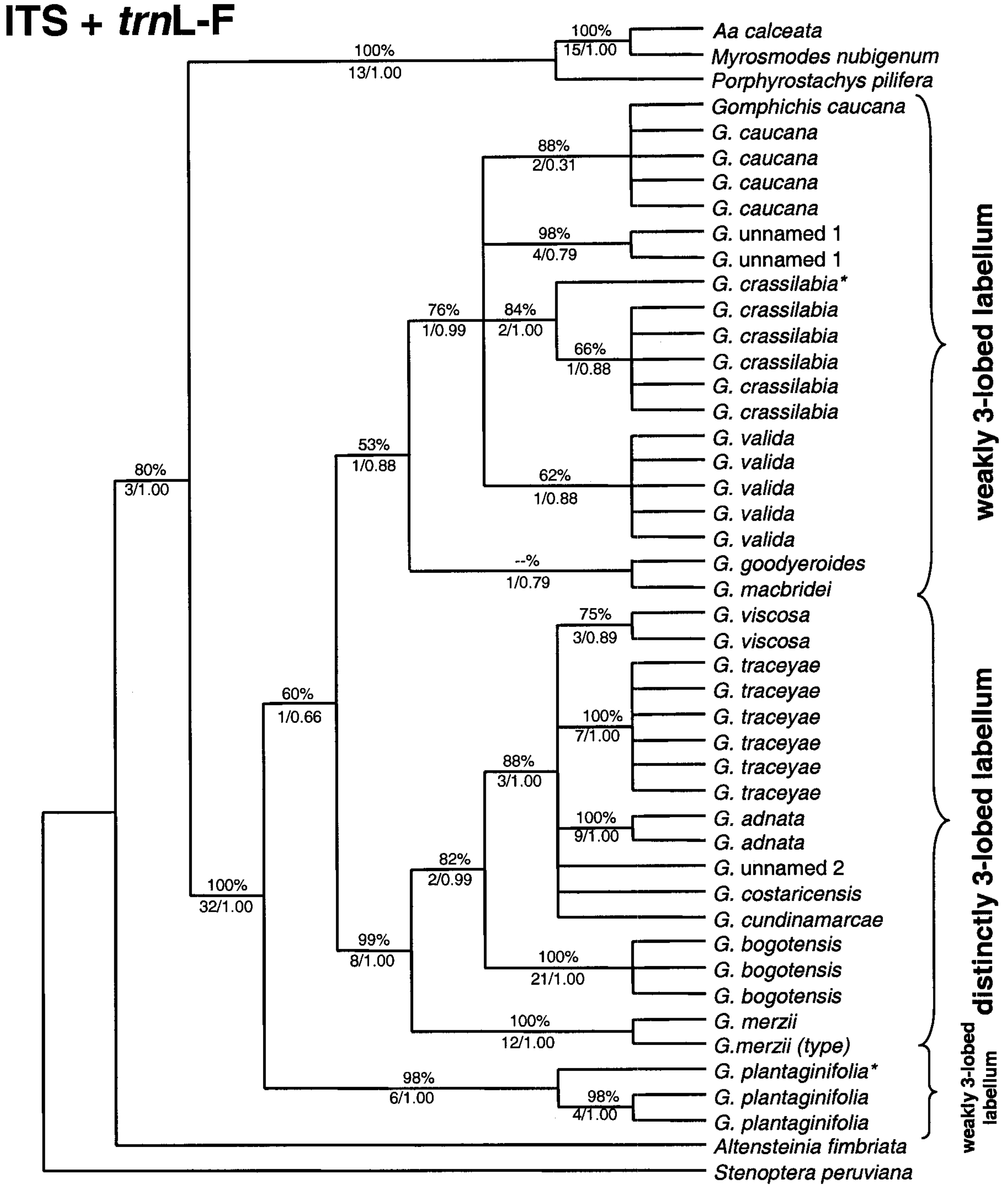

Fig. 5.5. Strict consensus of 168 trees from the parsimony analysis of ITS and *trn*L-F sequence data. L= 410, CI= 0.8341, and RI= 0.9099. Bootstrap values => 50% are indicated above branches; decay indices/posterior probabilities are indicated below branches.

