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**Systematics and evolution of *Centropogon* subgenus *Centropogon*
(Campanulaceae: Lobelioideae)**

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Washington University, 1987

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SYSTEMATICS AND EVOLUTION OF *CENTROPOGON* SUBGENUS *CENTROPOGON*
(CAMPANULACEAE: LOBELIOIDEAE)

by

Bruce Alan Stein

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University
in partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

Part of the research
was conducted at the
Missouri Botanical Garden

December 1987

Saint Louis, Missouri

Cecily

To my father,
who instilled in me a love
for wild places

CONTENTS

Acknowledgments	vi
Chapter I. Introduction	1
Chapter II. Ecology	7
Habitat	7
Sympatry	8
Phenology	9
Dispersal	11
Ant/Plant Interactions.....	11
Chapter III. Biogeography and Patterns of Diversification.....	15
Geological Background	15
Distribution of Sections	17
Distributional Ranges and Intraspecific Variation.....	19
Patterns of Diversification.....	20
Biogeographic Units.....	23
Chapter IV. Pollination Biology	30
Sicklebill Hummingbird Pollination.....	31
Nectar	38
Nectar-Robbers	40
Chapter V. Hybridization and Breeding Systems.....	44
Natural Hybridization in <i>Centropogon</i>	45
Experimental Hybridizations	49
Chapter VI. Morphology and Anatomy	67
Habit	67

Indument	68
Leaves	71
Inflorescence Structure	74
Pedicels	81
Sepals	83
Corolla	85
Androecium	90
Gynoecium	94
Seeds	96
Pollen	96
Cytology	97
Chapter VII. Systematic Treatment	120
Taxonomic History	120
Sectional Classification	124
Section <i>Centropogon</i>	133
Section <i>Amplifolii</i>	155
Section <i>Campylobotrys</i>	261
Section <i>Grandes</i> (not treated)	453
Excluded Species	457
Chapter VIII. Literature Cited	458

List of Tables

1. Species distributions with respect to elevation	26
2. Confirmed pollination records	42
3. Nectar concentrations.....	43

4. Fruit set by pollination class.....	61
5. Proportion of successful fruit set among crosses.....	62
6. Maximum number of seeds set by each species	63
7. Seed set among crosses.....	64
8. Comparison of cultivated and wild leaf shape and length.....	101
9. Pollen specimens examined	116
10. Chromosome counts for <i>Centropogon</i> and <i>Siphocampylus</i>	119
11. Sectional placement of species	129
12. Historical subdivisions of subgenus <i>Centropogon</i>	132
14. Principal differences between <i>Centropogon congestus</i> and <i>C. umbrosus</i>	198
15. Morphological comparison of fimbriate and non-fimbriate <i>C. roseus</i> leaf morphs from Atalaya, Cuzco, Department, Peru.....	224
16. Characters used in multivariate analysis of <i>Centropogon granulosus</i> subsp. <i>tortilis</i> and subsp. <i>mutans</i>	328
17. Principal differences between <i>Centropogon curvatus</i> and <i>C. loretensis</i>	359
18. Species recognized in Section <i>Grandes</i>	454

List of Figures

1. Distribution of subgenus <i>Centropogon</i>	27
2. Biogeographical units.....	29
3. Parental and hybrid leaf morphologies.....	65
4. SEM photomicrographs of corolla trichomes	99
5. Inflorescence structural types.....	102
6. Shoot apex fates	104
7. Corolla and androecium measurements	106

8. Representative flowers of subgenus <i>Centropogon</i>	108
9. SEM photomicrographs of antheridial scales	110
10. SEM photomicrographs of intersepalar nectaries.....	112
11. SEM photomicrographs of seeds	114
12. SEM photomicrographs of pollen.....	117
13. Distribution map of <i>Centropogon cornutus</i>	153
14. Principal components analysis of <i>Centropogon congestus</i>	199
15. Section <i>Amplifolii</i> illustrations: <i>Centropogon alectrolophos</i> and <i>C. undulatus</i>	247
16. Distribution map of <i>Centropogon capitatus</i>	249
17. Distribution map of <i>Centropogon macrophyllus</i> and <i>C. alsophilus</i>	251
18. Distribution map of <i>Centropogon umbrosus</i> , <i>C. gesneriiformis</i> , and <i>C. congestus</i>	253
19. Distribution map of <i>Centropogon hirtus</i> , <i>C. uncialis</i> , and <i>C. escobarae</i>	255
20. Distribution map of <i>Centropogon gamosepalus</i> and <i>C. roseus</i>	257
21. Distribution map of <i>Centropogon silvaticus</i> , <i>C. quebradanus</i> , <i>C. undulatus</i> , <i>C. eurystomus</i> , <i>C. alectrolophos</i> , and <i>C. escobarae</i>	259
22. Principal coordinates analysis of <i>Centropogon granulosus</i> subsp. <i>tortilis</i> and subsp. <i>nutans</i>	329
23. Section <i>Campylobotrys</i> illustrations: <i>Centropogon granulosus</i> subsp. <i>granulosus</i>	427
24. Section <i>Campylobotrys</i> illustrations: <i>Centropogon vargasii</i> and <i>C. cuatrecasanus</i>	429
25. Section <i>Campylobotrys</i> illustrations: <i>Centropogon papillosum</i>	431
26. Section <i>Campylobotrys</i> illustrations: <i>Centropogon pygmaeus</i>	433

27. Section <i>Campylobotrys</i> illustrations: <i>Centropogon lasiodorus</i> and <i>C. carpishensis</i>	435
28. Distribution map of <i>Centropogon granulosus</i> subsp. <i>granulosus</i> , subsp. <i>rutilus</i> , and subsp. <i>nutans</i>	437
29. Distribution map of <i>Centropogon granulosus</i> subsp. <i>lugens</i> , subsp. <i>tortilis</i> , and subsp. <i>lateriflorus</i>	439
30. Distribution map of <i>Centropogon cuatrecasanus</i> , <i>C. pulcher</i> , and <i>C. vargasii</i>	441
31. Distribution map of <i>Centropogon densiflorus</i> , <i>C. trachyanthus</i> , and <i>C. baezanus</i>	443
32. Distribution map of <i>Centropogon curvatus</i> , <i>C. vaughianus</i> , <i>C. papillosum</i> , <i>C. carpishensis</i> , and <i>C. bangii</i>	445
33. Distribution map of <i>Centropogon loretensis</i> , <i>C. amplicorollinus</i> , and <i>C. latifolius</i>	447
34. Distribution map of <i>Centropogon yungasensis</i> , <i>C. urubambae</i> , and <i>C. reflexus</i>	449
35. Distribution map of <i>Centropogon sciaphilus</i> , <i>C. lasiodorus</i> , <i>C. arcuatus</i> , and <i>C. pygmaeus</i>	451

ACKNOWLEDGMENTS

I am especially grateful to Peter H. Raven, chairman of my committee, for his continuing support, encouragement, and direction throughout my graduate work. Alwyn Gentry deserves special thanks both for initially suggesting neotropical Lobelioids as an worthwhile group on which to work, and for his on-going interest in my studies. I am also particularly obliged to Peter Hoch for the numerous ways in which he helped make my tenure at the Missouri Botanical Garden productive and pleasant.

I am indebted to the members of my committee, and especially to Peter Goldblatt, James Luteyn, and Alwyn Gentry for their detailed comments on drafts of this thesis.

Petra Malesevich and Mary Niswonger did an excellent job in propagating my plants in the greenhouses at the Missouri Botanical Garden. My experimental studies of hybridization were completely dependent upon their expertise in keeping these plants alive and happy. Bobbi Angell and John Meyers provided excellent illustrations that do justice to these beautiful plants. John Skvarla kindly prepared and photographed the pollen specimens and Michael Veith assisted me with electron microscopy and prepared the photographic plates included here. Jorge Crisci offered advice on the application of numerical taxonomic techniques.

Special thanks to Jaquelyn Kallunki for her support during the preparation of the thesis, and for critically editing the entire document.

My fellow graduate students at the Missouri Botanical Garden, particularly Hector Hernández, Porter P. Lowry II, James Miller, and David Neill, created a stimulating atmosphere in which to work and through our discussions contributed substantially to this study.

Many people assisted me in various ways during the course of my fieldwork in Central and South America. These include Alvaro Cogollo, Camillo Diaz, Calaway Dodson, Linda Escobar, Pilár Franco, Washington Galiano, Clement Hamilton, Jaquelyn Kallunki, Lucinda McDade, David Neill, Enrique Renteria, Abundio Sagástegui, David Smith, James Solomon, Carol Todzia, and Diane Tucker. Thanks to all.

I am also very appreciative for all of the help that was given me by the professional, curatorial, and support staff of the herbarium, library, and director's office of the Missouri Botanical Garden. I would also like to thank the curators of the following herbaria for loaning specimens or allowing me use of their facilities: A, AAU, B, BM, CAS, CM, COL, CUZ, DS, DUKE, F, FLAS, FUP, G, GB, GH, HUA, HUT, JAUM, K, LE, MICH, MO, MY, NA, NY, P, PR, PRC, QCA, QCNE, RSA, S, U, UC, UIS, US, USM, VALLE, VEN, W, WIS.

Financial support for my studies was provided by a Washington University fellowship, by the Bovard Scholarship Fund of the Missouri Botanical Garden, by a National Science Foundation doctoral dissertation improvement grant (BSR84-13912), and by a Garden Club of America Fellowship in Tropical Botany.

I. INTRODUCTION

Centropogon subgenus *Centropogon* is a speciose group of hummingbird-pollinated herbs, shrubs, and vines found primarily along the very wet slopes of the tropical Andes. The subgenus consists of approximately 55 species, which I divide into four sections; three of these sections (sects. *Centropogon*, *Amplifolii*, and *Campylobotrys*), comprising 40 species and nine subspecies, are treated taxonomically in this work. Nine of these species are described as new to science, and will be formally published elsewhere.

The neotropics are a center of diversity for Campanulaceae subfamily Lobelioideae. Of the approximately 1200 species in the subfamily, over 600 are found in Central and South America, principally in four large genera, *Lobelia*, *Siphocampylus*, *Centropogon*, and *Burmeistera*. Generic delimitations in the subfamily are problematic, however, and the circumscription of, and interrelationships between these genera are still unresolved. In particular, the baccate-fruited *Centropogon*, with over 200 species, may represent several lineages derived from the very diverse capsular-fruited *Siphocampylus*, which also contains more than 200 species. These genera as traditionally defined are probably artificial, and they are often considered categories of convenience (Gleason, 1925; McVaugh, 1940). As pointed out by Gleason (1921) in discussing the Lobelioideae of Bolivia, "the delimitation of species-groups and the determination of intrageneric relationships becomes a matter of some difficulty, which is increased rather than lessened by extending the study to other South American countries."

Centropogon subgenus *Centropogon*, however, is one of the few major groups of neotropical Lobelioideae that is widely regarded as natural (i.e., monophyletic)

(Wimmer, 1943; McVaugh, 1949a, 1965; Wilbur, 1977). The primary feature (synapomorphy) that characterizes the subgenus is the presence of a cartilaginous-like scale at the tip of the two lower anthers. This scale is produced by fusion of the apical anther trichomes, which in other groups of *Centropogon*, as well as in *Lobelia* and *Siphocampylus*, are free and brush-like. Another synapomorphy for the subgenus, recognized here for the first time, is the presence of extrafloral nectaries located on the hypanthium. These nectaries function to attract ants, and do not occur in any other group of *Centropogon*. I have also observed extrafloral nectaries on the hypanthia of certain *Siphocampylus* species. These differ in their arrangement and structure, however, and are probably a parallel development.

Inflorescence structure is also a distinctive feature for the subgenus. Although several species have solitary flowers borne in the axils of leaves, the inflorescence type characteristic of other groups of *Centropogon* and most species of *Siphocampylus*, the majority of species in subgen. *Centropogon* have the flowers clustered into discrete terminal inflorescences, often with very reduced bracts. Thus, while not a synapomorphy for the entire subgenus, inflorescence characters provide an immediately recognizable feature for most species of subgen. *Centropogon* and are of great importance in infrasubgeneric classification. Another characteristic (albeit plesiomorphic) that helps define the subgenus is the absence of branched or dendritic trichomes, such as characterize several other major groups of *Centropogon*, most notably the polyphyletic "stellato-tomentosi" group. Two species of the latter, *C. varicus* (McVaugh, 1965) and *C. solisii* (Jeppesen, 1981), were described as having anther trichomes fused into a scale, calling into question the validity of the antheridial scale as a synapomorphy for subgenus *Centropogon*. An examination of the type specimens of these species, and in the case of *C. varicus* study of fresh material at its only known locality, revealed that the anther

trichomes in these species are incompletely fused. These antheridial "scales" probably are the result of independent evolution, rather than an indication of phylogenetic relationship.

In contrast to the well-defined nature of the subgen. *Centropogon*, the component species exhibit a bewildering array of morphological variability and are often poorly differentiated from one another. This extensive intra- and interpopulational variation, coupled with the occurrence of many species in very remote and poorly collected regions, has led to a chaotic taxonomic situation. Since *Centropogon* was described by Presl in 1836, more than 165 names have been proposed for taxa included here in subgen. *Centropogon*. The only complete treatment of the subgenus was that included by Wimmer (1943) in his Das Pflanzenreich monograph of the entire subfamily Lobelioideae. Wimmer (1943) recognized a total of 79 species, 29 varieties, and 10 formas, with 48 of those species described by Wimmer himself. Several factors compromise the utility of Wimmer's treatment of the group. First, many of the areas where subgen. *Centropogon* is most diverse were poorly collected at that time (indeed many of the areas remain so today). A number of species were described on the basis of one, or very few collections. Furthermore, Wimmer never worked with the plants in the field. His treatment was based solely on herbarium specimens, and while he borrowed extensively from most major herbaria, he was not able to observe the considerable variation evident in the field. This may partially explain his tendency to overemphasize the importance of traits that are now considered to be variable within populations and species, such as leaf size and shape. Along with an inherently narrow species concept, this lead Wimmer to describe numerous species and varieties that are unsupported by the current study.

The primary objective of the present study was thus to clarify the systematics of this complex and taxonomically overly fragmented group of species. In the last forty years numerous new collections of *Centropogon* have been made throughout the Andes. These additional collections, and the increased accessibility of these regions, have made it possible to more thoroughly analyze patterns of variability within species, and to consolidate the many previously described taxa into modern taxonomic units. These new collections also included a number of new species that required taxonomic attention. To accomplish this monographic revision I undertook a program of herbarium study, field exploration, and laboratory work. More than 5,000 herbarium specimens were borrowed for study from the major North American and European herbaria, as well as from many important Latin American collections. To augment the information that can be gleaned from herbarium specimens, to gather information about intra- and interpopulational variability, and to investigate other aspects of the biology and ecology of these plants, I spent approximately 15 months conducting fieldwork throughout the main range of subgen. *Centropogon* -- principally the tropical Andes and adjacent lowland Amazonia. During the course of that fieldwork I covered over 20,000 km by road, collecting in Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, and Bolivia.

The subtropical and montane Andean forests, where subgen. *Centropogon* is centered, are botanically among the most species-rich regions on earth. The neotropics contain perhaps 90,000 plant species, far more than the paleotropics (Raven, 1976), and the lower Andean forests are one of the richest areas of the neotropics (Gentry, 1982). In spite of the exceptional species diversity found in these Andean forests relatively little work has focused on evolutionary patterns of primarily middle-elevation plant groups. Most reviews of evolutionary patterns

and processes in South American plants have dealt with either lowland Amazonia (e.g., Prance, 1982; Whitmore & Prance, 1987) or high elevations (e.g., Simpson, 1975; Vuilleumier & Monasterio, 1986). Factors that may have affected the diversification of plants in these middle-elevation forests include: the recent geological uplift and topographic diversity of the Andes (Simpson, 1975, 1979); Pleistocene climatic fluctuations (van der Hammen, 1974) that may have resulted in repeated episodes of species range fragmentation and coalescence; and increased opportunities for coevolution of precise plant-pollinator relationships (Gentry, 1982).

Subgenus *Centropogon* is a speciose group that achieves its maximum diversity at middle-elevations in the northern Andes -- precisely the kind of group that Gentry (1982) found accounts for so much of the overall neotropical species diversity. A secondary objective of this study, then, was to explore the patterns of evolution in this group as a way of perhaps elucidating more general reasons for the exceptionally species diversity of this region. In the case of subgen. *Centropogon*, patterns of diversification appear to be related primarily to the topographic variability and the exceptional opportunities for geographic isolation (Chapter III). Most species in the subgenus are restricted to upper elevations, even though the most plesiomorphic members occur at lower elevations. Thus, to a large degree speciation patterns in the subgenus reflect the diversification of upper-elevation taxa. Two major modes of diversification in these upper-elevation species can be distinguished; vertical (i.e., altitudinal) colonization and differentiation from widespread lower-elevation ancestors, and horizontal (i.e., latitudinal) colonization and diversification from upper-elevation ancestors.

Pollinator interactions (Chapter IV) are a major factor in the overall evolution of the subgen. *Centropogon*, and a very close relationship has developed

with the sicklebill hummingbird genus *Eutoxeres*. The shift from generalized hermit hummingbird pollination to sicklebill pollination is one of the major evolutionary trends within the subgenus. While the development of such a mutualistic relationship has interesting evolutionary implications, because of the limited number of hummingbird species involved, diversification of pollinator interactions cannot be regarded as a major factor in promoting speciation in this group. Many *Centropogon* species sharing the same pollinator could instead be expected to have the opposite effect, hindering diversification through increasing the likelihood of interspecific or interpopulational pollen transfer.

Reproductive isolating mechanisms among the species are rarely evident, and the maintenance of species integrity remains a puzzle. Sympatric species, many of which share the same pollinator (Chapter IV), are often common (Chapter II). Further, few phenological differences are evident that would allow temporal partitioning of these common pollinators (Chapter II). My observations into the occurrence of natural hybridization, and my experimental crossing studies also indicate that there are few internal reproductive isolating barriers (Chapter V). Given this difficulty in establishing the presence and nature of reproductive isolating mechanisms, the biological species concept as advocated by such authors as Mayr (1970) and Grant (1981) appears to be inappropriate for this group. Even if valid theoretically, the concept of a species as a "reproductively isolated system of breeding populations" (Grant, 1981) would be impossible to apply to the herbarium specimens that form the basis of this taxonomic work. Instead, the species concept used here is that of the taxonomic species as defined by Davis and Heywood (1963). Species in this context represent units held together by a constellation of shared morphological characters, a concept more suited to our current fragmentary knowledge of these plants.

II. ECOLOGY

Habitat

Plants of subgen. *Centropogon* are restricted to wet or moist habitats. They occupy a broad altitudinal range, from sea level to over 3000 m, but are represented most abundantly from 1000 to 2500 m. Most species are found in habitats ranging from upper elevation "cloud forest" to middle elevation subtropical forests, known locally as ceja de la monta a (Peru) or yungas (Bolivia). Certain species also occur in tropical lowlands at still lower elevations. Only one species, *C. amplicorollinus*, is found exclusively in lowland tropical forest. Within the context of the Holdridge lifezone system (Holdridge, 1967) subgen. *Centropogon* occupies tropical to montane, humid to pluvial forests.

The habitats in which most species occur are characterized by moderate to very high precipitation, usually occurring throughout the year. Species are absent from strongly seasonal habitats, and most of the vegetation types in which they occur can be regarded as aseasonal. The eastern slope of the Andes is one of the most continually wet parts of the continent (Hoffmann, 1975). Even though at the regional level there are marked wet and dry seasons (differing in time from north to south), their intensities are often ameliorated by local climatic features associated with tropical montane environments, such as the frequent presence of cloud cover or perpetual mist, and orographic precipitation.

Plants usually are found in relatively high light intensity environments, such as forest edges or around natural or artificial disturbances. When found in undisturbed forest most plants occur in microhabitats with higher light intensities, for instance along watercourses, in tree falls, or on landslides. They are often

which simulate forest edge habitats, and some plants may even be invigorated by the occasional trimming they receive during road maintenance. In regions that have suffered extensive deforestation, plants often may be found in the remnant vegetation along streams and *quebradas*.

Sympatry

The elevational and ecological preferences of different species can overlap broadly and many taxa often grow sympatrically. The most common type of sympatry is for two species from different taxonomic groups to be found together, for example *C. granulosus* of sect. *Campylobotrys* and *C. cornutus* of sect. *Centropogon*. In other instances up to seven species, some closely related, are known to co-occur.

The Carpish Pass region in Huánuco, Peru is the richest area known in terms of co-occurring species of subgen. *Centropogon*. From about 2100 to 2500 m at least seven species occur, often in extremely close proximity. These include *C. reflexus*, *C. granulosus*, *C. carpishensis*, *C. lasiodorus*, *C. macrophyllus*, *C. capitatus*, and *C. hirtus*. Although certain of these species are, in this area, found only at the upper or lower end of this range (e.g., *C. hirtus* at above 2400 m; *C. capitatus* and *C. macrophyllus* at below 2200 m) most of the species overlap broadly in elevation and habitat preference. Another area of exceptional diversity is the nearby Cordillera Azul, west of Tingo María. Here, at least five species are found including *C. umbrosus*, *C. macrophyllus*, *C. capitatus*, *C. granulosus*, and *C. latifolius*. *Centropogon cornutus* is also found in the region, but at slightly lower elevations. The Kosñipata Valley in Cuzco, southern Peru is yet another area with a very high concentration of sympatric species -- *C. cornutus*, *C. capitatus*, *C. roseus*, and *C. granulosus* at lower elevations (650-1000 m), and *C. yungasensis* and *C. umbrosus* at higher elevations.

There are numerous examples of three species occurring in close sympatry. A representative sampling of these are: La Gallera, Cauca, Colombia -- *C. congestus*, *C. pedicellaris*, *C. solanifolius*; Sasaima, Cundinamarca, Colombia -- *C. granulosus* subsp. *rutilus*, *C. vaughianus*, and *C. uncialis*; Finca Mehrenberg, Huila, Colombia -- *C. curvatus*, *C. congestus*, *C. semperflorens*; Plan de Milagro, Morona-Santiago, Ecuador -- *C. arcuatus*, *C. granulosus* subsp. *lateriflorus*, and *C. quebradanus*; Puya, Pastaza, Ecuador -- *C. loretensis*, *C. papillosum*, and *C. gamosepalus*; Pichinaki, Junín, Peru -- *C. cornutus*, *C. pulcher*, and *C. capitatus*. Additional species in *Centropogon* subgen. *Siphocampyloides* often co-occur with the above species.

Reproductive isolation through spatial isolation certainly occurs and may, in fact, be the most important isolating mechanism within the subgenus. The widespread co-occurrence of species, though, means that in many instances this type of reproductive isolation is not operative. It may be significant, however, that the most common form of sympatry is between species from different sections. Nonetheless, the common occurrence of sympatric species greatly increases the potential for interspecific hybridization, which is discussed in detail in Chapter V.

Phenology

Flowering apparently occurs throughout the year in most species, although there may be seasonal fluctuations in intensity. Detailed information on flowering phenology is difficult to gather, however. Simply documenting the temporal distribution of herbarium specimens can be particularly misleading; this approach merely documents the phenology of collectors rather than flowers. To get an accurate view of a particular species' phenology the same site must be revisited over the course of at least a year. Because my fieldwork has encompassed a broad geographical range, I have been unable

over the course of at least a year. Because my fieldwork has encompassed a broad geographical range, I have been unable to carry out such monitoring. My field observations, along with the observations of others, suggest that at least two patterns exist among species in the subgenus.

Most species apparently produce flowers throughout the year, a blooming behavior that corresponds to what Gentry (1974) has termed a "steady-state" flowering strategy. This flowering pattern may have more to do with the traplining behavior of their long-lived pollinators than with the relatively aseasonal habitats in which the plants occur. Stiles (1985, Appendix 1), for instance, classified *C. granulosus* at his study site in Costa Rica as a species in which the "population blooms fairly continuously, with irregular and variable peaks" throughout the year.

A few species show dramatic seasonal fluctuations in flowering intensity. Feinsinger (pers. comm.), for example, has collected two years of phenology data for *C. solanifolius* at Monteverde, Costa Rica. Flowers were found at low levels throughout the year, but prominent flowering peaks occurred during March and April, coinciding with the end of the dry season. At Colasay, in Cajamarca Department of northern Peru, I found that *C. vernicosus*, a species closely related to *C. solanifolius*, was completely vegetative in February (mid-wet season). The local people, who eat the leaves and thus know the plant's flowering behavior, informed me that flowers are produced at the end of the dry season.

Because most species of subgen. *Centropogon* flower throughout the year, even if at varying levels, temporal separation in flowering among species does not seem a likely reproductive isolating mechanism.

Dispersal

Little is known about the mode of seed dispersal in subgen. *Centropogon*.

The fleshy fruits and numerous, tiny seeds (from 1,000-3,500 per fruit, each 0.5-1 mm long) suggest bird dispersal through endochory. When ripe, most fruits are somewhat juicy and sweet. Expressed juice ranges from 15-30% sucrose-equivalent sugars. At maturity the fruits are normally 7-12 mm long by 10-20 mm in diameter. They remain green and are odorless, with the notable exception of *C. papillosum*, in which the fruits have a very sweet, fruity odor. The specific dispersal vectors are unknown, but could include a variety of small frugivorous birds such as tanagers, thrushes, or manakins. I have observed partially eaten fruits still attached to the plants. Because fruits typically abscise from the plants at maturity, it is also possible that they are eaten by ground dwelling frugivorous birds, such as tinamous, or by rodents.

Dispersal of the seeds by small birds could have several implications. The sedentary nature of most small Andean birds (Remson, 1984) would normally limit the area available for colonization, and the common occurrence of very localized morphological forms in the subgenus could partly be a result of such low average seed dispersal. Even normally sedentary birds, however, have a high potential vagility and could occasionally transport seeds relatively long distances. Rare dispersal events from one mountain drainage to another, or even between Andean slopes, could explain the distribution patterns of some of the widespread mid- and upper-elevation species.

Ant/Plant Interactions

Among the most distinctive features of subgen. *Centropogon* are the extrafloral nectaries present on the hypanthium, which I have termed intersepalar

Siphocampylus, although they are structurally different from those in subgen.

Centropogon. Within subgen. *Centropogon* these glands are not present in all species, nor in all members of the species in which they are found, nor are they functional in all individuals on which they are present. When present and functional, however, they secrete a very viscous, sugar-rich solution. The small quantity of nectar normally produced by the glands makes it difficult to obtain accurate secretion estimates. A two day accumulation of nectar from the three frontal glands on greenhouse-cultivated material of *C. cornutus* measured 3.12 ul, making the daily secretion for each gland approximately 0.5 ul. The nectar was extremely viscous and sweet and had to be diluted in order to fall within the range of the optical refractometer used to measure its sugar concentration. Based on a dilution series, the nectar ranged from 80-85% sucrose-equivalent sugars, an extraordinarily high value.

The function of these nectaries appears to be the attraction of ants, and in several instances I have observed ants collecting the nectar secreted by these glands. Presumably the presence of ants confers a selective advantage to the plants and justifies the production of this extremely concentrated nectar. The most likely advantage is protection from herbivory (Bentley, 1977). Ants that I observed on *Centropogon* were in only one instance aggressive and capable of deterring large mammals (paraponerid ants on *C. granulosus* subsp. *lugens* in Chocó, Colombia); most were small and non-aggressive. If the ants are truly beneficial to plants of subgen. *Centropogon*, a supposition that has not been empirically tested, it is because of their gleaning small herbivorous insects and eggs from the plant surface, rather than aggressively discouraging large herbivores.

The systematic and ecological distribution of the extrafloral nectaries provides a useful indicator of the direction of evolution within the subgenus. As mentioned above, not all species or individuals have the intersepalar glands. The presence or absence of

The systematic and ecological distribution of the extrafloral nectaries provides a useful indicator of the direction of evolution within the subgenus. As mentioned above, not all species or individuals have the intersepalar glands. The presence or absence of these structures correlates in a general way with elevation. For the most part, in those species that inhabit low elevations the glands are well-developed and functional intersepalar glands, while in species found at higher elevations (or in upper elevation populations of altitudinally wide-ranging species) the glands are often vestigial, non-functional, or entirely absent. Exceptions to this general trend occur, as evidenced by the normally well developed glands of the mostly upper-elevation *C. hirtus* species group.

Ants are most abundant and diverse in lowland tropical regions, and accordingly the greatest number of plants offering nectar rewards to them also occur in these environments (Bentley, 1977). Ant abundance and diversity declines with increasing elevation in tropical mountains. They are extremely rare in cloud forest, because ground nesting ants cannot live in very wet soils, and because arboreal species are sensitive to low air temperatures (Bentley, 1977). The loss of function and ultimately complete loss of glands in many higher elevation taxa would seem to be related to this paucity of ants. A similar loss of ant-related structures has been proposed by Rickson (1977) for island populations of *Cecropia*.

Extrafloral nectaries in subgen. *Centropogon* seem most likely, therefore, to have evolved in low elevation tropical habitats where (1) herbivore pressures are greatest, and (2) where ants are abundant and presumably able to provide a degree of protection from herbivores. In support of this supposition, *C. cornutus*, a lowland species that I regard as the sister group to the rest of the subgenus, exhibits some of the most well developed extrafloral nectaries in the subgenus. Extrafloral nectaries appear to be a synapomorphy for the subgenus as a whole (i.e., a

specialized ancestral condition within the subgenus). Thus, their degeneration or absence in upper elevation taxa can be interpreted as a derived condition. This further implies that upper elevation habitats, such as cloud forests, are not the ancestral habitat for the subgenus and that, instead, there has been a general migration from low to high elevations in the evolution of species within subgen.

Centropogon.

III. BIOGEOGRAPHY AND PATTERNS OF DIVERSIFICATION

Subgenus *Centropogon* ranges widely throughout the neotropics and is found from Nicaragua south to Bolivia, across much of Brazil, and into the West Indies (Fig. 1). In spite of this very extensive overall range, most species are concentrated in the Andes and adjacent lowland regions.

Geological Background

To interpret the patterns of distribution and differentiation in the subgenus it is necessary first to review the historical context in which it has developed. The primarily Andean distribution of most species of subgen. *Centropogon* makes the geological history of this mountain range particularly relevant. As reviewed by Berry (1982), three historical factors are of major importance in the development of the Andean flora: the separate geological history of different segments of the range, the relative recency of the main Andean uplift, and the climatic fluctuations that occurred during the Pleistocene.

The Andes are the longest mountain range in the world, extending from Venezuela to Tierra del Fuego. They are widely interpreted as representing the classic example of a volcano-plutonic orogeny that has developed along the margin of a convergent tectonic plate (Sillitoe, 1974). Because of its length the range has not developed uniformly, however; it is composed of a number of physiographic provinces with each segment having a distinctive geological history. These tectonically based structural units have been discussed for the central and southern Andes by Sillitoe (1974) and for the northern Andes by Hall and Wood (1985).

Simpson (1975, 1979) and Berry (1982) have both addressed the phytogeographical implications of these structural units. Within the area in which

subgen. *Centropogon* occurs Simpson (1975, 1979) recognizes five structural units: the eastern cordillera of Colombia, which includes the Andean spurs into Venezuela; the central Cordillera of Colombia together with the eastern Andes of Ecuador; the western cordillera of Colombia and Ecuador; the western cordillera of Peru; and the eastern cordillera of Peru and Bolivia.

Berry (1982) has modified this scheme slightly, recognizing a small structural unit in southern Ecuador and extreme northern Peru, the Amotape-Huancabamba zone. He also separated the eastern cordillera of Peru and Bolivia into northern and southern units. The Huancabamba deflection-upper Marañon basin of northern Peru is the lowest elevation gap along the entire eastern slope of the tropical Andes and has long been recognized as a biogeographic boundary, obstructing north-south migration of upper-elevation organisms. This gap is often considered the biological dividing line between the northern and central Andes (Duellman, 1979; Vuillumier, 1984). Sillitoe (1974) has noted, however, that geologically the central Andes extend into southern Ecuador to the so-called Amotape zone. Hall and Wood (1985) refer to this same zone as the Gulf of Guayaquil boundary, noting that it is a broad zone trending northeast-southwest in contrast to the northwest-southeast boundaries found further north. Berry's (1982) Amotape-Huancabamba zone encompasses the region within the differing biological and geological demarcations between the northern and southern Andes.

The northern part of the tropical Andes is in general much older than the central Andes, with the Cordillera Central of Colombia having been partially uplifted by late Cenozoic times (Zeil, 1979). Despite the varying histories and overall ages of the different structural units, most areas of the Andes appear to have achieved their maximum height only in the past five million years during Pliocene and Pleistocene times (van der Hammen, 1974; Zeil, 1979). The higher elevation portions of the Andes thus are extremely recent geologically.

Palynological work carried out over the last twenty years has provided insights into the very dynamic nature of the Andean environment during the Pleistocene. This emerging view shows that rather than the tropics having a long-stable climate, as thought previously, the cyclic Pleistocene glacial periods produced a general cooling and drying in the southern hemisphere (van der Hammen, 1974). Temperatures during glacial periods in the Andes may have been lowered by 6-7° causing a depression of vegetation belts by as much as 1500 m (van der Hammen, 1974). Along with a decrease in elevation, each vegetation band probably also became altitudinally compressed.

This cyclic lowering and raising of vegetation zones must have had a profound and complex influence on the Andean flora. During glacial periods the ranges of mesophytic lowland taxa would have decreased isolating previously contiguous populations, while during the interglacials their ranges would have re-expanded and coalesced or formed secondary contact zones (Haffer, 1982). High elevation páramo plants would have gone through exactly the opposite cycle, with ranges expanding during glacial periods and contracting during interglacials (Simpson, 1975). The effect of these cyclical changes on middle-elevation forest taxa may have been more complicated, combining aspects of both processes. The compression of vegetation zones would lead to a contraction in ranges. This range contraction may have been accompanied by fusion of previously disjunct populations, however, since the altitudinally depressed forests would be more continuous when occurring along the less dissected lower Andean slopes.

Distribution of Sections

The four sections recognized in this treatment have distinctive geographical patterns. Section *Centropogon*, considered the most plesiomorphic group, has the widest range. Its sole member, *C. cornutus*, usually is found at lower elevations and encompasses almost the entire distributional range of the subgenus -- from Panama to

Bolivia, through Brazil south to the Tropic of Capricorn, and north in the West Indies to the island of Antigua.

The three remaining sections, sects. *Amplifolii*, *Campylobotrys*, and *Grandes* are much more limited in their distribution. Section *Amplifolii* is found mostly in montane regions from central Costa Rica south through the Andes to southern Peru. Even though the section is well represented in Colombia, it is conspicuously absent from adjacent Venezuela, a distributional anomaly probably related to the specialized pollinators associated with this group (Chapter IV). Section *Campylobotrys* has a comparable distributional pattern, ranging from extreme southern Nicaragua to central Bolivia. This section, while best developed in montane or premontane habitats also includes low elevation members. Except for one collection of *C. granulosus* known from the border of Colombia, it too is absent from Venezuela, a distributional pattern again probably related to pollinator interactions.

Section *Grandes* has a more restricted range and is strictly montane. In Central America it occurs only in Costa Rica, while in South America it is found in Colombia and Venezuela, and reaches south in the western Andes as far as northern Peru. Although both sects. *Amplifolii* and *Campylobotrys* are well represented along the eastern slope of the Andes, sect. *Grandes* is entirely absent from that slope. The section is best developed in Colombia, occurring in all three cordilleras there. In the Cordillera Oriental, however, it does not cross over from the western to the eastern slope. A similar situation exists in Ecuador and northern Peru where members of this section are found only on the western (Pacific) slope of the Andes and are completely absent from the eastern (Amazonian) slope.

Distributional Ranges and Intraspecific Variation

Elevational differences play an important role in the distribution of species, and I have analyzed the 40 species comprising sects. *Centropogon*, *Amplifolii*, and *Campylobotrys* with respect to the elevational ranges at which they occur (Table 1). By far the largest number of species (55%) are found only at upper elevations (above 1500 m). Only three species (7.5%) are restricted to low elevations (0-500 m).

The differences in elevational distribution correlate with patterns in the extent of species ranges. Each species was scored as either widespread (with ranges greater than 250 km in any direction) or localized (ranges less than 250 km) (Table 1). Within the latter category there is much variation, some taxa being known from only a single locality, while others are restricted to a general region. The ratio of widespread to localized taxa was highly skewed for certain elevational classes. Although 40% of all species have widespread ranges, only 18% of those restricted to upper elevations are widespread. On the other hand, of the 12 species that are wide ranging elevationally (found in two or more elevational zones), 75% were also wide ranging geographically. Upper-elevation species thus tend to be much more localized in their distributions than either low elevation species, or species that span a broad altitudinal range.

The degree of intraspecific variation also differs among the various elevation and distributional classes. In general, widespread lower-elevation taxa show relatively limited amounts of intraspecific variation. Localized upper-elevation taxa tend to show little intra-populational, but often considerable interpopulational variation. Widespread middle- to upper-elevation species, however, tend to show much higher levels of intraspecific variation, both at the intra- and interpopulational levels. In the case of widespread lowland species the variation present is at least occasionally of a clinal nature, whereas variation patterns in middle- to upper-elevation species are usually discontinuous and geographically random.

Centropogon cornutus is a good example of a widespread lower elevation species that exhibits a surprising degree of morphological consistency. The reasons for this uniformity are not clear and, in a way, pose more of a puzzle than do the complex patterns of variation seen in many of the other species. The two major forces usually invoked to explain cohesion of species, gene flow and/or a common selective regime (Ehrlich & Raven, 1969), do not seem to explain this phenomenon. Clearly gene flow cannot be considered a viable cohesive force maintaining morphological integrity among populations as widely separated as Panama and southern Brazil. Neither are the ecological conditions uniform where the plants occur, even though most do grow in lowland tropical regions. Other species that to a lesser degree show this pattern of distribution include *C. capitatus*, *C. gamosepalus*, and *C. loretensis*. These latter species, however, generally exhibit a higher degree of morphological variation within their more limited ranges than does *C. cornutus*.

Widespread upper-elevation species, such as *C. congestus*, *C. umbrosus*, *C. granulosus*, *C. yungasensis*, and *C. solanifolius*, show extensive intraspecific variation and some have been finely subdivided taxonomically in the past. I have treated them as broadly circumscribed taxonomic species either because the variation is not well-correlated geographically (i.e., non-clinal) or because of the presence of numerous intermediate forms.

Patterns of Diversification

The historical factors discussed above have several implications for evolution in subgen. *Centropogon*. Given that over half the species in the subgenus are found in geologically recent upper-elevation habitats, discussion of modes of evolution in the subgenus must focus on these habitats. Based on analysis of morphological features and ecological factors (pollination syndromes and ant/plant adaptations) the subgenus appears

to have evolved at lower elevations in the humid tropics and later colonized middle and upper altitudes. This pattern differs sharply from that presumed for most other groups of Andean Lobelioideae, as well as for several other recently studied Andean groups, such as *Fuchsia* (Berry, 1982) and *Cavendishia* (Luteyn, 1983). For this reason, patterns of distribution and diversification may differ significantly from those of other groups even though they presently overlap broadly in habitat preferences.

A lowland origin for the subgenus implies that middle- and upper-elevation taxa would tend to be more recently evolved than those at lower elevations. The relatively recent age of the Andean uplift would reinforce this age difference, because habitats above about 2000 m have been available for colonization only since Pliocene times at the earliest (Simpson, 1979). Much of the diversification of these upper-elevation plants probably did not occur until the Pleistocene or more recently. Moreover, the high levels of morphological variability exhibited by many upper-elevation species suggest that they are still actively and rapidly evolving. It is not possible, however, to differentiate the relative contributions to these patterns of variation made by the present topographic and climatic diversity of the Andes, versus the putative cycles of fragmentation and secondary contact during the Pleistocene.

Two principal modes of diversification can be postulated for many of the high elevation species; derivation directly from lowland ancestors through vertical (i.e., elevational) colonization events or derivation from other upper-elevation taxa via horizontal (i.e., latitudinal) dispersal. Both appear to have been responsible for the origin of different species or populations. *Centropogon vargasii* and *C. reflexus*, for instance, are localized upper-elevation derivatives of *C. yungasensis*, a widespread upper-elevation species. Another example of a series of related species that probably derived from upper elevation horizontal colonizations is the group consisting of *C. densiflorus*, *C. trachyanthus*, and *C. baezanus*. An intriguing case involves *C. undulatus*

and *C. alectrolophos*. In spite of being separated by over 1000 km, these two upper-elevation members of the *C. gamosepalus* complex are sister species based on a preliminary cladistic analysis. It is not clear, however, whether these species are truly closest relatives and perhaps the result of horizontal upper-elevation dispersal events or are instead independent vertical derivations from the widespread, middle-elevation *C. gamosepalus*.

Centropogon quebradanus, an upper-elevation species, is almost certainly the product of vertical colonization and differentiation from *C. gamosepalus*. Another clear example of vertical differentiation is *C. cuatrecasanus*, which, as discussed elsewhere, must have been derived from a lower-elevation sicklebill-pollinated species. Unfortunately, in the absence of a detailed phylogenetic analysis of the subgenus it is not possible to unambiguously assign species to these categories or to estimate the relative importance of these two modes of diversification.

Biogeographic Units

Assuming the origin and initial differentiation of the subgenus occurred at lower elevations, and given the contemporary presence of widespread lower elevation species, the distribution and evolution of species in subgen. *Centropogon* may be less constrained by Andean structural units than were other groups of Andean plants that are more completely restricted to higher elevations. One would predict that the effect of these structural units on distributions would be of more importance in the formation or dispersal of species groups characterized by the "horizontal" rather than the "vertical" mode of differentiation. In the latter, the presence of the progenitor species in the more-or-less continuous lower montane and upper Amazon forests would circumvent any migrational barriers that applied primarily to upper elevation taxa. To assess the distribution of species in the subgenus with respect to these structural units, I tabulated the number of species present in, endemic to, and shared among the various Andean structural units (Fig. 2). To provide additional resolution in this analysis I included separately the six geographically based subspecies of *C. granulosus* and two subspecies of *C. densiflorus*.

The structural unit containing the largest number of species and endemics is the Cordillera Oriental of Peru and Bolivia, with 21 taxa, 15 of them endemic. This is also the largest unit considered, which may be partially responsible for its numerical dominance, although even taking size into account, its importance as a center of diversification for subgen. *Centropogon* is clear. The much smaller Cordillera Real of eastern Ecuador is almost as diverse with 17 species, 8 of which are endemic. Each of the three Colombia-centered cordilleras (Cordillera Occidental, including western Ecuador; Cordillera Central; and, Cordillera Oriental, including the extension into Venezuela) support approximately the same number of taxa, although these figures are more tentative due to the importance in these ranges of sect. *Grandes*, a group for which

the taxonomy has not yet been completely worked-out. Only a trickle of species enter Central America, and there has been little autochthonous diversification there.

The biogeographical/structural units used in this analysis differ from those proposed by either Simpson (1975, 1979) or Berry (1982), although they conform most closely to the former. The principal difference between this analysis and Simpson's is my use of the more traditional separation of the Ecuadorean Cordillera Real from the Cordillera Central of Colombia. Although there are structural similarities between these two units (Sauer, 1971), there is little overlap in the assemblage of *Centropogon* species, with only two shared species (one of which is the ubiquitous *C. cornutus*). Furthermore, Hall and Wood (1985) have noted that the Guairapungo Boundary, which passes through southern Colombia at about the latitude of Pasto, is one of the most conspicuous tectonic boundaries in the northern Andes and is a major physiographic break. This boundary corresponds to the Nudo de Pasto, where the Cordillera Oriental and Cordillera Central join together. In other groups the Nudo de Pasto appears to have been of major importance in the migration of upper-elevation species among cordilleras, but such is not the case in subgen. *Centropogon*. The Cordillera Occidental of Colombia and Ecuador are retained together as one unit, however, since the subgen. *Centropogon* flora of the latter is really just a depauperate version of that of the former.

Although other groups of *Centropogon*, especially the so-called "stellato-tomentosi," show an extraordinary development in the Amotape-Huancabamba zone of extreme southern Ecuador and northern Peru, the distribution of subgen. *Centropogon* does not support separate recognition of this biogeographic unit. Of the eight taxa found in this area, only the two subspecies of *C. densiflorus* are endemic.

The Huancabamba depression on the southern margin of this zone, however, does rather sharply separate the very diverse *Centropogon* assemblages found to its north and south. While seven taxa of subgen. *Centropogon* traverse this boundary, five of these are

widespread lower-elevation species (*C. cornutus*, *C. capitatus*, *C. gamosepalus*, *C. alsophilus*, and *C. loretensis*). The two remaining, *C. granulosus* subsp. *granulosus* and subsp. *lateriflorus*, are found at upper elevations on either side of the Huancabamba depression, but only the latter is restricted to higher elevations.

The subgen. *Centropogon* flora of southern Peru and Bolivia differs somewhat from that of central and northern Peru, but not sufficiently to endorse Berry's (1982) subdivision of this cordillera. The diversity of subgen. *Centropogon* drops sharply in Bolivia. Of the ten species that occur in Berry's (1982) southern unit of the Peruvian and Bolivian eastern cordillera, only two are endemic to there. However, slightly to the north of this boundary, near Satipo in Junín Department (about 11°S latitude), an interesting conjunction occurs in the northern ranges of two southern species, *C. urubambae* and *C. roseus*.

Table I
Species Distributions with Respect to Elevation
(Sections *Centropogon*, *Amplifolii*, and *Campylobotrys*)

Elevational Range	Number of Species	Distribution:	
		Widespread	Localized ^a
Low ^b	3 (7.5%)	1	2
Middle ^c	3 (7.5%)	2	1
Upper ^d	22 (55%)	4	18
Low to Upper	2 (5%)	2	0
Low to Middle	4 (10%)	3	1
Middle to Upper	6 (15%)	4	2
Total	40 (100%)	16	24

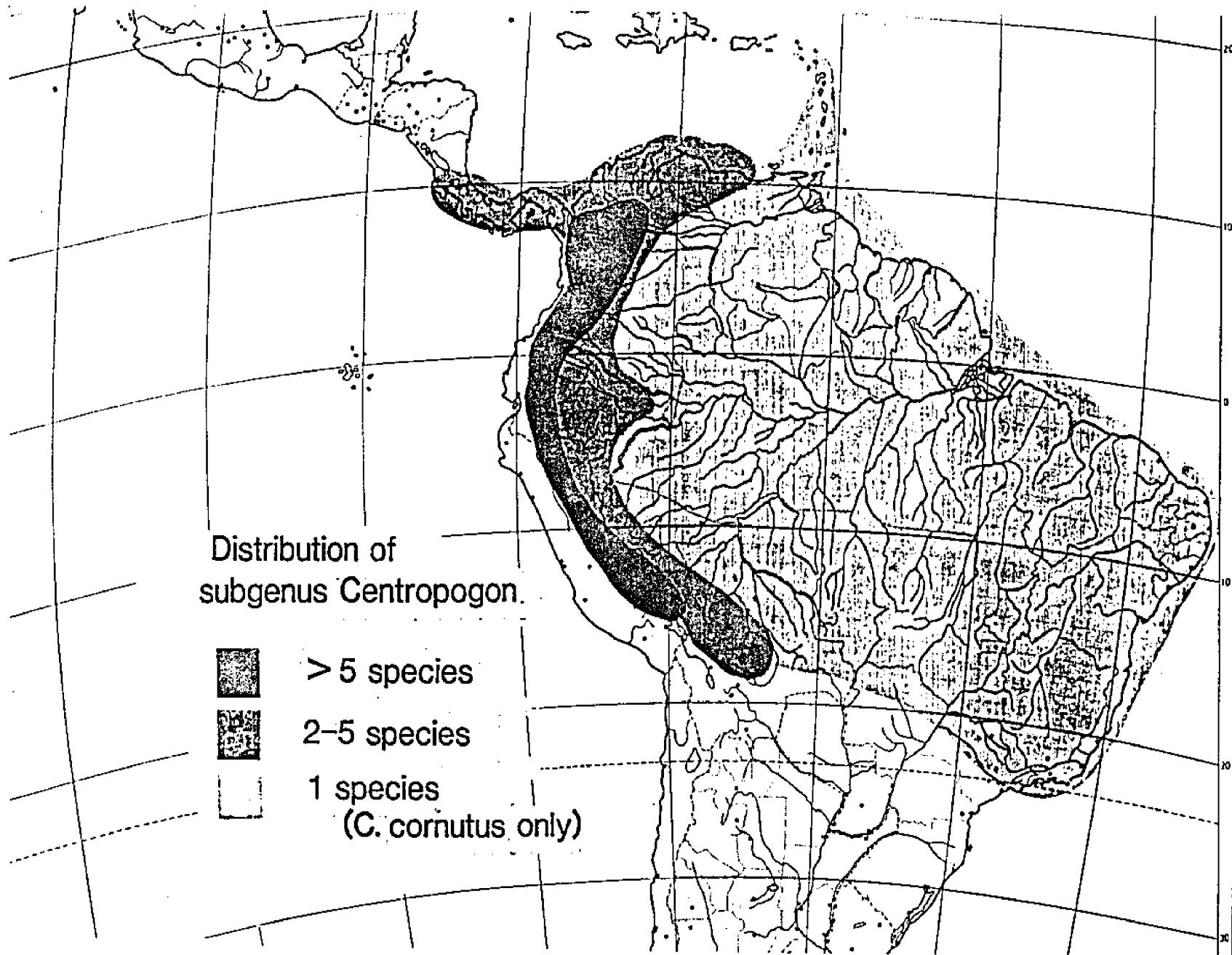
^a Species range less than 250 km.

^b Low Elevation = 0-500 m

^c Middle Elevation = 500-1500 m

^d Upper Elevation = 1500-3000 m

Fig. 1. Distribution of *Centropogon* subgenus *Centropogon*.



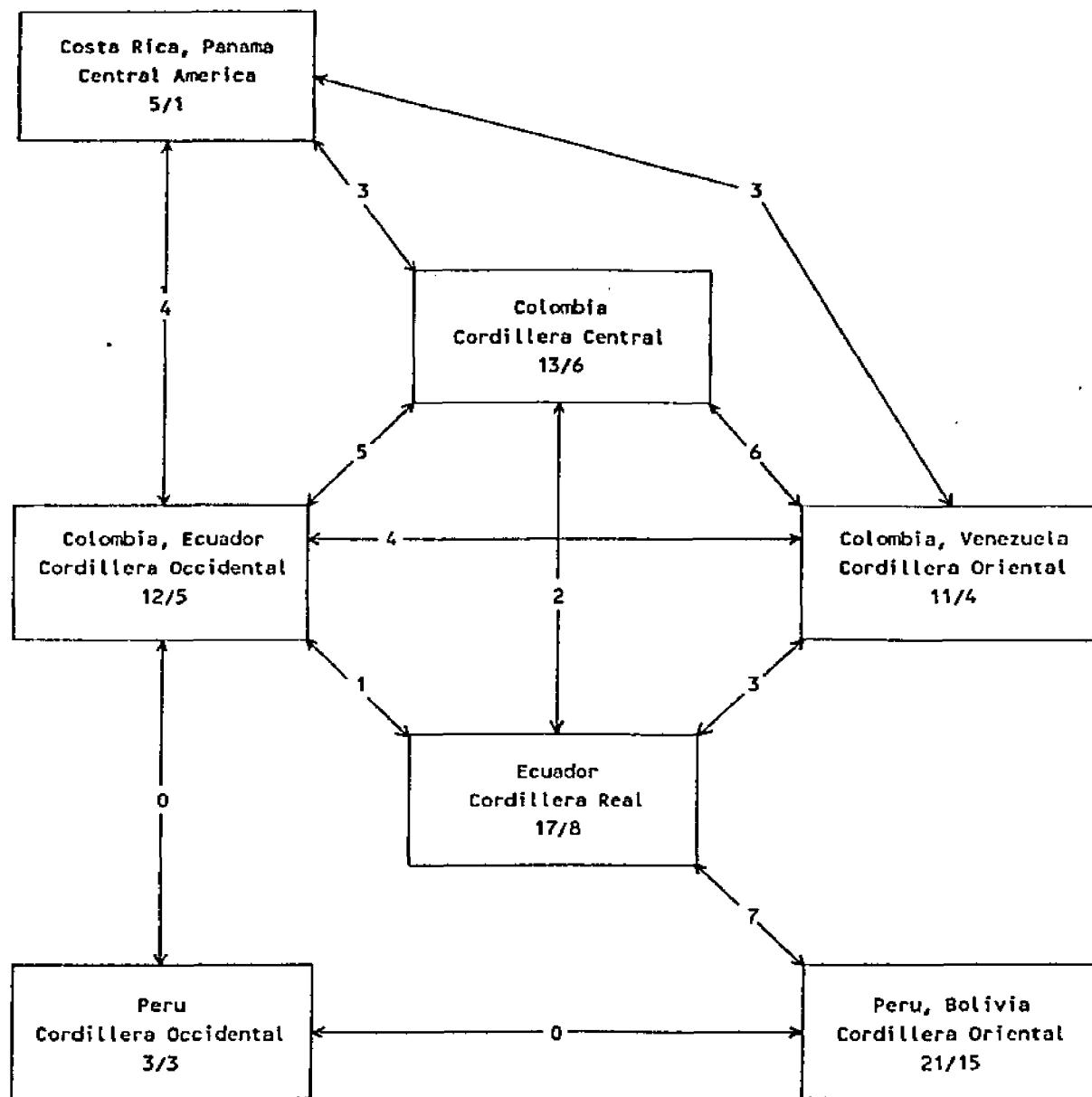


Fig. 2. Distribution of subgenus *Centropogon* among Andean structural units. Numbers refer to total number of taxa (species and subspecies) in unit/number of endemic taxa in unit. Figure includes all four sections of subgen. *Centropogon*.

IV. POLLINATION BIOLOGY

All species of subgen. *Centropogon* are hummingbird pollinated, although there are very few confirmed pollination records (Table 2). On the basis of the records that do exist, members of the subgenus fall into two general groups. The first is visited by hummingbirds with gently curving or relatively straight bills, many of them in the hermit hummingbird subfamily Phaethorninae. The second group is visited by *Eutoxeres* hummingbirds, a highly specialized genus of hermits that are commonly known as sicklebills in view of the long, exceptionally curved bills.

Corollas may be viewed as filtering devices that selectively allow access to pollinator rewards, in this case nectar. Ideally, corollas exclude visitors that would be ineffective pollinators. In hummingbird flowers this typically occurs through differences in the length or shape of the corolla that prevent ineffective visitors from reaching the nectar that accumulates at the base of the corolla. A straight-billed species is not able to fully insert its bill into a curved corolla, and a short-billed hummingbird cannot reach the base of a long corolla. In the absence of specific pollinator observations, corolla morphology alone can provide much information about the type of hummingbirds that can legitimately extract nectar from flowers. These relationships between the structure of corolla and bill are reflected in the corolla morphologies present in the subgenus. In the first group of species the corolla is usually moderately long to long, are almost always only gradually curved. In the second group, visited by sicklebill hummingbirds, the corolla is abruptly curved, closely matching the curvature of a sicklebill hummingbird's bill.

Sicklebill Hummingbird Pollination

Two major groups within the subgenus are characterized by sicklebill pollination, sects. *Amplifolii* and *Campylobotrys*. While a few species in both of these sections appear to be suited for other types of hummingbirds, the majority of the species in these groups have corolla morphologies that suggest an obligate reliance upon *Eutoxeres* pollinators. The geographic distribution of these sections and the range of the genus *Eutoxeres* are very closely correlated.

The genus *Eutoxeres* comprises only two species, *E. aquila* and *E. condamini*. *Eutoxeres aquila* ranges from Costa Rica south to northeastern Peru, while *E. condamini* is found from southeastern Colombia to northern Bolivia (Meyer de Shauensee, 1970; Hilty & Brown, 1986). Neither species has been recorded in Venezuela (Meyer de Shauensee & Phelps, 1978). The genus has a rather wide elevational range, occurring from lowlands up to 2650 m. The precise elevational range of these birds varies from country to country, but where the geographic distributions of the two species overlap, as in eastern Ecuador and northern Peru, *E. condamini* generally occurs at lower elevations than does *E. aquila*.

Section *Campylobotrys*, and notably its core species *C. granulosus*, extends from extreme southern Nicaragua to central Bolivia, almost precisely matching the overall range of *Eutoxeres*, the principal pollinator for this group. Along with this concordant overall distribution pattern, the geographic and elevational distribution of both plants and pollinators within each country also closely coincide. As an example of this coincidence, there are no reports of sicklebill hummingbirds from Venezuela, and even though apparently suitable *Centropogon* habitat exists there only a single Venezuelan collection of *C. granulosus* is known. This lone collection is from the Sierra de Perija near the border with Colombia, and I would predict that *Eutoxeres* occurs there although it has not yet been recorded. It is possible, on the other hand, that this single

C. granulosus collection represents a colonist that is persisting vegetatively in the absence of its legitimate pollinator.

The overall distribution pattern of sect. *Amplifolii* also correlates well with that of *Eutoxeres*. There are no members of this group in Venezuela either, again, perhaps due to the absence of sicklebills there.

Sicklebill hummingbirds are consummate "high-reward trapliners," in the terminology of Feinsinger and Colwell (1978). Hummingbirds of this type are typically large bodied and have moderate to high power output requirements that can be fueled only through access to abundant energy sources. Such birds will often travel long distances between individuals or clumps of energy-rich flowers. In turn, the so-called "dispersed-rich" flowers that they visit generally have corollas that exclude most insects and smaller hummingbirds from their substantial nectar supplies, insuring that the nectar will be available for the traplining hummingbirds (Feinsinger & Colwell, 1978).

Sicklebills are among the heaviest hummingbirds (over 9 grams) and have a high power output during hovering, as calculated using wing disk loading (the ratio of body weight to a circle whose diameter equals wing span) (Feinsinger et al., 1979). As a result, *Eutoxeres* do not hover while feeding, as do most hummingbirds, but instead perch during flower visits. They are strong fliers and apparently capable of covering long distances (Stiles, 1985).

Although sicklebills are not particularly rare, they are seldom seen, probably because of their large ranges and traplining behavior. In spite of working closely with one of their primary foodplants during a combined total of more than one and one-half years of fieldwork in Central and South America, I saw sicklebill hummingbirds on only three occasions. My best observation was of *E. aquila* visiting *C. baezanus* in montane eastern Ecuador at an elevation of 2400 m. The bird perched on the pendent inflorescence and completely inserted its bill into the upright corolla. With its face

against the mouth of the corolla the exserted anther tube pressed firmly against the top/back of the bird's crown. The hummingbird started at the bottom of the inflorescence and worked its way upwards, visiting only those flowers that were in an upright position. About 3-5 seconds were spent at each flower.

The most detailed work on sicklebill foraging habits has been done by Stiles (1975, 1985) in Costa Rica. At his La Montura study site at 1000 m in Braulio Carrillo National Park he found that *E. aquila* visits only two plant species, *C. granulosus* and *Heliconia trichocarpa* (Stiles, 1985). The abundance of the hummingbird at that location is statistically correlated with the abundance of *Centropogon* flowers but not with the abundance of *Heliconia* flowers, thus linking the presence of the bird with the flowering of *C. granulosus*. Stiles found that the flowering of *Centropogon* did not correspond to the putative breeding season of *E. aquila*, and he suggested that the energy to meet breeding demands is found at lower elevations (below 800 m) where other species of *Heliconia* are important foodplants. Stiles (1985) has even suggested that "given the extremely powerful flight of this large species, it is possible that the birds of the study area . . . might be commuting from lower elevations on a daily basis."

Evolutionary implications of sicklebill pollination

The specialization of many *Centropogon* species on this single pollen vector has several implications for the population dynamics and evolution of the plants. Because of *Eutoxeres'* traplining behavior and presumed ability to cover relatively long distances between flower visits, pollen dispersal in sicklebill-pollinated species may be greater than that in *Centropogon* species pollinated by more territorial hummingbirds with restricted ranges. To a lesser degree this also applies to species visited by more generalized hermit hummingbirds. Theoretically, increased pollen dispersal should increase the degree of gene flow between spatially separated populations. The very

localized morphological differentiation often observed in these plants, however, suggests that such increased gene flow, if it occurs, may be relatively insignificant. Even given long flight distances between foraging bouts, the most common types of pollinations would still be selfings (through geitonogamy) or nearest neighbor matings, both of which are capable of setting seed (Chapter V).

The traplining behavior of the hummingbirds may even have a negative effect on the immediate reproductive success of the plants. Populations of subgen. *Centropogon* often are characterized by very low fruit set, perhaps due to poor pollinator service. This could be related to the relative rarity of pollinator visits. It may also be the result of flowering individuals that have not been "discovered" and incorporated into a bird's foraging route. The relatively aseasonal flowering phenology of sicklebill-pollinated species may have as much to do with assuring that pollinators continue to visit them over the long-term to avoid this problem, as with the relatively aseasonal habitats in which the plants grow.

Sympatric species sharing the same pollinator also increases the likelihood of interspecific hybridization. The potential for long flight distances between foodplants increases the chance of interspecific pollen exchange even between species that are not strictly sympatric. The foraging behavior of sicklebill hummingbirds when several sympatric species are present is not known, however. While it is possible that they would concentrate on only one species during a foraging trip, from an energetics perspective one would expect the birds to visit whatever species were present and appropriate. I have, in fact, observed *E. condamini* visiting both *Heliconia* and *Centropogon* sequentially; exclusive search images probably are not operating.

Differential pollen placement on the bird may be one mechanism whereby interspecific pollen transfer is reduced or avoided. Stiles (1975) notes the different sites of pollen deposition by several species of *Heliconia* on hermit hummingbirds and

includes a photograph of pollen from *H. pogonantha* on the basal half of the maxilla on *Eutoxeres aquila*. The basic structure of lobelioid flowers limits the potential sites for pollen deposition to the dorsal surface of the bird's bill or head; pollen could not be deposited on the chin or lower surface of the bill. The androecium in most sicklebill-pollinated species of subgen. *Centropogon* is fairly well-exserted, and most would probably strike the hummingbird on the forehead or on the top/back of the crown as I observed in *C. baezanus*. The exertion of this structure varies among species and could have an effect on the pollen deposition site. Because the stigma emerges from the end of the anther tube the site of pollen deposition automatically correlates with the location of stigma receptivity.

An extreme example of differential pollen placement is *C. papillosum*, in which the androecium remains completely included in the corolla tube. Pollen from this species would probably be deposited on the bird's bill rather than on the forehead or crown, and the unusual coherent, rather than powdery, pollen found in that species may relate to the need to adhere to a smooth bill rather than to feathers. In experimental crosses I found that *C. papillosum* could readily cross with most species attempted, including *C. loretensis* with which it naturally occurs. The very distinctive pollen deposition site is probably an effective pre-mating isolation mechanism and may be one reason that *C. papillosum* is so fully fertile in interspecific crosses and has not developed any internal reproductive barriers. More subtle differences in deposition sites may also be important in reducing interspecific pollen transfer. For instance, *C. granulosus* subsp. *nutans* and subsp. *tortilis* are both found in Costa Rica and Panama, although rarely in sympatry. The filament exertion in the former ranges from 9-16 mm while in the latter the filament is exserted only 2-5(-7) mm, probably affecting the placement of pollen and the potential for interbreeding.

Origin of Sicklebill Pollination in Subgenus Centropogon

The pollinator-plant relationship between *Eutoxeres* and subgen. *Centropogon* has developed into a striking mutualism. The unusual corolla morphology of the species of *Centropogon* pollinated by *Eutoxeres* appears to preclude visits by other, more generalized hummingbirds, and these species would seem to depend entirely upon sicklebill hummingbirds for pollination. Corresponding dependency of the sicklebills on subgen. *Centropogon* is more complicated, however. At lower elevations sicklebills mostly rely upon *Heliconia* flowers for nectar (Ridgely, 1976; Stiles, 1975, 1985; J. O'Neill, pers. comm.), probably visiting *Centropogon* species when and where they are available. *Heliconia* is primarily a low elevation genus and usually does not occur much over 1000-1500 m. At higher elevations then, this preferred food source is absent and members of subgen. *Centropogon* appear to be the only nectar source morphologically suitable for sicklebills. A very limited number of other plant groups may have developed species that are visited by sicklebills. For example, *Pitcairnia* sp. (Stein 2987) from eastern Ecuador appears suitable for sicklebill pollination on the basis of corolla morphology. Nonetheless, no other group of plants as a whole are so completely adapted for sicklebill pollination as are sects. *Campylobotrys* and *Amplifolii* of subgen. *Centropogon*.

What are the origins of this close relationship between subgen. *Centropogon* and sicklebill hummingbirds? *Eutoxeres* probably first evolved/coevolved in partnership with *Heliconia* since (1) this is the bird's major food source and far more common than *Centropogon*, and (2) *Eutoxeres* is a member of a predominantly lowland hummingbird group (the subfamily Phaethorninae), which has undoubtedly had a long historical relationship with the lowland plant family Musaceae. Most neotropical lobelioids are upland plants, although the ancestral members of subgen. *Centropogon* were probably much like *C. cornutus* in being lowland plants pollinated by generalized hermit

hummingbirds. Unusual individuals at low or middle elevations may have begun to attract sicklebills, and subsequent morphological specialization could have refined the relationship. Given the ability of lobelioids to grow at elevations above the normal range of *Heliconia*, this new partnership allowed an expansion in the altitudinal range of the hummingbirds. At upper elevations (1500–2600 m) this has apparently become a more-or-less obligate relationship for the hummingbirds.

The systematic distribution of sicklebill pollination within subgen. *Centropogon* poses some interesting questions as to the number of times this pollination syndrome arose. Preliminary analysis suggests that sects. *Campylobotrys* and *Amplifolii* are not a monophyletic unit; sect. *Grandes* appears to be the sister group to sect. *Campylobotrys*, with sect. *Amplifolii* the sister group to both of those sections. If this is the case, sicklebill pollination either arose independently in sects. *Campylobotrys* and *Amplifolii*, an unlikely scenario given the overall rarity of this syndrome, or the generalist pollination syndrome in sect. *Grandes* may be a reversal from the sicklebill system, an equally unlikely scenario. It is also possible that the sicklebill pollination syndrome arose in one lineage and through hybridization was incorporated into the other, or conversely that sect. *Grandes* represents a lineage derived from hybridization between members of the generalized hermit-pollinated sect. *Centropogon* and the sicklebill-pollinated sect. *Campylobotrys*.

Apparent reversals in the presumed overall trend from generalized pollinators to obligate sicklebill pollinators do exist in the subgenus. *Centropogon cuatrecasanus*, for example, is found at 1850–2300 m in the Cordillera Occidental of Colombia. This species of sect. *Campylobotrys* shares many features with such sicklebill-pollinated species as *C. granulosus*. The corolla of *C. cuatrecasanus* is only gradually curved, however, and appears suited for pollination by generalized hermit hummingbirds rather than by *Eutoxeres*. According to Hilty and Brown (1986), *E. aquila*, the sicklebill

species present in that region, ranges only to about 1400 m in that area. I would suggest that *C. cuatrecasanus* is derived from a lower-elevation sicklebill-pollinated ancestor, but that the corolla morphology has straightened in response to the absence of that pollinator in its new habitat. A similar process appears to have occurred in *C. amplicorollinus*, a species apparently most closely related to *C. loretensis*, a sicklebill-pollinated species most abundant along the base of the Andes in eastern Ecuador and northern Peru.

Centropogon amplicorollinus is found in the Amazon lowlands south and east of Iquitos, where *Eutoxeres* is absent. The corolla in this species is very gradually curved, rather than sharply bent as in *C. loretensis*, and again, I presume that this shift in corolla structure has occurred in response to colonization of a region lacking the specialized sicklebill pollinator.

Nectar

In line with the type of energy-demanding hummingbirds that most species of subgen. *Centropogon* attract, the flowers produce relatively large quantities of energy-rich nectar. Nectar is secreted at the apex of the ovary and fills a nectar chamber bounded by the base of the adnate filaments. Nectar quantities measured in unvisited flowers (either bagged or cultivated) range from 23 ul (in *C. gamosepalus*) to 70 ul (in *C. cornutus* and *C. reflexus*). Because the structure of the nectar chamber requires destructive sampling to measure nectar volumes it was not possible to determine daily rates of nectar production. Nectar concentrations, as measured with a Reichert temperature-compensated optical refractometer, range from 27-40% sucrose-equivalents (percent weight by total weight). Mean values for seven species are given in Table 3; these average 34%, a relatively high value for hummingbird-pollinated plants, which as a whole averages about 23% (Pyke & Waser, 1981). The relatively energy-rich nectars in subgen. *Centropogon* probably relate to the large body size and traplining behavior of the

pollinators. Although the data are very incomplete, they support Baker's (1975) suggestion that dilute nectars in hummingbird flowers may partially be due to a balance between sugar concentration and nectar viscosity. In this interpretation, sugar concentrations are constrained by the energy expenditure required to drink highly viscose solutions while hovering. Of the species listed in Table 3, only *C. cornutus*, which has the lowest mean nectar concentration, is visited by hummingbirds that normally hover while feeding; the others are visited by *Eutoxeres*, which normally perches while feeding. Investigations into the mechanics of hummingbird feeding by Kingsolver and Daniel (1983) suggest that two different nectar concentration optima exist depending upon the quantity of nectar available and the size of the hummingbirds. For flowers with large nectar volumes they found the optimal concentration to be 35-40%, closely approximating the values reported here.

Nectar-Robbers

The relatively large quantities of rich nectar present in these flowers make them targets for nectar-robbers, flower visitors that extract nectar in a way that does not effect pollination. In *Centropogon* this usually involves piercing the basal portion of the corolla to obtain direct access to the nectar chamber. Most populations of subgen. *Centropogon* show little evidence of nectar robbing activity, however, and I have observed specialized nectar-robbing birds, such as *Diglossa*, completely ignore species of subgen. *Centropogon* while foraging. During one six-hour observation of *C. reflexus*, for instance, *Diglossa carbonaria* repeatedly passed the *Centropogon* while parasitizing species of *Cavendishia* (Ericaceae), which contain far less nectar. The birds paid no attention to inflorescences of the *Centropogon* that later analysis showed to contain up to 70 ul of high quality nectar per flower. During another observation period, however, I saw a species of small hummingbird, *Adelomyia melanogenys*, attempting to remove nectar by making a hole in the side of the nectar chamber with its bill. Because of the very thick tissue surrounding the nectar chamber, it is unclear how successful the bird was, but 81% of 33 flowers surveyed showed evidence of such attempts.

Several features found in subgen. *Centropogon* would appear to limit the extent to which nectar robbing can take place. First, the copious latex that exudes from the damaged corolla probably inhibits many potential nectar-robbers. This is a general feature of Lobelioideae, however, and its presence cannot be considered a response to selection against nectar robbery, even if it functions to lessen it. In a number of species, particularly in sect. *Campylobotrys*, the tissue surrounding the nectar chamber has become very thick and is difficult to penetrate. This tissue can be so tough that in sampling nectar I often had to first make an incision with a sharp metal object, since glass micropipettes could not penetrate the tissue without breaking. In species such as *C. baezanus* the tissue surrounding the nectar chamber may reach 4 mm thick, and

consequently the corolla often assumes an unusual "pregnant" shape. Connate sepals have developed independently in several lineages of *Centropogon* and may confer a selective advantage through creating an additional layer around the nectar chamber. Similarly, a number of species, such as *C. capitatus*, have inflorescence bracts that closely subtend and partially cover the lower portion of the flower.

Table 2

Confirmed Pollination Records for Subgenus *Centropogon*

Species	Pollinator	Country	Reference
<hr/>			
<i>C. cornutus</i>	<u>Glaucis hirsuta</u>	Trinidad	Snow & Snow, 1972
	<u>Phaethornis guy</u>	Trinidad	Snow & Snow, 1972
	<u>Phaethornis longuemareus</u>	Trinidad	Snow & Snow, 1972
<i>C. gamosepalus</i>	<u>Eutoxeres condamini</u>	Ecuador	pers. obs.
<i>C. silvaticus</i>	<u>Eutoxeres</u> sp.	Peru	J. O'Neill, pers. comm.
<i>C. granulosus</i>	<u>Eutoxeres aquila</u>	Costa Rica	Stiles, 1985
	<u>Phaethornis guy</u> (rarely)	Costa Rica	Stiles, 1985
<i>C. baezanus</i>	<u>Eutoxeres aquila</u>	Ecuador	pers. obs.
<i>C. loretensis</i>	<u>Eutoxeres aquila</u>	Peru	J. O'Neill, pers. comm.
<i>C. solanifolius</i>	<u>Phaethornis guy</u>	Costa Rica	P. Feinsinger, pers. comm.
	<u>Phaethornis syrmatophorous</u>	Colombia	pers. obs.
<i>C. beslerioides</i>	<u>Phaethornis syrmatophorous</u>	Colombia	pers. obs.
<hr/>			

Table 3
Nectar Concentrations in Species of Subgenus *Centropogon*¹

Species	Mean Nectar Concentration (%)
<i>C. cornutus</i>	28
<i>C. gamosepalus</i>	38
<i>C. granulosus</i> subsp. <i>nutans</i>	40
<i>C. baezanus</i>	34
<i>C. loretensis</i>	36
<i>C. reflexus</i>	32
<i>C. lasiodorus</i>	32

¹ sucrose-equivalent sugars in percent weight by total weight.

V. HYBRIDIZATION AND BREEDING SYSTEMS

Both natural and artificial hybrids are well-known in Lobelioideae, and particularly in the large genus *Lobelia*. Natural hybrids in *Lobelia* were reported at least as long ago as 1878 by Schneck. The most extensive work on hybridization in that genus was performed by Bowman (1961). Bowman made about 1400 experimental inter- and intraspecific crosses within *Lobelia* sect. *Lobelia*. He found that the species he tested were generally self-fertile and that interstrain crosses within a species also usually gave positive results. Among the interspecific crosses attempted, tetraploids crossed more easily than diploids (67% successful vs 29%).

Wood (1961) conducted an extensive crossing program with species of the small western North American genus *Downingia* and found that, in contrast to the situation in *Lobelia*, interspecific barriers to hybridization generally exist. Interspecific crosses either did not set seed, the seed produced inviable seedlings, or the progeny lacked the vigor of normal seedlings. The significance of these barriers to hybridization in *Downingia* is complicated by the existence of an aneuploid series, but even crosses between species with the same chromosome number generally failed.

Most recently Ayers (1986) attempted interspecific hybridizations among members of the polyphyletic genus *Heterotoma*, and with related species of *Lobelia*. Although most crosses failed, a small number yielded viable seed. These seed produced subviable plants, however, and those few plants that reached maturity had very low pollen viability or did not produce pollen at all.

Natural Hybridization in *Centropogon*

Because of the frequent sympatric occurrence of different species in subgen. *Centropogon* (Chapter II), the reliance by many of these species on the same pollen vector (Chapter IV), and an apparently common chromosome number (Chapter VI), there would seem to be a high potential for natural interspecific hybridization within this group. I have found relatively few clear examples of natural hybridization, however, and these are detailed below. This lack of clearly recognizable cases should be interpreted cautiously, because cases of hybridization may be obscured by the relative paucity of discrete, qualitative characters in the subgenus and by the high degree of intraspecific, and often intrapopulational, variability.

Hybrids Within Subgenus Centropogon

1). *Centropogon yungasensis* x *C. granulosus* subsp. *granulosus*, Kosñipata Valley, Cuzco, Peru. Along the Paucartambo road in Cuzco Department of southern Peru *C. yungasensis* ranges from about 2000-2400 m, while *C. granulosus* is found from about 700-2000 m. Principal features that distinguish *C. yungasensis* from *C. granulosus* in this area are the elongate and reflexed versus shorter and erect sepals, the glabrous versus pubescent corolla, and the glabrous, small, and lanceolate versus abaxially pubescent, larger, and often elliptic leaves. Further, the leaves in *C. yungasensis* have an unusual texture, discussed more fully elsewhere. Some plants found in the overlap zone at about 2000 m (e.g., Stein 2508) are intermediate between the two species in many of these features, having long, erect to spreading sepals, partially pubescent corollas, small to large, lanceolate to elliptic leaves that are pubescent beneath, and (as in *C. yungasensis*) a rather fleshy texture. The corolla morphology of these two species is very similar, and they are both almost certainly pollinated by sicklebill hummingbirds.

2). *Centropogon arcuatus* x *C. curvatus*, Plan de Milagro, Morona-Santiago, Ecuador. An unusual collection from around Plan de Milagro, (*Jorgensen OHJ-33*) appears to be a hybrid between the above two species, both of which are known from the area. In most respects, including the stout, abruptly curved and ventricose corolla, and the densely papillose-hirtellous inflorescence indument, the specimen resembles *C. curvatus*. The leaves, however, are serrate-lobate distally, a condition unknown in *C. curvatus*, and within subgen. *Centropogon* known only in the sympatric *C. arcuatus*. It is highly unlikely that this leaf margin condition would have evolved independently in *C. curvatus* in just that area, and instead a hybrid origin for the plant seems probable. Although the pollinator of *C. arcuatus* is not known, based on the very curved to arcuate corolla morphology it is probably visited by sicklebill hummingbirds, as I presume is *C. curvatus*.

3). *Centropogon solanifolius* x *C. beslerioides*, El Silencio above Ibagué, Tolima, Colombia. These two species differ strikingly in the length of the corollas. In this area the corolla tubes of *C. beslerioides* are 27-30 mm long whereas in *C. solanifolius* they are 44-51 mm long. I have seen the same hummingbird, *Phaethornis syrmatophorus*, visiting both species at this high elevation (2500 m) site. At least one plant present (*Stein 3539a*) was intermediate between these two species in corolla length (36 mm), bract shape, and inflorescence indument and most likely was the product of hybridization between these two closely related members of sect. *Grandes*.

Along with these more concrete examples of interspecific hybridization, certain geographically restricted morphological trends point to hybridization. For example, in northern Ecuador and southern Colombia several species in sect. *Campylobotrys* all have an unusual papillose or pustulate type of trichome base or surface protrusion. Since this surface feature does not occur elsewhere and the species involved do not appear to be a monophyletic assemblage, interspecific transfer of this unusual feature through

hybridization may be a possible explanation. Another case is the presence of lateral inflorescences among several taxa in the *C. granulosus* species complex in Ecuador and northern Peru. A number of specimens of *C. granulosus* subsp. *lateriflorus*, *C. trachyanthus*, and *C. baezanus* have lateral inflorescences, and while they are mostly found in a limited geographical region, again they do not appear to represent a monophyletic group. The condition can apparently be independently evolved, since at least one specimen of *C. granulosus* subsp. *lugens* from northwestern Colombia also exhibits this inflorescence type, but geographic consistency among the above mentioned species suggests that the trait may have been acquired by interspecific hybridization.

Hybrids Between Subgenus Centropogon and Subgenus Siphocampyloides

1). *Centropogon cornutus* x *C. warszewiczii*, Salgar, Antioquia, Colombia. This is a very clear example of hybridization between subgen. *Centropogon* (*C. cornutus*) and subgen. *Siphocampyloides* (*C. warszewiczii*). Both parental species were found together along with the putative hybrid. These two species have very different corolla and leaf morphologies. Rather than possessing intermediate character states, the hybrids combined a number of characters from each parent. Features resembling *C. cornutus* include leaf size and shape, hypanthium shape, the reflexed dorsal corolla lobe, and the deflexed ventral corolla lobe tip. Features resembling those of *C. warszewiczii* include the pedicel length, the narrow corolla tube, the deep red corolla color, and the unfused terminal anther trichomes. The length of the sepals in the hybrid was truly intermediate between the two species. Along with the above combination of characters, however, the most compelling reason for believing these plants to be hybrids is presence in Stein & McDade 3197 of unfused anther tubes with the thecae splayed and completely lacking pollen. Another putative hybrid from the same site (Stein & McDade 3198) had intact anther tubes with pollen.

Yet another aberrant plant at that site (*Stein & McDade 3199*) closely resembled *C. cornutus* except in its extremely short sepals. While I did not see any *C. trianae* in the immediate vicinity, that species (a member of subgen. *Centropogon* sect. *Grandes*) was found in abundance approximately 5 km away and probably also occurs near to the collection locality of this hybrid swarm. I suspect that this unusual specimen may be the product of hybridization between *C. cornutus* and *C. trianae*, which has very short sepals.

The unusual unfused and splayed anther tube found in the *C. cornutus* x *C. warszewiczii* hybrid is similar to the anther tube described by Wimmer (1948) for *Siphocampylus schizandrus*. After examining the type specimen of that species (Killip & Smith 15048), along with other specimens made by the collectors at the same time, I have come to the conclusion that this "species" is a similar hybrid in which the anthers do not develop properly. The parents of this hybrid are still unclear, but may be *S. densiflorus* and perhaps *S. longibracteolatus*.

Hybrids Within Subgenus Siphocampyloides

1) *Centropogon varicus* x *C. longifolius* x *C. featherstonei*, Pomacocha, Amazonas, Peru. A complicated three-way hybrid complex exists in the montane forest around Lago Pomacocha in northern Peru involving the above-named species. I observed the same species of hummingbird, *Coeligena torquata*, visiting all three parental species, and this common pollen vector undoubtedly provides the means for interspecific pollen transfer. Because *C. varicus* has several very unusual features, including a bilabiate, connate calyx, this hybrid situation offers an excellent opportunity to compare discrete character states among the parental species and putative hybrids. Those characters that in the hybrids are intermediate between the parental states include corolla length and curvature, corolla color, dorsal corolla lobe shape, calyx symmetry and fusion, and sepal length and width. In other features, such as filament pubescence, latex color, and

general trichome complement, the putative hybrids closely resemble one or another of the parental species.

Experimental Hybridization

In order to ascertain more precisely the potential for interspecific hybridization, I conducted an extensive series of crossing experiments using greenhouse-cultivated material. Very few crossing programs have been undertaken with perennial tropical plants, and even though species of *Centropogon* are mostly herbaceous, their perennial habit and long lifespan create practical difficulties in carrying out such work.

Methods

About twenty collections of *Centropogon* were successfully cultivated from seed in the research greenhouses of the Missouri Botanical Garden. Seeds were germinated under mist in vermiculite. Once established, seedlings were transplanted into clay pots with soil and removed from the mist bench. Temperatures were normally kept at 60°F night and 70°F day, although during the summer temperatures could range up to 80°F. No artificial illumination was provided, so plants were responding to natural photoperiod at 38° N latitude. Most plants that produced flowers did so only after two to three years in cultivation indicating that perhaps a maturity threshold must be reached before the plants allocate resources to flowering.

The structure and protandrous functioning of lobelioid flowers greatly facilitate crossing studies. The five stamens are fused together and form a tube that surrounds the style and stigma. At anthesis the anthers dehisce introrsely filling the anther tube with pollen. Because the anther tube orifice is closed-off by the downcurving upper anthers, the pollen is placed under pressure by the upwardly growing style and stigma. The scale at the tip of the anther in subgen. *Centropogon* functions as a trip lever.

Pushing on this scale opens the anther tube orifice slightly, allowing the pressurized pollen to discharge, and quantities of pollen can be obtained easily in this manner. In most cases if this lever is not activated, pollen eventually will issue from the anther tube nonetheless. The stigma remains tightly closed as it pushes up through the anther tube, and the lobes do not spread open and become receptive until they are exserted. As a result, except in unusual instances, no pollen is deposited on the moist receptive surface. The stigma normally emerges from the anther tube 3-5 days following the beginning of anthesis and remains receptive for approximately 2 days. The timing of emergence appears related to the presence of pollen within the anther tube, however, with stigmas emerging sooner from anthers in which pollen has been extracted. Occasionally, if pollen is not extracted from the anther tube, the stigma never emerges or the lengthening style bows-up and tears open the anther tube.

Flowers were cross-pollinated by collecting fresh pollen on a small stainless-steel spatula. To insure viability, pollen was harvested from male donors within two days of the flower's opening and was used immediately. Pollen used in crosses that was examined with Alexander's stain tested fully positive for cytoplasmic integrity. Fresh stigmas were selected for use as the female recipients, and were normally pollinated on the first day that they were fully spread. Because stigmas occasionally emerged from the anther tube deformed, only those that were well-formed and moist were used. Ample pollen was rubbed over the entire stigmatic surface using the spatula on which the pollen was collected. The spatula was cleaned with 70% ethanol between pollinations to avoid pollen contamination of stigmas.

Female recipients were not emasculated before crossing for several reasons. First, the limited number of flowering individuals necessitated the use of many flowers as both male and female parents. Emasculating one-half of the flowers for use as females would have substantially reduced the number of crosses possible. Second,

although certain lobelioids, such as *Hippobroma longiflora*, are autogamous with the stigma apparently becoming self-fertilized while in the anther tube, this does not seem to happen in subgen. *Centropogon*. Of the several hundred flowers left unpollinated during the crossing program, with only a few rare exceptions, unpollinated flowers did not set fruit. Because the flowers were not emasculated a small amount of self-pollen may have contaminated the stigma of certain crosses and produced selfed seed. The copious application of donor pollen to the stigma, however, would tend to overwhelm any self-pollen present. Further, a small amount of self-pollen could not possibly account for the very large number of seeds that were often set in cross-pollinations. Because the purpose of these crossing experiments was to ascertain the potential for hybridization in this group, and not to conduct detailed genetic analysis of the progeny, such possible low-levels of self-pollen contamination were considered acceptable in view of the constraints imposed by the number of available flowers.

Each flower was assigned a number through use of small jewelers tags placed around the pedicels, and the status of the flowers and fruits was checked daily. Several classes of pollinations were conducted: self-pollinations, intrastrain pollinations, interstrain pollinations, and interspecific pollinations. Because of the strongly protandrous condition, self-pollinations were made by transferring pollen from a male phase flower to a receptive stigma on the same individual. Intrastrain cross-pollinations were made between different individuals of the same collection, intraspecific pollinations were between different collections of the same species, and interspecific pollinations were between different species.

Each ripe fruit was measured and weighed after harvesting. In order to gain additional information about the success of the crosses, the number of seeds in each mature fruit was counted. Fruits were dissected and the small (0.5-1 mm) seeds were counted with the aid of a dissecting microscope. Because the ovary is bilocular, fruits

can be easily divided in half along the partition. Counts of both halves revealed that the number of seeds contained in each was roughly equivalent, and usually did not vary more than about ten percent. For this reason, in fruits that contained numerous seeds (more than 1,000) usually only one-half the fruit was counted, with the total number estimated by doubling that figure. Because seed of varying quality was produced by different crosses, the condition of the seed was also noted, with well-formed, plump seed counted separate from seed that was obviously abortive. The seed set figures presented below refer only to the well-formed, presumably viable seed.

Seed from a selected number of crosses was sown to examine the percent germination and the vigor of the plants produced. A limited number of progeny are in cultivation and will be grown to maturity in order to compare the morphology of the hybrid progeny with that of the parents.

Results

Fourteen different living collections representing ten different species bore flowers and were used in the crossing experiments. A total of 410 hand-pollinations of various combinations were performed over a period of approximately seven months. Of these, 13% were self-pollinations, 3% were cross-pollinations among individuals of a particular collection (intrastrain), 9% were pollinations among different collections of the same species (interstrain), and 75% were interspecific pollinations.

Changes in the flower following successful pollination were apparent usually within 24 hours. The most conspicuous alteration is a shift from the upright and erect attitude of the flower at anthesis to a drooping position. The corolla usually withers and turns brown, but in most species it remains attached to the fruit. Fruit normally took from 40-60 days to mature with an average of 48 days. *Centropogon cornutus* fruits took considerably longer to ripen (60-80 days) than fruits of other species. Ripe fruits could

be recognized by the development of an abscission layer at the base of the pedicel, or in rare instances the fruit began fissuring and exposing ripe seed before pedicel abscission (e.g., in *C. gamosepalus*).

Fruit Set

One-half of the 410 pollinations conducted set fruit. Although intrastrain crosses set slightly more and interstrain crosses slightly fewer, each of the pollination classes showed good fruit set (Table 4). The proportion of successful fruit set among the various crossing combinations attempted is given in Table 5. In addition to the fruit that was produced as a result of the hand-pollinations, six fruits formed from unpollinated flowers, apparently as a result of autogamy. Each of these autogamous fruits was rather small compared to their hand-pollinated relatives and contained few seeds. Nonetheless, their presence is significant.

Seed Set

Almost 250,000 seeds were produced by the 205 fruits that matured during this study. While the average number of viable seeds per fruit was 1,144, seed set varied widely, ranging from more than 3,700 to less than 100 per fruit. Because the number of seeds produced by different species appeared to vary in consistent ways, a standardized measure was needed to compare hybrid seed set data across species. The actual number of seeds set in any given cross should be viewed in the context of the maximum potential seed set for that particular female parent. Ideally the number of ovules should be used as the baseline for determining the proportion of potential seeds that actually developed. Unfortunately, the ovules in *Centropogon* are so small and their number within a single ovary so great that it was not possible to precisely establish the total number available in a given fruit. The second most desirable standard would be the

average number of seeds produced by cross-pollinated (intrastrain) fruits, information that for the most part is lacking for these plants, since many of the collections were represented in the study by only a single flowering individual. Because neither of these two methods were available to me, I have relied on a procedure with some clear shortcomings, but which given the circumstances provides consistent estimates of the relative seed set for different crosses.

The maximum number of seeds produced by each species in any crossing combination (Table 6) was used as an internal standard in calculating the relative seed set of crosses with that species as a female parent. The underlying assumption using this method is that the maximum seed set obtained for each species during this study represents 100% of the potential seed set, an assumption that is clearly unwarranted. Much higher seed sets may be possible but were not attained in these experiments because of the limited choice of crossing partners or environmental factors, or alternatively, heterotic effects may have occurred in some interspecific crosses giving an artificially high maximum seed set. The average number of seed produced by each cross, given as the proportion of the maximum seed set obtained in any cross of the female parent, is presented in Table 7. The maximum seed set for each given cross is also useful information since cases occur where the average seed set is very low, but an occasional highly fertile fruit is produced. When assessing the potential importance of hybridization, these high, if rare, seed set levels may be of more significance than the average figures. Maximum seed set data are thus given parenthetically in Table 7.

Germination and Viability

A number of crosses were selected for further investigation through planting. To determine percent germinability, seed from several interspecific crosses and self-fertilizations were accurately counted and sown on moist filter paper in petri dishes.

After three weeks 30-50% of the seed in each dish had germinated, approximating the germination percentages obtained from wild-collected seed. To test the growth and vigor of the progeny, seed from 52 crosses representing selfings, intraspecific crosses, and interspecific crosses were sown in vermiculite and kept on a mist bench for cultivation. Almost all of these crosses germinated well, with only one failing (i.e., *C. papillosus* x *C. gamosepalus*, although seed from another fruit of this same cross germinated well). The vigor of the seedlings was variable, but in general, they grew well, often surpassing the performance of the wild-collected parentals when they were at a comparable stage. Within 90 days of sowing certain of the more vigorous collections were 15-22 cm tall with leaves to 14 cm long. Whether this rapid growth is due to heterotic effects, or to improved cultivation techniques developed since the parentals were cultivated from seed is unknown.

Although the F1 progeny will not mature for at least one to two years (based on the performance of the parents in cultivation), leaf morphology already confirms the hybrid origin of several of the crosses. *Stein & Todzia 2169*, a collection of *C. cornutus*, has sharply serrate leaf margins and reflexed sepals, a form that has been known in the past as *C. puerilis*. These leaf margins contrast with the almost entire to only moderately serrulate leaves of most of the other collections in cultivation. Progeny of crosses using this collection as the male parent (e.g., with *C. granulosus* or other collections of *C. cornutus* as the female parents) clearly show the distinctive deeply serrate leaf margin (Fig. 3) and must be of hybrid origin, rather than the result of autogamy or of agamospermy induced by foreign pollen. Another example involves crosses with *C. cornutus* (*Plowman 13387*) as the female parent, which has generally lanceolate leaves and well-developed petioles, and *C. gamosepalus* (*Stein 3020*) as the pollen donor, with narrowly elliptic leaves and short or absent petioles. The hybrid progeny have leaves

with the widest point about at the middle (i.e., elliptic leaves) and short petioles as in *C. gamosepalus*.

Discussion

Breeding Systems

In addition to shedding light on the potential for interspecific hybridizations, the experimental pollinations have also elucidated the possible modes of reproduction available to plants in subgen. *Centropogon*. While in natural populations most plants may be modally outcrossing, self-fertilization is an apparently viable mode of reproduction among species of subgen. *Centropogon*. Forty-eight percent of self-pollinations set fruit, almost exactly the overall norm, and those fruits contained a respectably high average relative seed set of 70%. Because of the protandrous flowers, self-fertilizations in nature normally would result from geitonogamous pollinations rather than autogamy. In fact, as discussed elsewhere (Chapter IV), this is the most likely type of pollination to occur given the movement of the plant's hummingbird pollinators.

The ability to be self-fertilized is of critical importance in the establishment of new populations. A single individual that colonizes a new area is thereby able to reproduce sexually given the presence of appropriate pollinators. A period of self-fertilization following colonization may also markedly alter the genetic composition of the resulting population through the founder effect (Templeton, 1980). The ability to self, and the resulting differentiation of founder populations, may be a major factor in the bewildering patterns of differentiation evident among certain species complexes, such as the *C. granulosus* group. The capacity for self-fertilization is not uniform, however, and both *C. granulosus* and *C. urubambae* showed relatively low levels of fruit set from self-fertilizations, even though the fruits that were produced had relatively high levels of seed set.

Autogamy is apparently very rare, but can occasionally occur, as evidenced by the production of six such fruits during this study. This is significant, however, even at very low levels. Following colonization by a single propagule of a new area where appropriate pollinators may be absent, over long periods of time the infrequent production of autogamous fruits could play an important role in the development of a population. Certain species may be more prone than others to producing autogamous fruits. For example, *C. papillosus* produced three of the six autogamous fruits. This relatively high proportion in one species is likely a consequence of the completely included androecium of *C. papillosus*, in which the pollen is shed from the anther tube while inside the corolla tube and the receptive stigma is also spread within the corolla tube. The receptive surface of the stigma in these cases probably contacted pollen resting on the lower portion of the corolla throat rather than within the anther tube.

Fertility Relationships

Relative degree of fertility among different species has often been used as a measure of phylogenetic relationship, an inference that has recently come under much criticism (e.g., Rosen, 1979; Funk, 1985). These authors argue that ability to interbreed is difficult to interpret and may represent a plesiomorphic trait of little phylogenetic utility. In some instances closely related species may have been under selective pressures to become reproductively isolated from one another and developed internal barriers to hybridization, whereas more distantly related species never developed such barriers.

The crossing studies carried out here were not intended to determine relationships between the species involved, but it is of interest to examine the fertility relationships shown between presumably closely and more distantly related species. In general, no clear patterns emerge. Some obviously closely related species did not set any fruit even after numerous attempts (e.g., *C. granulosus* and *C. trachyanthus*), whereas

other closely related species crossed easily (e.g., *C. loretensis* and *C. papillosum*). Some more distantly related species also crossed with ease; *C. cornutus* of sect. *Centropogon*, phylogenetically considered to be the sister group to the rest of the subgenus, showed a relatively high fertility with most of the species with which it was crossed. *Centropogon papillosum* also was very fertile with all the species with which it was crossed regardless of presumed relationships.

The relative fertility between two species was not reciprocal. In certain instances crosses in one direction failed completely whereas crosses in the reverse direction were successful. This was the case with *C. granulosus* and *C. urubambae* where all 14 attempts using the former as the female parent failed but 56% of the 16 attempts using *C. urubambae* as the female parent successfully set fruit.

Centropogon gamosepalus was the only member of sect. *Amplifolii* included in the crossing studies and it showed an unusual response to interspecific crosses. Self-pollinations and intrastrain crosses were highly fertile for both fruit and seed set. Fruit set was also generally high when *C. gamosepalus* was used as a female parent in crosses with other species. Most of the fruits resulting from these interspecific crosses contained very low numbers of viable seed, however, and they often were filled almost completely with deformed, abortive seed. For example, of the 23 crosses with this species as the female parent and *C. granulosus* as the male, 69% successfully set fruit, an above average success rate. These fruit contained on average only 12% seed set, far below the norm for interspecific crosses.

There thus appear to be two general responses to incompatible crosses. The first, to which most of the species tested conform, involves abortion of the fruit soon after an incompatible pollination. The second, exemplified by *C. gamosepalus*, sets relatively high numbers of fruit regardless of the compatibility of the cross, with the relative fertility manifested in the seed set. This unusual response in *C. gamosepalus* may have

more to do with the mechanics of the flowering and fruiting in that species than with any evolutionary "strategy," since, as discussed in the morphology section, the pedicels in this species generally remain erect during the fruiting process and are often persistent even after fruits mature. While fruit abortion in most species occurs through development of an abscission layer at the base of the pedicel, the pedicel behavior in *C. gamosepalus* may somehow preclude this response.

Contrary to expectations based on the traditional biological species concept, intraspecific crosses among different genetic strains were not always very successful. Such intraspecific, interstrain crosses could only be attempted with three species due to limitations in the flowering material available (*C. cornutus*, *C. solanifolius*, and *C. granulosus*). In particular, *C. solanifolius* set low numbers of fruit and had poor seed set in those fruits that were produced. Crosses using *Stein 1740* as the female parent failed completely. These difficulties in making intraspecific crosses could imply that the taxonomic integrity of that species should be questioned, or could merely reflect the accumulation of many genetic differences in these two very disjunct strains (one from central Ecuador, the other from northern Venezuela).

Interspecific Hybridization

The significance of hybridization in subgen. *Centropogon* is still largely unresolved. The cases of natural hybridization discussed, along with the experimental crossing studies show that there is a very good potential for hybridization to occur extensively within subgen. *Centropogon*. The information gathered during the experimental studies is still incomplete, since although vigorous hybrid F1 progeny were obtained, the fertility of these plants will not be known until they flower. Nonetheless, it is fair to assume that given the ease of producing viable hybrids, some would be partially or fully fertile even if most were of reduced fertility. Hybridization thus is an

evolutionary force that must be considered of at least potential importance within the subgenus.

Given that hybridization among species of subgen. *Centropogon* can occur, the overriding questions become to what extent does it occur, and how important has it been evolutionarily. The first question, as discussed previously, is difficult to answer because the morphological distinctions between many of the species in the subgenus are so imprecise, and because such a wide range of intraspecific variability exists. It is possible that extensive hybridization, both intra- and interspecific, is partly responsible for the very patterns of morphological diversity that make discerning examples of it so difficult. Hybridization can play a role in the evolution of this group in several ways, the generation of novel morphological types (i.e., species) or the movement of genetic material across species boundaries (introgressive hybridization in the original sense of Anderson [1949]). If the novel form produced involves a fundamental shift in the corolla morphology, and thus alters the pollinator relationships, such a *de novo* hybrid "species" could become reproductively isolated to the extent that the morphological form would stabilize. Several species, such as *C. lasiodorus*, *C. carpishensis*, and *C. pygmaeus* have unusual combinations of features that make them anomalous in any of the major groups that are here treated as sections. Perhaps the solution to the perplexing relationships of these species lies with intersectional hybridization events.

Table 4
Fruit Set by Pollination Class

Class	Successful	Aborted	Total
<hr/>			
Intraspecific			
Self	25 (46%)	29 (53%)	54 (13%)
Intrastrain	9 (69%)	4 (31%)	13 (3%)
Interstrain	14 (39%)	22 (61%)	36 (9%)
Interspecific	151 (49%)	156 (51%)	307 (75%)
<hr/>			
Total	199 (49%)	211 (51%)	410 (100%)

Table 5

Proportion of Successful Fruit Set Among Crosses^a

<u>Male Parent</u>	<u>Female Parent</u>									
	<i>corn</i>	<i>als</i>	<i>gamo</i>	<i>sol</i>	<i>gran</i>	<i>trac</i>	<i>lor</i>	<i>pap</i>	<i>uru</i>	
<hr/>										
<u>Intraspecific Crosses</u>										
self	.80 (5)	1.00 (3)	.78 (9)	.50 (6)	.18 (17)	0.00 (1)	.60 (5)	.50 (4)	.14 (7)	
intrastrain			1.00 (4)	1.00 (1)	.25 (4)		.60 (5)	1.00 (1)		
interstrain	.62 (8)			.23 (13)	.35 (17)					
<hr/>										
<u>Interspecific Crosses</u>										
<i>cornutus</i>		1.00 (4)	.85 (13)	.42 (7)	.47 (17)	0.00 (2)	.60 (5)	1.00 (2)	1.00 (3)	
<i>alsophilus</i>	.80 (5)		.69 (23)	.80 (5)	.40 (5)			1.00 (2)		62
<i>gamocephalus</i>	.60 (5)			1.00 (2)	.40 (15)			1.00 (3)		
<i>solanifolius</i>	.25 (12)	.33 (3)	.40 (10)		.10 (19)		.43 (7)	.80 (5)	1.00 (2)	
<i>granulosus</i>	.20 (5)	.66 (3)	.69 (23)	.66 (6)		0.00 (9)	.57 (7)	1.00 (5)	.56 (16)	
<i>trachyanthus</i>				0.00 (1)	0.00 (5)		.28 (7)		.50 (2)	
<i>loretensis</i>		1.00 (1)		.50 (6)	.11 (9)	1.00 (3)		1.00 (5)		
<i>papillosum</i>	0.00 (3)		.25 (4)	.66 (3)	.50 (12)		.50 (2)			
<i>urubambae</i>					0.00 (14)	0.00 (2)	0.00 (4)			
<hr/>										

^a total attempted pollinations in parentheses.

Table 6
Maximum Number of Seeds Set by Each Species

Species	seed number	pollen donor that yielded maximum seed set
<i>C. cornutus</i>	1,482	self
<i>C. alsophilus</i>	2,102	<i>C. loretensis</i>
<i>C. solanifolius</i>	1,808	<i>C. cornutus</i>
<i>C. gamosepalus</i>	2,582	intrastrain cross
<i>C. granulosus</i>	3,088	intrastrain cross
<i>C. trachyanthus</i>	2,288	<i>C. loretensis</i>
<i>C. loretensis</i>	3,708	intrastrain cross
<i>C. papillosum</i>	3,016	self
<i>C. urubambae</i>	1,474	<i>C. granulosus</i> 2342

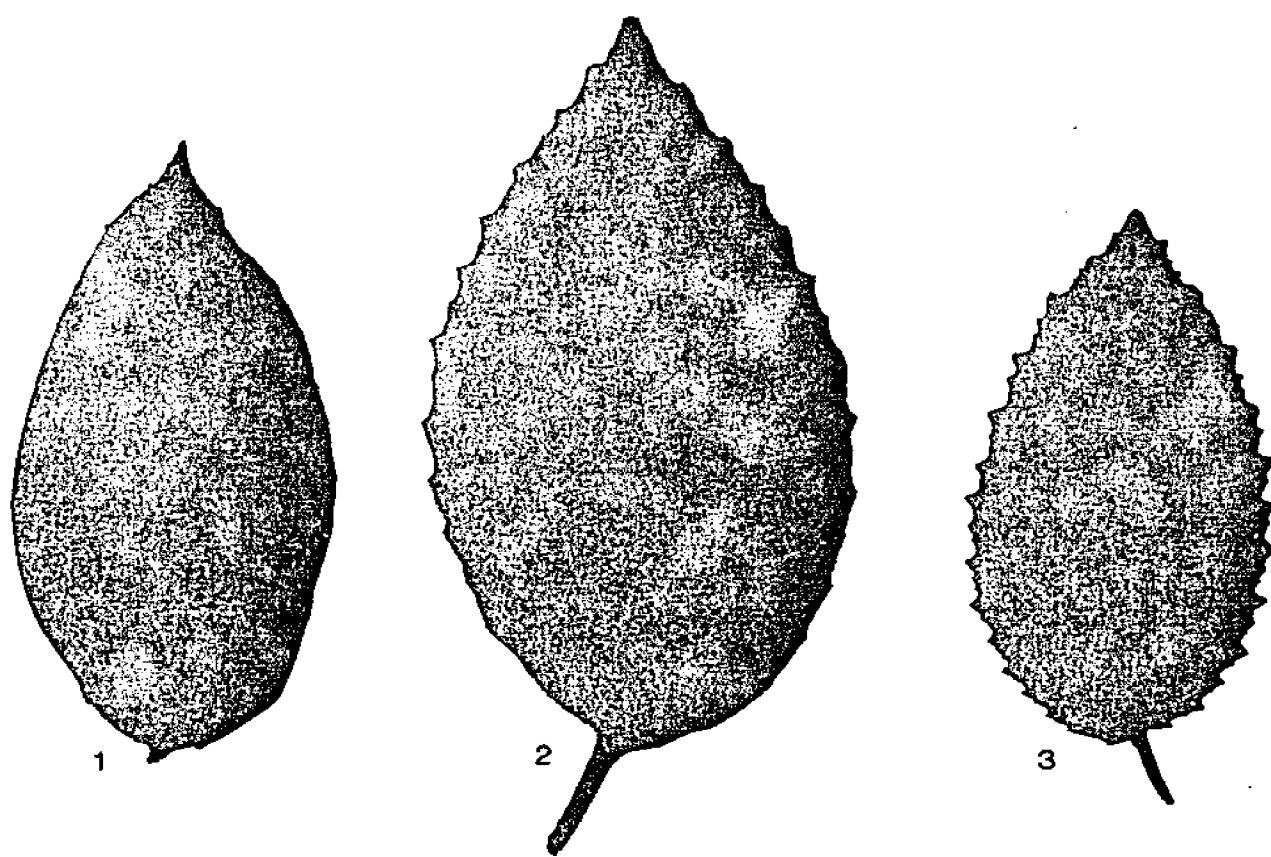
Table 7

Seed Set Among Crosses^a

<u>Male Parent</u>	<u>Female Parent</u>									
	corn	als	gamo	sol	gran	trac	lor	pap	uru	
<hr/>										
<u>Intraspecific Crosses</u>										
self	.78 (1.00)	.76 (.87)	.72 (.97)	.72 (.86)	.56 (.81)	F ^b	.74 (.86)	.97 (1.00)	.30 (.30)	
intrastrain				1.00 (1.00)	.18 (.18)	1.00 (1.00)			.85 (1.00)	.97 (.97)
interstrain	.75 (.88)				.11 (.13)	.53 (.70)				
<u>Interspecific Crosses</u>										
cornutus	--	.71 (.81)	.23 (.74)	.80 (1.00)	.76 (1.00)	F	.35 (.48)	.58 (.70)	.54 (.61)	
alsophilus	.72 (.92)	--		.56 (.78)	.62 (.78)				.39 (.49)	♂
gamosepalus	.72 (.76)		--	.52 (.79)	.39 (.58)				.56 (.64)	
solanifolius	.56 (.74)	.76 (.76)	.31 (.45)	--	.52 (.69)		.16 (.22)	.46 (.52)	.55 (.57)	
granulosus	.25 (.25)	.64 (.89)	.12 (.46)	.53 (.72)	--	F	.33 (.44)	.64 (.76)	.68 (1.00)	
trachyanthus				F	F	--	.14 (.15)		.56 (.56)	
loreensis		1.00 (1.00)		.30 (.50)	.62 (.62)	.83 (1.00)	--	.40 (.78)		
papillosum	F		.01 (.01)	.62 (.91)	.47 (.62)		.48 (.48)	--		
urubambae				F	F	F			--	

^a average proportion of seed set; maximum proportional seed set for a given cross in parentheses (see text for explanation of calculations).^b F = cross failed completely; no fruit set.

