To the Graduate Council:

I am submitting herewith a dissertation written by Jose L. Panero entitled "A monograph of the Andean genus Pappobolus." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

Edward E. Schilling, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

A MONOGRAPH OF THE ANDEAN GENUS PAPPOBOLUS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Jose L. Panero

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ABSTRACT

The genus Pappobolus S. F. Blake as circumscribed here includes the taxa previously placed in Pappobolus (sensu Blake 1916), the South American species of Helianthus L. (recently known as Helianthopsis H. Robinson) and one species transferred from Viguiera Kunth, V. acutifolia S. F. Blake. It consists of 45 taxa (38 species) 18 of which are newly described here, P. amoenus, P. andinus, P. cajamarcensis, P. davidii, P. decumbens, P. ecuatorianus, P. ecuatorianus var. lancifolius, P. juncosae, P. matthewsii var. occidentalis, P. matthewsii var. viridifolius, P. microphyllus var. dillonii, P. microphyllus var. liberus, P. microphyllus var. soukupii, P. robinsonii, P. sanchezii, P. schillingii, P. stork-hortonii, and P. youngiorum. The genus is distinguished from closely related genera such as Simsia Pers., Tithonia Desf. ex Gmelin and Viguiera by the deciduous disk achene pappus and a shrubby to arborescent habit. Pappobolus is endemic to the Andes of Colombia, Ecuador and Peru. It occupies habitats ranging from xerophytic and tropical deciduous forests to montane moist forests, and some species also occur in the Páramo or Jalca of northern Peru. The greatest concentration of species is encountered in northern Peru in the basin of the Marañón River. Leaf venation patterns and floral microcharacters such as endothecial cell morphology and style shape are essentially identical among the species of the genus. The genus is characterized by monochasial and dichasial thyrsoid capitulescences, although structural differences are common and apparently are tied to environmental conditions. Chromosome numbers obtained from a majority of the species

support a base chromosome number of $\underline{x}$ = 17 for the genus and indicate a lack of polyploidy. A cladistic analysis of the genus supports the recognition of two subgenera. Pappobolus subg. Apricus subg. nov. with nine species is distinguished by yellow anther thecae and disk flower lobes, large monochasial thyrsoid capitulescences and small heads. Pappobolus subg. Pappobolus with 29 species is distinguished by black anther thecae and disk flower lobes, monochasial and dichasial thyrsoid capitulescences (some associated with few, large heads) densely lanate herbage and sclerified leaves. Keys, distribution maps and illustrations are provided for all the species.

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1. INTRODUCTION

ABSTRACT

The genus Pappobolus S. F. Blake as circumscribed here includes the taxa previously placed in Pappobolus (sensu Blake 1916), the South American species of Helianthus L. (recently known as Helianthopsis H. Robinson) and one species transferred from Viguiera Kunth, V. acutifolia S. F. Blake. It consists of 45 taxa (38 species) 18 of which are newly described here, P. amoenus, P. andinus, P. cajamarcensis, P. davidii, P. decumbens, P. ecuatorianus, P. ecuatorianus var. lancifolius, P. juncosae, P. matthewsii var. occidentalis, P. matthewsii var. viridifolius, P. microphyllus var. dillonii, P. microphyllus var. liberus, P. microphyllus var. soukupii, P. robinsonii, P. sanchezii, P. schillingii, P. stork-hortonii, and P. youngiorum. The genus is distinguished from closely related genera such as Simsia Pers., Tithonia Desf. ex Gmelin and Viguiera by the deciduous disk achene pappus and a shrubby to arborescent habit. Pappobolus is endemic to the Andes of Colombia, Ecuador and Peru. It occupies habitats ranging from xerophytic and tropical deciduous forests to montane moist forests, and some species also occur in the Páramo or Jalca of northern Peru. The greatest concentration of species is encountered in northern Peru in the basin of the Marañón River. Leaf venation patterns and floral microcharacters such as endothecial cell morphology and style shape are essentially identical among the species of the genus. The genus is characterized by monochasial and dichasial thyrsoid capitulescences, although structural

differences are common and apparently are tied to environmental conditions. Chromosome numbers obtained from a majority of the species support a base chromosome number of x = 17 for the genus and indicate a lack of polyploidy. A cladistic analysis of the genus supports the recognition of two subgenera. Pappobolus subg. Apricus subg. nov. with nine species is distinguished by yellow anther thecae and disk flower lobes, large monochasial thyrsoid capitulescences and small heads. Pappobolus subg. Pappobolus with 29 species is distinguished by black anther thecae and disk flower lobes, monochasial and dichasial thyrsoid capitulescences (some associated with few, large heads) densely lanate herbage and sclerified leaves. Keys, distribution maps and illustrations are provided for all the species.

RESUMEN

El género Pappobolus tal como se circumscribe aquí, incluye los táxones previamente clasificados bajo Pappobolus (sensu Blake, 1916), las especies sudamericanas de Helianthus L. (recientemente conocidas como Helianthopsis H. Robinson) y una especie transferida del género Viguiera Kunth, V. acutifolia S. F. Blake. El género consiste de 45 táxones (38 especies) de los cuales, 18 son descritos como nuevos en este estudio, P. amoenus, P. andinus, P. cajamarcensis, P. davidii, P. decumbens, P. ecuatorianus, P. ecuatorianus var. lancifolius, P. juncosae, P. matthewsii var. occidentalis, P. matthewsii var. viridifolius, P. microphyllus var. dillonii, P. microphyllus var. liberus, P. microphyllus var. soukupii, P. robinsonii, P. sanchezii, P.

schillingii, P. stork-hortonii, P. youngiorum. El género se distingue de otros estrechamente relacionados tales como Simsia Pers., Tithonia Desf. ex Gmelin y Viguiera por tener el papus (vilano) del aquenio de la flor del disco deciduo y por un hábito sufruticoso a arborescente. Pappobolus es endémico de los Andes de Colombia, Ecuador y Perú con la mayor concentración de especies en el norte del Perú en la vertiente del Río Marañón. Se encontró que los patrones de nervación foliar así como microcaracteres florales tales como la morfología celular del endotecio y forma del estilo son esencialmente idénticos en las especies del género investigadas. Los números cromosómicos obtenidos indican un número cromosómico básico de x = 17 para el género y la ausencia de poliploidía. Un analisis cladistico del género apoya el reconocimiento de dos subgéneros. Pappobolus subg. Apricus subg. nov. con 9 especies se distingue por tener las tecas de las anteras y los lóbulos de las flores del disco amarillos o pardo-amarillos, capitulescencias tirseiformes monocasiales y capítulos relativamente pequeños. Pappobolus subg. Pappobolus con 29 especies se distingue por tener las tecas de las anteras y los lóbulos negros y capitulescencias tirseiformes monocasiales o dicasiales (algunas de estas asociadas con largos pedúnculos y capítulos grandes). Aunado a estas caracteristicas, algunos miembros de este subgénero se caracterizan por tener hojas duras y esclerificadas con una copiosa pubescencia lanada, particularmente en el envés de la hoja, así como en otras partes de la planta. Claves, mapas de distribución e ilustraciones son provistos para todas las especies.

GENERAL INTRODUCTION

Pappobolus S. F. Blake is a genus of 38 species (45 taxa) of shrubs and small trees of the Andes of Colombia, Ecuador and Peru with the greatest concentration of species in the Department of Cajamarca south of the Huancabamba deflection in the basin of the Marañón River, Peru. The genus is a member of the mostly Neotropical subtribe Helianthinae of the family Asteraceae. Because most of the genera of the subtribe are endemic to or have a majority of their species in North America, it is notable that Pappobolus, along with Scalesia and Syncretocarpus are endemic to South America.

Disk achene characters, especially discrete differences in pappus morphology, have been used to circumscribe genera within subtribe Helianthinae. Pappobolus was erected by Blake (1916) to accomodate three species having a disk achene pappus of a crown of deciduous awns reminiscent of those in Perymenium Schrad. and Steiractinia S. F. Blake. As circumscribed here, Pappobolus includes the South American members of Helianthus L. that were recently transferred to Helianthopsis H. Robinson, a species previously placed in Viguiera Kunth, V. acutifolia S. F. Blake and the species classified under Pappobolus.

Pappobolus is notable because the diverse types of habit, in addition to capitulescence, vestiture, and leaf and floral morphology of its members make it difficult to define generic morphological generalizations. In addition, Pappobolus is not defined by a discrete and distinctive morphological character but rather by a unique

combination of characters, all most of which are individually present in other allopatric, closely related genera such as Helianthus, Simsia Pers., Tithonia Desf. ex Gmelin and Viguiera. Pappobolus shares with the shrubby Mexican Viguieras, Helianthus, Tithonia and Simsia a similar leaf venation morphology that differs considerably from that exhibited by the perennial herb Viguieras sympatric with Pappobolus (see Morphology: Leaf Venation). The shrubby to arborescent Mexican Viguieras differ from Pappobolus in having a persistent and morphologically different disk achene pappus. Simsia is effectively separated from Pappobolus by its flat achenes, herbaceous phyllaries and style morphology. Helianthus shares with some members of Pappobolus a similar disk achene pappus morphology but differs from Pappobolus by having an annual or perennial herb habit and a distinct style morphology. Tithonia, endemic to Mexico and Central America differs from Pappobolus by having fistulose peduncles and cuspidate to aristate pale apices.

Pappobolus occurs in a wide variety of habitats between 650 and 4200 m. It inhabits premontane to lower montane dry scrub and dry forest of the western escarpment of the Andes and other dry interandean valleys. It also occurs in montane moist forest of the western and eastern Andean ranges with one species venturing into montane wet forest commonly referred as "la ceja de selva" (Weberbauer 1945). Approximately a third of the species are encountered in high, seasonally dry, interandean valleys or ranges with a few species being abundant and even dominant elements of the wet Jalca (local name for Páramo-like areas; Weberbauer 1945, p. 437) or Páramo of northern Peru.

Most of the species are apparently restricted to their particular habitats and only a few are somewhat wide-ranging and common. A few others are rare and often grow in areas of difficult access where the original vegetation still occurs amid the expanding agricultural and pasture lands. These narrowly endemic species are clearly threatened with extinction.

Pappobolus is the only genus of subtribe Helianthinae that is encountered at altitudes above 3000 m and certainly the only genus to occupy the peculiar Páramo habitat of the Andes of South America. Closely related genera are absent from equivalent areas in the Mexican or Central American highlands. The densely lanate herbage and thick leathery leaves exhibited by these high altitude species are only observed in the Heliantheae by genera in the subtribe Espeletiinae. Unlike Espeletia Mutis and related genera, Pappobolus is also common in several lower altitude habitats of the Andes. These wide environmental tolerances are only matched within the subtribe Helianthinae by the much larger genus Viguiera and by other distantly related Asteraceae such as Calea L., Bidens L. and Baccharis L.

Within Pappobolus two subgenera are recognized (Table 1; Tables and Figures may be found in Appendices 1, 2 and 9): P. subg. Apricus includes all the species with yellow anther thecae, small heads, large capitulescences, alternate leaves, and its species are mostly restricted to xerophytic or tropical deciduous forests. Pappobolus subg. Pappobolus comprises an heterogeneous group of species that occupies montane moist forest or dry scrub and Páramo or Jalca. The

subgenus is distinguished by black anther thecae and disk flower lobes, small to large heads, small and leafy capitulescences and either alternate or opposite leaves. Within P. subg. Pappobolus three somewhat distinctive groups based on morphology and habitat preferences can be distinguished: the nigrescens group, the discolor group and the stuebelii group. The nigrescens group is characterized by having broad and thin leaves with shallowly serrate to serrate margins and large heads in open, long-peduncled capitulescences. The discolor and stuebelii groups are characterized by having thick and somewhat coriaceous leaves with densely lanate white or tan abaxial surfaces. The stuebelii group is further distinguished from the discolor group by having much larger heads reminiscent of those of the nigrescens group and a more arborescent habit. The morphology and ecology of these four groups are discussed in more detail in the respective sections below.

This study is based on herbarium specimens, field studies and laboratory analyses and summarizes morphological, ecological and geographical information to provide a comprehensive monograph of the genus Pappobolus. Field studies were instrumental in obtaining a more inclusive concept of this highly heterogenous genus. Several trips were taken to Ecuador and Peru that resulted in the discovery of several new taxa; my collections substantially increased the number of specimens available for study. This monograph is part of an ongoing research project on Viguiera and related genera and represents the taxonomy of Pappobolus based on our present knowledge of the Colombian, Ecuadorian and Peruvian flora.

TAXONOMIC HISTORY

Pappobolus argenteus, P. microphyllus and P. verbesinoides, the first species of Pappobolus to be described, were collected by Humboldt and Bonpland and later classified by Kunth (1820) as part of the mostly North American genus Helianthus. Several decades later, Hieronymus (1895, 1901, 1905) named more species of Helianthus based on collections of Jelski, Lehmann, Sodiro and Stuebel. Blake (1916), while working on a revision of Viguiera, established Pappobolus with P. macranthus as its sole species based on a collection by Pearce from central Peru (Table 2). The new genus was diagnosed by a glabrous disk achene and disk achene pappus of a deciduous crown of awns. He allied the new genus to Perymenium, Melanthera Rohr., and Steiractinia but at the same time called attention to other achene and involucre characters that were reminiscent of Helianthus (Blake 1916). A few years later, in 1917 and later in 1926, he named two new species of Pappobolus, bringing the total to three. During the same time period (1917-1926) he also continued to name new species of South American Helianthus based on collections of Rose, Holway, and Macbride and Featherstone. All of the new species of Helianthus possessed the typical glabrous achene and a pappus of two deciduous awns as opposed to the crown of awns characteristic of Pappobolus. Cuatrecasas (1964, 1965) also followed achene characters when he described one species each of Helianthus and Pappobolus from Peru.

Heiser (1957) was the first to revise the South American species of Helianthus. In the process, he named two new species, P. lanatus

and P. nigrescens, and hinted as to the potentially polyphyletic nature of Helianthus s. l. The shrubby habit and isolated geographical position in South America (far from the southernmost elements of Helianthus in central Mexico) led him to propose informally Helianthus subg. Viguieropsis to accomodate the South American elements of the genus. Robinson (1979) went further and erected the new genus Helianthopsis to accomodate all of the South American species of Helianthus. He suggested that the affinities of the genus were with Viguiera and not Helianthus. In the same paper he named two new species of Helianthopsis. The latest publication dealing with the genus was by Robinson (1983) in which he named two additional new species, bringing the total of known species to 24. The new species described here, coupled with the transfers from other genera and the placement of a few in synonymy, result in a total of 38 species here recognized under the genus Pappobolus.

GENERIC RELATIONSHIPS

Morphological evidence (Heiser 1957; Robinson 1979, 1981) suggests that the genera Helianthus, Scalesia, Simsia, Syncretocarpus S. F. Blake, Tithonia and Viguiera are the closest relatives of the genus Pappobolus (Table 3). These genera, with the exception of Syncretocarpus and Viguiera, are mainly North American (Fig. 1). As stated above, all of these genera with the exception of Tithonia are recognized by discrete differences in the duration and morphology of the disk achene pappus, its presence or absence, and the shape and pubescence of the disk achene. The name Viguiera has been the

repository for many species of apparently varied affinities that happened to possess the generic pappus morphology of two awns and several intermediate squamellae. The other genera here discussed, although sometimes possessing the same pappus morphology, escaped inclusion in Viguiera s. l. by virtue of a peculiar or unusual but always discrete morphological trait (i.e. Syncretocarpus: corky-margined achene; Tithonia: fistulose peduncle; Simsia: flat achenes). The increment in collections, a better understanding of the ecology and distribution of these taxa and the use of chemical and molecular techniques have produced valuable information for a reexamination of these classification schemes.

A study of chloroplast DNA restriction fragment analysis of Pappobolus and related genera by Schilling and Jansen (1989) confirms the paraphyletic nature of Viguiera as presently circumscribed. Their study also reveals that Pappobolus is a monophyletic group whose sister genera are Helianthus, Simsia, Tithonia, and some infrageneric taxa of Viguiera such as V. series Aureae S. F. Blake, V. series Pinnatilobatae S. F. Blake, V. series Grammatoglossae S. F. Blake, and V. subg. Amphilepis S. F. Blake. More importantly, their data also show that Helianthus is not the immediate sister group of Pappobolus. Another important finding of their study is that all these groups are derived compared to the endemic Mexican members of Viguiera such as V. sect. Maculatae (S. F. Blake) Panero & E. Schilling, V. subg. Bahiopsis (Kellogg) E. Schilling, V. dentata (Cav.) Spreng. and the small genus Heliomeris Nutt (V. sect. Heliomeris).

The following paragraphs compare related genera to Pappobolus, particularly P. subg. Apricus. Pappobolus subg. Pappobolus is believed to be a highly specialized group of species specifically adapted to high altitude habitats and therefore distinguished by several apomorphies not shared by any other group of the subtribe. Any similarity between this group and related genera will probably be a plesiomorphy or a parallelism. It is believed that the morphological homogeneity of P. subg. Apricus, coupled with a predilection for xerophytic to tropical deciduous forest habitats typically inhabited by the purported sister genera, may have contributed to maintaining certain ancestral characters now difficult to discern in P. subg. Pappobolus.

Helianthus shares with Pappobolus a similar disk achene pappus morphology and duration, although other characters such as habit and floral microcharacters suggest a distant relationship. Helianthus is a genus of annual and perennial herbs of North America (Heiser et al. 1969). It is characterized by a deciduous disk achene pappus of two awns, and intermediate squamellae lacking or rarely present. In addition, most of the species also possess a pronounced tricuspidate pale apex. Another distinguishing morphological character of Helianthus is that the style branches are tapered and end in an appendage, although a somewhat similar morphology is also observed in Simsia and to a certain extent in Tithonia. The style in Pappobolus is acute and has no appendage, and the anther endothecium never exhibits polarized to radial cells somewhat common in at least a few species of Helianthus (see Morphology: Floral Micromorphology). However, the most

conspicuous difference between the two genera is the woody habit of Pappobolus.

Simsia shares with some species of Pappobolus a similar ray ovary and phyllary morphology. It is a genus of 18 species (Schilling & Spooner 1988) of annual and perennial herbs (some of these somewhat woody at the base) of Mexico and Central America with two or three species in South America. Simsia dombeyana DC. and S. fruticulosa (Spreng.) S. F. Blake are sympatric with some members of P. subg. Apricus. The genus is recognized by its flat achenes, auriculate leaf bases (nodal disks) exhibited by some of its members, sclerified cells exhibited by most of the species at the tip of the disk flower lobes, and long trichomes along the anther connective. These characters are not observed in any other related genera. Some species of Simsia, especially S. foetida (Cav.) S. F. Blake, share with some species of P. subg. Apricus stramineous-green, lanceolate to lageniform phyllaries conspicuously traversed by soft green longitudinal bands that coalesce into a green, herbaceous apex. Simsia also shares with the same group of species a long and thin ray ovary associated with oval to oblong, rather small ligules (rarely beyond 1.5 cm long).

There are no obvious morphological similarities between Pappobolus and Tithonia. Tithonia is a highly diverse genus primarily circumscribed by the presence of a fistulose peduncle (LaDuke, 1982) although in some species the hollow peduncle is difficult to discern (T. pedunculata Cronquist and some forms of T. calva Sch.-Bip.). It exhibits a wide variation of phyllary and disk achene pappus

morphologies and has no unifying habit, with annuals, perennial herbs, shrubs and trees all represented in the genus. The genus is mostly Mexican with a few species venturing into Central America. Some members of P. subg. Apricus share with the herbaceous species of Tithonia the tightly-packed, flat-topped apices of growing shoots. In addition, some members of P. subg. Apricus possess the soft, minutely hirsute to strigose vestiture that is so typical of the annual species of Tithonia. I have not observed the growing shoot morphology nor the vestiture characters oulined above in Simsia, Viguiera or Helianthus.

Based on pale trichome morphology, involucral characters and disk achene pubescence and pappus, Syncretocarpus appears to be significantly different from Pappobolus. Syncretocarpus consists of one or two species endemic to the western escarpment of the Andes of south-central Peru. It is characterized by a low, shrubby habit, sclerophyllous, small leaves (rarely exceeding 5 cm in length), a disk achene with a pappus of 2 awns and 2-4 broad squamellae and a prominent eliasome, and acute to tapered style branches. The pales are conspicuously glandular in contrast to any species of Pappobolus, and the involucre is composed of three loosely arranged series of phyllaries. The disk corolla is characterized by having 10-15 vascular bundles flanked by dark yellow resin ducts. This resin duct pattern is elsewhere observed in some species of Tithonia (T. tubaeformis (Jacq.) Cass. and T. rotundifolia (Miller) S. F. Blake). The taxonomic position of this genus is difficult to assess. The combination of a shrubby habit and the typical Viguiera achene are indeed unique considering that there are no shrubby Viguieras in the Andes and

probably in the rest of South America. In addition, some forms of Syncretocarpus sericeus, from the Santa River valley in Ancash Department, tend to have linear leaves and highly graduated involucres with prominent achenes densely covered by usually long trichomes of a type not seen in Viguiera or related genera but reminiscent of those in the genera Flourensia DC. and Encelia Adans.

Viguiera appears to represent a paraphyletic assemblage of species. The genus is widely recognized to have a diversity of types of involucre, capitulescence structures, habit, leaf morphology, herbage pubescence, disk achene morphology, etc. The only unifying theme among the species of the genus is the persistent disk achene pappus of 2 awns and several intermediate squamellae, although a sizable group of species are epappose. However, there are also differences in the width, color and attachment of the awns and the overall shape of the achenes, as well as in the diversity or absence of their pubescence. In other words, Viguiera defies a simple, straightforward generic definition.

Viguiera as presently understood is the most speciose genus in the Helianthinae and is estimated to comprise approximately 160-190 species. Although they are rare in hot, wet areas normally occupied by tropical rain or cloud forests, it occupies a great diversity of habitats. It is widely distributed from the southwestern United States to Argentina (Blake 1918). It has two major centers of diversity: one in central and southern Mexico and the other in southern Brazil, Paraguay and northeastern Argentina. The Mexican species are mostly

shrubby, and some are even arborescent (Panero & Schilling 1988), perennial herbs and annuals are also present, although in smaller numbers. They also comprise a series of highly diverse, discrete infrageneric taxa whose phylogenetic relationships are difficult to discern. In contrast, the South American Viguiera are, for the most part, variations on a single theme. Apparently all are perennial herbs, mostly with scabrous herbage and golden yellow to yellow-orange flowers. The major departures within this morphological syndrome are based in involucre seriation and leaf shape.

Heiser (1957) tentatively mentioned the genus Viguiera and especially its series Aureae as the possible ancestor of the South American species of Helianthus. Viguiera ser. Aureae comprises most of the species of Viguiera of the Andes as well as some of the Argentinian and Brazilian species. This series was defined by Blake (1918) on the basis of lacking the distinguishing features of other South American infrageneric taxa of Viguiera. In the Andes these species occupy recently disturbed areas such as agricultural fields or road edges. I never observed them as being part of an undisturbed, climax community (except V. sodiroi (Hieron.) S. F. Blake and V. szyszylowiczii Hieron. which are rare, high altitude species). The reason for considering these species to be the progenitors of Pappobolus may be based on geographical sympatry and the uncanny similarity in head morphology observed in dry, herbarium specimens of most of the species of the series. All of the species of this series are perennial herbs with scabrous herbage, yellow-orange ligules and disk flowers, which are characters not seen in Pappobolus. Another important character that

distinguishes Pappobolus from V. ser. Aureae is their leaf morphology (see Morphology: Leaf Morphology).

Among the Mexican species of Viguiera there are several shrubby groups that share with Pappobolus a few morphological characters. Viguiera ser. Pinnatilobatae is composed of three or four species of the dry areas of Oaxaca, Puebla and then north from San Luis Potosí to Texas. These species are characterized by deeply lobed, mostly opposite leaves and epappose achenes which are characters not observed in Pappobolus. The heads of the species of this series, especially those of V. pinnatilobata (Sch. Bip.) S. F. Blake and V. tripartita (Rob. & Greenman) S. F. Blake share with some members of P. subg. Apricus (i.e. P. ecuatorianus, P. matthewsii, P. sagasteguii) a tightly-packed, small, spherical head, and a similar number and morphology of phyllaries. Molecular data obtained from restriction fragment analysis of cpDNA (Schilling and Jansen, 1989) suggest that V. pinnatilobata along with Simsia, Tithonia and Pappobolus share a single mutation.

Viguiera ser. Grammatoglossae, an endemic Mexican group, is probably a paraphyletic assemblage of species (based on morphological and molecular evidence) as defined by Blake (1918). Some species of V. ser. Grammatoglossae share some characters with Pappobolus. Viguiera grammatoglossa DC. and allied species (those possessing a woody habit, opposite leaf phyllotaxy and cordate leaf bases, (e.g. V. bombycina S. F. Blake, V. hidalgoana E. Schilling & Panero and V. purpusii Brandegee) of southern and eastern Mexico possess the typical densely

velutinous-sericeous herbage pubescence somewhat similar to that of some species of Pappobolus. However, their disk achene, pappus and involucre morphology point to a closer relationship to Simsia. The rest of the series is composed of two distinct groups: the perennial herbs comprised by V. rhombifolia (Rob. & Greenman) S. F. Blake and allied species and the shrubs composed of two elusive species, V. pringlei Rob. & Greenman and V. seemannii Sch.-Bip. of Jalisco and Durango, respectively. Molecular and morphological data suggest that the species with a perennial herb habit are closely related if not conspecific with Simsia. The affinities of the shrubby species remain to be carefully evaluated.

The other significant group of Viguieras present in South America are the members of V. sect. Diplostichis S. F. Blake. These species are weak shrubs or ephemeral woody herbs that either grow in very wet, montane areas of Colombia and Venezuela, or along ditches or small rivers in the dry valleys of southern Ecuador, and Peru southward to northern Argentina. They are characterized by small heads, opposite leaves and either epappose achenes or with a pappus of a crown of very reduced awns or squamellae. They also have soft, ovate to deltate leaves with conspicuously crenate to serrate margins. Some of the members of this group are probably conspecific with Hymenostephium Benth. of Mexico and Central and South America. No species within these two groups share either superficial similarities or key technical characters with Pappobolus.

Scalesia Arn. is in many respects one of the most unusual genera in subtribe Helianthinae. Many of its members possess highly dissected

leaves, the capitulescences are sometimes axillary and solitary, the pales are conspicuously trifid, the achenes are either epappose or with a few awns or squamellae, only one species has a typical Viguiera pappus and many species are discoid (Eliasson 1974). In addition, their chromosome number is $x = 34$ indicating the genus is basically tetraploid. They are endemic to the Galápagos Islands which illustrates the potential dispersal abilities of the members of the subtribe. It is apparent that this genus has been evolving separately for a long time and many of its distinguishing characters are the result of its isolation. Morphological comparisons of Scalesia to any member of the subtribe inevitably highlights its distinctiveness.

ARTIFICIAL KEY TO PAPPOBOLUS AND RELATED GENERA IN SOUTH AMERICA.

(Para claves en español ver Apéndice 6)

1. Peduncles fistulose; shrubs, perennial herbs and annuals of SW U.S.A., Mexico and Central America, adventive in South America. Tithonia.

1. Peduncles not fistulose.

   2. Disk achenes flat; Plants of SW U.S.A., Mexico, Central America and sporadically along the Andean Region from Colombia to Argentina and NE Brazil. Simsia.

   2. Disk achenes biconvex, plump.

      3. Disk achenes with a pappus of several slender deciduous awns. Pappobolus.

      3. Disk achenes epappose or with a pappus of 2 awns with

or without intermediate squamellae or sometimes with a pappus of a crown of diminutive, persistent scales or awns.

4. Disk achenes with a conspicuous eliasome; Peru. Syncretocarpus.

4. Disk achenes without a conspicuous eliasome.

5. Disk achenes with a pappus of two deciduous awns, squamellae rarely present. Pappobolus.

5. Disk achenes with a pappus of two persistent awns and several squamellae or sometimes with a pappus of a crown of diminutive, persistent scales or awns or epappose.

6. Pales conspicuously trilobed; shrubs endemic to the Galápagos Islands. Scalesia.

6. Pales entire.

7. Disk achenes with a pappus consisting of a crown of reduced slender persistent awns or epappose.

Hymenostephium and Viguiera sect. Diplostichis in part.

7. Disk achenes with a pappus of 2 awns and several squamellae.

8. Shrubs with a softly villous, velutinous lanate or pilose herbage. Pappobolus.

8. Annuals or perennial herbs with scabrous, hispid herbage. Viguiera.

MATERIALS AND METHODS

General Considerations.—This study is based on material obtained from natural populations and herbarium specimens. Population samples of flowers and leaves of the 29 taxa collected were preserved in a mixture of 3:1 95% ethanol:glacial acetic acid. This mixture was found to maintain flower shape and orientation satisfactorily for measurement and other quantitative analyses. Most of the floral measurements stated in the descriptions are based on such material. Dried material was rehydrated by immersing it in a mixture of 4:1 water:liquid detergent and heating it at 40°C for two days. Permanent slides were prepared by mounting the material in Hoyer's solution and heating them at 40°C for two weeks. Appendix 3 summarizes the types and sources of material for all the morphological analyses performed for this investigation.

Fieldwork.—Trips were taken to Ecuador and Peru in June-July 1987, Feb-Apr 1988, and June-July 1988. Argentina was also visited in Apr 1988 to collect Viguiera mollis Griseb. which, at the time, was a strong potential candidate for inclusion as the southernmost element of the genus (see Doubtful and Excluded Species). Most of the species were collected along roads although, in some cases, a short walk of 3-5 kms from the road was taken that sometimes resulted in the discovery of larger populations. Collecting species, such as P. decumbens and P. jelskii, required extensive walks of up to 25 kms in the area of the Perlamayo River in north-central Cajamarca Department, Peru.

Descriptive Measurements.—To avoid any confusion as to how the several

measurements used in the key and descriptions were obtained, a summary is shown in Fig. 2. To standardize foliar measurements, the confluence of the three main veins was designated to separate the blade and petiole. The petiole (Fig. 2A) was considered to include the structure proximal to this point, the blade (Figs. 2B, C) anything distal to this point. Width was always measured at the widest point of the blade. The peduncle (Fig. 2D) was arbitrarily defined to include the axis subtending the head measured from the base of the head to the junction of this axis to another similar structure. Head width measurements were based on dry specimens and do not include ligule length. Head width (Fig. 2F) was measured at the base of the head to include the base of the phyllaries and disk diameter. Disk diameter (Fig. 2E) was measured in mature, fruiting heads. Head height (Fig. 2G) was measured from the base of the head up to include disk flower apices. Phyllaries (Figs. 2H, I) were categorized as to their respective series and subsequently their widths and lengths measured. Pales were flattened between two glass slides to obtain more faithful measurements of the width and length of this concave structure. All the pales measured were from fruiting heads. The disk achene and pappus were measured as indicated in Figs. 2L-N. The disk flower tube (Fig. 2O) was considered to include the area of the corolla ranging from the point of contact with the achene up to the point of adnation of the corolla and filament; in all of the species examined this point coincided with an abrupt expansion of the corolla. The throat (Fig. 2P) was quite variable in size and shape, so a lower and upper diameter were taken to

give a better understanding of shape. The lower diameter (Fig. 2R) was measured at the base of the throat and the upper diameter at the imaginary ring demarcated by the lobe sinuses (Fig. 2S). The lobes (Fig. 2Q) were measured from this imaginary ring to their apices. Styles and anthers were measured as indicated in Figs. 2T-V. Ray flower measurements (Figs. 2X-Z1) are self-explanatory.

Stamen and Style Morphology.—Stamens and styles of Pappobolus and related genera were obtained from natural populations or dried herbarium specimens (see Appendix 3). For the purpose of standardization, anthers and styles were dissected at the same developmental stage in all the specimens examined. Characters were measured and observed in three to ten mature disk flowers that were at the stage where the style was beginning to protrude from the exserted anthers. For more detailed observations of the cell thickenings and crystals, another set of slides was prepared as above, but the anthers and styles were cleared by immersion in 10% sodium hypochlorite (Clorox) for approximately ten minutes, followed by a rinse in water. Cell thickenings were observed with Nomarsky (DIC) optics. This method gave high contrast and enhanced observation of the cell thickenings. Anther macerations of species which showed all of the types of endothecium cell thickening patterns documented in this study were prepared following French (1985). Anther macerations were cleared in bleach and mounted in Hoyer's solution. Pressure followed by a slight movement of the cover slip was used to spread the cells and obtain various views of them. Line drawings of anther collars were performed with the aid of a camera lucida. Because of the complex surface

topography of the style and stigmatic surface, SEM was used to record it photographically. For this purpose, styles and anthers were dehydrated by a standard alcohol dehydrating series followed by critical point drying.

Leaf Morphology.—Dried leaves were removed from herbarium specimens (Appendix 3) and cleared, stained and mounted following the method outlined by Dilcher (1974). Toluene was substituted for xylene in the dehydration series to allow use of the toluene-based mounting media Permount (Fisher Laboratories). Cleared and stained leaves were mounted between two 1/16 inch thick glass plates. Mounted specimens were dried in an oven at 33°C for approximately three months. Weekly addition of mounting media was necessary to avoid bubble formation.

To obtain a more comprehensive knowledge of the variation in leaf architecture at the generic level, a series of slides was prepared using 1 cm wide cuttings from the midvein to the margin. These cuttings were treated as above but, instead of being subjected to the dehydrating series, temporary mounts were made in distilled water and sealed with nail polish. The prepared plates and slides were photographed using Technical Pan film and developed to maximize contrast. The venation pattern was highlighted by the use of a green filter. The cleared leaves and negatives are deposited at TENN.

Capitulescence studies—capitulescence patterns were analysed by examining herbarium specimens and natural populations. Given the difficulty in understanding this character in many of the collections of Pappobolus, special attention was made in the field to press

specimens depicting complete and clear capitulescence patterns. For easy and effective comparisons at the specific and generic level, capitulescence patterns and floral opening sequences were analysed and drawn on index cards. This method gave me greater flexibility to organize the information according to a specific variable (e.g. genus, geography, altitude, pattern).

Chromosome Studies.—Young heads from natural populations were fixed in a mixture of chloroform:methanol:propionic acid (6:3:2) or 95% ethanol:acetic acid (3:1), depending on local availability. When possible, heads were transferred to 75% ethanol and stored in cool conditions. Anthers were dissected from fixed heads and squashed in 2% lactic-acetic-orcein stain.

Distribution Maps.—Altitudinal maps used to depict species distributions are based on general topographic maps produced by the Geographic Military Institutes of Ecuador and Peru. A map summarizing place names and political divisions of Colombia, Ecuador and Peru mentioned in the text, as well as major roads and biogeographically significant areas is presented in Fig 26. The major river systems mentioned in the text are also presented in Fig 28.

Line Drawings.—Line drawings of the habit of species are based on photographs taken in natural populations. Special effort was made in the field to photograph habit and leaf disposition, as well as ligule and head angles. These studies aided me in interpreting these variables in dried specimens. Preserved material was used for depicting floral and reproductive characters. Species not collected by the author were drawn from herbarium specimens and rehydrated material,

always keeping in mind the habit and overall appearance of related species. The differential density of stipples used in these drawings were normally used to depict curvature or volume, although exceptions can be seen at the tips of pales and disk flowers to convey the phytomelanin black coloration of these structures. All drawings were executed at life size scale and reduced to fit this publication format.

MORPHOLOGY

Habit. All the species of Pappobolus exhibit a shrubby or weakly arborescent habit (Fig. 3). The species of P. subg. Apricus develop a weak shrubby habit characterized by a single stem that profusely branches a few centimeters from the ground level. From a distance the overall shape of these individuals is broadly obpyramidal. Vigorously growing young plants are reminiscent of the annual Mexican species of Tithonia. Exceptions to this general physiognomy are P. sagasteguii (Fig. 3B) and, to a lesser extent, P. matthewsii (Fig. 3C), which normally produce a single stem with branching restricted to the upper two-thirds of the plant. The habit of P. hutchisonii is exceptional in consisting of a dense mat of leaves from which flowering shoots arise. This habit is somewhat similar to that of Viguiera lanata of Baja California, Mexico. In P. subg. Pappobolus, species attain a more arborescent habit by producing a well-defined single stem, as exemplified by P. sanchezii. However, the attainment of this habit in the nigrescens group is apparently influenced by the surrounding vegetation. The largest individuals of P. sanchezii observed (3.5 m

tall) were in undisturbed areas where the surrounding shrubbery was giving support and protection from strong winds. The stems of this species are very brittle and snap easily. The other members of the nigrescens group tend to be more compact shrubs (i.e. a less well-defined single stem) which also require some kind of support by neighboring vegetation. The stuebelii and discolor groups exhibit different habits. Pappobolus stuebelii (Fig. 3D) and P. jelskii are compact shrubs or trees which exhibit well-developed trunks of up to 15 cm basal diameter. This "woodiness" has made these species useful as fuel wood. Pappobolus subniveus is the only species which seems to colonize disturbed areas at high altitudes. In undisturbed areas this species is a very compact shrub whereas in disturbed areas, especially along roads and at the edge of wheat fields, it only attains a weakly-branched single stem habit. The latter physiognomy may be the result of constant disturbance rather than being an adaptation to ruderal conditions but this was not tested experimentally. Field observations suggest that a lengthy period is required by this species to attain maturity. Another interesting adaptation is that of P. decumbens (Fig. 3E). This species is a profusely-branched decumbent shrub with succulent stems that root if in contact with the soil. It forms a mat of stems from which flowering shoots arise. After anthesis the shoots begin to grow, and the resulting gain in weight forces the shoot-bearing stems to the ground. These newly formed shoots eventually root and continue growing which results in an increase in the diameter of the plant. Eventually the central shoots die off leaving a grayish, bare center.

Leaf Morphology. Leaf shape and arrangement have been used with variable success in classification of neotropical Asteraceae. Some of the genera that have been studied are so variable in leaf characters that only a handful of species can be recognized in the sterile condition (Funk 1982; Jansen 1985). In other genera, most of the species are predictably constant for leaf characters, making them useful for recognition of specific taxa (Dillon 1984; Ezcurra 1985; Panero & Schilling 1988; Stuessy 1978).

In the case of Pappobolus, leaf morphology and arrangement have a limited but important use in circumscribing species. Two main groups based on superficial leaf characters can be circumscribed: P. subg. Apricus and the nigrescens group of P. subg. Pappobolus normally have broad leaves with a thin, soft texture. On the other hand, the rest of P. subg. Pappobolus has leaves with smaller blades, which are mostly lanceolate to narrowly ovate or linear in outline, and are thick, coriaceous and very pubescent abaxially. Pappobolus subg. Apricus tends to exhibit ovate to broadly ovate leaves with shallowly dentate to serrate margins and leaf bases that are always obtuse to attenuate or rarely truncate. Exceptions to this pattern occur in P. sagasteguii, which exhibits a strongly dentate leaf margin and copious pubescence which are useful indicators of this species; P. verbesinoides, P. acutifolius and P. ecuatorianus var. lancifolius share a lanceolate to narrowly ovate leaf shape which is not seen in any other species of the subgenus and a shallowly serrate or entire margin. The nigrescens group has leaf shapes and margins similar to

those of P. subg. Apricus. However, some forms of P. robinsonii from the area of Celendín, Peru, bridge the foliar morphology gap between the nigrescens and the stuebelii group of P. subg. Pappobolus. In this area it is not uncommon to find individuals of P. robinsonii with thick and conspicuously smaller leaves otherwise uncommon for this species. At the same time, plants of P. stuebelii sympatric with these individuals and growing approximately 500-1000 m below its major population center show a much larger and softer leaf than usual. It is not known whether this is indicative of the influence of high altitude factors such as low temperatures and intensity of solar radiation or the result of hybridization between these two species. The greatest differences in leaf morphology within Pappobolus are exhibited by the discolor group. In these taxa, leaf size is markedly smaller and the abaxial pubescence is so well-developed that it renders the leaf downy white to whitish-tan; leaf margins are always revolute and entire.

In Pappobolus, there are about equal numbers of species with alternate as with opposite phyllotaxy, although opposite phyllotaxy is absent in P. subg. Apricus. The question as to what leaf arrangement is ancestral to the genus is difficult, if not impossible, to ascertain. Sister groups of Pappobolus exhibit both arrangements sporadically, making the polarization of this character impossible.

Leaf Venation. Cuticular and venation characters of the leaves of angiosperms have been useful in the past to elucidate relationships of fossil remains (Dilcher 1974) and extant plants (Levin 1986). Leaf venation patterns have rarely been used in the Asteraceae to infer phylogenetic relationships at the specific or generic level. In an

effort to understand the generic relationships of Pappobolus and related genera, a limited sample (Appendix 4) of species was used to explore the potential differences in leaf architecture for classification purposes. Leaf venation terminology follows Hickey (1973).

Pappobolus and related genera exhibit an acro-brochidodromous venation pattern. This term is here used to describe the combination of a general brochidodromous leaf venation with two strong suprabasal secondary veins. However, some exceptions to this leaf architecture can be observed in species having narrowly lanceolate or linear leaves. For example, in Pappobolus decumbens the two suprabasal veins were only rarely prominent and only a weakly organized brochidodromous venation is seen. Another important general characteristic of the leaves of these genera is the percurrent arrangement of the tertiary veins. This arrangement, in which the tertiary veins from opposite secondary veins meet, is also responsible for the creation of a composite intersecondary which could be easily seen in many of the species here sampled. There appear to be important relationships between the thickness (sturdiness) of a leaf and relative thickness of the higher and lower orders of veins and the presence of sclereids.

Pappobolus exhibits a very uniform leaf venation pattern (Appendix 4; Figs. 4, 5). The highest order veins present range from six to seven; areolation is well-developed. It is surprising that this uniformity in leaf venation pattern is maintained given the wide range of environmental and altitudinal conditions encountered by different

species. The coriaceous leaves of the discolor and stuebelii groups have a similar leaf venation pattern as those of the low altitude species of P. subg. Apricus and the nigrescens group. All taxa exhibit a straight venation course with a gradual decrease in vein thickness from the lower to the higher vein orders. In addition, most of the species of the discolor and stuebelii groups exhibit branched sclereids. No species of Pappobolus exhibits sclereids associated with the veins, although they occur in most of the perennial herb members of Viguiera ser. Grammatoglossae (Figs. 7C, D).

A leaf venation pattern similar to Pappobolus is present in Tithonia (Figs. 6D-F), Viguiera sect. Maculatae, and ser. Pinnatilobatae, Iostephane (Figs 7, F), some species of Helianthus (Figs. 6A-C), and Hymenostephium (Figs. 8A-C), as well as some members of Viguiera sect. Diplostichis (Figs. 8D-F). Tithonia exhibits a very uniform leaf architecture with no apparent differences between the annual and shrubby species. Helianthus was one of the most heterogeneous genera for leaf venation characters showing a wide diversity of areole sizes and development. In H. argophyllus T. & G. differences in vein thickness were impossible to distinguish beyond the second and third order. This homogeneity in leaf venation or reticulum was rarely seen among Pappobolus and related genera. In this species, as well as in H. giganteus L., areolation was well-developed. The rest of the species of Helianthus examined (see Appendix 4) showed an imperfect areolation with little constancy in the complexity of veinlets within individual areoles. Another interesting aspect of Helianthus was the variability observed in vein order and areole size

(Appendix 4). These differences warrant a more detailed analysis because of their potential use in the classification of this genus.

Iostephane exhibits a very homogeneous leaf venation pattern (Figs. 6E, F; Appendix 4). The highest vein order observed ranged from four to five. Areolation is imperfect, resulting in highly branched veinlets within a given areole. In addition, a weakly-developed fimbrial vein runs close to the leaf margin. Another characteristic of Iostephane leaf morphology is the translucent nature of its veins which contrast highly against the soft green abaxial surface of the leaf. This macroscopic leaf character was also readily observed in some species of Helianthus (e.g. H. giganteus and H. heterophyllus Nutt.).

Hymenostephium, as well as the shrubby elements of Viguiera sect. Diplostichis, show a relatively well-developed areolation with the distinctive features being the conspicuous serration of their leaves and marginal teeth (Fig. 8). These similarities, in conjunction with other morphological features point, to a close phylogenetic relationship between these groups.

Simsia and some of the Baja California species of V. subg. Bahiopsis exhibit a zig-zag or sinuous vein course (Fig. 9; Appendix 4), a character not observed in any other group examined. Exceptions to this observation were seen in S. ghiesbreghtii (A. Gray) S. F. Blake and V. reticulata Watson. In S. ghiesbreghtii, leaf venation course is straight with little or no sinuousity. In V. reticulata, the primary to tertiary veins are disproportionately thicker than the higher order veins.

A distinctive leaf venation pattern was observed in species of Viguiera ser. Aureae, V. subg. Amphilepis and some of the perennial herbs of V. ser. Grammatoglossae. All of these species have sturdy, coriaceous leaves which exhibit conspicuous differences in the thickness of their lower versus higher vein order (Figs. 6A-D, 10). In addition, several species possess sclereid sheaths surrounding the veins (Figs. 6B-D). Viguiera ser. Aureae and V. subg. Amphilepis share a very similar leaf morphology. Both groups exhibit oval, lanceolate or ovate to narrowly ovate leaves with two strong suprabasal veins from which a series of tertiary veins arise (Fig. 11A). These tertiary veins are peculiar in all being of a constant length and gently loop to meet the superadjacent vein in an obtuse angle. This characteristic constancy in size roughly maintains the same curved trajectory of the suprabasal veins, rendering the characteristic oval to elliptical leaf shape seen in these groups. This leaf morphology, coupled with the coriaceous nature of the leaf and characteristic venation, translates into a set of effective and predictable characters useful in circumscribing some species within these groups. The rest of the species here examined exhibit a hierarchical growth of the tertiary veins arising from the two suprabasal secondary veins (Fig. 11B). In other words, the lower veins tend to be longer and gradually decrease in length as the suprabasal vein approaches the leaf margin. This venation pattern is characteristic of broadly ovate, deltate or obtusely-based leaves that occur in these species.

Foliar characters provide limited information. Many of the foliar characters observed in Pappobolus and related genera were too general

to be useful in circumscribing taxa. However, some groups showed specialized conditions that warrant further study as to their potential taxonomic use. Some species that are presumably closely related based on floral characters also have similar leaf morphologies. On the other hand species apparently not closely related sometimes shared similar leaf morphologies. These two situations highlight both the genetic and ecological factors influencing leaf morphology. The combination of these two factors and the uncertainty or difficulty in separating them limit the extent of the taxonomic conclusions that can be inferred from foliar characters.

Capitulescence. Although capitulescence arrangements provide a wealth of morphological information that is potentially useful in classification, they have been largely ignored in the Asteraceae. A majority of the revisionary treatments for the family have relegated capitulescence arrangement to overall shape without careful observation of head opening sequences and general structure or the relationship of these to phyllotaxy. Recent exceptions include studies by Cuatrecasas (1976) of subtribe Espeletiinae in which capitulescence structure is a useful character in the classification of several genera within the subtribe.

Before proceeding further, some clarification of terminology is necessary. All capitulescence morphological studies here discussed are based on what Cronquist (1977) termed the secondary inflorescence, this being the various arrangements into which the head-subtending stems (i.e. peduncles; see under Material and Methods—Descriptive

considered to represent a unit behaving as a single flower. Troll (1964) introduced the terms monotelic and polytelic to differentiate between capitulescences having a terminal flower and those lacking a clear terminal flower, respectively, as well as the term paracladia (i.e. accessory flowering branches) to represent repetitive units resembling the main structural axis of the capitulescence. The number and complexity of paracladia arrangements depends on the particular plant and growing conditions. The basic cymose capitulescence is common to most of the Asteraceae (Cronquist 1977), although solitary capitulescences are also present. A prominent feature of a cymose (monotelic) capitulescence is a terminal head which is the first to open. Cymose capitulescences could be of 2 two basic types: dichasial or monochasial. In dichasial capitulescences three heads or flowers arise from the same node (Fig. 12E). In a simple dichasium the central or terminal head opens first with the two opposite heads opening later at roughly the same time. In monochasial capitulescences the terminal head opens first but flowering is in an orderly centrifugal opening sequence down a sympodial axis (Fig. 12C). In both cases, enlargement of this basic pattern produces a thyrsoid capitulescence. There is an association between phyllotaxy and the type of cyme present in a particular capitulescence. In opposite-leaved plants there is a greater potential of encountering dichasial cymose inflorescences, whereas the contrary is true for alternate-leaved plants. However, exceptions to these observations are probably common in the Asteraceae.

All species of Pappobolus exhibit a monotelic thyrsoid

capitulescence but there is some variation in further details of its structure. Species of P. subg. Apricus all exhibit the same type of capitulescence structure. All the species exhibit a monochasial arrangement in which every leaf or prophyll subtends either a head or paracladium (Fig. 12A). There is greater variation in capitulescence morphology in P. subg. Pappobolus. The nigrescens group exhibits a capitulescence morphology similar to that of P. subg. Apricus, but they have fewer, larger heads per capitulescence (Fig. 12B). At the same time some leaves or prophylls associated with the peduncle do not exhibit heads or paracladia, although development of heads from these prophylls or leaves is possible if there is destruction or damage to developed heads or paracladia. It is possible that this adaptation is useful in extraordinary years in which the growing season is extended.

Within the nigrescens group the dichasial arrangement is rare but it is present in P. cinerascens. Pappobolus sanchezii and P. robinsonii also exhibit a tendency towards dichasial arrangements but, in these species, simple dichasia are only common on weak branches, and enrichment of this condition normally reveals the monochasial nature of the capitulescence. These three species occupy mesic environments of the Peruvian Andes, and P. sanchezii and P. cinerascens tend to become weak monocaulic treelets. However, it is not conclusive as to whether the evolution of a dichasial cymose capitulescence in Pappobolus is favored by a specific set of environmental conditions.

The discolor and stuebelii groups exhibit a monochasial thyrsoid capitulescence (Fig. 12C), with the exception of P. jelskii and P.

woodsonianus that have a dichasial arrangement (Figs. 12F, G). An important aspect of the capitulescence of these groups of species is the presence of the "leafy cyme". As in the nigrescens group, several leaves associated with the capitulescence fail to develop heads (fig. 13B, C). This condition becomes more prominent in the high altitude species in which the number of sterile leaves associated with the capitulescence increases considerably (Fig. 13D).

It is possible to hypothesize that the evolution of the monochasial capitulescence in Pappobolus has followed a gradual supression of paracladia as species colonized higher altitudes. Concomitant to this gradual reduction in the number of heads per capitulescence, an increase in head size (i.e. an increase in the number of disk flowers) has offset the potential loss in reproductive output.

The capitulescence morphology of Pappobolus is somewhat similar to those exhibited by related genera. Viguiera shows more variation in capitulescence morphologies than Pappobolus or any of the other related genera. This is not surprising given the extensive range and large number of species in Viguiera. However, the greatest diversity of habit and general morphology (including capitulescences) occurs in Mexico. Viguiera ser. Pinnatilobatae and the shrubby elements of V. ser. Grammatoglossae share with P. subg. Apricus a monochasial thyrsoid capitulescence. Other Mexican infrageneric taxa of Viguiera exhibit a similar morphology with subsequent specializations with the exception of Viguiera sect. Maculatae (except V. adenophylla, which has a monochasial arrangement) and V. ser. Brevifoliae which show a definite

dichasial arrangement. The arrangement of the latter group is reminiscent of that of P. woodsonianus (Fig. 12G) in which the lateral branches of the dichasium each give rise to two dichasia which, after anthesis repeat the same pattern over and over again. Given both the predictable branching pattern and the fact that the central leafy peduncle of the dichasium dies after flowering, it is possible to assess accurately the number of flowering episodes a particular individual has experienced. In the case of some species whose flowering seasons are intimately synchronous with climatic conditions, it is even possible to infer the approximate age of the individual.

The South American species of Viguiera are more homogeneous in their capitulescence morphologies than their Mexican counterparts. The Andean elements of the genus show a strongly monochasial thyrsoid capitulescence arrangement. The V. incana complex (V. brittonii Hochr. V. chimboensis Hieron., V. incana (Pers.) S. F. Blake, V. lehmannii Hieron., V. media S. F. Blake, V. mollis Griseb., V. pazensis Rusby, and V. procumbens (Pers.) S. F. Blake, V. sodiroi and V. szyszylowiczii), members of which are mostly ruderal species, tend to produce large capitulescences in which the main paracladium consisting of 3-5 heads is flanked by a series of lateral paracladia which produce simple cymes on leafy peduncles. The dormant meristems at the base of these leaves develop later in the growing season if conditions are suitable. This kind of capitulescence arrangement appears to be advantageous for the changing environmental conditions in which these perennial herbs occur. Viguiera sect. Diplostichis, apparently the

only group of shrubby viguieras in South America, exhibits a slender monochasial arrangement with short peduncles which tend to arch downward before and after anthesis. This kind of capitulescence morphology is reminiscent of Mexican Hymenostephium. Helianthus and Simsia exhibit dichasial and monochasial thyrsoid capitulescences similar to those encountered in Pappobolus. A few species in Simsia exhibit a very peculiar capitulescence structure not observed in any other genera. Species such as S. lagascaeformis DC. and some forms of S. foetida the capitulescence will be composed of two sets of heads. One set of heads will be well-developed and ready to open and another will be adjacent to these heads but in a very immature state. Once the well-developed heads have opened and are beginning to fruit, the second set of heads will begin flowering. The adaptive significance of this morphology is unknown. No specialized capitulescence morphology was observed to be shared between Pappobolus and these genera.

In conclusion, capitulescence structure, as in the case of leaf morphology and phyllotaxy, is only informative for Pappobolus at the specific and infrageneric level. Attempts to compare and identify homologous structures among genera are hindered by subtle specializations of the dichasial and monochasial conditions. This same argument can be extended to the problem of establishing the plesiomorphic state of the monochasial versus the dichasial arrangement. The fact that both arrangements are sporadic in related sister groups renders this character uninformative at the intergeneric level. However, capitulescence structure has proven invaluable in

identifying and understanding species concepts in the Asteraceae, especially the subtribe Helianthinae.

Vestiture. All species of Pappobolus have some sort of pubescence on their herbage. The different densities and kinds are sometimes useful in recognizing and even circumscribing species.

The most common type of trichome is one which is uniseriate with a tapered apical cell (Fig. 14A). The length, density and placement of such trichomes varies according to species and the type of surface it occupies. They vary in length from 0.1 to 10 mm long and can be hyaline, white, greenish-white, greenish-yellow, tan or ochreous. This trichome is responsible for the different types of vestiture present in the leaves, stems and phyllaries of Pappobolus explained below. Another important type, which is restricted only to photosynthetic structures, is the moniliform trichome (Fig. 14B). This is only present in some species of P. subg. Apricus and a few of the middle altitude species of P. subg. Pappobolus. It is most abundant along the veins of the leaves, is always arched and has a brownish-yellow coloration; the apical cell is always rounded. Another trichome mostly restricted to photosynthetic structures, although sometimes present in the anther appendages and flowers, is the sessile glandular trichome (Fig. 14C). This trichome differs from the above in being biseriate and in having a small or very reduced stalk. The uniseriate (Fig. 14D) and biseriate (Fig. 14E) stalked glandular trichomes are restricted to the flowers and are found in all species of the genus. Unicellular biseriate trichomes (Zwillingshaare; Fig. 14F) are restricted to

pubescent achenes of some of the species and are responsible for the silver or silvery-orange or silvery-purple sericeous quality of some of the achenes.

Given the many names used to describe the vestiture that the tapered trichome or a combination of this and other of the above described trichomes produce because of density or orientation, the following terms used in the descriptions are defined below (Fig 15):

floccose — Conspicuous balls or clumps of trichomes in an otherwise homogeneous indumentum.

hirsute — Erect, somewhat stiff trichomes which, given their orientation, are seldom evident unless touched.

lanate — Woolly, intertwined trichomes forming dense, cushiony mats.

pilose — Soft, long hairs mostly restricted to stems. In this genus only observed in P. sagasteguii.

puberulent — Microscopic trichomes mainly restricted to floral parts, normally multicellular with tapered apical cells. Evident to the unaided eye as a whitish film.

sericeous — Shiny, appressed trichomes arranged (combed) in only one direction.

strigose — Appressed, stiff trichomes that occur on the adaxial surfaces of the leaves.

velutinous — A velvety or cushiony indumentum composed of soft to somewhat stiff, straight to slightly curved trichomes.

villous — Erect, soft trichomes of different lengths having in common a capriciously twisted, tapered end. This

trichome sometimes clumps, forming the floccose condition.

Heads. The heads of Pappobolus are heterogamous and mostly hemispherical, although a few species have campanulate or oblong heads. The disk is always shallowly to moderately convex or flat. A useful character to separate species in the field was the shape, color and pubescence of the immature head, a set of characters that is remarkably constant in the species observed in the field. The characters of the immature head were seldom used to circumscribe a particular taxon because in dry herbarium specimens are difficult to discern.

Phyllaries. The phyllaries are always indurated at the base with herbaceous apices of different length and width. They are normally lanceolate or ovate, although oblong or deltate phyllaries are also present. They are normally arranged in 3-6 graduated or sometimes subequal series. Each species possesses a specific phyllary morphology, so there is a large degree of variation in size, shape, color and pubescence of this structure within the genus. Phyllary morphology was one of the most important characters used here to define and circumscribe species.

Pales. The pales, as in many other related genera are conduplicate, slightly to strongly keeled lengthwise and ovate to oblong in shape. A few species of P. subg. Apricus and some individuals of P. schillingii have pales that tightly wrap the disk flower under broad folds that overlap each other. This pale morphology is somewhat analogous to the one observed in the genus Sclerocarpus Jacq. The pale apices are either erect, reflexed or curved inward.

The sporadic occurrence of any of the three conditions in a given species minimizes the use of this character in classification, although P. acutifolius, P. hutchisonii, P. matthewsii and P. sagasteguii always have pales with strongly reflexed apices. Pales exhibiting curved inward apices are normally restricted to some species of P. subg. Pappobolus.

Pale coloration is always stramineous or stramineous-copper, rarely light green (restricted to P. subg. Apricus) with several brown, light green to dark greenish-black longitudinal bands of various width. Invariably these bands coalesce at the apex of the pale forming a conspicuous blackish area. In most of the species of P. subg. Apricus the bands tend to continue parallel to the apex and therefore rarely coalesce producing the blackish apex. However, P. hypargyreus, P. imbaburensis, some populations of P. ecuatorianus and P. verbesinoides exhibit pales with a conspicuously dark green distal half which are somewhat similar to those of the rest of the species of the genus.

Ray Corolla. The ray corolla is golden yellow, rarely orangish-yellow or light yellow, and oval to oblong in outline. The adaxial surface is papillose and never pubescent. The abaxial surface is always sparsely to densely puberulent and sometimes minutely pilose along the veins with interspersed uniseriate glandular trichomes. Biseriate glandular trichomes are normally restricted to intervenial tissue. This pubescence normally continues downward along the tube. In some species a clearly distinct tuft of trichomes is restricted to the sinus of the ligule. These trichomes are not present in all the

species of the genus and apparently are not correlated with any environmental or taxonomic group. It is hypothesized that these tufts may act as a mechanical deterrent to insects gaining access into the head through the ray corolla (see below, disk flower). The ray flower apex is either bifid or trifid with a few species presenting both conditions.

Disk Corolla. The disk corolla is yellow, orangish-yellow or lemon yellow. The lobes or their tips will be black abaxially and yellow adaxially especially in most of the species of P. subg. Pappobolus, but yellow on both surfaces in P. subg. Apricus. All of the species exhibit campanulate to lyrate or tubular disk flowers. The disk flower shape was not useful in circumscribing species because there is a large amount of variation within a species and there is little difference in overall shape within the genus. Differences in the degree of pubescence or the lack of it are an important character that was sometimes essential to circumscribe a species.

The pubescence on the disk corollas tends to be concentrated around the base and under the lobes with an irregular number of bands of trichomes occurring between the two areas. As in the case of the ray corolla, this conspicuous concentration of erect and stiff trichomes, coupled with the tight wrapping action of the pales, may act as a mechanical deterrent to pests working their way to the disk achene. Nearly all of the species of the genus show some kind of pubescence on the base of the throat. This pubescence pattern is also common in many other related genera but its apparently restricted to the Heliantheae and rarely seen in the Senecioneae (Nordenstam 1977).

Ray Ovary. The ray ovary is nearly always triquetrous and glabrous. The peculiar shape of this structure is probably due to the tight trigonal space it occupies between two folds of a pale and the flat surface of a phyllary. The species of P. subg. Apricus have a long and thin ray ovary, similar to those exhibited by Simsia. In P. subg. Pappobolus the ray ovary is wider and slightly flatter and not as pyramidal or tubular as in P. subg. Apricus. The ray ovary pappus exhibits a great deal of variability in the number, size and shape of awns and squamellae within and between species which, in turn, minimizes its usefulness in classification. An exception to this observation would be P. lehmannii, P. macranthus, P. mollicomus and P. cinerascens which exhibit a pappus of several awns.

Disk Achene. The disk achene is uniformly biconvex, oblong to obovate, rarely obpyramidal and shiny grayish-black to black or mottled. The achenes of most species are glabrous, although a few are sparsely to densely sericeous. The pubescent achenes have different trichome colorations ranging from silvery-gray to silvery-orange and silvery-purple. The pappus is quite variable and is useful in circumscribing species. The pappus can be easily deciduous or somewhat persistent and its duration is normally tied to its morphology. The pappus of two awns and several squamellae in between tends to be somewhat persistent and is more common in species of P. subg. Apricus. The deciduous pappus is normally composed of a crown of awns or of 2 awns and no squamellae.

Floral Micromorphology. Floral microcharacters (cellular or

surface structure of the corolla, endothecial pattern of the anther, anther collar and style branches, etc.) can be a valuable source of taxonomic information (King and Robinson 1970). They have been extensively used in the Asteraceae and more recently in the Araceae (French 1985, 1986). In the Asteraceae they have been useful in delimiting taxa, especially genera. King and Robinson (1987) applied them extensively as they circumscribed specific and generic concepts in the tribe Eupatorieae by proposing new genera and resurrecting others from synonymy. Robinson (1983) also has used anther microcharacters to imply phylogenies in the tribe Liabeae. However, their usefulness as specific or generic markers in the Asteraceae has been recently questioned by several authors. Wetter (1983), in his study of the Cacalioid group of Senecio, concludes that floral microcharacters should be used with caution because of their variability within a specimen, species or a geographic area. Sundberg (1985), in analyzing members of the Astereae, contended that floral microcharacters should be used in conjunction with other macro- and microcharacters, because their use alone may lead to inconsistent phylogenies and to the potential "disruption of natural classifications". In the present study the staminal endothecial tissue, anther collar, and style branch morphology are evaluated as sources of generic characters for Pappobolus and related genera (Appendix 3).

Two morphological features of the anthers appear to be taxonomically important: the endothecial tissue or fibrous layer (Dormer, 1962) and the anther collar. The endothecial tissue is

composed of several rows of cells. These cells vary in size and shape from quadratic to isodiametric and fusiform (Fig. 16).

Another important feature of the endothecial tissue cells is their pattern of cell wall thickening. In Pappobolus and related genera, the thickenings are very similar. All species show polarized thickenings in which one to three ribs emerge perpendicularly from the thin abaxial periclinal wall (Figs. 17B-D). These ribs run parallel to the anticlinal sides of each cell matching in width, number and position the ribs of the cells immediately above and below them. After reaching the adaxial perclinal wall of the cell, the ribs either end or meet each other forming differentially thickened bridges (Fig. 17D). These occur most commonly in the first three to five rows of endothecial cells closer to the connective. There is also variation in the number of ribs per cell, which apparently depends on the position of the row within the endothecial tissue. The last rows of the endothecium will normally have two to three ribs per cell compared to the one-ribbed cells of the middle rows. The most significant departure from this profile is exhibited by Tithonia and, to some extent, Helianthus (Fig. 16G-I). The thickenings in these genera are normally polarized, but thickenings at the corner of the periclinal wall are not uncommon producing a pattern described by Wetter (1983) as partially polarized.

The anther collar is structurally different from the endothecial tissue. According to Drury (1975), the anther collar is an extension of the connective tissue. The type of thickening exhibited by the cells of the anther collar of the species here studied has been traditionally labeled as radially-thickened (Dormer, 1962). This term

does not describe adequately the nature of these thickenings in Pappobolus and related genera. After a detailed observation it was discovered that they present randomly-thickened areas which translate into a reticulate or net pattern (Fig. 17A). Another interesting feature of the anther collar is the discontinuity in its adaxial surface. In all the species examined, the thickened cells of the anther collar disappear or are reduced to one or a few rows on the adaxial side (Fig. 18).

The overall morphology of the anther collar was not taxonomically important in Pappobolus (Figs. 19, 20). In Pappobolus the anther collars are mostly cylindrical, with the exception of P. stuebelii and P. subniveus in which the lower cells were more tightly packed to form a lyrate-shaped collar (Figs. 19K, L). Another anther collar morphology was observed in male sterile individuals of some species of P. subg. Apricus (Fig. 19J). These individuals possess a small, somewhat spherical anther collar, significantly different from other Pappobolus species (Fig. 20). In addition, no cell wall thickenings were discernable in the highly-reduced endothecial tissue layer of these individuals. In the rest of the species, the first (lowermost) rows of cells were roughly equal in size with general elongation of the cells as they converged into the connective.

There are subtle differences in anther collar morphology within and among related genera (Fig. 21). In Tithonia, the anther collar is somewhat lyrate-shaped (Fig. 21A). A somewhat similar shape was observed in Simsia, but the constriction of the lower rows of cells is not as pronounced (Figs. 21F, G). Simsia also differs from Tithonia in

having smaller, more tightly packed cells in its anther collar. Certain subgeneric taxa of Viguiera share with Pappobolus similar anther collar morphologies (Figs. 21H, I, L). This is especially true for the shrubby Mexican elements of the genus.

Overall, no Pappobolus species present heavily thickened walls in the anther collar. This contrasts with the heavily-thickened anther collar cell walls in Helianthus (Figs. 21B-D), V subg. Amphilepis (Fig. 21O) and some species of V. series Aureae (Figs. 21J, K) and to a lesser extent Simsia (Fig. 21G).

The stamen appendage is variable in shape and length. Variation is common at the specific and generic level and therefore it is not useful in delimiting taxa. The appendage is composed of two layers of elongated and many-sided cells. The cells are thinly-thickened with weak ribs sometimes present at the junction of one cell with another. The thickenings decrease in size (or magnitude) in cells that are progressively farther from the connective.

The style branch exhibits the most discrete and predictable differences among the genera examined (Fig. 22). Helianthus, Tithonia, Simsia and certain species of Viguiera ser. Grammatoglossae (i.e. V. potosina and V. sessilifolia) possess tapered style branches with small appendages at the tip of their style branches. Within this group, only a few species of Simsia and Viguiera also have papillae below the junction of the style branches. This style morphology is very different from that of Pappobolus and the rest of Viguiera in which the style branch is broadly acute and never tapered and the appendage is

very short or absent and the papillae are restricted to the distal two thirds of the style branches.

A variety of crystals, including raphids, square or rectangular slabs and druses are common in the endothecial tissue and styles of several species of Pappobolus and related genera. Druses were only observed in the style and style branch papillae, while raphids are common in all the structures examined. In all the species examined crystals are absent from the anther collar.

CHROMOSOME NUMBERS

All species of Pappobolus examined have chromosome counts of n = 17 (Appendix 5). However, many of the samples gave very poor preparations which may be the result of unsuitable field conditions. A count of n = 17 had previously been reported from P. imbaburensis, P. lehmannii, P. woodsonianus, and P. viridior. A count of n = 9 reported by Robinson et al. (1981) for a sample of P. ecuatorianus var. ecuatorianus (reported as P. hypargyreus) is unusual for the genus and the subtribe. Specimens of this species (Panero 1517, 1518) were collected in the same area and gave counts of n = 17.

Pappobolus, and related genera appear to have a base number of x = 17. The uniformity in chromosome counts indicates that polyploidy has not been involved in the evolution of the genus.

ECOLOGY, DISTRIBUTION AND REPRODUCTIVE BIOLOGY

Habitat. The genus Pappobolus occurs in a wide variety of habitats

(Fig. 23) ranging from xerophytic forest to Páramo between 650 and 4200 m (Fig. 24). These habitats correspond to the premontane and lower montane desert scrub, thorn woodland (Fig. 23B), dry scrub and dry forest, the montane desert scrub (Fig. 23A), steppe, moist forest (Figs. 23C, D) and, rarely, the wet forest and the subalpine moist (Fig. 23 E) to wet forest (Páramo) of the Holdridge life zone system (1967). All of these habitats have been greatly altered by human activities, resulting in the creation of multiple vegetation assemblages in an otherwise discrete life zone and thus permitting species such as P. sanchezii and P. microphyllus to be sympatric and produce hybrids (see Hybridization). It is probable that the extensions of Páramo covering parts of northern Peru today are the result of a long history of logging, burning and agriculture (Cuatrecasas 1968). In addition, the topography and climate of the Andes act together to produce special microclimates difficult to quantify and label but of paramount importance to specialized, narrow endemics adapted to these areas, such as P. argenteus, P. cinerascens, P. hutchisonii and P. sanchezii.

The species of P. subg. Apricus normally occur in lower montane to montane desert scrub, thorn woodland, dry forest and steppe from 650 to 3300 m. These areas are characterized by a dense cover of mostly spiny shrubs and small trees. In most of these areas species of P. subg. Apricus tend to occupy disturbed or exposed sites such as road edges and rocky vertical cliffs. They are normally associated with Buddleja L., Cortaderia Stapf., Dodonaea Mill., Jacquemontia Choisy., Lepechinia Willd., Onoseris Willd. and Wigandia Kunth, among others. Several

species, especially in Ecuador, are encountered at higher altitudes, sometimes up to 3300 m. At these altitudes they normally occupy human-made disturbed sites similar in physiognomy to montane to subalpine steppe or desert scrub.

The nigrescens group occupies montane moist forest with a few species venturing into somewhat wetter or drier sites between 1500 and 3000 m. All the species of this group differ from those of P. subg. Apricus in being part of the natural vegetation assemblage and rarely invading disturbed areas. However, in high montane wet forests they tend to occupy disturbed areas and rarely are part of the undisturbed habitat, an exception being P. cinerascens. They normally grow with such genera as Baccharis L., Clusia L., Drimys J. R. & G. Frost, Llagunoa Ruiz & Pav., Monactis Kunth, Monnina Ruiz & Pav., Oreocallis R. Br., Pineda Ruiz & Pav., and Viburnum L. Some species, notably P. lehmannii, form large stands covering large areas, whereas small aggregations restricted to specific, highly localized sites are common for the rest of the species of the group. Pappobolus cinerascens is the only member of the group that thrives in montane wet forests.

The discolor group occupies exposed, rocky hills or dry streambeds in interandean valleys or interior ranges between 1800 and 4200 m. They are normally associated with Acaena Mutis ex L., Alonsoa Ruiz & Pavón, Calceolaria L., Chaptalia Vent., Coreopsis L., Cosmos Cav., Cuphea P. Br., Lantana L., Lomatia R. Br., Onoseris, Puya Molina, Paranephelius Poepp. & Endl., Satureja L., Viguiera, Werneria Kunth, and several grasses, mostly Festuca L. and Calamagrostis Adans typical

the group are ruderal and apparently successful in colonizing human-made disturbed areas. Species such as P. microphyllus and P. subniveus have been successful in colonizing the disturbed areas surrounding the city of Cajamarca. On the other hand several species of this group, exemplified by P. decumbens, are narrow endemics restricted to natural exposed areas such as vertical cliffs and rocky outcrops.

The stuebelii group is mostly restricted to Páramo or Jalca of northern Peru. According to Cuatrecasas (1968) and Smith & Young (1987), these areas are characterized by low temperatures, normally ranging from -3 to 20°C, and by little seasonal variation in mean daily temperature. However, cloud cover and rainfall have significant seasonal variation. The combination of modest rainfall (1000 to 2000 mm/yr), low temperature, constant cloud cover and dew formation contribute to maintaining a constant high level of humidity in these areas. The soils are black and acid (pH 3.7-5.4) and saturated with water. Pappobolus stuebelii is a common member of the Jalca between the city of Cajamarca and the town of Celendín. The native vegetation of this area has been largely destroyed by human activity, although a few populations of this species flourish in rocky outcrops and deep crevices that apparently escape the periodic July-August man-made fires. This species grows with Alchemilla L., Berberis L., Buddleja, Cajophora Presl., Calceolaria, Fuchsia L., Gentianella Moench., Jungia L., Munnozia Ruiz & Pav., Paranephelius, Perezia Lag., Polymnia L. and Werneria.

The genus as a whole occurs in a wide range of edaphic conditions.

Most of the species in the dry and hot valleys of the western escarpment occur in alluvial, clay or alkaline soils. The high altitude species of the Páramo or Jalca thrive in black, organic and highly acidic soils.

Distribution. The range of Pappobolus extends from the province of Nariño in southern Colombia southward along the Andes of Ecuador, and northern and central Peru (Figs. 25, 26). The most distinctive aspect of the distribution of Pappobolus is the concentration of species in the numerous river valleys of the Marañón River basin just south of the Huancabamba River gorge (Figs. 27, 28). This area of northern Peru is characterized by a general lowering of the average altitude of the Andes that coincides with the deep and broad basins of the Chamaya and Marañón Rivers which effectively impede the migration of high altitude-adapted Andean fauna and flora. This is reflected in the observation that 30 of the 38 species of Pappobolus are endemic to Peru and seven to Ecuador with only one species, P. schillingii, found in both countries (Fig. 27).

The species of P. subg. Apricus inhabit the dry, Pacific drainage river valleys or basins of the western escarpment of the Andes from the valley of the Chanchán River in central Ecuador southward to the valley of the Santa River in Ancash Department in central Peru (Fig. 25). Some species also occur in the interior valleys of the basin of the Marañón River of northern Peru. The valleys or basins of northern Ecuador tend be drier than the eastern escarpment of the Andes because of the rainshadow effect and the consequent dryness associated with

are also affected by the southern anticyclone and the cold Humboldt current which promote extreme dry conditions in the western escarpment of the Andes. The western Andean slopes of southern Ecuador tend to harbor xerophytic or tropical deciduous forests at their base that are gradually replaced by sporadic and, finally, no vegetation southward into Peru and northern Chile. This aridity forces the vegetation belts to progressively higher altitudes in the Andes along an imaginary line in which the desert common at the base of the Andes of northern Peru creeps higher and higher in the Andes until it crosses them and merges with the dry associations of the Puna around the border of Bolivia (Johnson, 1976). The interplay of the above factors and the progressively higher altitudes needed to maintain equivalent growing conditions for a particular vegetation assemblage along a latitudinal north to south gradient are probably responsible for the subtle differences in the floristic composition of the many Pacific drainage river valleys of Ecuador and Peru. It has been hypothesized (Simpson, 1979) that at least the middle and high altitude areas of the western escarpment of the Andes were covered by a continuous forest which, in drier times such as occur at present, may have contracted to produce isolated pockets of vegetation. These pockets may have also experienced different climatic conditons that promoted the extinction, speciation or immigration of particular elements and consequently, with time, changed their floristic composition. The species of Pappobolus, and especially the species of P. subg. Apricus, tend to be endemic to a given valley, where they are discretely restricted to the basin of a

particular river and effectively separated from other such species. In Ecuador there are approximately ten basins or interandean valleys (most of them drained by Pacific drainage rivers), each with its own species of P. subg. Apricus. However, the distribution of Pappobolus imbaburensis is unusual because it is the only species that occupies both the western and eastern Andean ranges of Ecuador and it is widely distributed in several interandean basins north of the Chimborazo Volcano. This distribution may be the result of the adaptation of this species to slightly higher altitudes and consequently it has been able to colonize the climatically similar interandean basins along the eastern and western Andean ranges. On the other hand, P. hypargyreus, a species able to grow at higher altitudes than P. imbaburensis, is discretely restricted to the basins of the contiguous Cañar and Chanchán Rivers.

The Peruvian species of P. subg. Apricus are normally restricted to interandean valleys with river systems that empty their waters to the Marañón River, a tributary of the Amazon River. Only P. matthewsii var. occidentalis and P. acutifolius occupy the Peruvian Pacific drainage river valleys. No species has been discovered south of the Santa River valley. Similar river systems farther south along the western escarpment of the Andes are progressively drier and consequently potential habitats for members of P. subg. Apricus are gradually shifted to higher altitudes. Concomitant with these higher altitudes the potential for lower and even freezing temperatures clearly define a different set of growing conditions to which no member of P. subg. Apricus appears to have been able to adapt. Pappobolus

matthewsii like P. imbaburensis, occupies the western and eastern ranges of the Andes. This species is common along the river canyons of the tributaries of the Chamaya and northern Marañón Rivers as well as the Pacific drainage river canyons of Cajamarca Department. Pappobolus hutchisonii, P. sagasteguii and P. verbesinoides are narrow endemics restricted to small canyons of these river systems.

The nigrescens group normally occupies the same valleys as P. subg. Apricus but at higher altitudes in habitats that are consequently more mesic. The species of this group extend from just south of the Chimborazo volcano in central Ecuador southward to Huancavelica Department in south-central Peru (Fig. 25). The assessment of the distribution of these species is more difficult because of the paucity of collections and the difficulty in reaching potentially suitable habitats, especially in Peru; this is also true for the species of the discolor and stuebelii groups. The three Ecuadorian species, P. lehmannii, P. nigrescens and P. schillingii, like members of P. subg. Apricus, are restricted to the headwaters of Pacific drainage river systems. Pappobolus schillingii is the only species that colonizes several suitable habitats of southern Ecuador and northern Peru, an area that is irrigated by several river systems. The distribution of this species exemplifies the distribution of the Peruvian elements of the group which are rare but scattered along several, sometimes widely separated areas. Pappobolus sanchezii has been collected at the headwaters of the Chicama and Jequetepeque River systems in western Cajamarca Department. The distribution of this species represents the

southernmost for the nigrescens group along the western escarpment of the Andes. The highest concentration of species of the nigrescens group is along the Marañón River basin. Seven species are endemic to the eastern Andean range and only three are present south of the Nudo de Pasco (where the western and eastern ranges meet) in Junín and Huancavelica Departments. The tortuous course of the Mantaro River offers a suitable habitat for P. stork-hortonii, the southernmost element of the group and the genus. It is not known whether the genus extends any further south nor what forces are involved in defining its southern range. However, suitable habitats in Cuzco Department appear not to harbor species of Pappobolus (M. O. Dillon, pers. comm.). Another interesting aspect of the distribution of this group is that no species are shared between the eastern and western ranges flanking the Marañón canyon with the possible exception of P. robinsonii which is represented by an unusual collection (King & Bishop 9209) from Chachapoyas, Amazonas. Interestingly, it is the nigrescens group, with five species north of the Nudo de Pasco, that has the highest number of species in this range, as opposed to only one or two for each of the other two groups of P. subg. Pappobolus and P. subg. Apricus. This distribution pattern may reflect a rather recent colonization by the genus of the eastern range of the Andes of northern Peru, or more probably, the result of inherent ecological and climatic conditions of this range that promote suitable habitats for member of the nigrescens group and not for the other groups. The eastern range of the Andes of Peru north of the Nudo de Pasco is not as wide as its counterpart to the west with the result that the potential for interandean dry valleys

or extensive Jalca areas to exist is smaller. In addition, the eastern slopes of the range face the Amazon basin and consequently receive high amounts of rain, producing vegetation assemblages not suitable for the other groups of Pappobolus. Aside from the members of P. subg. Apricus, which appear to have reached the eastern Andean range by colonizing the river basins of the Marañón and adjacent rivers, the higher altitude species may be the result of a long-distance dispersal event or by the northward migration of a western Andean element along the eastern range from the Nudo de Pasco. The paucity of collections from the basin of the Marañón River in the Departments of Ancash, La Libertad and Huánuco makes it difficult to support either assumption. Irrespective of the mode of their arrival to the eastern range of the Andes, these species (P. acuminatus, P. cinerascens, P. macranthus, P. mollicomus, P. woodsonianus with the possible exceptions of P. youngiorum and P. smithii) are each characterized by several unique morphological features which may have arisen in isolation. These features effectively mask their phenetic relationships to other members of the genus.

The stuebelii group is known from Departments of Cajamarca and La Libertad of northern Peru (Fig. 25). Pappobolus stuebelii is common in the Páramo between the city of Cajamarca and the Marañón River although it is absent from other similar areas north or west of the city of Cajamarca. The peculiar distributions of P. jelskii and P. stuebelii suggest that these species appear to colonize the uppermost headwaters of major rivers, which are probably milder and more humid than the

surrounding Páramo. Pappobolus jelskii and P. stuebelii are also common in the subpáramo and sometimes dominate the vegetation assemblage. Pappobolus smithii is endemic to Páramo-like areas of the Cajamarquilla Peak above the town of Bolívar on the eastern Andean range of La Libertad Department.

Species of the discolor group exhibit two general patterns of distribution. Some are narrowly endemic to particular areas where they may be either abundant or rare. Others occupy a wider area in which they are rare. All the species of this group, with the exception of P. argenteus, are endemic to Peru. The discolor group occurs along the Pacific drainage river valleys from the valley of the Saña River in Cajamarca Department to the valley of the Rimac River in Lima Department (Fig. 25). The group also occurs in the interandean valleys and tributaries of the Marañón and Huallaga Rivers of central and northern Peru. Pappobolus woodsonianus is the only species that occupies the eastern range of the Andes (in Amazonas Department). Pappobolus viridior, endemic to Junín Department, is the only species of the group below the Nudo de Pasco on the eastern side of the Andes. Pappobolus argenteus is restricted to the valley of the Cañar River in central Ecuador and represents both the only Ecuadorian species of the discolor group and the only species of this group north of the Huancabamba deflection.

Phenology and Climate. The climatic information presented in this and other sections of this study is based mostly on Johnson (1976) very briefly supplemented by personal observations and specimen label data.

The climatic conditions of the Andes of Ecuador and Peru play an

important role in determining the time and duration of the flowering period of the species of Pappobolus. Most of the herbaceous and shrubby Asteraceae of this area tend to flower after completing their growth at the middle and end of the rainy season between February and June. The rainy season normally begins in September and ends in April or May in northern and central Ecuador. Farther south, the rainy season is progressively shorter so that it is concentrated in a few months of the year. However, the exact timing of rain schedules tend to vary slightly from year to year depending on global climatic cycles and peculiarities of a particular area, such as altitude and surrounding topography. These subtle differences in the climate of a particular area across the range of a given species are probably responsible for producing a staggered, as opposed to synchronous, flowering season in many of the species of the genus. In the case of the Peruvian species of P. subg. Apricus, flowering will be commonly observed in late March or April, and sometimes populations at slightly higher altitudes will flower well into May. In the case of the northern and central Ecuadorian species, flowering will be commonly observed in June and July. This is also the case for the species of the nigrescens group of P. subg. Pappobolus. The Peruvian species will have their peak flowering episodes in March through May while their Ecuadorian counterparts flower most commonly in June and July. On the other hand, the high altitude species inhabiting the Páramo or subpáramo of northern Peru will tend to flower year round. The discolor group of P. subg. Pappobolus is commonly seen in flower in

late March and April, although the beginning of the rainy season triggers a small, sporadic flowering period beginning in November. However, sporadic flowering in all the species is possible because of proximity to a stream, sporadic rains or peculiar microclimates.

There is variation within Pappobolus as to whether or not the leaves are evergreen. All of the species of P. subg. Apricus drop their leaves at the end of the rainy season after completing flowering. The tendency to drop leaves is not as widespread in P. subg. Pappobolus. The species of the nigrescens group will also drop their leaves in the dry season although the Ecuadorian species, especially P. lehmannii, are apparently evergreen. The discolor and stuebelii groups also appear to be evergreen. The species of the discolor group observed in the dry season kept a few small leaves and flowered sporadically. The species of the stuebelii group are evergreen, only shedding old, senescent leaves.

Seed dispersal. The species of Pappobolus exhibit no obvious seed dispersal mechanism. The disk achenes are glabrous and the pappus, a potential dispersal mechanism, is deciduous in most of the species although it is weakly persistent in a few species of P. subg. Apricus. The achenes also lack eliasomes, which in some other genera, may entice insects such as ants to collect, transport and bury the achenes.

Natural hybridization. The species pairs P. jelskii/P. decumbens and P. sanchezii/P. microphyllus, respectively, were observed growing sympatrically. In areas of sympatry putative hybrids between these pairs of species were observed. In both cases, the hybrids were easily recognized because of their intermediacy in all gross morphological

characters. The four species involved in these hybridization events are placed in the three informally recognized species groups of P. subg. Pappobolus.

Pappobolus jelskii x P. decumbens. Panero & Sánchez Vega 1344 (CPUN, F, GRI, TENN, US): Peru. Cajamarca: Prov. Hualgayoc, Cajamarca-Hualgayoc-Chugur road, 10-15 km before Chugur take road to Perlamayo, until first stream, then 3-5 km by foot to old school house, continue along right path to the gorge of the Perlamayo River for approximately 10-15 km, 3030 m, 20 Mar 1988. A summary of the distinctive morphological features of this hybrid and parents are summarized in Table 4. The hybrid population was composed of three plants scattered in a 10 m radius. The interesting aspect of this hybrid is that the parents exhibit significant morphological differences in many characters. The habit of the two species is very different, with plants of P. decumbens being weak and prostrate whereas those of P. jelskii are commonly big shrubs. The hybrid exhibits a weak, shrubby, erect habit. Pollen viability tested with lacto-phenol blue showed a 99.8% stainability based on 500 grains counted. The overall hybrid morphology is reminiscent of that of P. discolor and P. decumbens.

Pappobolus sanchezii x P. microphyllus. Panero 1289 (MEXU), 1290 (TENN) and 1291 (CPUN, F, GRI, K, SI, TENN, UC, US): Peru. Cajamarca: Km 154.8 on the Cajamarca-Pacasmayo road, then 1 km by foot along a narrow trail bordering the river gorge, 3040 m, 14 Mar 1988. A summary of the distinctive morphological features of the hybrid and parents are summarized on Table 5. The hybrid population was large and probably

composed of about 50 individuals. They were scattered in many areas of the river canyon but mostly in rocky outcrops. As in the previous example, the plants were intermediate in all gross features between the two parents, which were also present. Pollen stainability was only 5% based on 500 grains counted, indicating a high degree of sterility. This high sterility is intriguing given the large numbers of hybrid individuals and the obvious differences in age (based on trunk diameter, habit size) of the hybrid population. These peculiarities of the hybrid population may indicate either that some hybrid individuals not sampled are fertile or that the hybrid is commonly and continuously produced every flowering season. The general gestalt of the hybrid is similar to that of P. lanatus from central Peru. Most of the hybrid population was destroyed by a man-made fire a few days after these collections were made.

These two hybrids highlight the possibility that highly distinctive species of P. subg. Pappobolus may be separated by relatively weak genetic barriers. There is no doubt that hybridization could have played an important role in the speciation of the genus. Both hybrids gave chromosome counts of n = 17 with no apparent chromosomal abnormalities.

Another putative hybrid, between P. sagasteguii and P. robinsonii, was observed in dry herbarium collections: Hutchison & Wright 5398 (F, MO, UC, US) Peru. Cajamarca: Canyon of the Marañón River above Balsas, 11.5 km below the summit of the road to Celendín, 2630 m, 27 May 1964. This collection is also somewhat intermediate in gross morphological features between its putative parents, which are abundant in this area.

Male sterility. Male sterility was observed in five species of P. subg. Apricus: P. ecuatorianus, P. hypargyreus, P. matthewsii var. viridifolius, P. sagasteguii and P. verbesinoides; male sterile individuals of the first four taxa were observed in the field. In the case of the last two species, the type collection is based on male-sterile individuals. One individual of P. schillingii of P. subg. Pappobolus was observed to be male sterile. Male sterile individuals were easy to detect because of their abnormal anthers. In these plants the anthers are severely malformed and significantly smaller than in normal individuals of this species. In addition, the filament is very short and inelastic. The short and rigid filament coupled with the small anther are responsible for the naked style, a common trait in these individuals but rarely observed in hermaphrodite Asteraceae. Close inspection of the anthers revealed no pollen grains or sometimes a few, malformed grains. The severely malformed anthers and the lack of pollen production fit the structural male sterility type outlined by Kaul (1988).

