# A REVISION OF THE NEOTROPICAL GENUS LISIANTHIUS (GENTIANACEAE) 

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## TAXONOMIC TREATMENT

Lisianthius P. Browne, Civ. Nat. Hist. Jamaica 157. t. 9. 1756.
Lisianthus L. Mant. Pl. 43. 1767.
Leianthus Griseb. Gen. \& Sp. Gent. 196. 1839 [1838], nom. illegit. [Art. 63]. Petasostylis Griseb. in DC. Prodr. 9: 71. 1845.

Plants short-lived, coarse, perennial suffrutescent herbs or subshrubs, spindly shrubs, or even small trees, very rarely annual herbs, usually glabrous but occasionally puberulous; often monopodial, but occasionally with several main axes. Roots tufted, fibrous, often woody. Stems terete, but with 2 pairs of raised parallel ridges on opposite sides, these usually obscured below, the pairs sometimes diverging and the stems then 4 -angled. Leaves opposite, entire or rarely papillate or ciliolate, membranaceous or more rarely moderately coriaceous, the venation obscure or prominent on the lower surface of the leaf, of 1-2 pairs of primary lateral veins, when 2 pairs, the lower originating near the base of the blade, the upper closely paralleling the midvein for a distance before diverging, all ultimately curving to the leaf margin and closely paralleling it; petioles winged or not, or leaves sessile, the bases of the pairs fused, forming a sheath around the stem. Inflorescences often terminating the main stem and the upper lateral branches, the entire upper portion of the plant appearing as a single, large, diffuse inflorescence, equally often axillary or on modified lateral, leafy, determinate shoots, and then never terminating the main axis, or very rarely solitary flowers in the axils of the foliage leaves; basically branched systems of compound dichasia with the ultimate branches often monochasial, but frequently reduced and the dichasia appearing simple; inflorescence branches long and the inflorescences open, or branches contracted and the inflorescences dense and compact, rarely branches practically nonexistent and inflorescences appearing capitate or umbellate; bracts subtending the dichasia foliaceous but different in shape and reduced in size from the foliage leaves, or equally often greatly reduced and essentially scarious; flowers usually pedicellate, rarely sessile, the lateral pedicels in each dichasial unit subtended by a pair of opposite or subopposite bracteoles, these scarious or rarely foliaceous. Flowers nodding or horizontal, more rarely erect or ascending.

[^0]Calyx chlorophyllous, fused to the middle or more commonly only near the base, the inner surface of the tube covered to varying degrees with minute digitate squamellae; lobes 5 , long acuminate or rarely acute, usually with scarious margins, often carinate or even alate abaxially. Corolla marcescent and frequently persisting on the mature, dehisced capsule, usually with conspicuous fibrous bundles visible as longitudinal whitish lines when dried, tubular-funnelform (or tubular or tubularcampanulate), very rarely salverform; lobes ovate-lanceolate or oblonglanceolate (broadly ovate or even suborbicular), usually acuminate but rarely acute or obtuse, erect, spreading, or recurved. Stamens 5, usually inserted in the lower third of the corolla tube, only very rarely inserted in the throat, nearly always surpassing the corolla tube and occasionally surpassing the lobes; filaments elongate, filiform, expanded at the base and abruptly upturned at the apex, usually unequal in length, rarely subequal; anthers oblong, the connective slightly exserted or not, yellow (or purple). Pistil 2-carpellate; ovary oblong-ellipsoid or rarely ovoid, unilocular or bilocular, when unilocular the septum incomplete usually only at the base, the placentae scarcely protruding into the lumen of the ovary; style filiform, usually exceeding the corolla lobes, always longer than the filaments and usually exceeding them; stigma capitate or peltate, bilobed (often indistinctly), the lobes hemispherical. Capsule gray-brown, sometimes glaucous when immature, surrounded by the persistent calyx and marcescent corolla which often falls off before the seeds are shed, typically fusiform or oblong-ellipsoid, rarely ovoid, beaked, with the placentae, upon dehiscence, visible as whitish, erose bands along the margins of the valves adjacent to the suture. Seeds numerous, very small, angular, densely pitted with numerous small depressions. $\sqrt{ }$ Lectotype spectes: L. longifolius L., chosen by Britton \& Wilson, Sci. Surv. Porto Rico Virgin Is. 6:84. 1925.