Fig. 3. Parental and hybrid leaf morphologies; (1) female parent, *C. granulosus* (Stein & Todzia 2342), (3) male parent, *C. cornutus* (Stein & Todzia 2169), and (2) their progeny, showing serrate margins inherited from the male parent. All 0.5X.



VI. MORPHOLOGY AND ANATOMY

Habit

All members of subgen. *Centropogon* are perennial herbs, shrubs, or vines. Herbs are relatively uncommon with only a few species, such as *C. arcuatus*, *C. pygmaeus*, and *C. quebradensis* consistently less than 0.5 m in height. Shrubs are more frequent, normally reaching 1-2 m in height, or rarely, as in *C. loretensis*, to 3 m. Even in mostly erect species, however, some plants may be supported by other vegetation. There are also truly vining species that can reach 6-7 m in length. Most species of all habit types are primarily herbaceous above, but become increasingly suffrutescent toward the base, often forming thickened woody rootstocks. I have not seen any truly epiphytic members of this group, but some scandent species are sometimes mistaken as epiphytes.

Fresh stems are green and terete. Although the basal portion often reaches 2.5 cm in diameter or more, stems are mostly less than 1.5 cm in diameter, and can be very slender, especially in herbs and vines. When dry the frequently hollow stems often collapse, developing conspicuous longitudinal ridges on the surface. Under magnification elongate or cuboidal cells can be seen in the thickened surface cuticle. The basal part of the stem occasionally becomes cracked and striate in age as secondary lignification occurs. Although roots are basal, adventitious ones very rarely develop from upper shoots, and even inflorescences (seen in *C. electrophorus* and *C. granulosus* subsp. *lugens*). Adventitious inflorescence roots probably result from contact of pendent inflorescences with moist ground.

Habit is very important taxonomically and when known can easily separate some species that are very similar as dried specimens. This is particularly true in sect. *Campylobotrys* where erect, shrubby species such as *C. loretensis* can be easily confused

with related vining species if only floral characters are compared. On herbarium specimens inflorescence attitude is a good indication of plant habit, and can usually be deduced given that flowers at anthesis are always oriented upright. Branching pattern also correlates with growth form. Many shrubby species produce new branches only from the base, while vines and scrambling herbs usually branch extensively throughout the length of the plant.

Latex is present in virtually all parts of the plant, carried by an extensive system of anastamosing laticifers (Ydrac, 1905). In subgen. *Centropogon* the latex is usually white or opalescent (rarely yellowish) in color and often oxidizes tan or brownish following exposure to air.

Indument

An array of trichome types and surface features are taxonomically useful in subgen. *Centropogon*. The accurate description of trichome and surface features is difficult, however, owing to the proliferation and often ambiguous application of indument terms. Payne (1978) has provided a comprehensive glossary of such terms, but did not attempt to develop a uniform system of trichome and indument classification. Theobald et al. (1983) also have discussed trichome descriptive terminology and have emphasized the need to precisely detail the structural basis for the trichomes being described. The trichome and indument terminology used in this treatment derives in part from these two works, but also makes use of such standard descriptive glossaries as Stearn (1983), Lawrence (1951), and Radford et al. (1974).

In subgen. *Centropogon* the trichomes of foliage and stems normally are narrowly conical, stiff, and erect, while those of the corollas, and often of the sepals and hypanthia, are usually widely conical and appear triangular and collapsed when dry. The trichomes can be either unicellular or multicellular, but are almost invariably

uniserrate. Multicellular trichomes can be up to 10 cells long, and the individual cells are often clearly demarcated when the thin cell walls collapse after drying (Fig. 4B). Although trichome bases in the majority of species are not expanded, those in several members of sect. *Campylobotrys* have highly modified bases that are variously papillose, granulose, or pustulate (Fig. 4). A continuum exists in the prominence of these enlarged bases, ranging from only a slight swelling to, at the other extreme they can constitute a multicellular epidermal outgrowth that dwarfs the apical trichome. In *C. papillosus* the large papillose protrusions almost completely lack terminal trichomes (Fig. 25D).

In contrast to the dendritically branched or stellate hairs found in subgen. *Siphocampyloides*, particularly in the so-called "stellate-tomentose" group (sensu Wimmer, 1943), and in a few species of *Siphocampylus* (e.g., *S. furax* and *S. columnae*), those of the species of subgen. *Centropogon* are almost always unbranched. The only two exceptions are found in *C. trachyanthus* and *C. baezanus*. In the first, the trichomes are branched, while in the latter they are laterally bulbous (Fig. 4E and F). These "branched" trichomes do not appear to be homologous with those found in subgen. *Siphocampyloides*.

Trichomes range in length from less than 0.1 mm to over 2.5 mm. Because the individual trichomes are usually stiff and erect, the indument terms normally used in the descriptions are hirsute, hirsutulous, and hirtellous, depending upon the length of the trichomes. Since trichome length can vary within a single organ, these terms are used in an approximate way. As employed in this treatment, however, they can be summarized as follows: hirsute -- trichomes mostly greater than 1.5 mm in length; hirsutulous -- trichomes mostly from ca. 0.5 to 1.5 mm in length; hirtellous -- trichomes less than 0.5 mm in length. Of these, hirtellous is by far the most common indument type. Because this term denotes a size range rather than a definite trichome type, it is used in reference to both the narrowly conical trichomes characteristic of leaf and stem surfaces

and the more broadly conical or triangular trichomes often found on corolla tissue and floral parts. Descriptors of indument density used in this treatment are: (1) sparse -- trichomes scattered and often not conspicuous; (2) moderate -- indument conspicuous, but the plant surface easily visible; and (3) dense -- the plant surface mostly obscured by the indument.

Individual species are often characterized by the type and degree of pubescence present, and by the distribution of trichomes on different organs. All parts of the plant can bear trichomes but in general the upper, or younger, portions of the plant are more densely pubescent than the lower. This is because young, not fully expanded organs apparently contain their full complement of trichomes, which are thus more densely arrayed than on the expanded, mature organs. Secondly, trichomes are lost with age, as seen by the comparison of the glabrescent lower stems and the densely pubescent apical regions of many plants. Even in plants that are almost completely glabrous throughout, the apical portion of the stem and the inflorescence rachis often are slightly hirtellous. Leaf pubescence is often restricted to the abaxial venation, although it can occur over the entire surface, and even on the marginal hydathodes. Adaxial leaf surfaces are usually glabrous.

After drying, several species in sect. *Amplifolii* often exhibit unusual white, crustose excrescences on the surface of stems and leaves. Although the basis for these drying artifacts is not known, they also appear when fresh material is placed in 70 percent alcohol, indicating that it is the result of cell ruptures. While this phenomenon may be related to the presence of trichomes (most of the species involved have a rather dense indument), the excrescences are also found on glabrescent portions of the plants. In subgen. *Centropogon* these excrescences are found only in members of sect. *Amplifolii* (*C. macrophyllus* and the *C. hirtus* alliance), but I have observed similar features in species of subgen. *Siphocampyloides*, such as *C. ursinus*.

Leaves

In this discussion of leaf morphology and in the species descriptions that follow, terminology generally conforms to that proposed by Hickey (1973). These represent standardized terms for leaf architecture based on description of individual foliar elements, rather than the use of composite leaf descriptors.

Leaves in subgen. *Centropogon* are always alternate, with the orientation dependent upon the attitude of the shoot. On vertical shoots leaves are arranged spirally around the stem, occasionally appearing clustered near the apex due to the abscission of the lower leaves. When shoots are in a horizontal position, as in many vining species, the leaves are oriented in a planar and often distichous fashion through torsion of the petioles. This difference in orientation is not of taxonomic significance except as it correlates with general habit, because differently oriented shoots on a single individual can show both types. Clearly these different orientations are strategies for maximizing solar insolation and reducing self-shading.

Leaf shape is rather uniform throughout the subgenus but can be quite variable within particular species, spanning almost the entire range of shapes found throughout the subgenus. Leaves are mostly elliptic, although ovate and obovate leaves occur with some frequency as well. They are most commonly 1.5 to 3.5 times as long as wide, but can be much narrower, as in *C. silvaticus* (to 13 times longer than wide). Most medial caudine leaves are 10 to 25 cm long, with leaves to 35 cm long fairly common. The largest leaves in the subgenus are found in *C. gallerensis* (to 55 cm long) of the Chocó region of Colombia, a geographic pattern that has been documented in several other plant groups (Gentry, 1986). While most species overlap broadly in shape and size of leaves, certain taxa have characteristic leaf shapes, which can be useful in their

delimitation. The overemphasis on leaf shape and size in the past, however, has led to the recognition of numerous unsupported taxa.

Greenhouse propagation of a number of species under uniform conditions has allowed me to tentatively examine the extent to which variation in leaf shape and size are due to genetic versus environmental factors. Leaves produced by seed-grown plants were compared with those of their wild-collected parents (Table 8). There is a general concordance in the leaf length and shape (as measured by relative width and location of widest point), indicating that at least some of the variation in leaf shape does have a genetic component.

Leaf margins are normally serrulate or crenulate; less often they are almost entire with only slight denticulations, or they can be deeply and saliently toothed. Among the more unusual margins are long-fimbriate (in *C. sciaphilus* and *C. roseus*) and deeply sinuate (in *C. arcuatus*). Even in the species with atypical margins, however, there is considerable intraspecific variation with some populations and individuals exhibiting very reduced versions of these distinctive margins.

Small marginal callosities ranging in size from ca. 0.5 mm to 2 mm long are present in all species. These callosities are hydathodes (Tswett, 1907) that are vascularized by 3° or 4° veins. In spite of the presumed water excretion function of such glands, and the very wet environments where subgen. *Centropogon* occurs, I have never observed secretions from these structures. The shape and position of these hydathodes varies, but normally not in taxonomically significant ways. When the margin is serrulate the callosities are located at the apex of the teeth, even when the individual teeth extend as far as 6 mm as in some individuals of *C. roseus*. On crenulate margins the callosities are located in the sinuses. This shift from apex to sinus can be observed even within a single individual and is evidence that a continuum exists between serrulate and crenulate margins. In my interpretation the crenulate condition merely represents

very rounded "teeth" in which the "apex" becomes situated at the base of the superadjacent "tooth" or crenulation. The callosities are often slightly exserted from the leaf margin, and on a more-or-less entire leaf this produces a condition referred to here as callose-denticulate. Number of callosities per cm is a good indication of the density of marginal protrusions (whether they be serrations or crenulations), and this measurement is consistently made along the upper third of mature leaf margins. Number of callosities per cm varies from 1 to 12, but usually ranges from 3 to 6. Members of sect. *Amplifolii*; such as *C. congestus* and *C. umbrosus*, often have relatively numerous marginal callosities, while members of sects. *Campylobotrys* and *Grandes* usually have relatively few.

When fresh, the leaves are generally fleshy or thin, but are almost always pliable; they typically dry chartaceous to semi-membranaceous. Only rarely are leaves coriaceous and brittle when fresh, as in *C. baezanus*, or coriaceous and pliable, as in *C. loretensis*, and in both these cases they dry coriaceous. Leaves that are exceptionally fleshy when fresh, as in *C. gallerensis*, often dry very thin and membranaceous. An unusual leaf type is found in a group of four Peruvian species of sect. *Campylobotrys*: *C. reflexus*, *C. yungasensis*, *C. vargasii*, and *C. urubambae*. In these the abaxial aerenchyma layer is very well developed forming a layer several hundred microns thick. This gives the lower leaf surface a distinctive spongy appearance when fresh and a coriaceous texture when dry. The venation, particularly higher order veins, is almost completely embedded in the thickened aerenchyma layer rather than raised above the level of the lamina, and the individual veins appear somewhat diffuse.

Venation patterns in subgen. *Centropogon* are exclusively camptodromous, with the secondary veins not terminating at the margins (Hickey, 1973). The majority of species are eucamptodromous, although secondary veins occasionally form submarginal loops, joining with the superadjacent secondaries in a brochidodromous manner. The

angle of divergence from the mid-vein can vary within and between leaves, but normally is moderately acute (45-65°) or, in exceptional cases, widely acute (65-90°). The latter condition can be very distinctive, as in many populations of *C. congestus*. After diverging from the mid-vein the secondaries usually are strongly arcuately ascending. Number of secondary veins can also be a taxonomically useful character and greenhouse and herbarium studies indicate that this feature is under some genetic determination rather than merely a consequence of total leaf length. Although from 4 to 18 secondaries are present on each side of the mid-vein, 5 to 10 are most common. Many members of sect. *Amplifolii* have leaves with more than ten secondaries, which correlate with the generally more numerous marginal callosities found in these same species.

Petiole

Leaves are generally petiolate and only rarely sessile, a feature that helps to distinguish vegetative leaves from little-reduced inflorescence bracts, which are almost always sessile. Petioles usually measure from 5 to 25 mm long, but rarely can reach 60 mm, as in *C. escobarae*. Because leaf bases are normally cuneate or rounded, the petioles are generally quite distinct and unwinged, although they are usually slightly canaliculate adaxially.

Inflorescence Structure

Inflorescence structure is one of the most useful features in subgen. *Centropogon* for delimiting taxa and for assessing relationships. Inflorescences unfortunately are often difficult to use for comparative analysis, mainly due to inconsistencies in descriptive terminology and general lack of agreement about their classification. Troll (1964, 1969) has provided a major contribution to the study of inflorescence structure by

carefully documenting the spatial relationships of shoot, leaf, and flower organs as the basis for his system of classification. This has led to a clarification of terms and to a trend away from the generalized descriptive systems (e.g., Ricketts, 1944) that are still generally employed in taxonomy. Troll has been criticized severely, however, for following a very strict typological approach in the construction of his classification scheme, an approach that is largely independent of evolutionary considerations. More recently, Briggs and Johnson (1979) have attempted to provide a suitable inflorescence terminology that follows Troll in its attention to precise spatial relationships, but divorces itself from typology and theory-limited terms. In doing so they have retained certain traditional as well as Trollean terms, but have also proposed a number of new ones. In the discussion that follows many of the concepts of Briggs and Johnson (1979) are used, although not all of their terms have been adopted, particularly if standard terminology is easily understood and non-problematic within subgen. *Centropogon*.

Inflorescences in subgen. *Centropogon* are indeterminate, or in the terminology of Briggs and Johnson (1979) blastotelic, and are generally racemose. Within this basic framework the variety of inflorescences documented are based on modifications of six components: (1) orientation; (2) internode length; (3) shoot apex fate; (4) position; (5) bract length and differentiation; and (6) pedicel length and attitude. Figure 5 summarizes the inflorescence structures produced by variation in these features, principally in components 1, 2, and 5.

Orientation

The orientation of the inflorescence is closely tied to habit and provides a very useful distinction between many species. Ascending to erect inflorescences are the normal condition in the subgenus, matching the typically upright or scandent habits of most species. Within sect. *Campylobotrys*, however, habit ranges from erect herbs to

true vines and a comparable diversity of inflorescence orientations has developed, from strictly erect to strictly pendent. Pendent inflorescences with the apical portion of the rachis upturned (often appearing "pipe-shaped") are the most characteristic type found in that section. Based on observations of inflorescence development in live plants, it appears that this apically upturned-pendent condition has given rise to strictly pendent inflorescences rather than vice versa. The systematic distribution of these pendent inflorescences indicates that this transition must have occurred independently several times. The only truly vining species in sect. *Grandes*, *C. semperflorens*, also has developed a pendent inflorescence that occasionally has a slightly upturned tip.

Internode Length

Internode length is a reflection of the relative congestion of an inflorescence. In subgen. *Centropagon*, inflorescences can be considered either elongate, with the internodes usually from 0.5 to 3 cm in length, or congested, with the internodes generally less than 0.5 cm. Elongate inflorescences can be of two forms. Those in which the floral internodes are elongate throughout, including during anthesis, are considered truly elongate, while those with the flowers congested at anthesis and which subsequently elongate basally are considered secondarily elongate. The former type is found mostly in sect. *Campylobotrys*, and although inflorescences in this section are usually less than 50 cm in length, in *C. pulcher* the whip-like inflorescence rachis can reach over 250 cm, with internodes 3 to 6 cm long.

Well developed peduncles are rarely found in the subgenus and, when present, provide a useful character. In this context a peduncle is considered a leafless, elongate section of the shoot that subtends the first inflorescence bracts. True peduncles are mostly found in species with erect inflorescences, such as *C. sciaphilus*, *C. latifolius*, and *C. vaughianus* (Fig. 5F). In many members of sect. *Campylobotrys* pendent

inflorescences often appear pedunculate but are actually the result of the abscission of subtending vegetative leaves during the inflorescences' long blooming period.

Shoot Apex Fate

A useful inflorescence character at the sectional level is the fate of the shoot apex. In an indeterminate (i.e., blastotelic) inflorescence, two conditions are possible: (1) the terminal apex resumes vegetative growth, or (2) the apex withers and dies, terminating both the inflorescence and the shoot. These two conditions have been termed auxotelic -- growing at the end -- and anauxotelic -- not growing at the end (Briggs and Johnson, 1979). Studies of greenhouse plants, wild populations, and dried specimens indicate that both conditions are present in subgen. *Centropogon* and that they characterize different lineages.

Auxotelic inflorescences are characteristic of sect. *Amplifolii*, and certain members of that group often produce two to three discrete inflorescences on a single shoot, each of which is separated by a region of vegetative growth (Fig. 6A). Each inflorescence is formed at the current apex of the shoot and is thus "terminal," but after the subsequent acropetal production of vegetative leaves the inflorescence appears "subterminal." This growth pattern can be observed on dried specimens making it a useful taxonomic character. The abscission of the bracts and pedicels from the first-formed inflorescences leaves characteristic clusters of scars on the stem. These subterminal scars thus indicate an auxotelic inflorescence. Specimens collected at the right stage may actually show the crown of vegetative leaves emerging apically to the still-active inflorescence. Unfortunately, the subterminal scars are not always present on dried specimens, either because the plant was collected during the first inflorescence cycle or because the scars were located below the portion of the shoot gathered by the

collector. Additionally, not all individuals of auxotelic species appear to form multiple inflorescences, perhaps because of resource limitations.

In contrast to the situation described above, anauxotelic inflorescences terminate the shoot on which they occur. Further growth and flowering either takes place through activation of axillary buds basal to the old inflorescence (Fig. 6B) or through production of new basal shoots (Fig. 6C). In greenhouse plants the former pattern was observed in several species, including *C. granulosus* and *C. solanifolius*, while the latter occurred in species such as *C. papillosum* and *C. loretensis*.

Position

Except for truly axillary flowers, and ignoring the complexities of "subterminal" auxotelic inflorescences (discussed above), almost all inflorescences are borne in a terminal position. Lateral inflorescences are periodically encountered among several species of sect. *Campylobotrys* in Ecuador and northern Peru, including *C. granulosus* subsp. *lateriflorus*, *C. trachyanthus*, and *C. baezanus* (Fig. 5H). Lateral inflorescences are not found consistently in these taxa and, when present, are of the same structure as the species' normal terminal inflorescence, in these instances, upturned-pendent, short-bracteate, congested racemes. Because of this very derived structure they cannot be considered homologous with the lateral inflorescences found in the baccate Hawaiian lobelioids (Lammers & Stein, in prep.).

Bract Length and Differentiation

In characterizing inflorescences particular attention must be paid to the phyllomes subtending the flowers. These structures are generally referred to as bracts when small and as leaves when about the same size as vegetative leaves. Because of this dual terminology for homologous structures, Briggs and Johnson (1979) introduced the

term "pherophyll" to refer to the subtending foliar organ independent of its size relation to other leaves. Although sacrificing some precision, for the sake of readability and in view of historical usage for lobelioideae, I refer to these foliar organs as bracts. In addition to changes in relative size, bracts also can differ from vegetative leaves in shape and indument patterns.

Bracts can be grouped into three categories relative to the size of normal vegetative leaves: frondose (not reduced); frondulose (reduced but still foliaceous); and bracteose (much-reduced) (Briggs and Johnson, 1979). Inflorescences can thus be categorized as any of the above, or they can grade acropetally from one category to another, as in frondo-bracteose. A practical difficulty with this scheme arises in determining the limits between each of these size classes, particularly with regard to the difference between frondulose and bracteose. Furthermore, by rigorously adhering to these terms, "bracteose" inflorescences would be restricted to a very small subset of the inflorescence types found in the subgenus in spite of the fact that *all* contain "bracts," as the term is used in this treatment. For this reason, the terms frondose, bracteate, and short-bracteate are substituted for the above terms in this treatment.

Frondose inflorescences with solitary flowers in the axils of unreduced leaves occur in only a few species in the subgenus, but is the predominant inflorescence type elsewhere in *Centropogon* and must be considered the ancestral inflorescence type. Species with frondose inflorescences include *C. cormutus*, *C. hirtus*, *C. trianae*, *C. laxus*, and *C. scabellus* (Fig. 5A). In these instances, both the size and shape of the subtending floral phyllomes are substantially similar to the normal vegetative leaves.

Bracteate inflorescences are the most common type in the subgenus. The bracts are often quite foliaceous, but much smaller than the vegetative leaves. These bracts can be the end product of a gradual reduction series (Fig. 5B and C), differing little in shape

from the vegetative leaves, as in *C. carpishensis*, or they can exhibit an abrupt shift in both size and shape, as in *C. capitatus* (Fig. 5D-I).

In short-bracteate inflorescences (Fig. 5F-J), which are mostly restricted to sect. *Campylobotrys*, the bracts are generally less than 10 mm in length and are often less than 5 mm. These short bracts are often caducous, and thus, the lower inflorescence rachis is naked exposing the densely congested and raised pedicel abscission scars, which form a very conspicuous surface feature.

The ratio between pedicel length and bract length is often consistent within populations or species. While pedicels on short-bracteate inflorescences always much exceed the length of the subtending bracts, in bracteate inflorescences individual bracts can either be shorter than, equal to, or longer than the subtended pedicel. In *C. roseus*, for example, the bracts are normally shorter than or not much exceeding the pedicels, whereas in the closely related *C. gamosepalus* the bracts are almost always much longer than the pedicels and partially obscure the lower portion of the flowers. Similarly, many southern Colombia populations of *C. congestus* resemble *C. gesneriiformis* in having tightly appressed bracts that are shorter than the pedicels, while the more northerly populations have bracts that are normally longer than the pedicels. In certain species where the bracts both exceed the length of the pedicels and are appressed to, or partially envelope, the basal portion of the flowers, such as in *C. capitatus* and *C. gamosepalus*, they may function as additional protection against nectar-robbing.

While discussed separately later, pedicel length can have another effect on inflorescence structure. In general, racemose inflorescences have pedicels of approximately equal length, while in subcorymbose inflorescences the lower pedicels are longer than the apical ones, placing the flowers at approximately the same level. This subcorymbose condition is often present in congested, bracteate or short-bracteate inflorescences (Fig. 5C-D, F-I).

Bract shape is highly variable and may either reflect the overall shape of the vegetative leaves or differ from them sharply. The bracts are normally sessile and, as in vegetative leaves, they are mostly elliptic to narrowly elliptic. Obovate, oblanceolate, or spatulate bracts are frequent, however, and the relative width can be useful in differentiating closely related species.

Attitude of the bracts can also vary consistently. Although bracts in most inflorescences are loosely spreading to divaricate, in several members of sect. *Amplifolii* the bracts are upwardly ascending and often tightly appressed to one another. The imbricate disposition of these bracts forms a head-like structure that in *C. capitatus* (e.g., Killip & Smith 25772) can reach 11 cm in diameter.

The indument patterns on the bracts often differ from those found on the vegetative leaves. In species in which the vegetative leaves are adaxially glabrous but abaxially pubescent, the bracts commonly have trichomes on both surfaces. In the case of frondose or frondo-bracteate inflorescences, where there is a gradual transition in size from vegetative leaves to inflorescence bracts, this differential pubescence allows a fairly accurate determination of the interface between vegetative and inflorescence phyllomes.

Pedicels

All flowers in subgen. *Centropogon* are pedicellate, and although the pedicels range in length from 10 to 100 mm, most are 15 to 35 mm long. The most important characters of the pedicels include their attitude, length relative to the subtending bracts (discussed previously), and timing and degree of resupination. Persistence of the pedicel after fruit abscission was used as a character by Gleason (1925) in describing *C. pedicellaris*, but persistent pedicels occur occasionally in many species and are of relatively little taxonomic value.

At anthesis pedicels are always erect relative to the ground, even though this may be either acroscopic or basiscopic relative to the inflorescence axis. In fruit, pedicels are generally pendulous or nodding (Fig. 5). Only rarely do they remain erect, usually in species where inflorescence bracts closely subtend the lower portion of the pedicel, such as *C. capitatus*. Here, the pedicel either remains entirely erect, or droops apically.

Resupination of the flower by twisting of the pedicel is one of the subfamilial characteristics of Lobelioideae. This relatively rare condition, which is found also in such families as the Orchidaceae, involves a 180° torsion of the pedicel so that the ontogenetically ventral surface of the corolla is presented at anthesis as the dorsal surface. Thus, in the case of *Centropogon* the two larger lobes of the zygomorphic corolla that are uppermost at anthesis are actually developed in the ventral position. In this treatment, as elsewhere in the literature they are referred to simply as the dorsal lobes.

A detailed examination of living material of species with congested, radially symmetrical inflorescences, such as *C. capitatus* and *C. gamosepalus*, showed that the flowers resupinated with a clockwise twist, although it is possible that in species with less symmetrical inflorescences resupination may occur in the most convenient direction.

Floral resupination also may either be delayed or not occur at all. Because of the precise nature of the pollination mechanism in many subgen. *Centropogon* flowers, particularly those that are *Eutoxeres*-pollinated, an upright corolla orientation is essential. To be in the appropriate position for pollinators, flowers on a pendent inflorescence must be both upright and facing away from the inflorescence rachis. The pedicels on a pendent inflorescence must, therefore, become reflexed or recurved with respect to the main inflorescence axis in order for the corolla to be in an upright position. If, however, resupination takes place as well, the corolla would then be facing into the inflorescence rachis. As a result, in species such as *C. urubambae* and

C. reflexus, the pedicel reflexes but resupination is either delayed until after anthesis or does not take place at all. The fruiting pedicels in these two species often contain a corkscrew spiral, which is interpreted as the delayed resupination.

In at least one species, *C. papillosus*, resupination often appears not to occur at all. This *Eutoxeres*-pollinated species is a small herb with erect, congested, subcorymbose inflorescences. In greenhouse studies, the flowers consistently opened while facing inward towards the inflorescence axis, and the pollinated flowers and fruit typically recline backwards with no twisting of the pedicel.

Bracteoles

Two bracteoles are always present on the pedicels in subgen. *Centropogon*, although they occasionally are not visible in dried material. The bracteoles are normally in a basal or subbasal position (i.e., inserted on the lowest 1/4 of the pedicel), but in rare cases they can be medial or even sub-apical, as in *C. scabellus*. If the bracteoles are borne close enough to the pedicel base, they may be persistent on the stem after abscission of the pedicel, a feature characteristic of *C. cornutus*. Bracteoles normally range in size from very minute (less than 1 mm) to ca. 5 mm long, but can reach 15 mm. (In one collection of *C. capitatus*, Stein 3891, the 15 mm long bracteoles equalled the pedicels in length.) Smaller bracteoles are mostly subulate or linear, but longer ones can be somewhat foliaceous, even with distinctly serrulate margins. While bracteole size and shape is generally consistent within populations, except in rare cases they vary too widely among populations of the same species to have much taxonomic utility.

Sepals

The size and attitude of sepal lobes is often a useful taxonomic feature. Sepals range in size from ca. 2 mm to almost 20 mm long and can be triangular, narrowly

triangular, ligulate, or sometimes linear. The measurements given in the species descriptions indicate length by width at the base. Sepal attitude can also be a useful feature in distinguishing species. Most commonly the lobes are erect (Fig. 8A-C), although they are frequently slightly patent or arcuate (Fig. 8J, K). Less often, the lobes are reflexed, as in *C. reflexus* (Fig. 8E) and *C. yungasensis*, or have spreading or divaricate lobes, as in *C. cornutus*. In *C. urubambae* the divaricate lobes have upturned, erect tips (Fig. 8F). This species is also unusual in having a zygomorphic calyx, a feature extremely rare throughout the Lobelioideae (McVaugh, 1965). The typically recurved or reflexed sepal tips of *C. loretensis*, *C. amplicorollinus*, and *C. alsophilus* (Fig. 8D) are also distinctive.

Although sepals of most species in the subgenus are free to the base, gamosepalous calyces have developed independently at least three times. Connate sepals are most common in sect. *Amplifolii* and characterize a group of species centered around *C. gamosepalus*. In these species the calyx is fused from one-quarter to almost the entire length. Two other unrelated species also have connate sepals, *C. vaughianus* (Fig. 8G) in sect. *Campylobotrys* and *C. linnaeanus* in sect. *Grandes*. Given the periodic occurrence of gamosepalous calyces in several different groups of *Centropogon* both within and outside subgen. *Centropogon* (e.g., *C. nigricans*, *C. calycinus*, and *C. hazenii*), this condition must not be difficult to evolve. The presence of connate sepals, which surround the base of the corolla, may confer an advantage in protecting the nectar chamber from nectar robbers.

The shape of the sinuses between free sepal lobes have been used in the past as taxonomic characters (Gleason, 1925). Three types of sepal sinuses can be recognized, acute, rounded, and planar, which can be defined as follows. In acute sinuses the sepals are contiguous and have straight margins that form a sharp, usually acute angle where they meet (Fig. 8A-C, and E). In rounded sinuses the sepals are contiguous, but the

basal portion of the margins are concave so that no sharp angle is formed. With planar sinuses the sepals are non-contiguous, so that the margins of the individual lobes are separated by a straight or planar section of hypanthium summit (Fig. 8F, H, J, and K).

Corolla

The flowers of subgen. *Centropogon* are often strikingly beautiful, partly due to their brilliant colors, but also because of the unusual forms. These shapes, some of which are highly distinctive, are one of the most important features for both delimiting and grouping species. Form in this case follows function, and the unusual shapes are intimately related to modes of pollination.

The complex three dimensional structure of *Centropogon* flowers makes their description difficult. Corolla measurements can differ between fresh material and pressed, dried material depending primarily upon the thickness of the corolla tissue and the care taken in preparing the dried specimens. Thick tissue tends to shrink more than thin. Well-pressed corollas normally shrink very little, but corollas that are not under adequate pressure when drying (as when merely air-dried loose) can shrink considerably in both length and width. Although I have made detailed measurements of fresh material for many of the species, measurements presented in this treatment are from pressed, dried material, unless explicitly noted otherwise.

The corolla in subgen. *Centropogon* can be divided into two major parts, the tube and the lobes. An entire corolla tube is one of the defining features of the genus *Centropogon* and in theory separates it from *Pratia*, which has baccate fruits but a dorsally slit corolla tube, as does *Lobelia*. An entire corolla tube is a feature that *Centropogon* shares with the capsular-fruited genus *Siphocampylus* and is probably an adaptation to hummingbird pollination. Although there are hummingbird-pollinated species of *Lobelia* with corollas dorsally slit to the base (e.g., *L. cardinalis* and

L. laxiflora), a completely tubular corolla more effectively excludes non-pollinating visitors or nectar robbers, an especially important consideration given the large quantity of nectar produced by many species of *Centropogon* and *Siphocampylus*.

Several parts of the corolla tube can be distinguished: the basal portion, which extends from the summit of the hypanthium to the point of filament tube adnation and encompasses the nectar chamber; the mid-portion extending from the point of filament adnation to the base of the throat; and the throat, which is normally expanded in comparison to the lower and mid-portion and is very often curved forward (i.e., ventrally). The corolla tube descriptors provided in the species descriptions generally include overall length, width at base, location and width of narrowest point, as well as degree of differentiation, width, and curvature of the throat.

Because of the frequently curved nature of the tube, overall length can vary considerably depending upon where the measurement is made. For instance, the dorsal and ventral surface of the tube can differ in length by over 10 mm. To standardize corolla length measurements I have consistently used a measurement of the lateral side of the corolla from the summit of the hypanthium to the sinus between the dorsal and lateral lobes as illustrated in Fig. 7A-1. Measurement of the medial line running between these two points presents a minor problem in that the curvature of the corolla often makes it necessary to measure an arc rather than a straight line. This is most easily accomplished by using a flexible plastic ruler, although the results must generally be considered approximate. Given practice, however, measurement of the corolla in this fashion produces highly repeatable results and provides the most realistic estimate of overall corolla tube length. Further, on most pressed specimens the corollas are oriented laterally allowing measurement along this axis. Because this method accommodates differing degrees of corolla curvature, these measurements can be used in cross-species

comparisons. Although corolla tubes in subgen. *Centropogon* range from 17-50 mm long, the majority fall between 25-40 mm.

Three width measurements are important in conveying the form of the corolla tube, and measurements are usually made at the base (Fig. 7A-2), at the narrowest point, and at the throat (Fig. 7A-3). All width measurements are across the lateral plane unless stated otherwise. Of these width measurements, the throat is the most important, since many species have distinctively ampliate or ventricose throats, which is reflected in the width of this structure. Typically, moderately ampliate throats are in the range of 8-11 mm wide, while widely ampliate throats are 11-15 mm wide, or in extreme cases, such as *C. eurystomus*, to 21 mm. Along with the absolute width of the throat, the relative change in width from the lower portion of the tube to the throat must be taken into account. Thus, throats can be little differentiated and only gradually ampliate (e.g., Fig. 8B) (even if very wide in absolute terms such as *C. amplicorollinus*) or can be well-differentiated, that is abruptly ampliate to ventricose (e.g., Fig. 8A). The term ventricose describes a corolla throat in which the ventral side is somewhat saccate rather than smoothly expanding (e.g., Fig. 8G). In addition to a saccate ventral surface (a feature characteristic of several species in sects. *Campylobotrys* and *Amplifolii*), lateral distentions or pouches are occasionally present, as is, at least rarely, an elevated dorsal crest. The latter provides an elevated canal that invests the filament tube.

The lower portion of the corolla tube is usually cylindric but typically exhibits a conspicuous narrowing, or isthmus, at the point of filament adnation just above the nectar chamber (Fig. 8E). Occasionally the lower portion of the tube is ventrally distended giving the corolla a distinctive "pregnant" look (Fig. 8H). In this case the tube narrows gradually from the base and reaches its narrowest point just below the throat. This basal distention usually represents a thickening of the corolla tissue around the nectar chamber, perhaps for additional protection against nectar robbers as discussed

elsewhere. In extreme cases, such as in *C. baezanus*, tissue surrounding the nectar chamber can reach 4 mm thick.

Curvature

Corollas in subgen. *Centropogon* display a variety of curvatures; they can be more-or-less straight (Fig. 8I), can have the throat curving forward (Fig. 8, various), or can be sigmoid with the lower portion of the tube angled backward (dorsally) and the throat curving forward (ventrally) (Fig. 8F). Of these, the second is the most common, with the sigmoid condition less frequent. Straight corollas are extremely rare. Because of the taxonomic and biological importance of corolla curvature, a method was developed for providing consistent estimates of throat curvature. As shown in Fig. 7B, two straight lines are superimposed on the lateral surface of the corolla, one running along the medial axis of the lower portion of the corolla tube and one running along the approximate midline of the throat from the sinus of the dorsal and lateral lobes. The angle of intersection of these two lines is taken as an estimate of the corolla throat curvature. Because of the variation in corolla curvature present within many species, and the degree of error inherent in this measurement, corolla throat curvatures are generally presented as ranges or approximate figures. Two curvature classes can be easily noted without use of a protractor, slightly curved (10–30°) and moderately to sharply curved (40–70°).

As discussed in detail elsewhere, sharply curved corollas indicate pollination by the hummingbird genus *Eutoxeres*. Such species are characteristic of sects. *Amplifolii* and *Campylobotrys*, and corolla morphology is important in defining these two sections. This is particularly true with regard to the relationship between sect. *Campylobotrys* and sect. *Grandes*, the latter being characterized by gradually curved corollas with little-differentiated corolla throats and generalized hermit hummingbird pollination. Given

that *Eutoxeres* pollination is a derived condition in the subgenus, the sharply curved corollas seen in these two sections must also be interpreted as a derived feature. Examples of apparent reversals in corolla curvature are known in both sects. *Amplifolii* and *Campylobotrys*, however, as discussed individually under *C. gesneriiformis*, *C. cuatrecasanus*, and *C. amplicorollinus*.

Corolla lobes are fairly uniform within the subgenus and vary only slightly in shape; their length is closely related to the overall length of the corolla tube. The dorsal lobes are generally falcate in shape and at anthesis are either laterally spreading, or more commonly recurved or recoiled. I have seen only two species, *C. grandis* and *C. papillosus*, in which the dorsal lobes remain erect (directed forward) at anthesis. The lateral lobes are erect or, when fresh, are slightly spreading, and typically are assymetrically triangular or falcate with decurved tips. The ventral lobe is almost always erect usually with an abruptly deflexed tip. This lobe is often somewhat saccate, but this condition is difficult to see in pressed material.

Color

Flower color is an extremely useful character that unfortunately is not well preserved in herbarium specimens. Certain taxa that are difficult to distinguish as dried specimens are easily separable when fresh based upon their distinctive corolla colors (e.g., *C. urubambae* and *C. pulcher*). Corollas of subgen. *Centropogon* combine various shades of pink, red, orange, or yellow. Two major coloration patterns may be recognized, concolorous and bicolored. Concolorous corollas are composed entirely of one color; in bicolored corollas the color of the lower portion of the tube either grades into, or switches suddenly, to a contrasting color above. Corolla coloration is rather consistent at the sectional level, with sects. *Centropogon* and *Amplifolii* characterized by pink to red corollas. Orangish flowers are found only in some unusual and highly

derived members of sect. *Amplifolii*, such as *C. undulatus*, *C. electrolophos*, and *C. escobarae*. Sections *Campylobotrys* and *Grandes* also contain many species with red or pink corollas, but taxa with orange and yellow pigments are common. Although yellow or yellowish-orange is often found as a contrasting distal color in bicolored corollas, pure (i.e., concolorous) yellow corollas are relatively rare and occur consistently in only three taxa, *C. cuatrecasanus*, *C. granulosus* subsp. *lateriflorus*, and *C. densiflorus* subsp. *gracilis*. While there may be considerable variation in the corolla colors present throughout the range of a widespread species, within populations or given geographical regions coloration tends to be relatively constant. For example, in the wide-ranging and morphologically complex *C. granulosus*, corolla coloration provides a useful way to broadly partition the species on a geographic basis.

Androecium

The most characteristic feature of the subfamily Lobelioideae is the fusion of the stamens into a tube surrounding the style and stigma. The pollen is shed introrsely, filling the anther-tube chamber. As the style grows upwards and pushes through this chamber it puts the pollen under pressure, forcing it out the apical opening in the anther tube. The stigma eventually is exserted from the anther tube and becomes receptive when the two stigmatic lobes unfold.

Features of the androecium are important taxonomically in subgen. *Centropogon* with respect to separation of species, as well as delimitation of the subgenus as a whole. In general the androecium is composed of a completely fused filament tube, which is adnate to the corolla near the base, and a fused anther tube. The two ventral thecae of the anther tube are crowned by a tuft of elongate trichomes fused into what is here termed an antheridial scale, and this scale is the principal synapomorphy uniting the subgenus. Because of the importance of the androecium in separating species a number

of different measurements are included in the descriptions and are discussed below. Of these measurements, the most easily made is the total length of the androecium, from the base of the corolla to the tip of the anther tube (Fig. 7C-1), and this summary measurement is always given even though the component measurements (filament and anther tube lengths, Fig. 7C-2 & 5) are included as well. Total androecium length is a good predictor of overall flower length, and is important in determining the site of pollen deposition on pollinators.

Filaments

As mentioned above, the filaments are fused along their entire length, a feature that helps distinguish *Centropogon* from *Burmeistera*, in which the filaments are usually free at the base. Further, the filaments in *Centropogon* are adnate to the corolla tube, usually 4–6 mm above the base (although ranging from 2–8 mm) while in *Burmeistera* they typically are not adnate and instead are attached at the hypanthium summit. In subgen. *Centropogon* the location of filament tube adnation can usually be determined from the external corolla surface by the presence of slight depressions. Except in strongly sigmoid corollas, the two dorsal filaments are generally attached slightly (1–3 mm) higher than the three ventral filaments. In the descriptions measurements are given for both the location of filament tube adnation and the length of the filaments, as measured from the base of the corolla to the base of the anther tube (Fig. 7C-2). Although the latter measurement does not reflect only the "tubular" portion of the filaments, it is a more consistent measure than that of the distance from the site of adnation because of the above mentioned variation in dorsal and ventral attachment points. Exsertion of the filament tube from the corolla tube can occasionally be a useful feature for separating closely related taxa (e.g., *C. granulosus* subsp. *nutans* and subsp. *tortilis*) and can have potential importance in promoting reproductive isolation between

species through differential pollen placement on vectors. Filament exertion is measured from the sinus of the dorsal corolla lobes to the base of the anthers (Fig. 7C-4).

Filament tube cross-section is a previously unrecognized feature of importance at the sectional level within the subgenus. The usual condition in *Centropogon*, as well as in related genera, is a terete filament tube (round in cross-section). Within subgen. *Centropogon* there is a trend from narrow, subterete filament tubes to wide, semiterete ones (half-rounded in cross-section). For clarity the latter are termed "ventrally flattened." In sect. *Centropogon* the filament tube is generally subterete, although just below the anther tube it is occasionally somewhat flattened ventrally, and in sect. *Amplifolii* the tube is fairly narrow (1-2 mm wide) and subterete. In contrast, in sects. *Campylobotrys* and *Grandes* the tube is 2-3.75 mm wide and strongly ventrally flattened with the outer margins generally forming a sharp angle. Because features of the filament tube cross-section are not well preserved in dried specimens, filament tube width measurements (Fig. 7C-3) and cross-sections are given only when I have examined fresh material.

Color of the filaments also reflects sectional lines and closely follows the patterns in corolla coloration. In sects. *Centropogon* and *Amplifolii* whitish filaments are the norm, while in sects. *Campylobotrys* and *Grandes* pale yellow or orangish filament tubes predominate. In many species, however, the exserted summit of the tube is often tinged purplish-rose. Although the tube is usually glabrous, in many species with pilose anther tubes, the summit of the filament tube is also sparsely to densely pilose.

Anthers

Anther tube length and pubescence patterns also provide useful taxonomic characters. While anther tubes range in size from 3.5 to 10 mm long, most are from 6 to 8 mm in length. The three dorsal anthers are slightly longer than the ventral two and

curve downward at the apex effectively closing the orifice of the anther tube. Each anther contains two introrsely dehiscing thecae separated by connective tissue. The connectives often are beset with flattened, uni- or multicellular trichomes, and length, color, and distribution of which can be quite distinctive. Although trichomes are most commonly found only along the dorsal connectives (the three uppermost), in certain species the ventral connectives also contain hairs. In the descriptions long-pilose is generally used to refer to trichomes 1 to 2.5 mm long whereas short-pilose refers to trichomes generally shorter than 1 mm. In *C. cornutus* these trichomes are extremely well-developed and can reach 5 mm long. The connective trichomes can be either purplish or translucent, in which case they are referred to as white. The purple pigments are normally quite stable and persist in herbarium specimens, but occasionally they are lost during the drying process. Trichome color can often be a consistent feature for a species, or can be consistent for a particular geographic region within a species.

In most Lobelioideae, including the rest of *Centropogon*, the two ventral anthers are tipped with a tuft of free trichomes that operate as a lever to open the anther tube orifice slightly and allow the pressurized pollen to discharge. This action is normally tripped by a floral visitor, with the result that pollen is deposited on the pollen vector. In subgen. *Centropogon* this mechanism has been transformed into what is presumably a more effective trip lever through the fusion of these trichomes into a scale (Fig. 9A). This scale is normally triangular with an acute apex and is generally 1.5 to 3 mm long. Only rarely is the scale wider (deltoid), or, as in *C. papillosum*, longer (to 3.75 mm) and truncate at the apex. The antheridial scale is composed of translucent (white) trichomes (even when the connective trichomes are purple) and have a distinctive irregularly corrugated surface (Fig. 9D). Although the tuft of short unfused trichomes that is occasionally present at the base of the scale has been used taxonomically by Gleason (1925), I have rarely found this feature helpful in delimiting taxa.

Gynoecium

As the style grows through the anther tube the stigma remains closed to avoid self-fertilization, but once outside the tube the bilobed stigma unfolds and becomes receptive. The style normally is exserted from the anther tube 1 to 3 mm; occasionally the stigma is little-exserted and remains closely appressed to the anther tube. Once expanded the two lobes of the stigma normally measure 2 to 4 mm across.

Hypanthium

All species in subgen. *Centropogon* have strictly inferior bilocular ovaries in which the two placentae are attached at a medial position on the central column. At anthesis the hypanthium is mostly hemispheric to subcylindric, or rarely rhomboidal as in *C. sciaphilus*. The hypanthium base can be either rounded or truncate, but is always well-differentiated from and not tapering into the pedicel. The size of the hypanthium depends primarily on the overall size of the flower. Hypanthium sizes in the species descriptions are based on dried material and are usually somewhat smaller than if based on fresh material. Measurements are given as height by lateral width and range from 3 x 5 mm to 6 x 10 mm. The surface of the hypanthium is smooth, or more commonly moderately to deeply ridged.

A notable feature of the hypanthium is the glands that are often present just below the sepal sinuses (Fig. 10). These glands are extrafloral nectaries that secrete a very concentrated sugar solution, presumably to attract ants (see discussion in Chapter II). Because of the location and function, these glands are termed intersepalar nectaries. Certain species always have well-developed intersepalar nectaries while others lack them entirely. In still other species they are only occasionally present, or are small and

apparently non-functional. The presence of these nectaries appears to be the ancestral condition in the subgenus, while their degeneration or absence is a derived feature.

The intersepalar nectaries are generally best developed on the frontal (i.e., ventral) and two lateral sites on the hypanthium. They are normally round but can sometimes be transversely elongate. Although mostly 1-2 mm in diameter, they can occasionally reach 3 mm, and can be raised to 3 mm above the surface of the hypanthium. The glands are most readily observed on fresh material, but they can also be seen in dried specimens where they often appear as small flaps of tissue. Because the glands are almost always glabrous they are particularly apparent when the hypanthium is pubescent.

Fruits

Fruits are fleshy, indehiscent berries and typically contain between 1,000 and 3,500 seeds. They are usually spheroid, obloid, or ovoid, and normally 10 x 15 mm in size, but may reach 17 x 22 mm. Depending upon the surface features in the hypanthium they can be either smooth or moderately to deeply ribbed. When deeply five- or ten-ribbed they can be conspicuously star-shaped in cross-section. At maturity the placentae normally become juicy and sweet, and I have measured the sugar concentration of this juice at ca. 25% sucrose-equivalents. The mature fruits are scentless, except in rare instances, as in *C. papillosum* where they give off an intensely fruity aroma. In spite of apparent adaptation for dispersal by animals, the fruits remain green at maturity. With the notable exception of *C. cornutus*, in most species the nectar chamber, and at times the entire withered corolla tube, are persistent on the mature fruit.

Seeds

Seeds in subgen. *Centropogon* are rather variable in shape and size, but due to the intraspecific variation in these features they are of little taxonomic utility. The seeds can assume numerous shapes, from elliptic, oblong, oval, or, suborbicular to rectangular. They are either rounded along the edges or are irregularly angular (Fig. 11A-C). In only one species, *C. cornutus*, are seeds substantially terete, otherwise they are compressed. Seeds range in size from 0.5-1.2 mm long, with most species producing seeds in the 0.6-0.9 mm range. Seed size can be helpful in the delimitation of certain taxa, as in the small seeds (0.5-0.6 mm long) that are characteristic of the *C. gamosepalus* species group, and the large seeds, (0.8-1.1 mm long), that are found in *C. sciaphilus*.

The seed coat has a rather homogeneous reticulate-foveate surface sculpturing throughout the subgenus. The testa is composed of rows of 4-6-sided isodiametric cells ca. 30-50(-80) μm long. Each foveola consists of a single cell in which the ridges are formed by the thickened radial walls and the depression is created by the collapse of the thin outer tangential wall (Fig. 11D).

Pollen

Pollen within the Lobelioideae is rather homogeneous in both overall structure and exine sculpturing (Dunbar, 1975, 1984). Other than Belem's (1976) light microscope description of the pollen of *C. cornutus*, there are no published accounts of subgen. *Centropogon* pollen. To assess the potential usefulness of pollen characters within subgen. *Centropogon*, several species representing different parts of sections *Centropogon*, *Amplifolii*, and *Campylobotrys* were subjected to standard acetolysis and examined by Dr. John Skvarla of the University of Oklahoma under the scanning electron microscope. Species from *Centropogon* subgen. *Siphocampyloides* and the genus *Siphocampylus* were also included in this survey (Table 9). In spite of this wide taxonomic range

represented, no consistent, discernable differences were observed, and the grains we examined closely match those of *Siphocampylus biserratus* illustrated by Dunbar (1975). It appears unlikely that taxonomically important differences exist between species within subgen. *Centropogon*; thus, no further palynological investigations were pursued.

Pollen grains in subgen. *Centropogon* are colporate with the three colpi running almost to the poles. The grains are generally prolate to subprolate in shape, measuring 25-32 x 22-25 μm (polar axis vs. equatorial axis) (Fig. 12A, C, and E). The exine is ca. 1-1.5 μm thick (Fig. 12B), and has a minutely striate sexine with individual lirae 0.2-0.3 μm in width (Fig. 12D). The colpus membranes are conspicuously granular (Fig. 12F).

Cytology

The basic chromosome number in Lobelioideae appears to be $x=7$, based on numerous published counts. Polyploidy is common, particularly tetraploids, $n=14$, but hexaploidy, $n=42$, is also known. Aneuploidy has also been reported among Lobelioideae, most notably in the cytologically well-studied genus *Downingia*, in which, with the interesting exception of 7, all numbers from $n=12$ to 6 are represented (Weiler, 1962).

The large neotropical genera *Centropogon* and *Siphocampylus* are poorly known cytologically, but all available counts are $n=14$, a number consistent with that of large, shrubby lobelioids in other regions, such as eastern Africa and Hawaii. Only one count in subgen. *Centropogon* has previously been published, $2n=28$ for *C. cornutus* (Gibbs & Ingram, 1982). An additional, unpublished count for the subgenus was made by Marion Cave at the University of California during the 1960s, who recorded $n=14$ from field-collected buds of *C. granulosus* subsp. *granulosus* from Peru (*Hutchison 6050*). Six additional counts are reported here (Table 10), five for subgen. *Centropogon*, and one from *Siphocampylus*. Five of these counts are first records for the species.

Methods

Gametic counts were obtained from pollen mother cells in young, field collected buds fixed in 3 parts absolute ethanol : 1 part glacial acetic acid for 24 hours; buds were then transferred to 70% ethanol. Anthers were squashed and stained in aceto-carmine or in lacto-propionic orcein. The somatic chromosome count was obtained from actively growing root tips pretreated for 6 hours in 8-hydroxyquinoline, then fixed as above in acetic alcohol. Roots were hydrolyzed in 1 N HCL for 20 minutes at 60°C and squashed and stained in aceto-carmine.

Results

Six counts were obtained, and are listed in Table 10. All counts were tetraploid, $n=14$ or $2n=28$, consistent with the previously published reports for *Centropogon* and *Siphocampylus*. Although counts are available for only ten percent of the species in subgen. *Centropogon*, all four sections are represented. The common chromosome number of $n=14$ indicates that variation in chromosome number has not played a role at least in the evolution of major groups within the subgenus. This apparent uniformity in chromosome numbers may also be reflected in the ease with which widely divergent species can be artificially hybridized with one another.

FIG. 4A-F. SEM photomicrographs of trichomes. A-E, corolla trichomes. A, papillose cells, *C. granulosus* subsp. *lugens* (Alverson 32), X460. B, collapsed multicellular trichome, *C. densiflorus* subsp. *gracilis* (Espinosa 1504), X270. C, collapsed-conical trichome, *C. hirtus* (Ferreyra 1648), X500. D, collapsed-conical trichome atop papillose base, *C. baezanus* (Wiggins 10449), X1000. E, branching corolla trichomes in *C. trachyanthus* (Camp E-1573), X120. F, laterally bulbous pedicel trichomes in *C. baezanus* (Wiggins 10449), X160.



Table 8

Comparison of Wild and Cultivated Leaf Shape and Length

Collection	Shape (length/width)		Length (cm)	
	Wild	Cult.	Wild	Cult.
<i>C. alsophilus</i> BS-2801	2.78	2.08	16.6	18.3
<i>C. gamosepalus</i> BS-3020	3.00	2.40	18.9	15.8
<i>C. roseus</i> BS-2514	2.92	2.50	23.4	20.7
<i>C. umbrosus</i> BS-2510	3.42	1.83	26.1	16.4
<i>C. granulosus</i> BS-2342	2.91	1.78	16.0	13.7
<i>C. granulosus</i> BS-2757	1.91	2.02	12.1	16.0
<i>C. granulosus</i> BS-2627	1.96	1.81	14.2	14.7
<i>C. granulosus</i> BS-2755	3.11	2.28	12.8	12.4
<i>C. granulosus</i> BS-2802	2.14	2.21	13.5	15.6
<i>C. loretensis</i> BS-3066	2.80	2.01	20.9	17.9
<i>C. densiflorus</i> BS-2713	2.92	2.06	12.3	14.6
<i>C. trachyanthus</i> BS-2852	2.02	1.82	18.5	17.8
<i>C. baezanus</i> BS-2630	1.70	1.73	16.9	14.8
<i>C. papillosum</i> BS-3127	3.33	2.47	17.4	11.5
<i>C. urubambae</i> BS-2387	1.81	1.84	14.8	13.4
<i>C. solanifolius</i> BS-2689	3.28	2.38	19.5	13.5
Mean	2.63	2.07	17.1	15.4
s.d	0.59	0.26	4.02	2.39

n=5 for all measurements

Fig. 5. Inflorescence structural types.

	Orientation	Internodes	Bract Differentiation	Example
A.	erect to horizontal	elongate	foliaceous	<u>C. cornutus</u>
B.	erect to horizontal	elongate	foliaceous-bracteate	<u>C. solanifolius</u>
C.	erect to horizontal	congested	foliaceous-bracteate	<u>C. carpishensis</u>
D.	erect	congested	bracteate	<u>C. curvatus</u>
E.	erect	elongate	bracteate	<u>C. loretensis</u>
F.	erect ¹	congested	bracteate to short-bracteate	<u>C. sciophilus</u>
G.	upturned-pendent	congested	short-bracteate	<u>C. granulosus</u>
H.	upturned-pendent ²	congested	short-bracteate	<u>C. baezanus</u>
I.	pendent	congested	short-bracteate	<u>C. electrolophos</u>
J.	pendent	elongate	short-bracteate	<u>C. pulcher</u>

Note: () = flowering pedicels; () = fruiting pedicels.

¹ subtended by elongate peduncle

² lateral inflorescence present

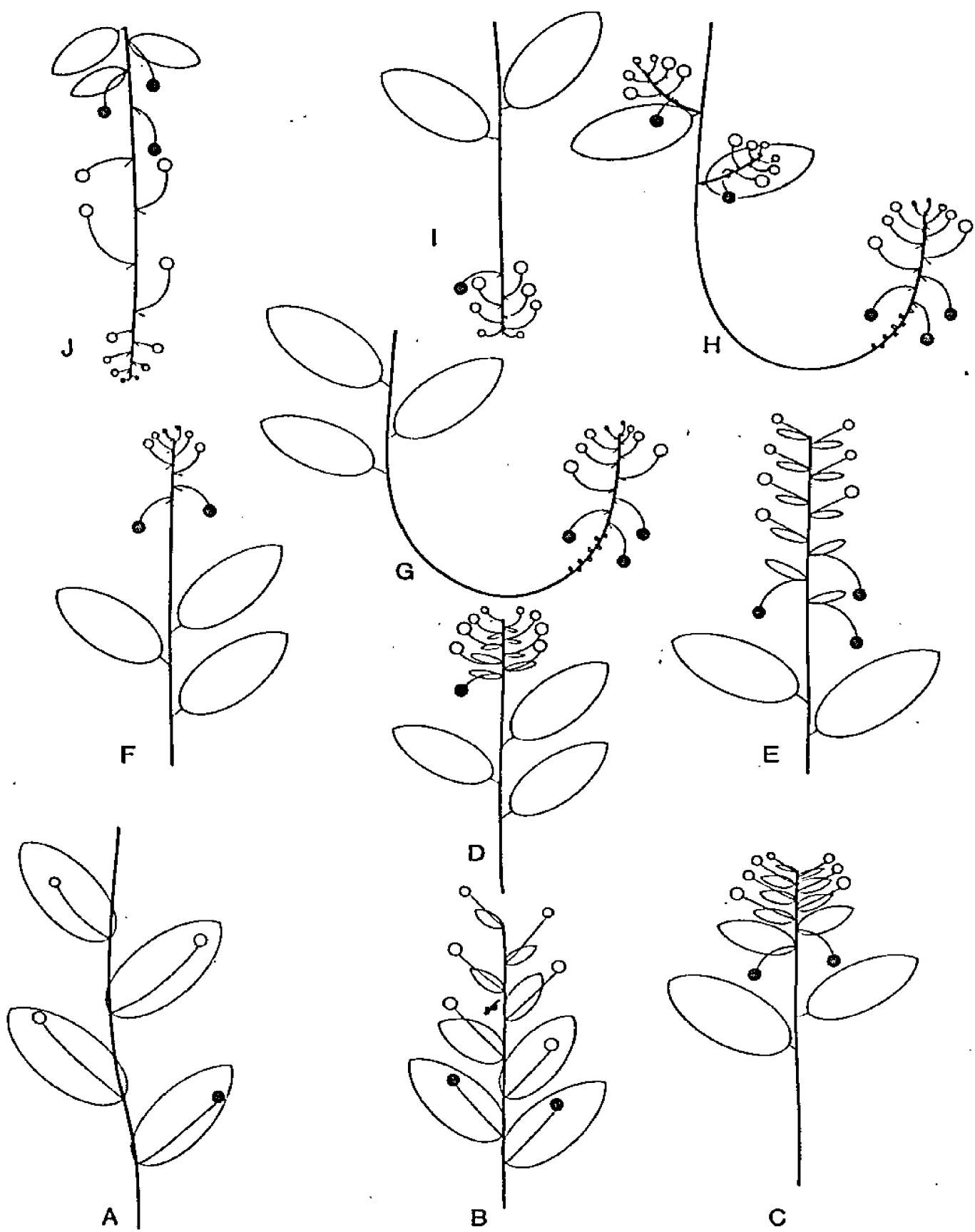


Fig. 6A-C. Shoot apex fates and production of sequential inflorescences. A, auxotelic inflorescence showing position of (1) original inflorescence and (2) subsequent, terminal inflorescence. B-C, anauxotelic inflorescences. B, (1) original inflorescence with (2) subsequent inflorescence developing from subterminal leaf axil. C, (1) original inflorescence and (2) subsequent inflorescence developing from basal shoot.

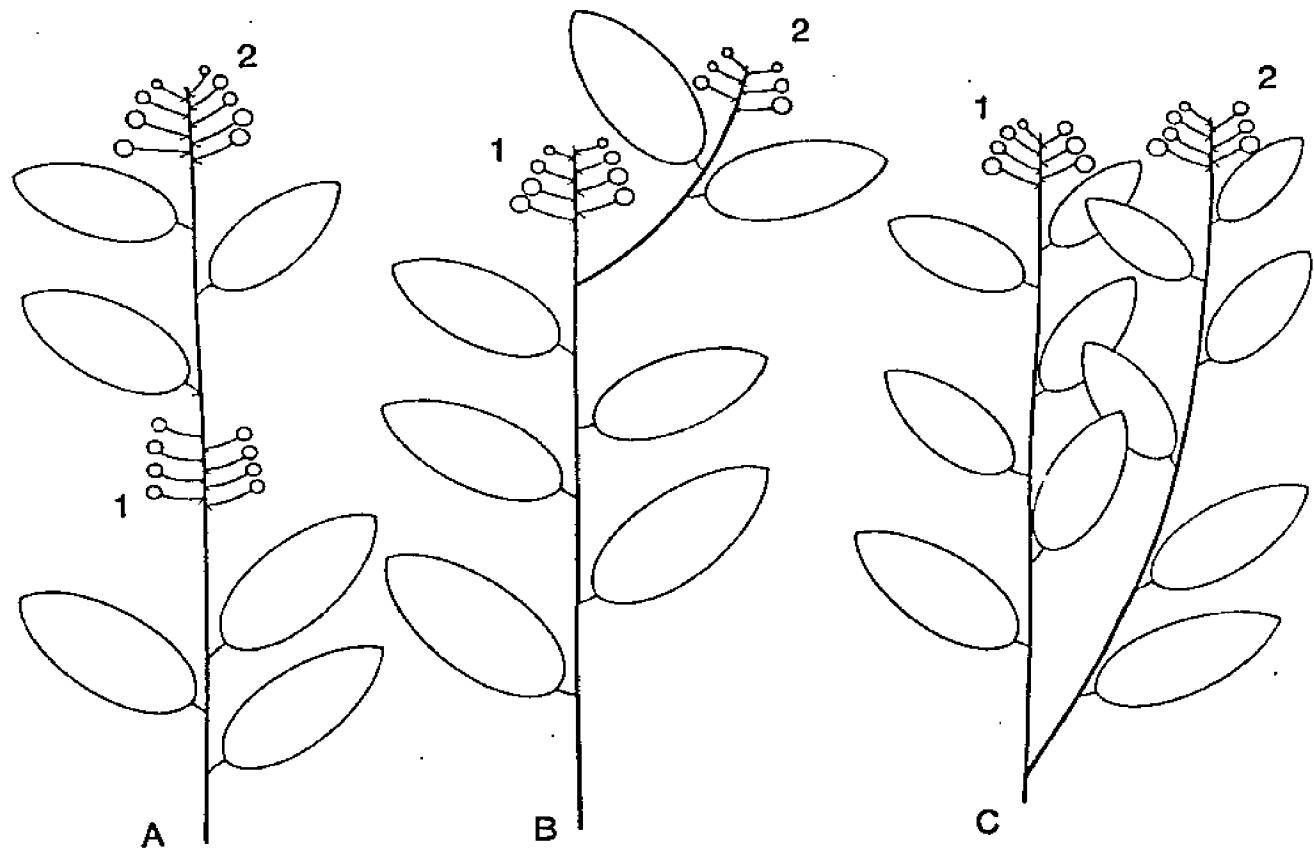


Fig. 7A-C. Corolla and androecium measurements. A, corolla length and width measurements. A-1, corolla tube length. A-2, corolla tube width at base. A-3, corolla tube width at throat. B, corolla tube curvature measured in intersection angle degree. C, androecium length and width measurements. C-1, overall androecium length. C-2, filament length. C-3, filament tube width. C-4, filament tube exsertion. C-5, anther tube length. C-6, stigma width.

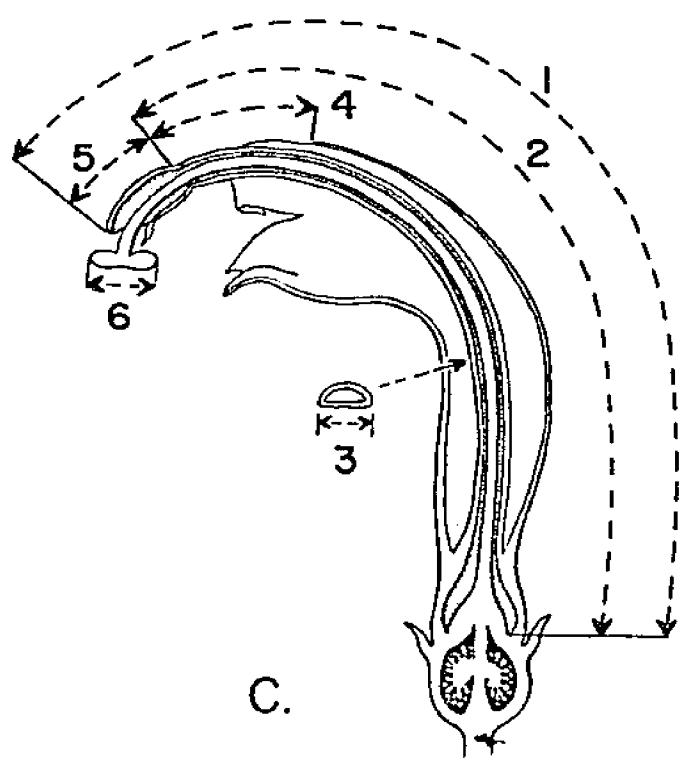
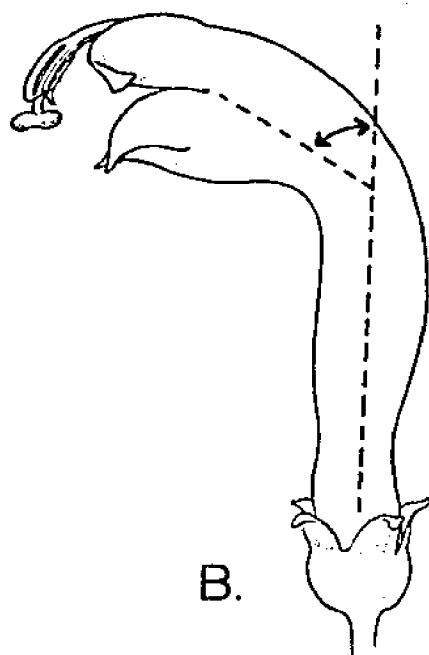
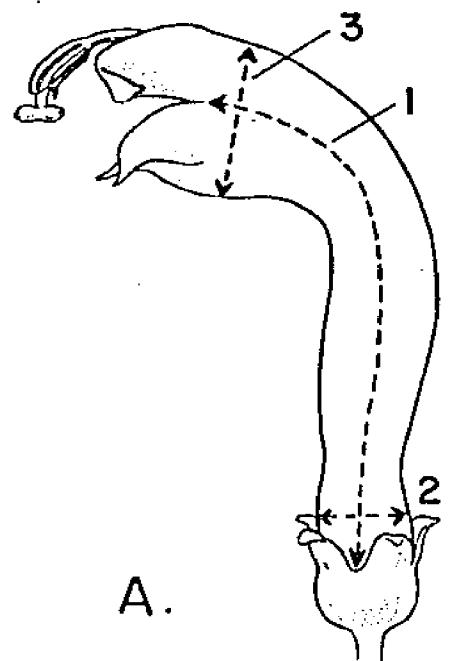


Fig. 8A-K. Representative flowers of subgen. *Centropogon*. A-D, sect. *Amplifolii*. A, *C. capitatus* (from Stein & Todzia 2401). B, *C. gesneriiformis* (from Stein 2845). C, *C. congestus* (from Stein 3740). D, *C. alsophilus* (from Stein 2800). E-H, sect. *Campylobotrys*. E, *C. reflexus* (from Stein & Todzia 2309). F, *C. urubambae*, lateral view of sigmoid flower and frontal view of zygomorphic calyx (from Stein & Todzia 2387). G, *C. vaughianus* (from Stein 3676). H, *C. granulosus* subsp. *lugens* (from Stein & Sierra 3600). I-K, sect. *Grandes*. I, *C. beslerioides* (from Stein 3465). J, *C. trianae* (from Stein & McDade 3204). K, *C. semperflorens* (from Stein 3739). (All drawn from pickled material and photographs.)

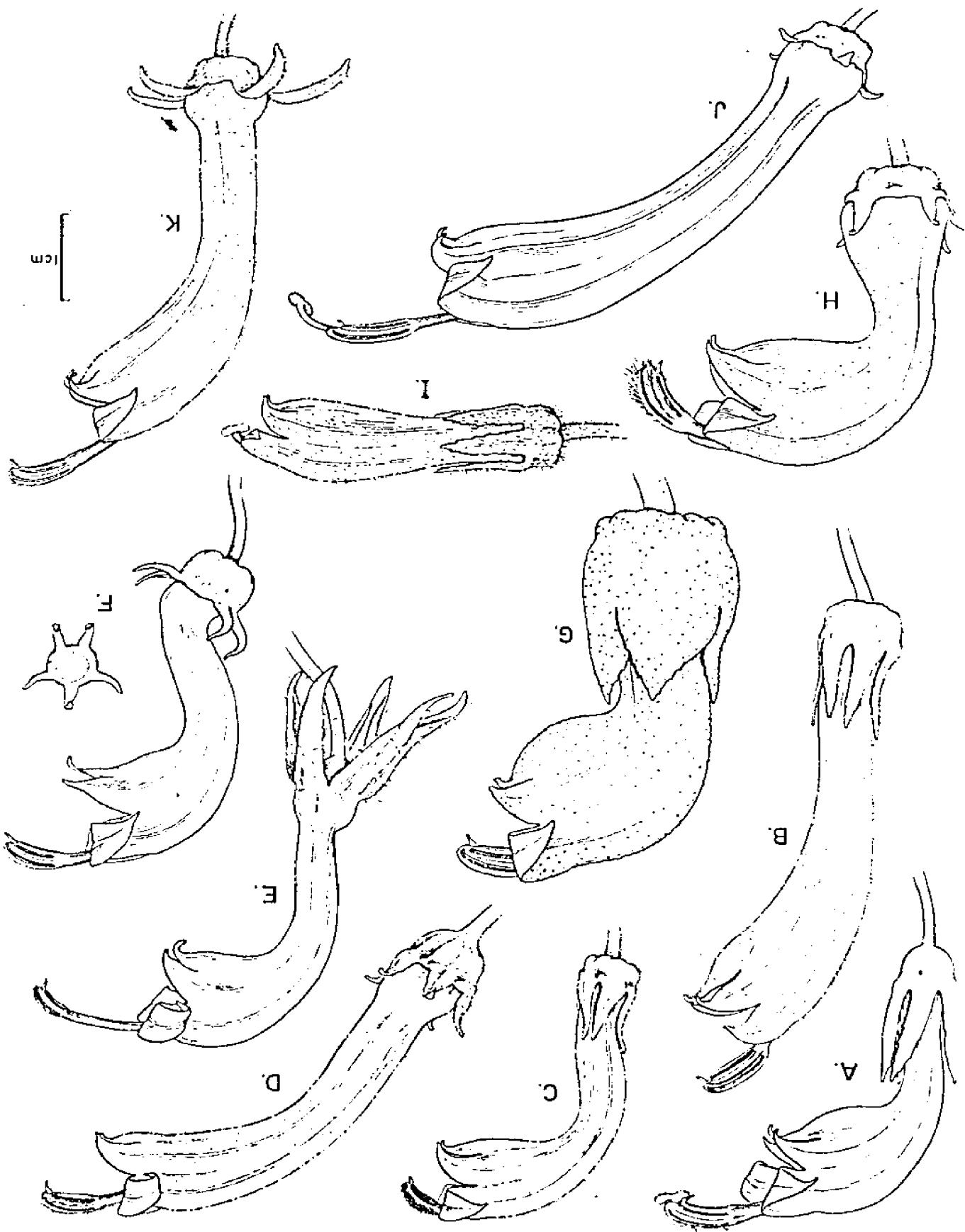


Fig. 9A-D. SEM photomicrographs of subgen. *Centropogon* antheridial scales. A-B, *C. granulosus* (cult. material of Stein & Todzia 2342). A, inner surface of scale, X40. B, detail of scale apex showing reticulate pattern from fused trichomes, X340. C-D, *C. papillosum* (cult. material of Stein & Tucker 3127). C, cross-section of trichome base showing fused trichomes, X750. D, detail of trichome apex, X2000.

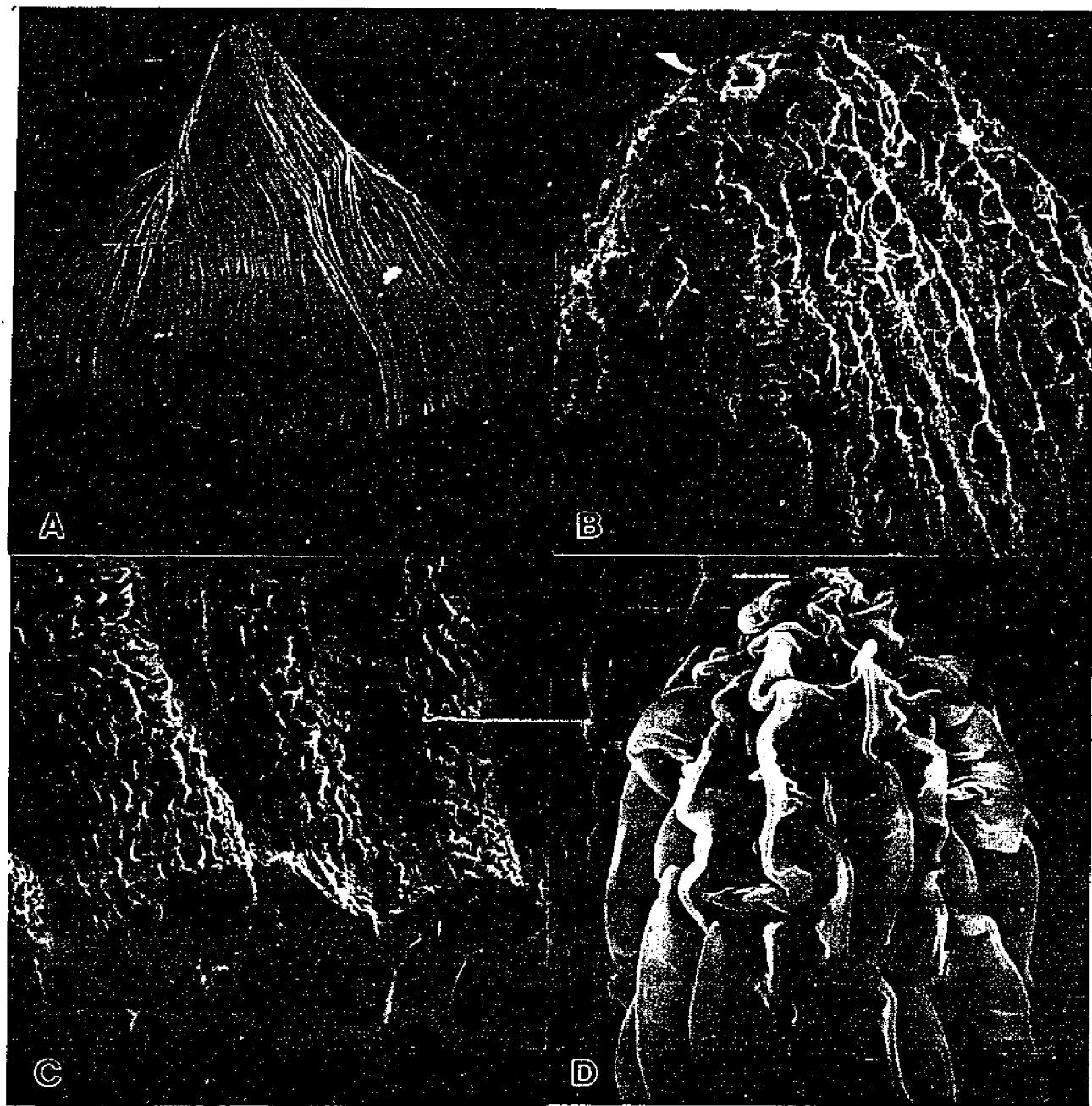


Fig. 10A~B. SEM photomicrographs of intersepalar nectaries. A, *C. umbratus* (Stein 2510), X40. B, *C. urubambae* (Stein & Todzia 2387), nectary surface showing stomata, X1500.

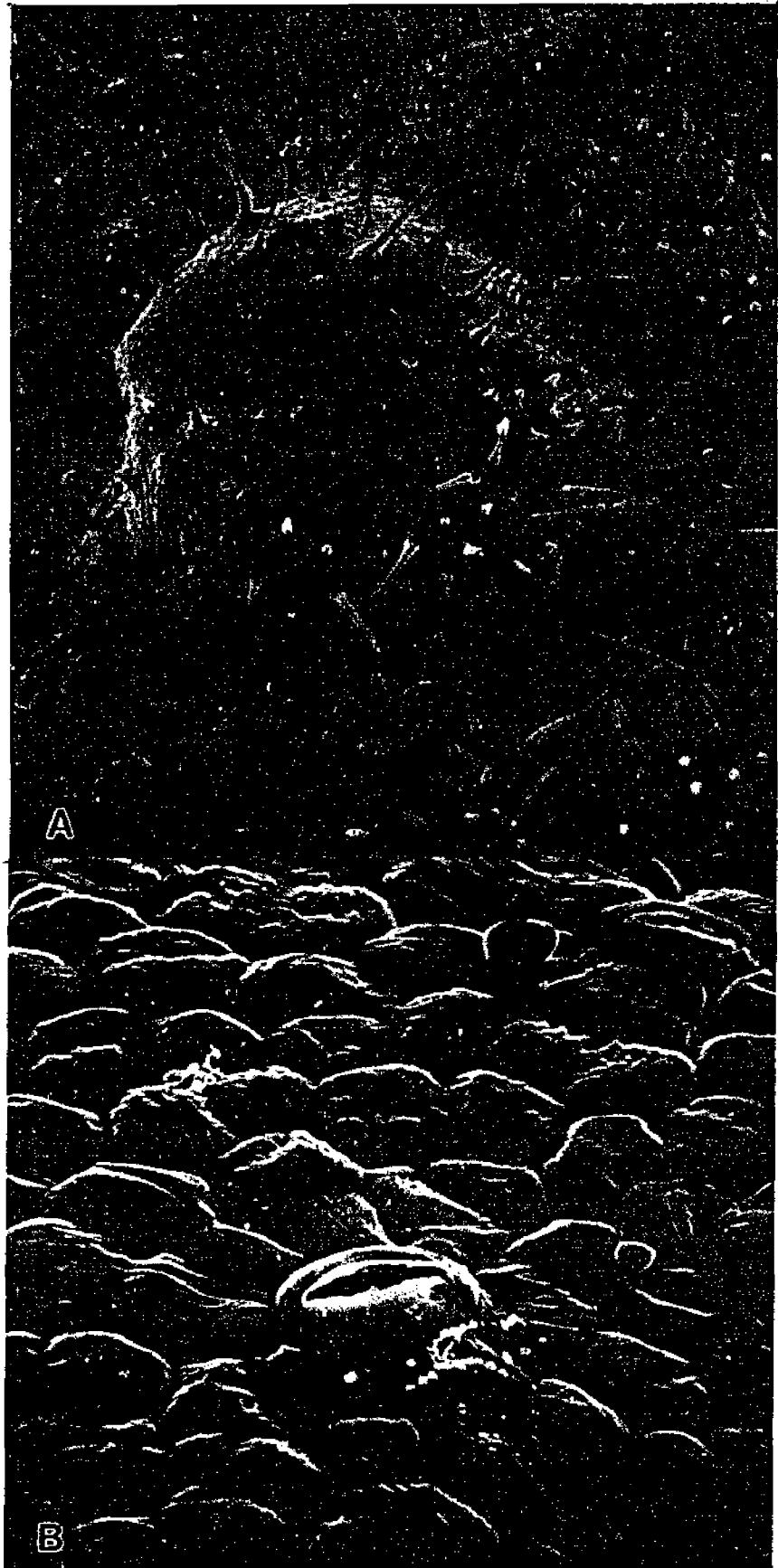


Fig. 11A-D. SEM photomicrographs of seeds. A, *C. urubambae* (Killip & Smith 23038), X150. B, *C. gamosepalus* (Schunke 4787), X150. C-D, *C. sciaphilus* (Killip & Smith 26672). C, entire seed, X90. D, detail of seed coat showing ridged radial walls and collapsed tangential wall of individual cells, X1000. Note difference in scale between A-B and C.

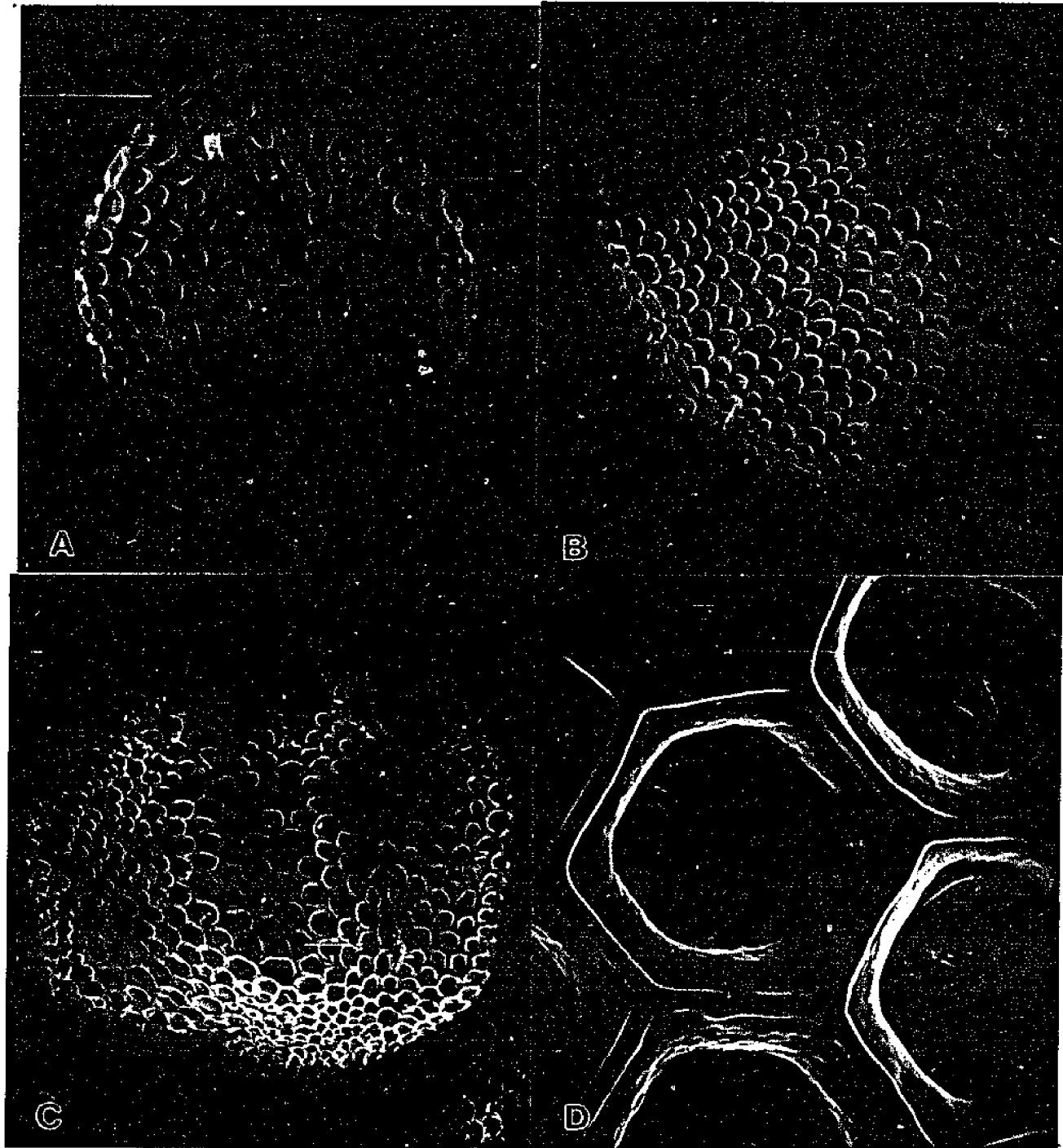


Table 9
Pollen Specimens Examined

Species	Locality	Collection
<i>Centropogon granulosus</i>	Panama, Chiriquí	Stein 1255
<i>Centropogon urubambae</i>	Peru, Cuzco	Boeke 1522
<i>Centropogon cornutus</i>	Colombia, Cundinamarca	Davidse 5520
<i>Centropogon capitatus</i>	Peru, San Martín	Schunke 7268
<i>Centropogon ferrugineus</i>	Panama, Chiriquí	Stein 1288
<i>Centropogon valerii</i>	Costa Rica, Cartago	Stein 1404
<i>Centropogon smithii</i>	Panama, Chiriquí	Hammel 6075
<i>Siphocampylus giganteus</i>	Ecuador, Pichincha	Ortiz 32

Fig. 12A-F, SEM photomicrographs of *Centropogon* pollen. A, *C. urubambae* (Boeke 1522), equatorial view, X2000. B, *C. ferrugineus* (Stein 1288), cross-section of exine, X10000. C-D, *C. cornutus* (Davidse & Llanos 5520). C, polar view, X2000. D, detail of striate sexine, X10000. E-F, *C. granulosus* (Stein 1255). E, polar view, X2000. F, detail of granular colpus membrane, X5000.

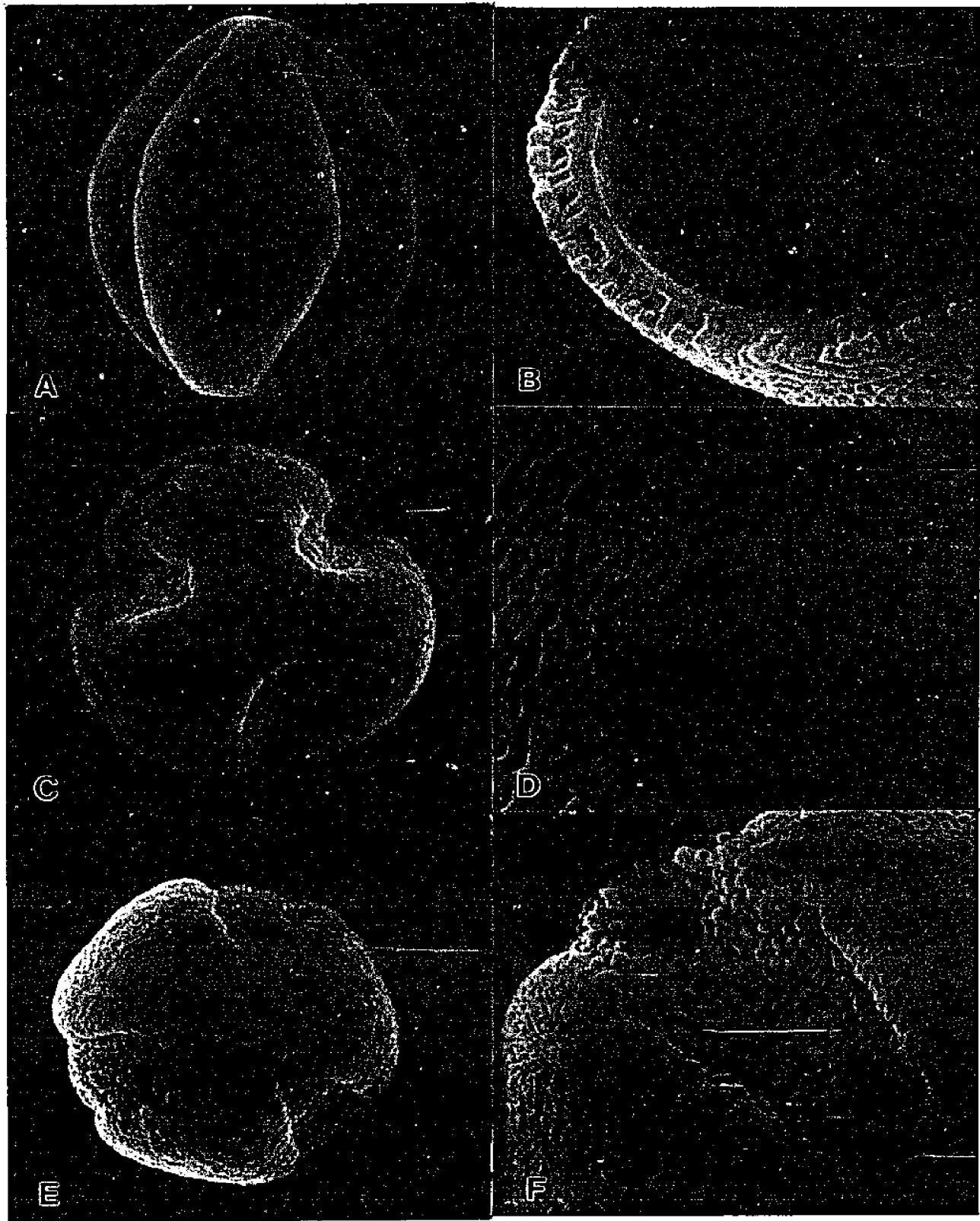


Table 10
Original Chromosome Counts for *Centropogon* and *Siphocampylus*

Species	Number	Voucher
<hr/>		
<i>C. cornutus</i> (L.) Druce	$2n=28$	Venezuela, <i>Plowman</i> 13387
<i>C. gesneriiformis</i> Drake	$n=14$ II*	Ecuador, Cañar, <i>Stein</i> 2845
<i>C. pulcher</i> A. Zahlbr.	$n=14$ II*	Peru, Junín, <i>Stein</i> 2386
<i>C. solanifolius</i> Benth.	$n=14$ II*	Ecuador, Pichincha, <i>Stein</i> 2661
<i>C. trachyanthus</i> F. Wimmer	$n=14$ II*	Ecuador, Azuay, <i>Stein</i> 2852
<i>Siphocampylus lucidus</i>	$n=14$ II*	Ecuador, Napo, <i>Stein</i> 2651
 F. Wimmer		
<hr/>		

* - indicates first record for species.

VII. SYSTEMATIC TREATMENT

Taxonomic History

In 1836 Presl described the genus *Centropogon* in his *Prodromous Monographiae Lobeliacearum*. The generic diagnosis and the species included clearly indicate that his concept of the genus agrees with what later authors have treated as section or subgenus *Centropogon* (Bentham and Hooker, 1876; Wimmer, 1943; McVaugh, 1949a; Wilbur, 1976). Noted in Presl's diagnosis are the entire, tubular corolla and baccate fruit, which are currently considered generic characters, as well as the presence of a fused anther scale, now a subgeneric character ("Antherae duae inferiores aculeo ovato-triangulari cartilagineo soliatario terminatae.").

Prior to Presl's erection of *Centropogon*, species now included in subgen. *Centropogon* mostly were assigned to *Lobelia*. The first of these was *Lobelia cornuta* L. (=*C. cornutus*), which was included by Linnaeus (1753) in the first edition of Species Plantarum. In the second edition, Linneaus (1763) described *L. surinamensis* L., now a synonym of *C. cornutus* as are most pre-Presl names. The only early subgen. *Centropogon* names in *Lobelia* that represent species other than *C. cornutus* are *L. grandis* L.f. (=*C. grandis*), *L. hirta* Cav. (=*C. hirtus*) and *L. beslerioides* H. B. K. (=*C. beslerioides*). Don (1834) transferred most of the above species into *Siphocampylus*, which had been established three years previously by Pohl, and described as new *S. macrophyllus* G. Don (=*C. macrophyllus*).

Presl (1836) included eight species in *Centropogon*, four of which had been described previously (*C. surinamensis* [=*C. cornutus*], *C. bonplandianus* [=*C. cornutus*], *C. grandis*, and *C. hirtus*), and three new (*C. exasperatus* [=*C. hirtus*], *C. granulosus*, and *C. reflexus*). The eighth species recognized by Presl, *C. edulis*, is a *nomen nudum* based on

an unpublished basionym in *Lobelia* that he attributed to Linneaus without providing any additional diagnosis. Presl's generic concepts in Lobelioideae differed significantly from those of most authors before and after him. For instance, he adopted the pre-Linnaean generic name *Rapuntium* for species with capsular fruits and dorsally slit corolla tubes (what are now considered *Lobelia*) reserving the name *Lobelia* for capsular-fruited species with entire tubular corollas (most of which are currently included in *Siphocampylus*). Although he was the first to emphasize fruit type (capsular and dehiscent versus baccate and indehiscent) in delimiting genera, the material available to him apparently did not always allow accurate assignment of species based on these features. Evidence of this is his placement of what are now known to be baccate-fruited species of *Centropogon* within his capsular-fruited genus *Lobelia*. This included three species of subgen. *Centropogon*, *L. andropogon* A. DC. (=*C. cornutus*), *L. beslerioides* H. B. K. (=*C. beslerioides*), and *L. macrophyllus* (G. Don) Presl (=*C. macrophyllus*). The identity of *L. cornuta* L. (=*C. cornutus*) remained obscure for many years because it too was not assigned to *Centropogon*. Instead, Presl listed it as "*Lobelia?* *cornuta* Lin." in an appendix containing species of uncertain generic placement ("Lobeliaeae quoad genus dubiae, vel solo nomine notae"). Not until 1913 did Druce make the appropriate combination, and establish the priority of *C. cornutus* over the widely used epithet *C. surinamensis*.

Centropogon was quickly accepted as a valid genus by Presl's contemporaries. Beginning with de Candolle (1839), new species with entire corollas and baccate fruits were referred to *Centropogon*. By 1876 Bentham and Hooker could state that more than 80 species of *Centropogon* were either published or could be distinguished in herbaria, and they provided the first infrageneric classification of the genus. Two sections were recognized based on whether the lower anthers were crowned with a cartilaginous appendage (sect. *Centropogon*) or had penicillate tips (sect. *Siphocampyloides*). Although

these sections have recently been elevated to subgeneric rank (Wilbur, 1976a), they retain the same basic definition as originally given by Bentham and Hooker (1876).

Zahlbruckner, in a series of publications from 1891 to 1915, meticulously described a number of new species of subgen. *Centropogon*, and in 1891 proposed an additional section, sect. *Amplifolii*, consisting of *C. sciaphilus*, *C. gamosepalus*, *C. capitatus*, and *C. amplifolius* (=*C. macrophyllus*). This section, composed entirely of species that previously would have been included in Bentham and Hooker's sect. *Centropogon*, was based principally on the bracteate, racemose or corymbose inflorescences found in these species. Although this section is still recognized in the current treatment, it differs somewhat in circumscription.

Gleason (1925) divided *Centropogon* into three groups of unspecified rank, the Stellate-tomentose, *Amplifolii*, and *Axillares* groups. These were "based largely on superficial characters and not always indicative of true relationships among the species" (Gleason, 1925). His *Amplifolii* group, contained only species with antheridial scales (thus belonging to subgen. *Centropogon*) and was subdivided into those species with "large leaves, a crowded inflorescence and erect sepals," and those with "small leaves, an elongate inflorescence, and reflexed sepals." His *Axillares* group, however, was divided into those species with "appendiculate anthers" and those with penicillate anthers. Based on the characters he employed to divide the genus, Gleason was certainly correct about the artificiality of his groupings. Of the 11 new species in subgen. *Centropogon* that Gleason described, only three are retained in this treatment.

By far the most prolific and diligent systematist to study *Centropogon* was Wimmer, who began publishing on neotropical Lobelioideae in the 1920s and eventually monographed the entire subfamily for Engler's *Das Pflanzenreich* (Wimmer, 1943, 1956, 1968). Wimmer's studies were based entirely on herbarium specimens, although he borrowed extensively from North American herbaria and studied most of the important

European collections. His monograph comprises the only complete prior treatment of subgen. *Centropogon*, and forms the foundation for my study. Wimmer (1931) followed Bentham and Hooker in recognizing two sections in *Centropogon*, dividing sect. *Centropogon* into several groups and subgroups of unspecified rank. In 1943, he modified and formalized this classification, which was based primarily on features of the inflorescence. Three subsections were designated within his sect. *Centropogon*, subsects. *Corymboides*, *Botryooides*, and *Axillares*. Wimmer (1943) also erected a new rank of "grex" below the level of subsection, which at times he formally treated as synonymous with Gleason's (1925) "groups" (e.g., *Amplifolii*). In other instances, however, he treated Gleason's "groups" as subsections (e.g., *Axillares*). Wimmer subdivided subsect. *Corymboides*, containing the majority of species, into grex *Campylobotrys* and grex *Amplifolii*. Within the key to the latter group, he also indicated two informal groups, the "Gamosepali" and "Lysisepali." In total Wimmer (1943) recognized 79 species, 29 varieties and 10 forms in sect. *Centropogon*, and his later supplements to the monograph (Wimmer, 1956, 1968) only slightly altered these figures. Although he made a major contribution to our understanding of subgen. *Centropogon*, Wimmer's treatment is plagued with problems, both in the infrasectional classification and the species delimitations. Many taxa were based on single collections, or on characters that are now known to be highly labile. Part of the inadequacy is related to Wimmer's lack of fieldwork and unfamiliarity with South American geography, but a large part is also due to his extremely narrow species concept.

Several other workers have included subgen. *Centropogon* in fairly recent regional floristic treatments. McVaugh's (1943) treatment of the Lobelioideae for *North American Flora* was published the same year as Wimmer's major work on *Centropogon*, but differs considerably in the circumscription of Central American taxa. In general, McVaugh uses a considerably more inclusive species concept. Treatments of *Centropogon* for both

Costa Rica (Wilbur, 1976) and Panama (Wilbur, 1977) largely follow McVaugh's concepts with respect to subgen. *Centropogon*. Wilbur's contribution is noteworthy for elevating sects. *Centropogon* and *Siphocampyloides* to subgeneric rank (Wilbur, 1976). Jeppesen's (1981) treatment of Lobeliaceae for the *Flora of Ecuador* provides the only recent evaluation of a portion of subgen. *Centropogon* in South America.

Sectional Classification

Previous attempts to subdivide subgen. *Centropogon* have produced highly artificial systems, either because of the limited number of species included, as in the case of Zahlbruckner (1891), or because of reliance upon a few relatively labile characters (e.g., Wimmer, 1931, 1943). The rather homogeneous structural makeup of the subgenus coupled with extensive intraspecific variation makes clustering of species along natural lines a difficult task. Further complicating infrasubgeneric alignments are apparently widespread reticulate character evolution and the potential for hybridization among even the most morphologically divergent species. During the course of this study several apparently natural groups have emerged, however, and these are used as the core of the sections recognized here. These groups are based to a large degree on inflorescence structure, corolla morphology, and filament tube cross-sectional shape. This infrasubgeneric classification must be considered tentative, with the hope that additional characters useful in determining relationships within the subgenus will be uncovered.

This treatment recognizes four sections, sects. *Centropogon*, *Amplifolii*, *Campylobotrys*, and *Grandes*, and Table 11 lists those species that are included in each. Because of the various ways in which sections and subsections have been interpreted in the past, it is difficult to precisely correlate my concept of the above groups with those

of past authors, but I have attempted to cross-reference those systems with my own (Table 12). The rather uniform morphology in the subgenus and the few characters that serve to unambiguously assign species to their respective groups necessitate that several characters often must be considered in combination. The following detailed key is thus presented as a means of characterizing and comparing these sections.

Key to Sections of Subgenus Centropogon

1. Flowers solitary in axils of unreduced leaves; pedicels elongate, spreading at anthesis; bracteoles basal, persistent on rachis after abscission of pedicel; sepals free, divaricate to reflexed; intersepalar nectaries well-developed; corolla gently curving, without well-differentiated throat, pinkish; filament tube whitish, subterete or less often ventrally flattened toward apex, well-exserted from corolla tube, the exserted portion arching upwards; anther tube curving ventrally; fruit ripening without persistent nectar chamber; seeds terete, relatively few maturing per fruit, 900-1,500; 1 species, widespread throughout much of tropical America.
.....sect. *Centropogon*.

1. Flowers usually in definite inflorescences, rarely solitary and axillary; pedicels short to elongate, generally erect at anthesis; bracteoles usually subbasal but from basal to subterminal, only rarely persistent on rachis after pedicel abscission; sepals free or fused at base, erect, divaricate, or reflexed; intersepalar nectaries present or absent; corolla tube gently to abruptly curving, with or without a well-differentiated throat, various shades of pink, red, orange or yellow; filament tube subterete or ventrally flattened, whitish or yellowish, when exserted from corolla tube, rarely arching upwards; anther tube straight or rarely curving; fruit

- normally ripening with the nectar chamber persistent; seeds compressed,
relatively few to numerous per fruit, ca. 1,000 to 3,500.....2
2. Erect herbs or shrubs, or very rarely scandent vines; leaves occasionally with white,
crustose, superficial excrescences; trichomes never with papillose bases or with
tuberculate papillae; inflorescences terminal, often auxotelic (i.e., the
inflorescence shoot apex capable of producing additional vegetative growth);
inflorescence bracts persistent, usually foliaceous, rarely reduced; corolla mostly
red or pink, rarely orangish, mostly concolorous, or the lobes colored only
slightly differently from tube, the tube usually abruptly curved forward above
middle and with a well-differentiated, usually ampliate throat, the tissue thin,
never thick and brittle; anther tube occasionally angling slightly to left when
fresh; filament tube subterete, mostly 1.5-2 mm wide, usually whitish or pinkish;
seeds small to medium, 0.5-0.8 mm long; 17 species, Costa Rica to Southern
Peru, mostly Andean.
-sect. *Amplifolii*.
2. Erect herbs or shrubs, or often scandent vines; leaves never with crustose superficial
excrescences; trichomes occasionally with papillose or pustulate bases, or rarely
with glabrous papillose tubercles; inflorescence terminal or rarely axillary,
anauxotelic (i.e., the inflorescence shoot apex not capable of further vegetative
growth); inflorescence bracts caducous or persistent, foliaceous or often much
reduced; corolla usually various shades of orange or red, rarely pink or yellow,
often bicolored with contrasting yellow or orange lobes, the tube either straight,
gradually curving with an indistinct throat, or abruptly curving forward above
middle with a well-differentiated ampliate and often ventricose throat, the tissue

thin or moderately to very thick and brittle; anther tube never angling to left when fresh; filament tube ventrally flattened, 2-4 mm wide, usually yellowish to orangish; seeds small to large, 0.6-1.1 mm long.....3.

3. Herbs, shrubs, or often vines; trichomes occasionally with expanded, papillose or pustulate bases, stem surface occasionally scabrous or granulose; inflorescence usually bracteate or short-bracteate, rarely folio-bracteose, the bracts often caducous, rachis erect or often pendent, and if pendent usually upturned at tip, occasionally subtended by a peduncle; hypanthium base rounded or occasionally truncate; corolla orange, red, pink, or yellow, often with lobes of contrasting colors; corolla tube mostly moderately to abruptly curved, 30-70(-90)°, the throat usually well-differentiated from lower portion of tube and somewhat ventricose, the tissue thin or thick and brittle; filament mostly well-exserted (5-15 mm) from corolla tube; 22 species, Nicaragua to Bolivia, mostly Andean and upper Amazon Basin.

.....sect. *Campylobotrys*.

3. Herbs shrubs, or rarely vines; trichomes almost never with expanded, papillose or pustulate bases, stem surfaces always smooth, rarely scaberulous; inflorescence foliose to foliobracteose, rarely bracteate but never short-bracteate, the bracts never caducous, the rachis normally erect to horizontal, rarely pendent, never subtended by a peduncle; hypanthium base usually truncate, rarely rounded; corolla orange to red, often with contrasting yellow or orange lobes; corolla tube straight to gradually curved, 0-30(-45)°, the throat usually not well-differentiated from lower portion of tube, the tissue thin, never thick and brittle; filament tube

usually exserted less than 5 mm from corolla tube; ca. 15 species, Costa Rica to northern Peru and Venezuela, mostly Andean.....sect. *Grandes*.