Male sterile individuals in P. subg. Apricus are common and appear to be a significant portion of the individuals of an otherwise hermaphrodite population. The combination of hermaphrodite and male sterile individuals or gynodioecy may be advantageous by promoting outcrossing and consequently genetic recombination. In the case of P. hypargyreus, which has been observed to be self-compatible (Heiser, 1957), male sterility of at least a few individuals will enhance genetic recombination by turning these male sterile individuals into

obligate outcrossers. The male sterile plants appear to be fertile if pollen reaches their stigmas. Achenes collected from a male sterile individual of P. ecuatorianus (Panero 1475) germinated, although only in very low numbers. It is not known if this low germination was the result of poor germination conditions or of inviability.

In overall morphology male sterile individuals are similar to the hermaphrodite individuals for vegetative traits. However, in flowering individuals the capitulescence as well as the aspect and size of the head are somewhat different. Male sterile individuals have capitulescences normally less well-organized and heads with smaller ligules not in the same plane, or of different color (Fig. 29) and in some cases smaller (i.e. P. matthewsii var. viridifolius)

PHYTOGEOGRAPHY

According to Clapperton (1983, other references therein), the Andes were formed by the subduction of the Antarctic, Cocos and Nazca plates under the South American plate which in turn is also responsible for the different Andean morphologies. Mountain uplift began in the late Cenozoic but significant elevations were not achieved until the upper Miocene. Based on analyses of vegetation fossil remains of the northern Andes, van der Hammen (1987) suggests that during the Tertiary the Andean range was probably higher than 1000 m. This altitude was gradually surpassed during the Miocene. The final uplift of at least the northern Andes to its present elevation was probably during the Pliocene. However, Clapperton (1983) concludes, based on evidence from glacier systems, that the Andes, aside from a few volcanic peaks, were

similar in elevation to those of today by the late Miocene. These somewhat different conclusions may be the result of differential orogenic rates or events along the different areas of the Andean range that have been investigated. Nevertheless, these geologic data suggest a relatively recent origin for the Andes and, by extension, of the vegetation assemblages they harbor. Based on these data, Andean montane endemic genera such as Pappobolus may be the result of relatively recent speciation events.

Palynological studies (van der Hammen 1974) of the northern Andes are the basis of the most detailed reconstruction yet of the vegetation history of this area. His studies suggest that by the late Pliocene some of the characteristic elements of the subandean forest were already present, as well as mountains perhaps as high as 2300 m. In addition, it is possible that nearby Andean peaks were high enough to support Páramo vegetation. In the Pliocene and Pleistocene conspicuous northern (Holarctic or Neotropical Mexican) elements such as Alnus Mill., Quercus L., Juglans L., Myrica L., as well as Hedyosmum Sw. appeared, some of them later to become dominant elements of the forest. The Páramo vegetation assemblage also experienced a marked enrichment in the same periods.

The enrichment of the Páramo flora took place by long distance dispersal and by a gradual adaptation of neotropical elements to these high altitude areas (Simpson 1975; Smith & Cleef 1988; van der Hammen & Cleef 1986). It is likely that Pappobolus represents an example of this phenomenon. The floristic enrichment of the Páramos of South

America may have been facilitated by the several Pleistocene glacial and interglacial periods. It is believed that between 15 and 20 glaciations have occurred in the last 2-2.5 million years (van der Hammen & Cleef 1986). Glacial periods were drier and colder at least in the northern Andes (van der Hammen 1974), resulting in a shift of the vegetation belts to at least 1500 m below present levels. These shifts in vegetation belts increased the surface area of the Páramo and facilitated the arrival and establishment of temperate elements. Fluctuations of the vegetation belts across an altitudinal gradient induced by climatic change probably resulted in the fragmentation, isolation and subsequent reunification of fragmented populations. This could have enhanced both the homogenization of diverging isolated groups such as Quercus or Alnus and the radiation of particular genera such as Pappobolus, Calceolaria (Molau 1988) or Cavendishia Lindl. (Luteyn 1983).

Dry forests and other xerophytic vegetation assemblages may have also responded to the drier and colder conditions of the glacial periods by expanding at the expense of humid forests. It is plausible to suggest that species such as the members of P. subg. Apricus adapted to dry forests may have expanded and colonized broader areas, while the ranges of species of P. subg. Pappobolus may have contracted. There are many interandean canyons influenced by descending dry, cooler air that harbor some sort of xerophytic plant community or dry forests which, under the above scenario, may have expanded and become connected as envisioned by Gentry (1982) in his "reverse refuges". The potential northern expansion of the dry forests of the western escarpment of the

Andes of Peru and Ecuador at the expense of the persistent Chocó wet forest may have facilitated the exchange of genera between this area and Central American, northern South American and Caribbean dry forest elements by reducing the distance between them. Phytogeographical studies (Sarmiento, 1975) show that, at least at the genus level, there are floristic affinities among these areas. Gentry (1982) also highlights the floristic affinities between the dry forests of eastern Ecuador and those of Brazil and southern Peru, Bolivia and Argentina. Gentry (1982), as well as Müller (1973), suggest that the Marañón valley acted as a bridge between these areas and for the same reason as an effective barrier for montane forest and Páramo elements (Simpson 1975).

Based on available information, dry habitats, such as those favored by Pappobolus, appear never to have been connected between North and South America. According to Simpson and Neff (1985), several factors suggest that the connection or existence of a tropical dry forest corridor between South and North America is difficult to support, including the paucity of shared groups, evidence that at least some amphitropical genera are the result of long-distance dispersal rather than the contraction of an otherwise continuous range and, most importantly, the distinctiveness of the bee faunas that forage amphitropical genera or species in each subcontinent. In addition, Gentry (1982) suggests that the Chocó wet forest, even in the driest periods, appears to have been present at the core of its present

distribution, effectively blocking the potential for a dry forest corridor.

The appearance in the central Andes of the ancestor of the genus Pappobolus and its subsequent diversification may have been the result of a long-distance dispersal event similar to the one responsible for the colonization and radiation of the apparently closely related Scalesia in the Galápagos Islands. In fact, several North American genera of Asteraceae with disjunct species in South America appear to have obtained their amphitropical distributions by long-distance dispersal. Most of these genera are adapted to similar dry habitats in the two hemispheres. The genus Flourensia has a total of 32 species with a slight majority located in South America (Dillon 1982, 1986). The genus is very speciose and is common in arid valleys of central and southern Peru south to Bolivia and Argentina. In Mexico, it is mostly restricted to the central Plateau where some species are quite common. This genus is not present in the regions from Ecuador north to Central America in spite of the presence of suitable arid habitats of the type normally inhabited by the genus. This is also true for the closely related genus Encelia which has all but one or two species in western Mexico and U.S.A. The other species occur in the Galápagos Islands and in the arid foothills of the western Andes of central Peru. Viguiera also exhibits a similar distribution pattern, being common in Mexico and in South America although it is rare or absent in Central America, Colombia and northern Ecuador.

The genera Tithonia and Simsia provide contrasting examples. They have some species adapted to hot, tropical scrub and moist forests that

have been successful in colonizing Central America but are absent in the South American middle and high altitude habitats similar to the ones they occupy in Mexico. In other words, these genera have apparently reached South America by first adapting to and colonizing Central American and northern South American habitats and later colonizing suitable habitats of the western escarpment of the Andes. This pattern, if true, would contrast with that of the other genera discussed in which an apparent speciation pulse and effective colonization of vast areas or habitats followed the presumed successful long-distance disperal of an ancestral species.

Pappobolus is one of the few Asteraceae genera endemic to the Andes that occupies lower montane dry forests and other vegetation assemblages up to the Páramo. Morphological and molecular data indicate that Pappobolus diversified in situ and that P. subg. Apricus is the sister group to the higher altitude species of the genus. These data, coupled with the presence of advanced characters in species at progressively higher altitudes in the Andes, follow the vertical speciation model advanced by Chardon (1938; see also Simpson, 1975). It is likely, based on the present distribution of its putative relatives, that the ancestor of Pappobolus was adapted to arid montane habitats. Initial colonization probably occurred in the Pacific drainage river valleys of Ecuador and Peru. Later it gradually adapted to higher altitudes and wetter conditions. Adaptations to major climatic zones were followed by horizontal speciation or radiation fostered by climatic fluctuations that may have fragmented and isolated

populations, eventually producing new species. This scenario explains the number of species discretely confined to one or two river valleys and effectively separated from other sister species by tenuous geographical or ecological barriers. These distribution patterns have also been observed for other Andean Asteraceae (Funk, pers. comm.) and Bignoniaceae (Gentry, 1979).

An alternative hypothesis for divergence in Pappobolus should be noted. Pappobolus could be composed of paraphyletic groups that have been subjected to essentially the same evolutionary pressures producing superficially similar individuals that under a phenetic classification scheme would tend to be seen as discrete, "natural" groups.

CLADISTIC ANALYSIS

This study represents the first attempt at constructing an infrageneric classification of Pappobolus. The phylogenetic analysis of the genus was performed under the assumption that Pappobolus represents a monophyletic assemblage of species. Although the genus presents few distinguishing generic characters, the deciduous pappus, the shrubby habit and geographical distribution are indicators of a common origin for the species here treated under Pappobolus. No other closely related genus exhibits these combination of characters.

Materials and Methods.—The phylogenetic analysis of Pappobolus is based on morphological data and field observations and it is here presented as a hypothesis of the evolutionary history of the genus. All the characters used in this analysis represent potential synapomorphies or shared derived characters (Appendix 2). No

autapomorphies were included in the analysis. Continuous characters were kept to a minimum to avoid the inherent problem of establishing character states. Nineteen of the 38 species were not used in the analysis because their character states were identical to other species. The genus Simsia was used as an outgroup based on morphological evidence (see Generic Relationships), molecular data (Schilling & Jansen 1989), geographical distribution and my familiarity with the genus. Character states shared by Simsia and Pappobolus were regarded as plesiomorphic. Certain characters (11 and 17) proved difficult to interpret given that the plesiomorphic and apomorphic conditions were present in both genera. For these two characters, the character states most commonly exhibited by Simsia were considered as the plesiomorphic condition. Cladograms were generated using version 2.4 of PAUP (D. Swofford) on an IBM-AT computer. The resulting network was rooted using the PAUP option ROOT = LUNDBERG. Other options such as multiple, equally parsimonious trees (MULPARS) and global branch swapping (SWAP = GLOBAL) were used to search for most parsimonious trees. The plesiomorphic condition was scored as "0" and the apomorphic as "1". Missing data were coded "9". The data matrix, consisting of 19 taxa and 21 characters is presented in Appendix 2. A strict consensus tree was generated using CONTREE (D. Swofford, version 1/3/86).

Results.— A total of 195 equally parsimonious trees was generated from which a strict consensus tree was produced and is shown in Fig. 30. The tree shows two major clades which are recognized taxonomically

as subgenera: the clade corresponding to P. subg. Apricus and the clade corresponding to P. subg. Pappobolus. Pappobolus subg. Apricus is characterized by yellow anther thecae (character 17), and shares with Simsia a similar ligule and ray ovary morphology (character 18) as well as a yellow disk flower lobe color (character 14). The relationships of the species of P. subg. Apricus are not fully resolved. Pappobolus hypargyreus and P. imbaburensis are not characterized by any additional synapomorphy. Pappobolus verbesinoides is characterized by lanceolate leaves as opposed to the the ovate to broadly ovate leaves of the rest of the species of the subgenus. The other six species of the subgenus are discretely characterized by pales with longitudinal bands not coalescing at the apex (character 11). Within this clade the Peruvian species and P. ecuatorianus are grouped in a clade characterized by a reversal of character 20 (pubescent disk achenes). Within these species, however, pubescent disk achenes are restricted to a few individuals or populations with the possible exception of P. hutchisonii which in all the collections examined (all from the same population) the achenes were invariably very pubescent.

The phylogeny of P. subg. Pappobolus is also highly unresolved. The lack of phylogenetically informative characters is evident in the many polychotomies within the P. subg. Pappobolus clade. The informally-recognized phenetic nigrescens group is not monophyletic based on this study because there are no synapomorphies that define its species. Within the nigrescens group, the clade represented by P. mollicomus, P. cinerascens and P. macranthus is characterized by the synapomorphy of a ray ovary pappus of several awns (character 19).

This clade is further characterized by a disk achene pappus of several awns (character 21), however, this character state is elsewhere seen in P. woodsonianus and P. decumbens. Reflexed ray flower ligules (character 12) which distinguish P. mollicomus and P. cinerascens from P. macranthus, appears also to be homoplasious and to have arisen spontaneously in other lineages within the genus. The discolor and stuebelii groups are characterized by several synapomorphies and form a well-defined clade. As in the case of the nigrescens group there are no synapomorphies that discretely define either group. Pappobolus stuebelii and P. smithii share a narrowly oval ray flower ligule morphology (character 13(2)) which contrasts with the oblong to ovate morphology of the other two species of the stuebelii group: P. jelskii and P. lodicatus. Pappobolus jelskii and P. woodsonianus form a clade defined by the apomorphic state of character 10, the dichasial thyrsoid capitulescences. This synapomorphy should be view with caution, however, given the profound morphological differences between these two species in the basic structure of the dichasial capitulescence, raising the potential that the character states in the two species are not truly homologous. According to this study, P. lodicatus is nestled within the species of the discolor group based on its ligule morphology and leaf shape. Pappobolus lanatus and P. senex phenetically are transitional between the stuebelii and discolor groups but are not characterized by any synapomorphy. The rest of the species of the discolor group forms a clade defined by lanceolate to linear leaf shape (character 2). Pappobolus cajamarcensis, P. discolor and P. decumbens

share a further synapomorphy of a shiny adaxial surface (character 7). The phenetically distinctive species, P. argenteus and P. viridior, exhibit a glabrous disk flower corolla (character 15), which is a very distinctive condition within the genus and subtribe. The northern Peruvian species P. davidii, P. lodicatus, P. microphyllus and P. subniveus fail to exhibit any phylogenetically informative character and form an unresolved polychotomy.

This study represents the initial classification framework of the genus upon which new species and information can be added. No clades below the subgenus level were recognized taxonomically because there is inadequate knowledge of the morphological variation, distribution and habitat of the genus. Given the lack of phylogenetically informative characters, the phenetic analysis presented below was used to organize the species based on overall morphological similarity within each subgenus. It is hoped that the relationships obtained may at least suggest some phylogenetic relationship.

PHENETIC ANALYSIS

The objective of this analysis was to produce a graphic representation of phenetic relationships or similarities and to highlight the major morphological characters that influenced my taxonomic decisions (Appendix 2). The phenetic relationships produced by this analysis are responsible for the order in which species appear in the taxonomic treatment below. For the purpose and scope of this study species were treated as OTUs (operational taxonomic units, Sneath and Sokal 1973).

Materials and Methods.—Data on 42 characters for the 37 OTUs (Appendix 2), were obtained from herbarium specimens, field observations and preserved material. A minimum of ten measurements for each OTU was obtained for each non-discrete character and the mean was used in the analysis. Gower's coefficient of resemblance (Gower 1971) was calculated between each pair of OTUs. This coefficient allows the use of mixed qualitative and quantitative data. Examination of the resulting matrix of coefficients for taxonomic structure utilized cluster analysis. The unweighted pair-group using arithmetic means (UPGMA) was used in the cluster analysis to produced a phenogram. Computations were performed on the VAX cluster at the University of Tennessee, using programs developed by Edward E. Schilling.

Results.—The phenetic analysis, similar to the cladistic analysis recognizes two major groups: P. subg. Apricus and P. subg. Pappobolus (Fig. 31). Additional information concerning morphological distinguishing features and relationships are discussed under the species' taxonomic treatments.

Pappobolus subg. Apricus is a cohesive morphological assemblage of species. All the species have yellow anther thecae, small heads, and large capitulescences, alternate leaves. Pappobolus subg. Pappobolus is distinguished from P. subg. Apricus by several characters. All the species of P. subg. Pappobolus have phytomelanins on the abaxial surface of the lobes of the disk corolla. These phytomelanins are also present in the veins of the ray corolla and anthers. The heads in at least some species tend to be significantly larger than those in P.

subg. Apricus. In addition, members of P. subg. Pappobolus tend to have fewer heads per capitulescence as well as longer peduncles and a much higher number of sterile leaves associated with the capitulescence (see Morphology: Capitulescence). Another distinguishing feature of P. subg. Pappobolus is that the ray ovary tends to be shorter and wider than in members of P. subg. Apricus. However, the herbage pubescence is the most striking difference between of P. subg. Pappobolus and P. subg. Apricus. The high altitude species of P. subg. Pappobolus exhibit densely lanate stems and petioles which are normally associated with thick, coriaceous leaves.

The most obvious differences among the species of P. subg. Apricus are those based on foliar and involucre characters. The phyllaries have in common a conspicuous banding pattern consisting of stramineous and green bands of various width running lengthwise. The phyllaries in P. acutifolius, P. ecuatorianus, P. hutchisonii, P. matthewsii, and P. sagasteguii, are lanceolate and rarely densely lanate. With the exception of some population of P. matthewsii and P. ecuatorianus, the phyllaries also have a long and reflexed herbaceous apex that give the head a stellate appearance. The pales are stramineous with brownish longitudinal lines which do not tend to coalesce at the apex. In addition, the pale tip is strongly reflexed particularly, in P. matthewsii and P. sagasteguii. Pappobolus acutifolius and P. hutchisonii are further distinguished by their densely puberulent disk corolla throat. These two species are the only members of the genus to have such a dense pubescence and high number of biseriate glandular trichomes in the tube of the disk corolla. In addition, they possess

lanceolate to narrowly ovate leaves with round to cuneate bases that are sparsely to moderately pubescent. These differences in the type and quantity of their foliar pubescence are in clear contrast to the rest of the species of the subgenus which have a moderately to densely lanate-villous pubescence. Pappobolus hutchisonii can also be distinguished by its strongly reflexed ligules, a character elsewhere only seen in some of the species of P. subg. Pappobolus. Pappobolus matthewsii and P. sagasteguii share broad leaves and pilose stems, although pilose herbaceous stems were only seen in some populations of P. matthewsii. Pappobolus ecuatorianus and P. verbesinoides have in common narrowly ovate to lanceolate leaves and densely villous to lanate abaxial leaf surfaces. However, this foliar character is only seen in P. ecuatorianus var. lancifolius and not in the nominal variety. In addition, the phyllaries of this species are morphologically more similar to the nominal variety of P. matthewsii and P. matthewsii var. viridifolius, P. hutchisonii and P. acutifolius. The phyllaries of P. verbesinoides tend to be oblong and stramineous-copper. This phyllary morphology is only seen in some populations of P. matthewsii var. matthewsii growing in northern Cajamarca Department close to the range of P. verbesinoides and in P. matthewsii var. occidentalis. Another morphological trait adding to the confusion is the blackish phyllary and pale coloration typical of Ecuadorian (see below) species seen in some individuals of both species. However, it is my belief that P. verbesinoides is probably an offshoot of P.

matthewsii that is adapted to the wetter and somewhat colder conditions of the basin of the Huancabamba River.

The central and northern Ecuadorian species P. hypargyreus, P. imbaburensis and P. juncosae all share broadly oblong to ovate-lanceolate phyllaries with densely lanate herbaceous apices especially on their abaxial surface. This phyllary morphology effectively circumscribes these three species, although this character is also shared by some individuals of the northernmost populations of P. ecuatorianus. Pappobolus verbesinoides has more lanceolate phyllaries simialr to those of P. matthewsii but these are blackish as in P. imbaburensis. In P. hypargyreus and P. juncosae the phyllaries tend to be broader sometimes even suborbicular, and conspicuously reflexed. In addition the involucre tends to be more pubescent than in P. imbaburensis. Pappobolus juncosae appears to be a highly specialized narrow endemic of the valley of the Mira River in northern Ecuador. The striking, dense pubescence of this species is not matched by any other member of the subgenus. This species is also unusual in possessing just a few heads per capitulescence. Pappobolus imbaburensis shares with P. verbesinoides and some populations of P. ecuatorianus dark to black inner phyllaries. At the northern edge of the range of this species individuals tend to have very small heads reminiscent of those of P. verbesinoides of northern Peru (see under P. imbaburensis).

Within P. subg. Pappobolus three groups can be recognized: the middle altitude group or the nigrescens group which consists of species with broad leaves similar to those of P. subg. Apricus and large, showy

heads, and two high altitude groups distinguished by the dense lanate pubescence of their herbage and their thick, coriaceous and somewhat smaller leaves. The high altitude species can be placed in two groups based on habit and head size: the stuebelii group, distinguished by its shrubby to arborescent habit and large heads, and the discolor group distinguished by smaller heads and a weak, low and sometimes prostrate shubby habit.

The nigrescens group of P. subg. Pappobolus shares a few characters with P. subg. Apricus. Both groups exhibit a velutinous to sericeous foliar pubescence and some members of the nigrescens group, especially P. lehmannii and P. nigrescens, have moniliform trichomes on both surfaces of the leaves, which also occur in several members of P. subg. Apricus. Pubescent disk achenes, common in P. subg. Apricus have been observed in at least two members of the nigrescens group, P. amoenus and P. robinsonii, although the achene pubescence of these two species is markedly different from the densely sericeous achenes of P. subg. Apricus. Both groups also share a similar growth habit distinguished by its robust, rapid growth that eventually produces a profusely-branched, open shrub or treelet. Pappobolus cinerascens, P. macranthus and P. mollicomus share a discrete disk achene pappus consisting of a crown of awns instead of the pappus of two awns, with or without squamellae, which is common in the rest of the genus. In addition, these species are apparently restricted to the Cordillera Oriental of the Andes of Peru. Pappobolus mollicomus has the same floral morphology of P. cinerascens, but the dense pubescence of its

herbage is reminiscent to densely pubescent forms of P. lehmannii. Pappobolus mollicomus and P. cinerascens have conspicuously reflexed ligules, a character seen in P. hutchisonii of P. subg. Apricus as well as in P. amoenus and P. robinsonii. Pappobolus macranthus can be easily distinguished its nearly round pale apices and large involucres consisting of long, lanceolate and reflexed phyllaries. This involucre morphology is not seen in any other species of the genus. Pappobolus lehmannii, P. nigrescens, P. acuminatus, P. stork-hortonii and P. andinus are distinguished by their phyllary morphology. The phyllaries in this group tend to be evenly pubescent or glabrescent with no marked difference between indurated and herbaceous parts and sometimes have a dense line of pubescence following the midrib on their abaxial surface. In the case of P. nigrescens and P. stork-hortonii the phyllaries are markedly glabrous to glabrescent and very dark green, drying black. In addition the phyllaries are only weakly graduated without great differences in morphology between the outer or innermost series. No other species exhibits this phyllary morphology. On the other hand, P. nigrescens and P. lehmannii share a well defined alternate phyllotaxy and similar foliar characters, such as type and density of pubescence, shape and leaf disposition. In addition, both species have several squamellae in their ray achenes and their style branches are black abaxially. Pappobolus lehmannii var. grandiceps shares a similar phyllary morphology with P. acuminatus and P. andinus of southern Peru. These three species can be recognized by their sparsely hirsute to villous phyllaries. Pappobolus acuminatus, P. andinus and P. stork-hortonii exhibit a villous-floccose herbage pubescence similar to that

of P. robinsonii. Pappobolus amoenus, P. robinsonii, P. sanchezii and P. schillingii possess a villous-floccose foliar pubescence and lanceolate to foliose phyllaries which are normally constricted between their indurated and herbaceous parts. Pappobolus youngiorum shares with the latter species similar phyllary morphologies, however, it possesses a velutinous-sericeous pubescence characteristic of P. lehmannii and P. nigrescens. Pappobolus schillingii and P. youngiorum share a whitish herbage pubescence and broad, blackish inner phyllaries which are glabrous to glabrescent on both surfaces and long-peduncled capitulescences. The other three species in this group, P. sanchezii, P. amoenus and P. robinsonii, share an ochreus to yellow-green herbage pubescence. The latter two species share reflexed ligules and disk achenes sparsely sericeous especially around the neck.

Pappobolus jelskii, P. smithii, P. stuebelii and P. lodicatus comprise the stuebelii group. Their striking, dense, lanate indumentum, the compact large heads and shrubby to arborescent habit represent a combination of morphological characters not seen elsewhere in the Helianthinae. These morphological characters are presumably the result of their adaptation to high altitude environments. Pappobolus jelskii possesses an opposite leaf phyllotaxy and dichasial thyrsoid capitulescences, which are both characters that effectively circumscribe this species. Pappobolus stuebelii and P. smithii share an alternate phyllotaxy and possess numerous narrowly oval-lanceolate ligules as opposed to the shorter and oval to oblong ligules of P. jelskii and P. lodicatus. Pappobolus lodicatus is morphologically

intermediate between P. stuebelii and P. microphyllus. It shares with P. stuebelii a similar herbage pubescence and with P. microphyllus a slightly larger but morphologically similar head and nearly identical leaf size and shape.

The discolor group is distinguished by small to medium heads (in the same size range as P. subg. Apricus), and phyllaries with dark green to black indurated bases and densely lanate herbaceous apices.

Pappobolus woodsonianus, P. lanatus and P. senex share an opposite leaf phyllotaxy, broad suborbicular to oval-ovate or elliptic leaves with densely lanate appressed pubescence on their abaxial surface. P. lanatus and P. senex the largest leaves of the group and have a similar head morphology. Pappobolus woodsonianus exhibits several specialized features that are not shared by any other species of the genus, such as a distinctive dichasial thyrsoid capitulescence, loosely-packed heads and disk achene pappus morphology. Pappobolus argenteus, P. davidii, and P. viridior, differ from the above three species by possessing, a more open habit, an alternate phyllotaxy, weakly sclerified, lanceolate leaves with margins that tend to be not as markedly revolute as the rest of the high altitude species. Pappobolus argenteus and P. viridior are further characterized by having glabrous disk corollas. The two species, however, have very different involucre and head morphologies and geographically they occupy the northern and southern end of the range of the group respectively. Pappobolus cajamarcensis, P. decumbens, P. discolor, P. microphyllus and P. subniveus share lanceolate to linear leaves with a prominent central vein. Their venation pattern is also slightly different from the rest of the genus,

having a mononerved to weakly triplinerved as opposed to the strongly triplinerved acrobrochidodromous venation pattern common in the rest of the genus. Pappobolus microphyllus and P. subniveus share a compact habit and lanceolate leaves with moderately strigose, white and dull adaxial surfaces. As mentioned above, some forms of P. microphyllus possess ovate to trullate leaves and phyllaries similar to those of P. lodicatus. Pappobolus cajamarcensis, P. decumbens, and P. discolor share a somewhat shiny, glabrous to sparsely strigose adaxial leaf surface. Pappobolus subniveus and P. cajamarcensis share phyllaries that are strongly reflexed and their herbaceous apices are heavily involuted and somewhat tubular. In addition, the last series of phyllaries is expanded and membranaceous as to cover the disk flowers. This phyllary morphology is conspicuously evident in P. cajamarcensis. On the other hand, P. discolor and P. decumbens have small ovate to lanceolate phyllaries forming a short involucre from which the pales protrude significantly. They both have a prostrate, weak habit, although most populations of P. discolor appear to form erect, compact shrubs reminiscent of those of the rest of the group.

SPECIES CONCEPT

The delimitation of taxa in this study has been mostly based on morphological characters. Ecological data and geographical distributions have also complemented the morphological information making easier the circumscription of certain taxa. Therefore, a morphological or phenetic species concept has been used. The term

variety is here used to recognize infraspecific variation confined to a discrete geographical area within a particular species' range. Given the poor knowledge of the distribution of many of the species, the paucity of collections, and the poor floristic knowledge of vast areas of the Andes, special emphasis was given to similarities rather than to differences in developing or maintaining species concepts. For the above reasons, and for the lack of tangible, discrete, defining characters, no effort was made to erect infrageneric taxa below the subgenus level.

2. TAXONOMIC TREATMENT

Pappobolus S. F. Blake, Hooker's Icon. Pl. 31:1-2. 1916.——TYPE: Pappobolus macranthus S. F. Blake.

Helianthopsis H. Robinson, Phytologia 44:258-259. 1979.——TYPE: Helianthus microphyllus H. B. K., [= Pappobolus microphyllus (H. B. K.) Panero].

Open or compact shrubs, rarely trees, variously with a conspicuous single stem, branching profusely from soil level, producing a multitude of stems with numerous leaves restricted to the lower third of their lengths, or rarely forming a dense central mat from where flowering shoots arise, these shoots densely covered by branchlets which root as they reach the ground, 1-40 dm tall; **stems** terete, light or dark brown, with or without creamy white lenticels, gray and glabrous, herbaceous parts purplish-brown, dark brown or white to ochreus pubescent, glabrous to glabrescent, puberulent, tomentose, hispid, sparsely pilose, villous or strigose, lanate to lanate-floccose, trichomes white, tan, green, yellowish-green, greenish-white, multicellular, tapered, 0.1-10 mm long; **leaves** alternate or opposite, sometimes both conditions present, triplinerved rarely mononerved, ovate, ovate-suborbicular, trullate to broadly trullate, rhombic, deltate, lanceolate to narrowly lanceolate, oblong or linear, adaxial surface light green, greenish-blue, greenish-gray, greenish-brown or shiny dark green, sparsely to moderately strigose or strigose-hirsute, sericeous or hirsute, trichomes hyaline, white to whitish-green, tan, multicellular, tapered, sometimes with raised multicellular bases, 0.1-2.5 mm long, sometimes with moniliform glandular trichomes restricted

to veins, arched, tan-brown, multicellular, apical cell rounded, 0.05-0.1 mm long, abaxial surface light creamy green, yellowish-green or tan, sparsely to densely villous, strigose, velutinous to lanate or lanate-floccose brownish-green or creamy green or white, sometimes silvery, trichomes white to light green or tan, multicellular, tapered, 0.15-7 mm long, pubescence along veins normally denser as to outline them against the background, sometimes with no clear difference in trichome density on and between veins, sometimes with moniliform glandular trichomes on adaxial surface; sessile glandular trichomes confined to abaxial surface 50-3000/cm^2, rarely on adaxial surface; **blades** 4-160 mm long, 1.5-110 mm wide, smaller or rarely similar in size upwards toward the capitulescence, apex acuminate, base obtuse, rarely truncate, sometimes narrowly attenuate along distal third to tenth of petiole, margins entire to serrate or revolute; petioles 3-60 mm long, terete to canaliculate, glabrous, puberulent, sparsely to densely villous, tomentose, sericeous or lanate on both surfaces; **capitulescences** monochasial or dichasial thyrsoid, with 1-50+ heads, peduncles 0.6-23 cm long, pubescence as stem; **heads** 7-32 mm across, 7.5-22 mm high, urceolate, campanulate or hemispherical; **receptacles** 3.8-18 mm in diameter in fruit, convex, rarely flat; **phyllaries** 17-81 in 3-6 subequal to graduated series, sometimes all series densely lanate as to mask phyllary morphology, first series 3-60 mm long, 1-19 mm wide, lanceolate to oblanceolate, oblong, obovate, ovate, sometimes constricted between indurated and herbaceous parts, base indurated, light green, stramineous or greenish-stramineous and glabrous

adaxially, light to dark green or stramineous and sparsely to densely tomentose, villous, velutinous or minutely hirsute, sometimes densely tomentose to lanate white, herbaceous apex reflexed, rarely appressed, sometimes foliaceous, light to dark green and sparsely to densely strigose or hirsute, sometimes densely sericeous or lanate white on both surfaces, margins sparsely to densely ciliate, second and third series 3.5-23 mm long, 1.3-11 mm wide, lanceolate to oblanceolate, oblong, fusiform, ovate, sometimes strongly constricted between indurated and herbaceous parts, light green, stramineous or greenish-stramineous and glabrous adaxially, dark green, greenish-black or stramineous and glabrous or sparsely to densely lanate, villous or velutinous abaxially, herbaceous apex slightly reflexed or appressed, light to dark green, sparsely to moderately strigose-hirsute adaxially, light green to dark greenish-black, glabrous or sparsely to moderately tomentose, lanate, villous or velutinous, margins glabrous to moderately ciliate, fourth, fifth and sixth series when present 6-18 mm long, 2.5-5 mm wide, oblong or lanceolate, rarely ovate, similar in morphology and pubescence to previous series, otherwise chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous or stramineous-green, glabrous or glabrescent; **pales** 4.9-12.5 mm long, 1.5-6.5 mm wide, oblong, lanceolate, ovate to broadly ovate, conduplicate, keeled lengthwise, stramineous or stramineous-copper, with several dark green or brown longitudinal bands of various width, bands sometimes coalescing at apex, glabrous to sparsely tomentose abaxially, apex coriaceous, acute, acuminate, rounded or cuspidate, pointed, reflexed or slightly curved inward, yellow-

stramineous or dark greenish-black, rarely densely pubescent silvery-gray; **ray flowers** 9-33, sterile, corolla bright yellow or light yellow, sometimes apex blackish abaxially, limb 5-45 mm long, 2.3-11.5 mm wide, oval to narrowly oval, oblong, lanceolate, sparsely to densely puberulent, sometimes puberulent-sericeous on veins of abaxial surface, apex acute to rounded, conspicuously to shallowly bifid or trifid, tube 0.6-3.1 mm long, yellow to yellowish-green, glabrous to densely puberulent, sometimes glandular; **ray ovaries** 1.4-5.1 mm long, biconvex or triquetrous, glabrous to glabrescent, pappus of 1-21 awns or 2-7 squamellae, awns 0.6-2 mm long, squamellae 0.2-2.4 mm long; **disk flowers** 45-400, fertile, flowers protruding 0.2-3 mm above pales, corollas deep yellow, orangish-yellow or lemon yellow, campanulate to narrowly campanulate, narrowly lyrate or tubular, throat 1.9-7 mm long, 0.6-1.8 mm wide at base, 0.6-2 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla or throat, glabrescent or sparsely to densely puberulent (sometimes pubescence conspicuously denser on the base), with uni- and biseriate multicellular glandular trichomes 0.05-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.4 mm long, tube 0.5-2.3 mm long, light yellow or yellowish-green, glabrous to moderately puberulent and glandular, trichomes as throat, lobes 0.5-1.4 mm long, yellow, sometimes blackish abaxially, sparsely to densely puberulent abaxially; anthers 5, 1.3-3.7 mm long, thecae yellow, orangish-yellow, yellowish-brown, brownish-black, purplish-black or black, appendages 0.3-0.7 mm long, ovate, ovate-suborbicular or lanceolate, stramineous, yellow, black or

purplish-black; styles 2.3-8.6 mm long, style branches 0.4-2.5 mm long; **disk achenes** 2.3-6.9 mm long, 0.7-2.5 mm wide, biconvex, obovate, with diminutive shoulders at the angles of the achene, shiny black, grayish-black, mottled gray and black or silvery sericeous, sometimes with silvery-orange or purple trichomes conspicuously contrasting with black coloration of achene wall, glabrous or sparsely to densely sericeous, pappus of 2-28 awns sometimes with 2-15 squamellae, awns slender, stramineous to purplish-stramineous, deciduous, rarely persistent, subequal, 1.3-5 mm long, squamellae free, to somewhat fused at the base, 0.3-2 mm long, same color as awns, deciduous, rarely persistent; Base chromosome number $\underline{x}$ = 17.

Phenology. Flowering at the middle and end of the rainy season, from late January to July. High altitude species from the Jalca regions of Peru flowering throughout the year.

Distribution. The Andean Cordillera from southern Colombia to Central Peru at altitudes of 650-4200 m.

ARTIFICIAL KEY TO THE SPECIES OF PAPPOBOLUS

(Para claves en español ver Apéndice 6)

1. Anther thecae yellow, orangish-yellow or brownish-yellow; disk flower lobes yellow abaxially.
   2. Pale apices slightly to strongly reflexed; phyllaries narrowly lanceolate with spreading to strongly reflexed linear herbaceous apices.
      3. Leaves ovate, deltate or broadly trullate; capitulescence associated with large leaves (just slightly smaller than

cauline leaves).

4. Leaves densely velutinous-sericeous to pilose abaxially, moderately to densely pilose adaxially; leaf margin serrate; herbaceous stem pilose.

2. P. sagasteguii.

4. Leaves glabrescent to moderately velutinous or villous abaxially, sparsely to moderately strigose adaxially; leaf margin entire to serrulate; herbaceous stem tomentose to moderately tomentose-hirsute.

1. P. matthewsii.

3. Leaves ovate to narrowly lanceolate, rarely linear; capitulescence with markedly smaller leaves than cauline leaves.

5. Disk flower throat 6-7 mm long; ray flower ligules reflexed; pales protruding 3-4 mm beyond phyllaries.

4. P. hutchisonii.

5. Disk flower throat 2.7-4.5 mm long; ray flower ligules not reflexed; pales protruding 1-1.5 mm beyond phyllaries.

5. P. acutifolius.

2. Pale apices straight; phyllaries oval to oblong, with appressed or slightly to moderately reflexed acute to suborbicular herbaceous apices.

6. Receptacles 3.9-4.2 mm in diameter in fruit; leaves narrowly lanceolate and densely lanate or velutinous

abaxially; leaves conspicuously and abruptly smaller upwards toward the capitulescence; phyllaries 17-21 in 3 subequal series. 6. P. verbesinoides.

6. Receptacles 5.7-8.5 mm in diameter in fruit; leaves lanceolate, ovate, trullate or rhombic sparsely to moderately villous, velutinous or lanate-sericeous; leaves progressively smaller upwards toward the capitulescence; phyllaries 19-30 in 3-4 subequal or graduated series.

7. Phyllaries of second to fourth series dark greenish-black or black and glabrescent abaxially; apex or distal half of pales conspicuously dark green or black. 8. P. imbaburensis.

7. Phyllaries of second to fourth series stramineous or stramineous-copper with conspicuous light green bands sometimes obscured by dense pubescence; apex or distal half of pales stramineous with light brown or green bands, rarely coalescing into a blackish apex.

8. Phyllaries broadly oval to suborbicular, sparsely to densely villous to lanate abaxially, herbaceous apices densely pubescent white or whitish-green.

9. Leaves and stems densely velutinous or villous to lanate white; pale apices stramineous with a few soft brown or green bands; capitulescence small with 1-5 heads. 9. P. juncosae.

9. Leaves and stems sparsely to densely tomentose to velutinous creamy green, never lanate white; pale apices dark green, rarely stramineous; capitulescence large with (3-) 12-40 heads. 7. P. hypargyreus.

8. Phyllaries narrowly oblong to lanceolate, minutely tomentose to villous but pubescence never obscuring color pattern of phyllary, indurated base stramineous with green longitudinal bands coalescing into a green herbaceous apex.

10. Disk flower throat 6-7 mm long; ray flower ligules reflexed; pales protruding 3-4 mm beyond phyllaries. 4. P. hutchisonii.

10. Disk flower throat 1.7-4.9 mm long; ray flower ligules not reflexed; pales protruding 0.2-0.6 mm beyond phyllaries.

11. Heads with 85-140 disk flowers; pale apices slightly to strongly reflexed; disk flower throat 1.9-2.9 mm long; pales protruding 0.2-0.6 mm beyond phyllaries. 1. P. matthewsii.

11. Heads with 60-90 disk flowers; pale apices pointed; disk flower throat 1.7-4.9 mm long; pales protruding 0.5-3 mm beyond phyllaries. 3. P. ecuatorianus.

1. Anther thecae black, brownish-black or purplish-black; disk flower lobes black, rarely yellow abaxially.
   12. Leaf margins subentire to serrate, never revolute; leaf texture thin; leaves not conspicuously bicolored; leaves ovate to deltoid to broadly lanceolate-elliptical and 25-160 mm long, 10-110 mm wide; petioles 5-52 mm long.
      13. Disk achene with a pappus of (5-) 8-28 awns and no squamellae; ray ovary with a pappus of (3-) 5-21 awns and no squamellae.
         14. Phyllaries oblong to ovate and appressed.
            15. Phyllaries densely lanate white abaxially. 16. P. mollicomus.
            15. Phyllaries glabrescent, dark green, drying black. 22. P. robinsonii.
         14. Phyllaries lanceolate and spreading or reflexed.
            16. Phyllaries 35-44, first and second series 10.5-11.5 mm long; leaf margins subentire to shallowly serrulate; ray flower ligules reflexed. 15. P. cinerascens.
            16. Phyllaries 38-62, first and second series 17-30 mm long; leaf margins serrate; ray flower ligules not reflexed. 17. P. macranthus.
      13. Disk achene with a pappus of 2 (-3) awns with or without squamellae; ray ovary with a pappus of 1-7 awns with or without squamellae or epappose.

17. Leaves alternate.

    18. Capitulescences compact, 1-3 heads on very short peduncles (see Fig. 12G). 12. P. andinus.

    18. Capitulescences open, 3-21 heads on long peduncles (see Fig. 12B).

        19. Leaf abaxial pubescence villous to lanate-floccose. 20. P. schillingii.

        19. Leaf abaxial pubescence velutinous to sericeous.

            20. Ray flower ligule 6.5-15 mm long, 3-5.3 mm wide.

                21. Ray flower ligules oblong-lanceolate, 14-15 mm long; phyllaries linear-lanceolate with blackish indurated bases. 23. P. szyszylowiczii.

                21. Ray flower ligules oval to oblong, 6.5-10.5 mm long; phyllaries oblong to oblanceolate without blackish indurated bases. 7. P. hypargyreus.

            20. Ray flower ligule 16.5-33.5 mm long, 6-11.5 mm wide.

                22. Ray ovary with 2-7 squamellae or small awns; style branches black abaxially.

23. Disk flower tube sparsely to moderately puberulent; disk achene 3.4-4.1 mm long; abaxial surface of phyllaries dark green drying black. 11. P. nigrescens.

23. Disk flower tube glabrous, disk achene 4.8-5.8 mm long; abaxial surface of phyllaries evenly hirsute, villous or lanate-sericeous. 10. P. lehmannii.

22. Ray ovary epappose or with 1 or 2 minute squamellae or awns; style branches yellow throughout. 13. P. stork-hortonii.

17. Leaves opposite.

24. First series of phyllaries 19-60 mm long, 7.5-19 mm wide, reflexed, twisted and foliaceous. 18. P. sanchezii.

24. First series of phyllaries 7.5-21 mm long, 3-10 mm wide, reflexed, twisted but not foliaceous.

25. Leaf abaxial surface lanate-floccose.

26. Leaf adaxial surface moderately to densely strigose-sericeous whitish -green; leaf margins entire; leaves

broadly ovate, bases obtuse to truncate. 14. P. acuminatus.

26. Leaf adaxial surface strigose, green; leaf margins shallowly serrulate to serrate; leaves ovate to ovate-lanceolate, bases attenuate to rounded.

27. First and second series of phyllaries oblong to spatulate, densely lanate or villous and reflexed, inner phyllaries appressed and dark green or black conspicuously lanate along acute tip of herbaceous apex abaxial surface. 22. P. robinsonii.

27. First and second series of phyllaries lanceolate to ovate, moderately tomentose to velutinous abaxially, inner phyllaries spreading and dark green, drying black, glabrescent to sparsely villous along acuminate to tapered tip of herbaceous apex abaxial surface.

28. Heads hemispherical; first

three series of phyllaries 12-21 mm long, 2.8-5 mm wide; ray flower ligules not reflexed; disk achene glabrous with a pappus of 2 awns and no squamellae. 20. P. schillingii.

28. Heads hemispherical-urceolate; first three series of phyllaries 7.4-12.5 mm long, 2.7-4.5 mm wide; ray flower ligules reflexed; disk achene with a few trichomes around the neck with a pappus of 2 awns sometimes 2-10 squamellae. 21. P. amoenus.

25. Leaf abaxial surface velutinous to sericeous. 19. P. youngiorum.

12. Leaf margins revolute and entire or rarely subentire; leaves thick and coriaceous; leaves bicolored due to conspicuous densely lanate pubescence on abaxial surface; leaves ovate to ovate-lanceolate, ovate-suborbicular, trullate, oblong, lanceolate to narrowly lanceolate or elliptical 4-115 mm long, 2-50 mm wide; petioles 1-30 mm long.

29. Disk achene pappus of more than 3 deciduous awns.

30. Leaves alternate, narrowly lanceolate to linear.

32. P. decumbens.

30. Leaves opposite, oval to elliptic.

33. P. woodsonianus.

29. Disk achene pappus of 2 or 3 deciduous awns squamellae rarely present.

31. Disk flowers 160-385; heads 16-32 mm across; leaves ovate to ovate-lanceolate, 10-115 mm long, 6-50 mm wide.

32. Leaves opposite. 26. P. jelskii.

32. Leaves alternate.

33. Leaves sparsely to moderately strigose, rugose adaxially, densely lanate tan.

24. P. stuebelii.

33. Leaves moderately to densely strigose -sericeous adaxially, densely lanate white abaxially. 25. P. smithii.

31. Disk flowers 35-160; heads 7-19 mm across; leaves ovate, ovate-suborbicular, trullate, oblong, lanceolate to narrowly lanceolate 4-80 mm long, 2-50 mm wide.

34. Leaves narrowly lanceolate to linear or minutely oblong (if trullate or ovate, heads smaller than 1 cm across [ligules not included]).

35. Leaf adaxial surface essentially

glabrous and shiny; innermost phyllaries suborbicular, membranaceous, covering immature head.

30. P. cajamarcensis.

35. Leaf adaxial surface pubescent and dull, rarely shiny; innermost phyllaries lanceolate to linear or oblong, chartaceous, never covering immature head.

36. Leaves narrowly lanceolate to linear and heavily revolute.

37. Pales protruding 1.5-2 mm beyond phyllaries; phyllaries abaxial base dark green or blackish and glabrescent, herbaceous apex appressed; leaf adaxial surface sparsely strigose, somewhat shiny; leaves decreasing in size and number upwards toward the capitulescence.

31. P. discolor.

37. Pales covered by phyllaries; phyllaries abaxial base densely lanate white,

herbaceous apex spreading; leaf adaxial surface moderately to densely strigose, dull whitish-green; leaves equivalent in size and number upwards toward the capitulescence. 29. P. subniveus.

36. Leaves ovate, oval to oblong, trullate (if narrowly lanceolate or linear then heads smaller than 1 cm across [ligules not included]). 28. P. microphyllus.

34. Leaves lanceolate to ovate or ovate-suborbicular, sometimes ovate to trullate.

38. Herbage pubescence ochreus. 27. P. lodicatus.

38. Herbage pubescence white or gray.

39. Leaves ovate to ovate-suborbicular, 10-80 mm long, 40-50 mm wide.

40. Disk flowers 115-160; ray flower limb 14.5-19.5 mm long; phyllaries 20-32 in 4 graduated series. 35. P. lanatus.

40. Disk flowers 45-85; ray flower limb 8.5-9.5 mm long;

phyllaries 19-26 in 3 subequal series. 36. P. senex.

39. Leaves lanceolate 11-65 mm long, 15-17 mm wide.

41. Disk flower corolla glabrous; ray flower ligules 8.2-25 mm long, 2.3-7 mm wide.

42. Pale apices pubescent; phyllaries 24-37. Plants of Ecuador. 37. P. argenteus.

42. Pale apices glabrous; phyllaries 20-23. Plants of Peru. 38. P. viridior.

41. Disk flower corolla sparsely to moderately puberulent and glandular; ray flower ligules 9-14 mm long, 2.5-4 mm wide. 34. P. davidii.

I. Pappobolus S. F. Blake subgenus Apricus Panero, subg. nov.—TYPE: Pappobolus hypargyreus (S. F. Blake) Panero.

Pappobolus subg. Apricus habet luteas vel atroluteas antherarum thecas, magnas monochasiales thyrsoideas synflorescentias, phyllaria pro parte maxima straminea cum pluribus atroviridibus longitudinalibus fasciis variae latitudinis, longa et tenuia radialia ovaria et parvos radiales flores.

Shrubs 3-35 dm tall; **leaves** alternate, triplinerved, lanceolate to narrowly lanceolate, ovate to broadly ovate, rhombic or deltoid; **blades** 8-125 mm long, 3-85 mm wide, petioles 5-60 mm long; **capitulescences** monochasial thyrsoid, with 1-50+ heads, peduncles 6-115 mm long; **heads** 7-14.5 mm across, 7.5-14 mm high, oblong-campanulate, campanulate, slightly urceolate or hemispherical; **receptacles** 4-8.5 mm in diameter in fruit, convex; **phyllaries** 17-31 in 3-4 subequal to graduated series; **pales** 5-11 mm long, 2.3-4 mm wide; **ray flowers** 10-20, limb 5-15 mm long, 2.3-5 mm wide, tube 0.7-1.7 mm long, sparsely to moderately puberulent and glandular; **ray ovaries** 1.8-4 mm long, epappose or with a pappus of 2-7 squamellae 0.3-0.6 mm long, sometimes with 1 awn 2-2.4 mm long or 1-3 awns 0.3-1.6 mm long; **disk flowers** 50-220, throat 1.9-7 mm long, 0.6-1.7 mm wide at base, 0.6-2 mm wide at junction with lobes, moderately to densely puberulent with interspersed uni- and biseriate glandular trichomes 0.05-0.2 mm long, tapered trichomes white to hyaline 0.1-0.3 mm long, tube 0.6-2.3 mm long, lobes 0.5-1.5 mm long; anthers 1.3-3.7 mm long, thecae yellow, orangish-yellow, brownish-yellow, yellowish-tan, appendages 0.3-0.7 mm long; styles 2.3-7.5 mm long, style branches 0.5-2.1 mm long; **disk achenes** 2.3-6.9 mm long, 0.7-2.5 mm wide, biconvex, oval-obovate to obpyramidal, with 2 diminutive shoulders, shoulders sometimes absent, shiny black, grayish-black, mottled, silver or with silvery-orange trichomes conspicuously contrasting with black coloration of achene wall, glabrous to densely sericeous, pappus of 2 awns and 2-15 squamellae, sometimes without squamellae, awns slender, stramineous, deciduous to somewhat persistent, subequal, 1.3-3.5 mm long, squamellae free to slightly

fused at the base, 0.4-1.5 mm long, same color as awns, deciduous to somewhat persistent.

Phenology. Flowering at the end of the rainy season from late March in central Peru to late July in Ecuador. Certain species flowering sporadically throughout the year. Flowering is clearly tied to availability of water. The onset of the dry season brings shedding of leaves and consequently a rest period.

Distribution. The members of P. subg. Apricus as the name implies are sun-loving. Known from seasonally dry, sunny valleys of the Pacific-drainage Rivers of Ecuador and Peru. They are also known from the interandean dry valleys of northern Peru, especially the basins of the Marañón and Chamaya Rivers. They range as far south as the Santa River valley of Ancash Department in Central Peru and north to Nariño Province, Colombia, the latter representing the northernmost extension of the genus; 650-3000 m.

1. Pappobolus matthewsii (Hochr.) Panero, comb. nov. Helianthus matthewsii Hochr., Bull. N.Y. Bot. Gard. 6:296. 1908-1910. Helianthopsis matthewsii (Hochr.) H. Robinson, Phytologia 44:264. 1979.——TYPE: PERU. Amazonas: Chachapoyas, Mathews 3061 (lectotype, here designated: K!, fragment at US!, photo: GH!; isolectotypes: BM(2)!, GH!; NY!, photo: GH!).

Profusely branched, open shrubs 10-35 dm tall; **stems** terete, brown with showy creamy white lenticels, glabrous, herbaceous parts dark brownish-purple, tomentose, villous to hirsute upwards toward the

capitulescence, trichomes hyaline or white, multicellular, tapered 0.2-0.5 mm long; **leaves** alternate, triplinerved, ovate, rhombic or broadly trullate, adaxial surface brown, green or dull brownish-green, sparsely to densely hirsute or strigose, trichomes hyaline to white, sometimes dull green, multicellular, tapered, 0.15-0.5 mm long, abaxial surface sericeous or velutinous creamy brownish-green, sometimes silvery iridescent, trichomes combed in opposite directions from secondary veins meeting at intersecondary composite veins, trichomes white to hyaline, multicellular, tapered, 0.4-1 mm long; sessile glandular trichomes confined to abaxial surface 500-1000/cm^2; **blades** 30-120 mm long, 10-75 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse and narrowly attenuate along distal half to third of petiole, margins entire to serrulate; petioles 5-45 mm long, terete to slightly canaliculate, densely tomentose to sparsely hirsute on both surfaces; **capitulescences** monochasial thyrsoid, with (3-) 9-50+ heads, peduncles 25-90 mm long, tomentose to villous-hirsute below the heads, trichomes as stem; **heads** 9-12.2 mm across, 7.5-10.5 mm high, urceolate to broadly campanulate; **receptacles** 5.7-6.3 mm in diameter in fruit, convex; **phyllaries** 19-27 in 3-4 subequal to strongly graduated series, first series 5-14.2 mm long, 1.2-2.6 mm wide, lanceolate or oblong, base indurated, stramineous-green and glabrous adaxially, densely tomentose-farinose creamy green abaxially, herbaceous apex appressed to strongly reflexed, green and tomentose to hirsute adaxially, densely tomentose to hirsute creamy green abaxially, margins ciliate, second and third series 5-11 mm long, 1.6-3.2 mm wide, lanceolate, oblong, obovate, deltate, base indurated, stramineous and

glabrous adaxially, stramineous, sometimes with several dark green longitudinal bands and sparsely to moderately tomentose or glabrescent, herbaceous apex foliaceous, reflexed, sometimes very reduced and appressed, green and sparsely to moderately tomentose to somewhat sericeous abaxially, margins puberulent to tomentose-sericeous, fourth series 4.5-12.3 mm long, 1.5-2.7 mm wide, oblong to oblanceolate, pyramidal, chartaceous to slightly indurated with no clear distinction between herbaceous and indurated parts, sometimes base strongly indurated, stramineous to dark green and glabrous to glabrescent abaxially, herbaceous apex appressed, rarely reflexed, green and sparsely tomentose adaxially, soft green, sparsely tomentose abaxially; **pales** 4.9-8.3 mm long, 2.5-3 mm wide, broadly ovate to oblong, conduplicate, shallowly to strongly keeled lengthwise, covered or sometimes protruding 0.5-3 mm beyond phyllaries, stramineous with several green or brown longitudinal bands of various width, bands rarely coalescing at apex, glabrous to sparsely puberulent abaxially, apex coriaceous to somewhat chartaceous, acuminate to acute, sometimes trifid, pointed to slightly reflexed, stramineous-yellow, rarely blackish; **ray flowers** 10-15, corolla golden yellow, limb 5-15 mm long, 3-5 mm wide, oval to oblong, sparsely to densely puberulent and glandular on veins of abaxial surface, apex acute, minutely to conspicuously bifid, tube 0.9-1.5 mm long, sparsely to moderately puberulent and glandular; **ray ovaries** 1.9-4 mm long, triquetrous, glabrous, pappus of 2-6 deeply lacerated squamellae 0.3-0.6 mm long; **disk flowers** 85-140, flowers protruding 0.2-0.6 mm above pales,

corollas deep golden yellow, cylindrical to narrowly campanulate, throat 1.7-5 mm long, 0.6-1 mm wide at base, 0.6-1.4 mm wide at junction with lobes, veins orange to orangish-green and discernable the whole length of the corolla, moderately to densely puberulent with interspersed uni- and biseriate glandular trichomes 0.05-0.2 mm long, tapered trichomes white to hyaline, 0.1-0.25 mm long, tube 0.7-2.3 mm long, yellowish-green, sparsely to moderately puberulent with a few scattered uni- and biseriate glandular trichomes, trichomes as throat, lobes 0.4-1 mm long, yellow, moderately puberulent and glandular abaxially; anthers 1.6-3.2 mm long, thecae yellow to tan-brown, appendages 0.4 mm long, ovate, yellowish-stramineous; styles 3-6.5 mm long, style branches 0.5-2 mm long; **disk achenes** 2.6-4 mm long, 0.9-1.7 mm wide, biconvex, oval-obovate, shoulders rarely present, shiny grayish-black, black, mottled, silver or with silvery-orange trichomes conspicuously contrasting with black coloration of achene wall, sparsely to densely sericeous, pappus of 2 awns, sometimes with 2-10 squamellae, awns slender, stramineous, deciduous to somewhat persistent, subequal, 1.5-2.8 mm long, squamellae free, 0.4-0.8 mm long, same color as awns, deciduous to somewhat persistent; $\underline{n}$ = 17.

Phenology. Flowering January to July.

Distribution. (Fig. 32). Known from Cajamarca and Amazonas Departments in northern Peru. Sometimes forming large colonies along the tributaries of the Chamaya, Marañón and Utcubamba Rivers. In the canyon of the Utcubamba River it is not uncommon to find roads densely lined for several kilometers by this species. It is also abundant around the towns of Chachapoyas and Jaén. Another large population is

found along the road Celendín-Balsas on the western side of the Marañón River canyon, although no individual of this species was observed in comparable habitats on the eastern side of the canyon. Isolated populations grow in the dry deciduous forests along several of the Pacific drainage rivers of Cajamarca; 650-2000 m.

Pappobolus matthewsii is morphologically very variable, although it can be recognized by its long and reflexed phyllaries, foliose capitulescence, broadly ovate to trullate leaves with mostly entire margins and reflexed pale apices. It is closely related to P. sagasteguii with which it shares a similar pale morphology and capitulescence structure (also see discussion under P. sagasteguii). Some forms of P. matthewsii, especially those coming from the area of Jaén and characterized by smaller and more appressed phyllaries and slightly reflexed pales may be confused with individuals of P. ecuatorianus from the Jubones River of central Ecuador. Both taxa can be separated by the disk flower number which in P. matthewsii is larger (see key characters) and the foliose capitulescence.

The spelling of the species name as originally described by Hochreutiner (1908-10) was Helianthus matthewsii. He named this species to honor the collector Andrew Mathews. There appears to be some degree of confusion, however, in the proper spelling of the name Mathews. Some label data indicate that his name should be spelled Mathews with one "t", whereas Vegter (1976) recognizes Matthews with a double "t". Given this conflicting evidence, the original spelling of the species is maintained.

Another source of controversy is the identity and authenticity of the syntypes. Although one of the specimens at BM and the ones at K and GH bear the number 3061, the rest of the purported syntypes lack this number. Hochreutiner based his description on the NY specimen and to a certain extent on the K specimen that he apparently saw. In the concluding paragraph of the description he mentions the undoubted common origin of both specimens. This statement and the fact that both the unnumbered specimen at NY and the numbered specimen at K were part of erecting this species concept inclined me to treat all of the specimens of this taxon collected by A. Mathews as syntypes whether they are numbered or not. The K specimen, being part of the original description and in better condition than the NY specimen, was chosen as the lectotype.

KEY TO THE VARIETIES OF Pappobolus matthewsii.

1. Leaves sparsely hirsute abaxially; ray corolla apex conspicuously bifid. 1c. P. matthewsii var. viridifolius.
1. Leaves densely lanate-sericeous or velutinous abaxially; ray corolla apex acute to minutely bifid.
   2. Phyllaries lanceolate in outline, herbaceous apex slightly to strongly reflexed. 1a. P. matthewsii var. matthewsii.
   2. Phyllaries oblong to obovate in outline, herbaceous apex conspicuously reduced and appressed. 1b. P. matthewsii var. occidentalis.

1a. Pappobolus matthewsii var. matthewsii.

Helianthopsis utcubambensis H. Robinson, Phytologia 54:53-54. 1983.——TYPE: PERU. Amazonas: Río Utcubamba valley, 3 km along road S of Tingo, 5500 ft, 21 Jan 1983 King & Bishop 9271 (holotype: US!; isotype: UC!).——PARATYPES: PERU. Amazonas: 3 km E of Chachapoyas along road to Mendoza, 7000 ft, 12 Jan 1983, King & Bishop 9155 (US!); 6 km along road W of Chachapoyas, 6600 ft, 13 Jan 1983, King & Bishop 9193 (K!, UC!, US!).

Leaves ovate, lanceolate, rhombic or broadly trullate, adaxial surface green or dull greenish-brown, sparsely to moderately hirsute-strigose, abaxial surface velutinous creamy green, sometimes sericeous silvery-green, iridescent; **blades** 36-120 mm long, 10-72 mm wide, margins entire to serrulate; **phyllaries** in 3-4 subequal series, lanceolate, base indurated, herbaceous apex foliaceous, strongly reflexed; **ray flowers** limb 7.8-15 mm long, 3.5-5 mm wide, apex acute, minutely bifid, tube 0.9-1.5 mm long; **disk flowers** cylindrical to narrowly campanulate, throat 1.7-2.8 mm long, 0.8-0.9 mm wide at base, 0.9-1.4 mm wide at junction with lobes, tube 0.8-1.1 mm long; anthers 1.6-1.8 mm long; **disk achenes** 2.5-3 mm long, 0.9-1.2 mm wide, shiny grayish-black, black, silver, glabrous or sparsely to densely sericeous. n = 17.

Phenology. Flowering from January through July. Major period in March and April.

Distribution (Fig. 32). Restricted to xerophytic forests of the many tributaries of the Chamaya, Utcubamba and Marañon Rivers of Northern Perú; 650-2000 m.

SPECIMENS EXAMINED. PERU. AMAZONAS: Prov. Chachapoyas, km 54-55 de la carretera Chachapoyas-Leimebamba, 1900-2000, 12 Apr 1950, Ferreyra 7104 (MO, TENN, US, USM); 34 km NW of Chachapoyas, on road to Bagua, 1370 m, 17 Jun 1978, Gentry et al. 23224 (F, TENN); 4 km S of Chachapoyas on road to Balsas, 1950 m, 23 Mar 1988, Panero 1354 (TENN); 10 km S of Chachapoyas on road to Balsas, 1300 m, 23 Mar 1988, Panero 1355 (F, GRI, TENN); Prov. Luya, entre Jazán y Pomacocha, borde de la carretera, 1800 m, 6 Jun 1978, Sánchez Vega J. et al. 2251 (CPUN); 12 W of Pedro Ruiz on road to Bagua Grande, 800 m, 22 Mar 1988, Panero 1352 (CPUN, F, GRI, TENN, US); 8 km W of Pedro Ruiz on road to Bagua Grande, 820 m, 22 Mar 1988, Panero 1353 (TENN).—CAJAMARCA: Prov. Cutervo, below Querocotillo, 1400 m, May 1915, Weberbauer 7122 (F(2), GH, US); Prov. Jaén, between Shumba and Jaén, Apr 1912, Weberbauer 6185 (GH, F, S, TEX, US); Quebrada de San Agustín, 1100-1200 m, 20 Jul 1982, Ferreyra & Sánchez 19658 (TENN, US, USM); Morro Solar, margen derecha del Río Jaén, 650 m, 11 Jul 1982, Ferreyra & Sánchez 19558 (TENN, US, USM); Km 14-15 of the road Chamaya-Jaén, 890 m, 22 Mar 1988, Panero 1351 (CPUN, F, GRI, MEXU, QCA, TENN, US); 69 km N along road from Jaén to San Ignacio, 1400 ft, 23 Jan 1983, King & Bishop 9296 (US); road between Santa Cruz and San Ignacio, ca 4 km N of Santa Cruz, 9 Jun 1966, Edwin & Schunke 3723 (US); entre Santa Cruz y Tamborapa, 650 m, 23 May 1963, López et al. 4127 (HUT).

This variety is the most common and also morphologically the most variable of the three. It can be recognized by the long and strongly reflexed, herbaceous apices of its phyllaries which give the head a

stellate appearance.

Some of the collections of this variety have unusual morphological specializations which require additional discussion. Panero 1351 of the area of Jaén in northern Cajamarca is representative of the collections coming from this area. This specimen exhibits phyllaries that are shorter and less reflexed and the heads tend to be slightly smaller than those of other parts of the range of the variety. On the other hand, Sánchez Vega J. et al. 2251 collected close to Lake Pomacocha in Amazonas Department exhibits the largest heads for this variety as well as very long, reflexed phyllaries. Ferreyra & Sánchez 19658 presents deltate phyllaries and large, campanulate-hemispherical heads, a combination of characters not seen in any other collection of P. matthewsii.

Robinson (1983) described Helianthopsis utcubambensis to accomodate a few collections of the area of Chachapoyas in Amazonas Department of northern Peru having reflexed phyllaries. The strongly reflexed phyllaries are precisely what characterizes the nominal variety of P. matthewsii, and therefore P. utcubambensis is placed in synonymy under it. In addition, P. utcubambensis has a similar capitulescence morphology, leaf size and shape and herbage pubescence. Another difference observed by Robinson (1983) was that the two taxa have a temporal difference in their flowering periods. Personal observations confirm that the populations around the city of Chachapoyas tend to flower in January and February while those at Jaén begin flowering in March and April. Given the large area covered by

this species and the significant differences in climatic conditions within its range is not improbable to observe these differences.

1b. Pappobolus matthewsii var. occidentalis Panero, var. nov.——TYPE: PERU. Cajamarca: Prov. Contumazá, SW of Magadalena along the trail to the locality of el Guayabo, 1600 m, 15 Apr 1988, Sánchez Vega 4699 (holotype TENN!; isotypes: F!, US!).——PARATYPE: same locality as type, 1 May 1986, Sánchez Vega 4036 (CPUN!).

Pappobolus matthewsii var. occidentalis differt a nominata varietate. Habet oblonga appressa phyllaria cum valde diminuto herbaceo apice.

Leaves ovate to broadly trullate, adaxial surface dull dark greenish-brown and moderately hirsute, abaxial surface moderately to densely strigose-lanate white; **blades** 30-120mm long, 10-70 mm wide, margins subentire to serrulate; **phyllaries** in 3-4 subequal series, oblong to obovate, base indurated, herbaceous apex conspicuously reduced, appressed; **ray flowers** limb 7.2-8 mm long, 4.4-4.6 mm wide, apex acute, minutely bifid, tube 1.4-1.6 mm long; **disk flowers** cylindrical, throat 2-3 mm long, 0.6-0.8 mm wide at base, 1 mm wide at junction with lobes, tube 0.7-1.4 mm long; anthers 1.6 mm long; **disk achenes** 2.5-3.4 mm long, 1-1.3 mm wide, shiny grayish-black, sparsely to moderately sericeous. Chromosome number unknown.

Phenology. Flowering from April through June.

Distribution (Fig. 32). Restricted to lower montane dry scrub or forest of the valleys of the Pacific drainage rivers of the Department of Cajamarca; 1400-1850 m. The type locality is approximately 2 km

from the Pacasmayo-Cajamarca road along a well-defined trail that begins at the end of a pedestrian bridge (that crosses the Jequetepeque River) approximately 1 km E of the town of Magdalena. The type locality is dominated by herbaceous Acanthaceae, Carica, Prosopis, arborescent Vernonia patens H. B. K., Simsia dombeyana and several Malvaceae. This area may have been dominated by forests given the few Ocotea trees that have been left behind for shade. This species was growing along a cornfield with the spectacular Rauhia, a genus in the Liliaceae thought to be endemic to the Marañón River basin and, like P. matthewsii, disjunct in this valley.

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Santa Cruz, entre Santa Cruz y Catache, 1850 m, 21 May 1965, López & Sagástegui 5185 (HUT, LP, TENN); antes de Catache, 1400 m, 7 Jun 1986, Quiroz 1891 (F, US).

All of the members of this variety have been collected west of the Andes along the canyons of Pacific drainage rivers of northern Peru, hence its name. This variety is recognized by phyllaries that are oblong and indurated. In addition, the herbaceous apex of the phyllary is very reduced and acute to rounded, and appressed. The collection López & Sagástegui 5185 represents a male sterile individual in which the heads are markedly smaller than the type and in the size range of those of P. verbesinoides, the smallest in the subgenus.

1c. Pappobolus matthewsii var. viridifolius Panero, var. nov.——TYPE: PERU. Cajamarca: Prov. Celendín, 48 km E of Celendín on road to

Balsas, 1390 m, 12 Mar 1988, Panero & Sánchez Vega 1257 (holotype F!; isotypes: CPUN!, GRI!, TENN!, NY!, US!, USM!).

Pappobolus matthewsii var. viridifolius differt a nominata varietate. Habet sparsim pubescentia, subviridia folia et conspicue indentatos apices radialium florum.

Leaves ovate to lanceolate, adaxial surface light green and sparsely hirsute, abaxial surface light green, slightly paler than adaxial surface and sparsely hirsute; **blades** 28-75 mm long, 10-42 mm wide, margins entire to shallowly serrulate; **phyllaries** in 3-4 slightly graduated series, lanceolate to oblong, base indurated, herbaceous apex foliaceous, reflexed; **ray flowers** cylindrical to narrowly campanulate, throat 3-3.5 mm long, 1 mm wide at base, 1.2 mm wide at junction with lobes, tube 1-1.2 mm long; anthers 2.3-2.4 mm long; **disk achenes** 2.8-3 mm long, 1.2-1.3 mm wide, shiny grayish-black or black, glabrous or sparsely sericeous especially along edges. n = 17.

Phenology. Flowering from March through April.

Distribution (Fig. 32). Known only from the western side of the valley of the Marañón River, along the road to the town of Balsas in the Department of Cajamarca; 1350-1850 m.

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Celendín, 47 km E of Celendín on road to Balsas, 1540 m, 12 Mar 1988, Panero & Sánchez Vega 1261 (GRI, TENN), 1262 (CPUN, F, GRI, US); 46 km E of Celendín on road to Balsas, 1570 m, 12 Mar 1988, Panero & Sánchez Vega 1263 (CPUN, F, GRI, K, MA, MEXU, QCA, SI, US), 1264 (B, TENN, UC); 41 km E of Celendín

on road to Balsas, 1830 m, 12 Mar 1988, Panero & Sánchez Vega 1265 (NY, TENN), 1267 (GRI).

Pappobolus matthewsii var. viridifolius shares with the nominal variety the strongly reflexed phyllaries but differs from it by the markedly less pubescent leaves and deeply notched ray flowers. In the field the leaves have a viscous and somewhat succulent texture and are very bright green, a combination of foliar characters that is not shown by any other taxon within the subgenus. These bright green leaves are responsible for the name of this variety.

2. Pappobolus sagasteguii (H. Robinson) Panero, comb. nov.——Helianthopsis sagasteguii H. Robinson, Phytologia 44:264-265. 1979.——TYPE. PERU. Cajamarca: Prov. Celendín, Canyon of Río Marañón, 11.5 km below summit of road Celendín-Balsas, 2630 m, 27 May 1964, Hutchison & Wright 5397 (holotype: US!, photos: GH!, TEX!; isotypes: F!, K!, GH!, MO!, NY!, UC!).——PARATYPE: PERU. Cajamarca: Prov. Celendín, Hacienda El Limón, 2150 m, 5 May 1970, Sagástegui 7415 (GH!, MO!).

Open shrubs 15-30 dm tall; **stems** brownish-gray, glabrous, herbaceous parts dark brownish-green, pilose, trichomes hyaline to white, multicellular, tapered 0.5-4.7 mm long; **leaves** alternate, ovate to deltoid, triplinerved, adaxial surface light green and moderately to densely strigose-sericeous, trichomes white to whitish-green, multicellular, tapered, 1.2-1.5 mm long, abaxial surface light creamy green and densely velutinous to somewhat villous, trichomes white to

light green, multicellular, tapered, 0.3-1 mm long, pubescence along veins moderately strigose-sericeous; sessile glandular trichomes 300-700/cm^2; **blades** 25-135 mm long, 13-110 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse to truncate and narrowly attenuate along distal eight of petiole, margin serrulate to strongly serrate; petioles 8-50 mm long, terete to slightly canaliculate, moderately to densely velutinous on both surfaces; **capitulescences** monochasial thyrsoid, with 3-40+ heads, peduncles 20-60 mm long, moderately hirsute-velutinous, pubescence slightly denser below the heads, trichomes as stem; **heads** 7.5-14.5 mm across, 10-13 mm high, hemispherical; **receptacles** 4-6.7 mm in diameter in fruit, convex; **phyllaries** 22-29 in 3-4 subequal series, first series 5-12 mm long, 1-2.3 mm wide, lanceolate, base indurated, stramineous-green and glabrous adaxially, stramineous-green with several dark green or brown longitudinal bands and tomentose to densely velutinous-sericeous abaxially, herbaceous apex reflexed, green and sparsely to moderately strigose adaxially, creamy green and densely strigose-sericeous abaxially, margins ciliate, second and third series 4.6-10.2 mm long, 1.9-3.7 mm wide, lanceolate, base indurated, stramineous and glabrous adaxially, stramineous-green, with several dark green longitudinal bands and moderately tomentose to moderately velutinous-sericeous abaxially, herbaceous apex reflexed, green and sparsely to moderately strigose adaxially, creamy green and sparsely to moderately strigose-sericeous abaxially, margins velutinous, fourth series 4.5-6.7 mm long, 1.2-1.8 mm wide, oblong to oblanceolate, chartaceous to slightly

indurated with no clear distinction between herbaceous and indurated parts, stramineous-green and glabrescent to tomentose on both surfaces, margins minutely tomentose to velutinous; **pales** 5.6-8.6 mm long, 2.9-4 mm wide, broadly ovate to oblong, conduplicate, shallowly to strongly keeled lengthwise, protruding 0.5-2.5 mm beyond phyllaries, stramineous with several green or brown longitudinal bands of various width, bands not coalescing at apex, glabrescent abaxially, apex coriaceous, acuminate, shallowly trifid, strongly reflexed, yellow; **ray flowers** 10-19, corolla golden yellow, limb 7.5-11.2 mm long, 3.6-4.7 mm wide, oval to oblong, sparsely puberulent and glandular on veins of abaxial surface, apex acute, minutely trifid, tube 0.7-1.4 mm long, moderately puberulent and glandular; **ray ovaries** 1.8-2.2 mm long, triquetrous, glabrous, pappus of 1-3 awns 0.3-0.6 mm long; **disk flowers** 70-145, flowers protruding 0.2-0.5 mm above pales, corollas deep golden yellow, narrowly campanulate, throat 2.4-3 mm long, 0.9-1.1 mm wide at base, 1.1-1.5 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, densely puberulent with interspersed uniseriate glandular trichomes 0.05-0.2 mm long, tapered trichomes hyaline, 0.1-0.3 mm long, tube 0.9-1.4 mm long, yellowish-green, glabrous, lobes 1-1.2 mm long, yellow, moderately puberulent and glandular abaxially; anthers 1.7-2.1 mm long, thecae yellowish-tan, appendages 0.5 mm long; styles 3.6-4 mm long, style branches 1.1-1.3 mm long; **disk achenes** 2.4-3.5 mm long, 1-1.4 mm wide, biconvex, oval-obovate, shoulders rarely present, shiny grayish-black, black or silver, glabrous or sparsely to densely sericeous, pappus of 2 awns, sometimes with 2-6 squamellae, awns slender, stramineous, sometimes

purplish, deciduous to somewhat persistent, subequal 1.3-1.9 mm long, squamellae free, 0.4-0.6 mm long, same color as awns, deciduous to somewhat persistent; n = 17.

Phenology. Flowering from March through June. Major floral display in May.

Distribution (Fig. 32). Known from the east-facing slopes of the valley of the Marañón River in the area of Celendín and Conga de Urquía, Cajamarca Department; 1950-2750 m.

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Celendín, Zigmalca, carretera Celendín-Río Marañón, 2300 m, 4 Jun 1960, López & Sagástegui 3373 (HUT); Cantange, (carretera Celendín-Sucre-Oxamarca), 2200 m, 19 May 1976, Sagástegui et al. 8456 (F, HUT, TENN); 36 km E of Celendín on road to Balsas, 2260 m, 12 Mar 1988, Panero & Sánchez Vega 1230 (CPUN, F, GRI, SI, TENN, US), 1231 (GRI, TENN), 1232 (F, TENN), 1234 (GRI, MA, US); 38 km E of Celendín on road to Balsas, 2150 m, 12 Mar 1988, Panero & Sánchez Vega 1236 (TENN), 1238 (TENN); entre la cumbre y la Hacienda Limón, 2400 m, 7 Aug 1958, Ferreyra 13315 (LP); Gelig, 2750 m, 24 Jul 1967, Aguado 6797 (LP); Atucmonte, entre Sucre y Oxamarca, 2600 m, 20 May 1976, Sánchez Vega & Ruiz Vigo 1779 (CPUN); entre Gelig y Limón, 2150 m, 5 May 1970, Sánchez Vega & Ruiz Vigo 494 (CPUN); Huasho, entre Gelig y Balsas, 2050 m, 14 May 1967, Sánchez Vega 340 (CPUN).

Pappobolus sagasteguii grows abundantly on the western side of the canyon of the Marañón River. Together with the shrubby mint Lepechinia it covers extensive areas of this canyon. This species is easily

recognized by its pilose stem and leaves and by the strongly reflexed apices of the pales. Another interesting aspect of this species is the arborescent habit. Mature individuals invariably have a central, well-developed stem.

This species shares with P. matthewsii a similar head and floral morphology. It can be effectively separated from P. matthewsii by the dense, pilose pubescence of its herbage and the large ovate to deltate leaves with conspicuously serrate margins. However, specimens collected at the lower end of the altitudinal range of the species and those collected around the town of Conga de Urquía tend to be less pubescent and reminiscent of the nominal variety of P. matthewsii especially those from around the city of Chachapoyas.

Pappobolus sagasteguii is one of the five species that can be easily observed along the Celendín-Balsas road. As is the case with the others, it occupies a discrete altitudinal belt with very little or no overlap with any other species of Pappobolus. Within this belt, this species is quite common. I speculate that this apparent dominance is due to the constant fires initiated by the locals to clear land for pasture. At the time I collected this species there were signs of the massive burning, which keeps many small plants, seedlings and shrubs from growing. In the case of P. sagasteguii the tall plants were apparently not affected by the fire. The fires are so repeated that grasses and other plants are never able to attain a large stature probably reducing the impact of the fire on taller plants like P. sagasteguii. I speculate that the periodic fires, coupled with the

apparent tolerance of this species to them and its fast growth, have created a very peculiar monoculture of this species.

3. Pappobolus ecuatorianus Panero, sp. nov.——TYPE: ECUADOR. Azuay: 74 km S of the intersection of the roads to Cuenca and Girón on road to Loja, 2120 m, 7 Jul 1988, Panero 1493 (holotype: QCA!; isotypes: F!, GRI!, QCNE!, TENN!, US!).

Pappobolus ecuatorianus differt a P. hypargyreo. Habet lanceolata folia sparsim pubescentia phyllaria et minora hemisphaerica vel campanulata capita.

Shrubs 4-20 dm tall; **stems** terete, dark brown, glabrous, herbaceous parts purplish-brown, tomentose, sometimes densely tomentose upwards toward the capitulescence, trichomes hyaline to white, multicellular, tapered, 0.2-0.5 mm long; **leaves** alternate, triplinerved, ovate, rhombic, broadly trullate or lanceolate, adaxial surface dull green to greenish-brown, sparsely to moderately strigose-hirsute, trichomes hyaline to white, multicellular, tapered, 0.4-0.6 mm long, abaxial surface velutinous-sericeous or villous to lanate creamy green or white, trichomes white to light green, multicellular, tapered, 0.5-0.8 mm long, moniliform trichomes restricted to veins, arched, tan-brown, multicellular, apical cell rounded, 0.5-0.1 mm long; sessile glandular trichomes on both surfaces 400-700/cm^2; **blades** 20-125 mm long, 10-85 mm wide, smaller upwards toward capitulescence, apex acuminate, base obtuse rarely truncate, decurrent and narrowly attenuate along distal third to fifth of petiole, margins subentire to

serrate; petioles 5-60 mm long, terete to slightly canaliculate, densely tomentose on both surfaces; **capitulescences** monochasial thyrsoid, with 3-40+ heads, peduncles 23-90 mm long, moderately to densely tomentose, pubescence slightly denser below the heads, trichomes as stem; **heads** 8.8-9.8 mm across, 11-11.8 mm high, oblong-campanulate, rarely hemispherical; **receptacles** 6-6.5 mm in diameter in fruit, slightly convex; **phyllaries** 20-28 in 3-4 subequal to somewhat graduated series, first series 6.6-7.5 mm long, 1.6-2.2 mm wide, lanceolate, base indurated, stramineous-green and glabrous adaxially, stramineous, with 3 conspicuous dark green longitudinal bands and sparsely to densely tomentose as to mask banding pattern abaxially, herbaceous apex slightly reflexed or appressed, rarely foliaceous, green and sparsely puberulent to tomentose adaxially, sparsely to densely tomentose white-green abaxially, margins ciliate, second and third series 6.8-8.5 mm long, 2.2-2.8 mm wide and 8.5-9.2 mm long, 2.2-2.6 mm wide respectively, differing from previous series by exhibiting less pubescence and mostly restricted to herbaceous distal portion, a more conspicuous banding pattern on indurated area and by a less prominent herbaceous apex, margin puberulent to tomentose, fourth series 5.8-6.5 mm long, 1.8-1.9 mm wide, oblong-lanceolate, resembling pales in general aspect, somewhat chartaceous, stramineous basally, puberulent abaxially, margins glabrescent; **pales** 5.8-6.5 mm long, 2.6-3 mm wide, ovate to oblong, conduplicate, keeled lengthwise, covered by phyllaries or sometimes protruding 0.2-0.6 mm, stramineous, with several green or soft brown longitudinal bands of various width, bands not coalescing at apex, glabrescent to puberulent abaxially, apex

coriaceous, acuminate, acute, rarely cuspidate, sometimes trifid, pointed to slightly reflexed, stramineous-yellow to blackish-green; **ray flowers** 9-14, corolla golden to orangish-yellow, limb 4.9-12.5 mm long, 2.5-6.5 mm wide, oval to oblong, sparsely to densely puberulent and glandular on veins of abaxial surface, apex acute to rounded, bifid, rarely trifid, tube 1-1.3 mm long, moderately puberulent and glandular; **ray ovaries** 3.2-3.4 mm long, triquetrous, glabrous, pappus of 3-7 deeply lacerated squamellae 0.3-0.5 mm long; **disk flowers** 60-90, flowers protruding 0.5-1 mm above pales, corollas golden yellow to greenish-yellow, cylindrical to narrowly campanulate, throat 1.9-2.9 mm long, 0.9-1.1 mm wide at base and at junction with lobes, veins orange and discernable the whole length of the corolla, moderately to densely puberulent, with interspersed uni- and biseriate, multicellular, glandular trichomes 0.8-1.2 mm long, tapered trichomes white to hyaline 0.1-0.3 mm long, tube 0.6-1.2 mm long, yellowish-green, glabrous, lobes 0.6-0.9 mm long, deltoid, deep yellow on both surfaces, sparsely to moderately puberulent and glandular abaxially; anthers 1.9-2.1 mm long, thecae yellow to brownish-yellow, appendages 0.5-0.6 mm long, ovate, stramineous to deep yellow; styles 3.5-4.3 mm long, style branches 0.7-1 mm long; **disk achenes** 1.8-3.2 mm long, 0.7-1.1 mm wide, biconvex, oval-obovate to obpyramidal, sometimes with 2 diminutive shoulders, shiny grayish-black, black or silver sericeous, glabrous or densely sericeous, pappus of 2 awns and (0-) 3-15 squamellae, awns slender, stramineous, deciduous to somewhat persistent, subequal, 2-3.2 mm long,

squamellae free, 0.4-0.5 mm long, same color as awns, deciduous to somewhat persistent; n = 9, 17.

Phenology. Flowering from February to August.

Distribution (Fig. 33). Lower montane or montane dry scrub or forest of the valleys of the tributaries of the Jubones, Chira and Paute Rivers of Azuay and Loja Provinces; 1600-2550 m. Growing with Barnadesia, Cacosmia, Dunalia, Erythrina, Onoseris, Prosopis, Viguiera, Wigandia. Forming large populations in alluvial soils, on the sandy beaches of rivers or in disturbed areas.

Pappobolus ecuatorianus is a morphologically variable and widespread species of southern Ecuador. The circumscription of this species is still tentative and more collections are needed to understand better its range and extent of morphological variation. Some of the key distinguishing characters of this species such as head size and phyllary morphology and pubescence appear to vary temporally. Some individuals will produce malformed, small heads especially at the beginning of the rainy season, quite different from the larger ones produced at the end of the rainy season by the same plants. Variation in floral characters contrasts with the apparent uniformity of two discrete leaf shapes confined to certain geographical areas which are effectively circumscribed by major geographical and ecological boundaries. The nominal variety is known from the valleys of the Girón and León and Paquishapa Rivers, which are tributaries of the Jubones River. This variety is characterized by broadly ovate to trullate leaves with serrulate to serrate leaf margins. Pappobolus ecuatorianus var. lancifolius is found south of the Cordillera Cordoncillo in the

dry valleys of the Catamayo and Guayuco Rivers, both of which are tributaries of the Chira River. This variety is recognized by its lanceolate to ovate leaves and soft velutinous to villous pubescence It also has a very uniform head and flower morphology which contrasts with the many subtle differences in head and flower morphology of the nominal variety.

This species shares with P. hypargyreus a similar capitulescence morphology and head disposition (see discussion under under nominal variety). On the other hand, head morphology is reminiscent of that of P. hutchisonii and some forms of P. matthewsii var. matthewsii in which the lanceolate phyllaries are stramineus with conspicuous green to brown longitudinal bands of various width and the herbaceous apices are either appressed or slightly reflexed. However, the heads in P. ecuatorianus are decidedly smaller and the pales do not protrude significantly beyond the involucre as in P. hutchisonii.

The species name honors the Republic of Ecuador. The name is a derivation of the Spanish word for Ecuadorian.

KEY TO THE VARIETIES OF Pappobolus ecuatorianus.

1. Leaves ovate, rhombic or deltoid, moderately to densely velutinous abaxially; ray flower limb 11-12.5 mm long; pale apices acuminate to acute. 3a. P. ecuatorianus var. ecuatorianus.
1. Leaves lanceolate, densely velutinous-sericeous to villous abaxially; ray flower limb 4.9-8 mm long; pale apices acuminate to cuspidate. 3b. P. ecuatorianus var. lancifolius.

3a. Pappobolus ecuatorianus var. ecuatorianus.

Shrubs 5-20 dm tall; **leaves** ovate, rhombic or deltoid, abaxial surface moderately to densely velutinous to sericeous creamy light green, rarely white, margins serrulate to serrate; **pales** 5.8-6.3 mm long, apex acuminate to acute, dark blackish-green, rarely yellowish-stramineous; **ray flowers** limb 11-12.5 mm long, 4.9-6.5 mm wide, tube 1.2-1.3 mm long; **disk achenes** shiny grayish-black, black or silver sericeous, glabrous or densely sericeous, pappus of 2 awns and (0-) 3-15 squamellae.

Phenology. Flowering from February to August.

Distribution (Fig. 33). Lower montane or montane dry scrub or forest in the valleys of the Girón and León Rivers tributaries of the Jubones River and along the canyons of the Sígsig and Paute Rivers in Azuay Province; 1600-2550 m.

SPECIMENS EXAMINED. ECUADOR. AZUAY: Along the road to Girón, ca 14 km SW of Girón, 6200 ft, 3 Feb 1974, King 6687 (MO, UC, US); along the road to Sígsig, ca 11 km N of Sígsig, 7600 ft, 1 Feb 1974, King 6646 (F, MO, UC, US); 14 km SE of Girón along the road Cuenca-Machala, 1620 m, 22 Feb 1988, Panero & Gómez 1088 (F, GRI, QCA, QCNE, TENN); 13 km S of Girón on road to Machala, 1740 m, 10 Jul 1988, Panero 1522 (GRI, QCNE, SI, US), 1523 (TENN), 1524 (TENN); 67 km S of the intersection of the roads to Cuenca and Girón on road to Loja, 2170 m, 3 Jul 1988, Panero 1439 (TENN); 72 km S of the intersection of the roads to Cuenca and Girón on road to Loja, 1990 m, 3 Jul 1988, Panero 1440 (TENN), 1441 (GRI); 22 km S of the intersection of the road to Paute on road to

Sígsig, 2390 m, 9 Jul 1988, Panero 1517 (TENN), 1518 (GRI, QCNE).—LOJA: Around Loja, 8 Sep 1865 Jameson 37 (K); 0.6 km N of Saraguro on road to Cuenca, 21 Feb 1988, Panero & Gómez 1069 (CPUN, QCNE, SI, TENN); 1070 (TENN); 1071 (TENN, US), 7 Jul 1988, Panero 1496 (TENN); 4 km NE of Saraguro along the road Loja-Cuenca, 2260 m, 21 Feb 1988, Panero & Gómez 1067 (F, MEXU, QCA, QCNE, S, TENN, US).