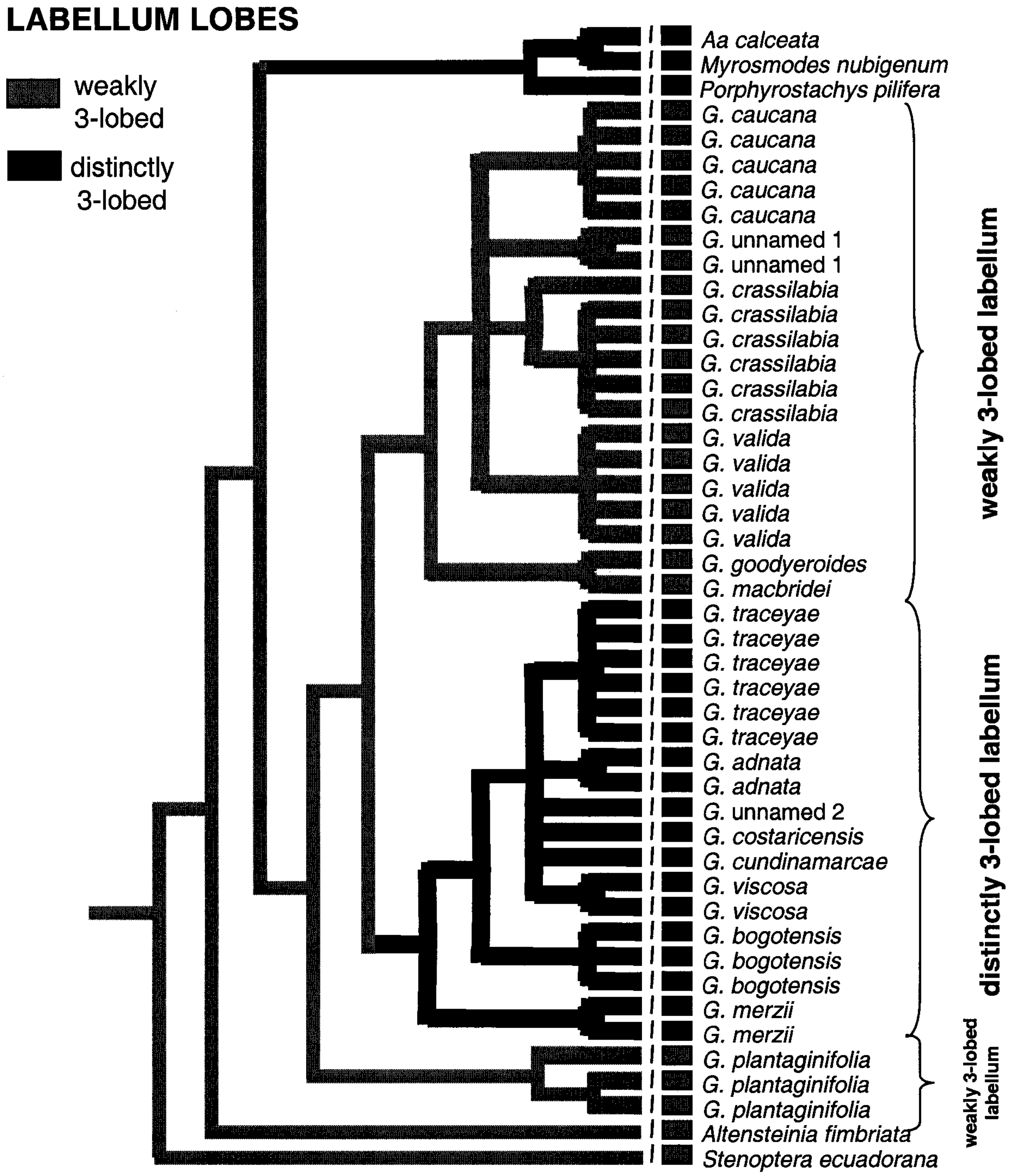

Figure 5.6. Optimization of labellum lobes onto the strict consensus tree from parsimony analyses of ITS and *trn*L-F.