Table 11
Sectional Placement of Species¹

Section *Centropogon*

1. *Centropogon cornutus* (L.) Druce

Section *Amplifolii*

2. *Centropogon capitatus* Drake
 3. *Centropogon macrophyllus* (G. Don) F. Wimmer
 4. *Centropogon umbrosus* F. Wimmer
 5. *Centropogon hirtus* (Cav.) Presl
 6. *Centropogon congestus* Gleason
 7. *Centropogon ventanaensis* B. A. Stein ined.
 8. *Centropogon gesneriiformis* Drake
 9. *Centropogon uncialis* McVaugh
 10. *Centropogon gamosepalus* A. Zahlbr.
 11. *Centropogon roseus* Rusby
 12. *Centropogon silvaticus* F. Wimmer
 13. *Centropogon quebradanus* F. Wimmer
 14. *Centropogon eurystomus* F. Wimmer
 15. *Centropogon undulatus* B. A. Stein ined.
 16. *Centropogon electrolophos* B. A. Stein ined.
 17. *Centropogon escobarae* B. A. Stein ined.
 18. *Centropogon alsophilus* F. Wimmer

¹ Numbers used here refer to the species throughout the treatment.

Section *Campylobotrys*

19. *Centropogon granulosus* Presl

19a. subsp. *granulosus*

19b. subsp. *lateriflorus* (F. Wimmer) B. A. Stein ined.

19c. subsp. *rutilus* (F. Wimmer) B. A. Stein ined.

19d. subsp. *lugens* (F. Wimmer) B. A. Stein ined.

19e. subsp. *tortilis* (F. Wimmer) B. A. Stein ined.

19f. subsp. *nutans* (Planchon & Oersted) B. A. Stein ined.

20. *Centropogon pulcher* A. Zahlbr.

21. *Centropogon cuatrecasanus* B. A. Stein ined.

22. *Centropogon densiflorus* Benth.

22a. subsp. *densiflorus*

22b. subsp. *gracilis* (Drake) B. A. Stein

23. *Centropogon trachyanthus* F. Wimmer

24. *Centropogon baezanus* Jepp.

25. *Centropogon curvatus* Gleason

26. *Centropogon papillosum* F. Wimmer

27. *Centropogon vaughianus* F. Wimmer

28. *Centropogon loretensis* F. Wimmer

29. *Centropogon amplicorollinus* (F. Wimmer) B. A. Stein ined.

30. *Centropogon latifolius* F. Wimmer

31. *Centropogon sciaphilus* A. Zahlbr.

32. *Centropogon yungasensis* Britton

33. *Centropogon reflexus* Presl

34. *Centropogon urubambae* F. Wimmer

35. *Centropogon vargasii* B. A. Stein ined.

36. *Centropogon arcuatus* F. Wimmer
37. *Centropogon pygmaeus* B. A. Stein ined.
38. *Centropogon bangii* A. Zahlbr.
39. *Centropogon carpishensis* B. A. Stein ined.
40. *Centropogon lasiodorus* B. A. Stein ined.

Section *Grandes* (not treated in this work)

- Centropogon grandis* (L. f.) Presl
- Centropogon solanifolius* Benth.
- Centropogon semperfolius* F. Wimmer
- Centropogon trianae* A. Zahlbr.
- Centropogon laxus* A. Zahlbr.
- Centropogon gallerensis* (Gleason) B. A. Stein ined.
- Centropogon pamplonensis* F. Wimmer
- Centropogon longipetiolatus* F. Wimmer
- Centropogon hypotrichus* F. Wimmer
- Centropogon vernicosus* A. Zahlbr.
- Centropogon albolimbatus* F. Wimmer
- Centropogon beslerioides* (H. B. K.) A. DC.
- Centropogon linnaeanus* F. Wimmer
- Centropogon pedicellaris* Gleason
- Centropogon scabellus* F. Wimmer

Table 12

Historical Subdivisions of Subgenus *Centropogon*

Previous Treatments	Present Treatment
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<u>Zahlbrückner 1891</u>	
Sect. <i>Amplifolii</i>	<i>Amplifolii</i> , <i>Campylobotrys</i> (in part)
<u>Gleason 1925</u>	
<i>Amplifolii</i>	<i>Amplifolii</i> , <i>Campylobotrys</i> , <i>Grandes</i>
<i>Axillares</i> (in part)	<i>Centropogon</i>
<u>Wimmer 1931</u>	
<i>Subumbellati</i>	<i>Amplifolii</i> , <i>Campylobotrys</i> (in part)
<i>Gamosepali</i>	<i>Amplifolii</i> (in part), <i>Grandes</i> (in part)
<i>Amplifolii</i>	<i>Campylobotrys</i> (in part)
<i>Corymboides</i>	<i>Grandes</i> , <i>Amplifolii</i> (in part)
<i>Botryoides</i>	<i>Campylobotrys</i>
<i>Axillares</i>	<i>Centropogon</i> , <i>Grandes</i> (in part)
<u>Wimmer 1943</u>	
Subsect. <i>Corymboides</i>	<i>Amplifolii</i> , <i>Campylobotrys</i> , <i>Grandes</i> (each in part)
<i>Grex Campylobotrys</i>	<i>Campylobotrys</i> (in part)
<i>Grex Amplifolii</i>	<i>Amplifolii</i> , <i>Campylobotrys</i> , <i>Grandes</i> (each in part)
Subsect. <i>Botryoides</i>	<i>Campylobotrys</i> (in part)
Subsect. <i>Axillares</i>	<i>Centropogon</i> , <i>Amplifolii</i> (in part), <i>Grandes</i> (in part)
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Section *Centropogon*

Centropogon Presl subgenus Centropogon section Centropogon.

Type species, *Centropogon surinamensis* (Linnaeus) Presl (=*Centropogon cornutus*).

Section *Centropogon* consists of a single species, *C. cornutus*, which combines many characters that are considered plesiomorphic for the subgenus. The most important of these features is the frondose inflorescence, consisting of solitary, axillary flowers. This type of inflorescence is found throughout the rest of the genus, but differs considerably from the congested racemes typical of the other sections of subgen. *Centropogon*. Other features of this section can be found in the detailed key to sections.

1. ***Centropogon cornutus* (Linnaeus) Druce, Bot. Exch. Club Soc. Brit. Isles 3: 416. 1914.**

Lobelia cornuta Linnaeus, Sp. Pl. ed. 1: 930. 1753. Type. French Guiana. "Habitat in Cayenna, plantam apud D. Royenum vidi," n.v.

Lobelia surinamensis Linnaeus, Sp. Pl. ed. 2: 1320. 1763. Type locality. "Surinam."

Collector not indicated and type not seen.

Lobelia obscura Linnaeus, Pl. Surin.: 14. 1775. Type. Surinam. This name is probably based on a Dahlberg collection, as are the other species in this work (Stafleu & Cowan, 1981). No specimens annotated with this name are present on the microfiche of the Linnaean herbaria in London or Stockholm, but it is possible that Linnaeus studied the Dahlberg specimen that was later annotated and published as *L. laevigata* by his son. Savage (1945) implies that two different elements are represented on that sheet.

Lobelia laevigata Linnaeus filius, Suppl. Pl.: 392. 1782. Type. Surinam. *Dalberg s.n.*, (holotype, LINN n.v., IDC microfiche).

Lobelia andropogon Cavanilles, Anales Hist. Nat. 2: 106. 1800. Type. Ecuador. Between Caracol and San Antonio, trail between Guayaquil and Quito, *Nee s.n.* (holotype, MA n.v., photo in LE & W).

Lobelia spectabilis Humboldt, Bonpland & Kunth, Nov. Gen. et Spec. 3: 306. 1819.

Type. Venezuela. Monagas: Cocollar, 800 m, Sep 1799, *Humboldt & Bonpland s.n.* (holotype, P n.v., IDC microfiche). Two additional *Humboldt & Bonpland* collections, 239 & 309 are in the Willdenow herbarium at B, but since the holotype is unnumbered neither of these are considered isotypes.

Lobelia bonplandiana Roemer & Schultes, Syst. Veg. 5: 57. 1819. Type. "In America Meridional," *Humboldt & Bonpland s.n.* (perhaps based on type of *L. dentata*).

Lobelia dentata Willdenow ex Roemer & Schultes, pro syn., Syst. Veg. 5: 57. 1819.

Type. without locality, *Humboldt & Bonpland s.n.* (holotype, B, IDC microfiche 3999).

Lobelia purpurea Velloso, Fl. Flum. 8: pl. 156. 1831. Type. Brazil. (lectotype here designated, plate 156 in Fl. Flum. 8). The diagnosis for this name was later published in Fl. Flum.: 353. 1888.

Siphocampylus macranthus Pohl, Pl. Brasiliæ Icon. Descr. 2: 105, pl. 168. 1831. Type. Brazil. Rio de Janeiro: "circa Rio de Janeiro, ad Mathias Ramos, Praja alta, Mangaritiba, Zapativa, etc., May, *Pohl & Schott* "5742 & 5373" (lectotype here designated, W; isolectotypes, W-2 sheets). The diagnosis does not specify collection numbers, but the locality information is identical to that written on the three specimens cited. All three are numbered "5724 & 5373," even though each contains only a single element, which together appear to represent one gathering. On the sheet here designated as the lectotype "*Siphocampylus [sic] macranthus*" is written, apparently in Pohl's hand; the other two sheets have later labels, perhaps written by Zahlbrückner, and are annotated as *Centropogon surinamensis*.

Siphocampylus andropogon (Cavanilles) G. Don, Gen. Syst. 3: 703. 1834.

Siphocampylus spectabilis (Humboldt, Bonpland & Kunth) G. Don, Gen. Syst. 3: 702. 1834.

Siphocampylus surinamensis (Linnaeus) G. Don, Gen. Syst. 3: 702. 1834.

Centropogon surinamensis (Linnaeus) Presl, Prodr. Monogr. Lobel.: 48. 1836.

Lobelia edulis Linnaeus ex Presl, pro syn., Prodr. Monogr. Lobel.: 48. 1836. Although Presl attributed this name to Linnaeus, it was never published by him. I have, however, seen at least one pre-Presl specimen (*Rohr* 87 at BM; collected in the West Indies from 1786-1791) annotated by this name in an unknown, but non-Linnaean, hand.

Centropogon edulis Presl nom. nud., Prodr. Monogr. Lobel.: 48. 1836.

Centropogon bonplandianus (Willdenow ex Roemer & Schultes) Presl, Prodr. Monogr. Lobel.: 48. 1836.

Centropogon laevigatus (Linnaeus f.) A. de Candolle, Prodr. 7:344. 1839.

Lobelia sphaerocarpa Jussieu ex A. de Candolle, pro syn., Prodr. 7: 345. 1839. Published as a synonym of *C. surinamensis*.

Centropogon andropogon (Cavanilles) A. de Candolle, Prodr. 7: 345. 1839.

Centropogon fastuosus Scheidweiler, Allg. Gartenzeitung 9: 396. 1841. Type not designated but said to come from "Mexico." An illustration labeled as "*C. fastuosum*," appeared as plate 16 in Jacques, Ann. Fl. Pomone II. 3: 118. 1845.

Centropogon oblongus Bentham, Plantae Hartwegianae 214. 1845. Type. Colombia.

Cundinamarca: Fusagasugá, 1843, *Hartweg* 1186 (holotype, K, photo USDA-neg. 78205; isotypes, B, BM, F, G-3 sheets, K, NY, P, W-3 sheets).

Centropogon surinamensis (Linnaeus) Presl var. *angustifolius* Zahlbruckner, Ann. K.K. Naturhist. Hofmus. 6: 437. 1891. Type. Venezuela. Carabobo, 600 m, Dec 1843,

Linden 1524 (lectotype here designated, W, photo F-neg. 30968; isolectotypes, BM, G-2 sheets, F, photo F-neg. 58355, K, W-3 sheets).

Centropogon cornutus (Linnaeus) Druce var. *vestita* Pilger, Bot. Jahrb. Engler 30: 200. 1901. Type. Brazil. Matto Grosso: Buriti-Bacher, 7 Sep 1899, Meyer 539 (holotype, B; isotypes, B, W).

Centropogon intermedius Zahlbruckner, Repert. Spec. Nov. Regni Veg. 14: 135. 1915. Type. Colombia. Cauca: Near Tocosá, 1600 m, 30 Dec 1883, Lehmann 3414 (lectotype here designated, G; isolectotypes, BM, LE, US). Because the G specimen is the only sheet I have seen on which Zahlbruckner included "n. sp." after the specific epithet, I have designated that specimen as the lectotype.

Centropogon bonplandianus (Roemer & Schultes) Presl forma *glabrescens* F. Wimmer, Pflanzenreich IV. 276b: 197. 1943. Type. Colombia. Cundinamarca: Fusagasugá, 1750 m, Feb, André 1325 (holotype, K n.v.).

Centropogon puerilis F. Wimmer, Repert. Spec. Nov. Regni Veg. 29: 68. 1931. Type. Peru. Matthews 1670 (holotype, K).

Centropogon cornutus (Linnaeus) Druce var. *laevigatus* (Linneaus filius) F. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13: 405. 1937.

Centropogon cornutus (Linnaeus) Druce forma *leucostomus* F. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13: 405. 1937. Type. Peru. Huánuco: between Monzón and the Río Huallaga, 600-700 m, 1903, Weberbauer 3630 (holotype, B n.v.; isotypes, G, W).

Centropogon cornutus (Linnaeus) Druce var. *intermedius* (Zahlbruckner) F. Wimmer, Pflanzenreich IV. 276b: 197. 1943.

Centropogon cornutus (Linnaeus) Druce forma *ynesae* F. Wimmer, Pflanzenreich IV. 276b: 200. 1943. Type. Brazil. Minas Gerais: Viçosa, 3 km on rd. to São Miguel, 685 m, 21 Dec 1929, Mexia 4142 (holotype, F n.v.; isotypes, GH, W).

Centropogon cornutus (Linnaeus) Druce forma *leucanthus* F. Wimmer, Pflanzenreich IV.

276b: 200. 1943. Type. Trinidad. On rd. to Maracas waterfall, 24 Oct 1928, Broadway 6698 (lectotype here designated, S; isolectotype, BM, MO, US). The S sheet is the only one I have seen that was annotated by Wimmer, although he used the equivalent Latin name "albiflorens."

Centropogon cornutus (Linnaeus) Druce forma *vellozianus* F. Wimmer, Pflanzenreich IV.

276b: 200. 1943. Type. Peru. (holotype, LE). Although specific collection data are unknown, the specimen was probably collected by either Ruiz & Pavón or Matthews. Two labels are affixed to the specimen reading "Herb. Fischer, Fielding," and "Herb. Fischer, Lobelia rosea, Fl. Per."

Centropogon cornutus (Linnaeus) Druce var. *angustifolius* (Zahlbruckner) F. Wimmer, Pflanzenreich IV. 276b: 201. 1943.

Sprawling to scandent, suffrutescent herbs, subshrubs, or vines 1-4 m long, much branched throughout; stems to 2 cm in diam. at base, smooth, glabrous or less often sparsely to moderately hirtellous or soft-puberulent with uni- or multicellular, uniseriate trichomes; latex white or tan. Leaves usually narrowly ovate to lanceolate, occasionally elliptic to oblong, 2.5-4(-6) times longer than wide, 8-17(-21) x 3-6(-8) cm, apex attenuate to acute, base rounded to obtuse, less often cuneate, margins serrulate to crenulate, rarely saliently serrate or doubly serrate, 3-8 callose-tipped teeth per cm; lamina usually rather thin and pliable when fresh, drying characeous or rarely coriaceous, adaxial surface dark green, glabrous, abaxial surface paler, glabrous or rarely sparsely to moderately hirtellous or soft-puberulent; secondary veins 5-9, arcuately ascending; petioles 5-10(-15) mm long. Inflorescence frondose, the flowers solitary in axils of unreduced, or only slightly reduced, apical leaves, the inflorescence either clustered at the apex or lax and elongate, floral internodes 5-30 mm long; pedicels

spreading or ascending at anthesis, usually spreading with a nodding apex in fruit, shorter than the subtending leaves, 25-70(-100) mm long, glabrous or sparsely to moderately hirtellous or puberulent, occasionally persistent, bracteoles normally basal and persistent on the stem after abscission of pedicel, less frequently subbasal, linear to narrowly ligulate, 4-10(-15) mm long. Flowers (55-)65-80 mm long, oriented horizontally; hypanthium hemispheric to subcylindric, rounded or slightly cuneate at base, 5-8 x 6-10 mm, smooth or slightly ribbed, glabrous or rarely sparsely to moderately hirtellous or puberulent, intersepalar nectaries usually prominent, especially laterally, often raised to 2 mm; sepals divaricate or arcuately spreading, occasionally reflexed or appearing so when pressed, very narrowly triangular to narrowly ligulate, 10-20 x 1.5-2(-3) mm, entire or more commonly irregularly serrulate to serrate, glabrous or sparsely puberulent, sinuses planar; corolla pale to bright pink or deep reddish-pink, the lobes usually paler than tube, occasionally whitish to greenish, completely glabrous or sparsely to moderately pubescent, especially along margins of lobes, the tissue thin and usually drying membranaceous; corolla tube (30-)35-50(-55) mm long, 6-9 mm wide at base, narrowing slightly at point of filament attachment and then gradually widening to limb, the throat 10-13(-15) mm wide, little differentiated from lower portion of tube, curving gradually 20-40(-45) $^{\circ}$; dorsal lobe recurved to recoiled, long-falcate, 12-20 mm long, often with attenuate tips, lateral lobes falcate, 6-10 mm long, often with long-attenuate and decurved tips, ventral lobe erect, 6-10 mm long, usually with a long-attenuate and deflexed tip; androecium (50-)55-70 mm long; filament tube (45-)50-65 mm long, subterete or ventrally flattened apically, 1.75-2.5 mm wide when fresh, white or pinkish, glabrous or sparsely long-pilose apically, adnate to corolla (6-)8-11 mm above base, exserted from corolla tube 10-15 mm and usually curving upwards; anther tube often ventrally curved, (6-)7-9 mm long, thecae gray, connectives tan, usually very densely long-pilose in dorsal and ventral connectives and especially towards apex,

occasionally only sparsely pilose or very rarely glabrescent throughout, the trichomes to 5 mm long, white or rarely purplish, antheridial scale triangular or narrowly triangular, (2-)2.5-3.5(-4) mm long; style exserted 2-5 mm from anther tube, the stigma ca. 3 mm wide. Fruit globose to ovoid, to 15 x 20 mm, smooth, nectar chamber not persistent; seeds terete when fresh, ellipsoid or subspheroid, usually smoothly rounded, 0.7-1.0 mm long.

Distribution. *Centropogon cornutus* is the most common and widespread species of neotropical Lobelioideae, and is found from Panama south to Bolivia, in Venezuela and the Guianas, throughout Brazil south to Sao Paulo (although surprisingly scarce in central Amazonia), and into the West Indies as far north as Antigua. Along the Pacific slope of the Andes it is found south as far as Tumbes Department, Peru. Reports of *C. cornutus* from Mexico appear to be unfounded, and are probably based upon old, vague references, such as found in the protologue of *C. fastuosus*. Collections from Costa Rica appear to be based upon cultivated material. A specimen reputedly from Valparaiso, Chile, Rusby 634, is almost certainly mislabeled and probably comes from Bolivia where Rusby is known to have collected this species. *Centropogon cornutus* is often very abundant and weedy. It is usually found growing in open areas, often along rivers, roadsides, or in other disturbed areas. Although normally found from sea level to 500 m, *C. cornutus* ranges as high as 1500 m in parts of the Andes.

Representative specimens examined. COSTA RICA. Puntarenas: Las Cruces Botanical Garden, 1300 m, 11 Jan 1978, Croat 44438 (MO); Las Cruces Botanical Garden, 7 km S of San Vito, perhaps cultivated, 1300 m, 15 Jul 1977, Wilbur et al. 22725 (DUKE).

PANAMA. Bocas del Toro: Fish Creek Hills, vic. of Chiriquí Lagoon, 7 May 1941, *Wedel* 2408 (MO). Canal Zone: Empire to Mandinga, 23 Feb 1923, *Piper* 5441 (BM, NY); nr. Culebra, 50-290 m, 1911, *Pittier* 2221 (F, NY). Coclé: Forest around Limón, 5 hours walk N of Alto Calvario, N of El Copé, 800-1000 m, 10 Oct 1977, *Folsom* 5803 (NY, DUKE-2 sheets); 46 km N from Penonome on rd. to Coclesito, 30 m, 22 Feb 1978, *Hammel* 1694 (DUKE). Colón: rd. to Portobelo, 1 mi SW of Porto Bello, 2 Nov 1975, *Davidson* 3335 (F); btwn. Río Guanche and Río Iguanita, 20 m, 19 Dec 1974, *Dressler* 4898b (DUKE); 1 km S of Portobelo, sea level, 10 Dec 1973, *Gentry & Nee* 8757 (AAU, DUKE-2 sheets, NY). Darién: Vic. of Cana, 500 m, 22 Jun 1959, *Stern et al.* 463 (LE, MO), 23 Jun 1959, *Stern et al.* 486 (MO); trail NW of Cana, 600 m, 28 Jul 1976, *Sullivan* 721 (DUKE). Panamá: Cerro Trinidad, 800-1000 m, 20 Oct 1946, *Allen* 3769 (G, MICH, MO); Capira, nr. settlement of Aguacate, 1 mi N of Cerro Trinidad, 350 m, 4 Feb 1971, *Foster* 2127 (DUKE). San Blas: Río Mandinga nr. village of Mandinga, nr. confluence with Río Cangandi, 3 Mar 1985, *McDade* 833 (DUKE), 4 Mar 1985, *McDade* 874 (DUKE).

LEEWARD ISLANDS. Antigua: Vic. of Saint John, Dec 1902, *Duss* 106 (NY).

WINDWARD ISLANDS. Guadeloupe: Matouba, 1 Nov 1938, *Bailey & Bailey* 168 (NY, US); Camp Jacob, 400-600 m, 1892, *Duss* 2409 (MO, NY, US); Matouba, 600 m, 29 Sep 1938, *Questel* 2089 (US); Matouba, 600 m, 3 Jan 1937, *Stehlé* 1571 (US). Martinique: Fond Saint Denis to Balata, 19-26 May 1950, *Howard* 11701 (MICH); Saint Joseph, 250 m, 24 Jan 1939, *Stehlé* 3654 (US); below Morne Calebasse, 3 km NE of Morne Rouge toward Ajoupa-Bouillon, 500-600 m, 23 Jul 1959, *Webster et al.* 9197 (DUKE, MICH). Grenada: Grand Etang, 21 Oct 1945, *Beard* 1314 (MO, S, UC, US); St. Andrew Parish, vic. of Grand Etang, 450-550 m, 30 Oct- 11 Dec 1957, *Proctor* 17036 (BM); border of Great Pond at Grand Etang, 28 Sep 1949, *Vélez* 3159 (US); St. Andrew,

Grand Etang Forest Reserve, 500 m, 8-9 Aug 1959, Webster et al. 9542 (DUKE, MICH, S).

COLOMBIA. Amazonas: Confluence of ríos Amazonas and Loretoyacu, 12 Apr 1975, Cabrera 3333 (COL). Antioquia: Below the summit nr. Santa Elena, rd. btwn. Medellín and Rio Negro, 2300-2500 m, Sep 1945, Pérez 94 (GH); 60 km S of Medellín on main hwy. to Manizales, 1350 m, 26 Jan 1986, Stein & McDade 3305 (COL, JAUM, MO); 3 km above Salgar on rd. to Las Margaritas, 1450 m, 12 Jan 1986, Stein & McDade 3187 (COL, JAUM, MO). Caldas: 10 km W of Manizales on old rd. to Arauca, 1650 m, 22 Feb 1986, Stein 3559 (COL, JAUM, MO); La Palmita, W of Armenia, 1100-1300 m, 23 Jul 1922, Pennell et al. 8597 (GH, NY, US), 8617 (GH, NY, US). Caquetá: Hwy. btwn. Rio Guayas and km 20 of Puerto Rico-San Vicente del Caguán hwy., 350-400 m, 26 Sep 1975, Cabrera 3507 (F); Rio Caquetá, Araracuara, 15 Jul 1977, Fernández-Pérez 20029 (COL); Río Caqueta, vic. of La Pedrera, Apr 1944, Schultes 5884 (GH, US). Cauca: Gorgona Island, 15 Oct 1924, "St. George Expedition" 586 (F, K, NY), 21 Nov 1924, "St. George Expedition" 710 (F, K, US). Chocó: Río Taparal off San Juan, 30 m, 19 Aug 1962, Robinson 257 (COL, US). Cundinamarca: Btwn. El Salto and El Colegio, 1900-2050 m, 3 Mar 1940, Cuatrecasas 8219 (COL, F, US); 20 km NW of Villavicencio along rd. to Bogotá, 800 m, 3 Jan 1974, Davidse & Llanos 5520 (AAU, MO, NY); rd. from Puerto Lleras to Cachipay, 1600-1700 m, 15 Mar 1986, Stein & Franco 3691 (COL, MO). Huila: Above Vega Larga in Río Fortalecillas valley, 26 km E of Neiva, 20 Jan 1943, Fosberg 19804 (NY, US); around Ladanta, rd. btwn. Garzón and Florencia, 900 m, 18 Feb 1949, Mason 13903 (US), 13913 (GH, MO, UC); above Guadalupe, 1000-1300 m, 20 Mar 1940, Pérez Arbelaez 8401 (NA). Magdalena: Finca Los Arroyitos, 10°56'N, 73°58'W, 1800 m, 7 Oct 1972, Kirkbride 2435 (NY-2 sheets, US); around San Andrés de la Sierra, 1000-1300 m, 1-6 Jun 1906, Pittier 1671 (BM p.p., NY, US), 1637 (US); Campo Alegre, Santa Marta, 450 m, 20 Nov 1898, H. H. Smith 1382 (AA, CM, F, G-2).

sheets, GH, MICH, MO, NY, US). Meta: 28 km beyond Las Acacias on rd. SW of Villavicencio, 500 m, 6 Jan 1986, Stein & McDade 3156 (COL, MO); above Villavicencio, 800 m, 12 Dec 1938, Haught 2455 (DS, NA, US). Putumayo: Margins of Río Guamués, San Antonio de Guamués, 310 m, Cuatrecasas 11174 (US); Mocoa, 750-850 m, 3-7 Dec 1942, Schultes 2090 (GH). Quindío: Quindío Pass, Ariste-Joseph s.n. (US). Santander: Río Suratá valley, btwn. El Jaboncillo and Suratá, 1500-1800 m, 3 Jan 1927, Killip & Smith 16443 (F, GH, NY); along rd. to Tona, 18 km E of Bucaramanga, 1800 m, 5 Mar 1986, Stein & Sierra 3605 (COL, MO, UIS). Tolima: Libano, 1000-1300 m, 26-29 Dec 1917, Pennell 3447 (GH, MO, NY, US); El Limón, 25 km SW of Chaparral on rd. to Rio Blanco, 1000 m, 16 Feb 1986, Stein 3500 (COL, JAUM, MO); 8 km NW of Ibagué on rd. to Juntas, 1350 m, 20 Feb 1986, Stein 3543 (COL, JAUM, MO). Valle: Rio Calima, La Trojita, 5-50 m, 19 Feb-10 Mar 1944, Cuatrecasas 16511 (F, MICH); 2 mi from Bitaco on rd. to Cali, 1500 m, 17 Nov 1963, Hutchison & Idrobo 3042 (F, G, GH, LE, MICH, MO, NY, UC); 5 km N of Darién along rd. to La Guajira, upper Rio Calima, 1550-1700 m, 24 Jan 1986, Stein & McDade 3287 (COL, JAUM, MO). Vaupes: Caño Grande-San José del Guaviare, 240 m, 2 Nov 1939, Cuatrecasas 7379 (US).

VENEZUELA. Amazonas: Cerro de la Neblina, Camp 5 at base of Pico Cardona, 1250 m, 14 Apr 1984, Stein & Gentry 1519 (NY, VEN); Sierra Parima, vic. of Simarawochi, Río Matacuni, 6-7 km W of Brasilian border, 795-830 m, 18 Apr-23 May 1973, Steyermark 107384 (MICH, MO, NY, VEN). Anzoátegui: Dist. Bolívar, Serranía de Turimiquire, Fila El Guácharo above Los Chorros and El Cielo, 1200-1350 m, 25 Nov 1981, Davidse & Gonzalez 19418 (MO); along Río León by Quebrada Danta, tributary to Río Neverí, NE of Bergantín, 500 m, 20 Feb 1945, Steyermark 61015 (F-2 sheets, MICH). Aragua: Btwn. Maracay and Choroni, 1500 m, 12 Dec 1856, Fendler 2010 (GH). Bolívar: Sierra de Lema, 80 km SW of El Dorado, 650 m, 22 Aug 1961,

Steyermark 89374 (MICH, NY-2 sheets, VEN); headwaters of Río Paramichi, E of Cerro Marutani, 400 m, 14 Feb 1981, *Steyermark et al.* 124270 (MO, VEN). **Carabobo:** Río Aguada, 1500 m, 9 Jan 1939, *Alston* 6276 (BM, WIS). **Delta Amacuro:** Sierra Imataca, nr. Guyana border on Río Amacuro, 65-80 m, 7 Nov 1960, *Steyermark* 87360 (F, MICH, NY); Dept. Antonio Diaz, Caño Atoiba, tributary of Boca Araguao, 50 m, 19 Oct 1977, *Steyermark et al.* 114969 (MO, VEN). **Falcón:** Serranía de San Luis, Cerro Galicia, 1500 m, 15 Dec 1977, *Ruiz et al.* 2837 (MY); Sierra de San Luis, vic. of Hotel Prador, 1400-1500 m, 17 Jul 1967, *Steyermark* 99039 (MICH). **Mérida:** Vic. of La Azulita, 900 m, Sep 1952, *Humbert* 26650 (US); btwn. La Azulita and Caño Zancudo, 800 m, 17 Nov 1966, *Bruijn* 1135 (MO, VEN). **Monagas:** Btwn. Guanoco and asphalt lake, 19 Mar 1965, *Ijjasz* 626 (MY, VEN); NE of Alto de Aguacate, btwn. Caripe and Caripito, 600-900 m, 19 Apr 1945, *Steyermark* 62176 (F). **Nueva Esparta:** Btwn. Valle del Espíritu Santo and Cerro Palma Real, 800 m, 22 Sep 1973, *Benítez* 1663 (MY); San Juan Mountain, 750 m, 6 Jul 1903, *Johnston* 88 (F, G, NY, UC, US, W). **Sucre:** Vic. of Cristobal Colon, the balcon, nr. the river, 5 Jan- 22 Feb 1923, *Broadway* 391 (GH-2 sheets, NY-2 sheets, US-2 sheets); Peninsula de Paria, headwaters of Río Cumaná, 15 km NW of Irapa, 800 m, 29 Nov 1979, *Steyermark* 120692 (MO, VEN). **Trujillo:** 74 km NNW of Boconó along rd. to Trujillo, 732 m, 23 Jan 1984, *Luteyn & Pipoly* 9363 (NY); Río Colorado, above Escuque, 12 Jan 1929, *Pittier* 13152 (F, G-2 sheets, MO, NY, UC, US). **Yaracuy:** Cumbre Gamelatal, 4-11 km N of Salom on rd. to Candelaria, 1000-1200 m, 19-20 Jan 1982, *Mori et al.* 14592 (F, NY); rd. btwn. Buenos Aires and Guamales, W part of Sierra de Aroa, 1200-1400 m, 18 Aug 1977, *Steyermark* 114092 (MO, NY).

TRINIDAD. **Trinidad:** Crest of northern Range, Arima Pass, 760 m, 10 Dec 1970, *Breedlove* 19001 (CAS); Maquiripe, 3 Mar 1920, *Britton et al.* 198 (NY, US); Aripo Savannah at Waller Field, 9-23 Feb 1950, *Howard* 10351 (BM, MICH); Arima Valley, Santa Isabel trail, nr. Simla, 250-350 m, 10 Mar 1956, *Smith* 10097 (MICH, NY, S, US).

Tobago: Castara, 30 Sep 1911, *Broadway* 4136 (NY, S); Roxborough-Parlatuvier rd., main ridge, 450-500 m, 4 Apr 1959, *Cowan* 1427 (NY, US); Pigeon Peak Trail, local rd. btwn. Speyside and Charlottville, 15 Mar 1980, *Read & Bell* 8052 (US).

GUYANA. Kaieteur Falls, Potaro River, 23 Oct- 3 Nov 1923, *de la Cruz* 4453 (CM, F, GH, MICH, MO, NY, UC, US); Morawhanna, Barima River, 14 Jan 1920, *Hitchcock* 17508 (GH-2 sheets, NY); Basin of Rupununi River, Isherton, 9-15 Nov 1937, *Smith* 2466 (AA, F, NY, S); NW slopes of Kanuku Mountains, Moku-moku Creek, 150-400 m, 31 Mar- 16 Apr 1938, *Smith* 3493 (GH, NY); Marudi Mountains, Mazoa Hill, nr. Norman Mines camp, 300-400 m, 8 Nov 1982, *Stoffers et al.* 198 (MO); Arabupu, slopes of Mount Roraima, 1250 m, 3 Jan 1928, *Tate* 218 (NY).

SURINAM. Nassau Mountains, Marowijne River, 415 m, 2 Jan 1955, *Cowan & Lindeman* 39084 (MICH, NY); Emmaketen, creek nr. main camp, 400 m, 24 Jul 1959, *Daniels & Jonkēr* 727 (US, WIS); W slopes of Bakhuis mountains, 700-850 m, 20 Feb 1966, *Florschütz & Maas* 2904 (F, U); Cottica River nr. Moengo, 9 Aug 1933, *Lanjouw* 404 (S); Lely Mountains, SW plateaus, 550-710 m, 19 Sep 1975, *Lindeman et al.* 79 (NY); Wilhelmina Mountains, Julianatop, 1000 m, 31 Jul 1963, *Schulz & Elburg* 10240a (GH, UC).

FRENCH GUIANA. Vic. of Cayenne, 4 Jun 1921, *Broadway* 420 (GH, NY), 8 Jul 1921, *Broadway* 708 (GH, NY); along rd. to Cayenne, 14-16 km from Saint Laurent, 20 Dec 1954, *Cowan* 38941 (NY); 40 km from Iracoubo on rd. to Saint Laurent, 19 Jan 1974, *Bescoings & Luu* 20473 (P); Montagne de la Trinité, NE summit, 550 m, 30 Jan 1984, *Granville* 6390 (MO); vic. of Kourou Juin, Jun 1969, *Petitbon* 104 (P).

ECUADOR. Azuay: Pasaje-Santa Isabel-Girón rd., valley of Río Jubones, 600-1600 m, 7 May 1974, *Harling & Andersson* 14459 (AAU, MO). Bolívar: Balsapampa E of Babahoyo, 700 m, Aug 1934, *Rimbach* 605 (F, NA). Carchi: Along Lita-Salinas rd., 1200-2000 m, 21 May 1987, *van der Werff et al.* 9576 (MO). El Oro: Km 19 on rd.

from Pinas to Santa Rosa, 460 m, 7 Oct 1979, *Dodson et al.* 8928 (MO, SEL); km 8 of Saracay-Loja rd., 550 m, 9 May 1985, *Stein & D'Alessandro* 2703 (AAU, CAS, MO, NY, QCA, QCNE, US). Esmeraldas: Quinindé (Rosa Zarate), 21 May 1955, *Asplund* 16447 (B, K, NY, S); Esmeraldas-La Tola hwy., 40 m, 28 Jul 1984, *Dodson et al.* 14589 (MO); San Lorenzo, 23 Jul 1964, *Jativa & Epling* 906 (NY, S). Guayas: Vic. of Naranjito, 30 m, 6-7 Jun 1945, *Camp E-3605* (GH, MICH, NY, US); Teresita, 3 km W of Bucay, 270 m, 5-7 Jul 1923, *Hitchcock* 20501 (F, GH, NY, P, US). Imbabura: Parambas, 540 m, 30 May 1949, *Solis* J2632 (F). Los Ríos: Hacienda Clementina on Río Pita, 28 Mar 1939, *Asplund* 5518 (CAS, G, S, US); Along Río Cristal nr. Montalvo, 70 m, 8-11 Jul 1962, *Jativa & Epling* 41 (MICH, NY, S, UC, US). Manabí: Portoviejo-Pichincha rd., 12 km E of San Plácido, 450 m, 2 May 1985, *Harling & Andersson* 24745 (GB); Bellavista, E of Jipijapa, 600-700 m, 13 Jul 1942, *Haught* 3393 (MICH, NA, NY, US). Napo: Trail Napo to Tena, 400 m, 31 Mar 1935, *Mexia* 7126 (NA, UC, US, W); Misahualli, 28 Mar 1969, *Lugo* 926 (AAU, GB, MO, NY); Río Anzu Valley, km 55 of Puyo-Puerto Napo rd., 550 m, 9 Jun 1985, *Stein* 3034 (AAU, MO, NY, QCA, QCNE, US). Pastaza: Río Curaray, 200 m, 5 Jun 1980, *Brandbyge & Asanza* 31616 (AAU); Río Bobonaza btwn. outlet into Río Pastaza and Chichirota, 350 m, 25 Jun 1980, *Ollgaard et al.* 35372 (AAU). Pichincha: Btwn. Quininde and Santo Domingo de los Colorados, Dec 1952, *Fagerlind & Wibom* 1716 (MO, S-2 sheets); 35 km N of Santo Domingo, vic. of Río Blanco, 250 m, 3 Feb 1974, *Gentry* 9585 (MO, NY).

PERU. Amazonas: Quebrada Huampami, Río Cenepa, 300 m, 8 Jun 1973, *Kayap* 921 (GH, MO); along Quebrada Miraná, km 277 of Marañon rd., above Cascadas de Mayasi, 450-500 m, 8 Sep 1962, *Wurdack* 1908 (F, GH, K, MICH, NY, UC, US). Cuzco: Nr. Pilcopata, Kosñipata Valley, 700 m, 5 Apr 1985, *Stein* 2512 (AAU, CUZ, DUKE, K, MO, US, USM), 7 Apr 1985, *Stein* 2516 (F, MO, NY, US, USM); btwn. Tambomayo and Asunción, 1200 m, 2 Jul 1936, *Vargas* 7147 (UC). Huánuco: Tingo

Tambomayo and Asunción, 1200 m, 2 Jul 1936, *Vargas 7147* (UC). Huánuco: Tingo María, Valley of Río Huallaga, 11-14 Jul 1937, *Belshaw 3064* (DUKE, F, GH, MICH, MO, NY, UC, US); Prov. Pachitea, 14 km from Puerto Inca on carretera marginal, 350 m, 13 Apr 1982, *D. N. Smith 1279* (MO); Cueva de las Pavas, 8 km S of Tingo María, 700 m, 17 Jan 1987, *Stein et al. 3892* (B, MO, U, US, USM). Junín: Rd. from Bajo Pichinaki to Alto Pichinaki, 650-900 m, 10 Mar 1985, *Stein & Todzia 2383* (B, CAS, DUKE, F, K, MO, NY, U, US, USM); 4 km W of Satipo on rd. to Concepción, 700 m, 12 Mar 1985, *Stein & Todzia 2399* (MO-2 sheets, NY, US, USM). Loreto: Yurimaguas, lower Río Huallaga, 135 m, 22 Aug- 9 Sep 1929, *Killip & Smith 27582* (BM, MO, NY, US); Florida, Rio Putumayo at mouth of Río Zubineta, 200 m, Mar-Apr 1931, *Klug 2096* (AA, BM, F, GH, MICH, MO, NY, US); Iquitos, trail to San Juan, 110 m, 7 Feb 1932, *Mexia 6495* (B, BM, CAS, F, G-2 sheets, GH, MO, NY, UC, US, WIS); Pebas, Jul 1929, *Ll. Williams 1790* (F, W). Madre de Dios: Shintuya, 550 m, 12 Oct 1971, *Chávez 851* (MO-2 sheets); Cocha Cashu, oxbow lake of Río Manu btwn. Panagua and Tayakome, 17-24 Aug 1974, *Foster et al. 3410* (DUKE, US). Pasco: Pozuzo, 600 m, 20-22 Jun 1923, *Macbride 4714* (F, GH, NA, NY, US); Río Chuchurras, 360 m, 19 Jun 1982, *D. N. Smith et al. 1977* (MO). San Martín: Tocache Nuevo, nr. Puerto Pizana, 15 Mar 1971, *Schunke 4773* (F, G, GH, MO, NY, US); nr. Tarapoto, 300-400 m, 12 Jul 1950, *Ferreyra 7792* (MICH, MO, US, USM); 2-8 km NE of Tarapoto, 400 m, 19 Jul 1982, *Gentry et al. 37751* (MO); 18 km W of Rioja on rd. to Pedro Ruiz, 820 m, 15 Feb 1985, *Stein & Todzia 2169* (B, F, K, MO, NY, U, US, USM). Tumbes: Prov. Zarumilla, Dist. Matapalo, in quebrada Trapazola nr. Campo Verde, 600-800 m, 21 Dec 1967, *Simpson & Schunke 454* (F, US). Ucayali: Bosque von Humboldt, km 86 on Pucallpa-Tingo María rd., 330 m, 2 Apr 1982, *D. N. Smith 1169* (MO); Boqueron del Padre Abad, 25 km W of Aguaytia on rd. to Tingo María, 500 m, 8 Jan 1987, *Stein et al. 3911* (F, MO, US, USM).

BRAZIL. Amazonas: Nr. mouth of Rio Embira, tributary of Rio Tarauaca, 17 Jun 1933, *Krukoff* 4901 (BM, F, G-2 sheets, GH, MICH, MO, NY, S, UC); Sao Paulo de Olivença nr. Palmares, 11 Sep- 26 Oct 1936, *Krukoff* 8054 (BM, F, G, GH, LE, MICH, MO, NY, S, US); Rio Javari, Palmeiras Army Post, 2 Aug 1978, *Lleras et al.* PI7064 (NY, S). Bahia: Itabuna, Saída to Uruçuca, 15 May 1968, *Belem* 3553 (CM, DUKE, MO, NY); Municipio de Mucuri, nr. bridge over Rio Mucuri on BR 101 rd., 15 Sep 1978, *Mori et al.* 10542 (AAU, NY-2 sheets); km 80 btwn. Betanha and Canavieiras, 13 Jul 1964, *Prance & Silva* 58422 (NY). Ceará: 3 km E of Guaramiranga, 720 m, 22 Mar 1945, *Cutter* 8308 (US); base of Serra do Araripe, 8 Aug 1948, *Duarte* 1390 (GH, NY).

Distrito Federal: Córrego Jeriva, 10 km E of Brasilia, 975 m, 15 Sep 1965, *Irwin et al.* 8347 (CM, DUKE, MICH, MO); Rio Torto, 10 km NE of Brasilia, 975 m, *Irwin et al.* 15661 (AAU, MICH, MO, NY). **Espírito Santo:** Reserva Florestal de Sooretama, 9 Aug 1965, *Belem* 1524 (MICH); Santa Tereza, 22 Nov 1953, *Duarte et al.* 3618 (F). **Goiás:** 25 km S of Caiapônia, 800 m, 1 May 1973, *Anderson* 9583 (DUKE, MO); Chapada dos Veadeiros, 15 km W of Veadeiros, 1000 m, 12 Feb 1966, *Irwin et al.* 12676 (MICH, NY).

Guanabara: Serra do Camorim, 30 May 1961, *Occhioni & Pereira* 5710 (B); Estrada do Sumaré, 28 May 1958, *Pereira et al.* 6698 (B). **Matto Grosso:** Municipio Cuiaba, Parque Aguas Quentes, 17 May 1973, *Hatschbach* 32056 (MICH, MO); Barra do Garças-Xavantina rd., 25 km from Xavantina, 10 Jun 1966, *Hunt* 5918 (MICH, NY, UC).

Minas Gerais: 27 km SE of Coroaci along hwy. MG-109, 350 m, 28 Mar 1976, *Davidse et al.* 11475 (MO); Viçosa, Fazenda de Aguada, 700 m, 26 Sep 1930, *Mexia* 5109 (B, BM, CAS, F, G, GB, GH, MICH, MO, NY, S, UC, US, WIS). **Pará:** Rio Jari, Monte Dourado, Bandeira, 14 Nov 1978, *Cavalcante* 3354 (NY); Lageira, airstrip on Rio Maicuru, 250 m, 17 Jul 1981, *Strudwick et al.* 3076 (MO), 3 Aug 1981, *Strudwick et al.* 3999 (MO). **Pernambuco:** Barreiro, 27 Aug 1954, *Falcao et al.* 842 (GH, MO, NY); Municipio de Bonita, 700 m, 23 Sep 1984, *Mizoguchi & OkaZaki* 2202 (MO); Recife, 20

Aug 1934, *Pickel* 449 (WIS-2 sheets). Rio de Janeiro: Corcovado, Rio de Janeiro, *Gardner* 71/9 (BM-2 sheets, GH-2 sheets, NY); btwn. Teodoro de Oliveira and Nova Friburgo, 800-1000 m, 20 Apr 1952, *Smith et al.* 6688 (MICH, US); Roraima: Serra Tepequem, beside Igarape Paiua, 1000 m, 19 Feb 1969, *Prance et al.* 4560 (DUKE, MO, NY); vic. of Auris, 760-800 m, 6 Feb 1969, *Prance et al.* 9659 (F, NY, S, US). Rondônia: São Lourenço mine, 20 km NW of Rio Madeira, across from Mutumparaná, 14 Jul 1979, *Calderon et al.* 2836 (MO, US); vic. of São Lourenço mines, 27 Nov 1968, *Prance* 8928 (DUKE, MO, NY). São Paulo: SW of Caraguatatuba, sea level, 20 May 1961, *Eiten & Eiten* 2797 (US); Caraguatatuba, Barra do Rio Juqueriqueré, sea level, 2 Jun 1968, *Krapovickas* 14383 (UC, WIS); Ubatuba, Praia do Lázaro, beira da estrada, 1 May 1977, *Ramos et al.* 4797 (F).

BOLIVIA. Beni: Prov. Ballivián, Rurrenbaque, 270 m, 9 Mar 1982, *Beck* 8228 (LPB, MO); Rio Chimane, nr. Ratima, 320 m, 3 Jun 1981, *Davis & Marshall* 1137 (F); Mapiri, 750 m, May 1886, *Rusby* 635 (BM, G, GH, MICH, NY-2 sheets, US); 3 km E of Riberalta on rd. to Guayaramerín, 230 m, 7 Jun 1982, *Solomon* 7967 (MO, NY). Cochabamba: Prov. Chapare, 110 km from Cochabamba on rd. to Villa Tunari, 1600 m, 25 Mar 1984, *Stein* 1454 (DUKE, LPB, MO); Incachaca, San Antonio, 500 m, Jul 1926, *Werderman* 2158 (MO). La Paz: Prov. Murillo, 44 km N of Lago Zongo dam, 1500 m, 19 Dec 1982, *Solomon* 9177 (MO); nr. Yolosa on rd. to Coroico, 1300 m, 9 Mar 1984, *Stein & Solomon* 1420 (LPB, MO), 22 Mar 1984, *Stein et al.* 1450 (LPB, MO). Santa Cruz: Prov. Sara, Río Surutú, Buena Vista, 400 m, 1-26 Apr 1921, *Steinbach* 5578 (F, MO, NY); Prov. Chiquitos, Serrania de Santiago, 2 km E of town of Santiago de Chiquitos, 750-800 m, 19 Jul 1983, *Daly et al.* 2128 (NY).

Vernacular names and local uses. "Crepe coq," Trinidad. "Deer meat" or "Deer food," Tobago. "Gallito Rosado," Caldas, Colombia. "Chepo," Antioquia, Colombia.

"Pacha-tuchto," Putumayo, Colombia. "Gallita de monte," Anzoátegui and Falcon, Venezuela. "Gallito de monte," Venezuela. "Tucuy-yariskú," (flor de tucusito), Venezuela. "Droengoe-droengoe," Surinam; used as a remedy for toothaches. "Pico de loro," Huanuco, Peru; the leaves are boiled and eaten. "Puínayma Gifire," Loreto, Peru. "Bico de papagago," Minas Gerais, Brazil. "Ki'i'mis," Beni, Bolivia; the vapors of cooked leaves are inhaled by children for chest ailments.

Discussion. *Centropogon cornutus* is the most common and widely distributed species in the genus and in many lowland tropical areas it is the only species of *Centropogon* present. It can be easily recognized in fruit as well as flower, and the distinguishing features include: usually narrowly ovate leaves with rounded bases and short petioles; solitary, axillary flowers; long, narrow bracteoles that often remain persistent on the shoot after abscission of the pedicel; long, narrow sepals that are normally divaricately spreading or sometimes reflexed, but never erect; long, stout, gradually curving, pink corollas; well-exserted filament tubes that usually curve upward after exiting the corolla; very densely pilose anther tubes with long (to 5 mm), usually white trichomes; and large, terete seeds. Although several other species in subgen. *Centropogon* have frondose inflorescences with solitary, axillary flowers, none share the combination of long, narrow, spreading sepals, long pink corollas, and densely long-pilose anther tubes. Of the other axillary-flowered species, *C. scabellus* of western Colombia is most similar in the size of flowers and length of sepals. It can be easily distinguished from *C. cornutus*, however, by its scaberulous rather than smooth stems, the elevated position of its bracteoles on the pedicels, and its almost straight rather than gradually curved corollas. Although the both species are found in the northern Cordillera Occidental, *C. scabellus* occurs at higher elevations (1950-2700 m) than does *C. cornutus*.

For such a widespread and common species, *C. cornutus* shows a surprising degree of morphological consistency. The numerous synonyms for this species do not reflect great morphological diversity so much as its wide range and long history of collection. Many early collections were uncritically described as new, starting with Linnaeus who applied three names to this species. Of the 34 names placed in synonymy, 20 are basionyms and another three were published as synonyms. A certain amount of morphological variability does occur within the species, particularly with regard to leaf serration, relative leaf width, sepal attitude, and pubescence. The variation present in these characters is not generally correlated with geography, and those features that do have some geographic consistency are relatively minor compared to the many features that unite this species. Because of this, I prefer not to recognize any of the numerous infraspecific taxa that have been described.

One of the most distinctive variations is the occasional presence of sharply serrate, rather than serrulate, leaf margins. Such margins occur periodically in various parts of the species' range, and are represented by such collections as *Stein & Todzia* 2129 and 2169, and *Klug* 3398 from Peru, *Ducke* 1630 from Brazil, and *Florshütz & Maas* 2904 from Surinam. These serrate, and at times doubly serrate, leaf margins are not simply an environmentally induced phenomenon since plants propagated from seed of *Stein & Todzia* 2169 have maintained their distinctive margins in cultivation. The trait appears to be genetically dominant, as it has been passed on to F1 progeny in crosses with *C. granulosus* and with other more entire-margined collections of *C. cornutus* (Fig. 3, Chapter V).

A few collections have relatively narrow leaves, reaching six rather than the more typical 2.5-4 times as long as wide. This narrow leaf morph was described as *C. cornutus* var. *angustifolius*, and has been collected twice in Carabobo, Venezuela (*Linden* 1524, the type, and *Alston* 6276). In other areas leaves can be almost as narrow, for

instance reaching five times as long as wide in *Stein & McDade 3187* from Antioquia, Colombia. For this reason, I prefer not to separate this leaf morph at the varietal or subspecific level. More collections from Carabobo would be desirable to determine the extent of variation in leaf shape among populations in that region.

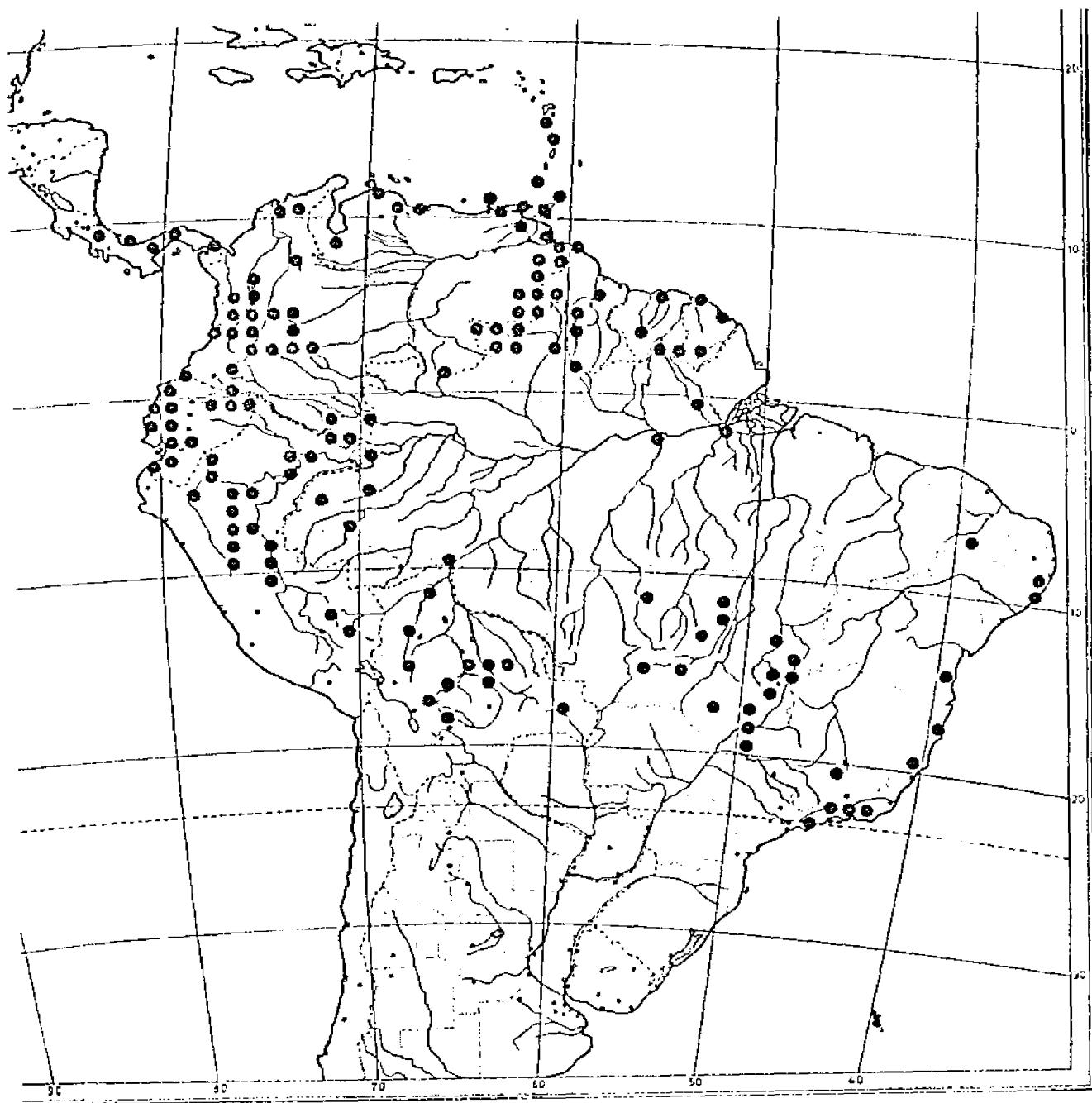
Reflexed sepals are another feature that occurs occasionally in *C. cornutus*. Divaricately spreading sepals, the normal condition in the species, often appear reflexed after being pressed complicating analysis of this feature. *Centropogon puerilis* was described on the basis of plants that combined reflexed sepals and sharply serrate leaf margins. The independent expression of both these characters in many areas, and the relatively few, widely separated, instances when they occur together in the same plants argues against recognition of this taxon. Crossing studies also show this serrate-leaved, reflexed sepal form to be highly interfertile with more normal forms of *C. cornutus*.

While plants in most populations of *C. cornutus* are almost entirely glabrous, certain regions are characterized by a higher degree of pubescence. Most collections from montane Colombia are somewhat pubescent, and the margins of the corolla lobes are often particularly ciliate. This pubescence form has been referred to as *C. bonplandianus*. Although pubescent corolla lobes are a general feature throughout this region, in other respects the plants are identical to those found in other areas. Further, ciliate corolla lobe margins occur occasionally in other regions, such as eastern Peru (e.g., *Gentry et al. 37751*) and Panama (e.g., *Dressler 4898b*). In Matto Grosso, Brazil, several collections (e.g., *Harley & Souza 11052*, and *Ratter et al. 566* and *1886*) are particularly hirsute, with trichomes spread over the entire abaxial leaf surface rather than restricted to the venation. Plants from this region have been described as *C. cornutus* var. *vestitus*.

Although one of the most characteristic features of *C. cornutus* is the long-pilose anther tube, the density and color of those trichomes can vary. While most plants have

very densely pilose anthers, glabrous or only sparsely pilose anther tubes are occasionally found in a number of areas, and Wimmer (1943) applied the name *C. cornutus* var. *laevigatus* to these widely scattered plants. Geographically more consistent is a tendency for the anther trichomes to be purple-pigmented, rather than white, in the West Indies, Trinidad, and parts of Venezuela (Nueva Esparta, Managas, and Sucre).

Fig. 13. Distribution map of *Centropogon cornutus*.



Section Amplifolii

Centropogon Presl subgenus **Centropogon** section **Amplifolii** Zahlbruckner, Ann.

Naturhist. Hofmus. 6: 435. 1891. Type species. *Centropogon amplifolius* Vatke (=*C. macrophyllus*).

Section *Amplifolii*, is a well delimited group of 17 species that ranges from Central America to Bolivia. The flowers are typically borne in terminal, densely bracteate inflorescences. The inflorescences are generally auxotelic, and this is the only group of species in subgen. *Centropogon* that exhibits this condition. Corollas are almost exclusively red or pink, and are thin-textured, moderately to sharply curved forward, and often have a well-differentiated throat. The filament tube in this section is subterete and rather narrow, which contrasts with the ventrally flattened and often much wider filament tubes found in sects. *Campylobotrys* and *Grandes*.

Two major species groups can be recognized within sect. *Amplifolii*, the *C. hirtus* and *C. gamosepalus* groups, and these two groups appear to be connected phylogenetically by the closely related species pair of *C. macrophyllus* and *C. capitatus*. The *C. hirtus* group is characterized by an often dense indument of multicellular trichomes, which are usually present on the adaxial leaf surface (a rarity in subgen. *Centropogon*) as well as the abaxial surface. Another feature uniting this group is the crustose surface excrescences that form when the plants are dried. These excrescences have not been observed in any other group of subgen. *Centropogon*. The *C. hirtus* species group includes *C. congestus*, *C. gesneriiformis*, *C. uncialis*, *C. ventanaensis*, *C. umbrosus* and *C. hirtus*, and ranges from Central America to southern Peru.

The *C. gamosepalus* group includes those members of the section with connate sepals. In addition to this feature they all have very small seeds (0.5-0.6 mm long) and

share a similar corolla morphology. This group includes *C. gamosepalus*, *C. quebradanus*, *C. eurystomus*, *C. roseus*, *C. silvaticus*, *C. aelectrolophos*, *C. undulatus*, *C. escobarae*. The only vining member of sect. *Amplifolii*, *C. aelectrolophos*, is found in this group.

Centropogon alsophilus is rather anomalous in this section given its stout, gradually curving corolla, but it does not fit well into any of the other sections recognized. It is tentatively assigned to this section on the basis of the subterete filament tube, and what appears in cultivation to be an auxotelic inflorescence. Alternatively the affinities of this species may lie with sect. *Centropogon*, as discussed in the treatment of *C. alsophilus*.

Key to Species of Section *Amplifolii*

1. Calyx gamosepalous, sepals fused at least 4 mm.....2
2. Bracts mostly reduced, normally shorter than or equaling the pedicels, usually not obscuring the lower portion of the flower, generally ovate to oblong, rarely obovate; bracteoles very small, less than 1.5 mm long, often not visible in dried material.3
3. Bracts 10-30 mm long; leaf margins denticulate to long-fimbriate with the teeth occasionally exserted 1-6 mm; corollas pinkish-red or deep red, never orangish.11. *C. roseus*.
3. Bracts very reduced, 4-10 mm long; leaf margins crenulate, denticulate, serrulate, or fimbriulate, with the teeth exserted 1 mm or less; corollas reddish or commonly orangish.4

4. Erect herbs; petioles 90-100 mm long; inflorescence erect, a congested, subcorymbose raceme; pedicels 10-20 mm long; anther tube glabrous.....17. *C. escobarae*.
4. Sprawling herbs or vines; petioles 5-25 mm long; inflorescence, pendent or sprawling, racemose but usually lax; pedicels 20-70 mm long; anther tube pilose in dorsal connectives.....5
5. Sprawling herbs; calyx 10-11 mm long, connate ca. 3/4 of length, the upper portion rotate-undulate with broadly triangular or rounded free lobes 3-4 mm long; inflorescence apparently spreading horizontally; pedicels 60-70 mm long; corolla tube 25-27 mm long.
-15. *C. undulatus*.
5. Vines or scandent herbs; calyx 12-20 mm long, completely connate except for short rounded or triangular free lobes 2-3 mm long; inflorescence pendent; pedicel 20-30(-40) mm long; corolla tube 30-33 mm long.....16. *C. aelectrolophos*.
2. Bracts foliaceous, as long as or exceeding length of the subtended pedicels, often obscuring lower portion of flower, mostly obovate or oblanceolate; bracteoles 1-3 mm long, usually visible in dried material.....6
6. Abaxial leaf surface glabrous or sparsely and minutely hirtellous, but if so restricted to major veins, adaxial surface glabrous.....7
7. Leaves very narrow, 6-13 times longer than wide; corolla throat little-expanded, 8-10 mm wide; anther tube densely long-pilose.
-12. *C. silvaticus*.

7. Leaves usually relatively wide, 2-3(-4) times longer than wide; corolla throat moderately to widely expanded, usually 10-15 mm wide; anther tube pilose or glabrous.....10. *C. gamosepalus.*
6. Abaxial leaf surface moderately to densely hirtellous or hirsutulous throughout, adaxial surface glabrous or sparsely pubescent.....8
8. Corolla 30-35 mm long, the throat only moderately expanded, 11-13 mm wide; calyx 13-18 mm long; adaxial leaf surface bullate when fresh, drying wrinkled, glabrous; anther tube densely short-pilose; filament tube exserted from corolla 0-4 mm.
.....13. *C. quebradanus.*
8. Corolla 37-40 mm long, the throat very inflated, 17-21 mm wide; calyx 11-12 mm long; adaxial leaf surface drying smooth, unwrinkled, sparsely appressed-hirtellous; anther tube glabrous; filament tube exserted from corolla 6-10 mm.
.....14. *C. eurystomus.*
1. Calyx with sepals free to base, or rarely slightly fused 1-2 mm.9
9. Plants mostly glabrous although adaxial venation often minutely hirtellous; leaves never drying with crustose surface excrescences; leaves sessile or petiolate.....10
10. Corolla gradually curving 20-30°, the throat not well-differentiated from the lower portion of tube; inflorescence elongating, the bracts mostly oblong; sepals tips often recurved or reflexed; leaves coriaceous when dry.
.....18. *C. alsophilus.*

10. Corolla moderately to abruptly curving, (30-)45-60°, the throat usually well-differentiated from lower portion of tube and often slightly ventricose; inflorescence mostly congested, or rarely elongating, the bracts mostly obovate or oblanceolate; sepals tips erect; leaves mostly chartaceous to membranaceous when dry, rarely coriaceous..... 11
11. Corolla tube 25-30 mm long, pinkish-red, the throat not ventricose, little expanded, 9-10 mm wide; bracts mostly narrow, oblanceolate or spatulate; subterminal inflorescence scars often present; leaves thin, 3° and 4° venation reticulum conspicuous both adaxially and abaxially.
- 3. *C. macrophyllus*.
11. Corolla tube 30-40 mm long, reddish or purplish, throat usually ventricose, abruptly ampliate, 10-12(-15) mm wide; bracts mostly obovate, or occasionally narrower; subterminal inflorescence scars never present; leaves fleshy, 3° and 4° venation reticulum usually not conspicuous adaxially. 2. *C. capitatus*.
9. Plants pubescent, mostly moderately to densely hirtellous to hirsute, rarely glabrescent; leaf and stem surfaces often drying with white crustose excrescences; leaves always petiolate..... 12
12. Corolla gradually curving, less than 30°, the throat usually not well-differentiated from lower portion of tube. 13
13. Corolla 40-45 mm long, 9-12 mm wide at throat; anther tube 6-7 mm long; sepals 8-11 mm long; pedicels well-exceeding subtending bracts.
- 8. *C. gesneriiformis*.

13. Corolla 17-20 mm long, 6-8 mm wide at throat; anther tube 3.5-4.5 mm long; pedicels either exceeding subtending bracts, or lowest flowers subtended by non-reduced leaves and well-exceeded by them.....9. *C. uncialis*.
12. Corolla moderately or abruptly curving, 30-70°, the throat usually well-differentiated from lower portion of tube.....14
14. Medial subtending inflorescence bracts or leaves much exceeding pedicels and flowers; leaves narrowly elliptic, 3.5-5 times as long as wide.....15
15. Flowers solitary in leaf axils; subtended by mostly unreduced leaves 70-300 mm long; pedicels 45-120 mm long; sepals (8-)10-16 mm long; leaves and stem densely hirsute; trichomes to 1.5 mm long.
.....5. *C. hirtus*.
15. Flowers in congested terminal inflorescences; subtended by leaf-like bracts 50-150 mm long; pedicels 25-30 mm long; sepals 7-8 mm long; leaves and stems scabridulous to hirtellous but never densely pubescent; trichomes less than 0.5 mm long.....7. *C. ventanaensis*.
14. Medial inflorescence bracts shorter than or slightly longer than pedicels, but never longer than the entire flower; leaves variously shaped, 2-3.5 times as long as wide.....16
16. Corolla tube 30-35 mm long; androecium length 42-50 mm; anther tube 4.5-6 mm long, usually short-pilose; sepals 6-15(-19) mm long; foliage sparsely to moderately pubescent, the trichomes mostly less than 1 mm long, occasionally glabrescent; petioles 20-40(-60) mm.....6. *C. congestus*.

16. Corolla tube 26-32 mm long; androecium length 36-42 mm long; anther tube 6-7 mm long, glabrous; sepals (4-)6-10 mm long; foliage indument moderately to densely pubescent, the trichomes often 1-1.5 mm long; petioles 10-20(-35) mm.

..... 4. *C. umbrosus*.

2. *Centropogon capitatus* Drake, J. Bot. (Morot) 3: 228. 1889. Type. Ecuador. Loja: "Huacabamba," Poortman 198 (holotype, P n.v., photo F neg. 30940, fragment, W).
Fig. 8A.

Centropogon capitatus forma *hirtus* A. Zahlbruckner, Ann. K. K. Naturhist. Hofmus. 6: 436. 1891. Type. Peru. [Huánuco?]: "Peruvia subandina. In sylvis densis locus subpaludososis," Jul 1829, Poeppig 1093 (holotype, W).

Centropogon capitatus var. *fieldii* F. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13: 406. 1937. Type. Peru. Junín: La Merced, Hacienda Schunke, 1200 m, 27 Aug-1 Sep 1923, Macbride 5662 (holotype, F; isotype, NY).

Centropogon capitatus var. *trichandrus* F. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13: 406. 1937. Type. Peru. Cuzco: Paucartambo, Kosñipata Valley, 800-1000 m, Herrera 9 (holotype, B n.v.).

Erect herbs or subshrubs, 0.5-1.5 m tall, single-stemmed or branching from the base, often succulent; stems entirely glabrous or puberulent to hirsutous above; latex white, tan, or ochre. Leaves oblanceolate to narrowly obovate, (15-)20-35(-45) x 6-15 cm, apex acuminate to acute, base narrowly cuneate to cuneate, margins serrulate, denticulate, or rarely crenulate, 5-7(-12) callose-tipped teeth per cm; lamina fleshy when fresh and often firm and coriaceous, drying coriaceous to chartaceous, adaxial surface dark green, glabrous or very rarely strigose with sparse, appressed trichomes to 1 mm long, abaxial surface paler, glabrous or commonly with the veins minutely puberulent to hirsutous, very rarely moderately hirsute throughout with multicellular trichomes to 0.5 mm long; secondary veins 10-15, diverging from mid-vein at a wide angle, almost straight or moderately arcuate-ascending, raised slightly abaxially but higher order venation generally not conspicuously raised; petioles absent, or to 2 cm long.
Inflorescence an erect, densely bracteate, terminal raceme, often capitate and

subcorymbose, mostly less than 8 cm long, but occasionally elongating to 35 cm, the flowers congested and numerous, usually 7-15 present at one time, the rachis glabrous or frequently hirtellous or minutely sordid puberulent; bracts foliaceous and persistent, often densely appressed-imbricate, entirely assurgent or with the upper portion flared outward, widely to narrowly obovate or spatulate, mostly 3-6(-7) x 2-4(-6) cm, much longer than the subtended pedicels and covering lower portion of flowers, apex usually mucronate, less often obtuse to rounded, base cuneate to narrowly cuneate, margins crenulate, denticulate, or serrulate, occasionally slightly revolute or crisped, when fresh the bracts often much darker than and contrasting with foliage leaves, both surfaces glabrous or rarely sparsely pubescent; pedicels erect at anthesis, remaining erect or recurving apically with age, 15-30(-40) mm long, glabrous or minutely hirtellous, bracteoles basal or sub-basal, mostly subulate and minute (less than 1 mm long), but occasionally filiform to 3 mm long, or very rarely foliaceous and oblanceolate, to 15 x 2.5 mm. Flowers 50-55 mm long; hypanthium hemispheric or subcylindric, basally rounded, 4-6 x 6-9 mm, 5 or 10 ribbed when fresh, glabrous or minutely hirtellous, intersepalar nectaries present; sepals erect, triangular, lanceolate, or ligulate, 10-18(-22) x 2-4(-5) mm, entire or remotely serrulate, glabrous or minutely puberulent, often drying membranaceous with apparent reticulate venation, sinuses acute to rounded, the lobes occasionally basally connate 1-2 mm; corolla bright to deep red or purplish-magenta, less often pinkish, whitish within, the tissue thin, drying chartaceous to membranaceous, glabrous or minutely puberulent; corolla tube often slightly sigmoid, 30-40 mm long, the basal portion cylindric, 15-18 x 5-8 mm, narrowing and re-expanding slightly ca. 4-6 mm above base, the throat abruptly ventricose, (7-)10-12(-15) mm wide, usually with lateral distentions or pouches and a dorsal crest, moderately to sharply curved 45-60°; dorsal lobes recurved to recoiled, 8-12 x 3-4 mm, lateral lobes asymmetrically triangular, 5-8 x 4-5 mm with attenuate, decurved tips, ventral lobe 6-

10 mm with an acute to attenuate, deflexed tip; androecium 45–60 mm long; filament tube 40–55 mm long, when fresh subterete and 1.5–2 mm in diam., white, or purple-rose where exserted, entirely glabrous or short-pilose at summit, adnate to corolla ca. 5–9 mm above base, exserted from corolla tube 4–8 mm; anther tube 5–7 mm long, when fresh often articulating to left from junction with filament tube, thecae gray, connectives white to purplish, completely glabrous or dorsal ones sparsely to moderately short to long-pilose with white, or rarely purple, trichomes, antheridial scale 1.5–2.5 mm long; style exserted 1–3 mm from anther tube, stigma lavender, ca. 3 mm in diam. Fruit spheroid, to 10 × 13 mm, smooth or with prominent ridges and star-shaped in cross-section, the nectar-chamber persistent; seeds irregularly rectangular to elliptic, ca. 0.7 mm long.

Distribution. A locally common understory and light-gap herb with a wide range of habitat tolerances, found in premontane, montane, and cloud forest. *Centropogon capitatus* occurs along the eastern slope of the Andes from Napo Province in central Ecuador south to Puno Department in southern Peru at elevations from 200–2400 m, but mostly between 500 and 1000 m.

Additional specimens examined. ECUADOR. Cañar: N slope of Rio Paute Canyon, across from Campamento Guarumales, 1650–1850 m, 21 May 1985, Stein 2850 (MO, QCA, QCNE, US). Loja: Huancabamba, 2 Oct 1879, André s.n. (K). Morona-Santiago: Taisha, Río Panguienza 5 km NW of military camp, 250–300 m, 21 Jun 1980, Brandbyge & Asanza 32187 (AAU); km 20 on Limón-Macas rd., 700–900 m, 26 Mar 1974, Harling & Andersson 12911 (AAU, GB, K, MO, NY); Pachicutza, km 140 on Loja-Gualaquiza rd., 900–1000 m, 26–27 Apr 1973, Holm-Nielsen et al. 4514 (AAU, K, NY); Río Yunganza, Limón-Méndez rd., 1100 m, 23 Sep 1979, Holm-Nielsen et al.

20389 (AAU), 20414 (AAU); Chiguinda, Andes E of Sigsig, 1400-1800 m, Lehmann 5768 (K-2 sheets); Lojtnant & Molau 14522 (NY, need locality information); km 8 on Limón-Macas rd, 1100 m, 18 May 1985, Stein 2827 (MO, NY, QCA, QCNE, US). Napo: Sinangua, Chuscuyacu, Río Dúe, 13 Jul 1980, Jaramillo & Coello 3070 (AAU, QCA). Pastaza: Centro Oriente, Tiwaeno, Río Tiwaeno, 400-500 m, 11 Aug 1980, Jaramillo 3455 (AAU). Tungurahua: Near El Topo, S side of Río Pastaza between Baños and Mera, 1500 m, 27 May 1944, Prescott & Wiggins 18 (DS). Zamora-Chinchipe: Km 42 on rd. to Zamora, 1400 m, 29 Sep 1961, Dodson & Thien 826 (MICH, MO); nr. Zumbi E of Zamora, 800 m, 20 Apr 1965, Knight 297 (WIS), 25 Feb 1965, Knight 374 (WIS); 1 km off Zamora-Gualaquiza rd. on rd. to Chicaña, 900 m, 16 May 1985, Stein & D'Alessandro 2790 (MO, QCA, US); between Panguintza and Zumbi on Zamora-Gualaquiza rd., 800 m, 16 May 1985, Stein & D'Alessandro 2793 (MO, QCA). Province unknown: Sine loco, Poortman 224(?) (P, perhaps a mis-numbered isotype).

PERU. Amazonas: La Poza, Río Santiago, 180 m, 23 Aug 1979, Asunción 272 (MO), 9 Aug 1979, Huashikat 24 (MO), 21 Aug 1979, Huashikat 112 (MO); 18 km below Montenegro on Mesones-Muro hwy., 700 m, 21 Jan 1964, Hutchison & Wright 3650 (F, MICH, UC, USM); Shillac, N by trail from Pedro Ruiz, 2300 m, 31 Aug-2 Sep 1983, Smith & Vasquez (MO); Río Marañon Valley, km 281 of Olmos-Marañon hwy., 470 m, 20 Feb 1985, Stein & Todzia 2225 (MO, USM); km 296 of Olmos-Marañon hwy., 700 m, 20 Feb 1985, Stein & Todzia 2225a (MO). Ayacucho: E massif of Cordillera Central, Huanhuachayo, 25 km walking distance SW of Hacienda Luisiana and the Río Apurimac, 1580 m, 18 Aug 1968, Dudley 11846 (NA), 23 km SW of Hacienda Luisiana, 1360-1400 m, 19 Aug 1968, Dudley 11873 (F, NA). Cuzco: Atalaya, nr. junction of Río Carbon with Río Alto Madre de Dios, 6-7 Aug 1974, Foster et al. 3055 (F); Marcapata Valley, 1200 m, Herrera 1164 (US), Herrera 1167 (NY); Río Arasa, NE Cuzco, 1050 m, Jan 1943, Sandeman 3658 (K); Asunción, Paucartambo, 24 Jul 1936, Vargas 87 (MO). Huánuco:

Ridge E of Tingo María, 625-1100 m, 30 Oct-19 Feb 1950, *Allard* 22585 (US); Cordillera Azul, 38 km N of Tingo María, 1740 m, 10 Nov 1975, *Davidson* 3463 (MO); Cueva de las Pavas, nr. Tingo María, 700-750 m, 8 Feb 1950, *Ferreyra* 6761 (US); Pachitea, Codo de Pozuzo, trail N towards Río Mashoca, 500 m, 19 Oct 1982, *Foster* 9297 (MO); La Divisora, Tingo María-Pucallpa rd., 1150-1350 m, 29 Mar 1977, *Gentry et al.* 18871 (MO); Carpish, 2400 m, Oct 1945, *Sandeman* 5183 (K); Cueva de las Pavas, 5 km S of Tingo María, 672 m, 29 Jun 1969, *J. Schunke* 3251 (F); Paty Trail, Carpish Hills, 5 km E of tunnel, 2100 m, 15 Jan 1987, *Stein et al.* 3866 (MO, NY, US, USM); Cueva de las Pavas, 8 km S of Tingo María, 700 m, 17 Jan 1987, *Stein et al.* 3891 (MO, US); La Divisora, 40 km E of Tingo María on rd. to Pucallpa, 1600-1700 m, 18 Jan 1987, *Stein et al.* 3900 (MO, USM). Junín: La Merced, 700 m, *Killip & Smith* 23763 (NY, US); Schunke Hacienda above San Ramón, 1400-1700 m, *Killip & Smith* 24665 (NY, US); Río Paucartambo Valley near Perené Bridge, 700 m, 19 Jun 1929 *Killip & Smith* 25285 (NY); nr. Puente Capelo along Río Perené, 700 m, 18 Mar 1976, *Plowman & Kennedy* 5675 (? sheet unmarked); Chanchamayo Valley, 1500 m, May 1929, *C. Schunke* 1603 (F), 1604 (F), 1400 m, 1609 (F); km 6 to 16 on rd from Bajo Pichinaki to Alto Pichinaki, 650-900 m, 10 Mar 1985, *Stein & Todzia* 2832 (MO, US, USM), 13 Mar 1985, *Stein & Todzia* 2401 (AAU, F, K, MO, NY, U, US, USM). Pasco: Puerto La Laguna, Amuesha village on upper Río Palcazu, 320 m, 14 Jun 1983, *Gentry et al.* 41988 (MO); Pichis Trail, Eneñas, 1600-1900 m, 30 Jun-2 Jul 1929, *Killip & Smith* 25745 (NY, US), *Killip & Smith* 25772 (NY, US-2 sheets); Pichis Trail between San Nicolás and Azupizú, 650-900 m, 6 Jul 1929, *Killip & Smith* 26115 (NY, US, W); Pichis Trail, between Azupizú and Santa Rosa, 625 m, 28 Jun-8 Jul 1929, *Killip & Smith* 26141 (NY, US); W side of Cordillera de San Matías, between Iscosacín and summit, 370 m, 22 Jun 1982, *D. N. Smith* 2073 (MO); Palcazu Valley, between Iscosacín and Villa América, 300 m, 22 Apr 1983, *D. N. Smith* 3870 (MO); Palcazu Valley, Río San José in the Río

Chuchurras drainage, 600 m, 12 May 1983, *Smith* 3960 (MO). Puno: Prov. Carabaya, nr. Sangabán, 600-800 m, 18 Oct 1984, *Maas et al.* 6087 (MO); trail from Aricoma Pass to Santo Domingo, 1600 m, 15 Sep 1939, *McCarroll* 19 (MICH). San Martín: Prov. Cáceres, Madre Mía, 760-880 m, 15 Mar 1977, *Boeke* 1272 (AAU, MO, NY); trail Desquite-Cuñunbuqui, en route to Tarapoto, 1000-1200 m, 25 Jul 1950, *Ferreyra* 7981 (US); trail Agua Blanca-Desquite, en route to Tarapoto, 800-900 m, *Ferreyra* 7978 (US); nr. Moyobamba, between Moyobamba and Tarapoto, 600-700 m, 18 Dec 1971, *Ferreyra* 17865 (USM); 12 km W of Tocache Nuevo of Carretera Marginal, 500-700 m, 12 Mar 1979, *Gentry et al.* 25584 (MO); km 15 on rd. from Tarapoto to Yurimaguas, 760-790 m, 9 Mar 1976, *Kennedy* 3547 (DUKE); Tarapoto, Alto Puca, 12-25 May 1987, *Montes* 17 (F); Palo Blaco, above Río Tocache, 500-550 m, 29 Jun 1978, *Plowman & Schunke* 7453 (F); 15 km SE of Tocache Nuevo on rd. to Tingo María, 500 m, 11 Dec 1981, *Plowman & Rury* (F, USM); E of Nuevo Progresso, Uchiza Dist., 500 m, 17 Jun 1969, *J. Schunke* 3145 (F-2 sheets); Fundo La Campiña, 2 km below Tocache, 400m, 7 Sep 1969, *J. Schunke* 3400 (F, US); Fundo Porvenir, Tocache Dist., 3 Sep 1970, *J. Schunke* 4331 (F, MICH, US); Santa Rosa de Mishollo, 4 km from Puerto Pizana on the Rio Huallaga, 14 May 1971, *J. Schunke* 4892 (F, MO, US, WIS); NE of Bambamarca, Tocache Nuevo Dist., 500-600 m, 15 Nov 1972, *J. Schunke* 5530 (NY); Quebrada Luis Sálas, 5 km N of Puerto Pizana, 350-370 m, 1 Aug 1973, *J. Schunke* 6590 (GH, MO); Cerro de Palo Blanco, left margin of Río Tocache, 600-700 m, 9 Jul 1974, *J. Schunke* 7268 (GH, MO); San Juan de Pacaizapa, km 72 on Tarapoto-Moyobamba rd., 1000-1050 m, 8 Jun 1977, *J. Schunke* 9641 (MO); nr. Tarapoto, 1855-1856, *Spruce* 4132 (K, W); 50 km SE of Moyobamba on rd. to Tarapoto, 1150 m, 10 Feb 1985, *Stein & Todzia* 2132 (AAU, F, K, MO, NY, US, USM), 14 Feb 1985, *Stein & Todzia* 2165 (MO, USM); Quebrada Ahuashyaco, 14 km NE of Tarapoto on rd. to Yurimagua, 800 m, 11 Feb 1985, *Stein & Todzia* 2133 (MO, USM); Cerro de Escaler, 1300 m, Jan 1903, *Ule* 6786 (G, K); San

Roque, 1350-1500 m, Jan-Feb 1930, Williams 7032 (F). Ucayali: Boquerón Padre Abad, 400 m, 16 May 1969, J. Schunke 3044 (F, NY), 20 May, 1969, J. Schunke 3069 (G, NY-2 sheets, US). Province unknown: without locality, Jul 1854, Lechler 2163 (K).

Discussion. *Centropogon capitatus* is a wide-ranging species of a variety of elevations and habitat types. This diversity of elevations and habitats, is reflected in a complex pattern of morphological variation, which does not, however, correlate with geography. The species is best characterized by the combination of: an erect, semi-succulent habit; the rather large, obovate leaves, which are generally fleshy; the erect, mostly compact inflorescences with densely imbricate, usually obovate bracts, which are typically much darker than the foliage leaves and often form a distinctive "head"; and the thin-textured, abruptly curved corolla with a ventricose throat.

A few morphological forms deserve mention although I do not consider them worthy of formal taxonomic rank. *Centropogon capitatus* forma *hirtus* was described by Zahlbruckner based on a specimen collected by Poeppig, probably in Huánuco Department of Peru. The type specimen differs from the other sheets of Poeppig 1093 (which are all *C. amplifolius*) in its dense abaxial pubescence and the moderately pubescent adaxial surface. In these features it resembles *C. umbrosus* and its allies, but the dense, capitate inflorescence and abruptly curved corolla leave little doubt about the specific placement of this specimen. I have recollected this pubescent form of *C. capitatus* in cloud forests in Huánuco Department at the Carpish Hills and at La Divisora in the Cordillera Azul (Stein et al. 3891 and 3900). Both of these localities are at relatively high altitudes for *C. capitatus* (2400 m and 1700 m, respectively), suggesting that it may represent a high elevation phase of the species. Other collections from La Divisora, agree with my collection in overall morphology but lack the dense pubescence. Until additional information is available about the distribution and extent of variability

in this pubescent form, I consider it to be a local variant, perhaps a result of introgression with pubescent sympatric species, such as *C. hirtus* or *C. lasiodorus* (at Carpish) or *C. umbratus* (at La Divisora).

Another rather distinctive phase of *C. capitatus* occurs in San Martín Department, where a number of collections have elongate, racemose inflorescences and purplish to magenta corollas rather than short-capitate inflorescences and reddish corollas (e.g., Stein & Todzia 2132 and Schunke 9641). Again, however, there is considerable gradation in inflorescence length and corolla color, and these populations should probably not be formally recognized.

A third morphological type is distinguished by the extreme development of the inflorescence bracts, which are closely appressed and imbricate forming a large head-like inflorescence. This structure occurs in several central and southern Peruvian collections including Gentry et al. 18871, Killip & Smith 25745 & 25772, and Vargas 87. This same type of inflorescence occasionally occurs in *C. gamosepalus*, as in the type specimen of *C. grandicephala*. Because this inflorescence type appears to have evolved independently several times within *C. capitatus* as well as within *C. gamosepalus*, it is probably best treated as a part of the normal variation pattern in the species.

Centropogon capitatus is closely related to *C. macrophyllus*, as discussed under that species. It is most easily differentiated from *C. macrophyllus* by the fleshier leaves in which the venation reticulum is not clearly visible and raised abaxially and by the wider, obovate bracts. Corolla color of *C. capitatus* is generally red rather than pink as in typical *C. macrophyllus*. Extensive fieldwork in central Peru has confirmed to me that the two species are clearly distinct. They occasionally occur sympatrically as well. A few intermediate collections, such as Schunke 3145 and 4331, may be the result of hybridization between these two species.

Centropogon capitatus also appears closely related to *C. gamosepalus* from which it differs principally in having free rather than connate sepal lobes. This relationship, and the possibility that *C. gamosepalus* may have been derived directly from *C. capitatus*, are discussed under that species.

Vernacular names and local uses. According to *Montes* 17, in San Martín Department, Peru the whole plant is cooked and used for baths. It is said to make children tranquil and works to cure "saladeras." The "corazon" (the inflorescence) is cooked and the infusion drunk by those that suffer from epilepsy. *McCarroll* 19 reports that in Puno Department, Peru the plant is used as a kidney remedy.

3. *Centropogon macrophyllus* (G. Don) F. Wimmer, Notizbl. Königl. Bot. Gart. Berlin
10: 733. 1929.

Siphocampylus macrophyllus G. Don, Gen. Syst. 3: 704. 1834. Type. Peru. Ruiz & Pavón s.n. (lectotype here designated, LE; isolectotypes, CGE n.v., MA n.v., photo F-neg. 2944).

Lobelia macrophylla (G. Don) Presl, Prodr. monogr. Lobel. 39. 1836.

Centropogon amplifolius Vatke, Linnaea 38: 716. 1874. Type. Peru. "Peruvia subandina," Poeppig s.n. (lectotype here designated, B).

Centropogon macrophyllus (G. Don) F. Wimmer forma *minoratus* F. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13: 419. 1937. Type. Peru. Junín: Chanchamayo Valley, 1200 m, Schunke 1778 (holotype, F n.v., photo DUKE).

Erect, suffrutescent herbs 0.5-1.5(-2) m tall, branching from base; stems hirtellous to minutely hirtellous, often with conspicuous scars from old subterminal, auxotelic inflorescences; latex white oxidizing yellowish-brown. Leaves oblanceolate, rarely narrowly obovate or elliptic, 15-30(-42) x 5-10(-13) cm, apex attenuate to acuminate, base narrowly cuneate to decurrent, margins serrulate to irregularly serrate, 4-7 callose-tipped teeth per cm; lamina very thin when fresh, drying chartaceous to membranaceous, adaxial surface glabrous or very sparsely pubescent with appressed, translucent trichomes to 0.5 mm long, dark green with a visible venation reticulum formed by the 2° to 4° veins (apparent both in fresh and dried material), abaxial surface paler, the venation well-raised and reticulum highly visible, the veins hirtellous; secondary veins 10-14, rather straight and widely ascending; petioles absent, or to 2 cm long and hirtellous abaxially. Inflorescence an erect, bracteate, terminal, subcorymbose raceme, normally less than 4 cm long, rarely elongating to 7 cm, the flowers congested and numerous, often 15 or more, the rachis densely hirtellous; bracts persistent,

oblanceolate to narrowly oblanceolate or spatulate, 25-40(-50) x 2-8(-10) mm, equalling or exceeding the subtended pedicels in length, apex acute to obtuse, margins serrulate, adaxial surface glabrescent to hirtellous, abaxial surface hirtellous; pedicels erect at anthesis, arcuately drooping with age, 20-35 mm long, hirtellous, occasionally persistent, bracteoles basal to sub-basal, subulate to linear, minute to 1.5 mm long. Flowers 45-50 mm long; hypanthium hemispheric to subcylindric, basally truncate, 4-5 x 4-7 mm, prominently 10-ribbed when fresh, minutely hirtellous or rarely glabrescent, intersepalar nectaries prominent, to 1.5 mm in diam.; sepals erect, narrowly triangular to ligulate, 8-15(-18) x 2-4 mm, entire or remotely serrulate, minutely hirtellous or glabrescent, thin-textured with prominent venation, the sinuses acute; corolla pink to rose-pink, whitish within throat and often on lower lobes, the tissue thin, densely and minutely hirtellous; corolla tube 25-30 mm long, lower portion of tube cylindric, straight or slightly angled back, 15-19 x 4-6 mm, often narrowing and re-expanding slightly 3-5 mm above base, the throat slightly ampliate, to 9-10 mm wide, with lateral distentions or pouches, moderately curved (35-)45°; dorsal lobes slightly spreading, little-recurved, ca. 9 x 3 mm, lateral lobes asymmetrically triangular, 5-7 mm long, with decurved, often caudate tips, ventral lobe 6-7 mm long with an acute to acuminate, deflexed tip; androecium (35-)40-45 mm long; filament tube (30-)35-40 mm long, subterete and ca. 1.5 mm in diam. when fresh, white or rose where exserted, sparsely to moderately short-pilose at summit with white trichomes, adnate to corolla ca. 5 mm above base, exserted from corolla tube 2-6 mm; anther tube 5-6 mm long, thecae dark gray, connectives purplish, the dorsal ones short-pilose with scattered purple trichomes, antheridial scale 1.5-2 mm long; style exserted 1-3 mm from anther tube, stigma purplish, 2-3 mm in diam. Fruit spheroid or ovoid, to 8 x 15 mm, prominently 10-ridged when fresh and star-shaped in cross-section, the nectar chamber persistent; seeds elliptic, ca. 0.6 mm long.

Distribution. An infrequent understory herb of subandean to cloud forests along the eastern slope of the Andes. Known from southern San Martín Department in Peru to northern Bolivia at elevations of 800-2100 m.

Additional specimens examined. PERU. Cuzco: Valle de Santa Ana, above Quillabamba, 1750 m, 20 Jan 1975, *Plowman & Davis* 4804 (GH). Huánuco: ridge E of Tingo María, 625-1100 m, 30 Oct 1949-19 Feb 1950, *Allard* 21945 (US), *Allard* 22321 (F); Cordillera Azul, 43 km E of Tingo María on rd. to Pucallpa, 1750 m, 21 Nov 1979, *Davidson & Jones* 9441 (MICH, MO, NY); La Divisora, divide between Tingo María and Aguaytia, 1500-1600 m, 3 Jun 1983, *Gentry et al.* 41454 (MO); Cuchero, 1829, *Poeppig* 1093 (W-4 sheets); Paty trail, Carpish Hills 5 km E of tunnel, 2100 m, 15 Jan 1987, *Stein et al.* 3869 (AAU, F, MO, NY, US, USM); La Divisora, 40 km E of Tingo María on rd. to Pucallpa, 1600-1700 m, 18 Jan 1987, *Stein et al.* 3896 (MO, NY, US). Junín: 40 km below Palca on rd. between Tarma and La Merced, 28 Sep 1943, *Evinger* 533 (NY, US-2 sheets); Prov. Chanchamayo, Pampatigre above Santa Ana, 1500 m, 14 Oct 1982, *Fernández et al.* 119 (MO, USM); E of Quimiri bridge, nr. La Merced, 800-1300 m, 1-3 Jun 1929, *Killip & Smith* 23836 (NY, US, W); Rio Rondayacu, 45 km from San Ramón, 1880 m, 15 Oct 1982, *Smith et al.* 2620 (MO); Rio Tulumayo Valley nr. Vitoc, trail above Chilpes, 1700 m, 15 Mar 1985, *Stein & Todzia* 2435 (MO); Prov. Tarma, Agua Dulce, 1800 m, 7 Mar 1948, *Woytkowski sub Goodspeed* 35424 (F, UC p.p.). Pasco: Pichis trail, Yapas, 1350-1600 m, 28 Jun 1929, *Killip & Smith* 25576 (NY, US); Pichis trail, Eneñas, 1600-1900 m, 30 Jun-2 Jul 1929, *Killip & Smith* 25726 (NY, US). Ucayali: Between La Divisora and El Boqueron, on rd. to Pucallpa, 840 m, 27 Mar 1976, *Plowman & Kennedy* 5765 (GH); La Divisora, 1500-1600 m, 6 Feb 1978, *Schunke* 9857 (MO-2 sheets). Department unknown: "Peruvia subandina", *Poeppig s.n.* (P, perhaps an isolectotype of *C. amplifolius*); *Warscewicz* 10 (B, syntype of *C. amplifolius*).

BOLIVIA. Department unknown: Santa Rosa, 2000 m, 4 Apr 1892, Kuntze s.n.
(NY, W).

Typification. The type of this species is a Ruiz and Pavón specimen seen by G. Don in the Lambert Herbarium. After Lamberts' death his herbarium was sold and the specimens were widely scattered among other collections. Of the two Ruiz and Pavón specimens of this taxon that I have seen (an LE sheet and the photo of the MA sheet), only the LE sheet bears an annotation in G. Don's hand of "Siph. macrophyllus." An additional presumed duplicate is cited by Wimmer (1943) at CGE, but he notes that this specimen bears the annotation "*Lobelia rosea*." Since the LE sheet is the only specimen known to have been both seen and annotated by G. Don, I am therefore designating it as the lectotype.

Discussion. *Centropogon macrophyllus* is a name that has been broadly interpreted and applied to a variety of taxa in sect. *Amplifolii*. Indeed, the type species for the has long been recognized correctly as a synonym of *C. macrophyllus*. As defined here however, *C. macrophyllus* is circumscribed rather narrowly and is restricted to the eastern Andean slopes from central Peru to northern Bolivia. *Centropogon macrophyllus* is morphologically transitional species between *C. capitatus*, with which it shares features of the calyx, leaves, and pubescence, and *C. umbrosus*, to which it is similar in inflorescence structure and corolla morphology and color.

Centropogon macrophyllus has often been confused with the more wide-ranging *C. capitatus*, as evidenced by the recent treatment (Jeppesen, 1981) of that species as a synonym of *C. macrophyllus*. In central Peru these two species occur sympatrically, and inclusion of *C. capitatus* within *C. macrophyllus* is untenable. A series of morphological features distinguishes these two species, but due to the highly variable nature of

C. capitatus some overlap does occur. One of the most important features distinguishing *C. macrophyllus* is the thin leaf texture so that when dry the venation reticulum is conspicuous on both the upper and lower leaf surfaces. All orders of veins, from 1° through 4°, are apparent and on the abaxial surface these are mostly raised with respect to the surface of the aereoles. In contrast, leaves of *C. capitatus* are generally fleshy with only the major veins (2° and some 3°) readily apparent when dry. The spatulate to oblanceolate inflorescence bracts of *C. macrophyllus* are in general much narrower than the typically obovate bracts of *C. capitatus* resulting in a much more open inflorescence in which the lower portion of the flowers is not obscured by bracts. This distinction is particularly apparent in central Peru where the two species are sympatric. Elsewhere the bracts on certain specimens of *C. capitatus* may approach or overlap those of *C. macrophyllus* in shape and width. Subterminal inflorescence scars are commonly found in *C. macrophyllus* indicating that auxotelic inflorescences occur frequently; this condition, however, has not been observed in *C. capitatus*. Differences in corolla color between the two species facilitates recognition in the field. In *C. macrophyllus* the flowers are consistently pink to rose-pink, whereas in *C. macrophyllus* they are somewhat more variable, but mostly reddish. The corolla of *C. macrophyllus* is narrower (9-10 mm wide at the throat) and typically less curved than in *C. capitatus* (10-12(-15) mm wide). Furthermore, *C. macrophyllus* usually occurs at higher elevations than *C. capitatus*. Specimens intermediate between these two species, such as Schunke 4331, are sometimes encountered, something that is not unexpected given the close relationship, occasional geographic overlap, and apparent ease of hybridization in subgen. *Centropogon*.

As mentioned above, *C. macrophyllus* also shares certain features with *C. umbrosus*, such as the predominantly pink corolla color, narrow, only moderately curved corolla, prominent intersepalar nectaries, and frequent subterminal inflorescence

scars. It differs from *C. umbrosus* principally in lacking the dense pubescence and long trichomes that characterize that rather variable species.

4. *Centropogon umbrosus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 19: 251. 1924.

Type. Peru. Ayacucho: Prov. La Mar, between Tambo and the Apurimac, below Yanamonte, 2600-2700 m, 1 Jun 1910, *Weberbauer 5616* (lectotype here designated, B-123/84, photo, B-neg. 3239A; isolectotypes, B, F-2 sheets, GH, US, W).

Centropogon caninus F. Wimmer, Notizbl. Königl. Bot. Gart. Berlin 10: 734. 1929. Type. Peru. Junin: between Tarma and Chanchamayo, *Raimondi 2849* (holotype, B n.v., perhaps destroyed during World War II, fragment of holotype, W).

Centropogon gesnerioides Gleason var. *zelans* F. Wimmer, Notizbl. Königl. Bot. Gart. Berlin 10: 734. 1929. Type. Peru. *Raimondi 2610* (holotype, B n.v., perhaps destroyed during World War II).

Centropogon gesnerioides Gleason var. *viperinus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 6. 1935. Type. Peru. Junin: Huacapistana, 1800-2400 m, 5-8 Jun 1929, *Killip & Smith 24096* (holotype, W; isotypes, NY, US).

Erect shrubs 0.5-2(-2.5) m tall, much branched; stems hirsute to hirsutulous, densely so towards apex, with uniseriate, multicellular trichomes to 1.5 mm long, often with conspicuous scars on stems from old inflorescences; latex white oxidizing yellowish. Leaves mostly elliptic, less often lanceolate or oblanceolate, 2.5-3.5 times longer than wide, (10-)15-30(-40) x 5-10(-12) cm wide, apex acuminate to attenuate, base narrowly cuneate, margins serrulate to denticulate, often densely so with 5-10 callose-tipped teeth per cm, these occasionally ciliolate; lamina thin and chartaceous when fresh, generally velutinous to the touch, drying chartaceous and often with numerous, small, white, crustose excrescences on the surface, adaxial surface pale to dark green, sparsely to moderately hirsutulous, the trichomes often appressed, 0.25-1(-1.5) mm long, abaxial surface pale green, moderately to densely hirsute to hirsutulous, especially along veins,

with spreading trichomes 0.5-1.5 mm long; secondary veins 10-16, mostly straight; petioles 10-20(-35) mm, pubescent on both surfaces, or absent. Inflorescence an erect, bracteate, auxotelic, terminal raceme, mostly less than 4 cm long, the flowers numerous and congested, often 8 or more present at one time, the rachis densely hirsutulous with tawny or silvery trichomes; bracts variable in size and shape, most commonly narrowly elliptic to narrowly oblanceolate and 25-35 x 4-10 mm, the lowermost often considerably larger and resembling normal leaves, the margins serrulate to denticulate, both surfaces with pubescence as on leaves; pedicels erect in bud and at anthesis, arching to pendent with age, 20-35(-50) mm long, normally about the same length as subtending bracts, moderately to densely hirtellous to hirsutulous, bracteoles basal to sub-basal, linear, 1-5(-7) mm long. Flowers 40-50 mm long; hypanthium hemispheric, 4-5 x 5-7 mm, prominently 10-ribbed, moderately to densely hirtellous to hirsutulous except for glabrescent surface of prominent intersepalar nectaries; sepals erect, narrowly triangular, (4-)6-10 x 2-3 mm, serrulate, moderately to densely hirtellous to hirsutulous, sinuses acute to rounded; corolla generally concolorous and pink to pinkish-red, or the lower lobes and inside throat somewhat paler, moderately to densely spreading hirtellous to hirsutulous with trichomes to 0.5-1 mm long, the lobes often ciliolate; corolla tube usually slightly sigmoid, 26-32 mm long, 5-7 mm wide at base, the lower portion of tube cylindric and narrowing to 3.5-5 mm wide before gradually re-expanding, or often remaining narrow to base of throat, the throat little ampliate, 6-9 mm wide, curved (30-)45-60°; dorsal lobes spreading to recurved, 8-11 mm long, lateral lobes 6-8 mm long with acute, decurved tips, ventral lobe 6-7 mm long with an acute, deflexed tip; androecium 36-43 mm long; filament tube 29-36 mm long, sub-terete when fresh, white except rose-purple where exserted, glabrous throughout, adnate to corolla 4-5 mm above base, exserted from corolla tube 5-8 mm; anther tube 6-7 mm long, thecae dark gray, connectives rose-purple, completely glabrous, antheridial scale ca. 2 mm long; style

exserted from anther tube 1-3 mm, stigma 2-3 mm in diam. Fruit spheroid to ovoid, to 9 x 14 mm, with 10 prominent, verrucose ribs, nectar chamber persistent; seeds oblong to suborbicular, 0.6-0.7 mm long.

Distribution. A locally common shrub of montane and cloud forests from Huánuco Department in central Peru to Puno Department in southern Peru, at 1000-3000 m.

Additional specimens examined: PERU. Cuzco: Vilcabamba District, trail Yupanqui to Río Apurímac, between Rumichurco and Alcobamba, 3000 m, 4 Jul 1981, *Davis et al.* 1241 (F-2 sheets, MO); Valle del Pilcopata, rd. from Patria to Pillahuata, 2000 m, 13 Dec 1983, *Foster & Wachter* 7467 (MO); rd. from Pillahuata to Patria, 2000 m, 4 Feb 1975, *Plowman & Davis* 4965 (F, GH); between Santa Isabel and Mistiana, Kosñipata Valley, 950 m, 23-31 Jul 1948, *Scolnik* 920 (MICH), *Scolnik* 921 (MICH); km 142 of Kosñipata rd., 14 km below Pillahuata, 2000 m, 5 Apr 1985, *Stein* 2510 (AAU, CUZ, F, K, MO, NY, US, USM); Paucartambo Province, between Tambomayo and Asunción, 1200-1500 m, Jul 1930, *Vargas* 293 (CUZ, F); Prov. Quispicanchis, between Tio and Murayaca, 1900 m, Jan 1943, *Vargas* 3157 (MICH); Paucartambo Province, Sapansachayocc, 1200 m, 7 Aug 1951, *Vargas* 10251 (CUZ, MICH); Suecia, 1900 m, 25 Dec 1952, *Woytkowski* 169 (USM); Paucartambo Province, Callanga, 1500 m, 1 Mar 1953, *Woytkowski* 498 (USM), 3 Mar 1953, *Woytkowski* 526 (USM). Huánuco: W of Divisora, 1400 m, 26 Jul 1940, *Asplund* 12512 (S, US); nr. Tingo María, between Huánuco and Pucallpa, 600-700 m, 10 Feb 1950, *Ferreyra* 6831 (F); La Divisora, Cordillera Azul, 1620-1760 m, 10 Aug 1980, *Gentry et al.* 29568 (MO), 1500-1600, 3 Jun 1983, *Gentry et al.* 41447 (MO); La Divisora, 21.8 km E of the Río Tulumayo, 1550 m, 27 Dec 1981, *Plowman & Schunke* 11704 (F, GB); Muña, 2100 m, 23 May-4 Jun 1923,

Macbride 3982 (S). Junín: Chuquishuinca, 2 km above Huacapistana, 2000-2200 m, 24 Jan 1946, *Ferreyra* 430 (MO, USM); Valle de Vitoc, 2 Nov 1863, *Isern* 2566 (F p.p.); above Huacapistana nr. Chusquichunca[?], 1927, *Juzepczuk* 10323[?] (LE, MO); Carpapata, above Huacapistana, 2700-3200 m, 7 Jun 1929, *Killip & Smith* 24470 (F, NY, US); Vitoc, 27 Dec 1878, *Martinet* 1583 (P); Huacapistana, 1700 m, Oct 1943, *Sandeman* 4449 (K), 2100 m, *Sandeman s.n.* (K); Fondo Romero, Pampatigre, above Santa Ana, SE of La Merced, 1500-1700 m, 7 Mar 1985, *Stein & Todzia* 2332 (AAU, F, MO, NY, US, USM); 59 km W of Satipo on rd. to Concepción, 2300 m, 15 Mar 1985, *Stein & Todzia* 2412 (F, MO, NY, US, USM). Pasco: Cordillera Yanachaga, new rd. in construction from Oxapampa to Villa Rica, 7-9 km E of main rd., 2100-2500 m, 1 Mar 1982, *Gentry & Smith* 35837 (MO); Cordillera Yanachaga, E of Oxapampa, lumber rd. to Chacas microwave station, 2040-2110 m, 2 Mar 1982, *Gentry & Smith* 35905 (MO); Chontabamba Valley, 2-8 km W of Oxapampa, 1800-1850 m, 2 Feb 1983, *Gentry et al.* 39906 (MO); Pichis trail, Eneñas, 1600-1900 m, 30 Jun-2 Jul 1929, *Killip & Smith* 25766 (NY, US); Oxapampa, 1600 m, Aug 1944, *Soukup* 2384 (US); Quillasú, 1700 m, Aug 1947, *Soukup* 3306 (US). Puno: Ollachea to San Gabon, 1000-2000 m, 17-24 Jul 1978, *Dillon et al.* 1136 (MO). Ucayali: Divisora between Tingo María and Pucallpa, 1500-1600 m, 7 Aug 1947, *Ferreyra* 2228 (F, MICH, US, US), 21 Jul 1948, *Ferreyra* 4303 (US), 1400-1500 m, 18 Aug 1965, *Ferreyra* 16430 (MO, USM); Río Chino W of Restaurant Acapulco, 1000-1100 m, 6 Jun 1976, *Schunke* 9178 (MO).