## Key to the Sections of Lisianthius

Corolla greenish or greenish-white, salverform, short, the tube 1.5 cm . or less in length; stamens inserted near the apex of the corolla tube, filaments of equal length in a given flower, very short, less than 9 mm . long.
I. Omphalostigma.

Corolla, at least the tube, yellow, red, or "black," tubular or funnelform, the tube more than 1.8 cm . long and usually much longer; stamens inserted in the lower $1 / 3-1 / 2$ of the corolla tube; filaments of unequal length in a given flower, more than 10 mm . long and usually much longer. .... II. Lisianthius.
I. Lisianthius sect. Omphalostigma (Griseb.) Weaver, comb. nov.

Leianthus sect. Omphalostigma Griseb., pro parte, Gen. \& Sp. Gent. 198. 1839 [1838].
Annual or perennial herbs, glabrous or minutely spiculate. Inflorescences terminal and axillary on the primary and secondary shoots, basically of compound dichasia. Corolla salverform, the limb widely flaring, greenish
or greenish-white, small, the tube 15 mm . long or less. Stamens inserted near the apex of the corolla tube, the filaments equal in one flower, less than 9 mm . long. Sculpturing of pollen grains reticulate. Lectotype species: L. saponarioides Cham. \& Schlecht.

The section Omphalostigma was defined more or less tentatively by Grisebach (1839) in his genus Leianthus to include the two Mexican species known at that time, L. saponarioides (Cham. \& Schlecht.) Griseb. ( = Lisianthius saponarioides Cham. \& Schlecht.) and L. nigrescens (Cham. \& Schlecht.) Griseb. (=Lisianthius nigrescens Cham. \& Schlecht.). These species reputedly differed from the West Indian species then known in having peltate rather than capitate stigmas and corollas swollen at the base and narrowed above, rather than narrowed at the base.

Stigmatic type has proved to be generally unreliable as an indicator of relationships in Lisianthius. According to my interpretation, L. nigrescens belongs in the typical section of the genus. Therefore L. saponarioides, by exclusion of $L$. nigrescens, becomes the lectotype species of Grisebach's section. At any rate, although both L. nigrescens and L. saponarioides have peltate stigmas, only L. saponarioides is characterized by corollas which are swollen at the base and narrowed above, and then only in older flowers. L. saponarioides therefore best demonstrates the characters mentioned above as supposedly distinctive of sect. Omphalostigma according to Grisebach, and, in any event, would be the better choice as a lectotype species.

## Key to the Species of Lisianthius Section Omphalostigma

Inflorescences compacted, the dichasia often sessile and appearing pleiochasial; calyx $5.5-10 \mathrm{~mm}$. long, the lobes $4-7.5 \mathrm{~mm}$. long, surpassing the ovary at anthesis; corolla $1.4-2.1 \mathrm{~cm}$. long, the lobes $4-7 \mathrm{~mm}$. long and cuspidateacuminate; filaments $3-8.5 \mathrm{~mm}$. long; flowers subsessile or very short pedicellate, the pedicels not more than 1 mm . long; plants glabrous or minutely spiculate, but the calyx and the midveins of the leaves always glabrous; calyx in fruit $2 / 3$ as long to nearly as long as the capsules. ....1. L. saponarioides.
Inflorescences diffuse, the dichasia always pedunculate and never appearing pleiochasial; calyx $3.5-5 \mathrm{~mm}$. long, the lobes $2-3 \mathrm{~mm}$. long, never surpassing the ovary; corolla $1.2-1.7 \mathrm{~cm}$. long, the lobes $2.5-4.5 \mathrm{~mm}$. long and acute or rarely short acuminate; filaments $2-4 \mathrm{~mm}$. long; flowers distinctly pedicellate, the pedicels $2-4 \mathrm{~mm}$. long; plants minutely spiculate, including the calyx tube and the midveins of the leaves; calyx in fruit usually $1 / 3$ and never more than $1 / 2$ as long as the capsule.
2. L. meianthus.

1. Lisianthius saponarioides Cham. \& Schlecht. Linnaea 6: 389. 1831 (as Lisianthus). Type. Mexico. Veracruz: Ad margines sylvarum Papantlae, Schiede (hal!).
Leianthus saponarioides (Cham. \& Schlecht.) Griseb. Gen. \& Sp. Gent. 198. 1839 [1838].