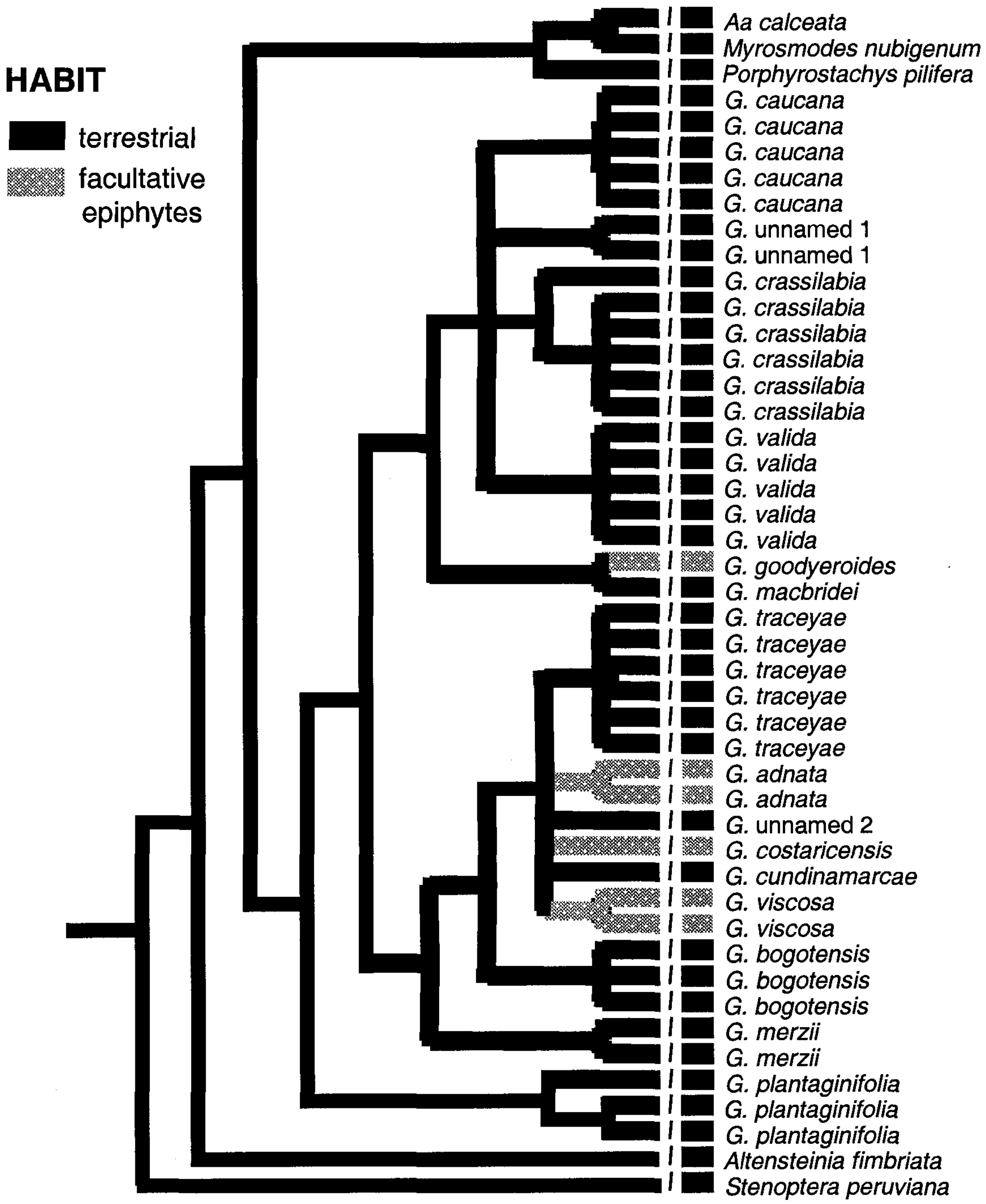

Figure 5.7. Optimization of habit preferences onto the strict consensus tree from parsimony analyses of the ITS and *trn*L-F sequence data.