Vernacular names. "Pico de Loro," Ucayali Department, Peru.

Discussion. *Centropogon umbrosus* is closely related to *C. hirtus*, as discussed in more detail under that species. It can be distinguished from that species primarily by the congested, racemose inflorescence, shorter pedicels, shorter sepals, generally smaller

flowers, and relatively wider leaves, which often have denser marginal serrulations. Morphologically it resembles certain populations of *C. congestus* from Colombia, which, however, tend to have tightly imbricate, rather than loose inflorescence bracts, shorter (4.5-6 vs. 6-7 mm) and pubescent anther tubes, and sparser foliar indument.

Centropogon umbrosus is highly variable with regard to density of indument, length of trichomes, and the shape and width of the bracts. Although collections from certain regions within its geographical range exhibit subtle but consistent differences, those morphological features involved intergrade extensively. Among the most distinctive of the morphological forms are collections from the Cordillera Azul at the northern limit of the species range. These have somewhat longer, yet often sparser, trichomes, and very narrow inflorescence bracts.

Centropogon umbrosus is very similar to *C. hirtus*, which has axillary flowers and narrowly elliptic leaves. Additional features for separating these two species are discussed under *C. hirtus*. *Centropogon umbrosus* is also quite similar to certain phases of *C. congestus* from Colombia and Central America. Specific characters for differentiating these two species are discussed under *C. congestus*.

5. *Centropogon hirtus* (Cavanilles) Presl, Prodr. Monog. Lobel. 48. 1836.

Lobelia hirta Cavanilles, Anales Hist. Nat. 2: 108-110. 1800. Type: Ecuador. San Antonio [locality probably in error, see below], *Née s.n.* (holotype, MA n.v., photo F-neg. 29443).

Siphocampylus hirtus (Cavanilles) G. Don, Gen. Syst. 3: 702. 1834.

Centropogon exasperatus Presl, Prodr. Monog. Lobel. 48-49. 1836. Type: Peru. "In montibus Peruviae prope Huanoco," *Haenke s.n.* (lectotype here designated, PR-502321; isolectotypes, PR-495571, photo NA-neg. 78245, W-5706 p.p., photo F-neg. 30955, W-15580).

Centropogon angustus Gleason, Bull. Torrey Bot. Club 6: 54, fig. 3. 1925. Type: Peru. Huánuco: Villcabamba on Rio Chinchao, 1825 m, 17-26 Jul 1923, *Macbride* 4967 (holotype, NY; isotype, F, photo F-neg. 58344).

Erect herbs 0.5-1(-1.5) m tall, single-stemmed or branching at base, generally densely hirsutulous but occasionally only minutely hirtellous; stems succulent, mostly hirsutulous, densely so towards apex, the trichomes multicellular, to 1(-1.5) mm long, stems rarely with pedicel scars from old inflorescences; latex opalescent. Leaves narrowly elliptic, 3.5-5 times as long as wide, 13-25(-30) x 2.8-5(6.5) cm, apex attenuate, base narrowly cuneate to decurrent, margins irregularly serrate to serrulate, with 4-8 callosities per cm; lamina thin and chartaceous when fresh, drying chartaceous, adaxial surface dark green, sparsely to moderately hirsutulous or hirtellous with mostly appressed trichomes 0.2-1 mm long, abaxial surface pale green or suffused purple, moderately to densely soft-hirsutulous to hirtellous, especially on major veins, with spreading trichomes mostly 0.5-1.5 mm long; secondary veins 10-13, arcuately ascending, prominently raised abaxially; petioles 1-2.5 cm long, densely pubescent on both surfaces. Inflorescence frondose, flowers solitary in axils of slightly to moderately reduced leaves,

these narrowly elliptic, 70-300 x 15-65 mm, similar to foliage leaves in pubescence and texture; pedicels erect in bud and at anthesis, drooping with age and in fruit, elongating to 45-120 mm but always shorter than the subtending leaves, occasionally persistent, densely hirsutulous to hirtellous, bracteoles basal to sub-basal, linear, 1-4 mm long.

Flowers often stout, 45-55 mm long; hypanthium hemispheric to slightly ovoid sometimes with a truncate base, 6-7 x 6-10 mm, densely hirsutulous, intersepalar nectaries prominent; sepals erect, narrowly triangular, (8-)10-16 x 2.5-4 mm, remotely serrulate, moderately to densely hirsutulous, the sinuses acute; corolla uniformly rose-pink to pinkish-red, moderately to densely soft-hirtellous, the lobes often short-ciliate; corolla tube usually slightly sigmoid in shape, 30-34 mm long, the basal portion 5-8(-10) mm wide, often narrowing just below throat, the throat little-ampliate, (7-)8-9 mm wide, curved 30-45°; dorsal lobes laterally recurved, 8-10 x 3 mm, lateral lobes 6-7 x 2.5-3.5 mm, with acuminate decurved tips, ventral lobe ca. 6 mm long, with an acuminate, deflexed tip; androecium 43-50 mm long; filament tube 37-44 mm long, subterete and 1.5-2 mm wide when fresh, white to pinkish-white, or rose-purple where exserted, glabrous throughout, inserted in corolla 4-5 mm above base, exserted from corolla 5-7 mm; anther tube 6-7 mm long, thecae gray, connectives purplish, completely glabrous, antheridial scale 2-2.5 mm long; style exserted from anther tube 1-2 mm, stigma ca. 2.5 mm in diam. Fruit spheroid to obloid, to 11 x 15 mm, moderately ribbed, nectar chamber persistent; seeds oblong, mostly 0.6 mm long.

Distribution. An uncommon cloud forest herb known only from Huánuco Department of central Peru, particularly around the Carpish Hills at 2400-2800 m.

Additional specimens examined. PERU. Huánuco: Carpish, 2700 m, 7 Aug 1940, Asplund 12810 (S, US), 2750 m, Asplund 12850 (S); Carpish tunnel, 46 km N of

Huánuco, 2720 m, 16 Nov 1979, *Davidson & Jones* 9197 (MO, NY); Cochero, *Dombey s.n.* (P); Carpish, 2800–2900 m, 4 Aug 1947, *Ferreyra* 2112 (F, G, NY-2 sheets, S, US), *Ferreyra* 2309 (US); without precise locality, *Haenke s.n.* (PR, W, W p.p. along with isolectotype of *C. exasperatus*); Huaguín, nr. Carpish, 2500 m, 4 Apr 1948, *Ochoa* 391 (US); Carpish Hills, 2650 m, 2 Mar 1985, *Stein & Todzia* 2270 (MO, NY, US, USM), 2500 m, *Stein & Todzia* 2277 (MO, US), 2450 m, 15 Jan 1987, *Stein et al.* 3844 (MO); Tumanga, 2400 m, 18 Apr 1963, *Wojtkowski* 7916 (MO); Carpish, 2500 m, 2 Jun 1981, *Young & Sullivan* 547 (MO).

Nomenclature: In the protologue of *Centropogon hirtus* Cavanilles (1800) noted the type locality as San Antonio, Ecuador, and elaborated further on that locality in the discussion of this species in his *Icones et Descriptiones* (Cavanilles, 1801). From the photograph of the holotype and the detailed illustration provided in *Icones et Descriptiones* (tab. 520) the identity of this species is very clear. No such plants, however, have been recollected in Ecuador, or anywhere outside Huánuco Department in central Peru. Thus, the locality, and possibly the collector, cited by Cavanilles are almost certainly incorrect. Both Née and Haenke were in Peru in 1790 as members of the Malaspina expedition. Née, however, did not accompany Haenke on his trip to Huánuco (Kühnel, 1960) and apparently collected only along the western slope of the Peruvian Andes between Lima and Cerro de Pasco (Weberbauer, 1945). Late in 1790 both Haenke and Née sent specimens back to Spain (Kühnel, 1960). It seems likely that one of Haenke's Huánuco specimens was accidentally included with those of Née and upon arrival in Madrid incorrectly attributed to Née. A Haenke collection from Huánuco in Presl's herbarium in Prague (PR) precisely matches the MA "Née" type of *C. hirtus*. This specimen of *Haenke s.n.* (PR-495678) as well as two others now in

Vienna but originally from Prague (W-15579 and W-5706 p.p.) are probably duplicates of the type collection.

While in Huánuco, Haenke also collected the type of *C. exasperatus*, which as discussed below merely represents a short-pubescent form of *C. hirtus*. One of the two Haenke specimens of *C. exasperatus* at PR is here designated as the lectotype. This sheet (PR-502321) was annotated by Presl as "*Centropogon exasperatus* Presl"; the second sheet (PR-495571) was annotated by Presl as "*Lobelia hirtus* Cavanilles B [beta] *exasperata*" but never reannotated as *Centropogon*.

Discussion. Within sect. *Amplifolii*, *C. hirtus* is characterized by narrowly elliptic leaves and axillary flowers with elongate pedicels. In these respects it superficially resembles the Colombian *C. ventanensis*, a species that has flowers in congested inflorescences (not truly axillary), smaller leaves (to 16 cm), much shorter pedicels (ca. 25 mm long), shorter sepals (7-8 mm), a puberulent rather than glabrous filament tube summit, and much more reduced foliar pubescence. *Centropogon hirtus* is most easily confused with *C. umbrosus*, with which it overlaps geographically. In general, however, *C. umbrosus* occurs at lower elevations than *C. hirtus*, and the two species are not known to occur sympatrically. In addition to the features mentioned above, *C. hirtus* can be differentiated from *C. umbrosus* by the usually longer sepals (10-16 vs. 6-10 mm) and the modally longer flowers (androecia 40-49 vs. 35-43 mm). Occasional specimens of *C. umbrosus* superficially appear to have axillary-flowered inflorescences. Typically, however, these are young inflorescences, in which, as in many species of subgen. *Centropogon*, the first flowers produced may appear axillary while later flowers are subtended by reduced bracts. In contrast, all flowers in an inflorescence of *C. hirtus* are axillary.

Given its very localized distribution at high elevations, *C. hirtus* can probably best be considered a derivative of the rather polymorphic *C. umbrosus*. While frondose inflorescences with solitary, axillary flowers are ancestral within subgen. *Centropogon*, in *C. hirtus* this condition appears to be a reversal from the congested inflorescence type found in *C. umbrosus*.

The density and length of the indument in *C. hirtus* varies significantly. Most individuals, including the type, are rather densely hirsutulous with trichomes from 0.5-1.5 mm in length. Occasional individuals found in the same geographic area have a much reduced indument with trichomes less than 0.1 mm long. Such minutely hirtellous specimens include the types of both *C. exasperatus* and *C. angustus*, as well as *Asplund* 12850. In all other respects these plants are identical to specimens with the typical pubescence form and are here included under *C. hirtus*.

6. *Centropogon congestus* Gleason, Bull. Torrey Bot. Club 6: 52, fig. 1. 1925. Type.

Colombia. Risaralda: thickets N of Pereira, 1400-1500 m, 30 Aug 1922, *Pennell 10169* (holotype, NY). Fig. 8C.

Centropogon ovalifolius A. Zahlbruckner var. *asperatus* A. Zahlbruckner, Repert. Spec. Nov. Regni Veg. 14: 137. 1915. Type. Colombia. Cauca: La Conga in Andes W of Popayan, 1700-2300 m, *Lehmann 5931* (holotype, B, W-fragment; isotype, K). A sheet of this number at F does not match the holotype or isotype, and is probably a mislabeled specimen of *Lehmann 1201*.

Centropogon gesnerioides Gleason, Bull. Torrey Bot. Club 6: 53, fig. 2. 1925. Type.

Colombia. Valle: Cuesta de Tocotá, rd. from Buenaventura to Cali, 1500-1900 m, Dec 1905, *Pittier 691* (holotype, US).

Centropogon diocleus F. Wimmer, Ann. Missouri Bot. Gard. 24: 209. 1937. Type.

Panamá. Chiriquí: Valley of Río Chiriquí Viejo, vic. of Monte Lirio, 1500 m, 27 Jun 1936, *Seibert 166* (holotype, W; isotypes, K, MINN, MO, NY, WIS).

Centropogon macrophyllus (G. Don) F. Wimmer var. *congestus* (Gleason) McVaugh, Ann. Missouri Bot. Gard. 27: 352. 1940.

Centropogon ovalifolius A. Zahlbruckner var. *sneidernii* F. Wimmer, Pflanzenreich IV. 276b: 187. 1943. Type. Colombia. Cauca: El Tambo, La Costa, 1000 m, 24 Jun 1936, von *Sneidern* 739 (lectotype here designated, S, photo F-neg. 30252), von *Sneidern* 738 (syntype, S).

Centropogon caninus F. Wimmer var. *hirsutulus* F. Wimmer, Pflanzenreich VI. 276b: 769. 1953. Type. Colombia. Huila: La Plata, 2600 m, 20 Mar 1939, von *Sneidern* 2707 (holotype, S).

Erect suffrutescent herbs to shrubs 1-2(-3) m tall, branching from base or above; stems fleshy to sub-ligneous when fresh, often drying with white, crustose excrescences on the surface, glabrescent to hirtellous or short-hirsute, especially apically, with stiff, uniserial, multicellular trichomes to 0.8 mm long, the older stems often with prominently raised pedicel scars from old inflorescences; latex opalescent to tan. Leaves variable in shape, narrowly to widely elliptic, lanceolate, or oblanceolate to slightly obovate, 15-37 x 6-16 cm, apex acute to attenuate, base cuneate, margins occasionally minutely crispate, densely serrulate to denticulate with 5-11 callose-tipped teeth per cm; lamina thin or sometimes slightly fleshy when fresh, often velutinous, rarely slightly bullate-wrinkled, drying chartaceous and usually with white, crustose excrescences, adaxial surface glabrescent or sparsely to moderately hirtellous with scattered, erect trichomes (0.1-)0.25-0.7 mm long, abaxial surface usually densely hirtellous to hirsutulous on veins with trichomes (0.1-)0.25-0.8 mm long; secondary veins 11-19, often diverging from mid-vein at a very wide angle, usually more or less straight and parallel, or in narrower leaves slightly arcuate-ascending; petioles 2-4(-6) cm long, hirtellous to hirsutulous. Inflorescence an erect, bracteate, auxotelic, terminal, subcorymbose raceme, normally less than 6 cm long, but occasionally elongating to 15 cm, the flowers congested and numerous, to 20 or more in total, often with 5-8 open at one time, the rachis moderately to densely hirtellous to hirsutulous, and with old pedicel and bract scars raised 2-4 mm from surface; bracts persistent, sometimes tightly erect-appressed forming a dense head, but more commonly divergent, oblanceolate to spatulate, or occasionally elliptic to narrowly elliptic, mostly 20-35 x 5-10 mm, apex acute, rarely obtuse to mucronate, base cuneate to narrowly cuneate, margins serrulate to denticulate, indument as on foliage leaves; pedicels erect at anthesis, often remaining erect in fruit with only the apical portion drooping, 20-35(-45) mm long, shorter than to well exceeding the subtending bracts, minutely hirtellous to densely hirsutulous,

bracteoles basal to sub-basal (inserted up to 1/4 the distance from base), subulate, linear or oblanceolate, 1-5(-7) mm long and to 1.5 mm wide. Flowers 45-50 mm long; hypanthium hemispheric to transversely obloid, usually truncate basally, the summit occasionally flaring outward at base of sepals, 3-5 x 5-9 mm, moderately to densely hirtellous to hirsutulous, intersepalar nectaries prominently raised, to 1.5 mm high when fresh; sepals erect, triangular to narrowly triangular, 5-15(-19) x 2-5 mm, entire to serrulate, moderately to densely puberulent to hirsutulous, sometimes drying membranaceous with prominent longitudinal venation, sinuses most commonly acute, otherwise planar, rounded, or the sepals rarely slightly connate at base; corolla concolorous, reddish, reddish-pink to rose-purple, sparsely to moderately spreading-puberulent to hirsutulous; corolla tube often slightly sigmoid, stout to very narrow, 30-35 mm long, the lower portion cylindric, 5-10 mm wide at base, narrowing to 3-5 mm at point of filament attachment and then re-expanding, or occasionally narrowest just below throat, the throat slightly to abruptly ampliate, 7-11 mm wide, sometimes with lateral distentions or pouches and a dorsal crest when fresh, moderately to abruptly curved 45-75°; dorsal lobes laterally recurved to recoiled, 8-10 x 3-4 mm, lateral lobes 6-8 x ca. 3 mm, falcate with decurved, acute tips, ventral lobe 6-8 mm long, erect with a decurved to deflexed, acute tip; androecium 42-50 mm long; filament tube 38-45 mm long, when fresh sub-terete and 1.25-1.75 mm wide, white except rose-purple at summit where exserted, entirely glabrous or pilose at summit, adnate to corolla tube 4-6 mm above base, exserted from corolla 3-7 mm; anther tube occasionally angled slightly to the left when fresh, 4.5-6(-7) mm long, thecae dark gray, connectives rose-purple, the dorsal connectives sparsely to moderately pilose with purple trichomes, less often completely glabrous, antheridial scale 1.5-2 mm long; style exserted from anther tube to 3(-4) mm, the stigma often rose-colored, ca. 3 mm in diam. Fruit obloid, to 11 x 20

mm, smooth to prominently ribbed; seeds oblong, sometimes irregularly angular, 0.6-0.7 mm long.

Distribution. A cloud forest and montane forest herb or shrub found in Central America from central Costa Rica to western Panamá and in South America to southern Colombia, mostly from 1400-2500 m. In Colombia it occurs along the length of the Cordillera Occidental, in the central and southern Cordillera Central, and in the southern portion of the Cordillera Oriental.

Additional specimens examined. COSTA RICA. Cartago: 6 km W and below Presa Tapanti, along Río Dos Amigos, 1 hr. upstream from junction with Río Grande de Orosi, 1600 m, 11 Aug 1980, *MacDougal* 1269 (CR, DUKE). Limón: Cordillera de Talamanca, Atlantic slope, Kamuk massif, ridge between the Río Tararia, and the NE-most Kamuk páramo, 1900-2300 m, 16 Sep 1984, *Davidse & Herrera* 29194 (MO). Puntarenas: Upper Río Burú, 2010 m, 19 Aug 1983, *Gómez et al.* 21468 (MO); Finca de Geronimo, 6 hrs. by foot above Las Meises on slopes of Talamancas between Río Coton and Rio Canasta, 1800-2100 m, *McAlpin* 2560 (DUKE); Parque Nacional Amistad, Las Tablas, nr. upper Río Coton, 1400-1500 m, 14 Jul 1982, *Todzia et al.* 1920 (CR). San José: 25 km N of San Isidro del General along Interamerican Hwy., 1800 m, 28-31 Dec 1969, *Burger & Liesner* 7044 (MO, NY); 15 km N of San Isidro del General, 1800 m, 26 Feb 1965, *Jiménez* 2993 (NY); between top of Cerro de la Muerte and San Isidro, 1760 m, 11 Jul 1976, *Smith et al.* 76-550 (DUKE); along Interamerican Hwy., 15 km N of San Isidro del General, 1500 m, 5 Mar 1985, *Taylor & Skotak* 4769 (DUKE).

PANAMA. Bocas del Toro: Róbalo trail, N slopes of Cerro Horqueta, 1800-2100 m, 5-7 Aug 1947, *Allen* 4936 (MO). Chiriquí: Vic. of "New Switzerland," central valley of Río Chiriquí Viejo, 1800-2000 m, 6-14 Jan 1939, *Allen* 1393 (MO, NA, NY);

Quebrada Velo, vic. of Finca Lerida, 1500 m, 24 Jul 1947, *Allen* 4673 (MO); 8 km W of Cerro Punta, vic. of Las Nubes, 1850-1950 m, 11 Feb 1978, *Almeda & Nakai* 3492 (CAS); 2.5 km N of Bambito, 4.5 km WNW of Cerro Punta, 2100 m, 3 Jan 1975, *Cochrane et al.* 6293 (WIS-2 sheets); vic. of Las Nubes, 2.7 mi. NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, 27 Feb 1973, *Croat* 22406 (MO); between Cerro Punta and Cerro Respinga, 8 Aug 1972, *D'Arcy & D'Arcy* 6577 (DUKE, MO-2 sheets); Bajo Chorro, Boquete District, 2100 m, 25 Jan 1938, *Davidson* 209 (MO); along trail between N fork of Río Palo Alto and Cerro Pate Macho, 6 km NE of Boquete, 1800-2200 m, 7 Feb 1986, *Grayum* 6421 (MO); Collins Finca, Aug 1965, *Hayden* 165 (MO); Volcán de Chiriquí, 1300 m, 15 Apr 1969, *Kennedy & Williams* 247 (WIS); E slopes of Cerro Pando, 2000-2300 m, 15 Oct 1981, *Knapp* 1665 (DUKE, MO); .5 km E of Cerro Pate Macho, headwaters of Río Palo Alto, 1800-2100 m, 12 Nov 1981, *Knapp et al.* 2102 (MO); above Las Nubes, NW of Cerro Punta, 1900-2100 m, 26 May 1973, *Luteyn* 3808 (DUKE); Bajo Chorro, trail from Paso Respingo to Fila de Respingo, 2360-2500 m, 27 May 1973, *Luteyn* 3815 (DUKE); hills behind Boquete, 1500 m, 8 Aug 1977, *McDade* 260 (DUKE); vic. of Cerro Punta, 2070 m, 31 May-1 Jun 1967, *Ridgway & Solis* 2392 (MO); nr. top of trail to Cerro Pate Macho, 5 Jun 1983, *Schmalzel* 1645 (MO); Alto Quiel, 1800 m, 5 Jul 1984, *Schmalzel* 1963 (MO); SE slopes and summit of Cerro Pate Macho, trail from Río Palo Alto, 4 km NE of Boquete, 1700-2100 m, 26 May 1981, *Sytsma et al.* 4873 (DUKE, MO); N of Cerro Punta, end of rd. to Las Nubes, 2000 m, 16 May 1984, *Taylor* 3301 (DUKE); Bambito, 1 mi. SW of Cerro Punta, 1700 m, 26 Jun 1969, *Tyson* 5650 (DUKE, MO-2 sheets); Las Nubes region, 3-5.5 km NW of Cerro Punta, 2 km NW of Las Mirandes, 2000-2410 m, 28 May 1972, *Utley et al.* 239 (DUKE); Cerro Punta, 2200 m, 23 Jan 1984, *van der Werff & Herrera* 6251 (DUKE, MO); Santa Clara to Cerro Pando, 28 Feb 1985, *van der Werff & Herrera* 7232 (DUKE, MO); Horqueta, 1980 m, 17 Apr 1940, *von Hagen & von Hagen* 2007 (NY); E of Guadelupe along the Río Chiriquí

Viejo 2 km NE of Cerro Punta, ridge of Cerro Respinga, 2100 m, 13 Jan 1971, *Wilbur & Teeri* 13098 (DUKE); 1 km N of Las Nubes, 5 km NW of town of Cerro Punta, 2000-2300 m, 24 Dec 1971, *Wilbur et al.* 15200 (CAS, CR, DUKE-4 sheets, MICH, NY); 2 km W of La Garita, about 3 km WNW of Cerro Punta, 2000 m, 24 Dec 1971, *Wilbur et al.* 15266 (DUKE-2 sheets, MICH, MO); upper Río Chiriquí Viejo, 2 km NE of Guadelupe, 25 Dec 1971, *Wilbur et al.* 15332 (DUKE, MICH, MO); nr. Guadelupe on N side of Río Chiriquí Viejo, 3.5 km from Cerro Punta, 25 Dec 1971, *Wilbur et al.* 15351 (DUKE); vic. of Las Nubes W of peak of Cerro Punta and 6 km NW of town of Cerro Punta, 1800-2200 m, 28 May 1972, *Wilbur & Almeda* 17067 (DUKE-3 sheets, MICH, MO); slope below summit of pass between Cerro Punta and Boquete, 2500 m, 31 May 1972, *Wilbur & Luteyn* 17250 (DUKE); slopes approaching Cerro Horqueta, 7 km NNE of Boquete, 1800 m, 4 Jan 1975, *Wilbur & Luteyn* 19236 (DUKE); W of Las Nubes, 2000-2100 m, 6 Jan 1975, *Wilbur & Luteyn* 19350 (DUKE-3 sheets, MICH), *Wilbur & Luteyn* 19395 (DUKE); Quebrada Velo, 1800 m, 8 Jul 1940, *Woodson & Schery* 273 (MO, NA); vic. of Bajo Chorro, 1900 m, 20-22 Jul 1940, *Woodson & Schery* 614 (MO, NA); Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, 1500-2000 m, 3 Jul 1938, *Woodson et al.* 1021 (MO, NA-2 sheets, NY). Darién: Cerro Tacarcuna massif between summit camp on W-most ridge and Pico Tacarcuna, 1650-1800 m, 22 Jul 1976, *Gentry et al.* 16919 (COL, DUKE, MO).

COLOMBIA. Antioquia: Rd. to La Blanquita, Río Cuevas drainage, Corregimiento Nutibara, 1630 m, 15 Jan 1987, *Sanchez et al.* 962 (MO). Caldas: La Linda, Manizales, 1950 m, 24 Feb 1985, *Avila* 199 (NY); San Bernardo, 2200 m, 28 Jun 1934, *Dryander* 1453 (B), 2400 m, 3 Jul 1934, *Dryander* 1465 (B). Caquetá: E slope of Cordillera Oriental, Quebrada del Rio Hacha, below Gabinete, 2100-2250 m, *Cuatrecasas* 8523 (COL). Cauca: E slope of Cordillera Central, Aguabonita, region of Moscopán, 2280 m, 31 Jan 1947, *Cuatrecasas* 23532 (MICH); Cordillera Occidental, La Gallera,

Micay Valley, 1400-1500 m, 29-30 Jun 1922, *Killip* 7700 (NY); Parque Nacional Munchique, km 50-55 along rd. above Uribe, 1875-2256 m, 25 Apr 1979, *Luteyn et al.* 7477 (COL, NY); W slope of Cordillera Occidental, Parque Nacional Munchique, km 42-58 of Uribe-La Gallera rd., 2000-2200 m, 27 Mar 1986, *Stein* 3784 (AAU, B, F, K, MO, NY, U, US). Chocó: Ansermanuevo-San José del Palmar rd., between El Alto del Galápago and San José del Palmar, 1900 m, 29 Aug 1976, *Forero et al.* 2286 (COL); Alto del Galápago, border with Valle Department, 2000 m, 19 Feb 1977, *Forero et al.* 2947 (COL, MO); W slope of Cordillera Occidental, 64 km W of Ansermanuevo on rd. to San Jose del Palmar, 1500 m, 25 Jan 1986, *Stein & McDade* 3298 (COL, JAUM, MO, NY, US). Huila: Finca Altadecas, hills above Finca Virginia, S side of valley Río Neiva, 40 km SSE of Neiva, 2100 m, 5 Dec 1942, *Fosberg* 19254 (US); Balsillas, on Río Balsillas, 2100-2200 m, 3-5 Aug 1917, *Rusby & Pennell* 790 (GH, NY, US, W), *Rusby & Pennell* 816 (NY); W slope of Cordillera Oriental, 29 km above (SE of) Guadalupe on rd. to Florencia, 2250-2350 m, 22 Mar 1986, *Stein* 3707 (COL, FUP, MO, NY, US); E slope of Cordillera Central, Finca Mehrenberg, km 101 of La Plata-Popayán rd., 13 km E of Santa Leticia, 2300 m, 24 Mar 1986, *Stein* 3740 (COL, FUP, K, MO, NY, US). Quindío: Quindío, 2000 m, 1918, *Dawe* 804 (K, NY); W of Salento, 1600-1900 m, 25-31 Jul 1922, *Killip & Hazen* 8764 (NY); Río Quindío above Armenia, 1400-1600 m, *Pennell et al.* 8726 (NY); San José, Quindío, 1200 m, *Triana* 1561 (P); San José en el Quindío, 1200 m, Jul 1853, *Triana s.n.* (BM). Tolima: Río Saldaña, 1600-1800 m, 19 Nov 1944, *Cole* 1611 (MICH). Valle: Pass above Queremal, 1500 m, 5 Mar 1939, *Alston* 7933 (BM, S); km 18.5 on rd. between Cali and Buenaventura, 1910 m, 27 Aug 1976, *Croat* 38521 (MO); W slope of Cordillera Occidental, Las Colonias above Queremal, 1950-2050 m, 20 Mar 1947, *Cuatrecasas* 23930 (MICH, US); San Antonio, 2000 m, 1 Mar 1939, *Dryander* 2272 (BM); Alto Mercedes, hwy. to the ocean, 2200 m, *Dryander* 2424 (NA, US); km 17, 1700 m, May 1946, *Dryander* 2929 (F); Bosque de San Antonio, W of Cali, nr. television

tower, 1950-2050 m, 15 Jul 1984, *Gentry et al.* 48119 (MO, US); km 18 of Cali-Buenaventura rd., finca Zingara, 1900-2100 m, 29 Sep 1985, *Giraldo 21* (MO), 27 Oct 1985, *Giraldo 33* (MO); Campamento Tokio (Telecom towers), above Queremal, 2000-2075, 22 Apr 1979, *Luteyn 7372* (COL, NY); 30-37 km W on Ansermanuevo-San José del Palmar rd., 1850-1875 m, *Luteyn et al.* 10399 (NY); above Cali, 1800 m, Aug 1939, *Sandeman s.n.* (K); Cali, hwy. to the ocean, 2000 m, 23 Jul 1953, *Schneider 1278* (COL); Cerro Horqueta, San Antonio above Cali, 2050-2200 m, 20 Jan 1986, *Stein et al.* 3235 (COL, MO); nr. km 18 on rd. from Cali to Buenaventura, 1840 m, 23 Jan 1986, *Stein et al.* 3277 (COL, MO, US); 50 km W of Ansermanuevo on rd. to San Jose del Palmar, nr. border with Chocó Depart., 1950 m, 25 Jan 1986, *Stein & McDade 3288* (COL, MO-2 sheets); Buenaventura, via del Dagua, 1200 m, Jun 1853, *Triana 1560* (BM). Department unknown: *Dryander 999* (W); La Balsa, *Goudot s.n.* (K); *Lehmann B.T. 1201* (NY, F-sub *Lehmann 5931*).

Discussion. As indicated by the extensive synonymy *C. congestus*, as here defined, is a highly variable species. To a degree the morphological variability found in *C. congestus* can be partitioned according to geography. In order to more thoroughly assess the morphological relationships between the different populations of *C. congestus* a multivariate analysis of 31 specimens from throughout Colombia was conducted using 20 floral and vegetative characters (Fig. 13; Table 13). This analysis indicates that while some of the geographic variants form fairly distinctive units, extensive intergradation occurs between the groups. For this reason I prefer a more conservative and inclusive species concept at this time. The different morphological phases of the species are discussed below according to their geographical location: the placement of previously described taxa within these informal groupings is noted.

Southern Colombia. In the southern portion of the Colombian cordilleras Oriental and Central (Huila and eastern Cauca Departments) *C. congestus* typically has narrow leaves (2.5-4.5 times longer than wide), relatively short sepals (6-10 mm long), erect-appressed bracts forming congested, almost capitate inflorescences, pedicels that generally exceed the bracts, rather narrow and often only moderately curved corollas, and generally very short anther tubes (4.5-5 mm long). Although certain of these features of the flowers and inflorescences indicate an affinity with *C. gesneriiformis* of Ecuador, the latter is immediately distinguishable by its much longer and straighter corolla, longer (6-7 mm), glabrous anther tube, and larger, wider leaves. Collections such as *Stein 3707 & 3740*, *Rushy & Pennell 790 & 816*, and *Cuatrecasas 23532* exemplify this morphological type, and the type of *C. caninus* var. *hirsutulus* is from this region.

Cordillera Occidental. A diversity of morphological forms occur in the western mountain range, with the most distinctive occurring in the central portion of the cordillera above Cali. Plants from this region have very long, foliaceous sepals (often 15-19 mm long) that often bulge out at the summit of the hypanthium and moderately dense, relatively long pubescence. The leaves are fairly wide (1.7-2.5 times longer than wide) with numerous close-set secondary veins. This is the most frequently collected Colombian form of *C. congestus* owing to its presence along one of the historic trade routes over the western cordillera. It has previously been described as *C. gesnerioides*.

Further south in the Cordillera Occidental, around the latitude of Popayán, populations are intermediate between the long-sepaled Cali form and the southern Colombian form discussed above. These intermediate plants have the more robust indument and wider leaves of the Cali populations, but the shorter sepals (8-11 mm long), narrower corollas, and shorter anthers of the southern form, as well as pedicels that well-exceed the bracts. The type of *C. ovalifolius* var. *asperatus* is of this form.

North of Cali, in the region west of Ansermanuevo the sepal length also decreases in size (to ca. 10 mm long) but the plants retain many of the other robust features of the Cali populations. At a slightly higher elevation in this same area, at Alto del Galápago, four unusual collections have been made (*Forero* 2286 & 2947, *Luteyn* 10399, & *Stein* 3288), which are almost entirely glabrescent and have sepals of intermediate length (12-13 mm long) and pedicels well-exserted above the bracts.

Cordillera Central. The "typical" form of *C. congestus* from the middle region of the Cordillera Central (Quindío, Caldas, and Tolima Departments) has moderately long sepals (8-13 mm) and generally elongate inflorescences with non-imbricate bracts. The leaves are moderately wide (2.5-3.5 times as long as wide), but pubescence is often very reduced.

Central America. *Centropogon congestus* from Costa Rica and Panama is very similar to the mid-Cordillera Central form of the species. Although an unusual crinkly leaf texture occasionally occurs in plants of this region, in other respects these specimens are identical to those with normal leaves. The type of *C. diocleus* exhibits this unusual crispate/sub-bullate texture.

At least certain phases of *C. congestus*, particularly the southern Colombian form, resemble some populations of *C. umbrosus* of Peru. Both of these species are quite variable and there are few clearcut morphological features that separate them. In spite of the poorly defined morphological traits for each of the species as a whole, I treat them separately for several reasons. In a multivariate analysis including the entire *C. hirtus* species group, *C. congestus* and *C. umbrosus* formed separate clusters with virtually no overlap. Thus, while many individual characters intergrade between the two species, the distribution and correlation of these characters within any given population are distinctive and non-overlapping.

The most important of the morphological characters that can be used to separate *C. congestus* and *C. umbrosus* are given in the key and summarized in Table 14. Probably the most striking difference is the indument density and trichome length, with the Peruvian plants typically much more pubescent and with modally longer trichomes. In *C. congestus* there is a significant trend toward very short pubescence or even glabrescence. The only form of *C. congestus* in which the density of pubescence approaches that of *C. umbrosus* is that of the Cali populations (i.e., "*C. gesnerioides*"), which can be easily distinguished by the much longer sepals. Although the inflorescence in *C. congestus* typically is elongate in age, some populations, particularly from southern Colombia, have congested, little-elongate inflorescences, as in *C. umbrosus*. These southern populations can almost always be distinguished from *C. umbrosus* as they generally have very tightly imbricate bracts forming dense heads, rather than the loosely divaricate bracts typical of *C. umbrosus*. Furthermore, the pedicels often exceed the bracts in these populations of *C. congestus* (a rare condition in *C. umbrosus*), and the anther tubes are much shorter (4.5-5 vs. 6-7 mm) and are normally pubescent rather than glabrous.

In addition to the morphological distinctions between these two species listed in Table 14, there is a significant disjunction in their distribution. *Centropogon umbrosus* ranges north only to Huánuco Department in central Peru, while *C. congestus* is found no further south than southern Colombia, a gap of some 2500 km.

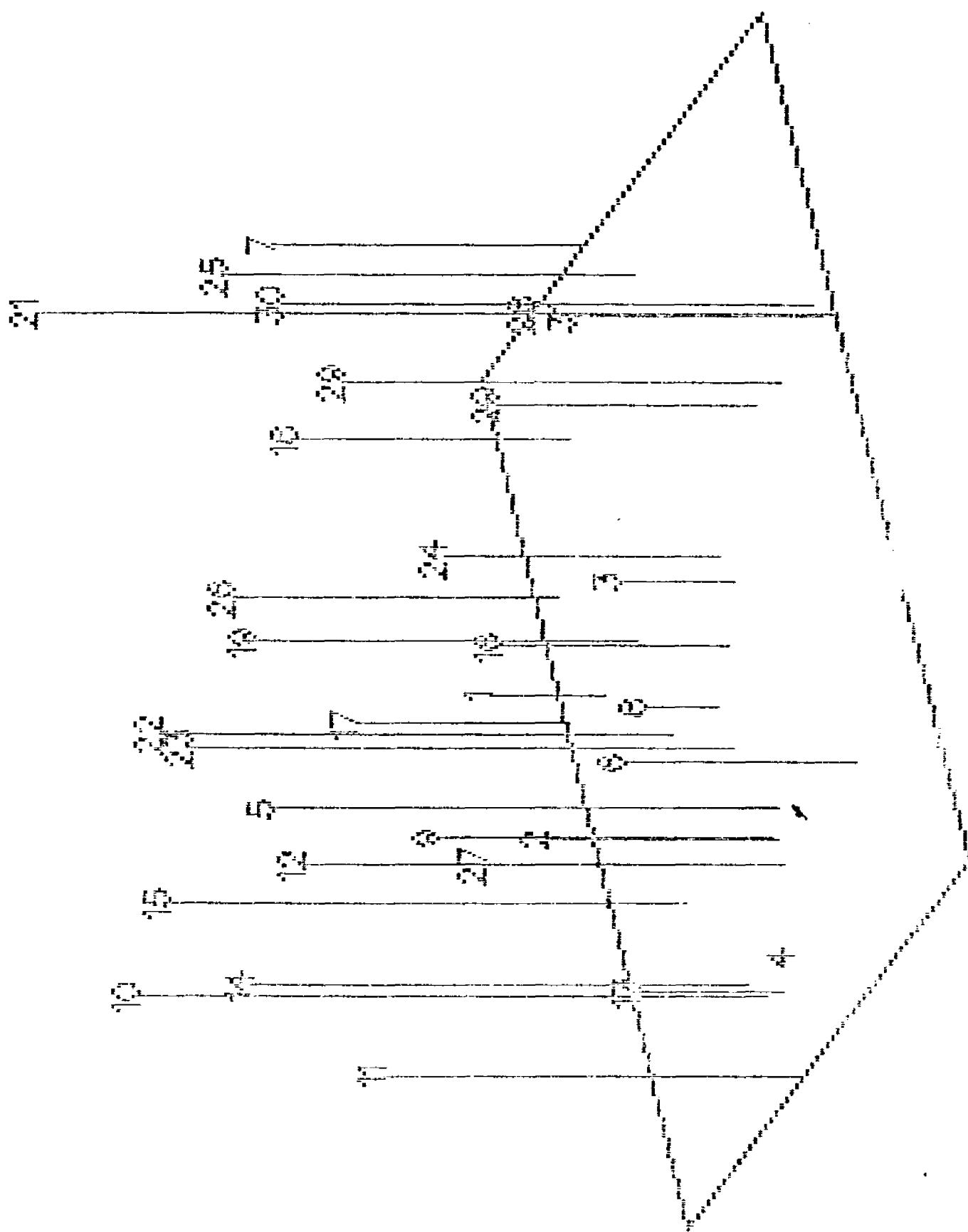
Table 14

Principal differences between Centropogon congestus and Centropogon umbrosus

	<u>C. congestus</u>	<u>C. umbrosus</u>
Petiole length	2-4(-6) cm	(0-)1-2(-3.5) cm
Indument density	sparse to moderate	moderate to dense
Leaf trichome length		
Adaxial	(0-)0.1-0.5 mm, $x = 0.37^*$	0.25-1.5, $x = 0.76^*$
Abaxial	(0-)0.1-1.0 mm, $x = 0.47^*$	0.25-1.5, $x = 0.96^*$
Sepals length	6-19 mm	6-10 mm
Corolla tube length	30-35 mm	26-32 mm
Androecium length	42-50 mm	36-42 mm
Anther tube length	4.5-6 mm	6-7 mm
pubescence	usually short-pilose	glabrous

* $n = 26$ for each

Fig. 14. Principal components analysis of *Centropogon congestus*, factors 1, 2, and 3.



7. **Centropogon ventanensis** B. A. Stein, sp. nov. Type. Colombia. Antioquia: 1-5 km off Pan American hwy. on rd. to Briceño, 25 km N of Yarumal, 7°07'N, 75°28'W, 1850 m, 7 Feb 1986, Stein & Cogollo 3378 (holotype, COL; isotypes, AAU, B, DUKE, F, JAUM, K, MO, NY, U, US).

Erect to subscandent shrubs to 2 m tall, diffusely branched; stems narrow and spindly, mostly 4 mm in diam. or less, moderately to densely hirtellous with stiff, multicellular trichomes ca. 0.05 mm in length, with up to 3 sets of prominently raised, subterminal inflorescence scars on stems below leaves; latex tan. Leaves clustered near apex of stems, the blades narrowly elliptic or rarely oblanceolate, 3.5-4.5 times longer than wide, 14-20 x 3.5-5 cm, apex attenuate to acuminate, base narrowly cuneate or slightly decurrent, margins serrulate with 5-9 callose-tipped teeth per cm; lamina thin when fresh, drying chartaceous with small, white, crustose excrescences on the surface, adaxial surface dark green, slightly scabridulous due to moderately dense, very minute, erect trichomes, abaxial surface paler, hirtellous, densely so along veins; secondary veins 8-10, acutely arcuate-ascending, prominently raised abaxially; petioles 1.5-2 cm long, hirtellous on both surfaces. Inflorescence an erect, long-bracteate, terminal raceme, elongating to 5 cm, the flowers few (to 4 open at a time) and mostly congested, but often appearing axillary, the rachis densely hirtellous; bracts little-reduced with most resembling normal leaves, the medial ones ca. 5 x 1.3 cm, but lower bracts to 11 cm long, similar in indument and margin to normal leaves; pedicels erect at anthesis, drooping with age and in fruit, 25-30 mm long, much shorter than the subtending bracts, hirtellous, bracteoles sub-basal, linear, 1-2 mm long. Flowers ca. 50 mm long; hypanthium hemispheric, 2-4 x 5-7 mm, hirtellous, intersepalar nectaries prominent; sepals erect, triangular, 7-8 x 2 mm, minutely serrulate, hirtellous, sinuses acute to rounded; corolla pinkish-red, whitish within throat, moderately hirtellous externally;

corolla tube slightly sigmoid, 32-35 mm long, basal portion cylindric, 5-7 mm wide at base, narrowing slightly then gradually re-expanding to base of throat, the throat moderately ampiate, 8-10 mm wide, curved ca. 50°; dorsal lobes laterally spreading, 9 x 3 mm, with cuspidate tips, lateral lobes asymmetrically triangular, 6 x 3 mm, with acuminate, decurved tips, ventral lobe triangular, 6 x 3 mm, with an attenuate, erect or deflexed tip; androecium 47-49 mm long; filament tube 42-44 mm long, sub-terete and 1.5 mm wide when fresh, white except rose-purple at summit, sparsely short-pilose at summit with purplish trichomes, adnate to corolla ca. 6 mm above base, exserted from corolla tube 6-8 mm; anther tube 5-6 mm long, thecae black, connectives purplish-rose and sparsely short-pilose with purplish trichomes, antheridial scale 1.5-2 mm long; style exserted from anther tube 0-1 mm, stigma tinged rose, ca. 2.5 mm in diam. Fruit obloid, to 7 x 17 mm, with 10 prominent ribs when fresh creating a star-shaped cross-section, nectar chamber persistent; seeds oblong to ovoid and irregularly angular, 0.5-0.6 mm long.

Distribution: Known only from the type locality in the northern Cordillera Central near Alto de Ventanas, Antioquia Department, Colombia. Found in cloud forest understory and along forest edges at 1500-1850 m.

Additional specimen examined: COLOMBIA. Antioquia: To 5 km down rd. to San Fermin de Briceño, W from Pan American Hwy., ca. 25 km N of Yarumal, 1525-1830 m, 26 May 1984, Luteyn et al. 10767 (NY).

Discussion. This species is closely related to *C. congestus* and shares with it a similar corolla morphology, the presence of subterminal inflorescence scars, and of white, crustose leaf excrescences that form upon drying, and a short-pilose anther tube

and filament summit. It differs from *C. congestus* in having very narrow leaves, 3.5-4.5 times longer than wide, and very reduced trichomes on the upper leaf surface that give the leaves a slightly roughened texture. The most distinctive feature, however, is the little-reduced inflorescence bracts that result in an inflorescence that is congested but in which the flowers appear axillary due to the leaf-like bracts. As a result, the pedicels are much shorter than the subtending bracts, in contrast to most other species in this group. The only other species in the *C. hirtus* complex that has a similar bract to pedicel ratio is *C. hirtus* itself, a truly axillary-flowered species of Central Peru. The shrubs of *C. ventanensis* are also much more spindly and diffusely branching than those typical of *C. congestus* or other members of the *C. hirtus* complex.

In a multivariate analysis of the *C. hirtus* complex, *C. ventanensis* appeared distinctive regardless of which other species it was analysed with.

8. *Centropogon gesneriiformis* Drake, J. Bot. (Morot) 3: 229. 1889. Type. Ecuador.

Loja: Huacapamba [Huancabamba], *Poortman* 224 (holotype, P, photo F-neg. 30942). Fig. 8B.

Erect suffrutescent herbs to shrubs 0.5-1.5 m tall, single-stemmed or branching from base, generally with velutinous pubescence, but rarely glabrescent or glabrous throughout; stems often with conspicuous pedicel scars from old inflorescences, glabrescent below, densely hirtellous above with multicellular trichomes to 0.3 mm long, the stems to 2 cm in diam. at base; latex tan. Leaves often clustered near apex, the blades elliptic to oblong or slightly obovate, 2-3 times longer than wide, 17-35(-45) x 7-13(-17) cm, apex acute to acuminate, rarely obtuse, base narrowly cuneate and tapering into petiole, margins densely ciliate, dentate to denticulate or serrulate, the callose-tipped teeth salient and well-exserted, often 1-2 mm long, 6-10 teeth per cm; lamina thin and chartaceous with a velutinous indument when fresh, drying chartaceous, often with small white excrescences on surface, adaxial surface sparsely strigose with scattered, appressed trichomes to 0.2 mm long, abaxial surface moderately to densely hirsutulous throughout, but most densely along major veins, the trichomes to 0.5 mm long, the leaves very rarely glabrescent or merely hirtellous; secondary veins 10-14, diverging from mid-vein at a widely acute angle and arcuately ascending; petioles 1-2 cm long and hirtellous, or absent. Inflorescence an erect, densely bracteate, auxotelic, subcorymbose raceme, mostly 4 cm long or less, occasionally elongating to 8 cm, the flowers numerous (to 20 in total) and congested, the rachis hirtellous to hirsutulous; bracts persistent, erect and tightly appressed forming a dense head, oblanceolate to spatulate, mostly 25-35 x 6-10 mm, occasionally wider, apex acute to obtuse, base decurrent and sessile, margins denticulate, both surfaces hirsutulous to hirtellous; pedicels erect at anthesis, arcuate-drooping with age, usually very long and much

exceeding the subtending bracts, 30-70 mm long, densely hirsutulous to hirtellous, bracteoles sub-basal, linear or filiform, to 5 mm long. Flowers very long, (50-)58-63 mm, oriented vertically at anthesis; hypanthium hemispheric, 4-5 x 6-8 mm, moderately pubescent, intersepalar nectaries prominent; sepals erect and appressed to corolla tube, narrowly triangular to sub-deltoid, (5-)8-11 x 3 mm, the dorsal lobe often slightly longer than others, entire to irregularly serrate, moderately spreading pubescent, sinuses acute; corolla bright pink to reddish-violet, whitish internally and along inner base of lobes, moderately to densely soft-puberulent externally; corolla tube gently expanding from base to throat and only gradually curved, (34-)40-45 mm long, 5-7 mm wide at base, narrowing slightly to 3-4 mm, then expanding to (7-)9-12 mm wide at throat, the throat not well differentiated, gently curving ca. 20°; dorsal lobes recurved, 9-11 mm long, lateral lobes ca. 7 mm long, with caudate, decurved tips, ventral lobe ca. 7 mm long with a caudate, deflexed tip; androecium (45-)50-55 mm long; filament tube (40-)45-50 mm long, adnate to corolla 7-8 mm above base, exserted from corolla tube 1-3 mm, white, or purplish where exserted, glabrous throughout; anther tube 6-7 mm long, thecae gray to black, connectives rose-purple, glabrous, or with few scattered trichomes in connectives, antheridial scale triangular, 2 mm long, with few shorter, unfused trichomes at base; style exserted from anther tube to 3 mm, stigma white, ca. 3 mm in diam. Fruit obloid, to 9 x 18 mm, prominently 10-ribbed and star-shaped in cross-section when fresh, nectar chamber persistent; seeds elliptic, 0.6-0.7 mm long.

Distribution: A rare understory herb to subshrub of montane forest and cloud forest. Known from the eastern slope of the Andes in Cañar, Loja, Morona-Santiago, and Zamora-Chinchipe provinces in Ecuador, and from Cajamarca Department in northern Peru, and rarely found on the western slope of the Andes in Bolívar, Cañar, and Cotopaxi provinces. It is found at elevations from 1150-2700 m.

Additional specimens examined. ECUADOR. Azuay: Jesús María-Molleturo rd., 12 km from Guayas border, 1150 m, 16 Jul 1977, Boeke & Loyola 2172 (NY). Bolívar: Balsapampa, 1200 m, 19 May 1968, Harling et al. 9646 (GB); Alto de Pucará, 1500 m, 23 Nov 1943, Solis 6998 (F). Cañar: 10 km E of Cochencaí on Guayaquil-Cuenca rd., 1970-2000 m, 26 Jan 1981, Gentry et al. 30808 (MO, SEL, US); N slope of Río Paute Canyon, across from Campamento Guarumales, 1650-1850 m, 21 May 1985, Stein 2845 (AAU, DUKE, F, K, MO-2 sheets, NY, QCA, QCNE, US). Cotopaxi: 1-3 km S of El Corazón on trail to Facundo Vela, 1300-1400 m, 17 May 1980, Harling & Andersson 19221 (GB). Loja: Km 16-22 on Loja-Zamora rd., 2300-2700 m, 16 Apr 1974, Harling & Andersson 13642 (GB). Morona-Santiago: 7-8 km N of Gualaquiza on rd. to Indanza, 1450 m, 16 Apr 1985, Harling & Andersson 24194 (GB); Gualaquiza-Indanza rd., km 20 between Túmbez and Tucumbatza, 1600 m, 20 Apr 1985, Harling & Andersson 24355 (GB); Limón-Cuenca rd., 3 km above Plan de Milagro, 1900-2000 m, 18 May 1985, Stein 2818 (MO); Arenillas along Río Tintas, 2195 m, 13 Jul 1943, Steyermark 53560 (F). Zamora-Chinchipe: Loja-Zamora rd., E of the pass, 2600 m, 15 Feb 1985, Harling & Andersson 22106 (GB); Quebrada Achupallas, 3000-3500 m [elevation perhaps erroneous], 9 Oct 1943, Steyermark 54510 (F).

PERU. Cajamarca: San Ignacio Prov., along trail 7 km W of La Coipa, 1200 m, 8 Feb 1978, Wasshausen & Encarnación 871 (NY, US).

Nomenclature. This species was originally published by Zahlbrückner as "*Centropogon gesneraeformis*," and this spelling has been followed by all subsequent authors. In accordance with Article 73.8 and Recommendation 73G of the International Code of Botanical Nomenclature (Voss et al., 1983), the compounding form "ae" is

considered an orthographic error, and the name is here corrected to *C. gesneriiformis*, reflecting classical Latin usage.

Discussion. *Centropogon gesneriiformis* is a well-defined species with a rather localized distribution. It can be distinguished easily by the vertically oriented flowers, by its very long, little-curved corolla in which the throat is not well differentiated, by the erect, tightly appressed, oblanceolate bracts that form a congested head, by the erect, usually very elongate pedicels that far exceed the subtending bracts, and by the combination of a generally velutinous abaxial leaf surface, sparsely hirsute adaxial surface, and common presence of white leaf excrescences. There is a trend toward glabrescence in *C. gesneriiformis*, and at least one specimen, *Wasshausen & Encarnación* 871, is completely glabrous. Because this specimen is concordant with *C. gesneriiformis* in all other characters, including the presence of leaf excrescences, and because it originates from the southern periphery of the species range, it is here treated as an anomalous member of this species. More problematic are several collections from the western slope of the Ecuadorean Andes, which in addition to being less pubescent than typical *C. gesneriiformis*, have relatively short pedicels that do not exceed the length of the bracts (e.g., *Dodson & Thien* 2108 and *Gentry et al.* 30808, and *Solis* 6998). Because of the vertically oriented, relatively long and straight corollas, and the long, linear bracteoles, these anomalous specimens are tentatively treated under this species.

Within the *C. hirtus* species complex *C. gesneriiformis* is a highly derived species. It is perhaps most closely related to the southern Colombian populations of *C. congestus*, with which it shares the basic inflorescence structure of erect, tightly appressed bracts that are exceeded by the pedicels. The corolla in *C. congestus*, however, is more typical of other members of the *C. hirtus* complex in its length, and its moderate curvature.

The much longer, gently curving corolla in *C. gesneriiformis*, suggests that a fundamental shift in pollinators has taken place in the origin of this species.

9. Centropogon uncialis McVaugh, J. Wash. Acad. Sci. 39: 159. 1949. Type. Colombia.

Cundinamarca: Between Pacho and Rio Negro, 1000-1200 m, 22-26 Feb 1942,

García Barriga 10744 (holotype, MICH; isotypes, COL, US, photo US-neg. 3382).

Erect herbs to subshrubs 0.5-1.5 m tall, branching at base, hirsutulous throughout; stems to ca. 1 cm in diam. at base, densely silver-hirsutulous with multicellular trichomes to 0.7 mm long, the stems often with scars from old inflorescences; latex opalescent to pale tan. Leaves elliptic to very narrowly elliptic, 2-5 times longer than wide, 15-23 x 3-8 cm, apex attenuate to acute, base narrowly cuneate and decurrent along petiole, margins saliently serrate to serrulate, with 5-9 ciliate, callose-tipped teeth per cm; lamina thin and chartaceous when fresh, drying chartaceous to membranaceous and with scattered white excrescences, adaxial surface sparsely to moderately strigose with scattered trichomes to 0.5 mm long, abaxial surface densely hirsutulous, especially along veins, the trichomes to 0.7 mm long; secondary veins numerous, 13-17, diverging from mid-vein at a wide angle (even in very narrow leaves) and arcuately ascending, deeply impressed adaxially when fresh, prominently raised abaxially; petioles 0.5-1.5 cm long, hirsutulous. Inflorescence frondo-bracteate, the basal-most flowers often solitary in axis of unreduced leaves, the upper flowers grading into an erect, bracteate, auxotelic, subcorymbose raceme, elongating to 5 cm, the flowers congested and numerous, often more than 15 in total, the rachis densely hirsutulous; bracts narrowly obovate to oblanceolate, 20-40 x 7-17 mm, apex acute to obtuse, base cuneate and sessile, margins serrulate, adaxial surface sparsely hirsutulous, the abaxial surface densely so; pedicels erect at anthesis, drooping with age, densely hirsutulous, 30-50(-60) mm long, much exceeding the subtending bracts, the pedicels longest when axillary to unreduced leaves, bracteoles inserted medially or on upper third of pedicel, occasionally sub-basal, linear and 1-4 mm long. Flowers 25-30 mm long, oriented

horizontal or somewhat assurgent; hypanthium subcylindric, rounded or truncate at base, 3-4 x 5-7 mm, slightly ribbed, moderately to densely hirsutulous, intersepalar glands prominent; sepals erect and appressed to corolla, triangular to narrowly triangular, 5-7 x 2.5-3 mm, ciliate, entire to irregularly serrulate, sparsely to moderately hirsutulous, sinuses acute to planar; corolla uniformly bright pink to rose-red, whitish within tube, sparsely to moderately hirsutulous externally with soft, flaccid trichomes to 0.7 mm long, these especially dense along margins of lobes; corolla tube 17-20 mm long, 4-5 mm wide at base narrowing quickly to an isthmus 1.5-3 mm wide, then expanding to 6-8 mm wide at throat, the throat only moderately ampliate and gradually curving 15-30°; dorsal lobes recurved, 6-7 x 2.5 mm, lateral lobes 4-5 mm, with acute, decurved tips, ventral lobe 4-5 mm, with an acute, deflexed tip; androecium 23-28 mm long; filament tube 19-24 mm long, subterete and 1.5 mm in diam. when fresh, white, glabrous or sparsely short-pilose at summit, adnate to corolla 2-3 mm above base, exserted from corolla tube ca. 2 mm; anther tube 3.5-4.5 mm long, thecae gray and connectives purplish, or both tan, glabrous or dorsal connectives sparsely short-pilose with white trichomes, antheridial scale narrowly triangular, ca. 1.5 mm long, often with few unfused trichomes at base. Fruits depressed globose, to 13 x 20 mm, smooth, nectar chamber persistent; seeds oblong to elliptic, 0.6-0.8 mm long.

Distribution. A montane forest herb, restricted to the western slope of the Cordillera Oriental in Cundinamarca Department, Colombia, at elevations of 1800-2400 m.

Additional specimens examined. COLOMBIA. Cundinamarca: Chiquinquirá nr. Bogotá, 18 Aug 1909, Apollinaire s.n. (G); Pacho, Hacienda Patasia, 1820-2400 m, 5-7 Aug 1947, García-Barriga 12527 (COL); Villegas-Utica rd., 540-800 m [elevation

doubtful], 15 Nov 1959, *Garcia-Barriga* 17202 (COL, NY, US); Pacho-Palma hwy., 2200 m, 13 Aug 1947, *Haught* 6072 (US); Alto de San Miguel, 19-24 km SW of Sibaté on rd. to Fusagasugá, 2300-2450 m, 4 Jan 1986, *Stein et al.* 3140 (COL, MO, NY, U, US); La Magnolia, 10 km N of San Francisco on rd. to Supatá, 2050 m, 13 Mar 1986, *Stein* 3678 (AAU, B, CAS, COL, DUKE, F, K, MO, NY, US); quebrada 2 km W of Salto de Tequendama, 12 km W of Bogotá-Fusagasugá hwy., 2300 m, 15 Mar 1986, *Stein & Franco* 3685 (COL, MO); Pacho, forests of Patasia, 2100 m, Feb 1948, *Uribe* 1651 (US), 2200-2300 m, May 1949, *Uribe* 1975 (US).

Discussion. *Centropogon uncialis* is a well defined and localized member of the *C. hirtus* species complex. Its most distinctive feature is the very small flower with the corolla only mildly curved. It is the only pubescent-leaved member of sect. *Amplifolii* to have this combination of floral features. Three other species, *C. pygmaeus*, *C. bangii*, and *C. carpishensis*, have similar flowers, but differ significantly from *C. uncialis* vegetatively and in inflorescence structure, and the similar corolla morphology is probably due to convergence. Two other features characteristic of *C. uncialis* are the elongate pedicels, which greatly exceed the subtending bracts (when present), and the frequently elevated placement of the bracteoles on the pedicels.

Centropogon uncialis has foliose-bracteose inflorescences that show a gradation from solitary, axillary flowers to a congested, corymbose terminal inflorescence. This transition can be seen on the same plant, and reflects a developmental sequence. The basal flowers are subtended by normal leaves, but as the inflorescence matures the floral internodes become compressed and the subtending leaves/bracts become reduced in size. The inflorescence is also auxotelic, and after termination of flowering, the apical meristem may continue to elongate and produce a new flush of leaves distal to the inflorescence. As many as three inflorescences may develop on a single shoot as

evidenced by distinctive clusters of pedicel scars. The material of *C. uncialis* studied by McVaugh (1949b) contained only axillary flowers, explaining his incomplete description of the inflorescence structure, and for Wimmer's (1956) later inclusion of this species in his subsect. *Axillares*.

10. *Centropogon gamosepalus* A. Zahlbruckner, Ann. K. K. Naturhist. Hofmus. 6: 434.

1891. Type. Peru. San Martín: Tarapoto, 1855-1856, Spruce 4131 (holotype, W, photo F-neg. 30952; isotypes, K-2 sheets).

Centropogon grandicephalus A. Zahlbruckner, Bot. Jahrb. Syst. 37: 454. 1906. Type.

Peru. Amazonas: E of Chachapoyas between Tambo Almirante and Incatambo, 1800-1900 m, Weberbauer 4461 (holotype, B, photo F-neg. 30218; isotype, W).

Erect succulent herbs to subshrubs 0.5-1.5 m tall, single-stemmed or branching from base; stems fleshy and often drying conspicuously ridged, glabrous to hirtellous, the older stems occasionally with scars from old inflorescences, slightly woody at base, to 1.5 cm in diam.; latex white. Leaves well-distributed along stems, mostly elliptic or narrowly elliptic to oblanceolate, 2-3(-4) times as long as wide, 14-25(-30) x 5-10(-12) cm, apex acute to attenuate, very rarely obtuse, base cuneate, the margins serrulate to denticulate with 4-9 callose-tipped teeth per cm, these sometimes slightly exserted to 1 mm; lamina firm but fleshy when fresh, drying chartaceous to membranaceous, adaxial surface dark green, glabrous, abaxial surface normally paler, glabrous to minutely hirtellous or puberulent especially along mid-vein and secondaries; secondary veins 9-14, mostly arcuate-ascending, often prominently raised abaxially; petioles usually stout, 5-20 mm long, glabrous to hirtellous, or rarely absent in upper leaves. Inflorescence an erect, densely bracteate, auxotelic, terminal, corymbose raceme, mostly less than 4 cm long but occasionally elongating to 10 cm, the flowers congested or becoming lax basally, the rachis glabrous to moderately or densely hirtellous; bracts assurgent with the distal portion flaring outward, variable in shape but generally obovate to spatulate, rarely oblanceolate, 20-50 x (5-)10-30 mm, longer than and closely subtending the pedicels, often enveloping the basal portion of flowers, apex rounded to mucronate, rarely acute, base decurrent and sessile, margins serrulate to denticulate, adaxial surface glabrous or

sparingly puberulent, abaxial surface glabrous or minutely hirtellous along veins, the lower bracts sometimes grading into vegetative leaves in size and shape; pedicels erect at anthesis and remaining erect but drooping distally in fruit, slender, occasionally persistent, 15-30(-70) mm long, glabrous to hirtellous, the bracteoles basal, subulate to linear, 1-2 mm long. Flowers 50-55(-60) mm long; hypanthium hemispheric or depressed-cylindric, rounded or truncate basally, 4-6 x 5-7 mm, prominently 10-ribbed when fresh, drying 10-veined, glabrous, intersepalar nectaries present; calyx gamosepalus, 11-19 mm long, connate basally for 1/4 to 1/2, rarely 2/3 of length, glabrous, the tube 6-10 mm wide, the free lobes triangular to narrowly triangular, apex acute, entire or with few callose teeth; corolla red, pinkish-red, or pink, the lobes usually paler, inside of tube often whitish, corolla tissue thin, drying membranaceous, glabrous or puberulent; corolla tube often slightly sigmoid, 32-37 mm long, the basal portion cylindrical 4-5 mm wide, the throat abruptly ampliate and ventricose, 9-15(-18) mm wide, often with lateral distentions or pouches, moderately to sharply curved 45-65°; dorsal lobes spreading to recoiled, 8-11 x 3-5 mm, lateral lobes 5-7 mm long with attenuate, decurved tips, ventral lobe often saccate, 5-8 mm long with an acute, deflexed tip; androecium 45-55 mm long; filament tube 40-50 mm long, subterete and ca. 1.5-2 mm wide when fresh, white or purplish-rose where exserted, glabrous or sometimes pilose at summit, adnate to corolla 6-7 mm above base, exserted from corolla tube 3-8 mm; anther tube 5-6 mm long, thecae dark gray, connectives rose-purple, glabrous or dorsal and ventral connectives densely long-pilose with white trichomes, antheridial scale 1.5-2 mm long; style exserted from anther tube 2-3(-4) mm, stigma purplish, rarely greenish-white, ca. 3 mm in diam. Fruit rhomboid to obloid, to 8 x 20 mm, usually with 10 very pronounced longitudinal ridges to 4 mm high and appearing star-shaped in cross-section when fresh, the calyx and nectar chamber persistent; seeds orbicular to elliptic, occasionally angular, ca. 0.5 mm long.

Distribution. A locally common herb in premontane rainforest along the foothills of the eastern slope of the Andes from Napo Province in central Ecuador to southern San Martin Department in central Peru. Occurring from 600-1800 m, but most frequently at about 1000 m in altitude.

Additional specimens examined. ECUADOR. Morona-Santiago: Just below Chontal on trail from Sevilla de Oro to Mendez, valley of the ríos Negro and Chupianza, 15-16 Dec 1944, *Camp s.n.* (NY), between Santa Elena and Tres Ranchos, 900-1000 m, 1 Nov 1944, *Camp E-832* (MICH, NY); Río Paute 2-3 km W of Mendez, 580 m, 13 Dec 1944, *Camp E-1477* (MICH, NY); Indanza-Limón, 1300-1600 m, 23 Mar 1974, *Harling & Andersson 12749* (GB); Trail Macas-Arapicos, La Punta 10 km N of Macas, 1000 m, 29 Mar 1974, *Harling & Andersson 12980* (GB); 8 km E of Limón on rd. towards La Unión, 1400-1500 m, 22 Apr 1985, *Harling & Andersson 24419* (GB); 3 km N of Tucumbatza on Gualaquiza-Indanza rd., 1200 m, 19 Apr 1985, *Harling & Andersson 24342* (GB); Sucua-Macas rd., km 10, 24 Sep 1979, *Holm-Nielsen et al. 20433* (AAU, K, NY); Río Tutanagosa, Sucúa-Huarani rd., 850 m, 25 Sep 1979, *Holm-Nielsen et al. 20527* (AAU); km 24, General Plaza (Limón)-Mendez rd., 850 m, 10 Jun 1979, *Lojtnant & Molau 14522* (AAU). Napo: Mission Shandia, Río Jatun Yaku, 14 Aug 1957, *Barclay 4861* (COL); Tena-Pano rd., 550 m, 18-19 Jul 1982, *Besse et al. 1661* (SEL); Talag, 15 km SSW from Tena, 600 m, 11 Jul 1960, *Grubb et al. 124* (NY); Baeza-Tena rd., between Osayacu and Jondachi, 10-20 km N of Archidona, 900 m, 5 Feb 1980, *Harling & Andersson 16250* (GB); 2 km NW of Santa Rosa de Quijos, 1500 m, 12 Feb 1980, *Harling & Andersson 16483* (GB); Archidona, Feb 1857, *Jameson s.n.* (K); km 114, Lago Agrio-Baeza rd., 1750 m, 8 Aug 1980, *Ollgaard et al. 35782* (AAU-2 sheets); 17 km W of Lubaque, 73 km W of Lago Agrio on rd. to Quito, 1200 m, 9-10 Mar 1983, *Pipoly*

6365 (AAU, MO, NY). Pastaza: Km 31 on Puyo-Canelos rd., 870 m, 21 Jul 1982, Besse et al. 1693 (SEL); along new rd. towards Canelos departing from Puyo-Macas rd. at km 32, 850 m, 3 May 1984, Croat 58974 (MO); 1-5 km SW of Diez de Agosto, Puyo-Arajuno rd., 900 m, 4 Mar 1980, Harling & Andersson 16879 (GB); San José, 17 km NE of Puyo on Puyo-Puerto Napo rd., 800 m, 10 Mar 1980, Harling & Andersson 17133 (GB, NY); Puyo, 1000 m, 18 Mar 1978, Jaramillo III (AAU, NY); Pacayacu, 17 km SE of Canelos, 29 Oct 1974, Lugo 4347 (AAU, GB, K, MO); 34-36 km N of Puyo on Puerto Napo rd., 1000 m, 25 Apr 1978, Luteyn & Lebrón-Luteyn 5832 (AAU, MO, NY, QCA); 5 km E of Veracruz beyond Puyo, 970 m, 23 Apr 1972, MacBryde 1526 (AAU, MO); 1 km N of Shell, 1100 m, 17 Mar 1985, Neill et al. 6143 (MO, NY); Teniente H. Ortiz, 18 km from Puyo on rd. to Tena, 1100 m, 3 Sep 1976, Ollgaard & Balslev 9223 (AAU); near Puyo, 17 Feb 1953, Prescott 886 (NY); Puyo, 850 m, 12 May 1935, Schultze-Rhonhof 1856 (B); km 2.4 on rd. towards Canelos departing Puyo-Macas rd. 8 km S of Puyo, 1000 m, 9 Jun 1985, Stein 3018 (AAU, B, DUKE, F, K, MO, NY, QCA, QCNE, US); side rd. past radio antenna, departing Puyo-Puerto Napo rd. at km 35, 1000-1050 m, 9 Jun 1985, Stein 3020 (AAU, CAS, F, MO-2 sheets, NY, QCA, QCNE, US); trail towards Colonia 24 de Mayo, 2.5 km W of km 9 of Puyo-Tena rd., 1050 m, 3 Jul 1985, Stein & Tucker 3124 (MO-2 sheets). Tungurahua: Hacienda La Merced, 7 Apr 1931, Benoist 4173 (P). Zamora-Chinchipe: Río San Francisco above Canillones, 15-18 km ENE of Loja, 1800-1830 m, 20 Feb 1945, Fosberg 23166 (US); km 30 on rd. in construction Zamora-Zumba, along Río Jamboe, 1400-1500 m, 22 Apr 1974, Harling & Andersson 13840 (AAU, GB, MO); 10 km S of Zamora along Río Jamboe, 1100 m, 12 Apr 1985, Harling & Andersson 24051 (GB); 10 km E of Paquisha, 1400-1500 m, 13 Apr 1985, Harling & Andersson 24058 (GB); 4 km W of Panguintza on rd. to Panguintza Alto, 1100-1200 m, 14 Apr 1985, Harling & Andersson 24149 (GB). Province unknown: Mille 34 (W).

PERU. Amazonas: Río Marañón above Cascadas de Mayai nr. Campamento Montenegro, kms 276-280 of Marañón rd., 450 m, 3-4 Sep 1962, Wurdack 1835 (MICH, US). San Martín: Río Huallaga Valley, Carretera Marginal nr. top of divide between Puerto Pinzana and Punta Arenas, 1000-1100 m, 4 Feb 1984, Gentry & Smith 44918 (F, MO, US); Zepelacio nr. Moyobamba, 1200-1600 m, Jan 1934, Klug 3500 (F, GH, MO, K, S, US, WIS); Roque S of Moyobamba, 26 Mar 1925, Melin 292 (S); Tocache Nuevo District, Río Huallaga, Quebrada de Huasca Yacu, 5 Apr 1971, Schunke 4787 (COL, F, G, GH, NY, US); Venceremos, km 390 Pedro Ruiz-Moyobamba rd., 1800 m, 27 Jul 1983, Smith 4423 (MO); Tarapoto, Spruce s.n. (K).

CULTIVATED. Lyon Arboretum, Hawaii, from material collected at km 20 along rd. from Tena to Salsedo, Napo Province, Ecuador, 28 Dec 1983, Nagata 2760 (MO).

Vernacular names. "Cuyul," Napo Province, Ecuador.

Discussion. *Centropogon gamosepalus* is the core species within the *C. gamosepalus* species group. It is very closely related to, and probably derived from *C. capitatus*. It shares with that species an erect habit, a usually condensed and corymbose inflorescence with bracts widest above the middle, and a thin-textured, abruptly curved and pouched corolla. *Centropogon gamosepalus* overlaps *C. capitatus* in most morphological features and often must be differentiated solely by the connate sepals. While the feature of connate versus free sepals is easily observed in (although the bracts often obscure the base of the calyx) and provides a convenient qualitative character to distinguish these two species, the phylogenetic reliability of this single character is questionable. Because it occurs in several species of *Centropogon* from clearly unrelated lineages, basal connation of the sepals through intercalary fusion must

be relatively easy to evolve. Also, in *C. capitatus* many collections show an incipient basal fusion of 1-2 mm. The possibility thus exists that connate sepals have developed independently several times in *C. capitatus*-like ancestors, and if so *C. gamosepalus*, as the species as here defined, would represent a polyphyletic species.

II. *Centropogon roseus* Rusby, Bull. New York Bot. Gard. 8: 122. 1912. Type. Bolivia.

La Paz: Tumupasa [Prov. Iturralde, 14° 09'S, 67°55'W], 550 m, 10 Jan 1902,
Williams 584 (holotype, NY; isotype, BM).

Centropogon inflatus F. Wimmer, Repert. Spec. Nov. Regni Veg. 29: 60, pl. 117, fig. 9.

1931. Type. Peru. cultivated at St. Albans, England [probably from seed collected by L. Forget], 25 Aug 1910, *Sander & Sons s.n.* (holotype, K).

Erect herbs 0.25-1.75 m tall, few- to many-branched at base; stems glabrous, often drying with prominent ridges. Leaves oblanceolate to elliptic or narrowly elliptic, 14-30 x 4-9 cm, apex acuminate to attenuate, base narrowly cuneate, margins denticulate to long-fimbriate with 6-10(-14) callose-tipped teeth per cm, these occasionally exserted 1-6 mm from margin with the longest teeth separated by several shorter teeth, sometimes minutely ciliate-hirtellous; lamina thin to fleshy when fresh, drying chartaceous to membranaceous, adaxial surface dark green and nitid, glabrous, abaxial surface paler, minutely hirtellous along veins; secondary veins 10-15, widely arcuate-ascending, prominently raised abaxially; petioles less than 10 mm long, glabrous or glabrescent. Inflorescence an erect, terminal raceme, congested when young but elongating to 7 cm, somewhat lax basally in age, rachis glabrous to hirtellous, sometimes with sordid pubescence; bracts persistent, obovate to oblong, 10-30 mm long, equalling or usually shorter than the subtended pedicels, apex acute to mucronate, rarely obtuse, margins serrulate to fimbriulate, both surfaces glabrous; pedicels erect at anthesis, drooping with age and in fruit, 15-25(-30) mm long, conspicuously 5-angled in cross-section when fresh, drying ridged, bracteoles basal, linear, to 1.5 mm long, often not visible in dried material. Flowers 50-60 mm long; hypanthium oblate to shallowly cylindric, often truncate basally, 3-4 x 5-7 mm, 10-ribbed, glabrous, intersepalar nectaries present; calyx gamosepalus, erect, 11-21 mm long, connate for basal 1/2 to 3/4 of length, glabrous, the

tube 8-12 mm wide, the lobes broadly ovate to narrowly triangular, 3-7(-11) x 4-6 mm, apex acute to apiculate, the margins serrulate to fimbriulate; corolla bright pinkish-red to deep red, the lobes same color as tube or rose-lilac, the tissue thin, glabrous; the corolla tube 28-35 mm long, basal portion cylindric and straight, obscured by calyx tube, 5-6 mm wide at base, often narrowing to 4-5 mm just below throat, the throat abruptly ampiate and saccate, 10-15 mm wide, laterally and ventrally distended when fresh, curved 45-60°; dorsal lobes spreading to recoiled, 7-9 x 4 mm, lateral lobes deltoid or asymmetrically triangular, 3-6 mm long, with decurved, attenuate to caudate tips, ventral lobe saccate, triangular, 3.5-6 mm long, with an erect or deflexed, acuminate tip; androecium 45-50(-55) mm long; filament tube 40-45(-50) mm long, subterete, glabrous, white except rose-colored where exserted, adnate to corolla 5-8 mm above base, exserted from corolla tube 2-8 mm; anther tube 5-6 mm, thecae dark gray, connectives whitish or rose-purple, glabrous or rarely sparsely short-pilose with white trichomes, antheridial scale 1.5-2 mm long; style exserted 0-3 mm from anther tube, stigma to 4 mm in diam. Fruit rhomboid, to 10 x 20 mm, prominently 10-ridged, star-shaped in cross-section when fresh, with the calyx persistent and enlarging with age; seeds orbicular, slightly angular, ca. 0.5 mm long.

Distribution. An infrequent understory herb of Andean foothill forests from Junín Department in central Peru to La Paz Department of northern Bolivia, between 550-1600 m.

Additional specimens examined. PERU. Ayacucho: Prov. La Mar, Río Apurimac Valley, Hacienda Luisiana, 585 m, 8 Jun 1968, Dudley 10026 (MO, NA, US); Río Apurimac Valley, near Kimpitiriki, 400 m, 10-11 May 1929, Killip & Smith 22880 (NY). Cuzco: Atalaya, near junction of Río Carbón and Río Alto Madre de Dios, 31 Jul

1976, *Foster* 2376 (DUKE); Marcapata Valley, 1200 m, Aug 1926, *Herrera* 1161 (US); Pilcopata, rd. to Villa Carmen, 700 m, 6 Feb 1975, *Plowman & Davis* 5021 (GH, F); Rio Carbón, 0.5 km S of Atalaya, 10 km from Pilcopata on rd. to Shintuya, 650-700 m, 6 Apr 1985, *Stein* 2514 (AAU, B, CUZ, DUKE, F, K, MO, NY, U, US, USM); Atalaya along Rio Carbon, 10 km from Pilcopata on rd. to Shintuya, 650-700 m, 6 Apr 1985, *Stein* 2515 (F, MO, NY, US, USM); 2.5 km W of Pilcopata on rd. to Patria, 700 m, 7 Apr 1985, *Stein* 2518 (CUZ, F, MO-2 sheets, NY, US, USM). Paucartambo Prov., Tambomayo, 1600 m, Jul 1935, *Vargas* 87 (MICH); Prov. Quispicanchis, Mándor Marcapata, 1200 m, 11 Dec 1943, *Vargas* 3730 (CUZ, MICH); Paucartambo Prov., near Santa Isabel, 1200 m, 26 Jul 1936, *Vargas* 7152 (CUZ, UC); Quispicanchis between Quince Mil and Huacyumbe, 500-700 m, 21-28 Jan 1949, *Vargas* 7805 (CUZ); San Lorenzo, Marcapata, 700 m, 23 Oct 1950, *Vargas* 9741 (CUZ); Paucartambo Prov., Callanga, 1500 m, *Wojtkowski* 435 (USM). Junín: Satipo, May 1941, *Cubas s.n.* (USM, mixed collection with *C. cornutus*). Madre de Dios: Prov. Manu, Shintuya, 550 m, 11 Oct 1971, *Chávez* 831 (MO); Prov. Manu, Manu Park, Cocha Cashu uplands, 400 m, 19 Aug 1986, *Núñez* 5825 (MO).

Discussion. *Centropogon roseus* bears a close resemblance to *C. gamosepalus*, but can be distinguished from that species by: the more elongate, usually glabrous inflorescence; the bracts usually shorter than the pedicels and thus not covering the lower portion of the flowers; the calyx proportionately more connate (0.5-0.75 vs. 0.25-0.5); and the often narrower leaves (3-4 times vs. 2-3 and only rarely 4 times as long as wide). Furthermore, many collections of *C. roseus* have distinctive fimbriate leaf margins, a feature never found in *C. gamosepalus*. The only other member of subgen. *Centropogon* with fimbriate leaf margins is the central Peruvian *C. sciaphilus*, a species not easily confused with *C. roseus* on account of its free sepal lobes and pedunculate

inflorescence. *Centropogon roseus* can be easily differentiated from the southern Peruvian form of *C. capitatus* with which it sometimes occurs. In addition to the free sepals, *C. capitatus* has a characteristically little-elongate, "capitate" inflorescence with large bracts that cover the lower portions of the flowers. Furthermore, the anther tube in these southern populations of *C. capitatus* is densely pilose rather than glabrous (or rarely sparsely pilose) as in *C. roseus*.

The leaf margin in *Centropogon roseus* is quite variable, ranging from almost entire with only slight denticulations to fimbriate with marginal processes to 6 mm long. The type specimen, *Williams 584*, has relatively short but salient teeth between 1 and 2 mm long, whereas the type of *C. inflatus* has teeth to 3 mm long. A thorny problem is whether to consider the fimbriate-leaved morph as taxonomically distinct from the more entire- or denticulate-leaved morph.

During fieldwork in Cuzco Department, Peru, both leaf forms of *C. roseus* were found growing intermixed in the forests around Atalaya. A detailed analysis of this population revealed several floral characters that appeared to correlate with leaf margin type (see Table 15). Whether these differences are an artifact of the limited sample size available for the fimbriate morph, or reflect the maintenance of genetic integrity of these morphs is open to question. In view of the extreme similarity in corolla morphology and overall inflorescence structure, the two morphs must be visited by the same sicklebill hummingbird pollinator, *Eutoxeres condamini*. Although the differences noted in corolla and androecium length and style exertion could theoretically indicate a subtle spatial partitioning of this shared pollen vector, given the ease of crossing widely divergent species in subgen. *Centropogon*, including the closely related *C. gamosepalus* (see Chapter V), it is unlikely that these nearly identical morphs represent non-intergrading biological entities. Examination of the other available collections of *C. roseus* shows a general intergradation between the two leaf morphs with respect to the

corolla characters noted in Table 15. Greenhouse-grown plants from seed of *Stein 2514* maintained the basically denticulate leaf margin of the parental plant but also developed a slight tendency towards more salient and prominent teeth. In *C. sciaphilus*, the other Peruvian species with fimbriate marginal projections, a similar variation range in leaf margins occurs, with certain plants developing only slightly-exserted callose-denticulations. For these reasons, an inclusive concept of *C. roseus* is used here, which accommodates considerable variation in leaf margin dentition.

Table 15

Morphological comparison of fimbriate and non-fimbriate Centropogon roseus intrapopulational

leaf morphs from Atalaya, Cuzco Department, Peru

	non-fimbriate morph (Stein 2514)	fimbriate morph (Stein 2515)
Leaf margins	teeth less than 1 mm long	teeth fimbriate, 1-4 mm
Calyx length	11-17 mm	13-21 mm
Calyx connation (proportion)	0.66-0.83 ($x = 0.73$)	0.50-0.62 ($x = 0.58$)
Corolla tube length	36-40 mm	32-35 mm
Dorsal corolla lobe		
Length:	8-9 mm	7 mm
Attitude:	recoiled	spreading
Androecium length	47-55 mm	45-47 mm
Filament exertion	4-8 mm	0-2 mm

12. *Centropogon silvaticus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 6. 1935.

Type: Peru. Loreto: Balsapuerto, 220 m, May 1933, Klug 3062 (lectotype here designated, US; isolectotypes, B, BM, F, G, photo MICH-negs. 123 & 124, GH, K, MO, NY, S, W).

Erect suffrutescent herbs to 0.5 m tall; stems glabrous, often with close-set, spiralling petiole scars and occasionally with pedicel scars from old auxotelic inflorescences. Leaves clustered near stem apex, blades narrowly lanceolate to very narrowly elliptic, 6-13 times longer than wide, 10-20 x 0.7-2.7 cm, apex attenuate, base decurrent, margins serrulate, 5-10 callose-tipped teeth per cm; lamina drying chartaceous to membranaceous, adaxial surface dark green, glabrous, abaxial surface paler, minutely hirtellous on midvein and secondaries; secondary veins 9-13, acutely ascending but intersecting midvein at a obtuse or right angle; petioles 5-20 mm long, minutely hirtellous. Inflorescence an erect, bracteate, auxotelic, subcorymbose raceme, the flowers congested, the rachis 1-2.5 cm long and minutely hirtellous; bracts persistent, lanceolate or narrowly elliptic, 2.5-4 cm long or often longer and only slightly shorter than vegetative leaves, always longer than the subtended pedicels, apex acute, margins serrulate and occasionally ciliolate, adaxial surface sparsely pubescent or rarely glabrescent, abaxial surface sparsely to moderately hirtellous; pedicels erect at anthesis, remaining erect or drooping with age, 15-20 mm long, moderately to densely hirtellous, bracteoles basal, ca. 1 mm long. Flowers ca. 50 mm long; hypanthium subcylindric, rounded or slightly tapering basally, 4-6 x 4-5 mm, moderately puberulent to hirtellous, intersepalar nectaries present; calyx gamosepalous, erect, 11-22 mm long, connate at base 5-7(-9) mm, the lobes narrowly triangular, 2-3 mm wide at base, minutely puberulent; corolla deep red to rose-red, the tissue thin, sparsely to moderately puberulent or hirtellous; corolla tube 30-35 mm long, the basal portion rather narrow and cylindric, 4-

6 mm wide at base narrowing above to (2.5-)3-4 mm wide, the throat only slightly expanded, 8-10 mm wide, curved ca. 45°; dorsal lobes 7-8 x ca. 3 mm, lateral lobes asymmetrically triangular, 5-6 mm long, with caudate, decurved tips, ventral lobe 4-6 mm long with an acute, deflexed tip; androecium 45-48 mm long; filament tube 40-42 mm long, entirely glabrous, adnate to corolla ca. 7 mm above base, exserted from corolla tube 5-7 mm; anther tube 5-6 mm long, densely long-pilose in dorsal and ventral connectives with white trichomes, antheridial scale 2-2.5 mm long; style exserted to 2 mm from anther tube, stigma ca. 3 mm in diam. Fruit spheroidal, to 9 x 11 mm; seeds orbicular or widely elliptic, ca. 0.5 mm long.

Distribution. A rare herb of lowland forests, in understory or on riverine rocks. Known only from Amazonas and Loreto departments of northeastern Peru at 220-350 m.

Additional specimens examined. PERU. Amazonas: Upper Rio Cenepa region, creek flowing into Quebrada Huampami, 300 m, 10 Sep 1972, Berlin 22 (MO); Bagua Prov., N of Mesones-Mura, along quebrada, 350 m, 7 Jul 1984, Knapp & Mallet 6573 (BH, K, MO, NY, US). Loreto: between Balsapuerto and Moyobamba, Aug 1938, Sandeman 152 (K).

Discussion. *Centropogon silvaticus* is closely related to *C. gamosepalus*, but can be distinguished by the extremely narrow leaves and bracts and by the narrow corolla with little-expanded throat. The growth habit appears distinctive as well, with the leaves clustered near the stem apex, leaving a characteristic spiralling of petiole scars on the bare lower portion of the stem. In leaf width, *C. eurystomus* approaches *C. silvaticus*, but the extremely wide (17-21 mm) corolla throat and glabrous anther tube

of the former contrasts sharply with the narrow corolla and pilose anthers of *C. silvaticus*.

The leaves on the four known collections of *C. silvaticus* vary from 10-13 times longer than wide in *Klug 3062* (the type collection) and *Sandeman 152* to 6-7.3 times in *Knapp & Mallet 6573*. *Berlin 22* is intermediate at 7.6-10 times longer than wide. Although the two latter collections have leaves relatively wider than those found on the type, they are still far narrower than those of *C. gamosepalus*, which ordinarily are 2-3 times longer than wide, and only exceptionally as much as 4 times, longer than wide (e.g., *Stein 3020*).

13. *Centropogon quebradanus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 29: 61, pl. 116, fig. 1. 1931. Type: Ecuador. Zamora-Chinchipe: Quebrada Honda, 19 Sep 1876, André 4602 (holotype, K; isotype, K p.p.).

Erect herbs 25 to 75 cm tall, branching at base; stem sparsely pubescent with short, spreading trichomes, glabrescent below; latex white. Leaves clustered near apex of stem, narrowly elliptic, 10-20(-25) x 4-6(-7) cm, apex attenuate, base cuneate, margins irregularly serrate, from 3 coarse callose-tipped teeth per cm to 5-7(-9) finer serrations per cm; lamina thin but stiff when fresh, somewhat concave and conspicuously bullate from deeply impressed secondary and tertiary veins, drying chartaceous and wrinkled, adaxial surface very dark green, glabrous, abaxial surface paler, moderately hirsutulous especially along veins with spreading uniserial, multicellular trichomes 0.25-0.75 mm long; secondary veins 8-10, acutely ascending; petioles elongate, 15-30 mm long, hirsutulous to hirtellous. Inflorescence an erect, terminal, capitate raceme, to 3 cm long, the flowers congested, the rachis moderately to densely hirtellous; bracts obovate to widely spatulate, apex apiculate to rounded, middle bracts usually 2-3 x 2-2.5 cm, exceeding the length of the subtended pedicels, the lower bracts longer, grading gradually into vegetative leaves, adaxial surface glabrous, dark green and bullate when fresh, abaxial surface densely hirtellous; pedicels erect at anthesis, 10-15 mm long, densely hirtellous, bracteoles sub-basal, filiform, 2-3 mm long. Flowers 45-50 mm long; hypanthium hemispheric, 3-4 x 4-6 mm, slightly 5-ribbed, moderately to densely hirtellous, intersepalar nectaries not seen; calyx gamosepalous, 13-18 mm long, connate 1/2 to 2/3 of length, erect, moderately hirtellous to puberulent, the tube slightly inflated, 8-11 mm wide, the lobes triangular 4-8 x 4-5 mm, serrulate; the corolla pale to deep pink, whitish within tube, the tissue thin, puberulent to hirtellous with spreading trichomes 0.5-0.75 mm long, the lobes ciliate; corolla tube 30-35 mm long, the lower

portion hidden by calyx, straight, 4-5 mm wide but narrowing slightly just below throat, the throat moderately expanded, 11-13 mm wide, laterally and ventrally distended or pouched, curved ca. 50-65°; dorsal lobes spreading to recoiled, 9-10 x ca. 4 mm, lateral lobes asymmetrically triangular, 6-7 x ca. 4 mm wide at base, with decurved, caudate tips, ventral lobe ascending-erect, triangular ca. 7 mm long, with an acute, deflexed tip; androecium 45 mm long; filament tube ca. 40 mm long, white except purplish where exserted, entirely glabrous or pilose at summit, adnate to the corolla 4-5 mm above the base, exserted 0-4 mm from the corolla tube; anther tube 5-6 mm long, thecae gray, connectives purplish, dorsal and ventral ones densely short-pilose with white trichomes, antheridial scale 2-2.5 mm long; style exserted from anther tube to 3 mm, stigma purplish ca. 3 mm in diam. Fruit not seen.

Distribution: A very rare understory herb known only from cloud forests of Morona-Santiago and Zamora-Chinchipe provinces of southern Ecuador at 1900-2000 m.

Additional specimen examined. ECUADOR. Morona-Santiago: 3 km above Plan de Milagro on Limón-Cuenca rd, 1900-2000 m, 18 May 1985, Stein 2820 (AAU, K, MO, NY, QCA, QCNE, US).

Discussion. *Centropogon quebradanus* is an upper elevation derivative of *C. gamosepalus* from which it is distinguished by the unusual bullate leaves, very low habit, pale pink rather than pink-red or red corolla, and pubescent to hirsutulous lower leaf surfaces, inflorescence rachis, and flower parts. The dark green, bullate leaves are very striking and when fresh, are reminiscent of many Gesneriaceae.

The type of this species, André 4602, was collected in the Nudo de Sabanilla region of Zamora-Chinchipe Province, Ecuador, not in Colombia as stated by Wimmer

(1931). McVaugh (1949) has noted that all of André's numbers over 4500 were collected in Ecuador, and the date of this collection (19 September 1876) accords well with his presumed presence south of Loja. Furthermore, a "Quebrada Honda" exists near the village of Valladolid. This locality was visited by Steyermark in the 1940s where he collected several other localized endemics first found by André. *Centropogon quebradanus* should be expected in cloud forests between the type locality and the Plan de Milagro region, some 200 km north, where I have recently recollected the species.

14. *Centropogon eurystomus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 29: 60, pl. 116, fig. 4. 1931. Type. Ecuador. Pastaza: "Bombonasa" [Rio Bobonaza], May 1856, Spruce s.n. (holotype, K).

Herbs to 0.6 m tall; stems to 5 mm in diam., moderately hirtellous becoming densely so towards apex, the trichomes stiff, uniseriate, and multicellular, to 0.5 mm long. Leaves narrowly elliptic, 4 times longer than wide, 12-17 x 3-3.8 cm, apex acute to attenuate, base cuneate, margins serrulate with 4-6 callose-tipped teeth per cm, ciliolate; lamina drying chartaceous to membranaceous, adaxial surface very sparsely covered with short, appressed trichomes, abaxial surface moderately hirtellous with stiff, spreading trichomes, densely so on midvein and secondaries; secondary veins 8-10, acutely ascending; petioles 5-15 mm long, hirtellous except along adaxial groove. Inflorescence an erect, bracteate, terminal raceme to 2 cm long, the flowers congested, the rachis densely hirtellous; bracts oblanceolate, 1.5-4 cm long, generally as equaling or exceeding the length of the subtended pedicels, apex acute, margins serrulate and ciliolate, adaxial surface sparsely hirtellous, abaxial surface moderately so; pedicels erect, slender, 15-20 mm long, moderately hirtellous or glabrescent, bracteoles basal, linear, 1.5-2 mm long. Flowers 65 mm long; hypanthium subcylindric, 4-5 mm long, ca. 4 mm wide at summit, the base tapering slightly into pedicel, glabrous, intersepalar nectaries not seen; calyx, erect, 11-12 mm long, basally connate 4-5 mm, glabrous, the tube mostly appressed to corolla, 5-6 mm wide, the lobes narrowly triangular to ligulate, 2-3 mm wide at base, apex acute, margins with few callose-tipped teeth; corolla bright red, the tissue very thin, drying membranaceous, glabrous; corolla tube 37-40 mm long, basal portion straight and cylindrical, 15-18 x 4-6 mm, the throat ventricose and abruptly inflated, 17-21 mm wide, laterally and ventrally distended or pouched, curved ca. 45°; dorsal lobes recoiled, 10-12 x ca. 6 mm, lateral lobes asymmetrically triangular from

wide base, ca. 6-7 mm long, ventral lobe saccate, ca. 6 mm long with a long, acute to attenuate, deflexed tip; androecium ca. 60-65 mm long; filament tube ca. 55-60 mm long, glabrous, adnate to corolla 6-7 mm above base, exserted from corolla 6-10 mm; anther tube 6 mm long, glabrous, antheridial scale 1.5-2 mm long; style little-exserted, stigma 3 mm in diam., appressed to anther tube. Fruit spheroid to obloid, to 10 x 14 mm, apparently smooth; seeds orbicular to oblong-angular, ca. 0.65 mm long.

Distribution. A rare herb of lowland rainforest, known only from the the confluence of the ríos Bobonaza and Pucayacu in Pastaza Province of eastern Ecuador at ca. 300 m.

Additional specimen examined. ECUADOR. Pastaza: Río Bobonaza, on elevated ground below Montalvo (Limon), 300 m, 17 Jul 1980, Ollgaard et al. 34544 (AAU).

Discussion. Known from only two collections made 124 years apart, *C. eurystomus* is one of the rarest species in subgen. *Centropogon*. It is almost certainly derived from the widespread *C. gamosepalus*, which occurs to the west along the base of the Andes. The most striking aspect of *C. eurystomus*, and one that immediately distinguishes it from *C. gamosepalus*, is the extremely inflated, almost balloon-like corolla throat to which the name refers. The pressed width of the corolla throat in *C. gamosepalus* rarely exceeds 15 mm, while in *C. eurystomus* the throat is commonly wider than 20 mm. Several other features serve to separate these two species as well. The leaves of *C. eurystomus* are narrower than those typical of *C. gamosepalus* (4 vs. 2-3 times longer than wide), but some populations of the latter species (e.g., Stein 3020) occasionally approach this. *Centropogon eurystomus* also has a much more hirtellous

lower leaf surface with longer trichomes (to 0.5 mm) and a sparsely pubescent rather than glabrous upper leaf surface. Its flowers are also slightly longer than those of *C. gamosepalus* (65 vs. 50-60 mm).

The type of *C. eurystomus* was collected by Spruce along the Río Bobonaza in May of 1856. Although the exact locality is not noted on the specimen label, it was most likely collected during his twenty-day stay in Pucayacu (Spruce, 1908). This accords well with the recent recollection of this species at precisely that locality, the confluence of the Río Pucayacu and Río Bobonaza, a site now known as Montalvo (2°05'S, 76°55'W).

15. **Centropogon undulatus** B. A. Stein, sp. nov. Type. Peru. Pasco: Oxapampa Prov., El Tunqui alto, 57 km from Oxapampa, 10°15'S, 75°30'W, 1700 m, 14 May 1982, Smith et al. 1571 (holotype, MO; isotypes, AMAZ, F, NY, US, USM). Fig. 15F-I.

Creeping herbs to 1 m long, glabrous throughout; stems drying with prominent ridges. Leaves elliptic to narrowly elliptic, 10-15 x 3.5-6.5 cm, apex acuminate, base cuneate, margins serrulate with 4-5 callose-tipped teeth per cm; lamina drying chartaceous to membranaceous, adaxial surface dark green, abaxial surface paler; secondary veins 10-13, arcuate-ascending and occasionally forming submarginal loops with superadjacent secondaries, slightly raised abaxially; petioles 20-25 mm long. Inflorescence a lax, terminal, short-bracteate raceme, elongating to 20 cm, the floral internodes ca. 1 cm long at anthesis, the rachis drying ridged; bracts persistent, elliptic to obovate, mostly 4-10 x 2-4 mm, apex acute, base cuneate, margins serrulate; pedicels flexuous, 60-70 mm long, bracteoles sub-basal, minute, less than 1 mm long and often not apparent. Flowers ca. 45 mm long; hypanthium spheroid to obloid, rounded basally, 5-6 x 6-9 mm, smooth with 5 prominent veins, intersepalar nectaries not seen; calyx gamosepalous, 10-11 mm long, connate basally for ca. 3/4 of length, the lower portion of calyx tube erect and cylindric, 2-3 x 5-6 mm, the upper portion of tube rotate-undulate, 5-7 mm long and spreading to 15-20 mm wide, the lobes broadly rounded to broadly triangular 3(-4) x 5-7 mm, apex rounded but callose-apiculate, margins denticulate; corolla red to orange-red externally, yellow-orange within, the tissue thin, entirely glabrous; corolla tube 25-27 mm long, the lower portion of tube straight and cylindric, ca. 2.5 mm wide at base, gradually widening to 4 mm just below throat, the throat abruptly ampliate, 10-12 mm wide, sharply curved ca. 55-65°; dorsal lobes reflexed at anthesis, ca. 9 x 5 mm, lateral lobes asymmetrically triangular, ca. 5-6 x 4

mm with attenuate, decurved tips, ventral lobe triangular, 5 mm long with an acute, deflexed tip; androecium 35-40 mm long; filament tube 30-35 mm long, orange-yellow except purplish where exserted, glabrous throughout, adnate to corolla ca. 6 mm above base, exserted 3-5 mm from corolla; anther tube 5-6 mm long, densely pilose in dorsal and ventral connectives with purple trichomes to 1 mm long, antheridial scale 2 mm long, obtuse or truncate at apex; style exserted 0-2 mm from anther tube, stigma 2-3 mm in diam. Fruit obloid to depressed obloid, to 10 x 20 mm, with 5 prominent ridges and star-shaped in cross-section; seeds elliptic, ca. 0.6 mm long.

Distribution. A creeping herb of wet mossy slopes and stream-banks in montane forest, known only from the Río Tunqui area of the Cordillera Yanachaga in Pasco Department of central Peru at 1700-1800 m.

Additional specimen examined. PERU. Pasco: Headwaters of Río Tunqui, trail to Chuchurras-Palcazu, 1800 m, 2 Jan 1984, Foster et al. 7728 (F, K, MO, NY, US).

Etymology. The epithet *undulatus* (Latin for wavy) is in reference to the distinctive rotate-undulate calyx that characterizes this species.

Discussion. *Centropogon undulatus* is an upper-elevation member of the *C. gamosepalus* species group, with which it is allied based on the fused sepals, the similar corolla morphology, texture, and color, and the small seeds. It differs from all other species in this group by its creeping habit and unusual rotate-undulate calyx. Morphologically it is most similar to *C. alectrolophos* from northern Ecuador and southern Colombia, sharing with that species a non-erect habit, a lax inflorescence (at least in some *C. alectrolophos*), very short floral bracts, minute and inconspicuous

bracteoles, an almost completely fused calyx, a lack of intersepalar nectaries, and reddish-orange to yellowish-orange corollas. These two species are separated by some 1200 kilometers, both being restricted to eastern outliers of the Andes. It is not clear whether these two taxa represent independent upper-elevation derivations from *C. gamosepalus*, or are widely disjunct sister species derived from an upper-elevation ancestor.

16. *Centropogon electrolophos* B. A. Stein sp. nov. Type. Ecuador. Napo: Baeza-Tena rd., 37 km from Baeza, S of Cosanga, 2150 m, 28 Mar 1979, *Holm-Nielsen* 16250 (holotype, AAU). Fig. 15A-E.

Climbing vines or scandent herbs to 2 m long, glabrous throughout; rooting from base or rarely with adventitious roots from upper stem and inflorescence. Leaves distichously retrorse on pendent shoots, otherwise spirally arranged, the blades narrowly ovate to elliptic, 13-18(-23) x 5-10 cm, apex acute to attenuate, base rounded to acute, rarely subcordate, margins occasionally tinged purple, serrulate to fimbriulate with 7-9 salient callose-tipped teeth per cm, these short-exserted to 1 mm; lamina drying chartaceous, both surfaces glabrous; secondary veins 11-13, close-set, the veins straight to slightly arcuate-ascending, intersecting the midvein at ca. 60-70°; petioles 10-15(-25) mm long. Inflorescence a pendent, short-bracteate, terminal raceme to 10 cm long, the flowers congested at apex, becoming lax basally, often secund, the rachis glabrous with prominent pedicel abscission scars to 5 mm high; bracts persistent, oblong to elliptic, mostly 4-10 mm long and usually less than 1/4 the length of the subtended pedicels, apex acute to obtuse, margins fimbriulate; pedicels slender, occasionally flexuous, retrorsely assurgent at anthesis, assurgent to nodding or pendulous with age, 20-30(-40) mm long, bracteoles not visible. Flowers 50-55 mm long; hypanthium stout, hemispheric to spheroid with rounded base or slightly obconic and tapering into pedicel, 5-8 mm long, 6-10 mm wide at summit, intersepalar nectaries lacking; calyx 12-20 mm long, almost completely connate, the tube moderately inflated, 8-12 mm wide, enlarging with age, the lobes 2-3 mm long, rounded to triangular with undulate and fimbriulate margins; corolla orangish-red to orange, rarely canary-yellow, the tissue thin, glabrous; corolla tube 30-33 mm long, the basal portion cylindric and straight, hidden by calyx, 6-8 mm wide at base narrowing to 3-4.5 mm wide just below throat, the throat abruptly

expanded, 9-12 mm wide, curved ca. 50°; dorsal lobes 9-10 x 4-5 mm, lateral lobes asymmetrically triangular 6-7 x ca. 4 mm with attenuate, decurved tips, ventral lobe 4-5 mm long with an acute, deflexed tip; androecium 45-50 mm long; filament tube 40-45 mm long, glabrous, adnate to corolla 6-7 mm above base, exserted from corolla tube 3-5 mm; anther tube 5-6 mm long, thecae gray, connectives purplish, dorsal and ventral ones densely short-pilose with purple trichomes, antheridial scale 1.5-2 mm long; style exserted from anther tube to 2 mm, stigma ca. 3 mm in diam. Fruit oblate to rhomboid, to 10 x 20 mm, prominently 5-ridged and star-shaped in cross-section; seeds widely ellipsoid to ellipsoid, ca. 0.6 mm long.

Distribution. A rare cloud forest vine or scandent herb known only from the Cordillera de Guacamayos of Napo Province in central Ecuador and the Cordillera Portachuelo of Putumayo Department in extreme southern Colombia, found from 1500-2500 m.

Etymology. A common vernacular name for members of subgenus *Centropogon* in South America is *Cresta de Gallo*, or "cockscomb," in reference to the showy curved reddish or orangish flowers, a feature that this beautiful new species ably illustrates. The specific epithet *alectrolophos* is of Greek derivation: *alectros* meaning rooster and *lophos* signifying crest. As a Greek substantive, the ending *-os* is here retained rather than substituting the latinized adjectival *-us* ending.