Petasostylis saponarioides (Cham. \& Schlecht.) Griseb. in DC. Prodr. 9: 71. 1845.

Lisianthus congestus Standl. Carnegie Inst. Publ. 461: 82. 1935. ${ }^{\text {Thpe. }}$ Guatemala. Petén: Sabana de San Francisco, La Libertad, Lundell 2479 ( F !).

Rather coarse, erect, monopodial, perennial (?) herbs, glabrous or minutely spiculate. Stems $8-14 \mathrm{dm}$. tall, green, minutely spiculate (with magnification) or more rarely essentially glabrous, terete below but 4 -angled above, the angles usually minutely serrulate. Leaves (1.6)3.2-12 cm . long and ( 0.7 ) $1.3-4 \mathrm{~cm}$. broad, dull textured on both surfaces, papillose above and with the margins of the upper leaves often very minutely ciliolate, the lateral veins inconspicuous below; the principal foliage leaves narrowly elliptic (or ovate-lanceolate), long-acuminate, long-attenuate at the base, essentially sessile or with a short, winged petiole to 3 mm . long; the upper leaves and those on the secondary branches distinctly ovate or ovate-lanceolate, rounded or subcordate at the base, distinctly shortpetiolate. Inflorescences of sessile or pedunculate dichasia, these usually $1-2(-4)$ times compound but often reduced and appearing simple, borne singly or in groups of 3 , the terminal one often sessile and the whole unit appearing pleiochasial; inflorescence branches usually contracted and the dichasia or groups of dichasia dense and compact, more rarely somewhat elongate and the dichasia more diffuse, 4 -angled, 2 of the angles often expanded into scarious wings, minutely spiculate; bracteoles scarious, subulate. Flowers erect or ascending, subsessile or very short pedicellate, the pedicels not exceeding 1 mm . in length. Calyx $5.5-10 \mathrm{~mm}$. long, fused for $2 / 10-3 / 10$ its length; the lobes $4-7.5 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, lanceolate, long-acuminate, scarious margined, ridged abaxially; the tube $1.5-2.5 \mathrm{~mm}$. long. Corolla $1.4-2.1 \mathrm{~mm}$. long, salverform, greenish-white or green; the tube at anthesis narrow, $10-15 \mathrm{~mm}$. long and ca. 1.5 mm . in diameter, conspicuously white-striate at least at the base; the lobes $4-7 \mathrm{~mm}$. long and $2-4.5 \mathrm{~mm}$. broad, flaring and recurved, ovatelanceolate or more rarely somewhat elliptic, long-acuminate, conspicuously longer than broad, usually $1 / 3$ as long as the tube but varying from $3 / 10-4 / 10$ as long. Stamens inserted near the apex of the corolla tube, in the upper $1 / 6-1 / 3$, at or just above the apex of the calyx lobes; filaments subequal, (3) $4.5-7.5$ (8.5) mm . long, surpassing the corolla tube but not the lobes, usually surpassing the style; anthers $1.5-2.5 \mathrm{~mm}$. long and ca. 1 mm . broad, oblong, becoming almost sagittate upon dehiscence. Style $6-10 \mathrm{~mm}$. long, surpassing the corolla tube; stigma peltate. Capsule oblong-ellipsoid, $5-10 \mathrm{~mm}$. long and $3-4 \mathrm{~mm}$. broad; the marcescent corolla apparently not persisting until the seeds are shed. Flowering: All year.

Distribution: From 600 to 1200 meters on rocky limestone hillsides and in secondary scrub from the State of Veracruz, Mexico, south and east to Chiapas, the departments of Huehuetenango and Petén, Guatemala, and western British Honduras (Map 1).