Pappobolus ecuatorianus var. ecuatorianus is a common taxon of the dry valleys of southern Ecuador. It can be recognized by its deep orangish-yellow ligules (somewhat similar in color to the flowers of species of Viguiera ser. Aureae), slightly graduated involucre with lanceolate phyllaries, small heads and broadly ovate to deltate leaves. The circumscription of this taxon was especially difficult because of the temporal variation in characters such as head morphology that was observed in populations along the Jubones River of southern Azuay. This species was collected in this area in February and later the same year in July. Flowering specimens were difficult to obtain in February and at this time flowering heads were always produced by weak, secondary branches under the growing foliage. These off-season flowering shoots produced densely pubescent and malformed heads. At the peak of the flowering period in July the same individuals produced heads with the typical phyllary and floral morphologies for the taxon. This morphological variation was taken into account in erecting this species concept, and is indicative of the great morphological plasticity of this taxon. Specimens collected along the León River, a tributary of the Jubones River, were similar in morphology to the above

population. Specimens collected along the Paute River and tributaries of northern Azuay province superficially resemble P. hypargyreus of central Ecuador because of their slightly reflexed phyllaries although phyllary, achene and pale morphology as well as head size are similar to that of other P. ecuatorianus populations.

3b. Pappobolus ecuatorianus var. lancifolius Panero, var. nov.——TYPE: ECUADOR. Loja: 20 km S of Loja on road to Vilcabamba, 2210 m, 4 Jul 1988, Panero 1451 (holotype: QCA!; isotypes: AAU!, QCNE!, TENN!, US!).

Pappobolus ecuatorianus var. lancifolius differt a nominata varietate. Habet lanceolata folia cum moderate vel dense pubescentibus abaxialibus paginis.

Shrubs 4-12 dm tall; **leaves** lanceolate to narrowly ovate, abaxial surface densely velutinous to villous-lanate creamy shiny white, margins subentire to serrulate; **pales** 6.2-6.5 mm long, apex trifid, acuminate to cuspidate, yellowish-stramineous; **ray flowers** limb 4.9-8 mm long, 2.5-2.9 mm wide, tube 1-1.1 mm long; **disk achenes** shiny grayish-black, black, glabrous, pappus of 2 awns and (0) 1-5 squamellae.

Phenology. Flowering from March to July (August).

Distribution (Fig. 33). Known only from the dry valleys of the western Andes of the Province of Loja of southern Ecuador; 2200-2350 m.

SPECIMENS EXAMINED. ECUADOR. LOJA: 4 km N of Loja on road to Cuenca, 2320 m, 3 Jul 1988, Panero 1449 (CPUN, GRI, TENN); 20 km S of Loja on

road to Vilcabamba, 2210 m, 4 Jul 1988, Panero 1452 (TENN), 1453 (MEXU, S, UC); 20 km al S de Catamayo sobre la carretera a Cariamanga, 5 Jul 1988, Panero 1465 (B, C, COL, LP, MA); 19 km S of Cariamanga on road to Amaluza, 5 Jul 1988, Panero 1475 (AAU, F, GRI, QCNE, SI, TENN, UC, US); 27 km S of Cariamanga on road to Amaluza, 5 Jul 1988, Panero 1476 (GRI, TENN).

This taxon can be recognized by its lanceolate to narrowly ovate leaves with densely velutinous sericeous to lanate abaxial surfaces, and small heads. The phyllaries are reminiscent of those of P. hutchisonii. Some individuals produce a pungent camphor odor when their leaves are crushed, a characteristic not observed in any other Pappobolus collected by the author. This taxon was always collected in disturbed areas growing with Onoseris salicifolius H.B.K. and Viguiera aff. incana.

This taxon has a superficial similarity to P. verbesinoides and to a certain extent with P. acutifolius. These two species have narrowly ovate or lanceolate leaves that are slightly to markedly smaller upwards toward the capitulescence as is the case of P. ecuatorianus var. lancifolius. However, both species differ significantly from this variety in head and floral morphology. Pappobolus verbesinoides has the smallest heads of the genus and the phyllaries are appressed, oval to oblong, rarely lanceolate and dark green or black in color. Pappobolus acutifolius has lanceolate to linear phyllaries that have a prominent reflexed herbaceous apex. In addition, the leaves of P. acutifolius are glabrescent to sparsely strigose to velutinous on both

surfaces, and clearly contrast with the densely velutinous abaxial leaf surface of P. ecuatorianus var. lancifolius.

4. Pappobolus hutchisonii (H. Robinson) Panero, comb. nov.

Helianthopsis hutchisonii H. Robinson, Phytologia 44:262-263. 1979.——TYPE: PERU. Cajamarca: Prov. Celendín, Río Marañón opposite Balsas and upstream 1 km, 800 m, 29 May 1964, Hutchison & Wright 5436 (holotype: US!, photo: GH!; isotypes: F!, NY!, UC!, WIS!).

Shrubs 7-15 dm tall, composed of a multitude of stems, with significant amounts of leaves only on the lower third of their length, the rest of the shoot diffuse and open with only a few small leaves associated with the branching capitulescence; **stems** terete, soft brown or gray, glabrous, herbaceous parts dark brown, rarely purplish-brown, puberulent, tomentose upwards toward the capitulescence, trichomes hyaline or white, multicellular, tapered, 0.25-0.35 mm long; **leaves** alternate, ovate, triplinerved, adaxial surface light green, hirsute, trichomes hyaline, multicellular, tapered, 0.25-0.4 mm long, abaxial surface light creamy green, villous, trichomes white, multicellular, tapered, 0.5-0.7 mm long, pubescence along veins densely villous and clearly outlining them against the soft green background; sessile glandular trichomes confined to abaxial surface, 1800-2200/cm^2; **blades** 12-100 mm long, 10-65 mm wide, significantly smaller upwards toward the capitulescence, apex acuminate, base obtuse and narrowly attenuate along distal fourth of petiole, margins minutely serrulate, sometimes

entire; petioles 8-35 mm long, terete to slightly canaliculate, villous adaxially, minutely hirsute and glandular abaxially; **capitulescences** monochasial thyrsoid, with (2-) 9-28+ heads, peduncles 20-115 mm long, tomentose, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 8.5-13 mm across, 12.5-14 mm high, broadly campanulate; **receptacles** 4.2-5.5 mm in diameter in fruit, slightly convex; **phyllaries** 20-27 in 4 graduated series, first series 5.3-6 mm long, 1.6-2 mm wide, ovate, base heavily indurated, with 1-2 dark green ribs, stramineous-green and glabrous adaxially, light green and hirsute abaxially, herbaceous apex green, hispid adaxially, soft green, hirsute and glandular abaxially, margins puberulent, second series 5.5-7.5 mm long, 2-3.2 mm wide, ovate, indurated and appressed at base, stramineous-green and glabrous adaxially, light green, with 1-3 dark green ribs, hirsute and glandular abaxially, herbaceous apex appressed, the tip slightly reflexed, green and hirsute to villous adaxially, dark green, glandular and hirsute abaxially, margins minutely puberulent, third series 7.2-8.2 mm long, 2.8-3.2 mm wide, ovate, similar to second series in general morphology, pubescence and color, margins glabrous to puberulent, fourth series 5.5-7.8 mm long, 1.4-2.4 mm wide, ovate or oblong, some resembling pales, somewhat chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous and glabrous adaxially, stramineous to light green and puberulent abaxially; **pales** 9-11 mm long, 2.5-4 mm wide, ovate to oblong, conduplicate, shallowly keeled lengthwise, protruding 3-4 mm beyond phyllaries, light greenish-stramineous with several green longitudinal

bands of various width, bands not coalescing at apex, sparsely tomentose abaxially, pubescence denser towards apex, apex trifid, with a central coriaceous, narrowly acuminate, pointed yellowsih-stramineous; **ray flowers** 9-14, corolla golden yellow, limb 14-16.5 mm long, 4.8-6 mm wide, oval, sparsely puberulent and glandular on veins of abaxial surface, apex acute, conspicuously bifid or trifid, tube 1-1.5 mm long, densely puberulent and glandular; **ray ovaries** 2.9-3.7 mm long, trigonal, slightly puberulent along edges, with a pappus of 2-3 deeply lacerated squamellae 0.4-0.6 mm long, sometimes with 1 awn 2-2.4 mm long; **disk flowers** 54-85, flowers protruding slightly above pales, corollas deep yellow, narrowly campanulate, throat 6-7 mm long, 1.4-1.7 mm wide at base, 1.6-1.9 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sometimes with additional short straight veins arising from the tips of the corolla lobes and running down the whole length of the lobe, densely puberulent with interspersed uni- and biseriate glandular, multicellular trichomes 0.06-0.15 mm long, tapered trichomes white to hyaline, multicellular, 0.10-0.25 mm long, tube 0.9-1.2 mm long, greenish-yellow, densely glabrous or glabrescent, trichomes similar in size and morphology to those on throat, lobes 1.1-1.4 mm long, deltoid, deep yellowish-orange; anthers 3.5-3.7 mm long, thecae light yellow to orangish-brown, appendages 0.6-0.7 mm long, ovate, stramineous; styles 6.4-7.4 mm long, style branches 1.6-2.1 mm long; **disk achenes** 3.2-3.8 mm long, 1.1-1.4 mm wide, biconvex, obovate-obtriangular, with no shoulders, silvery-gray, densely sericeous, pappus of 2 awns and 6-10 squamellae, awns slender, stramineous, somewhat persistent, subequal, 2-3.2 mm long,

squamellae barely fused at base or rarely free, 0.6-1.5 mm long, same color as awns, somewhat persistent; n = 17. Fig. 34.

Phenology. Collected in flower in March through May, with its major flowering peak in late March.

Distribution (Fig. 33). Known from the banks of the Marañón River around the town of Balsas in Amazonas and Cajamarca Departments. Growing in lower montane dry scrub with Aristolochia chachapoyensis Ahumada, Bouganvillea peruviana H.B.K., Cienfuegosia tripartita (H. B. K.) Gürke, Dalechampia hutchisoniana Webster, Jacquemontia, Jatropha, Nicotiana, Onoseris aff. albicans (D. Don) Ferreyra, Pectis, Trixis, and several Cactaceae; 800-1250 m.

SPECIMENS EXAMINED. PERU. AMAZONAS: 3 km SE of Balsas on road to Chachapoyas, 1000 m, 23 Mar 1988, Panero 1358 (TENN).—CAJAMARCA: 56 km E of Celendín on road to Balsas, Canyon of the Río Marañón, 1220 m, 12 Mar 1988, Panero & Sánchez Vega 1241 (B, CPUN, F, GRI, MA, MEXU, TENN, US); 0.5 km SE of Balsas on road to Celendín, along the Marañón River, 900 m, Panero & Sánchez Vega 1242 (HUT, K, MEXU, S, SI, UC), 1245 (TENN).

Pappobolus hutchisonii can be easily recognized by its long disk corolla throat, densely puberulent and glandular disk corollas, reflexed ray corollas and the conspicuous protrusion of the pales beyond the phyllary/ray corolla level. Another notable distinguishing character of this species is its growth habit (see Morphology: Habit) which is unique within the genus.

This species is apparently endemic to the low, eroded hills along the banks of the Marañón River (Fig. 3B). Panero & Sánchez Vega 1241 was the only individual observed growing at substantially higher altitudes (1220 m, as opposed to 800-1000 m along the banks of the Marañón River). The lack of any other collection further SE along the river may either indicate a specialized set of growing conditions at the collection site or possibly the paucity of collections from this area; probably the latter. However, some of the species native to this canyon show similar extreme degrees of endemism. An example is Dalechampia hutchisoniana Webster which is only known from this and another nearby site (I. Sánchez Vega, pers. comm.).

Pappobolus hutchisonii shares with P. acutifolius a similar floral pubescence and leaf morphology. They also share stramineous pales with slightly reflexed apices (also seen in P. mathewsii and P. sagasteguii, although not as reflexed as in these two species).

5. Pappobolus acutifolius (S. F. Blake) Panero, comb. nov. Viguiera acutifolia S. F. Blake, Bot. Jahrb. Syst. 54:48. 1916.——TYPE: PERU. Ancash: Caráz, open formations, 2200-2500 m, 19 May 1903, Weberbauer 3008 (holotype: B, destroyed, photo: GH!; lectotype, here designated: fragment ex B at GH!).

Shrubs 10-20 dm tall; **stems** terete, brownish-gray, glabrous, herbaceous parts purplish-brown, glabrescent, puberulent upwards toward the capitulescence, trichomes hyaline or white, multicellular, tapered, 0.10-0.25 mm long; **leaves** alternate, triplinerved, linear to narrowly

ovate or ovate, adaxial surface dull green-brown, sparsely strigose, trichomes hyaline, multicellular, tapered, 0.1-0.2 mm long, abaxial surface slightly lighter in color than adaxial surface, sparsely to moderately strigose to velutinous with no clear difference in trichome density on and between veins, trichomes white, multicellular, tapered, 0.15-0.25 mm long; sessile glandular trichomes confined to abaxial surface 500-700/cm^2; **blades** 10-110 mm long, 2-40 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse and narrowly attenuate along distal third of petiole, margins entire to subentire; petioles 4-40 mm long, slightly canaliculate to terete, glandular farinose to tomentose adaxially, puberulent and tomentose abaxially; **capitulescences** monochasial thyrsoid, with (2-) 9-30+ heads, peduncles 20-55 mm long, puberulent, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 9.2-10.7 mm across, 11-12.2 mm high, slightly urceolate to hemispherical; **receptacles** 5.8-7.5 mm in diameter in fruit, slightly convex; **phyllaries** 20-31 in 3-4 graduated series, first and second series 8.5-10.5 mm long, 1.2-1.8 mm wide, lanceolate, base indurated, stramineous and and glabrous adaxially, stramineous, with 1-3 dark green ribs and strigose abaxially, herbaceous apex reflexed, green and puberulent to minutely hirsute adaxially, light green and sparsely hirsute and glandular abaxially, margins puberulent, third series 8.3-10 mm long, 1.8-2.5 mm wide, ovate-lanceolate, less pubescent than previous series, color similar to previous series, margins glabrous to puberulent, fourth series 7.2-7.8 mm long, 1.6-2 mm wide, ovate-lanceolate, resembling pales in general aspect, somewhat chartaceous with no clear distinction between

indurated and herbaceous parts, stramineous to hyaline, both sides glabrous, margins glabrous; **pales** 6.2-7.2 mm long, 2.7-4 mm wide, ovate to oblong, conduplicate, shallowly or rarely keeled lengthwise, protruding 1-1.5 mm beyond phyllaries, stramineous with several green or brown longitudinal bands of various width, bands not coalescing at apex, glabrous abaxially, apex coriaceous, narrowly acuminate, pointed to slightly reflexed, yellowish-stramineous; **ray flowers** 9-14, corolla golden yellow, limb 8.4-12 mm long, 3.1-4.8 mm wide, oval, sparsely puberulent and glandular on veins of abaxial surface, apex acute to rounded, conspicuously trifid, tube 1-1.5 mm long, sparsely puberulent and glandular; **ray ovaries** 2-2.6 mm long, triquetrous, slightly puberulent along edges, pappus of 2-6 deeply lacerated squamellae 0.3-0.6 mm long, and 1 awn 2-2.4 mm long; **disk flowers** 65-90, flowers protruding 0.2-0.4 mm above pales, corollas deep golden yellow, narrowly campanulate, throat 2.7-4.5 mm long, 0.9-1.1 mm wide at base, 1-1.5 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, moderately to densely puberulent with interspersed uni- and biseriate, multicellular glandular trichomes 0.05-0.1 mm long, tapered trichomes white to hyaline, multicellular, 0.1-0.15 mm long, tube 0.9-1.4 mm long, yellowish-green, sparsely puberulent with a few scattered uni- and biseriate trichomes, size and morphology similar to those on throat, lobes 0.6-1.2 mm long, deltoid, deep yellowish-orange, densely puberulent and glandular abaxially; anthers 1.5-2.5 mm long, thecae yellow to orangish-brown, appendages 0.3-0.7 mm long, ovate, stramineous; styles 2.3-4.8 mm long, style

branches 0.5-1 mm long; **disk achenes** 3-3.2 mm long, 1.1-1.3 mm wide, biconvex, oval-obovate, with no shoulders, silvery or silver-orange trichomes conspicuously contrasting with black coloration of achene wall, moderately sericeous, pappus of 2 awns and 3-10 squamellae, awns slender, stramineous, somewhat persistent, subequal, 1.9-2.5 mm long, squamellae free, 0.8-1.1 mm long, same color as awns, somewhat persistent; n = ca 17. Fig. 35.

Phenology. Collected in flower in January through June. Major flowering period in April and May.

Distribution (Fig. 33). Known from the valley of the Santa River in Ancash Department especially around the city of Caráz, and southeastern Cajamarca Department in the valley of the Crisnejas River, a tributary of the Marañón River. Growing on limestone rocks in xerophytic forests with Flourensia macrophylla S. F. Blake, Onoseris, Schinus molle and several Cactaceae and Euphorbiaceae; 1600-2600 m.

SPECIMENS EXAMINED. PERU. ANCASH: Prov. Carhuaz, along highway 3, 6 km S of Carhuaz, 7000 ft, 10 Jan 1982, King & Collins 9026 (US); Prov. Huaylas, Cañón del Pato, (Caráz-Huallanca), borde de la carretera, 1650 m, 18 May 1976, López et al. 8382 (HUT, SI); 7 km NE of Caráz on road to Huallanca, 2070 m, 5 Apr 1988, Panero & Galán 1399 (QCA, S, TENN, USM); 6 km SW of Caráz on road to Yungay, 2200 m, 5 Apr 1988, Panero & Galán 1400 (CPUN, GRI, HUT, F, MEXU, US).——CAJAMARCA: Prov. Cajabamba, 8 km NW of Cajabamba, 2550 m, 10 Jan 1983, Dillon et al. 2856 (TEX).

Pappobolus acutifolius is the southernmost species of subg. Apricus. It is recognized by its lanceolate leaves, urceolate-

hemispherical heads and reflexed phyllaries. Within subg. Apricus only P. verbesinoides and P. ecuatorianus var. lancifolius exhibit lanceolate leaves. However, the adaxial leaf surfaces of P. ecuatorianus are densely lanate-sericeous, contrasting with the sparsely to moderately strigose abaxial surfaces of P. acutifolius. Another useful distinguishing character of P. acutifolius is the presence of glandular, biseriate, multicellular trichomes on the disk flower tube.

Originally this species was described by Blake (1916) as Viguiera acutifolia, presumably because of its pubescent achenes with a pappus of two awns and several squamellae. However, its herbage pubescence, floral morphology, and habit override achenial considerations as to the proper placement of this species. Aside from the species of Viguiera sect. Diplostichis, there are no shrubby Viguieras in the Andes. It is clear, based on morphological considerations, that its closest relatives are within the genus Pappobolus.

6. Pappobolus verbesinoides (H. B. K.) Panero, comb. nov.——Helianthus verbesinoides H. B. K., Nov. gen. sp. qt. 4:221. 1820.——Helianthopsis verbesinoides (H. B. K.) H. Robinson, Phytologia 44:266. 1979.——TYPE: PERU. Piura: between Huancabamba and Páramo de Guamaní, Humboldt & Bonpland 3534 (lectotype, here designated: P-HBK, IDC 6209.108:III.1!, fragment US!, photo: GH!; isolectotype: B, fragment F!, photo: GH!, TENN!).

Shrubs 10-20 dm tall; **stems** terete, brown with showy creamy white

lenticels, glabrous, herbaceous parts dark brown-purple, tomentose, tomentose-villous upwards toward the capitulescence, trichomes hyaline to white, multicellular, tapered, 0.2-0.5 mm long; **leaves** alternate, triplinerved, lanceolate to narrowly-lanceolate, adaxial surface dull dark green and sparsely to densely strigose, trichomes hyaline to white, multicellular, tapered, 0.15-0.6 mm long, abaxial surface whitish-green and moderately to densely villous to lanate, trichomes white to light green, multicellular, tapered, 0.5-1.2 mm long; sessile glandular trichomes confined to abaxial surface 500-700/cm^2; **blades** 8-60 mm long, 3-11 mm wide, conspicuously smaller upwards toward the capitulescence, apex acuminate, base obtuse and narrowly attenuate along distal third of petiole, margin entire; petioles 5-17 mm long, terete to slightly canaliculate, densely tomentose on both surfaces; **capitulescences** monochasial thyrsoid, with 5-40+ heads, peduncles 25-43 mm long, tomentose to tomentose-hirsute below the heads, trichomes as stem; **heads** 7-8.2 mm across, 7.7-8.3 mm high, campanulate; **receptacles** 3.9-4.2 mm in diameter in fruit, convex; **phyllaries** 17-21 in 3 subequal series, first series 3.8-6 mm long, 1-1.8 mm wide, lanceolate, base indurated, stramineous-green and glabrous adaxially, sparsely to moderately tomentose-villous whitish-green abaxially, herbaceous apex slightly reflexed, green and moderately tomentose-villous on both surfaces, margins ciliate, second and third series 5.3-6.8 mm long, 1.3-1.5 mm wide, oblong to obovate, base indurated, stramineous and glabrous adaxially, stramineuos, sometimes with several dark green-brown longitudinal bands and sparsely to moderately tomentose or

glabrescent, herbaceous apex very reduced and appressed, green and sparsely tomentose abaxially, margins glabrous to puberulent; **pales** 4.9-5.2 mm long, 2.3-2.5 mm wide, broadly ovate to oblong, conduplicate, shallowly keeled lengthwise, covered by phyllaries, stramineous with several dark green longitudinal bands of various width, bands coalescing at apex, glabrous abaxially, apex coriaceous, acuminate to cuspidate, pointed to slightly reflexed, blackish; **ray flowers** 11-13, corolla golden yellow, limb 6.9-7 mm long, 2.3-2.5 mm wide, oval to oblong, sparsely puberulent and glandular on veins of abaxial surface, apex acute, minutely bifid, tube 1-1.2 mm long, moderately puberulent and glandular; **ray ovaries** 2 mm long, triquetrous, glabrous, pappus of 3-4 squamellae 0.1-0.3 mm long; **disk flowers** 45-65, flowers protruding 0.2-0.4 mm above pales, corollas deep golden yellow, cylindrical, throat 2-2.3 mm long, 0.6 mm wide at base, 0.7 mm wide at junction with lobes, veins orange and discernable the whole length of the throat, moderately to densely puberulent with interspersed uni- and some biseriate, multicellular glandular trichomes 0.5-0.1 mm long, tapered trichomes white to hyaline, 0.1-0.2 mm long, tube 1 mm long, yellowish-green, moderately puberulent with a few scattered uniseriate glandular trichomes, trichomes as throat, lobes 0.6 mm long, yellow, moderately puberulent and glandular abaxially; anthers 1.3-1.5 mm long, thecae yellowish-brown, appendages 0.4-0.5 mm long, ovate, stramineous; styles 2.5-2.6 mm long, style branches 1 mm long; **disk achenes** 2.3-2.7 mm long, 0.9-1.1 mm wide, biconvex, oval-obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 1.8-2.3 mm long;

Chromosome number unknown.

Phenology. Flowering August to September.

Distribution (Fig. 36). Known from the Canyon of the Huancabamba River and the Páramo de Guamaní at the headwaters of the Quiróz River; 2000-2300 m.

SPECIMENS EXAMINED. PERU. PIURA: Huancabamba, 1909-1914, Weberbauer 6072 (F, GH, US); Huaringas, sobre el camino a Salalá, 2100-2200 m, 16 Sep 1985, Ferreyra & Chanco 20463 (TENN, US, USM); Huancabamba, 6000 ft, Aug 1943, Laudeman 4316 (K).

Pappobolus verbesinoides is recognized by the marked reduction in leaf size upwards toward the capitulescence and the villous to lanate abaxial leaf surface. Another distinguishing character is the flowering head and flowers which are among the smallest in the genus.

The relationships of this species are not very clear. The sometimes densely pubescent and blackish phyllaries are reminiscent of those of P. imbaburensis of central Ecuador. These superficial similarities with P. imbaburensis are so convincing that they prompted Watson (1929) to deride Hieronymus' rationale in erecting P. pseudoverbesinoides var. gracilis when according to him it was obviously a central Ecuadorian collection of P. verbesinoides. This species also shows pales that at least in some collections are blackish at the apex, a character otherwise only observed in Ecuadorian species. However, the overall morphology is reminiscent to some forms of P. matthewsii var. matthewssii from the geographically close area of Jaén

in northern Cajamarca. The densely pubescent, narrow leaves of this species are somewhat similar to those of P. ecuatorianus var. lancifolius which in other characters such as head and flower morphology is significantly different from P. verbesinoides.

7. Pappobolus hypargyreus (S. F. Blake) Panero, comb. nov. Helianthus hypargyreus S. F. Blake, Bot. Gaz. 74:421-422. 1922. Helianthopsis hypargyrea (S. F. Blake) H. Robinson, Phytologia 44:263. 1979.——TYPE: ECUADOR. Chimborazo: Huigra, 3 Aug 1920, Holway & Holway 815 (holotype: US!).

Monocaulic shrubs, sometimes profusely-branched from soil level 5-20 dm tall; **stems** terete, brownish-gray, glabrous, herbaceous parts dark brown-green, tomentose, or hirsute to villous upwards toward the capitulescence, trichomes white to light green, multicellular, tapered, 0.5-2.5 mm long; **leaves** alternate, triplinerved, ovate to broadly trullate, rarely lanceolate or deltoid, adaxial surface dull greenish-brown and sparsely strigose, trichomes hyaline to white, multicellular, tapered, 0.2-0.5 mm long, abaxial surface creamy light green and moderately to densely velutinous-sericeous, densely velutinous-sericeous along veins, trichomes hyaline to white, multicellular, tapered, 0.3-1.2 mm long, moniliform glandular trichomes restricted to veins, tan-brown, arched, multicellular, apical cell rounded, 0.05-0.1 mm long; sessile glandular trichomes confined to abaxial surface 500-800/cm^2; **blades** 30-125 mm long, 10-85 mm wide, slightly smaller upwards toward the capitulescence, apex acuminate, base obtuse to truncate and

narrowly attenuate along distal fifth to seventh of petiole, margin crenate, serrulate or serrate; petioles 10-60 mm long, terete to slightly canaliculate, densely hirsute velutinous-sericeous on both surfaces; **capitulescences** monochasial thyrsoid, with (5-) 12-40+ heads, peduncles 17-105 mm long, villous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 8.5-14.5 mm across, 9.8-11.2 mm high, hemispherical; **receptacles** 6.5-8.5 mm in diameter in fruit, shallowly convex; **phyllaries** 24-28 in 4 graduated series, first series 10.3-12.5 mm long, 3.9-4.5 mm wide, oblong to oblanceolate, base indurated, stramineous-green and glabrous adaxially, densely velutinous-sericeous and creamy green to white abaxially, herbaceous apex foliaceous, spreading, green and densely strigose-sericeous adaxially, densely velutinous-sericeous creamy green to white abaxially, margins hispid-sericeous, second and third series 10.5-13.5 mm long, 3.7-7 mm wide, oblanceolate, base heavily indurated, stramineous and glabrous adaxially, stramineous with 3 conspicuous dark green longitudinal bands and sparsely tomentose abaxially, herbaceous apex acuminate, acute to suborbicular, foliaceous, reflexed, green and densely strigose-sericeous adaxially, dark green and hirsute-sericeous, glandular abaxially, margins tomentose to villous, fourth series 7.3-8.3 mm long, 1.6-1.9 mm wide, ovate-lanceolate, resembling pales in general aspect, somewhat chartaceous with no clear distinction between indurated and herbaceous parts, stramineous basally, puberulent to tomentose abaxially, margins puberulent; **pales** 6.5-7.3 mm long, 2.4-2.6 mm wide, ovate to oblong, conduplicate, shallowly keeled lengthwise, covered by phyllaries, stramineous with several dark greenish-black

longitudinal bands of various width, bands coalescing at apex, glabrescent to tomentose abaxially, apex coriaceous, acuminate to acute or rounded, pointed, rarely reflexed, greenish-black; **ray flowers** 16-20, corolla golden yellow, limb 6.5-10.5 mm long, 4.4-5.3 mm wide, oval-suborbicular to oblong, sparsely to densely puberulent and glandular on veins of abaxial surface, apex acute to rounded, bifid, tube 1.3-1.7 mm long, moderately puberulent and glandular; **ray ovaries** 2.9-3.8 mm long, triquetrous, glabrous, pappus of 3-4 deeply lacerated squamellae 0.3-0.5 mm long; **disk flowers** 125-220, flowers protruding 0.4-0.6 mm above pales, corollas golden yellow, cylindrical to narrowly campanulate, throat 3.4-3.7 mm long, 1.2-1.4 mm wide at base and at junction with lobes, veins orange and discernable the whole length of the throat, moderately puberulent with interspersed uni- and some biseriate, multicellular glandular trichomes 0.08-0.15 mm long, tapered trichomes white to hyaline, 0.1-0.25 mm long, tube 1.3-1.7 mm long, greenish-yellow, glabrous, lobes 0.7-0.8 mm long, deltoid, deep yellowish-orange adaxially, sometimes black abaxially, sparsely to densely puberulent and glandular abaxially; anthers 2-2.3 mm long, thecae yellow, brownish-yellow or black, appendages 0.3-0.5 mm long, ovate, stramineous to deep yellow; styles 4-4.8 mm long, style branches 1.3-1.5 mm long; **disk achenes** 2.9-3.8 mm long, 1.2-1.3 mm wide, biconvex, oval-obovate to obpyramidal, sometimes with 2 diminutive shoulders, shiny grayish-black or black, sometimes with a few trichomes along edges or around the neck, pappus of 2 awns and 2-6 squamellae, awns slender, stramineous, deciduous, subequal, 2.6-3.5 mm long,

squamellae free, flanking the awns, 0.7-1.2 mm long, same color as awns, deciduous; n = ca 17.

Phenology. Main flowering period May through July. Apparently flowering sporadically the rest of the year.

Distribution (Fig. 36). Known from the canyons of the Chanchán and Cañar Rivers of Central Ecuador; 1200-3000 m. Growing in xerophytic vegetation with Barnadesia spinosa L., Barnadesia lehmannii Hieron., Onoseris hyssopifolia Kunth, Viguiera incana, Croton, Baccharis, and Wigandia.

SPECIMENS EXAMINED. ECUADOR. CAÑAR: Road Cañar-El Tambo, 3 km from Cañar, 3000 m, 18 Jan 1984, Madsen 50070 (QCA); 2 Km N of Cañar along the road to Riobamba, 3000 m, 19 Jun 1987, Panero 733 (TENN).—CHIMBORAZO: Huigra, 1200 m, either 4, 16, 20-27, Jul 1923, Hitchcock 20321 (GH, NY, US), 20334 (GH, NY, US), 20366 (GH, NY, US), 20634 (GH, US); 21 km N of Chunchi along the road Riobamba-Cuenca, 2260 m, 19 Feb 1988, Panero & Gómez 1061 (GRI, QCA, QCNE, TENN); Sibambe, 2500 m, Apr 1966, Knight 732 (WIS); Below Alausí, at Río Chanchán, 2400 m, 4 Feb 1984, Madsen 50153 (QCA); 17.2 km S of Alusí, along the road Riobamba-Cuenca, 2 Jul 1988, 2400 m, Panero 1414 (GRI, QCA, QCNE, TENN, US); 4.4 km NE of Huigra on road to Sibambe, 1710 m, 8 Jul 1988, Panero 1510 (B, CPUN, GRI, F, QCA, QCNE, TENN, US); 5.4 km NE of Huigra on road to Sibambe, 1720 m, 8 Jul 1988, Panero 1511 (K, MEXU, QCNE, SI); vicinity of Huigra, mostly in the Hacienda de Licay, 18 Aug 1918, Rose & Rose 22171 (GH, NY, US), Sep 6 1918, 22568 (GH, US); canyon of the Río Chanchán near Huigra, 4000-4500 ft, 7-14 May 1945, Camp E-3142 (GH,

K, MO, UC, US); Sibambe, canyon of Río Sibambe, 2460-2550 m, 28 Jan 1945, Fosberg & Giler 22620 (F, NY, US); 3.2 km W of Sibambe on road to Chunchi, 1900 m, 8 Jul 1988, Panero 1513 (GRI, TENN), 1514 (F, UC, US); Sibambe, on dry hillsides, 1900 m, 27 May 1942, Haught 3317 (GH, LP, US); Entre Chunchi y Huigra, ca 7 km al S de Chunchi, 2500 m, 28 Oct 1978, Albert de Escobar & Berry 656 (TEX).

This species grows abundantly along the road to the town of Huigra off the Pan American Highway in the Canyon of the Chanchán River. It forms large colonies in recently disturbed areas. It was not observed growing within the native vegetation assemblage, but only in disturbed or open areas, suggesting the importance of disturbance in the life cycle and survival of this species. Another interesting aspect of this species is its wide altitudinal tolerance. Those individuals growing at lower altitudes, from 1200 to 2400 m, exhibit a larger habit and capitulescence. The heads also tend to be significantly larger. Those growing at higher altitudes tend to have a smaller habit and significantly smaller heads. However, the basic circumscribing character of the species, the reflexed, broadly oblong phyllaries, is maintained across this altitudinal gradient.

Pappobolus hypargyreus can be recognized by its broadly ovate to oblong reflexed phyllaries which are normally densely villous to lanate especially on the abaxial surface of the herbacous apex. The heads tend to be the largest of the subgenus, only rivaled by those of the southernmost populations of P. imbaburensis and P. juncosae. It shares with these two species a similar phyllary morphology, although the

phyllaries of P. imbaburensis tend to be more lanceolate and conspicuously black, a coloration never seen in P. hypargyreus. Pappobolus juncosae differs from P. hypargyreus by the lanate pubescence of its herbage and by its significantly smaller capitulescence. In addition the ligules of P. hypargyreus tend to be oval-suborbicular to oblong and golden yellow whereas in P. juncosae and P. imbaburensis the ligules are more oval to oblong and have a slightly lighter yellow color, especially in P. imbaburensis. Some forms of P. ecuatorianus var. ecuatorianus share with P. hypargyreus a similar leaf shape and phyllary morphology (see under P. ecuatorianus var. ecuatorianus).

8. Pappobolus imbaburensis (Hieron.) Panero, comb. nov. Helianthus imbaburensis Hieron., Bot. Jahrb. Syst. 21:348-349. 1895. Helianthopsis imbaburensis (Hieron.) H. Robinson, Phytologia 44:264. 1979.——TYPE: ECUADOR. Imbabura [Pichincha ?]: Cangahua, near Loma de Canaballa, 2100-2300 m, Stuebel 135 (holotype: B, destroyed; lectotype, here designated: fragment ex B at US!).

Helianthopsis pseudoverbesinoides (Hieron.) H. Robinson, Phytologia 44:264. 1979. Helianthus pseudoverbesinoides Hieron., Bot. Jahrb. Syst. 29:40-41. 1901.——TYPE: ECUADOR. Tungurahua: Tumbaco, Sodiro 36/3 in part (holotype: B, destroyed, photo: GH!; lectotype, here designated: fragment ex B at US!).

Helianthus pseudoverbesinoides var. gracilis Hieron. Bot. Jahrb. Syst. 29:41. 1901. ——TYPE: ECUADOR. Tungurahua: near Tumbaco,

Sodiro 36/3 in part (holotype: B, destroyed; lectotype, here designated: fragment ex B at US!).

Monocaulic shrubs sometimes profusely-branched from soil level 5-20 dm tall; **stems** terete, brown, glabrous, herbaceous parts dark brownish-green, sparsely to densely tomentose or moderately hirsute-villous upwards toward the capitulescence, trichomes white to light green, multicellular, tapered, 0.5-2.5 mm long; **leaves** alternate, triplinerved, ovate to broadly trullate, rhombic or lanceolate, adaxial surface dull greenish-brown, sparsely to moderately strigose, trichomes hyaline to white, multicellular, tapered, 0.2-0.5 mm long, abaxial surface sparsely to moderately velutinous-sericeous creamy yellowish-green to white, pubescence denser along veins, trichomes hyaline to white or yellowish-green, multicellular, tapered, 0.3-1.2 mm long, moniliform trichomes restricted to veins, yellowish-brown, arched, multicellular, apical cell rounded, 0.05-0.1 mm long; sessile glandular trichomes confined to abaxial surface 500-800/cm^2; **blades** 20-100 mm long, 6-50 mm wide, smaller upwards toward capitulescence, apex acuminate, base obtuse and narrowly attenuate along distal fifth of petiole, margin entire to serrulate or serrate; petioles 10-55 mm long, terete to slightly canaliculate, sparsely to densely hispid-sericeous on both surfaces; **capitulescences** monochasial thyrsoid, with 3-40+ heads, peduncles 6-45 mm long, sparsely to moderately villous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 7.5-11.5 mm across, 7.5-12 mm high, broadly campanulate hemispherical; **receptacles** 6.5-8 mm in diameter in fruit, shallowly convex; **phyllaries**

24-30 in 4 graduated series, first series 5-8.2 mm long, 1.7-2.3 mm wide, lanceolate, base indurated, stramineous-green and glabrous adaxially, densely velutinous-sericeous creamy green to white abaxially or dark green and sparsely tomentose, herbaceous apex slightly reflexed, dark green and moderately strigose adaxially, densely velutinous-sericeous creamy green to white abaxially, margins ciliate, second and third series 5-10 mm long, 1.8-3.2 mm wide, lanceolate-oblong or deltoid, base heavily indurated, stramineous and glabrous adaxially, dark green and sparsely tomentose or glabrous abaxially, herbaceous apex appressed, dark green green, and sparsely to moderately strigose adaxially, dark green and sparsely tomentose abaxially, margins glabrescent to sparsely ciliate, fourth series 6.9-8.3 mm long, 2-2.4 mm wide, ovate to lanceolate or oblong, similar in all characters to previous series, otherwise somewhat chartaceous with no clear distinction between indurated and herbaceous parts, stramineous basally, puberulent to tomentose abaxially, margins glabrous or puberulent; **pales** 5.5-6.3 mm long, 2.8-3.8 mm wide, ovate to oblong, conduplicate, shallowly keeled lengthwise, covered by phyllaries, stramineous with several dark green-blackish, longitudinal bands of various width, bands coalescing halfway between the base and apex, glabrescent abaxially, apex coriaceous, acuminate to acute, pointed, blackish-green; **ray flowers** 11-16, corolla bright yellow, limb 7-14 mm long, 3.8-6.2 mm wide, oval to oblong, sparsely puberulent and glandular on veins of abaxial surface, apex acute to rounded, bifid, tube 0.5-1.9 mm long, moderately puberulent and glandular; **ray ovaries**

2-2.4 mm long, triquetrous, glabrous, pappus of 3-4 squamellae or awns 0.5-1.6 mm long; **disk flowers** 50-135, flowers protruding 0.4-0.6 mm above pales, corollas golden yellow, cylindrical to narrowly campanulate, throat 2.3-3.7 mm long, 1.2-1.4 mm wide at base and at junction with lobes, veins orange and discernable the whole length of the throat, sparsely puberulent with interspersed uniseriate glandular trichomes 0.08-0.15 mm long, tapered trichomes white to hyaline, 0.1-0.25 mm long, tube 1.3-1.7 mm long, yellowish-green and glabrous or sparsely puberulent, lobes 0.5-0.7 mm long, deltoid, deep yellowish-orange adaxially, sparsely puberulent and glandular abaxially; anthers 1.6-2.4 mm long, thecae yellow, orangish-brown, appendages 0.3-0.5 mm long, ovate, stramineous to deep yellow; styles 3.5-5.6 mm long, style branches 1.1-1.4 mm long; **disk achenes** 2.5-3.2 mm long, 0.9-1.4 mm wide, biconvex, oval-obovate to obpyramidal, with 2 diminutive shoulders, shiny grayish-black, black or mottled, pappus of 2 awns and 2-4 squamellae, awns slender, stramineous, deciduous, subequal, 2.5-3.2 mm long, squamellae free, flanking the awns, 0.7-1.2 mm long, same color as awns, deciduous; $\underline{n}$ = 17.

Phenology. Flowering throughout the year.

Distribution (Fig. 36). Known from all of the interandean valleys north of the Chimborazo Volcano to the valley of the City of Tulcán in northern Ecuador and Colombia. Growing along dry stream beds or recently disturbed areas, sometimes growing on steep cliffs along river gorges; 1500-3300 m.

SPECIMENS EXAMINED. COLOMBIA. NARIÑO: Pasto; Cebadal, on highway to

Yacuanquer, kms 15-25, 2700-2800 m, 2 Jun 1946 Schultes & Villareal 7932 (K, F, US).— ECUADOR. BOLIVAR: between Guaranda and Ambato, in alpine meadow, 3900 m, 11 Jun 1979, Fallen 690 (MO); along the road to Guaranda, ca 21 km SW of Ambato, 10,000 ft, 25 Jan 1974, King 6583 (F, MO, UC, US).—CARCHI: 1 km N of Mira on road to El Angel, 2450 m, 25 Feb 1988, Panero & Gómez 1100 (CPUN, GRI, QCA, QCNE, TENN, US).—CHIMBORAZO: 1 km al N del puente sobre el Río Chambo, 2500 m, 10 Jul 1988, Panero 1526 (GRI, QCA, QCNE), 1527 (B, SI); steep slopes overlooking the Chambo River Gorge, just across the intersection of the roads to Puela and Riobamba-Baños, 2650 m, 18 Jun 1987, Panero 718 (COL, GRI, MA, MEXU, NY, QCA, QCNE, TENN); road from Riobamba to Pungalá and Alao, ca 0.5 km W toward river below Pungalá, 2900 m, 9 May 1971, MacBryde & Montanucci 230 (QCA, US); 2 km SW of Penipe along the road Riobamba-Baños, 2700 m, 10 Jul 1988, Panero 1525 (TENN).—COTOPAXI: road Salcedo-Ambato, 2 km from Salcedo, 2600 m, 2 Mar 1984, Madsen 50368 (QCA); Km 102 of the road Quito-Ambato, 2720 m, 2 Jul 1988, Panero 1405 (GRI, TENN), 1406 (GRI, QCA, QCNE).—IMBABURA: San Vicente, 6 Jun 1876, André 3538 (GH, K, F); Pimampiro, along path towards Carpuela, 1800 m, 24 Nov 1981, Filskov et al. 37388 (AAU); between Ibarra and Salinas, 2000 m, 30 Jan 1962, Heiser 4824 (US);Ibarra, 31 Dec 1930, Benoist s n. (MO, US); 1 km W of the intersection of the road to the Mirador of Volcán Pululahua and the road to Calacalí, 2800 m, 25 Jun 1987, Panero 822 (GRI, QCA, QCNE, TENN, US); entre el Río Chota y el partidero de la carretera a El Angel, 1500 m, 1 Jan 1963, Mora 2545 (US); Cima de Aluburo, 2600 m, 26 May 1949, Acosta 12503 (F); Shanshipamba, 2700 m, 12 Nov 1949, Acosta

14218 (F); 0.3 km from the intersection of the roads to Salinas and the road to Ibarra on road to Salinas, 1500 m, 25 Feb 1988, Panero & Gómez 1094A (TENN); En la cima del Pinllar, 2708 m, 18 Feb 1928, Firmin 365 (F, US).—PICHINCHA: 10 km N of Guayllabamba, 2650 m, 25 Feb 1988, Panero & Gómez 1103 (GRI, QCA, QCNE, TENN); 2 km N of San Antonio, 2450 m, 30 Jan 1973, Humbles 6172 (F, MO(3)); Otón, 2500-2600 m, 29 Nov 1945, Acosta 11269 (F); Río Guayllabamba, 1 km from the Pan-American Highway, 2200 m, 4 Apr 1979, Holm-Nielsen 16672 (QCA, US); 30 km N of Quito on Pan American Highway, 2180 m, 25 May 1977, Olsen & Escobar 438 (TEX); near Pifo, 2600 m, Jul 1904, Mille 495 (K, MO).—TUNGURAHUA: along Río Ambato, 2700 m, 29 Oct 1932, Heinrichs 5 (NY); Ambato, 8500 ft, 7 Sep 1939, Balls 7150 (US); Km 142 of the road Quito-Riobamba, 3110 m, 2 Jul 1988, Panero 1407 (CAN, CPUN, K, LIL, UC); entre Casigana y Chilcaloma, 2900-3300 m, 28 Nov 1944, Acosta 9107 (F); Ambato, Dec 1918, Pachano 76 (US); entre Pelileo y La Tranquilla, 2200-2550 m, 14 Nov 1944, Acosta 8922 (F), 8928 (F); 7 km NW of Baños on road to Ambato, 2500 m, 17 Jun 1987, Panero 711 (AAU, GRI, MA, MEXU, LE, TENN, US); entre el Mirador y Tilulúm, 2850-3000 m, 29 Nov 1944, Acosta 9199 (F); entre Ambato y Pishilata, 2500-2680 m, 25 Oct 1944, Acosta 8652 (F); along the road to Baños, ca 25 km SE of Ambato, 7400 ft, 23 Jan 1974, King 6577 (MO, UC, US); 7 km W of Ambato, 3000 m, 11 Nov 1981, Madsen et al. 36546 (AAU, QCA, US); Ambato, 2600 m, 21 Sep 1923, Hitchcock 21743 (GH, US); along the road to Baños, ca 1 km SE of Ambato, 8700 ft, 20 Jan 1974, King 6533 (F, MO, US); Sodiro s. n. (NY); Ambato, 2400-3000 m, Sep-Oct, Lehmann 5215 (F, K, NY, US; photo of K

specimen GH); Chaupi, 7.7 km E of Pelileo, 2200 m, 29 Jul 1979, Stuessy et al. 4948 (TEX); 32 km S of Ambato on road to Baños, 2040 m, 27 May 1977, Olsen & Escobar 461 (TEX, WIS).

Pappobolus imbaburensis can be easily recognized by its dark greenish-black or black phyllaries. In some individuals, especially those at the southern end of the range, the first series of phyllaries will be densely pubescent white dramatically contrasting with the blackish coloration of the inner phyllaries. It shares with P. verbesinoides a similar phyllary and pale coloration, as well as appressed phyllaries, a condition otherwise only shared with some forms of P. matthewsii. On the other hand, the somewhat broader phyllaries of P. imbaburensis coupled with the coloration of its pales suggest a relationship with P. hypargyreus.

Pappobolus imbaburensis is the northernmost species of the genus. Across its geographical range it exhibits a gradual change in certain key morphological characters such as head size and foliar morphology. At the southernmost end of the range, and especially in the populations along the Pastaza and Chambo Rivers in Tungurahua Province, the largest heads and floral characters occur. Individuals from other parts of the range show markedly smaller heads and floral characters. Another character that has been used to differentiate taxonomic groups within this taxon is leaf morphology. There are two extreme leaf morphologies with many intermediate forms bridging them. The lanceolate to trullate leaf with entire margins is mostly restricted to the southernmost end of the range and occurs sporadically in other parts. The broadly ovate

leaf with entire to serrate margins is mostly encountered in the north. Another important aspect is that leaf and head size and shape are not necessarily correlated; a particular leaf shape can be associated with several head sizes and shapes and vice versa.

The existence of numerous intermediate forms that connect P. imbaburensis and P. pseudoverbesinoides suggest that maintenance latter as a distinct entity is not tenable. The original collections of P. pseudoverbesinoides came from the area of Ambato in Tungurahua province; specimens from this area, as noted above, tend to be more pubescent, have larger lanceolate to trullate leaves and larger heads than individuals from other areas. The long history of human disturbance in the interandean valleys of Ecuador and the ruderal nature of this species may have contributed to mask the potential geographical and morphological integrity of otherwise discrete taxa. However, given the uniformity in overall morphology of all the species of the subgenus, it is remarkable that all populations of these species show the same phyllary morphology and coloration, an unusual character only observed elsewhere to an extent in P. verbesinoides.

9. Pappobolus juncosae Panero, sp. nov.——TYPE: ECUADOR. Imbabura: Highway Salinas-Lita, along the canyon of Río Mira, 1400-1500 m, 25 Feb 1988, Panero & Gómez 1094 (holotype: QCA!; isotypes: AAU!, F!, QCNE!, TENN!, US!).

Pappobolus juncosae differt ab aliis speciebus subgeneris Aprici. Habet villosas et lanatas herbas, capita magna et parvas

synflorescentias. Differt quoque a P. imbaburensi non habens atroviridia vel nigra phyllaria et paleas.

Weak, open shrubs 3-7 dm tall; **stems** terete, brown, glabrous, herbaceous parts tomentose to densely veillous white, trichomes white, multicellular, tapered, 0.5-4.5 mm long; **leaves** alternate, triplinerved, rhombic to ovate, adaxial surface silvery brownish-green and moderately strigose, trichomes white, multicellular, tapered, 0.3-0.7 mm long, abaxial surface lanate-floccose white, pubescence along the veins densely sericeous, trichomes white, multicellular, tapered, 0.3-4 mm long; sessile glandular trichomes confined to abaxial surface, 500-700/cm^2; **blades** 30-76 mm long, 9-43 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse and narrowly attenuate along distal third of petiole, margins serrulate; petioles 4-33 mm long, terete to slightly canaliculate, densely villous to lanate on both surfaces; **capitulescences** monochasial thyrsoid, with 1-5 heads, peduncles 17-105 mm long, densely villous to lanate, pubescence denser below heads, trichomes as stem; **heads** 10.8-11.2 mm across, 10.6-11 mm high, broadly campanulate to hemispherical; **receptacles** 7-7.5 mm in diameter in fruit, shallowly convex; **phyllaries** 21-24 in 4 slightly graduated series, first series 8.7-10.2 mm long, 2.6-3.6 mm wide, oblong to obovate, sometimes constricted between indurated and herbaceous parts, base strongly indurated, stramineous and glabrous adaxially, densely lanate white abaxially, herbaceous apex slightly reflexed, silvery greenish-brown and densely sericeous-strigose adaxially, densely lanate white abaxially, margins lanate, second and third series, 8.3-11 mm high, 3.4-4.5 mm wide, rhombic-oblong, base

strongly indurated, stramineous-brown, glabrous adaxially, stramineous-brown with several dark brown longitudinal bands and glabrescent abaxially, herbaceous apex appressed to shallowly reflexed, dull greenish-brown and sparsely strigose adaxially, sparsely to moderately lanate white abaxially, margins glabrescent to lanate, fourth series 8.8-10 mm long, 1.7-2.7 mm wide, ovate-oblong, resembling pales in general aspect, base somewhat indurated, stramineous, glabrous on both surfaces, herbaceous apex appressed, green-stramineous, puberulent adaxially, sparsely lanate whitish-green abaxially; **pales** 6.4-6.9 mm long, 2.3-2.5 mm wide, ovate to oblong, conduplicate, keeled lengthwise, covered by phyllaries, stramineous, with several green or brown longitudinal bands of various width, bands not coalescing at apex, glabrous abaxially, apex coriaceous, narrowly acuminate, pointed or reflexed, yellowish-stramineous; **ray flowers** 11-15, corolla bright yellow, limb 11.4-13.4 mm long, 4.4-5.2 mm wide, oblong, sparsely puberulent and glandular on veins of abaxial surface, apex rounded to acute, minutely bifid or trifid, tube 1.8-2 mm long, moderately puberulent; **ray ovaries** 3.7-4 mm long, triquetrous, glabrous, epappose; **disk flowers** 99-135, flowers protruding 0.2-0.5 mm above pales, corollas deep golden yellow, narrowly campanulate to cylindrical, throat 3.6-3.8 mm long, 0.9-1.1 mm wide at base, 0.9-1.3 mm wide at junction with lobes, veins deep orange and discernable the whole length of the throat, sparsely puberulent with interspersed uniseriate glandular trichomes 1-1.5 mm long, tapered trichomes white to hyaline, 0.1-0.2 mm long, tube 1.4-1.5 mm long, yellowish-green, glabrous, lobes

0.6-0.7 mm long, deltoid, deep yellowish-orange, sparsely puberulent and glandular abaxially; anthers 2.2-2.3 mm long, thecae yellow to orangish-brown, appendages 0.4-0.5 mm long, ovate, stramineous to yellow; styles 5.3-5.5 mm long, style branches 1.1 mm long; **disk achenes** 6.4-6.9 mm long, 2.3-2.5 mm wide, biconvex, oval-obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.2-2.7 mm long; n = 17.

Phenology. Flowering February and March.

Distribution (Fig. 36). Known from the valley of the Mira River of northern Ecuador; 1100-1500 m. This valley is a narrow gorge dominated by xerophytic vegetation at its headwaters. It gradually opens to the coastal lowlands of the Province of Esmeraldas and consequently elements of the coastal rain forest intermingle with the xerophytic vegetation and eventually dominate the lower altitude and wetter areas of the canyon. Pappobolus juncosae grows sporadically in the driest areas of this canyon (260-300 mm/yr). This species is rare, and only two plants were observed aside from the population that was the source of the type collectin which consisted of six individuals growing along an intermittent stream under the shade of a Leguminosae tree.

SPECIMEN EXAMINED. ECUADOR. IMBABURA: Highway Salinas-Lita, Río Mira gorge, 900-1100 m, 22 Feb 1984, Juncosa 2307 (QCA).

Pappobolus juncosae is a distinctive and unusual species. It possesses a combination of characters not observed in any other member of the subgenus. It can be easily recognized by its wide, oblong phyllaries, the densely velutinous-sericeous to lanate pubescence of

its leaves and stems and small capitulescences sometimes composed of one or two heads. In addition, the pales of this species have stramineous bands that do not coalesce at the apex as in other northern Ecuador species. The species epithet honors the original collector.

Pappobolus juncosae shares with P. hypargyreus a similar head size and phyllary morphology, although they differ significantly in herbage pubescence, leaf shape and capitulescence size. Its overall morphology is also somewhat similar to densely pubescent forms of P. imbaburensis, although the blackish phyllaries, large capitulescences and smaller heads effectively distinguish this species from P. juncosae.

II. Pappobolus S. F. Blake subgenus Pappobolus.—TYPE: Pappobolus macranthus S. F. Blake.

Shrubs 1-40 dm tall; **leaves** alternate or opposite, triplinerved or mononerved, lanceolate to narrowly lanceolate, ovate to broadly ovate, ovate-suborbicular, rhombic, trullate to broadly trullate, deltoid or oblong; **blades** 4-160 mm long, 1.5-50 mm wide; petioles 1-30 mm long; **capitulescences** monochasial or dichasial thyrsoid, with 1-22+ heads, peduncles 10-230 mm long; **heads** 7-32 mm across, 8.5-22 high, campanulate to broadly campanulate, urceolate-hemispherical or hemispherical; **receptacles** 3.8-18 mm in diameter in fruit, convex; **phyllaries** 19-81 in 2-6 graduated, rarely subequal series; **pales** 5-12.5 mm long, 1.5-6.5 mm wide; **ray flowers** 10-33, limb 8.5-45 mm long, 3.2-11.5 mm wide, tube 0.6-3.1 mm long, glabrous or sparsely to densely

puberulent and glandular; **ray ovaries** 1.4-5.1 mm long, epappose or with a pappus of 1 or 10-21 awns, sometimes 1-2 awns and 2-12 squamellae, awns 1-3 mm long, squamellae 0.2-2.4 mm long; **disk flowers** 45-385, throat 2.8-5.8 mm long, 0.7-1.8 mm wide at base, 0.8-2 mm wide at junction with lobes, glabrous or sparsely to moderately puberulent with interspersed uni- and biseriate glandular multicellular trichomes 0.1-0.2 mm long, tapered trichomes white to hyaline 0.1-0.4 mm long, tube 0.5-2 mm long, lobes 0.5-1.3 mm long; anthers 1.8-3.5 mm long, thecae black, yellowish-brown, brownish-black or purplish-black, appendages 0.3-0.9 mm long; styles 4.2-8.6 mm long, style branches 0.4-2.5 mm long; **disk achenes** 2.4-5.8 mm long, 0.9-2 mm wide, with 2 diminutive shoulders, shoulders sometimes absent, shiny black, grayish-black, mottled, sometimes with silvery-orange or purplish trichomes conspicuously contrasting with black coloration of achene wall, glabrous to sparsely sericeous, pappus of 2-28 awns, sometimes with 2-12 squamellae, awns slender, stramineous, rarely purplish-stramineous, deciduous to somewhat persistent, subequal, 1.3-5 mm long, squamellae free, 0.3-2 mm long, same color as awns, deciduous to somewhat persistent.

Phenology. Flowering at the middle and end of the rainy season from January to Late July or August, some species flowering throughout the year.

Distribution. Montane moist forest, rarely venturing into wet forest of the western range of Ecuador south of the Chimborazo volcano southward along the Andes to the valley of the Chicama River in southern Cajamarca Department. Also in the eastern Andean range of Peru

from Amazonas department south to the valley of the Mantaro River in Huancavelica Department. Some species are are known from subalpine moist or wet forests or Páramo of central Cajamarca and La Libertad Departments. Some species are also known fom montane to subalpine dry scrub or steppe of the interandean and western escarpment valleys of the central and northern Andes of Peru; 1800-4200 m.

A. THE NIGRESCENS GROUP

Open to to slightly compact shrubs 10-35 dm tall with broadly ovate to ovate, trullate, rarely deltate or lanceolate, soft leaves. Capitulescences of large, showy heads on long peduncles. Known from tropical deciduous to moist and wet forests of the western range of the Andes of Ecuador and Peru.

10. Pappobolus lehmannii (Hieron.) Panero, comb. nov. Helianthus lehmannii Hieron., Bot. Jahrb. Syst. 29:39-40. 1901. Helianthopsis lehmannii (Hieron.) H. Robinson, Phytologia 44:264. 1979.——TYPE: ECUADOR. Bolívar: Chapacoto, 2500-3000 m, Lehmann 7966 (lectotype, here designated: US!; isolectotype: K!, photo: GH!).

Open shrubs 10-30 dm tall; **stems** terete, soft brown, glabrous, herbaceous parts dark brown and sparsely tomentose to villous, densely villous-lanate upwards toward the capitulescence, trichomes hyaline or white, multicellular, tapered, 1.5-3.5 mm long; **leaves** alternate, triplinerved, ovate-deltoid, rarely cordate or rhombic, adaxial surface

light to dark green and strigose, trichomes white to hyaline, multicellular, tapered, 0.5-0.7 mm long, moniliform trichomes restricted to veins, arched, tan-brown, multicellular, apical cell rounded, 0.05-0.1 mm long, abaxial surface creamy light green and moderately to densely velutinous to velutinous-sericeous, sometimes silvery iridescent with trichomes combed in opposite directions from secondary veins meeting at intersecondary composite veins, trichomes white, multicellular, tapered, 0.7-1.3 mm long, moniliform trichomes similar in size, morphology and distribution to those of abaxial surface, pubescence along major veins densely velutinous-sericeous; sessile glandular trichomes confined to abaxial surface 700-900/cm^2; **blades** 35-115 mm long, 20-55 mm wide, similar in size and morphology throughout stem and capitulescence, apex acuminate, base obtuse rarely truncate, sometimes narrowly attenuate along distal third of petiole, margins serrulate to serrate; petioles 5-35 mm long, slightly canaliculate, densely tomentose adaxially, densely velutinous-sericeous rarely villous abaxially; **capitulescences** monochasial thyrsoid, with 3-19+ heads, peduncles 5-42 mm long, velutinous to villous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 15-22 mm across, 17-19.5 mm high, hemispherical; **receptacles** 11-15 mm in diameter in fruit, flat to shallowly convex; **phyllaries** 31-38 in 4 somewhat subequal to graduated series, first series 11-21 mm long, 3.5-10 mm wide, lanceolate or ovate to obovate, sometimes slightly constricted between indurated and herbaceous parts, base indurated, light green and glabrous adaxially, moderately to densely lanate or

villous dark green to blackish or white abaxially, herbaceous apex sometimes foliaceous, spreading or conspicuously appressed, light green and sparsely to moderately strigose or minutely hirsute adaxially, dark green and minutely hirsute or densely lanate-sericeous, sometimes pubescence conspicuously denser along midrib abaxially, margins tomentose to velutinous, second and third series 13-22 mm long, 3.6-11 mm wide, lanceolate, oval to fusiform, base indurated, stramineous-green, and glabrous adaxially, dark green with several dark green longitudinal ribs and glabrescent to sparsely tomentose abaxially, herbaceous apex foliaceous, spreading or appressed, light green and sparsely to moderately strigose-velutinous or minutely hirsute adaxially, dark green and minutely hirsute or moderately to densely velutinous, sometimes pubescence conspicuously denser along midrib abaxially, margins as previous series, fourth series 7-17 mm long, 2.4-5.3 mm wide, oblong-lanceolate, somewhat chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous with several dark green bands coalescing at apex and glabrous aadaxially, glabrescent to tomentose abaxially; **pales** 9.5-11.5 mm long, 3-4 mm wide, broadly ovate, conduplicate, strongly keeled lengthwise, covered by phyllaries, stramineous-copper, with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrescent or glabrous abaxially, apex coriaceous, acute, pointed or slightly curved inward, dark green or black; **ray flowers** 16-22, corolla bright yellow, sometimes apex blackish abaxially, limb 22-30 mm long, 10.2-11.5 mm wide, lanceolate-oval to obovate, sparsely puberulent and glandular on veins of abaxial surface, apex acute, bifid, tube 1.6-2.6

mm long, basal half glabrous, distal half puberulent; **ray ovaries** 4.2-5 mm long, triquetrous, glabrous, pappus of 2-7 squamellae, 0.8-2.4 mm long; **disk flowers** 120-175, flowers protruding 0.4-0.6 mm beyond pales, corollas golden yellow, narrowly campanulate, throat 4.8-5.8 mm long, 1.4-1.6 mm wide at base, 1.7-1.8 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, glabrescent or sparsely puberulent especially at the base, glandular trichomes rarely present, tapered trichomes hyaline to white, 0.15-0.2 mm long, tube 1.2-1.6 mm long, yellowish-green, glabrous, lobes 0.7-1 mm long, deltoid-lanceolate, yellow adaxially, black abaxially; anthers 2.8-3.4 mm long, thecae black, appendages 0.3-0.5 mm long, ovate, stramineous; styles 7.3-7.8 mm long, style branches 1.5-2 mm long; **disk achenes** 4.8-5.8 mm long, 1.8-2 mm wide, biconvex, obovate, with diminutive shoulders, shiny black, glabrous, pappus of 2 awns, sometimes with 5-12 squamellae, awns slender, stramineous, deciduous, subequal, 3-4.7 mm long, squamellae free, 1-1.1 mm long, same color as awns, deciduous; n = 17.

Phenology. Flowering profusely from April to August and sporadically throughout the rest of the year.

Distribution (Fig. 37). Moist forests surrounding the canyons of the Chanchán, Cañar and Chimbo Rivers of central Ecuador; 1800-3500 m.

Pappobolus lehmannii is a very common species of the montane moist forest of central Ecuador. It grows abundantly along the Pan-American Highway, sometimes forming large colonies. It grows with Fuchsia loxensis, several Calceolaria spp., Monnina, Barnadesia spinosa,

Cortaderia, Oreocallis grandiflora, Clusia, and Coriaria thymifolia Humb. & Bonpl., among others.

This species is the northernmost element of P. subg. Pappobolus. It can be recognized by its glabrous disk flower tube, phyllary structure and color, and the largest achenes and ray flower ovaries in the genus. It shares with P. nigrescens from southern Ecuador an alternate leaf phyllotaxy, a velutinous-sericeous herbage pubescence and style branches with black abaxial surfaces. It can be confused with P. schillingii of southern Ecuador but is effectively separated by characters of the leaf such as shape and the abaxial surface pubescence. In P. lehmannii the leaf tends to be ovate with an obtuse base while an ovate to ovate-deltate leaf with an obtuse to truncate base is common in P. schillingii. In addition, the leaf abaxial surface pubescence in P. lehmannii is always velutinous-sericeous while P. schillingii exhibits a floccose-villous to sometimes lanate-floccose pubescence. The phyllaries of these three species also provide important characters to separate one from another. In P. lehmannii the phyllaries are densely villous to lanate and lanceolate, or rarely sparsely villous or hirsute and ovate. In the case of P. nigrescens the phyllaries are sparsely tomentose or villous and very dark green and drying black, and the herbaceous apex is somewhat appressed which contrasts with the strongly reflexed or sometimes twisted apices of the other two species. Pappobolus nigrescens shares with P. schillingii a somewhat similar phyllary color and pubescence, however, the phyllaries in the latter species tend to be strongly reflexed, larger and

conspicuously constricted between the indurated and herbaceous portions.

KEY TO THE VARIETIES OF Pappobolus lehmannii.

1. Phyllaries lanceolate, spreading to strongly reflexed, those of first and second series moderately to densely villous to lanate. 10a. P. lehmannii var. lehmannii.

1. Phyllaries ovate to obovate or somewhat fusiform, appressed or slightly reflexed, those of first and second series glabrescent to densely minutely hirsute or velutinous abaxially. 10b. P. lehmannii var. grandiceps.

10a. Pappobolus lehmannii var. lehmannii.

Phyllaries 31-37 in 4 somewhat subequal to graduated series, first series 11-21 mm long, 3.5-7 mm wide, lanceolate, base indurated, light green and glabrous adaxially, densely lanate or villous white abaxially, herbaceous apex somewhat foliaceous, spreading, light green and sparsely to moderately strigose adaxially, green-white and densely lanate or villous abaxially, margins densely ciliate, second and third series 14.5-22 mm long, 3.6-6 mm wide, lanceolate, base indurated, stramineous-green and glabrous adaxially, dark green with several dark green longitudinal ribs and sparsely tomentose abaxially, herbaceous apex foliaceous, spreading, light green and sparsely to moderately strigose-velutinous adaxially, dark green or moderately to densely velutinous white abaxially, margins ciliate.

Phenology and distribution as indicated above.

SPECIMENS EXAMINED. ECUADOR. BOLIVAR: Carretera Guaranda-Pueblo Viejo, a 12 km de Guaranda, 3100 m, 2 Aug 1985, Larsen 83 (F, QCA); Simiatug, 3500 m, 15 Aug 1982, Falconí & Argüello 71 (QCA).—CAÑAR: 16 km N of El Tambo, 2950 m, 8 Jul 1988, Panero 1501 (B, GRI, QCA, QCNE, TENN, US), 1502 (QCNE, UC), 1503 (TENN), 1504 (TENN); Chimbo, 2800 m, Jun 1936, Rimbach 763 (F); Casichagua, 2860 m, 29 Sep 1943, Acosta 5993 (F); 17 km NW of El Tambo, 2950 m, 19 Jun 1987, Panero 720 (CAN, CPUN, MA, MEXU, QCA, QCNE, S, SI, TENN), 720A (TENN).—CHIMBORAZO: Bosquecito El Carmen, parroquia Sibambe, 2450 m, 22 Aug 1943, Acosta 5533 (F); Above Tixan, along the road Riobamba-Cuenca, 3040 m, 2 Jul 1988, Panero 1408 (GRI, TENN), 1412 (F, QCA, QCNE, US), 1413 (AAU, K); 35 km SW of Cajabamba on road to Bucay, 2900 m, 2 Sep 1979, Stuessy & Nesom 5843 (LP, SI); along the road to Riobamba, ca 25 km SW of Riobamba, 10600 ft, 31 Jan 1976, King & Garvey 6970 (MO, UC, US); Pallatanga Valley, 1800 m, Sodiro 36/1 (US); road Pallatanga-Cajabamba, 29-30 km from Pallatanga, 2950 m, 28 Aug 1976, Øllgaard & Balslev 8981 (NY, US); Guanojo, Jul 1876, André K233 (K, NY); Quimiac, [Quimiag ?], 2600 m, Mille 496 (GH, US).

This taxon is easily recognized by the densely velutinous-sericeous to lanate lanceolate phyllaries with strongly reflexed and twisted herbaceous apices. Superficially it resembles P. mollicomus from Amazonas Department in northern Peru. Both species share a similar herbage and phyllary pubescence although the phyllaries of P. mollicomus are somewhat appressed and smaller. A more discrete and effective character separating the two species is the disk achene

pappus, which in P. mollicomus is of several awns and not the 2 (-3) awns typical in P. lehmannii.

10b. Pappobolus lehmannii var. grandiceps (S. F. Blake) Panero, stat. et comb. nov. Helianthus grandiceps S. F. Blake, Contr. U.S. Natl. Herb. 22:621. 1924. Helianthopsis grandiceps (S. F. Blake) H. Robinson, Phytologia 44:262. 1979.——TYPE: ECUADOR. Chimborazo: Huigra, mostly on the Hacienda de Licay, 19 Aug 1918, Rose & Rose 22231 (lectotype, here designated: US!; isolectotypes: GH!, NY!).

Phyllaries 31-38 in 4 graduated series, first series 11.6-13 mm long, 5-10 mm wide, ovate to obovate, sometimes slightly constricted between indurated and herbaceous parts, base indurated, light green and glabrous adaxially, dark green to blackish and moderately minutely hirsute to velutinous-sericeous abaxially, herbaceous apex conspicuously appressed, light green and sparsely minutely hirsute adaxially, dark green and moderately to densely minutely hirsute, sometimes pubescence conspicuously denser along midrib, margins tomentose to velutinous, second and third series 13-19 mm long, 5-11 mm wide, oval to fusiform, constricted between indurated and herbaceous parts, base indurated, stramineous-green and glabrous adaxially, dark green with several dark green longitudinal ribs and glabrescent to sparsely tomentose abaxially, herbaceous apex appressed rarely spreading, light green and sparsely to moderately minutely hirsute adaxially, dark green and minutely hirsute to moderately velutinous,

sometimes pubescence conspicuously denser along midrib abaxially, margins tomentose.

Phenology. Flowering April to July (August).

Distribution. (Fig. 37). Known from a small area just above the town of Huigra a few miles south of Chunchi along the Pan-American Highway in Chimborazo Province; 2800-2850 m.

This taxon can be recognized by its ovate to lanceolate, appressed and sparsely to moderately pubescent phyllaries. This phyllary morphology is somewhat similar to that of P. acuminatus from central Peru. However, P. acuminatus shows an opposite phyllotaxy, entire leaf margins and a mostly dichasial capitulescence, characters which are not present in P. lehmannii.

The decision to consider H. grandiceps a variety of P. lehmannii was a difficult one. After several visits to the collection area (see below) and a careful comparison of several specimens of this taxon I arrived at the conclusion that this variety is identical in most respects to the nominal variety. The only difference that justifies the present varietal recognition is the phyllary structure and restricted geographical distribution of this phyllary morphology. Even within this variety there is significant variation in the pubescence and phyllary morphology. Panero 1415 and 1507 show more lanceolate and slightly more pubescent phyllaries whereas Panero 1508 exhibits ovate and sparsely pubescent phyllaries. However, these differences in phyllary morphology do not bridge the gap between the two varieties.

SPECIMENS EXAMINED. ECUADOR. CAÑAR: Between Tambo and Suscal, 23 Apr

1945, Camp E-2784 (GH, K, US).—CHIMBORAZO: 40 km N of El Tambo, 2830 m, 2 Jul 1988, Panero 1415 (GRI, QCA, QCNE, SI, TENN, US), 8 Jul 1988, 1507 (B, CPUN), 1508 (F, GRI, QCA, TENN, US).

11. Pappobolus nigrescens (Heiser) Panero, comb. nov. Helianthus nigrescens Heiser, Brittonia 8:287. 1957. Helianthopsis nigrescens (Heiser) H. Robinson, Phytologia 44:264. 1979.——TYPE: ECUADOR. Azuay: along the Río Tarquí, 4 km S of Cuenca, 8300 ft, 27 Jun 1945, Camp E-3903 (lectotype, here designated: NY!; isolectotypes: MO!, UC!).

Shrubs 15-35 dm tall; **stems** terete, soft brown, glabrous, herbaceous parts dark brown-green and tomentose to minutely velutinous, trichomes whitish-green, multicellular, tapered, 0.7-2.2 mm long; **leaves** alternate, triplinerved, ovate to broadly trullate, adaxial surface dull brown-green and moderately strigose, trichomes white, multicellular, tapered, 0.4-0.6 mm long, moniliform trichomes restricted to veins, arched, tan-brown, multicellular, apical cell rounded, 0.05-0.1 mm long, abaxial surface creamy light green to white-green and moderately to densely velutinous to sericeous, rarely floccose, trichomes white to yellowish-green, multicellular, tapered, 0.7-1.3 mm long, moniliform trichomes similar in size, morphology and distribution to those of abaxial surface, pubescence along major veins densely lanate-sericeous; sessile glandular trichomes confined to abaxial surface 2700-3000/cm^2; **blades** 2.5-13.5 cm long, 15-110 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse,

sometimes narrowly attenuate along distal fifth of petiole, margins serrulate to serrate; petioles 8-52 mm long, slightly canaliculate, moderately to densely velutinous-sericeous on both surfaces; **capitulescences** monochasial thyrsoid, with (3-) 5-21+ heads, peduncles 1.5-11.5 cm long, moderately tomentose to velutinous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 14-16 mm across, 13-16.5 mm high, hemispherical; **receptacles** 9-12.5 mm wide, flat to shallowly convex; **phyllaries** 34-48 in 5 graduated series, first and second series 8.5-12.5 mm long, 2-4.2 mm wide, ovate, base indurated, light greenish-stramineous and glabrous adaxially, shiny blackish-green and glabrescent to sparsely tomentose-villous abaxially, herbaceous apex appressed to slightly reflexed, dark greenish-black and sparsely velutinous-sericeous adaxially, dark greenish-black to creamy greenish-white and glabrescent to densely tomentose-villous abaxially, margins ciliate, third and fourth series 10-14.2 mm long, 2.9-5 mm wide and 14.5-18 mm long, 3.2-4.8 mm wide respectively, oblong, lanceolate, base indurated, stramineous-light green and glabrous adaxially, shiny dark greenish-black and glabrous abaxially, herbaceous apex appressed or slightly reflexed, dark greenish-black and glabrous adaxially, shiny dark green-black and glabrescent, sometimes pubescence denser along midrib abaxially, margins glabrescent to minutely ciliate, fifth series 10-16.5 mm long, 2.3-3.6 mm wide, oblong-lanceolate, somewhat chartaceous with no clear distinction between indurated and herbaceous parts, stramineous basally, stramineous-green apically, glabrous on both surfaces; **pales** 7.7-8.3 mm long, 3.1-3.6 mm wide, broadly ovate, conduplicate, keeled lengthwise, covered by phyllaries, stramineous-

copper, with several dark green or brown longitudinal bands of various width, bands coalescing at apex and fold, glabrous abaxially, apex coriaceous, acute, pointed or slightly curved inward, dark green or black; **ray flowers** 16-23, corolla bright golden yellow, apex blackish abaxially, limb 16.5-33.5 mm long, 6-7 mm wide, lanceolate-oval, moderately puberulent on veins of abaxial surface, apex acute, bifid or trifid, tube 1.6-3 mm long, sparsely puberulent; **ray ovaries** 3.5-3.7 mm long, triquetrous, glabrous, pappus of 2-5 squamellae 0.3-0.8 mm long; **disk flowers** 115-170, flowers protruding 1.2-1.6 mm beyond pales, corollas golden yellow, cylindrical to narrowly campanulate, throat 4.5-5.6 mm long, 1.2-1.6 mm wide at base, 1.2-2 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, moderately puberulent especially at the base with interspersed uni- and biseriate multicellular glandular trichomes 0.05-0.15 mm long, tapered trichomes hyaline to white, 0.1-0.3 mm long, tube 0.9-2 mm long, yellowish-green, sparsely to moderately puberulent, lobes 0.6-1 mm long, deltoid, yellow adaxially, black abaxially; anthers 2.9-3.4 mm long, thecae black, appendages 0.4-0.5 mm long, ovate-lanceolate, stramineous; styles 6.2-7.2 mm long, style branches 1.7-2.4 mm long, conspicuously black abaxially; **disk achenes** 3.4-4 mm long, 1.6-1.7 mm wide, biconvex, obovate, with or without two diminutive shoulders, shiny grayish-black or black, glabrous, with a few trichomes around the neck, pappus of 2 awns and 3-5 squamellae, awns slender, stramineous, deciduous, subequal, 1.3-3.2 mm long, squamellae free, 0.8-1.2 mm long, same color as awns, deciduous; $\underline{n}$ = ca 17.

Phenology. Flowering from April to August and apparently sporadically the rest of the year.

Distribution (Fig. 37). Montane moist or dry forests along the canyons of the Girón and León Rivers in Azuay Province and at the headwaters of the Paquishapa River in northern Loja Province. Sometimes growing along the roads in disturbed areas especially along the several rivers that cross the valley of the city of Cuenca; 2100-3000 m.

SPECIMENS EXAMINED. ECUADOR. AZUAY: carretera Cuenca-San Joaquín al lado del Río Yanuncay, 2200 m, 3 Nov 1978, Albert de Escobar et al. 685 (QCA, TEX); 17 km S of the intersection of the road to Loja and Girón, on road to Girón, 2950 m, 21 Jun 1987, Panero 755 (GRI, QCNE, TENN); 758 (B, F, GRI, QCA, QCNE, US), 10 Jul 1988, 1520 (LE, MA, MEXU, SI), 22 Feb 1988, Panero & Gómez 1092 (TENN); 2.9 km S of Girón on road to Machala, 2120 m, 10 Jul 1988, Panero 1521 (COL, QCNE); Along the road to Girón, ca 11 km NE of Girón, 8900 ft, 3 Feb 1974, King 6676 (MO, UC, US); 61 km S of Cuenca on road to Loja, 2670 m, 7 Jul 1988, Panero 1492 (GRI, QCA, QCNE, TENN, US); road Cuenca-Loja, upper northern slopes of Valle del Río León and southern parts of Páramo de Tinajillas, 2800 m, 9 May 1974, Harling & Andersson 14531 (AAU); 9 km from the intersection of the roads Cuenca-Loja and the road Cuenca-Girón on road to Loja, 2830 m, 3 Jul 1988, Panero 1416 (QCA, QCNE, TENN); 59 km S of the intersection of the roads to Cuenca and Girón on road to Loja, 2910 m, 3 Jul 1988, Panero 1434 (QCNE, TENN), 1436 (TENN), 1437 (F, GRI, QCNE, TENN), 1438 (CPUN, MICH).—LOJA: 10 km N of Saraguro on road to Oña,

2190 m, 3 Jul 1988, Panero 1444 (CPUN, QCA, QCNE, TENN, UC); 0.6 km N of Saraguro, 2760 m, 7 Jul 1988, Panero 1494 (AAU, F, GRI, QCA, QCNE, TENN), 1495 (B, K, MA, MEXU, RB); 1.1 km NE of Saraguro on road to Cuenca, 2450 m, 21 Feb 1988, Panero & Gómez 1077 (AAU, QCA, QCNE, TENN, US); 4 km al N de Saraguro, 8000-8500 ft, 2 Feb 1979, Albert de Escobar 1053 (TEX); Near Loja, 8 Sep 1865, Jameson 20 (K).

This is an attractive species of central and southern Ecuador. It sometimes grows abundantly along the roads, especially around the town of Cumbe on the road to Loja and around the town of Saraguro in Loja Province. It can be easily recognized by its dark, shiny green phyllaries and the gently curved or "wavy" ligules. Some populations, especially those north of the town of Girón and the ones surrounding the town of Saraguro, tend to have slightly tomentose to villous outer phyllaries. This phyllary morphology is somewhat similar to that of some individuals of P. lehmannii. These forms can be easily separated by the pubescent disk flower tube in P. nigrescens as opposed to the glabrous disk flower tube in P. lehmannii. Other similarities and differences between these two species are discussed under P. lehmannii.

12. Pappobolus andinus Panero, sp. nov.——TYPE: PERU. Junín: Prov. Tarma, upper mouth of the gorge of Río Huasahuasi, 2600 m, 27 Feb 1964, Hutchison & Tovar 4153 (holotype: F!; isotypes: UC!, US!).

Pappobolus andinus similis P. lehmannii est sed differt habens minores synflorescentias et ovata vel lanceolata folia.

Open shrubs 10-15 dm; **stems** terete, light brown and glabrous, herbaceous parts sparsely tomentose to moderately villous brownish-white, trichomes white, multicellular, tapered, 1-1.5 mm long; leaves alternate, triplinerved, ovate, adaxial surface brownish-green moderately to densely hirsute, trichomes hyaline, multicellular, tapered, 0.5-0.8 mm long, abaxial surface creamy greenish-white and densely villous-floccose, trichomes white, multicellular, tapered, 1-1.5 mm long; sessile glandular trichomes confined to abaxial surface 50-100/cm^2; **blades** 25-50 mm long, 12-30 mm wide, markedly smaller upwards toward capitulescence, apex acuminate, base obtuse and narrowly attenuate along distal fourth of petiole, margins serrulate; petioles 7-15 mm long, slightly canaliculate, densely tomentose-villous on both surfaces; **capitulescences** monochasial thyrsoid, with 1-3 heads, peduncles 15-40 mm long, densely tomentose to densely villous-lanate under heads, trichomes as stem; **heads** 9.5-15.5 mm across, 12.5-16 mm high, hemispherical; **receptacles** 6.5-9 mm in diameter in fruit, shallowly convex; **phyllaries** 25-42 in 4 slightly graduated series, all series with a conspicuous densely tomentose midrib on the abaxial surface, first series 7.5-12 mm long, 2.5-3.2 mm wide, ovate-lanceolate, base indurated, light green and glabrous adaxially, dark green and sparsely tomentose abaxially, herbaceous apex appressed or reflexed, light green and sparsely strigose-hirsute adaxially, dark green and moderately hirsute to velutinous abaxially, margins sparsely ciliate, second and third series 10-16 mm long, 3.5-5 mm wide, lanceolate-oblong, base indurated, stramineous and glabrous adaxially,

dark green-stramineous and glabrescent to sparsely tomentose abaxially, herbaceous apex appressed, light green and sparsely strigose adaxially, dark green and sparsely tomentose abaxially, margins sparsely ciliate, fourth series 13-17 mm long, 3.3-4 mm wide, oblong, somewhat chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous with several dark green longitudinal bands of various width, bands coalescing at apex, glabrous adaxially, glabrescent to sparsely tomentose abaxially, margins glabrous to minutely ciliate; **pales** 9.5-10.5 mm long, 4.2-5.2 mm wide, broadly ovate, conduplicate, strongly keeled lengthwise, protruding 1-2 mm beyond the phyllaries, stramineous-copper, with several dark green longitudinal bands of various width, bands coalescing at apex, glabrescent to glabrous abaxially, apex coriaceous, acute to acuminate, pointed, dark green or black; **ray flowers** 22-28, corolla bright yellow, sometimes apex blackish abaxially, limb 19-28 mm long, 5-8.5 mm long, lanceolate-oval, sparsely puberulent and glandular on veins of abaxial surface, apex acute, bifid, rarely trifid, tube 1.9-2.3 mm long, moderately puberulent and glandular; **ray ovaries** 3-3.4 mm long, triquetrous, glabrous, pappus of 2-4 squamellae 0.3-0.5 mm long; **disk flowers** 75-200, flowers protruding 0.5 mm beyond pales, corollas golden yellow, campanulate, throat 4.3-4.7 mm long, 1.4-1.5 mm wide at base, 1.5-1.7 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, moderately puberulent especially at the base, with interspersed uniseriate multicellular glandular trichomes 0.05-0.15 mm long, tapered trichomes white to hyaline, multicellular, 0.1-0.2 mm long, tube 1.6-1.8 mm long, greenish-yellow,

glabrous, lobes 0.8-1.1 mm long, yellow, apices black abaxially, moderately puberulent and glandular abaxially; anthers 2.9-3.2 mm long, thecae black, appendages 0.4-0.6 mm long, lanceolate, stramineous; styles 6-6.6 mm long, style branches 2-2.2 mm long; **disk achenes** 3.8-4.4 mm long, 1.7-1.9 mm wide, biconvex, oval-obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.3-2.8 mm long; Chromosome number unknown.

Phenology. Flowering February and March.

Distribution (Fig. 38). Central Junín, in the canyon of the Huasahuasi River, a tributary of the Palca River; 2600 m.

The few sheets of the only collection known of this species indicate a weak, open shrub of a definite alternate phyllotaxy. The defining character of this species is the gradual reduction in leaf size upwards toward the capitulescence. In most of the species of the genus the leaves tend to be smaller upwards toward the capitulescence with a marked drop in size for the leaves associated with the branching capitulescence. In P. andinus the growing shoots are short and exhibit a significant reduction of leaf size that is abruptly interrupted by a capitulescence composed of 1 to 3 heads. The peduncles are short and have no leaves associated with them. These capitulescence and growth morphologies are unique within the genus. The phyllaries are appressed to slightly reflexed with a soft hirsute to tomentose pubescence. This phyllary morphology is elsewhere only observed in P. acuminatus and P. lehmannii var. grandiceps. Another important aspect of the phyllaries

is the conspicuously denser line of trichomes along the midrib of the abaxial surface which is also observed in the above two species and in P. nigrescens and P. stork-hortonii.

Pappobolus andinus, like the other two southernmost species of the group, P. acuminatus and P. stork-hortonii, share with the northernmost Ecuadorian species, P. nigrescens and P. lehmannii, a similar phyllary morphology. In addition, P. andinus also shares with the latter two an alternate phyllotaxy, and is the only Peruvian species in the nigrescens group that exhibits this character. It is difficult to ascertain if these characters are shared by common descent or are the result of convergence. Given the wide geographical separation between the Ecuadorian and Peruvian species it is plausible that convergence is responsible for the similarities observed between the two groups.

13. Pappobolus stork-hortonii Panero, sp. nov.——TYPE: PERU. Huancavelica: Quebrada, 3 km N of Salcabamba, 3500 m, Jan 9 1939, Stork & Horton 10316 (holotype: UC!; isotype: F!).

Pappobolus stork-hortonii similis P. lehmannii est sed differt habens minores radiales flores, ovata folia, disciformes flores et disciformia achenia.

Shrubs 15-30 dm tall; **stems** terete, soft brown, glabrous, herbaceous parts brownish-green and tomentose to minutely velutinous upwards toward growing apex, trichomes whitish-green, multicellular, tapered, 0.7-2.5 mm long; **leaves** alternate (opposite?), triplinerved, ovate, adaxial surface dull brownish-green and moderately strigose-

hirsute, trichomes white, multicellular, tapered, 0.4-0.6 mm long, moniliform trichomes restricted to veins, arched, tan-brown, multicellular, apical cell rounded, 0.05-0.1 mm long, abaxial surface creamy light green to whitish-green and moderately to densely velutinous, trichomes white to yellowish-green, multicellular, tapered, 0.7-1.0 mm long, moniliform trichomes as adaxial surface, pubescence along major veins densely velutinous-sericeous; sessile glandular trichomes confined to abaxial surface 1000-1300/cm^2; **blades** 25-95 mm long, 10-50 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse and narrowly attenuate along distal fifth of petiole, margins serrulate; petioles 10-25 mm long, slightly canaliculate, moderately to densely lanate-sericeous on both surfaces; **capitulescences** monochasial thyrsoid, with 2-12+ heads, peduncles 15-85 mm long, moderately velutinous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 14-17 mm across, 15-21 mm high, hemispherical; **receptacles** 7.5-11.5 mm wide, shallowly convex; **phyllaries** 32-44 in 4 graduated series, first and second series 8.5-11.5 mm long, 3.5-5 mm wide, ovate, base indurated, light greenish-stramineous and glabrous adaxially, shiny blackish-green and glabrescent to sparsely tomentose-villous abaxially, herbaceous apex slightly reflexed and twisted, dark greenish-black and sparsely hirsute-sericeous adaxially, dark greenish-black glabrescent to densely tomentose-villous abaxially, margins ciliate, third series 16-22 mm long, 4-5.5 mm wide, oblong or lanceolate, base indurated, stramineous-light green and glabrous adaxially, shiny dark greenish-black and glabrous abaxially, herbaceous apex appressed or slightly reflexed,

dark greenish-black and glabrous adaxially, shiny dark green-black and glabrescent, sometimes pubescence denser along midrib abaxially, margins glabrescent to sparsely ciliate, fourth series 10-16.5 mm long, 2.3-3.6 mm wide, oblong-lanceolate, somewhat chartaceous with no clear distinction between indurated and herbaceous parts, stramineous basally, stramineous-green apically, glabrous on both surfaces; **pales** 7.7-8.5 mm long, 3-3.6 mm wide, broadly ovate, conduplicate, keeled lengthwise, covered by phyllaries, stramineous-copper, with several dark green or brown longitudinal bands of various width, bands coalescing at apex and fold, glabrous or sparsely tomentose abaxially, apex coriaceous, acute, pointed or slightly curved inward, dark green or black; **ray flowers** 18-23, corolla bright golden yellow, apex blackish abaxially, limb 16.5-28.5 mm long, 6-7 mm wide, lanceolate-oval, moderately puberulent on veins of abaxial surface, apex acute, bifid or trifid, tube 1.6-3 mm long sparsely puberulent; **ray ovaries** 3.2-3.5 mm long, triquetrous, glabrous, epappose?; **disk flowers** 125-250, flowers protruding 1-1.2 mm beyond pales, corollas golden yellow, campanulate-cylindrical throat 4.8-5.5 mm long, 1.7-1.8 mm wide at base, 1.9-1.8 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely puberulent especially at the base with interspersed uniseriate multicellular glandular trichomes 0.05-0.15 mm long, tapered trichomes hyaline to white, 0.1-0.3 mm long, tube 1.5-1.7 mm long, yellowish-green, glabrous, lobes 1-1.2 mm long, deltoid, yellow adaxially, black abaxially; anthers 2.9-3.4 mm long, thecae black, appendages 0.5-0.6 mm

long, ovate-lanceolate, stramineous; styles 7.2-7.5 mm long, style branches 1.8-2 mm long; **disk achenes** 3.4-4 mm long, 1.6-1.7 mm wide, biconvex, obovate, with diminutive shoulders, shiny grayish-black or black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 1.3-3.2 mm long; Chromosome number unknown.