Additional specimens examined. COLOMBIA. Putumayo: E slope of the Cordillera Oriental, between El Silencio and La Cabaña (Sibundoy-Urcusique rd.), 2200-2400 m, 31 Dec 1940, Cuatrecasas 11511 (F, US); km 90-91 on rd. between Sibundoy and Mocoa, 2500 m, 26 Jan 1976, Luteyn et al. 5040 (COL).

ECUADOR. Napo: Baeza-Tena rd., S slope of Cordillera de Guacamayos, above Jondachi, 1500 m, 7 Feb 1980, *Harling & Andersson 16331* (GB), 1700 m, *Harling & Andersson 16362* (GB).

Discussion. *Centropogon electrolophos* is an upper-elevation derivative of *C. gamosepalus*, but is differentiated from that species by its vining habit and pendent inflorescences as well as by the very short, fimbriulate bracts, the pronounced pedicel abscission scars, the almost entirely connate and tubular calyx with short-fimbriulate lobes, the very reduced (absent?) bracteoles, and the orangish-red to yellow corolla. Another unique feature found in this species are the adventitious roots on the upper stem and inflorescence in *Harling & Andersson 16362*, which presumably were produced when the pendent inflorescence contacted the soil surface.

Collections from southern Colombia differ somewhat from those near the type locality in Ecuador. The three collections known from the Cordillera de Guacamayos have strictly pendent inflorescences with the flowers retrorse and secund; those from the Cordillera Portachuelo are less obviously pendent and have slightly longer, more flexuous pedicels. The attitude of the flowering and fruiting pedicels on these Colombian collections, however, indicates that the inflorescences were also directed downward, and the label information on *Cuatrecasas 11511* states that the plant was in fact vining ("hierba robusta, trepadora"). This specimen is unusual in that the corolla color given by the collector is canary yellow ("amarillo de canario"), a color uncommon in subgen. *Centropogon* as a whole and the only instance known in sect. *Amplifolii*. Because label information on the other collections of *C. electrolophos* note corolla colors ranging into the orange spectrum, rather than the typical reds and pinks of *C. gamosepalus*, a yellow pigment is not completely anomalous but merely an endpoint in the spectral range present in this species. While the Colombian collections differ slightly, I prefer to include them

in the same species until more collections of this rare plant clarify the degree of geographic variability.

17. *Centropogon escobarae* B. A. Stein, sp. nov. Type. Colombia. Antioquia:

Municipality of Urrao, trail btwn. Incarnación and Parque de las Orquídeas, from el Alto del Páramo to the house of Don Emilio, Río Calles, 1200-2500 m, 13 Jun 1981, *Escobar et al.* 1625 (holotype, HUA).

Herb 1.5 m tall, almost entirely glabrous; stem deep maroon, zig-zig at apex.

Leaves widely elliptic, to 27 x 17 cm, apex acute, base cuneate, denticulate to crenulate-denticulate with 3-4 small, purple callosities per cm, these protruding from leaf margin to 0.5 mm; lamina drying chartaceous, adaxial surface dark green, glabrous, abaxial surface paler, glabrous, but with minutely muricate veins; secondary veins ca. 18, diverging from mid-vein at a very wide angle, widely arcuate; petioles elongate, 9-10.5 cm long, deep maroon, abaxial surface glabrescent or minutely sordid-puberulent.

Inflorescence an erect, short-bracteate, terminal, subcorymbose raceme, 4.5 cm long, with 15 or more densely congested flowers; bracts very reduced, triangular, 6-8 x 2.5-4 mm, apex acute, margins minutely serrulate; pedicels erect at anthesis, 10-20 mm long, glabrescent to minutely puberulent, bracteoles not visible. Flowers 45-50 mm long; hypanthium, oblong to obovoid, 5-7 x 4-6 mm, with 5 prominent ridges opposite sepals, glabrous, intersepalar nectaries not seen; calyx 8-10 mm long, connate basally 6-7 mm, the tube, 5-7 mm wide, the lobes erect, triangular, 2.5-4 x 2.5-3 mm, entire or margins slightly revolute; corolla orangish, glabrous, the corolla tube 25-30 mm long, the basal portion obscured by gamosepalous calyx, straight and cylindric, 15-20 x 3-4 mm, the throat moderately ampliate, 7-9 mm wide, curved 40-60°; androecium 35-40 mm long, glabrous throughout; filament tube 30-35 mm long, yellowish-orange except purplish where exserted, adnate to corolla ca. 4 mm above base, exserted from corolla tube ca. 5 mm; anther tube 6 mm long, thecae dark gray, connectives deep purplish, antheridial

scale ca. 1.5 mm long; style exserted from anther tube 0-2 mm, stigma ca. 2 mm in diam. Mature fruit not seen.

Distribution. Known only from a single collection made in the northern Cordillera Occidental of Antioquia Department, Colombia between 1200 and 2500 m.

Etymology. This very distinctive new species is named in honor of its discoverer, Dr. Linda Albert de Escobar.

Discussion. This imperfectly known new species displays a unique combination of features that make it unmistakably distinctive, even on the basis of the single specimen available. It can be recognized by the gamosepalous calyx, widely elliptic leaves with extremely long petioles, unusual "zig-zag" upper stem, very congested inflorescence with very short bracts, and moderately sized, orangish corolla. On the basis of leaf shape and venation pattern it would appear to be *C. congestus*, a species well-represented in the Cordillera Occidental of Colombia. However, the general lack of both indument and leaf excrescences, as well as the fused sepals and orangish corolla argue against this alignment. Rather, it appears that *C. escobarae* may be related to *C. electrolophos* of extreme southern Colombia and northern Ecuador. In addition to gamosepalus calyces, these two species share a number of other presumably derived features, including flower color (orange is elsewhere unknown in the *C. gamosepalus* species complex), inconspicuous bracteoles, very short inflorescence bracts, rather prominent hypanthium ridges opposite the sepal lobes, and very regular, parallel secondary venation. *Centropogon escobarae* differs from *C. electrolophos* in many other features, including habit (erect vs. scandent or vining); shorter flowers (androecium 35-40 mm vs. 45-50 mm); an erect and congested (rather than pendent and lax)

inflorescence; denticulate rather than fimbriate leaf margins; and much larger leaves with longer petioles.

If *C. escobarae* is related most closely to *C. alectrolophos* it poses an interesting phytogeographic puzzle, because they occur on the opposite slopes of the Andes and are separated by over 600 kilometers. It may be significant, though, that *C. alectrolophos* is found adjacent to the Nudo de Pasto, an area of relatively close proximity between the Cordillera Oriental and Occidental.

18. *Centropogon alsophilus* F. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13: 402. 1937.

Type. Peru. San Martin: Jepelacio near Moyobamba, 1200-1600 m, Klug 3432 (holotype, US; isotypes, F, S). Fig. 8D.

Erect, stout, suffrutescent herbs to subshrubs 0.5-2 m tall, branching from base; stems glabrous, striate towards base; latex opalescent, oxidizing brownish. Leaves mostly oblanceolate to narrowly obovate, occasionally oblong or elliptic, (10-)14-21 cm long, 4.5-8.5 cm wide, apex acute to short acuminate, rarely obtuse, base cuneate to rounded, margins from almost entire to serrulate, 3-4(-5) little-exserted callosities per cm; lamina thick and coriaceous when fresh, drying coriaceous, abaxial surface dark green and nitid, glabrous, adaxial surface pale green, minutely puberulent along veins; secondary veins 6-9, acutely to arcuate-ascending, prominently impressed abaxially and raised adaxially; petioles 5-20 mm long. Inflorescence an erect, bracteate, terminal, raceme, or rarely sub-foliate and appearing axillary through non-reduction of subtending bracts, racemes elongating to 60 cm, floral internodes congested at apex, elongating to 1-2 cm with age, rachis minutely hirtellous with short, erect trichomes, rarely scaberulous; bracts persistent, short-petiolate, narrowly oblong to oblanceolate, narrowly elliptic, or lanceolate, mostly 3-6 x 1-2 cm, both surfaces sparsely to moderately pubescent; pedicels erect at anthesis, recurved with age, 2-4 cm long, indument as on inflorescence rachis, often persistent, bracteoles subbasal or rarely inserted medially, subulate to narrowly oblanceolate, 1-5(-7) mm long. Flowers 50-60(-65) mm; hypanthium hemispheric to cylindric, rounded at base, 4-7 x 6-9 mm, moderately 10-ribbed when fresh, sparsely to moderately hirtellous, intersepalar nectaries prominent; sepals erect, tips often spreading or recurved, triangular to narrowly triangular, 5-10(-12) mm long, 2-3 mm wide at base, mostly entire or with 1-3 marginal callosities, sparsely to moderately hirtellous, sinuses planar; corolla deep to pale pink, the lobes mostly cream-colored, sparsely hirtellous or

puberulent; corolla tube (30-)35-45 mm long, 6-8 mm wide at base, narrowing very slightly above 4-5 mm-long nectar chamber, then expanding gradually throat, the throat 8-11 mm wide, not well-differentiated from lower portion of tube, curved ca. 20-30°; upper lobes recurved to recoiled, 11-13 x 3 mm, lateral lobes spreading, falcate, ca. 8-9 mm long, with acuminate, decurved tips, ventral lobe erect, triangular, ca. 7-8 mm long, with an acuminate, deflexed tip; androecium 40-55 mm long; filament tube 32-47 mm long, subterete and ca. 2 mm wide when fresh, white or purple-rose where exserted, glabrous or sparsely pilose at base of anthers, adnate to corolla 7-10 mm above base, exserted from corolla tube 2-4 mm, the exserted portion often arching upwards; anther tube 7-8 mm long, straight or slightly curved, thecae greyish or tan, connectives rose-purple, the dorsal ones sparsely white-pilose, sometimes densely so at apex, antheridial scale usually with truncate apex, ca. 3 mm long; style exserted from anther tube 0-3 mm, stigma white or greenish, ca. 3 mm in diam. Fruit widely ovoid, to 17 mm long and 23 mm wide, prominently ribbed, nectar chamber persistent; seeds oblong to widely ellipsoid, ca. 0.8 mm long.

Distribution. A locally abundant herb to subshrub in disturbed forest edges and moist roadsides. *Centropogon alsophilus* is restricted to a relatively limited region of extreme southern Ecuador and northeastern Peru, from the eastern foot of the Andes into the Amazon lowlands at 200-1100 m.

Additional specimens examined. ECUADOR. Morona-Santiago: La Misión Salesiano, 5 km S of Río Bomboiza, nr. Zamora-Gualaquiza rd., 800 m, 10 May 1985, Baker 6136 (NY); near Yurupaza on rd. Limón-Macas, 600 m, 28 Mar 1974, Harling & Andersson 12950 (GB); Misión Bomboiza, 800 m, 23 Apr 1973, Holm-Nielsen et al. 4156 (AAU, K, NY); camino Gualaquiza-Churujaco, 850 m, 24 Dec 1948, Scolnik 1494

(MICH); Zamora-Gualaquiza rd., 5 km N of El Chamico, 10 km S of Zumbi, 980 m, 16 May 1985, Stein 2800 (MO, NY, QCA, QCNE, US); 10 km S of Gualaquiza on rd. to Zamora, 880 m, 17 May 1985, Stein 2801 (AAU, F, K, MO, NY, QCA, QCNE, US). Pastaza: Río Capihuari, tributary of Río Pastaza, 285 m, 23 Jul 1980, Ollgaard et al. 35063 (AAU). Zamora-Chichipe: trail N across bridge from Zamora, 1030-1270 m, 17 Aug 1982, Clemants 2365 (NY); Horse-trail Guadalupe-San José de Yacuambi, 900-1000 m, 24 Apr 1974, Harling & Andersson 13948 (AAU, GB, MO, NY), 13949 (AAU, K); Namírez, 5 km N of Cumbaraza, 900 m, 24 Apr 1974, Harling & Andersson 13963 (AAU, GB, QCA); La Saquea on Río Yacuambi-Yanzatza and near Pincho, 900-1000 m, 26 Apr 1974, Harling & Andersson 1410 (AAU, GB); 3 km E of Paquisha, 1100 m, 11 Apr 1985, Harling & Andersson 23971 (GB); 16 miles E of Zamora, 1 Sep 1972, Humbles 6011 (MO); Zamora-Gualaquiza rd., 1 km S of Cumbaratza, 15 km N of Zamora, 900 m, 16 May 1985, Stein & D'Alessandro 2799 (AAU, F, K, MO, NY, QCA, QCNE, NY).

Peru. Loreto: Andoas, Río Pastaza near Ecuador border, 230 m, 16 Nov 1979, Gentry & Diaz 28126 (MO); Andoas, Río Pastaza near Ecuador border, 210 m, 15 Aug 1980, Gentry et al. 29727 (MO); Andoas, 180 m, 8 Sep 1983, Vásquez 4393 (MO). San Martín: 1 km SE of Moyobamba on Carretera Marginal to Tarapoto, 830 m, 10 Feb 1985, Stein & Todzia 2126 (AAU, DUKE, MO, NY, US, USM), 2127 (F, K, MO, NY, US, USM), 2128 (B, F, MO, U, US, USM).

Centropogon alsophilus is a well delimited species, and is characterized by an erect habit; thick, coriaceous, generally oblanceolate leaves; an elongate inflorescence with oblong bracts; erect sepals often with recurved tips; and pink, little-ampliate and gradually curved corollas. A latitudinal gradient exists in the size of flowers. Plants from the southern portion of the range (e.g., Moyobamba, Peru) have significantly shorter corolla tubes and androecia than do populations further north. Although sepal

length is variable within the Moyobamba populations, they are also often much shorter than those found in Ecuador. In contrast, plants from the northernmost portion of the range (e.g., Gualaquiza, Ecuador) have the longest corolla tubes, androecia, and sepals.

The affinities of *C. alsophilus* are problematic, and it is treated here as member of sect. *Amplifolii* primarily on the basis of the subterete filament tube and apparently auxotelic inflorescence. The species may instead be related to the widespread *C. cornutus*, with which it shares a preference for low elevation disturbed habitats, a similar corolla morphology and color, an upwardly arching filament tube, and, at least occasionally, axillary flowers. It is immediately distinguishable from that species, however, on the basis of its erect habit, the erect and usually shorter sepals, its typically racemose inflorescence, the shorter often persistent pedicels, and the thick, leathery leaves. Interestingly, in southeastern Ecuador where *C. alsophilus* is most abundant, *C. cornutus* is unknown. Elsewhere along the eastern base of the Andes *C. cornutus* is a common element in these same habitat types. Its puzzling absence suggests that *C. alsophilus* may represent an ecological, and perhaps phylogenetic, replacement in this region. Although these two species both occur in the southern portion of the range of *C. alsophilus*, I have not seen them growing sympatrically.

Jeppesen (1981) erroneously referred the Ecuadorean collections of this species to *Centropogon planchonis* Zahlbruckner. *Centropogon planchonis* is actually a synonym of *C. solanifolius*, and is based upon collections from the Cordillera Central of Colombia. *Centropogon planchonis* should not be considered a component of the Ecuadorean flora.

Fig. 15. A-E, *Centropogon alectrolophos* (A-D, from Holm-Nielsen 16250; E, from Luteyn et al. 5040). A, habit with detail of fimbriulate leaf margin. B, flower. C, longitudinal section of lower portion of flower. D, close-up of anther tube with exserted stigma. E, fruit. F-I, *Centropogon undulatus* (from Smith et al. 1571). F, habit with detail of leaf margin. G, flower. H, longitudinal section of lower portion of flower. I, anther tube.

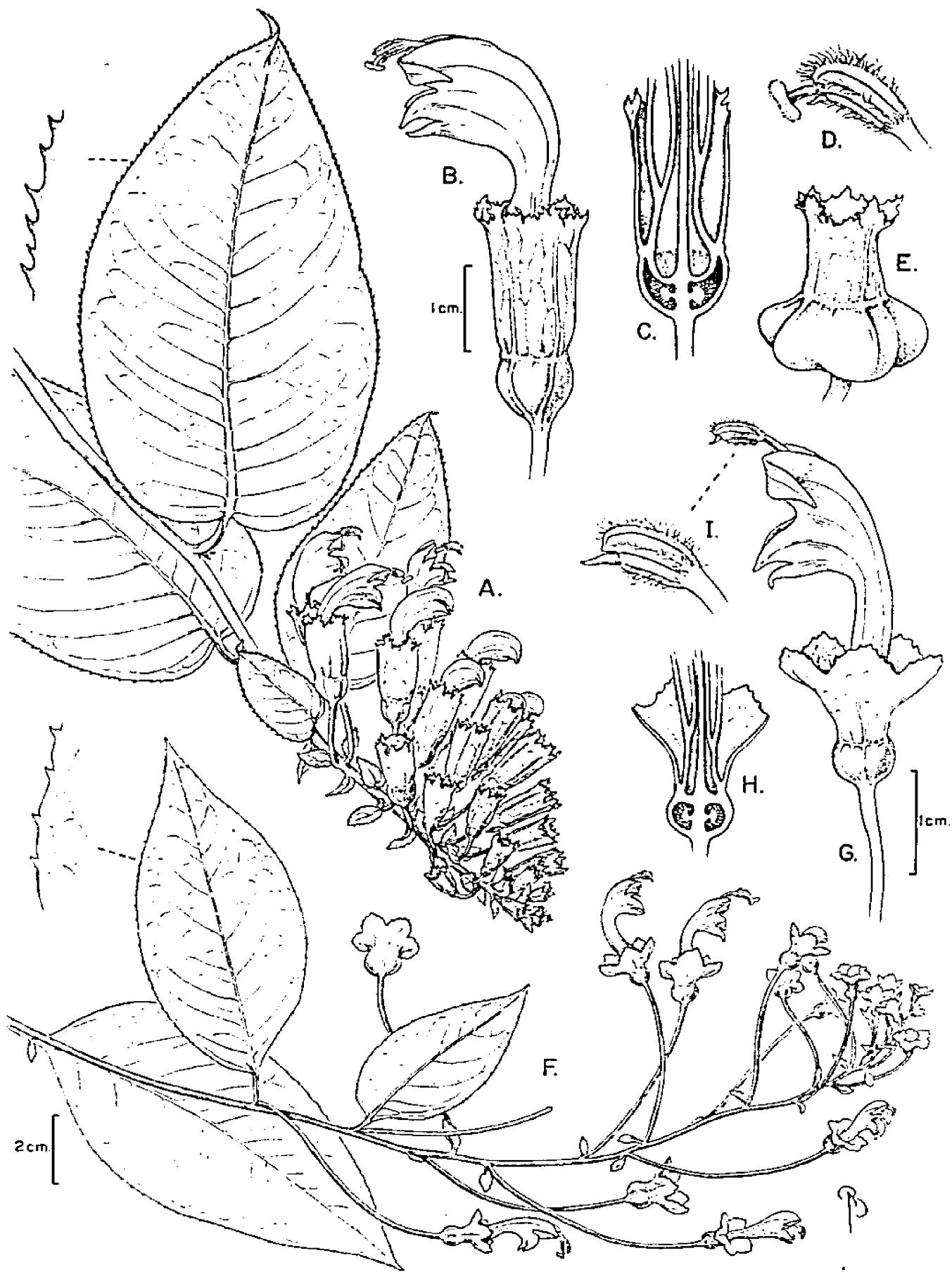


Fig. 16. Distribution map of *Centropogon capitatus*.

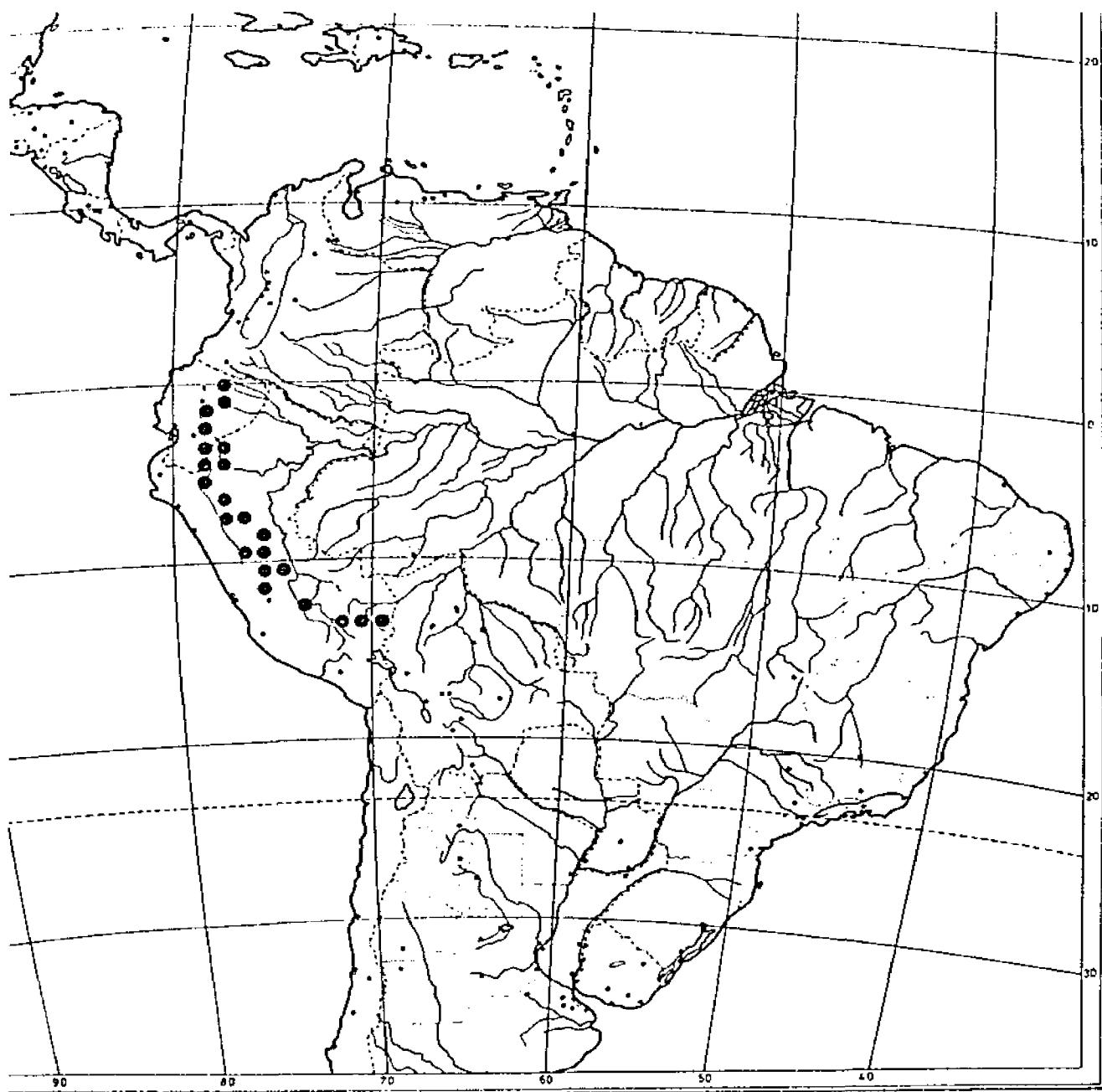


Fig. 17. Distribution map of: (●) *Centropogon macrophyllus* and (■) *C. alsophilus*.

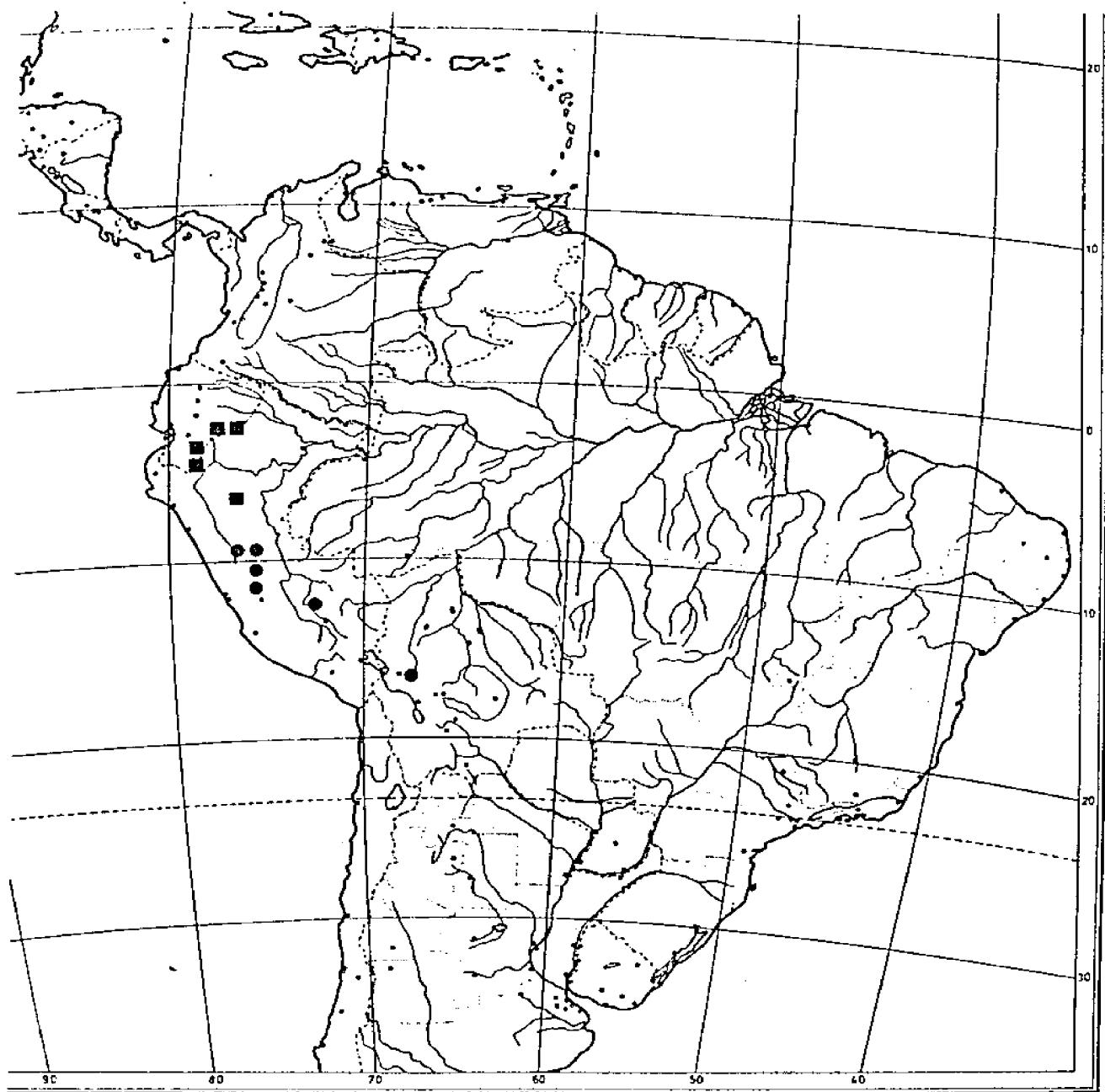


Fig. 18. Distribution map of: (●) *Centropogon umbrosus*, (○) *C. gesneriformis*, and (■) *C. congestus*.

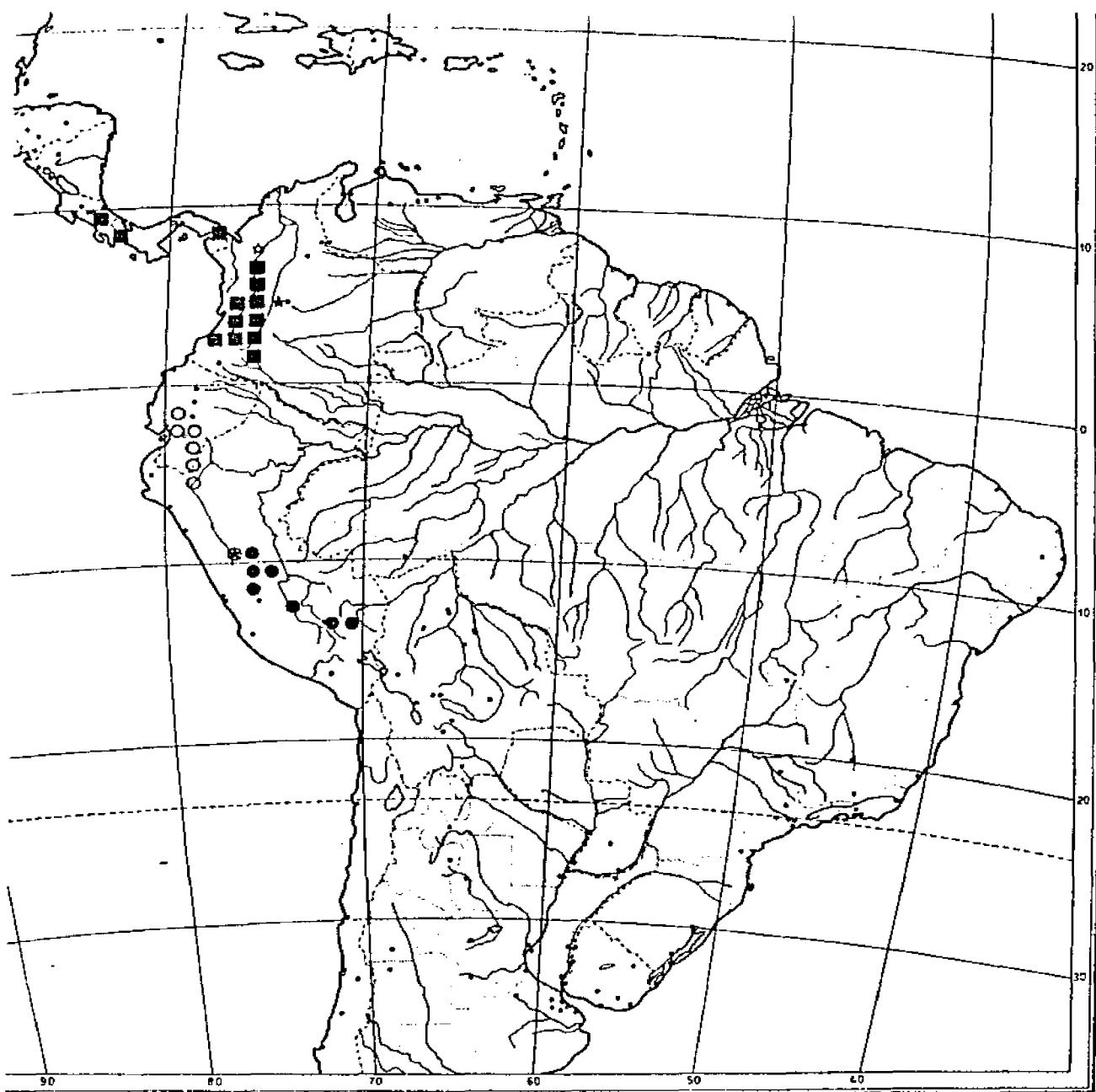


Fig. 19. Distribution map of: (●) *Centropogon hirtus*, (■) *C. uncialis*, and (▲) *C. escobarae*.



Fig. 20. Distribution map of: (●) *Centropogon gamosepalus* and (■) *C. roseus*.



Fig. 21. Distribution map of: (●) *Centropogon silvaticus*, (■) *C. quebradanus*,
(★) *C. undulatus*, (○) *C. eurystomus*, (⊕) *C. electrolophos*, and
(☆) *C. escobarae*.



Section *Campylobotrys*

Centropogon subgenus **Centropogon** section **Campylobotrys** (F. Wimmer) B. A. Stein, stat. et comb. nov.

Centropogon section *Centropogon* subsection *Corymboides* F. Wimmer grex *Campylobotrys* F. Wimmer, Pflanzenreich IV, 276b: 167. 1943. Type species here designated, *Centropogon granulosus* Presl.

The 22 species of sect. *Campylobotrys* include a wide array of morphological forms, but are centered around the widespread and highly variable *C. granulosus*. Most of the core species, as exemplified by *C. granulosus* (Fig. 15), are vines with short-bracteate, upturned-pendent inflorescences, and have moderately to abruptly curved and ventricose corollas. In addition to the typical upturned-pendent inflorescence, however, there is a great deal of variation in inflorescence structure, related primarily to the habit of the plants. In several vining species inflorescences are strictly pendent, whereas erect species normally have upright inflorescences. Well-developed peduncles are occasionally present, a feature not found in any of the other sections. Variation also exists in the length and persistence of the bracts. Caducous bracts are common, and when present the inflorescence rachis usually shows very prominent pedicel abscission scars, another good sectional character. Indument features can be distinctive in this section, with plants ranging from completely glabrous to densely pubescent and with variously modified trichomes. Trichomes with expanded papillose or pustulate bases are occasionally present, and in at least one species, *C. trachyanthus*, branched trichomes occur. The stem surface is occasionally scabrous or scaberulous, a feature that is rare elsewhere within the subgenus.

Wimmer (1943) placed most of the species included here in his grex *Campylobotrys*, which appropriately means in Greek "hook-shaped raceme", and I have used this as the basis for the sectional name. Those species with lax and strictly pendent inflorescences he included in his subsect. *Botryoides*, although it is now clear that this inflorescence type has evolved independently several times from the pendent-upturned inflorescences more typical of this section. Wimmer placed many of the species with erect habits in his grex *Amplifolii*.

Section *Campylobotrys* appears to be most closely related to sect. *Grandes* on the basis of the unusual ventrally flattened filament tube. Several anomalous species that do not fit well into any of the sections recognized (e.g., *C. pygmaeus*, *C. carpishensis*, *C. bangii*, and *C. lasiodorus*) are tentatively placed in sect. *Campylobotrys*, and are discussed in detail under the respective species.

Key to Species of Section *Campylobotrys*

1. Erect herbs or shrubs; inflorescences erect; bracts persistent.....2
2. Corolla abruptly curved (30-)45° or more, the throat well-differentiated from lower portion of tube.3
3. Sepals connate at base, the calyx tube 3-6 mm long.....27. *C. vaughianus*.
3. Sepals free to base.....4
4. Corolla less than 25 mm long, 1.5-2.5 mm wide at middle; leaves occasionally sinuate-lobate.....5

5. Corolla sharply curved or arcuate, 50-75(-90)°; leaves mostly longer than 9 cm, crenulate, serrulate or often sinuate-lobate; anther tube glabrous, antheridial scale 2.5-3.5 mm long; inflorescence trichomes never with papillose or pustulate-bases.....36. *C. arcuatus*.
5. Corolla only curved ca. 30°; leaves less than 9 cm long, serrulate, never sinuate-lobate; anther tube sparsely pilose, antheridial scale 1.25-1.5 mm long; inflorescence trichomes often with papillose or pustulate-bases.....37. *C. pygmaeus*.
4. Corolla longer than 25 mm and wider than 2.5 mm at middle; leaves never sinuate-lobate.....6
6. Inflorescence rachis, pedicels, and corolla with verrucate papillae.....7
7. Inflorescence and flower parts densely papillose-verrucose; dorsal corolla lobes remaining erect at anthesis; androecium completely included in corolla; anther tube 6 mm long; antheridial scale 3.5-3.75 mm long, often truncate.....26. *C. papillosus*.
7. Inflorescence and flower parts occasionally with verrucate papillae, but if present only sparsely so; dorsal corolla lobes recurved or recoiled at anthesis; filament tube exserted from corolla tube 4-8 mm; anther tube 7-8(-9) mm long; antheridial scale 2-3 mm long, mostly acute.....25. *C. curvatus*.
6. Inflorescence rachis glabrous, hirtellous, or tomentose, but without verucate papillae..8
8. Inflorescence rachis and peduncle densely tomentose; bracts 5-10 mm long, much shorter than subtended pedicels.....40. *C. lasiodorus*.

8. Inflorescence rachis and peduncle glabrous or hirtellous but not densely tomentose; bracts shorter to longer than subtended pedicel. 9
9. Inflorescence subtended by a slender, elongate peduncle. 10
10. Leaves fimbriate-serrate, rarely merely exserted callose-denticulate; sepals 6-10 mm long; inflorescence rachis and peduncle glabrous; corolla concolorous, reddish or pinkish-red or with yellow to orange lobes; hypanthium rhomboid to turbinate; seeds 0.8-1.1 mm long. 31. *C. sciaphilus*.
10. Leaves crenulate or denticulate; sepals 2-4 mm long; inflorescence rachis and peduncle hirtellous, occasionally glabrescent; corolla bicolored, reddish-orange basally and yellowish-orange at lobes; hypanthium hemispheric; seeds 0.6-0.7 mm long. 30. *C. latifolius*.
9. Inflorescence not subtended by a peduncle, or the peduncles relatively short and stout.
- 11
11. Corolla concolorous, pink or rose-red; filament tube exserted from corolla tube 2-5 mm; sepals occasionally longer than 10 mm, the tips erect; intersepalar nectaries absent; Central America.
- 19. *C. granulosus*.
11. Corolla bicolored, usually orangish or reddish basally and yellow or orange at lobes, rarely concolorous; filament tube ususally exserted from corolla tube more than 5 mm; sepals never longer than 10 mm, the tips erect or recurved; intersepalar nectaries present; South America 12
12. Inflorescence subcorymbose at maturity, rarely elongating more than 3 cm; sepals mostly 4-6 mm long, the tips not recurved; anther tube 7-8(-9) mm long, the

dorsal connectives densely short-pilose with purple trichomes; hypanthium often purple tinged, occasionally with papillose or pustulate-based trichomes.

..... 25. *C. curvatus*.

12. Inflorescence racemose at maturity, usually elongating to 15-30 cm; sepals mostly 5-10 mm long, the tips often recurved; anther tube (8-)9-10 mm long, dorsal and ventral connectives normally densely long-pilose with white trichomes; hypanthium green, never with papillose or pustulate-based trichomes.

..... 28. *C. loretensis*.

2. Corolla gradually curved, 30° or less, throat not well-differentiated from lower portion of tube.

13. Flowers very large, corolla 40-45 mm long, the throat widely ampliate, 15-17 mm wide; inflorescence elongating, usually at least 10 cm..... 29. *C. amplicorollinus*.

13. Flowers very small, corolla 17-22 mm long, throat little-ampliate, 6-9 mm wide; inflorescence little-elongate, to 2 cm long..... 14

14. Upper stem and inflorescence rachis densely hirsutulous with tawny trichomes; leaves glabrous adaxially, hirsute or hirsutulous abaxially; corolla (18-)20-22 mm long; sepals 7-8 mm long.

..... 39. *C. carpishensis*.

14. Upper stem and inflorescence rachis hirtellous; leaves sparsely hirtellous adaxially, moderately hirtellous abaxially; corolla 17 mm long; sepals 5-6 mm long.

..... 38. *C. bangii*.

1. Scandent vines; inflorescences pendent or horizontal; bracts caducous or persistent....15

15. Inflorescence strictly pendent and elongating; floral internodes lax; rachis slender, not showing secondary thickening; bracts persistent..... 16
16. Leaves fleshy when fresh, drying coriaceous, the abaxial venation mostly embedded in a thickened layer of aerenchyma, the veins often tinged purple; inflorescence rarely elongating more than 50 cm; sepals divaricate or reflexed, linear or ligulate..... 17
17. Corolla bright pink; calyx zygomorphic, the sepals linear, 5-8 mm long, divaricate, rarely reflexed in fruit, but if so shorter than the hypanthium... 34. *C. urubambae*.
17. Corolla orangish-red or orangish-pink; calyx actinomorphic, the sepals ligulate, rarely sublinear, 10-15 mm long, strictly reflexed and much exceeding the hypanthium..... 33. *C. reflexus*.
16. Leaves thin when fresh, drying chartaceous, the abaxial venation slightly raised, not embedded in lamina; inflorescence often elongating to 100-250 cm; sepals mostly erect, linear or narrowly triangular..... 20. *C. pulcher*.
15. Inflorescence pendent or rarely horizontal but usually sharply upturned and forming a U-shaped rachis; floral internodes remaining congested, only rarely becoming lax basally; rachis often becoming secondarily thickened and with conspicuous raised pedicel abscission scars; bracts often caducous..... 18
18. Corolla gently curved, 40-45 mm long, the throat not well-differentiated from lower portion of tube; corolla bright yellow; anther tube completely glabrous.
..... 21. *C. cuatrecasanus*.
18. Corolla abruptly curved, 30-40 mm long, the throat usually abruptly ampliate and often ventricose, well-differentiated from lower portion of tube; corolla rarely

- yellow, usually various shades of red, orange or pink; anther tube pilose or
glabrous.....19
19. Leaves fleshy when fresh, drying coriaceous, the abaxial venation embedded in a
thickened aerenchyma layer; sepals ligulate, erect or reflexed.....20
20. Sepals 10-17 mm long, erect or slightly patent; bracteoles foliaceous, 3-5 mm long.
.....35. *C. vargasii.*
20. Sepals (4-)7-12(-15) mm long, mostly strictly reflexed, rarely divaricate or spreading,
but if so less than 10 mm long; bracteoles subulate, 1 mm long or less.....32.
C. yungasensis.
19. Leaves drying coriaceous or membranaceous but lacking a thickened arenchyma
layer, the abaxial venation usually somewhat raised and not embedded in the
lamina; sepals triangular or rarely ligulate, erect or arcuate,21
21. Corolla, hypanthium, pedicels, and abaxial leaf surface densely papillose-verrucose
but glabrous; corolla usually ventrally distended at base and narrowest just below
throat, the tissue thick and brittle, often shrinking when drying.
.....24. *C. baezanus.*
21. Floral parts and leaves glabrous, hirsutulous, or strigose, the trichomes occasionally
with papillose or granulose bases; corolla sometimes distended ventrally, but
usually narrowest just above nectar chamber, the tissue thin or thick.....22
22. Corolla, inflorescence rachis, pedicels and abaxial leaf surface densely tawny hispid-
strigose, the trichomes occasionally with papillose bases or branched.
.....23. *C. trachyanthus.*

22. Flowers and foliage never densely hispid-strigose nor with branched trichomes.....23
23. Sepals foliaceous, ligulate or narrowly triangular, 10-14 mm long and 4-5 mm wide at base, the margins conspicuously dentate or serrate; inflorescence and corollas moderately to densely scaberulous or hirtellous, often with the trichomes arising from papillose bases; corollas red or golden yellow.22. *C. densiflorus*.
23. Sepals variable, mostly less than 10 mm long, but if longer then not conspicuously serrate; corollas usually hirtellous with conical trichomes, often with granulose bases, rarely glabrous; corollas variable in color, yellow, red, orange, or pink.
.....19. *C. granulosus*.

19. **Centropogon granulosus** Presl, Prodr. Monogr. Lobel.: 49. 1836. Type. Peru.

Huánuco: "Peruvia subandina. In sylvis densis, versus Cuchero, ripas rivorum colens," Sep 1929, Poeppig s.n. (neotype here designated, W; probable isoneotypes, LE, W). Figs. 8H & 15.

Suffrutescent vines or rarely arching to erect shrubs, stems smooth to scabrous, glabrous to densely hirtellous or hirsutulous; latex opalescent to tan. Leaves variable in shape, narrowly to widely elliptic, oblong, ovate or obovate, (8-)10-10(-35) x (3-)4-11(-14) cm, apex usually acute to acuminate, rarely cuspidate to obtuse, base cuneate to rounded, margins crenulate to serrulate with 2-5 callosities per cm; lamina fleshy or thin when fresh, drying coriaceous to chartaceous, rarely membranaceous, adaxial surface dark green, glabrous, abaxial surface glabrous or the veins minutely muricate or minutely hirtellous, rarely hirtellous to hirsutulous over entire surface; secondary veins 5-11, arcuately ascending; petioles 0.5-2(-3) cm long. Inflorescence a bracteate or short-bracteate, subcorymbose raceme, normally pendent and upturned but rarely erect (as in subsp. *tortilis*), terminal or occasionally lateral, often elongating to 7-15(-30) cm, the flowers numerous and very congested, floral internodes either remaining congested in age or rarely elongating basally, the rachis often densely covered with prominent pedicel scars and occasionally thickening in age, scaberulous to moderately or densely hirtellous; bracts caducous or persistent, usually abscissuing at least after fruit abscission, mostly much-reduced and 10 mm long or less, sometimes foliaceous and to 30 mm long, both surfaces moderately to densely hirtellous, rarely glabrescent; pedicels erect at anthesis, drooping with age, (5-)15-30(-90) mm long, moderately to densely hirtellous or scaberulous, bracteoles basal to subbasal, usually linear and 1-2(-5) mm long. Flowers 55-65(-70) mm long; hypanthium usually hemispheric to broadly hemispheric, 3-5(-7) x 5-10 mm, glabrous to moderately hirtellous, intersepalar nectaries often present,

especially prominent laterally; sepals erect, triangular to narrowly triangular or ligulate, 3-16 x (1-)2-4(-5) mm, entire to irregularly serrulate, glabrous to moderately hirtellous, sinuses planar; corolla variously colored, pink, red, orange, or yellow, either concolorous or bicolored (the lobes contrasting in color with tube), glabrous or usually moderately to densely hirtellous with short (0.1-0.2 mm) conical trichomes, these occasionally with granulose or pustulate bases; corolla tube often slightly sigmoid, cylindric basally and with an abruptly ampliate and sharply curved throat distally, the tube (28-)32-40 mm long, the throat (9-)10-15 mm wide; dorsal lobes recurved to recoiled at anthesis, (8-)10-15 mm long, lateral lobes falcate, (5-)7-10 mm long, ventral lobe erect, often saccate, (5-)7-10 mm long with a deflexed tip; androecium 45-60(-65) mm long; filament tube 38-55 mm long, ventrally flattened and 2-3.75 mm wide when fresh, yellow or whitish, glabrous throughout or pilose at summit, adnate to corolla 4-8 mm above base, exserted from corolla tube (2-)5-12(-16) mm; anther tube 6-9(-10) mm long, thecae and connectives either dark gray and purplish-rose, or yellow-tan and yellow to brown, the connectives glabrous to densely pilose with short to long, white or purple trichomes, antheridial scale usually triangular and acute, 2-3 mm long, often with tuft of short, unfused, white trichomes at base; style exserted from anther tube 1-3(-6) mm, stigma 3-4(-4.5) mm in diam. Fruit spheroid to ovoid, 10-17 x 15-23 mm, smooth or variously ribbed and verrucate, nectar chamber persistent; seeds elliptic to suborbicular, occasionally irregularly angular, 0.6-0.8 mm long.

Distribution. One of the most widespread species in subgen. *Centropogon* and certainly the most variable, *C. granulosus* is found from southern Nicaragua to Bolivia. It occurs in a wide spectrum of habitat types, from lowland tropical forest to high-elevation cloud forest, and ranges from sea level to 3000 m in elevation.

Typification. No type was designated in the protologue of *C. granulosus* and the only collection information given was that the species came from Peru. Although several of Presl's other Peruvian *Centropogon* species were based upon material presumably collected by Haenke, no Haenke specimens of this species are known in spite of his visit to an area where *C. granulosus* is known to occur. Presl also examined Peruvian material collected by Poeppig and made at least one reference to this in the same work in which *C. granulosus* was published (page 34, under *Lobelia virgata* "Poeppig pl. peruv. exs. n. 1"; Presl, 1836). I have searched unsuccessfully for original material of *C. granulosus* in the two herbaria in Prague that now contain Presl's herbarium (PR and PRC). Three Poeppig specimens from Cuchero, Peru are extant, *Poeppig 16* (W), *Poeppig s.n.* (W), and *Poeppig s.n.* (LE), and I believe them to be part of the original collection studied by Presl. Wimmer (1943) apparently shared this view because he cites the W sheet of *Poeppig s.n.* as "fortasse typus Preslii." This specimen was not annotated as *C. granulosus* by Presl, but the handwriting on the label is almost certainly his. Although there is thus strong circumstantial evidence for considering this collection as the type, I have opted to be conservative and have designated the W sheet of *Poeppig s.n.* as a neotype for *C. granulosus* rather than as a lectotype.

Key to Subspecies of *Centropogon granulosus*

1. Corolla bright pink to pinkish-red, concolorous or predominantly so; anther trichomes normally purple and less than 1.5 mm long; shrubs to vines. 2
1. Corolla orange to deep red or yellow, either concolorous or bicolored and the lobes contrasting with the tube; anther trichomes purple or white, variable in length but often longer than 1.5 mm; vines. 3

2. Erect to slightly scandent shrubs; inflorescence erect or rarely bent upward at an obtuse angle; bracts persistent; anther tubes densely short-pilose; intersepalar nectaries absent; Central America..... 19e. subsp. *tortilis*.
2. Vines or rarely scandent shrubs; inflorescence normally acutely upturned; bracts caducous; anther tubes short-pilose to glabrous; intersepalar nectaries present; Colombia and adjacent Panamá and Venezuela. 19d. subsp. *lugens*.
3. Corolla concolorous, bright to golden yellow; anthers tan to yellow, mostly glabrous or with apical tuft of white trichomes; northern Peru to central Ecuador 19b. subsp. *lateriflorus*.
3. Corolla bicolored, orange, orangish-red, or reddish basally with orangish-yellow to yellow lobes; anthers yellowish-tan or greyish and purple, pilose or glabrescent with white or purple trichomes 4
4. Corolla completely smooth and glabrous; inflorescence rachis elongate (to 30 cm), and usually markedly thickened in age; bracts caducous; anther gray/purplish with purple trichomes dorsally; stems smooth, never scaberulous; Colombia.
..... 19c. subsp. *rutilus*.
4. Corolla usually hirtellous to granulose, rarely glabrous and smooth; inflorescence rachis occasionally elongating, but usually not markedly thickened; bracts caducous or persistent; anther tube yellowish-tan to brown, trichomes usually white; stems smooth to scabrous.
..... 5
5. Sepals usually 7-16 mm long; pedicels 25-45(-90) mm long; bracts persistent; anthers normally densely pilose on both dorsal and ventral connectives, with long, white trichomes; Central America, rarely northwestern Ecuador and southwestern Colombia.
..... 19f. subsp. *nutans*.

5. Sepals usually 3-6 mm long; pedicels 15-30 mm long; bracts caducous; anthers pilose on dorsal connectives or glabrescent, with white or rarely purple trichomes;
Colombia to Bolivia along eastern slope of Andes 19a. subsp. *granulosus*.

19a. ***Centropogon granulosus* Presl subsp. *granulosus*. Fig. 15.**

Centropogon cuspidatus A. de Candolle, Prodr. 7: 346. 1839. Type. Peru. *Dombey s.n.* (holotype, P n.v., photo F-neg. 38188).

Siphocampylus aggregata Rusby, Bull. New York Bot. Gard. 8: 122. 1912. Type. Bolivia. Río Machichoiris, 1000 m, 4 Aug 1902, *Williams* 1579 (holotype, NY; isotypes, BM, K, US).

Centropogon cardinalis A. Zahlbruckner & Rechinger, Meded. Rijks-Herb. 19: 51. 1913. Type. Bolivia. Cochabamba: Tablas, 1400 m, May 1911, *Herzog* 2142 (lectotype here designated, S; isolectotypes, B n.v., probably destroyed in World War II, photo F-neg. 9101, W). Although Zahlbruckner worked at Vienna, the W specimen examined was not accessioned into that herbarium until 1922 and thus cannot be considered a holotype. Because the two specimens that I have seen were annotated by the authors in an identical fashion, I have chosen the more complete S sheet as the lectotype.

Centropogon aggregatus (Rusby) Gleason, Bull. Torrey Bot. Club 48: 199. 1921.

Centropogon parvulus Gleason, Bull. Torrey Bot. Club 6: 56, fig. 6. 1925. Type. Peru. Huánuco: Cushi, 1500 m, 19-23 Jun 1923, *Macbride* 4848 (holotype, NY n.v.; isotypes, F, photo F-neg. 58350, US).

Centropogon casapiensis F. Wimmer, Repert. Spec. Nov. Regni Veg. 29: 66. 1931. Type. Peru. Huánuco: Casapi, *Matthews* 1693 (holotype, K).

Centropogon granulosus Presl var. *cuspidatus* (A. de Candolle) F. Wimmer, Repert. Spec.

Nov. Regni Veg. 29: 67. 1931.

Centropogon granulosus Presl var. *aggregatus* (Rusby) F. Wimmer, Pflanzenreich IV.

276b: 170. 1943.

Centropogon granulosus Presl var. *aggregatus* (Rusby) F. Wimmer forma *cardinalis* (A. Zahlbrückner & Rechinger) F. Wimmer, Pflanzenreich IV. 276b: 170. 1943.

Scandent, suffrutescent vines to 4 m long, much-branched throughout; stems scaberulous to scabrous with stiff pustulate or granulose-based protrusions, rarely smooth, glabrous to densely hirtellous or hirsutulous. Leaves elliptic, oblong, ovate or occasionally obovate, 10-20(-33) x 3.5-10(-13) cm, secondary veins 5-9. Inflorescence a pendent, upturned, short-bracteate, terminal raceme, elongating to 8 cm, the rachis covered with prominent pedicel scars in age, not thickening appreciably, scaberulous to densely scabrous, or merely hirtellous, rarely smooth and glabrous; bracts normally caducous, oblong, elliptic or lanceolate, 3-8(-20) mm long, apex obtuse to acute; pedicels 15-30(-40) mm long, with surface and indument similar to those of inflorescence rachis, occasionally persistent and thickened, bracteoles 1-2 mm long. Flowers 55-60 mm long; hypanthium hemispheric, intersepalar nectaries normally present, at least laterally; sepals triangular to narrowly triangular, 3-6(-10) x 1.5-3 mm; corolla bicolored, orange, reddish-orange or red basally grading to yellowish-orange or yellow at lobes, moderately to densely hirtellous or scaberulous, with short, conical trichomes, often with swollen, granulose or pustulate bases, rarely glabrescent; corolla tube 28-35 mm long, the basal portion of tube with prominently thickened nectar chamber, 5-8 mm wide and 4-5 mm long, the tube narrowing to 2.5-4 mm above this then re-expanding to base of throat, or occasionally narrowing gradually from base and reaching narrowest point just below throat, the throat abruptly to moderately ampiate, 9-13 mm wide, curving sharply 45-

70°; androecium 45–55 mm long; filament tube 38–50 mm long, ventrally flattened and 2–2.5 mm wide when fresh, pale yellow, usually densely pilose at summit, rarely glabrous, exserted from corolla tube 7–12 mm; anther tube (6–)7–8(–9) mm, thecae yellowish to tan, connectives tan to brown, rarely purplish, dorsal ones densely pilose with short to long (to 2 mm) trichomes, these white or occasionally purplish, the anther tube very rarely glabrous throughout or merely with an apical or basal tuft, antheridial scale with few or no free trichomes at base. Fruit to 17 x 20 mm, smooth or moderately ridged when fresh; seeds elliptic.

Distribution. A common vine of forest edges and light gaps along the eastern slope of the Andes mostly from northern Peru to central Bolivia, but also in northern Ecuador and extreme southern Colombia. Found in a variety of habitats from 200–2500 m, but most common at 500–1500 m elevation.

Additional specimens examined. COLOMBIA. Caquetá: E slope of Cordillera Oriental, Quebrada del Río Hacha in Cajón de Pulido, 1700 m, 26 Mar 1940, Cuatrecasas 8748 (COL, F); E slope of Cordillera Oriental, Sucre, 1000–1300 m, 4 Apr 1940, Cuatrecasas 9084 (COL, US)[intermediate with subsp. *rutilus*]; 29 km SE of Guadalupe on rd. to Florencia, nr. Huila border, 2300 m, 12 Jan 1974, Davidse et al. 5785 (COL, MO). Putumayo: Between Sachamates and San Francisco de Sibundoy, Planada de Minchoy, 2100 m, 30 Dec 1940, Cuatrecasas 11430 (COL, F, US); Sachamates, opposite mouth of Quebrada Payoyaco, Río Susunga, 17 km W of Mocoa, 1750 m, 27–28 Mar 1943, Fosberg 20379 (S, UC, US-2 sheets); Sibundoy-Mocoa rd., Cordillera de Portachuelo, 2200 m, 8 Oct 1965, García-Barriga et al. 18632 (COL, NY); El Mirador between San Francisco and Mocoa, 2130 m, 5 Jan 1957, Idrobo & Ospina-Hernández 2375 (COL); Mocoa and vic. to N, 750–850 m, 3–7 Dec 1942, Schultes &

Smith 2016 (COL, GH); Sibundoy-Mocoa rd., 2450-2800 m, 15 Mar 1953, *Schultes & Cabrera 18826* (GH); Buenos Aires point, Cerro Portachuelo, 2800 m, 25 Jul 1964, *Soejarto 1081* (GB).

ECUADOR. Morona-Santiago: 25 km from Limón on rd. to Macas, 700 m, 28 Mar 1974, *Harling & Andersson 12921* (AAU, GB, QCA); 24 km from Limón on rd. to Méndez, 850 m, 10 Jun 1979, *Lojtnant et al. 14515* (AAU). Napo: Río Salado, 49 km from Baeza on rd. to Lago Agrio, 1400 m, 24 Oct 1976, *Balslev & Madsen 10275* (AAU), Río Oyacachi, 23 km from Baeza, 1500 m, 29 Oct 1976, *Balslev & Madsen 10455* (AAU, NY); Auca oil field, 60 km S of Coca, 300 m, Jan 1979, *Besse et al. 33* (F, QCA, SEL)[locality doubtful]; 44 km E of El Chaco, 1400 m, 4 Nov 1974, *Gentry 12415* (DUKE, MO); 1 km NW of El Chaco, 1400 m, 12 Feb 1980, *Harling & Andersson 16493* (GB); 5 km S of Reventador towards Baeza, 1000 m, 3 Apr 1985, *Neill & Palacios 6191* (MO, NY); Baeza-Lago Agrio rd., 1400 m, 7 Aug 1980, *Ollgaard et al. 35713* (AAU); Río Salado, 1425 m, 29 Jul 1974, *Plowman 3908* (F, GH); km 74 km on Lago Agrio-Baeza rd., 1050 m, 26 Apr 1985, *Stein 2618* (MO, QCA, QCNE); 2-5 km N of Reventador on rd. to Lago Agrio, 1400 m, 26 Apr 1985, *Stein 2626* (AAU, MO, QCA, QCNE, US), 2627 (AAU, F, K, MO, NY, QCA, QCNE, US); 3 km N of Salado pump station, km 118 of Lago Agrio-Baeza rd., 1250 m, 26 Apr 1985, *Stein 2632* (MO, NY, QCA, QCNE, US). Zamora-Chinchipe: Km 6-8 along Valladolid-Río Palanda, 1500 m, 31 Jan 1985, *Harling & Andersson 21318* (GB, NY); rd. from Loja to Zumba, 5 km above Valladolid, 1920 m, 11 May 1985, *Stein & D'Alessandro 2756* (MO); between Palanuma and Zumba on Valladolid-Zumba rd., 1050-1250 m, 12 May 1985, *Stein & D'Alessandro 2757* (AAU, F, MO-2 sheets, NY, QCA, QCNE, US).

PERU. Amazonas: Guamalito, Mendoza-Chachapoyas rd., 2000 m, 5 Jul 1978, *López & Aldave 8563* (NY); Mendoza, 1500 m, 23 Jul 1963, *Woytkowski 8041* (GH, MO), 1600 m, 29 Aug 1963, *Woytkowski 8284* (GH, MO, US). Ayacucho: E massif of

Cordillera Central, halfway between San Jose and Huanhuachayo, 23 km SW of Hacienda Luisiana and Río Apurimac, 12°47'S, 73°47'W, 1360-1400 m, 19 Aug 1968, *Dudley 11855* (NA); W slope of Rio Apurimac valley on Caprichio-Puncu trail, 12°43'S, 73°47'W, 1592 m, 15 Jul 1970, *Madison 10263-70* (NA). Cajamarca: Tiruyas, 30 km SE of Huancabamba, Río Tabaconas Valley, 1600 m, 11 Jun 1947, *Fosberg 27759* (MO).

Cuzco: 12 km NE of Hacienda Luisiana and Río Apurimac, 1700 m, 23 Jun 1968, *Dudley 10365* (F, NA-2 sheets); Atalaya, nr. junction of Río Carbón with Río Alto Madre de Dios, 27 Aug 1973, *Foster 2750* (DUKE); km 195 of Paucartambo-Madre de Dios rd., 9 km N of Pilcopata, 550 m, 30 Jun 1978, *Gentry et al. 23575* (MO); Marcapata Valley, 1200 m, Aug 1926, *Herrera 1160* (US), 1168 (US); Quincemil, 800 m, Jun 1949, *Marin 1535* (F); Quincemil, 800-1500 m, *Kanti-Hirsch [?J] 1260a* (F); upper valley of Río Sambray, W affluent of Vilcanota, 1800 m, 14 May 1936, *Mexia 8063a* (GH, K, UC, US); Kosñipata Valley, rd. from Pillahuata to Patria, 1850 m, 5 Feb 1975, *Plowman & Davis 4987* (GH); btwn. Yanamayo and Santa Isabel, Kosñipata Valley, 1500 m, 23-31 Jul 1948, *Scolnik 846* (MICH); km 159 of Kosñipata rd., 5 km below San Pedro, 1320 m, 5 Apr 1985, *Stein 2511* (AAU, CUZ, F, MO, NY, US, USM); 5-10 km E of Pilcopata on rd. to Shintuya, 680-750 m, 5 Apr 1985, *Stein 2513* (F, K, MO, NY, US, USM); 2.5 km W of Pilcopata on rd. to Patria, 700 m, 7 Apr 1985, *Stein 2517* (MO, US, USM); Prov. Quispicanchis, Tio to Murayaca, 1900 m, Jan 1943, *Vargas 3165* (CUZ, MICH); 4 km W of Quincemil, 960 m, 6 Oct 1976, *Wasshausen & Encarnación 721* (MO, K, NY, US); Callanga, 1500 m, 18 Feb 1953, *Woytkowski 393* (USM). Huánuco: Tingo María, 8 Jul 1940, *Asplund 12061* (S, US), 12062 (S); Cordillera Azul, 40 km E of Tingo María, 1600 m, 19 Nov 1979, *Davidson & Jones 9331* (MO, NY), 1700-1800 m, 21 Nov 1979, *Davidson & Jones 9409* (MO); La Divisora, 28 Feb 1947, *Ferreyra 1648* (F, GH, NY, UC, US); Cayumba, between Huánuco and Tingo María, 800-850 m, 8 Feb 1950, *Ferreyra 6746* (US); Fundo Sinchono, Rio Chino, affluent of Yuroc-yacu, Cordillera

Azul, 1500 m, 21 Oct 1947, *Fosberg* 28817 (MO); Pampayacu, hacienda at mouth of Río Chinchao, 19-25 Jul 1923, *Macbride* 5088 (F-2 sheets, NY, S, US); Casapi, 1835, *Matthews* 1676 (K); rd. Mirador to Chinchao, 2300 m, 6 Nov 1935, *Mexia* 4155 (GH, MO, W); Dist. Churubamba, trail Puente Durand to Exito, W slopes of Santo Toribio, 1450 m, 8 Sep 1936, *Mexia* 8154 (BM, F, G, GB, GH, K, MO, NA, NY, S, U, US, W); Carpiscillo, Tingo María, 1800 m, Jun 1938, *Sandeman s.n.* (BM); Jacintillo, left bank of Río Monzón, 672 m, 14 Nov 1971, *J. Schunke* 5154 (F, G, GH, MO, NY, US); Chinchao, 1850 m, 10 Sep 1948, *Scolnik* 1077 (MICH); km 493 on rd. between Huánuco and Tingo María, 1000 m, 30 Jun 1977, *Solomon* 3345 (MO); Paty Trail, 5 km E of Carpish Tunnel, 2100-2400 m, 15 Jan 1987, *Stein et al.* 3871 (MO), 3872A (DUKE, F, MO, NY, US); outskirts of Chinchavito S of Tingo María, 750 m, 16 Jan 1987, *Stein et al.* 3875 (AAU, DUKE, F, K, MO, NY, US, USM); Cueva de las Pavas, 8 km S of Tingo María, 700 m, 17 Jan 1987, *Stein et al.* 3888 (MO, USM); La Divisora, 40 km E of Tingo María, 1550 m, 18 Jan 1987, *Stein et al.* 3894 (MO, US, USM); Tingo María, 26 Oct 1938, *Stork & Horton* 9507 (F, UC), 650 m, 2 Nov 1938, *Stork & Horton* 9599 (F, UC); 0.5 km above San Miguel, Chinchao, 1900 m, 2 Jun 1981, *Young & Sullivan* 626 (MO), 629 (MO). Junín: Chanchamayo Valley nr. San Ramón, 800-900 m, 27 Jun 1954, *Constance & Tovar* 2234 (UC); below Huacapistana, 1700-1800 m, 21 Sep 1955, *Ferreyra* 11202 (USM); Tulumayo Valley, 5-10 km S of San Ramón, above La Esperanza, 1000-1500 m, 5 Sep 1982, *Foster* 8524 (MO); Puente Pan de Azucar, above San Ramón, 1200 m, 29 Jun 1982, *Gentry & Tredwell* 37275 (MO); Chilpes, 8 km S of Vitoc, 1420-1700 m, 8 Feb 1983, *Gentry et al.* 40173 (MO, MO); Cumbre Yacunay, above La Merced, 2000 m, 15 Aug 1957, *Hutchison* 1187 (F, G, GH, K, MICH, NY, S, UC, US); Pomamarca, 12 km NW of San Ramón, 1200 m, 31 Nov 1962, *Iltis & Iltis* 259 (MICH, WIS-2 sheets); Schunke Hacienda above San Ramón, 1700 m, 8-12 Jun 1929, *Killip & Smith* 24708 (NY, S, US, W), 1400-1700 m, *Killip & Smith* 24805 (NY, US), 1200 m, 27

Aug-1 Sep 1923, *Macbride* 5654 (F, NY); Pangoa, Jul, *Matthews* 1188 (K); Chanchamayo Valley, Sep 1924-1927, *C. Schunke* 347 (F), 1500 m, Apr 1929, *C. Schunke* 1582 (F), 1583 (F); Fondo Romero, Pampatigre, above Santa Ana SE of La Merced, 1500-1700 m, 7 Mar 1985, *Stein & Todzia* 2342 (AAU, F, K, MO-2 sheets, NY, U, US, USM); 10 km W of San Ramón on rd. to Tarma, 1200 m, *Stein & Todzia* 2346 (AAU, CAS, MO, US, USM); rd. to San Vicente S of San Ramón, 980 m, 8 Mar 1985, *Stein & Todzia* 2353 (MO, NY, US, USM); Río Tulumayo Valley, trail above Chilpes, 1500-1700 m, 15 Mar 1985, *Stein & Todzia* 2434 (F, MO, NY, US, USM); Huatsiroke, 1800 m, 21 Feb 1960, *Woytkowski* 5544 (F, LE, MO); Utuyacu, 1800 m, 25 Feb 1948, *Woytkowski* sub *Goodspeed* 35376 (F, MO, UC). Pasco: Río Palcazu, 51-60 km NW of Villa Rica towards Puerto Bermudez, 700 m, 4 Mar 1982, *Gentry & Smith* 36067 (MO); Pichis Trail, Yapas, 1350-1600 m, 28-29 Jun 1929, *Killip & Smith* 25474 (F, NY, US, W); Pichis Trail, Dos de Mayo, 1700-1900 m, 2-3 Jun 1929, *Killip & Smith* 25799 (NY, US, W); Pichis Trail, Santa Rosa, 625-900 m, 6-7 Jul 1929, *Killip & Smith* 26171 (F, NY, US); Puerto Yessup, 400 m, 10-12 Jun 1929, *Killip & Smith* 26335 (F, NY, US, W); Río El Tunqui, 50 km from Oxapampa, 1620 m, 27 May 1982, *Smith et al.* 1737a (MO); Oxapampa-Cerro de Pasco rd., La Suiza to San Gotardo, 2100-2650 m, 19 May 1983, *Smith* 4095 (MO); Gran Pajonal, 3 km N of Chequitavo, 1200 m, 21 Sep 1983, *Smith* 5086 (MO); nr. Shiringamazu, up Río Mamuriz from Río Palcazú, 350 m, 12 Sep 1984, *Smith* 8368 (MO); Oxapampa, 1800 m, 3 Mar 1986, *van der Werff et al.* 8328 (MO). Puno: Ollachea to San Gabon, 1000-2000 m, 17-24 Jul 1978, *Dillon et al.* 1168 (MO); Tambopata Valley, 2100-2200 m, 14 May 1966, *Ferreyra* 16734 (USM); Prov. Sandia, Oroya-Santo Domingo Trail, 1200 m, 23 May 1943, *Hodge* 6027 (US-2 sheets, USM); Río Inambari region, trail from Aricoma Pass to Santo Domingo, 1730 m, 13 Sep 1939, *McCarroll* 13 (MICH); Prov. Sandia, nr. Sagrario, 1000-1300 m, 26 May 1942, *Metcalf* sub *Goodspeed* 30637 (UC, US); between Río Azata-Colorado, 1100 m, 22 Jun 1986,

Núñez & Muñoz 5250 (MO); *Muruncunca*, 1800 m, *Vargas* 16365 (MICH);
 Chunchusmayo, 900 m, 13 Jun 1902, *Weberbauer* 1166 (B). *San Martín*: 20-27 km NE of
 Tarapoto on rd. to Yurimaguas, 900-1000 m, 21 Jul 1982, *Gentry et al.* 37876 (MO);
 Roque, 7 May 1925, *Melin* 126 (S); Quebrada de Santiago, E of Puerto Pizana, 350-380
 m, 27 Jul 1973, *J. Schunke* 6496 (GH, MO); Cachiyacu de Lepuna, Uchiza District, 450-
 500 m, 10 Jul 1974, *J. Schunke* 7283 (GH, MO); San Juan de Pacaizapa, km 72 on
 Tarapoto-Moyobamba rd., 1000-1050 m, 30 May 1977, *J. Schunke* 9567 (AAU, MO); nr.
 Tarapoto, 1855-1856, *Spruce* 3954 (BM, G-2 sheets, K-2 sheets, W); rd. between
 Moyobamba and Jepelacio, 1100 m, 9 Feb 1985, *Stein & Todzia* 2125 (B, COL, DUKE,
 GH, MICH, MO, UC, USM); 19 km SE of Moyobamba on rd. to Tarapoto, 870 m, 10
 Feb 1985, *Stein & Todzia* 2130 (F, K, MO, US, USM); 48 km SE of Moyobamba on rd.
 to Tarapoto, 1110 m, 10 Feb 1985, *Stein & Todzia* 2131 (DUKE, MO, US, USM);
 Quebrada Ahuashyaco, 14 km NE of Tarapoto, 800 m, 11 Feb 1985, *Stein & Todzia*
 2134 (MO, US); 50 km E of Moyobamba on rd. to Tarapoto, 1150 m, 14 Feb 1985, *Stein*
 & *Todzia* 2166 (F, MO, US, USM); Cerro de Escalar, 1200 m, Feb 1903, *Ule* 6787 (B,
 G); San Roque, 1350-1500 m, Jan-Feb 1930, *Williams* 7018 (F-2 sheets, NY), 7214 (F,
 NA), 7693 (F). *Ucayali*: Boquerón del Padre Abad at puente "Velo de Novia," 5 Dec
 1978, *Diaz & Aronson* 742 (MO); 28 km NNE of Tingo María on rd. to Pucallpa, 22 Jul
 1981, *Dillon* 2693 (MO); La Divisora, 1500-1600 m, 7 Aug 1947, *Ferreyra* 2224 (F,
 MICH, US); below Divisora, 1200-1300 m, 21 Jul 1948, *Ferreyra* 4278 (US); Boquerón,
 between Tingo María and Pucallpa, 500-550 m, 2 Oct 1950, *Ferreyra* 8117 (K, MICH,
 US), 16 Jan 1981, *Ferreyra* 19344 (MO); Cordillera Azul, N of Tingo María, 1200-1650
 m, 18 Jun 1958, *Humbert* 31045 (P); lower Boquerón del Padre Abad, 480 m, 25 Jul
 1964, *Hutchison* 6050 (MICH, UC); nr. Rio Chino, La Divisora, 1400-1600 m, 11 Jun
 1976, *J. Schunke* 9211 (MO); Pucallpa, 200 m, 4 Aug 1946, *Soukup* 3047 (F); 50 km E of
 Tingo María on rd. to Pucallpa, 1450 m, 18 Jan 1987, *Stein et al.* 3908 (CAS, F, MO),

NY, US, USM); Boquerón del Padre Abad, 300 m, 9 Aug 1946, Woytkowski sub *Goodspeed* 34346 (F, G, MO, UC). Department unknown: *Maclean* s.n. (K); 27 Dec 1878, *Martinet* 1543 (P); 1835, *Matthews* 1676 (K).

BOLIVIA. Cochabamba: Antahacana, Espíritu Santo, 160 km N of Cochabamba, 750 m, Jun 1909, *Buchtien* 2255 (NY, US-3 sheets); nr. Chimore, rd. to Todos Santos, 130 km NE of Cochabamba, 800 m, 10 Mar 1939, *Eyerdam* sub *Goodspeed* 24829 (UC); Solitario, 1600 m, 21 Feb 1929, *Steinbach* 9293 (NY); Incachaca-San Antonio, 2000 m, Jul 1926, *Werdermann* 2098 (MO, S). Department unknown: Locality not given, *Pearce* 234 (K), 729 (K).

Vernacular names. "Musanga," Cuzco, Peru; the leaves used locally in soups. "Gallito," Huánuco and San Martín, Peru. "Gallo custa," Ucayali Department.

19b. *Centropogon granulosus* Presl subsp. *lateriflorus* (F. Wimmer) B. A. Stein comb. et stat. nov.

Centropogon lateriflorus F. Wimmer, Pflanzenreich IV 276b: 193, fig. 45b. 1943. Type.

Ecuador. Morona-Santiago: Chiguinda, *Lehmann* K.157 (holotype, K).

Suffrutescent vines, to 5 m long, much-branched throughout; stems smooth or rarely scaberulous with muricate protrusions, glabrescent to hirtellous. Leaves elliptic to narrowly elliptic or lanceolate, (8-)11-20(-25) x (3-)4-10(-12) cm, glabrous on both surfaces; secondary veins 5-9; petioles 0.5-1.5 cm long. Inflorescence a pendent, upturned, short-bracteate, terminal or lateral raceme, elongating to 6 cm but if lateral usually much shorter and occasionally less than 1 cm long, the rachis occasionally thickening and with numerous, close-set, raised pedicel scars; bracts caducous, narrowly

triangular, oblanceolate or ligulate, less than 10 mm long, glabrous to hirtellous; pedicels (5-)10-25 mm long, glabrescent to moderately hirtellous, bracteoles to 1.5 mm long. Flowers 55-65(-70) mm long; the hypanthium, sepals and lower portion of corolla often drying black, rest of corolla often drying black or dark brown; hypanthium smooth to verrucose, intersepalar glands present at least laterally; sepals deltoid to narrowly triangular, (2-)3-8 x (1-)2-3 mm, glabrous to minutely hirtellous; corolla concolorous, bright canary yellow to golden yellow when fresh, glabrous or sparsely to moderately hirtellous; corolla tube often slender, 33-40 mm long, 5-8 mm wide at base then narrowing and re-expanding slightly, the throat abruptly ampliate, 10-13 mm wide, sharply curving 45-70°; androecium 55-60(-65) mm; filament tube 47-55 mm long, pale yellow throughout or rarely purplish at summit, entirely glabrous or sparsely pilose at summit, long-exserted from corolla tube 10-13 mm; anther tube 6-8(-9) mm long, thecae yellowish or tan, connectives yellowish to brown, completely glabrous or usually with densely pilose dorsal tufts at apex and base, the trichomes to 2.5 mm long, white to yellowish, very rarely purplish, antheridial scale often with a tuft of unfused white trichomes at base. Fruit to 11 x 25 mm, usually prominently ribbed and often verrucose; seeds elliptic, occasionally irregularly angular.

Distribution. An infrequent to locally common vine of mid-elevation montane forest to cloud forest at elevations from 1000-2000 m. Found from northern Peru to Central Ecuador, with an unusual form as far south as Huánuco Department, Peru.

Additional specimens examined. ECUADOR. Azuay: Contego encampment, Cuenca-Cola de San Pablo hwy., 1640 m, 15 Feb 1977, Boeke & Loyola 1021 (AAU, MO, NY-2 sheets, QCA). Morona-Santiago: 9-10 km SE of San Juan Bosco, 1540-1600 m, 27 Jan 1981, Gentry et al. 30888 (AAU, DUKE, MO, SEL); Indanza-Limón, 1300-

1600 m, 23 Mar 1974, *Harling & Andersson* 12775 (AAU, MO); Tumbes, 17-18 km N of Gualaquiza on rd. to Indanza, 1700-1800 m, 17 Apr 1985, *Harling & Andersson* 24252 (GB); Km 20 between Tumbes and Tucumbatza on Gualaquiza-Indanza rd., 20 Apr 1985, 1600 m, *Harling & Andersson* 24365 (GB); Pachicutza, km 140 on Loja-Gualaquiza rd., 900-1000 m, 26-27 Apr 1973, *Holm-Nielsen et al.* 4425 (AAU, NY); Plan de Milagro, 10 km NW of Indanza, 1725 m, 2-16 Oct 1944, *Jorgensen OHJ-35* (NY); NW range of Cordillera del Condor, camp overlooking Rio Zamora at headwaters of Rio Piuntza, 1850 m, 6 Jan 1972, *MacBryde* 998 (AAU, MO, QCA); 7 km S of Tucumbatza on Gualaquiza-Limón rd., 1650 m, 17 May 1985, *Stein* 2802 (AAU, B, DUKE, F, K, MO, NY, QCA, QCNE, US); 5 km S of Plan de Milagro, on rd. to Indanza, 1650 m, 17 May 1985, *Stein* 2810 (AAU, F, K, MO, NY-2 sheets, QCA, US-2 sheets); 3 km above Plan de Milagro, Limón-Cuenca rd., 1900-2000 m, 18 May 1985, *Stein* 2819 (MO, QCA). Pastaza: 5 km W of Rio Negro, 1500 m, 8 Jan 1962, *Dodson & Thien* 1935 (WIS); Rio Pastaza Valley 8 km W of Mera, 1150-1200 m, 15 Sep 1933, *Schimpff* 1078 (B). Tungurahua: Rio Pastaza Valley between Baños and Cashurco, 8 hours E of Baños, 1300-1800 m, 25 Sep 1923, *Hitchcock* 21874 (GH, NY, US) (syntype of *C. holtonis* var. *albanensis*); Colónia Mexico, 4 km from Rio Topo, 5 Mar 1969, *Lugo* 658 (GB); between Rio Mapoto and Rio Margaritas, 1225 m, 20 Mar 1939, *Penland & Summers* 172 (F, GH, NA); Volcán Tungurahua, Dec 1904, *Sodiro* 35 (W) (syntype of *C. granulosus* var. *rutilus*). Zamora-Chinchipe: Trail N across bridge from Zamora, 1030-1270 m, 17 Aug 1982, *Clemants* 2363 (MO, NY); Rio Zamora, 1000 m, 24 Aug 1938, *Espinosa* 703 (B); Rio San Francisco, above Canillones, 15-18 km ENE of Loja, 1800-1830 m, 20 Feb 1945, *Fosberg* 23163 (US); rd. in construction Zamora-Zumba along Rio Jamboe, 30 km S of Finca Cruz-Kaya, 1400-1500 m, 22 Apr 1974, *Harling & Andersson* 13854 (AAU, GB); 10 km E of Paquisha, 1400-1500 m, 13 Apr 1985, *Harling & Andersson* 24098 (GB); 16 mi. E of Zamora, 1 Sep 1972, *Humbles* 6012 (MO); Rio Zamora across from

Hacienda Alegre, N of Cumbaratza, 24 Jul 1960, *Mathias & Taylor* 5249 (F); 5 km above Valladolid on Loja-Zumba rd., 1920 m, 11 May 1985, *Stein & D'Alessandro* 2755 (AAU, F, MO-2 sheets, NY, QCA, QCNE, US); Quebrada Achupallas, 2500-2800 m, 9 Oct 1943, *Steyermark* 54534 (F, MICH); Quebrada del Diablo, new rd. Loja-Zamora, 2000-2400 m, 1 May 1987, *van der Werff & Palacios* 9242 (MO, QAME).

PERU. Amazonas: Prov. Bagua, 20 km E of La Peca by trail, 2000 m, 22 Jul 1978, *Barbour* 2806 (MO); 25 km E of La Peca, 1900 m, 13 Aug 1978, *Barbour* 2955a (MO), 2975 (MO); Cordillera Colán SE of La Peca, 1900-2200 m, 10 Oct 1978, *Barbour* 3906 (MO), 1800-1875 m, 17 Oct 1978, *Barbour* 4117 (MO); 17 trail km E of La Peca in Serranía de Bagua, 1850-1900 m, 14 Jun 1978, *Gentry et al.* 22974 (MO); Prov. Pongará, Buenos Aires, across Rio Chiriaco from Yambrasbamba, 40 km N of Jumbilla, 1860-2000 m, 2 Mar 1967, *Tillett* 673-257 (US). Huánuco: Trail to Hacienda Paty below Carpish, 2300-2400 m, 23 Jun 1953, *Ferreyra* 9409 (USM); Río Chinchao above Hacienda Pati, below Carpish Pass, 2800 m, 24 Oct 1947, *Fosberg* 28865 (MO); Carpish Divide, 2500 m, Oct 1945, *Sandeman* 5174 (K); Carpish Hills, Paty Trail 5 km E of tunnel, 2100-2400 m, 15 Jan 1987, *Stein et al.* 3872 (MO, USM). San Martín: Venceremos, nr. Amazonas border, km 391 on Rioja-Pomacocha rd., 1850 m, 10 Feb 1984, *Gentry et al.* 45345 (MO); km 399 of Carretera Marginal, trail to Quebrada Venceremos and Río Serranoyacu, 1400-1500 m, 13 Jun 1986, *Knapp & Alcorn* 7786 (MO); Venceremos, km 390 on Pedro Ruiz-Moyobamba rd., 2100 m, 7-9 Aug 1983, *Smith & Vasquez* 4689 (MO); Venceremos area, Río Serrano Valley, 64 km from Pomacocha on rd. to Moyobamba, 1500 m, 9 Feb 1985, *Stein & Todzia* 2124 (AAU, B, DUKE, F, K, MO, NY, US, USM); 15 Feb 1985, *Stein & Todzia* 2170 (MO-2 sheets, US, USM).

19c. ***Centropogon granulosus* Presl subsp. *rutilus* (F. Wimmer) B. A. Stein, comb. et stat. nov.**

Centropogon chrysostoma Cortés nom. nud., Flora de Colombia 1: 35. 1897. The publication of this name consists only of an illustration of a single flower and lacks a diagnosis or reference to a type. It is thus considered a *nomen nudum*. I have tentatively placed the name under *C. granulosus* subsp. *rutilus*, however, on the basis of the corolla color implicit in the name, the likely geographic origin of the plant given Cortes' location in Bogotá, and the illustrations' general concordance with features of this subspecies.

Centropogon granulosus Presl var. *rutilus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 22: 201. 1926. Type. Cundinamarca: Bogotá, forests of Fusagasugá, Dec 1842, Linden 855 (lectotype here designated, G, photo F-neg. 27228; isolectotypes, BM, W). Wimmer also cited another collection in the protologue, Sodiro 35 (W), from Volcán Tunguragua in Ecuador. Since the diagnosis applies much more to the Linden specimen than to the very incomplete and fragmentary Sodiro specimen, I have chosen the Linden specimen as the lectotype. The Sodiro syntype is here excluded from this taxon, and instead I consider it taxonomically to be a part of *C. granulosus* subsp. *lateriflorus*.

Centropogon holtonis F. Wimmer, Repert. Spec. Nov. Regni Veg. 29: 66, tab. 116, fig. 6. 1931. Type. Colombia. Cundinamarca: Citra Gena [?], 19 Dec 1853, Holton 404 (holotype, K; isotype, NY).

Centropogon holtonis F. Wimmer var. *albanensis* F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 8. 1935. Type. Colombia. Cundinamarca: Albán, 1500 m, Guevara Amórtegui 297 (lectotype, US). Wimmer cited another collection in the protologue, Hitchcock 21874, from Ecuador. In 1943, however, he excluded this syntype from his conception of this taxon and effectively lectotypified this name

with the Guevara Amórtegui collection by explicitly declaring it the type (Wimmer, 1943).

Scendent vine to 5 m long; stems glabrescent to hirtellous. Leaves elliptic to oblong or slightly ovate, 10-19 x 4.5-10 cm, apex acute, margins serrulate; abaxial surface glabrous or minutely hirtellous to minutely muricate on veins; secondary veins 9-10. Inflorescence a pendent, upturned, short-bracteate terminal raceme, the flowers numerous although few open at any one time, older inflorescences with an extremely elongate and thickened rachis to 35 cm long and 2.5 cm in diam., covered with numerous close-set and raised pedicel scars and often subtended by an elongate, pendent "peduncle," to 1.5 m, formed through abscission of the subtending stem's vegetative leaves; bracts caducous, ovate, triangular, or oblong, to 15 mm long, the apex acute to rounded; pedicels 20-30 mm long, glabrescent to hirtellous, bracteoles lanceolate, to 5 x 2 mm. Flowers 60-65 mm long, the hypanthium, sepals and lower portion of corolla often drying deep maroon; hypanthium apparently lacking intersepalar glands; sepals erect with patent tips when fresh, narrowly triangular to ligulate, 6-9 x 2.5-4 mm, apex acute to rounded, margins entire; corolla bi-colored, orangish-red below grading into orangish-yellow at the lobes, completely smooth and glabrous; corolla tube usually stout, 35(-38) mm long, the basal portion often distended ventrally, (6-)8-11 mm wide, narrowing to 5-6 mm just below throat, the throat ventricose, abruptly ampliate to 11-15(-18) mm wide, sharply curved 45-60°; androecium 55-60 mm long; filament tube 46-52 mm long, pale yellow, glabrous throughout, long-exserted from corolla tube 9-12 mm; anther tube slightly arching, 8-10 mm long, thecae dark gray, connectives rose-purple, the dorsal ones densely pilose with purple trichomes 1-2 mm long, antheridial scale deltoid, occasionally sub-truncate at apex and often with a dense tuft of short, unfused, white trichomes at base. Fruit to 12 x 17 mm, smooth; seeds elliptic.

Distribution: A fairly common vine of montane forests, on the western slope of the Cordillera Oriental of Colombia in Cundinamarca and adjacent Tolima departments at 1000-2300 m.

Additional specimens examined. COLOMBIA. Cundinamarca: Villeta, 2500 m, 14 Jun 1875, André 681 (K); Laguna de Pedro Palo, Vereda El Rosario, 2000-2100 m, 9 Apr 1983, Ayala 6 (COL); Sierra de Subia, 5 km N of Cumaca along rd. to Viotá, 1725 m, 20 Jun 1972, Barclay et al. 3517 (NA); Albán, Jun 1932, Cáceres 297 (COL); between El Salto and El Colegio, 1900-2050 m, 3 Mar 1940, Cuatrecasas 8221 (COL); vic. of San Bernardo, towards Sasaima, 1600-1800 m, 23 Jun 1940, Cuatrecasa 9638 (COL); above Santandercito, 1720 m, 13 Jun 1943, Dugand 3176 (COL); Estación Santana above Sasaima, 1600-1700 m, 25-29 Jul 1945, Dugand 3867 (COL); Río La Aguadita, 1820 m, 27 Jan 1983, Escobar et al. 3010 (HUA); between quebradas La María and La Victoria nr. Sasaima, 1750-1940 m, García-Barriga 12564 (US); Pacho-La Palma hwy., 1100 m, 28 Jul 1947, Haught 6008 (COL, US); rd. between Zipaquirá and Pacho, 12 May 1961, Pinto 639 (COL); Sasaima, San Bernardo, 1700 m, 8 Dec 1945, Schneider 178 (S); 9 km S of San Francisco on rd. to Supatá, 2000 m, 13 Mar 1986, Stein 3677 (COL, DUKE, F, K, MO, NY, US); rd. from Puerto Lleras to Cachipay, 1600-1700 m, 15 Mar 1986, Stein & Franco 3692 (COL, MO, US); 6-8 km W of Zipacón on rd. to Cachipay, 2100-2300 m, 15 Mar 1986, Stein & Franco 3693 (COL, F, MO, NY, U, US); Fusagasugá, 2000 m, Aug 1855, Triana s.n. (BM); Santandercito, 1650 m, Nov 1945, Uribe 1096 (COL). Tolima: Between headwaters of Río Cuindé Feo and Río Cuindé Blanco, 9 km E of Andalucía, 2000-2100 m, 18 Nov 1943, Fosberg 21341 (US). Department unknown: "Prov. Popayan, La Horqueta, 1600 m, Jul 1853, Triana s.n. (BM)[probably a mislabeled duplicate of *Triana s.n.* from Fusagasugá].

19d. *Centropogon granulosus* Presl subsp. *lugens* (F. Wimmer) B. A. Stein, comb. et stat. nov. Fig. 8H.

Centropogon densiflorus Bentham var. *lugens* F. Wimmer, Repert. Spec. Nov. Regni Veg. 22: 196. 1926. Type. Colombia. Norte de Santander: "Prov. de Ocaña, forêts Pericos," 1200 m, May 1846-1852, *Schlism* 703 (lectotype here designated, G, photo F-neg. 2722; isolectotypes, BM, G). Norte de Santander: "Prov. de Ocaña, paramos," 2400-3000 m, May 1846-1852, *Schlism* 571 p.p (syntype G, n.v.).

Schlism 571 is apparently a mixed collection, because Wimmer (1926) cites it as the type of *C. majalis* (=*C. pamplonensis*), and the 5 sheets of this collection I have seen are all in accord with that taxon. Wimmer (1943) later made reference to the mixed nature of this collection, and I assume that the one aberrant sheet he observed at G is actually a mislabeled duplicate of *Schlism* 703. Because the original diagnosis is in complete accord with the collections of *Schlism* 703 that I have seen, I am therefore designating that collection as the lectotype.

Centropogon cumulatus F. Wimmer, Pflanzenreich IV. 276b: 178. 1943. Type. Colombia. Cauca: El Tambo, La Costa, 800 m, von Sneidern 833 (holotype, S, photo F-neg. 30250).

Centropogon vinosus F. Wimmer, Pflanzenreich IV. 276b: 179. 1943. Types. Colombia. Chocó: between La Oveja and Quibdo, 1-2 Apr 1931, Archer 1707 (lectotype here designated, US). Cauca: El Tambo, La Costa, 800 m, von Sneidern 1029 (syntype, S n.v., photo F-neg. 30253).

Scandent vines to 5 m long, or rarely arching to scandent shrubs to 2 m tall, usually much-branched above; stems smooth or rarely scaberulous, glabrous to hirtellous.

Leaves elliptic to widely elliptic, oblong, or ovate, 15–30(-36) x 6–15 cm, rarely sharply serrate; secondary veins 8–10(-12), often diverging from mid-vein at a wide angle and widely arcuate-ascending. Inflorescence a pendent, upturned, bracteate, terminal raceme, elongating to 20 cm although mostly less than 10 cm long, the floral internodes congested throughout, the rachis densely covered with pedicel scars in age, moderately to densely hirtellous, rarely scaberulous; bracts caducous or deciduous with age, lanceolate, oblong or elliptic, 10–25 mm long; pedicels 15–30 mm long, glabrescent to moderately short hirtellous, bracteoles linear, lanceolate or oblanceolate, 1–5 mm long and to 2 mm wide. Flowers 55–65 mm long; hypanthium often with truncate base, intersepalar nectaries usually prominent, especially laterally; sepals narrowly triangular to ligulate, 6–16 x 2–4(-5) mm; corolla mostly concolorous, pink to bright rose-red, glabrescent or more commonly moderately covered with short conical trichomes, these occasionally with swollen granulose bases; corolla tube 32–38 mm long, often with ventrally distended base 5–10 mm wide, the tube reaching narrowest point either at filament attachment or at base of throat, the throat ventricose and abruptly ampliate, 10–15 mm wide, sharply curved 50–70°; androecium 50–60 mm long; filament tube 45–52 mm long, white with purplish summit, rarely pale yellow, glabrous throughout, exserted from corolla tube 4–8(-12) mm; anther tube 7–9 mm long, thecae dark gray, connectives rose-purple, the dorsal ones pilose with short to moderately long (0.5–2 mm), usually purple trichomes, occasionally partially or completely glabrous, antheridial scale with tuft of short, unfused, white trichomes at base; stigma large, to 4.5 mm in diam. Fruit to 12 x 23 mm, moderately ribbed; seeds elliptic to suborbicular.

Distribution. *Centropogon granulosus* subsp. *lugens* is a locally common scandent shrub to vine with wide ecological tolerances ranging from lowland wet tropical forests to montane forests and occurring from sea level to 2300(-3000?) m. It is found

primarily in Colombia, but also occurs in extreme eastern Panama (Darién Province) and in northeastern coastal Ecuador, and is known from a single collection from Venezuela in the Sierra de Perija near the Colombian border. In Colombia it occurs throughout the Chocó region and up the Magdalena valley on both the western slopes of the Cordillera Oriental and the eastern slopes of the Cordillera Central.

Additional specimens examined. PANAMA. Darién: Río Tacarcuna, vic. of old Tacarcuna village, 580 m, 15 Jan 1975, *Gentry & Mori* 13568 (MO); trail along ridge S of Río Setigandi, nr. Colombian border, 800-1100 m, 19 Apr 1980, *Gentry et al.* 28594 (MO).

COLOMBIA. Antioquia: Río Anorí nr. Quebrada La Tirana, 400-700 m, 20 Feb 1977, *Alverson et al.* 32 (NY, WIS); vic. of Villa Arteaga, 200 m, 14 Aug 1948, *Araque & Barkley* 18C742 (COL, MICH, UC, US); Medellín-Bogotá hwy. Río Samaná-Río Claro section, 935 m, 11 Nov 1982, *Cogollo & Cecilia* 158 (MO); Quebrada El Piñal, Municipality of Campamento, 800-1300 m, 3 Jun 1986, *Cogollo & Alzate* 2295 (MO); between Madreseca and Providencia along Rio Anorí, 600-700 m, 10 May 1944, *Core* 665 (US); between Dos Bocas and Anorí, Rio Anorí Valley, 400-700 m, 15 Dec 1974, *Denslow* 2571 (WIS); Finca Montepinar, Municipality of Guatapé, 1800-1900 m, 1 Oct 1982, *Escobar & Folsom* 2418 (HUA), 5 Sep 1982, *Escobar et al.* 2343 (HUA); between Dos Bocas and Anorí, Rio Anorí Valley, 400-900 m, 24 Jan 1976, *Fonnegra et al.* 575 (HUA); Hacienda La Soledad, region of Rioverde, Municipality of Sonsón, 1430-1800 m, 21 Jan 1947, *Gutiérrez sub Goodspeed* 35504 (UC), 23 Jan 1947, *Gutiérrez sub Goodspeed* 35539 (UC); Río Grande, 20 km SE of Turbo, 100 m, 9 Apr 1945, *Haught* 4551 (COL, MICH, US); Medellín-Bogotá Hwy., Río Samaná-Río Claro section, 730 m, 11 Nov 1982, *Hernández et al.* 575 (HUA), 623 (HUA); Salto de Guadalupe, 1600 m, 27 Jul 1947, *Hodge* 6962 (MICH, US); El Castrillón, San Luis, 1470 m, 3 Mar 1981, *Loaiza et*

al. 164 (HUA); Municipality of San Luis towards Vereda Manizales, 1460-1760 m, Orozco *et al.* 525 (COL); between Caldera and San Luis, 14 Apr 1949, Romero-Castañeda 1504 (COL), 1512 (COL); along Río Dormilón, 1000-2000 m, 8 Oct 1978, Santas 392 (HUA); Fuentes Termales de Santo Domingo, 1200 m, 7 May 1949, Scolnik *et al.* 19An487 (US); Río Anorí Valley nr. Planta Providencia, 350-600 m, 27 Jun 1976, Shepherd 461 (WIS); old rd. between Tirana Creek and hydroelectric plant on Río Anorí, 500 m, 10 Feb 1971, Soejarto & Villa 2721 (COL, GH-2 sheets); between Dos Bocas and Anorí, 400-900 m, 6 Feb 1972, Soejarto *et al.* 3241 (HUA), 26 Apr-3 May 1973, Soejarto *et al.* 3917 (GH); Medellín-Bogotá hwy. 15 km E of Río Samará, 700 m, 31 Jan 1986, Stein & McDade 3325 (COL, MO, NY, US); Finca Montepinar, 10 km NE of Guatapé, 1800 m, 10 Feb 1986, Stein 3426 (COL, DUKE, F, HUA, JAUM, K, MO, NY, US); Nariño, quebradita El Oso, 1900 m, 8 Jan 1949, Uribe 1917 (COL, US). Boyacá: Chapon region, 100 mi NW of Bogotá, 1200 m, 8 May 1932, Lawrence 19 (AA, BM, F, MICH, MO, NY, US). Cauca: W of Tambo, W flank of Cordillera Occidental, 1000 m, 12 Nov 1946, Haught 5259 (COL, US); El Tambo, La Costa, 900 m, 5 Oct 1935, von Sneidern 504 (S), 1000 m, 28 May 1936, von Sneidern 699 (S), 900 m, 5 Oct 1935, von Sneidern 1047 (S). Chocó: La Equis, 200 m, 22 Jan 1949, Araque & Barkley 19Ch079 (COL, MICH, US); Río Bebará, sector La Calle, 12 Apr 1984, Córdoba 429 (MO); 31 mi E of Quibdó on rd. to Medellín, 18 Dec 1980, Croat 52306 (MO); km 175 of Medellín-Quibdó rd., 24 km E of Tutunendo, 430 m, 22 Apr 1983, Croat 56320 (MO), km 155, 77 km E of Quibdó, 500 m, 11 Mar 1984, Croat 57307 (MO, NY, US); Comunidad Indígena El 21, 8 Aug 1982, Escobar *et al.* 2188 (HUA); Bahía de Solano, climbing up Quebrada Seca towards la Chorrera, 11 Jun 1950, Fernández 320 (NY, US); Río Mutatá, 7 Jan 1973, Forero & Gentry 682 (COL, MO-2 sheets); San José del Palmar-Nóvita rd., nr. Curundó, Río Ingárá, 450 m, 31 Aug 1976, Forero *et al.* 2401 (COL, MO), beyond Curundó, 300 m, 20 Feb 1977, Forero *et al.* 3028 (COL, MO); Tutunendo-

El Carmen rd., 200-350 m, 26 Apr 1979, *Forero et al.* 5842 (COL, DUKE, MO), nr. "El 12," 600 m, 27 Apr 1979, *Forero et al.* 5891 (DUKE, MO, NY); Rio Torito, tributary of Rio Hábita, Finca Los Guaduales, 730-830 m, 1 Mar 1980, *Forero et al.* 6281 (COL, MO); left bank of Rio Ingára, Vereda Curundó, 720 m, 13 Jan 1983, *Franco et al.* 1139 (COL); between Carmen de Atrato and Tutunendo, 500-600 m, 25-26 Jul 1944, *Garcia-Barriga* 11129 (COL, US); Rio Mutata, tributary of Rio El Valle between base of Alto de Buey and mouth of river, 100-150 m, 7 Aug 1976, *Gentry & Fallen* 17289 (MO); 11 km E of Tutunendo on rd. to Medellín, 100-200 m, 12 Aug 1976, *Gentry & Fallen* 17533 (COL, MO); 6 km E of Rio Pato, 48 km W of Las Animas on Pan American Hwy., 250 m, 11 Jan 1979, *Gentry & Renteria* 24051 (COL, HUA-2 sheets, MO); 33 km E of Tutunendo on rd. to Medellin, 350 m, 14 Jan 1979, *Gentry & Renteria* 24171 (MO); Vereda Torito, Finca Los Guaduales, 630-890 m, 20 Mar 1981, *Guerra* 20 (COL); Rio Catripe, 100 m, 17 Jan 1947, *Haught* 5447 (COL, MICH, US); El Carmen-Quibdo Hwy., 490 m, 28 Dec 1982, *Juncosa* 522 (MO, US); N of Bahia Solano, Quebrada La Platanilla, 50 m, 10 Jan 1984, *Juncosa* 1863 (MO, US); Bahia Solano, nr. airport, 10 m, 17 Jan 1984, *Juncosa* 1944 (MO); km 137 of Bolívar-Quibdo hwy., 930 m, 11 Mar 1984, *Juncosa* 2464 (MO); Bahia Solano, nr. Ciudad Mutis, 0-75 m, 21-23 Feb 1939, *Killip & Garcia* 33476 (US); 8 km from Puerto Mutis along rd. to El Valle, 50 m, 28 Jan 1971, *Lellinger & de la Sota* 92 (US); Medellín-Quibdó rd., km 177-179, 450-500 m, 5 Apr 1979, *Luteyn & Lebrón-Luteyn* 7214 (COL, HUA, NY); Medellín-Quibdó rd., km 136, 16 km W of El Carmen de Atrato, 950 m, 28 Jan 1986, *Stein & McDade* 3309 (COL, JAUM, MO-2 sheets, US); Medellín-Quibdó rd., 35 km E of Quibdó, 450 m, 29 Jan 1986, *Stein & McDade* 3316 (AAU, COL, DUKE, F, JAUM, K, MO, NY, U, US-2 sheets); Nuquí, Alto de Buey, 1000 m, 3 Jun 1940, *von Sniedern* A.37 (S).
Cundinamarca: Caparrapí, 1280 m, 8-13 Jun 1939, *García-Barriga* 7700 (US); Balsonera Creek, 5 km SE of Yacopí, nr. Boyacá border, 740 m, 5 May 1944, *Grant* 9140 (NA).

US); Tenasuca, 1800 m, Jul 1853, *Triana* 1568 (BM, P). Norte de Santander: "Dep. Santander," Espíritu Santo, 30 Nov 1878, *Kalbreyer* 318 (B, K-2 sheets); Pueblo Nuevo, Ocaña, Jun 1845, *Purdie s.n.* (K-4 sheets). Risaralda: Santa Cecilia, Pueblo Rico, Tatamá, 800 m, 14 Nov 1945, *von Sneidern* 5001 (F, S, UC, US). Santander: Virolín, Vereda El Reloj, 1750-1800 m, 29 Nov 1979, *Diaz* 1289 (AAU, COL); from Virolín to Charalá, 29 May 1958, *Romero Castañeda* 6769 (COL); vic. of Puerto Berrio, between Carare and Magdalena rivers, headwaters of Dorado Creek, 11 km S of Raizudo, 300 m, 7 May 1937, *Haught* 2195 (COL, F, NA, NY, US, W); San Fernando, between Rio Carare and Puerto Berrio, 300 m, 30 Jun 1939, *Haught* 2852 (COL, NA, NY, US); Quebrada Boquerona, at confluence with Quebrada La Putana, W of Cordillera de la Paz, 3200 m, 7 Jul 1944, *St. John* 20558 (MICH, NY, UC, US); along rd. to Tona, 18 km E of Bucaramanga, 1800 m, 5 Mar 1986, *Stein & Sierra* 3600 (COL, MO-2 sheets, NY, U, UIS, US). Tolima: Río Saldaña, 1600-1800 m, 19 Nov 1944, *Core* 1601 (MICH, US), 1610 (US); Ibagué, El Palmar, 2200 m, 8 Oct 1975, *López-Palacios* 3902 (COL); La Virginia, Libano, 1200-1500 m, 22 Dec 1917, *Pennell* 3272 (NY); Municipality of Santa Isabel, Vereda La Pava, Finca La Pavita, 2030 m, 4 Aug 1980, *Idrobo et al.* 10502 (COL); Río Saldaña Valley, 9 km E of Herrera on rd. to Río Blanco, 2000 m, *Stein* 3501 (B, COL, DUKE, F, JAUM, K, MO, NY, U, US); Finca El Palmar, 5 km Above Juntas on rd. from Ibagué toward Nevado del Tolima, 2150 m, 20 Feb 1986, *Stein* 3541 (AAU, COL, F, JAUM, K, MO, NY, US-2 sheets); El Libano, 1600 m, 18 Jul 1945, *Uribe* 990 (COL); Toche, 2300 m, 19 May 1942, *von Sneidern s.n.* (S). Valle: Río Anchicayá, Quebrada del Retiro, 300 m, 19 Dec 1942, *Cuatrecasas* 13683 (F-2 sheets, MICH, US); without locality, *Duque Jaramillo* 1965 (F); Río Anchicayá nr. CVC hydroelectric plant, 400-500 m, 15 Dec 1981, *Gentry* 35675 (COL, MO); Río Digua Valley, La Margarita, 760 m, 4-5 Apr 1939, *Killip* 34893 (US); old rd. Cali-Buenaventura, 2-13 km N of Anchicayá, 300-490 m, 9 May 1984, *Luteyn et al.* 10363 (NY); 34-39 km from

Buenaventura along Río Anchicayá on old rd. to Cali, 150–400 m, 23 Jan 1986, Stein et al. 3279 (B, COL, CUVC, DUKE, MO, NY, US). Department unknown: Los Corales, Dec 1844, Goudot s.n. (P).

VENEZUELA. Zulia: Sierra de Perijá, W of Dakuma, 1000 m, 22 Sep 1974, Jangoux 10212 (MICH).