## Representative collections

Mexico. Chiapas: Laguna Ocotal Grande, ca. 25-30 km. se. of Cerro Líbano, Dressler 1481 (IJ, mexu, us). Veracruz: ad margines sylvarum Papantlae, Schiede \& Deppe s.n. (bM). Guatemala. Huehuetenango: cafetal of Finca Soledad, 5 mi . se. of Barillas, Sierra de los Cuchumatanes, Steyermark 49547 (f). Petén: La Cumbre, w. of km. 139 of Cardenas Road, Contreras 6205 (F); Lake Petén Itza, 2 km . s. of Santa Elena, on La Cueva Road, Contreras 2060 (Ll) ; Sabana San Francisco, La Libertad, Lundell $2479^{2}(\mathrm{MICH}$, isotype of $L$. congestus) ; Tikál, on top of Temple IV, Contreras 166 (F, IJ, LL). British Honduras. Cayo Dist.: hill se. of Millionario, Proctor 29820 (duke, iJ); near Camp 6, Gentle 2363 (A, F, LL, Ny).

Lisianthius saponarioides is a rather poorly collected plant of which only 28 specimens were available for study. With their small, greenish, salverform corollas and short stamens inserted near the apex of the corolla tube, L. saponarioides and L. meianthus form a very distinctive group unlikely to be confused with any other species in the genus.

Despite its distinctiveness, Lisianthius saponarioides has had a rather confused history. Until recently, the name usually was applied incorrectly to plants recognized here as L. acuminatus and L. quichensis, both morphologically very different from $L$. saponarioides. The reason for the confusion is unclear. Chamisso and Schlechtendal, in the original description of L. saponarioides, describe the corolla as ". . . hypocrateriformis, tubo tertia circiter parte calycem superans . .." Certainly no other species in the genus, known then or now, is characterized by having a salverform corolla with the calyx reaching to $2 / 3$ of the length of the corolla tube.

Grisebach $(1839,1845)$ evidently applied the name correctly (as Leianthus saponarioides, 1839, and Petasostylis saponarioides, 1845). Hemsley (1882) cited Sumichrast 1558, a fragment of this collection now the lectotype of $L$. acuminatus Perk., as representative of L. saponarioides. Gilg (1895) included a figure of a plant (p. 92, Figure 41-A) which he called L. saponarioides, but which undoubtedly represents $L$. acuminatus Perk., a fact recognized and pointed out by Perkins (1902, p. 493). However, Perkins (loc. cit., p. 491) cited Heyde \& Lux 2921, from Dept. Quiché Guatemala, as representative of L. saponarioides. Heyde \& Lux 2921 superficially resembles L. acuminatus much more than it does $L$. saponarioides. The specimen of Heyde \& Lux 2921 (Us) was later selected by John Donnell Smith as the holotype of L. quichensis.

Although Williams $(1968,1969)$ considered Lisianthius congestus Standl. to be synonymous with $L$. saponarioides, he did it with some reservation. I have seen the holotypes of both $L$. congestus and L. saponarioides; they are similar in all respects and undoubtedly represent the same taxon.