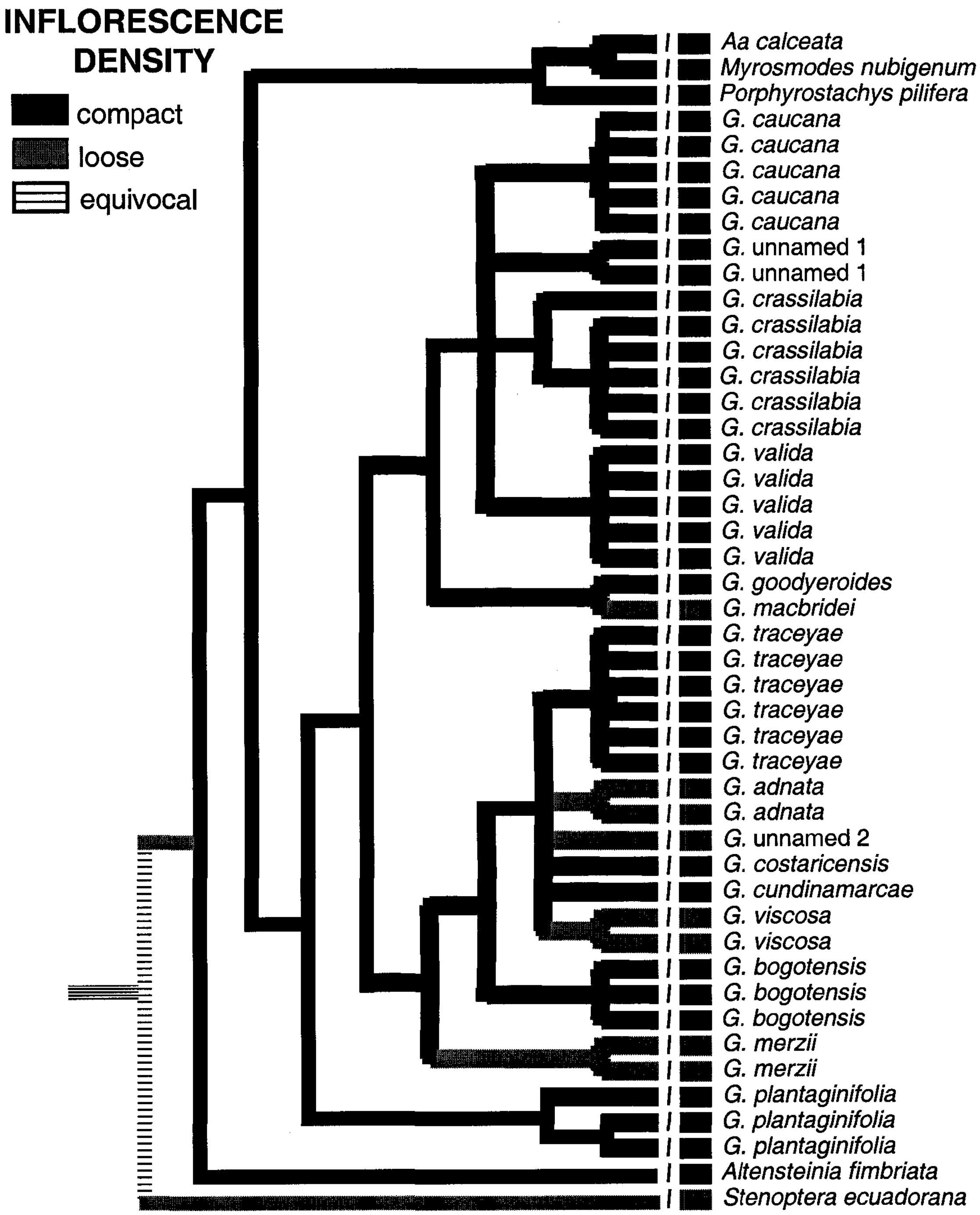

Figure 5.8. Optimization of inflorescence density onto the strict consensus tree from parsimony analyses of the ITS and *trn*L-F sequence data.

APPENDIX 1

GLOSSARY

Definitions are adopted or modified from Lawrence (1951), van der Pijl and Dodson (1966), Quer (1979), Dressler (1981; 1993), Stearn (1983), Stern et al. (1993), Harris and Harris (1994), Schuh (2000), Kiger and Porter (2001).

Abaxial: The side away from the stem, generally the lower surface.

Adaxial: The side towards the stem, generally the upper surface.

Amyloplasts: Organelles that synthesize and store starch grains.

Apomorphic: Advanced, as opposed to primitive or ancestral features; a character unique to a group and therefore group defining.

Apomorphy: An advanced character; a group-defining character.

Autapomorphic: Derived feature, unique to a taxon (see apomorphy).

Bootstrap: A technique that uses resampling and replication of characters in an attempt to understand in what degree a data set supports a given tree topology.

Bract: A scale, sheath, or leaflike structure.

Cladogram: A depiction of hierarchic relationships in the form of a treelike diagram with the intent of showing relative recency of relationship, without the connotation of amount of difference.

Claw: The narrow basal portion of a labellum or petal.

Column: The central structure of an orchid flower, made up of the style united with the filaments of one to three anthers.