Vernacular names and local uses. "Kol de Monte," Antioquia Department, Colombia; leaves eaten after cooking." "Col de Montaña," Chocó Department, Colombia. "Flor de verano," Chocó Department, Colombia; leaves and fruit eaten. "Cresta de Gallo"; Tolima Department, Colombia. "Mountain cabbage," Norte de Santander Department, Colombia.

19e. *Centropogon granulosus* Presl subsp. *tortilis* (F. Wimmer) B. A. Stein, comb. et stat.

nov.

Centropogon tortilis F. Wimmer, Repert. Spec. Nov. Regni Veg. 22: 217. 1926. Type.

Costa Rica. Limón: ravine along Río Chirripó (N), Feb 1900, Pittier 16033 (holotype, W, photo F-neg. 30969; isotypes, BM, CR n.v., GH n.v., photo-DUKE).

Centropogon panamensis Wilbur, Ann. Missouri Bot. Gard. 63: 628, fig. 3. 1977. Type.

Panama. Coclé: W slopes of Cerro Pajita in crater of El Vallé de Antón, 650 m, 31 Dec 1971, Wilbur et al. 15611 (holotype, DUKE; isotypes, CAS, DUKE, MICH, MO, NY).

Erect to scandent shrubs 1–2.5 m tall, mostly branching from the base; stems glabrescent or hirtellous apically. Leaves elliptic to widely elliptic, oblong, ovate, or

obovate, 15-25(-35) x 6-14 cm, apex acute to acuminate, base cuneate; lamina thick and fleshy when fresh, abaxial surface glabrous or minutely hirtellous to minutely muricate along veins; secondary veins 8-11, very conspicuous, strongly parallel and usually widely arcuate-ascending. Inflorescence an erect, bracteate, terminal, subcorymbose raceme, elongating to 30 cm but usually less than 15 cm long, the flowers numerous, floral internodes congested at apex, remaining congested in age or becoming somewhat lax basally, the rachis moderately hirtellous, occasionally subtended by an erect peduncle to 10(-15) cm long; bracts persistent, rarely deciduous in age, elliptic, oblong to lanceolate, mostly 15-30 mm long and often exceeding the length of the subtended pedicels; pedicels short, 5-20(-25) mm long, densely hirtellous or rarely with verrucate protrusions, bracteoles 1-4 mm long. Flowers 55-60 mm long; hypanthium broadly hemispheric, apparently lacking intersepalar nectaries; sepals narrowly triangular to ligulate, (4-)7-12(-16) x 2-3 mm, moderately to densely hirtellous, especially on adaxial surface; corolla concolorous, bright pink to rose-red, densely hirtellous; corolla tube 33-38 mm long, 6-9 mm wide at base, narrowing to 4-5 mm either at point of filament attachment, or more often just below throat, the throat ventricose and abruptly ampliate, 10-13(-14) mm wide, sharply curving 50-70°; androecium 48-53 mm long; filament tube 38-43 mm long, white, usually short-pilose at summit, scarcely exserted from corolla tube 2-5(-7) mm; anther tube (7-)8-9 mm long, thecae gray, connectives rose-purple, the dorsal ones densely short-pilose with purple trichomes 0.5-1.5 mm long, the anther tube rarely glabrescent, antheridial scale deltoid and often concave, the apex occasionally truncate, a tuft of short, unfused, white trichomes often present at base. Fruit to 15 x 20 mm; seeds elliptic to suborbicular.

Distribution. *Centropogon granulosus* subsp. *tortilis* is found from central Panamá to southern Nicaragua at elevations of 100-1300 m. It occurs in montane and

cloud forests at mid-elevations along the peaks and continental divide in Central Panama, and in lowland tropical forest along the Caribbean coast from western San Blas Comarca through Costa Rica and into adjacent Nicaragua. Additional collections from San Blas will probably reveal populations linking this taxon with *C. granulosus* subsp. *lugens* in eastern Darién Province and the Chocó of Colombia.

Additional specimens examined. NICARAGUA. Río San Juan: Nr. Caño Chontaleño, 20 km NE of El Castillo, 200 m, 7-9 Mar 1978, *Neill* 3394 (MO).

COSTA RICA. Limón: Nr. the Río Catarata (Río Sand Box) in the hills between BriBri on the Río Sixaola and the Caribbean coastal plain, 50-100 m, 28-29 Nov 1975, *Baker & Burger* 132 (DUKE, F), 10-13 Feb 1977, *Burger et al.* 10482 (DUKE, MO); Alto Urén, trail between finca Fila Dimat and finca Sukut, 22 Oct 1985, *Gómez et al.* 23769 (MO).

PANAMA. Bocas del Toro: Along road between Chiriquí Grande and Fortuna, 13.2 mi W of Chiriquí Grande, 310 m, 9 Mar 1985, *Croat & Grayum* 60118 (DUKE), 8.5 mi N of bridge over the Fortuna Lake, 4.3 km N of the Continental Divide, 590 m, 10 Mar 1985, *Croat & Grayum* 60170 (DUKE); Río San Pedro, Jan 1978, *Gordon* 32 (MO); Río Teribe, near Q. Lukulon, 100 m, 12 Apr 1968, *Kirkbride & Duke* 515 (MO); Chiriquicito to 5 mi S along Río Guarumo, 5-7 Jun 1967, *Lewis et al.* 2026 (DUKE, MO). Coclé: N rim of El Valle, 800-1000 m, 14 Feb 1937, *Allen* 211 (MO); vic. of El Valle, 600-1000 m, 8 Dec 1938, *Allen* 1213 (MO, US); trail to La Mesa N of El Valle de Antón, 1000 m, 31 Aug 1941, *Allen* 2709 (MO); nr. La Mesa, 1000 m, 12 May 1941, *Allen* 2392 (MO); N of El Valle de Antón, 700-800 m, 7 Feb 1947, *Allen* 4217 (MO); N of El Copé nr. sawmill, 730 m, 16 Oct 1979, *Antonio* 2169 (DUKE, MO), *Antonio* 3269 (DUKE); El Valle, 2 km E of La Mesa, N slope of Cerro Gaital, 800 m, 16 Nov 1983, *Churchill* 3868 (DUKE); 2.5 mi above El Valle on rd. to La Mesa, 11 Feb 1971, *Croat*

13371 (MO-2 sheet, NY); La Mesa, 13 Apr 1971, *Croat* 14368 (DUKE, MO); on Atlantic slope near the continental divide 9.4 km above El Copé, 750-900 m, 20 Jan 1978, *Croat* 44604 (MO); hills above El Valle, 13 Aug 1972, *D'Arcy & D'Arcy* 6736 (DUKE, MO-2 sheets); top of ridge N of El Copé, El Petroso, 9 Apr 1977, *D'Arcy* 1317 (DUKE, MO, MO); trail from Caño Blanco del Norte to continental divide N of El Copé, 400 m, 5 Feb 1983, *Davidse & Hamilton* 23671 (DUKE); slopes of Cerro Pilon nr. El Valle, 700-900 m, 10 Jun 1967, *Duke* 12102 (MO), 900 m, 5 Oct 1967, *Duke & Correa* 14656 (MO); El Valle, 12 Jul 1962, *Dwyer* 1928 (MO-2 sheets); El Valle de Antón at the foot of Cerro Pilón, 600 m, 15 Aug 1967, *Dwyer & Correa* 7992 (MO); La Mesa, above El Valle, 4 Jan 1974, *Dwyer & Nee* 11923 (MO); summit at El Calvario, 900 m, 4 Apr 1977, *Folsom & Robinson* 2430 (MO), 2431 (DUKE, MO); Alto Calvario, 800-900 m, 20 Apr 1977, *Folsom & Jaslon* 2673 (DUKE, MO); around Limón, 5 hours walk N of Alto Calvario, 800-1000 m, 10 Oct 1977, *Folsom* 5825 (DUKE, MO-2 sheets, MO, NY); vic. of La Mesa, N of El Valle, 1000 m, 23 Dec 1972, *Gentry* 6849 (DUKE, F, MO); Caribbean side of divide at El Copé, 200-400 m, 3 Feb 1983, *Hamilton & Davidse* 2609 (DUKE); 8 km above El Copé, 600 m, 10 Jan 1978, *Hammel* 811 (DUKE, MO-2 sheets); rd. from El Valle to La Mesa, 700 m, 24 Apr 1982, *Hust* 1938 (MO); El Valle, along Río Indio trail, 500-700 m, 30 Jan 1935, *Hunter & Allen* 299 (G, MO); El Valle WEPCOR site, 24 Apr 1968, *Kirkbride* 1083 (MO); Atlantic slope of the Continental Divide nr. sawmill above El Copé, 750-800 m, 13 Feb 1982, *Knapp & Dressler* 3403 (MO), 3479 (DUKE); Cerro Pilon, 1968, *Lallathin* 6002 (MO); mts. N of El Valle de Antón, 750-900 m, 28 May 1967, *Lewis et al.* 1760 (MO); Cerro Pilon, 900-1173 m, 16 Mar 1973, *Liesner* 776 (MO); 5 mi N of El Valle de Antón, 1000 m, 7 Jul 1970, *Luteyn* 1184 (DUKE), 1227 (DS, DUKE); about 8 mi N of El Valle de Antón, 2 Aug 1970, *Luteyn & Kennedy* 1680 (DUKE, MICH); along trail to Las Minas, N of El Valle de Antón, 800-900 m, 18 Jun 1972, *Luteyn* 3159 (DUKE); 4 mi NW of El Valle de Antón, 850-900 m, 10 Jun 1973,

Luteyn 4077 (DUKE); nr. El Valle del Antón, 650-700 m, 15 Sep 1974, *Maas et al.* 1728 (U); above Copé, 700-750 m, 27 Nov 1985, *McPherson* 7674 (MO); La Mesa, 4 km N of El Valle, 875 m, 3 Jan 1974, *Nee & Dwyer* 9173 (DUKE, MO); foot of Cerro Pilón, 600 m, 27 Mar 1969, *Porter et al.* 4421 (MO); W slope of Cerro Gaital, N of El Valle, ca. 1.2 km N of N edge of town, 720 m, 3 Feb 1979, *Reveal & Burns Balogh* 4974 (MO); along rd. from El Valle to La Mesa, 750 m, 10 Aug 1971, *Spellman et al.* 581 (MO); El Valle, 2 km N along rd. to La Mesa, 750 m, 12 Dec 1982, *Stein & Hamilton* 961 (MO); La Mesa, 2 km W of Cerro Pilon, 860 m, 21 Jul 1976, *Sullivan* 450 (DUKE, MO-2 sheets, NY); above El Petroso sawmill at continental divide, 1200-1300 m, 25 Oct 1980, *Sytsma* 1868 (DUKE, MO); between Continental Divide above El Copé and El Petroso sawmill and the Rio Blanco to the N, 250 m, 13 Dec 1980, *Sytsma et al.* 2423 (MO), 2442 (MO); 4 mi past Llano Grande on rd. to Cascajal, ca. 2 km W along continental divide, 600 m, 10 Apr 1981, *Sytsma* 3959 (MO); NE slopes of Cerro Caracoral, N rim of El Valle, 850 m, 4 May 1981, *Sytsma et al.* 4316 (DUKE, MO); above El Potroso sawmill at Continental Divide, N of El Copé, 1200-1300 m, 13 May 1981, *Sytsma & Andersson* 4552 (DUKE); La Mesa, 5 mi N El Valle, 750 m, 10 Nov 1965, *Tyson et al.* 2430 (NY); La Mesa, above El Valle de Antón, 1000 m, 14 Sep 1968, *Weaver & Foster* 1644 (DUKE-3 sheets, MICH); Distr. Penonomé, along headwaters of Rio Guaybo, W slopes of Cerro Pajita, 8°38'N, 80°8'W, 700 m, 2 Jul 1971, *Webster* 16822 (DUKE); inside the crater of El Valle de Antón on La Mesa below the N rim, ca. 1000 m, 20 Jan 1970, *Wilbur et al.* 11108 (DUKE-2 sheets, F, GH, MICH, MO, NY); along trail to La Mesa ca. 4.5 mi beyond El Valle de Antón, 21 May 1970, *Wilbur & Luteyn* 11689 (DUKE, MICH); nr. La Mesa, ca. 5 mi N of El Valle, 22 May 1970, *Wilbur & Luteyn* 11732 (DUKE); W slopes of Cerro Pajita in crater of El Valle de Antón and ca. 3 mi N of El Valle, 650 m, 31 Dec 1971, *Wilbur et al.* 15611 (CAS, DUKE-2 sheets, MICH, MO, NY); La Mesa, in crater of El Valle ca. 3 km N of El Valle de Antón, 850 m, 31 Dec 1971,

Wilbur et al. 15640 (DUKE, F, MICH, MO). Panamá: Trail to top of Cerro Pelado, 1000 m, 16 Jun 1979, *Antonio* 1095 (DUKE, MO); Cerro Campana, 700 m, 19 Jun 1966, *Blum et al.* 2373 (MO); hwy. nr. top of Cerro Campana, 10 Sep 1970, *Croat* 12091 (MO); along rd. to Cerro Campana, 25 May 1971, *Croat* 14708A (MO); Cerro Campana above Su Lin Motel, 25 May 1971, *Croat* 14745 (MO); Campo Tres, 3 mi NE of Altos de Pacora, 500-800 m, 10 Mar 1973, *Croat* 22728 (DUKE, MO); Serrania de Pirre, headwaters of Rio Escucho Ruido, ca. 16 km due N of Alto de Nique, 1530-1550 m, 27 Jul 1976, *Croat* 37939 (MO); Cerro Campana, 10 May 1971, *D'Arcy* 5501 (DUKE, MO), 800 m, 29 Mar 1977, *D'Arcy* 11136 (DUKE, MO), 750 m, 17 Aug 1982, *D'Arcy & Hamilton* 14945 (DUKE); Cerro Jefe, 10-13 mi. beyond Goofy Lake, 12 Feb 1966, *Duke* 8006 (MO); Cerro Campana, 900 m, 11 Aug 1967, *Dwyer & Kirkbride* 7856 (MO); Cerro Campana, 8 Jul 1960, *Ebinger* 330 (F, MICH, MO); Cerro Campana, 19 Aug 1967, *Garner* 24 (DUKE), 800-1000 m, 3 Apr 1972, *Gentry* 4919 (MO), 800 m, 17 Aug 1982, *Hamilton & D'Arcy* 687 (DUKE), Jul 1965, *Hayden* 115 (MO), 800 m, 4 Jun 1967, *Lewis et al.* 1910 (DUKE), 8.6 mi SW of Capira, 700 m, 28 Jun 1970, *Luteyn* 977 (DS, DUKE, GH), 8 Aug 1970, *Luteyn & Kennedy* 1788 (DUKE), 850 m, 6 Jun 1973, *Luteyn* 3976 (DUKE), 2900 m, 28 Aug 1965, *McDaniel* 6861 (DUKE, MO), ca. 10 km SW of Capira, 870-1000 m, 7 Dec 1974, *Mori & Kallunki* 3558 (DUKE, MO); 5-10 km NE of Altos de Pacora, 750 m, 6 Mar 1975, *Mori & Kallunki* 4949 (MO); Cerro Campana, above Su Lin Motel, 25 Mar 1969, *Porter et al.* 4176 (DUKE, MO), 4214 (DUKE-2 sheets, MO), 4265 (DUKE-2 sheets, MO-2 sheets); Cerro Campana, 800 m, 17 Sep 1980, *Sytsma* 1137 (DUKE), 800 m, 3 Jan 1981, *Sytsma* 2915 (DUKE), 750 m, 19 Mar 1972, *Tyson & Lazor* 6234 (NA), 750-850 m, 14 Feb 1978, *Utley* 5710 (CAS, DUKE); Cerro Campana, 850 m, 11-12 Jun 1971, *Webster & Breckon* 16498 (DUKE), 820 m, 23 Jan 1970, *Wilbur & Weaver* 11285 (DS, DUKE-2 sheets, F, GH, MICH, MO), 13 Sep 1975, *Witherspoon & Witherspoon* 8376 (DUKE, MO-2 sheets). San Blas: Nusagandi, El Llano-Carti rd., 350

m, 20 Feb 1985, *van der Werff* 7016 (DUKE). Veraguas: Slopes of Cerro Tute, nr. Santa Fé, 750 m, 25 Mar 1947, *Allen* 4368 (MO); rd. to Río Calovébora above Escuela Agrícola nr. Río Santa María, 850 m, 7 Oct 1979, *Antonio* 2026 (MO); along trail to top of Cerro Tute, 1000-1250 m, 30 Nov 1979, *Antonio* 2921 (MO), 700 m, 26 Jan 1980, *Antonio* 3524 (MO); 5 mi W of Santa Fe on Pacific side of divide, 800-1200 m, 18 Mar 1973, *Croat* 22984 (DUKE, MO); Río Primero Braso, nr. Santa Fe, 700-750 m, 24 Jul 1974, *Croat* 25481 (MO-2 sheets); valley of Río Dos Bocas on rd. between (above Santa Fe) and Calovebora, 350-400 m, *Croat* 27379 (MO); nr. Escuela Agrícola on rd. to Río Calovebora, 750 m, 3 Apr 1976, *Croat & Folsom* 33870 (DUKE, MO); 0.6 mi beyond Escuela Agrícola, 730 m, 4 Apr 1976, *Croat & Folsom* 34015 (DUKE, MO); along Santa Fe-Calovebora rd. 3 mi. beyond Escuela Agrícola, 700 m, 1 Dec 1979, *Croat* 49023 (DUKE); E side of Cerro Tute W of Escuela, 5 mi NW of Santa Fé, 750-800 m, 10 Sep 1982, *D'Arcy* 15006 (MO); 3.9-5 mi. N of Santa Fé, 500-1000 m, 12 Dec 1971, *Gentry* 2967 (MO); past Escuela Agrícola on rd. to Calovebora, 1200 m, 9 Sep 1982, *Hamilton et al.* 1257 (DUKE); Cerro Tute, ridge above Escuela Agrícola, Santa Fé, 800-1000 m, 20 Feb 1983, *Hamilton & Dressler* 2983 (MO); mountains W of Alto de Piedras, school N of Santa Fe, on E slope of Cerro Arizona, 915 m, 11 Sep 1978, *Hammel* 4745 (DUKE, MO); trail from Barera S to gold mine "Cocuyo," 30-180 m, 17 Oct 1978, *Hammel* 5200 (MO); Caribbean slope above Río Primero Brazo, 5 mi. NW of Santa Fe, 700-1200 m, 18-19 Mar 1973, *Liesner* 834 (MO); trail on ridge to summit of Cerro Tute, 750-950 m, 15 Dec 1981, *Knapp & Sytsma* 2542 (DUKE); rd. beyond Escuela Agrícola, above Santa Fé, 700-800 m, 1 Jan 1975, *Luteyn & Wilbur* 4577 (DUKE); N of Santa Fé, 2 km N of Escuela Agrícola Alto de Piedra, 18 Oct 1974, *Mori & Kallunki* 2630 (MO); N of Santa Fé 11 km from Escuela Agrícola Alto de Piedra, along Río Dos Bocas on Atlantic slope, 14 Nov 1974, *Mori & Kallunki* 3081 (MO); valley of Río Dos Bocas, Atlantic slope NW of Santa Fé, 450-550 m, 20 Dec 1974, *Mori & Kallunki* 3837 (MO); 6-7 km W of Santa

Fé, 880 m, 16 Feb 1974, Nee 9734 (DUKE, MO, NY); trail to summit of Cerro Tute, 3 km above Escuela Agrícola, 790-850 m, 4 Jan 1981, Sytsma & Antonio 2979 (DUKE); headwaters of Río Coloveborita, 15 km past Escuela Agrícola, 500 m, 16 May 1981, Sytsma & Andersson 4759 (MO); slopes N of Escuela Agrícola, 2 km N of Santa Fé, 1 Jan 1975, Wilbur & Luteyn 19123 (CAS, DUKE-2 sheets, MICH, MO, NY).

Specimens intermediate between *C. granulosus* subsp. *tortilis* and *C. granulosus* subsp. *nutans* (see discussion): PANAMA. Chiriquí: N of San Felix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine rd. along continental divide, 1525-1675 m, 5 May 1979, Mori & Kallunki 5919 (DUKE, MO). Coclé: Top of ridge N of El Copé, El Petroso, 9 Apr 1977, D'Arcy 11317 (DUKE, MO-2 sheets); elfin forest, Cerro Caracoral, 1000 m, 19 Jan 1968, Duke & Dwyer 15122 (NY); summit of Alto Calvario, low montane cloud forest, ridge-type vegetation, 900 m, 4 Apr 1977, Folsom & Robinson 2430 (DUKE, MO); forest around Rivera sawmill, Alto Calvario, 7 km N of El Copé, 13 May 1977, Folsom 3230 (MO, DUKE); Cerro Pilon, 5 km NE of El Valle, 800-1045 m, 14 Jun 1975, Mori et al. 6623 (MO); cloud forest on divide SW of La Mesa, 900 m, 26 Dec 1982, Stein & Hamilton 988 (MO); above El Petroso sawmill at continental divide, 1200-1300 m, 24 Oct 1980, Sytsma 1771 (MO); above El Petroso sawmill at Continental Divide, N of El Copé, 1200-1300 m, 13 May 1981, Sytsma & Andersson 4577 (MO) - collected along with normal form, 4552.

19f. *Centropogon granulosus* Presl subsp. *nutans* (Planchon & Ørsted) B. A. Stein comb
et stat. nov.

Centropogon nutans Planchon & Ørsted, Vidensk. Meddel. Dansk Naturhist. Foren.

Kjobenhavn 1857: 156. 1857. Type. Costa Rica. Cartago: Turrialba, 900-1200 m, May, Ørsted s.n. (holotype, C n.v.).

Centropogon corymbiflorus Koch, nom. nud., Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 8: 60. 1864.

Centropogon warszewiczii Vatke, Linnaea 38: 716. 1874, non *Centropogon warszewiczii* Van Houtte (1858). Types. Costa Rica or Panama. "Costa Rica et Veragua," Warszewicz 5 (lectotype here designated, B, photo B-neg. 5633a; isolectotype, G); "Costa Rica et Veragua," Warszewicz 3 (syntype, B); "Sud-America," Warszewicz 12 (syntype, B).

Centropogon augostanus F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 9. 1935. Type. Costa Rica. Cartago: Angosta [?], 10 Nov 1875, Polakowsky 431 (holotype, B).

Centropogon erastus F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 8. 1935. Costa Rica. Palma, 5 Mar 1909, Brade 2395 (holotype, B, photo F-neg. 30217).

Suffrutescent scandent herbs or vines to 3 m long, usually much-branched throughout; stems smooth to scaberulous, glabrous or minutely hirtellous, especially toward apex. Leaves widely elliptic, elliptic, oblong or ovate, (8-)10-24(-32) x 4-11(-13) cm, base usually obtuse to rounded, margins mostly crenulate, abaxial surface glabrous or the veins minutely muricate to minutely hirtellous; secondary veins 7-10, usually diverging from mid-vein at a wide angle and arcuately ascending. Inflorescence a horizontal or pendent, upturned, bracteate, subcorymbose raceme, elongating to 15(-30) cm but usually shorter, the flowers congested at tip, either remaining congested or becoming lax basally following rachis elongation, the rachis hirtellous and usually scaberulous, occasionally with granular-pustulate protrusions or pustulate-based trichomes, often subtended by a short peduncle; bracts normally persistent, rarely caducous, lanceolate or ovate to oblanceolate, 8-20 mm long, glabrous or both surfaces sparsely to moderately hirtellous; pedicels assurgent or spreading, often elongate, (15-)25-45(-90) mm long, moderately to densely puberulent to hirtellous, bracteoles rarely

submedial, linear to ligulate, 1-5(-9) mm long. Flowers (55-)60-70 mm long; hypanthium with intersepalar nectaries at least occasionally present; sepals erect or slightly spreading, narrowly triangular to linear or ligulate, (3-)7-16 x (1-)2-3 mm; corolla bicolored, orangish-red to reddish-orange basally grading into yellowish-orange or yellow at lobes, the corolla rarely glabrescent, usually sparsely to densely hirtellous with short conical trichomes, these occasionally with swollen or granulose bases; corolla tube (32-)35-40 mm long, the base 6-10 mm wide, narrowing to 2.5-5 mm at point of filament attachment then gradually re-expanding to base of throat, the throat often not well differentiated from lower portion of tube, moderately ampliate, 10-13(-15) mm wide, gradually to sharply curved 35-55°; androecium (50-)55-65 mm long; filament tube ca. 45-55 mm long, pale yellow, glabrous throughout or long-pilose at summit, long-exserted from corolla tube 9-13(-16) mm; anther tube slightly arching, (7-)8-9(-10) mm long, thecae yellowish-tan, connectives brown, dorsal and ventral ones sparsely to densely long-pilose with white trichomes 2-3 mm long, or rarely partially or completely glabrous, antheridial scale with a dense tuft of unfused trichomes at base. Fruit to 15 x 20 mm, prominently ridged; seeds suborbicular.

Distribution. *Centropogon granulosus* subsp. *mutans* is centered in Central America where it is found from western Panama to northern Costa Rica, and also occurs in the coastal regions of southwestern Colombia and northeastern Ecuador. It occupies a wide variety of habitats ranging from montane and cloud forests to low elevation moist forests. In Chiriquí Province, Panamá it is found primarily at upper elevations in montane and cloud forest (700-2650 m), while in Costa Rica it occurs over a wider elevational range, being most abundant in montane regions (900-2300 m), but infrequently reaching low elevations along both the Pacific (to 150 m) and Atlantic slopes (to 300 m). In northwestern South America it is found from 500-1900 m.

Additional specimens examined. COSTA RICA. Alajuela: Nr. border with Heredia Province, 7 km beyond Varablanca junction on CR 9, 1450 m, 11 Dec 1975, *Almeda & Almeda* 2658 (CAS); Lake Achandi nr. Cariblanco, 750 m, 3 Mar 1965, *Blaisdell* 248 (MO); La Palma de San Ramón, 1250 m, Nov 1922, *Brenes* 3730 (F), 7 Dec 1926, *Brenes* 5165 (F, NY), 9 Sep 1928, *Brenes* 6304 (F); Los Angeles de San Ramón, 1025 m, 20 Nov 1923, *Brenes* 3945 (F), 11-12 Dec 1928, *Brenes* 6026 (F); upper drainage of Río Peñas Blancas, Monteverde Reserve, 1250-1350 m, 25-26 Feb 1977, *Burger et al.* 10781 (F); upper Rio Sarapiquí nr. Cariblanco, along rd. to Colonia Virgen del Socorro, 800 m, 17-18 Sep 1978, *Burger & Antonio* 11146 (DUKE, F); 8.5 km NE of Villa Quesada along Hwy. 15 between Naranjo and Aguas Zarcas, 600 m, 3 Feb 1979, *Croat* 46956 (MO); 4 km S of San Miguel, 600 m, 17 Oct 1968, *Davidse and Pohl* 1312 (F); region of Zarcero, 1400 m, 3 Feb 1938, *Donnell-Smith* H-266 (F); La Peña de Zarcero, 1550 m, 22 Oct 1938, *Donnell-Smith* 1282 (F, NY); San Luis de Zarcero, 1400 m, 20 Jan 1939, *Donnell-Smith* 1523 (NY); La Peña, 1300 m, 26 Dec 1939, *Donnell-Smith* 2180 (NA), 4 Jan 1941, *Donnell-Smith* 10112 (F); Río Peñas Blancas, Monteverde Reserve, 1100-1200 m, 26 Mar 1977, *Dryer* 1271 (F); Rio Cataratitas, 20 km NW of San Ramón, 850 m, 3 Feb 1986, *Grayum et al.* 6325 (MO); Peñas Blancas, Monteverde Reserve, 1200 m, 20 Oct 1984, *Haber* 734 (MO), 1300 m, *Haber* 743 (MO), 960 m, 27 Oct 1984, *Haber* 844 (MO), 1100 m, 20 Nov 1984, *Haber* 990 (MO); 20 Jan 1985, *Haber* 1242 (MO), 1257 (MO); between Finca Los Ensayos and Zapote de Alfaro Ruiz, 1400 m, 4 Mar 1963, *Jiménez* 449 (F); N of San Ramón between Angeles and Balsa, 1300 m, 23 Jul 1970, *Lellinger & White* 1210 (DUKE); 17-20 km NNW of San Ramón, 4-7 km N of Balsa, 750 m, 24 Apr 1983, *Liesner & Judziewicz* 14693 (DUKE, WIS); 18 km N of San Ramón on rd. through Los Angeles, 1200 m, 11 Jun 1970, *Luteyn* 700 (DUKE); Balsa, 10 km N of San Ramón, 1000 m, 9 Aug 1974, *Maas & Lent* 1227 (F, U); vic. of Coliblanco, 1950

m, 30 Apr-2 May 1906, *Maxon* 311 (NY); N of San Ramón on rd. to Santa Clara, 900 m, 13 Jul 1977, *McDade* 223 (DUKE); nr. Artezalea 8 km NE of Villa Quesada, 550 m, 17 Feb 1966, *Molina et al.* 17301 (F, NY); Río San Rafael 2 km W of La Marina, Llanura de San Carlos, 550 m, 17 Feb 1966, *Molina et al.* 17389 (F, WIS-2 sheets); Cariblanco, on rd. 4 mi. toward Laguna Hulé, 10 Jun 1972, *Primack & Stone* 52 (DUKE); rd. from San Ramón N to Balsa, 900-1000 m, 29 Aug 1979, *Stevens* 13745 (DUKE, MO), 700-800 m, *Stevens* 13858 (MO); N of San Ramón , km 15-35 of rd. to La Tigra and Fortuna, 400-600 m, 14 Jun 1984, *Taylor & Tingley* 4236 (DUKE); Buena Vista de San Carlos, 15 Apr 1903, *Pittier* 16665 (B); N of San Ramón 4 km beyond Río Balsa, 1100-1200 m, 27 Jun 1972, *Utley* 370 (DUKE); 13 km N of La Balsa, *Utley & Utley* 4066 (DUKE); 19 km N of San Ramón, 1000 m, 16 Jan 1968, *Wilbur & Stone* 9704 (DUKE-2 sheets, F-2 sheets), 21 Mar 1968, *Wilbur & Stone* 10110 (DS, DUKE-2 sheets, F, GH, MICH, NY); 13.5 mi. E of Arenal and 6.5 mi. W of Fortuna, 28 Mar 1968, *Wilbur & Stone* 10264 (DUKE); 19 km N of San Ramón, 1000 m, 3 Sep 1968, *Wilbur & Stone* 10675 (DUKE); 4 mi. N of Varablanca on rd. to Sarapiquí, 1450 m, 29 Jan 1971, *Wilbur & Teeri* 13705 (DUKE, F, MICH); 9-11 mi. N of Varablanca, 900 m, 1 Feb 1971, *Wilbur & Teeri* 13832 (DUKE), 13853 (DUKE); 3-7 km N of Angeles Norte, 1000 m, 15 Dec 1974, *Wilbur & Luteyn* 18194 (DUKE), 18214 (DUKE, MO); 1.5 km S of Los Angeles Norte, 12 km N of San Ramón, 1200 m, 15 Dec 1974, *Wilbur & Luteyn* 18223 (DUKE, DUKE, MICH, MO); rd. to Laguna Hulé, 5-9 km NW of Cariblanco, 900 m, 16 Dec 1974, *Wilbur & Luteyn* 18276 (DUKE), 18294 (DUKE-2 sheets); Colonia Virgen del Socorro, 900 m, 2 Aug 1976, *Wilbur* 21681 (DUKE); 28 km NNW of San Ramón nr. Río Cataratas, 600 m, 6 Jul 1977, *Wilbur et al.* 22097 (DUKE); 3-4 km NW of Río Balsa, 1100 m, 23 Feb 1978, *Wilbur* 24799 (DUKE), *Wilbur* 24824 (DUKE); nr. San Juan de Laja, 15 km N of Zarcero, 1350 m, 7 Feb 1965, *Williams et al.* 28947 (F); Hacienda la Marina, Río San Rafael, Cantón de Aguas Zarcas, 450-550 m, 8 Feb 1965, *Williams et*

al. 29099 (BM, F, NW, WIS). Cartago: 11–20 km E of Orosi, beyond Tapanti, 1500–1700 m, 29 Dec 1973, *Almeda et al.* 2191 (DUKE), 5 Jan 1974, 2372 (DUKE, F); 2.5 km S of Muñeco, 1500 m, 25 Feb 1978, *Almeda & Nakai* 3944 (CAS); 7 km NE of Santa Cruz on rd. beyond Agua, 1950 m, 8 Mar 1978, *Almeda & Nakai* 4163 (CAS); 15 km S of Tapanti, 1500 m, 12–17 Dec 1969, *Burger & Liesner* 6754 (F, MO, NY); beyond Pavones on rd. from Turrialba, 26 Jan 1957, *Carlson* 3396 (F); Estrella, 1350 m, Mar 1888, *Cooper* 5844 (B, G, G); Tapanti watershed preserve 20 mi. SW of Paraíso, 5 Feb 1979, *Croat* 46998 (MO); rd. from Tapanti to ICE watershed area, 1000 m, 3 Feb 1976, *Durkee* 76-25 (F); Reserva de Tapanti, 1300–1800 m, Nov 1982, *Gómez* 18749 (MO), 7 Dec 1982, *Gómez* 19222 (DUKE, MO); Río Grande de Orosi, Tapanti, 1200 m, 19 Jan 1964, *Jiménez* 1617 (F, BM); SE of Orosi, nr. Purisil, 1800 m, 9 Aug 1970, *Lettenger & White* 1488 (DUKE); 3 km S of Tres Equis, 600 m, 24 Apr 1965, *Lent* 538 (F); Río Grande de Orosi, 3 km SE of Tapanti, 1400 m, 16 Apr 1967, *Lent* 823 (F, NY, WIS); nr. Río Villegas, Valley of Río Grande de Orosi, 1650 m, 11 Jan 1970, *Lent* 1863 (F, NY); Finca La Palmira, 12 km NW of Turrialba, 1800 m, 19 Jan 1972, *Maas* 816 (F, U); Río Aquiares, 0.5 km W of Santa Cruz, 1500 m, 17 May 1973, *Luteyn* 3636 (DUKE); Volcán Turrialba, 1400 m, Jan 1899, *Pittier* 7517 (BM p.p., F, MO); N of Muñeco, along Río Sombrero, 1400 m, 25 Jun 1972, *Primack et al.* 194 (DUKE); El Copey, 2280 m, 19 Apr 1928, *Stork* 1543 (F, MINN); Turrialba, 900 m, 10 Jun 1928, *Stork* 2633 (F); 10 km along rd. to Tablón, 1600–1700 m, 29 Apr 1984, *Taylor* 2835 (DUKE); Río Taus, 1000 m, 2 Aug 1972, *Taylor & Taylor* 11495 (MO); Tapanti, 1250 m, 7 Jul 1964, *Tessene* 1292 (WIS); forests of Copey, 1800 m, Mar 1898, *Tonduz* 11840 p.p. (B, G, P); along Río Blanco, El Copey, 1800–1900 m, Feb 1898, *Tonduz* 11910 (BM); Las Vueltas, Tucurrique, 635 m, Jan 1899, *Tonduz* 13104 (G, P); Valley of Río Grande del Orosi, Tapanti, 21 Dec 1970, *Tryon & Tryon* 7103 (F); Tapanti, 23 Jun 1972, *Utley* 324 (DUKE); S of Muñeco, 5 Apr 1974, *Utley & Utley* 763 (DUKE); Tapanti, 1500–1900 m,

13 Dec 1974, Utley & Utley 1595 (DUKE), 13 Dec 1975, Utley & Utley 3624 (DUKE, F, MO), 7 April 1976, Utley & Utley 4518 (DUKE); El Retiro, Santa Cruz de Turrialba, 1400 m, Jan 1941, Valerio 1347 (F); 10 km E of Caché toward Tucurrique, 1090 m, 23 Sep 1967, Whitmore 99 (DUKE, F); above Platanillo, 600 m, 25 Mar 1967, Wilbur & Stone 8663 (DUKE); 6 km S of Tapantí, 30 Mar 1967, Wilbur & Stone 8899 (DUKE); Tapantí, 1300 m, 22 Mar 1968, Wilbur & Stone 10146 (DUKE), 1400 m, 27 Aug 1968, Wilbur & Stone 10482 (DUKE); 2.5 km NE of Pacayas towards Santa Cruz de Turrialba, 1580 m, 31 Jan 1971, Wilbur & Teeri 13806 (DUKE); Volcán Turrialba above Pastora or Trinidad, 2000 m, 10 May 1971, Wilbur 14360 (DUKE); 3 km NE of Pacayas, 1500 m, 7 Jan 1972, Wilbur 16087 (DUKE, F, MICH); 10-20 km SE of Tapantí, 1400-1900 m, 13 Dec 1974, Wilbur & Luteyn 18028 (DUKE, MICH), 18082 (DUKE), 20 Dec 1974, Wilbur & Luteyn 18546 (DUKE); 4 km S of Muñeco, 1800-2000 m, 26 Dec 1974, Wilbur & Luteyn 18887 (DUKE); Río Grande de Orosi 3 km above Tapantí, 1250 m, 9 Jul 1977, Wilbur et al. 22332 (DUKE); 3-5 km above Muñeco, 1400-1500 m, 25 Feb 1978, Wilbur 24958 (DUKE), 24984 (DUKE); 10 km N of Santa Cruz, 1950 m, 8 Mar 1978, Wilbur 25470 (DUKE); rd. to Taus above Tapantí, 1600 m, 17 Jul 1981, Wilbur 31593 (DUKE); Río Grande de Orosi, 12 km SE of Tapantí, 1500 m, 11 Aug 1981, Wilbur 33068 (DUKE); El Copey, Cordillera de Talamanca, 1900 m, 17 Apr 1949, Williams 16411 (MICH); nr. Pavones, 15 km E of Turrialba, 600 m, 7 May 1956, Williams 19732 (MICH). Guanacaste: Los Ayotes nr. Tilarán, 600-700 m, 21 Jan 1926, Standley & Valerio 45385 (F); slopes of Volcán Arenal on rd. from Lake Arenal to Lake Cote, 500-700 m, 2 Mar 1985, Taylor & Skotak 4680 (DUKE). Heredia: Río Guácimo, Magasasay, Zona Protectora, 300 m, 13 Jan 1983, Chacón 54 (MO); 8 km N of Vara Blanca on rd. to Sarapiquí, 1450 m, 25 Dec 1974, Cochrane et al. 6220 (DUKE, WIS-2 sheets); Brualio Carrillo National Park, Río Bajo de Honduras, La Palma, 1150 m, 23 Jan 1983, Garwood et al. 466 (MO); along Río Peje 0.5 km SW of Vargas property, 20 Feb 1982, Hammel

11199 (DUKE); Zona Protectora La Selva, 6 km from Río Peje, 5 km SSE of Magasasay, 280-300 m, 25 Jan 1983, Schatz & Grayum 718 (DUKE); Vara Blanca de Sarapiquí, 1370 m, Feb 1938, Skutch 3492 (MO, NY, S); nr. Cariblanco, Río Sarapiquí, N of Volcán Poas, 850 m, 24 Apr 1956, Williams 20258 (MICH). Limón: Suerre, Llanuras de Santa Clara, 300 m, Feb 1896, Donnell-Smith 6622 (B, BM p.p., G, NY); lake at foot of Fila Lleskila Talamanca, 1160 m, 4 Nov 1984, Gómez et al. 23083 (MO); W side of Lago Dabagri toward Río Llei, 4 Nov 1984, Gómez et al. 23189 (MO); Las Brisas de Pacuarito, Siquirres, 300 m, 18 Apr 1985, Gómez et al. 23403 (MO); Alto Guayacán, SE of Siquirres, 700 m, 12 Oct 1967, Lent 1407 (F, NY). Puntarenas: Above Palmar Norte, trail to Buenos Aires, 830 m, 17 Feb 1951, Allen 5897 (DS, F-2 sheets); E of Paso Los Indios and due NE of Quepos, 190-225 m, 4 Aug 1977, Almeda et al. 3404 (CAS, MO); slopes E of Las Cruces, 5-6 km S of San Vito, 1100-1200 m, 15-16 Jan 1967, Burger & Matta 4375 (F, BM); between Agua Buena and Villa Neily, 1000 m, 19 Jan 1967, Burger & Matta 4592 (F); mountains E of Quepos, 150-250 m, 19 Feb 1977, Burger et al. 10583 (AAU, DUKE, F); Las Cruces Tropical Botanical Garden, 12 Jul 1976, Cooper-Smith 9a (DUKE); between Cortu and La Union nr. San Miguel, 8 Aug 1974, Croat 26522 (MO-2 sheets); rd. between La Union and Coton, between Río Negro and Río Coto Brus, 9 Aug 1974, Croat 26569 (MO); hills N of Palmar Norte, trail to Jalisco, 50-700 m, 21 May 1976, Croat 35148 (DUKE, MO); Las Cruces, 1300 m, 11 Jan 1978, Croat 44408 (MO); trail between Las Alturas and Cotonsito, along Río Cotón, 1400 m, 31 Aug-1 Sep 1983, Davidse 24392 (DUKE, MO); 17 km N of San Vito on rd. to potrero Grande, 845 m, 30 Mar 1978, Davidson 7156 (MO); Rincón, Osa Peninsula, 9 Feb 1969, Duke 16118 (F, MO), 3 Mar 1965, Godfrey 66522 (MO, NY); ridge between Quebrada Aguabuena and Quebrada Banegas, 5 km W of Rincón de Osa, 300-400 m, Grayum et al. 4047 (DUKE, MO); San Vito, 1200 m, 24 Dec 1970, Heithaus 1 (MO); between Pedernal and Canderlarita, 900 m, 29 May 1966, Jiménez 3963 (F); Finca Las Cruces, 1200-1300 m,

29 May 1973, *Luteyn* 3853 (DUKE); San Vito de Java, 1100 m, 9 Jan 1964, *McKee* 11181 (P), 1400 m, 19 May 1984, *Murphy* 1145 (DUKE), 1200 m, 19 Aug 1967, *Raven* 21978 (DS, F, NY); Río Naranjo, 240-250 m, Mar 1893, *Tonduz* 7580 (BM, G-5 sheets); Finca Las Cruces, 5 mi. S of San Vito, 1200-1300 m, 5 Jul 1972, *Utley & Utley* 443 (DUKE); 15 km ENE of La Union, 30 km NE of San Vito, 1300-1500 m, 12 May 1976, *Utley & Utley* 4793 (DUKE); 10 km N of Villa Neily towards San Vito, 800 m, 13 May 1971, *Wilbur* 14428 (DUKE, F, MICH, MO, U); 5 km S of San Vito, 1400 m, 14 May 1971, *Wilbur* 14465 (DUKE, MICH); 10 km N of Villa Neily towards Agua Buena, 14 Jul 1977, *Wilbur et al.* 22642 (DUKE); 3 km E of Paso Los Indios, 12 km NE of Quepos, 150 m, 4 Aug 1977, *Wilbur et al.* 23929 (DUKE, F); 9 km NW of San Vito de Java, 2 Aug 1981, *Wilbur* 32554 (DUKE); Río Sonador, nr. Panamerican hwy., El General Valley, 600 m, 31 Jan 1965, *Williams et al.* 28794 (F). San José: 15 km NE of Vicente between Alto La Palma and Bajo La Honduras, 1400-1500 m, 4 May 1971, *Almeda* 615 (DUKE, MO); 16-24 km S of San Isidro del General, 850 m, 15 Dec 1975, *Almeda & Almeda* 2695 (DUKE); 5 km NE of Cascajal, 1650 m, 17 Feb 1978, *Almeda & Nakai* 3619 (CAS); slopes below La Palma, Río Claro, along trail to Guapiles 1100-1200 m, 16 Dec 1966, *Burger* 3906 (F), 3936 (F, WIS); Rio Claro valley below La Palma, NE of San Jerónimo, 1000-1200 m, 19 Nov 1969, *Burger & Liesner* 6291 (BM, DUKE, F), 23 Oct 1975, *Burger & Liesner* 9424 (F); above Alfombra along rd. from San Isidro del General to Dominical, 1000 m, 19 Nov 1975, *Burger & Baker* 10112 (F, WIS); La Palma area NE of San Jerónimo, 1500 m, 15 Sep 1978, *Burger & Antonio* 11069 (F); Panamerican Hwy. on Cerro de la Muerte nr. Villa Mills, 16 Aug 1967, *Gentry s.n.* (WIS); Braulio Carrillo, Estación Montura, 1050 m, 22 Jan 1984, *Gómez et al.* 20891 (MO); Quebrada El Mochote, Cerro Zurquí, 12 Feb 1984, *Gómez et al.* 21049 (DUKE, MO); between La Honduras and Río Claro, 1100 m, 24 Feb 1963, *Jiménez* 412 (F); Cerbatana, Puriscal, 1050 m, 13 Apr 1963, *Jiménez* 649 (F, G); 13 km NW of San Isidro del General, 1500

m, 30 Jul 1964, Jiménez 2221 (F); vic. of San Isidro del General, 900 m, 28 Feb 1966, Molina et al. 18108 (DS, F, NY); nr. Cascajal, 14-17 km from San Isidro de Coronado, 1400 m, 28 Apr 1984, Murphy 738 (DUKE), 26 May 1984, Murphy & Jacobs 1267 (DUKE); vic. of El General, 1000 m, Dec 1935, Skutch 2196 (MO, NY, S), Feb 1939, Skutch 4145 (MO, S); Río Bajo de Honduras, Parque Braulio Carrillo, 25 km N of San José, 1120 m, 23 Jan 1983, Sousa et al. 12671 (MO), 12673 (MO); from La Montura to Los Chorritos, 1200 m, 28 Jan 1984, Gómez 20908 (DUKE, MO); La Honduras, 1200-1500 m, 9 Mar 1926, Standley & Valerio 51860 (F); 4 mi. N of Las Nubes junction on rd. to Cascajal, 25 Apr 1972, Stone 3244 (DUKE); 4-9 km beyond Cascajal, 14-19 km from San Isidro de Coronado, 1600-1700 m, 5 Aug 1981, Taylor 970 (DUKE); nr. Santa Marta, 10 km toward ocean from Puriscal, 6 Aug 1981, Taylor 998 (DUKE); above Río Honduras at Baja La Honduras, 1150 m, 31 Dec 1974, Taylor 17893 (F); rd. between San Isidro del General and Dominical, 0-1000 m, 20 Oct 1974, Utley & Utley 1498 (DUKE); between Alto de La Palma and Baja La Honduras, 1300-1500 m, 6 Apr 1976, Utley & Utley 4511 (DUKE); 12 km NNE of San Vicente de Moravia, nr. Bajo La Honduras, 1200 m, 4 May 1971, Wilbur 14113 (DUKE); from Alto de La Palma to Bajo La Honduras, 1500 m, 14 Dec 1974, Wilbur & Luteyn 18120 (DUKE); 19 km N of San Isidro, 28 Dec 1974, Wilbur & Luteyn 18963 (DUKE); 13 km SW of San Isidro del General on rd. to Dominical, 30 Jul 1977, Wilbur et al. 23576 (DUKE); 31 km SW of Puriscal, 3 Aug 1977, Wilbur et al. 23835 (DUKE); 3-5 km NE of Cascajal, 1750 m, 17 Feb 1978, Wilbur 24451 (DUKE); 2-3 km NE of Alfombra, 900 m, 5 Mar 1978, Wilbur 25377 (DUKE); 15 km N of San Isidro del General, 1600 m, 16 Dec 1979, Wilbur 28952 (DUKE-2 sheets); Salitiales, 22 km SW of Santiago de Puriscal, 6 Aug 1981, Wilbur 32740 (DUKE); vic. of Boquete, 20 km N of San Isidro del General, 2000 m, 8 Aug 1981, Wilbur 32880 (DUKE), 32900 (DUKE); forest N of San Isidro del General, 1400 m, 12 May 1956,

Williams 19976 (F, MICH); 25 km N of San Isidro del General along Pan American Hwy., 29 Jan 1965, Williams et al 28600 (F).

PANAMA. Bocas del Toro: Robalo trail, N slopes of Cerro Horqueta, 1800-2100 m, 5-7 Aug 1947, Allen 4923 (G, MICH, MO, S); Oleoducto rd., nr. Continental Divide, Fortuna Dam area, 1000 m, 5 Feb 1984, Churchill et al. 4496 (DUKE, MO); along continental divide from rd. N of Fortuna-Chiriquí Grande Hwy., 1200 m, 11 Mar 1985, Croat & Grayum 60329 (MO); between Quebrada Hiqueron and Gutierrez, Chiriquicito-Caldera trail, Kirkbride & Duke 743 (MO, NY); rd. to Chiriquí Grande N of Fortuna Dam, 650-700 m, 29 Jun 1987, McPherson 11125 (MO). Chiriquí: Llanos on slopes of Volcán Chiriquí Viejo and along Río Chiriquí Viejo, 1200 m, 20 Apr 1935, Allen 985 (G, MO); vic. of "New Switzerland," valley of Río Chiriquí Viejo, 1800-2000 m, 6-14 Jan 1939, Allen 1420 (F, MO, US); vic. of Cerro Punta, 2000-2500 m, 24 May 1946, Allen 3519 (G, MICH, MO, NY, S); Bajo Mono, Robalo trail, W slopes of Cerro Horqueta, 1500-2100 m, 27 Jul 1947, Allen 4792 (MO); 8 km W of Cerro Punta nr. Las Nubes, 1850-1950 m, 11 Feb 1978, Almeda & Nakai 3488 (CAS); Cerro Pata de Macho, 5 mi. NE of Boquete, 22 Nov 1979, Antonio 2636 (MO); Monte Azul, 1.4 mi. N of Entre Ríos on E slopes of Cerro Punta, 2250 m, 22 Nov 1979 (MO); 10 mi. along Gualaca-Fortuna Dam rd., NW of Los Planes de Hornito, 1300 m, 8 Apr 1980, Antonio 4056 (DUKE, MO); nr. Gualaca 11 mi. from Planes de Hornito, 1200 m, 9 Jul 1980, Antonio 5039 (MO); Cerro Punta, 2100 m, 28 Mar 1965, Blaisdell 368 (MO); Cerro Punta, 2100 m, 3 Jul 1966, Blum et al. 2423 (MO); Cerro Horqueta, 2100 m, 24 Jul 1966, Blum & Dwyer 2593 (MO, MO); 2.5 km N of Bambito, 4.5 km WNW of town of Cerro Punta, 2100 m, 3 Jan 1975, Cochrane et al. 6292 (DUKE-2 sheets, MO, WIS); between Bambito and Cerro Punta, 30 May 1970, Croat 10557 (DUKE, MO); 9 mi. from Paso Canoas on rd. to Cañas Gordas, 25 Feb 1973, Croat 22207 (DUKE, MO); 1 mi. E of Cañas Gordas nr. Costa Rican border on rd. to Volcán, 26 Feb 1973, Croat 22333 (DUKE, MO); vic.

of Las Nubes, 2.7 mi. NW of Río Chiriquí Viejo, 2200 m, 27 Feb 1973, *Croat* 22382 (DUKE, MO-2 sheets, NY); Cerro Punta, 700 m, 7 Aug 1974, *Croat* 26332 (MO, U); vic. of Monte Azul, 1.4 mi. N of Entre Ríos on slopes of Cerro Punta, 2250 m, 25 Nov 1979, *Croat* 48599 (MO), *Croat* 48610 (MO); S of Cerro Pando, 7 Aug 1972, *D'Arcy & D'Arcy* 6496 (DUKE, MO-2 sheets, NY); Bajo Chorro, 1000-2000 m, 21 Mar 1977, *D'Arcy* 10919 (DUKE, MO-2 sheets, NY); Fortuna Dam area, Quebrada Bonita, N of reservoir, 1100 m, 30 Jul 1984, *D'Arcy et al.* 15878 (MO); Bajo Chorro, 1800 m, 5 Jan 1938, *Davidson* 33 (F, MO); Cerro Horqueta, 1500-1750 m, 13 Dec 1966, *Dwyer et al.* 457 (MO, NY, UC); Cerro Colorado, 1500 m, 17-18 Feb 1977, *Folsom & Collins* 1783 (MO); Boquete, 20 Mar 1977, *Folsom* 2169 (DUKE, MO); lower rd. to Bajo Mono, 21 Mar 1977, *Folsom et al.* 2241 (DUKE, MO); ridge rd. at Cerro Colorado, 1450-1750 m, 15 Aug 1977, *Folsom et al.* 4846 (DUKE, MO); above Guadeloupe, 2400 m, 25 Dec 1977, *Folsom et al.* 7122 (DUKE, MO-2 sheets); Cerro Respinga on Boquete Trail, 2000-2500 m, 11 Sep 1972, *Gentry* 5908 (MO); 7 mi. S of Volcán on rd. from David, 600-750 m, 28 Dec 1963, *Graham* 256 (MICH); 6 km E of Cerro Punta above Paso de Respingo, 2200 m, 12 Feb 1978, *Hammel* 1482 (DUKE, MO); E slopes of Cerro Pando, 2000-2300 m, 15 Oct 1981, *Knapp* 1662 (BM, DUKE, MO); S slopes of Cerro Pate Macho along Río Palo Alto, 1300-1800 m, 11 Nov 1981, *Knapp et al.* 2072 (MO), *Knapp et al.* 2088 (DUKE, MO), 12 Nov 1981, *Knapp et al.* 2129 (DUKE, MO), *Knapp et al.* 2131 (DUKE, MO); Bajo Mono trail NW of San Ramón, 1600-1700 m, 23 May 1973, *Luteyn* 3733 (DUKE); Bajo Chorro trail from Paso Respinga to Fila de Respinga, 2360-2500 m, 27 May 1973, *Luteyn* 3826 (DUKE); Fortuna Dam, above Gualaca, 1200 m, 9 Mar 1985, *McPherson* 6719 (DUKE, MO); Cerro Punta, 2.5 km SE of town, 20 Apr 1975, *Mori & Kallunki* 5641 (DUKE, MO, NY); NW of Cerro Punta, 2500 m, 14 May 1984, *Murphy* 1043 (DUKE); Bajo Grande, 1-3 km E of town of Cerro Punta, 2000-2200 m, 24 Feb 1974, *Nee* 10063 (DUKE, MO); vic. of Cerro Punta, 2100 m, 31 May-1

Jun 1967, *Ridgway & Solis* 2390 (DUKE, MO); Cerro Punta, 1675 m, 2 Mar 1967, *Sawyer s.n.* (MO, WIS-2 sheets); Río Cochea, 6 May 1983, *Schmalzel* 1545 (MO); trail up Cerro Pate Macho, 1500-1700 m, 6 Jan 1983, *Stein et al.* 1205 (MO, MO), 7 Jan 1983, *Stein et al.* 1255 (MO); NE of Cerro Punta on rd. through Bajo Grande, 2250-2400 m, 9 Nov 1980, *Stevens* 18218 (MO); 4 km NE of Cerro Punta on rd. through Bajo Grande, 2250-2400 m, 9 Nov 1980, *Sytsma & Stevens* 2078 (DUKE, MO); SE slopes and summit of Cerro Pate Macho, 1700-2100 m, 26 May 1981, *Sytsma et al.* 4890 (MO); NW of Cerro Punta, 2000-2100 m, 14 May 1984, *Taylor* 3247 (DUKE); 3 mi. S of El Volcán, 1200 m, 23 Aug 1962, *Tyson* 880 (MO); Bambito, 1 mi. SW of Cerro Punta, 1700 m, 26 Jun 1969, *Tyson* 5647 (MO); 6 mi. above Cerro Punta on Boquete trail, 2300 m, 7 Mar 1974, *Tyson* 7153 (NA); 8 km W of Cerro Punta in vic. of Las Nubes, 1850-1900 m, 11 Feb 1978, *Utley* 5663 (DUKE); Cerro Punta, 2200 m, 23 Jan 1984, *van der Werff & Herrera* 6288 (DUKE, MO), 24 Jan 1984, *van der Werff & Herrera* 6300 (DUKE, MO); Fortuna Dam site, 1200 m, 6 Feb 1984, *van der Werff & van Hardeveid* 6553 (DUKE, MO); Santa Clara to Cerro Pando, 28 Feb 1985, *van der Werff & Herrera* 7237 (DUKE, MO); Cerro Horqueta, 1950 m, 8 May 1940, *von Hagen & von Hagen* 2091 (NY); 2.5 mi. NE of Volcán, 16 Jun 1971, *Webster* 16625 (DUKE); between El Volcán and Cerro Punta, 15 Mar 1938, *White* 13 (MO, MO, MO, NA); slope above Cerro Punta toward Bajo Grande, 1980 m, 14 Jan 1970, *Wilbur et al.* 10913 (DUKE-2 sheets, GH, MICH-2 sheets); above Rio Caldera beyond Bajo Mono, 1800 m, 17 Jan 1970, *Wilbur et al.* 11080 (DUKE, F, MICH, MO); trail between Cerro Punta and Quebrada Bajo Grande, 2000-2100 m, 28 May 1970, *Wilbur et al.* 11917 (DUKE-2 sheets, MICH-2 sheets, MO-2 sheets); E of Guadeloupe along Rio Chiriquí Viejo, 13 Jan 1971, *Wilbur & Teeri* 13110 (DUKE); Quebrada Bajo Grande, 2 mi. E of Cerro Punta, 2100 m, 14 Jan 1971, *Wilbur & Teeri* 13131 (DUKE); between town of Cerro Punta and Las Nubes, 15 Jan 1971, *Wilbur & Teeri* 13261 (CAS, DUKE-2 sheets, F, MICH, MO, NY, WIS); S slopes of

Cerro Horqueta, 1700 m, 21 Jan 1971, *Wilbur et al.* 13438a (DUKE-3 sheets, MICH, MO); slopes above village of San Ramón nr. Bajo Mono, 1825 m, 22 Jan 1971, *Wilbur et al.* 13538 (DUKE); 1 km N of Las Nubes, 2000-2300 m, 24 Dec 1971, *Wilbur et al.* 15204 (DUKE-3 sheets, F-2 sheets, MICH, MO, NY); 2 km W of La Garita, WNW of Cerro Punta, 2000 m, 24 Dec 1971, *Wilbur et al.* 15265 (DUKE, MICH, MO); 2 km NE of Guadalupe, 25 Dec. 1971, *Wilbur et al.* 15333 (DUKE, MO), *Wilbur et al.* 15354 (DUKE-2 sheets); SW slopes of Cerro Horqueta, 1700-1800 m, *Wilbur et al.* 15427 (DUKE); Boquete-Cerro Punta trail, 2650 m, 29 May 1972, *Wilbur et al.* 17141 (DUKE); 2.5 km NE of Cerro Punta, 2200 m, 29 May 1972, *Wilbur et al.* 17150 (DUKE); Bajo Mona Trail, 1800 m, 31 May 1972, *Wilbur et al.* 17242 (DUKE, MICH, MO); summit of pass between Cerro Punta and Boquete, 2500 m, 31 May 1972, *Wilbur et al.* 17251 (DUKE, F, MICH, MO); Cerro Horqueta, 1500-1800 m, 4 Jan 1975, *Wilbur & Luteyn* 19212 (DUKE), *Wilbur & Luteyn* 19242 (DUKE); ravine W of Las Nubes, 2000-2100 m, 6 Jan 1975, *Wilbur & Luteyn* 19348 (DUKE); Quebrada Bajo Grande, 2200 m, 12 Feb 1978, *Wilbur* 24251 (DUKE); Quebrada Velo, 1800 m, 8 Jul 1940, *Woodson & Schery* 271 (MO, NA); vic. of Bajo Mona and Quebrada Chiquero, 1500 m, 18 Jul 1940, *Woodson & Schery* 525 (MO, NA); vic. of Casita Alta, Volcán de Chiriquí, 1500-2000 m, *Woodson et al.* 844 (MO).

COLOMBIA. Nariño: Altaquer, 1050 m, 10 Nov 1946, *Foster & Foster* 2092 (AA); Ricáurte, 1300 m, 4 Apr 1941, *von Sniedern s.n.* (S), 24 Apr 1941, *von Sniedern s.n.* (S).

ECUADOR. Carchi: El Pailon, 45 km below Maldonado along path to Tobar Donoso, 800 m, 3 Dec 1979, *Madison & Besse* 7273 (QCA); 6 km above Maldonado on rd. to Tulcán, 1900 m, 30 May 1985, *Stein* 2895 (MO-2 sheets, QCA); 7 km below Maldonado on rd. to Chical, 1300 m, 30 May 1985, 2896 (MO, US); Maldonado, 1500 m, 8 Oct 1981, *Werling & Leth-Nissen* 384 (QCA). Esmeraldas: Lita, 1000 m, 20 Jul 1964,

Jativa & Epling 837 (UC, US); Lita-Ibarra rd., nr. Lita, 660 m, 23 May 1983, Lawesson et al. 43969 (AAU); vic. of Lita on the Ibarra-San Lorenzo railroad, 550-650 m, 11 Jun 1978, Madison 5230 (SEL); nr. Lita, 600 m, 19 May 1987, van der Werff et al. 9486 (MO, QAME). Imbabura: Lita, 500 m, 22 Apr 1949, Acosta Solis 12166 (F).

Discussion. *Centropogon granulosus* is by far the most variable and problematic species in subgen. *Centropogon*. It is more widespread than any species except *C. cornutus*, and exhibits extensive regional and local differentiation. In certain instances this differentiation has been so profound that the result can easily be accommodated in separate species, and several such segregate species are recognized elsewhere in this treatment. With the general exception of these segregates, however, most of the forms in the *C. granulosus* complex intergrade extensively with one another. In addition, the plants often exhibit a great deal of intrapopulational variability further confounding attempts to sort them into discontinuous morphological units. This combination of local and regional differentiation, intergradation, and intrapopulational variability has created an exceedingly complex situation that is at present only possible to approach in a tentative way.

As the core species of the *C. granulosus* species complex of sect. *Campylobotrys*, this species shares many fundamental features with the derivative, or segregate taxa. As a result, *C. granulosus* itself lacks sharp definition; it contains those synapomorphies that define the species group as a whole (relating to corolla morphology, inflorescence structure, etc.), but lacks autapomorphies. In large part, *C. granulosus* can be considered the residual of the species complex after exclusion of the most distinctive and highly differentiated units. The result is that *C. granulosus* as here constituted must be

considered a paraphyletic species, a situation that is unavoidable given the present fragmentary knowledge of this complicated group.

After detailed fieldwork throughout the geographic range of *C. granulosus*, from Costa Rica to Bolivia, I have come to discern several geographically based morphological forms that I recognize at the subspecific level. Where possible I have attempted to define these subspecies in such a way as to constitute truly monophyletic units, but certain of the more wide-ranging and polymorphic subspecies (e.g., subsp. *granulosus* and *lugens*) almost certainly include more than one phylogenetic lineage.

As the 17 specific epithets placed in synonymy indicate, *C. granulosus* as here defined subsumes numerous species proposed by previous workers. In the last complete treatment of subgen. *Centropogon*, Wimmer (1943) recognized 12 of these species along with three varieties within *C. granulosus*. He distinguished the many taxa primarily using leaf shape, sepal length, corolla length, anther pubescence, and stem surface. Although some of these characters are relatively stable, others, in particular leaf shape and sepal length, can be highly labile both among and within populations. More recent treatments (e.g., Wilbur, 1977; Jeppesen, 1981) have tended to treat *C. granulosus* in a broader manner, and my treatment in general follows this approach while at the same time attempting to formally recognize some of the major morphological and geographical trends. This treatment differs most notably from Wilbur's (1977) work on Central American *Centropogon* in considering *C. tortilis* (=*C. panamensis*) a subspecies of *C. granulosus* rather than a distinct species as discussed below.

The subspecies may in general be distinguished from one another by the characters given in the key. The differentiating features of each subspecies will be discussed below, along with additional features for separating particular subspecies pairs, especially those that are geographically contiguous. Not all specimens encountered will easily "key-out" or fit into the subspecies classification here proposed, especially those

that may be intermediates between subspecies. Particular regions, such as the Cordillera de Colán in northern Peru, show a high preponderance of unusual specimens that are not well accommodated in these subspecific concepts. Too few specimens are available from such areas to determine if these unusual collections are hybrids, aberrant individuals, or distinct entities. The presence of occasional specimens morphologically intermediate between the subspecies, however, is a compelling argument to recognize them as subspecies rather than species.

As can be seen from the key to subspecies, corolla color is one of the most useful features for broadly partitioning the species over its wide range. This character unfortunately is not well-preserved in dried material. My field observations, however, are supported by available specimen label information. Label information about colors must be interpreted cautiously since color perception is very individualistic and many collectors tend to be unspecific about color patterns, i.e., whether a corolla is uniformly one color (concolorous) or has lobes that contrast with the lower portion of the tube (bicolored). The general patterns of corolla coloration correlate with other suites of characters, primarily details of the inflorescence structure and floral morphology, and, to a lesser degree, leaf morphology and indument.

Subspecies granulosus

This subspecies is found exclusively along the eastern slope of the Andes from southern Colombia to central Bolivia. The most distinctive manifestation is in central Peru, which includes the type locality for the species. Populations in this region are quite homogeneous and are characterized by: orange or reddish-orange corollas with yellow to pale orange lobes; short sepals (3-6 mm long); an androecium that is densely pilose with white trichomes at the summit of the filament tube and along the dorsal connectives of the anther tube; relatively short anther tubes (7-8 mm long) which are

yellowish to tan; few or no free trichomes at the base of the antheridial scale; short-bracteate inflorescences in which the bracts are caducous; and often scabrous to scaberulous upper stems and inflorescence rachises. Synonyms that apply to this central Peruvian morphological type include *C. cuspidatus*, *C. parvulus*, and *C. casapiensis*.

In southern Peru and Bolivia subsp. *granulosus* becomes more variable, with the flowers often more reddish than orangish and with certain collections exhibiting either completely glabrous corollas, purple anther trichomes, slightly longer sepals, or somewhat persistent bracts. Within a given area a variety of morphological forms are found, however, and discrete morphological units cannot be recognized. Collections with non-scabrous stems from these southern populations form the basis for the synonyms *C. cardinalis* and *C. aggregatus* (the latter also has a glabrous corolla).

In northern Ecuador and southern Colombia populations also have more reddish corollas, but the androecium is similar to that of subsp. *lateriflorus*, the predominant form of *C. granulosus* between these northern populations and the main body of the subspecies in Peru. The androecium in these populations is relatively glabrous, often with only an apical tuft of white trichomes. The northernmost populations in Caquetá, Colombia have slightly longer sepals than is typical for the subspecies and in this show some intergradation with subsp. *rutilus*. In particular, Cuatrecasas 9084 has a very glabrous corolla as in subsp. *rutilus*, although the very long sepals in that collection (to 15 mm long) exceed those usually found in either subspecies. The northern Ecuador populations occur in very close proximity to, and possibly sympatric with, *C. baezanus*, but I have not found evidence of hybridization between these two taxa.

Subspecies lateriflorus

This subspecies is easily recognized by its bright yellow to golden corolla, a distinctive feature that is shared only with *C. densiflorus* subsp. *gracilis* and

C. cuatrecasanus. *Centropogon densiflorus* subsp. *gracilis* can be readily distinguished from *Centropogon granulosus* subsp. *lateriflorus* by its dense pubescence, long sepals, and strictly pendent inflorescence, and the Colombian *C. cuatrecasanus* can be differentiated by its long, gently curved corolla. Other features that characterize subsp. *lateriflorus* include: often glabrous corollas; anther tubes tan to yellowish, and these glabrous or with only apical and/or basal tufts of white trichomes; a tendency for development of lateral inflorescences; and completely glabrous leaves.

Wimmer (1943) described *C. lateriflorus* on the basis of its supposedly few-flowered lateral umbels, and he noted that in this inflorescence it appeared very similar the Hawaiian genus *Clermontia*, but that it was also very close to *Centropogon pulcher*. Accordingly, he assigned it to his subsect. *Botryoides*. Wimmer's description was based on a rather young flowering branch with few flowers present and a little-elongate rachis that makes the inflorescences appear subumbellate. In reality, the inflorescences of subsp. *lateriflorus* are typically campylobotrous in being pendently upturned, densely flowered, subcorymbose racemes. Inflorescences in the subspecies are borne either terminally or laterally, with the position consistent within populations. Although lateral inflorescences are unusual in subgen. *Centropogon*, they are found occasionally in several other species and subspecies of the *C. granulosus* complex and cannot be considered an autapomorphy for this taxon.

Several morphological and geographical trends can be recognized within the subspecies. Populations with predominantly lateral inflorescences tend to have narrower leaves than populations with strictly terminal inflorescences. Collections of subsp. *lateriflorus* from the outlying ranges of the Andes in southern Ecuador and northern Peru, such as the Cordillera del Condór and Cordillera Colán usually have lateral inflorescences, whereas most of those found at mid-elevations of the main Andean chain have terminal inflorescences.

An aberrant population from the Carpish Hills of central Peru is here somewhat hesitantly assigned to this subspecies. These plants have bright yellow, glabrous corollas and glabrous anther tubes, features that fit well within my concept of subsp. *lateriflorus*, but they have a very unusual non-elongating inflorescence that forms an umbellate "knot" at the tip of pendent, whip-like shoots. Given the very disjunct distribution, it is possible that these populations represent an independent derivation from the sympatric subsp. *granulosus*.

Although subspecies *lateriflorus* overlaps in range with subsp. *granulosus* in northern Peru and central Ecuador, in these areas there is usually an altitudinal separation between the two subspecies with subsp. *lateriflorus* found mostly at higher elevations. For example, in Morona-Santiago Province subsp. *granulosus* occurs at ca. 700 m while subsp. *lateriflorus* is found between 1000 m and 2000 m. Similarly, in San Martin Department of northern Peru, subsp. *granulosus* is common at lower elevations around Moyobamba and Tarapoto, while subsp. *lateriflorus* is found at about 1500 m further west in the Venceremos area.

Wimmer (1943) erroneously cited the type specimen of *C. lateriflorus* as from Colombia; Chiguinda, the locality given on the Lehmann type specimen, is actually in Morona-Santiago Province of Ecuador near where recent collections of this taxon have been made. Because subsp. *lateriflorus* has never been collected in Colombia, it should not be regarded as a component of the Colombian flora.

Subspecies rutilus

Subspecies *rutilus* is the most geographically localized of the recognized subspecies, being restricted to the Cordillera Oriental of Colombia and centered around Cundinamarca Department. It is characterized by: completely smooth and glabrous corollas, which are reddish-orange grading to yellowish at the lobes; well-exserted

filament tubes; anther tubes that are densely pilose with short purple trichomes; very short, caducous inflorescence bracts; and an exceptional inflorescence that becomes very elongate and thickened in age. In addition, the sepals are entire and often rounded at the apex, and intersepalar nectaries appear to be lacking.

The completely glabrous corolla is the most obvious feature that differentiates subsp. *rutilus* from subsp. *lugens*, which occurs to the north and west. This feature is probably responsible for Wimmer's (1943) inclusion of members of subsp. *lateriflorus*, which also have glabrous corollas, in the protogues of both *C. granulosus* var. *rutilus* and *C. holtonis* var. *albanensis* (=*C. granulosus* var. *rutilus*). As explained in the discussion of types for these two names, this resulted in nonconcordant syntypes being designated, which are excluded from this *C. granulosus* var. *rutilus*; the lectotypes for these names selected reflect the Colombian populations upon which this subspecies is based.

The inflorescence is the most unusual feature of this subspecies, however. The typically campylobotryous inflorescence type is developed to an extreme in terms of length and girth; some rachises reach 35 cm long and 2.5 cm in diameter. Because of its weight the inflorescence does not remain vertical, but lists to a horizontal position. I have counted up to 250 pedicel scars on a single inflorescence (Stein 3677). Since only about three flowers are open at a time with each flower remaining open for several days, a single inflorescence may last for well over a year. The rich growth of bryophytes on the basal portion of that particular inflorescence supports this conclusion.

Subspecies lugens

Subspecies *lugens* encompasses a wide range of forms found throughout much of Colombia and some adjacent regions, and can be characterized by the following features. The corollas are pink to pinkish- or rose-red, which sharply contrast with those

subspecies found further south. The inflorescence often elongates, but never shows secondary thickening as in subsp. *rutilus*; the bracts are either caducous or tardily deciduous, but never persistent; and the floral internodes remain congested even after rachis elongation. I have seen only one collection, Hodge 6962, in which lateral inflorescences were formed. The stem is almost always smooth, rather than scaberulous.

The following trends can be noted in this rather polymorphic taxon. Throughout most of its range subsp. *lugens* assumes a vining habit, with typical pendently upturned inflorescences. At two ends of its range, however, it intergrades with more shrubby taxa with erect inflorescences. Populations from the Río Saldaña Valley of Tolima Department on the eastern slope of the southern Cordillera Central in Colombia often have sub-erect inflorescences, and in this feature show affinities with *C. curvatus*, an erect shrub that occurs further south in the same Cordillera. The flower color, trichome morphology, and upward curve of the inflorescence rachis in these Río Saldaña plants lead me tentatively to place these populations in *C. granulosus* subsp. *lugens*. A more problematic situation occurs at the interface between subsp. *lugens* and subsp. *tortilis* in the Chocó region of western Colombia and eastern Panama, and is discussed in more detail under the latter subspecies.

Anther tubes in subsp. *lugens* are typically densely short-pilose with purple trichomes in the dorsal connectives. On the western slope of the Cordillera Occidental in southern Chocó and Valle Departments most populations have completely glabrous anthers, but the plants are identical in other respects to those from further north.

Lower elevation populations from the Chocó region and the lower Río Magdalena Valley have quite wide leaves that reach the maximum size found in *C. granulosus*. The venation pattern is often very distinctive in that the conspicuous secondary veins diverge from the mid-vein at a wide angle and are strongly arcuate-ascending. This venation pattern is shared with subsp. *tortilis* and subsp. *nutans*.

Subspecies tortilis

Subspecies tortilis is fairly distinctive in being an erect to subscandent shrub. It is further characterized by: bright pink to pinkish-red, abruptly curved and ventricose corollas; short-exserted (2-5 mm) filament tubes; anther tubes moderately to densely short-pilose with purple trichomes; short pedicels (5-20 mm long); persistent bracts; and large, often wide leaves with strongly arcuate secondary veins.

This subspecies is contiguous with subsp. *lugens* with which it intergrades. This intergradation is the primary reason for treating it here as a subspecies of *C. granulosus* rather than as a distinct species, as has been done in the past (i.e., *C. panamensis* sensu Wilbur, 1977). Subspecies *tortilis* differs from the Chocóan populations of subsp. *lugens* principally in its erect habit. Such a shift, from a vining to an erect habit, has necessary consequences for inflorescence structure. Rather than the pendent and upturned, pipe-shaped inflorescences characteristic of the vining subsp. *lugens*, subsp. *tortilis* has a mostly erect inflorescence rachis that is often subtended by a short erect peduncle. My fieldwork in the Chocó has shown, however, that plants of subsp. *lugens* often start as semi-erect to arching shrubs and only later assume a scandent or vining habit. At maturity most have the typical pendent inflorescences that are upturned at an acute angle. In contrast to this generalized condition, occasional collections of subsp. *lugens*, (e.g., *Forero et al. 2401, 3028, 5842, Forero & Gentry 682, Franco 1139, and Guerra 20*) have inflorescences that appear to be erect, while other collections, particularly from the coastal regions, have inflorescences upturned at only an obtuse angle (45-90°). Similar to these, some collections of subsp. *tortilis* also have inflorescences upturned at an obtuse angle (e.g. *Croat 13371, Hammel 811, Lallathin 6002, and Luteyn 1184*) although no acutely upturned inflorescences are known in that subspecies.

In most other features subsp. *lugens* from the Chocó and subsp. *tortilis* are indistinguishable, sharing such characteristics as pink to pink-red corollas, scarcely exserted filament tubes, short pedicels, densely short-pilose anther tubes with purple trichomes, and large leaves with conspicuous, widely arcuate venation. One character that does differ rather consistently is the inflorescence bracts, which are almost always persistent in subsp. *tortilis*, but caducous or tardily deciduous in subsp. *lugens*. The lower floral internodes in subsp. *tortilis* are also more likely to become elongate in age rather than remaining congested as in subsp. *lugens*. This results in the older portion of the inflorescence in subsp. *tortilis* remaining bracteate and occasionally becomes slightly lax, while the basal portion of the inflorescence in subsp. *lugens* is naked with the prominent, tightly congested pedicel scars exposed. Subspecies *tortilis* also appears to lack intersepalar nectaries, which are usually very prominent in subsp. *lugens*.

Subspecies *tortilis* is sharply demarcated from subsp. *nutans*, with which it overlaps in range, by the latter's reddish-orange, bicolored corolla, its much more exserted (9-13 mm vs. 2-5 mm) filament tube, and its densely long-pilose anther tube with white trichomes. These two subspecies overlap geographically but apparently do not occur sympatrically. In central Panama, where subsp. *nutans* does not occur, subsp. *tortilis* is found mostly at mid-elevations. In western Panama, however, subsp. *tortilis* inhabits only the Caribbean lowlands, while subsp. *nutans* occurs mostly at upper elevations. This apparent elevational separation occurs also in Costa Rica where subsp. *tortilis* is found at low elevations along the Caribbean coastal plain. Subspecies *nutans*, though it occupies a wide range of habitats and altitudes in Costa Rica, descends only to about 300 m on the Caribbean slope and apparently does not come into contact with subsp. *tortilis*.

A number of unusual collections have been made in central and western Panama that have the erect habit and inflorescence of subsp. *tortilis*, but the bicolored corollas of

subsp. *nutans*. In order to more thoroughly assess the status of these collections a multivariate statistical analysis was performed using 12 floral and inflorescence characters, but excluding corolla coloration, overall habit, and vegetative features (Table 16). Twenty-five collections of subsp. *tortilis* from throughout its geographical range, including the types of both *C. tortilis* and *C. panamensis*, 14 collections of subsp. *nutans* from Panama and Costa Rica, and all 14 complete collections available of the "bicolored *tortilis*" were analysed. Principal component analysis, principal coordinate analysis, and cluster analysis were performed using NTSYS-pc version 1.21, a numerical taxonomy and multivariate analysis system developed by James Rohlf. The first two techniques yielded comparable results, and a plot of the first two principal coordinates is shown in Figure 16. The groups recognized *a priori* were strongly supported by this analysis, with the delineation of three distinct clusters. In particular, my interpretation of the type of *C. tortilis* as consubspecific with *C. panamensis* is clearly supported. The types of *C. tortilis* and *C. panamensis* fall within the same cluster in the PCA, and in the phenogram these two collections actually appear as closest neighbors. Also supporting this interpretation are characters that were not included in the PCA, such as the erect and elongating inflorescence found in the type of *C. tortilis*.

While the "bicolored *tortilis*" collections appear distinct from both subspecies on the basis of these floral and inflorescence features, their interpretation is problematic. They are truly intermediate between the two subspecies for Factor 1, which is most heavily influenced by (in descending order) filament exsertion length, overall androecium length, anther trichome color, anther trichome length, and bract length. The "bicolored" cluster differs from both subspecies in terms of Factor 2, which is most influenced by anther tube length, pedicel length, anther pubescence density, and anther trichome length. The biological interpretation of this group eludes me at present. It is unlikely that these collections are local hybrids between subsp. *tortilis* and subsp. *nutans*.

given their scattered distribution, and the absence of subsp. *nutans* in these regions. Also, certain features such as the completely glabrous anther tubes are not characteristic of either of these two subspecies.

Subspecies nutans

In western Panama and Costa Rica, populations of *C. granulosus* once more assume a vining habit and have bicolored corollas (orangish-red to reddish-orange basally with yellow to yellowish-orange lobes). In addition to these features, which also are present in subsp. *granulosus* of South America, subsp. *nutans* can be characterized by: leaves that, while quite variable, usually have obtuse to rounded bases; elongate pedicels, usually 25-45 mm long, but occasionally to 90 cm; upturned inflorescences that often elongate with the basal floral internodes becoming lax rather than remaining congested; inflorescence bracts persistent; a long, rather narrow corolla with the throat often not abruptly curved or ventricose and thus not well-differentiated from the lower portion of the tube; and a long-exserted filament tube, usually exserted 9-13 mm, but rarely to 16 mm. As discussed above, subsp. *nutans* can be readily distinguished from subsp. *tortilis* primarily by the habit, corolla color, filament exsertion, and color and length of the anther trichomes (white and usually 2-3 mm long). Subspecies *nutans* can be distinguished from subsp. *granulosus* by the elongate pedicels, persistent bracts, usually longer sepals (3-6 mm vs. 7-16 mm), and frequently pilose ventral as well as dorsal anther connectives.

Sepals in subsp. *nutans* are generally long and strap-shaped, but occasional specimens from Chiriquí Province of Panama (e.g., Allen 4923 and Knapp 2129) have exceptionally short lobes only 3-4 mm long. That other flowers in the same collections, and other collections from the same areas exhibit more normal sepals indicate that such

short sepals are not characteristic of entire populations, but rather represent individual anomalies.

Populations of *C. granulosus* from the western slope of the Cordillera Occidental in Nariño Department of southern Colombia and Carchí, Esmeraldas, and Imbabura Provinces of northwestern Ecuador are tentatively aligned with subsp. *nutans*. These South American populations share with that subspecies the bicolored corollas with little-differentiated throats, persistent inflorescence bracts, occasionally elongate pedicels, well-exserted filament tubes, and tan anther tubes. They differ most conspicuously in the glabrous rather than densely long-pilose anther tubes, although occasional specimens do have sparse white anther trichomes either apically, basally, or dorsally. Three very unusual collections from the vicinity of Maldonado in Carchí Province (Stein 2895, 2896 and Werling & Leth-Nissen 384) are densely pubescent throughout, and superficially resemble *C. trachyanthus* in their dense leaf pubescence; this is almost certainly a very localized derivation.

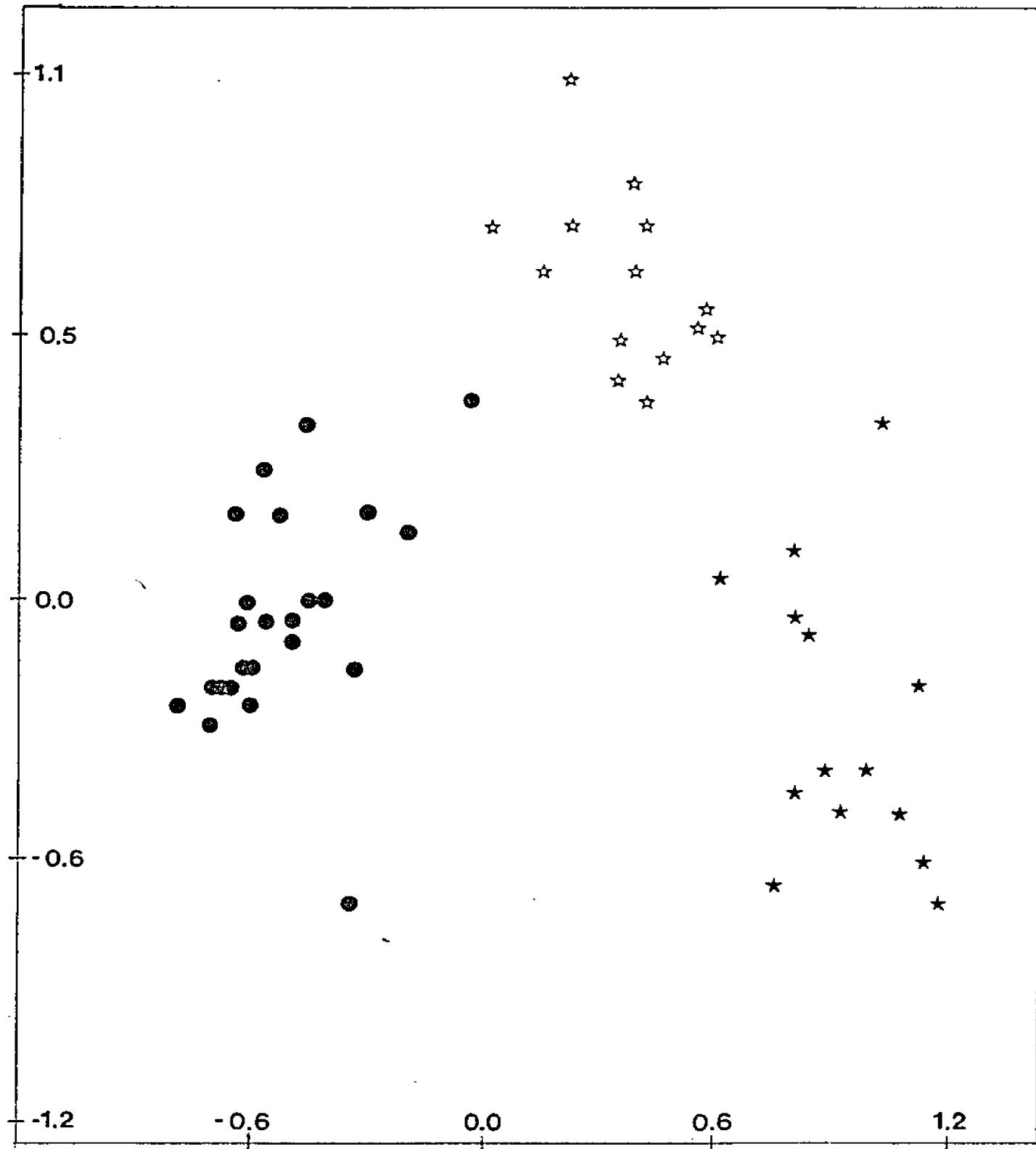
Several possible explanations exist for the morphological similarity between these South American populations and subsp. *nutans* from Costa Rica and Panama. Geographically these populations are contiguous with subsp. *lugens*, and they occur at the periphery of that subspecies range in the southern end of the Chocó phytogeographic region. It is possible that this South American form of subsp. *nutans* has been independently derived from subsp. *lugens*. Several collections from western Cauca Department, Haught 5259, von Sneidern 504, 699, and 1047, also have bicolored corollas and are somewhat intermediate between subsp. *lugens* and these disjunct subsp. *nutans*. Alternatively, these populations could be derived from Central American subsp. *nutans*, or perhaps vice versa, through a long-distance dispersal event. Given that this disjunction occurs between the Pacific coast of northwestern South America and the Pacific coast of southern Central America such an event is at least conceivable.

Table 16

Characters used in multivariate analysis
of *Centropogon granulosus* subsp. *tortilis* and subsp. *nutans*

1. Corolla length
2. Corolla width at throat
3. Androecium length
4. Filament exsertion from dorsal slit in corolla tube
5. Anther tube length
6. Anther pubescence density (1 = glabrescent to sparse; 2 = dense)
7. Anther trichome color (1 = white; 2 = purple)
8. Anther trichome length (1 = to 1.5 mm; 2 = greater than 1.5 mm)
9. Sepal length
10. Sepal width at base
11. Pedicel length
12. Bract length

Fig. 22. Principal coordinates analysis of *Centropogon granulosus* subsp. *tortilis* and subsp. *nutans*; factor 1 X factor 2. (●) subsp. *tortilis*, (★) subsp. *nutans*, and (☆) "bicolored" intermediates (see text).



20. *Centropogon pulcher* A. Zahlbruckner, Bot. Jahrb. Syst. 37: 451. 1906. Type. Peru.

Junin: mountains E of Huacapistana, 2000 m, 14 Jan 1903, Weberbauer 2164

(lectotype here designated, B, photo F-neg. 30221; isolectotypes, B, G, photo F-neg. 27269, W-fragment).

Scandent, herbaceous vines to 8 m long, much-branched above; stems glabrous below, glabrescent or occasionally scaberulous above. Leaves often distichously arranged, narrowly ovate to lanceolate, rarely elliptic, 7-15 x 3-6 cm, apex acute to attenuate, base obtuse to cuneate, occasionally rounded, margins serrulate to irregularly serrate, with 2-4(-5) callose-tipped teeth per cm; lamina thin when fresh, drying chartaceous, adaxial surface dark green, glabrous, abaxial surface slightly paler, glabrous or with minutely hirtellous venation; secondary veins few, 5-6, acutely to arcuately ascending, secondaries and higher order venation conspicuous and slightly raised abaxially; petioles 8-15(-20) mm long, glabrous or rarely minutely hirtellous.

Inflorescence a pendent, short-bracteate, lax, terminal raceme, elongating to 250 cm, the floral internodes 0.5 to 3 cm long, the rachis 1-2 mm wide, glabrescent or minutely hirtellous, rarely scaberulous; bracts persistent, lanceolate to oblanceolate, occasionally ligulate, mostly 7-15 x 2-2.5 mm, apex acute, rarely truncate, base narrowly cuneate, sessile or short petiolate, both surfaces sparsely to moderately hirtellous, basal bracts often resembling normal or slightly reduced vegetative leaves; pedicels retrorsely assurgent at anthesis, drooping in fruit, 10-15(-25) mm long, moderately to densely hirtellous, bracteoles subbasal to submedial, linear or lance-linear, ca. 1 mm long, hirtellous, often inconspicuous when dry. Flowers 60-65 mm long, assurgent and directed away from inflorescence rachis at anthesis; hypanthium hemispheric, 4-6 x 6-8(-9) mm, slightly 5-ribbed, glabrescent to sparsely hirtellous, intersepalar nectaries present; sepals erect or sometimes twisted, linear to narrowly triangular, (3-)5-15 x ca. 1

mm, entire to denticulate, glabrescent to moderately hirtellous, sinuses widely planar; corolla orange to reddish-orange with yellow-orange throat and lobes, sparsely to densely covered with short (to 0.2 mm long), stiff, conical or triangular trichomes; corolla tube moderately sigmoid, 30-35 mm long, the basal portion of tube cylindric and angled backwards ca. 35°, 5-8 mm wide at base narrowing slightly above nectar chamber, then gradually expanding to base of throat, the throat abruptly ampliate, 10-15 mm wide, sharply curved forward 50-60°; dorsal lobes recoiled 12-15 x 5-6 mm, lateral lobes asymmetrically triangular 7-8 x 3-4 mm with attenuate, decurved tips, ventral lobe triangular, 5-6 mm long, with an attenuate, deflexed tip; androecium 55-60 mm long; filament tube ca. 43-48 mm long, ventrally flattened when fresh, pale yellow, glabrous throughout, or occasionally pilose at summit, adnate to corolla 5-6 mm above base, exserted from corolla tube 10-12(-15) mm; anther tube 7-8 mm long, gently arching, thecae tan to brown, connectives pale yellow, the dorsal ones mostly densely long-pilose with white trichomes to 2 mm long, antheridial scale ca. 3 mm long; style exserted from anther tube to 4 mm, stigma 3-3.5 mm in diam. Fruit widely ovoid, to at least 7 x 12 mm, smooth, nectar chamber persistent; seeds widely elliptic, ca. 0.7 mm long.

Distribution. A locally common vine of mid-elevation forests, often at forest edges or in disturbed secondary forest. Restricted to Junin Department of central Peru at elevations of 650-1900 m.

Additional specimens examined. PERU. Junin: Btwn. Pichanaki and Alto Pichinaki, 1300 m, 18 Sep 1981, *Fernández* 13 (NY, USM); Huacapistana, 1800-1900 m, 24 Jan 1946, *Ferreyra* 472 (USM), 22 Sep 1955, *Ferreyra* 11259 (USM); Rio Pinedo, N of La Merced, 700-900 m, 30 May 1929, *Killip & Smith* 23569 (F, NY, US); La Merced, 700 m, 29 May-4 Jun 1929, *Killip & Smith* 23762 (F, NY, US); Huacapistana, 1800-2400

m, 5-8 Jun 1929, Killip & Smith 24266 (NY, US); Colonia Perene, 680 m, 14-25 Jun 1929, Killip & Smith 25048 (F, NY, US, W); above Huacapistana, 1800 m, Jun 1938, Sandeman 89 (K), Oct 1943, Sandeman 4428 (K-2 sheets); km 6-16 on rd. from Bajo Pichinaki to Alto Pichinaki, 650-900 m, 10 Mar 1985, Stein & Todzia 2380 (MO, NY, US, USM), 2384 (K, MO, US, USM), 2385 (AAU, B, MO, USM), 2386 (CAS, DUKE, F, MO-2 sheets, NY, UC-2 sheets, US, USM); Satipo, 750 m, 28 Aug 1960, Woytkowski 5923 (GH, MO, US); Yaupe, 1400 m, 26 Jun 1961, Woytkowski 6334 (MICH, MO).

Department unknown: Martinet 1281 (P); Utubamba[?], Apr 1877, Vidal-Sénège s.n. (P).

Discussion. *Centropogon pulcher* is best characterized by the pendent inflorescences that are often exceedingly long. Although they are often less than 50 cm in length, I have found whip-like pendent racemes to 250 cm long, by far the longest inflorescences in the genus, and perhaps in the subfamily Lobelioideae. Along with this feature, the species can be recognized by the bicolored, abruptly curved corollas, relatively short and hirtellous pedicels, persistent lanceolate to oblanceolate bracts, and glabrescent stems and inflorescence rachis.

The corolla morphology and coloration is almost identical to that of *C. granulosus* subsp. *granulosus*, and *C. pulcher* appears to be a local derivative of that taxon. In addition to the elongate, pendent inflorescence, several characters serve to differentiate these two taxa, which both occur in Junin Department. The pedicels in *C. pulcher* are consistently short (10-15 mm) rather than somewhat elongate as are the basal pedicels of the subcorymbose inflorescences of *C. granulosus*. Further, the bracts in *C. pulcher* are persistent and rather long and narrow rather than caducous and short, and the inflorescence rachis is glabrescent rather than scaberulous or hirtellous. The leaves of *C. pulcher* are thin and generally smaller and narrower (narrowly ovate to lanceolate) than those of *C. granulosus*. Derivation from a *C. granulosus*-like ancestor is supported

by the occasional presence in that species of individuals (e.g., the US sheet of *Hutchison* 1187) with somewhat lax and pendent inflorescences. *Centropogon pulcher* and *C. granulosus* apparently co-occur in the Chanchamayo region but I do not know if they are found sympatrically. While *C. granulosus* is very abundant in the Chanchamayo region, it is completely absent slightly further south around Pichinaki, where I have found *C. pulcher* to be common. There, *C. pulcher* may represent a local ecological replacement for *C. granulosus*.

Centropogon pulcher can also be confused with *C. urubambae*, another species with a lax pendent inflorescence. Differences between these two species are given in the key and discussed under that species.

Jeppesen (1981), with some hesitation, referred several Ecuadorean collections with lax elongate inflorescences to *C. pulcher*. Such collections include specimens from the provinces of: Azuay -- *Boeke & Loyola* 990 (AAU); Cañar -- *Fosberg & Prieto* 22703 (US), 22743 (US), 22748 (US); and Morona-Santiago -- *Acosta-Solis* 5036 (F) and *Steyermark* 53571 (F, MICH). These Ecuadorean collections are quite distinct from the Peruvian material and are not included here in *C. pulcher*. They differ most conspicuously in the pustulate or scaberulous stems and inflorescence rachis and the usually short, deltoid sepals. These collections probably represent an independent derivation of the elongate inflorescence, and additional collections of this morphological form are needed to determine whether they warrant separate taxonomic recognition.

21. **Centropogon cuatrecasanus** B. A. Stein sp. nov. Type. Colombia. Valle:

Ansermanuevo-San José del Palmar rd., 36 km W of Ansermanuevo, 1850 m, 25 Jan 1986, *Stein & McDade 3301* (holotype, COL; isotypes, JAUM, K, MO, NY, US). Fig. 17E-I.

Scendent suffrutescent vine, to 4 m long, much branched above; stems densely granulose-scaberulous, to 2.5 cm in diam. at base; latex opalescent. Leaves narrowly ovate to elliptic, (10-)13-16 x (4-)6-8 cm, apex acuminate, base cuneate, margins serrulate to crenulate with 3-5 callosities per cm; lamina thin when fresh, drying chartaceous, adaxial surface dark green, glabrous, abaxial surface paler, hirtellous to hirsutulous, especially on rather prominently raised venation; secondary veins 7-10, acutely arcuate-ascending; petioles 1-1.5(-3) cm long, to 3 mm wide when pressed, hirtellous and occasionally granulose-scaberulous. Inflorescence a pendent, short-bracteate, terminal raceme, sharply upturned distally and elongating to 15 cm, flowers congested, rachis densely hirtellous with stiff, crinkly, multicellular, tawny trichomes to 0.2 mm long, and with prominent pedicel abscission scars to 5 mm high; bracts caducous, ovate, 10-13 mm long, apex acute, margins denticulate, both surfaces moderately pubescent; pedicels erect at anthesis, drooping in fruit, 25-35 mm long, with indument as on inflorescence rachis, occasionally persistent, bracteoles subbasal, usually inserted ca. 7 mm above base, foliaceous, 4-5 x ca. 1.5 mm. Flowers 60-70 mm long, oriented horizontally; hypanthium very shallow, depressed hemispheric with a truncate base, 3-4 x 6-8, moderately ribbed, moderately to densely hirtellous, intersepalar nectaries not present; sepals erect and appressed to corolla, triangular but often slightly narrowed at base, 5-8 x 3.5-5 mm, entire to minutely serrulate, moderately hirtellous, sinuses mostly planar; corolla uniformly bright yellow, moderately hirtellous with short, collapsed-conical trichomes; corolla tube gently ampliate and only gradually curved, 40-

45 mm long, 5-9 mm wide at base, narrowed slightly above the 5-6 mm long nectar chamber and then gradually expanding to (9-)10-13 mm wide at throat, the throat not well-differentiated from lower portion of tube, gently curving 25-40°; dorsal lobes laterally recurved, 10-12 x 4 mm, lateral lobes asymmetrically triangular, 5-6 mm long with decurved tips, ventral lobe slightly saccate, 4-6 mm long with an erect to deflexed tip; androecium 60-65 mm long; filament tube ca. 55 mm long, ventrally flattened and 3 mm wide when fresh, pale yellow, glabrous throughout, adnate to corolla ca. 7 mm above base, exserted 10-12 mm from corolla tube and arching slightly upwards; anther tube 7-8 mm long, thecae tan, connectives tan to gray, glabrous, antheridial scale 1.5-2 mm long; style exserted from anther tube to 5 mm, stigma greenish, ca. 3 mm in diam. Fruit widely ovoid, to 10 x 18 mm, deeply 10-ridged and star-shaped in cross-section when fresh, nectar chamber persistent; seeds mostly orbicular, ca. 0.6 mm long.

Distribution. A rare vine of moist montane forests near the summit of the Cordillera Occidental of Valle Department, Colombia at 1850-2300 m.

Additional specimens examined. COLOMBIA. Valle: Cordillera Occidental, ridge above Las Brisas, between El Tabor and Alto de Mira, 2200-2300 m, 22 Oct 1946, Cuatrecasas 22422 (F, MICH); Cordillera Occidental, W slope N of Albán, 2100 m, 17 Aug 1941, Dugand & Jaramillo 3041 (COL); Ansermanuevo-San José del Palmar rd., ca. 30-37 km W of Ansermanuevo, 1850-1875 m, 13 May 1984, Luteyn et al. 10400 (NY).

Etymology. This new species is named in honor of Dr. José Cuatrecasas, whose explorations of the Cordillera Occidental of Colombia has brought to light numerous botanical novelties, including an early collection of this species.

Discussion. *Centropogon cuatrecasanus* is easily recognized by the bright yellow corolla (the only Colombian *Centropogon* with flowers this color) and the granulose-scaberulous stems. *Centropogon cuatrecasanus* is unusual in combining features characteristic of both sect. *Campylobotrys* and sect. *Grandes*. The vining habit, the pendulous, sharply upturned inflorescence with short, caducous bracts and prominent pedicel scars, and the wide, ventrally flattened filament tube are all characteristics of sect. *Campylobotrys*; the gently curved and gradually ampulate corolla, however, is reminiscent of sect. *Grandes*. The species is aligned here with sect. *Campylobotrys* on the basis of the unusual inflorescence structure, which comprises a suite of characters unlikely to have arisen independently. The relatively little-curved corolla, which constitutes a deviation from the form typically found in members of this section, is probably related to a shift in pollinator. As discussed in Chapter IV, the abruptly curved corollas found in sect. *Campylobotrys* are an adaptation that allows visits by sicklebill hummingbirds of the genus *Eutoxeres*. According to Hilty and Brown (1986), *E. aquila*, the only species of sicklebill present in western Colombia, ranges no higher than 1400 m in the Cordillera Occidental. *Centropogon cuatrecasanus* occurs at higher elevations (1850–2300 m) where this pollinator is presumably not present. Thus, a shift in corolla morphology that allows access by more generalized hummingbird species with less abruptly curved bills appears to have taken place. At its type locality, *C. cuatrecasanus* occurs sympatrically with *C. solanifolius*, a species visited by such generalized hermit hummingbirds.

Centropogon cuatrecasanus is also similar in certain features to *C. scabellus*, an axillary-flowered species found further north in the Cordillera Occidental. These similarities include the thin, narrowly elliptic to ovate leaves that dry chartaceous and have hirtellous abaxial venation, the granulose-scaberulous stems, the foliaceous bracteoles, and an upwardly arching filament tube with a glabrous anther tube.

Although the profound difference in inflorescence types, generally considered a character of fundamental importance, argues against a close relationship between these two species, these shared characters, some of which are rather derived in nature, may reflect some link. *Centropogon cuatrecasanus* is also similar in certain respects to the disjunct populations of *C. granulosus* subsp. *nutans* that occur in southwestern Colombia and northwestern Ecuador. These populations share with *C. cuatrecasanus* a similar inflorescence type, glabrous anther tube, well-exserted filament tube, and at least occasionally moderately hirtellous to hirsutulous abaxial leaf surfaces. Because as interpreted above, this species is probably derived from a lower elevation member of the *C. granulosus* species complex, these populations of *C. granulosus* subsp. *nutans* may well represent the progenitor, or at least the sister group of this species.

22. **Centropogon densiflorus** Bentham, Pl. Hartw. 138. 1844. Type. Ecuador. Loja: mountains of Yangana, Hartweg 775 (holotype, K, photo USDA-neg. 78196; isotype, CGE n.v., photo F neg-30191, K p.p.).

Scandent herbaceous or suffrutescent vines, to 5 m long, much branched above; stems glabrous below, moderately to densely tuberculate-scaberulous or hirsute above; latex cream-colored to pale yellow. Leaves narrowly elliptic to narrowly oblong or ovate, 6-17(-22) 3-7(-8.5) cm, apex acute to acuminate, base cuneate to rounded, margins slightly revolute, serrulate to serrate, ca. 4 callose-tipped teeth per cm, the callosities slightly exserted; lamina fleshy, pliable or somewhat stiff when fresh, drying coriaceous, adaxial surface dark green and nitid, glabrous, abaxial surface pale green, sparsely to moderately soft-pubescent or hirsutulous, especially along veins; secondary veins 6-8, straight and acute to arcuate-ascending, occasionally forming loops with superadjacent secondaries; petioles 1-1.5 cm long, puberulent to hirtellous. Inflorescence a congested, short-bracteate, terminal raceme, either strictly pendent or pendent apically upturned, the slender rachis elongating to 8 cm, densely scabrous or hirsute with stiff conical trichomes, these often from elongate-bulbous bases, the basal portion of rachis with prominently raised pedicel abscission scars, often subtended by a pendent peduncle; bracts caducous, ovate to oblong, mostly less than 12 mm long, margins serrulate to serrate, moderately to densely hirtellous on both surfaces; pedicels acroscopic in bud, assurgent at anthesis, and pendulous in fruit, 10-20(-30) mm long, with indument as on inflorescence rachis, bracteoles subbasal, small and subulate, or longer and foliaceous, 1.5-6 mm long. Flowers ca. 55-60 mm long; hypanthium very shallow, depressed hemispheric and truncate basally, 3-4 x 6-8 mm wide, prominently 10-ribbed, moderately to densely hirsutulous, intersepalar nectaries not present; sepals foliaceous, erect or slightly patent, ligulate to narrowly triangular, (8-)10-14 x (3-)4-5 mm,

conspicuously dentate or serrate, moderately to densely hirtellous on both surfaces, the bases often auriculate with sinuses planar or adjacent sepals contiguous; corolla deep to bright red, or golden to bright yellow, the tissue rather thick and brittle, densely scaberulous or hirtellous with mostly collapsed-conical trichomes often arising from papillose-bases; corolla tube 35-40(-45) mm long, the lower portion of tube cylindric and straight, 6-9 mm wide at base, narrowing above the thickened nectar chamber then gradually expanding to base of throat, the throat abruptly and widely ampliate, 12-17(-20) mm wide with prominent distended lateral pouches, and often with a dorsal ridge, sharply curved 45-60(-80) $^{\circ}$; dorsal lobes recurved, 10-15 x 4-6 mm, lateral lobes asymmetrically deltoid, 5-8 mm long with acuminate, decurved tips, ventral lobe deltoid, 5-8 mm long with an acute, deflexed tip; androecium 47-53 mm long; filament tube 40-45 mm long, ventrally flattened and ca. 3 mm wide when fresh, pale yellow throughout, or purplish where exserted, entirely glabrous or sparsely pilose at summit, adnate to corolla 6-8 mm above base, exserted from corolla tube 2-7 mm; anther tube 7-8 mm long, thecae gray to purplish, connectives purplish, the dorsal ones usually densely short-pilose with purple trichomes, antheridial scale 2.5-3 mm long; style exserted from anther tube to 4 mm, stigma ca. 4 mm in diam. Fruit ovoid to flattened hemispheric with a truncate base, to 10 x 22 mm, prominently 10-ribbed and verrucose, nectar chamber or entire corolla persistent; seeds elliptic, ca. 0.7 mm long.