There was no correctly determined material of Lisianthius saponarioides in American herbaria in 1935 when Standley described L. congestus. Therefore, in view of the confused application of the name at that time, it is quite possible that Standley did not consider L. saponarioides when describing his new species. He did not compare L. congestus to any known
species but rather stated that it is "distinguishable at once" from other Central American species "by the densely flowered, congested inflorescence."
2. Lisianthius meianthus Donn. Sm. Bot. Gaz. 52: 51. 1911 (as Lisianthus). Type. Guatemala: Sacolal, bei Pansamalá, von Tuerckheim 1436 (US!).
Rather coarse, annual herbs, minutely pubescent. Stems 7-14 dm. tall and to 5 mm . in diameter, erect, green, terete below but 4-angled above, minutely and densely spiculate in the upper portions. Leaves (0.7)1.5-9 cm . long and ( 0.3 ) $1.3-3.5 \mathrm{~cm}$. broad, dull textured on both surfaces, densely papillose above and with very minutely ciliolate margins, the midvein and the principal lateral nerves conspicuous below, minutely spiculate; principal foliage leaves lanceolate or ovate-lanceolate, rarely tending toward elliptic, long-acuminate, attenuate at the base, essentially sessile or with short, winged petioles to 2 mm . long; the upper leaves and those on the secondary branches distinctly lanceolate, rounded or subcordate at the base, distinctly short-petiolate. Inflorescences of distinctly pedunculate dichasia, these usually 1-2 times compound but often reduced and appearing simple, borne singly or in groups of 3, the ultimate branches often scorpioid; inflorescence branches elongate and the dichasia or groups of dichasia loose and open, 4 -angled, densely spiculate. Flowers ascending or horizontal, the pedicels $2-4 \mathrm{~mm}$. long and minutely spiculate; bracteoles subulate, scarious. Calyx $3.5-5 \mathrm{~mm}$. long, fused for $3 / 10$ - nearly $1 / 2$ its length; the lobes $2-3 \mathrm{~mm}$. long and ca. 1 mm . wide, lanceolate, acuminate, scarious-margined, ridged abaxially; the tube $1-2 \mathrm{~mm}$. long, minutely spiculate. Corolla 12-16.5 mm. long, salverform; the tube at anthesis narrow, $9-12.5 \mathrm{~mm}$. long and ca. 1.5 mm . in diameter at the base, greenish, conspicuously white-striate at least at the base; the lobes flaring, 2.5-4.5 mm . long and $1.5-2.5 \mathrm{~mm}$. broad, oblong-oblanceolate or oblong-elliptic, acute or rarely short-acuminate, longer than broad, $1 / 3-1 / 5$ as long as the tube. Stamens inserted near the apex of the corolla tube, in the upper $1 / 5$, well above the apex of the calyx lobes; filaments subequal $2-4$ mm . long, surpassing the corolla tube, equalling or slightly exceeding the style; anthers ca. 1.5 mm . long and 1 mm . broad, oblong, becoming almost sagittate upon dehiscence. Style $5-8 \mathrm{~mm}$. long, surpassing the corolla tube; the stigma peltate. Capsule oblong-ellipsoid, beaked, $6-9 \mathrm{~mm}$. long, not including the $1-3.5 \mathrm{~mm}$. long beak, and $2-4 \mathrm{~mm}$. in diameter; the marcescent corolla not persisting until the seeds are shed. Flowering: Oct.-Apr.

Distribution. From near sea level to 1500 meters in pine forests, limestone thickets, and along roadsides in central, southern, and eastern Guatemala (Map 1).

[^1](F); woods between Finca Gubilguitz and Hacienda Yaxcabanal, Steyermark 44821 ( $\mathrm{F}, \mathrm{NY}$ ). Izabal: along Highway CA-9 near turnoff to Mariscos, Weaver 2186 (DUKE) ; between milla 49.5 and ridge 6 mi . from Izabal, Montaña del Mico, Steyermark 38534 (Gh, f). Suchitepequez: Finca Moca, Skutch 1568 ( $\mathrm{F}, \mathrm{US}$ ).

A very poorly collected species, Lisianthius meianthus is the only one in the genus definitely known to be an annual.

Lisianthius meianthus is similar to L. saponarioides and was combined with it by Williams $(1968,1969)$. As outlined in the key, L. meianthus differs from $L$. saponarioides in having the principal veins of the leaf (lower surface) and the calyx tube spiculate; an open loose inflorescence; pedicels at least 2 mm . long; calyx shorter and never equalling the ovary; and the corolla lobes shorter, and acute or short-acuminate. These differences are constant and diagnostic, and all of the available specimens are easily assignable to one taxon or the other.

Whether the two taxa, L. meianthus and L. saponarioides, are specifically or only varietally distinct is perhaps open to question. Until more complete collections are available for both, I prefer to treat $L$. meianthus and $L$. saponarioides as distinct species.

## II. Lisianthius section Lisianthius.

Subshrubs, shrubs, or slender trees, more rarely suffrutescent, perennial herbs, very rarely annual, glabrous or puberulous. Inflorescences terminal and axillary on primary and secondary shoots, or on specialized determinate flowering branches, of compound or apparently simple dichasia, more rarely reduced to single flowers. Corolla tubular or funnelform, the limb erect, spreading, or recurved, the tube yellow, or more rarely red or black. Stamens inserted in the lower $1 / 3-1 / 2$ of the corolla tube, the filaments of unequal length in a given flower, more than 10 mm . in length, usually much longer. Type species: L. longifolius L.

This, by far the larger section, may be divided into two subsections, based primarily on differences in habit.