Column foot: A ventral extension at the base of the column; the lip is attached at its tip.

Consensus: The collection of groups (components) that is contained exactly in all (most parsimonious) trees resulting from a phylogenetic analysis.

Consensus tree: The tree depicting the consensus.

Consistency index: A value computed as the ratio of minimum possible number of changes in a character on a tree divided by the observed number of changes.

Dichotomy: A node on a cladogram from which two branches arise.

Exine: The outer wall of a pollen grain.

Extrinsic data: Data derived from sources not subject to genetic inheritance.

Heuristic: A numerical cladistic result determined through the use of algorithms applied to data sets so large that all possible trees cannot be examined.

Hamulus: A pollinium stalk developed from the apex of the rostellum.

Holotype: The unique specimen designated to represent the concept for a named species; the name bearer for a taxon of the species group.

Intrinsic data: Data subject to genetic inheritance

Labellum: One of the three petals which is usually larger and different in shape from the other two; the median petal.

Lectotype: A specimen, serving the function of a holotype, as designated from the members of a syntype series.

Lineage: A terminal taxon or monophyletic group.

Mapping (of characters): The practice of plotting extrinsic character data on a cladogram produced from a matrix of intrinsic data; determining the distribution of any character not used in a prior analysis.

Monophyletic: A group defined by synapomorphies; a group containing a hypothetical common ancestor and all of its descendents.

Most parsimonious tree (MPT): For a given data set, the tree(s) of minimum length as computed under the parsimony criterion.

Node (on a cladogram): The point of intersection in a hierarchy that identifies a component; a hypothetical taxonomic unit.

Natural group: A monophyletic group.

Paraphyletic: A group containing a hypothetical common ancestor and some, but not all, of its descendants.

Parsimony: Simplicity of explanation; the principle of accepting the simplest explanation or hypothesis that is consistent with the data.

Petiole: The narrow, stemlike basal portion of a leaf.

Peduncle: Stalk of an inflorescence or solitary flower when that flower is the remaining member of an inflorescence.

Plesiomorphic: Primitive, as opposed to advanced.

Plesiomorphy: A primitive character, not group defining at the level at which it is being observed; the quality of being primitive.

Polyphyletic: A group of taxa not including their hypothetical ancestor.

Polytomy: Four or more branches arising from a single node on a cladogram.

Resupination: Having the labellum on the lower side as a result of the twisting of the pedicel.

Retention index: The fraction of potential synapomorphy retained as synapomorphy on a cladogram.

Reticulate: Netlike, it is used in reference to veins that form a branched network, or to netlike sculpturing of a pollen grain.

Rostellum: A portion of the median stigma lobe that aids in gluing the pollinia to the pollinator; the tissue that separates the anther form the fertile stigma.

Root: The point at which a cladogram is given directions; the taxon or outgroup, used to determine the polarity of the characters used to compute a cladogram.

Sectile: Soft and granular pollinia subdivided into small packets usually connected by elastic material.

Sister group(s): A pair of taxa united by one or more unique characters.

Spiranthosomes: Specialized amyloplasts.

Stalk: A supporting axis or column that bears a structure at its apex. The axis may be ontogenetically distinct from the structure that it bears, or it may be the basal portion of an ontogenetic entity that includes both the stalk and the structure that it bears. The stalk is usually narrower than the structure that it bears.

Stigma: The sticky, receptive part of the pistil.

Stipe: Any pollinium stalk not derived from the anther. A non-viscid band or strap of tissue derived from the column which connects the pollinia to the viscidium.

Symplesiomorphy: Shared, primitive, traits defining groups at higher levels.

Synapomorphy: Shared, derived, group-defining trait.

Synonym: Two or more different names applied to the same taxon.

Syntype: Two or more specimens examined by the original author of the species, none of which was designated to serve as the name bearer for the taxon.

Topology (of a cladogram): The geometric form of a cladogram; the pattern of branching of a cladogram.

Tree: Any branching diagram that specifies hierarchic relationships among taxa; sometimes, a branching diagram specifying ancestor-descendant relationships or patterns of speciation.

Trichotomy: Three branches arising from a single node on a cladogram.

Velamen: One or more layers of spongy cells on the outside of a root; in origin related to the epidermis.

Viscidium: A viscid part of the rostellum which is removed with the pollinia as a unit and serves to attach the pollinia to the pollinator.

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