Phenology. Collected in flower in January and April.

Distribution (Fig. 38). Vicinity of the town of Salcabamba along the canyon of the Mantaro River in Huancavelica Department, central Peru; 3000-3500 m.

Vernacular name: Sacha-sunchu (fide Tovar 3581).

SPECIMEN EXAMINED. PERU. HUANCAVELICA: Prov. Tayacaja, alrededores de Salcabamba, 3000-3100 m, 11 Apr 1962, Tovar 3581 (LP).

This species is known only from the type locality and another collection from the same vicinity. Its distinctive features are the large heads, dark green and sparsely villous phyllaries which have a twisted and reflexed herbaceous apex, and the evenly tomentose stem which is pubescent even well below the capitulescence. The phyllary morphology and capitulescence structure are somewhat similar to specimens of the southern end of the range of P. nigrescens which exhibit a less well-organized (series of phyllaries, especially the innermost not complete) involucre in which the phyllaries are slightly reflexed or twisted and pubescent. The heads in P. stork-hortonii are larger and have smaller ligules than in P. nigrescens. On the other hand some of the phyllaries tend to be slightly constricted and reflexed as in P. youngiorum from La Libertad and Amazonas Departments.

As is the case of the other southernmost species of the genus such as P. andinus and P. acuminatus the relationships of this species are not very clear. This species, unlike the majority in the genus, is defined by only subtle differences in characters shared by several species and not by unique or specific characters.

14. Pappobolus acuminatus (S. F. Blake) Panero, comb. nov. Helianthus acuminatus S. F. Blake, J. Wash. Acad. Sci. 16:219. 1926. Helianthopsis acuminata Phytologia 44:262. 1979.——TYPE: PERU. Huánuco: rocky slope at Tomaiquichua [Tomay Kichwa], three miles below [N of] Ambo, 2590 m, 19 Sep 1922, Macbride & Featherstone 2429 (lectotype, here designated: F!; isolectotypes: GH!, K!, S!, US!).

Shrubs 10-25? dm; **stems** terete, soft brown, glabrous, herbaceous parts dark brown, sparsely tomentose to lanate, densely villous upwards toward the growing apex, trichomes white, multicellular, tapered, 1-1.5 mm long; **leaves** opposite, triplinerved, ovate or deltoid, adaxial surface dark greenish-gray and moderately to densely strigose-sericeous, trichomes white to hyaline, multicellular, tapered, 0.5-0.7 mm long, abaxial surface creamy greenish-white and moderately to densely villous-floccose, trichomes white, multicellular, tapered, 1-1.5 mm long; sessile glandular trichomes confined to abaxial surface 50-100/cm^2; **blades** 25-65 mm long, 25-50 mm wide, slightly smaller upwards toward capitulescence, apex acuminate, base obtuse or truncate, sometimes narrowly attenuate along distal fifth of petiole, margins

entire; petioles 8-30 mm long, slightly canaliculate, densely tomentose-villous adaxially, densely villous-lanate abaxially; **capitulescences** dichasial thyrsoid, with 2-20+ heads, peduncles 50-125 mm long, densely tomentose to densely villous-lanate under heads, trichomes as stem; **heads** 11.5-16.5 mm across, 12.5-20 mm high, hemispherical; **receptacles** 6.5-12 mm in diameter in fruit, flat to shallowly convex; **phyllaries** 25-37 in 4 graduated series, first series 7.5-9.5 mm long, 4-4.8 mm wide, ovate, base indurated, light green and glabrous adaxially, dark green and sparsely tomentose abaxially, herbaceous apex appressed, light green and sparsely strigose-hirsute adaxially, dark green and moderately hirsute or tomentose to villous abaxially, margins sparsely ciliate, second and third series 11.5-14 mm long, 5-6.5 mm wide, oval-oblong, base indurated, stramineous and glabrous adaxially, dark green and glabrescent to sparsely tomentose abaxially, herbaceous apex appressed, light green and sparsely strigose adaxially, dark green and sparsely villous abaxially, margins sparsely ciliate, fourth series 10.5-11 mm long, 3.3-3.6 mm wide, oblong, somewhat chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous with several dark green longitudinal bands of various width, bands coalescing at apex, glabrous adaxially, glabrescent to sparsely tomentose abaxially, margins glabrous to minutely ciliate; **pales** 10-12.5 mm long, 4.2-5.2 mm wide, broadly ovate, conduplicate, strongly keeled lengthwise, protruding 1-2 mm beyond the phyllaries, stramineous-copper, with several dark green longitudinal bands of various width, bands coalescing at apex,

glabrescent to glabrous abaxially, apex coriaceous, acute to acuminate, pointed, dark green or black; **ray flowers** 17-28, corolla bright yellow, sometimes apex blackish abaxially, limb 20-28 mm long, 5.2-7 mm long, lanceolate-oval, sparsely puberulent and glandular on veins of abaxial surface, apex acute, bifid, rarely trifid, tube 1.5-1.6 mm long, densely puberulent and glandular; **ray ovaries** 3.7-4 mm long, triquetrous, glabrous, pappus of 2-4 squamellae 0.3-0.5 mm long; **disk flowers** 75-230, flowers protruding 1-1.5 mm beyond pales, corollas golden yellow, narrowly campanulate to tubular, throat 4.3-4.7 mm long, 0.9-1.4 mm wide at base, 1.3-1.5 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, moderately puberulent especially at the base, with interspersed uni- and biseriate multicellular glandular trichomes 0.05-0.15 mm long, tapered trichomes white to hyaline, multicellular, 0.1-0.2 mm long, tube 1.6-1.8 mm long, greenish-yellow, sparsely to moderately puberulent and glandular, trichomes as throat, lobes 0.6-0.8 mm long, yellow, apices black abaxially, moderately puberulent and glandular abaxially; anthers 2.9-3.2 mm long, thecae black, appendages 0.5-0.6 mm long, lanceolate, stramineous-black; styles 6-6.6 mm long, style branches 1.3-1.6 mm long; **disk achenes** 4.3-4.6 mm long, 1.7-1.9 mm wide, biconvex, oval-obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.3-2.8 mm long; Chromosome number unknown.

Phenology. Probably flowering from January to May. Known only from the type which was collected late in the fruiting season in September.

Distribution (Fig. 38). Known only from the upper Huallaga River valley around the towns of Ambo and Tomay Kichwa in central Huánuco; 2500-2600 m.

This species is known only by the type collection. It can be recognized by its ovate to deltate leaves with entire margins, opposite phyllotaxy, monochasial to dichasial thyrsoid capitulescences and ovate to oblong, sparsely pubescent phyllaries reminiscent of those of P. lehmannii var. grandiceps. Blake (1926) mentioned its relationship to P. lehmannii var. grandiceps and to P. jelskii based on leaf and involucral characters. Pappobolus lehmannii var. grandiceps in many respects is very different from this species. Pappobolus lehmannii var. grandiceps possesses an alternate phyllotaxy, the leaves have serrulate to serrate margins and there are certain floral characters, such as ligule size, number and shape and disk achene and ray ovary size, which in P. lehmannii var. grandiceps tend to be larger. Pappobolus jelskii differs from P. acuminatus in many respects. Although P. jelskii shares with P. acuminatus an opposite phyllotaxy, the leaves are rugose, coriaceous and scabrous clearly contrasting with the softly pubescent and thin leaves of P. acuminatus. In addition, the phyllaries in P. jelskii are broad, reflexed, and densely lanate very different from the appressed, sparsely to moderately tomentose to villous or sometimes hirsute phyllaries of P. acuminatus.

15. Pappobolus cinerascens S. F. Blake, J. Wash. Acad. Sci. 16(8):223-224. 1926.——TYPE: PERU. Amazonas: Prov. Chachapoyas, 1836,

Mathews s. n. (lectotype, here designated: K!, fragment and photo: US!; isolectotypes: BM!, K!).

Open shrubs 5-25 dm tall; **stems** terete, brown, glabrous, herbaceous parts brownish-green and moderately tomentose to villous, trichomes hyaline or white, multicellular, tapered, 0.5-1.5 mm long; **leaves** opposite, triplinerved, ovate to lanceolate, adaxial surface dark green and strigose, trichomes white to hyaline, multicellular, tapered, 0.3-0.8 mm long, abaxial surface creamy light green to white and sparsely to moderately velutinous to somewhat villous, trichomes white or yellowish-green, multicellular, tapered, 0.5-1.3 mm long, pubescence along major veins moderately velutinous-sericeous; sessile glandular trichomes confined to abaxial surface 500-800/cm^2; **blades** 40-125 mm long, 15-65 mm wide, slightly smaller upwards toward the capitulescence, apex acuminate, base obtuse, sometimes slightly attenuate along upper fifth of petiole, margins subentire to shallowly serrulate; petioles 10-40 mm long, slightly canaliculate, moderately tomentose adaxially, moderately tomentose-villous abaxially; **capitulescences** dichasial, rarely monochasial thyrsoid, with 3-12+ heads, peduncles 90-145 mm long, tomentose to villous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 13.5-17.5 mm across, 13-15 mm high, hemispherical; **receptacles** 8-10.5 mm in diameter in fruit, slightly convex; **phyllaries** 35-44 in 4 subequal series, first and second series 10.5-11.5 mm long, 2.5-4.6 mm wide, oblanceolate or lanceolate, slightly constricted between indurated and herbaceous parts, base indurated, stramineous and glabrous adaxially,

dark green and sparsely tomentose abaxially, herbaceous apex somewhat foliaceous, reflexed and twisted, dark green and sparsely to moderately strigose adaxially, densely velutinous tp villous whitish-green abaxially, margins ciliate, third series 12.5-13 mm long, 4.8-5.2 mm wide, obovate to oblanceolate or lanceolate, base indurated, stramineous and glabrous adaxially, dark green and glabrescent to sparsely tomentose to villous abaxially, herbaceous apex reflexed and slightly twisted, dark green and sparsely to moderately strigose-hirsute adaxially, dark green and moderately villous abaxially, margins as previous series, fourth series 10-11 mm long, 3-3.5 mm wide, oblong, somewhat chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous with several dark green bands coalescing at apex and sparsely tomentose adaxially, dark green and sparsely tomentose abaxially; **pales** 9.5-10.5 mm long, 4.5-5.5 mm wide, broadly ovate, conduplicate, keeled lengthwise, covered by phyllaries, stramineous-copper, with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrescent or glabrous abaxially, apex coriaceous, acute or acuminate, pointed or slightly curved inward, dark green or black; **ray flowers** 19-28, corolla bright yellow, sometimes apex blackish abaxially, limb 14-35 mm long, 6.5-8 mm wide, oval or narrowly elliptical, sparsely puberulent and glandular on veins of abaxial surface, apex acute, bifid or trifid, tube 0.9-1.3 mm long, sparsely puberulent; **ray ovaries** 2.4-2.8 mm long, triquetrous, glabrous, pappus of 14-21 awns or 2-5 squamellae, awns 1-2 mm long, squamellae 0.3-0.5 mm long; **disk flowers** 95-225, flowers protruding 0.6-1 mm beyond pales, corollas greenish-yellow, campanulate, throat

4.5-5 mm long, 1.2-1.5 mm wide at base, 1.6-2 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely puberulent especially at the base, with uniseriate multicellular glandular trichomes 0.1 mm long, tapered trichomes hyaline to white, 0.15-0.2 mm long, tube 0.9-1.1 mm long, yellowish-green, glabrous or moderately puberulent, lobes 0.7-1.1 mm long, deltoid-lanceolate, yellow adaxially, black abaxially, sparsely to densely puberulent abaxially, anthers 2.5-3.2 mm long, thecae black, appendages 0.5 mm long, ovate, purplish-red or black; styles 6-6.5 mm long, style branches 1.5-1.8 mm long; **disk achenes** 3.5-4.2 mm long, 1.5-1.7 mm wide, biconvex, obovate, with diminutive shoulders, shiny black, glabrous, pappus of 2-28 awns, slender, stramineous, deciduous, subequal, 1.8-3 mm long; n = 17.

Phenology. Flowering January to June.

Distribution (Fig. 39). Wet, cloud forests south of the town of Leimebamba in Amazonas Department along the road to Balsas; 2800-2900 m.

SPECIMEN EXAMINED. PERU. AMAZONAS: 7 km S of Leimebamba on road to Balsas, at the point where the road meets the Utcubamba River, 2830 m, 23 Mar 1988, Panero 1357 (CPUN, F, GRI, LP, S, TENN, US).

Pappobolus cinerascens can be distinguished by its mostly dichasial thyrsoid capitulescence, disk achene pappus of several deciduous awns, and its involucre composed of heavily indurated phyllaries with strongly reflexed, herbaceous apices. Pappobolus

mollicomus and P. macranthus are the only species that share with P. cinerascens a similar disk pappus morphology (aside from P. decumbens and P. woodsonianus of the discolor group which, based on other morphological characters, appear to be distantly related to these species). Pappobolus mollicomus differs by its dense lanate-sericeous herbage pubescence and oblong and densely lanate phyllaries, although it shares with P. cinerascens conspicuously reflexed ray flower ligules. Pappobolus macranthus can be distinguished from P. cinerascens by its larger involucre, longer ray flower ligules, and pales with an acute to rounded apex.

Pappobolus cinerascens appears to be the only species of the genus encountered in wet forests. The dense, lush and wet forest south of Leimebamba contrasts with the tropical deciduous, xerophytic or moist forests where many of the species of the genus are encountered. Pappobolus cinerascens tends to grow in a straggly, open fashion within the vegetation mass, and the only evidence of its presence are the flowering shoots which develop above the dense vegetation. A few individuals were observed growing on vertical cliffs where they attained a more shrubby, dense habit.

Specimen Panero 1357 differs from the type collection only by having considerably larger, broadly ovate leaves. The head and other floral characters are essentially identical.

16. Pappobolus mollicomus S. F. Blake, Contr. Gray Herb. 52:49-50. 1917.——TYPE: PERU. Amazonas: Prov. Chachapoyas, 1836, Mathews

s. n. (lectotype, here designated: BM!; isolectotypes: GH(2)!, K(2)!).

Open shrubs 10-25 dm tall; **stems** terete, brown, glabrous, herbaceous parts moderately tomentose to lanate white, trichomes hyaline or white, multicellular, tapered, 1.5-3.5 mm long; **leaves** opposite or alternate, triplinerved, lanceolate to elliptical, adaxial surface dark green and strigose, trichomes white to hyaline, multicellular, tapered, 0.5-1.2 mm long, abaxial surface creamy light green to white and moderately to densely villous to lanate, trichomes white, multicellular, tapered, 0.7-1.3 mm long, pubescence along major veins densely velutinous-sericeous; sessile glandular trichomes confined to abaxial surface 200-300/cm^2; **blades** 40-95 mm long, 20-40 mm wide, slightly smaller upwards toward the capitulescence, apex acuminate, base decurrent, margins subentire to shallowly serrulate; petioles 5-30 mm long, slightly canaliculate, densely tomentose adaxially, densely lanate abaxially; **capitulescences** monochasial thyrsoid, with 1-12+ heads, peduncles 35-115 mm long, villous, pubescence denser below the heads, trichomes as stem; **heads** 15.5-21 mm across, 10-14.5 mm high, hemispherical; **receptacles** 6.5-9 mm in diameter in fruit, shallowly convex; **phyllaries** 31-40 in 4 graduated series, first and second series 11-16 mm long, 2.5-3.2 mm wide, lanceolate, sometimes slightly constricted between indurated and herbaceous parts, base indurated, stramineous and glabrous adaxially, densely lanate white abaxially, herbaceous apex somewhat foliaceous, reflexed and twisted, dark green and sparsely to moderately strigose

adaxially, densely lanate white abaxially, margins velutinous, third series 10-13 mm long, 3-3.5 mm wide, lanceolate, base indurated, stramineous and glabrous adaxially, dark green and glabrescent to sparsely villous abaxially, herbaceous apex slightly reflexed or appressed, dark green and sparsely to moderately strigose-hirsute adaxially, dark green and moderately to densely velutinous abaxially, margins as previous series, fourth series 7.5-9.5 mm long, 1.6-2.3 mm wide, oblong, somewhat chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous with several dark green bands coalescing at apex and glabrous adaxially, glabrescent to tomentose abaxially; **pales** 7.5-8 mm long, 2.6-3 mm wide, broadly ovate, conduplicate, keeled lengthwise, covered by phyllaries, stramineous-copper, with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrescent or glabrous abaxially, apex coriaceous, acute, pointed or slightly curved inward, dark green or black; **ray flowers** 19-23, corolla bright yellow, sometimes apex blackish abaxially, limb 15-23 mm long, 5-6.5 mm wide, narrowly oval, sparsely puberulent and glandular on veins of abaxial surface, apex acute, bifid or trifid, tube 0.9-1.3 mm long, moderately puberulent; **ray ovaries** 2.8-3.3 mm long, triquetrous, glabrous, pappus of (2-) 3-5 awns, 0.8-1.6 mm long; **disk flowers** 125-225, flowers protruding 0.6-1 mm beyond pales, corollas golden yellow, narrowly campanulate, throat 4.5-5 mm long, 0.9-1.2 mm wide at base, 1.4-1.6 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely puberulent especially at the base, with uniseriate multicellular glandular trichomes 0.1 mm long, tapered trichomes

hyaline to white, 0.15-0.2 mm long, tube 0.9-1.1 mm long, yellowish-green, glabrous, lobes 0.7-1.1 mm long, deltoid-lanceolate, yellow adaxially, black abaxially, densely puberulent abaxially, anthers 2.3-2.5 mm long, thecae black, appendages 0.3-0.5 mm long, ovate, stramineous; styles 5-5.5 mm long, style branches 1.5-1.8 mm long; **disk achenes** 3.2-3.7 mm long, 1.3-1.6 mm wide, biconvex, obovate, with diminutive shoulders, shiny black, glabrous, pappus of (2-) 3-8 awns, slender, stramineous, deciduous, subequal 1.3-2.5 mm long; Chromosome number unknown. Fig. 40.

Phenology. Flowering November, probably through April.

Distribution (Fig. 39). Probably growing in moist forest of the Provinces of Luya and Chachapoyas in central Amazonas Department; 2500-2800 m.

Vernacular Name. "Monte Plomo" (Lead weed; fide Cevasco 13391). The word Monte is used to describe useless plants (i.e. those with no commercial or curative uses) by the native people of the farm regions of many of the countries of Latin America. For that reason I translated Monte as weed to convey to the reader the disdain by the locals for this and many other "useless" plants of the forest. I believe that lead is used here to stress the silvery white-greenish color of the herbage of this species.

SPECIMEN EXAMINED. PERU. AMAZONAS: Luya, Hacienda Shañi, Nov 1943, Cevasco 13391 (USM).

Pappobolus mollicomus is apparently restricted to a very small

area of the province of Luya in Amazonas Department. According to label data from the representative specimen this species appears to be common at the collection site.

Pappobolus mollicomus can be easily recognized by its densely velutinous to lanate leaf abaxial surfaces and phyllaries. Another distinguishing character is the presence of several awns in the pappus of the disk achenes and ray ovaries. It is closely related to P. cinerascens and P. macranthus with which it shares a similar pappus structure, although superficially it is very similar to densely pubescent forms of P. lehmannii of central Ecuador. This species, like P. cinerascens, has reflexed and somewhat small ray flowers.

17. Pappobolus macranthus S. F. Blake, Hooker's Icon. Pl. 31:1-2. 1916.——TYPE: PERU. Huánuco: Muña, 2135-2440 m, May 1863, Pearce 121 (holotype: K!, photo and fragment ex K at GH!).

Open shrubs 10-30 dm tall; **stems** terete, brown, glabrous, herbaceous parts brownish-green and sparsely to moderately tomentose to villous, trichomes hyaline or white, multicellular, tapered, 0.5-1.5 mm long; **leaves** opposite or alternate, triplinerved, ovate to lanceolate, adaxial surface dark green and strigose, trichomes white to hyaline, multicellular, tapered, 0.3-0.8 mm long, abaxial surface creamy light green to brownish-green and sparsely to moderately velutinous to somewhat velutinous-sericeous, trichomes white or whitish-green, multicellular, tapered, 0.5-1.3 mm long, pubescence along major veins moderately velutinous-sericeous; sessile glandular trichomes confined

to abaxial surface 50-3000/cm^2; **blades** 35-160 mm long, 10-80 mm wide, slightly smaller upwards toward the capitulescence, apex acuminate, base obtuse, sometimes slightly attenuate and cuneately narrowed along distal fourth of petiole, margins serrate; petioles 15-50 mm long, slightly canaliculate, moderately tomentose-velutinous adaxially, moderately to densely tomentose-villous abaxially; **capitulescences** monochasial thyrsoid, with 3-7+ heads, peduncles 50-110 mm long, sparsely tomentose to moderately villous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 19-25 mm across, 12-21 mm high, hemispherical; **receptacles** 9.5-13 mm in diameter in fruit, slightly convex; **phyllaries** 38-62 in 4-5 subequal series, first, second, third and fourth series 17-30 mm long, 3.5-5.5 mm wide, lanceolate, base indurated, stramineous and glabrous adaxially, dark green and sparsely tomentose or glabrous abaxially, herbaceous apex, reflexed and twisted, dark green and sparsely to moderately strigose adaxially, densely velutinous-sericeous whitish-green or sparsely tomentose dark green abaxially, margins glabrous to sparsely ciliate, fifth series, 12-14 mm long, 2.5-3 mm wide, oblong-lanceolate, somewhat chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous or stramineous, with several dark green bands coalescing at apex and sparsely tomentose adaxially, dark green and sparsely tomentose abaxially; **pales** 9-10.5 mm long, 3-3.2 mm wide, ovate, conduplicate, keeled lengthwise, covered or protruding 1-3 mm beyond phyllaries, stramineous-copper, with several dark green or brown longitudinal bands of various width, bands coalescing at apex, or dark green and glabrescent or glabrous abaxially, apex coriaceous, acute to

rounded or acuminate, pointed or slightly curved inward, dark green or black; **ray flowers** 20-32, corolla bright yellow, sometimes apex blackish abaxially, limb 20-30 mm long, 5.8-7 mm wide, oval or narrowly elliptical, sparsely puberulent and glandular on veins of abaxial surface, apex acute, trifid, tube 2-2.2 mm long, sparsely puberulent; **ray ovaries** 3.3-3.6 mm long, triquetrous, glabrous, pappus of 10-16 awns 1-1.8 mm long; **disk flowers** 150-325, flowers protruding 1-1.5 mm beyond pales, corollas bright yellow, campanulate, throat 4.5-5 mm long, 1.2-1.3 mm wide at base, 1.5-1.6 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely puberulent, trichomes hyaline to white, 0.15-0.2 mm long, tube 1.4-1.6 mm long, greenish-yellow and glabrous, lobes 0.8-1.2 mm long, deltoid-lanceolate, yellow adaxially, black abaxially, sparsely puberulent abaxially, anthers 2.5-3.2 mm long, thecae black, appendages 0.5 mm long, ovate, stramineous; styles 7-7.5 mm long, style branches 1.5-1.9 mm long; **disk achenes** 3.9-4.2 mm long, 1.7-2 mm wide, biconvex, obovate, with diminutive shoulders, shiny black, glabrous, pappus of 10-25 awns, slender, stramineous, deciduous, subequal 1.8-3 mm long; Chromosome number unknown. Fig. 41.

Phenology. Flowering February to July.

Distribution. (Fig. 39). Headwaters of the Huallaga River NE of the city of Huánuco. Also around the city of Huacapistana along the Palca River of central Junín; 2100-2950 m.

SPECIMENS EXAMINED. PERU. HUANUCO: Pillao, anywhere in open sunny places, in hedges, 2700 m, 17 Feb 1946, Woytkowski 34133a (F, MO, LIL,

UC, US); Chaglla, 9000 ft, 12 May 1923, Macbride 3646 (F, GH, US); Mito, 9000 ft, 8-22 Jul 1922, Macbride & Featherstone 1384 (F, GH, US).—JUNIN: Huacapistana, 5 Feb 1940, Woytkowski 2 (US).

Pappobolus macranthus produces very large heads reminiscent, when dried, of heads of Helianthus strumosus L. and closely related species of North America. The large heads and long, lanceolate, reflexed phyllaries coupled with the numerous awns on the disk achene and ray ovary are a unique combination within the genus. Based on achenial characters it appears to be related to P. cinerascens and P. mollicomus (see under P. cinerascens for distinguishing features of these three species).

According to various label data this taxon appears to be very common in the collection sites of the Department of Huánuco. A single collection from Junín Department suggests a potentially wider geographical distribution. This last specimen, Woytkowski 2, is more pubescent than the other collections and the leaves are not as serrated (another collection labeled as Woytkowski 2 from the area of Celendín is Viguiera aff. procumbens and not a Pappobolus).

18. Pappobolus sanchezii Panero, sp. nov.——TYPE: PERU, Cajamarca: Km 154.8 of the road Pacasmayo-Cajamarca, then 1 km by foot along a narrow trail bordering the river gorge, 3040 m, 9 Mar 1988, Panero 1195 (holotype F!; isotypes: B!, C!, CAN!, COL!, CPUN!, GRI!, HUT!, K!, LE!, LIL!, MA!, MEXU!, MICH!, NY!, QCA!, RB!, S!, SI!, TENN!, TEX!, U!, UC!, US!).

Pappobolus sanchezii differt a P. schillingii. Habet reflexa et foliosa exteriora phyllaria, ovata folia et ochreoviridem pubescentiam herbarum.

Monocaulic shrubs or small trees 10-35 dm tall; **stems** terete, brownish-gray, glabrous, herbaceous parts dark brown and sparsely villous becoming densely villous toward growing apex or below heads, trichomes white, multicellular, tapered, 0.6-2 mm long; **leaves** opposite, triplinerved, ovate, adaxial surface dull dark green and strigose, trichomes white to slightly greenish, multicellular, tapered, 0.4-0.65 mm long, moniliform trichomes restricted to veins, arched, tan-brown, multicellular, apical cell rounded, 0.5-0.1 mm long, abaxial surface soft green and moderately villous to floccose, trichomes white to light green or yellowish-green, multicellular, tapered, 0.4-0.9 mm long, moniliform trichomes similar in size, morphology and distribution to those of adaxial surface, veins densely villous to lanate; sessile glandular trichomes confined to the abaxial surface, 1700-2000/cm^2; **blades** 35-130 mm long, 10-90 mm wide, similar in size and morphology throughout stem and capitulescence, apex acuminate, base obtuse sometimes slightly attenuate, margins serrulate; petioles 15-40 mm long, somewhat canaliculate, glabrescent adaxially, sparsely villous to tomentose abaxially; **capitulescences** simple dichasia, dichasial or monochasial thyrsoid, with 1-15+ heads, peduncles 25-110 mm long, sparsely to densely villous, pubescence conspicuously denser below the heads, trichomes as stem; **heads** 17-23 mm across, 15.5-18.3 mm high, hemispherical; **receptacles** 10-15.2 mm in diameter in fruit, slightly

convex; **phyllaries** 28-38 in 4 graduated series, first series 19-60 mm long, 7-19 mm wide, lanceolate to oblanceolate, constricted between indurated and herbaceous parts, base strongly indurated, light green and glabrous adaxially, dark green or blackish and sparsely villous to floccose abaxially, herbaceous apex spreading, sometimes foliaceous, wider than base, light to dark green and sparsely hirsute adaxially, creamy green and villous abaxially, margins villous, second series 16.5-21 mm long, 4.5-6.1 mm wide, similar in shape to first series but smaller and somewhat less pubescent, pubescence restricted to distal herbaceous portion, margins villous, third series 15-17.5 mm long, 3-5 mm wide, ovate, base indurated, stramineous and glabrous adaxially, dark green and glabrous abaxially, herbaceous part slightly reflexed, color and pubescence as previous series, margins tomentose, fourth series 6-12 mm long, 3-5 mm wide, lanceolate, and normally covered by outer phyllaries, chartaceous, with no herbaceous part, stramineous adaxially, dark greenish-black abaxially, essentially glabrous on both surfaces, margins glabrescent to tomentose; **pales** 8.7-9.1 mm long, 4.8-5.3 mm wide, ovate, conduplicate, keeled lengthwise, covered by phyllaries, stramineous-copper with a few dark green longitudinal bands of various width, bands coalescing at apex, glabrous abaxially, apex coriaceous, rounded, pointed or slightly curved inward, dark greenish-black; **ray flowers** 14-21, corolla golden yellow, limb 22-32 mm long, 8.5-11 mm wide, oval-lanceolate, sparsely to moderately puberulent on veins of abaxial surface, apex acute, bifid or trifid, tube 1.1-2.5 mm long, sparsely puberulent; **ray ovaries** 2.4-3 mm long, biconvex or

triquetrous, glabrous, epappose or with 2-5 squamellae, 0.2-0.5 mm long; **disk flowers** 90-180, flowers protruding 1-1.3 mm beyond pales, corollas yellow sometimes distal portion and lobes black, narrowly campanulate to lyrate, throat 3.8-5.2 mm long, 1.2-1.8 mm wide at base, 1.1-1.4 mm wide at junction with lobes, veins orange sometimes discernable the whole length of the corolla, essentially glabrous, tube 0.8-1.3 mm long, yellow, pubescent, lobes 0.8-1.3 mm long, deltoid, yellow, black abaxially, sparsely puberulent to glabrous abaxially; anthers 2.4-3.3 mm long, thecae yellowish-brown to black, appendages 0.4-0.7 mm long, lanceolate, stramineous, sometimes rimmed with black; styles 5.8-7.5 mm long, style branches 1.6-2.5 mm long; **disk achenes** 3.8-4.7 mm long, 1.5-2 mm wide, biconvex, obovate, with diminutive shoulders, shiny black or dark gray, rarely mottled, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal 3.8-4.8 mm long; n = 17. Fig. 42.

Phenology. Flowering March through June; major floral display early in the flowering season.

Distribution (Fig. 43). Known only from the cloud forests at the headwaters of the Chicama and Jequetepeque River systems of southwestern Cajamarca, Peru. Growing on steep canyons interspersed in the thick shrubbery with shrubby or arborescent Baccharis, Begonia, Llagunoa nitida, Monactis, several Myrtaceae, Oreocallis grandiflora R. Br., Perymenium bishopii H. Robinson, Pineda incana Ruiz & Pav., Sebastiania obtusifolia Pax & K. Hoffm., and Puya; 2900-3100 m.

SPECIMENS EXAMINED. PERU. CAJAMARCA: sobre el km 156 de la carretera

Pacasmayo-Cajamarca, 2900 m, 5 Abr 1982, Sánchez Vega 2756 (CPUN, F); surroundings of Cajamarca, 2700-3700 m, 21 May 1986, Becker & Terrones 1211 (US); Sunchubamba, Chicama River valley, 3100 m, 3 Jun 1957, Ellenberg 1767 (U).

Pappobolus sanchezii is one of the most attractive species of the genus. The tree-like habit, large heads and large number of capitulescences come together to create an impressive floral display reminiscent of the members of Viguiera sect. Maculatae (Panero & Schilling, 1988) of Mexico. In the area of Cajamarca, this species grows along steep river canyons where the original vegetation still survives. I did not observe any individual established in the man-made disturbed areas surrounding these vegetation pockets. The accelerated destruction of the vegetation clinging to these deep ravines and the apparent inability of this species to exploit disturbed areas surely paint a bleak picture for the survival of this species, at least in this area.

Pappobolus sanchezii can be distinguished by its large heads, mostly dichasial thyrsoid capitulescences, and strongly foliose involucre. It shares with P. schillingii a somewhat similar involucre morphology (see discussion under P. schillingii). The immature heads are reminiscent of those of P. robinsonii; both are round with reflexed outer phyllaries in the shape of a miniature, open rose. Pappobolus sanchezii also shares with P. robinsonii a similar leaf shape and foliar pubescence.

On the other hand, the gestalt of this species is somewhat

intermediate between P. amoenus and lower altitude forms of P. jelskii. Pappobolus amoenus grows in the same river canyon as P. sanchezii but 300-400 m below. Superficially both species are very similar, but P. amoenus can be distinguished by its reflexed ray flowers, less foliaceous and strongly urceolate involucres (a character only evident in live or pickled material), and a deltate to ovate leaf shape. In addition P. amoenus tends to be ruderal and apparently better adapted to cope with human and natural disturbance (see under P. amoenus). Pappobolus jelskii, although being a well-circumscribed and readily recognizable species, has lower altitude forms that exhibit larger leaves and less pubescence in its herbage which are reminiscent of P. sanchezii. These forms, centered between the towns of Hualgayoc and Bambamarca in central Cajamarca, can be easily separated by the creamy stramineous color of their pale apices and the consistently lanate herbaceous stems and peduncles which are never present in P. sanchezii.

Pappobolus sanchezii is named after Dr. Isidoro Sánchez Vega, chairman of the Botany Department at the Universidad Nacional Técnica de Cajamarca. His contagious and indefatigable passion for the botanical exploration of northern Peru and especially the department of Cajamarca were a constant source of encouragement and knowledge. His hospitality, comments and optimism helped me enormously in my Peruvian collecting efforts. If not for his efforts the northern Peru chapter of this investigation would not have been possible.

19. Pappobolus youngiorum Panero, sp. nov.——TYPE: La Libertad: Prov.

Patáz, along trail from Yalen to Los Alisos, 2800-3300 m, 21 Feb 1986, Young 2936 (holotype F!; isotype: TENN!).

Pappobolus youngiorum differt ab P. schillingii. Habet angustiora phyllaria, ovata folia et maiores radiales flores.

Monocaulic shrubs 7-25 dm tall; **stems** terete, dark brown and glabrous, herbaceous parts greenish-brown and sparsely to moderately hirsute to villous, trichomes white or hyaline, multicellular, tapered, 0.8-3 mm long; **leaves** opposite, triplinerved, ovate, adaxial surface light to dark dull green and sparsely to moderately strigose, trichomes white to hyaline, multicellular, tapered, 0.4-0.8 mm long, moniliform trichomes restricted to veins, arched, tan-brown, multicellular, apical cell rounded, 0.05-0.1 mm long, abaxial surface creamy white-green to white and moderately velutinous to sericeous, trichomes white, multicellular, tapered, 0.4-0.9 mm long, moniliform trichomes similar in size, morphology and distribution to those of abaxial surface, pubescence along major sparsely villous; sessile glandular trichomes confined to abaxial surface 1200-1500/cm^2; **blades** 32-110 mm long, 16-55 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse, sometimes narrowly attenuate along distal fourth of petiole, margins entire to serrulate; petioles 5-22 mm long, slightly canaliculate, puberulent adaxially, densely velutinous abaxially; **capitulescences** monochasial or dichasial thyrsoid, with 3-18+ heads, peduncles 45-130 mm long, hirsute-velutinous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 16-19.5 mm across, 14-18 mm high, hemispherical; **receptacles** 11.5-15.5 mm in diameter in

fruit, slightly convex; **phyllaries** 29-40 in 4 subequal series, first and second series 12-15 mm long, 3.5-5 mm wide, lanceolate, base indurated, stramineous and glabrous adaxially, light green and moderately tomentose to velutinous abaxially, herbaceous apex somewhat foliaceous, reflexed and twisted, greenish-brown and sparsely to moderately strigose adaxially, moderately velutinous or villous whitish-green abaxially, margins ciliate, third series 14-20 mm long, 3.8-4.4 mm wide, lanceolate, base indurated, stramineous and glabrous adaxially, stramineous with dark green longitudinal bands and glabrescent to sparsely tomentose abaxially, herbaceous apex reflexed and slightly twisted, dark green and sparsely villous to velutinous or tomentose adaxially, dark green and moderately hirsute abaxially, margins as previous series, fourth series 10-11 mm long, 3-3.5 mm wide, oblong, somewhat chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous with several dark green bands coalescing at apex and sparsely tomentose adaxially, dark green and sparsely tomentose abaxially; **pales** 6.5-10 mm long, 3.5-5 mm wide, ovate, conduplicate, keeled lengthwise, protruding 1-2 mm beyond phyllaries, stramineous, with several dark green or brown longitudinal bands of various width, bands coalescing at apex, sparsely tomentose abaxially especially along fold, apex coriaceous, acute to somewhat rounded, pointed, dark green or black; **ray flowers** 19-28, corolla bright yellow, sometimes apex blackish abaxially, limb 20-33 mm long, 5-7.5 mm wide, oval, sparsely puberulent and glandular on veins of abaxial surface, apex acute or rounded, bifid, tube 1.3-1.8 mm long, puberulent; **ray ovaries** 0.3-0.5 mm long, glabrous, pappus of 2-5

squamellae, 1.2-1.5 mm long; **disk flowers** 125-245, flowers protruding 0.5-2 mm beyond pales, corollas golden yellow, campanulate, throat 4-5 mm long, 1.3-1.6 mm wide at base and at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely to moderately puberulent especially at the base, with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.15-0.3 mm long, tube 1.2-1.4 mm long, yellowish-green, glabrous, lobes 0.6-0.9 mm long, deltoid-lanceolate, black abaxially, sparsely puberulent abaxially; anthers 2.5-3.2 mm long, thecae black, appendages 0.3-0.4 mm long, ovate, black; styles 6.5-7 mm long, style branches 1.0-1.3 mm long; **disk achenes** 3.5-4.5 mm long, 1.3-1.7 mm wide, biconvex, obovate, with diminutive shoulders, shiny grayish-black or black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2-3 mm long; Chromosome number unknown.

Phenology. Flowering January to July.

Distribution (Fig. 43). Tropical deciduous to cloud forests of the eastern range of the Andes bordering the canyon of the Marañón River; 2000-3300 m.

SPECIMENS EXAMINED. PERU. AMAZONAS: 38-41 km NE of Balsas on road to Chachapoyas, 2700-2800 m, 5 Jan 1979, Dillon & Turner 1715 (F); 25 km E of Balsas on road to Leimebamba, 2080 m, 17 Jun 1978, Gentry et al. 23129 (F).

This species shares with P. schillingii of southern Ecuador and

northern Peru some important characters (see discussion under P. schillingii). It can be recognized by its ovate leaves, reflexed phyllaries and large heads with long ray flowers reminiscent of those of P. macranthus.

Ken Young and Blanca León, collectors of the type specimen, describe (in litt.) this taxon as rare. Their attempts to relocate and collect this species were unsuccessful, and apparently the individual from which the type specimen was collected has disappeared. I tried unsuccessfully to locate this species above the town of Balsas.

In the type locality this plant grows in forests similar in floristic composition to those of the headwaters of the Pacific drainage rivers of Cajamarca Department. Other plants listed (in litt.) by Ken Young and Blanca León growing in the type locality include: Alnus acuminata H. B. K., Bocconia integrifolia Humb. & Bonpl., Buddleja bullata H. B. K., B. incana Ruiz & Pav., Cacosmia rugosa H. B. K., Caesalpinea tinctoria DC., Calceolaria, Delostoma, Dodonaea viscosa Jacq., Euphorbia laurifolia Lam., Ephedra americana Willd., Hesperomeles, Llagunoa nitida, Lomatia hirsuta (Lam.) Diels, Myrsine manglilla R. Br., Oreocallis grandiflora, Pineda incana, Polymnia glabrata DC., Prunus huantensis Pilger, Randia boliviana Rusby, Satureja sericea Briq., S. weberbauerii Mansfeld, Sebastiania obtusifolia, Solanum glutinosum Dun., Tecoma stans Juss., and Vallea stipularis L.

The species name honors the collectors Ken Young and his wife Blanca León or "The Youngs" as they are know in Peru to friends and botanists. The collections that he and his wife have made have greatly

increased the knowledge of the flora of Parque Nacional Río Abiseo and surrounding areas and will serve as an invaluable reference for biogeographical and floristic studies of the eastern Peruvian Andes and of Peru itself. Their friendship, courage, advice and love for nature were a constant source of inspiration in my collecting trips.

20. Pappobolus schillingii Panero, sp. nov.——TYPE: ECUADOR. Loja: 25 km S of Catamayo on road to Cariamanga, 2300 m, 5 Jul 1988, Panero 1472 (holotype: QCA!; isotypes: AAU!, F!, GRI!, MA!, MEXU!, QCNE!, SI!, TENN!, US!).

Pappobolus schillingii ab P. youngiorum. Habet maiora interiora phyllaria cum constrictis herbaceis apicibus, deltatis foliis cum floccosis et lanatis abaxialibus paginis et longioribus pedunculis.

Monocaulic shrubs 10-25 dm tall; **stems** terete, dark brown and glabrous, herbaceous parts greenish-brown and sparsely to moderately hirsute to villous, trichomes white or hyaline, multicellular, tapered, 0.5-2.2 mm long; **leaves** opposite, triplinerved, ovate to deltate, adaxial surface light to dark dull green and sparsely to moderately hirsute or strigose, trichomes white to hyaline, multicellular, tapered, 0.3-0.65 mm long, moniliform trichomes restricted to veins, arched, tan-brown, multicellular, apical cell rounded, 0.05-0.1 mm long, abaxial surface creamy white-green to white and densely villous to floccose, trichomes white, multicellular, tapered, 0.4-0.9 mm long, moniliform trichomes similar in size, morphology and distribution to those of abaxial surface, pubescence along major veins densely villous

to lanate; sessile glandular trichomes confined to abaxial surface 1200-1500/cm^2; **blades** 28-130 mm long, 9-80 mm wide, similar in size and morphology throughout stem and capitulescence, apex acuminate, base obtuse or truncate, margins serrulate to serrate; petioles 5-36 mm long, slightly canaliculate, puberulent adaxially, densely villous abaxially; **capitulescences** monochasial thyrsoid, with 3-12+ heads, peduncles 30-200 mm, hirsute-villous, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 12-20.5 mm across, 12.5-17.5 mm high, hemispherical; **receptacles** 9.5-14.5 mm in diameter in fruit, slightly convex; **phyllaries** 30-38 in 4 graduated series, first series 12-18.5 mm long, 3-5 mm wide, lanceolate to oblanceolate, sometimes constricted between indurated and herbaceous parts, base indurated, light green and glabrous adaxially, sparsely to densely villous dark green to blackish or white abaxially, herbaceous apex spreading, foliaceous, light to blackish-green and hirsute to strigose or glabrous adaxially, white villous or blackish-green and glabrous to densely villous abaxially, margins densely ciliate, second series 12.5-20.5 mm long, 3-5 mm wide, lanceolate-oblong or oblanceolate, strongly constricted between indurated and herbaceous parts, spreading, foliaceous, base indurated, dark green and glabrous adaxially, dark green and puberulent abaxially, herbaceous apex conspicuously wider than base, dark green drying black and puberulent or glabrous on both sides, margins moderately villous, third series 14.5-21 mm long, 2.8-4 mm wide, lanceolate-oblong, base slightly indurated, stramineous and glabrous adaxially, stramineous with dark green longitudinal bands and

glabrous abaxially, herbaceous apex dark green drying black, glabrous on both sides, margins puberulent, fourth series 10-18.5 mm long, 1.8-3.5 mm wide, oblong, lanceolate, chartaceous, with no clear distinction between indurated and herbaceous parts, stramineous with several dark green bands coalescing at apex, glabrous on both sides, margins glabrous; **pales** 6.3-10 mm long, 3-6.5 mm wide, lanceolate to broadly ovate, conduplicate, keeled lengthwise, rarely protruding beyond phyllaries, stramineous, with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrescent abaxially, apex coriaceous, acute to somewhat rounded, pointed or slightly curved inward, dark green or black; **ray flowers** 15-24, corolla bright yellow, sometimes apex blackish abaxially, limb 12-20 mm long, 6-8.2 mm wide, lanceolate, oval to suborbicular, sparsely puberulent and glandular on veins of abaxial surface, apex acute or rounded, bifid, tube 1.6-2.8 mm long, basal half glabrous, distal half puberulent; **ray ovaries** 3.4-4 mm long, triquetrous, glabrous, pappus of 1 awn 1.2-1.5 mm long; **disk flowers** 110-200, flowers protruding 0.5-2 mm beyond pales, corollas golden yellow, narrowly lyrate, throat 3-5 mm long, 1.2-1.5 mm wide at base, 0.9-1.6 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely to moderately puberulent especially at the base, with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.15-0.3 mm long, tube 1.2-1.6 mm long, light yellowish-green, glabrous, lobes 0.5-0.9 mm long, deltoid-lanceolate, yellow, sometimes black abaxially, sparsely puberulent abaxially; anthers 2.3-3 mm long, thecae black, appendages 0.3-0.4 mm

long, ovate, stramineous-orange; styles 4.8-6.5 mm long, style branches 1.5-1.6 mm long; **disk achenes** 3.3-4.3 mm long, 1.3-1.7 mm wide, biconvex, obovate, with diminutive shoulders, shiny grayish-black or black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2-3 mm long; n = 17.

Phenology. Flowering in May to August.

Distribution (Fig. 43). Montane dry and moist forests along the canyons of the Pacific drainage rivers of southern and central Loja Province, Ecuador and Piura Department in adjacent Peru. Also growing along the headwaters of the Río Zamora around the City of Loja; 2000-2600 m.

SPECIMENS EXAMINED. ECUADOR. LOJA: Argelia, 4 km al S de Loja, 2300 m, 18 Jun 1947, Espinosa 1533 (F); 5 km S of Catamayo on road to Cariamanga, 2300 m, 5 Jul 1988, Panero 1471 (TENN); 29 km N of Loja along the road to Cuenca, 2480 m, 3 Jul 1988, Panero 1446 (TENN); 1 km S of the Universidad Nacional de Loja on road to Vilcabamba, 2210 m, 4 Jul 1988, Panero 1450 (CPUN, F, GRI, QCA, QCNE, TENN, US); 5 km S of the Universidad Nacional de Loja on road to Vilcabamba, 2400 m, 4 Jul 1988, Panero 1456 (TENN); eastern slopes of Cerro Villanaco, 2500-2600 m, 12 Apr 1974, Harling & Andersson 13440 (AAU); 28 km N of Loja along the road Oña-Cuenca, 2480 m, 3 Jul 1988, Panero 1445 (AAU, GRI, MEXU, MICH, QCA, QCNE, TENN, US); 27 km N of Loja on road to Oña-Cuenca, 2480 m, 3 Jul 1988, Panero 1447 (QCA, TENN); 14 km S of Vilcabamba on road to Yangana, 1980 m, 6 Jul 1988, Panero 1477 (AAU, CPUN, GRI, MA, MEXU, QCA, QCNE, S, TENN, US) distribute); 16 km S of Vilcabamba on road to

Yangana, 2080 m, 6 Jul 1988, Panero 1478 (B, CAN, COL, F, GRI, LE, RB, SI, UC).—PERU. PIURA: Prov. Ayabaca, Yacupampa, borde del camino, 26 May 1971, 2650 m, López et al. 7787 (HUT).

Pappobolus schillingii can be distinguished by its sparsely to moderately lanate-floccose foliar pubescence, long peduncles, large and foliose involucre with dark green to black inner phyllaries, which are conspicuously constricted between their indurated and herbaceous parts. Another useful character to distinguish this species is the deltate leaf with a truncate base observed in a few populations of this species, but rarely seen in any other species of the genus.

Several of the distinguishing morphological features of this species are shared by P. youngiorum of La Libertad and Amazonas Departments of northern Peru. Both species have a similar phyllary morphology, although P. youngiorum has markedly narrower inner phyllaries. In addition, P. youngiorum also exhibits a mostly dichasial thyrsoid capitulescence which is not seen in P. schillingii despite its opposite phyllotaxy. Another important distinguishing feature is that the leaves of P. youngiorum tend to have obtuse bases and are not floccose as in P. schillingii. On the other hand, the large foliose involucre exhibited by some populations of P. schillingii is reminiscent of individuals of P. sanchezii of Cajamarca Department with which it shares a similar foliar pubescence. However, the pubescence in P. sanchezii is always tan or yellowish-green as opposed to the white pubescence of P. schillingii. The immature heads are also a source of important characters to separate these two species. P.

schillingii has oval, dark green to black immature heads while P. sanchezii has densely pubescent, rounded heads with reflexed, herbaceous phyllary apices similar to those of P. robinsonii.

This species grows sporadically in a few isolated ranges and mountaintops of the Province of Loja. The apparent geographical isolation between populations may be responsible for a myriad of subtle morphological differences which for this study were encompassed under one broader species concept. Panero 1450 and 1456 exhibit densely pubescent outer phyllaries, narrowly lyrate disk corollas and ovate, rarely deltate leaves. In the case of the type collection collected just north of Gonzanamá the phyllaries are markedly less pubescent and the disk corollas more tubular in outline, and the leaves tend to be deltate with truncate bases. This leaf morphology also occurs in the only Peruvian collection. Another interesting combination of key morphological characters is exhibited by the scattered individuals I found around the town of Yangana. These individuals exhibit significantly smaller heads and leaves and grow in slightly drier areas. However, one individual in this area growing in a wet streambank had dramatically larger leaves and heads identical to those of the type collection. Environmental conditions can apparently influence certain key morphological features of this species.

The species name honors my advisor, Edward E. Schilling.

21. Pappobolus amoenus Panero, sp. nov.——TYPE: PERU. Cajamarca: 2-3 km by foot along trail to Yumagual thermal baths, (off the road

Pacasmayo-Cajamarca), 2620 m, 8 Mar 1988, Panero & Sánchez Vega 1156 (holotype: F!; isotypes: CPUN!, GRI!, HUT!, K!, SI!, TENN!, UC!, US!).

Pappobolus amoenus differt ab P. sanchezii. Habet hemisphaerica vel urceolata capita in longis pedunculis et minora appressa phyllaria.

Much-branched shrubs 10-25 dm tall; **stems** terete, dark brown, glabrous, herbaceous parts greenish-brown, glabrous to sparsely tomentose, trichomes white to hyaline, multicellular, tapered, 0.2-0.4 mm long; **leaves** opposite, triplinerved, ovate to deltoid, adaxial surface light dull green and sparsely to moderately hirsute, trichomes white to hyaline, multicellular, tapered, 0.2-0.5 mm long, abaxial surface creamy greenish-white and densely villous to floccose, trichomes white, multicellular, tapered, 0.3-1 mm long, pubescence along major veins densely villous to lanate; sessile glandular trichomes confined to abaxial surface 1000-1300/cm^2; **blades** 20-130 mm long, 8-90 mm wide, slightly smaller upwards toward the capitulescence, apex acuminate, base obtuse or truncate and narrowly attenuate along distal fourth of petiole, margins serrulate to serrate; petioles 7-35 mm long, slightly canaliculate, puberulent adaxially, densely villous abaxially; **capitulescences** monochasial thyrsoid, with 1-12+ heads, peduncles 40-230 mm long, sparsely to moderately tomentose, pubescence slightly denser below heads, trichomes as stem; **heads** 16-17.5 mm across, 14-15.5 mm high, urceolate-hemispherical; **receptacles** 9.5-11 mm in diameter in fruit, slightly convex; **phyllaries** 29-35 in 4 graduated series, first series 7.4-9.5 mm long, 2.7-3.4 mm wide, oblong to

spatulate, slightly constricted between indurated and herbaceous parts, base heavily indurated, light green-stramineous and glabrous adaxially, sparsely tomentose whitish-green abaxially, herbaceous apex reflexed, foliaceous, light green and sparsely hirsute to strigose adaxially, sparsely tomentose-villous whitish-green abaxially, margins sparsely ciliate, second and third series 8-12.5 mm long, 3-4.5 mm wide, ovate, conspicuously constricted between indurated and herbaceous parts, base heavily indurated, whitish-stramineous and glabrous adaxially, rows of dark green and greenish-stramineous bands of various width coalescing at herbaceous apex and glabrous abaxially, herbaceous apex reflexed and twisted, light greenish-stramineous and puberulent adaxially, dark green and glabrescent abaxially, margins glabrous to sparsely ciliate, fourth series 7.5-9.5 mm long, 2.5-3.5 mm wide, oblong, chartaceous, base slightly indurated sometimes chartaceous, light stramineous and glabrous on both surfaces, herbaceous apex very reduced, appressed, light greenish-stramineous and glabrescent adaxially, light green and sparsely tomentose abaxially, margins glabrous to sparsely ciliate; **pales** 8-8.5 mm long, 3.5-3.8 mm wide, oblong-ovate, conduplicate, keeled lengthwise, protruding slightly beyond phyllaries, stramineous with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrous or sparsely puberulent along fold and tip, apex slightly coriaceous, acute to acuminate, pointed, dark greenish-black; **ray flowers** 16-21, corolla golden yellow, apex blackish on both surfaces, limb 13.5-15.5 mm long, 6.5-7 mm wide, broadly oval, sparsely to moderately puberulent on veins of abaxial surface, apex acute to rounded, bifid or trifid, tube 2.5-3.1 mm long, moderately

puberulent and glandular; **ray ovaries** 3.9-4.2 mm long, triquetrous, glabrous, pappus of 2-5 squamellae 0.3-0.4 mm long; **disk flowers** 100-145, flowers protruding 1-1.5 mm beyond pales, corollas greenish-yellow, narrowly campanulate to tubular, throat 4.2-4.4 mm long, 1.3-1.5 mm wide at base, 1.5-1.6 mm wide at junction with lobes, veins orange and discernable the whole length of the throat, moderately puberulent, with interspersed uni- and biseriate glandular trichomes 0.1-0.15 mm long, tapered trichomes hyaline to white, 0.1-0.2 mm long, tube 1.4-1.5 mm long, light yellowish-green, moderately puberulent and glandular, trichomes as throat, lobes 0.7-1.2 mm long, deltoid, yellow, apices black on both surfaces, moderately puberulent abaxially; anthers 2.7-2.8 mm long, thecae black, appendages 0.4-0.5 mm long, ovate, stramineous; styles 6.1-6.7 mm long, style branches 1.3-1.5 mm long; **disk achenes** 2.4-3.3 mm long, 0.9-1.3 mm wide, biconvex, oval-obovate, shoulders rarely present, shiny black, or with silvery-orange or purplish trichomes conspicuously contrasting with black coloration of achene wall, sparsely to moderately sericeous, pappus of 2 awns, sometimes with 2-10 squamellae, awns slender, stramineous or purplish, deciduous, subequal, 2.3-2.8 mm long, squamellae free or fused at the base, 0.3-0.4 mm long, same color as awns somewhat persistent; $\underline{n}$ = 17.

Phenology. Flowering March to July.

Distribution. (Fig. 43). Montane moist to dry forests of the headwaters of the many Pacific-flowing rivers in Cajamarca and Piura Departments in northern Peru; 1900-2900 m.

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Cajamarca, Yumagual, 2550 m,

26 Jun 1966, Sánchez Vega & Contreras 246 (CPUN, F, TENN); Prov. Contumazá, alrededores de Guzmango, borde del camino, 2500 m, 24 May 1978, Sagástegui & Mostacero 9172 (F, HUT, TENN, SI); El Puquio, Guzmango, 2900 m, 21 Jun 1962, Sagástegui 3923 (HUT, LP, US).—PIURA: Prov. Huancabamba, Abra de Porculla. Road from Olmos to Pucará, Km 45 E of Olmos, 1920 m, 13 Jul 1986, Plowman et al. 14278 (F, TENN).

Pappobolus amoenus is a rare but widely scattered species of the western Andes. In the area of Cajamarca it grows abundantly in recently disturbed, open areas scattered with shrubs of Myrtaceae and Euphorbiaceae that form remnants of the previously thick shrubbery.

This species can be distinguished by its weak, profusely-branched habit normally supported by adjacent vegetation, urceolate to urceolate-hemispherical heads on long peduncles and strongly reflexed ray flowers. The urceolate head shape is unique within the genus, as well as the heavily indurated base and the reduced and twisted herbaceous apex of the outer series of phyllaries. It shares with P. robinsonii a similar leaf shape and pubescence as well as reflexed ray flowers. Sagástegui 3923 from Contumazá Province, Cajamarca Department, has slightly longer and reflexed phyllaries reminiscent of those of of P. sanchezii but head size is markedly smaller and well within the range of P. amoenus.

22. Pappobolus robinsonii Panero, sp. nov.——TYPE: PERU. Cajamarca: Prov. Celendín, 2-3 km E of Celendín on road to Balsas, along a river creek, 2560 m, 5 Jul 1987, Panero et al. 955 (holotype:

F!; isotypes: B!, CPUN!, GRI!, HUT!, K!, MEXU!, SI!, TENN!, UC!, US!).

Pappobolus robinsonii differt ab P. amoenus. Habet hemisphaerica capita, anguste ovata vel lanceolata folia, reflexa exteriora phyllaria discrepantia cum fere glabris perviridibus vel nigris appressis interioribus phyllariis.

Much-branched, weak shrubs 10-22 dm tall; **stems** terete, dark brown, glabrous, herbaceous parts greenish-brown and moderately tomentose to villous or lanate-floccose, densely villous or lanate upwards toward growing apex, trichomes white, greenish-white or tan, multicellular, tapered, 0.5-1.5 mm long; **leaves** opposite, rarely alternate, triplinerved, ovate to ovate-lanceolate, adaxial surface light to dark dull green and sparsely to moderately strigose or hirsute, trichomes white to hyaline, multicellular, tapered, 0.3-0.5 mm long, abaxial surface creamy whitish-green, yellowish-green or greenish-tan and densely villous to floccose, trichomes white, greenish-white or tan, multicellular, tapered, 0.8-2.5 mm long, veins densely villous brown and clearly outlined; sessile glandular trichomes confined to abaxial surface 800-1000/cm^2; **blades** 20-130 mm long, 7-75 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse and slightly attenuate along distal fourth of petiole, margins subentire to serrulate; petioles 4-30 mm long, somewhat canaliculate, glabrescent to sparsely tomentose adaxially, densely villous abaxially; **capitulescences** monochasial thyrsoid, with 2-14+ heads, peduncles 50-120 mm long, sparsely to densely villous or

tomentose, pubescence denser below the heads, trichomes as stem; **heads** 13.5-18 mm across, 11.5-14 mm high, hemispherical; **receptacles** 7-11 mm in diameter in fruit, slightly convex; **phyllaries** 35-48 in 4-5 graduated series, first and second series 8-14.5 mm long, 2.5-7.5 mm wide, spatulate, constricted between indurated and herbaceous parts, base strongly indurated, light green and glabrous adaxially, dark greenish-black and sparsely villous or tomentose abaxially, herbaceous apex spreading, sometimes foliaceous, light to dark green and sparsely strigose-hirsute adaxially, densely villous creamy green or greenish-yellow abaxially, margins sparsely ciliate to densely villous, third and fourth series 10-16 mm long, 3.5-4.2 mm wide, lanceolate-oblong, base indurated, stramineous and glabrous adaxially, dark green with several light greenish-stramineous longitudinal bands coalescing at herbaceous apex and glabrous abaxially, herbaceous apex slightly reflexed or appressed, light green and sparsely strigose adaxially, glabrescent to densely villous or tomentose yellowish-green or whitish-green abaxially, margins glabrous to sparsely villous, fifth series 7.5-10.8 mm long, 2-2.8 mm wide, oblong, normally covered by outer phyllaries, chartaceous, base stramineous and glabrous on both surfaces, apex greenish-stramineous, sparsely tomentose on both surfaces, margins glabrous or sparsely tomentose; **pales** 8.4-9 mm long, 3-3.3 mm wide, ovate to oblong, conduplicate, keeled lengthwise, protruding 1-2 mm beyond the phyllaries, stramineous, with a few dark green longitudinal bands of various width, bands coalescing at apex, glabrescent abaxially, apex coriaceous, acute, pointed or slightly

reflexed, dark greenish-black; **ray flowers** 19-29, corolla golden yellow, limb 17-26 mm long, 8-10.5 mm wide, oval-lanceolate or broadly oval, sparsely to moderately puberulent on veins of abaxial surface, apex acute, bifid or trifid, tube 1-2.7 mm long, sparsely puberulent; **ray ovaries** 2.4-3 mm long, triquetrous, glabrous, epappose or with 2-5 squamellae 0.2-0.3 mm long; **disk flowers** 125-200, flowers barely protruding beyond pales, corollas yellow, distal portion of throat and lobes black, narrowly campanulate to tubular, throat 3.9-4.5 mm long, 1.3-1.5 mm wide at base, 1.4-1.7 mm wide at junction with lobes, veins orange and discernable the whole length of the throat, sparsely puberulent, trichomes hyaline, multicellular, tapered, 0.05-0.25 mm long, tube 0.5-1.1 mm long, yellow, sparsely puberulent, trichomes as throat, lobes 0.9-1.2 mm long, deltoid, black on both surfaces; anthers 2.8-3.2 mm long, thecae black or purplish-black, appendages 0.5-0.6 mm long, ovate or lanceolate, black or purple; styles 5-6.2 mm long, style branches 1.3-1.9 mm long; **disk achenes** 3.4-4.2 mm long, 1.6-1.9 mm wide, biconvex, obovate, with two diminutive or no shoulders, shiny grayish-black or black, glabrous or sparsely sericeous, pappus of 2 awns sometimes with 2-5 squamellae, awns slender, stramineous, deciduous, subequal, 3-3.5 mm long, squamellae free, 0.5-0.7 mm long, same color as awns, deciduous; $\underline{n} = 17$.

Phenology. Apparently flowering throughout the year.

Distribution (Fig. 43). Along narrow water courses, in disturbed areas or growing along the roads around the town of Celendín especially along the road to Balsas in the canyon of the Marañón River; 2400-3000 m. Growing with Alnus acuminata, Brachyotum, several Calceolaria, Coreopsis celendinensis

Ságastegui & Sánchez, C. connata Cabrera, C. woytkowskii Sherff., Coriaria thymifolia, Elleanthus, Myrcianthes, Oncidium, Oreopanax, Viburnum, Viola arguta DC., among others.

SPECIMENS EXAMINED. PERU. AMAZONAS: along road ascending mountain SE of Chachapoyas, 8200 ft, 14 Jan 1983, King & Bishop 9209 (US).—CAJAMARCA: Prov. Celendín, Conga de Urquía, (Sucre-Oxamarca), 2500 m, 19 May 1976, Sagástegui et al. 8422 (F, HUT, SI, US); canyon of Río Marañón above Balsas, 3-4 km below summit of the road to Celendín, 2950 m, 21 May 1964, Hutchison & Wright 5224 (F, K, MO, NY, UC, US); rocky hillsides 4 km E of Celendín, 2700 m, 19 May 1964, Hutchison & Wright 5175 (C, GH, F, LIL, MO, TENN, S, UC, US, USM); vicinity of Celendín, 2625 m, 6 Jun 1936, Woytkowski 25 (F); 21-25 km E of Celendín on road to Balsas, 3000 m, 18 Oct 1984, Dillon & Whalen 4055 (F); bajando a Conga de Urquía, entre Sucre y Oxamarca, 2800 m, 20 May 1976, Sánchez Vega & Ruiz Vigo 1751 (CPUN); 32 km E of Celendín on road to Balsas, 2430 m, 12 Mar 1988, Panero & Sánchez Vega 1223 (COL, WIS), 1224 (TENN), 1225 (MICH, USM); 21 km E of Celendín on road to Balsas, 2800 m, 11 Mar 1988, Panero & Sánchez Vega 1208 (CPUN, TENN); 20 km E of Celendín on road to Balsas, 2830 m, 11 Mar 1988, Panero & Sánchez Vega 1210 (TENN), 1211 (F, GRI, RB); 18 km E of Celendín on road to Balsas, 2900 m, 11 Mar 1988, Panero & Sánchez Vega 1212 (CAN, CPUN, F, HUT, TENN, US, USM), 1213 (B, GRI, MEXU, NY, RB, S, SI, TENN), 1215 (AAU, QCA).—PIURA: Huancabamba, western cordillera opposite Huancabamba, 8000-9500 ft, 26 Sep 1911, Townsend A206 (F).

Pappobolus robinsonii is recognized by its distinctive involucre. The first and second series of phyllaries normally have a densely lanate or villous abaxial surface and they are conspicuously reflexed. The third and fourth series are conspicuously appressed and dark shiny green, drying black. The pubescence in these phyllaries is restricted to the very distal end of the abaxial surface. These two dramatically different phyllary morphologies are very helpful to distinguish this species especially when dry. Another interesting aspect of this species is that there is relatively little variation in key morphological characters across its wide geographical distribution. Only one specimen (King & Bishop 9209) from Chachapoyas, Amazonas Department exhibits a disk achene pappus of several deciduous awns typical of P. cinerascens and related species. On the other hand the phyllaries are glabrescent and blackish, and the leaves are densely lanate-floccose or lanate abaxially similar to some forms of P. robinsonii from the area of Celendín. The placement of this collection under this species is tentative, and more collections are needed to fully evaluate the relationships and status of this population.

This species is sympatric with and sometimes difficult to separate from lower altitude forms of P. stuebelii. Both share conspicuously long internodes, opposite leaves and superficially similar heads. However, they can be separated by the densely lanate herbaceous stems and phyllaries commonly found in P. stuebelii. In addition, the rugose, thick leaves of P. stuebelii contrast with the soft and much larger leaves of P. robinsonii.

The species name honors Dr. Harold Robinson, curator at the U.S. National Herbarium.

23. Pappobolus szyszylowiczii (Hieron.) Panero, comb. nov. Helianthus szyszylowiczii Hieron., Bot. Jahrb. Syst. 36:491. 1905.——TYPE: PERU. Cajamarca: around Callacate, May 1879, Jelski 732 (holotype: B destroyed; lectotype, here designated: F! as photo F-15276!, also at LIL!, TEX!).

Shrubs? 10-20 dm tall; stems terete, glabrous, herbaceous parts sparsely to moderately puberulent to pilose; **leaves** alternate (opposite ?), triplinerved, ovate to broadly trullate, abaxial surface deep green, strigose, abaxial surface much lighter in color, moderately velutinous; **blades** 30-150 mm long, 10-80 mm wide, smaller upwards toward the capitulescence, apex acuminate, base obtuse and narrowly attenuate along fourth to third of petiole, margins serrulate to serrate; petioles 10-30 mm long, slightly canaliculate; **capitulescence** monochasial thyrsoid with (3-) 5-18+ heads, peduncles 4-7 cm long, softly tomentose to villous, trichomes 1-1.3 mm long; **heads** 10-15 mm across, hemispherical; **receptacles** 5-10 mm in diameter in fruit, slightly convex; **phyllaries** 20-25 in 3 graduated series, 12-13 mm long, 2-2.5 mm wide, linear-lanceolate, acute, dark green to black and densely villous abaxially; **pales** 6 mm long, 2 mm wide, oblong, conduplicate, stramineous, apex dark green; **ray flowers** 5-10, corolla yellow, limb 14-15 mm long, 3.5 mm wide, oblong-lanceolate, puberulent and glandular on veins of abaxial surface, bifid, tube 1.5-2 mm long,

pubescent; **disk flowers** corolla yellow, throat 3-3.5 mm long, pubescent, tube 1-1.5 mm long, lobes 0.5 mm long, deltoid, slightly greenish-black?; **disk achenes** (immature) 2.5 mm long, glabrous, pappus of 2 awns, 2 mm long.

Phenology. Flowering in May.

Distribution. (Fig. 43). Callacate near the towns of Chota and Cutervo in central Cajamarca Department; 2600-2800 m.

The description of this species is based on the photograph of the type and the original description. Based on this information, the species appears to be part of the nigrescens group. The long peduncles, broad leaves, the dark disk flower lobes and the capitulescence structure point to a close relationship to P. youngiorum and P. schillingii. Blake (1918) placed this species in synonymy under Viguiera lanceolata Britton of southern Peru and Bolivia notwithstanding the fact that this species differs from V. lanceolata by the soft pubescence of its herbage, broad and serrate leaves, size and arrangement of the capitulescence and involucre, and geographical distribution. Viguiera lanceolata is apparently endemic to the Puna of Bolivia and southern Peru where it grows in disturbed areas; a completely different habitat from the moist forest of the canyon of the Chotano and Cutervo Rivers of northern Peru where P. szyszylowiczii was collected. It is interesting to note that Blake's description of V. lanceolata does not include certain key characters of the leaves and petioles obvious in the photograph of the type of H. szyszylowiczii. These important omissions lead me to believe that this specimen was peripheral to the circumscription of V. lanceolata.

B. THE STUEBELII GROUP.

Compact to open shrubs or small trees 5-40 dm tall with ovate to trullate, sclerified to coriaceous leaves. Capitulescences of a few large and showy heads on short, very leafy peduncles. Known from the Jalca or Páramo of central Cajamarca and northern La Libertad Departments.

24. Pappobolus stuebelii (Hieron.) Panero, comb. nov. Helianthus stuebelii Hieron., Bot. Jahrb. Syst. 21:349. 1895. Helianthopis stuebelii (Hieron.) H. Robinson, Phytologia 44:266. 1979.——TYPE: PERU. Cajamarca: near Celendín, between Pacasmayo and Moyobamba, 3200 m, Stuebel 34e (holotype: B destroyed; lectotype, here designated: fragment US!).

Helianthopsis bishopii H. Robinson, Phytologia 54:52-53. 1983.——TYPE: PERU. Cajamarca: 62 km NE of Cajamarca along road to Celendín, 11,000 ft, 9 Jan 1983, King & Bishop 9141 (holotype US!; isotypes: F!, GH!, UC!).

Compact to open shrubs or trees, 10-40 dm tall; **stems** terete, brownish-gray and glabrous, herbaceous parts densely lanate tan rarely white, trichomes white or tan, multicellular, tapered, 3-8 mm long; **leaves** alternate, sometimes opposite, triplinerved, ovate to ovate-lanceolate, adaxial surface dark green, somewhat rugose and moderately strigose, trichomes white or hyaline, multicellular, tapered, sometimes

with raised multicellular bases, 0.3-1.2 mm long, abaxial surface densely lanate sometimes lanate-floccose tan, trichomes white or tan, multicellular, tapered, 0.5-5 mm long; sessile glandular trichomes confined to abaxial surface 100-200/cm^2; **blades** 10-115 dm long, 7-50 mm wide, similar in size and morphology throughout stem and capitulescence, apex acuminate, base obtuse, sometimes attenuate along distal fifth of petiole, margins subentire to entire and revolute; petioles 1-2.5 cm long, canaliculate, glabrescent adaxially, densely lanate abaxially; **capitulescence** monochasial thyrsoid, with 1-12+ heads, peduncles, 40-115 mm long, densely lanate, trichomes as stem; **heads** 16-32 mm across, 13-22 mm high, hemispherical; **receptacles** 12-18 mm in diameter in fruit, convex; **phyllaries** 45-81 in 5-6 subequal series, all series densely lanate as to mask phyllary morphology, 20-29 mm long, 3-5.5 mm wide, lanceolate, base indurated, stramineous-green and glabrescent to sparsely sericeous adaxially, densely lanate tan abaxially, herbaceous apex slightly reflexed or appressed, densely lanate tan on both surfaces, margins densely lanate-velutinous; **pales** 7.8-8.6 mm long, 3.2-3.5 mm wide, ovate, conduplicate, strongly keeled lengthwise, covered by phyllaries, stramineous with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrous abaxially, apex coriaceous, acute to rounded, pointed or slightly curved inward, blackish; **ray flowers** 20-33, corolla bright yellow, apex blackish abaxially, limb 16-45 mm long, 6-9 mm wide, oval to narrowly oval, moderately puberulent-sericeous and glandular on veins of abaxial surface, apex acute, bifid, tube 1.2-1.9 mm long, basal half glabrous, distal half moderately puberulent; **ray ovaries**

3.5-4.2 mm long, triquetrous or biconvex, glabrous, pappus of 1 awn 1.7-2.5 mm long; **disk flowers** 160-385, flowers not protruding significantly beyond pales, corolla golden yellow, broadly campanulate-tubular, throat 3.5-5 mm long, 1.1-1.6 mm wide at base and at junction with lobes, veins orange and discernable the whole length of the throat, sparsely puberulent with interspersed uni- and biseriate glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.3 mm long, tube 1.1-1.8 mm long, light yellow, essentially glabrous, lobes 0.8-1.2 mm long, deltoid, yellow adaxially, black abaxially, sparsely puberulent abaxially; anthers 2.5-3.5 mm long, thecae black or brownish-black, appendages 0.4-0.6 mm long, ovate, stramineous-black; styles 6.3-7.5 mm long, style branches 1.1-1.3 mm long; **disk achenes** 3.5-4 mm long, 1.4-1.7 mm wide, biconvex, obovate, with incipient shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.8-3.6 mm long; n = 17. Fig. 50.

Phenology. Flowering throughout the year.

Distribution (Fig. 45). Endemic to protected rocky outcrops in the Jalca between Kumulka and the town of Celendín along the road Cajamarca-Celendín; 2850-3700 m. Growing with Alnus acuminata, Berberis, Buddleja incana, Cajophora, Calamagrostis, Calceolaria balloti̇folia Kranzl., C. dentifolia Edwin, C. melissiifolia Benth., C. rhododendroides Krzl., Fuchsia mathewsii J. F. Macbride, Gentianella, Jungia stuebelii (Hieron.) Crisci, Munnozia, Ranunculus, and Werneria among others.

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Celendín, Chalhuayaco, 3600 m, 18 May 1976, Sagástegui et al. 8404 (F, HUT, US); Jalca de Kumulka, 3350 m, 17 Aug 1984, Sagástegui et al. 12050 (HUT); entre Kumulka y Celendín, 3700 m, 6 Aug 1958, Ferreyra 13265 (LP); 64-68 km NE of Cajamarca, along the road to Celendín, 3300-3500 m, 4 Jan 1979, Dillon & Turner 1636 (F, K, MO, TEX); 62 km NE of Cajamarca, near Micuypampa, 3500 m, 15 Jan 1983, Dillon et al. 2990 (F, TEX); 60 km N of Cajamarca on road to Celendín, 3480 m, 7 Mar 1988, Panero 1150 (F, GRI, TENN), 1151 (GRI, TENN, US), 1152 (B, SI); Quebrada de Sendamal, 3000 m, 16 Jun 1969, Sánchez Vega 423 (F, LP); Km 65 of the road Cajamarca-Celendín, 3520 m, 3 Feb 1985, Todzia & Stein 2623 (TEX); 1 km W of Chalhuayaco, on road to Celendín, 3450 m, 4 Jul 1987, Panero et al. 932 (CAN, COL, CPUN, HUT, LE, MEXU, USM, US); Cerro Gelig, summit of the road Celendín-Balsas, 3000 m, 5 Jul 1987, Panero et al. 995 (C, GRI, MA, LP, TENN, US); between Cajamarca and Celendín, 19 Apr 1904, Weberbauer 4241 (US); 65 km de Cajamarca sobre la carretera a Celendín, 3500 m, 14 Jul 1979, Albert de Escobar & Berry 1493 (TEX(2)); 62 km NE of Cajamarca on road to Celendín, 3490 m, 10 Mar 1988, Panero & Sánchez Vega 1196 (TENN), 1197 (GRI), 1202 (F); 13 km SW of Celendín on road to Cajamarca, 2800 m, 13 Mar 1988, Panero & Sánchez Vega 1270 (GRI, TENN); 70 km SW of Celendín on road to Cajamarca, 3190 m, 11 Mar 1988, Panero & Sánchez Vega 1206 (F, UC); 59 km SW of Celendín on road to Cajamarca, 2960 m, 11 Mar 1988, Panero & Sánchez Vega 1207 (COL, CPUN); Chalhuayaco, entre la Encañada y Celendín, 3520 m, 3 Jul 1975, Sánchez Vega et al. 1703 (CPUN); Quebrada de Sendamal, entre Cajamarca y

Celendín, 12 Jun 1969, 3000 m, Sánchez Vega & Ruiz Vigo 423 (CPUN); Kumulka, entre la Encañada y Celendín, 7 Apr 1966, Sánchez Vega & Alvaz 191 (CPUN, F, LP, TENN); Celendín, Cerro Gelig al S [E] de Celendín, 2900 m, 11 Sep 1984, Cowan et al. 4355 (TENN, TEX, USM); 5 km E of Celendín on road to Balsas, 2870 m, 12 Mar 1988, Panero & Sánchez Vega 1217 (F, GRI, TENN).

Pappobolus stuebelii is a very attractive large shrub or treelet of the perpetually humid habitats common to the Jalca of northern Peru. Its large habit and heads, and the conspicuous tan to ochreus vestiture come together to create one of the most beautiful species within the Helianthinae.

Pappobolus stuebelii shares with P. jelskii and P. smithii similar habit, pubescence and floral characters. The main populations of this species are restricted to Jalca habitat but a few individuals are encountered at lower altitudes. These individuals are less pubescent, and have larger leaves and larger capitulescences. These forms of P. stuebelii are morphologically reminiscent of P. robinsonii. It is not clear if hybridization or ecological conditions are responsible for these morphological extremes.

Robinson (1979) considered the name P. stuebelii to apply to P. robinsonii and erected Helianthopsis bishopii to accomodate the individuals considered here to be P. stuebelii. Fragments of the type specimen and some key observations by Watson (1929) of the type in Berlin leave no doubt as to the identity of P. stuebelii. Watson (1929) says: "The species is remarkable for the dense wool on the stem

and lower surface of the leaves, the very numerous narrow rays, the sessile heads and the small crowded leaves". In addition Stuebel collected the type near Celendín at 3200 m on his journey between Pacasmayo and Moyobamba. The only areas around Celendín that would be along this route and that are at or above 3200 m are the habitats of P. stuebelii. Careful examination of floral fragments of the type shows they match modern specimens of P. stuebelii.

25. Pappobolus smithii (Ferreyra) Panero, comb. nov. Helianthopsis smithii Ferreyra, Bol. Soc. Peruana Bot. 8(1-2):77-80. 1980.——TYPE: PERU. La Libertad: Bolívar, cerca del Nevado de Cajamarquilla, Ferreyra 1296 (holotype: USM!).

Compact, monocaulic shrubs 5-25 dm tall; **stems** terete, brownish-gray and glabrous, herbaceous parts densely lanate white, trichomes white, multicellular, tapered, 3-10 mm long, **leaves** alternate, triplinerved, ovate to ovate-lanceolate, adaxial surface light to creamy green and moderately sericeous, trichomes white, multicellular, tapered, 0.3-2.5 mm long, abaxial surface densely lanate white, trichomes white, multicellular, tapered, 0.5-5 mm long; sessile glandular trichomes confined to abaxial surface 900-1200/cm^2; **blades** 20-50 mm long, 10-25 mm wide, similar in size and morphology throughout stem and capitulescence, apex acuminate, base obtuse to rounded, margins entire and slightly revolute; petioles 4-10 mm long, conspicuously canaliculate, glabrous adaxially, densely lanate abaxially; **capitulescences** monochasial thyrsoid with 1-3+ heads,

peduncles 60-120 mm long, densely lanate, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 17-26 mm across, 13-19.5 mm high, hemispherical; **receptacles** 9-15 mm in diameter in fruit, convex; **phyllaries** 35-48 in 4-5 graduated series, series 1-3 densely lanate as to mask phyllary morphology, base indurated, stramineous and glabrous adaxially, densely lanate white abaxially, herbaceous apex moderately to densely lanate on both surfaces, first series 11-24 mm long, 4-8.6 mm wide, very variable in size and shape, generally ovate or lanceolate, constricted between herbaceous and indurated parts, herbaceous apex reflexed, foliaceous, second series 11.5-23 mm long, 3-6.2 mm wide, similar in shape and indumentum to previous series, third series 13-22 mm long, 3.4-5.5 mm wide, lanceolate, less pubescent than previous series, pubescence localized at distal abaxial portion, fourth and fifth series 8-23 mm long, 2.6-4.6 mm wide, lanceolate, resembling pales in general aspect, chartaceous, apical portion blackish, sparsely pubescent, otherwise both sides stramineous and glabrous; **pales** 9.3-11 mm long, 2.5-3.5 mm wide, ovate, conduplicate, keeled lengthwise, rarely protruding beyond phyllaries, stramineous with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrous abaxially, apex coriaceous, acute to rounded, pointed or slightly curved inward, blackish; **ray flowers** 23-30, corolla bright yellow, apex blackish abaxially, limb 22-30 mm long, 5-6 mm wide, oval, moderately puberulent and glandular on veins of abaxial surface, apex acute, bifid, tube 1.2-1.6 mm long, basal half glabrous, distal half densely puberulent; **ray ovaries** 2.1-3.2 mm long, triquetrous, glabrous, pappus of 1 or 2 awns 2-3.1 mm long; **disk flowers** 160-340, flowers not

protruding significantly beyond pales, corolla yellow, campanulate, throat 3.3-3.6 mm long, 1.2-1.4 mm wide at base, 1.4-1.9 mm wide at junction with lobes, veins orange and discernable the whole length of the throat, moderately to densely puberulent especially at the base with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.6 mm long, tube 1.2-1.9 mm long, light yellow, glabrous or sparsely to moderately puberulent, trichome size and morphology similar to those on throat, lobes 0.9-1.3 mm long, deltoid, yellowish-green, apices black abaxially, sparsely puberulent abaxially; anthers 2.6-3 mm long, thecae black, appendages 0.4-0.5 mm long, broadly ovate to suborbicular, black; styles 6-6.3 mm long, style branches 1.3-1.4 mm long; **disk achenes** 3.8-4.1 mm long, biconvex, obovate, with diminutive shoulders at the angles of the achene, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 3-4.2 mm long; Chromosome number unknown. Fig. 46.

Phenology. Apparently flowering throughout the year.

Distribution (Fig. 45). Known from the base of the Nevado de Cajamarquilla SE of the town of Bolívar along the Eastern Andean Cordillera bordering the canyon of the Marañón River in NE La Libertad Department; 3300-3500 m.

Vernacular name. Antarahuaita (fide López & Ságastegui 3309).

SPECIMENS EXAMINED. PERU. LA LIBERTAD: Bolívar. Camino a Cujibamba, en ladera pedregosa, 3300 m, 1 Jun 1960, López & Sagástegui 3309 (HUT, LP, TENN); Cajamarquilla, 6 Nov 1946, Infantes 4424 (LIL).

Pappobolus smithii is a compact shrub of the Jalca just above the town of Bolívar. According to Dr. Ferreyra (pers. comm.) this species is rare and threatened by the burning of grasses in the short dry season in August. The few individuals he observed are restricted to protected rocky areas where the fires do not penetrate.

This species can be easily recognized by the moderately sericeous adaxial leaf surfaces and the deep white-silver pubescence of its herbage. It shares with P. stuebelii and P. jelskii the large heads, short peduncles and densely lanate, lanceolate phyllaries and herbage.

26. Pappobolus jelskii (Hieron.) Panero, comb. nov. Helianthus jelskii Hieron., Bot. Jahrb. Syst. 36:490-491. 1905. Helianthopsis jelskii (Hieron.) H. Robinson, Phytologia 44:264. 1979.——TYPE: PERU. Cajamarca: between Chota and Cutervo, Jun 1879, Jelski 713 (holotype: B, destroyed; lectotype, here designated: fragment ex B at US!).

Compact, monocaulic shrubs 5-25 dm tall; **stems** terete, orangish-brown, glabrous, herbaceous parts densely lanate white, tan or whitish-green, trichomes white, green or tan, multicellular, tapered, 3-10 mm long, **leaves** opposite, triplinerved, ovate to ovate-lanceolate, adaxial surface dark green, rugose and moderately strigose to hirsute, trichomes white, multicellular, tapered, sometimes with raised multicellular bases, 0.3-2.5 mm long, abaxial surface white to tan or green pubescent and densely lanate and somewhat floccose, trichomes

white or tan-green, multicellular, tapered, 0.5-7 mm long; sessile glandular trichomes confined to abaxial surface 900-1200/cm^2; **blades** 10-65 mm long, 6-33 mm wide, similar in size and morphology throughout stem and capitulescence, apex acuminate, base obtuse to rounded, margins entire and slightly revolute; petioles 4-30 mm long, conspicuously canaliculate, glabrous adaxially, densely lanate abaxially; **capitulescences** simple dichasia or dichasial thyrsoid, with 3-15+ heads, peduncles 20-120 mm long, densely lanate, pubescence evenly distributed along peduncle, trichomes as stem; **heads** 17-26 mm across, 13-19.5 mm high, hemispherical; **receptacles** 9-15 mm in diameter in fruit, convex; **phyllaries** 35-48 in 4-5 graduated series, series 1-3 densely lanate as to mask phyllary morphology, base indurated, stramineous and glabrous adaxially, densely lanate tan or white abaxially, herbaceous apex moderately to densely lanate on both surfaces, first series 11-24 mm long, 4-8.6 mm wide, very variable in size and shape, generally ovate or lanceolate, constricted between herbaceous and indurated parts, herbaceous apex reflexed, foliaceous, second series 11.5-23 mm long, 3-6.2 mm wide, similar in shape and indumentum to previous series, third series 13-22 mm long, 3.4-5.5 mm wide, lanceolate, less pubescent than previous series and localized at distal abaxial portion, fourth and fifth series 8-23 mm long, 2.6-4.6 mm wide, lanceolate, resembling pales in general aspect, chartaceous, apical portion blackish, sparsely pubescent, otherwise both sides stramineous and glabrous; **pales** 9.3-11 mm long, 2.5-3.5 mm wide, ovate, conduplicate and, sometimes (especially inner ones) strongly keeled lengthwise, rarely protruding beyond phyllaries, stramineous with

several dark green or brown longitudinal bands of various width, bands coalescing and abruptly ending 0.3-0.5 mm below tip, glabrous abaxially, apex coriaceous, acute to rounded, pointed or slightly curved inward, orangish-stramineous; **ray flowers** 20-30, corolla bright yellow, apex blackish abaxially, limb 13-18 mm long, 5-7.8 mm wide, oval, densely puberulent to sericeous and glandular on veins of abaxial surface, apex acute, bifid, tube 1.2-1.6 mm long, basal half glabrous, distal half densely puberulent to minutely pilose; **ray ovaries** 2.1-3.2 mm long, triquetrous, glabrous, pappus of 1 awn 1.7-2.6 mm long; **disk flowers** 160-340, flowers not protruding significantly beyond pales, corolla lemon-yellow, broadly campanulate, throat 3.6-4.5 mm long, 1.2-1.7 mm wide at base, 1.4-2.3 mm wide at junction with lobes, veins orange and discernable the whole length of the throat, moderately to densely puberulent especially at the base, with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.4 mm long, tube 1.2-1.9 mm long, light yellow, glabrous or sparsely to moderately puberulent, size and morphology similar to those on throat, lobes 1-1.3 mm long, deltoid, yellowish-green, apices black abaxially, sparsely puberulent abaxially; anthers 2.6-3 mm long, thecae black, appendages 0.5-0.9 mm long, broadly ovate to suborbicular, stramineous-orange; styles 4.2-8.6 mm long, style branches 0.5-1.4 mm long; **disk achenes** 3.8-4.6 mm long, biconvex, obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.5-4.8 mm long; n = ca 17. Fig. .

Phenology. Apparently flowering throughout the year.

Distribution (Fig. 45). Protected outcrops and narrow crevices around the town of Hualgayoc, at the headwaters of the Llaucano River. Also in the gorge of the Perlamayo River NNW of the town of Hualgayoc and south of Chota. The type came from a locality NNW of the town of Hualgayoc between Chota and the town of Cutervo. This area has been heavily disturbed by human activity and neither this species nor Viguiera szyszylowiczii Hieron., both of which were collected by Jelski in the same area, have not been relocated at the type locality (I. Sánchez Vega, pers. comm.; fortunately, the latter taxon has also been recollected above La Encañada, Cajamarca Department, Panero et al. 863 [B, F, K, LP, MA, MEXU, QCA, TENN, US]); 2900-3900 m.