## Key to the Subsections of Lisianthius section Lisianthius

Perennial, suffrutescent, very rarely annual, herbs, dying back to the woody base after each flowering season; plants monopodial, the main axis determinate; branching excurrent; inflorescences typically of compound dichasia, terminal and axillary on the primary and secondary shoots, never reduced to solitary axillary flowers; capsules ovoid or more rarely oblong-ellipsoid; principal foliage leaves sessile and usually clasping; corolla tube yellow, red, or black. Subshrubs, shrubs, or slender trees, persisting for more than a single season; plants not monopodial, the main axes branched above, at least in older plants, the branches indeterminate; branching seldom excurrent; inflorescences of apparently simple dichasia, rarely of compound dichasia and either axillary or axillary and terminal on determinate lateral shoots, occasionally reduced to
solitary, axillary flowers; capsules oblong-ellipsoid or fusiform; principal foliage leaves petiolate (or subsessile), never clasping; corolla tube yellow or very rarely red.
B. subsect. Fruticosi.

Lisianthius sect. Lisianthius subsect. Herbacei Weaver, subsect. nov.
Herbae perennae suffrutescentes, grossae monopodiales, raro herbae annuae, omnino glabrae. Ramificatio excurrens. Folia sessilia plerumque amplexicauliaque. Dichasia vulgo composita, terminalia axillariaque. Capsulae ovoideae vel raro oblongo-ellipsoideae. Species typica: L. nigrescens Cham. \& Schlecht.
$\angle 13801236$
The species in subsect. Herbacei, in contrast to those in subsect. Fruticosi, are suffrutescent herbs with terminal inflorescences. One of them, Lisianthius silenifolius, is possibly an annual. Six of the seven species are distributed in Mexico and Guatemala, the remaining one, L. silenifolius, in Cuba.

## Key to the Species of subsection Herbacei

A. Corolla tube dull red; corolla lobes obtuse and somewhat erose, very rarely acute; calyx fused for $1 / 3-1 / 2$ its length, fleshy, the lobes narrowly ovate, acute or short-acuminate, completely ecarinate; anthers purple.