Distribution. A locally common vine of cloud and elfin forests. Restricted to the eastern slope of the Andes in Loja and Zamora-Chinchipe provinces in extreme southern Ecuador at elevations of 1800-2800 m.

Key to the subspecies of *Centropogon densiflorus*

1. Corolla red; inflorescence sharply upturned and pipe-shaped with age, trichomes often with elongating, bulbous bases; corolla throat generally less than 14 mm wide, and lacking a dorsal ridge; filament exserted ca. 7 mm from corolla tube; bracteoles often foliaceous.....22a. subsp. *densiflorus*.
1. Corolla golden yellow; inflorescence entirely pendent, trichomes lacking swollen bases; corolla throat often more than 14 mm wide, globose and with a prominent dorsal ridge when fresh; filament generally exserted less than 4 mm from corolla tube; bracteoles generally subulate.22b. subsp. *gracilis*.

22a. *Centropogon densiflorus* Bentham subsp. *densiflorus*.

Inflorescence upturned and pipe-shaped, rachis to 6 cm long, densely hirtellous with stiff, conical, multicellular tawny trichomes, often arising from elongate, bulbous bases; pedicels with similar pubescence, bracteoles generally foliaceous with serrate margins, 4-6 x ca. 2 mm. Flowers: hypanthium and sepals often dark maroon or tinged purplish, with scattered, stiff, conical trichomes, the tissue occasionally thick and warty when fresh; corolla deep to bright red, orangish internally, the tube 30-35 mm long, the throat 11-14(-15) mm wide, with distended lateral pouches but no dorsal ridge; filament tube exserted ca. 7 mm from corolla tube.

Distribution. An uncommon vine of lower cloud forest to elfin forest. Endemic to the Nudo de Sabanilla region of southern Ecuador in southern Loja and adjacent Zamora-Chinchipe provinces at elevations of 2400-2800(-3000) m.

Additional specimens examined. ECUADOR. Loja: Km 5 of antenna maintenance rd. climbing to crest of Cordillera Oriental E of Yangana, 2400 m, 10 May 1985, Stein & D'Alessandro 2713 (MO, NY, QCA, QCNE, US). Zamora-Chinchipe: Above Valladolid on rd. to Yangana, 2700 m, 2 Feb 1985, Harling & Andersson 21467 (GB, NY); Nudo de Sabanilla, just E of pass on rd. to Valladolid, 2800 m, 4 Feb 1985, Harling & Andersson 21513 (GB), 21572 (GB); Nudo de Sabanilla, E slope ca. 5 km from pass on Yangana-Valladolid rd., 2700 m, 4 April 1985, Harling & Andersson 23659 (GB); S side of Nudo de Sabanilla Pass, rd. from Loja to Zumba, 2600 m, 11 May 1985, Stein & D'Alessandro 2741 (MO, QCA, QCNE, US); S side of Nudo de Sabanilla Pass, rd. from Loja to Zumba, 2460 m, 11 May 1985, Stein & D'Alessandro 2750 (MO, QCA, US); Quebrada Achupallas, 3000-3500 m, 9 Oct 1943, Steyermark 54512 (F, MICH). Province unknown: Rio Coichaco, 18 Dec 1876, André 4581 (K-2 sheets).

22b. *Centropogon densiflorus* Bentham subsp. *gracilis* (Drake) B.A. Stein, comb. et stat. nov.

Centropogon gracilis Drake, J. Bot. (Morot) 3: 238. 1889. Type. Ecuador. Loja: vic. of Loja, 9 Nov 1881, Poortmann 150 (holotype, P, photo F neg.-30943; isotype, W).

Stems densely silver-hirsute on young growth. Inflorescence strictly pendent, rachis to 8 cm long, densely hirsute with stiff, or occasionally flaccid, multicellular trichomes, these not arising from elongate, bulbous bases; pedicels directed acroscopically downward in bud, recurved-assurgent at anthesis, often very densely hirsutulous, bracteoles mostly small, 1.5-2 mm long, subulate, rarely larger and more foliaceous. Flowers: hypanthium and sepals green, often very densely hirsutulous with translucent, silvery trichomes, these conical, or more commonly collapsed in dried material, the tissue

not warty when fresh; corolla golden to bright yellow, often appearing galeate, the tube 30-40 mm long, the throat 12-20 mm wide, relatively globose with distended lateral pouches and an elevated dorsal ridge when fresh; filament exserted ca. 2-4 mm from corolla tube.

Distribution: A locally common cloud forest vine. Endemic to the region directly E of Loja, along the eastern slope of the Cordillera Oriental descending toward Zamora at elevations of (1800-)2250-2700 m.

Additional specimens examined. ECUADOR. Loja: Huancabamba, 10 Nov 1876, André 4401 (K); Crest of Cordillera de Zamora, E of Loja, 2900 m, 2 Jul 1944, Camp E-79 (MICH, NY). Zamora-Chinchipe: Pass between Loja and Zamora, along trail toward Zamora, 2360-2800 m, 29 Jul 1982, Clements et al. 2258 (DUKE, MO, NY); Hacienda Zamora-Huaico, 2250-2300 m, 17 Jul 1946, Espinosa 630 (MICH); Hacienda Montecristi, 40 km NE of Loja, 9 Jun 1947, Espinosa 1504 (MICH); Cordillera El Condor-Zamora, 2700 m, 28 Aug 1938[?], Espinosa 1764 (B); Zamora-Huaico, SE of Loja, 2300 m, 15 Dec 1947, Espinosa 2255 (MICH); Río San Francisco above Canillones, 15-18 km ENE of Loja, 1800-1830 m, 20 Feb 1945, Fosberg 23171 (US), Fosberg 23177 (US); Loja-Zamora rd., km 16-22 from Loja, 2300-2700 m, 16 Apr 1974, Harling & Andersson 13646 (AAU, GB, MO); Loja-Zamora rd., E of pass, 2400-2700 m, 11 Feb 1982, Harling et al. 20597 (GB, NY), 2600 m, 15 Feb 1985, Harling & Andersson 22111 (GB); km 17 on Loja-Zamora rd., 2400 m, 16 Apr 1973, Holm-Nielsen et al. 3600 (AAU, NY); km 21 on Loja-Zamora rd., 2400 m, 20 Apr 1973, Holm-Nielsen et al. 4000 (AAU, NY); rd. from Loja to Zamora, E slope of Cordillera Oriental, 2280-2560 m, 15 May 1985, Stein & D'Alessandro 2781 (AAU, F, MO, NY, QCA, QCNE, US).

Discussion. *Centropogon densiflorus*, as treated here, is represented by two subspecies, which are distinctive morphologically and, nonoverlapping geographically in spite of their very localized distributions in extreme southern Ecuador. Subspecies *densiflorus* was first collected by Hartweg around the village of Yangana in Loja Province. Populations in this vicinity, and slightly further south around the Nudo de Sabanilla, are characterized by having corollas of various shades of red. In addition, the inflorescence is of the typical campylobotrous type in being pendent but sharply curved upwards. The majority of the collections of this subspecies have been made since 1985, when a newly constructed road linking Loja with Zumba on the Peruvian border opened and provided access to a region previously accessible only by foot.

Centropogon densiflorus subsp. *gracilis* is found further north on the eastern Andean escarpment along the well-collected road between the towns of Loja and Zamora. Consequently, this subspecies is better represented by collections and has long been confused with subsp. *densiflorus*. Populations in this region consist entirely of plants with golden or yellow corollas and inflorescences that are strictly pendent, i.e., the apex does not turn upwards. The corolla morphology also differs between the two subspecies. Although they both have rather stiff, brittle corollas with unusual lateral pouches that resemble cheeks, subsp. *gracilis* also has a pronounced dorsal ridge, which can attain a height of 5 mm in fresh material. This dorsal ridge provides a groove that partially envelopes the filament tube. In subsp. *gracilis* the corolla throat is also often wider and more globose, creating a saccate or galeate appearance.

Centropogon gracilis was described from material that clearly belongs to yellow-flowered populations. Since Drake proposed this species in 1889, it has been treated as a synonym of *C. densiflorus*. Although the two taxa are separable on the basis of several morphological characters, they are united by a suite of features such as the slightly patent, enlarged and foliaceous sepals, thick corollas with lateral cheeks, densely

scaberulous or hirsute inflorescence rachis, and coriaceous, mildly revolute leaves with a similar abaxial indument. This suggests that whether the two taxa are treated as species or as subspecies, they are closest relatives within sect. *Campylobotrys*. Of the characters that separate the two subspecies, subsp. *gracilis* exhibits the derived conditions for most of these features: yellow corolla color, strictly pendent inflorescence, and a unique dorsal ridge. However, one derived feature, the peculiar inflorescence trichomes with elongated, bulbous bases, is mostly restricted to subsp. *densiflorus*. It seems likely, then, that subsp. *gracilis* has been derived from a subsp. *densiflorus*-like ancestor rather than vice versa.

23. *Centropogon trachyanthus* F. Wimmer, Report. Spec. Nov. Regni Veg. 29: 65. 1931.

Type. Ecuador. Tungurahua: woods near Baños, Jul 1835, Jameson 31 (holotype, K).

Vines to scandent shrubs to 3 m long, much branched above; stems densely scaberulous and strigose, or hispid with tuberculate-based, spreading, uniseriate, multicellular, tawny trichomes to 1.5 mm long, glabrescent basally; latex white to tan. Leaves elliptic to lanceolate, 8-20(-25) x 4-10(-12.5) cm, apex acute to attenuate, base cuneate to obtuse, margins often slightly revolute, serrulate to serrate with 2-5 callose-tipped teeth per cm, these often purple and prominently exserted; lamina thin and pliable to coriaceous when fresh, drying coriaceous to chartaceous, adaxial surface glabrous, sometimes bullate from deeply impressed venation, abaxial surface densely hispid, especially along veins, the acicular trichomes 1-1.5 mm long, spreading; secondary veins 6-10, acute or arcuately ascending, occasionally forming submarginal loops with superadjacent secondaries; petioles 1-2 cm long, densely hispid except on adaxial surface. Inflorescence a pendent, upturned, short-bracteate, subcorymbose raceme, elongating to 11 cm, normally terminal, but occasionally lateral on the same flowering branch, the flowers congested and internodes remaining congested in age, the rachis normally slender, ca. 5 mm, rarely to 10 mm in diam., densely hispid or strigose, with raised pedicel abscission scars to 2 mm tall and 4 mm in diam., often subtended by a pendent peduncle; bracts caducous, lanceolate, lance-oblong, or elliptic, sessile, mostly 15 mm long or less, shorter than the subtended pedicels, apex acute, both surfaces moderately to densely hispid-strigose; pedicels erect at anthesis, pendent with age and in fruit, 20-30(-40) mm long, densely hispid to hirsutulous, bracteoles subbasal, subulate to lanceolate, 2-5 mm long. Flowers 50-55(-60) mm long overall; hypanthium hemispheric, rounded or truncate basally, 3-5 x 5-7 mm, 10-ribbed, densely hispid or hirsutulous,

intersepalar nectaries present but poorly developed; sepals erect, arcuate distally, triangular, 6-10(-12) x 2-3 mm, entire to irregularly serrulate, moderately to densely hispid or hirsutulous on both surfaces, but less so than hypanthium, sinususes planar; corolla red, reddish-orange or orange, with inner surfaces of tube and lobes golden-orange, densely papillose-verrucose externally, each papilla topped with one or more stiff trichomes, occasionally numerous trichomes radiating laterally and appearing stellate, or rarely merely hispid without well-developed papillae; corolla tube 30-35 mm long, the basal portion cylindric, often ventrally distended at base, 5-8 mm wide, and narrowing to just below throat, the throat moderately ampliate, 8-11 mm wide, occasionally distended with lateral pouches and a dorsal crest when fresh, curved 45-60°; dorsal lobes laterally spreading, 8-10 x 3-4 mm, lateral lobes asymmetrically deltoid, 5-7 mm long, with acute, decurved tips, ventral lobe erect and often saccate, 5-7 mm long, with an acute, deflexed tip; androecium 50-55 mm long; filament tube 42-48 mm long, ventrally flattened and 3 mm wide when fresh, yellowish, often pilose at summit, otherwise glabrous, adnate to corolla 6-7 mm above base, exserted from corolla tube 3-8 mm; anther tube 7-8 mm long, thecae gray to purplish, connectives rose-purple, the dorsal ones densely short-pilose with purple trichomes, antheridial scale deltoid, ca. 2 x 2-3 mm; style exserted from anther tube 0-3 mm, stigma greenish to purplish, to 4 mm in diam. Fruit depressed-spheroidal, to 10 x 19 mm, ribbed, nectar chamber persistent; seeds elliptic to oblong, angular, ca. 0.7 mm long.

Distribution. An uncommon montane and cloud forest vine of the eastern Andean slope. Known from Tungurahua, Morona-Santiago, and Azuay provinces of central Ecuador, from 1900-2800 m.

Additional specimens examined. ECUADOR. Azuay: Km 88, Cuenca-Cola de San Pablo hwy., 2540 m, 14 Feb 1977, Boeke & Loyola 989 (AAU, MO, NY); Río Paute Canyon, 3 km below Amaluza at km 85 of Cola de San Pablo rd., 1900 m, 21 May 1985, Stein 2852 (MO, QCA, QCNE, NY, US). Cañar: Hacienda Frutillas, canyon of Río Paute nr. confluence of Río Jubal, 2430-2500 m, 4 Feb 1945, Fosberg & Prieto 22739 (US). Morona-Santiago: Campanas, E of El Pan, 2700-2850 m, 16 Jul 1943, Acosta Solis 5041 (F); between Río Sordo and La Esperanza, en route to Huamboya, 2000-2600 m, 13 Feb 1944, Acosta Solis 7362 (F); Tambo Chontal to Tambo Consuelo, valley of ríos Negro and Chupianza, along trail from Sevilla de Oro to Mendez, 1750-2450 m, 16 Dec 1944, Camp E-1573 (MICH, NY). Tungurahua: Baños, 4 Apr 1931, Benoist 4142 (P); Mount Abitagua, Oct 1857, Spruce 5087 (K-2 sheets); Hacienda San Antonio nr. Baños, 4 km up Río Ulba canyon from Ulba, 2100 m, 2 Jun 1985, Stein 2930 (AAU, B, DUKE, F, K, MO, NY, QCA, QCNE, US); Hacienda San Antonio nr. Baños, 8 Dec 1937, Sydow 472 (B-2 sheets).

Discussion. *Centropogon trachyanthus* is an uncommon upper elevation vine known only from central Ecuador. The densely hispid inflorescence and underleaf surface make this species easily recognizable within sect. *Campylobotrys*. It belongs to the group that includes *C. densiflorus* and *C. baezanus* and is intermediate between those two species morphologically and geographically. It combines the ventrally distended corolla base, papillose-verrucose corolla surface, and propensity for lateral inflorescences of *C. baezanus* with the dense indument and lateral and dorsal corolla throat distentions of *C. densiflorus*.

Three collections from the western slopes of the Andes in northern Ecuador exhibit similar densely pubescent inflorescences and abaxial leaf surfaces. These collections, Stein 2895 & 2896 and Werling & Leth-Nissen 384, are from a very restricted

area near the town of Maldonado in Carchí Province. They appear to be pubescent derivatives of the generally glabrous *C. granulosus* subsp. *nutans* that is found in the surrounding region, rather than a disjunct population of *C. trachyanthus*.

24. *Centropogon baezanus* Jeppesen, Fl. Ecuador 14: 59. 1981. Type: Ecuador. Napo: 1 km E of pump station on Papallacta-Baeza rd., 2050 m, Holm-Nielsen et al. 6932 (holotype, AAU n.v., photograph MO; isotypes, K, NY, S).

Vine to scandent shrub to 5(-7) m high; stems coarsely scabrous with tubercles to 1.5 mm long, often becoming smooth beneath; latex tan. Leaves mostly elliptic, 10-20(-27) x 5-10(-14) cm, apex acute, rarely obtuse, base cuneate, occasionally obtuse, margins often slightly revolute when fresh, denticulate to serrulate, 3-5 exserted callosities per cm; lamina often coriaceous and brittle when fresh, drying coriaceous to chartaceous, adaxial surface dark green, glabrous, abaxial surface paler green, often suffused with purple, coarsely scabrous, especially on mid-vein and secondaries, to smooth and glabrescent; secondary veins 7-12, mostly arcuately ascending, rarely forming intramarginal loops with superadjacent secondaries, conspicuously raised abaxially; petioles thick, 0.5-1.5 cm long, to 3 mm wide, scabrous to glabrescent. Inflorescence of terminal or lateral racemes, usually pendent and upturned at tip, occasionally sub-erect, normally less than 7 cm long, the flowers congested, a peduncle sometimes subtending terminal racemes, the rachis densely and coarsely golden-scabrous with papillate-sided tubercles, these often with mucronate tips and lateral protrusions, older rachis with prominent raised pedicel abscission scars; bracts caducous, lanceolate to triangular with an acute apex, generally less than 10 mm long, much shorter than subtended pedicels, hirtellous to glabrescent, rarely scaberulous; pedicels erect at anthesis, pendent with age, 15-30 mm long, densely scabrous with papillate-tubercles as on inflorescence rachis, occasionally persistent and thickening, bracteoles basal to subbasal, lanceolate and foliaceous, 2-5 mm long. Flowers 55-65 mm long; hypanthium hemispheric, 3-5 x 5-8 mm, prominently ribbed when fresh, densely papillose-verrucose to hirtellous, intersepalar nectaries not seen; sepals erect to arcuate-spreading, triangular to ligulate, 5-

10(-14) x 2-3(-4) mm, entire to irregularly serrulate, sparsely to moderately hirtellous or papillose-verrucose, less densely so than hypanthium, sinuses planar to rounded; corolla bright orange to reddish-orange, rarely red, the lobes and within the tube mostly orange to yellowish-orange, the tissue very thick and brittle, often shrinking when dry, densely covered with verrucose papillae; corolla tube 30-38 mm long, the basal portion ventrally distended, (6-)8-12 mm wide with tissue to 4 mm thick (when fresh) surrounding the nectar chamber, narrowing to 5-9 mm wide just below throat, the throat moderately ampliate, 10-14 mm wide, curved 40-60°; dorsal lobes recurved to recoiled, 12-15 x 4-5 mm wide, lateral lobes asymmetrically deltoid, 7-10 mm long with decurved tips, ventral lobe slightly pouched or plane when fresh, 7-10 mm long with an acute, deflexed tip; androecium 45-55(-60) mm long; filament tube ca. 40-52 mm long, ventrally flattened and 3-4 mm wide when fresh, pilose at summit, otherwise glabrous, adnate to corolla 4-5 mm above base, exserted from corolla tube 5-10 mm; anther tube 7-8 mm long, thecae and connectives purplish, moderately to densely purple-pilose in dorsal connectives, rarely glabrescent, antheridial scale acute to somewhat rounded at tip, 2.5-3 mm long; style exserted to 4 mm, stigma often purplish, 3-5 mm in diam. Fruit oblate, to 10 x 21 mm, prominently 10-ribbed and verrucose, nectar chamber persistent; mature seed not seen.

Distribution. A locally common vine of montane and cloud forests, restricted to the eastern slope of the Andes in Napo and (rarely) Imbabura provinces of central Ecuador, from 1400-2600 m.

Additional specimens examined: ECUADOR. Imbabura. Rio San Pedro just below mouth of Rio Clavadero, E of Cayambe peak, 2100 m, 25 Jul 1944, Wiggins 10449 (DS, US). Napo: Cosanga, 20 km S of Baeza, 2000-2100 m, 26 Oct 1976, Balslev

& Madsen (AAU, K, NY); Puente Sardinas Grandes, 18 km from Baeza on rd. to Lago Agrio, 1650-1700 m, 2 Nov 1976, Balslev & Madsen 10570 (AAU); Cosanga, 1 Dec 1976, Boeke & McElroy 356 (AAU, NY); 5 km S of Baeza on rd. to Tena, 1800 m, 26 Jun 1983, Bohlin & Bohlin 686 (GB); vicinity of Baeza, 1900 m, 27 Mar 1972, Dwyer & MacBryde 9582 (AAU, QCA); Baeza, 2000 m, 6 Jun 1975, Gilli 319 (W); E of Borja, 1800 m, 28 Jul 1960, Grubb et al. 1072 (K, NY); Baeza, 2000 m, 3 Feb 1980, Harling & Andersson 16162 (GB); Cosanga, 1800-1900 m, 4 Feb 1980, Harling & Andersson 16229 (GB); above Jondachi, Baeza-Tena rd., S slope of Cord. de Guacamayos, 1500 m, 7 Feb 1980, Harling & Andersson 16345 (GB); union of Rio Borja and Rio Quijos, 1750 m, 19 Sep 1980, Holm-Nielsen et al. 26075 (AAU, NY); 5 km NW of Borja, 1950 m, 20 Sep 1980, Holm-Nielsen et al. 26443 (AAU); Rio Borja, 1740 m, 21 Sep 1980, Holm-Nielsen et al. 26491 (AAU), 1780 m, Holm-Nielsen et al. 26613 (AAU); slopes of Guagra Urcu, above Rio Bretania, 2000-2200 m, 22 Sep 1980, Holm-Nielsen et al. 26775 (AAU), 2500 m, 24 Sep 1980, Holm-Nielsen et al. 26853 (AAU), 2600 m, 26 Sep 1980, Holm-Nielsen et al. 27077 (AAU), 2650 m, 26 Sep 1980, Holm-Nielsen et al. 27100 (AAU); Baeza, Mar 1865, Isern 1746(2) (GB), Isern 1747(2) (GB); S of Cosanga, km 24-29 from Baeza, 2300 m, 28 Mar 1979, Lojtnant & Molau 11471 (AAU); km 40 from Baeza on rd. to Tena, 1900 m, Lojtnant & Molau 11496 (AAU); Baeza, 1800-2000 m, 20 Sep 1977, Maas et al. 3032 (QCA); Rio Azuela on Baeza-Lago Agrio rd., 1740 m, 21 Oct 1971, MacBryde 779 (AAU, MO, QCA); Baeza, 2000 m, 20 Oct 1976, Ollgaard & Balslev 10179 (AAU, K, NY); km 134 on Lago Agrio-Baeza rd., 1800 m, 7 Aug 1980, Ollgaard et al. 35618 (AAU); km 93-95 on Lago Agrio-Baeza rd., 1550 m, 26 Apr 1985, Stein 2630 (AAU, MO, NY, QCNE, QCA, US); 1 km above Santa Elena on S slope of Cordillera de Guacamayos, km 35 on Baeza-Tena rd., 1800 m, 27 Apr 1985, Stein 2643 (MO, QCA, QCNE, US); km 31 from Archidona on rd. to Baeza, 1400 m, 11 Jun 1985, Stein 3068 (MO-2 sheets, QCA, QCNE, US-2 sheets); Km 34 from Archidona on rd. to

Baeza, 1600 m, 11 Jun 1985, Stein 3069 (F, K, MO, NY, QCA, QCNE, US); trail up Volcán Reventador, km 100 Lago Agrio-Baeza rd., 1500-1700 m, 17 Jun 1985, Stein 3080 (F, K, MO, NY, QCA, QCNE, US). Province unknown: locality not indicated, *Mille 33* (W).

Discussion. *Centropogon baezanus* is a member of the upper-elevation species group that includes *C. densiflorus* and *C. trachyanthus* of central and southern Ecuador. Although *C. baezanus* is rather localized in distribution, it is well-collected owing to its occurrence along the frequently traveled roads passing through Baeza. It shares a number of features with *C. trachyanthus*, such as the tendency toward lateral inflorescences, a ventrally distended basal portion of the corolla tube, and elongate bracteoles. The hispid pubescence characteristic of the latter species, however, is not present. Instead, the stems and inflorescences are very scabrous, but non-pubescent, with unusual tuberculate protrusions. There is much variability within the species in the density and coarseness of these tubercles. In general, collections from lower elevation (1400-2000 m) are more densely and coarsely scabrous than those from higher elevations. In particular, a series of specimens collected by Holm-Nielsen *et al.* on the upper slopes of Guagra Urco are unusual for the species in being only lightly tuberculate.

Along the northern edge of its range *Centropogon baezanus* overlaps with the local form of *C. granulosus* subsp. *granulosus*, and these two taxa are probably sympatric at least occasionally. While the scabrous stem and inflorescence of *C. baezanus* easily separate it from this form of *C. granulosus*, it can be distinguished also by the much thicker corolla tissue, which is usually orange rather than deep red, the purplish rather than tan anther tube, and the purple-pilose rather than glabrous dorsal connectives.

25. *Centropogon curvatus* Gleason, Bull. Torrey Bot. Club 6: 55, fig. 5. 1925. Type.

Colombia. Huila: Cordillera Oriental, E of Neiva, 1300-1800 m, 1-8 Aug 1917,
Rusby & Pennell 948 (holotype, NY).

Centropogon colombiensis F. Wimmer, Repert. Spec. Nov. Regni Veg. 22: 196, pl. 31, fig.

9. 1926. Wimmer, Planzenreich IV. 276b: 168. 1943. Type. Colombia. Huila:
 above Jigante [Gigante], Tolima, 2000 m, 29 Dec 1882, *Lehmann* 2307 (lectotype
 here designated, G; isolectotypes, LE, W).

Centropogon curvatus Gleason var. *pearcei* F. Wimmer, Repert. Spec. Nov. Regni Veg. 29:
 62. 1931. Type. Ecuador. Eastern Andes, Cuenca, 1500-2400 m, *Pearce* 337
 (holotype, K).

Centropogon curvatus Gleason var. *pearcei* F. Wimmer forma *minor* F. Wimmer, Repert.
 Spec. Nov. Regni Veg. 29: 62. 1931. Type. Ecuador. Morona-Santiago:
 Chiguinda, *Lehmann* K.158 (holotype, K).

Suffrutescent herbs to subshrubs 0.5-1.5(-2.5) m tall, erect or occasionally
 scendent, mostly branching from base; stems glabrescent below, usually scaberulous
 above; latex white. Leaves variable in shape, mostly elliptic to obovate, but at times
 narrowly elliptic or narrowly obovate, 14-25(-30) x (4-)6-10(-13) cm, apex generally
 acuminate, sometimes acute or attenuate, rarely mucronate, base cuneate, margins
 crenulate to serrulate, occasionally coarsely crenate or obtusely serrate, with (2-)3-4
 callosities per cm; lamina fleshy when fresh, drying chartaceous to coriaceous, adaxial
 surface dark green and glabrous, occasionally semi-bullate from impressed secondary and
 tertiary venation, abaxial surface paler, glabrous or the veins minutely puberulent to
 hirtellous; secondary veins 7-10, mostly arcuately ascending; petioles 1-2(-4) cm long.
 Inflorescence an erect, bracteate, terminal, corymbose raceme, rarely elongating more

than 3 cm, flowers usually numerous and congested, the rachis mostly scaberulous to scabrous with tawny, stiff, multicellular, conical trichomes, these occasionally with papillose bases, or the trichome portion reduced or lacking and the rachis entirely verrucose-papillose; bracts persistent, elliptic to lanceolate, mostly less than 30 mm long and shorter than the subtended pedicels, sparsely to densely hirtellous on both surfaces; pedicels erect at anthesis, drooping with age, 10-25(-30) mm long, indument as on inflorescence rachis, bracteoles subbasal, subulate to lanceolate, 1-4 mm long. Flowers 50-55 mm long, pedicels, hypanthium, and sepals often tinged deep purple; hypanthium hemispheric to depressed hemispheric, 3-5 x 7-9 mm, prominently 10-ribbed, moderately to densely hirtellous, occasionally with papillose trichome bases, or completely verrucose-papillose, rarely glabrescent, intersepalar nectaries present; sepals erect to arcuately spreading, deltoid to narrowly triangular, variable in length, (2-)4-6(-8) x 2-4 mm, serrulate, sparsely to moderately hirtellous on both surfaces, sinuses planar to acute; corolla bicolored, bright orange, reddish-orange, or rarely red, with the lobes paler and often yellowish-orange, densely hirtellous, the short, collapsed-conical trichomes often with papillose bases, or rarely entirely papillose-verrucose; corolla tube 32-38 mm long, the lower portion of tube straight and stout, the base slightly distended ventrally, 7-9(-11) mm wide narrowing gradually to 5-6 mm just below throat, the throat abruptly ampliate to 12-15(-17) mm wide, occasionally with distended lateral pouches when fresh, sharply curved 40-60°; dorsal lobe recurved to recoiled, 11-14 x 4-5 mm, lateral lobes asymmetrically deltoid, 7-9 x 4-5 mm, with acuminate, decurved tips, ventral lobe ascending-saccate and coherent with the lateral lobes, 5-7 mm long, with an acute, deflexed tip; androecium 47-55 mm long; filament tube 40-48 mm long, ventrally flattened and 3.5-4 mm wide when fresh, yellow throughout or rose-purple where exserted, often pilose at summit, otherwise glabrous, adnate to corolla 5-6 mm above base, exserted 4-8 mm from corolla tube; anther tube 7-8 mm long, rose-purple,

dorsal connectives densely short-pilose with purple trichomes, antheridial scale acute or occasionally truncate, 2-3 mm long, often with tuft of short, unfused, white trichomes at base; style exserted from anther tube to 2 mm, stigma lavender, ca. 4 mm in diam. Fruit oblate to ovoid to 10 x 16 mm, deeply 10-ribbed, nectar chamber persistent; seeds elliptic, 0.7-0.8 mm long.

Distribution. A rare to locally common understory herb or subshrub of upper elevation montane forests. Found in the Cordillera Oriental of central and southern Colombia, the Cordillera Central of southern Colombia, and the eastern Andean slopes of northern and central Ecuador, and occurring at 1550-2350 m.

Additional specimens examined. COLOMBIA. Cauca: E slope of Cordillera Central, Moscopán region, Río San José, Aguabonita, 2280 m, 30-31 Jan 1947, Cuatrecasas 23470 (F, MICH). Cundinamarca: Guayabetal, Río Progreso, 1650 m, 13 Dec 1947, Schneider 464 (S). Huila: Finca Mehrenberg, 2350 m, 6 Jul 1984, D'Arcy et al. 15645 (MO), 11 Jul 1975, Diaz et al. 403 (COL), 15 Jul 1975, Diaz et al. 558 (COL); Quebrada Perdiz, government trail SE of Algeciras, 42 km S of Neiva, 2030 m, 11 Dec 1942, Fosberg 19309 (US); below Finca la Estrella on Quebrada Cucaracha, headwaters of Quebrada Damas, 12 km ESE of Garzón, 2000 m, 1 Feb 1943, Fosberg 19915 (US-2 sheets); Finca Mehrenberg, 2300 m, 3 Apr 1986, Gentry et al. 53971 (MO); Mcpio. de San José de Isnos, Vereda El Hornito, 1960-2000 m, 23 Jul 1980, Lozano 3375 (COL); Finca Mehrenberg, km 100 Popayan-La Plata rd., 2300 m, 16 Feb 1983, Murcia 24 (CUVC); Pitalito, 18 Mar 1899, Sprague 235 (K); La Plata-Popayan rd., 8 km W of Belén, 2300 m, 23 Mar 1986, Stein 3719 (F, FUP, MO, NY); Finca Mehrenberg, km 101 La Plata-Popayan rd., 2300 m, 24 Mar 1986, Stein 3738 (AAU, FUP, K, MO, US); La Plata, 2600 m, 6 Mar 1938, von Sneidern 2705 (S). Meta: Btwn. Paso de Las Cruces and

Buenavista, drainage of Rio Tigre, Colombia-Uribe trail, 25 km ESE of Colombia, 1540 m, 24 Dec 1942, *Fosberg 19540* (US); ridge between Rio Manzanares and Quebrada Playón, 30 km W of La Esperanza, 32 km W of Villavicencio, 1600 m, 3 Sep 1944, *Grant 10127* (MICH, NA, NY, US, WIS-2 sheets); Cordillera La Macarena, extreme NE, Renjifo massif, summit and surroundings, 1300-1900 m, 6-20 Jan 1951, *Idrobo & Schultes 1030* (COL). Putumayo: San Francisco-Mocoa rd., km 92 from Pasto, sitio Los Monos, 2200 m, 30 Oct 1974, *Plowman & Davis 4323* (COL). Department unknown: locality unknown, *Triana 1568* (K).

Ecuador. Napo: Santa Bárbara-La Bonita rd., trail towards La Bonita, 25-28 km S of Santa Bárbara, along Rio Chingual, 2150-2350 m, 17 May 1982, *Luteyn et al. 8445* (NY); Trail to La Bonita, 1-2 km from end of Tulcán-Santa Bárbara rd., ca. 25 km below Santa Bárbara, 2100-2150 m, 28 May 1985, *Stein 2872* (AAU, F, MO, NY, QCA, QCNE, US). Morona-Santiago: 6 km E of Limón on rd. towards La Unión, 1300 m, 23 Apr 1985, *Harling & Andersson 24487* (GB); Plan de Milagro, 10 km NW of Indanza, 1750 m, 2-16 Oct 1944, *Jorgensen OHJ-33* (NY) [probable hybrid with *Centropogon arcuatus*], *Jorgensen OHJ-39* (NY); nr. Rio Calagrás on Limón-Gualaquiza rd., 1600 m, 19 Sep 1980, *Luer et al. 5491* (SEL).

Discussion. *Centropogon curvatus* is a rather polymorphic member of sect. *Campylobotrys* and is characterized by an erect habit, an erect corymbose inflorescence, rather stout orangish or reddish corollas that are usually slightly distended at the base giving them a "pregnant" appearance, and often purple-pigmented hypanthia and sepals. The species, as here defined, is highly variable in leaf shape and sepal length.

The type specimen of *C. curvatus* is rather unusual in having narrowly elliptic leaves 3.5 to 4.5 times longer than wide, whereas most collections exhibit elliptic to obovate leaves 2.5 to 3.5 times longer than wide. The type specimen of *C. colombiensis*

contains the more common, wider leaf shape. At least one collection examined, *Grant 10127*, spans this range (2.3 to 3.8) and indicates that the single sheet of the *C. curvatus* type collection likely represents an extreme on a continuum that includes the broader forms. Likewise, the sepals of the type specimen are exceptionally short, but a range of sepal lengths is apparent in the specimens examined with no apparent correlation with geography or other morphological features. The type specimens of both *C. curvatus* and *C. colombiensis* were collected in the same region of the Cordillera Oriental in Huila Department at comparable elevations. Thus, while the type of *C. colombiensis* represents the more usual form, this species is here treated under the older name, *C. curvatus*.

Centropogon curvatus appears to be closely related to *C. loretensis* and shows some intergradation with that primarily lowland rainforest species. While low elevation *C. loretensis* is well-characterized by having long sepals recurved at the apex, elongate racemes, generally longer flowers, and large, obovate, leathery leaves, certain middle-elevation populations in central Ecuador approach *C. curvatus* in the short congested inflorescence and the shorter, completely erect sepals. Although it is sometimes difficult to unambiguously assign some of the problematic collections, several features can normally be used to differentiate the two species in this region of overlap (Table 17). The most consistent of these are the length and pubescence of the anthers and the color of the hypanthium and sepals. *Centropogon curvatus* has an anther tube 7-8 mm long with mostly short, purple trichomes emanating only from the dorsal connectives. In contrast, *C. loretensis* has an anther tube 9-10 mm long with dense long, white trichomes in both the ventral and dorsal connectives. There are rare exceptions, but in general these features are reliable in separating those populations that overlap in both inflorescence type and sepal attitude. In *C. curvatus* the hypanthium, sepals, and often the pedicel are usually tinged deep purple, whereas in *C. loretensis* these parts are

always green. Furthermore, papillose-based trichomes or papillose-verrucose protrusions are never present in *C. loretensis* as they occasionally are in *C. curvatus*.

Table 17

Principal differences between Centropogon curvatus and Centropogon loretensis

	<u>C. curvatus</u>	<u>C. loretensis</u>
Sepals		
Length	2-8 mm long	3-8 mm long
Attitude	erect to spreading	erect
Apex	tips not recurved	tips recurved or erect
Color	purple	green
Anther tube		359
Length	7-8 mm long (rarely 9 mm)	9-10 mm long (rarely 8 mm)
Pubescence	dorsal connectives	dorsal and ventral connectives
Trichome color	purple	white
Inflorescence		
Type	corymbose	elongate racemose
Length	less than 3 cm long	between 3 and 45 cm

26. *Centropogon papillosum* F. Wimmer, Pflanzenreich IV. 276b: 177. 1943. Types.

Ecuador. Napo: Archidona, 900-1000 m, Jan, *Hopp 1030* (holotype, B n.v., probably destroyed in World War II); Archidona, Apr-May 1865, *Isern 1347(2)* (neotype here designated, GB). Fig. 18.

Erect herbs 0.5-1(-1.5) m tall, single-stemmed or branching from the base, glabrous below, becoming papillose-verrucate towards apex and throughout the inflorescence, the papillae fleshy when fresh, to 0.4 mm long, drying irregularly verrucate, occasionally tipped by minute spiculate or elongate, multicellular trichomes; latex white. Leaves narrowly elliptic to elliptic, rarely oblanceolate, 14-20(-23) x 4-6(-7) cm, apex acuminate to acute, base cuneate, margins usually sharply serrate, with 2-3 prominent callose-tipped teeth per cm; lamina rather stiff and often convex with revolute margins when fresh, drying chartaceous, adaxial surface dark green and glabrous, bullate from the deeply impressed secondary veins, abaxial surface paler, glabrous or the veins minutely muricate, the venation prominently elevated; secondary veins 10-12, acutely to arcuately ascending; petioles 5-15(-25) mm long, canaliculate adaxially and occasionally slightly winged to base. Inflorescence an erect, bracteate, terminal, subcorymbose raceme, usually less than 4 cm long, but occasionally elongating to 11 cm, densely flowered and congested, often subtended by a peduncle 5-10 cm long, the rachis glabrescent below, becoming increasingly papillose-verrucate toward the apex, often tinged maroon as are the pedicels, hypanthium and sepals; bracts much reduced and persistent, narrowly elliptic to ovate, sessile, medial and upper bracts mostly less than 15 mm long, margins callose-serrulate, both surfaces sparsely hirtellous, or abaxial veins papillose-verrucate; pedicels erect at anthesis, reclining with age, 10-15 mm long, very densely papillose-verrucate, bracteoles basal, subulate, 1-2 mm long. Flowers 40-50 mm long, not resupinating and directed inward at anthesis; hypanthium hemispheric,

rounded at base, 7-9 x 5-6 mm, surface smooth to verrucose, sparsely to densely papillose-tuberculate, intersepalar nectaries not present; sepals erect or with slightly patent tips, triangular, 4-7 x 2-3 mm, entire to minutely denticulate, mostly smooth and glabrescent in sharp contrast to hypanthium, sinuses planar or slightly rounded; corolla bright reddish-orange, the lobes and withing throat orange to yellowish-orange, the tissue thick and brittle, densely papillose-verrucose; corolla tube 30-35 mm long, the lower portion cylindric and thickened, ca. 15 mm long, 7-9 mm wide at base, narrowing to 5-7 mm wide at base of throat, the throat abruptly ventricose, 12-15 mm wide, with laterally distended pouches and a slight dorsal ridge when fresh, with a very small orifice almost closed off by the coherent lobes, sharply curved 50-60(-80) $^{\circ}$; dorsal lobes remaining erect at anthesis, 10-11 mm long, lateral lobes deltoid, ca. 6 mm long, with falcate tips, ventral lobe ascending and coherent with lateral lobes, 4-6 mm long, with an acute, deflexed tip; androecium 35-40 mm long, completely included within corolla; filament tube 30-35 mm long, ventrally flattened and 3 mm wide when fresh, pale yellow, glabrous, adnate to corolla ca. 5 mm above base; anther tube 6 mm long, thecae yellow, connectives tan or grayish-brown, sparsely white-pilose along dorsal connectives and at tube apex, antheridial scale often truncate and poorly fused at apex, exceptionally long, 3.5-3.75 mm; pollen grains pale yellow, coherent and not powdery; style exserted from anther tube to 3 mm, stigma longitudinally conduplicate, ca. 2.5 mm in diam. Fruit spheroidal, to 9 x 13 mm, intensely sweet-fragrant when ripe, thickened nectar chamber persistent; seeds oblong-rectangular, 0.8-0.9 mm long.

Distribution. A rare understory herb with a limited range and restricted to primary premontane tropical forest. It is endemic to the region between Puyo and Tena in Morona-Santiago, Napo, and Pastaza provinces of central Ecuador at 800-1050 m.

Additional specimens examined. Ecuador. Morona-Santiago: Puerto Santana, ca. 5-6 km from Shell-Mera, 16 Sep 1968, *Lugo* 445 (AAU, WIS). Pastaza: Km 31 on Puyo-Canelos rd., 870 m, 21 Jul 1982, *Besse et al.* 1694 (SEL); Puyo-Puerto Napo rd, San José ca. 17 km NE of Puyo, 800 m, 10 Mar 1980, *Harling & Andersson* J7134 (GB); Colonia 24 de Mayo, 18-20 km from Puyo, 13 Sep 1968, *Lugo* 395 (F, GB), 396 (GB, WIS), 27 Jun 1972 *Lugo* 2468 p.p. (K); 25.7 km NNE of Puyo on Puerto Napo rd, 0.5 km W on rd to Estación Llania, 1040 m, 22 Apr 1972, *MacBryde* 1499 (AAU); 6.5 km from Puyo on Napo rd, 17 Feb 1953, *Prescott* 411 (DS; NY sheet of this number is *C. loretensis*); trail towards Colonia 24 de Mayo, 2.5 km W on rd departing main Puyo-Tena rd at km 9, 1050 m, 3 Jul 1985, *Stein & Tucker* 3127 (fAAU, F, MO, NY, QCA, QCNE, US). Tungurahua: 5 km W of Baños, 2300 m [locality undoubtedly wrong], 9 Oct 1961, *Dodson & Thien* 982 (MO).

Typification. The holotype of this species, *Hopp* 1030, can not be found in the herbarium at Berlin, and may have been a casualty of the bombing that took place during World War II. I have searched unsuccessfully for the specimen at B as well as at W, where many of the Berlin specimens were on loan during the war and where fragments of other presumably lost Berlin types have been located. I am therefore designating a neotype for this species, *Isern* 1347(2) at GB. This specimen was chosen for several reasons. Foremost, it is concordant with the protologue in all details. Second, it is a collection of historical interest as Isern was one of the first botanists to visit eastern Ecuador, and he undoubtedly made the first collection of this species. Finally, the collection is from the type locality, Archidona, whereas all other collections I have seen are from elsewhere in its limited range. Because this species is found in the understory of mostly undisturbed forest, the lack of recent collections from the type

locality is probably due to the widespread forest destruction that has taken place in the vicinity of Archidona during the last few decades.

Discussion. *Centropogon papillosum* is one of the most distinctive species in sect. *Campylobotrys*, displaying a number of unique or unusual characteristics. The feature that most clearly sets this species apart from all others is the completely included androecium, a condition found nowhere else in subgen. *Centropogon*. Several other floral features may be related to the included androecium. The longitudinally conduplicate stigma is unique to this species and probably is related to space restrictions within the corolla throat. Similarly, the relatively long and truncate antheridial scale and the coherent, rather than powdery pollen may relate to the pollen deposition method developed in this species.

The papillose-verrucose floral and inflorescence tubercles which give the species its name are very distinctive, and though papillae are found in several other species (e.g., *C. curvatus* and *C. pygmaeus*), they are nowhere near as well developed as in *C. papillosum*. When present in other species, the papillae generally form enlarged bases for trichomes, whereas in *C. papillosum* trichomes are absent or reduced to a small mucronate tip on the papillae. Occasional collections, such as the DS sheet of *Prescott* 411 (the NY sheet is *C. loretensis*), show well-developed conical trichomes arising from the papillae indicating that the papillae probably did once serve as trichome bases. The papillae are very fleshy multicellular structures that have the same elongate-reticulate cell arrangement as the epidermis (Fig. 18D), whereas the associated trichomes are well-differentiated uniseriate conical structures with transverse cell divisions.

The narrowly elliptic and bullate leaves are another characteristic feature of this species. The only other species in subgen. *Centropogon* with bullate leaves is *C. quebradanus* a member of the *C. gamosepalus* alliance in sect. *Amplifolii*.

Centropogon papillosum may be most closely related to *C. curvatus*, a mid-elevation species of northern Ecuador and southern Colombia. These two species share a number of derived features, including an erect habit with upright, generally congested inflorescences, inflorescence papillae (only occasionally in *C. curvatus*, and in these instances they are clearly trichome bases), and purple to maroon pedicels and hypanthia. Furthermore, at least one specimen, Cuatrecasas 11411 from near Mocoa in Putumayo, Colombia, is somewhat intermediate between these two species supporting their possible relationship. The absence of intersepalar nectaries in *C. papillosum* is unusual for a lowland species, suggesting that it may have been derived from a higher elevation ancestor, similar to *C. curvatus*, in which the nectaries were lost.

27. *Centropogon vaughianus* F. Wimmer, Brittonia 8: 110. 1955. Type. Colombia.

Cundinamarca: Subatá-San Francisco rd., 2000 m, 26 Aug 1947, Haught 6107
(holotype, MICH; isotypes, COL, US, W). Fig. 8G.

Erect suffrutescent herbs 0.5–1.5 m tall, single-stemmed from base; stem thick, succulent, to 1.5 cm in diam., glabrous beneath, scaberulous or hirtellous towards apex; latex pale yellowish-tan. Leaves obovate to narrowly obovate (17–)20–34 x (5.5–)8–12 cm, apex mucronate to acuminate, base cuneate, margins almost entire, minutely callose-denticulate to crenulate, 2–3 callosities per cm; lamina very thick and fleshy when fresh, often drying chartaceous, adaxial surface dark green, glabrous, abaxial surface pale green, glabrous; secondary veins 7–9, widely arcuate-ascending, prominently raised abaxially; petioles 2–10 mm long, often thick, to 3 mm wide. Inflorescence an erect, bracteate, terminal, subcorymbose raceme, elongating 5 cm, few flowered, the floral internodes congested throughout, the rachis hirtellous or scaberulous, subtended by a thick, bractless peduncle 5–12 cm long and 3–5 mm in diam.; bracts persistent, mostly ovate, 15–20 x 8–17 mm, apex mucronate to obtuse, base rounded to cuneate, sparsely to moderately hirtellous on both surfaces and along the minutely serrulate margin; pedicels erect at anthesis, drooping with age, 15–25 mm long, moderately to densely hirtellous, bracteoles conspicuous, basal to subbasal, narrowly triangular, 4–7 x 1–2 mm, often persistent on inflorescence rachis after abscission of pedicel. Flowers 50–55 mm long; hypanthium transversely oblong or depressed hemispheric, rounded or truncate basally, 3–5 x 8–10(–13) mm, prominently ridged when fresh, moderately to densely hirtellous, intersepalar nectaries absent; calyx gamosepalus, 10–15 mm long, connate basally for 1/3 to 1/2 of length, the tube 12–15 mm wide, pentagonal in cross-section when fresh, the lobes erect, triangular, 7–10 x 5 mm, hirtellous throughout; corolla concolorous, cardinal or deep red, the tissue very thick and stiff, shrinking somewhat when dried, moderately

to densely hirsutous with collapsed-conical trichomes, these occasionally with small papillose-verrucose bases; corolla tube 30-35 mm long, obscured by the stout lower portion of calyx tube, the tube 8-10 mm wide at base, narrowing to 5-7 mm just below throat, the throat ventricose and abruptly ampliate, 13-15 mm wide, when fresh ca. 15 mm in diam. with prominent laterally distended pouches and a slight dorsal ridge, curved 40-50°; dorsal lobes spreading to recurved, 10-12 mm long, lateral lobes deltoid ca. 6 mm long, with attenuate to acuminate, decurved tips, ventral lobe coherent with lateral lobes, ascending-saccate, ca. 6 mm long, with a short, deflexed tip; androecium ca. 45 mm long; filament tube ca. 40 mm long, ventrally flattened and ca. 3.5 mm wide when fresh, pale yellow throughout, entirely glabrous or short-pilose at summit, adnate to corolla ca. 5 mm above base, exserted from corolla tube 4-5 mm; anther tube 7-8 mm long, thecae greyish, connectives rose-purple, the dorsal ones densely short-pilose with purple trichomes, antheridial scale deltoid, ca. 2 mm long; style exserted 0-2 mm from anther tube, stigma to 4 mm in diam., purplish. Fruit oblate, to 8 x 19 mm, prominently 5-ribbed, calyx and nectar chamber persistent; seeds elliptic, 0.8-0.9 mm long.

Distribution. An uncommon herb of moist montane forest, endemic to the west slope of the Cordillera Oriental in western Cundinamarca Department of Colombia at 1650-2100 m.

Additional specimens examined. COLOMBIA. Cundinamarca: Ravine 3 km S of San Francisco, 2100 m, 29 Apr 1973, Cleef 9670 (COL); Albán, Guevara Amórtegui 297 p.p. (US; mixed collection, including lectotype of *C. holtonis* var. *albanensis*); Albán, Guayabetal, 1650 m, 13 Dec 1947, Schneider 464-A (COL p.p.); Sasaima, San Bernardo,

2000 m, 22 Sep 1951, Schneider 1116 (COL); San Francisco-Subatá rd., 9 km N of San Francisco, 1 km S of La Magnolia, 2000 m, 13 Mar 1986, Stein 3676 (COL, MO, US).

Discussion. *Centropogon vaughianus* is a very distinctive species owing to the combination of an abruptly curved and ventricose campylobotrous corolla and a gamosepalous calyx, the latter occurring nowhere else in sect. *Campylobotrys*. Other characteristic features of this species include the erect habit with succulent stems, the large, fleshy, obovate leaves with mucronate apices, the erect inflorescence subtended by a peduncle, the enlarged bracteoles that are often persistent after abscission of the pedicel, and the very thick and stiff corollas with both lateral and dorsal distentions.

Wimmer (1955) aligned this species with *C. gamosepalus*, a member of sect. *Amplifolii*, on the basis of the fused calyx, but he admitted that it differed in features of the leaves and corolla. Wimmer's placement was apparently based on his reliance on sepal fusion as a conservative character. It is now clear that fused sepals have developed independently in several different lineages within subgenus *Centropogon*. On the basis of corolla morphology, filament tube cross-section, and inflorescence structure *C. vaughianus* belongs to sect. *Campylobotrys* and is not at all related to *C. gamosepalus*.

The relationships of *C. vaughianus* apparently lie with *C. curvatus*, and *C. vaughianus* may well represent a direct descendent of that species. These two species share the relatively unusual features (for sect. *Campylobotrys*) of an erect habit and erect, congested inflorescences as well as thick, obovate leaves. In general aspect the corolla resembles that of *C. curvatus*, but the lateral and dorsal distentions of the throat and the coherent lower corolla lobes are reminiscent of *C. papillosum*, another species seemingly closely related to *C. curvatus*. Distribution also supports the derivation of *C. vaughianus* from a *C. curvatus*-like ancestor. The latter species ranges from eastern Cundinamarca Department south to central Ecuador and *C. vaughianus* occurs in a very

restricted area on the northwestern periphery of that range. They are not known to occur sympatrically; in Cundinamarca Department *C. curvatus* is found only on the eastern slope of the Cordillera Oriental, while *C. vaughianus* is endemic to the western slope of this range. Such an isolated peripheral location is precisely where such an evolutionary novelty might develop following dispersal over the cordillera.

Centropogon vaughianus and *C. granulosus* subsp. *rutilus* occur in close sympatry and they presumably share the same pollinator, but I have found no evidence of hybridization between these two species.

28. **Centropogon loretensis** F. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13: 417. 1937.

Type. Peru. Loreto: Río Marañón below Pongo de Manseriche, 155 m, 29 Aug 1924, *Tessmann* 3906 (lectotype here designated, G). The holotype at B was apparently destroyed during World War II, but is represented by a Field Museum type photograph, F-neg. 9092.

Erect or subscandent suffrutescent herbs or shrubs 1-2.5(-4) m tall, single-stemmed, or branching from the base; stems glabrous, striate basally, to 2.5 cm in diam. at base; latex normally tan. Leaves mostly narrowly oblong, oblanceolate, or narrowly elliptic, occasionally broader, (15-)20-40 x 6-12.5 cm, apex acute to short acuminate, rarely obtuse, base cuneate, or occasionally obtuse, margins denticulate with minutely exserted callosities, or more commonly serrulate to serrate, especially along distal half of margin, 2-5 callose-tipped teeth per cm; lamina normally very thick and leathery, drying coriaceous, adaxial surface dark green and glabrous, abaxial surface paler, glabrous or minutely pubescent along rather prominent venation; secondary veins 10-14, arcuately to acutely ascending, occasionally forming loops with superadjacent secondaries; petioles short and thick, 5-10(-20) mm long. Inflorescence an erect, bracteate, terminal raceme, elongating to 45 cm, but usually shorter, rarely little-elongate and sub-corymbose, flowers congested near apex, internodes elongating to ca. 1 cm basally, often subtended by a peduncle to 15 cm long, inflorescence rachis and peduncle moderately to densely scaberulous with tawny, stiff, uniseriate, multicellular trichomes; bracts persistent, narrowly oblong, lanceolate, or rarely oblanceolate, 1.5-4 x 0.5-1 cm, about as long as subtended pedicels, apex acute, base cuneate, sessile, margins callose-denticulate to serrulate, both surfaces sparsely to moderately hirtellous; pedicels erect at anthesis, recurved with age, 20-35 mm long, usually densely scaberulous-hirtellous, occasionally persistent, bracteoles basal to subbasal, subulate, 1-3 mm long. Flowers 55-75 mm long;

hypothecium hemispheric to cylindric, rounded basally, (4-)5-7 x (5-)6-10 mm, smooth, moderately to densely hirtellous, intersepalar nectaries prominent; sepals erect, usually with recurved tips, triangular to lance-oblong, highly variable in length, (3-)5-10 x 2-3.5 mm, entire and often with 2-4 marginal callosities, sparsely to moderately hirtellous, sinuses planar to rounded; corolla usually bicolored, of varying hues from orange to deep-red (rarely pink?), the lobes and inside of throat normally yellowish-orange, sparsely to densely hirtellous with short, conical trichomes; corolla tube 35-45 mm long, (4-)6-8(-10) mm wide at base, usually narrowing to (2-)4-6 mm wide above the 4-5 mm-long nectar chamber, then gradually expanding to base of throat, or occasionally the basal portion of tube uniformly stout with the narrowest point just below throat, the throat abruptly ampliate, (8-)11-15 mm wide, sharply curved ca. 50-60°; dorsal lobes recoiled, long-falcate, 10-18 x 4-5 mm wide, lateral lobes asymmetrically deltoid to falcate, 7-10 mm long, ventral lobe erect, slightly pouched, triangular 6-9 mm long, with an acute, deflexed tip; androecium 45-65(-70) mm long; filament tube 40-55(-60) mm long, ventrally flattened and 2-4 mm wide when fresh, pale yellow throughout, pilose at summit, otherwise glabrous, adnate to corolla 7-10 mm from base, exserted from corolla tube 5-10 mm; anther tube (8-)9-10 mm long, thecae gray, connectives tan to yellowish, the dorsal and ventral ones normally densely long-pilose with white, or very rarely purple trichomes, rarely glabrescent, antheridial scale deltoid to triangular, 2-3 mm long, apex acute or irregularly truncate; style exserted from anther tube 0-3 mm, stigma whitish, to 7 mm in diam., although usually less. Fruit globose, oblate, or depressed ovoid, 8-12 x 15-20 mm, smooth, nectar chamber persistent; seeds elliptic to suborbicular, often angular, 0.6-0.8 mm long.

Distribution: A locally common understory herb to shrub primarily of lowland tropical rainforest and premontane rainforest. Widespread in Andean foothills and adjacent Amazonia from southern Colombia to northern Peru at 200-1100 m alt.

Representative specimens examined: COLOMBIA. Caquetá: 9 km S of San José de Fragua, 320 m, 10 Jan 1974, *Gentry et al.* 9122 (COL); Morelia, 300 m, 4 Sep 1941, *von Sneidern s.n.* (S); Mocoa, 23 May 1899, *Sprague* 390 (K-2 sheets). Cauca: Puerto Limón, Rio Caquetá, Loma de José María and Negro Agapito, 300-350 m, 27 Nov 1967, *Mora* 4428 (COL). Putumayo: Between Puerto Asis and San Pedro, 25 Jul 1957, *Barclay* 4737 (COL); Rio San Miguel nr. mouth of Rio Conejo, 300 m, 9 Dec 1940, *Cuatrecasas* 10932 (COL); between Rio Chipayacu and Finca Pedrogoso en route to Puerto Asis, 700 m, 10 Jan 1945, *Ewan* 16742 (MICH); 4 km S of San Antonio de Guamues, 18 Feb 1970, *Foster* 1555 (DUKE); 40 km NW of Puerto Asis, 300 m, 31 Jul 1965, *King & Guevara* 6127 (NY, US).

ECUADOR. Morona-Santiago: Taisha, Rio Guambime, 400 m, 19 Jun 1980, *Brandbyge & Asanza* 32066 (AAU), 22 Jun 1980, *Brandbyge & Asanza* 32204 (AAU); Pampuenteza, 250 m, 27 Jun 1980, *Brandbyge & Asanza* 32326 (AAU); km 20 on Limón-Macas rd., 700-900 m, 26 Mar 1974, *Harling & Andersson* 12893 (GB); horse trail Macas-Riobamba, 7 km NW of General Proaño, 1100 m, 30 Feb 1974, *Harling & Andersson* 13025 (MO, NY); Cumandá, 6 km W of Mera, 1000 m, 14 Mar 1980, *Harling & Andersson* 17294 (GB); Puerto Santan, 5-6 km from Mera, 16 Sep 1968, *Lugo* 450 (GB); Rio Palora, 2-5 km downstream from Arapicos, 800-900 m, 9 Apr 1981, *Lugo* 6064 (GB). Napo: INIAP experimental station, San Carlos, 6 km SE of Los Sachas, 250 m, 10 Apr 1985, *Baker* 5976 (NY); 40 km SE of Coca, 300 m, 4 Nov 1976, *Balslev & Madsen* 10584 (AAU, NY); Mission Shandia, Rio Jatun Yaku, 15 Aug 1957, *Barclay* 4902 (COL); 12 km W of Coca on rd. to Loreto, 6 Jul 1983, *Bohlin & Bohlin* 304 (GB);

Río Palanda Yacu, 45 km N of Coca on Lago Agrio rd., 7 Jun 1983, *Bohlin & Bohlin* 320 (GB); Payomino, 200 m, 25 Feb 1980, *Brandbyge & Asanza* 30021 (AAU); 5 km N of Coca on rd. to Lago Agrio, 200 m, 16 Mar 1980, *Brandbyge et al.* 30193 (AAU); Coca-Lago Agrio rd., 9 km NE of Rio Coca, 200 m, 20 Mar 1980, *Brandbyge et al.* 30238a (AAU); San Pablo de los Secoyas, Río Wai si aya, a tributary of the Río Aguarico, 300 m, 7 Aug 1980, *Brandbyge et al.* 32600 (AAU), 29 Aug 1980, *Brandbyge et al.* 36210 (AAU); Dureno, 350 m, 30 Apr 1986, *Cerón* 280 (MO); 17.3 km N of Lago Agrio on rd. to Rio San Miguel, 450 m, 3 Oct 1980, *Croat* 50335 (MO, NY); 7.2 km S of Río Aguarico, nr. Lago Agrio, 270 m, 28 Apr 1984, *Croat* 58667 (MO); Archidona-Cotundo rd., 800 m, 14 Dec 1976, *Davis* 461 (U); Limoncocha, 243 m, 25 Sep 1977, *Foster* 3829 (AAU, F, NY); 12 km W of Lago Agrio, 270 m, 5 Nov 1974, *Gentry* 12463 (MO); 8 km W of Lumbaque on Quito-Lago Agrio rd., 5 km N of hwy., 500 m, 21 Jul 1986, *Gentry & Miller* 54939 (MO); Hacienda Cotapino, 500 m, 19-20 Feb 1968, *Harling et al.* 6997 (GB); Cañon de los Monos, 12 km N of Coca, 350 m, 4 Feb 1974, *Harling & Andersson* 11723 (AAU, GB); Shushufindi, on Coca-Lago Agrio rd., 400 m, 16 Feb 1974, *Harling & Andersson* 12011 (GB); 5 km N of Jondachi on Baeza-Tena rd., 1100 m, 8 Feb 1980, *Harling & Andersson* 16410 (GB); Lago Agrio-El Conejo rd., 300 m, 16 Feb 1980, *Harling & Andersson* 16577 (GB); 60 km W of Coca along Río Payomino, 350 m, 18 Jun 1968, *Holm-Nielsen & Jeppesen* 791 (AAU, NY); San Pablo de las Secoyas along Río Aguarico, 21 Feb 1980, *Holm-Nielsen et al.* 21702 (AAU); San José de Payamino, 40 km W of Coca, 300-600 m, 29 Apr 1984, *Irvine & Jipa* 1076 (F); Archidona, Apr 1865, *Isern* 1057(2) (GB), 1058(2) (GB); Sarayacu nr. Río Aguarico, 29 Jun 1980, *Jaramillo & Coello* 2595 (AAU), 2642 (QCA); Secoya, nr. junction of Río Eno and Río Aguarico, 3 Jul 1980, *Jaramillo & Coello* 2784 (AAU, QCA); Puerto Bolívar, Río Cuyabeno, 6 Jul 1980, *Jaramillo & Coello* 2841 (AAU); Dureno, right margin of Río Aguarico, 10 Jul 1980, *Jaramillo & Coello* 2987 (AAU); Campanacocha, left margin of Río Napo, 360-

400 m, 22 Aug 1980, *Jaramillo & Coello* 3784 (QCA); Laguna Grande, Cuyabeno, Pica Saladero de Dantas, 30 Jul 1984, *Jaramillo* 6850 (MO); Latas, 12 Aug 1968, *Lugo* 277 (AAU, GB, WIS); Santa Rosa at Río Napo, 27 Apr 1972, *Lugo* 1971 (AAU, GB, MO); Río Sumino, tributary of Río Napo, 5 km NE of Santa Rosa, 2 May 1972, *Lugo* 2102 (AAU, GB, MO); Río Bueno, tributary of Río Suno, 5 km N of Santa Rosa, 7 May 1972, *Lugo* 2156 (GB); Río Napo 3-4 km S of Coca, 8 Jan 1973, *Lugo* 2551, (AAU, GB); Armenia Vieja, 12 km W of Coca, 12 Jan 1973, *Lugo* 2635 (AAU, F, GB, NY); Coca, 17 Jan 1973, *Lugo* 2784 (AAU, GB); Río Payomino, nr. Payomino-Capihuara, 19 Jan 1973, *Lugo* 2846 (AAU, GB, MO); Cañon de los Monos, 12 km N of Coca, 24 Jan 1973, *Lugo* 2972 (AAU, F, GB); Lago Agrio, 4 Feb 1973, *Lugo* 3134 (AAU, GB, WIS); Río Aguarico, 5 km S of Lago Agrio, 7 Feb 1973, *Lugo* 3183 (AAU, GB, NY); Las Sachas, 30-40 km E of Coca, 13 Feb 1973, *Lugo* 3346 (AAU, GB, MO); Limoncocha, 240 m, 16 Jun 1978, *Madison et al.* 5332 (AAU, F, QCA, SEL); nr. Archidona, 650 m, 19 Apr 1935, *Mexia* 7274 (UC); Limoncocha, Apr 1969, *Mowbray* 69422 (MO); 9 km downriver from Misahualli on Río Napo, 450 m, 5-6 May 1985, *Neill* 6440 (MO); Río Tigre, 10 km S of Lumbaqui, 800 m, 6 Dec 1986, *Neill* 7538 (MO); Añangu, Yasuni National Park, 260-350 m, 30 May-21 Jun 1982, *Ollgaard et al.* 39154 (AAU); Dureno along Río Aguarico, 450 m, 1 Aug 1974, *Plowman* 4036 (COL, GH); Cañon de los Monos, 15 km N of Coca, 250 m, 20 Apr 1985, *Stein et al.* 2549 (AAU, B, CAS, DUKE-2 sheets, MO, NY, QCA, QCNE, U, US); 9 km below Puerto Misahualli on the Río Napo, 400 m, 10 Jun 1985, *Stein & Suarez* 3050 (K, MO, QCA, QCNE, US); S slope of Cordillera de Guacamayos, new rd. Cotunda-Coca, 3-5 km from turn-off, 1150 m, 11 Jun 1985, *Stein* 3066 (MO, QCA, QCNE, US). Pastaza: 19 km S of Puyo along rd. to Macas, 1200 m, 9 Oct 1980, *Croat* 50535 (MO, NY); 2.7 km W of Mera along Puyo-Baños rd., 1110 m, 5 May 1984, *Croat* 59085 (MO); Mera, 1100 m, 27-28 Mar 1968, *Harling et al.* 7842 (GB), 25 May-6 Jun 1968, *Harling et al.* 9787 (GB), *Harling et al.*

10200 (GB); 3 km SE of Veracruz, Puyo-Macas rd., 900 m, 3 Mar 1980, *Harling & Andersson*; 16832 (GB); 1-5 km NW of Mera, 1100-1200 m, 7 Mar 1980, *Harling & Andersson* 17020 (GB, NY); 2 km N of Mera, 1050 m, 6 Jun 1968, *Holm-Nielsen* 376 (AAU, NY); E side of Puyo, 25 Sep 1974, *Hudson* 811 (MO); Toñampari, 400-500 m, 14 Aug 1980, *Jaramillo & Coello* 3502 (AAU, MO); Tzapino, 400-500 m, 16 Aug 1980, *Jaramillo* 3587 (AAU); Montalvo, 250 m, 17-19 May 1979, *Lojtnant & Molau* 13340 (AAU); Colonia Jativa, 15 km from Mera, 4 Jul 1968, *Lugo* 102 (AAU, F, GB); Motolo, 11 Mar 1969, *Lugo* 679 (GB); Colonia Alvarez Miño, 6 km from Mera, 19 Mar 1969, *Lugo* 835 (AAU, GB); Mera, 1100 m, 27 Apr 1971, *Lugo* 1873 (AAU, MO, GB); Pindo, 6 km E of Mera, 15 Jun 1972, *Lugo* 2389 (AAU, GB); Colonia 24 de Mayo, 27 Jun 1972, *Lugo* 2468 (AAU, GB, MO); Cushillo Urco, 8 km N of Puerto Sarayacu, 6 Oct 1974, *Lugo* 3916 (AAU, GB); Parayacu, 10 km E of Canelos, 8 Nov 1974, *Lugo* 4566 (AAU, MO); 12 km N of Puyo on Puerto Napo rd., 3 Dec 1974, *Lugo* 4727 (AAU, GB); El Porvenir, 5 km N of Puyopungu, 17 Sep 1976, *Lugo* 4883 (AAU, GB, NY); Pacayacu on Rio Bobonaza, 16 km NW of Sarayacu, 10 Aug 1979, *Lugo* 5221 (GB); Sarayacu on the Río Bobonaza, 14 Mar 1979, *Lugo* 5398 (GB); Sarayaquillo, 5 km N of Sarayacu, 16 Aug 1979, *Lugo* 5434 (GB, NY); Arajuno, 3 Sep 1979, *Lugo* 5767 (GB, NY); Tzapino, 420 m, 25 May 1976, *Oldeman & Arevalo* 74 (NY, QCA); Rio Bobonaza between Cachitama and outlet of Rio Bufeo, 300 m, 19 Jul 1980, *Ollgaard et al.* 34683 (AAU); Montalvo on the Rio Bobonaza, 300-350 m, 28 Jul 1980, *Ollgaard et al.* 35504 (AAU); 6.5 km from Puyo, 17 Feb 1953, *Prescott* 411 (NY; DS sheet of this number is *C. papillosus*); 4 km E of Puyo, 16 Feb 1953, *Prescott* 454 (NY); nr. Puyo, 17 Feb 1953, *Prescott* 876 (DS); 8 km W of Mera, 1150-1200 m, 15 Sep 1933, *Schimpff* 1094 (B); Puyo, 750-1000 m, Sep 1939, *Skutch* 4553 (A, K, NY); Mera, 1150 m, 7 Jun 1985, *Stein* 3000 (AAU, MO, NY, QCA, QCNE, US); new rd. to Río Bobonaza, leaving Puyo-Macas rd. at Km 15, 1050 m, 8 Jun 1985, *Stein* 3014 (MO, NY, QCA, QCNE, US); km 31 on

Puyo-Puerto Napo rd., 1000 m, 7 Jun 1985, *Stein* 3019 (MO-2 sheets); side rd. off Puyo-Puerto Napo rd. at km 35, 100-1050 m, 9 Jun 1985, *Stein* 3033 (MO-2 sheets); trail towards Colonia 24 de Mayo, 9 km N of Puyo, 1050 m, 3 Jul 1985, *Stein & Tucker* 3126 (MO, QCA, QCNE, US).

PERU. Amazonas: Quebrada Sasa, Río Cenepa, 270 m, 30 May 1973, *Ancuash* 499 (GH, MO); Quebrada Kachaig, Río Cenepa, 11 Jun 1973, *Ancuash* 620 (MO); Quebrada Wampusik entsa, 250 m, 5 Aug 1974, *Ancuash* 719 (GH, MO); Ridge 7 km SE of Huampami overlooking Río Cenepa, 300 m, 12 Oct 1972, *Berlin* 260 (MO); trail E of Huampami to Shaim, 300-525 m, 1 Aug 1974, *Berlin* 1915 (MO); Caterpiza, 65 km N of Pinglo, Río Santiago Valley, 180 m, 27 Aug 1979, *Huashikat* 207 (MO), 24 Mar 1980, *Huashikat* 2340 (MO); Kasu, Río Numpatkin, 350 m, 10 Mar 1973, *Kayap* 533 (MO); Quebrada de apigkagentsa, Río Cenepa, 215 m, 9 Apr 1973, *Kayap* 608 (MO); Huampami, 250 m, 29 Jul 1974, *Kayap* 1356 (MO); left bank of Río Marañon above Cascadas de Mayasi, 425-500 m, 12 Sep 1962, *Wurdack* 1956 (MICH, NY, US, USM). Loreto: Andoas, Río Pastaza nr. Ecuador border, 210 m, 15 Aug 1980, *Gentry et al.* 29812 (MO); between Yurimaguas and Balsapuerto, 135-150 m, 26-31 Aug 1929, *Killip & Smith* 28342 (NY, US, W); Balsapuerto, 150-350 m, 28-30 Aug 1929, *Killip & Smith* 28648 (NY, US, W); Río Macusari, Nuevo Jerusalem, 10-11 Jun 1986, *Lewis et al.* 11035 (MO, USM); Río Huasaga, Washintsa, 16-28 Jun 1986, *Lewis et al.* 11173 (MO, USM), 13-15 Nov 1986, *Lewis et al.* 11795 (MO, USM); Río Sinchiyacu, Puranchim, 25-27 Nov 1986, *Lewis et al.* 12256 (MO, USM), 30 Mar-1 Apr 1987, *Lewis et al.* 13368 (MO, USM); Prov. Alto Amazonas, Capahuari Sur oil camp, 200 m, 25 Mar 1982, *Vasquez et al.* 3040 (MO). San Martín: 36 km NE of Tarapoto, Río Cainarachi, 520-650 m, 22 Jul 1982, *Gentry et al.* 37935 (MO); Convento, trail to Nuevo Lamas, km 68 Tarapato-Yurimaguas rd., 200 m, 10 Aug 1986, *Knapp* 7953 (MO).

Discussion. *Centropogon loretensis* is one of the few species of subgen.

Centropogon that inhabits almost exclusively low elevation Amazonian forests. Along with this characteristic ecological preference, it is recognized by the erect usually shrubby habit, the large, leathery, mostly oblong or obovate leaves, the erect, elongating, racemose inflorescences with oblong or elliptic bracts about as long as the pedicels, the abruptly curving campylobotrous corolla, and the generally recurved or reflexed sepal tips.

Three discernable morphological groups exist within this species, which are detailed below. Because these forms intergrade extensively, however, I do not consider them worthy of formal recognition.

Group 1: Ecuadorean populations in the eastern portion of the species range, at low elevations from 200-500 m, generally have the largest and most robust plants.

These plants have the longest corollas and long sepal lobes with strongly recurved tips.

Group 2: At higher elevations along the Andean foothills of central Ecuador the size of the sepals progressively becomes shorter and the sepal tips remain erect. In these regions, where the species reaches its maximum elevations of 900-1100 m, populations are also characterized by a relatively short (ca. 2 mm long) and truncate antheridial scale and less-elongate, often sub-corymbose inflorescences. The corollas are often shorter and stouter than in Group 1 with the tube narrowest just below the throat, rather than above the nectar chamber.

Group 3: Collections from northern Peru, particularly from the region of the Rio Marañon and Rio Santiago, are characterized by somewhat shorter and more slender corollas, which according to label information are more frequently reddish (even pinkish?) rather than orangish. Although elsewhere anther tubes are consistently 9-10 mm long, in this region are only ca. 8 mm long.

The specimens here assigned to *Centropogon loretensis* have had a checkered taxonomic past, probably owing to the great variation found in the species. Wimmer (1943) included one Ecuadorean collection (Schimpff 1904) under his *C. colombiensis*, retained the Peruvian type specimen (Tessmann 3906) under *C. loretensis*, and later annotated still others (e.g., Killip & Smith 28342, 28648, and Ewan 16742) as *C. planchonis*. Jeppesen (1981), probably relying on Wimmer's determination of the Schimpff specimen, treated all Ecuadorean *C. loretensis* as *C. colombiensis*. As discussed elsewhere, I regard *C. colombiensis* as a synonym of *C. curvatus*, which in turn I regard as distinct from *C. loretensis* (see below). *Centropogon planchonis* is completely unrelated to this group, being a synonym of *C. solanifolius* in sect. *Grandes*.

Because the corolla morphology of *C. loretensis* is of the typical campylobotrous form with an abruptly curved and ampliate throat, an indication of habit is sometimes necessary to differentiate collections of *C. loretensis* (particularly those with only immature inflorescences and short sepals) from *C. granulosus*, a highly variable vining species with pendent, upturned inflorescences. There is little overlap in the ecological distribution of these two species; where the two are found in the same general region, *C. granulosus* is usually at higher elevations than *C. loretensis* and is completely absent from the lowland Amazonian forests of eastern Ecuador where *C. loretensis* is most abundant.

A more troublesome taxonomic problem is the relationship between *C. loretensis* and *C. curvatus*, both of which are erect and shrubby. *Centropogon curvatus* is a species centered in the highlands of southern and central Colombia and occurs sporadically in northern and central Ecuador. In addition to an abruptly curving campylobotrous corolla, it shares with *C. loretensis* such features as an erect habit, often coriaceous, obovate leaves, and an erect, terminal inflorescence with a scaberulous rachis. The differences between these two species are summarized in Table 17. These differences

include the length of the inflorescence (sub-corymbose and not elongating in *C. curvatus*; racemose and usually elongating in *C. loretensis*), the anther tube size and vestiture (7-8 mm long and short purple-pilose in the dorsal connectives in *C. curvatus*; 9-10 mm long and long white-pilose, normally in both ventral and dorsal connectives in *C. loretensis*), and the hypanthium and sepal color (often tinged deep maroon in *C. curvatus*; green in *C. loretensis*). The two species are also separated from each other by their altitudinal ranges and habitat preferences. *Centropogon curvatus* occurs in montane forest from 1500-2300 m, while *C. loretensis* occupies lowland to premontane forests from 200-1100 m. The most problematic region for differentiating these two species is central Ecuador where some populations of *C. loretensis*, belonging to the morphological Group 2 discussed above, resemble phases of *C. curvatus* in having short completely erect sepals, little-elongate subcorymbose inflorescences, and stout corollas. Some specimens from mid-elevations in this region (1100-1300 m) are only referred to one or the other species with difficulty.

Vernacular names and local uses. Ecuador. Pastaza: "Cresta de gallo." Napo: "Uttetsuttetto'cho" (Cofán language: Cerón 280); the ground flowers are reported to be mixed in dog food to make puppies strong. "Dumbiqui sulima aula," (Irvine & Jipa 1076), meaning: toucan "sulima" grandmother. Reportedly used to cure infected sores, the leaves are pounded, wrapped in leaves, and heated over a fire. The hot poultice is applied to the sores. The collector notes, however, that it is not clear whether this remedy applies to this plant (called toucan sulima grandmother) or to the "true" toucan sulima.

Peru. Loreto: "pakupkus" (Achual Jívaro: Lewis 11795); "jempetsetsa mukuntairi," (Achual Jívaro: Lewis 13368); "uyanchi tsukankari" (Huambisa: Huashikat 2340); "iyanchi tsukagkari" (Huashikat 207). "Ujik kuntutkam" (Ancuash 620).

29. *Centropogon amplicorollinus* (F. Wimmer) B. A. Stein, comb. et stat. nov.

Centropogon planchonis A. Zahlbruckner var. *amplicorollinus* F. Wimmer, Pflanzenreich IV. 276b: 184. 1943. Types. Peru. Loreto: Pebas on the Amazon, Jul 1929, Williams 1904 (lectotype here designated, F; isolectotype, W), 1695 (syntype, F), 1788 (syntypes, F, W), 1798 (syntype, F).

Erect herb to subshrub 0.7-2 m tall; stems glabrescent beneath, increasingly hirsutulous or scaberulous above. Leaves narrowly elliptic to lanceolate, (15-)20-30 x 5-8.5 cm, apex acuminate to attenuate, base cuneate, margins crenulate to obtusely serrulate with small callosities either at apex of teeth or in sinuses of crenulations, 2-3 such callosities per cm; lamina fleshy when fresh, drying chartaceous to membranaceous, adaxial surface dark green, glabrous, abaxial surface often paler, glabrous or minutely hirtellous to minutely muricate on major veins; secondary veins 8-11, arcuately ascending, conspicuously raised on adaxial surface; petioles 5-20 mm long, glabrous. Inflorescence an erect, bracteate, terminal raceme, mostly less than 10 cm long but occasionally elongating to 25 cm, the flowers congested apically, internodes elongating to 5-10 mm basally, the rachis hirtellous or scaberulous with stiff, conical, tawny or translucent trichomes, these occasionally multicellular, sometimes subtended by a peduncle 5-10 cm long; bracts persistent, narrowly oblong to narrowly elliptic, mostly 20-35 x 8-10 mm, equalling or longer than the subtended pedicels, apex acute to acuminate, base acute to cuneate, sessile, margins serrulate, both surfaces glabrous or sparsely hirtellous; pedicels erect at anthesis, drooping with age, 10-20 mm long, hirtellous, bracteoles basal to subbasal, subulate, 1-2 mm long. Flowers very large, 50-60 mm long; hypanthium hemispheric, 5-6 x 6-7 mm, minutely hirtellous, intersepalar nectaries present; sepals erect but often with recurved or reflexed tips, narrowly triangular, 6-7 x 1.5 mm, serrulate, glabrescent or sparsely hirtellous, sinuses planar to

rounded; corolla "carmine pink" (*Plowman 7185*), the tissue thin and drying membranaceous, minutely hirtellous with short, collapsed conical trichomes; corolla tube infundibular, 40-45 mm long, 5-6 mm wide at base gradually dilating to 15-17 mm wide at throat, sometimes slightly contracted at base of lobes, the throat not well differentiated from basal portion of tube, gently curving ca. 15-30°; dorsal lobes apparently spreading or recurved, 12-13 x ca. 6 mm, lateral lobes asymmetrically deltoid, 5-7 x 5-6 mm with acuminate, decurved tips, ventral lobe deltoid, ca. 5 mm long, with an acute, deflexed tip; androecium 48-55 mm long, barely exserted from corolla, or completely covered by non-reflexed corolla lobes; filament tube 40-48 mm long, pilose at summit, otherwise glabrous, adnate to corolla ca. 6 mm above base, usually completely included in corolla tube; anther tube 7 mm long, densely long-pilose in dorsal and ventral connectives with white trichomes 1-2 mm long, antheridial scale 2-2.5 mm long; style exserted 0-2 m from corolla, stigma ca. 2.5 mm in diam. Fruit obloid, to 10 x 15 mm, nectar chamber persistent; seeds widely elliptic, rounded, or angular, 0.8-0.95 mm long.

Distribution. A rare understory herb of lowland tropical forest, known only from the region along the Amazon River from Iquitos, Peru (particularly around Pebas) to Puerto Nariño, Colombia at 100-150 m.

Typification. In the protologue of *C. planchonis* var. *amplicorollinus*, Wimmer (1943) cited four collections made by Williams but did not designate a holotype. I have selected the F sheet of *Williams 1904* as the lectotype because it is the most complete specimen available and because Wimmer clearly studied this sheet as evidenced by his annotations and the presence of a duplicate of the same number at W.

Additional specimens examined. COLOMBIA. Amazonas: Trail E of Puerto Nariño, Río Loreto-Yacu, 3 Aug 1972, *Glenboski C-8* (COL); Puerto Nariño, 24 Jul 1965, *Lozano et al. 582* (COL); Altura de Loretoyacu, 30 minutes walk from Puerto Nariño on trail to Putumayo, August 1964, *Raffauf 101* (COL).

PERU. Loreto: Guarnición Pijuayal, nr. Pebas, 3 hours walk behind military base, 130 m, 7 Sep 1978, *Diaz et al. 549* (MO); Río Ampiyacu, trail from Pebas to Corutú, 3 May 1977, *Plowman et al. 7185* (GH); trail from Pebas toward Corutú, 140 m, 30 Jan 1987, *Stein et al. 3967* (MO); Nauta-Iquitos rd., 4°29'S, 73°35'W, 150 m, 17 Jul 1981, *Vásquez 2247* (MO); Pebas on the Amazon, Jul 1929, *Williams 1695* (F), 1788 (F, W), 1798 (F).

Discussion. *Centropogon amplicorollinus* is the only species in subgen. *Centropogon* that is entirely restricted to lowland tropical forest. The species is distinctive in its erect, elongating terminal inflorescence with persistent bracts and its extremely ampiate corolla throat, which is among the widest found in the subgenus. The gently curving corolla is reminiscent of *C. cornutus*, a rather common axillary-flowered lowland species, but *C. amplicorollinus* is easily distinguished from that axillary-flowered species, by its erect habit, terminal bracteate inflorescence, erect (rather than patent) sepals, short and subulate (rather than long and linear) bracteoles, and consistently larger leaves.

The affinities of *C. amplicorollinus* are probably with *C. loretensis*, another species of lowland forests, which is distributed along the base of the Andes from northeastern Peru to southern Colombia. *Centropogon amplicorollinus* agrees quite well with that species in overall habit, in inflorescence structure and indument, in the long-pilose dorsal and ventral anther connectives, and in the erect sepals with recurved tips. In corolla color and texture, and in leaf shape and texture it most closely approaches the

northeastern Peruvian form of *C. loretensis*. It differs from *C. loretensis* most conspicuously in the gently curving and gradually flanged corolla, rather than abruptly ampliate and sharply curved corolla found in that species. Although *C. loretensis* often occurs at low elevations, it is not found as far east as Iquitos, perhaps constrained by the distribution of its presumed sicklebill hummingbird pollinators, which do not range that far into the Amazon basin. It is possible that *C. amplicorollinus* has been derived directly from a *C. loretensis*-like ancestor. Because sicklebill hummingbirds are not present in the the lowland region where *C. amplicorollinus* is found, following initial establishment of this species in this area a shift in corolla morphology may have occurred enabling non-sicklebill hummingbirds to visit the flowers and effect pollination. Because these birds would have less abruptly curved bills than the highly specialized sicklebills, the consequent shift in corolla morphology would be towards the more gradually curved corolla now present in this species. Another possibility is that *C. amplicorollinus* is the product of hybridization between a *C. loretensis*-like ancestor and *C. cornutus*, with which it shares a similar corolla color and texture. Notably, Williams collected both species at the type locality of *C. amplicorollinus*.

Wimmer's (1943) placement of *C. amplicorollinus* as a variety of *C. planchonis* was certainly in error, since *C. planchonis* is a synonym of *C. solanifolius*, and that name was based on a collection from montane forests of the Cordillera Central of Colombia.

30. *Centropogon latifolius* F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 7. 1935.

Type: Peru. Pasco: Pichis trail, Porvenir, 1500-1900 m, 3-4 Jul 1929, Killip & Smith 25918 (holotype, US; isotype, NY).

Erect herbs to subshrubs 0.5-1.5 m tall, usually single-stemmed; stems glabrous, to 1 cm in diam. at base; latex white. Leaves narrowly elliptic to elliptic, occasionally oblong, 10-20(-25) x 4.5-8 mm, apex attenuate or occasionally mucronate, base cuneate or rarely rounded, margins serrulate to crenulate with 3-5 callose-tipped teeth per cm; lamina glabrous, relatively thick and fleshy when fresh, drying coriaceous, adaxial surface dark green, abaxial surface paler or tinged purplish; secondary veins (7-)9-11, arcuate-ascending, occasionally forming weak intramarginal loops; petioles absent or to 5 mm long. Inflorescence an erect, short-bracteate, terminal, subcapitiate raceme, elongating to 7 cm, the flowers congested and numerous (to 15 flowers and buds), the rachis hirtellous or occasionally glabrescent, subtended by a mostly bractless, elongate peduncle 5-15 cm long, the peduncle, along with pedicels and hypanthium sometimes tinged purple; bracts usually persistent, lanceolate, 4-7(-9) x 3-6 mm, glabrous; pedicels erect at anthesis, drooping with age, 20-25 mm long, hirtellous to scaberulous, the trichomes rarely multicellular, bracteoles basal to subbasal, subulate, 0.5-1 mm long.

Flowers ca. 40 mm long, often very slender in dried specimens; hypanthium hemispheric, 3-5 x 4-6(-7) mm, moderately ribbed when fresh, glabrescent to hirtellous, intersepalar nectaries present; sepals erect, triangular to deltoid, (1-)2-4 x (1-)1.5-2 mm, glabrescent to hirtellous; corolla reddish-orange, the lobes and inside of throat yellowish-orange, sparsely to densely minutely hirtellous; corolla tube 26-32 mm long, the basal portion slender or occasionally rather thick, 3-6(-7) mm wide at base narrowing slightly above nectar chamber and then expanding gradually to base of throat, the throat slightly to moderately ampliate, 7-9 mm wide when dried, but when fresh to 12 mm wide, curved

ca. 50°; dorsal lobes laterally recurved, 10–12 mm long, lateral lobes deltoid-falcate, 6–7 mm long, ventral lobe 4–6 mm long with an acute, deflexed tip; androecium 35–42 mm long; filament tube 28–34 mm long, ventrally flattened and 2–2.5 mm wide when fresh, yellowish throughout, glabrous or rarely short-pilose at summit, adnate to corolla ca. 6 mm above base, exserted ca. 4 mm from corolla tube; anther tube 6–7 mm long, tan to yellow, dorsal connectives long-pilose, especially apically, with white trichomes, antheridial scale 2–2.5 mm long; style exserted from anther tube 0–1 mm, stigma ca. 3 mm in diam. Fruit oblate, to 10 × 12–15 mm, nectar chamber persistent; seeds suborbicular, oblong to ovate, 0.6–0.7 mm long.

Distribution. A rare cloud forest herb known only from the Cordillera Azul and Cordillera de Yanachaga in Huánuco and Pasco Departments of central Peru at 1400–1900 m.

Additional specimens examined. PERU. Huánuco: La Divisora, 59 km from Tingo María on rd. to Pucallpa, 1600 m, 17 Nov 1949–15 Jan 1950, Allard 21232 (US), 1540 m, Allard 21302 (US); Cordillera Azul, La Divisora, 1620–1760 m, 10 Aug 1980, Gentry et al. 29562 (MO), 1500–1600 m, 3 Jun 1983, Gentry et al. 41450 (MO); La Divisora, rd. from Pumahuasi to the summit, 1600–1660 m, 26 Jun 1978, Plowman & Schunke 7376 (F, MICH, U); La Divisora, 1500–1600 m, 8 Feb 1978, Schunke 9866 (MO); La Divisora, 1600–1700 m, 18 Jan 1987, Stein et al. 3895 (MO, US, USM).

Discussion. *Centropogon latifolius* appears to be closely related to, and partially co-occurs with *C. sciaphilus* (see discussion of features distinguishing these two species under *C. sciaphilus*). The corolla morphology of this species place it within the *C. granulosus* species complex, but within that group it is well-distinguished by the erect habit, the elongate peduncles, short sepals, and serrulate to crenulate leaves. It is known from only two localities, the fairly well-collected low-elevation cloud forest of La

Divisora in the Cordillera Azul, an isolated front range of the Andes, and the type locality not far to the south in the Cordillera de Yanachaga. These two populations appear to differ primarily in leaf size and shape: the single collection from the Cordillera de Yanachaga has broadly elliptic to oblong leaves with mucronate tips (hence the epithet "latifolius"), whereas all La Divisora plants examined have narrowly elliptic to elliptic leaves with attenuate apices. Given that only two specimens are available of the typical form, the common occurrence of intrapopulational variability in leaf shape among other species of subgenus *Centropogon*, and the general agreement of the two populations on other characters, I would not consider the La Divisora population to be worthy of special taxonomic recognition.

An additional collection from the Cordillera de Yanachaga, Gentry & Smith 35993, appears to be related to *C. latifolius* but may represent a new species. It shares with *C. latifolius* the erect herbaceous habit, the general corolla form, and short sepals. However, it lacks the distinctive peduncle, the leaves are considerably smaller, the inflorescence rachis, pedicels, and to some extent underleaf veins are densely covered with stiff multicellular tawny trichomes, the anther tube is glabrous, and the corolla has unusual bulbous protrusions at the filament attachments. Unfortunately, only a single specimen of this form exists and additional collections from this very interesting region are needed to ascertain the range of variability found in *C. latifolius* and to determine if this unusual collection is truly distinct.

31. *Centropogon sciaphilus* A. Zahlbruckner, Ann. K. K. Naturhist. Hofmus. 6: 435.

1891. Type. Peru. "Peruvia subandina. In sylvis maxime obscuris et valde humidis," Jan 1830, Poeppig 1651 (holotype, W, photo F-neg. 30966).

Centropogon ciliatus Gleason, Bull. Torrey Bot. Club 52: 58, pl. 3, fig. 9. 1925. Type. Peru. Huánuco: Muña, 2100 m, 23 May-4 Jun 1923, Macbride 4028 (holotype, NY; isotypes, BM, F, photo CM-neg. 50038).

Erect herbs to subshrubs 0.3-1(-1.2) m tall, entirely glabrous, single-stemmed, stems 4-6 mm in diam. near base; latex opalescent. Leaves very narrowly elliptic to elliptic, occasionally oblanceolate, 12-25(-30) x (2.5-)5-10 cm, apex acute to attenuate, base acute to cuneate, margins conspicuously fimbriate-serrate, the teeth with terminal callosities or rarely the teeth merely exserted-callosities, usually ca. 6 large teeth per cm, each 1-2.5(-3) mm long, separated by 0-4 smaller teeth, 0.5-1 mm long; lamina thin but fleshy when fresh, drying chartaceous to membranaceous, uniformly dark green or mottled with green or white spots, abaxial surface occasionally tinged purple; secondary veins 9-14, arcuate-ascending, occasionally forming loops with superadjacent secondaries; petioles 5-10(-25) mm long or less commonly absent. Inflorescence an erect, terminal, short-bracteate, subcapitate raceme with congested flowers, elongating to 2-5(-8) cm and subtended by a bractless peduncle (3-)5-20 cm long; bracts persistent, lanceolate to ovate, the lowermost to 40 x 20 mm, the medial ones 10-15(-20) x 4-8(-10) mm, margins coarsely serrate to fimbriate-serrate; pedicels erect at anthesis, recurved in fruit, 10-25 mm long, bracteoles basal to subbasal, linear to narrowly lanceolate with toothed margins, 3-5(-7) mm long. Flowers 40-50 mm long; hypanthium rounded-rhomboid to turbinate in shape, widest at mid-point, 4-5 x 4-6 mm, prominently 5-ribbed, intersepalar nectaries not seen; sepals erect or with slightly spreading tips, lanceolate to ligulate, often widest at mid-point, 6-10 x 1.5-2.5 mm, coarsely serrate

with 3-6 teeth or rarely entire; corolla bright red to red-orange, the lobes either same color as tube or orange to yellow, the tissue thin, glabrous to minutely puberulent; corolla tube 30-35 mm long, basal portion of tube cylindric and straight, 5-7 mm wide at base narrowing to 3-4 mm wide at point of filament adnation, widening gradually to base of throat, the throat moderately ampliate, ca. 10(-14) mm wide, gradually to rather abruptly curving 40-60°; dorsal lobes spreading to recurved, ca. 8 x 4 mm, falcate, lateral lobes deltoid, ca. 5 mm long, with acuminate, decurved tips, ventral lobe ca. 5 mm long, deltoid with an acute, deflexed tip; androecium 40-45 mm long; filament tube 35-40 mm long, ventrally flattened and ca. 2-2.5 mm wide when fresh, glabrous, pale yellow, adnate to corolla 4-6 mm above base, exserted from corolla 0-4 mm; anther tube 5-7 mm long, thecae dark grey, connectives purplish, the dorsal ones sparsely to densely pilose with white or purple pigmented trichomes, antheridial scale narrowly triangular, 2-3 mm long; style little-exserted from anther tube, stigma ca. 2.5-3 mm in diam. Fruit spheroidal, ca. 15 mm in diam.; seeds elliptic to oblong, often angular, relatively large, 0.8-1.1 mm long.

Distribution. An infrequent understory herb of mid-elevation and lowland tropical forest and occasionally in low elevation cloud forest, at 200-1500 m. It is found along the eastern Andean slope and foothills in a very limited area of Central Peru, from the upper Huallaga Valley of San Martin Department in the north (ca. 9°S latitude) south to the Chanchamayo region in Junín Department (ca. 11°S) .

Additional specimens examined. PERU. Huánuco: Cueva de las Pavas, nr. Tingo Maria, 700-800 m, 25 Feb 1947, Ferreyra 1607 (GH); La Divisora, Tingo Maria-Pucallpa rd. nr. Loreto [Ucayali] border, 1150-1250 m, 29 Mar 1977, Gentry et al. 18848 (MO, USM); Don Diogenes', woods on high ground SE of house, 29 Jun 1960, Mathias &

Taylor 5046 (F); vicinity of Tingo María, cliffs above Rio Monzón, 23 Jun 1961, *Mathias & Taylor* 5346 (F, USM); Casapí, *Matthews* 189 (K); left bank of Rio Monzón, W of Tingo María, 700 m, 12 Apr 1976, *Plowman* 5891 (GH, USM); Cucharas, 400 m, 2 Feb 1954, *Woytkowski* 1080 (USM); Cucharas, 500 m, 11 Feb 1954, *Woytkoski* 1123 (USM); Cucharas, 500 m, 14 Mar 1954, *Woytkoski* 1181 (USM). Junín: Chilpes, 8 km S of Vitoc, trail overlooking Rio Tulumayo, 1420-1700 m, 8 Feb 1983, *Gentry et al.* 40192 (MO); Rio Tulumayo Valley, trail above Chilpes (9 km above Vitoc), 1700 m, 19 Mar 1985, *Stein & Todzia* 2429 (MO); Prov. Tarma, Agua Dulce, 1800 m, 7 Mar 1948, *Woytkowski* 35424 p.p.(MO); Prov. Tarma, Agua Dulce, 2600 m, 12 Mar 1948, *Woytkowski sub Goodspeed* 35458 (UC). Pasco: Serranía de San Matías, W slope, E of Loma Linda, 400-700 m, 15 Jun 1983, *Gentry et al.* 42008 (MO); La Esperanza, Rio Pichis 1 hr. below Puerto Bermudez, 200 m, 17 Jun 1983, *Gentry et al.* 42008 (MO); Pichis trail, between Ayupiyú and Santa Rosa, 625 m, 28 Jun-8 Jul 1929, *Killip & Smith* 26146 (NY, US); Puerto Bermudez, 375 m, 14-17 Jul 1929, *Killip & Smith* 26581 (NY, US, W); Puerto Bermudez, 375 m, 14-17 Jul 1929, *Killip & Smith* 26672 (NY, US, W). San Martín: Uchiza Dist., border of quebrada E of Nuevo Progresso (Rio Hullaga), 17 Jun 1969, *Schunke* 3141 (F, COL); Tocache Nuevo Dist., Puerto Pizana, right margin of Rio Huallaga, 350-400 m, 15 Jun 1974, *Schunke* 6962 (GH, MO). Ucayali: Summit of La Divisora, 1500-1600 m, 3 Feb 1978, *Schunke* 9865 (MO).

Discussion. *Centropogon sciaphilus* is easily recognized by the fimbriate leaf margins and sepals and the well-developed peduncle topped by a short-bracteate inflorescence. Although the usual condition in the species is long-fimbriate leaf margins, considerable variation occurs, with at least some collections completely lacking the fimbria. In these instances, however, the callosities that normally are found at the tip of the fimbria are still present, forming a denticulately exserted leaf margin.

Fimbriate leaf margins are also found in the central and southern Peruvian *C. roseus*, which exhibits a similar latitude in the degree of marginal protrusions. That species, a member of sect. *Amplifolii*, is easily distinguished from *C. sciaphilus* by its gamosepalous calyx and lack of an elongate peduncle.

Centropogon sciaphilus appears to be closely related to another central Peruvian species *C. latifolius*, with which it shares a well-developed peduncle and a similar corolla morphology. That species differs, however, in having crenate-denticulate leaf margins, shorter, entire sepals, smaller bracteoles, generally more pubescent inflorescence parts (rachis, pedicel, and corolla), and red-orange and yellow bicolored corollas. The two species occur sympatrically in the Cordillera Azul at La Divisora. Given the seemingly close relationship between these two species, I include *C. sciaphilus* in sect. *Campylobotrys*, although it is rather atypical for that section as a whole. It does, however, have the ventrally flattened filament tube that is characteristic of that group.

32. *Centropogon yungasensis* Britton, Bull. Torrey Bot. Club 19: 371-372. 1892. Type: Bolivia. La Paz: Yungas, 1200 [1800?] m, Rusby 642 (holotype, NY; isotypes, NY, US, W).

Centropogon yungasensis Britton var. *angustior* A. Zahlbruckner, Bot. Jahrb. Syst. 37: 451. 1906. Type: Peru. Junin: Prov. Tarma, mountains of Yanangu, E of Huacapistana, 2100-2200 m, 12 Jan 1903, Weberbauer 2131 (holotype, B; isotype, W).

Centropogon ostrinus F. Wimmer, Report. Spec. Nov. Regni Veg. 29: 67, pl. 115, fig. 9. 1931. Type: Peru. Maclean s.n. (holotype, K).

Scendent or sprawling herbaceous vines to 4 m long; stems glabrous, rarely hirtellous or scaberulous above, much branched; roots basal or occasionally adventitious along stem. Leaves variable in shape, mostly elliptic, but from very narrowly elliptic or lanceolate to widely ovate, (5-)7-12(-15) x (1.5-)2.5-4(-5) cm, apex attenuate to acute, base mostly cuneate, occasionally acute to obtuse, margins crenulate to serrulate with 3-4 glandular callosities per cm; lamina fleshy and firm when fresh, drying coriaceous, adaxial surface dark green, glabrous or rarely sparsely hirtellous, abaxial surface paler, glabrous or occasionally hirtellous; secondary veins few, 4-6, arcuate-ascending or in narrower leaves acutely ascending and almost straight, the higher order venation embedded in lamina; petioles 5-20 mm long, occasionally fleshy and flattening to 2 mm wide when dry, glabrous or hirtellous. Inflorescence horizontal or somewhat pendently-upturned, short-bracteate racemes, terminal, or occasionally several short lateral racemes along the same branch, generally less than 5 cm long, but rarely elongating to 10 cm, floral internodes congested, mostly less than 5 mm long, sometimes lax and to 30 mm, the rachis glabrescent or rarely densely hirtellous with stiff, conical or narrowly triangular, multicellular, tawny trichomes to 0.2 mm long, an elongate and pendent

peduncle sometimes subtending the terminal racemes; bracts often caducous, similar in shape, texture, and indument to foliage leaves but much reduced, generally less than 10 mm long; pedicels assurgent at anthesis, drooping with age, often elongate, (20-)30-60 mm long, slender or rarely fleshy and flattening to 2 mm wide when dry, indument as on inflorescence rachis, bracteoles sub-basal, mostly subulate and less than 1 mm long. Flowers (40-)50-65 mm long (including reflexed sepals), hypanthium and sepals often tinged dark purple; hypanthium hemispheric, 3-5 x 5-7 mm, smooth or slightly 10-ribbed at anthesis, glabrous to densely hirtellous, intersepalar nectaries occasionally present; sepals strictly reflexed to arcuately recurved, very rarely only spreading to divaricate, ligulate to linear, usually exceeding the hypanthium in length, (4-)7-12(-15) x 1-2 mm, acute to obtuse at apex, entire to gland-denticulate, glabrescent to densely hirtellous, sinuses acute to planar; corolla bright reddish-orange or orange, with orange or yellowish-orange lobes, glabrescent, or usually hirtellous with scattered, stiff, conical or triangular trichomes; corolla usually slightly sigmoid, the tube (22-)27-32 mm long, the basal portion cylindric, 4-6 mm wide at base narrowing to 2.5-4 mm wide at point of filament attachment, then gradually expanding to base of throat, the throat moderately ampliate, 9-12 mm wide, moderately to sharply curved ca. 45-60°; dorsal lobes laterally recurved to recoiled at anthesis, 8-10 x 4-5 mm, lateral lobes triangular, 7-8 x ca. 3 mm, with decurved tips, ventral lobe triangular 5-7 x ca. 4 mm, with a deflexed, acute tip; androecium (35-)40-50 mm long; filament tube (30-)35-42 mm long, ventrally flattened, orangish-yellow, except purplish where exserted, glabrous throughout, adnate to corolla (4-)5-6 mm above base, exserted 6-8 mm from corolla tube; anther tube (5-)6(-7) mm long, thecae gray, connectives reddish-purple, the dorsal ones short-pilose either apically or throughout with purple trichomes, antheridial scale 2-2.5 mm long; style exserted 0-3 mm from anther tube, stigma ca. 3 mm in diam.

Fruit spherical to oblate, to 10 x 17 mm, prominently 10-ribbed and verrucose, thickened nectar chamber persistent; seeds elliptic to oblong, ca. 0.8 mm long.

Distribution: A locally common upper elevation cloud forest vine, found from central Peru to central Bolivia mostly at 2100-2700 m.

Additional specimens examined: PERU. Cuzco: Cordillera Vilcabamba, 12°38'S, 73°36'W, 1980 m, 30 Jun 1968, *Dudley* 10643 (F, NA), 1 Jul 1968, *Dudley* 10671 (NA); Pillahuata, Cerro de Cusilluyoc, 2100-2300 m, 3-6 May 1925, *Pennell* 13957 (F, GH, NY); nr. Rio Yanamayo below Pillahuata, 2000-2300 m, 4-5 May 1925, *Pennell* 14055 (F, GH, NY); Kosñipata Valley, rd. from Pillahuata to Patria, 2050 m, 4 Feb 1975, *Plowman & Davis* 4982 (GH); btwn. Yanamayo and Sta. Isabel, Kosñipata Valley, 1500 m, 23-31 Jul 1948, *Scolnik* 850 (MICH); 10-12 km below Pillahuata, 2250 m, 5 Apr 1985, *Stein* 2506 (CUZ, MO, NY, US, USM), 2180 m, *Stein* 2507 (F, MO, NY, US, USM); 5 km below Pillahuata, 2420 m, 7 Apr 1985, *Stein* 2530 (AAU, F, K, MO, US, USM). Huánuco: SW slope of Rio LlullaPichis watershed, Cerros del Sira, 1750 m, 28 Jul 1969, *Dudley* 13384 (NA), 1950 m, 30 Jul 1969, *Dudley* 13484C (NA), 1535 m, 28 Jul 1969, *Wolfe* 12398 (F, NA). Junín: Huacapistana, 2100 m, Oct 1943, *Sandeman* 4562 (K). Pasco: SW of Oxapampa on rd. to María Teresa and Llaupi, 2700 m, 28 Dec 1983, *Foster* 7620 (MO); Cordillera Yanachaga, new rd. from Oxapampa to Villa Rica, 7-9 km E of main rd., 2100-2500 m, 1 Mar 1982, *Gentry & Smith* 35845 (MO); Cordillera Yanachaga, lumber rd. 12 km E of main Oxapampa-Villa Rica rd., 2100-2200 m, 2 Mar 1982, *Gentry & Smith* 35935 (MO); top of Cordillera Yanachaga, 14 km E of main Oxapampa-Villa Rica rd., 2450 m, 2 Mar 1982, *Gentry & Smith* 35962 (MO); La Suiza to San Gotardo on Oxapampa-Cerro de Pasco rd., 2100-2650 m, 19 May 1983, *Smith* 4101 (MO); Río San Alberto, E of Oxapampa, 2550 m, 25 Jul 1984, *Smith & Pretel* 8012

(MO). San Martín: nr. Pajaten ruins, Río Abiseo National Park, 2600-2700 m, 22-23 Jul 1985, Young 1257 (MO); nr. La Playa camp, Río Abiseo National Park, 2600-2700 m, 16 Aug 1985, Young 1467 (MO), 30 Aug 1985, Young 1519 (MO). Ucayali: Margarita, La Divisoria, 1500-1600 m, 14 Aug 1946, Ferreyra 1005 (MICH, US).