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Hualgayoc, La Tahona, entre Bambamarca y Hualgayoc, 2900 m, 16 Aug 1952, Ferreyra 8499 (MO, TENN, USM); Laderas verticales al NW de Hualgayoc, sobre el camino a la Mina "La Predilecta", 3410 m, 8 Aug 1981, Sánchez Vega et al. 2666 (CPUN, F, SI), 6 Mar 1988, Panero & Sánchez Vega 1122 (B, C, CPUN, F, GRI, QCA, MA, TENN, US); Road Cajamarca-Hualgayoc-Chugur, 10-15 km before Chugur take road to Perlamayo until first river, then 3-5 km by foot to old school house, continue along right path to the gorge of the Perlamayo River for approximately 10-15 km, 3030 m, 20 Mar 1988, Panero & Sánchez Vega 1343 (F, TENN, US); 4-5 km from the intersection of the road Cajamarca-Hualgayoc on road to Chugur, then 200 m up the mountain to a protected rocky area, 3850 m, 20 Mar 1988, Panero & Sánchez Vega 1342

(COL, GRI, MEXU, RB, SI, TENN); Centro Minero CEMSA, entre Hualgayoc y Bambamarca, 3200 m, 1 Jul 1977, Sánchez Vega et al. 2086 (CPUN).

Pappobolus jelskii can be easily recognized by its opposite phyllotaxy, long internodes, and densely lanate herbage. It shares with P. stuebelii and P. smithii a similar pubescence, head size and morphology, and habit. It differs from these two species by having ray flower ligules that are fewer, smaller, and of an oval shape (as compared to the narrowly lanceolate ligules of P. smithii and P. stuebelii). Specimens of P. lanatus collected prior to Heiser's revision (1957) were incorrectly identified as P. jelskii. These confusion was in part due to the similarities in some key distinguishing features between the two species. Pappobolus jelskii and P. lanatus share opposite leaves, densely lanate herbage and phyllaries and a somewhat similar head size and morphology (see under P. lanatus).

This species grows sporadically around the town of Hualgayoc in protected rocky outcrops or vertical cliffs of difficult access. In this area the overall pubescence tends to be whitish-tan to somewhat greenish-white or slightly tan. In the area of the Perlamayo River gorge, where this species is very abundant, the pubescence is deep white and the shrubs tend to be larger. In addition the heads tend to be larger and with longer ray flowers. These morphological differences between the populations of these two sites probably reflect differences in altitude and the concomitant changes in growing conditions.

27. Pappobolus lodicatus (Cuatr.) Panero, comb. nov. Helianthus lodicatus Cuatr., Proc. Biol. Soc. Wash. 77:144-145. 1964. Helianthopsis lodicata (Cuatr.) H. Robinson, Phytologia 44:264. 1979.——TYPE: PERU. Cajamarca: Sunchubamba on the way to Huallabamba, 3000-3700 m, 3 Jun 1957, Ellenberg 1756 (holotype: U!, fragment ex U at US!).

Open shrubs 10? dm tall; **stems** terete, light brown sometimes blackish and glabrous, herbaceous parts densely lanate white or tan, trichomes white or tan, multicellular, tapered, 2-4 mm long; **leaves** alternate, triplinerved, trullate, ovate, adaxial surface greenish-blue to grayish-green and moderately strigose or sericeous, trichomes white or tan, multicellular, tapered, 0.4-0.7 mm long, abaxial surface very densely lanate white or tan, trichomes white or tan, multicellular, tapered, 1-1.5 mm long; sessile glandular trichomes confined to abaxial surface 100-200/cm^2; **blades** 11-24 mm long, 4-14 mm wide, similar in size throughout stem and capitulescence, apex acute to acuminate, base obtuse or slightly attenuate along distal fourth of petiole, margins entire to shallowly serrulate, revolute and undulate; petioles 14-27 mm long, canaliculate, densely lanate on both surfaces; **capitulescences** monochasial thyrsoid, with 1-3+ heads, peduncles 40-125 mm long, densely lanate, trichomes as stem; **heads** 13-15 mm across, 11-15 mm high, hemispherical; **receptacles** 6-7.5 mm in diameter in fruit, convex; **phyllaries** 28-40 in 4 graduated series, first and second series 6.5-10.5 mm long, 3.8-5 mm wide, lanceolate to oblanceolate, base indurated, light green or stramineous and glabrous adaxially, densely

lanate white or tan abaxially, herbaceous apex appressed, sparsely strigose greenish-blue adaxially, densely lanate white or tan abaxially, margins densely lanate, third and fourth series 13-14.5 mm long, 4.5-5 mm wide, lanceolate or oblong, base slightly indurated, light green or stramineous and glabrous adaxially, dark green and glabrous to sparsely tomentose abaxially, herbaceous apex appressed, light greenish-blue and sparsely strigose adaxially, sparsely to densely lanate or tomentose white or tan abaxially, pubescence restricted to distal portion of herbaceous apex, margins glabrous to moderately ciliate to lanate; **pales** 7.8-8.1 mm long, 3.2-3.6 mm wide, oblong-ovate, conduplicate, keeled lengthwise, covered by phyllaries or protruding 1 mm beyond them, stramineous with several dark green or purplish longitudinal bands of various width, bands coalescing at tip, glabrous, or with a few trichomes along the fold, apex coriaceous, acute to acuminate, pointed, blackish-green; **ray flowers** 12-19, corolla golden yellow, apex blackish abaxially, limb 18-23 mm long, 5.5-7.5 mm wide, narrowly oval, sparsely to moderately puberulent on veins of abaxial surface, apex acute to rounded, shallowly bifid or trifid, tube yellow, 1.2-1.4 mm long, sparsely puberulent to glabrous; **ray ovaries** 2.5-3 mm long, triquetrous, glabrous, epappose; **disk flowers** 115-160, protruding 0.5 mm beyond pales, corolla golden yellow, narrowly campanulate to tubular, throat 3.8-4.1 mm long, 0.9-1.1 mm wide at base, 1.3-1.4 mm wide at junction with lobes, veins orange and discernable the whole length of the throat, sparsely to moderately puberulent especially at the base with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes

hyaline to white, 0.1-0.4 mm long, tube 1.1 mm long, light yellow, glabrous, lobes 0.6-1 mm long, deltoid, yellow, rarely black, sparsely puberulent abaxially; anthers 2.4-2.9 mm long, thecae black, appendages 0.5-0.6 mm long, ovate, stramineous or yellow; styles 6-6.2 mm long, style branches 1.1-1.2 mm long; **disk achenes** 2.7-3.3 mm long, 1.3-1.6 mm wide, biconvex, obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.8-3.5 mm long; Chromosome number unknown.

Phenology. Collected in flower and fruit in June, probably flowering throughout the year.

Distribution (Fig. 45). Known only from the highlands (Macizo Collán) between the Jequetepeque and Chicama River systems of SW Cajamarca Department of northern Peru; 3000-3700 m.

Pappobolus lodicatus shares several morphological characters with P. microphyllus and P. stuebelii. It shares with P. microphyllus a similar leaf morphology and involucre. The leaves tend to be trullate to ovate and of the same size range as P. microphyllus. The involucre is larger but otherwise similar to those common in P. microphyllus var. microphyllus. The ochreus, densely lanate pubescence of the stems and abaxial surface of the phyllaries is reminiscent of that of P. stuebelii. The habit of this species is apparently slightly larger than that of P. microphyllus.

C. THE DISCOLOR GROUP

Small, compact to open shrubs 1-15 dm tall with narrowly ovate,

oblong, trullate, lanceolate or linear, sclerified and coriaceous leaves. Capitulescences of small to medium heads on short, leafy peduncles. Known from dry, high interandean valleys and Jalca areas of central and northern Peru, one species in south-central Ecuador.

28. Pappobolus microphyllus (H. B. K.) Panero, comb. nov. Helianthus microphyllus H. B. K., Nov. gen. sp. qt. 4:220. 1820., pl. 375. Leighia microphylla Cass., Dict. Sci. Nat. 25:436. 1822. Viguiera microphylla (H. B. K.) Hieron., Bot. Jahrb. Syst. 36: 490. 1905. Note: Blake (1918) was the first to attribute the combination Viguiera microphylla to Hieronymus. Hieronymus implied from Bentham and Hooker Gen. pl. 2:375 that Bentham had transferred Helianthus microphyllus H. B. K. (already transferred to Leighia by Cassini in 1822) to Viguiera when he identified the collection Jelski 739 as Viguiera microphylla (H. B. K.) ex Benth. in Bentham & Hooker. Based on articles 33.1 and 33.3 of the International Code of Botanical Nomenclature (1988) this combination is not valid. Helianthopsis microphylla (H. B. K.) H. Robinson, Phytologia 44:264. 1979.——TYPE: PERU. Cajamarca: around Cajamarca and Páramo de Yanaguanga Humboldt & Bonpland 3683 (lectotype, here designated: P-HBK, IDC 6209.108:II.6!, fragment US!; isolectotype: B, destroyed, photo ex B at GH!).

Compact or open shrubs 2-10 dm tall; **stems** terete, light brown or gray and glabrous, herbaceous parts densely lanate white or glabrous to

sparsely tomentose shiny brownish-purple, trichomes white, multicellular, tapered, 0.3-0.6 mm long; **leaves** alternate, rarely opposite, triplinerved or mononerved, oval to oblong, trullate, linear, adaxial surface dull dark green or greenish-blue to grayish-green and moderately strigose or sericeous, trichomes white, multicellular, tapered, 0.5-1 mm long; sessile glandular trichomes confined to abaxial surface 100-200/cm^2; **blades** 4-25 mm long, 1.5-11 mm wide, similar in size throughout stem and capitulescence, rarely smaller upwards toward the capitulescence, apex acute, base obtuse or slightly attenuate along distal third of petiole, margins entire to shallowly serrulate, revolute, sometimes undulate; petioles 5-10 mm long, canaliculate, densely lanate or somewhat sericeous on both surfaces; **capitulescences** monochasial thyrsoid, with 1-12+ heads, peduncles 40-125 mm long, densely lanate or tomentose, trichomes as stem; **heads** 8-11.5 mm across, 9-12 mm high, campanulate, rarely hemispherical; **receptacles** 4.5-5.5 mm in diameter in fruit, convex; **phyllaries** 23-31 in 4 graduated or subequal series, first series 3-6.5 mm long, 1-2.5 mm wide, linear, lanceolate to oblanceolate or obovate, base indurated, light green or stramineous and glabrous adaxially, densely lanate white or silver or glabrescent to glabrous light green abaxially, herbaceous apex reflexed or appressed, sparsely strigose light green to densely lanate or tomentose white or whitish-green adaxially, densely lanate white or whitish-green abaxially, margins densely ciliate to lanate, second and third series 4-9.5 mm long, 1.8-3.7 mm wide, lanceolate, oblong, trullate, linear or obovate to spatulate, base slightly indurated, light green or stramineous and glabrous adaxially, stramineous suffused

with green and glabrous to sparsely tomentose abaxially, herbaceous apex appressed, light green and sparsely strigose adaxially, sparsely to densely lanate or tomentose white or greenish-white abaxially, margins glabrous to moderately ciliate to lanate, fourth series 4.5-9 mm long, 1.3-2.2 mm wide, similar to previous series in shape, color and pubescence, but differing by having a smaller herbaceous apex with a larger dark green or stramineous glabrous area, some phyllaries somewhat chartaceous, hyaline, margins glabrous to sparsely ciliate; **pales** 5.5-7 mm long, 2-3 mm wide, oblong-ovate, conduplicate, slightly keeled lengthwise, covered by phyllaries or protruding 1-1.5 mm beyond them, stramineous with several dark green or purplish longitudinal bands of various width, bands coalescing at apex, glabrous, or with a few trichomes along the fold, apex coriaceous, acuminate sometimes acute, pointed, blackish-green; **ray flowers** 11-18, corolla golden yellow, apex sometimes blackish abaxially, limb 9-17.5 mm long, 4.5-7.5 mm wide, broadly to narrowly oval, sparsely to moderately puberulent on veins of abaxial surface, apex acute to rounded, shallowly bifid or trifid, tube 0.8-1.4 mm long, sparsely puberulent to glabrous; **ray ovaries** 1.7-2.7 mm long, triquetrous, glabrous, epappose; **disk flowers** 55-95, protruding 0.5 mm beyond pales, corolla golden yellow, rarely yellowish-purple, narrowly lyrate to tubular, throat 2.8-3.8 mm long, 0.9-1.4 mm wide at base, 1-1.3 mm wide at junction with lobes, veins orange and discernable the whole length of the throat, sparsely to moderately puberulent especially at the base with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered

trichomes hyaline to white, 0.1-0.4 mm long, tube 0.6-1.1 mm long, light yellow, glabrous, lobes 0.6-1 mm long, deltoid. yellow or purple, apices sometimes blackish abaxially, sparsely puberulent abaxially; anthers 1.8-2.4 mm long, thecae black to brownish-yellow, appendages 0.5-0.7 mm long, ovate-lanceolate, black or stramineous; styles 4.5-5.6 mm long, style branches 0.8-1.2 mm long; **disk achenes** 3.3-4.2 mm long, 1.3-1.7 mm wide, biconvex, obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns sometimes with 2-5 squamellae, awns slender, stramineous, sometimes suffused with purple, deciduous, subequal, 2.5-4 mm long, squamellae free, 0.4-1 mm long, same color as awns, somewhat deciduous; n = 17.

Phenology. Flowering throughout the year. Major flowering period at the end of the rainy season, February to April.

Distribution (Fig. 47). Abundant around the cities of Cajamarca and Santiago de Chuco in Cajamarca and La Libertad Departments respectively. Sporadic along the Hualgayoc-Bambamarca road and further NW along the same road around the town of Huambos in central Cajamarca Department; 2000-3400 m.

Pappobolus microphyllus is a morphologically variable species, typical of dry, exposed hills, disturbed habitats and Jalca regions of northern Peru. This morphological variation is discretely confined to four major assemblages, here recognized as varieties, which are restricted to specific areas within the range of the species.

This species can be recognized by the small ovate, oblong or trullate leaves, the densely lanate white or greenish-white abaxial leaf surfaces and small heads. It is closely related to P. subniveus

from which it can be separated by its lanceolate leaves and ligule color, which in this species is light yellow as opposed to the deep yellow to golden yellow ligules common to P. microphyllus. Another important character is the consistently larger head and narrower and longer ligules of P. subniveus.

KEY TO THE VARIETIES OF Pappobolus microphyllus.

1. Leaves linear, 4-7 mm long, 1.5-2.5 mm wide; phyllaries lanceolate to linear, densely lanate and silvery-white abaxially. 28b. P. microphyllus var. dillonii.
1. Leaves oval, oblong, ovate to trullate, 6-25 mm long, 3-11 mm wide; phyllaries ovate or oblong never linear.
   2. Leaves ovate to lanceolate, abaxial surface densely lanate and yellowish-green; leaves smaller and fewer upwards toward the capitulescence. 28c. P. microphyllus var. liberus.
   2. Leaves ovate to oblong, lanceolate, rarely linear, abaxial surface densely lanate or sericeous gray or white; leaves similar in size and number throughout stem and capitulescence.
      3. Leaves ovate to oblong, adaxial surface moderately sericeous, grayish-green, abaxial surface densely sericeous, white or gray. 28d. P. microphyllus var. soukupii.
      3. Leaves ovate, lanceolate or linear, adaxial surface sparsely to moderately strigose green, abaxial surface

densely lanate, white.

28a. P. microphyllus var. microphyllus.

28a. Pappobolus microphyllus var. microphyllus.

Leaves oval, lanceolate or ovate, adaxial surface dull green and moderately strigose, abaxial surface densely lanate white; **blades** 4-22 mm long, 2-9 mm wide; **phyllaries** in 4 graduated series, first series 4-6.5 mm long, 1.7-2.5 mm wide, lanceolate to oblanceolate or obovate, base indurated, light greenish-stramineous and glabrous adaxially, densely lanate white abaxially, herbaceous apex reflexed, light green and sparsely strigose adaxially, densely lanate white abaxially, second and third series 4-9.5 mm long, 1.8-3.7 mm wide, lanceolate, oblong, or obovate to spatulate, base slightly indurated, light green or stramineous and glabrous adaxially, stramineous suffused with green and glabrous to sparsely tomentose abaxially, herbaceous apex appressed, light green and sparsely strigose adaxially, sparsely to densely lanate white abaxially, fourth series 4.5-9 mm long, 1.3-1.8 mm wide, similar in shape, size and pubescence to previous series, but differing by having a smaller herbaceous apex with a larger dark green or brownish-stramineous area, some phyllaries somewhat chartaceous and hyaline; n = 17.

Phenology. Flowering throughout the year. Major flowering period February to April

Distribution (Fig. 47). Abundant in the valley of the city of Cajamarca and along the road Pacasmayo-Cajamarca between the town of San Juan and the city of Cajamarca; 2450-3100 m.

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Cajabamba, entre Cajabamba y Lluchubamba, ladera, 3050 m, 17 Nov 1983, Sagástegui et al. 11216 (HUT, TENN); Prov. Cajamarca, Puylucana, arriba de Baños del Inca, 2650 m, 17 Aug 1984, Sagástegui et al. 12005 (F, TENN); 5 km al S de Cajamarca, 2800 m, 22 Mar 1984, Sánchez Vega 3261 (F); Arboretum Chancay II de CICAFOR, entre Chancay y Valle Condebamba 2450 m, 29 Mar 1981, Sánchez Vega et al. 2397 (CPUN); entre el Gavilán y San Juan, siguiendo la carretera Cajamarca-Pacasmayo, 2500 m, 18 May 1986, Sánchez Vega 4055 (F); 22.5 km S of Cajamarca on road to Chilete, 2740 m, 19 Jan 1983, Dillon et al. 3033 (F, TEX); 11 km NE of Cajamarca, on road to Celendín, 2800 m, 4 Jan 1979, Dillon & Turner 1551 (F, MO, TEX); Chotén, en el Arboretum CICAFOR, 2990 m, 23 May 1981, Sánchez Vega et al. 2540 (CPUN); 3 km from the intersection of the road to Polloquito and the road to la Encañada on road to Polloquito, 3030 m, 13 Mar 1988, Panero & Sánchez Vega 1275 (TENN), 1276 (TENN); Km 25 of the road Cajamarca-Cajabamba, 2520 m, 15 Mar 1988, Panero et al. 1293 (TENN), 1296 (F); Bellavista, entre Cajamarca y Cumbemayo, 2850 m, 25 May 1976, Sánchez Vega et al. 1854 (CPUN); alrededores de Namora, ladera abierta, 2600 m, 16 Aug 1973, Sagástegui 7739 (F, HUT, MO, US); Baños del Inca, May 1958, Soukup 4632 (F, US); Prov. de Cajamarca, Arriba de San Juan (km 145), al borde de la carretera, 2600 m, 16 Jun 1981, López 8737 (F, HUT); Caserío Otuzco, 2700 m, 16 Jun 1975, Sagástegui et al. 8050 (MO, SI, TEX); 4 km N of Baños del Inca on road to Celendín, 2840 m, 7 Mar 1988, Panero 1124 (GRI, MEXU, TENN), 1125 (F, SI, UC, US), 1127 (TENN), 1128 (GRI, S); 6 km N of Baños del Inca on road to Celendín, 2920 m, 7

Mar 1988, Panero 1132 (MO), 1133 (TENN), 1134 (TENN), 1135 (TENN); 25 km km N of Cajamarca on road to Celendín, 3050 m, 7 Mar 1988, Panero 1143 (F, GRI, MO, QCA, TENN, US); 5 km N of Cajamarca on road to Bambamarca, 8600 ft, 8 Jan 1983, King & Bishop 9104 (K, US); along the road Cajamarca-Pacasmayo at the intersection of this road and the trail to Yumagual, 8 Mar 1988, 2750 m, Panero & Sánchez Vega 1174 (TENN), 1175 (TENN), 15 Mar 1988, Panero & Eriksen 1298 (TENN), 1299 (TENN); 11 km E of Cajamarca on road to Pacasmayo, 2950-3100 m, 2 Jul 1987, Panero et al. 864 (F, MO, UC), 865 (B, COL, MA, MEXU, SI); 9 Mar 1988, Panero 1177 (F, TENN, US), 1178 (CAN, TENN), 1179 (SI), 1180 (TENN), 1181 (TENN), 1182 (TENN), 1183 (NY), 1184 (MO), 1185 (TENN), 1186 (TENN), 1187 (GRI), 1188 (TENN); Prov. Celendín Pumarrume, 2850 m, 30 Jul 1985, Mostacero et al. 1002 (HUT), 1022 (F, TENN); Prov. Hualgayoc, entre Bambamarca y Hualgayoc, en ladera rocosa, 2720 m, 27 May 1965, López & Sagástegui 5493 (HUT, LP); Bambamarca, 2600 m, 28 Jun 1968, Soukup & Carmona 4939 (US).

This variety can be distinguished from the other three by its graduated involucre with broadly ovate to oblong phyllaries that normally cover the pales. The phyllaries tend to be copper-stramineous when dry with a conspicuous tuft of white, lanate pubescence at the reduced herbaceous apex. The leaves are very variable and can be narrowly lanceolate to oblong or suborbicular but their abaxial surface tends to dry bluish-green, a character elsewhere seen only in P. subniveus. As discussed above, the overall morphology of this taxon is very similar to P. subniveus.

28b. Pappobolus microphyllus var. dillonii Panero var. nov.——TYPE: PERU. La Libertad: Prov. Huamachuco, 20 km W of Huamachuco, 3400 m, 7 Jan 1983, Dillon et al. 2805 (holotype: F!; isotypes: TEX!, US!).

Pappobolus microphyllus var. dillonii differt a nominata varietate. Habet linearia folia et phyllaria.

Leaves linear, adaxial surface dull green and sparsely strigose, abaxial surface densely lanate white; **blades** 4-7 mm long, 1.5-2.5 mm wide; **phyllaries** in 4 subequal series, all series 6-7.5 mm long, 1.6-1.9 mm wide, narrowly lanceolate to linear, base indurated, stramineous and glabrescent adaxially, sparsely to densely lanate-sericeous silver abaxially, herbaceous apex appressed, dark green and sparsely strigose adaxially, densely lanate-sericeous silver abaxially; Chromosome number unknown.

Phenology. Collected in flower and fruit in January.

Distribution (Fig. 47). Known only from the type locality; 3400 m.

Pappobolus microphyllus var. dillonii is a very distinctive variety. It can be easily recognized by the nearly linear small leaves which have heavily revolute margins. The phyllaries are linear to oblong and densely pubescent silvery-white. These characters coupled with the delicate and weak habit and small heads are not found in any other taxon within the genus.

This variety honors its collector, Michael O. Dillon, curator at

the Field Museum of Chicago. His excellent collections of South American Asteraceae have been instrumental in obtaining a better understanding of this family's diversity in Peru.

28c. Pappobolus microphyllus var. liberus Panero, var. nov.——TYPE: PERU. La Libertad: Prov. Santiago de Chuco, carretera Santiago de Chuco-Cachicadán, 2700 m, 14 Jun 1984, Sagástegui et al. 11820 (holotype: F!; isotypes: HUT!, NY!, TENN!).

Pappobolus microphyllus var. liberus differt a nominata varietate. Habet pauciora folia consociata una cum synflorescentia et minora, minus pubescentia phyllaria non tegentia paleas.

Leaves ovate to lanceolate sometimes trullate, adaxial surface dull green and moderately strigose, abaxial surface densely lanate yellowish-green; **blades** 10-25 mm long, 4-11 mm wide; **phyllaries** in 4 somewhat graduated series, first series 3.2-3.5 mm long, 1-1.5 mm wide, lanceolate to oblanceolate, base indurated, light green-stramineous and glabrous adaxially, densely lanate white abaxially, herbaceous apex slightly reflexed, light green and sparsely strigose adaxially, densely lanate greenish-white abaxially, second, third and fourth series 3.9-6 mm long, 1-2.4 mm wide, trullate, base slightly indurated, light green or stramineous and glabrous adaxially, brownish stramineous to dark green and glabrous to sparsely tomentose abaxially, herbaceous apex appressed, light green and sparsely strigose adaxially, sparsely to densely lanate white or greenish-white abaxially; Chromosome number unknown.

Phenology. Collected in flower and fruit in June. Probably

flowering sporadically throughout the year.

Distribution (Fig. 47). Known from the valley of the city of Santiago de Chuco in central La Libertad Department; 2700-3000 m.

SPECIMENS EXAMINED. PERU. LA LIBERTAD: Prov. Santiago de Chuco, alrededores de Santiago de Chuco, 2800 m, 13 Jun 1984, Sagástegui et al. 11786 (F, NY); Carretera Santiago de Chuco-Cachicadán, al borde del camino, 3000 m, 8 Jun 1953, López 1955 (HUT, US); Mollepata, 2900 m, 20 Jun 1954, López 2338 (HUT).

This variety is easily recognized by the densely lanate greenish-white abaxial leaf surfaces, the conspicuous reduction in the number of leaves along the peduncle upwards toward the head, and the distinctive phyllaries which tend to be dark greenish-black, glabrescent, and only densely pubescent white on the very reduced herbaceous tip and around the rim. It can readily be distinguished from the nominal variety by its protruding pales which are in fruit approximately twice as long as the involucre.

All the specimens collected of this variety are located around the city of Santiago de Chuco in La Libertad Department. It is named for this Peruvian Department.

28d. Pappobolus microphyllus var. soukupii Panero, var. nov.——TYPE: PERU. Cajamarca: Prov. Chota, Huambos, ± 2000 m, 9 Sep 1956, Soukup 4548 (holotype: US!).

Pappobolus microphyllus var. soukupii differt a nominata

varietate. Habet opposita folia et perviridia vel nigra appressa phyllaria.

Leaves oval to oblong, adaxial surface greenish-blue gray and moderately sericeous, abaxial surface lanate-sericeous white to gray; **blades** 8-17 mm long, 2.5-6 mm wide; **phyllaries** in 4 somewhat graduated series, first series 3.2-3.8 mm long, 2-2.4 mm wide, lanceolate, base indurated, light greenish-stramineous and glabrous adaxially, sparsely tomentose whitish-gray, sometimes dark green and glabrous abaxially, herbaceous apex appressed, moderately tomentose grayish-white on both surfaces, second, third and fourth series 4-6.5 mm long, 2.3-2.8 mm wide, lanceolate, base slightly indurated, light green to stramineous and glabrous adaxially, brownish-stramineous to dark green and glabrous abaxially, herbaceous apex appressed, light green, sparsely sericeous adaxially, sparsely to moderately tomentose white or greenish-white abaxially; Chromosome number unknown.

Phenology. Collected in flower and fruit in September.

Distribution (Fig. 47). Known only from the type locality; 2000 m.

This variety is the most distinctive of the four and it exhibits moderately to densely sericeous or lanate-sericeous leaves and lanceolate phyllaries. It can be distinguished from the other varieties by its opposite phyllotaxy which is also maintained in the capitulescence, a condition never observed in the other varieties. The name honors its collector, J. Soukup.

29. Pappobolus subniveus (S. F. Blake) Panero, comb. nov. Helianthus

subniveus S. F. Blake, Contr. U.S. Natl. Herb. 22:621. 1924. Helianthopsis subnivea (S. F. Blake) H. Robinson, Phytologia 44:266. 1979. Helianthus niveus Hieron, Bot. Jahrb. Syst. 21:350. 1895, not Helianthus niveus (Benth.) T. S. Brandegee, Proc. Calif. Acad. Sci. 2:173. 1889.——TYPE: PERU. Cajamarca: Prov. Celendín, around Celendín, between Pacasmayo and Moyobamba, 3200 m, Stuebel 34d (holotype: B, destroyed, photos: GH!, TEX!; lectotype, here designated: fragment US!, photos: GH!, TEX!).

Open, monocaulic, weak shrubs 2-5 dm tall when young, profusely branched, compact, cushion-like 50-70 cm tall when mature; **stems** terete, soft brown and glabrous, herbaceous parts, densely lanate brownish-white to white, trichomes white, multicellular, tapered, 3.5-6 mm long; **leaves** opposite and/or alternate depending on individual and growth stage, triplinerved, lanceolate, to linear, adaxial surface dull white-green and moderately to densely strigose-sericeous, trichomes white, multicellular, tapered, 0.5-1 mm long, abaxial surface densely lanate white, trichomes white, multicellular, tapered, 0.2-0.6 mm long; sessile glandular trichomes 200-400/cm^2; **blades** 10-40 mm long, 2-9 mm wide, similar in size throughout stem and capitulescence, apex acute-acuminate, base obtuse, margin entire, revolute; petioles 3-12 mm long, canaliculate, glabrous to moderately strigose-sericeous adaxially, densely lanate abaxially; **capitulescences** monochasial thyrsoid, with 1-12+ heads, peduncles 10-85 mm long, densely lanate, trichomes as stem; **heads** 9-15 mm across, 12-15 mm high, broadly campanulate to

hemispherical; **receptacles** 3.8-7.7 mm in diameter in fruit, convex; **phyllaries** 26-36 in 4 graduated series, first series 7.5-15 mm long, 1.8-3.4 mm wide, lanceolate to linear, base indurated, light green and glabrous to sparsely strigose adaxially, densely lanate white abaxially, herbaceous apex reflexed, light greenish-white and moderately strigose adaxially, densely lanate white abaxially, margins densely lanate, second and third series 11-15 mm long, 2.5-4 mm wide, lanceolate to oblong, base indurated, light greenish-stramineous and glabrous to sparsely strigose adaxially, sparsely to densely lanate white abaxially, herbaceous apex reflexed to appressed, light greenish-white and moderately strigose adaxially, densely lanate white abaxially, margins densely lanate, sometimes revolute, fourth series 8.5-13 mm long, 1.5-3.5 mm wide, oblong, somewhat chartaceous throughout, sometimes base slightly indurated, light greenish-stramineous, with several dark green longitudinal bands and glabrous to glabrescent adaxially, basal half light greenish-stramineous and glabrous, distal half densely lanate white, margins glabrous to lanate; **pales** 8-8.7 mm long, 2.8-3.6 mm wide, ovate, conduplicate, shallowly to prominently (especially inner ones) keeled lengthwise, covered by phyllaries, stramineous with several dark green or brown longitudinal bands of various wifth, bands coalescing at apex, glabrescent distally otherwise glabrous, apex coriaceous, acute, pointed to slightly curved inward, dark greenish-black; **ray flowers** 12-19, corolla light yellowish-green, sometimes apex blackish abaxially, limb 10-26 mm long, 3.5-6 mm wide, narrowly oval, moderately puberulent on veins of abaxial

surface, apex acute, bifid, tube 1.1-1.6 mm long, moderately puberulent; **ray ovaries** 2.6-3.1 mm long, biconvex or triquetrous, glabrous, epappose; **disk flowers** 95-140, protruding 1-1.5 mm beyond pales, corollas yellowish-green, cylindrical, throat 3.7-4.7 mm long, 1.1-1.4 mm wide at base and at junction with lobes, veins orange and discernable the whole length of the throat, densely puberulent at base, otherwise sparsely puberulent, tube 0.5-1 mm long, light yellowish-green, glabrous, lobes 0.7-0.9 mm long, deltoid, yellowish-green, sometimes black abaxially, glabrescent abaxially; anthers 2.1-2.8 mm long, yellowish-brown or black, appendages suborbicular-lanceolate, stramineous; styles 5.2-5.4 mm long; style branches 1.2-1.3 mm long; **disk achenes** 3-3.6 mm long, 1.3-1.6 mm wide, biconvex, obovate, with two diminutive shoulders, shiny black or mottled, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.4-4 mm long; $\underline{n}$ = 17.

Phenology. Flowering throughout the year.

Distribution. (Fig. 48). Known from the valley of the Pampa de la Culebra and adjacent mountains surrounding the town of La Encañada in south-central Cajamarca Department. Also growing in the small valley of the Cumbemayo peak NW of the city of Cajamarca; 2600-3550 m. Growing with Acaena, Barnadesia dombeyana Less., Calceolaria argentea H. B. K., Chaptalia, Coreopsis obovatifolia Sagástegui, C. senaria S. F. Blake & Sherff, Cosmos paucedanifolius Wedd., Satureja sericea, Stenomesson, and Viguiera szyszylowiczii, among others.

Vernacular Name. Llune. The people of the area use the pink resinous exudate found at the base of the trunk to cover small wounds

to hasten healing. According to the local lady who explained to me the proper use of the resin: "Llune is the medicine of the poor".

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Cajamarca, La Encañada, 2750 m, 17 Aug 1984, Sagástegui et al. 12014 (F, HUT, NY); Cumbemayo Peak, approximately 21 km E of the City of Cajamarca, from parking area follow Inca aqueduct for 1 km then right along a wide gorge for approximately 1 km, just 3 plants, 3550 m, 15 Mar 1988, Panero et al. 1310 (GRI, TENN, US); Pampa de la Culebra, cerca de la Encañada, 2900 m, 17 Jun 1975, Sagástegui et al. 8078 (F, HUT, TENN, MO); on road to Celendín, 31 km E of Cajamarca, 3240 m, 16 May 1964, Hutchison & Wright 5114 (F, K, MICH, MO, UC, US); 17 km N of Cajamarca on road to Celendín, 3060 m, 7 Mar 1988, Panero 1136 (MA, MEXU, MO, SI, TENN), 1137 (TENN); 20 km N of Cajamarca on road to Celendín, 2880 m, 7 Mar 1988, Panero 1139 (TENN), 1140 (F), 1141 (TENN); 22 km N of Cajamarca on road to Celendín, 2990 m, 7 Mar 1988, Panero 1142 (B, COL, K, MICH, NY); 27 km N of Cajamarca on road to Celendín, 3130 m, 7 Mar 1988, Panero 1144 (TENN, UC); 29 km N of Cajamarca on road to Celendín, 3170 m, 7 Mar 1988, Panero 1145 (GRI, TENN, US); 31 km N of Cajamarca on road to Celendín, 3250 m, 7 Mar 1988, Panero 1146 (TENN); 39 km N of Cajamarca on road to Celendín, 3420 m, 2 Jul 1987, Panero et al. 862 (B, C, CAN, GRI, RB, S, TENN, US), 7 Mar 1988, Panero 1148 (F, MO, TENN); Km 61 de la carretera Cajamarca-Celendín, 3350 m, 10 Nov 1984, Cowan et al. 4418 (TEX); 30 km NE of Cajamarca along the road to Celendín, 10,000 ft, 9 Jan 1983, King & Bishop 9133 (UC, US); surroundings of Cajamarca, 2700-3700 m, 13 Dec 1985, Becker & Terrones

239 (US), 11 Sep 1986, 1826 (US); 32 km E of Cajamarca, 13 km W of La Encañada, 3000 m, 15 Jan 1983, Dillon et al. 2970 (F); Prov. Celendín, vicinity of Celendín, 2625 m, 3 Jun 1936, Woytkowski 21 (F).

Pappobolus subniveus is a very common species of central Cajamarca Department. Interestingly, this abundance is only in a very restricted and small area just around the town of La Encañada along the Cajamarca-Celendín road. It is certainly puzzling that a species that can grow and cover unworked wheat fields and any disturbed area with notable success has such a small range. Another aspect of this species is the difference in habit in disturbed and non-disturbed areas (see Morphology: Habit). This species also exhibits the shortest internodes in the genus. This condition is responsible for the compact and tight growth typical of undisturbed populations.

In the field this species is very easy to recognize by the light yellow ligule color unique within the genus. Its overall morphology indicates a very close relationship with P. microphyllus (see discussion under that species).

30. Pappobolus cajamarcensis Panero, sp. nov.——TYPE: PERU. Cajamarca: Prov. Cajamarca, 7 km from the intersection of the road to Polloquito and the road La Encañada-Celendín, on road to Polloquito, then 2 km by foot to nearby mountains, very rare, 3130 m, 13 Mar 1988, Panero & Sánchez Vega 1282 (holotype: F!; isotypes: C!, CPUN!, K!, MA!, MEXU!, MO!, QCA!, SI!, TENN!, USM!, US!).

Pappobolus cajamarcensis differ a P. subniveus. Habet folia cum glabris, nitidis, adaxialibus paginis, longiora internodia, maiora et latiora phyllaria et aureos radiales flores.

Weak, open shrubs 10-15 dm tall; **stems** terete, glabrous, dull to shiny brown, herbaceous parts shiny brown-green and glabrous to sparsely floccose towards growing apex, trichomes white, multicellular, tapered, 0.5-1.2 mm long; **leaves** alternate, triplinerved, lanceolate, adaxial surface shiny dark green and glabrous or glabrescent, trichomes white, multicellular, tapered, 0.1-0.2 mm long, abaxial surface densely lanate white, trichomes white, multicellular, tapered, 0.3-0.5 mm long; sessile glandular trichomes 50-100/cm^2 or absent; **blades** 12-40 mm long; 1.8-9.5 mm wide, similar in size throughout stem and capitulescence, apex acuminate, base obtuse, margins entire, revolute; petioles 3-10.5 mm, canaliculate, glabrous adaxially, moderately lanate-floccose abaxially; **capitulescences** monochasial thyrsoid, with 1-18+ heads, peduncles 35-55 mm long, sparsely floccose, trichomes as stem; **heads** 10-19 mm across, 12-16 mm high, broadly campanulate to hemispherical; **receptacles** 5.5-9 mm in diameter in fruit, convex; **phyllaries** 23-30 in 4 graduated series, first and second series 10-16.5 mm long, 2.2-4 mm wide, lanceolate, base indurated, light green and glabrous adaxially, light green with several dark green longitudinal bands and glabrescent abaxially, herbaceous apex strongly reflexed, light green and glabrous adaxially, sparsely lanate white abaxially, margins glabrous to moderately lanate and conspicuously revolute at herbaceous apex, third series 14.5-18.5 mm long, 3.5-4.2 mm wide, oblong, base indurated,

light greenish-stramineous with several dark green longitudinal bands and glabrous on both surfaces, herbaceous apex appressed, somewhat chartaceous, light green and glabrous adaxially, moderately lanate white abaxially, margins glabrous to lanate, fourth series 13.5-16.5 mm long, 2.6-4 mm wide, similar in morphology, color and pubescence to previous series; **pales** 7.7-8.6 mm long, 3-3.6 mm wide, ovate, conduplicate, shallowly to prominently keeled lengthwise, covered by phyllaries, stramineous with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrous abaxially, apex coriaceous, acute, pointed to slightly curved inward, dark green or blackish; **ray flowers** 15-18 corolla golden yellow, sometimes apex blackish abaxially, limb 21.5-24.5 mm long, 6-7.5 mm wide, narrowly oval, sparsely to moderately pubescent on veins of abaxial surface, apex acute to rounded, bifid, tube 1-1.4 mm long, sparsely puberulent; **ray ovaries** 1.9-2.2 mm long, biconvex or triquetrous, glabrous, epappose or with a single awn 2.8-3 mm long; **disk flowers** 72-115, protruding 1-1.5 mm beyond pales, corollas deep yellow-green, narrowly campanulate, throat 4.3-4.6 mm long, 1.4-1.6 mm wide at base, 1.7-1.9 mm wide at junction with lobes, veins orange and discernable the whole length of the throat, sparsely puberulent, with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.4 mm long, tube 1-1.2 mm long, yellowish-green, glabrous, lobes 0.8-1.3 mm long, narrowly deltoid, yellowish-green, blackish abaxially, glabrescent abaxially; anthers 2.7-2.9 mm long, black, appendages 0.4-0.5 mm long lanceolate, black or stramineous-black; styles 5.9-6.5 mm long, style branches 1.4-1.7 mm long; **disk**

achenes 3.4-4.2 mm long, 1.3-1.6 mm wide, biconvex, obovate, with two diminutive shoulders, shiny black rarely mottled, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 3-4.3 mm long; n = 17.

Phenology. Collected in flower in March and April; probably flowering sporadically throughout the year.

Distribution. (Fig 48). Known only from dry, exposed hillsides NE of the town of Polloquito in central Cajamarca Department. The only two plants found were growing at the ecotone between a humid riverbank and the xerophytic, heavily disturbed hills; 3000-3100 m.

SPECIMEN EXAMINED. PERU. CAJAMARCA: Hacienda Polloquito, distrito Namora, 3100 m, 1 Apr 1967, Sánchez Vega 300 (CPUN, F, LP, TENN).

Pappobolus cajamarcensis is a very rare and elusive species of the dry hills overlooking the Pampa de la Culebra in central Cajamarca Department. It possesses a straggly and open habit that conspicuously contrasts with the more compact habit observed in the phenetically similar P. subniveus. In addition, this species has essentially glabrous and shiny adaxial leaf surfaces, rare in the genus and only seen elsewhere in P. discolor and P. decumbens. Another important distinguishing feature of this species are the broadly ovate to suborbicular herbaceous apices of the inner phyllaries which effectively enclose the disk flowers until anthesis. This morphology is somewhat reminiscent of the Mexican species of Viguiera subg. Amphilepis.

31. Pappobolus discolor (S. F. Blake) Panero, comb. nov. Helianthus discolor S. F. Blake, J. Wash. Acad. Sci. 16:220. 1926. Helianthopsis discolor (S. F. Blake) H. Robinson, Phytologia 44:262. 1979.——TYPE: PERU. Huánuco: eastern side of canyon at Llata, 2135 m, 21 Aug 1922, Macbride & Featherstone 2240 (lectotype, here designated: F!; isolectotypes: GH!, K!, US!).

Much-branched, compact shrubs 3-15 dm tall; **stems** terete, soft brown and glabrous, herbaceous parts shiny brown-green and brown-canescent to velutinous upwards toward growing apex, trichomes white, multicellular, tapered, 0.3-0.7 mm long; **leaves** alternate or opposite, triplinerved or mononerved, narrowly lanceolate, adaxial surface dull, rarely shiny brownish-green, sparsely to moderately strigose, trichomes white, multicellular, tapered, 0.2-0.4 mm long, abaxial surface densely lanate white, trichomes white, multicellular, tapered, 0.3-0.5 mm long; sessile glandular trichomes confined to abaxial surface 200-500/cm^2; **blades** 6-35 mm long, 1.5-7 mm wide, smaller in size upwards toward the capitulescence, apex acuminate to acute, base obtuse to attenuate, margins entire and revolute; petioles 1-5.5 mm long, canaliculate, densely sericeous on both surfaces; **capitulescence** monochasial or dichasial thyrsoid, with 1-10+ heads, peduncles 65-155 mm long, sparsely to densely velutinous, pubescence denser below the heads, trichomes as stem; **heads** 7-12.5 mm across, 9-16.5 mm high, campanulate to hemispherical; **receptacles** 4.5-7.5 mm in diameter in fruit, convex; **phyllaries** 20-28 in 3-4 graduated series, first series 4.5-5.2 mm long, 1.4-1.7 mm wide, lanceolate, base indurated, light green and glabrous

adaxially, light to dark green with several dark green longitudinal bands and glabrescent abaxially, herbaceous apex appressed to slightly reflexed, light to dark green and strigose adaxially, canescent brown to light green or densely lanate white and sparsely tomentose, sericeous or lanate abaxially, margins glabrescent to moderately villous, sometimes revolute, second series 6.5-8 mm long, 2.7-3.2 mm wide, ovate-lanceolate or lanceolate, base indurated with several shallow ribs, light greenish-stramineous adaxially or dark greenish-black and glabrescent to sparsely tomentose abaxially, herbaceous apex appressed, light green and puberulent to strigose adaxially, canescent-tomentose green or densely lanate white abaxially, margins glabrescent to villous, sometimes revolute, third and fourth series 5.5-9.5 mm long, 1.3-3.2 mm wide, both series similar to second series in shape, color and pubescence, but differing by having a smaller herbaceous apex with a consequently larger dark greenish-black, glabrous or glabrescent indurated base, innermost phyllaries sometimes resembling pales, somewhat chataceous, margins puberulent, sparsely villous or glabrous; **pales** 6-10 mm long, 1.5-4.3 mm wide, ovate, conduplicate, slightly keeled lengthwise, protruding 1.5-2 mm beyond phyllaries, stramineous with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrous, sometimes with a few trichomes along the fold and tip, apex coriaceous, acuminate, pointed, dark greenish-black; **ray flowers** 11-19, corolla golden yellow, apex blackish abaxially, limb 11.5-17 mm long, 4.5-6.2 mm wide, narrowly oval, sparsely puberulent on veins of abaxial surface, apex acute, bifid or trifid, tube yellow, 0.7-1.2 mm long, moderately puberulent; **ray**

ovaries 1.8-2.5 mm long, triquetrous, glabrous, epappose; **disk flowers** 55-105, protruding 1-2 mm beyond pales, corolla golden yellow, narrowly campanulate, throat 3.5-5.5 mm long, 0.8-1.1 mm wide at base, 1-1.2 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely puberulent with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.4 mm long, tube 0.7-1.2 mm long, yellowish-green, glabrous, lobes 0.5-0.7 mm long, deltoid, deep yellow adaxially, black abaxially, sparsely puberulent abaxially; anthers 2.4-3.2 mm long, thecae black or brownish, appendages 0.5-0.7 mm long, black or black-stramineous; **disk achenes** 3.5-4.3 mm long, 1.6-2 mm wide, biconvex, obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.8-3.2 mm long; n = 17.

Phenology. Flowering from March to August.

Distribution (Fig. 48). Widely scattered in Jalca, dry hillsides or montane to high montane dry scrub or forests in central and northern Peru; 2100-3500 m.

SPECIMENS EXAMINED. PERU. ANCASH: Prov. Huaráz, 3 km SW of Huaráz on road to Lima, 3120 m, 4 Apr 1988, Panero & Galán 1367 (CPUN, TENN), 1368 (B, C, F, MA, MEXU, QCA, RB, SI, TENN, UC, US).—CAJAMARCA: Prov. Celendín, Celendín, 2600 m, 26 Jun 1969, Sagástegui 7339 (HUT).—LA LIBERTAD: Prov. Otuzco, Cerro Ragache (Salpo), 3500, 23 May 1984, Sagástegui et al. 11641 (F, TENN, US).

Pappobolus discolor is an elusive and apparently rare and widely scattered species. My collections in Ancash Department were totally serendipitous in contrast to my diligent search in the area of Celendín, Cajamarca Department in which I was unsuccessful.

Although this species can be recognized by the lanceolate and somewhat shiny leaf adaxial surfaces reminiscent of P. cajamarcensis and the ovate, somewhat appressed phyllaries, there are a few subtle differences that warrant special mention in light of the poor knowledge about the range and extent of morphological variation. Collections from Ancash Department, Panero & Galán 1367 and 1368 possess an opposite phyllotaxy all the way up to the capitulescence. In addition the phyllaries are much smaller and slightly more pubescent than those observed in the type collection. These collections are somewhat similar to those collected in La Libertad and Cajamarca Departments with the exception that the phyllotaxy in the latter collections is alternate.

Pappobolus discolor shares with P. decumbens a similar head morphology. The heads in both species have long pales that protrude significantly from the small involucre as well as disk flowers that protrude 1 to 2 mm beyond the pale apex. The leaves of P. discolor are mostly mononerved and narrowly lanceolate to linear, somewhat similar to those of P. decumbens, but not as wide as those of P. cajamarcensis and P subniveus.

32. Pappobolus decumbens Panero, sp. nov.——TYPE: PERU. Cajamarca: Prov. Hualgayoc, road Cajamarca-Hualgayoc-Chugur, 10-15 km

before Chugur take road to Perlamayo, until first river creek, then 3-5 km by foot to old school house, continue along right path to the gorge of the Perlamayo River for approximately 10-15 km, 3030 m, 20 Mar 1988, Panero & Sánchez Vega 1345 (holotype: F!; isotypes: CPUN!, GRI!, K!, MEXU!, QCA!, SI!, TENN!, US!).

Pappobolus decumbens differt a P. discolor. Habet linearia folia, disciformem achenii pappum cum pluribus deciduis aristis et parvas monochasiales thyrsoideas vel solitarias synflorescentias.

Low, prostrate, compact shrubs 1-5 dm tall, composed of a dense central mat from where flowering shoots arise, these shoots densely covered by branchlets, which root as they reach the ground; **stems** terete, brown-gray and glabrous, somewhat succulent, herbaceous parts, shiny white-silver to brown, strigose to sericeous upwards toward growing apex, trichomes white, multicellular, tapered, 0.25-0.6 mm long; **leaves** alternate, mononerved, linear, adaxial surface shiny light to dark green and sparsely strigose-sericeous, trichomes white, multicellular, tapered, 0.25-0.35 mm long, abaxial surface whitish-green pubescent, sericeous, especially along the prominent central vein, trichomes white or greenish-white, multicellular, tapered, 0.4-0.7 mm long; sessile glandular trichomes absent; **blades** 10-60 mm long, 0.9-3.2 mm wide, similar in size and morphology throughout stem and capitulescence, apex acute to rounded, base attenuate, margins entire and heavily revolute; petioles 1.5-6.5 mm long, canaliculate, densely sericeous on both surfaces; **capitulescences** monochasial thyrsoid, rarely solitary, with 1-3 heads, peduncles 75-145 mm long, moderately

strigose to densely sericeous under heads, trichomes as stem; **heads** 9-11 mm across, 10-12 mm high, campanulate-hemispherical; **receptacles** 6.3-7.5 mm in diameter in fruit, slightly convex; **phyllaries** 23-36, in 3-4 subequal series, first series 4.5-7.5 mm long, 1.6-2.1 mm wide, lanceolate, base indurated, with one prominent rib, light green and sparsely sericeous adaxially, dark green, drying black and sparsely sericeous abaxially, herbaceous apex reflexed, light green and sparsely strigose adaxially, densely villous-sericeous silvery-white abaxially, margins tomentose, second series 4.9-6.8 mm long, 2.1-2.8 mm wide, ovate, base indurated, with 2-3 ribs, light green and glabrous adaxially, dark green, drying black and glabrous abaxially, herbaceous apex appressed, light green and puberulent adaxially, moderately to densely villous-sericeous silvery-white abaxially, margins tomentose, third and fourth series 5.9-6.5 mm long, 2.3-2.8 mm wide, and 4.9-7 mm long, 1.6-2.6 mm wide, respectively, both series similar to second series in shape, color and pubescence, but differing by having a smaller herbaceous apex with a consequently larger black and glabrous indurated base, innermost phyllaries sometimes resembling pales, margins puberulent to glabrous; **pales** 7.5-9.5 mm long, 2.5-3.8 mm wide, ovate, conduplicate, slightly keeled lengthwise, protruding 2-4 mm beyond phyllaries, stramineous with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrous sometimes with some trichomes along the fold and tip, apex coriaceous, acuminate, pointed, dark greenish-black; **ray flowers** 12-19, corolla golden yellow, sometimes apex blackish abaxially, limb 12.5-16.5 mm

long, 4.9-5.9 mm wide, narrowly oval, moderately puberulent on veins of abaxial surface, apex acute to rounded, bifid or trifid, tube yellow, 0.6-1 mm long, moderately puberulent; **ray ovaries** 1.4-2.5 mm long, trigonal, glabrous, with a pappus of 3-9 awns, 0.5-2.3 mm long; **disk flowers** 68-95, protruding 1-2 mm beyond pales, corollas golden yellow, narrowly campanulate-tubular, throat 4-4.5 mm long, 1.1-1.4 mm wide at base and at junction with lobes, veins orange and discernable the whole length of the corolla, essentially glabrous with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.4 mm long, tube 0.8-1.1 mm long, yellowish-green, essentially glabrous, lobes 0.7-1.2 mm long, deltoid, deep yellow, sometimes black abaxially, glabrescent abaxially; anthers 2.4-2.9 mm long, thecae black, appendages 0.6 mm long, lanceolate, stramineous; styles 5-6.3 mm long, style branches 1.3-1.7 mm long; **disk achenes** 2.8-3.7 mm long, 1.3-1.5 mm wide, biconvex, obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 4-10 awns and no squamellae, slender, stramineous, deciduous, subequal, 1.5-5 mm long; n = 17. Fig. 49.

Phenology. Flowering January to July. Probably throughout the year.

Distribution (Fig. 48). Scattered in Jalca and dry exposed hillsides of Cajamarca and La Libertad Departments; 2850-3350 m.

SPECIMENS EXAMINED. PERU. CAJAMARCA: Prov. Hualgayoc, Desvío carretera Chugur-Tingo-Perlamayo-Tambillo, borde de camino, 2850 m, 22 Jul 1986, Cabanillas 257 (CPUN, TENN); Prov. Cajamarca, Jalca de Kumulka, 3350 m,

17 Aug 1984, Sagástegui et al. 12288 (F).—LA LIBERTAD: 12 km SE of Otuzco/Huamachuco junction on road to Agallpampa, 2950 m, 6 Jan 1983, Dillon et al. 2758 (F).

Pappobolus decumbens is recognized by its linear leaves and decumbent habit. Another interesting feature of this species is its succulent stems which tend to root at contact with the soil.

Pappobolus decumbens shares with P. discolor a similar head and leaf morphology. They can be readily separated by the linear leaves and weak monochasial thyrsoid capitulescences of P. decumbens which contrast with the narrowly lanceolate, rarely linear leaves and the more profusely-branched capitulescences of P. discolor. The capitulescence character, although sometimes difficult to appreciate in incomplete herbarium specimens, is very useful to separate the two species. Pappobolus decumbens always has only one open flowering head per capitulescence at any given time and produces a second or third only after a very wide time interval. In the case of P. discolor the capitulescence is either dichasial or monochasial thyrsoid but with the difference that all the heads are simultaneously present and the time interval between flowering is negligible. On the other hand, P. decumbens exhibits some characters that are rarely seen in any other species; the habit is prostrate and weak, a condition sometimes observed in P. discolor, and the disk achene pappus is composed of a crown of deciduous awns similar to the pappus of P. woodsonianus and P. cinerascens, P. macranthus and P. mollicomus.

33. Pappobolus woodsonianus Cuatr., Ann. Missouri Bot. Gard. 52: 308-309. 1965.——TYPE: PERU. Amazonas: Prov. Chachapoyas, Caño de Santa Lucía just E of Chachapoyas, 2200-2400 m, 28 May 1962, Wurdack 584 (holotype: US!; isotype: GH!, F!, TEX!, UC!, USM not located).

Open shrubs 3-10 dm tall; **stems** terete, dark brown to black and glabrous, herbaceous parts densely tomentose-lanate white, trichomes white, multicellular, tapered, 0.2-0.6 mm long; **leaves** alternate or opposite, ovate-elliptical, adaxial surface dull dark green and moderately hirsute-strigose, trichomes white to hyaline, multicellular, tapered, 0.15-0.25 mm long, abaxial surface densely lanate white, veins contrastingly less pubescent, trichomes white to cream, multicellular, tapered, 0.3-0.6 mm long; sessile glandular trichomes on both surfaces, less than $1/cm^2$ on adaxial surface, $1200-1600/cm^2$ on abaxial surface; **blades** 1.2-3.5 cm long, 0.7-2 cm wide, similar in size and morphology throughout stem and capitulescence, apex acute, base obtuse, slightly attenuate along distal fifth of petiole, margins subentire to entire, rarely revolute; petioles 5-15 mm long, canaliculate, sparsely tomentose adaxially, densely lanate abaxially; **capitulescences** monochasial or dichasial thyrsoid, with 1-3 heads, peduncles 1.6-3.8 cm long, densely lanate trichomes as stem; **heads** 11-14 mm across, 8.5-13 mm high, broadly campanulate to slightly urceolate or hemispherical; **receptacles** 6-8 mm in diameter in fruit, slightly convex; **phyllaries** 22-33 in 4 somewhat graduated series, first and second series, 3.9-4.4 mm long, 1.6-2.1 mm wide, oblong to obovate, base indurated,

stramineous-green and glabrous adaxially, dark greenish-black and glabrescent abaxially, herbaceous apex very reduced, slightly rflexed or appressed, green and sparsely strigose adaxially, densely lanate white or tomentose-glandular somewhat farinose green-white abaxially, margins minutely velutinous, third series 5.8-8.5 mm long, 2.2-3.7 mm wide, similar in pubescence and morphology to previous series, fourth series 5.3-9.5 mm long, 1.7-2.2 mm wide, base slightly indurated, similar in pubescence and morphology to previous series, although innermost resembling pales in general aspect, somewhat chartaceous, glabrescent on both surfaces, margins glabrous to minutely ciliate; **pales** 8.5-9.2 mm long, 3-3.2 mm wide, ovate, conduplicate, strongly keeled lengthwise, protruding 2-4 mm beyond phyllaries, stramineous with several brown or green longitudinal bands of various width, bands coalescing at tip, glabrous or sparsely puberulent along fold and tip, apex coriaceous, acute, pointed to slightly curved inward, blackish; **ray flowers** 10-14, corolla yellow, limb 9-10.5 mm long, 4.5-5.5 mm wide, oval, moderately puberulent and glandular on veins of abaxial surface, apex acute to rounded, minutely bifid or trifid, tube 1.5-1.7 mm long, moderately puberulent and glandular; **ray ovaries** 2-2.5 mm long, triquetrous or biconvex, glabrous, epappose or with a pappus of 1 awn 2.3-2.5 mm long; **disk flowers** 35-115, flowers protruding 0.2-0.4 mm beyond pales, corollas yellow, narrowly campanulate, throat 4-5 mm long, 1-1.4 mm wide at base, 1.4-1.8 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, glabrous to sparsely puberulent with uniseriate multicellular glandular trichomes 0.05-0.1 mm long, tapered trichomes white to hyaline, 0.1-0.2

mm long, tube 0.9-1.2 mm long, yellowish-green, essentially glabrous, lobes 0.7-1.1 mm long, deltoid, deep yellow, glabrescent abaxially; anthers 2.6-3.1 mm long, thecae black, appendages 0.4-0.5 mm long, ovate, reddish-stramineous; styles 6-8 mm long, style branches, 1.4-1.8 mm long; **disk achenes** 3.4-3.8 mm long, 1.3-1.7 mm wide, biconvex, obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2-8 awns and no squamellae, slender, stramineous, deciduous, 1.4-3.6 mm long; n = 17.

Phenology. Collected in flower in May.

Distribution. (Fig. 50). Known from the canyons and small gorges E of the city of Chachapoyas in Amazonas Department, Peru; 2200-2400 m.

Pappobolus woodsonianus is an unusual and distinctive species of northeastern Peru. It is readily recognized by its ovate-elliptical, opposite leaves, loose and dark greenish-black involucre and disk achene pappus. Its overall morphology suggests a possible relationship with P. microphyllus especially its variety soukupii.

The disk achene pappus of several awns and no squamellae of P. woodsonianus is elsewhere only exhibited by the three original Pappobolus species named by Blake. These three species possess no other morphological characters to suggest a close relationship with P. woodsonianus. On the other hand, Pappobolus decumbens shares with P. woodsonianus a similar disk achene pappus and herbage pubescence. However, these two species can be readily separated by characters of the involucre, leaf morphology and phyllotaxy. The involucre of P. woodsonianus, which consists of large, conspicuously greenish-black and

sparsely pubescent phyllaries, contrasts highly with the much smaller involucre of P. decumbens. In addition, the species differ in leaf characters and phyllotaxy. Another distinguishing feature P. woodsonianus is the loosely-packed head that contains far fewer disk flowers for its size than in any other species in the genus.

34. Pappobolus davidii Panero, sp. nov.——TYPE: PERU. Ancash: Prov. Huaylas, Huascarán National Park, Auquispuquio area of ruins, 3800-3900 m, 7 Apr 1986, Smith et al. 11984 (holotype: TENN!; isotype: HUT!).

Pappobolus davidii differt ab P. argenteus. Habet longiores, glabrescentes vel lanatos pedunculos, foliorum margines integras vel serrulatas et minores radiales flores et capita.

Much-branched, low shrubs 3-7 dm tall; **stems** terete, soft brown, glabrous, herbaceous parts shiny brownish-green to sparsely velutinous-lanate white upwards toward growing apex, trichomes white, multicellular, tapered, 0.3-0.7 mm long; **leaves** alternate, triplinerved, lanceolate, adaxial surface dull brownish-green, sparsely to moderately strigose, trichomes white, multicellular, tapered, 0.2-0.4 mm long, abaxial surface moderately velutinous white, trichomes white, multicellular, tapered, 0.3-0.7 mm long; sessile glandular trichomes confined to abaxial surface 800-1000/cm^2; **blades** 35-43 mm long, 1.5-7 mm wide, similar in size throughout the stem and capitulescence, apex acuminate, to acute, base obtuse to attenuate, margins subentire to serrulate; petioles 4.5-5.5 mm long, somewhat

canaliculate, densely villous on both surfaces; **capitulescences** monochasial thyrsoid, with 3-10+ heads, peduncles 50-140 mm long, sparsely to densely velutinous, pubescence denser below the heads, trichomes as stem; **heads** 9-12.5 mm across, 9-15.5 mm high, hemispherical; **receptacles** 4.5-7.5 mm in diameter in fruit, convex; **phyllaries** 23-33 in 3-4 graduated series, first series 5-7.5 mm long, 2.0-2.5 mm wide, lanceolate, base indurated, light green and glabrous adaxially, light to dark green with several dark green longitudinal bands and glabrescent abaxially, herbaceous apex reflexed, light to dark green and strigose adaxially, moderately lanate to sparsely tomentose white abaxially, margins glabrescent to moderately villous, second series 6.5-8 mm long, 2.5-2.7 mm wide, ovate-lanceolate or lanceolate, base indurated, light greenish-stramineous adaxially or dark greenish-black and glabrescent to sparsely tomentose abaxially, herbaceous apex appressed or slightly reflexed, light green and puberulent to strigose adaxially, canescent-tomentose green or densely lanate white abaxially, margins glabrescent to villous, third and fourth series 5.5-9.5 mm long, 1.3-2.8 mm wide, both series similar to second series in shape, color and pubescence, but differing by having a smaller herbaceous apex with a consequently larger dark greenish-black, glabrous or glabrescent indurated base, innermost phyllaries sometimes resembling pales, somewhat chartaceous, margins puberulent, sparsely villous or glabrous; **pales** 8.5-10 mm long, 2.8-4.2 mm wide, ovate, conduplicate, slightly keeled lengthwise, protruding 1.5-2 mm beyond phyllaries, stramineous with several dark green or brown longitudinal bands of various width, bands coalescing at apex, glabrous abaxially,

sometimes with a few trichomes along the fold and tip, apex coriaceous, acuminate, pointed, dark greenish-black; **ray flowers** 14-19, corolla golden yellow, apex blackish abaxially, limb 9-14 mm long, 2.5-4 mm wide, oval, sparsely puberulent on veins of abaxial surface, apex acute, bifid or trifid, tube yellow, 0.7-1 mm long, moderately puberulent; **ray ovaries** 2-2.5 mm long, triquetrous, glabrous, epappose; **disk flowers** 65-105, protruding 1-2 mm beyond pales, corolla golden yellow, narrowly campanulate, throat 3.5-4.5 mm long, 1-1.2 mm wide at base, 1.2-1.5 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely puberulent, with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.4 mm long, tube 1.2-1.3 mm long, yellowish-green, glabrous, lobes 0.5-0.7 mm long, deltoid, deep yellow adaxially, black abaxially, sparsely puberulent abaxially; anthers 2.4-3 mm long, thecae black, appendages 0.5-0.7 mm long, ovate, black; **disk achenes** 3.5 ? mm long, 1.6 ? mm wide, biconvex, obovate, with two diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal 2.8-3.2 mm long; Chromosome number unknown.

Phenology. Collected in flower in April.

Distribution (Fig. 50). Known only from the type locality in the Cordillera Blanca of central Peru; 3800-3900 m.

According to David N. Smith (pers. comm.) this species is very common in the type locality in one of the many narrow canyons at the northern edge of the Huascarán National Park in the Cordillera Blanca

of central Peru. This species in its overall morphology resembles P. discolor and weak individuals of P. lanatus. It can be separated from these two species by the small, lanceolate leaves which do not have a conspicuously white abaxial leaf surface nor a heavily revolute margin.

This species honors its collector, David N. Smith, whose Flora of the Huascarán National Park will be of tremendous help to any botanist or phytogeographer interested in the area.

35. Pappobolus lanatus (Heiser) Panero, comb. nov. Helianthus lanatus Heiser, Brittonia 8:291. 1957. Helianthopsis lanata (Heiser) H. Robinson, Phytologia 44:264. 1979.——TYPE: PERU. Ancash: Prov. Bolognesi, Chiquián, 16 Apr 1949, Ferreyra 5808 (lectotype, here designated: US!; isolectotype: USM!).

Compact or open shrubs 4-12 dm tall; **stems** terete, soft brown and glabrous, herbaceous parts shiny brownish-green and glabrous or sparsely tomentose-velutinous to densely velutinous-lanate white towards growing apex, trichomes white, multicellular, tapered, 0.3-2 mm long; **leaves** opposite or alternate (especially those associated with the capitulescence), triplinerved, ovate to ovate-suborbicular, adaxial surface dull dark brownish-green and moderately hirsute-strigose, trichomes white or hyaline, multicellular, tapered, 0.15-0.25 mm long, abaxial surface densely lanate white, trichomes white, multicellular, tapered, 0.3-0.8 mm long; sessile glandular trichomes confined to abaxial surface 200-500/cm^2; **blades** 10-80 mm long, 4-50 mm wide, similar in size and morphology throughout stem and capitulescence, apex

acute or acuminate, base obtuse, sometimes slightly attenuate along distal fifth of petiole, margins entire, revolute; petioles 1-17 mm long, canaliculate, densely lanate on both surfaces; **capitulescences** monochasial thyrsoid, with 2-12+ heads, peduncles 25-140 mm long, densely lanate-velutinous, trichomes as stem; **heads** 10-17.5 mm across, 11-16 mm high, broadly campanulate to hemispherical; **receptacles** 6-9.5 mm in diameter in fruit, convex; **phyllaries** 20-32 in 4 graduated series, first series 5-17 mm long, 2.4-6.2 mm wide, ovate to lanceolate, base indurated, light green-stramineous and glabrous adaxially, dark greenish-black and glabrescent to sparsely tomentose abaxially, herbaceous apex strongly reflexed, foliaceous, dull green and moderately strigose-hirsute adaxially, densely lanate white abaxially, margins sparsely tomentose to densely lanate, second and third series 6-13.5 mm long, 1.8-3.5 mm wide, lanceolate-oblong, base indurated, stramineous and glabrous adaxially, dark greenish-black abaxially, herbaceous apex slightly reflexed or appressed, greenish white and moderately strigose-hirsute adaxially, densely lanate white abaxially, margins glabrous to densely lanate, fourth series 6.5-9.5 mm long, 1.8-2.6 mm wide, slightly chartaceous with no clear distinction between indurated and herbaceous parts, base stramineous and glabrous on both surfaces, apex greenish-white and sparsely lanate on both surfaces, margins glabrescent; **pales** 7-11 mm long, 2.8-3.8 mm wide, ovate, conduplicate, keeled lengthwise, covered by phyllaries or protruding 2-5 mm beyond phyllaries, stramineous with several dark green longitudinal bands of various width, bands coalescing at apex, densely puberulent at fold and apex, apex coriaceous, acuminate,

pointed or slightly curved inward, moderately tomentose silver-dark green or black; **ray flowers** 12-16, corolla golden yellow, apex blackish abaxially, limb 14.5-19.5 mm long, 6.5-9.5 mm wide, oval, moderately puberulent on veins of abaxial surface, apex acute to rounded, bifid or trifid, tube 0.6-1.4 mm long, yellow, moderately puberulent; **ray ovaries** 2-2.7 mm long, biconvex or triquetrous, glabrous, epappose or with a pappus of one awn 1.2-1.6 mm long; **disk flowers** 80-155, protruding 2-3 mm beyond pales, corollas golden yellow, narrowly campanulate to tubular, throat 3.8-5.5 mm long, 1-1.4 mm wide at base, 1-1.7 mm wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely puberulent with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.3 mm long, tube 0.7-1.2 mm long, yellowish-green, essentially glabrous, lobes 0.5-1.2 mm long, yellow, apices black abaxially, sparsely puberulent abaxially; anthers 1.6-3.4 mm long, thecae black or brownish-black, appendages 0.5-0.9 mm long, lanceolate, black or stramineous-black; styles 4.5-7.5 mm long, style branches 0.4-1.3 mm long; **disk achenes** 3.5-4.2 mm long, 1.3-1.7 mm wide, biconvex, obovate, with diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 3-3.8 mm long; $\underline{n}$ = 17.

Phenology. Flowering March to June

Distribution. (Fig. 50). Occasional along the canyon of the Rimac River in Lima Department. Also known from around the town of Chiquián at the headwaters of the Pativilca River and just north of the city of

Huaráz along the Santa River in Ancash Department. One collection from Yanahuanca in Cerro de Pasco Department from the eastern slopes of the Western Andean Range; 1800-3300 (-3500) m.

SPECIMENS EXAMINED. PERU. ANCASH: Prov. Bolognesi, Ainin, puente entre Chiquián y Aquia, 2900 m, 18 May 1950, Cerrate 758 (MO, TENN, USM), Ferreyra 7557 (US); Cerro San Jerónimo, arriba de Aquia, 3500-3600 m, 29 May 1962, Ferreyra 14493 (MO, TENN, USM); 8 km NE of Huaráz on road to Carhuáz, 2800 m, 5 Apr 1988, Panero & Galán 1398 (CPUN, F, GRI, MEXU, QCA, TENN, US); Jerusalem, cerro al E de Aquia, 3200-3260 m, 18 May 1950, Cerrate 724 (MO, TENN, USM), Ferreyra 7523 (MO, US).—CERRO DE PASCO: Prov. Daniel Carrion, Yanahuanca, 10,000 ft, 16-22 June 1922, Macbride & Featherstone 1171 (F, GH, US).—LIMA: Prov. Huarochirí, valley of Río Rimac, near Lima-La Oroya highway, ca 90 km E of Lima, 2800 m, 15-22 Mar 1942, Goodspeed & Weberbauer 33063 (MO, UC, US), 70 km E of Lima, 1850 m, 21-26 Apr 1942, Goodspeed 33121 (GH, UC, US); Infiernillo, Km 106 de la carretera Lima-La Oroya, 3200-3300, 19 Jun 1950, Ferreyra 7713 (MO, TENN, US, USM), 10 May 1952, Ferreyra 8311 (MO, TENN, USM), 17 Jan 1949, Ferreyra 5280 (LIL, US); Km 85 of the road Lima-La Oroya, 2650 m, 1 Apr 1988, Panero 1362 (B, CPUN, F, GRI, MA, MEXU, TENN, US); Km 95 of the road Lima-La Oroya, 3160 m, 1 Apr 1988, Panero 1363 (SI, TENN, UC); arriba de San Mateo, 3300 m, 15 May 1958, Cabrera & Farris 13432 (K, S, LP, TEX); Río Blanco, 3000-3500 m, 15-17 Apr 1929, Killip & Smith 21698 (F, US); Matucana, 12 Apr-3 May 1922, Macbride & Featherstone 345 (F,GH, US); entre San Matéo y Río Blanco, 3300-3400 m, 17 May 1959, Ferreyra 13602 (TENN, USM);

Infiernillo, sobre la carrereta Lima-La Oroya, 3000-3200 m, 15 May 1963, Ferreyra 14911 (TENN, USM).

Pappobolus lanatus is a common species of the Pacific drainage River canyons of the Departments of Lima and Ancash. This species can be easily recognized by its large heads and ovate to ovate-suborbicular leaves. It appears to be closely related to P. senex of the upper Huallaga River canyon of Huánuco Department with which it shares a similar leaf size and morphology and herbage pubescence. Most of the differences between these two species occur in the heads, which in P. lanatus are normally twice as large. An interesting specimen, Macbride & Featherstone 1171 from Yanahuanca, exhibits significantly smaller heads but they are still larger than those of P. senex, and the disk flower and pale size and morphology are within the lower size range for these structures in P. lanatus. The population of the valley of the Santa River differs considerably in several important morphological features from the populations of the Pativilca and Rimac River valleys. Panero & Galán 1398 exhibits an open and straggly habit, ovate leaves and smaller phyllaries, morphological features that depart considerably from the compact habit, ovate-suborbicular leaves and larger heads typical of the individuals of the other populations examined.

Many of the specimens of P. lanatus collected before Heiser's revision (1957) were misidentified as P. jelskii. Both species possess densely pubescent herbage and heads and opposite phyllotaxy. However, they can be easily separated by habit, which in P. lanatus is low in comparison to the large and compact shrubs of P. jelskii, and by the

pale apices which are pubescent and somewhat reflexed in P. lanatus as opposed to the glabrous, cream or stramineous, pointed pale apices of P. jelskii.

36. Pappobolus senex (S. F. Blake) Panero, comb. nov. Helianthus senex S. F. Blake, J. Wash. Acad. Sci. 16:220-221. 1926. Helianthopsis senex (S. F. Blake) H. Robinson, Phytologia 44:265. 1979.——TYPE: PERU. Huánuco: canyon slope at Mito, 2745 m, 8-22 Jul 1922, Macbride & Featherstone 1572 (lectotype, here designated: F!; isolectotypes: GH!, K!, S!, US!).

Compact shrubs 5-12 dm tall; **stems** terete, glabrous, dark brown with conspicuous creamy white lenticels, herbaceous parts drying brownish-red, glabrous or sparsely tomentose-velutinous to densely velutinous-lanate white upwards toward growing apex, trichomes white, multicellular, tapered, 0.3-5 mm long; **leaves** opposite or alternate (especially those associated with the capitulescence), triplinerved, ovate-suborbicular, adaxial surface dull brownish-green to brownish-red and moderately hirsute-strigose to sericeous, trichomes white or hyaline, multicellular, tapered, 0.15-1 mm long, abaxial surface densely lanate white, trichomes white, multicellular, tapered, 0.3-0.8 mm long; sessile glandular trichomes confined to abaxial surface 200-500/cm^2; **blades** 16-70 mm long, 13-46 mm wide, conspicuously smaller upwards toward the capitulescence, apex acute, base obtuse, rarely attenuate along distal sixth of petiole, margins entire to subentire, revolute; petioles 5-23 mm long, canaliculate, densely lanate on both

surfaces; **capitulescences** monochasial thyrsoid with 2-9+ heads, peduncles 35-80 mm long, densely lanate-velutinous, trichomes as stem; **heads** 9.5-10.5 mm across, 11.5-13.5 mm high, campanulate; **receptacles** 4.2-5 mm in diameter in fruit, slightly convex; **phyllaries** 19-26 in 3 subequal series, first and second series 3.9-5.5 mm long, 1.9-2.5 mm wide, oblong, base indurated, light greenish-stramineous and glabrous adaxially, dark green and glabrescent to sparsely tomentose abaxially, herbaceous apex appressed or slightly reflexed, dull green and sparsely to moderately hirsute-strigose adaxially, densely lanate white abaxially, margins densely tomentose to lanate, third series 5.8-6.5 mm long, 1.2-2.1 mm wide, oblong, base slightly indurated, light greenish-stramineous and glabrous adaxially, dark green and glabrous or glabrescent abaxially, herbaceous apex appressed, dull green and sparsely strigose or glabrescent on both surfaces, margins minutely velutinous; **pales** 6.3-8.5 mm long 2.5-3.3 mm wide, ovate, conduplicate, rarely keeled lengthwise, protruding 2-5 mm beyond phyllaries, stramineous with several dark green longitudinal bands of various width, bands coalescing at apex, sparsely to moderately puberulent at fold and apex, apex coriaceous, acute to acuminate, pointed or slightly reflexed, blackish; **ray flowers** 10-14, corollas yellow, limb 8.5-9.5 mm long, 3.2-4 mm wide, oval, moderately puberulent on veins of abaxial surface, apex acute, bifid or trifid, tube 1.2-1.5 mm long, yellow and moderately puberulent; **ray ovaries** 2.2-2.5 mm long, trigonal, epappose or with a pappus of one awn 1.4-1.8 mm long; **disk flowers** 45-85, protruding 1-1.5 mm beyond pales, corollas golden yellow, narrowly campanulate, throat 4.5-5 mm long, 0.7-0.9 mm wide at base, 1-1.2 mm

wide at junction with lobes, veins orange and discernable the whole length of the corolla, sparsely puberulent with interspersed uniseriate multicellular glandular trichomes 0.1-0.2 mm long, tapered trichomes hyaline to white, 0.1-0.3 mm long, tube 1-1.2 mm long, yellowish-green, glabrous, lobes 0.7-0.8 mm long, yellow, sparsely puberulent abaxially; anthers 2.7-3.3 mm long, thecae black, appendages 0.5 mm long, ovate, stramineous-black; styles 5.5-6.2 mm long, style branches 1.7-1.9 mm long; **disk achenes** 3.8-4.2 mm long, 1.4-1.6 mm wide, biconvex, obovate, with diminutive shoulders, shiny black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 3.3-3.6 mm long; Chromosome number unknown.

Phenology. Collected in flower April to July.

Distribution. (Fig. 50). Known only from the valley of the Huallaga River in central Huánuco Department, especially around the city of Huánuco; 2100-2745 m.

SPECIMENS EXAMINED. PERU. HUANUCO: Hills E of Acomayo, 2100 m, 25 Apr 1946, Woytkowski 34247 (F, LIL, MO, S, UC); Prov. Ambo, Hacienda Quicacán, 2400-2500, 18 Jun 1953, Ferreyra 9241 (MO, TENN, USM).

This species can be recognized by its small heads and ovate-suborbicular leaves. In addition, the leaf adaxial surfaces tend to turn brownish-red upon drying. It shares several morphological characters with P. lanatus (see discussion under P. lanatus).

37. Pappobolus argenteus (H. B. K.) Panero, comb. nov. Helianthus

argenteus H. B. K., Nov. gen. sp. qt. 4:221. 1820., pl. 376.——TYPE: ECUADOR. Azuayan Andes, near Los Paredones, Humboldt & Bonpland s.n. (lectotype, here designated: P-HBK, IDC 6209.108:II.7!; isolectotype: B, destroyed, photo ex B at GH!).

Much-branched, compact shrub 6-12 dm tall; **stems** terete, brown-gray and glabrous, herbaceous parts dark brown and tomentose, woolly at growing apex, trichomes white, multicellular, tapered, normally appressed but spreading where longer or denser, 0.5-2.3 mm long; **leaves** alternate, sometimes opposite on first or second node of growing branch, narrowly ovate to lanceolate, adaxial surface light to dull dark green and strigose, trichomes white or hyaline, multicellular, tapered, 0.15-0.2 mm long, denser and longer along veins, abaxial surface densely lanate white to whitish-green, densely sericeous on veins, trichomes white or greenish-white, multicellular, tapered, 0.3-0.8 mm long; sessile glandular trichomes, confined to the abaxial surface 1700-2000/cm^2; **blades** 11-41 mm long, 2-12 mm wide, similar in size and morphology throughout stem and capitulescence, apex acute to acuminate, base attenuate, margins serrulate, sometimes entire, slightly revolute; petioles 2-4.5 mm long, slightly canaliculate, densely tomentose to sericeous on both surfaces; **capitulescences** monochasial thyrsoid, with 1-5 heads, peduncles 25-100 mm long, densely tomentose, villous under heads, trichomes as stems; **heads** 10-14 mm across, 12-17 mm high, hemispherical; **receptacles** 6-10 mm in diameter in fruit, slightly convex; **phyllaries** 24-37 in 4 graduated series, first series 6-9 mm long, 1.8-2.5 mm wide, ovate to lanceolate,

spreading, mostly indurated, margins slightly revolute, silvery-greenish and lanate on both surfaces, margins villous to lanate, second series 6.5-10.5 mm long, 3-3.8 mm wide, ovate to lageniform, base indurated, stramineous-orange and glabrous adaxially, dark greenish-black and glabrous abaxially, herbaceous apex somewhat appressed, margins revolute, densely sericeous to lanate silvery-white on both surfaces, margins villous to lanate, third and fourth series 7.5-9 mm long, 3.3-3.5 mm wide, ovate to obovate, base indurated, stramineous suffused with black and glabrous adaxially, green or black and glabrous abaxially, herbaceous apex similar in morphology and pubescence to those of previous series, margins puberulent, fourth series 6.7-7.5 mm long, 1.5-2.3 mm wide, oblong, chartaceous, resembling pales in general aspect; **pales** 8.5-11 mm long, 4.2-5 mm wide, ovate, conduplicate, strongly keeled lengthwise, protruding 4-5 mm beyond phyllaries, stramineous with several dark green or black longitudinal bands of various width, bands coalescing at apex, glabrescent, conspicuously tomentose apically, apex acute to somewhat rounded, pointed or slightly curved inward, silver-black; **ray flowers** 12-18, corolla golden yellow, limb 15-25 mm long, 5.8-7.5 mm wide, oval, moderately puberulent and glandular on veins of abaxial surface, apex acute, bifid or trifid, tube 0.6-0.8 mm long, moderately puberulent; **ray ovaries** 2-3.1 mm long, trigonal, glabrous, with a pappus of 8-12 free or slightly fused squamellae, 0.3-0.5 mm long; **disk flowers** 65-125, flowers rarely protruding beyond pales, corollas yellow, narrowly campanulate, throat 3.6-4.5 mm long, 0.9-1 mm wide at base, 1.4-1.6 mm wide at junction with lobes, veins orange and discernable the whole length of the

corolla, essentially glabrous, tube 1.7-1.9 mm long, yellow, glabrous, lobes 0.7-0.9 mm long, deltoid, golden yellow, slightly black abaxially, sparsely pubescent abaxially; anthers 2.5-2.9 mm long, thecae black, appendages 0.5-0.6 mm long, lanceolate, stramineous; styles 5.2-5.6 mm long, style branches 1.5-1.6 mm long; **disk achenes** 3.9-5.5 mm long, 1.3-1.7 mm wide, biconvex, obovate to obtriangular, with two diminutive shoulders, shiny black or mottled, glabrous or with a few trichomes around the neck, pappus of 2 awns and sometimes with 3-8 intermediate squamellae, peripheral achenes normally lacking squamellae, inner achenes exhibiting squamellae of various size and number, awns slender, stramineous, sometimes suffused with orange, deciduous, sometimes somewhat persistent, subequal, 2.8-4.5 mm long, squamellae fused at base, rarely free, 0.8-2 mm long, same color as awns, deciduous or persistent; n = 17. Fig. 51.

Phenology. Collected in flower from February through July; major floral display in June-July.

Distribution (Fig. 52). Known only from the high, somewhat xerophytic hillsides of the mountains surrounding the valley of the city of Cañar and El Tambo of southern Ecuador. Growing with Fransieria artemisiifolia, Onoseris hyssopifolia, and Pappobolus hypargyreus; 3100-3200 m.

SPECIMENS EXAMINED. ECUADOR. CAÑAR: 1 km S of Cañar along the road Cañar-Cuenca, 3190 m, 20 Jun 1987, Panero 736 (AAU, CPUN, F, MEXU, QCA, QCNE, SI, TENN), 23 Feb 1988, Panero & Gómez 1089 (CAN, COL, MA, MICH, NY); Steep hill planted with Eucalyptus at southern edge of the City of

Cañar, 3190 m, 8 Jul 1988, Panero 1499 (GRI, MO, US), 1500 (F, QCA, TENN); Ingapirca, 21 Dec 1986, Warnock & Warnock 5619 (TEX).

This elusive species grows on a hillside just south of the city of Cañar in south-central Ecuador. In this area the plant still hangs on to certain protected rocky outcrops apparently left untouched after the reforestation of the hill with Eucalyptus. A few scattered individuals grow approximately 1 km south of this area.

Pappobolus argenteus is a distinct and beautiful compact shrub that can hardly be confused with any other species of the genus in Ecuador. This species is the only Ecuadorian member of the discolor group. It shares with P. viridior of central Peru a similar habit, leaf shape and pubescence, and as well as glabrescent or glabrous disk flowers, a condition not observed in any other species. However, this similarity is only superficial, for the two species are definitely very different in several floral characters. Pappobolus argenteus has densely tomentose and acute pale apices, an involucre composed of oblong phyllaries with very contrasting greenish-black indurated parts and densely lanate silvery-white herbaceous parts and a well organized head (i.e. all the ligules tend to be in one plane and the buds are always upright and never nodding). In P. viridior the pales are very chartaceous, acuminate, and with conspicuously black apices, the involucre is weakly organized in 4 strongly graduated series, and the phyllaries are rarely bicolored. Another unique feature of P. viridior are the heads which are loosely organized with the ligules in several planes, either reflexed or dramatically projecting forward and the buds

nod before opening, a floral behavior I did not observed in any other species that I collected.

Previous workers in the genus (Heiser, 1957; Robinson, 1979) regarded this species as rare, extinct or a morphological misfit due to the lack of modern specimens and the poor condition of the type. Given the widespread destruction of the habitat of this rare species, its extinction may be unfortunately true in a few years.

38. Pappobolus viridior (S. F. Blake) Panero, comb. nov.——Helianthus viridior S. F. Blake, J. Wash. Acad. Sci. 16:221-222. 1926.——Helianthopsis viridior (S. F. Blake) H. Robinson, Phytologia 44:266. 1979.——TYPE: PERU. Junín: Tarma, 3965 m, 1-6 Jun 1922, Macbride & Featherstone 1070 (lectotype, here designated: F!; isolectotypes: GH!, US!).

Compact shrubs 5-20 dm tall; **stems** terete, brown and glabrous, herbaceous parts soft brown, puberulent or slightly villous upwards toward the capitulescence, trichomes hyaline or white, multicellular, tapered, 0.15-0.7 mm long; **leaves** alternate, triplinerved, lanceolate to narrowly lanceolate, adaxial surface light soft green to grayish blue-green and moderately strigose to sericeous, trichomes white, multicellular, tapered, 0.25-0.7 mm long, abaxial surface light green to light gray pubescent, tomentose, villous or woolly between veins, trichomes white, multicellular, tapered, 0.6-1 mm long, pubescence on major veins densely strigose to sericeous; sessile glandular trichomes confined to abaxial surface 150-1800/cm^2; **blades** 7-65 mm long, 2-17 mm

wide, similar in size and morphology throughout stem and capitulescence, apex acuminate to acute, base obtuse and narrowly attenuate along upper half of petiole, margins entire to shallowly serrulate, petioles 0.2-1.3 cm long, canaliculate to terete, densely strigose to sericeous on both surfaces; **capitulescences** monochasial thyrsoid, with 2-5 heads, peduncles 50-140 mm long, puberulent to strigose, pubescence markedly denser below heads, trichomes as stem; **heads** 10-13 mm across, 11-12.5 mm high, campanulate to hemispheric; **receptacles** 4.7-6.2 mm in diameter in fruit, convex; **phyllaries** 20-23 in 4 strongly graduated series, first series 5.7-9.6 mm long, 2.2-3.5 mm wide, broadly ovate, indurated throughout, stramineous-dark green and glabrous adaxially, densely tomentose to villous whitish-silver abaxially, second series, 9.8-11.6 mm long, 3.7-4.6 mm wide, base heavily indurated with 1 central prominent dark green rib and 2 parallel smaller ones, these contrasting with stramineous background, soft green and glabrous adaxially, strigose to villous and glandular sometimes glabrescent abaxially, herbaceous apex broadly ovate to oblong, reflexed and involuted, green with dark green longitudinal veins and villous adaxially, similar in morphology and color but more pubescent abaxially, third series 11.5-14 mm long, 3.5-4.5 mm wide, oblong-lanceolate, otherwise similar in morphology and pubescence to previous series, herbaceous apex slightly reflexed, fourth series 9.8-12 mm long, 2.3-2.7 mm wide, lanceolate, resembling pales in general aspect, chartaceous with no clear distinction between indurated and herbaceous parts, stramineous and glabrous adaxially, stramineous-green

and sparsely puberulent abaxially; **pales** 7.5-9.7 mm long, 2.3-3.6 mm wide, ovate to lanceolate, conduplicate, rarely keeled lengthwise, covered by phyllaries, light stramineous with several light brown longitudinal bands of various width, bands coalescing in a conspicuous dark green or blackish tip, glabrescent abaxially, apex chartaceous to coriaceous, acuminate, pointed, black; **ray flowers** 10-15, corolla bright yellow, sometimes apex blackish abaxially, limb 8.2-23 mm long, 2.3-5 mm wide, oval, puberulent to minutely tomentose and glandular on veins of abaxial surface, apex acute, minutely bifid, tube 1-1.8 mm long, glabrescent; **ray ovaries** 3-3.2 mm long, biconvex, glabrous, pappus of 2-4 lacerated squamellae at angles with ovary, 0.5-0.6 mm long; **disk flowers** 80-105, flowers not protruding significantly beyond pales, corollas lemon-yellow, narrowly campanulate, throat 4.3-5 mm long, 1-1.5 mm wide at base, 1.5-1.9 mm wide at junction with lobes, veins dark orange and discernable the whole length of the corolla, essentially glabrous, tube 0.9-1.1 mm long, lemon-yellow, glabrous, lobes 1-1.4 mm long, deltoid, lemon yellow, glabrescent abaxially; anthers 2.5-3 mm long, thecae black, appendages 0.6-0.7 mm long, ovate-lanceolate, stramineous-orange; styles 5.5-7.2 mm long, style branches 1.2-2 mm long; **disk achenes** 3.1-4.2 mm long, 1.4-1.8 mm wide, biconvex, oval-obovate with 2 diminutive shoulders shiny dark gray or black, glabrous, pappus of 2 awns, slender, stramineous, deciduous, subequal, 2.5-3.5 mm long; $\underline{n}$ = 17. Fig. .

Phenology. Flowering December to June and probably sporadically the rest of the year.

Distribution. (Fig. 52). Montane to subalpine dry scrub or forest

of the valley of the Palca River and tributaries of Junín Department, central Peru; 2850-4200 m.

SPECIMENS EXAMINED. PERU. JUNIN: Prov. Tarma, 19 km NE of Tarma on road to San Ramón, 2850 m, 17 Dec 1978, Dillon & Turner 1329 (F, MO, TEX); 26 km W of the intersection of the roads to Tarma and Huánuco on road to Tarma, 3210 m, 1 Apr 1988, Panero 1365 (CPUN, F, GRI, MO, SI, US), 1365A (TENN); Acobamba, 3500-4200 m, 3 Jun 1940, Woytkowski 57 (F).

Pappobolus viridior is notable among the high altitude species of Peruvian Pappobolus for its compact habit, long peduncles and sometimes glabrescent herbage. However, this species exhibits a significant degree of morphological variability. The type and the specimens Panero 1365 and 1365a have very glabrescent herbage. This lack of a copious pubescence in the stems, peduncles and leaves contrasts with the rest of the specimens known of this species which show densely velutinous-sericeous to lanate leaves, stems and peduncles. Its overall morphology suggests a possible relationship with P. argenteus of central Ecuador (see discussion under P. argenteus).

DOUBTFUL AND EXCLUDED NAMES

Included are all the names of Helianthus for South America which are not included in the revision of Pappobolus herewith.

Helianthus angustifolius Baker, Abh. Königl. Ges. Wiss. Göttingen

24:221. 1884. = Viguiera anchusaefolia (DC.) Baker, Mart. Fl. Bras. 6(3): 222. 1884, fide Blake (1918).

Helianthus araucanus Phil., Anal. Univ. Chile 90:39. 1895. Flourensia corymbosa var. araucana (Phil.) Reiche, Anal. Univ. Chile 112:145. 1903.—TYPE: CHILE. without exact locality, F. Philippi s. n. (holotype: B, destroyed). = Viguiera revoluta (Meyen) S. F. Blake, fide Blake (1918).

Helianthus argentinus (Griseb.) Sáenz, Darwiniana 22:65. 1979. Viguiera mollis Griseb. Abh. Königl. Ges. Wiss. Göttingen 19:183. 1874.—TYPE: ARGENTINA. Tucumán, Cuesta del Garabatal, between Siambon and Juntas 18 Mar 1872, P. G. Lorentz 502 (holotype B: destroyed; fragment GH). = Viguiera mollis Griseb.

Helianthus atacamensis Phil., Anal. Mus. Nac. Chile. Bot. 1891:48. 1891. Flourensia atacamensis (Phil.) Reiche, Ann. Univ. Chile 112:146. 1903.—TYPE: CHILE. Antofagasta: Atacama, F. Philippi s. n. (holotype B: destroyed). Viguiera pazensis Rusby, fide Blake (1918).

Helianthus aureus H.B.K., Nov. gen. sp. 4:224. 1820. = Viguiera incana (Pers.) S. F. Blake, (see H. incanus Pers. below) fide Blake (1930).

Helianthus australis Phil. Anal. Univ. Chile 90:36. 1895. = Grindelia chiloensis (Corn.) Cabrera, fide Heiser (1957).

Helianthus besseriana (Meyen & Walp) J. D. Hook. & A. B. Jackson Ind. Kew. 1:1112. 1893. Flourensia besseriana Meyen & Walp., Nov. Act. Aca. Caes. Leop. Carol. 19:270.—TYPE: CHILE. No exact locality, B. Besser s. n. (holotype, B, destroyed: lectotype, designated by Dillon, 1984: fragment ex B at GH; photograph of B specimen, F, GH). = Flourensia thurifera (Molina) DC., fide Dillon (1984).

Helianthus calvus Sch.-Bip., Bull. Soc. Bot. France 12:79. 1865. = Viguiera pflanzii Perkins, Bot. Jahrb. Syst. 49:226. 1913. Fide Blake (1918).

Helianthus campestris (Griseb) Kuntze, Rev. Gen. Pl. 3:157. 1889. Flourensia campestris Griseb. Abh. Königl. Ges. Wiss. Göttingen 19:184. 1874.—TYPE: ARGENTINA. Córdoba, abundant in field SE of Córdoba, 1871, P. G. Lorentz 245 (holotype: GOET; isotype CORD, fragment GH). = Flourensia campestris Griseb., fide Dillon (1984).

Helianthus canescens Juss. Syn. Pl. 2:475. 1807. = Viguiera incana (Pers.) S. F. Blake, (see H. incanus Pers. below) fide Blake (1930).

Helianthus copiapinus Phil. Anal. Univ. Chile 90:37. 1895. = Wedelia copiapina (Phil.) Reiche.

Helianthus corymbosus Poepp. ex DC., Prodr. 5:592. 1836. pro syn., Flourensia corymbosa DC., Prodr. 5:592. 1836.—TYPE: CHILE, Bío-bío,

Jan 1830, Poeppig 791 (holotype: G-DC; isotype: F) = Viguiera revoluta (Meyen) S. F. Blake, fide Blake (1918).

Helianthus cumingii H. & A. J. Bot. (Hooker) 3:315. 1841.—TYPE: CHILE, Maule, 1831, Cumming 849 (holotype: K). = Viguiera revoluta (Meyen) S. F. Blake, fide Blake (1918).

Helianthus floribundus E. E. Watson, Papers Mich Acad. Sci. 9:405, pl. 59.—TYPE: BOLIVIA, San Luis, 2000 m, Fiebrig 2758 (holotype: B, destroyed). = Viguiera australis S. F. Blake, Contr. Gray Herb. 54:148-149. 1918.

Helianthus gayanus Phil., Anal. Univ. Chile 90:39. 1895. Flourensia gayana (Phil.) Reiche, Anal. Univ. Chile 112:145. 1903.—TYPE: CHILE. without exact locality, F. Philippi s. n. (holotype: B, destroyed). = Viguiera revoluta (Meyen) S, F, Blake, fide Blake (1918).

Helianthus glutinosus Hook. & Arn., Bot. Beechey Voy. p. 32. 1830.—TYPE: CHILE. Valaparaíso, Bridges s. n. (holotype: GL). = Flourensia thurifera (Molina) DC., fide Dillon (1984).

Helianthus heteropappus Gill. ex Hook. & Arn., J. Bot. (Hooker) 3:314. 1841.—TYPE: ARGENTINA. Mendoza: San Pedro Mendoza, Gillies 68 (holotype: K). = Viguiera gilliesii (Hook. & Arn.) S. F. Blake, fide Blake (1918).

Helianthus incanus Pers. Syn. Pl. 2:475. 1807. = Viguiera incana Pers. (S. F. Blake, fide Blake (1930).

Helianthus insulatus E. E. Watson nom. herb. This name was applied by Watson to a specimen of Viguiera aff. peruviana A. Gray, Jelski 714 at B. He labeled this specimen as the "type" when he visited B in June 1926, but he never published the name. The name does not appear in his treatment of Helianthus of 1929 nor in Index Kewensis. Hieronymus (1905) identified this specimen as Helianthus rugosus Meyen. Jelski 714 appears to have been destroyed, however, a photograph of the specimen labeled as the type of Helianthus insulatus is deposited at F (photo: 15431).

Helianthus lanceolatus Meyen, Reise um die Erde 1:311. 1834. Flourensia corymbosa var. lanceolata (Meyen) Reiche, Anal. Univ. Chile 112:144. 1903.—TYPE: CHILE. without exact locality F. J. F. Meyen s. n. (holotype: B, destroyed). = Viguiera revoluta (Meyen) S. F. Blake, fide Blake (1918).

Helianthus mandonii Sch.-Bip. Bull. Soc. Bot. France 12:79. 1865, nomen nudum.

Helianthus montevidensis Baker, Abh. Königl. Ges. Wiss. Göttingen 24:221. 1884. = Viguiera anchusaefolia (DC.) Baker, Mart. Fl. Bras. 6(3):222, 1884, fide Blake (1918).

Helianthus navarri Phil. Anal. Univ. Chile 90:37. 1895. Flourensia navarri (Philippi) Reiche, Anal Univ. Chile 112:145. 1903.—TYPE: CHILE. without exact locality, F. Philippi s. n. (holotype: B, destroyed). = an undetermined species of Wedelia, fide Blake (1921).

Helianthus procumbens Pers. Syn. pl. 2:475. 1807. = Viguiera procumbens (Pers.) S. F. Blake, fide Blake (1930).

Helianthus prostratus (prostratum) Pers. Syn. pl. 1807. = Viguiera procumbens (Pers.) S. F. Blake, fide Blake (1930).

Helianthus revolutus Meyen, Reise um die Erde 1:311. 1834.—TYPE: CHILE. without exact locality F. J. F. Meyen s. n. (holotype: B, destroyed). = Viguiera revoluta (Meyen) S. F. Blake, fide Blake (1918).

Helianthus riparia (Griseb.) Kuntze, Rev. Gen. Pl. 3:157. 1889. Flourensia riparia Griseb., Abh. Königl. Ges. Wiss. Göttingen 24:196. 1879.—TYPE: ARGENTINA: Salta, passage of the Río Turamento, Feb 1873, G. Hieronymus & P. G. Lorentz 268 (holotype: GOET; isotypes: CORD, F, GH, NY, SI, US). = Flourensia riparia Griseb., fide Dillon (1984).

Helianthus rugosus Meyen, Reis. Erd. 2:45. 1835. = Viguiera peruviana A. Gray Proc. Amer. Acad. Arts 5:124. 1861. Fide Blake (1930).

Helianthus sodiroi Hieron. Bot. Jahrb. Syst. 39:41. 1900.—TYPE: ECUADOR. Pichincha: dry hills near Pifo, Sodiro 34/3 (holotype: B, destroyed). = Viguiera sodiroi (Hieron.) S. F. Blake, fide Blake (1918).

Helianthus thurifera Molina, Sagg. Stor. Nat. Chil. 160. 1782.—TYPE: CHILE. Valparaíso, sonnige Abhänge, 7 Oct 1895, Buchtien s. n. (neotype, designated by Dillon, 1984: US; isoneotype: GH). = Flourensia thurifera (Molina) DC., fide Dillon (1984).

Helianthus truxillensis H. B. K. Nov. gen. sp. 4:223.—TYPE: PERU. La Libertad: Trujillo, near the sea. Humboldt & Bonpland s. n. (type: P). = Viguiera truxillensis (H. B. K.) S. F. Blake, fide Blake (1918).

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APPENDICES

APPENDIX 1

TABLES

Table 1. Comparison of treatments and taxa assignments in *Pappobolus*.

Previous Workers	Heiser (1957)	Robinson (1979, 1983)	Panero (herein)
Viguiera acutifolia (Blake 1916)			*Pappobolus*
Helianthus (16) (South America)	*Helianthus* (17)	*Helianthopsis* (24)	*Pappobolus*
Pappobolus (4) (Blake 1916)			*Pappobolus* (38)

Table 2. Infrageneric classification and species groups in Pappobolus proposed in this treatment.

Subgenus Apricus	Subgenus Pappobolus		
	nigrescens group	stuebelii group	discolor group
P. acutifolius	P. acuminatus	P. jelskii	P. argenteus
P. ecuatorianus	P. amoenus	P. smithii	P. cajamarcensis
P. hutchisonii	P. andinus	P. stuebelii	P. davidii
P. hypargyreus	P. cinerascens		P. decumbens
P. imbaburensis	P. lehmannii		P. discolor
P. juncosae	P. macranthus		P. lanatus
P. mathewsii	P. mollicomus		P. lodicatus
P. sagasteguii	P. nigrescens		P. microphyllus
P. verbesinoides	P. robinsonii		P. senex
	P. sanchezii		P. subniveus
	P. schillingii		P. viridior
	P. stork-hortonii		P. woodsonianus
	P. szyszylowiczii		
	P. youngiorum		

Table 3. Morphological comparison of Pappobolus and related genera.

					Viguiera		
	Pappobolus	Tithonia	Simsia	Helianthus	Aureae	Grammatoglossae	Pinnatilobatae
Habit	Shrubs	Annuals, Shrubs	Annuals, Perennial herbs	Annuals, Perennial herbs	Perennial herbs	Shrubs, Perennial herbs	Shrubs
Leaf margin	Entire	Entire, Lobed	Entire, Lobed	Entire	Entire	Entire	Lobed
Leaf auricles	Not Present	Present	Present	Not Present	Not present	Present	Not Present
Synflorescence	Monochasial Dichasial	Monochasial	Monochasial Dichasial	Monochasial Dichasial	Monochasial	Monochasial	Monochasial
Herbage Pubescence	Soft; Glabrescent to lanate	Soft; Glabrescent to Villous	Soft to Scabrous; Glabrescent, Pilose-hispid, Villous	Soft to Scabrous; Glabrescent to Lanate	Scabrous; Hirsute-hispid to Lanate	Soft or Scabrous; Pilose-hispid to Lanate.	Soft: Glabrescent to Villous-lanate
anther color	yellow or black	yellow or black	yellow or black	yellow or black	black	yellow or black	yellow
Style shape	deltate; no appendage	deltate to tapered; small appendage	tapered; small appendage	tapered; appendage	deltate; no appendage	deltate; no appendage	deltate; no appendage
Endothecium cell shape and thickenings	polarized; cells oblong	polarized-radial; cells oblong to isodiametric	polarized; cells mostly oblong a few isodiametric	polarized, rarely radial; cells oblong to isodiametric	polarized; cells oblong	polarized; cells oblong	polarized; cells oblong
Trichomes on anther connective	not present	present	present	present	not present	present (V. rhombifolia)	not present

Table 3. (continued).

Sclerified cells on disk flower lobes	not present	not present	present	not present	not present	present	not present
Achene shape	biconvex	biconvex	flat	biconvex	biconvex	biconvex	biconvex
Disk achene pappus duration	deciduous	persistent	persistent	deciduous	persistent	persistent	persistent
Disk achene pappus shape	2 awns with or without squamellae; a crown of awns	fused band of squamellae with without awns; epappose; 2 awns and squamellae or only squamellae	2 awns with or without squamellae	2 awns; squamellae rarely present	2 awns with squamellae	2 awns with squamellae; epappose	epappose

Table 4. Comparison of key distinguishing characters of *Pappobolus decumbens*, *P. jelskii* and a putative hybrid.

Character	*P. decumbens*	Hybrid	*P. jelskii*
Leaf length (mm)	10-60	22-65	10-65
Leaf width (mm)	0.9-3.2	3-14	6-33
Petiole length (mm)	1.5-6.5	17-19	4-30
Receptacle (mm)	6.3-7.5	12	9-15
Phyllary number	23-36	35	35-48
Pale length (mm)	7.5-9.5	9-9.8	9.3-11
Ligule length (mm)	12.5-16.5	22-23	13-18
Ligule width (mm)	4.9-5.9	4.5-6	5-7.8
Disk flower number	68-95	195-220	160-340
Disk flower throat (mm)	4-4.5	4.2-4.5	3.6-4.5

Table 5. Comparison of key distinguishing characters of Pappobolus microphyllus, P. sanchezii and a putative hybrid.

Character	P. microphyllus	Hybrid	P. sanchezii
Leaf length (mm)	4-22	18-41	35-130
Leaf width (mm)	2-9	10-24	10-90
Petiole length (mm)	5-10	9-12.5	15-40
Receptacle (mm)	4.5-5.5	7.5	10-15.2
Phyllary number	23-31	27-29	28-38
Pale length (mm)	5.5-7	7.5	8.7-9.1
Ligule length (mm)	9-17.5	17.3-18	22-32
Ligule width (mm)	4.5-7.5	8.2-8.7	8.5-11
Disk flower number	55-95	95-115	90-180
Disk flower throat (mm)	2.8-3.8	3.5-3.7	3.8-5.2

APPENDIX 2

DATA MATRICES

2.1. Characters and their states used in the cladistic analysis of Pappobolus.

1. Leaves pinnately-lobed	present	absent
2. Leaf shape	ovate to broadly ovate	lanceolate to linear
3. Leaf nodal disks	present	absent
4. Leaf margin	serrate	revolute
5. Leaf texture	thin	sclerified
6. Leaf color	not contrasting	conspicuously bicolored
7. Leaf adaxial surface	dull and pubescent	shiny and glabrescent
8. Leaf venation	triplinerved	mononerved
9. Capitulescence	full	some sterile leaves (1) multiple sterile leaves (2)
10. Capitulescence structure	monochasial	dichasial
11. Pale coloration	lines not converging	lines converging
12. Ray flower ligule orientation	horizontal	reflexed
13. Ray flower ligule morphology	oval to suborbicular	oval to lanceolate (1) narrowly lanceolate (2)
14. Disk flower lobe color	yellow	black
15. Disk corolla pubescence	present	absent

16. Style branch morphology	tapered	truncate
17. Anther color	yellow	black
18. Ray ovary	thin and long	biconvex and broad
19. Ray ovary pappus	2-3 awns	5-15 awns
20. Disk achene pubescence	pubescent	glabrous to glabrescent
21. Disk achene pappus	2-4 awns	8-30 awns

2.2. Data matrix for cladistic analysis of Pappobolus.

0 = plesiomorphic; 1, 2 = apomorphic. 9 = missing data.

	VER	ECU	HYP	JUN	HUT	AMO	SAN	MOL	MAC	SMI	JEL	WOO	LOD	CAJ	DIS	DEC	ARG	LAN	SIM
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
2	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
4	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0
5	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0
6	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
9	0	0	0	0	0	1	1	1	1	2	9	9	1	2	2	2	2	2	0
10	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
11	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
12	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	1	1	1	1	2	1	1	1	1	1	1	1	1	0
14	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
16	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
17	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
18	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
19	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
20	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
21	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0

2.3. Characters and their states used in the phenetic analysis of Pappobolus.

Habit. 1. Stems erect, not rooting at nodes (0), stems decumbent, rooting at nodes (1).

Leaves. 2. Texture: thin, not sclerified (0), coriaceous, sclerified (1). 3. Margins: serrate to entire (0), entire and revolute (1). 4. Margins: not undulate (0), undulate (1). 5. Shape: broadly ovate to ovate (0), ovate to suborbicular or elliptical (1), ovate (2), lanceolate (3), lanceolate to linear or narrowly oblong (4). 6. Leaf main vein: not sunken (0), sunken (1). 7. Abaxial surface: dull and pubescent (0), shiny and glabrescent (1). 8. Venation: triplinerved (0), mononerved (1). 9. Pubescence color: hyaline to white or greenish white (0), ochreus (1). 10. Leaf abaxial and adaxial surface color: not contrasting (0), contrasting, conspicuously-bicolored (1). 11. Pubescence: velutinous (0), villous to floccose (1), sparsely to densely lanate (2). 12. Disposition: not tightly-packed with visible internodes (0), tightly-packed without visible internodes (1). 13. Phyllotaxy: alternate (0), variable (1), opposite (2).

Capitulescence. 14. Monochasial (0), dichasial (1). 15. Monochasial capitulescence structure: all leaves associated with capitulescence subtending a head or paracladium (0), some sterile leaves visible (1), numerous sterile leaves (2).

Heads. 16. Diameter (ligules not included; mm): 8-15 (0), 15-20 (1), ≥ 20 (2).

Receptacle. 17. Diameter (mm): 5-10 (0), 10-20 (1).

Phyllaries. 18. Abaxial surface with green longitudinal lines (0), without green lines (1). 19. Somewhat indurated: lanceolate to linear (0), oval to suborbicular (1). 20. Somewhat indurated: herbaceous apex reflexed (0), variable (1), appressed (2). 21 Herbaceous apex: conspicuous (0), very reduced or missing (1). 22. Shape: not constricted between indurated and herbaceous apex (0), constricted (1). 23. Pubescence: not masking phyllary shape (0), densely lanate as to mask phyllary morphology (1). 24. Pubescence and color: evenly pubescent or not conspicuously-bicolored (0), conspicuously bicolored (1). 25. Pubescence and shape: lanceolate to suborbicular, variously pubescent and colored (0), ovate to oblong, pubescence and color evenly distributed (1). 26. Average number: ≤ 30 (0), 30-40 (1), ≥ 40 (2).

Pales. 27. Color: bands not coalescing at apex (0), coalescing at apex (1). 28. Apex orientation: straight (0), reflexed (1).

Ray flowers. 29. Ligule orientation: horizontal (perpendicular to the head) (0), reflexed (1). 30. Shape: oval to suborbicular (0), oval to lanceolate (1), narrowly lanceolate (2). 31. Average number: 10-15 (0), 15-25 (1), ≥ 26 (2). 32. Length (mm): 10-15 (0), ≥ 16 (1).

Disk flowers. 33. Anther color: yellow (0), black (1). 34. Style color: yellow throughout (0), style branches black abaxially (1). 35. Anther appendage color: black to dark red (0), stramineous (1). 36. Lobe color: yellow (0), black (1). 37. Corolla pubescence: present (0), essentially glabrous (1). 38. Tube pubescence: sparsely pubescent to glabrous (0), densely pubescent (1).

Ray ovary. 39. Shape: long, tubular and triquetrous (0), oval, biconvex to triquetrous (1). 40. Pappus: 2 (-3) awns with or without several squamellae (0), multiple awns (more than 5) (1).

Disk achene. 41. Pubescence: present (0), glabrescent (1). 42. Pappus: 2 (-3) awns with or without squamellae (0), multiple awns (more than 5) (1).

2.4. Data matrix for the phenetic analysis of Pappobolus.

9 = missing data. Pappobolus szyszylowiczii 23 not included in the analysis.

MAT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	2	0
SAG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	2	0
VER	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
ECU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0
HYP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0
IMB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
JUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
HUT	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	2	0
ACU	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	2	0
AMO	0	0	0	0	1	0	0	0	0	0	1	0	2	0	1	1	1	1	9	9	0	1	0	0	0	1	1	0	1	1	1	0	1	0	1	1	0	0	0	0	1	0
SAN	0	0	0	0	1	0	0	0	0	0	1	0	2	0	1	1	1	1	9	9	0	1	0	0	0	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0
AND	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	9	9	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0
ACM	0	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	0	1	9	9	0	0	0	0	1	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0
STO	0	0	0	0	1	0	0	0	0	0	0	0	9	0	1	1	0	1	9	9	0	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0
LEH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	9	9	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0
NIG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	9	9	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0
SCH	0	0	0	0	1	0	0	0	0	0	1	0	2	0	1	1	1	1	9	9	0	1	0	0	0	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0
YOU	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	1	1	1	9	9	0	1	0	0	0	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0
CIN	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	1	1	1	9	9	0	1	0	0	0	1	1	0	1	1	1	1	1	0	0	1	0	0	0	1	0	1
MOL	0	0	0	0	1	0	0	0	0	0	1	0	2	0	1	1	1	1	9	9	0	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	0	0	0	1	0	1
MAC	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	2	1	1	9	9	0	0	0	0	0	2	1	0	0	1	2	1	1	0	1	1	0	0	0	1	0	1
ROB	0	0	0	0	1	0	0	0	0	0	1	0	2	0	1	1	1	1	9	9	0	0	0	0	0	2	1	0	1	1	1	1	1	0	0	1	0	0	0	0	1	0
STU	0	1	1	0	2	0	0	0	1	1	2	1	0	0	2	2	1	1	9	9	0	0	1	0	0	2	1	0	0	2	2	1	1	0	0	1	0	0	0	0	0	0
SMI	0	1	1	0	2	0	0	0	0	1	2	1	0	0	2	2	1	1	9	9	0	0	1	0	0	2	1	0	0	2	2	1	1	0	0	1	0	0	0	0	0	0
JEL	0	1	1	0	2	0	0	0	0	1	2	0	2	1	9	2	1	1	9	9	0	0	1	0	0	2	1	0	0	1	2	1	1	0	1	1	0	0	0	0	0	0
LOD	0	1	1	1	4	0	0	0	1	1	2	0	0	0	2	0	0	1	9	9	0	0	1	0	0	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0
MIC	0	1	1	1	4	1	0	0	0	1	2	1	1	0	2	0	0	1	9	9	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0
WOO	0	1	1	0	2	0	0	0	0	1	2	0	2	1	9	0	0	1	9	9	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1
SUB	0	1	1	0	4	1	0	0	0	1	2	1	1	0	2	0	0	1	9	9	0	0	0	1	0	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0
CAJ	0	1	1	0	4	1	1	0	0	1	2	1	0	0	2	0	0	1	9	9	0	0	0	1	0	0	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0
DIS	1	1	1	0	4	1	1	1	0	1	2	1	1	0	2	0	0	1	9	9	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0
DEC	1	1	1	0	4	1	1	1	0	1	2	1	0	0	2	0	0	1	9	9	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1
DAV	0	1	1	0	3	0	0	0	0	1	2	0	0	0	2	0	0	1	9	9	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0
ARG	0	1	1	0	3	0	0	0	0	1	2	0	0	0	2	0	0	1	9	9	0	0	0	1	0	1	1	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0
VIR	0	1	1	0	3	0	0	0	0	1	2	0	0	0	2	0	0	1	9	9	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0
LAN	0	1	1	0	2	0	0	0	0	1	2	0	2	0	2	1	0	1	9	9	0	0	0	1	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0
SEN	0	1	1	0	2	0	0	0	0	1	2	0	2	0	2	0	0	1	9	9	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0

APPENDIX 3

Voucher Specimens for Anatomical Studies

Vouchers are deposited at TENN. An asterisk denotes material preserved in ethanol or ethanol:acetic acid (3:1); all other material was rehydrated by boiling in water or in a mixture of liquid soap and water at 40 C for 2 days. Letters in parentheses indicate structures studied: f = disk flower microcharacters; l = leaf clearings.

Helianthus:

angustifolius: Panero UT17* (f, l).

argophyllus: Schilling & Clements 85- (l).

arizonensis: Panero UT41* (f, l).

atrorubens: Panero UT6* (f, l).

decapetalus: Panero 1623 (f, l).

floridanus: Panero UT15* (f, l).

giganteus: Wofford & Panero 87-100 (f, l).

hirsutus: Panero UT33* (l).

maximilianii: Panero UT4* (f).

microcephalus: Panero et al. 408* (f, l).

occidentalis: Patrick 3571 (l).

praecox: Panero UT11* (f).

Heliomeris

multiflora: Schilling & Panero 88-10* (f).

Hymenostephium

superaxillare: Schilling & Panero 88-9 (f, l).

Iostephane

heterophylla: Panero & Schilling 1561* (f, l).

madrensis: Schilling & Panero 88-22* (f, 1).

papposa: Panero et al. 617 (f).

trilobata: Schilling & Panero 88-34* (f).

Pappobolus

acuminatus: Macbride & Featherstone 2429 (f).

acutifolius: Panero & Galán 1399* (f, 1); 1400* (f); Weberbauer 3008 (f).

amoenus: Panero & Sánchez Vega 1156* (f, 1); Sánchez Vega & Contreras 246 (f); Sagástegui & Mostacero 9172 (f); Plowman et al. 14278 (f).

andinus: Hutchison & Tovar 4153 (f).

argenteus: Panero 736* (f); 1499* (f, 1).

cajamarcensis: Panero & Sánchez Vega 1282* (f, 1).

cinerascens: Mathews s. n. (f); Panero 1357* (f, 1).

davidii: Smith et al. 11984 (f, 1).

decumbens: Panero & Sánchez Vega 1343* (f, 1).

discolor: Macbride & Featherstone 2240 (f); Panero & Galán 1367* (f, 1).

ecuatorianus var. ecuatorianus: Panero & Gómez 1088* (f); Panero 1440* (f, 1); 1517* (f).

ecuatorianus var. lancifolius: Panero 1453* (f, 1); 1475* (f).

hutchisonii: Panero & Sánchez Vega 1242* (f, 1).

hypargyreus: Panero 733 (f); 1510* (f, 1).

imbaburensis: Panero 711* (f); 718* (f); 1405 (f); 1526 (f, 1); Panero & Gómez 1069* (f, 1); 1100* (f).

jelskii: Panero & Sánchez Vega 1122* (f, 1); 1343* (f).

juncosae: Panero & Gómez 1094* (f, 1).

lanatus: Panero 1362* (f, 1); Panero & Galán 1398* (f, 1).

lehmannii var. lehmannii: Panero 720* (f, 1); 1408* (f, 1); 1501* (f, 1).

lehmannii var. grandiceps: Panero 1508* (f, 1).

lodicatus: Ellenberg 1756 (f, 1).

macranthus: Macbride & Featherstone 1384 (f); Woytkowski 34133a (f, 1).

matthewsii var. matthewsii: Panero 1351* (f); 1354* (f, 1).

matthewsii var. occidentalis: López & Sagástegui 5185 (f); Sánchez Vega 4699 (f).

matthewsii var. viridifolius: Panero & Sánchez Vega 1257* (f, 1); 1261 (f); 1263 (f).

microphyllus var. microphyllus: Panero et al. 864* (f, 1); Panero 1179 (f); 1186 (f) Panero & Eriksen 1298* (f, 1); Panero & Sánchez Vega 1275 (f, 1).

microphyllus var. dillonii: Dillon et al. 2805 (f, 1).

microphyllus var. liberus: Sagástegui et al. 11820 (f, 1)

microphyllus var. soukupii: Soukup 4548 (f, 1).

mollicomus: Cevasco 13391 (f, 1); Mathews s. n. (f).

nigrescens: Panero 755* (f); 1436* (f, 1); 1492* (f); 1495* (f); 1520 (f, 1).

robinsonii: Panero & Sánchez Vega 1223* (f); Panero et al. 955* (f, 1).

sagasteguii: Panero & Sánchez Vega 1230* (f, 1); 1231* (f);

sanchezii: Panero 1195* (f, 1).

schillingii: Panero 1446* (f); 1450* (f, 1); 1472* (f, 1); 1477* (f, 1).

senex: Ferreyra 9241 (f, 1).

smithii: López & Sagástegui 3309 (f, 1).

stork-hortonii: Stork & Horton 10316 (f).

stuebelii: Panero 1150* (f, 1); Panero & Sánchez Vega 1196 (f); Panero et al. 932* (f, 1); 995* (f, 1); Stuebel 34e (f).

subniveus: Panero 1140* (f, 1); Panero et al. 862* (f, 1); Stuebel 34d (f).

verbesinoides: Ferreyra & Chanco 20463 (f, 1).

viridior: Panero 1365* (f, 1).

woodsonianus: Wurdack 584 (f, 1).

youngiorum: Young 2936 (f, 1).

Simsia

amplexicaulis: Panero & Schilling 448 (f, 1)

annectens var. annectens: Spooner 2845 (f, 1).

calva: Shinners 31753 (f); Panero UT1* (f, 1).

chaseae: Spooner 2880 (f).

dombeyana: Panero & Sánchez Vega 1360 (f).

eurylepis: Spooner 2481 (f); Spooner 2885 (f).

foetida var. foetida: Spooner & Dorado 2691 (f).

foetida var. grandiflora: Spooner & Dorado 2699 (f).

foetida var. megacephala: Spooner & Dorado 2867 (f).

fruticulosa: Panero & Gómez 1102 (f, 1).

ghiesbreghtii: Spooner 2781 (f, 1).

holwayi: Spooner & Dorado 2692 (f).

lagascaeformis: Spooner & Villaseñor 2489 (f).

molinae: Spooner & Dorado 2701 (f).

sanguinea: Panero et al. 651 (f, 1); Spooner & Burgos (f).

setosa: Spooner & Villaseñor 2528 (f).

steyermarkii: Spooner & Dorado 2748 (f).

Syncretocarpus

sericeus: Panero 1336* (f, 1)

Tithonia

calva: Schilling & Panero 88-4* (f, 1).

diversifolia: Panero et al. 521* (f, 1).

rotundifolia: Panero & Schilling 451 (f).

tubaeformis: Schilling & Panero 88-8* (f, 1)

Viguiera

adenophylla: Panero & Panero 2 (f).

atacamensis: López et al. 7381 (f).

bicolor: Schilling & Panero 88-29* (f).

bombycina: Schilling et al. 85-29 (f).

brevifolia: Schilling & Panero 88-14* (f).

cordata: Spooner & Burgos 2629 (f).

cordifolia: Schilling & Panero 88-11* (f, 1).

eriophora: Panero et al. 609 (f).

excelsa: Schilling & Panero 88-26 (f).

flava: Schilling & Panero 88-51 (f, 1).

grammatoglossa: Panero & Panero 12* (f, 1).

hemsleyana: Schilling & Panero 88-32 (1).

hidalgoana: Schilling & Panero 88-28* (f).

hypargyrea: Schilling & Panero 88-12* (f, l).

hypochlora: Panero et al. 540 (f, l).

incana: Panero 732 (f, l).

latibracteata: Schilling & Panero 88-7* (f, l).

linearis: Schilling & Panero 88-17* (f).

microphylla: Schilling & Schilling 82 (l).

mollis: Panero et al. 1380* (f).

oaxacana: Panero et al. 599 (f, l).

ovata: Schilling & Panero 88-33* (f, l); 88-36* (f, l); 88-38* (f).

parkinsonii: Schilling & Panero 88-1* (f, l); 88-45 (f).

pazensis: Solomon 7221 (f).

pinnatilobata: Panero et al. 634 (f, l).

purisimae: Rieseberg & Schilling 10E (f).

quinqueradiata: Panero & Panero 7 (f).

quitensis: Panero 782 (f, l).

reticulata: Schilling & Rieseberg 83-16 (l).

revoluta: Nuñez & Labra s.n. (f).

rhombifolia: Schilling & Panero 88-31* (f, l).

rosei: Schilling & Panero 88-20* (f, l).

schultzii: Schilling & Panero 88-47* (f, l).

sessilifolia: Schilling & Panero 88-21* (f, l); 88-44* (f); 88-18* (f, l).

simsioides: Sagástegui 9804 (f).

sphaerocephala: Panero et al. 569 (f, l).

szyszylowiczii: Panero et al. 863* (f, 1).

tenuis: Panero et al. 531 (f, 1).

tomentosa: Schilling & Rieseberg 83-23 (1).

trachyphylla: Panero & Schilling 1563 (f, 1).

tripartita: Panero et al. 635 (f, 1).

APPENDIX 4

Summary of leaf venation patterns in Pappobolus and related genera. Character: 1. Vein course, 2. Highest venation order present, 3. Number of veinlets within areoles, 4. Presence of a resticulum, 5. Conspicuous contrast in vein thickness between primary or secondary veins and higher orders, 6. Degree of development of areolation.

	Characters					
Taxon	1	2	3	4	5	6
Helianthus						
argophyllus	st	7-8	0-s	p	np	wd
arizonensis	st	4-5	1-2	np	np	im
atrorubens	st-sn	5-6	1-2	np	np	im
carnosus	st	4-5	1-2	np	np	im
floridanus	st	4-5	1-3	np	np	im
giganteus	st-sn	5-6	1-2	np	np	wd
hirsutus	st	5-6	s-1	np	np	im
occidentalis	st-sn	5-6	1-2	np	np	im
Iostephane						
madrensis	st	4-5	1-2	np	np	im
heterophylla	st-sn	5	2-3	np	np	im
Pappobolus all species	st	6-7	0-2	np	np	wd
Simsia						
amplexicaulis	z	6-7	s-1	np	np	wd
annectens	z	6-7	s-1	np	np	wd

dombeyana	z	6-7	s-1	np	np	wd
foetida	z	6-7	s-1	np	np	wd
ghiesbreghtii	st	6-7	s-1	np	np	wd
Tithonia						
calva	st	6	s-1	np	np	wd
diversifolia	st	6	s-1	np	np	wd
tubaeformis	st	6	s-1	np	np	wd
Viguiera						
subg. Amphilepis						
excelsa	st	5-6	0-s	p	np	wd
flava	st	5-6	s-1	p	np	wd
hemsleyana	st	5-6	s-2	np	p	wd
hypochlora	st	5-6	0-s	p	np	wd
latibracteata	st	6-7	s-2	np	np	wd
schultzii	st	6	s-2	np	np	im
sect. Aureae						
incana	st	6-7	s-1	np	p	wd
szyszylowiczii	st	6-7	s-1	np	p	wd
ser. Grammatoglossae						
cordifolia	st	6-7	2-3	np	p	wd
aff. ovata	st	5	1-2	np	np	im
parkinsonii	st	6-7	2-3	np	p	wd
rhombifolia	st	6-7	1-3	np	p	wd
sessilifolia	st	5-6	1	np	np	im
sect. Hypargyrea						

rosei	st	6-7	s-1	np	p	wd
sect. *Maculatae*						
oaxacana	st	6	1-2	np	np	wd
quinqueradiata	st	6	s-1	np	np	wd
trachyphylla	st	7-8	s-1	np	np	wd
ser. *Pinnatilobata*						
pinnatilobata	st	6-7	s-1	np	np	wd
subg. *Bahiopsis*						
microphylla	z	6-7	s-1	np	np	im
reticulata	st	5-6	2-3	np	p	wd
tomentosa	z	5-6	s-1	np	np	im

sn = sinuous, st = straight, z = zig-zag
p = present, np = not present
im = imperfect, wd = well-developed

APPENDIX 5

Chromosome numbers of species of Pappobolus. Vouchers deposited at TENN. References to previously published results are cited in parentheses. All the counts preceded by ca are approximations in which either n = 16, 17 or 18 were counted but where 17 was the most common count.

Pappobolus acutifolius: n = ca 17, PERU: Ancash, Panero & Galán 1399.

Pappobolus amoenus: n = 17, PERU: Cajamarca, Panero & Sánchez Vega 1156.

Pappobolus argenteus: n = 17, ECUADOR: Cañar, Panero 736.

Pappobolus cajamarcensis: n = 17, PERU: Cajamarca, Panero & Sánchez Vega 1282.

Pappobolus ecuatorianus var. ecuatorianus: n = ca 17, ECUADOR, Azuay, Panero 1518.

Pappobolus ecuatorianus var. lancifolius: n = 17, ECUADOR, Loja, Panero 1475.

Pappobolus decumbens: n = 17, PERU: Cajamarca, Panero & Sánchez Vega 1345.

Pappobolus discolor: n = 17, PERU: Ancash, Panero & Galán 1367; 1368.

Pappobolus hutchisonii: n = ca 17, PERU: Cajamarca, Panero & Sánchez Vega 1242.

Pappobolus hypargyreus: n = ca 17, ECUADOR: Chimborazo, Panero 1510; (Heiser, C. 1957).

Pappobolus imbaburensis: n = ca 17, ECUADOR: Carchi, Panero & Gómez 1100; (Heiser, C. 1957); Tungurahua, Panero 718; 1407; (Robinson,

H. et al. 1981).

Pappobolus jelskii: n = ca 17, PERU: Cajamarca, Panero & Sánchez Vega 1122.

Pappobolus juncosae: n = ca 17, ECUADOR: Imbabura, Panero & Gómez 1094.

Pappobolus lanatus: n = 17, PERU: Lima, Panero 1362; PERU: Ancash, Panero & Galán 1398.

Pappobolus lehmannii var. lehmannii: n = ca 17, ECUADOR: Chimborazo, Panero 1501; (Robinson, H. et al. 1981).

Pappobolus lehmannii var. grandiceps: n = ca 17, ECUADOR: Chimborazo, Panero 1415; 1508.

Pappobolus matthewsii var. matthewsii: n = ca 17, PERU: Cajamarca, Panero 1352; 1353; 1356.

Pappobolus matthewsii var. viridifolius: n = 17, ECUADOR: Cajamarca, Panero & Sánchez Vega 1257.

Pappobolus microphyllus: var. microphyllus: n = 17, PERU: Cajamarca, Panero 1124; 1143; 1177; 1178.

Pappobolus nigrescens: n = ca 17, ECUADOR: Azuay, Panero 1416; 1438; 1492.

Pappobolus robinsonii: n = 17, PERU: Cajamarca, Panero et al. 955; Panero & Sánchez Vega 1225.

Pappobolus sagasteguii: n = ca 17, PERU: Cajamarca, Panero & Sánchez Vega 1230.

Pappobolus sanchezii: n = 17, PERU: Cajamarca, Panero 1195.

Pappobolus schillingii: n = 17, ECUADOR: Loja, Panero 1450; 1472; 1477; 1478.

Pappobolus stuebelii: n = 17, PERU: Cajamarca, Panero et al. 932;

Panero 1207; Panero & Sánchez Vega 1217.

Pappobolus subniveus: n = 17, PERU: Cajamarca, Panero et al. 862; Panero 1136.

Pappobolus viridior: n = 17, PERU: Junín, Panero 1365; (Dillon, M. & B. L. Turner 1982).

Pappobolus woodsonianus: n = 17, (Turner, B. L. et al. 1967).

HYBRIDS

Pappobolus decumbens X Pappobolus jelskii: n = 17, PERU: Cajamarca, Panero & Sánchez Vega 1344.

Pappobolus microphyllus X Pappobolus sanchezii: n = 17, PERU: Cajamarca, Panero 1290.

APPENDIX 6

CLAVE ARTIFICIAL PARA PAPPOBOLUS Y GENEROS RELACIONADOS EN SUDAMERICA.

1. Pedúnculos fistulosos; Arbustos, hierbas perennes o anuales del SW de E.U.A., México y América Central, pioneras en Sudamérica (especialmente en el NW de Argentina). Tithonia.

1. Pedúnculos no fistulosos.

   2. Aquenios del disco planos; SW E.U.A., México, América Central y esporádicamente a lo largo de la Cordillera de los Andes desde Colombia hasta La Argentina, también en el NE del Brasil. Simsia.

   2. Aquenios del disco biconvexos, rellenos.

      3. Aquenios del disco con un papus de varias aristas delicadas y deciduas. Pappobolus.

      3. Aquenios del disco sin papus, con un papus de 2 aristas con o sin escamitas intermedias o

         4. Aquenios del disco con un eliasoma conspicuo; Peru. Syncretocarpus.

         4. Aquenios del disco sin eliasomas.

            5. Aquenios del disco con un papus de 2 aristas deciduas, escamitas rara vez presentes. Pappobolus.

            5. Aquenios del disco con un papus de 2 aristas persistentes y varias escamitas, sin papus, o a veces con una corona de escamitas minúsculas persistentes.

6. Páleas trilobadas conspicuamente; arbustos endémicos de las Islas Galápagos. Scalesia.

6. Páleas enteras.

7. Aquenios del disco con un papus consistente en una corona de aristas muy reducidas o sin papus.

Hymenostephium y Viguiera sect. Diplostichis en parte.

7. Aquenios del disco con un papus de 2 aristas y varias escamitas.

8. Arbustos con una suave pubescencia villosa, velutinosa, lanada o pilosa. Pappobolus.

8. Anuales o hierbas perennes con una pubescencia escabrosa o híspida. Viguiera.

CLAVE ARTIFICIAL PARA LAS ESPECIES DE PAPPOBOLUS.

1. Teca de las anteras amarillas, amarillo-naranjas o café-amarillas; lóbulos de la flor del disco amarillos en su superficie abaxial.

2. Apices de la pálea tenue a fuertemente reflexos; filarias estrechamente lanceoladas con ápices herbáceos lineales extendidos a fuertemente reflexos.

3. Hojas ovadas, deltadas o ampliamente truladas; tubo de la flor del disco escasamente pubérulo o glabro; capitulescencia asociada con hojas grandes (tan sólo ligeramente menores que las hojas caulinas).

4. Hojas densamente velutinoso-sericeas a pilosas en su superficie abaxial, moderada a densamente pilosas en su superficie adaxial; margen foliar aserrado; tallos herbáceos pilosos.

2. P. sagasteguii.

4. Hojas glabrescentes a moderadamente velutinosas o villosas en su superficie abaxial, escasa a moderadamente estrigosas en su superficie adaxial; margen foliar entero a aserrulado; tallos herbáceos tomentosos a moderadamente tomentoso-hirsutos.

1. P. matthewsii.

3. Hojas ovadas a estrechamente lanceoladas, rara vez lineales; tubo de la flor del disco densamente pubérulo y glandular; capitulescencia con hojas marcadamente más pequeñas que las hojas caulinas.

5. Garganta de la flor del disco 6-7 mm de longitud; lígula reflexa; páleas sobresaliendo 3-4 mm sobre el nivel de las filarias. 4. P. hutchisonii.

5. Garganta de la flor del disco 2.7-4.5 mm de longitud; lígula no reflexa; páleas sobresaliendo 1-1.5 mm sobre el nivel de las filarias. 5. P. acutifolius.

2. Apices de las páleas derechos; filarias ovales a oblongas, con ápices herbáceos agudos a suborbiculares adpresos o tenue a moderadamente reflexos.

6. Receptáculos 3.9-4.2 mm de diametro en frutificación;

hojas estrechamente lanceoladas y densamente lanadas o velutinosas en su superficie abaxial; hojas abruptamente más pequeñas arriba hacia la capitulescencia; filarias 17-21 en 3 series equivalentes. 6. P. verbesinoides.

6. Receptáculos 5.7-8.5 mm de diametro en fructificación; hojas lanceoladas, ovadas, truladas o rómbicas escasa a moderadamente villosas, velutinosas o lanado-sericeas; hojas progresivamente más pequeñas arriba hacia la capitulescencia; filarias 19-30 en 3-4 series graduadas o equivalentes.

7. Filarias de la segunda a cuarta serie verde-negruzcas o negras y glabrescentes en su cara abaxial; el ápice o la mitad distal de la pálea conspicuamente verde obscura o negra. 8. P. imbaburensis.

7. Filarias de la segunda a cuarta serie estramineas o estramineo-cobrizas con conspicuas bandas verde claro, éstas a veces no evidentes por la densa pubescencia; ápice o la mitad distal de la pálea estraminea con bandas café claro o verdes, rara vez juntandose para formar un ápice verde obscuro o negruzco.

8. Filarias anchamente ovales a suborbiculares, escasa a densamente villosas a lanadas en su cara abaxial, ápices herbáceos blancos o blanco-verdosos.

9. Hojas y tallos densamente velutinosos o villosos a blanco lanados; ápices de la pálea estramineos con unas cuantas bandas café claro o verdes;

capitulescencia pequeña con 1 a 5 capítulos.

9. P. juncosae.

9. Hojas y tallos escasa a densamente tomentosos a velutinosos, verde cremosos, nunca blanco lanados; ápices de la palea verde obscuros, raramente estramineos; capitulescencia amplia con (3-) 12-40 capítulos. 7. P. hypargyreus.

8. Filarias estrechamente oblongas a lanceoladas, minúsculamente tomentosas a villosas, más nunca tapando el patrón de coloración de la filaria, la base endurecida, estraminea con bandas longitudinales verdes, éstas uniendose, formando un ápice herbáceo verdoso.

10. Garganta de la flor del disco 6-7 mm longitud; lígulas reflexas; las páleas sobresaliendo 3-4 mm sobre el nivel de las filarias.

4. P. hutchisonii.

10. Garganta de la flor del disco 1.7-4.9 mm longitud; lígula no reflexas; las paleas sobresaliendo 0.2-0.6 mm sobre el nivel de las filarias.

11. Capítulos con 85-140 flores del disco; ápices de las páleas tenue a fuertemente reflexos; garganta de la flor del disco

1.9-2.9 mm de longitud; las páleas sobresaliendo 0.2-0.6 mm sobre el nivel de las filarias. 1. P. matthewsii.

11. Capítulos con 60-90 flores del disco; ápices de las páleas derechos; garganta de la flor del disco 1.7-4.9 mm de longitud; las páleas sobresaliendo 0.5-3 mm sobre el nivel de las filarias. 3. P. ecuatorianus.

1. Teca de la antera negra, café-negruzca o morado-negruzca; lóbulos de la flor del disco negros, rara vez amarillos en su superfici abaxial.

12. Margenes foliares subenteros a aserrados, nunca revolutos; textura de la hoja suave y delgada; las hojas sin gran diferencia en color entre ambas caras; hojas ovadas a deltadas a anchamente lanceolado-elípticas y 25-160 mm de longitud, 10-110 mm de ancho; pecíolos 5-52 mm de longitud.

13. Aquenio del disco con un papus de (5-) 8-28 aristas y sin escamitas; ovario de la flor ligulada con un papus de (3-) 5-21 aristas y sin escamitas.

14. Filarias oblongas a ovadas y adpresas.

15. Filarias densamente blanco-lanadas en su superficie abaxial. 16. P. mollicomus.

15. Filarias glabrescentes, verde obscuras, negras cuando secas. 22. P. robinsonii.

14. Filarias lanceoladas y expandiendose o reflexas.

16. Filarias 35-44, primera y segunda series 10.5-11.5 mm de longitud; margenes foliares subenteros a escasamente aserrulados; lígulas reflexas. 15. P. cinerascens.

16. Filarias 38-62, primera y segunda series 17-30 mm de longitud; margenes foliares; lígulas no reflexas. 17. P. macranthus.

13. Aquenios del disco con un papus de 2 (-3) aristas con o sin escamitas; ovario de la flor ligulada con un papus de 1-7 aristas con o sin escamitas, a veces sin papus.

17. Hojas alternas.

18. Capitulescencias compactas, 1-3 capítulos en pedúnculos muy cortos (ver Fig.). 12. P. andinus.

18. Capitulescencias abiertas, 3-21 capítulos en pedúnculos largos (ver Fig.).

19. Pubescencia abaxial de la hoja villosa a lanado-flocosa. 20. P. schillingii.

19. Pubescencia abaxial de la hoja velutinosa a sericea.

20. Lígula 6.5-15 mm de longitud, 3-5.3 mm de ancho.

21. Lígulas oblongo-lanceoladas, 14-15

mm de longitud; filarias lineal-lanceoladas con bases negruzcas endurecidas. 23. P. szyszylowiczii.

21. Lígulas ovales a oblongas, 6.5-10.5 mm de longitud; filarias oblongas a oblanceoladas sin bases negruzcas endurecidas. 7. P. hypargyreus.

20. Lígula 16.5-33.5 mm de longitud, 6-11.5 mm de ancho.

22. Ovario de la flor ligulada con 2-7 escamitas o pequeñas aristas; ramas del estilo negras en su superficie abaxial.

23. Tubo de la flor del disco escaso a moderadamente pubérulo; aquenio del disco 3.4-4.1 mm de largo; superficie abaxial de las filarias verde obscuro, negras cuando secas. 11. P. nigrescens.

23. Tubo de la flor del disco glabro, aquenio del disco 4.8-5.8 mm de longitud; superficie abaxial de las filarias uniformemente hirsuta,

villosa lanado-sericea.

10. P. lehmannii.

22. Ovario de la flor ligulada sin papus o con 1 o 2 pequeñas escamitas o aristas; ramas del estilo completamente amarillas.

13. P. stork-hortonii.

17. Hojas opuestas.

24. Primera serie de filarias 19-60 mm de longitud, 7.5-19 mm de ancho, reflexas, dobladas y foliáceas. 18. P. sanchezii.

24. Primera serie de filarias 7.5-21 de largo, 3-10 mm de ancho, reflexas, dobladas más no foliáceas.

25. Superficie abaxial de la hoja lanado-flocosa.

26. Superficie adaxial de la hoja moderada a densamente estrigoso-sericea, blanco -verdosa; margenes foliares enteros; hojas anchamente ovadas, bases obtusas a truncadas. 14. P. acuminatus.

26. Superficie adaxial de la hoja estrigosa, verde; margenes foliares escasamente aserrulados a aserrados; hojas ovadas a ovado-lanceoladas, bases

atenuadas a redondeadas.

27. Primera y segunda serie de filarias oblongas a espatuladas, densamente lanadas o villosas y reflexas, filarias interiores adpresas y verde obscuras o negras, conspicuamente lanadas a lo largo de la superficie abaxial del agudo ápice herbáceo. 22. P. robinsonii.

27. Primera y segunda serie de filarias lanceoladas u ovadas, moderadamente tomentosas a velutinosas sobre la superficie abaxial, filarias interiores extendiendose, verde a verde obscuras, secando negras, glabrescentes a escasamente villosas a lo largo de la superficie del acuminado ápice herbáceo.

28. Capítulos hemisféricos; las primeras 3 series de filarias 12-21 mm de longitud, 2.8-5 mm de ancho; lígulas no reflexas; aquenios del disco, glabros con un papus de 2 aristas y sin escamitas.

20. P. schillingii.

28. Capítulos hemisférico-urceolados; las primeras 3 series de filarias 7.4-12.5 mm de longitud, 2.7-4.5 mm de ancho; lígulas reflexas; aquenios del disco con unos cuantos tricomas alrededor del cuello con un papus de 2 aristas y a veces con 2-10 escamitas. 21. P. amoenus.

25. Superficie abaxial de la hoja velutinosa a sericea. 19. P. youngiorum.

12. Margenes foliares revolutos y enteros o rara vez subenteros; las hojas gruesas y coriáceas; las hojas conspicuamente bicoloras y densamente lanadas en su superficie abaxial; las hojas ovadas a ovado-lanceoladas, ovado-suborbiculares, truladas, oblongas, lanceoladas a estrechamente lanceoladas o elípticas 4-115 mm de longitud, 2-50 mm de ancho; pecíolos 1-30 mm de largo.

29. Papus del aquenio del disco de más de 3 aristas deciduas.

30. Hojas alternas, estrechamente lanceoladas a lineales. 32. P. decumbens.

30. Hojas opuestas, ovales a elípticas.

33. P. woodsonianus.

29. Papus del aquenio del disco de 2 o 3 aristas deciduas, escamitas rara vez presentes.

31. Flores del disco 160-385; capítulos 16-32 mm de ancho; hojas ovadas a ovado-lanceoladas, 10-115 mm de largo, 6-50 mm de ancho.

32. Hojas opuestas. 26. P. jelskii.

32. Hojas alternas.

33. Hojas escasa a moderadamente estrigosas y rugosas en su superficie adaxial, densamente lanadas, ocre cobrizas en su superficie abaxial. 24. P. stuebelii.

33. Hojas moderada a densamente estrigoso-sericeas en su superficie adaxial, densamente lanadas, blancas en su superficie abaxial. 25. P. smithii.

31. Flores del disco 35-160; capítulos 7-19 mm de ancho; hojas ovadas a ovado-suborbiculares, truladas, oblongas, lanceoladas a estrechamente lanceoladas 4-80 mm de longitud, 2-50 mm de ancho.

34. Hojas estrechamente lanceoladas o lineales o minúsculamente oblongas (sí truladas u ovadas, entonces los capítulos más pequeños que 1 cm de ancho [lígulas no incluidas]).

35. Superficie foliar adaxial esencialmente

glabra y brillante; filarias interiores suborbiculares, membranaceas, cubriendo el capítulo inmaduro.

30. P. cajamarcensis.

35. Superficie foliar adaxial pubescente y parda, rara vez brillante; filarias interiores lanceoladas a lineales o oblongas, cartáceas, nunca cubriendo el capítulo inmaduro.

36. Hojas estrechamente lanceoladas a a lineales y fuertemente revolutas.

37. Páleas sobresaliendo 1.5-2 mm sobre el nivel de las filarias; base abaxial de las filarias verde obscuro o negruzca y glabrescentes, ápice herbáceo adpreso; superficie foliar adaxial escasamente estrigosa y algo brillante; hojas disminuyendo en tamaño y número arriba hacia la capitulescencia. 31. P. discolor.

37. Páleas cubiertas por las filarias; base abaxial de las filarias densamente

lanadas, blancas, ápice herbáceo extendiendose; superficie foliar adaxial moderada a densamente estrigosa, blanco-verdosa, opaca; hojas equivalentes en en tamaño y número arriba hacia la capitulescencia. 29. P. subniveus.

36. Hojas ovadas, ovales a oblongas, truladas (sí estrechamente lanceoladas o lineales entonces los capítulos más pequeños que 1 cm de ancho [lígulas no incluidas]). 28. P. microphyllus.

34. Hojas lanceoladas a ovadas o ovado-suborbiculares, a veces ovadas a truladas.

38. Pubescencia del hábito ocre a bronceada. 27. P. lodicatus.

38. Pubescencia del hábito blanca a incana.

39. Hojas ovadas a ovado-suborbiculares, 10-80 mm de longitud, 40-50 mm de ancho.

40. Flores del disco 115-160; lígulas 14.5-19.5 mm de longitud; filarias 20-32 en

4 series graduadas. 35. P. lanatus.

40. Flores del disco 45-85; lígulas 8.5-9.5 mm de longitud; filarias 19-26 en 3 series equivalentes. 36. P. senex.

39. Hojas lanceoladas 11-65 mm de longitud, 15-17 mm de ancho.

41. Corola de la flor del disco glabra; lígulas 8.2-25 mm de longitud, 2.3-7 mm de ancho.

42. Apices de las páleas pubescentes; filarias 24-37. Plantas del Ecuador. 37. P. argenteus.

42. Apices de las paleas glabros; filarias 20-23. Plantas del Perú. 38. P. viridior.

41. Corola de la flor del disco escasa a moderadamente pubérula y glandular; lígulas 9-14 mm de longitud, 2.5-4 mm de ancho. 34. P. davidii.

APPENDIX 7

NUMERICAL LIST OF SPECIES

I. Subgenus Apricus

1a. P. matthewsii var. matthewsii

1b. P. matthewsii var. occidentalis

1c. P. matthewsii var. viridifolius

2. P. sagasteguii

3a. P. ecuatorianus var. ecuatorianus

3b. P. ecuatorianus var. lancifolius

4. P. hutchisonii

5. P. acutifolius

6. P. verbesinoides

7. P. hypargyreus

8. P. imbaburensis

9. P. juncosae

II. Subgenus Pappobolus

10a P. lehmannii var. lehmannii

10b. P. lehmannii var. grandiceps

11. P. nigrescens

12. P. andinus

13. P. stork-hortonii

14. P. acuminatus

15. P. cinerascens

16. P. mollicomus

17. P. macranthus

18. P. sanchezii

19. P. youngiorum

20. P. schillingii

21. P. amoenus

22. P. robinsonii

23. P. szyszylowiczii

24. P. stuebelii

25. P. smithii

26. P. jelskii

27. P. lodicatus

28a. P. microphyllus var. microphyllus

28b. P. microphyllus var. dillonii

28c. P. microphyllus var. liberus

28d. P. microphyllus var. soukupii

29. P. subniveus

30. P. cajamarcensis

31. P. discolor

32. P. decumbens

33. P. woodsonianus

34. P. davidii

35. P. lanatus

36. P. senex

37. P. argenteus

38. P. viridior

INDEX TO NUMBERED COLLECTIONS CITED

The numbers in parentheses refer to the corresponding taxa in the text and the Numerical List of Species presented above.

Acosta, M. 5533 (10a); 5993 (10a); 8652 (8); 8922 (8); 8928 (8); 9107 (8); 9199 (8); 11269 (8); 12503 (8); 14218 (8).

Aguado 6797 (2).

Albert de Escobar, L. 1053 (11).

Albert de Escobar, L., & P. Berry 656 (7); 1493 (24).

Albert de Escobar, L., et al. 685 (11).

André, E. K233 (10a); 3538 (8).

Balls, E. K. 7150 (8).

Becker & Terrones 239 (29); 1211 (18); 1826 (29).

Cabanillas 257 (32).

Cabrera, A., & Farris 13432 (35).

Camp, W. H. E-2784 (10b); E-3142 (7); E-3903 (11).

Cevasco 13391 (16).

Cerrate, E. 724 (35); 758 (35).

Cowan, C. P., et al. 4355 (24); 4418 (29).

Dillon, M. O., & B. L. Turner 1329 (38); 1551 (28a); 1636 (24); 1715 (19).

Dillon, M. O., & Whalen 4055 (22).

Dillon, M. O., et al. 2758 (32); 2805 (28b); 2856 (3); 2970 (29); 2990 (24); 3033 (28a).

Edwin & Schunke 3723 (1a).

Ellenberg 1756 (27); 1767 (18).

Espinosa 1533 (20).

Fallen 690 (8).

Falconí & Argüello 71 (10a).

Ferreyra, R. 1296 (25); 5280 (35); 5808 (35); 7104 (1a); 7523 (35); 7557 (35); 7713 (35); 8311 (35); 8499 (26); 9241 (36); 13265 (24); 13315 (2); 13602 (35); 14493 (35); 14911 (35).

Ferreyra, R., & M. Chanco 20463 (6).

Ferreyra, R., & Sánchez 19558 (1a); 19658 (1a).

Filskov et al. 37388 (8).

Firmin 365 (8).

Fosberg, F. R., & M. A. Giler 22620 (7).

Gentry A., et al. 23129 (19); 23224 (1a).

Goodspeed, T. H. 33121 (35).

Goodspeed, T. H., & A. Weberbauer 33063 (35).

Harling & Andersson 13440 (20); 14531 (11).

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APPENDIX 8

INDEX TO SCIENTIFIC NAMES

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  chachapoyensis Ahumada

Baccharis L.

Barnadesia Mutis

  dombeyana Less.

  lehmannii Hieron.

  spinosa L.

Begonia L.

Berberis L.

Bidens L.

Bocconia L.

  integrifolia Humb. & Bonpl.

Bouganvillea Comm. ex Juss.

  peruviana H. B. K.

Brachyotum Triana

Buddleja L.

  bullata H. B. K.

incana Ruiz & Pav.

Cacosmia Kunth

rugosa H. B. K.

Caesalpinia L.

tinctoria DC.

Calceolaria L.

argentea H. B. K.

ballotifolia Kranzl

dentifolia Edwin

melissifolia Benth.

rhododendroides Kranzl

Calea L.

Cajophora Presl.

Calamagrostis Adans.

Carica L.

Cavendishia Lindl.

Cienfuegosia Cav.

tripartita (H. B. K.) Gürke

Chaptalia Vent.

Clusia L.

Coreopsis L.

celendinensis Sagástegui & Sánchez

connata Cabrera

obovatifolia Sagástegui

senaria S. F. Blake & Sherff

woytkowskii Sherff

Coriaria L.

thymifolia Humb. & Bonpl.

Cortaderia Stapf.

Cosmos Cav.

paucedanifolius Wedd.

Croton L.

Dalechampia L.

hutchisoniana Webster

Delostoma D. Don

Dodonaea L.

viscosa Jacq.

Dunalia Kunth

Elleanthus Presl.

Encelia Adans.

Ephedra L.

americana Willd.

Erythrina L.

Espeletia Mutis

Euphorbia L.

laurifolia Lam.

Festuca L.

Flourensia DC.

macrophylla S. F. Blake

Frankenia L.

Franseria Cav.

Fuchsia L.

loxensis H. B. K.

mathewsii J. F. Macbr.

Gentianella Moench.

Hedyosmum Sw.

Helianthopsis H. Robinson

acuminata (S. F. Blake) H. Robinson

discolor (S. F. Blake) H. Robinson

grandiceps (S. F. Blake) H. Robinson

hutchisonii H. Robinson

hypargyrea (S. F. Blake) H. Robinson

imbaburensis (Hieron) H. Robinson

jelskii (Hieron.) H. Robinson

lanata (Heiser) H. Robinson

lehmannii (Hieron.) H. Robinson

matthewsii (Hochr.) H. Robinson

microphylla (H. B. K.) H. Robinson

nigrescens (Heiser) H. Robinson

pseudoverbesinoides (Hieron.) H. Robinson

var. *gracilis* Hieron.

sagasteguii H. Robinson

senex (S. F. Blake) H. Robinson

smithii Ferreyra

stuebelii (Hieron.) H. Robinson

subnivea (S. F. Blake) H. Robinson

utcubambensis H. Robinson

verbesinoides (H. B. K.) H. Robinson

viridior (S. F. Blake) H. Robinson

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acuminatus S. F. Blake

angustifolius L.

argenteus H. B. K.

argophyllus T. & G.

arizonensis R. C. Jacks.

atrorubens L.

carnosus Small

decapetalus L.

discolor S. F. Blake

floridanus A Gray ex Chapman

giganteus L.

grandiceps S. F. Blake

heterophyllus Nutt.

hirsutus Raf.

hypargyreus S. F. Blake

imbaburensis Hieron.

jelskii Hieron.

lanatus Heiser

lehmannii Hieron.

lodicatus Cuatr.

matthewsii Hochr.

maximilianii Schrader

microcephalus T. & G.

microphyllus H. B. K.

nigrescens Heiser

niveus Hieron.

niveus (Benth.) T. S. Brandegee

occidentalis Riddell

praecox Engelm. & A. Gray

pseudoverbesinoides Hieron.

senex S. F. Blake

stuebelii Hieron.

subniveus S. F. Blake

szyszylowiczii Hieron.

verbesinoides H. B. K.

viridior S. F. Blake

Heliomeris Nutt.

multiflora Nutt.

Hesperomeles Lindl.

Hymenostephium Benth.

superaxillare S. F. Blake

Iostephane Benth.

heterophylla (Cav.) Hemsl.

madrensis (S. Wats.) Strother

papposa Fay

trilobata Hemsl.

Jacquemontia Choisy.

Jatropha L.

Juglans L.

Jungia L.

  stuebelii (Hieron.) Crisci

Lantana L.

Lepechinia Willd.

Llagunoa Ruiz & Pav.

  nitida H. B. K.

Lomatia R. Br.

  hirsuta (Lam.) Diels

Masdevallia Ruiz & Pav.

Melanthera Rohr.

Monactis Kunth

Monnina Ruiz & Pav.

Munnozia Ruiz & Pav.

Myrcianthes Berg.

Myrica L.

Myrsine L.

  manglilla R. Br.

Nicotiana L.

Ocotea Aubl.

Oncidium Sw.

Onoseris Willd.

  albicans (Don) Ferreyra

  hyssopifolia Kunth

  salicifolia H. B. K.

Oreocallis R. Br.

grandiflora R. Br.

Oreopanax Decne & Planch.

Pappobolus S. F. Blake

subg. Apricus Panero

subg. Pappobolus

acuminatus (S. F. Blake) Panero

acutifolius (S. F. Blake) Panero

amoenus Panero

andinus Panero

argenteus (H. B. K.) Panero

cajamarcensis Panero

cinerascens S. F. Blake

davidii Panero

decumbens Panero

discolor (S. F. Blake) Panero

ecuatorianus Panero

var. ecuatorianus

var. lancifolius Panero

hutchisonii (H. Robinson) Panero

hypargyreus (S. F. Blake) Panero

imbaburensis (Hieron.) Panero

jelskii (Hieron.) Panero

juncosae Panero

lanatus (Heiser) Panero

lehmannii (Hieron.) Panero

var. lehmannii

var. grandiceps (S. F. Blake) Panero

lodicatus (Cuatrecasas) Panero

macranthus S. F. Blake

matthewsii (Hochr.) Panero

var. matthewsii

var. occidentalis Panero

var. viridifolius Panero

microphyllus (H. B. K.) Panero

var. microphyllus

var. dillonii Panero

var. liberus Panero

var. soukupii Panero

mollicomus S. F. Blake

nigrescens (Heiser) Panero

robinsonii Panero

sagasteguii (H. Robinson) Panero

sanchezii Panero

schillingii Panero

senex (S. F. Blake) Panero

smithii (Ferreyra) Panero

stork-hortonii Panero

stuebelii (Hieron.) Panero

subniveus (S. F. Blake) Panero

szyszylowiczii (Hieron.) Panero

verbesinoides (H. B. K.) Panero

viridior (S. F. Blake) Panero

woodsonianus Cuatrecasas

youngiorum Panero

Paranephelius Poepp. & Endl.

Pectis L.

Perezia Lag.

Perymenium Schrad.

Pineda Ruiz & Pav.

incana Ruiz & Pav.

Polymnia L.

glabrata DC.

Prosopis L.

Prunus (Tourn.) L.

huantensis Pilger

Puya Molina

Quercus L.

Randia L.

boliviana Rusby

Ranunculus L.

Rauhia Traub.

Satureja L.

sericea Briq.

weberbauerii Mansfeld

Scalesia Arn.

Schinus L.

molle L.

Sclerocarpus Jacq.

Sebastiania Spreng.

obtusifolia Pax & K. Hoffm.

Simsia Pers.

amplexicaulis (Cav.) Pers.

annectens S. F. Blake

var. annectens

calva (A. Gray & Engelmann ex A. Gray) A. Gray

chaseae (Millspaugh) S. F. Blake

dombeyana DC.

eurylepis S. F. Blake

foetida (Cav.) S. F. Blake

var. foetida

var. grandiflora (Benth.) D. M. Spooner

var. megacephala (Sch.-Bip. ex S. F. Blake) S. F. Blake

fruticulosa (Spreng.) S. F. Blake

ghiesbreghtii (A. Gray) S. F. Blake

hoıwayi S. F. Blake

lagascaeformis DC.

molinae H. Robinson

sanguinea A. Gray

setosa S. F. Blake

steyermarkii H. Robinson

Solanum L.

glutinosum Dun.

Steiractinia S. F. Blake

Stenomesson Herb.

Syncretocarpus S. F. Blake

sericeus (DC.) S. F. Blake

Tecoma Juss.

stans Juss.

Tithonia Desf. ex Gmelin

calva Sch.-Bip.

diversifolia (Hemsl.) A. Gray

pedunculata Cronquist

rotundifolia (Miller) S. F. Blake

tubaeformis (Jacq.) Cass.

Trixis P. Br.

Vallea Mutis ex L.

stipularis L.

Vernonia Schreb.

patens H. B. K.

Viburnum L.

Viguiera Kunth

subg. Amphilepis S. F. Blake

subg. Bahiopsis (Kellogg) E. Schilling

sect. Diplostichis S. F. Blake

sect. Maculatae (S. F. Blake) Panero & E. Schilling

series Aureae S. F. Blake

series Brevifoliae S. F. Blake

series Grammatoglossae S. F. Blake

series Pinnatilobatae S. F. Blake

acutifolia S. F. Blake

adenophylla S. F. Blake

atacamensis Phil.

bicolor S. F. Blake

bombycina S. F. Blake

brevifolia Greenm.

brittonii Hochr.

chimboensis Hieron.

cordata (Hook. & Arn.) D'Arcy

cordifolia A. Gray

dentata (Cav.) Spreng.

eriophora Greenm.

excelsa (Willd.) B. & H.

flava (Hemsl.) S. F. Blake

grammatoglossa DC.

hemsleyana S. F. Blake

hidalgoana E. Schilling & Panero

hypargyrea Greenm.

hypochlora (S. F. Blake) S. F. Blake

incana (Pers.) S. F. Blake

lanata (Kellogg) A. Gray

lanceolata Britton

latibracteata (Hemsl.) S. F. Blake

lehmannii Hieron.

linearis (Cav.) Sch.-Bip.

media S. F. Blake

microphylla Vasey & Rose

mollis Griseb.

oaxacana (Greenm.) S. F. Blake

ovata (A. Gray) S. F. Blake

parkinsonii (Hemsl.) S. F. Blake

pazensis Rusby

pinnatilobata (Sch. Bip.) S. F. Blake

pringlei Rob. & Greenman

procumbens (Pers.) S. F. Blake

purisimae Brandegee

purpusii Brandegee

quinqueradiata (Cav.) A. Gray

quitensis (Benth.) S. F. Blake

reticulata S. Watson

revoluta (Meyen) S. F. Blake

rhombifolia (Rob. & Greenm.) S. F. Blake

rosei Greenm.

schultzii S. F. Blake

seemannii Sch. Bip.

sessilifolia DC.

simsioides S. F. Blake

sodiroi (Hieron.) S. F. Blake

sphaerocephala (DC.) Hemsl.

szyszylowiczii Hieron.

tenuis A. Gray

tomentosa A. Gray

trachyphylla S. F. Blake

tripartita (Rob. & Greenman) S. F. Blake

tuberosa Griseb.

Viola L.

arguta DC.

Werneria Kunth

Wigandia Kunth

APPENDIX 9

List of Figure captions and Figures

FIG. 1. Distribution of Pappobolus and related genera.

FIG. 2. Diagrams indicating points of reference for the major morphological features measured for Pappobolus and used in the Taxonomic Treatment. Figures explained in the text.

FIG. 3. Examples of growth habit in Pappobolus. A. P. argenteus (Panero 1500), Ecuador: Prov. of Cañar, south of Cañar. B. P. sagasteguii (Panero 1230), Peru: Dept. of Cajamarca, along the road Celendín-Balsas. C. P. matthewsii var. matthewsii (Panero 1351), Peru: Dept. of Cajamarca, south of Jaén. D. P. stuebelii (Panero 1150), Peru: Dept. of Cajamarca, along road Cajamarca-Celendín. E. P. decumbens (Panero & Sánchez Vega 1345), Peru: Dept. of Cajamarca, in the gorge of the Perlamayo River.

FIG. 4. Variation in blade morphology in Pappobolus. A. P. acutifolius (Panero & Galán 1399). B. P. robinsonii (Panero et al. 955). C. P. sanchezii (Panero 1195). D. P. hypargyreus (Panero 1510). E. P. lehmannii var. grandiceps. (A-E, bar = 1 cm).

FIG. 5. Leaf clearings of Pappobolus. A-B. P. acutifolius (Panero

& Galán 1399). C. P. cinerascens (Panero 1357). D. P. stuebelii (Panero 1150). E. P. argenteus (Panero 1500). F. P. stuebelii (Panero 1150). (A, C, E and F bar = 0.5 mm; B and D bar = 0.1 mm).

FIG. 6. Leaf clearings of Viguiera and Iostephane. A-B. V. cordifolia (Schilling & Panero 88-11). C. V. aff. ovata (Schilling & Panero 88-33). D. V. rhombifolia (Schilling & Panero 88-20). E. I. heterophylla (Panero & Schilling 1561). F. I. madrensis (Schilling & Panero 88-22).

FIG. 7. Leaf clearings of Helianthus and Tithonia. A-C. H. floridanus (Panero UT15). D-F. T. calva. (A and D bar = 1 cm; B, C and E bar = 0.5 mm; F bar = 0.2 mm).

FIG. 8. Leaf clearings of Hymenostephium and Viguiera. A. H. superaxillare (Schilling & Panero 88-9). B. Areolation in H. superaxillare. C. Areolation and mucronate tooth of H. superaxillare. D. Areolation in V. quitensis (Panero 782). E. Areolation in V. quitensis. F. Areolation and mucronate tooth of V. quitensis. (A and D bar = 1 cm; B, C, E and F bar = 0.5 mm).

FIG. 9. Leaf clearings of Simsia and Viguiera. A. S. amplexicaulis (Panero & Schilling 448). B-C. Areolation in S. amplexicaulis. D. V.

tomentosa. E. Areolation in V. tomentosa. (A and D bar = 1 cm; B bar = 0.5 mm; C and E bar = 0.1 mm).

FIG. 10. Leaf clearings of Viguiera. A. V. szyszylowiczii (Panero et al. 863). B. Areolation in V. szyszylowiczii. C. Areolation in V. rosei (Schilling & Panero 88-20). D. V. parkinsonii (Schilling & Panero 88-1). E. V. hemsleyana ( ). F. V. hypargyrea (Schilling & Panero 88-12). (A, D, E and F bar = 1 cm; b and C bar = 0.5 mm).

FIG. 11. Basic leaf venation patterns of Pappobolus and related genera. A. Pappobolus hypargyreus. B. Viguiera szyszylowiczii.

FIG. 12. Diagrams showing variation in synflorescence morphology in Pappobolus. A-D. Examples of monochasial thyrsoid synflorescences. A. P. hypargyreus (Panero 1510). B. P. nigrescens (Panero 755). C. P. stuebelii (Panero 1150). D. P. andinus (Hutchison & Tovar 4153). E-G. Examples of dichasial thyrsoid synflorescences. E. P. cinerascens (Panero 1357). F. P. jelskii (Panero & Sánchez Vega 1122). G. P. woodsonianus (Wurdack 584).

FIG. 13. Morphological variation in the synflorescence structure of Pappobolus along an altitudinal and environmental gradient. 1. P. hypargyreus (Panero 1510). 2. P. nigrescens (Panero 755). 3. P. stuebelii (Panero 955). 4. P. stuebelii (Panero 1150).

FIG. 14. Trichomes of Pappobolus. A. Tapered trichome (P. hypargyreus). B. Moniliform trichome (P. hypargyreus). C. Sessile glandular trichome (P. hypargyreus). D. Uniseriate glandular trichome (P. acutifolius). E. Biseriate glandular trichome. (P. robinsonii). F. Zwillingshaare. (P. hutchisonii).

FIG. 15. Variation in tapered trichomes. A. P. robinsonii. B. P. lehmannii var. lehmannii. C. P. microphyllus.

FIG. 16. Cleared endothecial tissue of Pappobolus and related genera viewed under DIC optics, scale bar = 10 μm. A. Simsia amplexicaulis (Panero & Schilling 448). B. S. annectens (Spooner 2845). C. Viguiera sessilifolia (Schilling & Panero 88-21). D. V. rhombifolia (Schilling & Panero 88-31). E. V. ovata (Schilling & Panero 88-33). F. V. sessilifolia (Schilling & Panero 88-21. G. Helianthus maximilianii (Panero UT4). H. H. tomentosus (Panero .UT25). I. Tithonia diversifolia (Panero et al. 521). J. V. incana (Panero 732). K. V. simsioides (Sagástegui 9804). L. Pappobolus stuebelii (Panero 1150). M. P. hutchisonii (Panero & Sánchez Vega 1242). N. Syncretocarpus sericeus (Panero 1336).

FIG. 17. Maceration of anther collar and endothecial tissue,

viewed with DIC optics, scale bar = 10 μm. A. Anther collar cell wall thickenings of P. stuebelii (Panero et al. 932). B. Anther connective and first rows of endothecial tissue of P. stuebelii (Panero et al. 932). C. Endothecial cell wall thickenings of P. hypargyreus (Panero 733). D. Rows of endothecial cell wall thickenings of P. stuebelii (Panero et al. 932).

FIG. 18. Anther collar of P. stuebelii (Panero et al. 932). A. Adaxial surface showing uneven cell wall thickenings, 310 X. B. Abaxial surface, 140X.

FIG. 19. Camera-lucida drawings of Pappobolus anther collars, scale bar = 0.5 mm. A. P. robinsonii (Panero et al. 955). B. P. stuebelii (Panero et al. 995). C. P. stuebelii (Panero et al. 932). D. P. jelskii (Ferreyra 8499). E. P. senex (Ferreyra 9241). F. P. lehmannii var. lehmannii (Panero 720). G. P. imbaburensis (King 6583). H. P. macranthus (Woytkowski 34133a). I. P. sagasteguii (Hutchison & Wright 5398). J. P. mathewsii var. mathewsii (King 9271). K. P. smithii (López & Sagástegui 3309. L. P. subniveus (Panero et al. 862).

FIG. 20. Camera-lucida drawings of Pappobolus anther collars, scale bar = 0.5 mm. A. P. discolor (Sagástegui 11661). B. P. imbaburensis (Panero 711). C. P. viridior (Dillon & Turner 1329). D. P. argenteus (Panero 736). E. P. imbaburensis (Panero 822). F. P.

microphyllus (Panero et al. 864). G. P. andinus (Hutchison & Tovar 4153). H. P. davidii (Smith et al. 11984). I. P. sagasteguii (Hutchison & Wright 5397). J. P. mathewsii var. occidentalis (López & Sagástegui 5185. K. P. lehmannii (King & Garvey 6970).

FIG. 21. Camera-lucida drawings of Helianthus, Simsia, Tithonia and Viguiera anther collars, scale bar = 0.5 mm. A. T. diversifolia (Panero et al. 521). B. H. praecox (Panero UT11). C. H. carnosus. D. H. tomentosus (Panero UT25). E. V. porteri. F. S. calva (Panero UT1). G. S. foetida var. grandiflora (Spooner & Dorado 2699). H. V. subincisa. I. V. szyszylowiczii Panero et al. 861). J. V. incana (Panero 732). K. V. mollis (Venturi 5496). L. V. puruana (Panero et al. 659). M. V. potosina (Panero UT2). N. V. pinnatilobata (Panero et al. 634). O. V. pachycephala (Panero & Panero 8).

FIG. 22. Style branch morphology in Pappobolus and related genera. A. Pappobolus discolor. B. Viguiera puruana. C. Tithonia diversifolia. D. Helianthus resinosus. E. Simsia calva. F. Viguiera potosina.

FIG. 23. Habitats of species of Pappobolus. A. Canyon slopes of the Chanchán River south of Alausí, Ecuador. Pappobolus hypargyreus occurs on the slopes at right and left foreground. B. Banks of the Marañón River close to the town of Balsas, Dept. of Cajamarca, Peru.

Pappobolus hutchisonii flowering at left foreground. C. Valley of the Santa River, Dept. of Ancash, central Peru, the Huascarán peak in the background. D. High Andean stream just north of El Tambo, Prov. of Chimborazo, central Ecuador. Pappobolus lehmannii var. lehmannii flowering at right foreground. E. Gentle slopes overseeing the town of Celendín, Dept. of Cajamarca in northern Peru. Pappobolus stuebelii occurs on the slopes at right foreground.

FIG. 24. Elevational ranges of species of Pappobolus.

FIG. 25. Distribution of Pappobolus subg. Apricus and the three groups of Pappobolus subg. Pappobolus.

FIG. 26. Place names and Political division of Colombia, Ecuador and Peru. Biogeographical barriers are indicated with stipples.

FIG. 27. Number of Pappobolus species per 1° grid square. Set of numbers after country name indicate to the left of the slash total species per country; to the right, number of endemic species per country.

FIG. 28. Major rivers of Colombia, Ecuador and Peru.

FIG. 29. Examples of perfect and male sterile heads in P. sagasteguii (Panero & Sánchez Vega 1231). A. Top view of heads. Right head perfect, left head male sterile. B. Bottom view of heads. Right head perfect, left head male sterile.

FIG. 30. Cladogram showing relationships among the species of Pappobolus. The acronym for each species is derived from the first three letters of the species name, except P. acuminatus = ACM. Acronym SIM = the genus Simsia.

FIG. 31. Dendrogram of similarities among species of Pappobolus. P. szyszylowiczii 23 was not included in the analysis.

FIG. 32. Distribution of Pappobolus matthewsii and varieties, and P. sagasteguii.

FIG. 33. Distribution of Pappobolus acutifolius, P. ecuatorianus and varieties, and P. hutchisonii.

FIG. 34. Habit of Pappobolus acutifolius (Drawn from Panero 1399).

FIG. 35. Pappobolus hutchisonii (Drawn from Panero & Sánchez Vega 1242). A. Habit. B. Disk flower. C. Ray flower. D. Pale. E. Disk

achene. F. Head. G. General aspect of the plant in the field. (A, bar = 1 cm; B-E, bar = 1 mm; F, bar = 2 mm; G, bar = 1.5 m).

FIG. 36. Distribution of Pappobolus hypargyreus, P. imbaburensis, P. juncosae, P. verbesinoides.

FIG. 37. Distribution of Pappobolus lehmannii and varieties, and P. nigrescens.

Fig. 38. Distribution of Pappobolus acuminatus, P. andinus and P. stork-hortonii.

FIG. 39. Distribution of Pappobolus cinerascens, P. macranthus, and P. mollicomus.

FIG. 40. Habit of P. mollicomus (Drawn from Mathews s.n.).

FIG. 41. Habit of P. macranthus (Drawn from Woytkowskii 3434133a).

FIG. 42. Pappobolus sanchezii (Drawn from Panero 1195). A. Habit. B. Disk flower. C. Ray flower. D. Pale. E. Disk achene. F. Head. G.

General aspect of the plant in the field. (A, bar = 1 cm; B, D and E, bar = 1 mm; C, bar = 4 mm; F, bar = 8 mm; G, bar = 2.5 m).

FIG. 43. Distribution of Pappobolus amoenus, P. robinsonii, P. sanchezii, P. schillingii, P. szyszylowiczii, P. youngiorum.

FIG. 44. Pappobolus stuebelii (Drawn from Panero 1150). A. Habit B. Disk flower. C. Ray flower. D. Disk achene. E. Pale. F. General aspect of the plant in the field. (A, bar = 1 cm; B-E, bar = 1 mm; F, bar = 2 m).

FIG. 45. Distribution of Pappobolus jelskii, P. lodicatus, P. smithii, and P. stuebelii.

FIG. 46. Pappobolus smithii (Drawn from López & Sagásteguii 3309).

FIG. 47. Distribution of Pappobolus microphyllus and varieties.

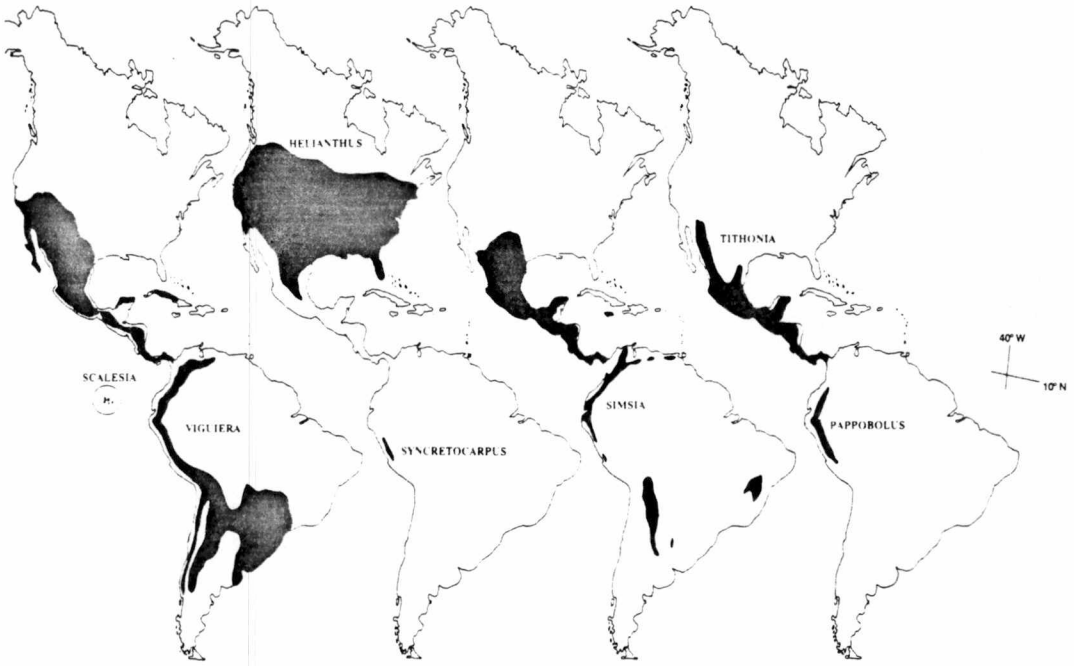
FIG. 48. Distribution of Pappobolus cajamarcensis, P. decumbens, P. discolor, and P. subniveus.