BOLIVIA. Cochabamba: Incachaca 80 mi. NE of Cochabamba, 2400 m, 22 Aug 1950, Brooke 6773 (BM, F, NY). La Paz: Coroico, Sep 1894, Bang 2432 (B, BM, F, G-2 sheets, K, MICH, MO, NY, US, W-2 sheets).

Vernacular names. "Col de monte," San Martín Department, Peru.

Discussion. *Centropogon yungasensis* is distinguished by the combination of a horizontal or slightly pendent inflorescence that is upturned at the tip, reflexed sepals that are narrow and elongate and usually exceed the hypanthium in length, and very fleshy leaves with a well-developed aerenchyma layer. This last feature gives the leaves a characteristic coriaceous appearance when dried, with the venation imbedded in the lamina, an unusual character in common with *C. reflexus*, *C. vargasii*, and *C. urubambae*.

The species is very poorly known from Bolivia, from where it was described, and the three collections from that country have atypically short sepals. The collection from the extreme southern part of the species' range in Cochabamba Department (Brooke 6773) also has very short corollas, but still seems best assigned to this species on the basis of the inflorescence structure, overall corolla morphology, anther length and pubescence, and leaf shape and texture. Collections from Junin and Pasco Departments in Peru are also somewhat unusual in being quite pubescent, with larger, more persistent bracts, slightly longer anther tubes, and sepals that are not always strictly reflexed. The

collections from the northern part of the species range in San Martín Department have sepals even less frequently reflexed but exhibit the more usual glabrous condition. The type of *C. ostrinus*, although labeled "Maclean," was probably collected by Matthews. It is very similar to these northern populations and, given Matthews collecting itinerary, may well be from that region.

Centropogon yungasensis appears closely related to *C. granulosus* and probably can be best considered an upper elevation derivative of that species. It generally occupies higher elevations, and where the two overlap there is some evidence for hybridization (see Chapter V). *Centropogon yungasensis* also appears to be related to the three species above-mentioned species (*C. reflexus*, *C. ostrinus*, and *C. urubambae*) that have the derived feature of thickened laminar aerenchyma. In particular, *C. reflexus* and *C. vargasii* may well be direct offshoots from *C. yungasensis*.

33. *Centropogon reflexus* Presl, Prodr. Monogr. Lobel. 49. 1836. Type. Peru. "Peruano montano ororouensis," 1790, *Haenke* 1919 (neotype here designated, F). Fig. 8E.
Centropogon auratus F. Wimmer, Repert. Spec. Nov. Regni Veg. 19: 243. 1924. Type.
 Peru. Huánuco: above Muña, 2400-2500 m, 1 Jul 1913, *Weberbauer* 6716
 (holotype, B; isotypes, B, F, W).

Centropogon rubrovenosus Gleason, Torreya 25: 93. 1925. Type. Peru. Huánuco:
 Huacachi, near Muña, 2000 m, 20 May-1 Jun 1923, *Macbride* 4104 (holotype, F,
 photo F-neg. 58351; isotypes, NY, S).

Suffrutescent vines to 5 m long, scandent or rarely epiphytic; stems numerous and many branched, glabrous; roots basal, or occasionally adventitious along stems; latex opalescent. Leaves ovate to lanceolate, (4-)5-11 x (1.5-)3-4.5 cm, apex acute to attenuate, rarely obtuse, base rounded to acute, margins crenulate to serrulate, 2-4 callosities per cm in sinuses of crenulations or at apex of teeth; lamina thick and fleshy when fresh, drying coriaceous, adaxial surface dark green, glabrous, abaxial surface pale green, often with conspicuous reticulate purple venation or mottled purplish throughout, glabrescent to sparsely pubescent on veins; secondary veins few, 4-6, arcuate-ascending, somewhat impressed adaxially, embedded in fleshy lamina and little-raised abaxially, higher order venation irregularly reticulate and completely embedded in expanded aerenchyma; petioles 5-15 mm long, glabrous to hirtellous. Inflorescence a lax, pendent, short-bracteate, terminal raceme, elongating to 30 cm, the floral internodes mostly less than 2 cm, but to 6 cm basally, the rachis glabrescent or sparsely hirtellous toward apex; bracts persistent, glabrous to hirtellous, especially beneath, sessile, ovate, elliptic or spatulate, mostly 5-10 x 4-7 mm, margins gland-denticulate, the basal bracts occasionally unreduced and resembling vegetative leaves; pedicels acroscopically pendent in bud, reflexed-ascending at anthesis, drooping and twisted with age and in fruit, 3-6

cm long, glabrescent to moderately hirtellous with uni- or multicellular trichomes to 0.5 mm long; bracteoles basal, subulate, 1 mm long or less. Flowers 60-75 mm long, delayed resupinate; hypanthium often tinged maroon, hemispheric, 3-4 x 4-6 mm, slightly ridged, glabrescent to hirtellous, intersepalar nectaries absent; sepals much exceeding the hypanthium, erect to spreading in bud, strictly reflexed at anthesis, ligulate, or rarely linear, sometimes narrowed basally, (6-)10-15 x (1-)2-3(-4) mm, acute to obtuse at apex, irregularly serrulate distally, often undulate and ciliate, pubescence as on pedicels, sinuses rounded to acute; corolla bright orangish-red to orangish-pink, the lobes and inside of throat mostly orangish, glabrous or sparsely covered with minute, flaccid, conical trichomes; corolla tube often somewhat sigmoid, 28-38 mm long, the basal portion cylindric, prominently thickened at base and 5-7 mm wide, narrowing above this to 2-4 mm, then gradually expanding to base of throat, the throat abruptly ampliate, 9-13 mm wide, curved 45-60°; dorsal lobes recurved, 9-11 x 3-4 mm, lateral lobes deltoid to asymmetrically triangular, 5-8 x ca. 3 mm, with attenuate, decurved tips, ventral lobe deltoid, 5-6 mm long, with an acute, deflexed tip; androecium 50-60 mm long, well-exserted from corolla tube; filament tube 45-55 mm long, ventrally flattened and ca. 2.5 mm wide when fresh, pale yellow except reddish-purple where exserted, glabrous throughout, adnate to corolla 7-9 mm from base, exserted from corolla tube 8-10 mm; anther tube 6-7 mm long, thecae grey, connectives purple, the dorsal ones normally short-pilose apically with purple trichomes, antheridal scale 1.5-2.5 mm long; style exserted 0-4 mm from anther tube, stigma 2-3 mm in diam. Fruit broadly ovoid, truncate basally, to 10 x 16 mm, with 10 prominently raised ridges, the surface verrucose, nectar chamber persistent; seeds ovate to elliptic, ca. 0.8 mm long.

Distribution. A locally common cloud forest vine that is restricted to a very limited region of central Peru. It is known exclusively from the Carpish Hills and the area around Muña in Huánuco Department at 2400-2700 m.

Additional specimens examined: PERU. Huánuco: S side of divide between Acomayo and Tingo María, 2860 m, 3 Apr 1984, *Croat* 57838 (MO); Cerro Carpish, just S of tunnel, 2700 m, 7 Nov 1975, *Davidson* 3381 (MO), 16 Nov 1979, *Davidson & Jones* 9199 (MO, NY); Carpish, 2700 m, 11 Nov 1964, *Ferreyra* 16152 (MO); Gloriapampa, 2450 m, *Huapalla Yábar* 2285 (USM); Carpish, 2560-9100 m, 26 Feb 1978, *Luteyn & Lebrón-Luteyn* 5455 (NY), 27 Feb 1978, *Luteyn & Lebrón-Luteyn* 5473 (NY); Huagin, 2500 m, 4 Apr 1948, *Ochoa* 408 (US); Carpish, 8 Feb 1982, *Ochoa* 14540 (US); Muña, 2500-3000 m, May 1863, *Pearce* 151 (BM); Muña, *Pearce* 235 (K); N of Carpish Pass, 2570 m, 6 Dec 1981, *Plowman & Rury* 11110 (DUKE, F, NY); Carpish Hills, 2650 m, 2 Mar 1985, *Stein & Todzia* 2268 (MO, US, USM), 2500 m, *Stein & Todzia* 2272 (F, MO, US, USM), 2600 m, 4 Mar 1985, *Stein & Todzia* 2309 (F, K, MO, NY, US, USM), *Stein & Todzia* 2311 (MO), 2450 m, 15 Jan 1987, *Stein et al.* 3845 (DUKE, F, MO, NY, US, USM); Paty Trail, Carpish Hills, 2400 m, 15 Jan 1987, *Stein et al.* 3873 (MO); Tumanga, 2400 m, 18 Apr 1963, *Woytkowski* 7917 (GH, MO); Saraypampa, 2700 m, 13 Mar 1946, *Woytkowski sub Goodspeed* 34189 (UC, F). Locality unknown: "Columbia," [locality probably in error] *Lobb s.n.* (K).

Typification. The identity of *Centropogon reflexus* has long remained obscure due to the absence of original material of this species. I have searched the herbaria in which Presl's material is located (PR and PRC), but I was unable to locate any material of *C. reflexus*. Fortunately, a Haenke specimen found at F is almost certainly a duplicate of the original collection seen and described by Presl. This specimen, *Haenke*

1919, was not annotated by Presl and now lacks flowers. The very distinctive shape, texture, and purple-reticulation of the leaves, however, eliminates all doubt as to its specific identity. Haenke is known to have collected in the vicinity of Huánuco, where this species is found, and also collected the type of *C. exasperatus* (=*C. hirtus*), another species described by Presl and known only from the same limited area. The majority of Haenke's Peruvian collections were described by Presl (1825-1835) in *Reliquiae Haenkeanae*, but Lobeliaceae was omitted from this treatise, probably because Presl was preparing a separate comprehensive work on that family. In that volume, *Prodromous Monographiae Lobeliacearum*, published in 1836, Presl generally does not cite collectors or collection numbers. Thus, no specific collection is referred to in the protologue of *C. reflexus*, and its locality is given merely as "hab. in Peruvia." Haenke's collection number 1919 must have been seen by Presl, however, since the printed label reads "Reliquiae Haenkeanae, Herbarium Musei Regni Bohemiae," and the writing on the specimen, "Peruano montano ororouensis," is in the hand of one of Presl's assistants (pers. comm., J. Sojak). Furthermore, the specimen agrees with the protologue in all observable details. Although the evidence outlined above convinces me that this specimen is indeed a part of the type collection of this species, I am taking a conservative approach and designating the F sheet of *Haenke 1919* as a neotype rather than lectotype.

Discussion. *Centropogon reflexus* can be easily recognized by the combination of an elongating, pendent inflorescence, reflexed, ligulate sepals that are much longer than the hypanthium, and fleshy leaves with an expanded aerenchyma layer that give the leaves a coriaceous texture when dry. The venation reticulum is usually completely embedded in this thickened layer and is often conspicuously purplish tinged.

Centropogon reflexus appears to be most closely related to *C. yungasensis* and probably

represents a localized derivative from that much more widely distributed species. These two species share a similar corolla morphology, reflexed sepals, and the fleshy leaves described above, but *C. yungasensis* can be distinguished by its horizontal or upturned, rather than strictly pendent, inflorescence, shorter flowers (androecium 40-50 vs. 50-60 mm), and general lack of purple pigmentation on the adaxial leaf surface.

Within the small geographic range of *C. reflexus* some variation occurs in the length and width of the sepals. Plants from the Muña area in general show somewhat shorter and narrower sepals than do those from the much better collected Carpish Hills region. A great deal of intrapopulational variation occurs in the pigmentation of the adaxial leaf surface, with those of some individuals entirely green, others green with purple-pigmented veins, and still others with the underleaves entirely suffused with purple.

34. *Centropogon urubambae* F. Wimmer, Repert. Spec. Nov. Regni. Veg. 38: 7. 1935.

Types. Peru. Cuzco: San Miguel, Urubamba Valley, "monte ñucja," 27 May 1915, Cook & Gilbert 942 (lectotype here designated, US); Valle de Urubamba, 2050 m, Sep., Herrera 2682b (syntype, B n.v., probably destroyed in World War II).

Fig. 8F.

Centropogon urubambae F. Wimmer var. *estrellanus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 8. 1935. Type. Peru. Ayacucho: Estrella, between Huanta and Río Apurimac, 500 m, 8-14 May 1929, Killip & Smith 22643 (holotype, US; isotype, NY).

Centropogon estrellanus (F. Wimmer) F. Wimmer, Pflanzenreich IV. 276b: 192. 1943.

Scandent suffrutescent vines to 5 m or longer, much branched above, generally glabrous throughout; stems to 2 cm in diam. at base; latex white. Leaves often retrorsely distichous, the blades mostly ovate, less often oblong, elliptic, or narrowly ovate, 9-16(-24) x 4.5-7.5(-11) cm, apex obtuse to acuminate, base rounded or occasionally cuneate, margins crenulate to serrulate, very rarely retrorsely serrulate, 2-5 callosities per cm, either at tip of teeth or in sinuses of crenulations; lamina thick and fleshy when fresh with expanded abaxial aerenchyma, drying semi-coriaceous, both surfaces glabrous; secondary veins few, 4-6, widely arcuate-ascending, moderately raised on abaxial surface but the higher order venation completely imbedded in aerenchyma; petioles slender, (0.5-)1-2.5 cm long, glabrous or very rarely sparsely puberulent. Inflorescence a pendent, lax, short-bracteate, terminal raceme, elongating to 1 m, the floral internodes 0.5-3(-5) cm long, inflorescence glabrous or rarely sparsely hirtellous; bracts persistent, narrowly spatulate to linear, 10-20 x 1-2 mm, apex acute to obtuse, base narrowly cuneate, both surfaces glabrous or abaxial surface sparsely to moderately hirtellous, the basal bracts sometimes similar to vegetative leaves; pedicels acroscopic to divaricate in

bud, retrorseously assurgent in flower, arcuate-drooping with age and in fruit, 15-25 mm long, glabrous to hirtellous, bracteoles sub-basal to medial, often retrorse, linear, 1-2 mm long. Flower 45-70 mm long, not resupinate; hypanthium hemispheric, 4-5 x 6-9 mm, 5-ribbed with 2 discrete swellings between each rib when fresh, intersepalar nectaries present; calyx zygomorphic, sepal lobes erect in bud, at anthesis divaricate with upturned tips or occasionally reflexed, linear, 5-8(-10) x 1-1.5 mm, entire to denticulate, sinuses widely planar; corolla pink to magenta, the lobes sometimes paler, whitish within throat, the tissue thin, drying chartaceous to membranaceous, glabrous or sparsely hirtellous; corolla tube 25-35 mm long, strongly sigmoid, the lower portion of tube cylindric, 15-20 mm long, angled backwards 30-50°, 6-8 mm wide at base, narrowing to (2-)3-5(-6) mm wide above thickened 3-5 mm-long nectar chamber and then gradually widening to base of throat, the throat abruptly ampiate to 8-12(-14) mm wide, curved forward ca. 45°; dorsal lobes recurved to recoiled, 10-15 x 3-5 mm, lateral lobes 5-8 x 3-4 mm, ventral lobe triangular, 5-8 mm with an attenuate, deflexed tip; androecium (35-)45-65 mm long; filament tube (30-)40-55 mm long, ventrally flattened and ca. 2 mm in diam. when fresh, white throughout or rose-purple where exserted, entirely glabrous, adnate to corolla 3-7 mm above base, exserted from corolla tube 6-15 mm; anther tube 5-6(-7) mm long, thecae gray, connectives purplish, the dorsal ones moderately to densely short-pilose with purple or white trichomes, antheridial scale 1.5-2.5(-3) mm long; style exserted 0-3 mm from anther tube, stigma greenish or lavender, ca. 3 mm in diam. Fruit oblate to spherical, to 11 x 15 mm, smooth, nectar chamber not persistent; seeds elliptic, 0.5-0.6 mm long.

Distribution. A locally common vine, often climbing to considerable heights in mid-elevation forest-edge habitats. Occurring along the eastern slope of the Andes in

southern Junin, Ayacucho, and Cuzco departments of southern Peru at elevations of 400-2000 m.

Additional specimens examined. PERU. Ayacucho: Huanhuachayo, 25 km SW of Hacienda Luisiana and Rio Apurimac, 1570 m, 18 Aug 1968, *Dudley 11835* (NA); Ccarrapa, between Huanta and Rio Apurimac, 1500 m, 5-17 May 1929, *Killip & Smith 22337* (NY, US); Rio Apurimac Valley, nr. Kimpitiriki, 400 m, 10-11 May 1929, *Killip & Smith 23038* (NY, US); Aina, between Huanta and Río Apurimac, 750-1000 m, 7-17 May 1929, *Killip & Smith 23096* (NY); Huanhuachayo on the Caprichio-Puncu trail, W slope of Rio Apurimac Valley, 1600 m, 15 Jul 1970, *Madison 10264-70* (F, NA). Cuzco: Aguas Calientes, nr. tracks, 18 Apr 1977, *Boeke 1522* (MO, NY); Prov. La Convención, 12°38'S, 73°39'W, 1260-1500 m, 18 Jun 1968, *Dudley 10251* (NA); Río Mapitunuari, 2 hrs walk from Hacienda Luisiana on Río Apurimac, 780 m, 29 Jul 1968, *Dudley 11416* (NA); Macchu Pichu, 2000-2500 m, 24 Jul 1983, *Gentry & Emmons 43228* (MO); Macchu Pichu, 2000 m, *Kanti-Hirsch P852* (F); Valle de Santa Ana, above Quillabamba, 1750 m, 20 Jan 1975, *Plowman & Davis 4814* (F, GH); Río Mapitunuari, E side of Cordillera Vilcabamba, 660 m, 11 Jun 1970, *Madison 10018-70* (NA); Prov. Calca, San Pedro Lares, 2000 m, May 1950, *Marin 2177* (F); upper valley of Río Sambray, western affluent of Vilcanota, 1800 m, 14 May 1936, *Mexia 8064* (GH, UC, US, W); 5 km N of Aguas Calientes, 2000 m, 7 Jun 1977, *Solomon 3163* (MO); Santa María, Jan 1938, *Soukup 816* (F, GH); along railroad tracks between Aguas Calientes and Machu Picchu, 2020 m, 26 Mar 1985, *Stein & Todzia 2438* (CUZ, MO-2 sheets, USM); along railroad below Machu Picchu, 2000 m, 11 Jan 1983, *Stevens 22095* (MO); Machu Picchu, 2200 m, Mar 1938, *Vargas 956* (CUZ, GH, MO); Potrero, 1300 m, Jan 1940, *Vargas 1735* (GH, MICH); Hacienda Amaibamba, 1700 m, 28 Jul 1943, *Vargas 3472* (MICH); Itma, 1400-1600 m, 30 Oct 1949, *Vargas 8533* (CUZ); San Miguel to Aobamba, 1900 m, 5 Oct 1950, *Vargas*

9590 (CUZ); vic. of Tunquimayo, Itma, 1800 m, 21 Apr 1952, Vargas 10641 (CUZ); Potrero, 1250 m, 19-20 Apr 1959, Vargas 12712 (MICH); Itma, 1650 m, 28 Jun 1967, Vargas 19820 (MICH); along Rio Apurimac, 10 km NW of Pte. San Francisco on rd. to Pichari, 600 m, 24 Sep 1976; Wasshausen & Encarnación 709 (K, NY, US). Junín: San Martin de Pangoa, 650 m, 16 Sep 1981, Fernandez 8 (NY, USM); Pangoa, Matthews 1189 (K, K); Satipo, 500 m, Aug 1945, Soukup 2853 (F); Rio Satipo Valley, km 18-23 on Satipo-Concepción rd., 900-1000 m, 12 Mar 1985, Stein & Todzia 2387 (AAU, B, CAS, DUKE, F, K, MO-2 sheets, NY-2 sheets, U, US-2 sheets, USM). Department unknown: Monterico, Mar 1867, Pearce s.n. (K).

CULTIVATED. Lyon Arboretum, Hawaii (originally from Plowman & Davis 4814), 13 Jan 1984, Nagata 2790 (MO-2 sheets).

Discussion. *Centropogon urubambae* is a well-delimited species characterized by pendent, short-bracteate inflorescences; thick fleshy leaves that are generally rounded at the base and have few secondary veins; a zygomorphic calyx (the only such occurrence in subgen. *Centropogon*) with linear, divaricate sepal lobes; and strongly sigmoid, bright pink corollas. This species has in the past been confused with *C. pulcher*, which occurs slightly to the north of its range. That species is most easily differentiated by the flower color; *C. pulcher* has bicolored corollas that are reddish-orange basally and yellowish orange at the lobes. Furthermore, the sepals in *C. pulcher* are generally erect rather than divaricate, and are often shorter than those in *C. urubambae*, and the bracts are typically wider, although there is some overlap in this. In contrast to those of *C. urubambae*, the leaves of *C. pulcher* are narrower, usually lanceolate to narrowly ovate, and lack the expanded aerenchyma that gives *C. urubambae* leaves their coriaceous texture when dried. Within *C. urubambae* a gradient in flower size exists, with the northern populations (Junin and Ayacucho) having corollas considerably shorter (ca. 25 mm long)

than those from Cuzco Department. The expanded leaf aerenchyma of *C. urubambae* is an unusual feature that it shares with *C. yungasensis*, *C. reflexus*, and *C. vargasii*, and the relationships of *C. urubambae* may lie with that species group.

35. *Centropogon vargasii* B. A. Stein, sp. nov. Type. Peru. Cuzco: Puncuyoj, 10 km SW of Incatambo, Machu Picchu, Urubamba, 2385 m, 3 Oct 1982, *Peyton & Tilney-Peyton 1364* (holotype, MO). Fig. 17A-D.

Scandent vines to 4 m long; stems glabrous below to hirtellous towards apex. Leaves elliptic to narrowly ovate, 5-10 x 2.5-4 cm, apex acute to attenuate, base cuneate to rounded, margins crenulate to serrulate, 2-4 small callosities per cm; lamina apparently fleshy when fresh, drying semi-coriaceous, adaxial surface dark green, glabrous or hirtellous, rarely velutinous, abaxial surface paler, occasionally with faint purple vein reticulations, glabrous or hirtellous; secondary veins 6-7, acutely to arcuately ascending, slightly raised abaxially, higher order venation embedded in lamina; petioles 4-10 mm long. Inflorescence a terminal, slightly upturned, bracteate or short-bracteate, subcorymbose raceme, to at least 5 cm long, flowers congested at anthesis but the floral internodes elongating to 3 cm basally, the rachis probably pendent or horizontal, sparsely to densely hirtellous, with stiff multicellular trichomes, 0.2-0.4 mm long, occasionally subtended by a bractless peduncle; bracts apparently persistent, ovate to lanceolate, 5-12(-25) mm long, glabrescent to hirtellous; pedicels assurgent in bud and at anthesis, drooping with age and in fruit, 15-30 mm long, sparsely to densely hirtellous, rarely persistent; bracteoles enlarged and foliaceous, ligulate to spatulate with ciliate margins, 3-5 x 1-2 mm. Flowers ca. 50-55 mm long, hypanthium and sepals often tinged purple; hypanthium hemispheric to depressed hemispheric, rounded or truncate basally, 3-4 x 6-7 mm, smooth or deeply ribbed, glabrescent to densely hirtellous, no intersepalar nectaries evident; sepals erect or slightly patent, coriaceous, ligulate with an acute apex, 10-17 x 2-4 mm, entire or minutely gland-denticulate, abaxial surface glabrescent to hirtellous, adaxial surface moderately to densely hirtellous, sinuses acute or lobes occasionally slightly fused at base; corolla "deep yellow orange" to "orange," glabrous or

moderately hirtellous with short (0.1-0.2 mm long), collapsed conical-trichomes, these sometimes with papillose bases; corolla tube somewhat sigmoid, 28-30 mm long, 5-7 mm wide at base, narrowing to 3-4 mm above nectar chamber, then gradually expanding to base of throat, the throat moderately ampliate, 9-10 mm wide, curved ca. 50°; dorsal lobes probably spreading or recurved at anthesis, 10-12 x ca. 4 mm, lateral lobes triangular, 6-7 x 4-5 mm, with acuminate, decurved tips, ventral lobe triangular, 5-7 mm long, with a deflexed tip; androecium ca. 45-50 mm long; filament tube 40-45 mm long, entirely glabrous, adnate to corolla 5-7 mm from base, exserted from corolla tube 7-10 mm; anther tube 6-7 mm long, entirely glabrous or short-pilose apically in the dorsal connectives, antheridial scale 2.0-2.5 mm long; style exserted 0-2 mm from anther tube, stigma ca. 3 mm in diam. Fruit widely ovate, base truncate, to 15 x 20 mm; seeds ellipsoid, 0.7-0.8 mm long.

Distribution. A rare vine of humid montane forests or cloud forests, known from only three collections in Cuzco and Ayacucho departments of southern Peru at 2400-2600 m.

Additional specimens examined: PERU. Ayacucho: Nr. Yuraccyacu, ca. 40 km NE of Tambo, W slope of Rio Apurímac valley, 2600 m, 22 Jul 1970, *Madison* 10312-70 (F). Cuzco: Prov. Convención, Quillomayo, 2600 m, Jul 1944, *Vargas* 4531 (CUZ, MICH).

Etymology. This new species is named in honor of Dr. Ceasar Vargas C., a longtime student of the flora of southern Peru. Through his many collections, including the first collection of this new species, Dr. Vargas has contributed significantly to our knowledge of the plants of Cuzco Department.

Discussion. *Centropogon vargasii* is closely related to, and presumably derived from, the more common and widespread *C. yungasensis*. This new species is distinguished from *C. yungasensis* chiefly by the erect, rather than reflexed, ligulate sepals and the enlarged foliaceous bracteoles. It shares several derived features with that species, as well as with *C. reflexus*, another probable offshoot from *C. yungasensis*. These include the fleshy leaves that dry coriaceous and that have mostly embedded abaxial leaf venation. This venation occasionally forms a very distinctive purple-reticulate pattern, a feature particularly well developed in *C. reflexus*, but also found to varying degrees in both *C. vargasii* and *C. yungasensis*. All three of these species have elongate, generally ligulate sepals that are strictly reflexed in *C. reflexus* and *C. yungasensis*, but are erect in *C. vargasii*. In addition, all three species have a similar corolla morphology and all produce fruit of a relatively unusual shape, i.e., widely ovate with a truncate base.

36. *Centropogon arcuatus* F. Wimmer, Repert. Spec. Nov. Regni Veg. 19: 242. 1924.

Type. Ecuador. Tungurahua: Volcán Tungurahua, 1861, Spruce 5375 (holotype, W, photo; isotypes, BM, G-3 sheets, photo F-neg. 31666, K, LE, P, P n.v., photo F-neg. 27218, W).

Erect herb 0.5-1 (-1.75) m tall, normally single-stemmed; stems glabrous below, scabrous to hirtellous above, to 5 mm wide at base. Leaves elliptic to lanceolate or oblanceolate, (9-)12-15(-21) x 3-5(-8) cm, apex acuminate or attenuate, base cuneate, margins variable, from almost entire and slightly crenulate or serrulate with 2-3 callose-tipped teeth per cm, or more commonly deeply and irregularly sinuate-lobate, the lobes largest in the distal half and reaching 2 cm long and 1 cm wide, the lobe sinuses rounded and the apices obtuse with an apiculate gland tip; lamina fleshy but pliable when fresh, drying chartaceous to membranaceous, adaxial surface dark, velvety green, glabrous, abaxial surface pale green or tinged purple, completely glabrous, minutely puberulent on the major veins, or rarely sparsely so over entire surface, the trichomes uni- or multicellular; secondary veins 7-10, arcuate-ascending to more or less straight, occasionally forming loops with the superadjacent secondaries; petioles slender, 1-2 cm long. Inflorescence an erect, bracteate, terminal, subcorymbose raceme 2-6 cm long and few flowered, the rachis densely hirtellous with stiff, conical, multicellular, tawny trichomes to 0.75 mm long, occasionally subtended by a short peduncle to 3.5 cm long; bracts narrowly ovate to lanceolate, mostly 10-20 x 5-10 mm, the lowermost grading into vegetative leaves, apex acute to acuminate, margins serrulate, both surfaces glabrescent to densely hirtellous; pedicels erect at anthesis, recurved with age, 10-20 mm long, densely hirtellous, bracteoles subbasal, subulate, to 1.5 mm long. Flowers ca. 30-35 mm long, occasionally not resupinate; hypanthium hemispheric to subcylindric, 4-6 x 4-6 mm, smooth, moderately to densely hirtellous, intersepalar nectaries present at least

laterally; sepals erect with the tips recurved, deltoid to narrowly triangular, 2-3 x 1.5-2.0 mm, minutely hirtellous, sinuses planar; corolla orangish-red to red, the lobes sometimes orange, moderately to densely puberulent with trichomes to 0.25 mm long; corolla tube 20-25 mm long, the basal portion of tube cylindric and very slender, 4-6 mm wide at base narrowing rapidly to 1.5-2.5 mm wide, then remaining narrow or gradually expanding to base of throat, the throat abruptly ampiate, 7-10(-12) mm wide, sharply curved or arcuate, 50-75 (-90) $^{\circ}$; dorsal lobes erect, not recurving, 6-8 mm long, lateral lobes deltoid, 4-6 mm long, with decurved tips, ventral lobe 4-6 mm long, with an apiculate, deflexed tip; androecium ca. 30 mm long, exserted from corolla tube, but normally obscured by the non-reflexed dorsal corolla lobes; filament tube ca. 25 mm long when fresh ventrally flattened and 2.25 mm wide, yellowish, glabrous; anther tube 5-6 mm long, yellowish-tan, glabrous, antheridial scale often truncate and poorly fused, 2.5-3.5 mm long (conspicuously long relative to size of anther tube); style exserted 0-2 mm from anther tube, stigma ca. 2 mm in diam. Fruit ovoid to subspheric, 7 x 10 mm; ripe seed not seen.

Distribution. A rare understory herb of undisturbed cloud forest. Restricted to the eastern slope of the Andes in Tungurahua, Cañar, and Morona-Santiago provinces in central Ecuador at elevations of 1500-2500 m.

Additional specimens examined. ECUADOR. Cañar: Rio Paute drainage, E side of valley of Rio Monay, 40 km ENE of Anzogues, 2350-2620 m, 3 Feb 1945, Fosberg & Prieto 22712 (US); Hacienda Frutillas, Rio Paute Canyon, 2430-2500 m, 4 Feb 1945, Fosberg & Prieto 22745 (US-2 sheets). Morona-Santiago. Btwn. El Rio Sordo and La Esperanza, trail to Huamboya, 2000-2600 m, 13 Feb 1944, Acosta Solis 7341 (F), Acosta Solis 7363 (F); Limón-Cuenca rd., trail 3 km above Plan de Milagro, 1900-2000 m, 18

May 1985, Stein 2811 (MO); valley at Arenillas along Rio Tintas, ca. 50 km SE of El Pan, 2195 m, 13 Jul 1943, Steyermark 53570 (F, MICH). Tungurahua: Baños, 4 Apr 1931, Benoist 4145 (P); E of Baños, 1500 m, 23 Jan 1934, Schimpff 644 (B).

Discussion. *Centropogon arcuatus*, one of the most distinctive species in the subgenus, is characterized by the often sinuate-lobate leaves and the small, extremely slender and abruptly curved corolla with non-recurved dorsal lobes. Sinuate lobate leaves are not found in any other species in subgen. *Centropogon* and are rare within the genus as a whole. Only *C. grandidentatus* of Mexico and *C. australis* of Venezuela, both members of subgen. *Siphocampyloides*, have leaves that occasionally approach those of the sinuate-leaved form of *Centropogon arcuatus*. The unusually small and slender corollas are similar in certain respects to those of *C. carpishensis* of central Peru and *C. pygmaeus* from northern Ecuador. *Centropogon arcuatus* can be differentiated from *C. pygmaeus* by the latter species' much shorter antheridial scale (ca. 1.5 mm long), smaller unlobed leaves, less acutely curved corolla with a generally narrower throat and consistently spreading upper lobes, shorter, pubescent anther tubes, and longer sepals. *Centropogon carpishensis* can be easily separated by such features as the much longer sepals, less acutely curved corolla with a thicker tube and recurved upper lobes, and a pubescent anther tube with a shorter antheridial scale.

The overall relationships of *C. arcuatus* are problematic, however. On the basis of the trichome morphology, corolla shape, and filament tube cross-sectional shape it appears to be a member of sect. *Campylobotrys*. It stands out sharply from all other species in that group, though, and must be considered very derived, perhaps closest to *C. papillosum*.

An apparent hybrid between *C. arcuatus* and another member of sect. *Campylobotrys*, perhaps *C. curvatus*, has been collected near Plan de Milagro, Morona-

Santiago Province. This rather anomalous specimen, Jorgensen OHJ-33 (NY), approaches *C. arcuatus* in its erect habit and inflorescence, persistent bracts, nonreflexed corolla lobes, red-orange corolla color, small sepals with recurved tips, and, most importantly, serrately lobed distal leaf margin. It has, however, a much stouter corolla, apical anther pubescence, and papillose pubescence. *Centropogon curvatus*, which is known from the same region and is represented by another Jorgensen collection, shares many of these features.

37. *Centropogon pygmaeus* B. A. Stein, sp. nov. Type. Ecuador. Napo: Above Río Chingual along trail to La Bonita, 1-2 km from end of Tulcán-Santa Bárbara rd., ca. 25 km below Santa Bárbara, 0°35'N, 77°30'W, 2100-2150 m, 28 May 1985, Stein 2869 (holotype, MO; isotypes, AAU, K, NY, QCA, QCNE, US). Fig. 26.

Erect to sprawling terrestrial herbs 20-40(-50) cm tall, branched at base from a thickened rootstock; stems 3-6 mm wide, sometimes prominently ridged, often purplish, glabrescent below, moderately hirsutulous with verrucate, papillose or pustulate-based trichomes toward apex, slightly woody at base; latex white. Leaves elliptic, narrowly elliptic, to narrowly ovate, 2.5-7(-9) x 1.5-4 cm, apex attenuate to acute, base acute to cuneate, margins serrulate, rarely crenulate, 2-5 teeth per cm, these tipped by apiculate-exserted purple callosities; lamina thin but fleshy when fresh, drying chartaceous, adaxial surface dark green, glabrous, abaxial surface paler green or purple tinged, minutely hirtellous on veins; secondary veins 5-7, prominent, often purple, acutely ascending or in broader leaves arcuate-ascending, occasionally forming loops with superadjacent secondaries; petioles 10-20(-30) mm long, glabrous or sparsely hirtellous. Inflorescence an erect, folio-bracteose, terminal raceme, the lower flowers often axillary to unreduced leaves, apical flowers congested, the rachis elongating to 2 cm, moderately to densely strigulous with irregularly verrucate, papillose or pustulate-based trichomes; bracts persistent, the upper ones much reduced and sessile, narrowly ovate to narrowly elliptic, 10-20 x 5-7 mm, gland-serrulate, adaxial surface glabrous or sparsely hirsutulous, abaxial surface hirsutulous, lower bracts resembling normal vegetative leaves; pedicels erect at anthesis, spreading to recurved with age, (5-)10-25 mm long, densely covered with 0.1-0.2 mm long verrucate or pustulate trichomes, bracteoles basal to subbasal, subulate, ca. 1 mm long, occasionally the distal portion composed of a purple callosity. Flowers small, 25-32 mm in length; hypanthium ovoid to obovoid, rounded or somewhat

truncate at base, 1.5-3 x 2-4 mm, moderately to densely covered with papillose or pustulate-based trichomes, these friable and often only a portion of the base remaining, intersepalar nectaries not present; sepals erect, triangular to narrowly triangular, 2-3(-4) x 1-1.5 mm, glabrescent or sometimes sparsely hirtellous; corolla cardinal red, moderately covered with short (ca. 0.1 mm) collapsed-conical trichomes arising out of verrucate-papillose bases; corolla tube 17-22 mm long, 2-4 mm wide at base narrowing quickly to (1-)1.5-2.5 mm wide and remaining narrow to base of throat, the throat abruptly ampiate, 4-6 mm wide (to ca. 7.5 mm when fresh), curving ca. 30°; dorsal lobes spreading but often appearing erect when pressed, narrowly falcate, 8-10 mm long, lateral lobes triangular, 5-6 mm long, with decurved tips, ventral lobe triangular, 5-6 mm long, with an acute, deflexed tip; androecium 24-28 mm long, well-exserted from corolla tube; anther tube ca. 4 mm long, thecae greyish-blue, connectives purple, the dorsal ones sparingly short-pilose with purple trichomes, antheridial scale 1.25-1.5 mm long; filament tube 20-24 mm long, ventrally flattened when fresh, pale yellow and often purplish where exserted, glabrous, adnate to corolla 3-4 mm above base, exserted from corolla tube 1-2 mm; style exserted from anther tube 0-1 mm, stigma ca. 1.5 mm in diam. Fruit depressed ovoid, to 5 x 10 mm, conspicuously star-shaped in cross-section when fresh with 10 prominent longitudinal ridges; seeds elliptic to oblong, 0.6-0.7 mm long.

Distribution. A locally common herb of cloud forest edge and disturbed pastures, known from only two localities along the eastern slope of the Andes in northern Napo Province at 1900-2700 m.

Additional specimens examined. ECUADOR. Napo: ca. 5 km E of Santa Bárbara, 2700 m, 4 March 1974, Harling & Andersson 12453 (AAU, GB); km 40 from El

Carmelo on rd. towards La Bonita, ca. 5 km below La Alegria, 2350 m, 8 April 1979, Lojtnant et al. 11914 (AAU); Santa Bárbara-La Bonita rd., trail towards La Bonita, ca. 25-28 km S of Santa Bárbara, along Rio Chingual, 2100-2350 m, 17 May 1982, Luteyn et al. 8453 (NY); 140 km from Lago Agrio on rd. to Baeza, pass S of Río Salado, 1940-2000 m, 8 August 1980, Ollgaard et al. 35716 (AAU).

Discussion. *Centropogon pygmaeus* is the most diminutive member of subgen. *Centropogon*, and hence the name of this new species. It is well-characterized by its low habit, the small and slender corollas, extremely short anther tubes, and unusual papillose-pustulate inflorescence and floral trichomes. The small, gradually curved, but ventricose corolla of *C. pygmaeus* is reminiscent of *C. uncialis*, a Colombian member of the *C. hirtus* species group or sect. *Amplifolii*, but this similarity is undoubtedly due to convergence as these species differ in numerous floral and vegetative features. The only other species in subgen. *Centropogon* with such small corollas are *C. arcuatus* of central Ecuador, *C. carpishensis* of central Peru, and *C. bangii* of Bolivia. *Centropogon pygmaeus* can easily be distinguished from those species by the unusual indument present and the much smaller leaves.

The overall relationships of *C. pygmaeus* are obscure. The very distinctive trichomes are similar to those found in certain members of sect. *Campylobotrys*, particularly *C. pilosus*, and the sympatric *C. curvatus*. The ventricose corolla, even in this small, gradually curving form, also suggests an affinity with this group, perhaps near to *C. arcuatus* of central Ecuador. For these reasons, I am tentatively placing this species in sect. *Campylobotrys*.

The pollinator of this species is unknown. Because of the very short, gently curving corolla and the plant's low stature and preference for relatively open habitats, it is probably visited by short-billed hummingbirds. This type of hummingbird is very

different from the sicklebill hummingbirds that presumably visit the sympatric *C. curvatus*, and these two species would thus be well-isolated ethologically.

38. **Centropogon bangii** A. Zahlbruckner, Bull. Torrey Bot. Club 24: 372. 1897. Types.

Bolivia. La Paz: Yungas, 1890, *Bang 500* (lectotype here designated, W—"Acqu.

1890 No. 965"; isolectotypes, BM, G, K, MO, NY-2 sheets, W-2 sheets); near Yungas, 1200 m, 1885, *Rusby 1093* (syntypes, NY, US).

Erect suffrutescent herb; stems hirtellous, to 5 mm in diam., green or tinged maroon. Leaves elliptic, (8-)10-17 x (3-)4.5-7 cm, apex acuminate to attenuate, base cuneate, margins serrulate with 5-7 callose-tipped teeth per cm. or occasionally doubly serrulate, with 2 larger teeth (to 1.5 mm) per cm interspersed by 2-4 shorter teeth; lamina drying chartaceous, adaxial surface with the reticulum of 2°-4° veins readily apparent, glabrescent or sparsely hirtellous on venation, abaxial surface with the venation well raised and the reticulum highly visible, moderately hirtellous along veins with trichomes to 0.1 mm long; secondary veins 9-11, acutely to arcuately ascending; petioles to 1.5 cm long, hirtellous abaxially, or absent. Inflorescence an erect, frondobracteose, terminal, subcorymbose raceme, to 3.5 cm long, the flowers few (4-10 in total) and congested, the rachis hirtellous; upper bracts oblanceolate, mostly less than 20 x 4 mm and slightly shorter than pedicels, apex acute, margins serrulate, both surfaces sparsely to moderately hirtellous, lower bracts generally unreduced leaves and well-exceeding the subtended pedicels; pedicels erect at anthesis and apparently remaining erect with a nodding tip in fruit, 15-25 mm long, hirtellous, occasionally persistent, bracteoles basal, subulate, ca. 1 mm long. Flowers 28-33 mm long; hypanthium hemispheric, 3 x 5-6 mm, 10-ribbed, moderately hirtellous, intersepalar nectaries present; sepals erect, triangular, 5-6 x (2-)3 mm, entire or remotely serrulate, hirtellous, sinuses acute; corolla reddish when dry, moderately to densely hirtellous; corolla tube 17 mm long, 3-5 mm wide at base, narrowing rapidly to 1.5-2.5 mm then gradually ampiate to throat, the throat 7-9 mm wide not well differentiated from lower portion of

tube, gradually curving 25(-45)°, ; dorsal lobes apparently recurved, ca. 5-6 x 3 mm, lateral lobes ca. 5 x 3 mm with cuspidate, decurved tips, ventral lobe ca. 5 mm long with a cuspidate, deflexed tip; androecium 25-28 mm long; filament tube 20-23 mm long, sparsely short-pilose at summit with white trichomes, adnate to corolla 3-4 mm from base, exserted from corolla tube 3-5 mm; anther tube 5 mm long, connectives purplish, the dorsal ones sparsely short-pilose with white trichomes, antheridial scale narrowly triangular, 1.5-2 mm long, with short unfused trichomes at base; style exserted from anther tube ca. 1 mm, stigma ca. 2.5 mm in diam. Fruit globose to ovoid, to 8 x 12 mm, smooth, the nectar chamber persistent; seeds oblong to elliptic, often angular, ca. 0.6 mm long.

Distribution. A very rare herb of the Yungas region of northern Bolivia, occurring at elevations of 1200-1650 m. Because this species is known from only three collections made around the turn of the century, no information is available about its habitat preferences.

Additional specimen examined. BOLIVIA. La Paz: Sud Yungas, Sirupaya nr. Yanacachi, 1650 m, 19 Nov 1906, *Buchtien* 4743 (US).

Typification. *Centropogon bangii* was originally published by Zahlbruckner in 1897 as "*C. bangi*"; this orthographic error was corrected subsequently by Wimmer (1937). In the protologue for *C. bangii* Zahlbruckner cited two collections, *Bang* 500 and *Rusby* 1093, without designating either as the type. Gleason (1925) referred to the Bang collection as the type, but no herbarium citations were given. To unambiguously typify this species, I have designated one of the three W sheets of *Bang* 500 as the lectotype. This specimen was annotated by Zahlbruckner as "*C. bangi* nov.," and because

it was accessioned into the Vienna herbarium in 1890, he presumably did so prior to the 1897 publication of the name. The only other specimen of this species that I have seen annotated in Zahlbruckner's hand is the G specimen of *Bang 500*, which bears an annotation date of 1908. Of the two sheets I have seen of *Rusby 1093*, neither was annotated by Zahlbruckner.

Discussion. *Centropogon bangii* is most easily recognized by its very small flowers with little-curved corollas and its frondo-bracteose inflorescence. The leaf texture, with its readily apparent venation reticulum, and the pedicels that remain erect after anthesis resembles those found in *C. macrophyllus*. In inflorescence structure, however, these two species are fundamentally different, with *C. bangii* having anauxotelic inflorescences. This is shown by the Rusby specimens in which a new vegetative shoot has emerged from a leaf axil near the base of the old inflorescence rather than from the apex. The affinities of this species appear to be with *C. carpishensis* of central Peru and are discussed in more detail under that species.

39. *Centropogon carpishensis* B. A. Stein, sp. nov. Type. Peru. Huánuco: Carpish Hills, quebrada 0.5 km E of tunnel on rd. from Huánuco to Tingo María, 9°42'S, 76°05'W, 2650 m, 2 Mar 1985, *Stein & Todzia* 2265 (holotype, MO; isotypes, F, NY, US, USM). Fig. 27F-I.

Erect suffrutescent herbs 0.5-0.75(-1.2) m tall; single-stemmed or branching from base, stems to 1 cm in diam. at base, glabresent below, increasingly hirsute toward apex with uniseriate, multicellular, conical, tawny trichomes, 0.5-1.5 (-2.0) mm long; latex white. Leaves narrowly elliptic to elliptic, (9.5-)12-16 x (3-)4-6 cm, apex attenuate, base narrowly cuneate, margins serrulate with 5-6 purple-callose-tipped teeth per cm; lamina fleshy when fresh, drying chartaceous to membranaceous, adaxial surface dark green, glabrous, with deeply impressed secondary veins when fresh, abaxial surface paler, midvein and secondaries raised and sparsely to moderately hirsutulous or hirsute; secondary veins 7-8, arcuately ascending; petioles 10(-30) mm long, hirsute abaxially. Inflorescence an erect, frondo-bracteose, terminal raceme, 1.5-2 cm long with 8 or more congested flowers, the rachis densely tawny-hirsute; bracts persistent and sessile, ovate to lance-ovate, (8-)10-15 x 4-10 mm, apex acute to attenuate, margins serrulate and short ciliate, adaxial surface glabrous, abaxial surface glabrescent or hirsute along veins, the lower bracts grading in size and shape into vegetative leaves; pedicels erect at anthesis, drooping with age, 15-25 mm long, densely hirsute, bracteoles basal, subulate, ca. 1 mm long. Flower ca. 32-37 mm long; hypanthium hemispheric to subcylindric, rounded or slightly tapering at base, 4-5(-6) x (3-)4-5(-6) mm, slightly 5-ribbed, moderately to densely hirtellous with short (ca. 0.1 mm), triangular trichomes occasionally interspersed with longer ones, intersepalar nectaries not present; sepals foliaceous, erect but the tips often patent, triangular to ligulate, 7-8 x (2-)3 mm, remotely serrulate, glabrescent to moderately hirtellous, sinuses acute or planar; corolla

reddish-orange to pinkish-orange, lower lobes and inside of throat orange to orangish-yellow, external surface moderately hirtellous with collapsed conical, uni- or multicellular trichomes, 0.1-0.2 mm long; corolla tube (18-)20-22 mm long, 3-4.5 mm wide at base, narrowing just above this to (1.5-)2-3 mm and gradually expanding to (6-)7-9 mm wide at the throat, the throat not well-differentiated from lower portion of tube, gently curving ca. 30°; dorsal lobes recurved, 8-10 x 3-4 mm, lateral lobes 5-6 mm long, with decurved, cuspidate tips, ventral lobe 4-6 mm long, with a short, deflexed, cuspidate tip; androecium (27-)30-32 mm long; filament tube (22-)23-26 mm long, ventrally flattened and ca. 2 mm wide when fresh, yellowish orange, pilose to short pubescent at summit, adnate to corolla 5-6 mm above base, exserted 0-3 mm from corolla tube; anther tube 5-6 mm long, thecae gray, connectives purplish, the dorsal ones pilose with purple trichomes to 0.5 mm long, antheridial scale often splitting into two segments, ca. 2 mm long; style exserted from anther tube 0-1 mm, stigma ca. 3 mm in diameter. Fruit unknown.

Distribution. An uncommon cloud forest herb found along streams and in forest understory and light gaps. Known only from the Carpish Hills of Huánuco Department in central Peru at 2250 to 2700 m.

Additional specimens examined. PERU. Huánuco: Rd. to Huánuco, 40 minutes from Tingo Maria, 21 Mar 1982, *King* 340 (F); trail from S entrance of Carpish tunnel, 2700 m, 27 Feb 1978, *Luteyn & Lebron-Luteyn* 5467 (NY); quebrada 2 km E of Carpish tunnel, 2600 m, 4 Mar 1985, *Stein & Todzia* 2310 (MO, US); quebrada 1 km E of Carpish tunnel, 2450 m, 15 Jan 1987, *Stein et al.* 3846 (MO, US, USM); trail below San Pedro de Carpish, 3 km E of Carpish tunnel, 2250-2450 m, 15 Jan 1987, *Stein et al.*

3847 (MO, USM); Paty trail, 5 km E of Carpish tunnel, 2400 m, 15 Jan 1987, Stein et al. 3867a (MO).

Discussion. *Centropogon carpishensis* is distinguished by the following features: its low stature; an erect, subcorymbose, anauxotelic, frondo-bracteose inflorescence in which the lower bracts consistently are composed of unreduced leaves (and much exceed the subtended pedicels) whereas the upper bracts are generally shorter than the subtended pedicels; a relatively small corolla that is rather narrow at the base and gradually curves and expands towards the poorly differentiated throat; and an extremely dense indument of stiff, tawny trichomes covering the upper stem and inflorescence rachis. The species resembles and appears most closely related to *C. bangii* from northern Bolivia. It differs from that species in several vegetative and floral features, however. The adaxial leaf surface in *C. carpishensis* is entirely glabrous rather than sparsely hirtellous, while the abaxial surface is hirsutulous to hirsute instead of merely hirtellous as in *C. bangii*. The flowers of *C. carpishensis* are longer overall (32-37 vs. 28-33 mm) and have slightly longer sepals (7-8 vs. 5-6 mm). Furthermore, the anther pubescence is purple in *C. carpishensis* and white in *C. bangii*.

That these two closely related species are separated north to south by approximately 1000 km may be to some degree an artifact of the relatively few collections available from upper elevation forest habitats along the eastern Andean slope in southern Peru. As an example, *C. carpishensis* is a conspicuous but infrequent component of the cloud forests in the Carpish Hills of Central Peru. Although this area is one of the most accessible and thoroughly collected cloud forests in all of Peru, and botanists have visited the region since the late 1700s, *C. carpishensis* was collected for the first time only in 1978. If such is the case for one of the most well explored cloud

forests in Peru, then it is likely that additional populations of either of these two species may occur elsewhere in the intermediate zones.

The overall relationships of these two species are problematic. Certain morphological features suggest an alignment with sect. *Amplifolii*. For example, the conspicuous venation reticulum apparent on the abaxial and adaxial leaf surfaces of *C. bangii* suggests a similarity to *C. macrophyllus*, as does the corolla shape, and the indument of *C. carpishensis* is similar to that found in *C. hirtus*. Several other features, however, argue against inclusion in that section. The inflorescences in both species are anauxotelic, and at least in *C. carpishensis*, where fresh material was available, the filament tube is yellowish with a ventrally flattened cross-section and the corolla is orangish internally, all features not typical of section *Amplifolii*. On the basis of these last characters these two species are provisionally assigned to sect. *Campylobotrys*, although they are recognized as being rather anomalous there as well.

40. **Centropogon lasiodorus** B. A. Stein sp. nov. Type. Peru. Huánuco: Paty Trail, Carpish Hills 5 km E of tunnel on Huánuco-Tingo María rd., 2100-2400 m, 15 Jan 1986, *Stein et al.* 3868 (holotype, MO; isotypes, AAU, B, CAS, DUKE, F, K, NY, U, US, USM). Fig. 27A-E.

Erect, suffrutescent herbs 1-2 m tall, occasionally branched at base; stems moderately to densely tomentose with soft and spreading, acicular, uniseriate, multicellular, amber-colored trichomes to 2.5 mm long, glabrescent below; latex opalescent-white. Leaves narrowly obovate to elliptic, 14-23(-26) x (5-)7-11 cm, apex acuminate, base cuneate, margins denticulate to serrulate, rarely coarsely dentate, usually with 5-8 ciliate, callose-tipped teeth per cm, these exserted to 1.5 mm; lamina thin and pliable when fresh, drying chartaceous, adaxial surface dark green, glabrous, abaxial surface paler, densely tomentose with pale tawny, spreading hairs to 2 mm long, especially dense along mid-vein and secondaries, but also present on higher order venation and areoles; secondary veins 7-9, arcuately ascending, often forming loops with superadjacent secondaries, prominently raised abaxially; petioles often short and thick, 5-10(-20) mm long, densely tomentose except glabrous along canaliculate adaxial face. Inflorescence an erect, terminal, short-bracteate, sub-corymbose raceme, elongating to 20 cm, flowers numerous, to 22 per inflorescence, congested in bud but becoming lax with age, subtended by an erect peduncle to 12 cm long, the rachis and peduncle very densely tomentose; bracts persistent, triangular to oblong, 5-10 mm long and much shorter than pedicels, apex acute, base sessile, margins serrulate, both surfaces hirtellous to tomentulous or adaxial surface occasionally glabrescent; pedicels erect in bud and at anthesis, drooping with age and often tortuous, 20-45 mm long, very densely tomentose, bracteoles basal to subbasal, lance-linear, 2-2.5 mm long. Flowers 50-60 mm long; hypanthium hemispheric, 4-6 x 4-6 mm, ribbed when fresh, moderately to densely

hirtellous or tomentulous but much less so than pedicels, intersepalar nectaries not present; sepals erect to spreading, deltoid to narrowly triangular, 2.5-4(-8) x 2-2.5 mm, entire to serrulate, moderately to densely hirtellous or tomentulous, sinuses acute, rarely planar; corolla pinkish-red externally and yellowish-orange within throat, or "canary yellow" (*Barbour 4116*), with a rather narrow lower tube and a slightly ampliate, moderately curved throat, densely pubescent throughout with short, soft, collapsed-conical trichomes; corolla tube 30-37 mm long, the lower portion 20-25 mm long, straight or slightly angled back, 4-7 mm wide but narrowing and re-expanding slightly above the 4-5 mm-long nectar chamber and again at base of throat, often somewhat laterally compressed when fresh, the throat only slightly ampliate, 7-11 mm wide and curved 45-60°; dorsal lobes recurved, usually narrowly falcate, 10-12 x 2.5-3.5(-5) mm, lateral lobes asymmetrically triangular, ca. 7 x 3(-5) mm, with long decurved tips, ventral lobe triangular to deltoid, ca. 7 mm long with an acute, deflexed tip; androecium 42-45(-55) mm long; filament tube 40-50 mm long, ca. 2 mm wide and ventrally flattened when fresh, white, pilose at base of anthers but otherwise glabrous, adnate to corolla ca. 8 mm above base, exserted from corolla 4-6 mm; anther tube 6-7(-8) mm long, thecae dark grey, connectives rose-purple, the dorsal ones densely short-pilose with purple trichomes, antheridial scale triangular, 2-3 mm long; style exserted from anther tube 0-2 mm, stigma purplish, ca. 2.5 mm in diam. Fruit spheroid to slightly ovoid, to 10 x 14 mm, prominently ribbed and star-shaped in cross-section when fresh, nectar chamber persistent; seeds irregularly angular, ca. 0.8 mm long.

Distribution. A rare herb of the eastern slope of the Andes in central and northern Peru, where it is known only from cloud forest in Huánuco and Amazonas departments at 1800-2450 m.

Additional specimens examined. PERU. Amazonas: Third camp, Cordillera Colán SE of La Peca, 1800-1860 m, 17 Oct 1978, Barbour 4116 (MO). Huánuco: Trail downslope from San Pedro de Carpish, Carpish Hills 3 km E of tunnel on Huánuco-Tingo Maria rd., 2250-2450 m, 15 Jan 1987, Stein et al. 3849 (MO, NY, US, USM).

Etymology. The epithet *lasiодорус* (Greek: *lasiοs* -- shaggy, *dory* -- shaft or spear) is in reference to the densely tomentose peduncle and inflorescence rachis that characterize this species.

Discussion. This new species is characterized chiefly by the densely tawny-tomentose inflorescence rachis, peduncle, pedicels, and underleaves. *Centropogon lasiodorus* is fairly common at the type locality in the Carpish Hills, a cloud forest region that has been the source of many botanical collections since the beginnings of plant explorations in Peru. It is therefore surprising that this species was not collected there previously. The type was gathered along the Paty Trail, a popular locality for ornithologists visiting the country. This trail apparently has been almost totally neglected by botanists, however, since *C. lasiodorus* was growing there along with at least five other species of *Centropogon*, most of which were previously unknown from the vicinity. One can extrapolate that a similar paucity of collections exists for other groups present in this fast-disappearing cloud forest.

The Amazonas collection referred here to *C. lasiodorus* (Barbour 4116) agrees well with the type in most important respects, particularly the erect habit and the erect pedunculate, densely tomentose, terminal inflorescence. There are, however, several conspicuous differences. The leaf margins in this collection are more coarsely dentate, the corolla and androecium are slightly longer and the throat slightly wider, the corolla is indicated as "canary yellow" rather than pinkish-red, and the sepals are two to three

times as long (8 vs. 2.5-4 mm). Additional material from this northern population or geographically intermediate areas are needed to ascertain the full range of morphological variability in this species and to discern if two distinct taxa exist. I hesitate to describe a subspecific taxon on the basis of the single specimen available from Amazonas. Unfortunately, the upper Andean slopes of northern Peru are extremely poorly collected due to their inaccessibility, and the burgeoning illicit drug trade in the region does not improve the prospects of increased botanical attention.

In habit, trichome type, and corolla morphology, *C. lasiodorus* resembles members of the *C. hirtus* species group of sect. *Amplifolii* that occur nearby in the Carpish Hills. Several important features differentiate it from that group, however. The inflorescence in *C. lasiodorus* is anauxotelic, with each long-pedunculate and subcorymbose inflorescence terminating the axis upon which it is borne. New growth occurs from lateral buds at the base of the inflorescence, rather than as a continuation of the inflorescence axis as in the auxotelic inflorescences of sect. *Amplifolii*. The pedunculate and very short-bracteate condition found in this species are other features atypical of sect. *Amplifolii*. Furthermore, while the pinkish-red external corolla color of the type collection closely matches that of many members of sect. *Amplifolii*, yellow and orange pigments, as in the internal corolla color of the type and the Amazonas collection, are also extremely rare in that section. The ventrally flattened instead of subterete filament tube is another feature that differentiates this species from sect. *Amplifolii*. While *C. lasiodorus* can confidently be excluded from sect. *Amplifolii* based on the above suite of characters, the true sectional relationships of this species remain elusive. On the basis of the filament tube cross-section, short-bracteate raceme, and peduncle, it is tentatively placed in sect. *Campyllobotrys*. A hybrid origin from members of sect. *Campyllobotrys* and sect. *Amplifolii* is at least a possible explanation for the sectional ambiguity of this species.

Fig. 23. *Centropogon granulosus* (from cultivated material of Stein & Todzia 2342). A, habit showing upturned inflorescence rachis. B, flower.

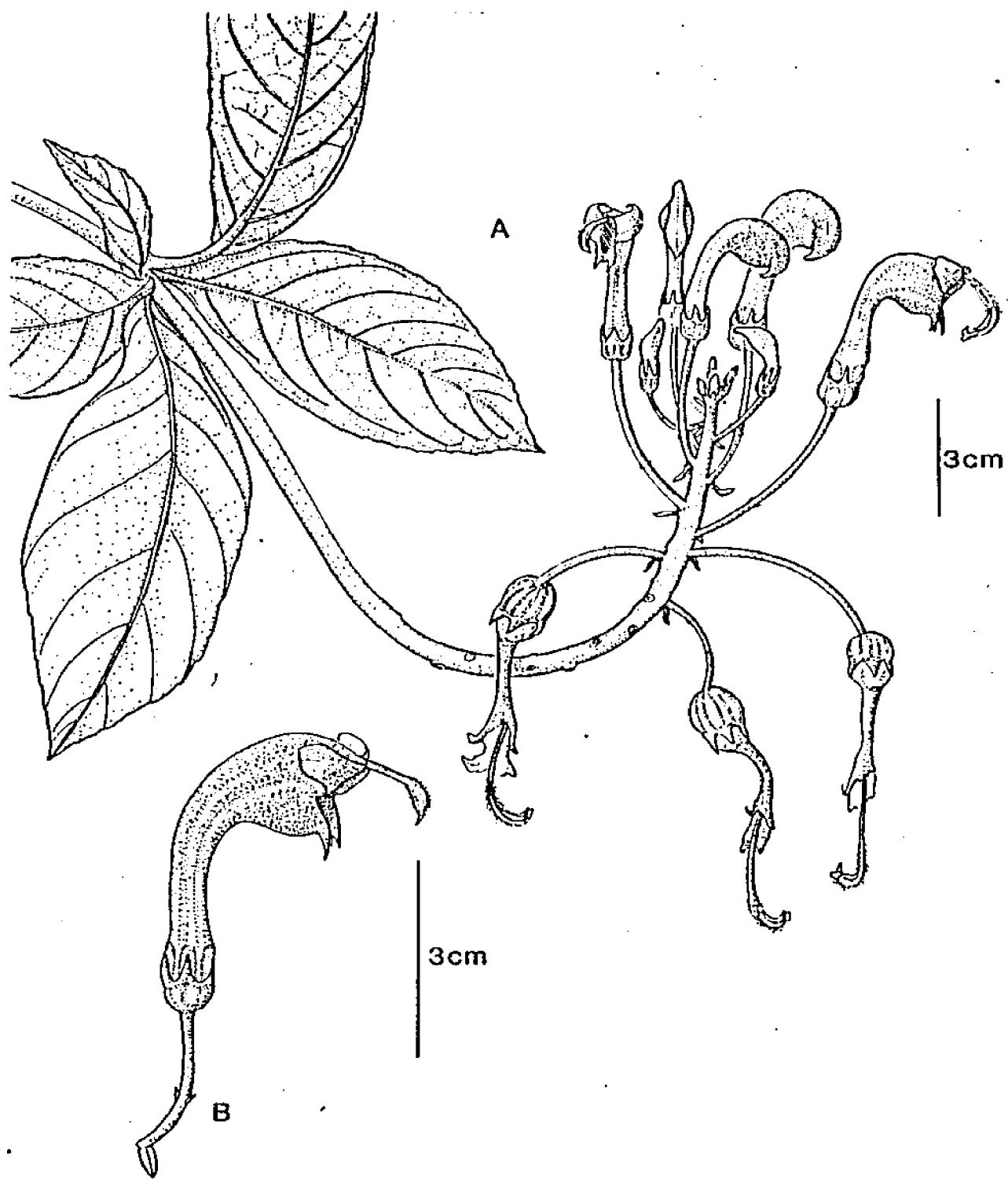


Fig. 24. A-D, *Centropogon vargasii* (from Peyton & Tilney-Peyton 1364). A, habit. B, flower with close-ups of papillose-based corolla trichomes and multicellular pedicel trichomes. C, anther tube with exserted stigma. D, seed. E-F, *Centropogon cuatrecasanus* (E-F from Luteyn et al. 10400; G-I from Stein & McDade 3301). E, habit with close-up of scaberulous stem surface. F, detail of leaf margin. G, flower with detail of hirtellous corolla surface. H, close-up of inflorescence showing reduced bracts and foliaceous bracteoles. I, longitudinal section of lower portion of flower.

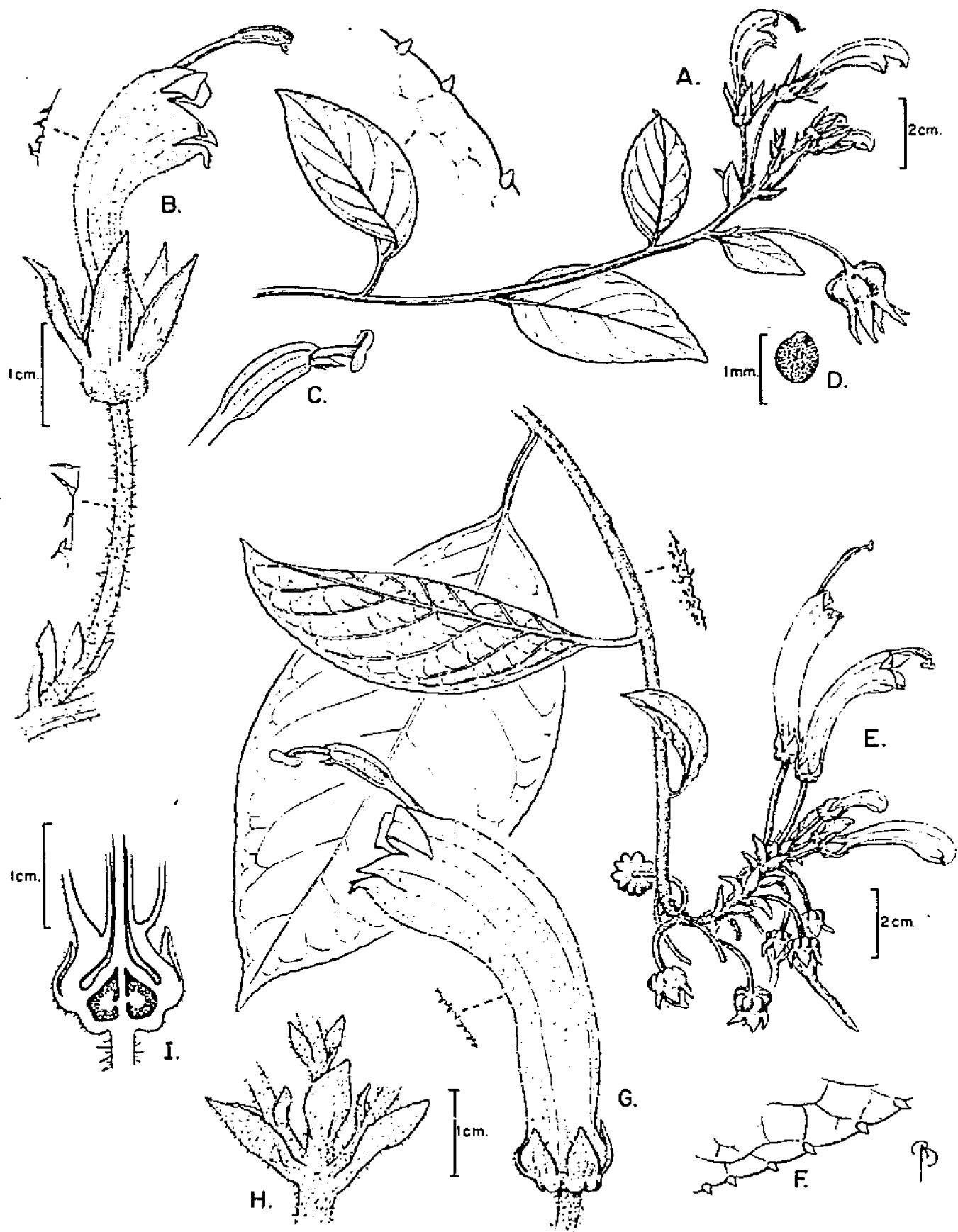


Fig. 25. *Centropogon papillosum* (from cultivated material of Stein & Tucker 3127). A, habit. B, flower at anthesis with non-reflexed lobes. C, close-up of papillose stem. D, detail of papillae, X30.

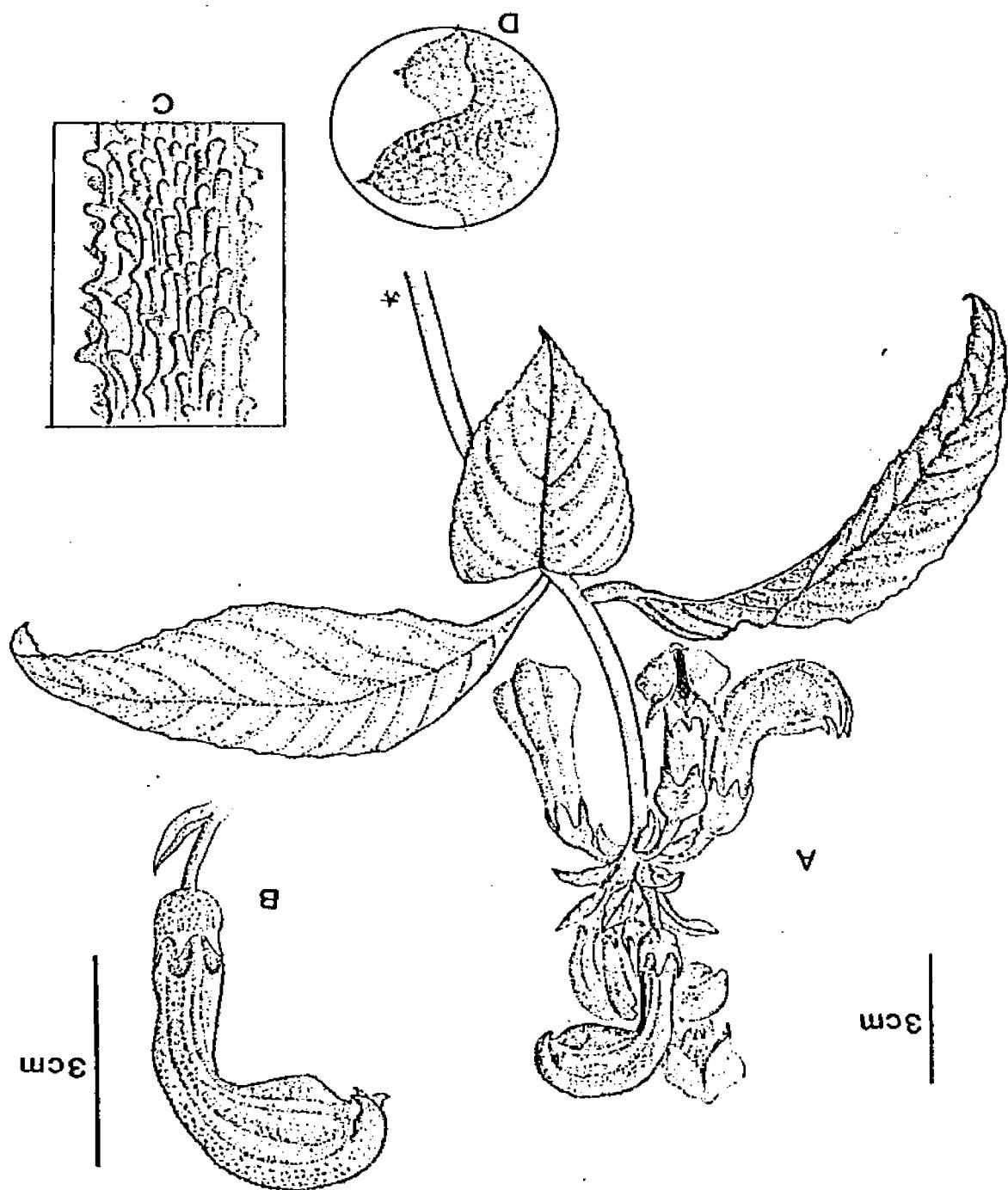


Fig. 26. A-D, *Centropogon pygmaeus* (from Stein 2869). A, habit, entire plant. B, flower and portion of subtending leaf with close-ups of pustulate-based pedicel and corolla trichomes. C, longitudinal section of lower portion of flower. D, anther tube. E, mature fruit.

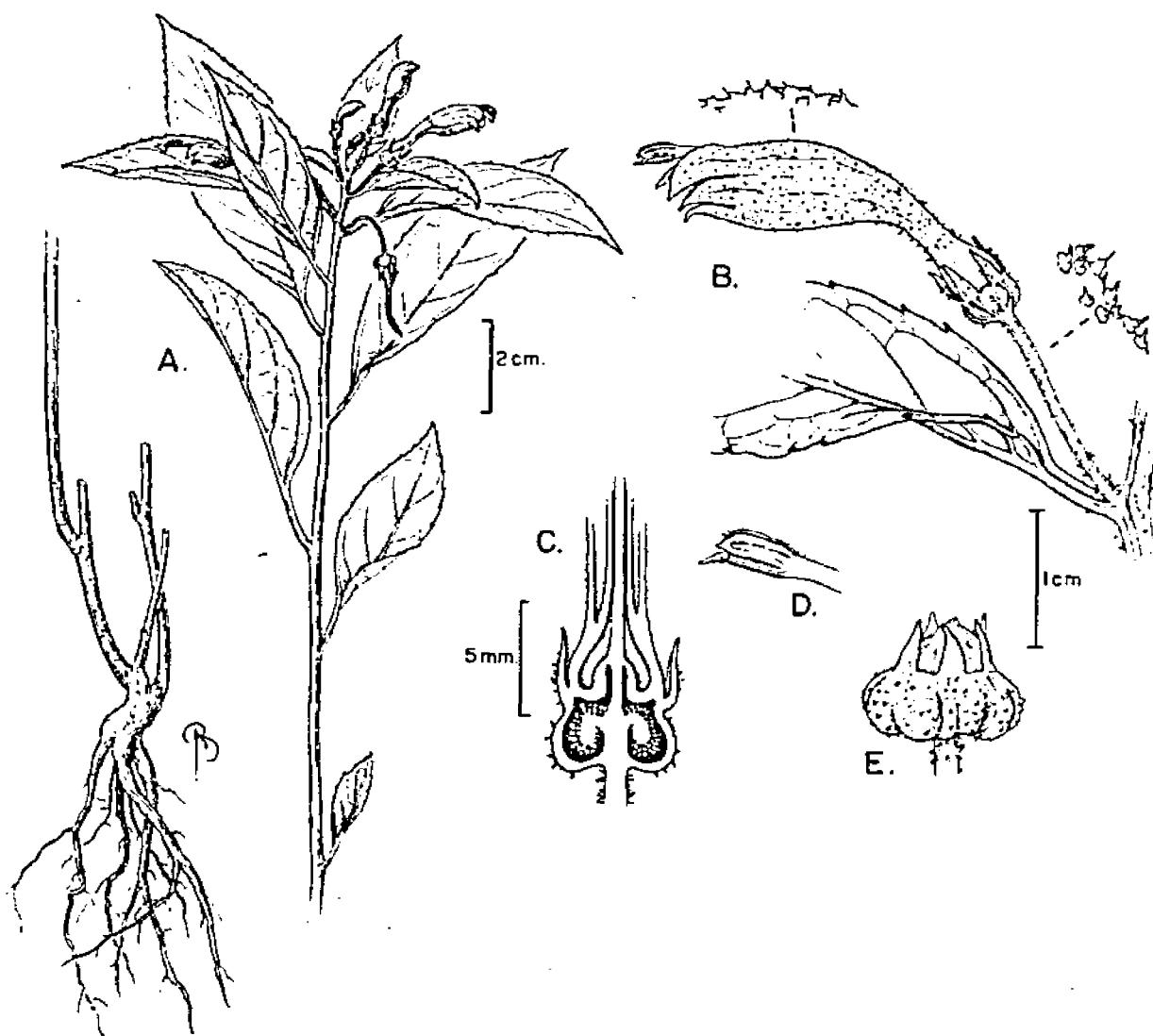


Fig. 27. A-E, *Centropogon lasiodorus* (from Stein et al. 3868). A, habit with close-up of ciliate marginal callosities. B, detail of abaxial leaf surface. C, flower and pedicel with close-up of multicellular trichome. D, frontal view of corolla orifice, anther tube, and exserted stigma. E, longitudinal section of flower and ventrally flattened filament tube cross-section. F-I, *Centropogon carpishensis* (from Stein & Todzia 2310). F, habit with close-up of leaf margin. G, detail of inflorescence. H, longitudinal section of flower with close-up of multicellular trichome. I, anther tube.



Fig. 28. Distribution map of: *Centropogon granulosus* (●) subsp. *granulosus*,
(■) subsp. *rutilus*, and (▲) subsp. *nutans*.

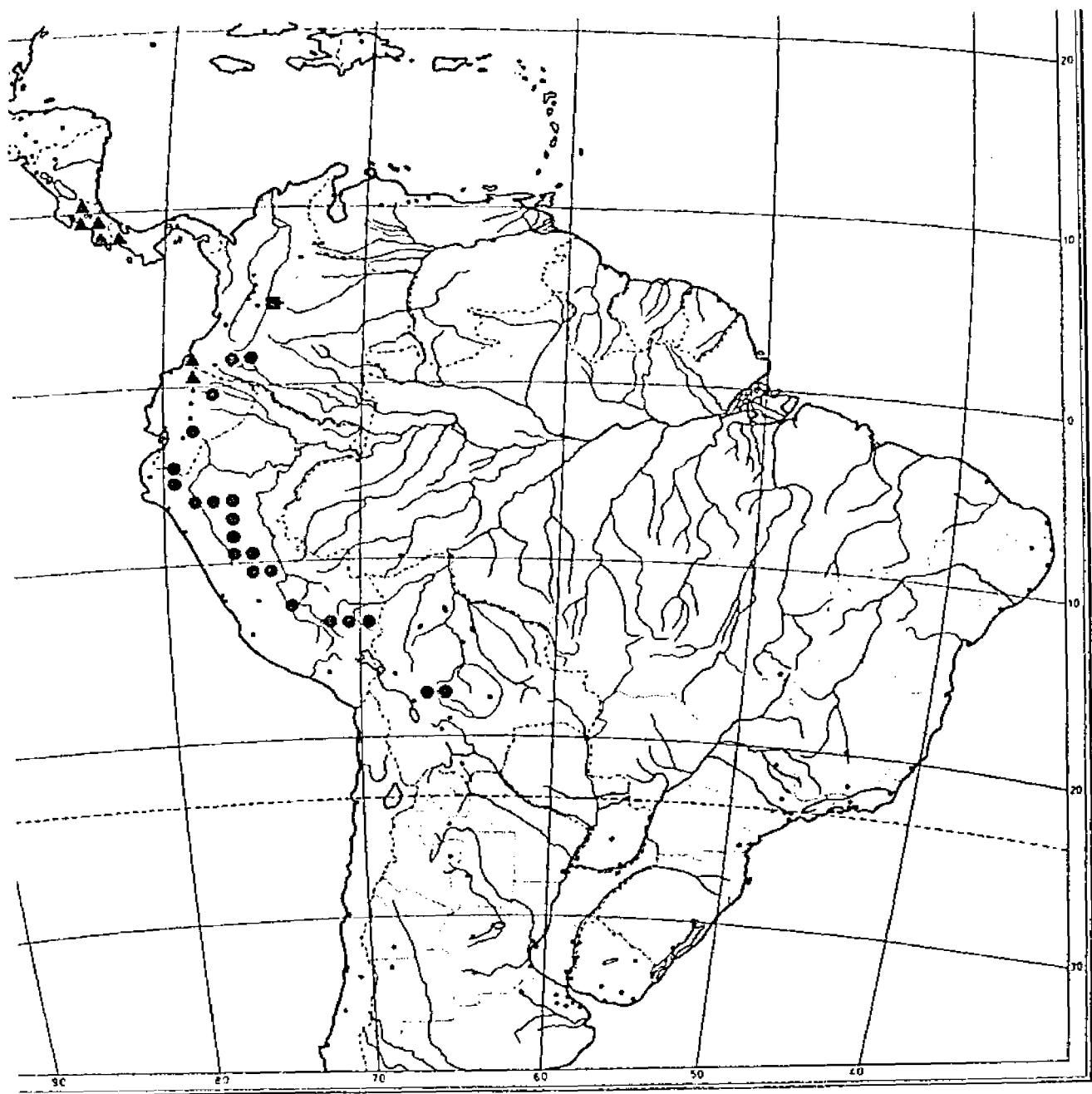


Fig. 29. Distribution map of: *Centropogon granulosus* (●) subsp. *lugens*, (■) subsp. *tortilis*, and (▲) subsp. *lateriflorus*.

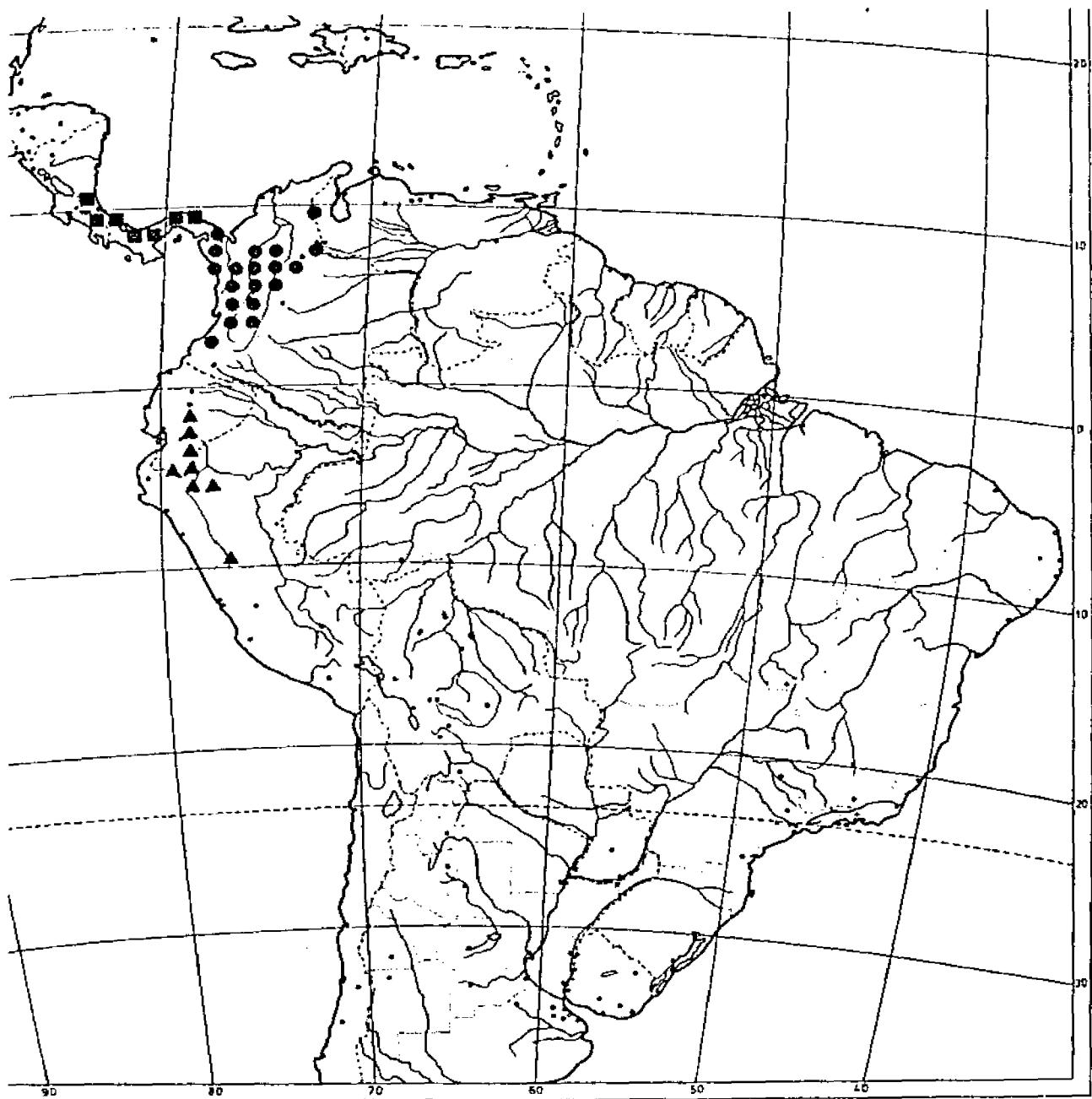


Fig. 30. Distribution map of: (●) *Centropogon cuatrecasanus*, (■) *C. pulcher*, and (▲) *C. vargasii*.

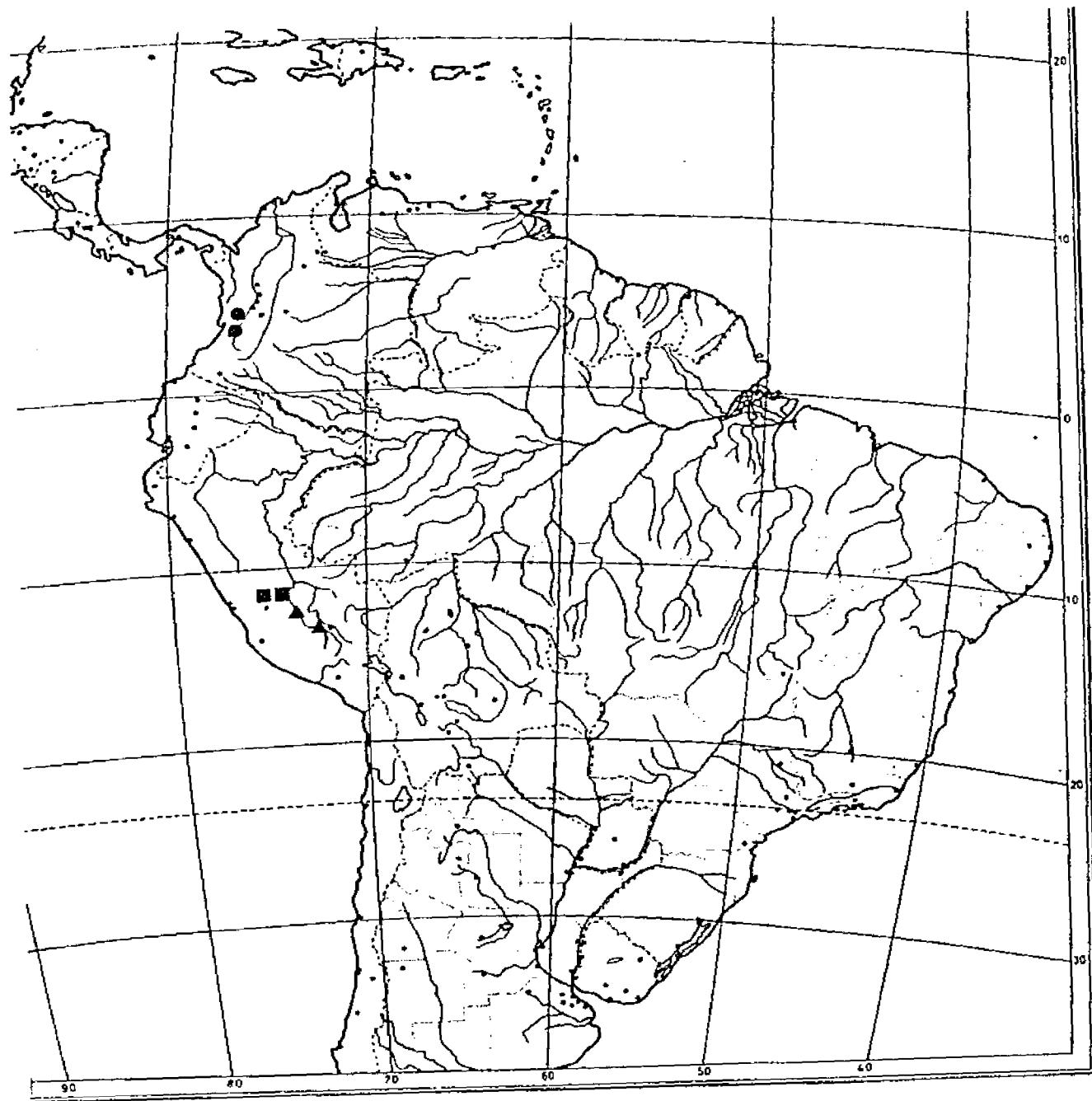


Fig. 31. Distribution map of: *Centropogon densiflorus* (●) subsp. *densiflorus*, and
(★) subsp. *gracilis*, (■) *C. trachyanthus*, and (○) *C. baezanus*.

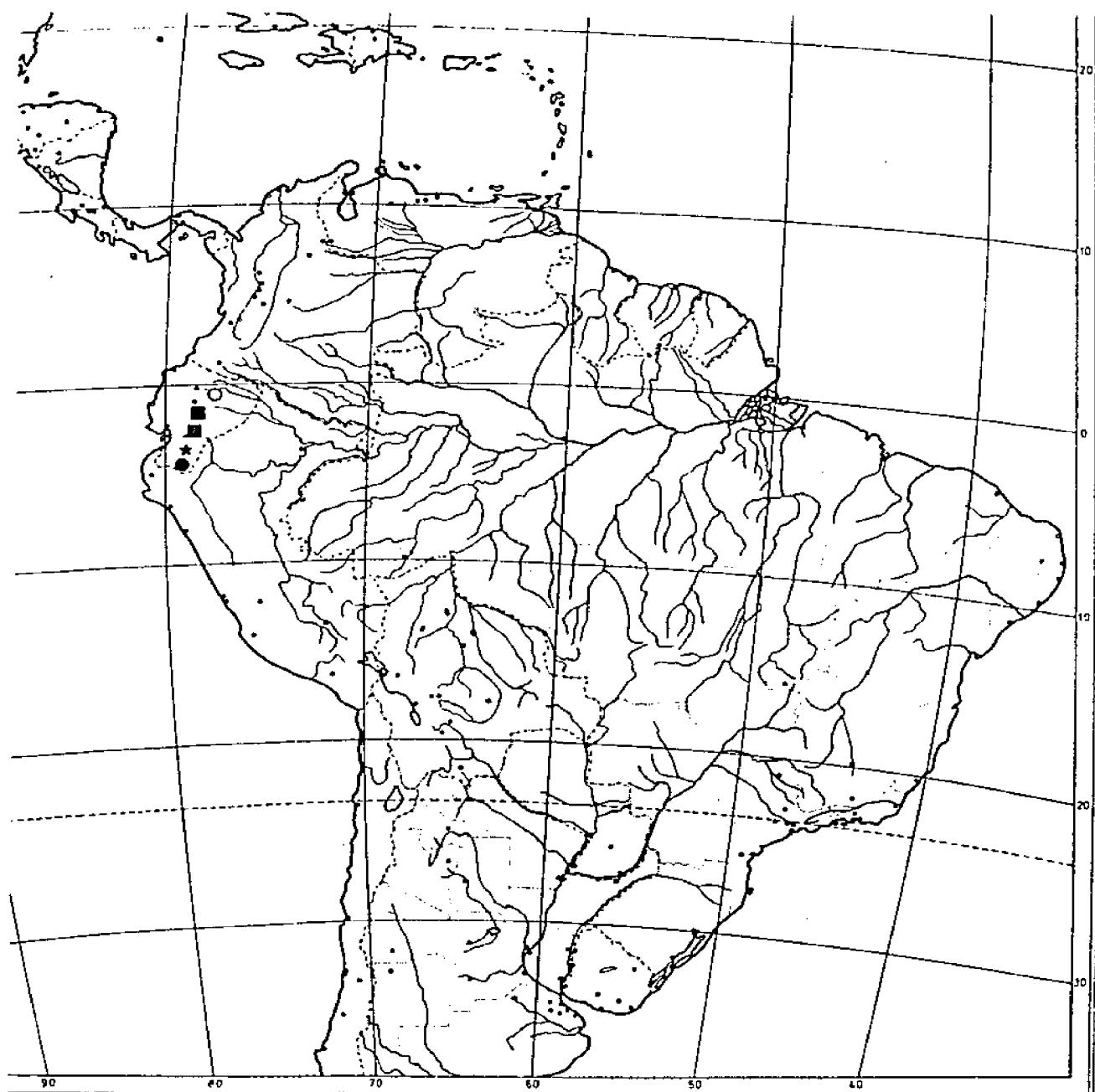


Fig. 32. Distribution map of: (●) *Centropogon curvatus*, (■) *C. vaughianus*,
(○) *C. papillosum*, (★) *C. carpishensis*, and (⊕) *C. bangii*.



Fig. 33. Distribution map of: (●) *Centropogon loretensis*, (■) *C. ampicorollinus*, and (○) *C. latifolius*.

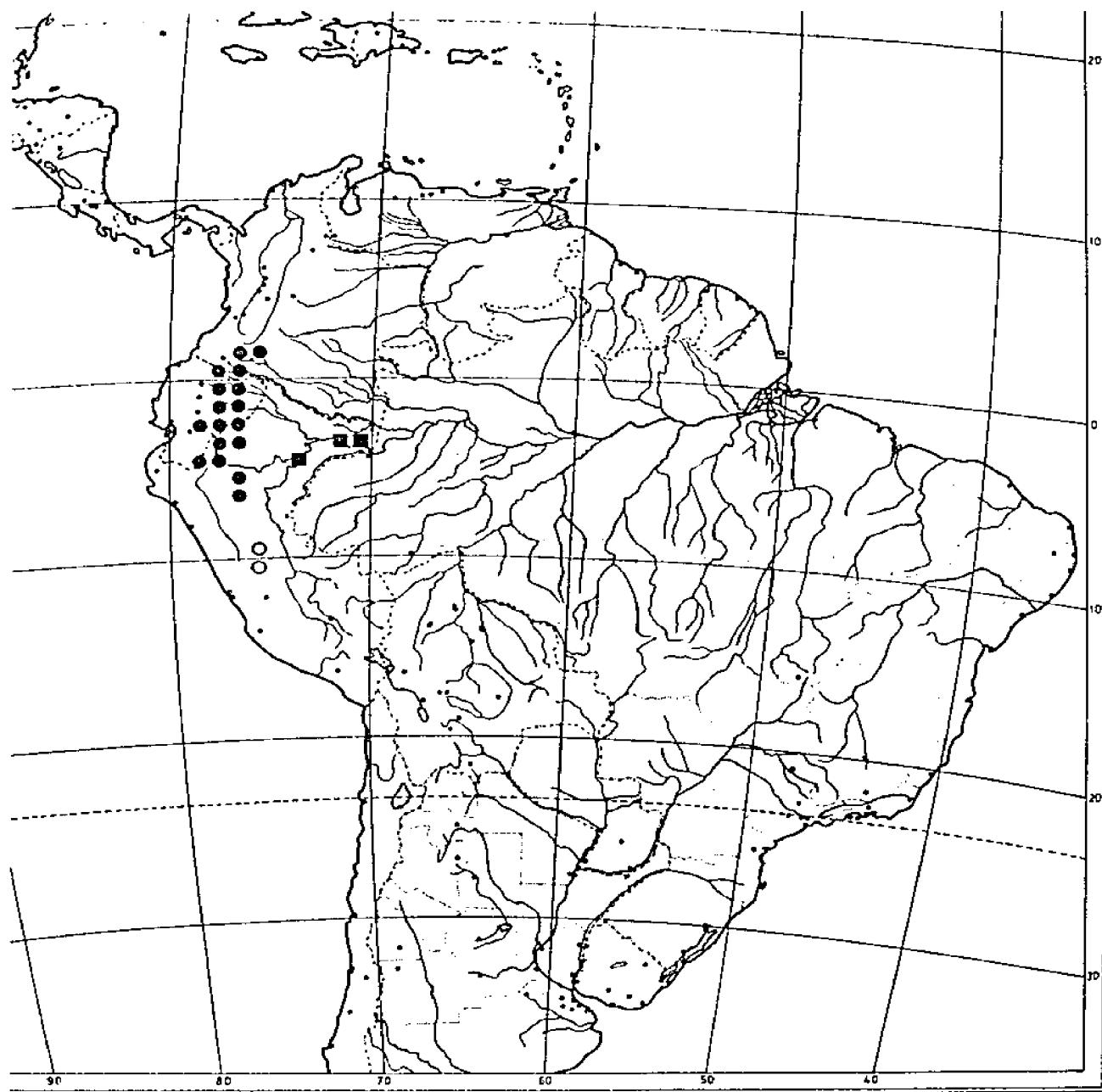


Fig. 34. Distribution map of: (●) *Centropogon yungensis*, (■) *C. urubambae*, and (▲) *C. reflexus*.

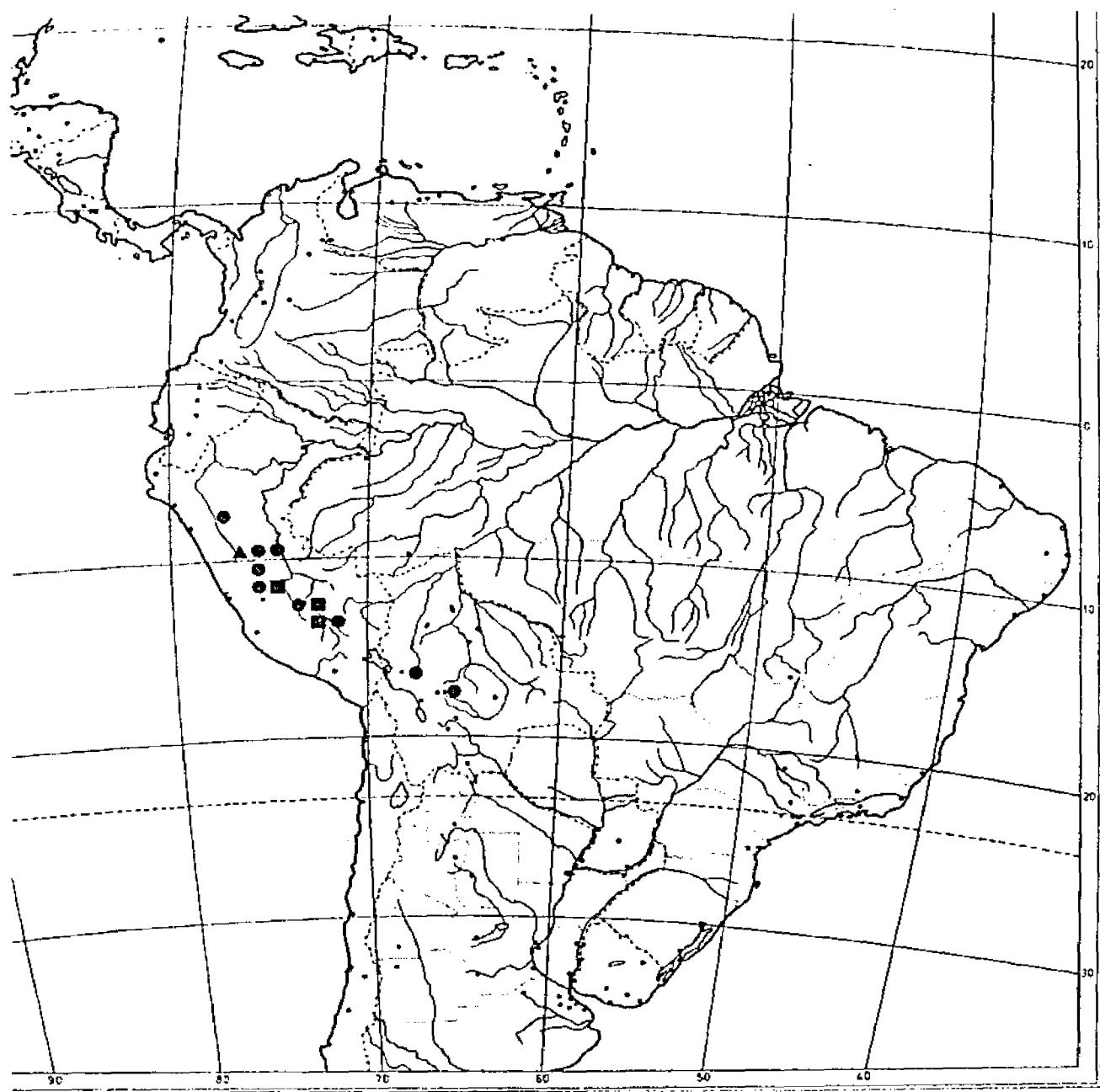


Fig. 35. Distribution map of: (●) *Centropogon sciaphilus*, (■) *C. lasiodorus*,
(○) *C. arcuatus*, and (⊕) *C. pygmaeus*.



Section *Grandes*

Centropogon subgenus **Centropogon** section **Grandes** B. A Stein, sect. nov.

Type species. *Centropogon grandis* (Linnaeus filius) Presl.

Section *Grandes* consists of a group of species centered around *C. grandis* and *C. solanifolius*. It is characterized by a normally erect to sprawling habit, upright, bracteate, folio-bracteose, or rarely foliose inflorescences, mostly long, gradually curving corollas without well-differentiated throats, and ventrally flattened filament tubes that are rarely exserted more than 5 mm from the corolla tube. This section appears closely related to sect. *Campylobotrys* based on the unusual filament tube, and occasional species, such as the vining *C. semperflorens* approach that section in some respects. Although this section is rather widespread, ranging from Central America to northern Peru, it displays an unusual distributional pattern. In spite of occurring in all three cordilleras of Colombia, and along the western slope of the Ecuadorean Andes, members of this section are not found anywhere along the eastern slope of the Andes.

A detailed treatment of the approximately 15 species in this section is in preparation and is not included in the present work. Those species that are tentatively recognized in this section, however, are indicated in Table 18, along with the synonyms.

Table 18

Species Currently Recognized in Section *Grandes*
and Their Synonyms

***Centropogon albolimbatus* F. Wimmer**

Centropogon albolimbatus var. *concolor* F. Wimmer

Centropogon albolimbatus var. *serratus* (Gleason) F. Wimmer

Centropogon albolimbatus var. *villosus* F. Wimmer

Centropogon serratus

***Centropogon beslerioides* (H.B.K.) A. DC.**

Lobelia beslerioides H.B.K.

Siphocampylus beslerioides (H.B.K.) G. Don

Centropogon aristi var. *subterpilis* F. Wimmer

Centropogon pilosulus var. *quindiuensis* F. Wimmer

***Centropogon gallerensis* (Gleason) B. A Stein ined.**

Centropogon pedicellaris var. *gallerensis* Gleason

***Centropogon grandis* (L.f.) Presl**

Lobelia grandis L.f.

Siphocampylus grandis (L.f.) G. Don

Centropogon aristi F. Wimmer ? (or *Centropogon beslerioides*?)

Centropogon grandis var. *hirtellus* F. Wimmer

Centropogon rostellatus

***Centropogon hypotrichus* F. Wimmer**

***Centropogon laxus* A. Zahlbr.**

Centropogon brachyandrus F. Wimmer

***Centropogon linnaeanus* F. Wimmer**

***Centropogon longipetiolatus* F. Wimmer**

Centropogon pamplonensis F. Wimmer

Centropogon pamplonensis var. *fratellus* F. Wimmer

Centropogon majalis F. Wimmer

Centropogon pedicellaris Gleason

Centropogon scabellus F. Wimmer

Centropogon altibracteolatus F. Wimmer

Centropogon semperflorens F. Wimmer

Centropogon solanifolius Benth.

Centropogon austin-smithii Standl.

Centropogon discolor Kunth, & Bouche

Centropogon flexuosus F. Wimmer

Centropogon longipes Regel

Centropogon montanus F. Wimmer

Centropogon nubicola Gomez-L & L.D. Gomez

Centropogon ovalifolius A. Zahlbr.

Centropogon prostratus Benth.

Centropogon psilandrus F. Wimmer

Centropogon riparius F. Wimmer

Centropogon solanifolius var. *hirtellus* F. Wimmer

Centropogon solanifolius var. *inconstans* F. Wimmer

Centropogon solanifolius var. *speciosus* (Planch.) F. Wimmer

Centropogon speciosus Planch.

Centropogon subfalcatus A. Zahlbr.

Centropogon xestus F. Wimmer

Centropogon trianae Zahlb.

Centropogon decemlobus Gleason

Centropogon purdieanus Gleason

Centropogon trianae var. *cuspidatus* Zahlb.

Centropogon trianae var. *decemlobus* (Gleason) F. Wimmer

Centropogon trianae var. *purdieanus* (Gleason) F. Wimmer

Centropogon vernicosus Zahlb.

Centropogon pamplonensis var. *glabrisflorus* F. Wimmer

Centropogon pamplonensis var. *peruvianus* F. Wimmer

Centropogon pilosus F. Wimmer

Centropogon flexuosus var. *ethnicus* F. Wimmer

Excluded Species

***Centropogon dubius* (A. Zahlbruckner) F. Wimmer, Pflanzenreich IV, 276b: 196, 1943.**

= *Siphocampylus dubius* A. Zahlbruckner, Bull. Torrey Bot. Club 24: 385, 1897.

Type. Bolivia. La Paz: Unduavi, 2400 m, Oct 1885, Rusby 637 (holotype, NY; isotypes, MICH, NY).

In publishing this species, Zahlbruckner (1897) expressed his uncertainty about the generic placement of *Siphocampylus dubius* by inserting a parenthetical question mark after the genus name, and he suggested that perhaps it was instead a *Centropogon*. The lack of mature fruit in the material he saw, however, did not allow him to unambiguously ascertain the generic placement. Wimmer (1943) placed this species in his subsect. *Axillares* based on the axillary flowers, and what appeared to both he and Zahlbruckner to be a fused antheridial scale similar to that found in subgen.

Centropogon. Recent collections of this species show the fruit to be capsular, establishing its position in *Siphocampylus* rather than *Centropogon*. Furthermore, I have examined the anthers of this species, both fresh and dried, and find that the terminal trichomes are not truly fused into a scale.

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