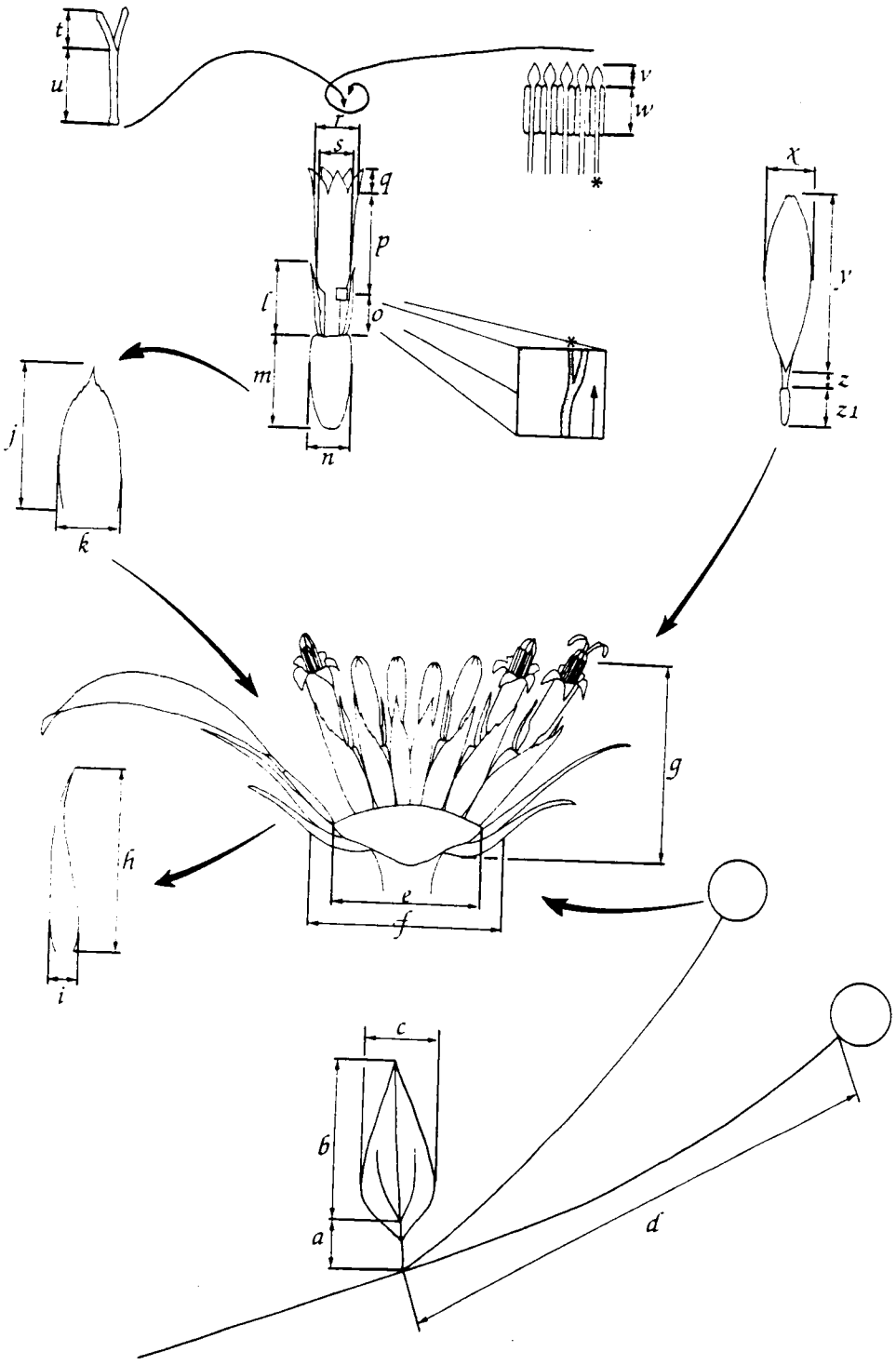
FIG. 49. Pappobolus decumbens (Drawn from Panero & Sánchez Vega 1345). A. Habit. B. Ray flower. C. Disk flower. D. Pale. E. Disk achene. F. Head. (A, bar = 1 cm; B-E, bar = 1 mm; F, bar = 4 mm).

FIG. 50. Distribution of Pappobolus davidii, P. lanatus, P. senex, and P. woodsonianus.

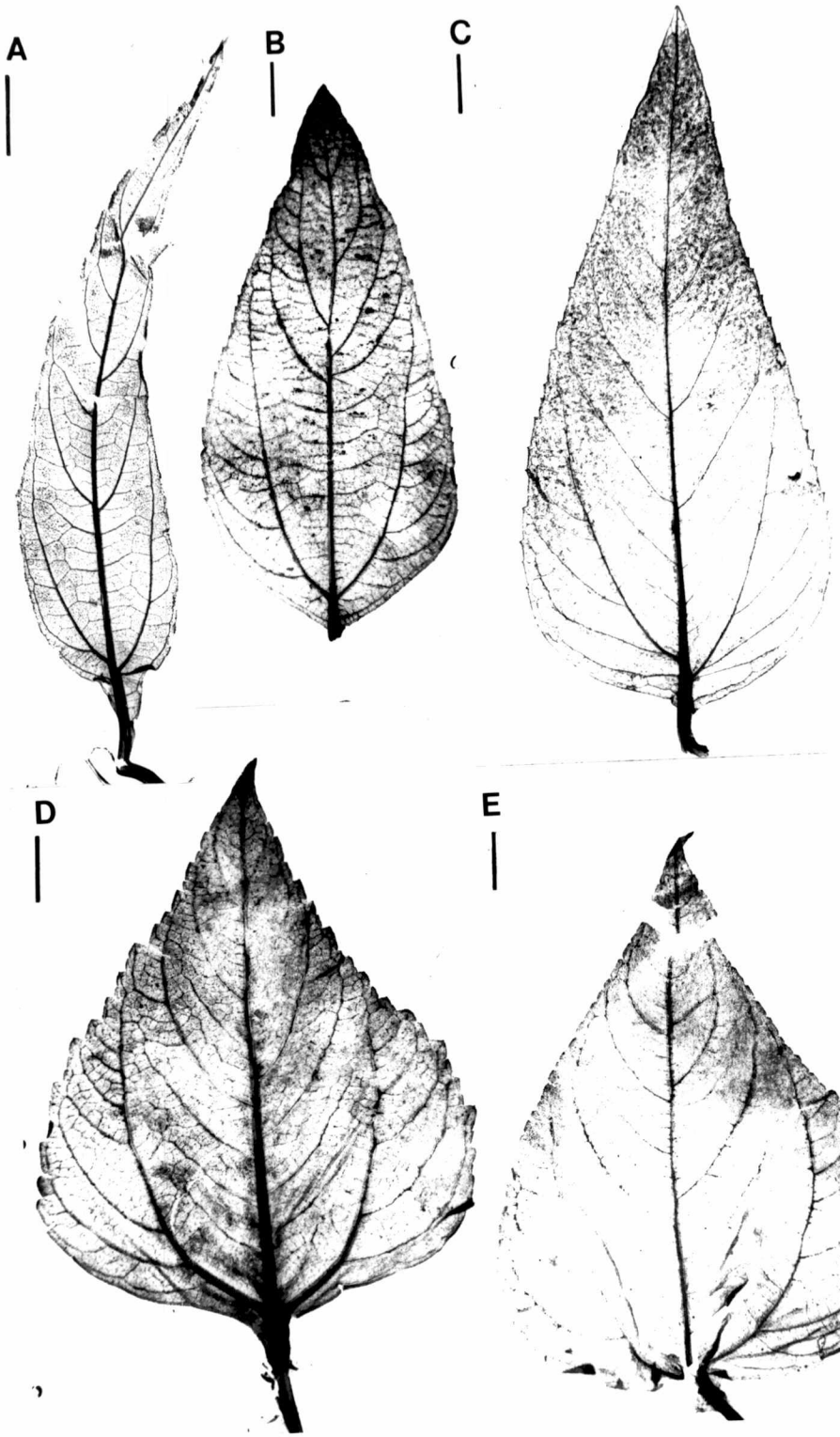
FIG. 51. Pappobolus argenteus (drawn from Panero 736). A. Habit. B. Disk flower. C. Ray flower. D. Pale folded and unfolded view. E. Disk achene. F. Head (ligules not shown). G. General aspect of the plant in the field. (A, bar = 1 cm; B, D and E, bar = 1 mm; C, bar = 2 mm; F, bar = 5 mm; G, bar = 1.2 m).

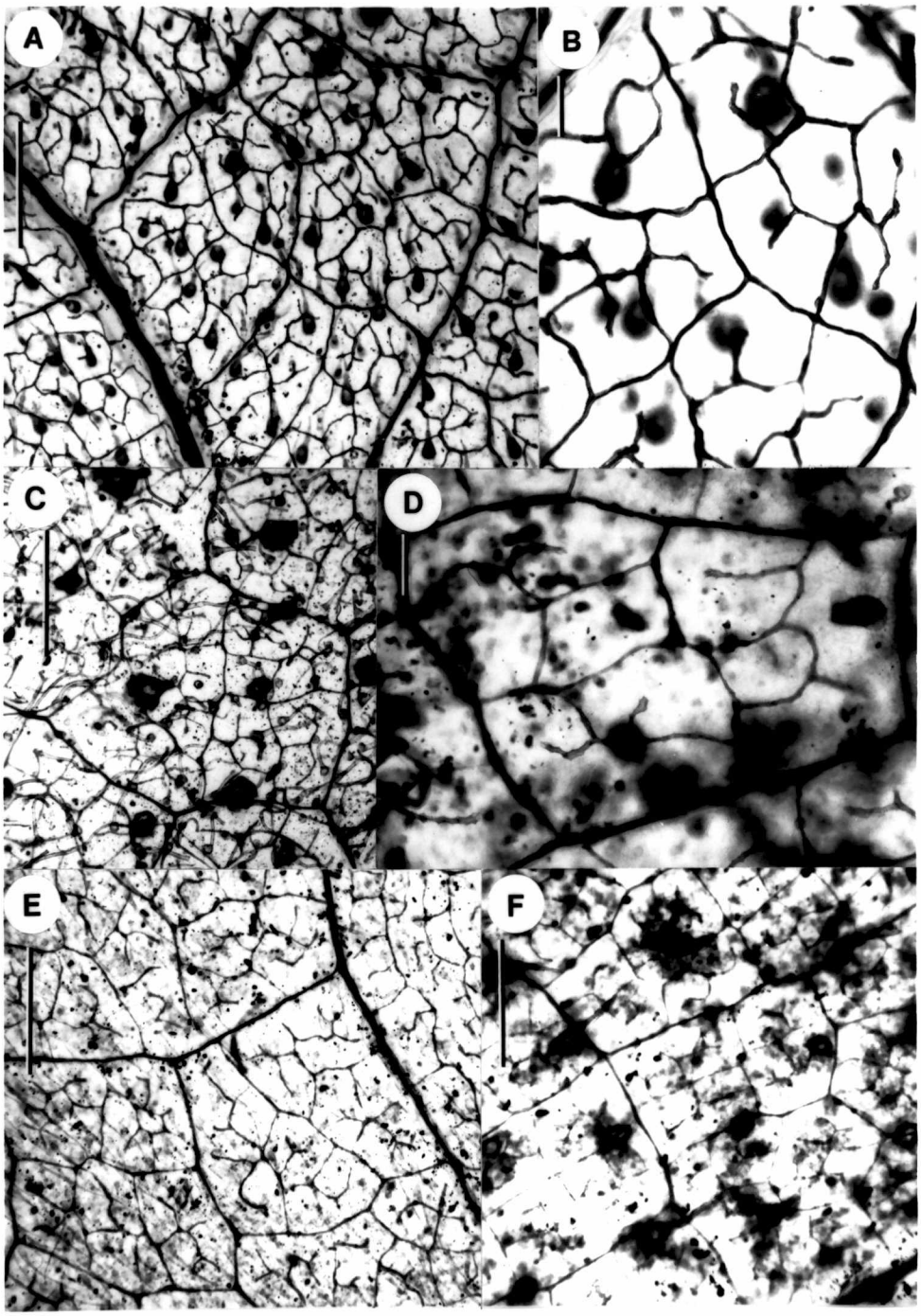
FIG. 52. Distribution of Pappobolus argenteus and P. viridior.

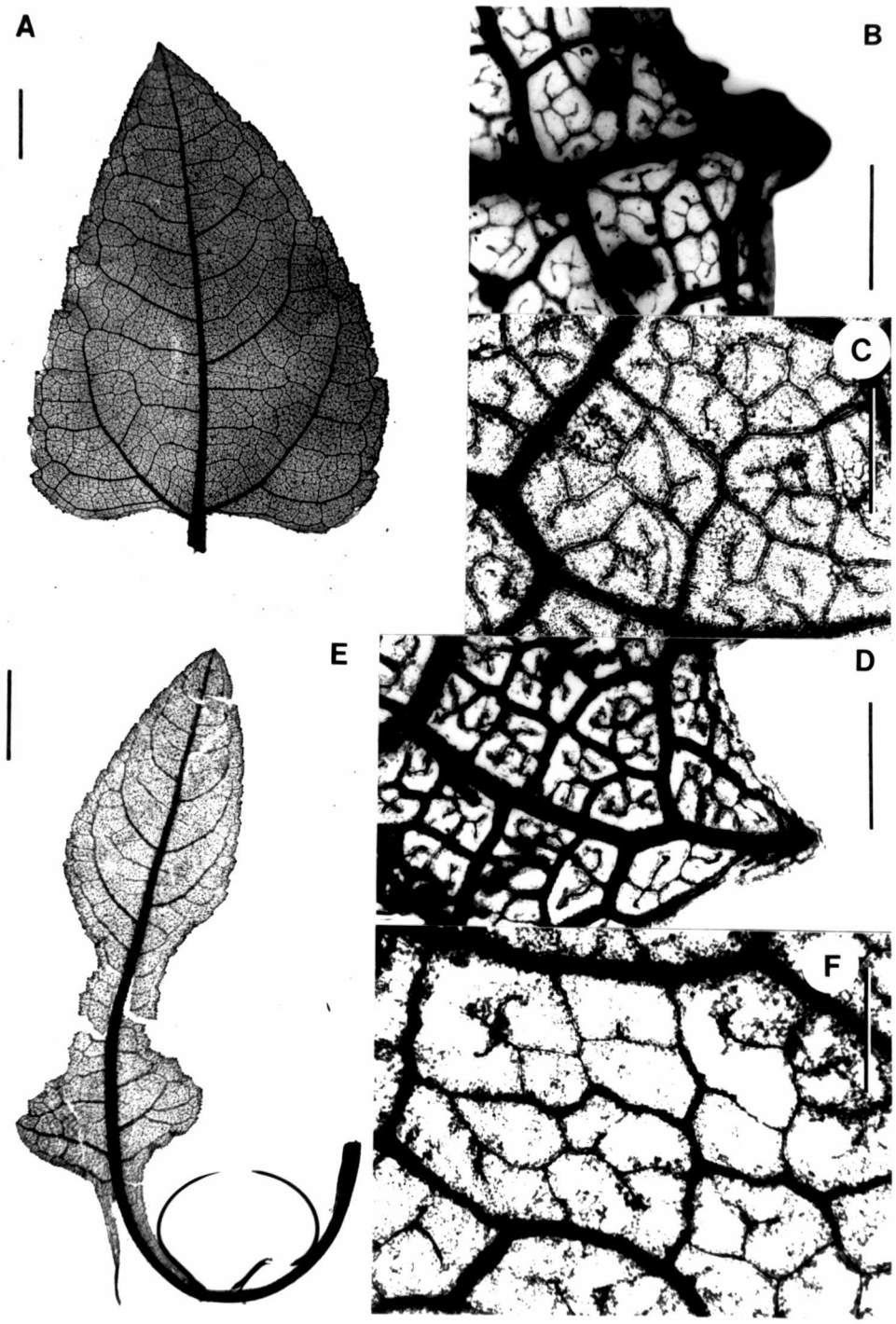

HELIANTHUS
TITHONIA
SCALESIA
VIGUIERA
SYNCRETOCARPUS
SIMSIA
PAPPOBOLUS
40° W
10° N

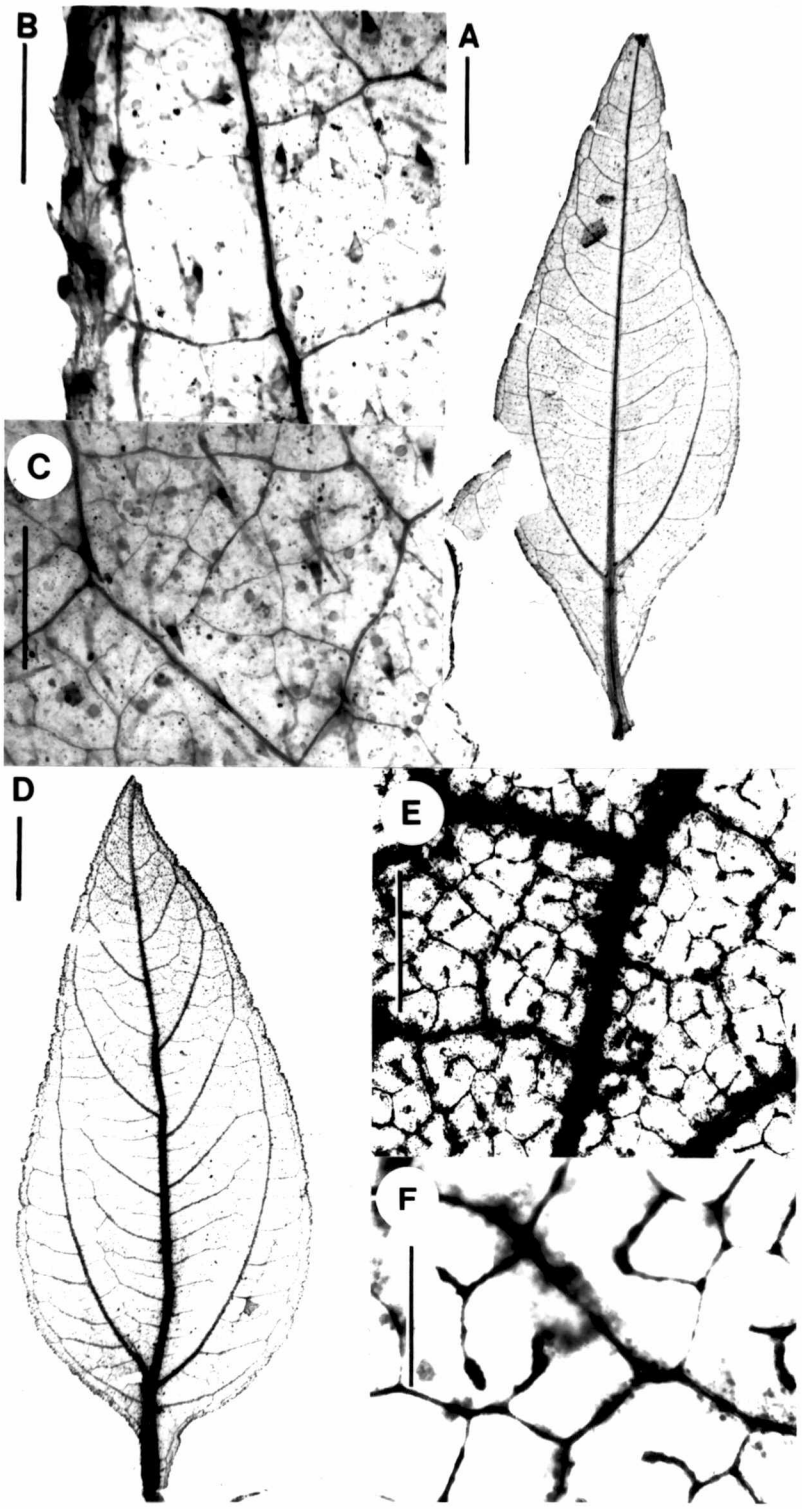

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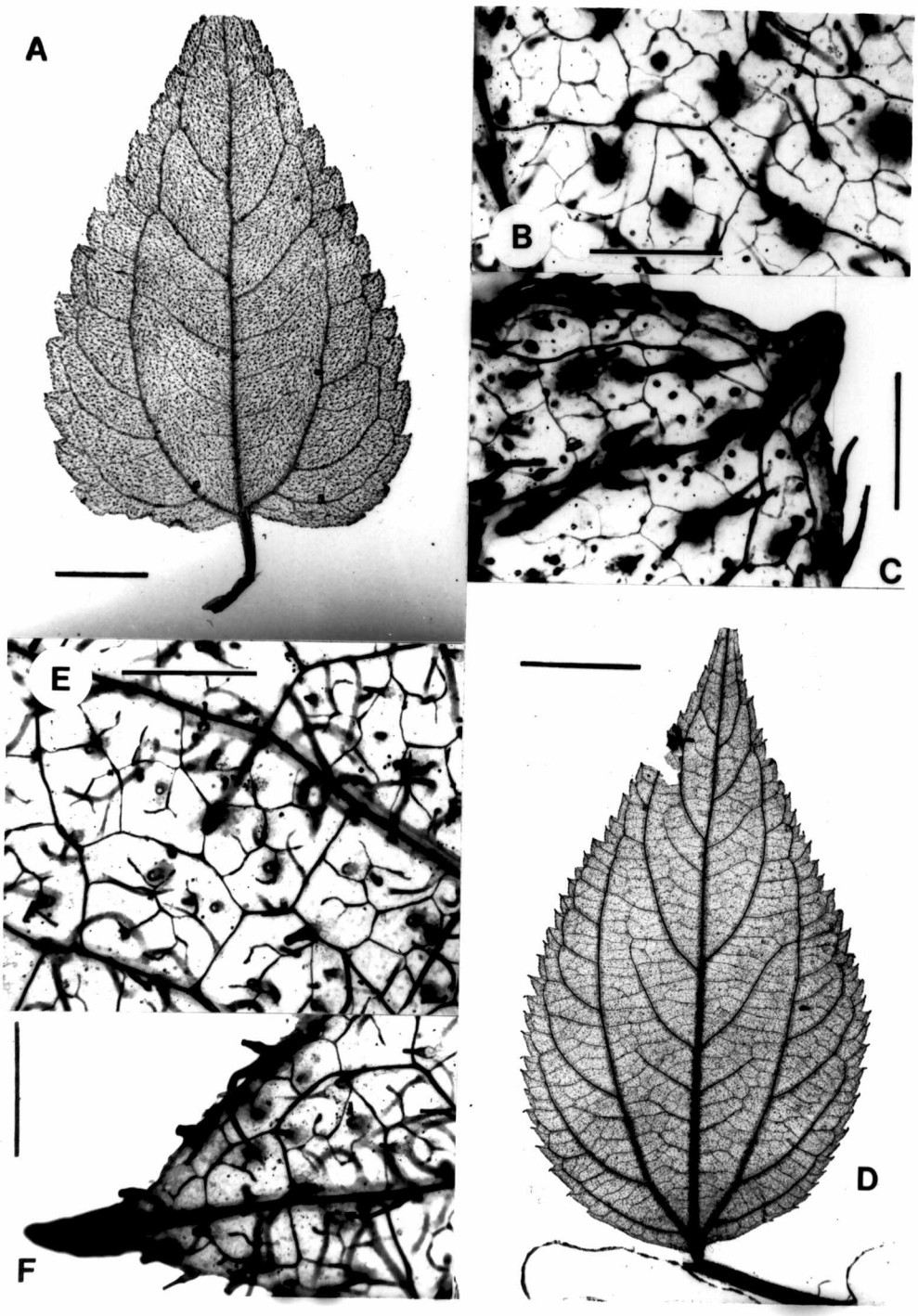

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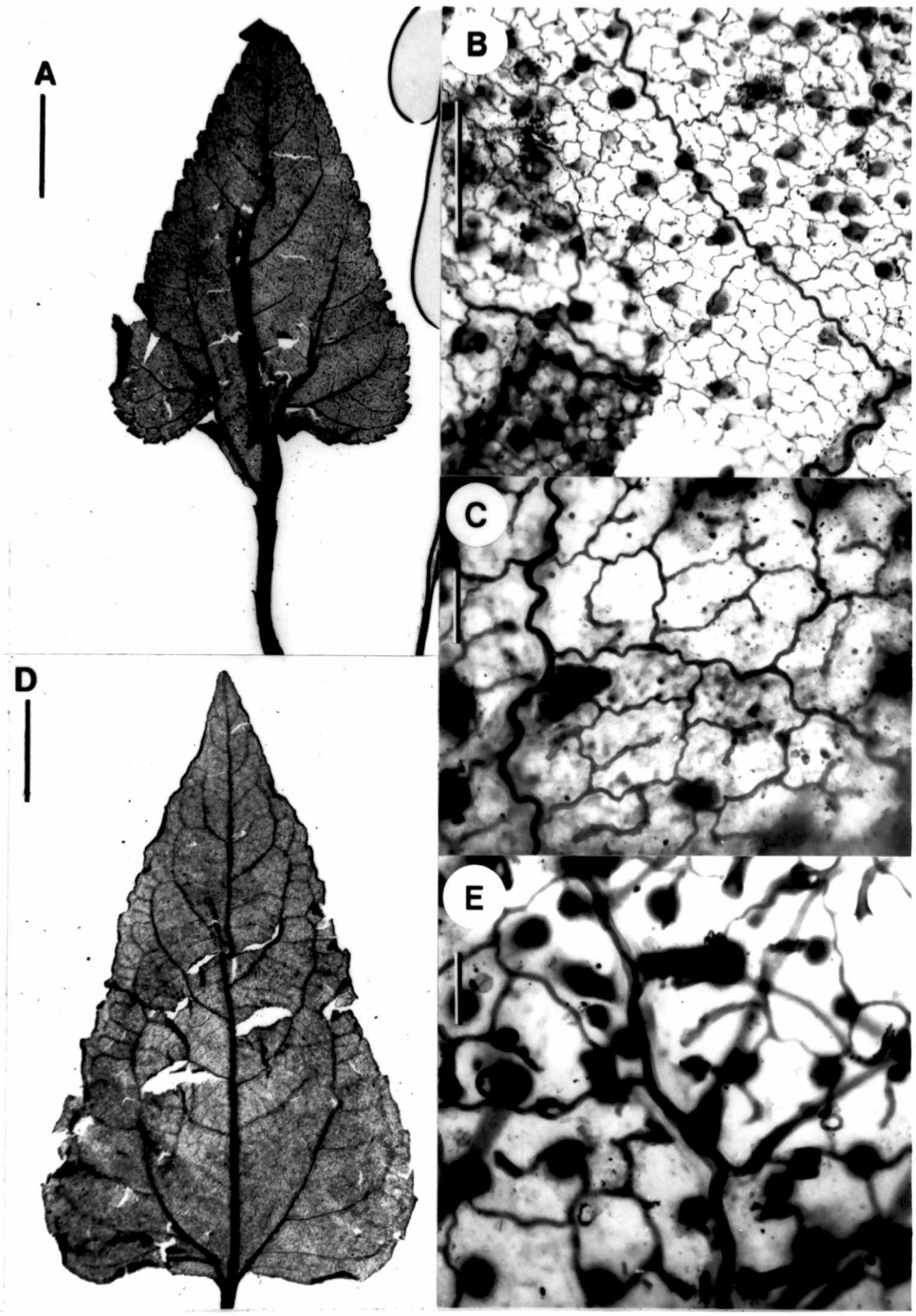

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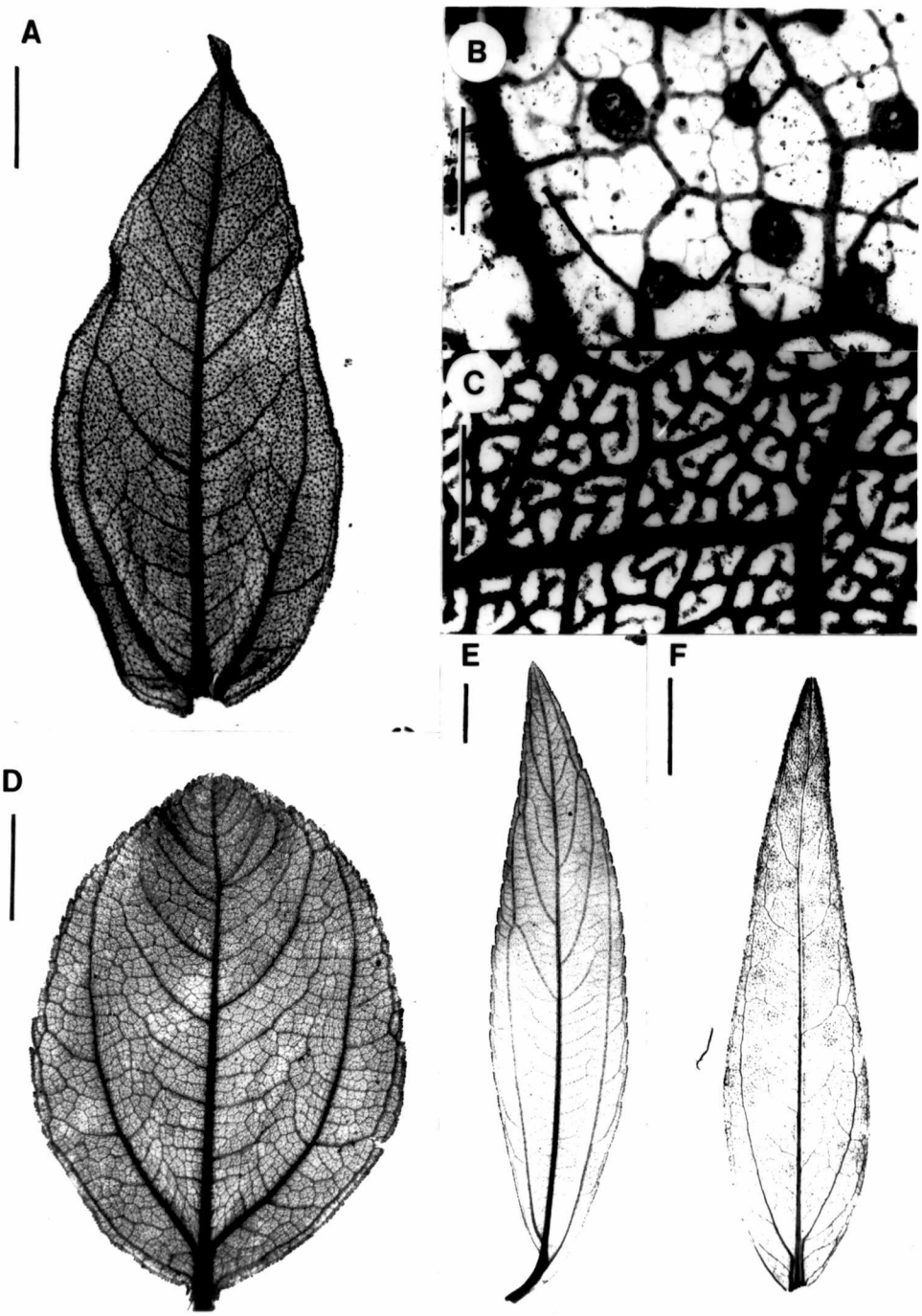

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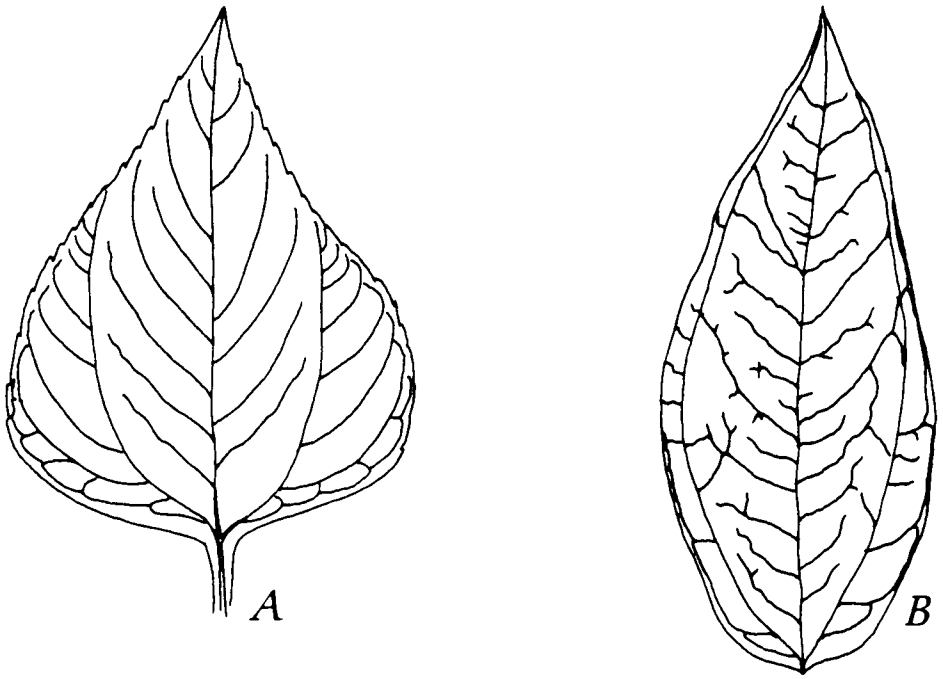

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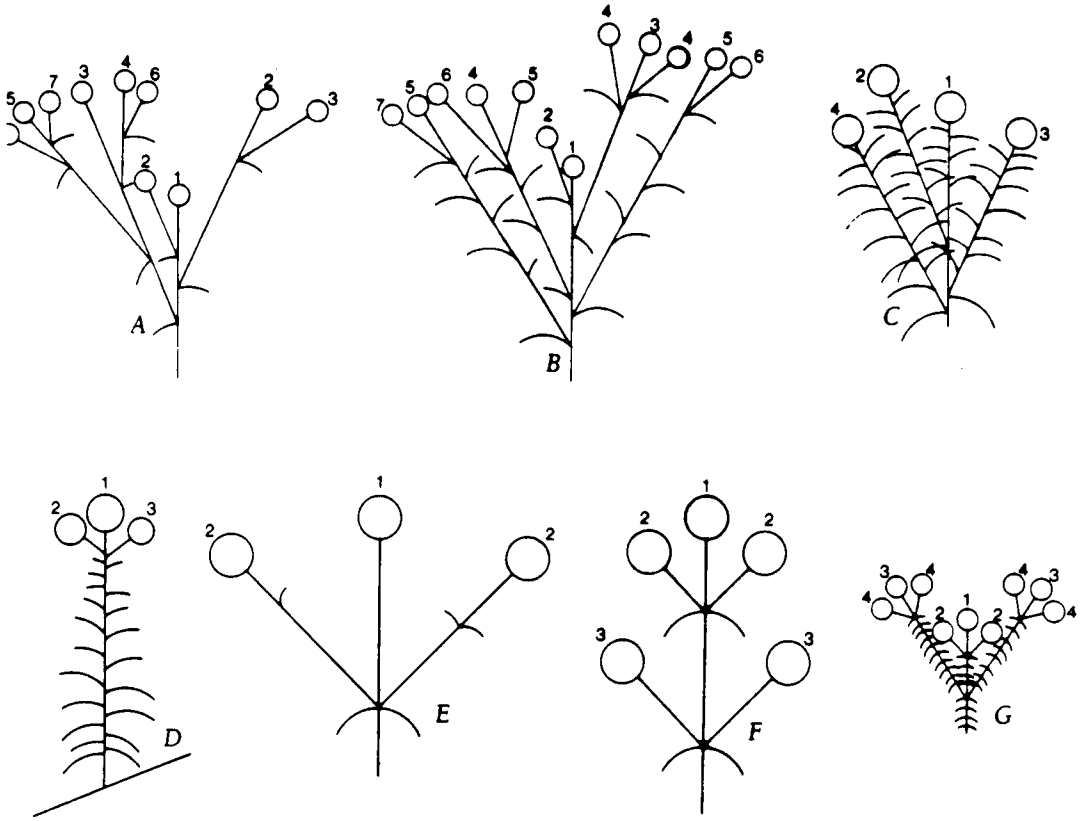

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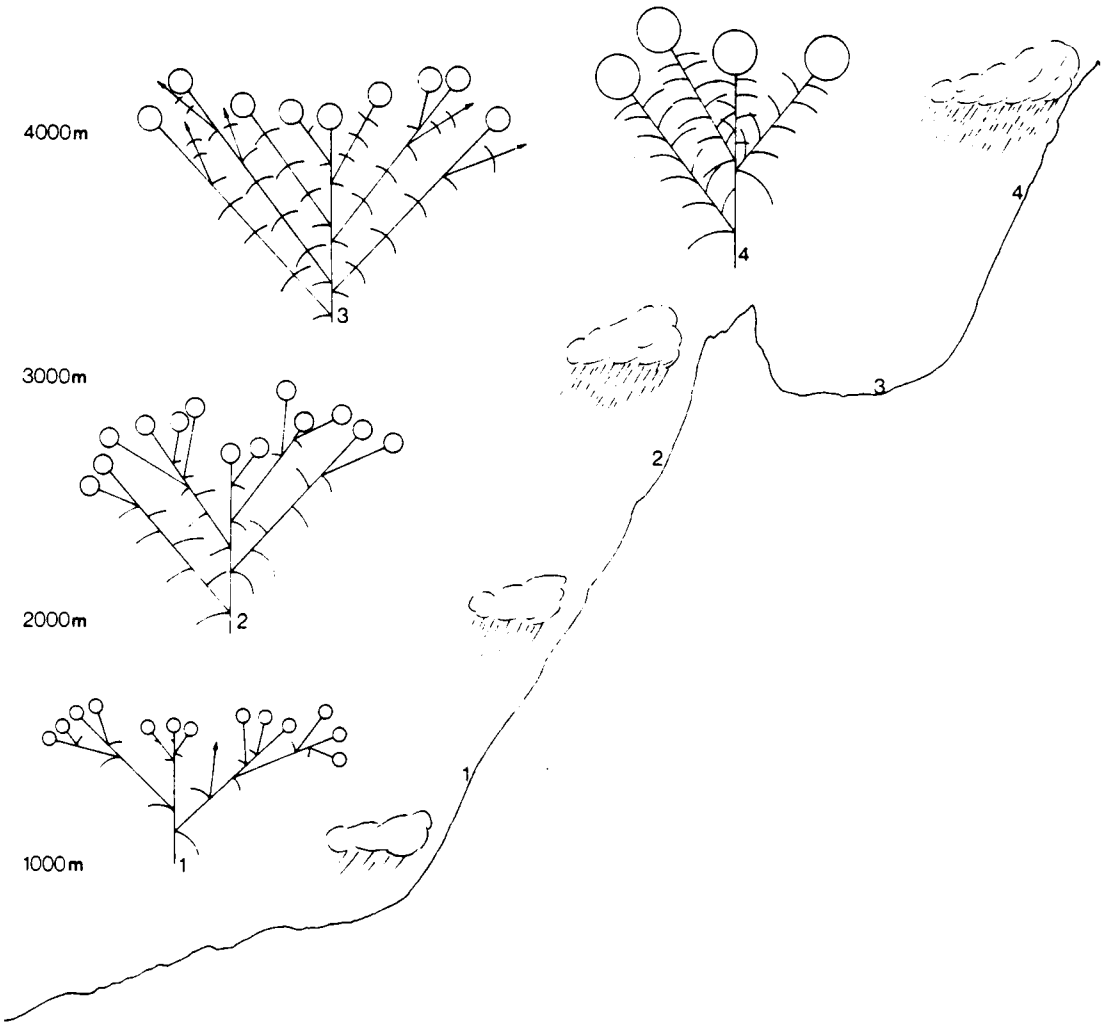

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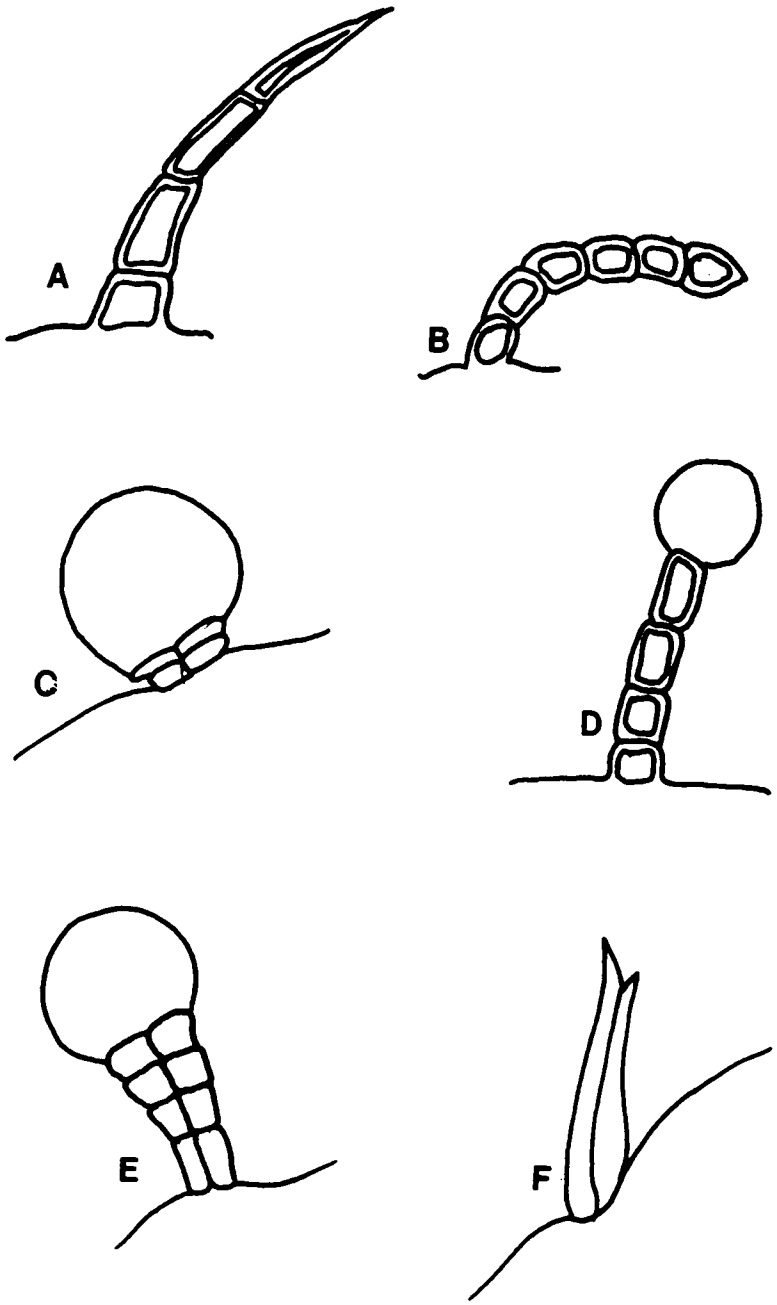

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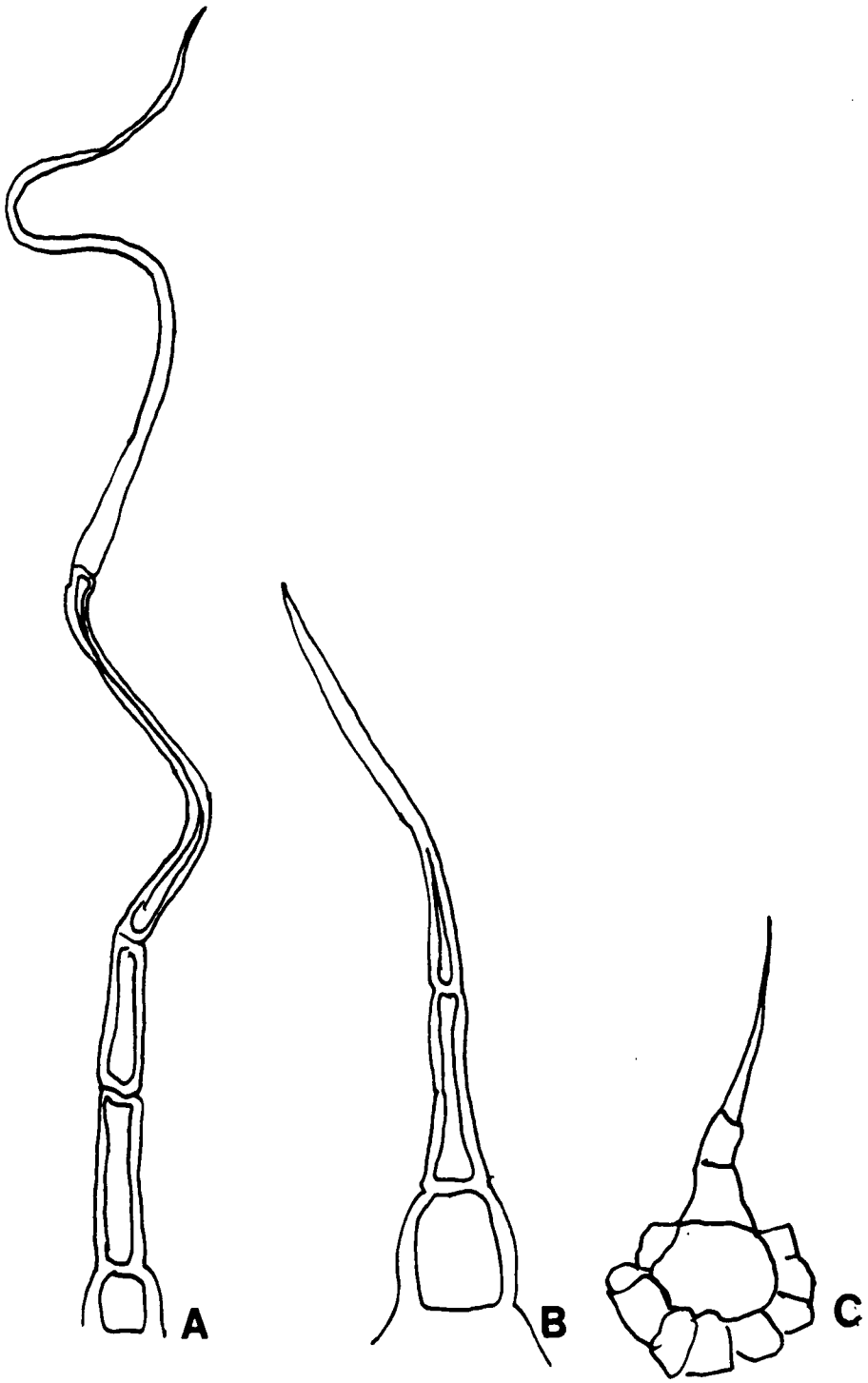

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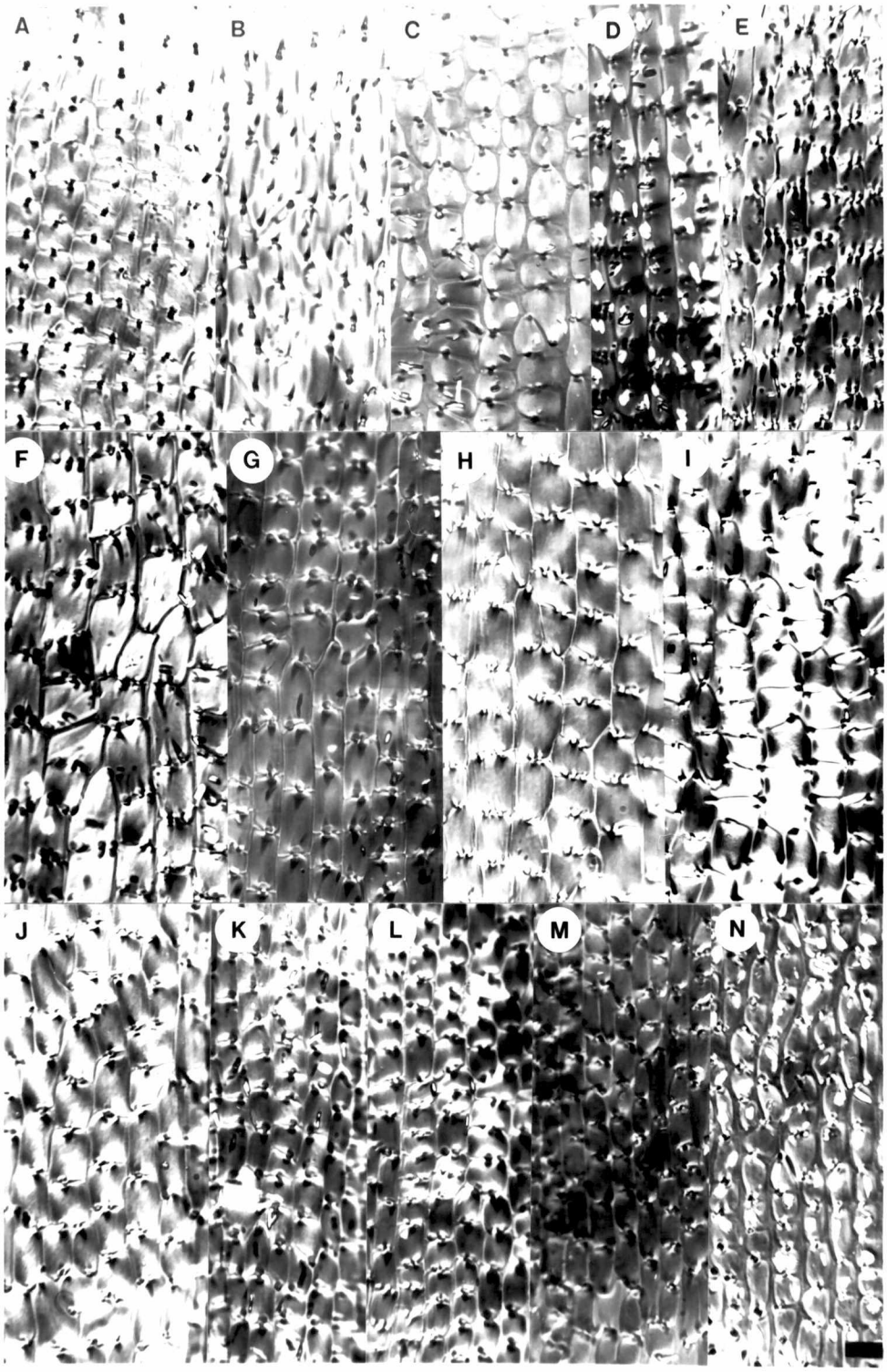

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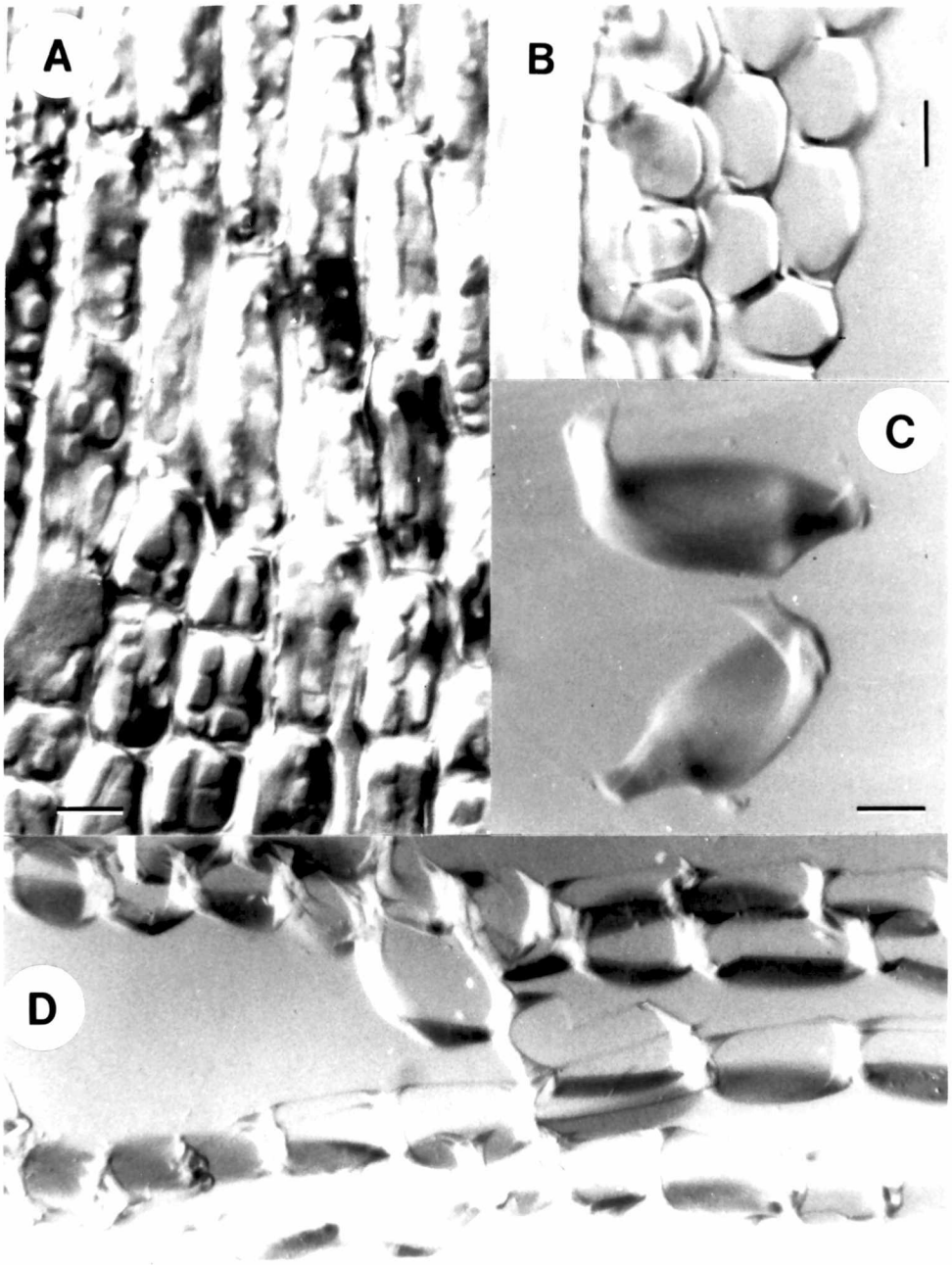

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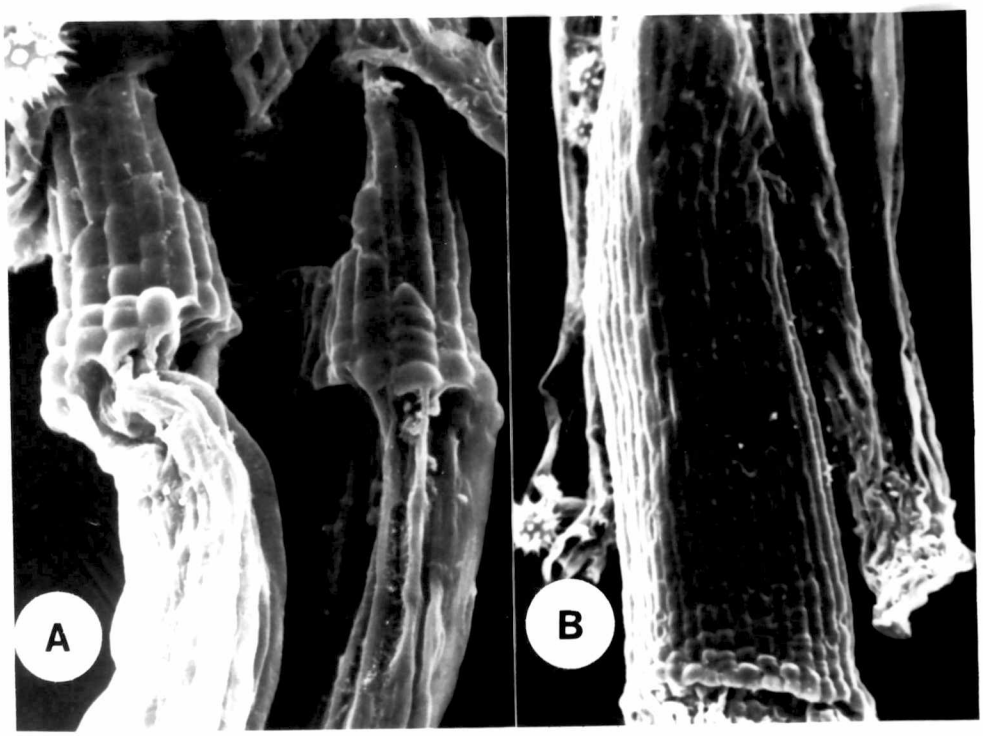

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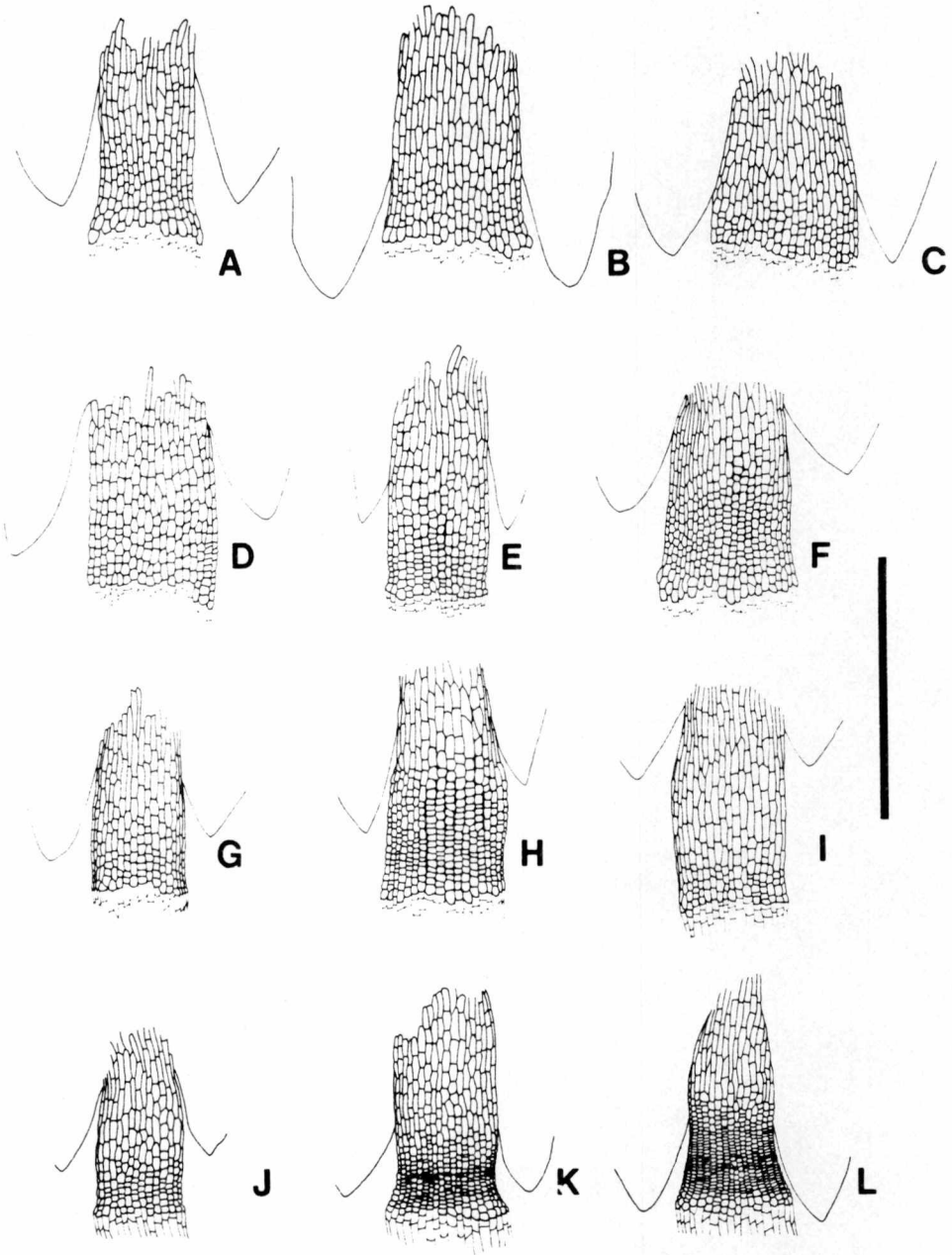

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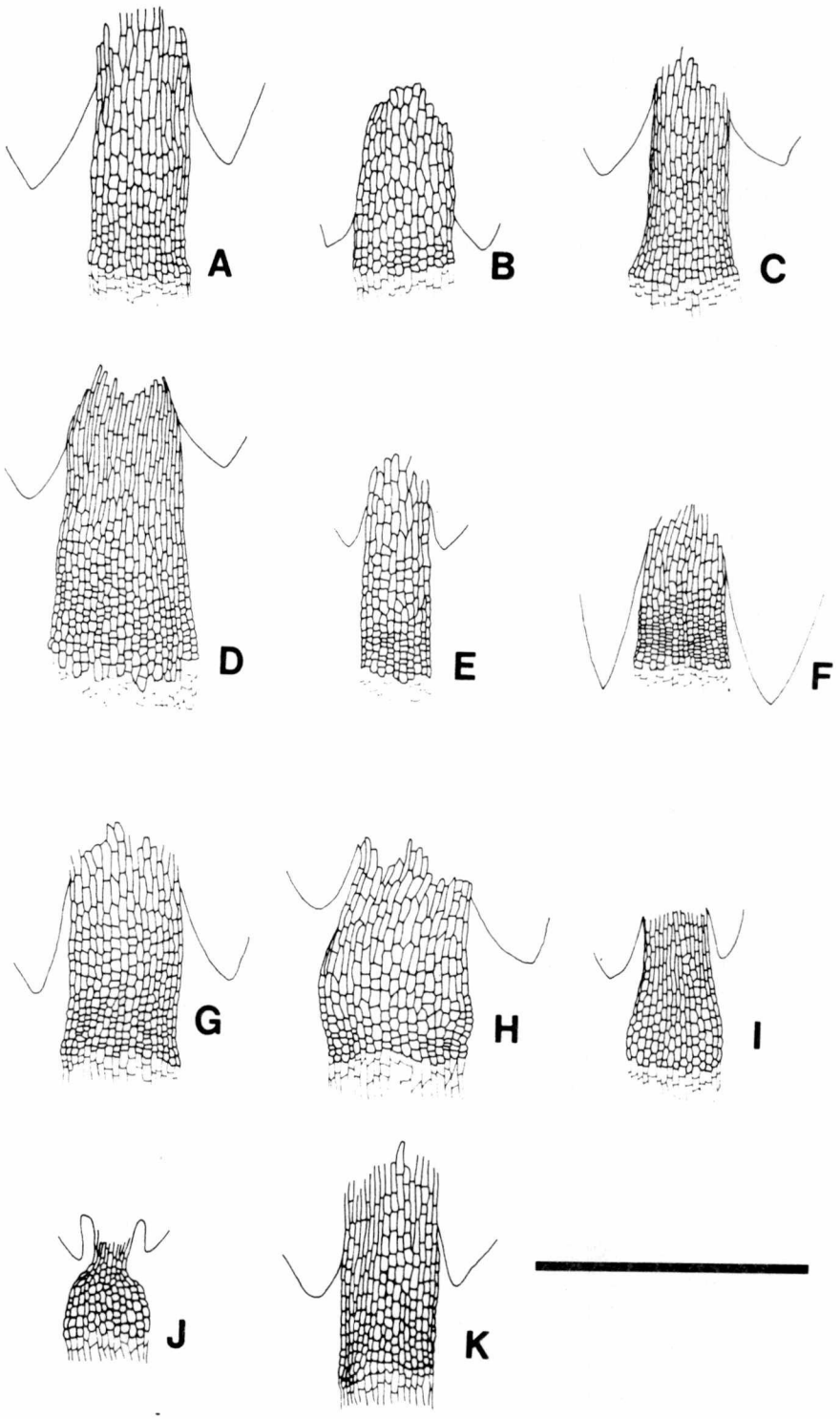

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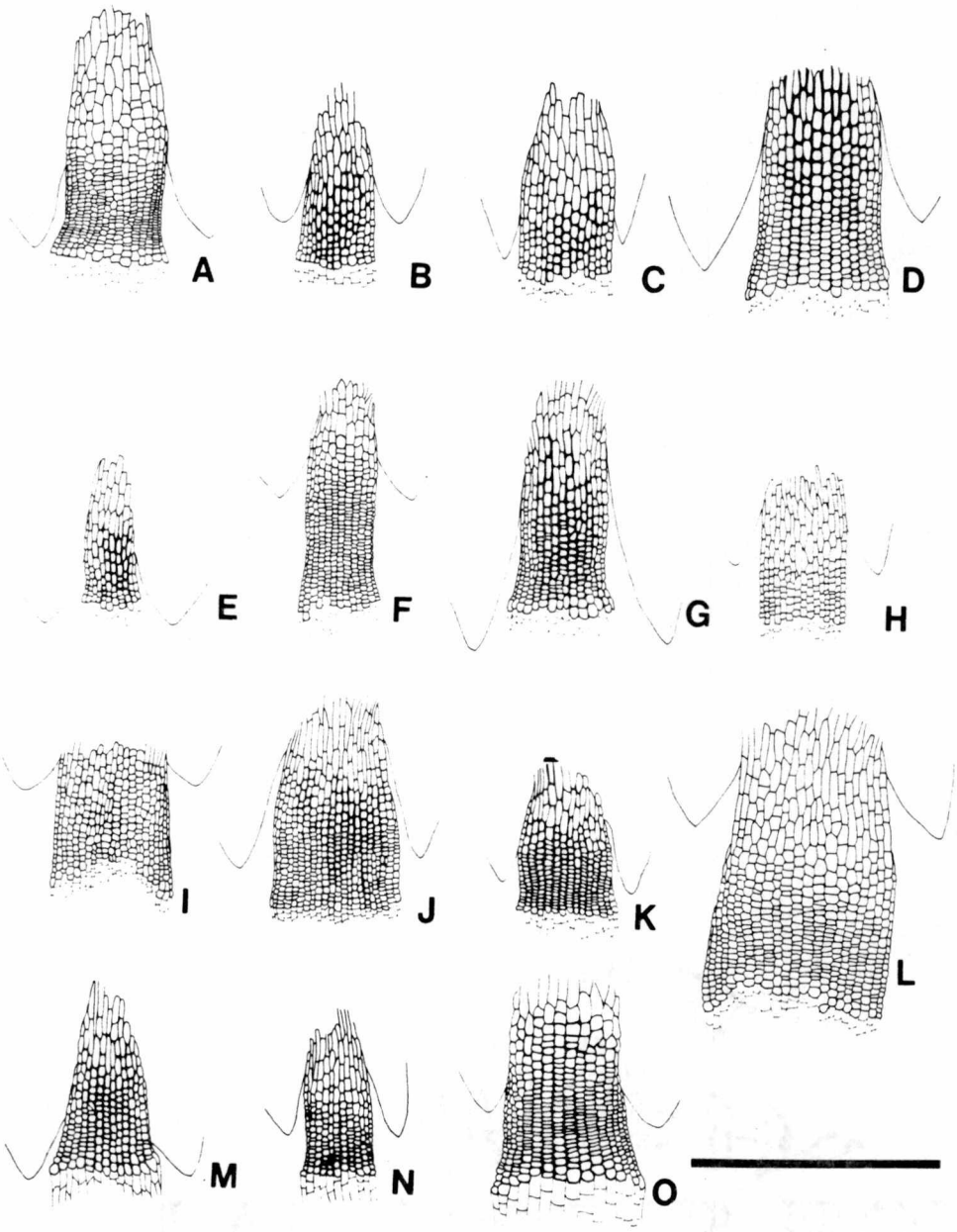

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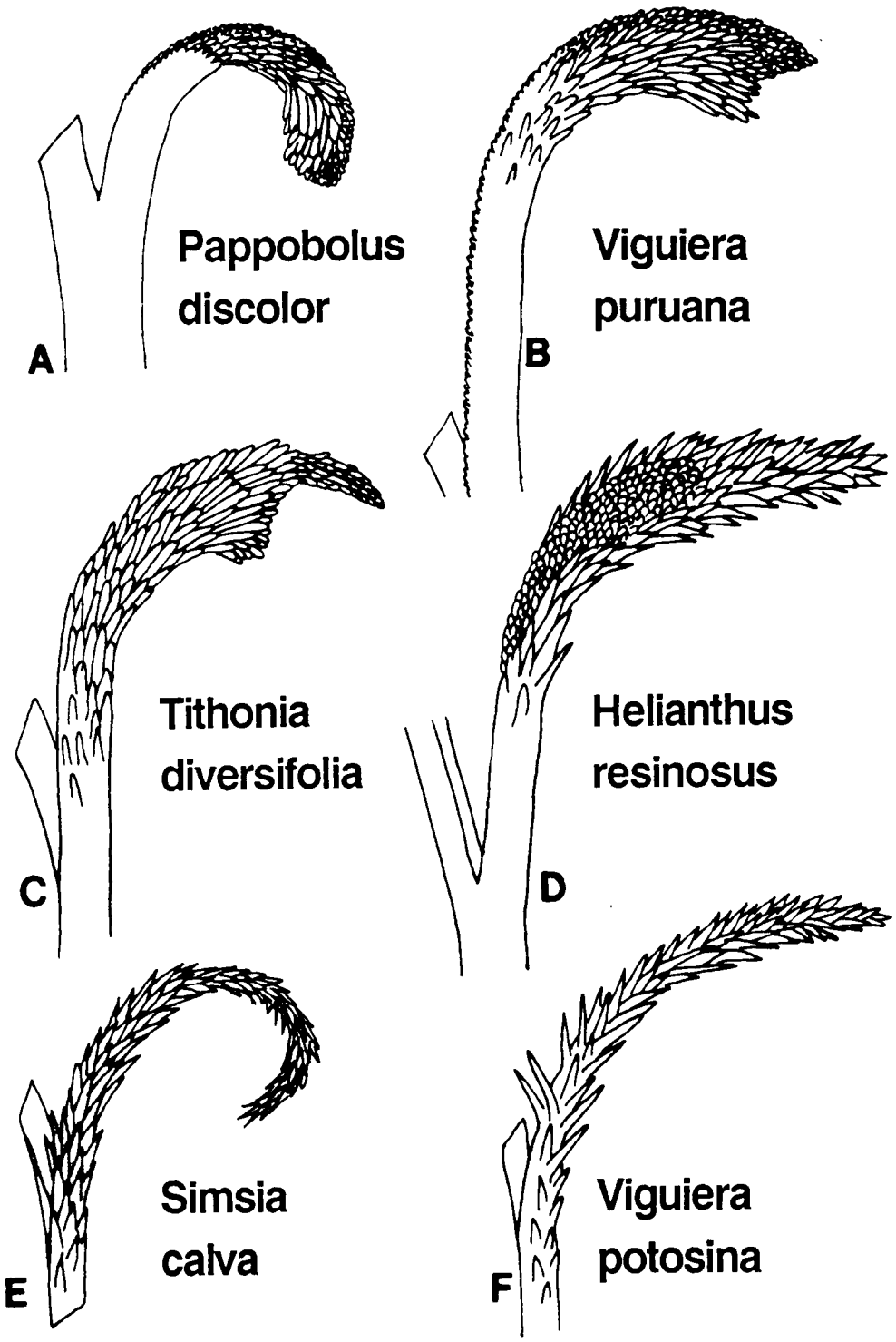

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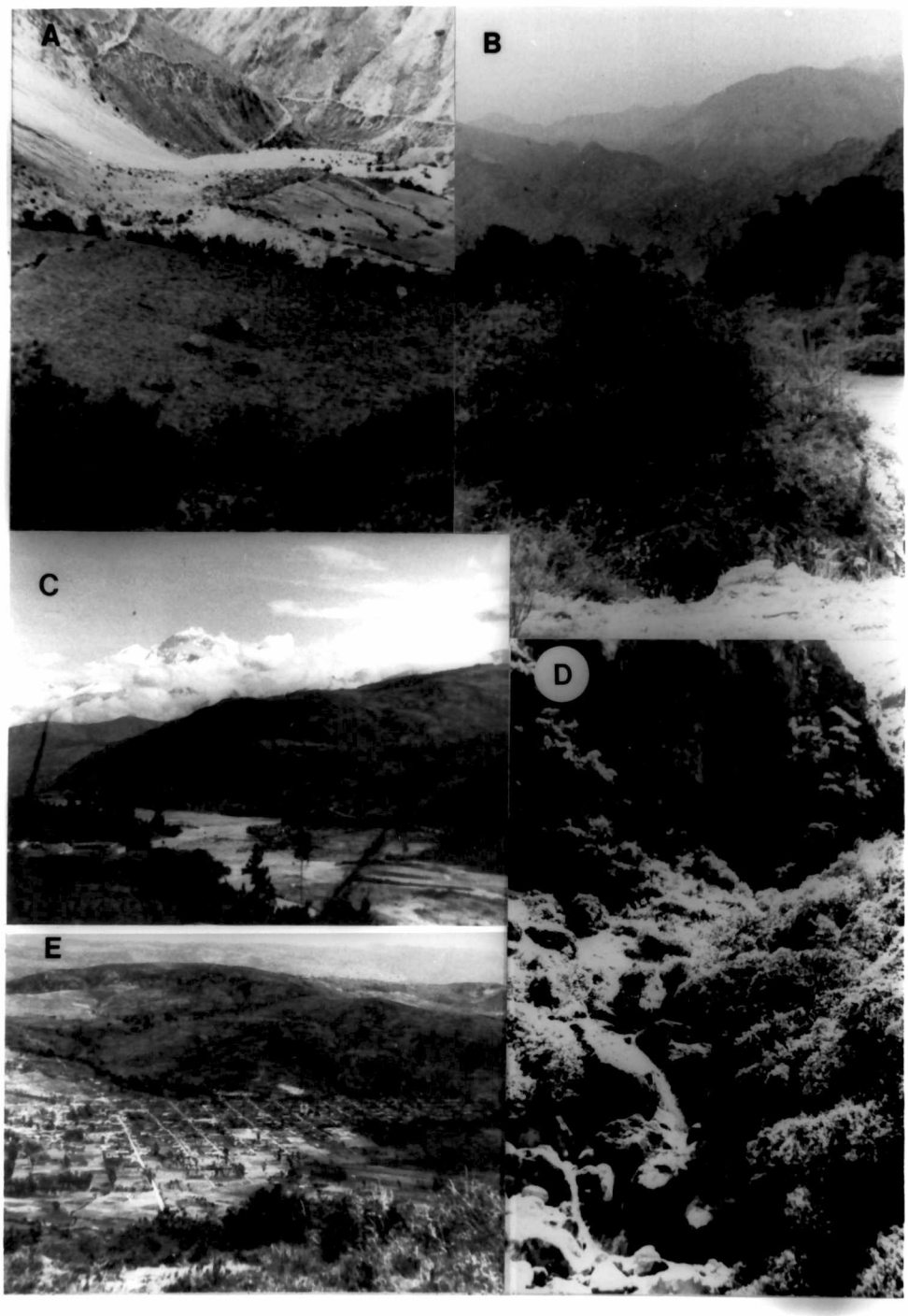

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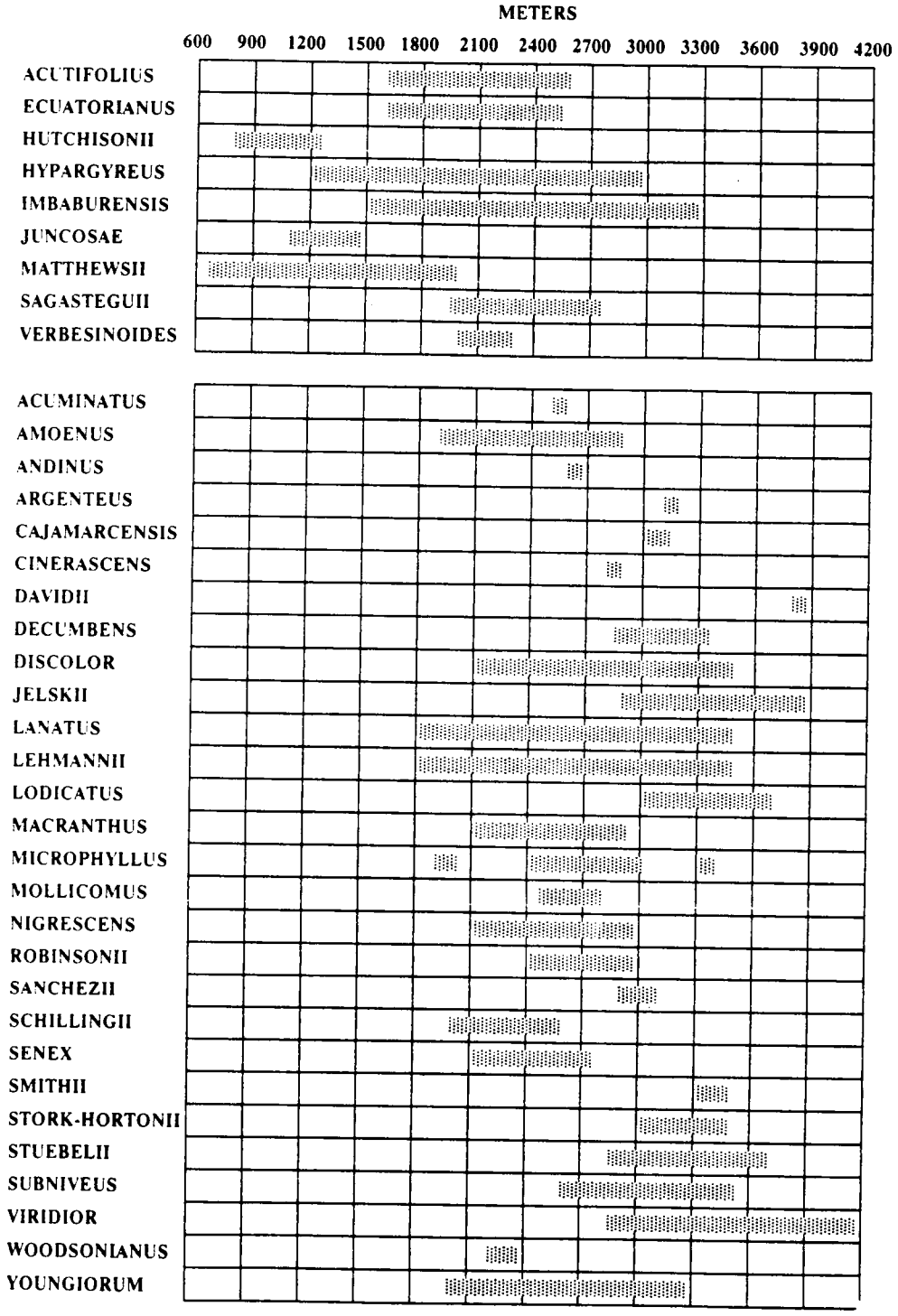

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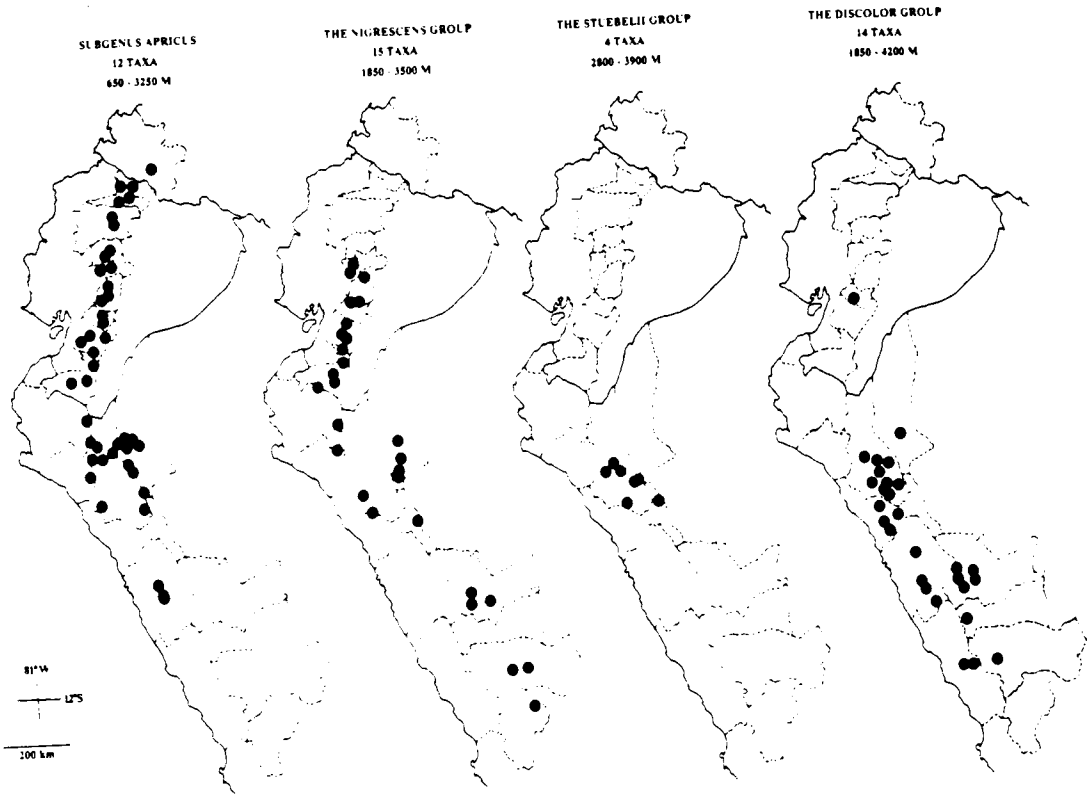

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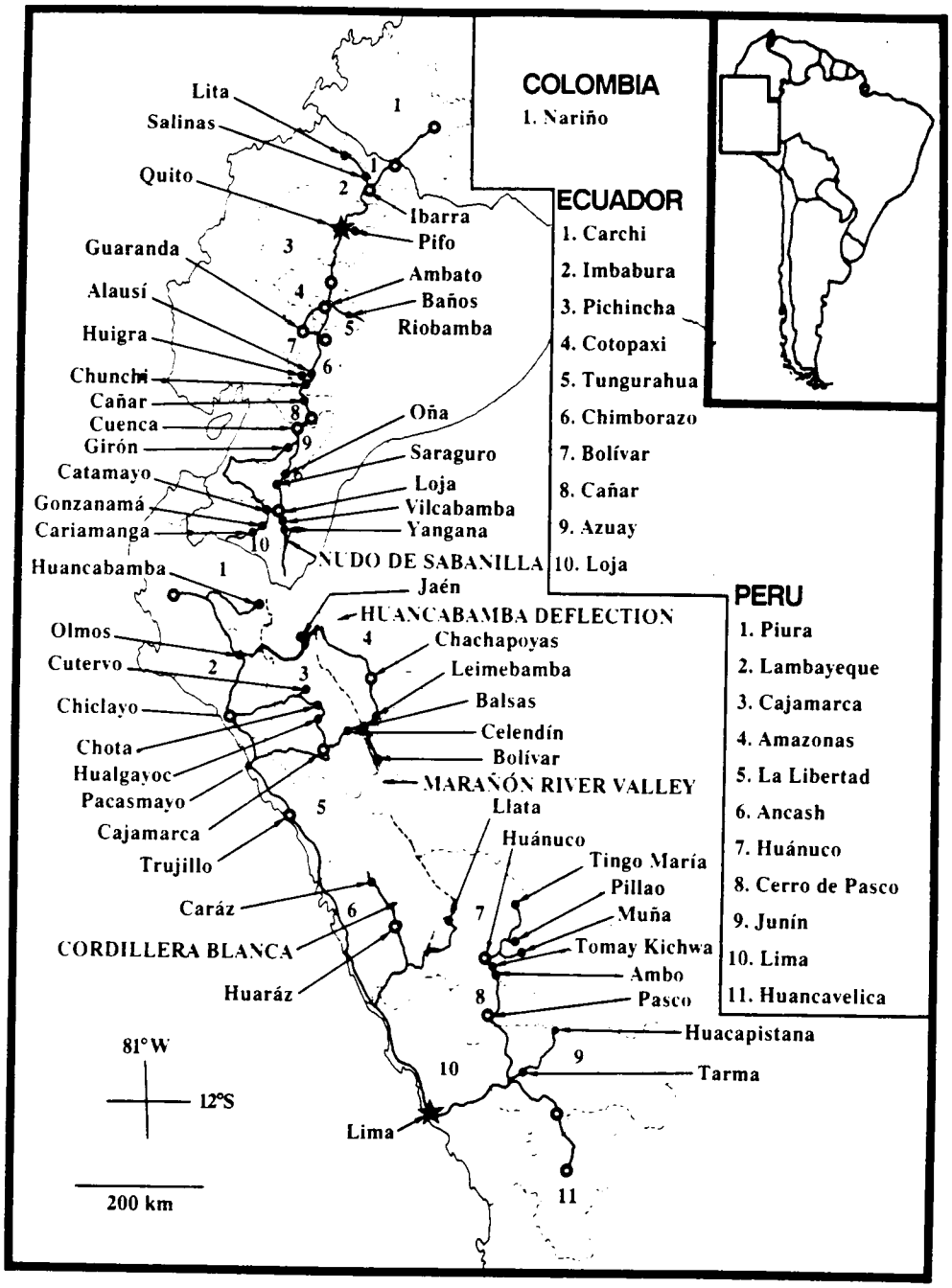

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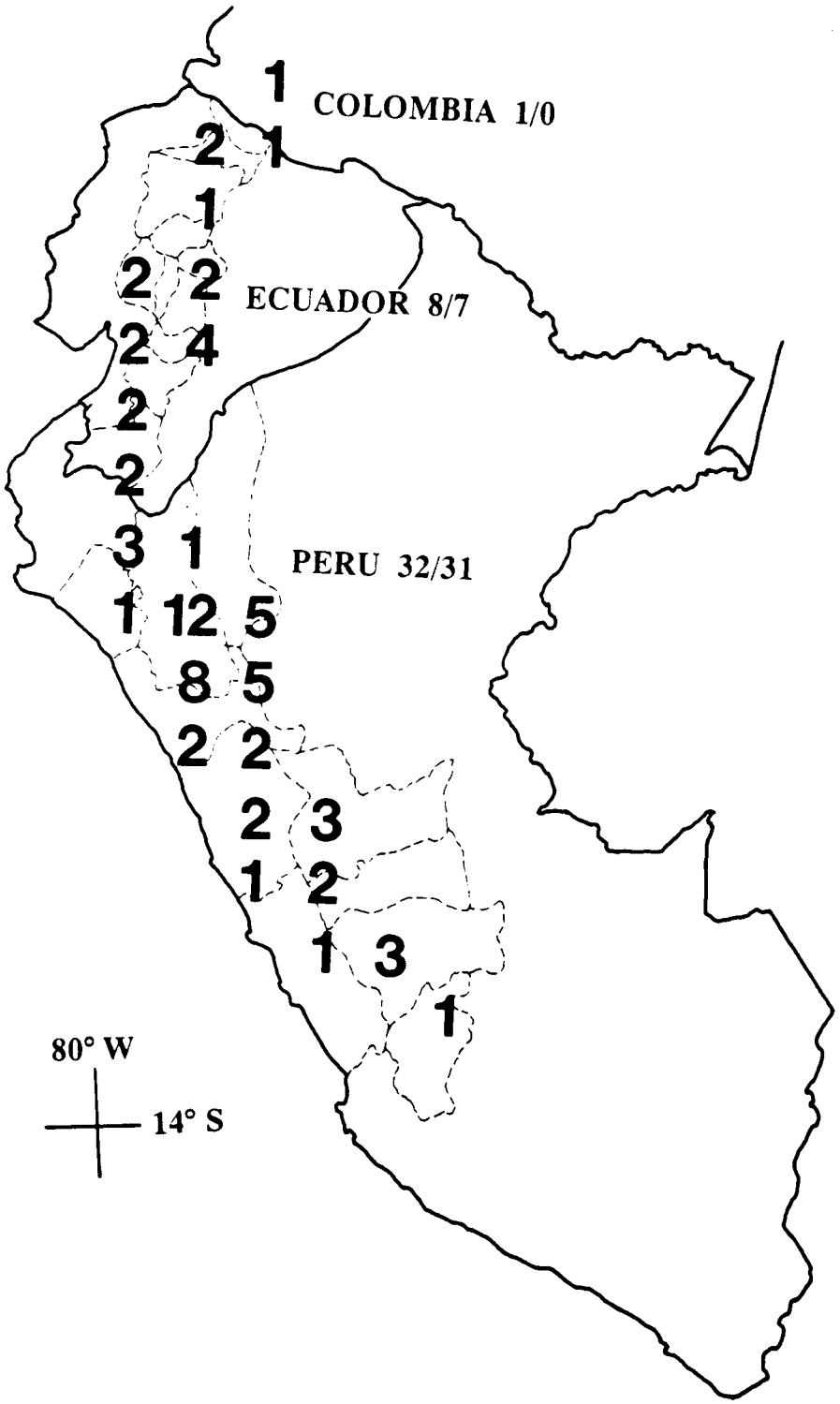

Pappobolus
discolor
A
Viguiera
puruana
B
Tithonia
diversifolia
C
Helianthus
resinosus
D
Simsia
calva
E
Viguiera
potosina
F

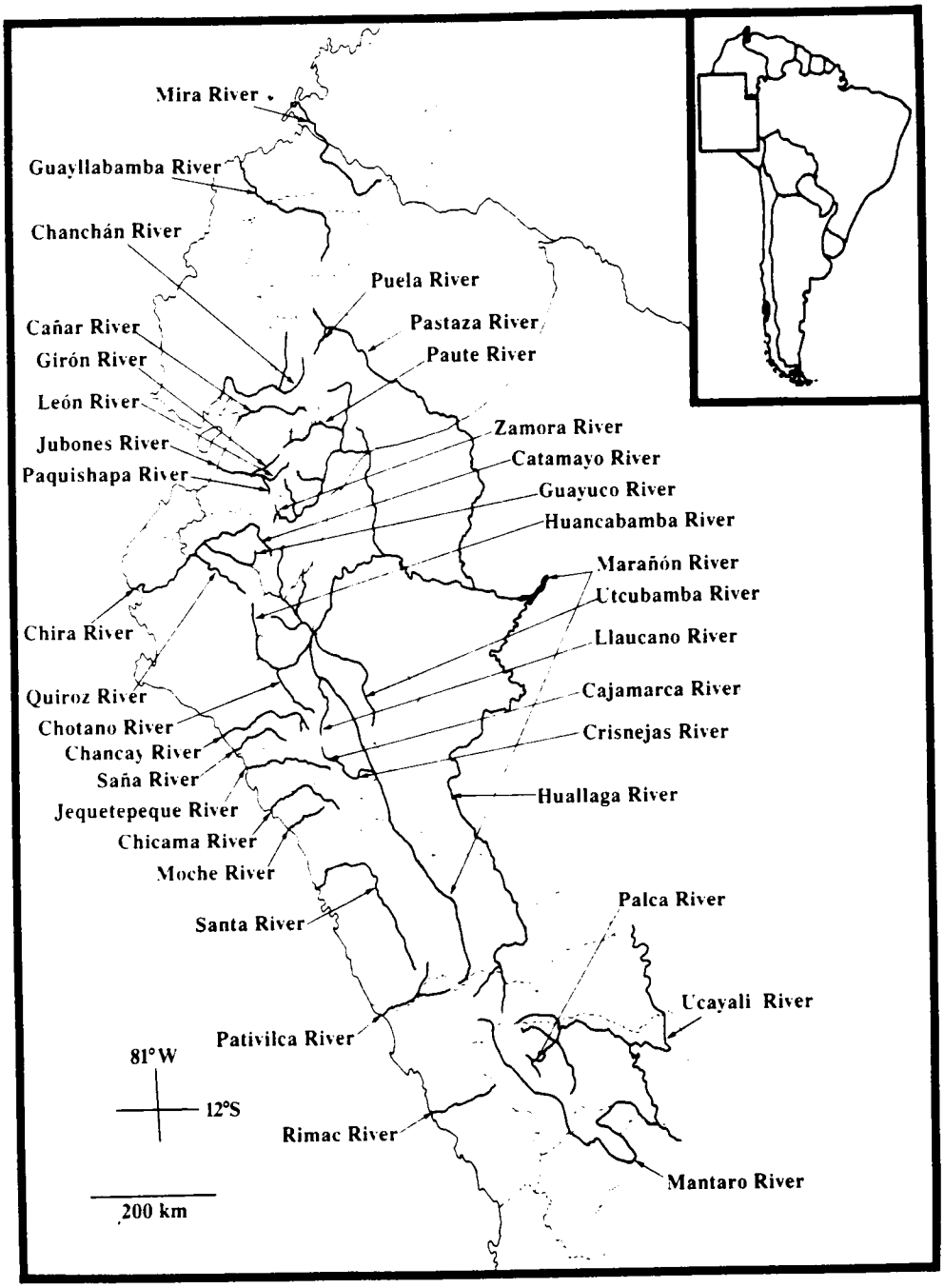

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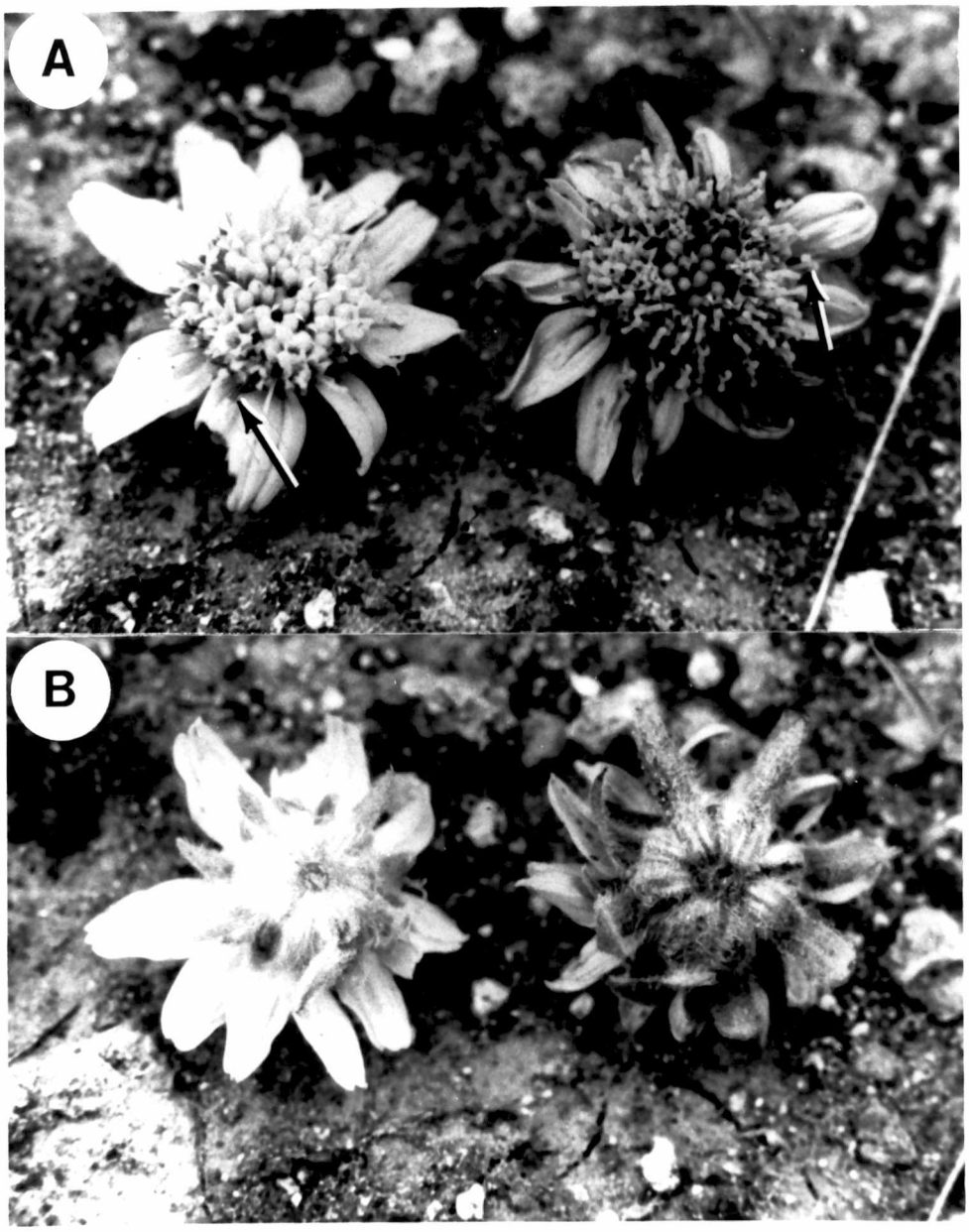

METERS
600 900 1200 1500 1800 2100 2400 2700 3000 3300 3600 3900 4200
ACUTIFOLIUS
ECUATORIANUS
HUTCHISONII
HYPARGYREUS
IMBABURENSIS
JUNCOSAE
MATTHEWSII
SAGASTEGUII
VERBESINOIDES
ACUMINATUS
AMOENUS
ANDINUS
ARGENTEUS
CAJAMARCENSIS
CINERASCENS
DAVIDII
DECUMBENS
DISCOLOR
JELSKII
LANATUS
LEHMANNII
LODICATUS
MACRANTHUS
MICROPHYLLUS
MOLLICOMUS
NIGRESCENS
ROBINSONII
SANCHEZII
SCHILLINGII
SENEX
SMITHII
STORK-HORTONII
STUEBELII
SUBNIVEUS
VIRIDIOR
WOODSONIANUS
YOUNGIORUM

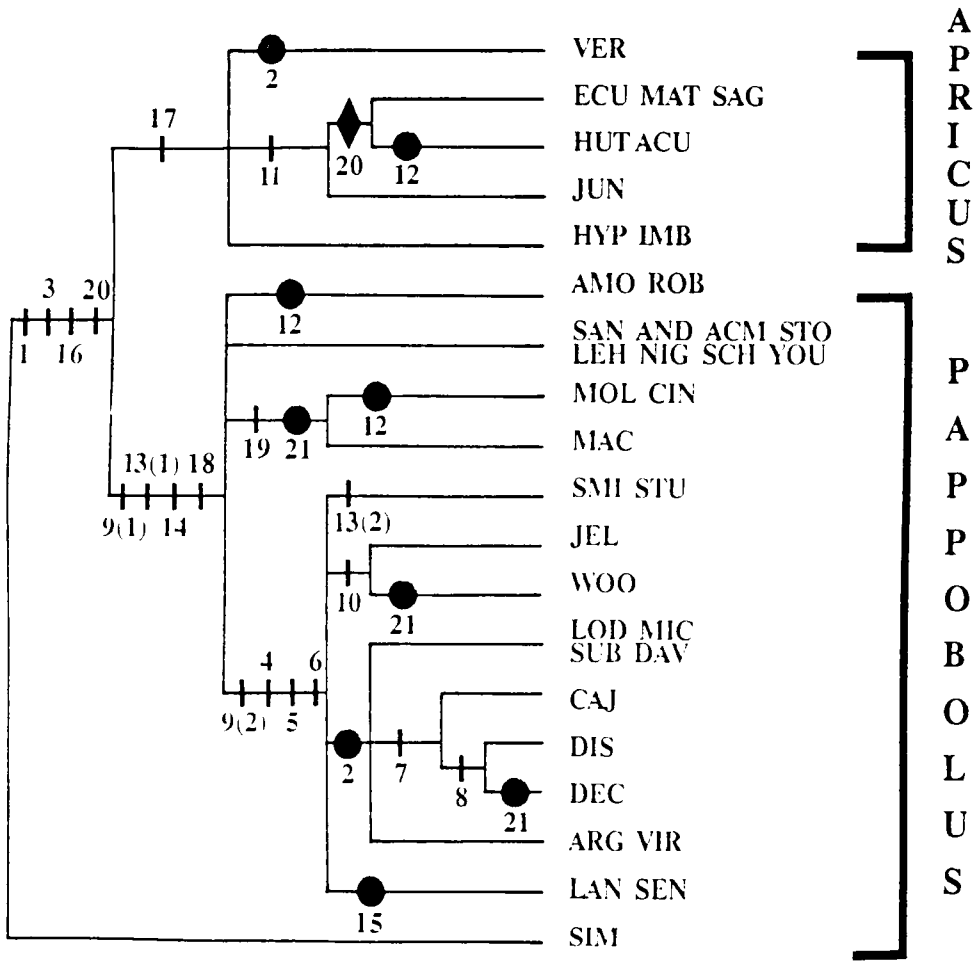

SUBGENUS APRICUS
12 TAXA
650 - 3250 M
THE NIGRESCENS GROUP
15 TAXA
1850 - 3500 M
THE STUEBELII GROUP
4 TAXA
2800 - 3900 M
THE DISCOLOR GROUP
14 TAXA
1850 - 4200 M
81°W
12°S
200 km

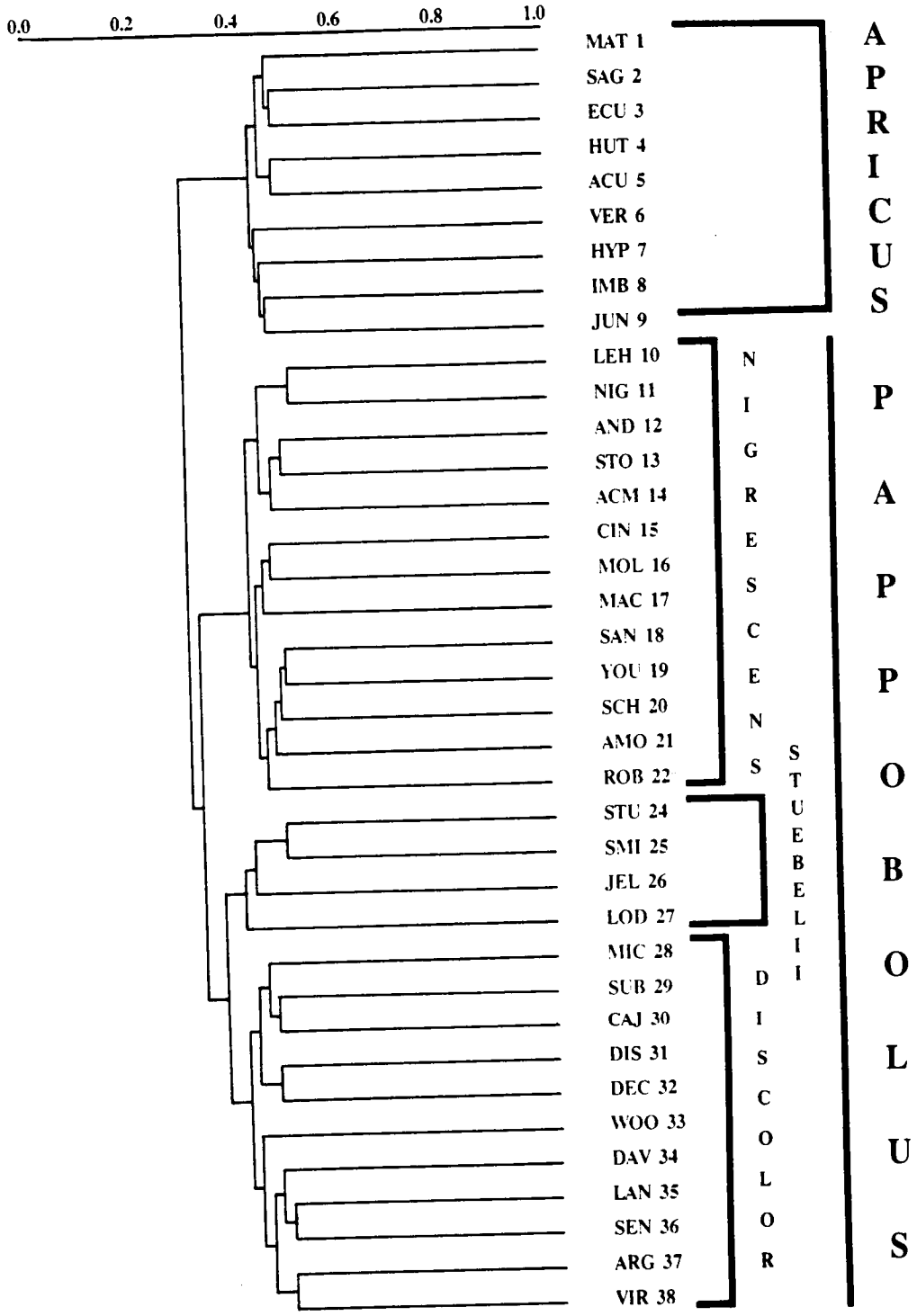

COLOMBIA
1. Nariño
ECUADOR
1. Carchi
2. Imbabura
3. Pichincha
4. Cotopaxi
5. Tungurahua
6. Chimborazo
7. Bolívar
8. Cañar
9. Azuay
10. Loja
PERU
1. Piura
2. Lambayeque
3. Cajamarca
4. Amazonas
5. La Libertad
6. Ancash
7. Huánuco
8. Cerro de Pasco
9. Junín
10. Lima
11. Huancavelica
Lita
Salinas
Quito
Ibarra
Pifo
Guaranda
Ambato
Alausí
Baños
Riobamba
Huigra
Chunchi
Cañar
Cuenca
Girón
Oña
Saraguro
Catamayo
Loja
Gonzanamá
Vilcabamba
Cariamanga
Yangana
NUDO DE SABANILLA
Huancabamba
Jaén
HUANCABAMBA DEFLECTION
Olmos
Chachapoyas
Cutervo
Leimebamba
Chiclayo
Balsas
Celendín
Chota
Bolívar
Hualgayoc
MARAÑÓN RIVER VALLEY
Pacasmayo
Llata
Cajamarca
Huánuco
Trujillo
Tingo María
Pillao
Caráz
Muña
CORDILLERA BLANCA
Tomay Kichwa
Ambo
Huaráz
Pasco
Huacapistana
Tarma
81°W
12°S
Lima
200 km

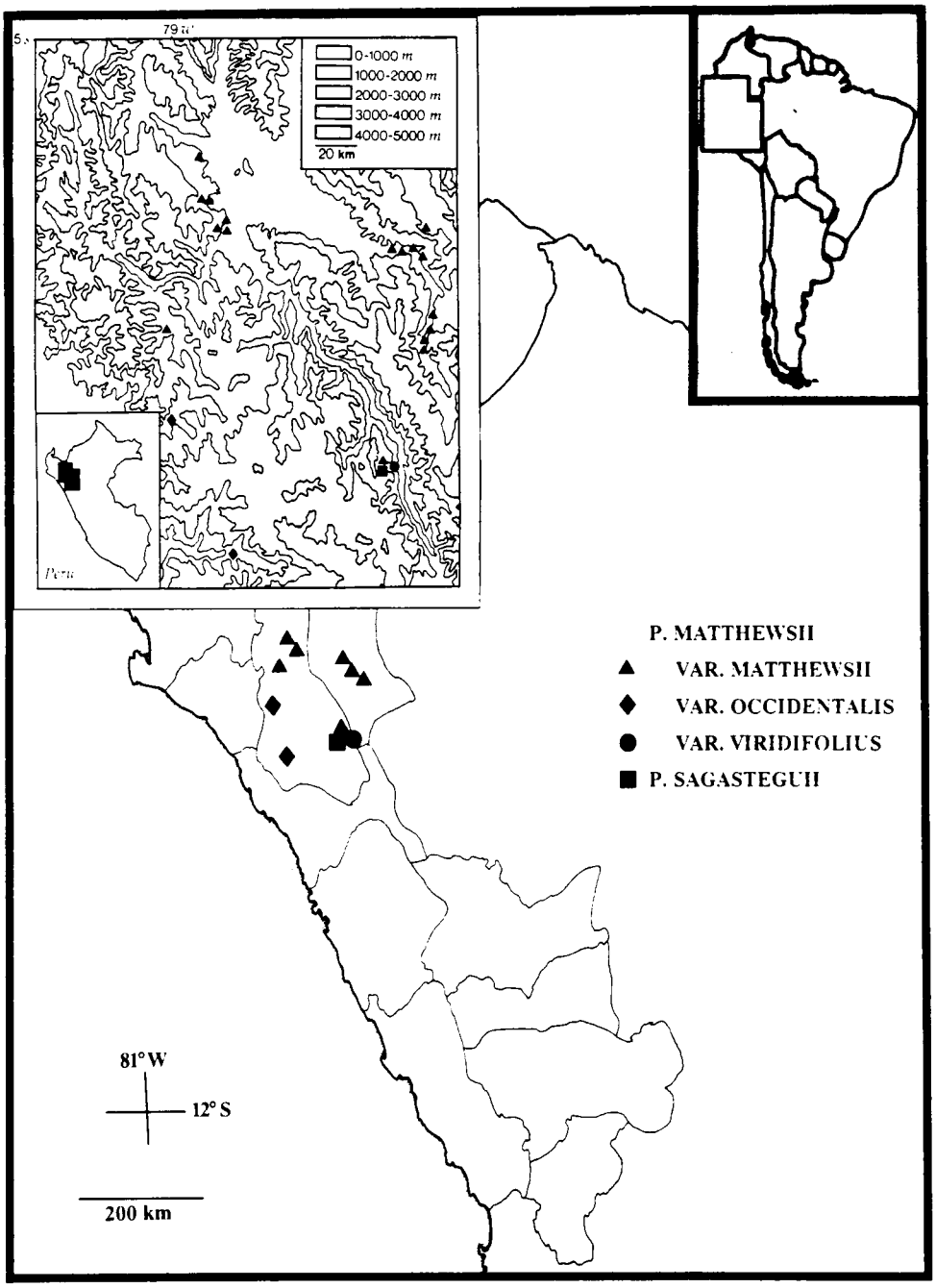

1
COLOMBIA 1/0
2 1
1
2 2
ECUADOR 8/7
2 4
2
2
3 1
PERU 32/31
1 12 5
8 5
2 2
2 3
1 2
1 3
1
80° W
14° S

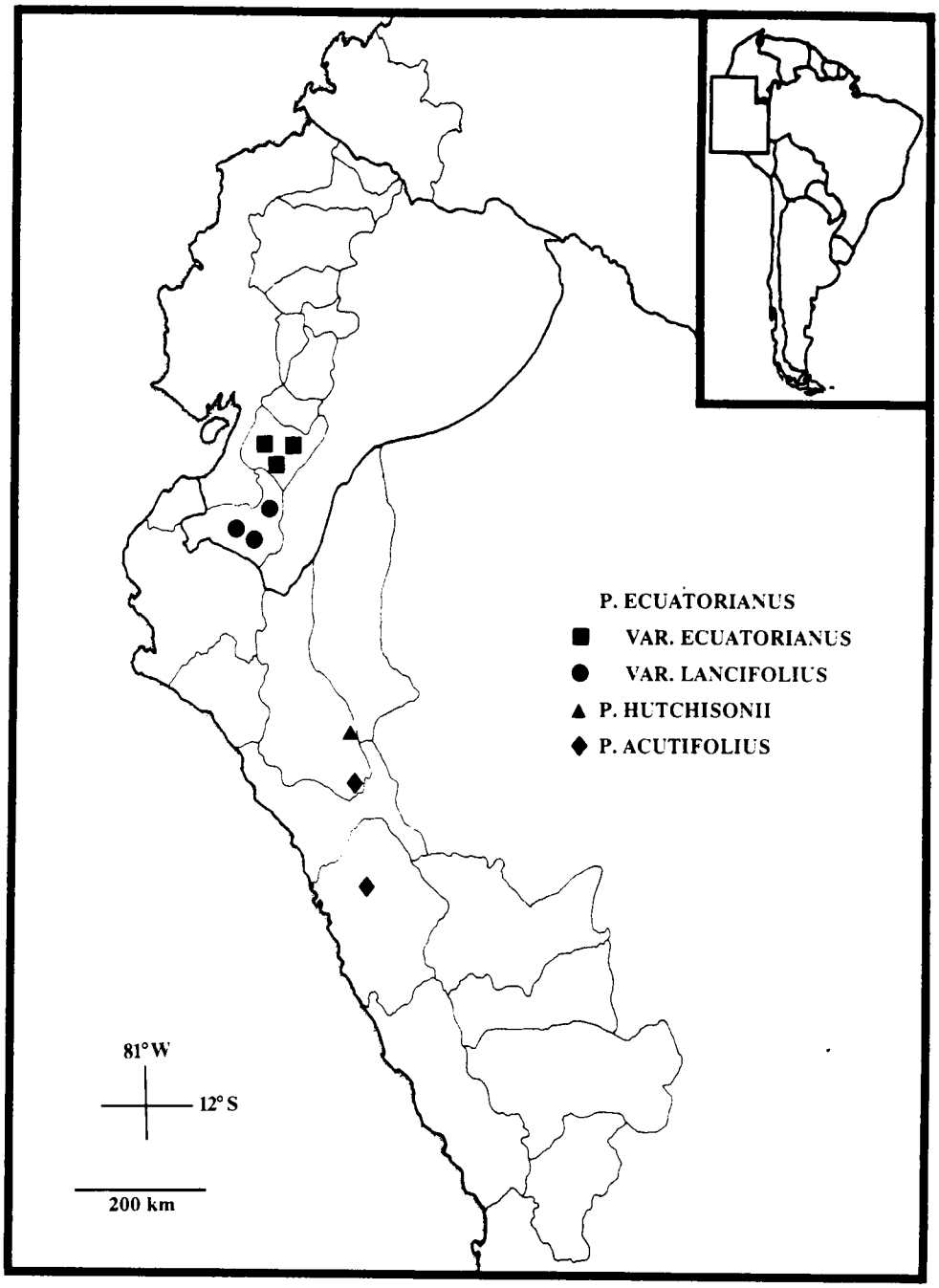

Mira River
Guayllabamba River
Chanchán River
Puela River
Pastaza River
Paute River
Cañar River
Girón River
León River
Jubones River
Paquishapa River
Zamora River
Catamayo River
Guayuco River
Huancabamba River
Marañón River
Utcubamba River
Llaucano River
Cajamarca River
Crisnejas River
Huallaga River
Chira River
Quiroz River
Chotano River
Chancay River
Saña River
Jequetepeque River
Chicama River
Moche River
Santa River
Palca River
Ucayali River
Pativilca River
Rimac River
Mantaro River
81°W
12°S
200 km


A
B

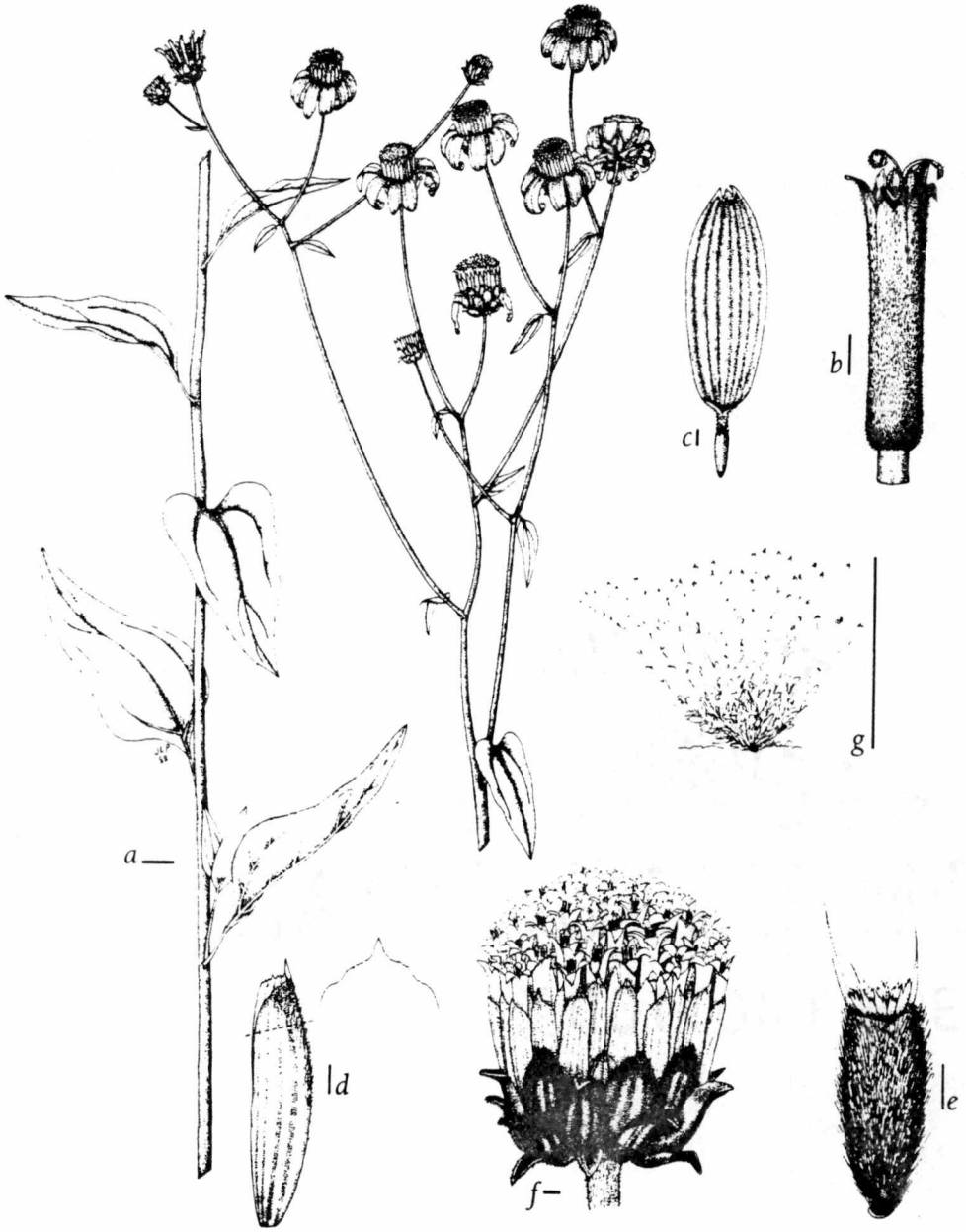

VER
ECU MAT SAG
HUT ACU
JUN
HYP IMB
AMO ROB
SAN AND ACM STO
LEH NIG SCH YOU
MOL CIN
MAC
SMI STU
JEL
WOO
LOD MIC
SUB DAV
CAJ
DIS
DEC
ARG VIR
LAN SEN
SIM
APRICUS
PAPPOBOLUS
2
17
11
20
12
3 20
1 16
12
19 21
12
13(1) 18
9(1) 14
13(2)
10
21
4 6
9(2) 5
2
7
8
21
15
— SYNAPOMORPHY
● PARALLELISM
◆ REVERSAL

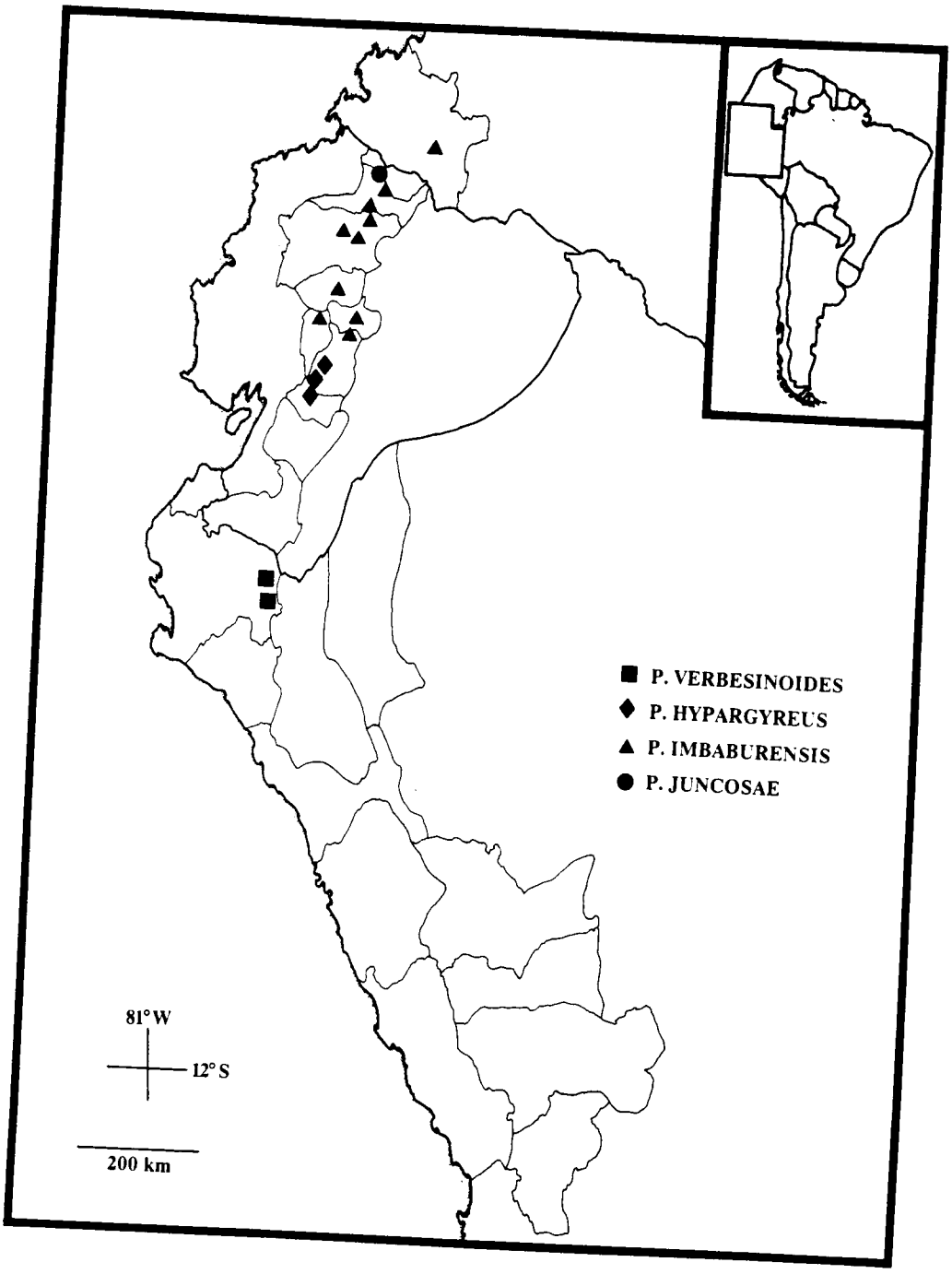

0.0
0.2
0.4
0.6
0.8
1.0
MAT 1
SAG 2
ECU 3
HUT 4
ACU 5
VER 6
HYP 7
IMB 8
JUN 9
LEH 10
NIG 11
AND 12
STO 13
ACM 14
CIN 15
MOL 16
MAC 17
SAN 18
YOU 19
SCH 20
AMO 21
ROB 22
STU 24
SMI 25
JEL 26
LOD 27
MIC 28
SUB 29
CAJ 30
DIS 31
DEC 32
WOO 33
DAV 34
LAN 35
SEN 36
ARG 37
VIR 38
APRICUS
NIGRESCENS
STUEBELII
DISCOLOR
PAPPOBOLUS

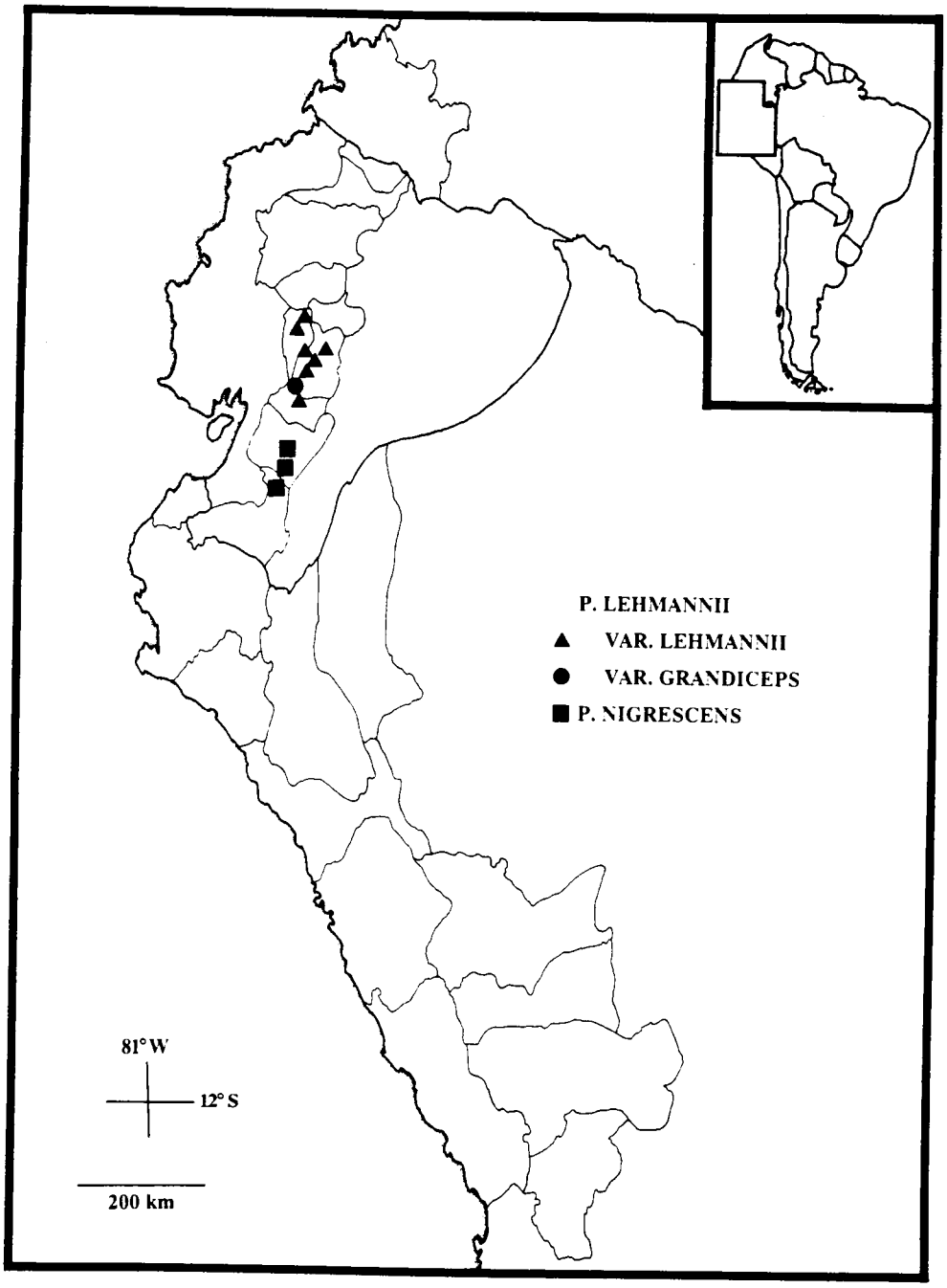

79°W
5°
0-1000 m
1000-2000 m
2000-3000 m
3000-4000 m
4000-5000 m
20 km
Peru
P. MATTHEWSII
VAR. MATTHEWSII
VAR. OCCIDENTALIS
VAR. VIRIDIFOLIUS
P. SAGASTEGUII
81°W
12° S
200 km

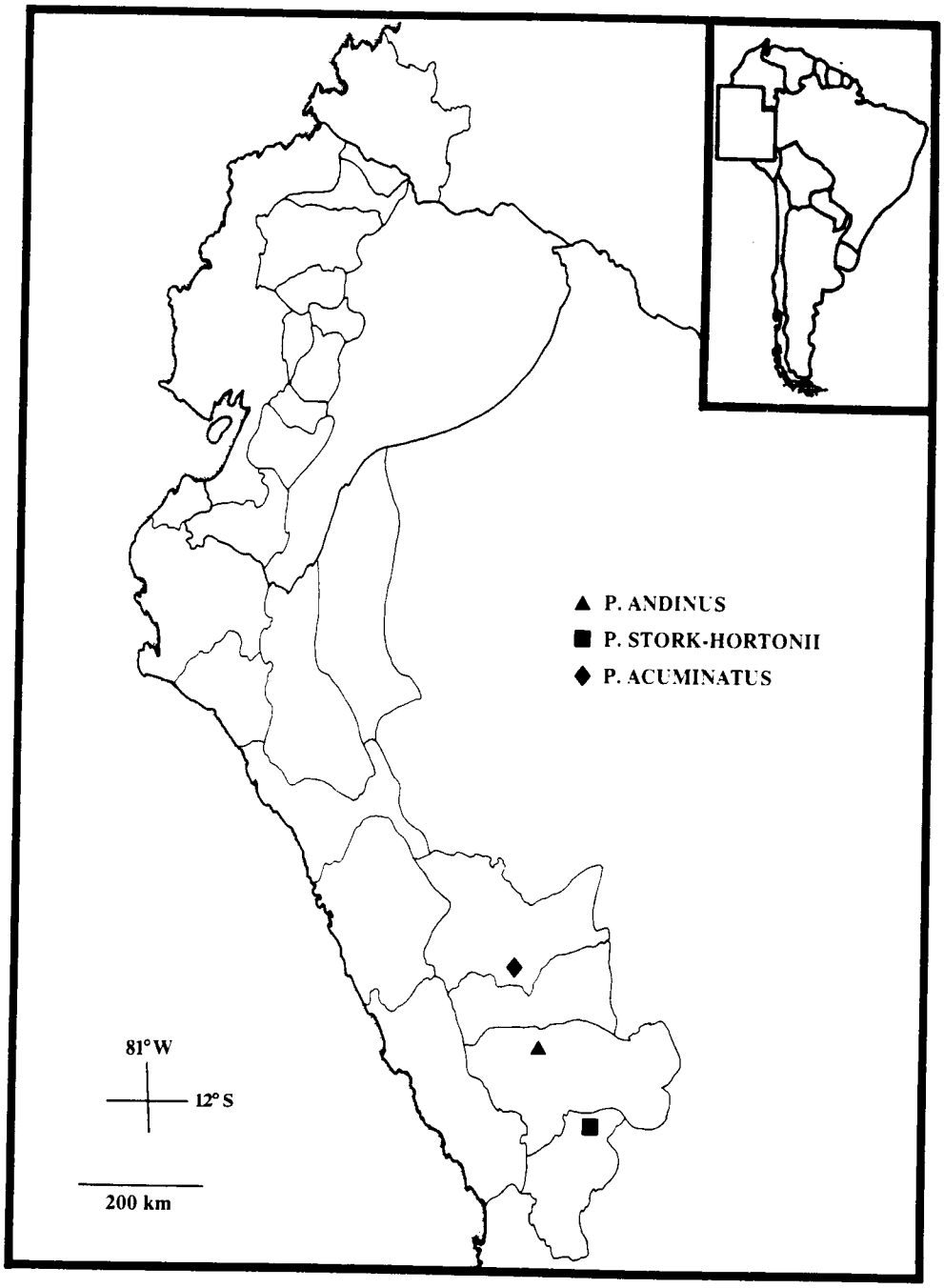

P. ECUATORIANUS
VAR. ECUATORIANUS
VAR. LANCIFOLIUS
P. HUTCHISONII
P. ACUTIFOLIUS
81°W
12° S
200 km

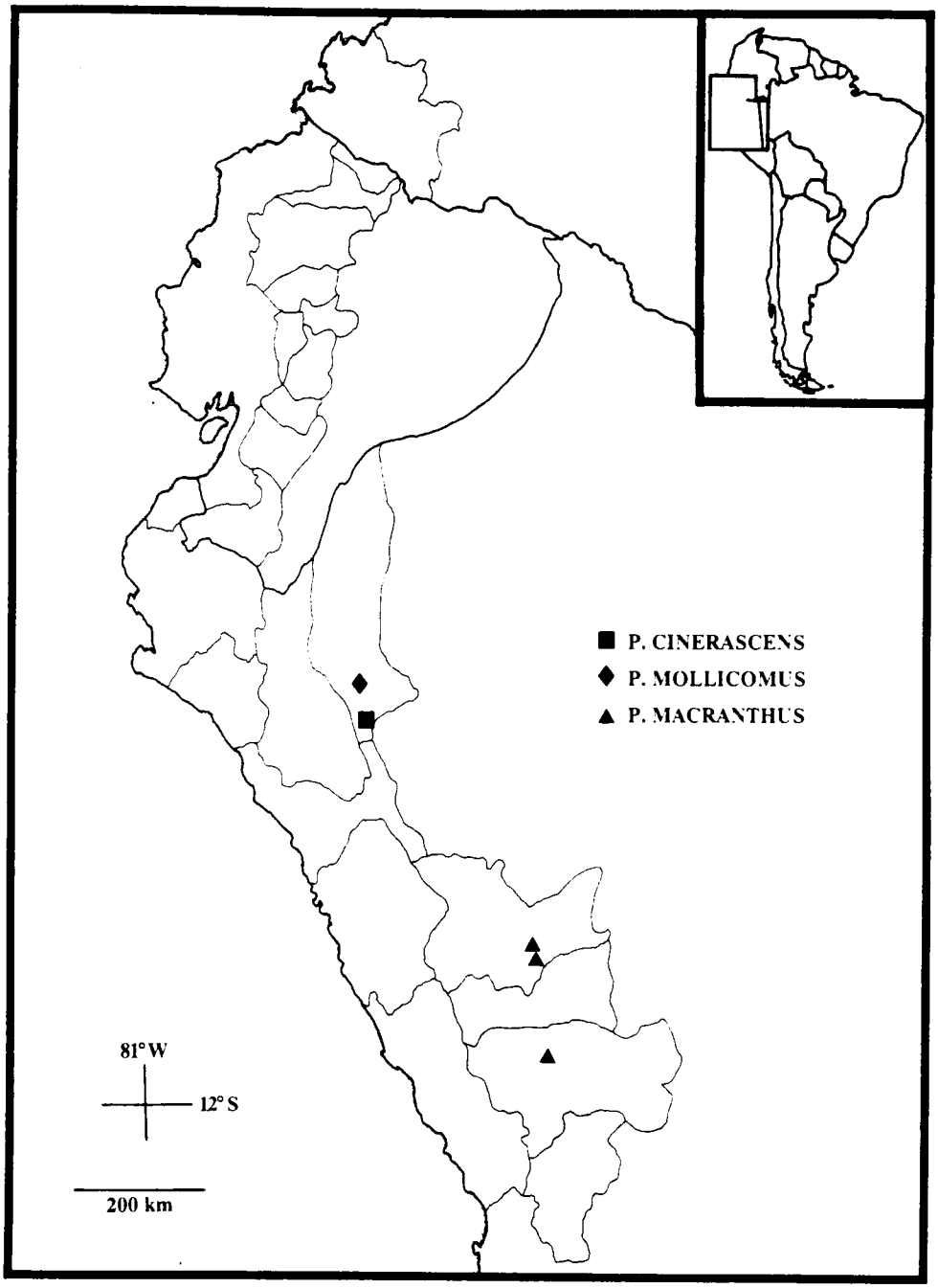



a
b
c
d
e
f
g


P. VERBESINOIDES
P. HYPARGYREUS
P. IMBABURENSIS
P. JUNCOSAE
81°W
12° S
200 km

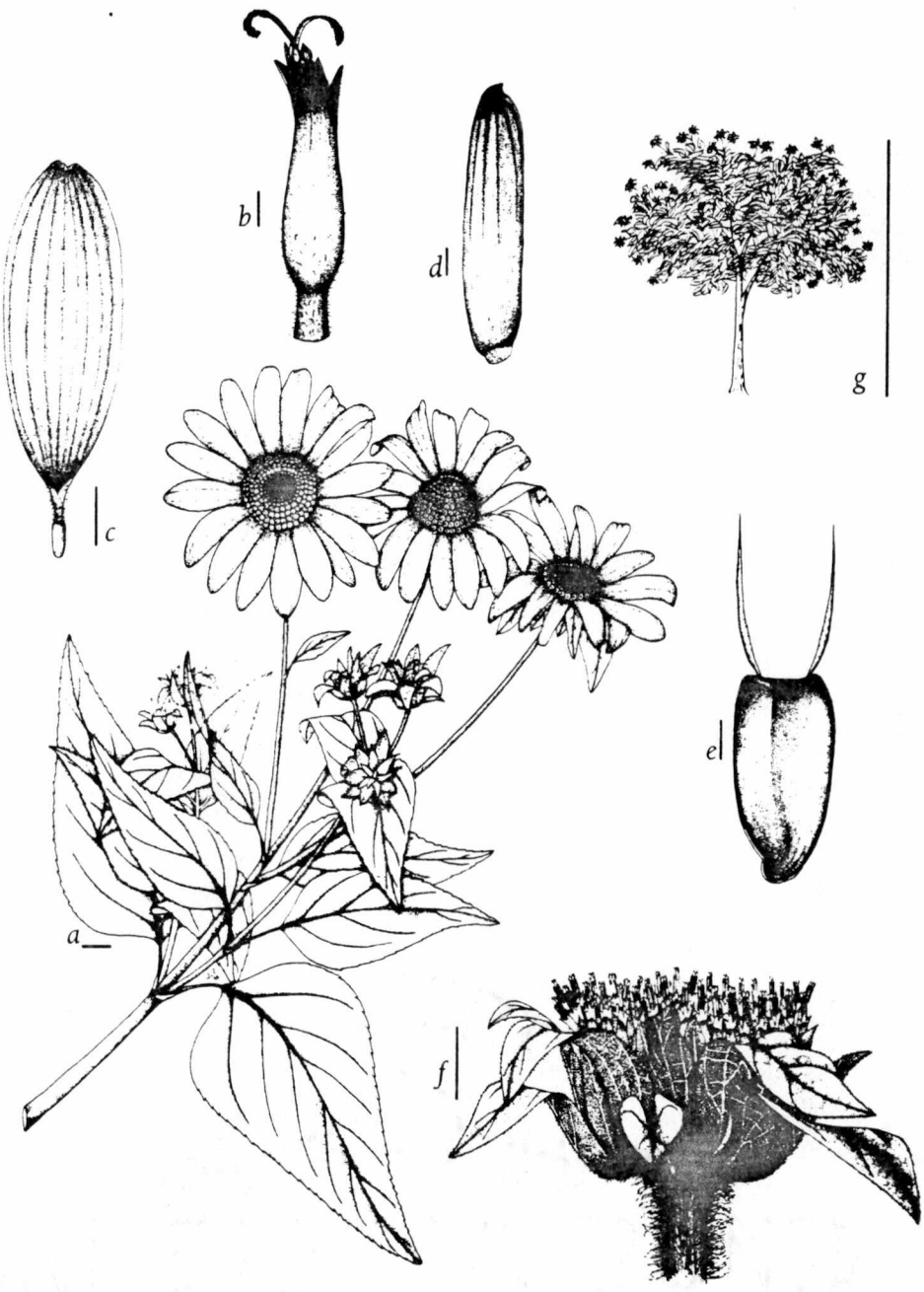

P. LEHMANNII
VAR. LEHMANNII
VAR. GRANDICEPS
P. NIGRESCENS
81° W
12° S
200 km

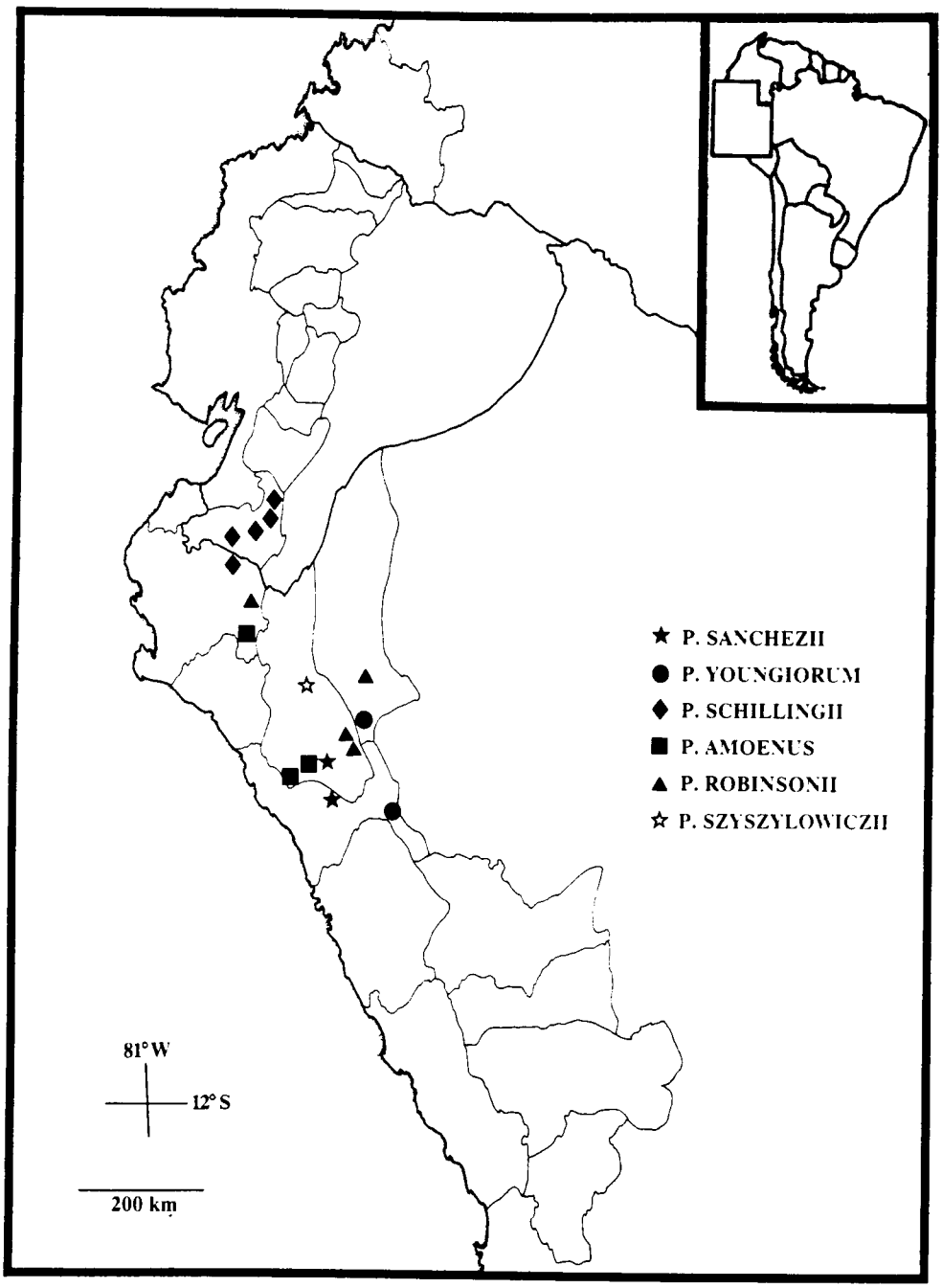

▲ P. ANDINUS
■ P. STORK-HORTONII
◆ P. ACUMINATUS
81°W
12° S
200 km

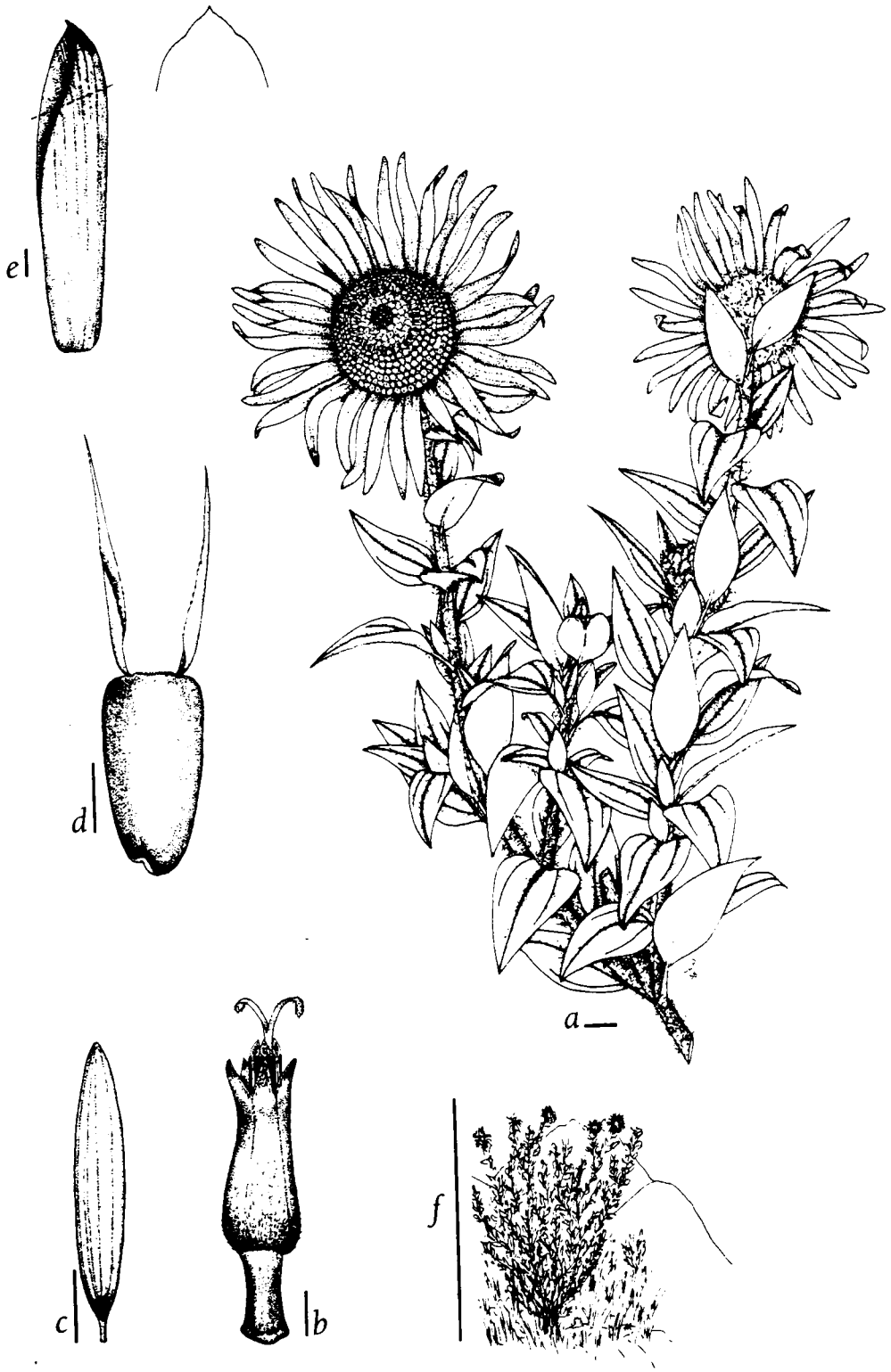

P. CINERASCENS
P. MOLLICOMUS
P. MACRANTHUS
81° W
12° S
200 km

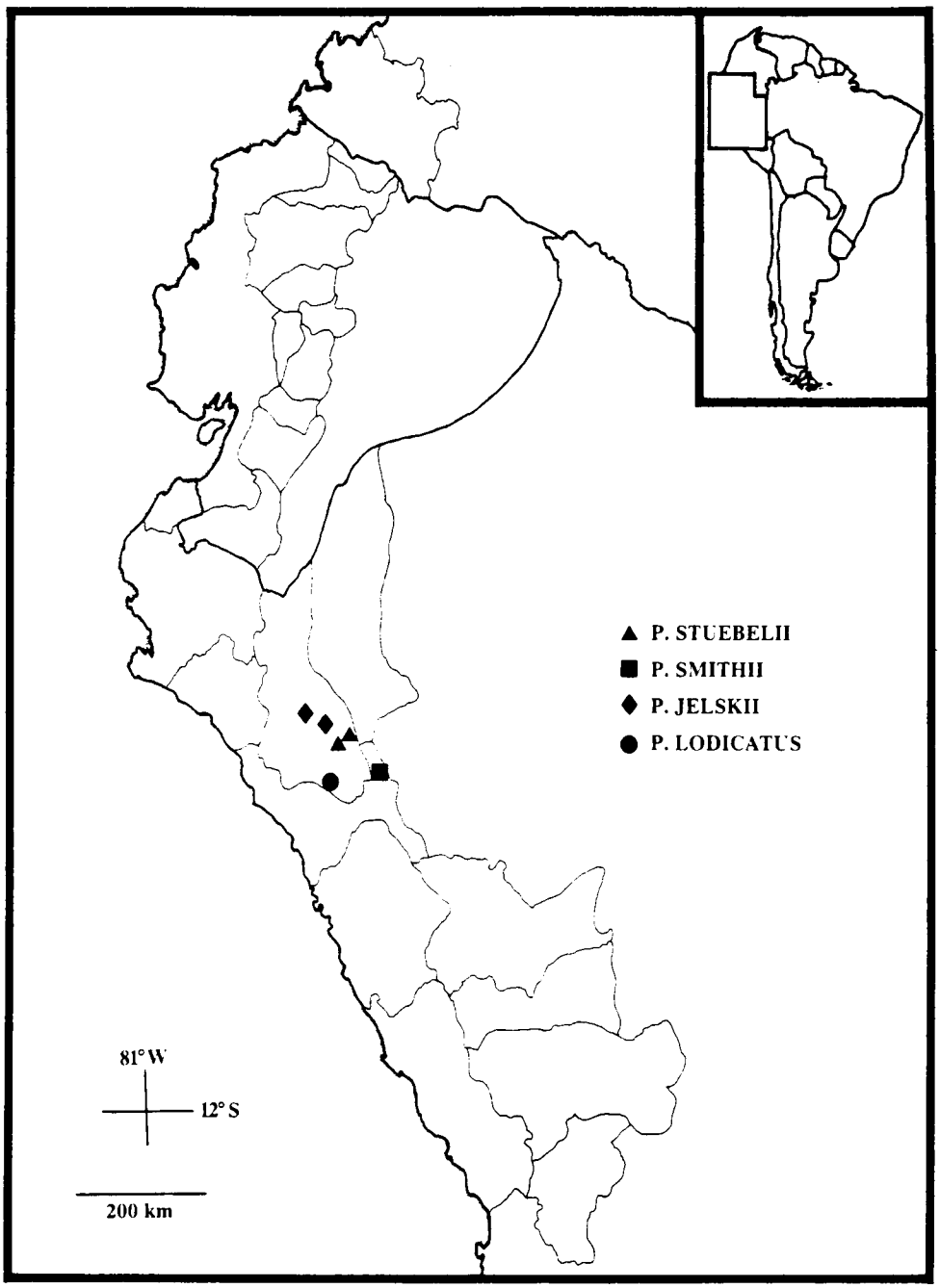


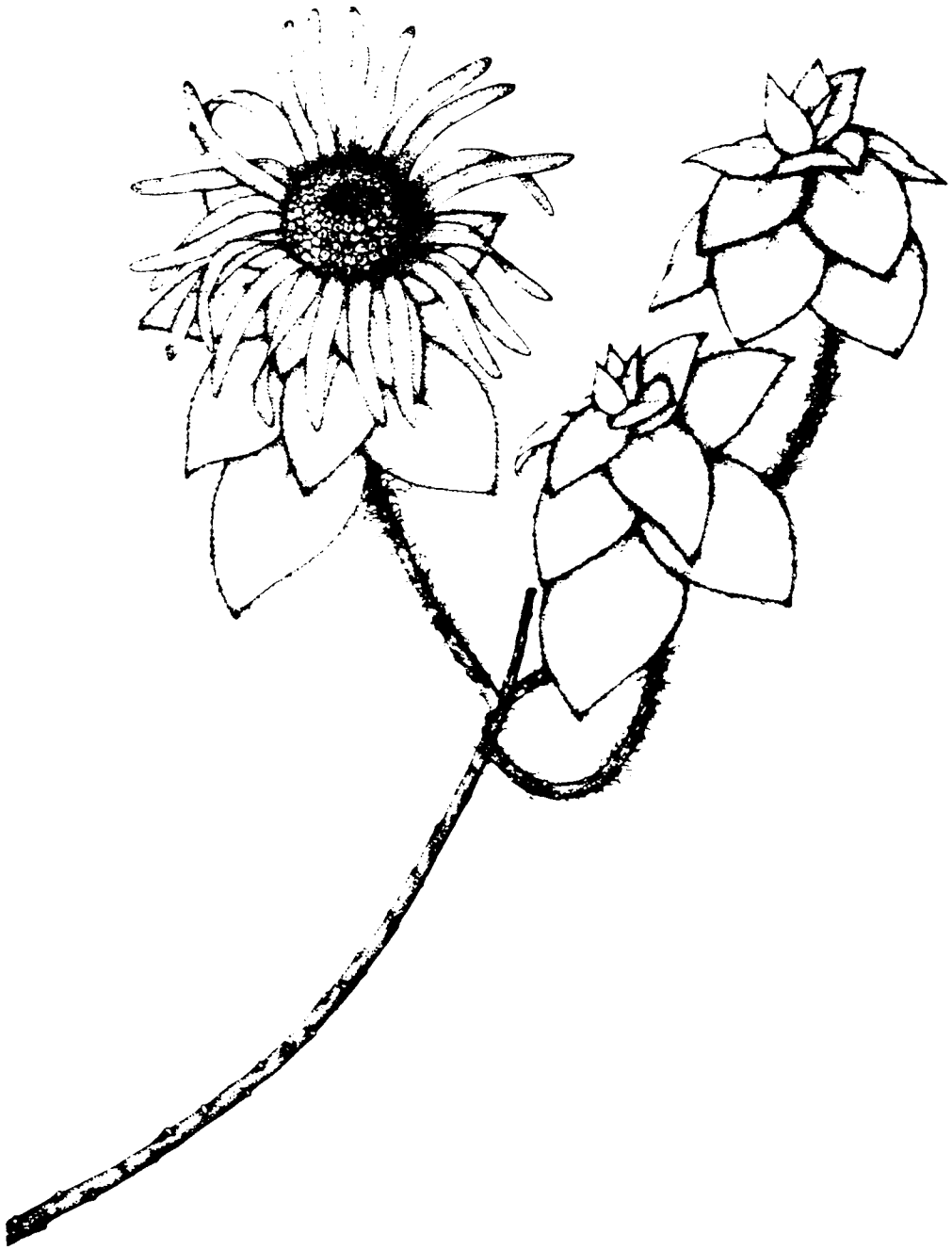


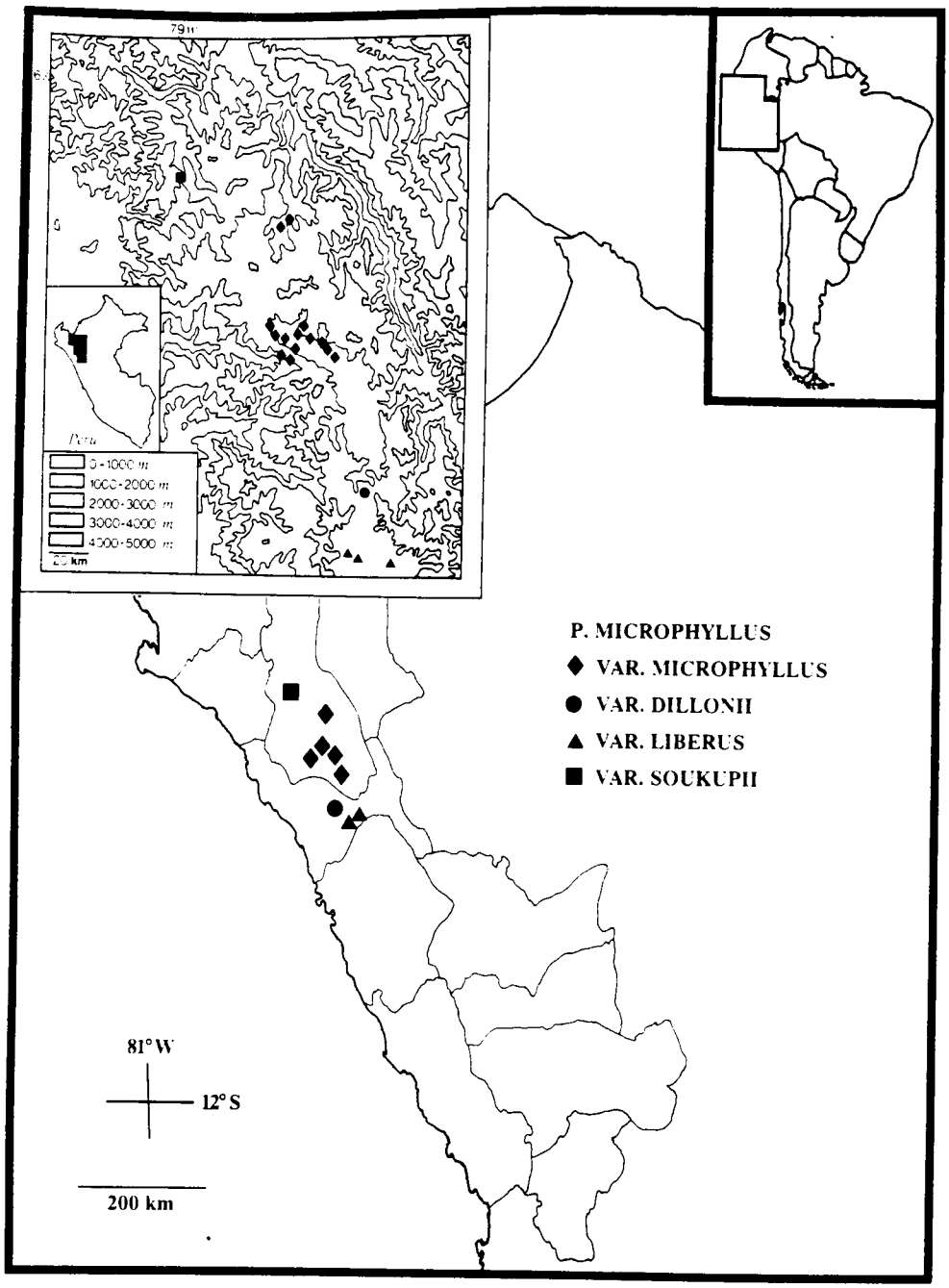

b
d
g
c
e
a
f

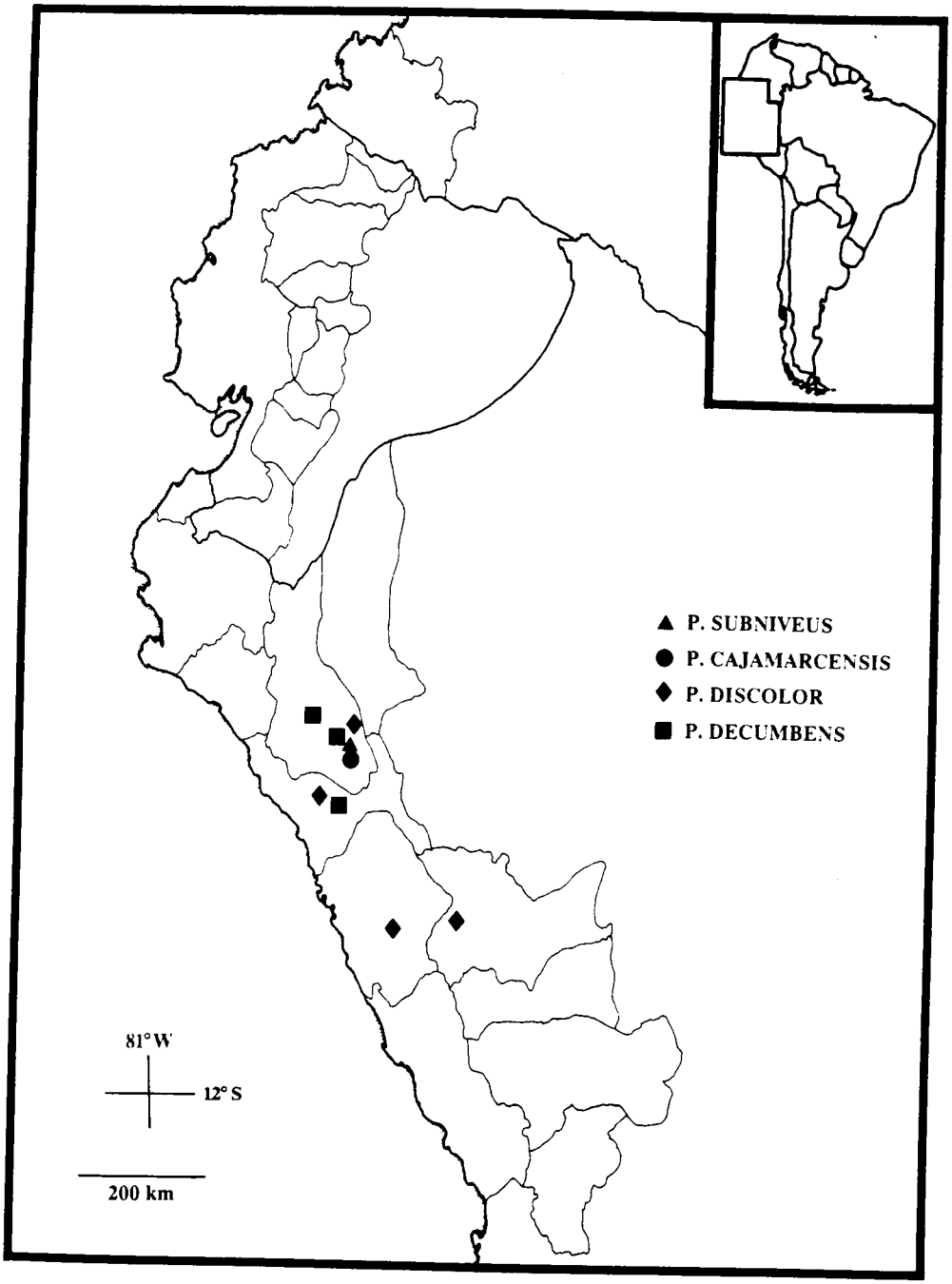

P. SANCHEZII
P. YOUNGIORUM
P. SCHILLINGII
P. AMOENUS
P. ROBINSONII
P. SZYSZYLOWICZII
81°W
12°S
200 km

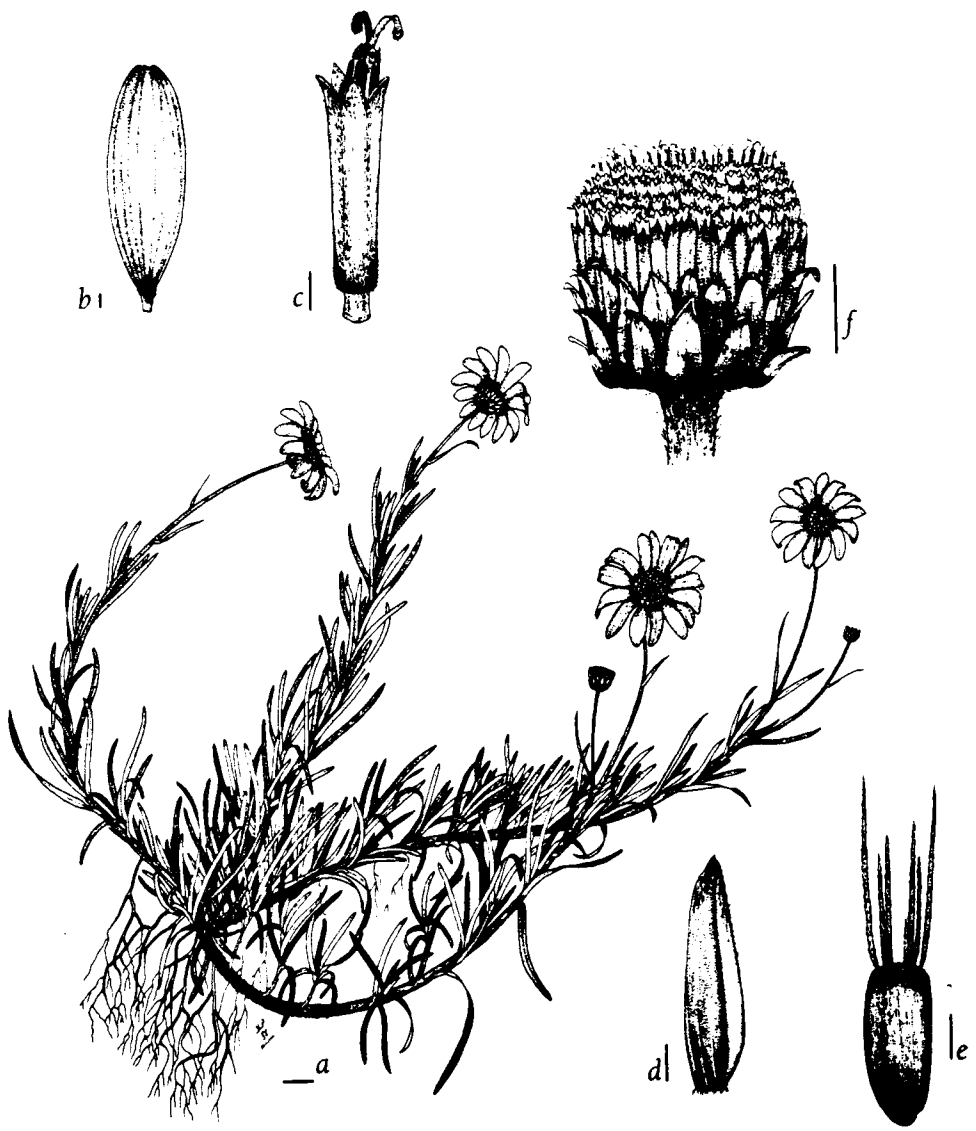

e
d
a
c
b
f

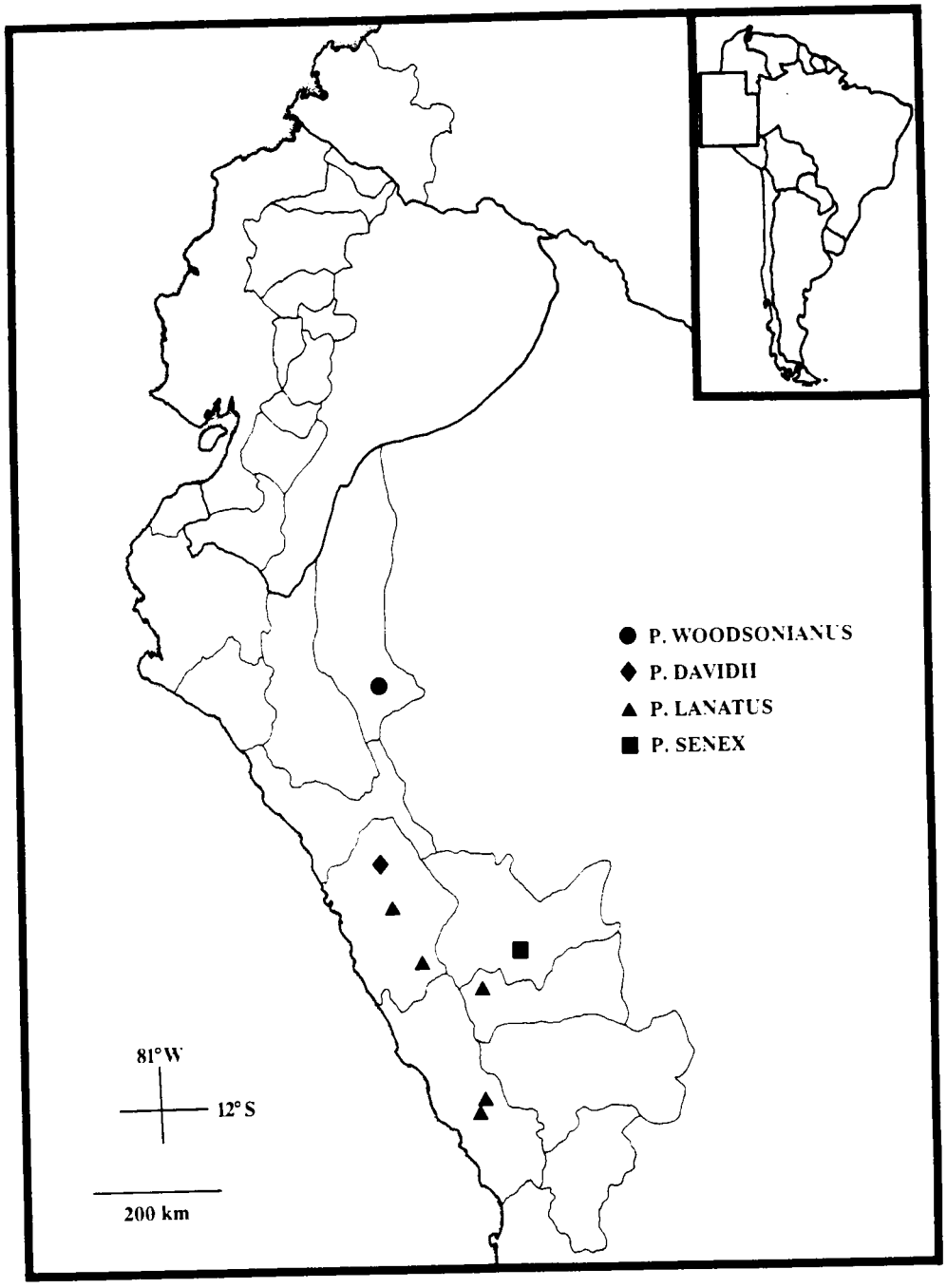

P. STUEBELII
P. SMITHII
P. JELSKII
P. LODICATUS
81° W
12° S
200 km

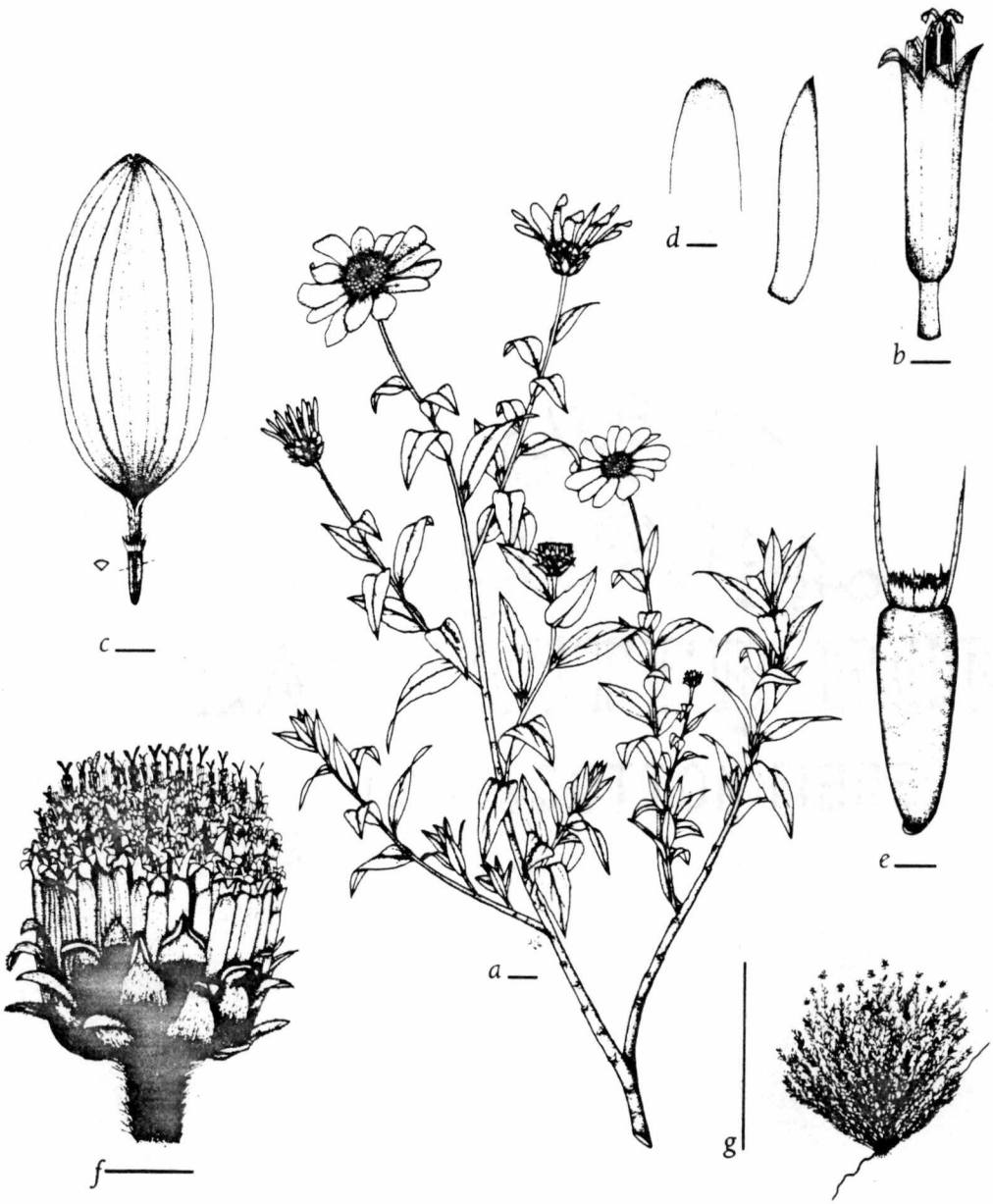


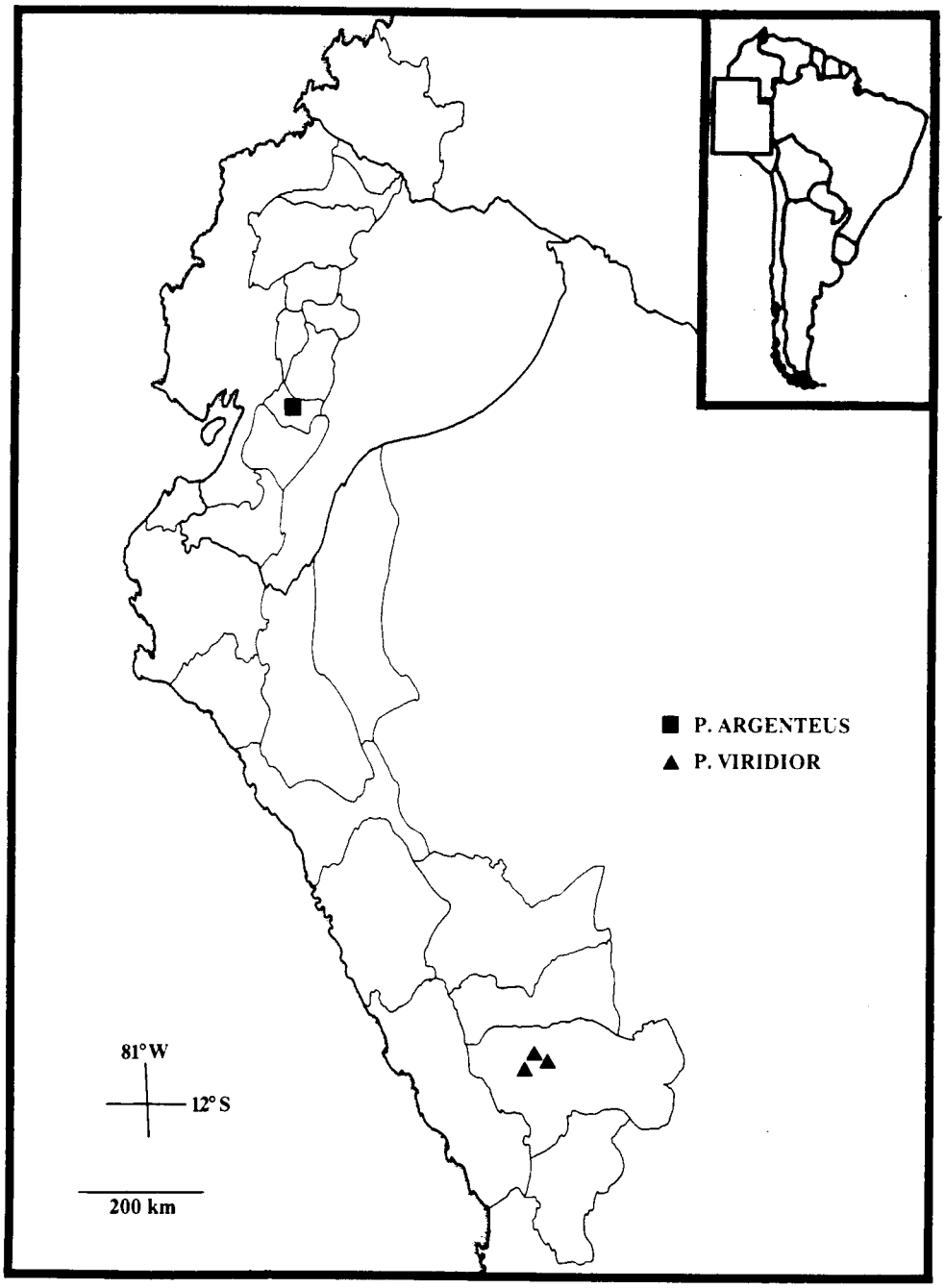

79°W
6°
5°
Peru
0-1000 m
1000-2000 m
2000-3000 m
3000-4000 m
4000-5000 m
200 km
P. MICROPHYLLUS
VAR. MICROPHYLLUS
VAR. DILLONII
VAR. LIBERUS
VAR. SOUKUPII
81°W
12°S
200 km


P. SUBNIVEUS
P. CAJAMARCENSIS
P. DISCOLOR
P. DECUMBENS
81° W
12° S
200 km


b
c
f
a
d
e


P. WOODSONIANUS
P. DAVIDII
P. LANATUS
P. SENEX
81°W
12°S
200 km


d
b
c
a
e
f
g


P. ARGENTEUS
P. VIRIDIOR
81°W
12° S
200 km

VITA

Jose L. Panero was born December 8, 1959 in Havana, Cuba. He received a Bachelor of Arts degree from the University of Miami in June 1984, with a major in Biology. In September 1984 he entered the University of Tennessee, Knoxville and received a Master of Science degree with a major in Botany in August 1986 and a Ph.D. in May 1990.