> 9. L. viscidiflorus.
A. Corolla tube yellow or black; corolla lobes acuminate or more rarely acute; calyx fused for $1 / 4$ its length or less, not fleshy, the lobes lanceolate, longacuminate or more rarely acute, ridged or carinate abaxially; anthers yellow.
B. Corolla lobes ovate to squarish or suborbicular, less than twice as long as broad, $2-4 \mathrm{~mm}$. long, $1 / 10-1 / 8$ as long as the tube; corolla narrowly tubular; inflorescences congested or rarely diffuse, the dichasia often sessile and appearing pleiochasial; inflorescence branches strongly winged; stamens inserted on the corolla tube ca. $1 / 2$ the distance from the base to the apex.
8. L. brevidentatus.
B. Corolla lobes ovate-lanceolate or lanceolate, more than twice as long as broad, (3) $5-24 \mathrm{~mm}$. long, more than $1 / 5$ as long as the tube; corolla broadly tubular or funnelform; inflorescences diffuse, the dichasia never sessile or appearing pleiochasial; inflorescence branches terete or indistinctly 4 -angled, very rarely with narrow, scarious wings; stamens inserted on the corolla tube ca. $1 / 3$ of the distance from the base to the apex.
C. Corolla black; capsules ovoid or fusiform.
D. Capsules fusiform; inflorescence branches distinctly 4 -angled, the angles expanded into narrow, scarious wings, these minutely serrulate; inflorescences of apparently simple dichasia, very rarely of compound dichasia; leaves dull green and papillose on the upper surface, weakly clasping at the base; corolla lobes more than $1 / 2-3 / 4$ as long as the tube; stamens inserted below the apex of the calyx lobes; styles seldom surpassing the midpoint on the corolla lobes.
3. L. cuspidatus.
D. Capsules ovoid and often broadly so; inflorescence branches terete or indistinctly 4 -angled, the angles not serrulate or expanded into
narrow scarious wings; inflorescences of compound dichasia, rarely of apparently simple dichasia; leaves glossy and not papillose on the upper surface, strongly clasping at the base; corolla lobes usually $1 / 6-1 / 2$ as long as the tube, very rarely more than $1 / 2$ as long; stamens inserted above the apex of the calyx lobes; styles nearly always equalling or surpassing the corolla lobes.
4. L. nigrescens.
C. Corolla yellow; capsules ovoid and usually broadly so.
E. Foliage leaves rounded or truncate at the base, clasping; corolla lobes spreading or recurved; corolla tube not at all inflated, widest at the apex; styles not surpassing to conspicuously surpassing the corolla lobes.
F. Corolla lobes recurved, $11-20 \mathrm{~mm}$. long, more than $1 / 3$ as long as the tube; calyx $9-15 \mathrm{~mm}$. long; style equalling to conspicuously surpassing the corolla lobes; plants of Mexico.
5. L. oreopolus.
F. Corolla lobes spreading, $5.5-9 \mathrm{~mm}$. long, less than $1 / 3$ as long as the tube; calyx $6-11.5 \mathrm{~mm}$. long; style never surpassing the corolla lobes; plants of Cuba. ......... 6. L. silenifolius.
E. Foliage leaves narrowed at the base, not clasping; corolla lobes erect; corolla tube slightly inflated, widest below the apex; styles always surpassing the corolla lobes.
7. L. quichensis.
3. Lisianthius cuspidatus Bertol. Nov. Comm. Bonon. 4: 408. t. 37. 1840 (as Lisianthus). Type. Guatemala, without exact locality, Velásquez, presumably at Bologna (bolo) but not seen.
Leianthus cuspidatus (Bertol.) Griseb. in DC. Prodr. 9: 82. 1845.
Lisianthus nigrescens var. cuspidatus (Bertol.) L.O. Wms. Fieldiana Bot. 31:
408. 1968.
Rather coarse, perennial herbs. Stems $0.7-3 \mathrm{~m}$. tall and to 1 cm . in diameter, erect or ascending, green or often purplish, terete below and 4 -angled above, the angles expanded into narrow, scarious wings. Leaves ( 0.9 ) $2.4-10.1 \mathrm{~cm}$. long and ( 0.1 ) $0.4-2.7 \mathrm{~cm}$. broad, firmly membranaceous, the margins minutely papillose, the principal foliage leaves lanceolate or more rarely ovate-lanceolate, long-acuminate, narrowly tapered to rounded at the base, weakly clasping, the base usually less than twice the diameter of the stem; upper leaves and those on the secondary branches lanceolate, the bases rounded or cuneate, short-petiolate or sessile but not clasping. Inflorescences composed of dichasia, usually $2-3$-flowered and appearing simple, rarely 1 -compound, long-pedunculate; inflorescence branches strongly 4 -angled, elongate and the inflorescences appearing loose and open. Flowers drooping, long-pedicellate, the pedicels $0.5-2.2 \mathrm{~cm}$. long; bracteoles subulate, scarious. Calyx $10-14.5 \mathrm{~mm}$. long, fused for $1 / 6-1 / 5$ its length; the lobes $8-12 \mathrm{~mm}$. long, lanceolate, long-acuminate, scariousmargined, ridged abaxially; the tube $1.5-2.5 \mathrm{~mm}$. long. Corolla funnelform, uniformly black, $4-5.6 \mathrm{~cm}$. long; the tube $2.6-3.3 \mathrm{~cm}$. long and $7-8 \mathrm{~mm}$. in diameter at the apex; the lobes $1.4-2.4 \mathrm{~cm}$. long and $3-5 \mathrm{~mm}$. broad, spreading and slightly recurved at the tips, lanceolate or oblong-
lanceolate, long cuspidate-acuminate, $1 / 2-3 / 4$ as long as the tube. Stamens inserted on the corolla tube ca. $1 / 3$ of the distance from the base to the apex; filaments $1.8-2.9 \mathrm{~cm}$. long, only slightly surpassing the corolla tube; anthers oblong, 2-2.5 mm. long and $1-1.5 \mathrm{~mm}$. broad. Style $2.1-2.9 \mathrm{~cm}$. long, surpassing the corolla tube but not reaching to more than the midpoint on the corolla lobes; stigma peltate. Capsule fusiform, beaked, $1.1-1.5 \mathrm{~cm}$. long, not including the $1-2 \mathrm{~mm}$. long beak, and $3-5 \mathrm{~mm}$. in diameter; the marcescent corolla seldom persisting until the seeds are shed. Flowering: Aug.-Nov.

Distribution: In pine forests about 2000 meters elevation in central Guatemala (MAP 2).

## Specimens examined

Guatemala: without locality, Bernoulli 320 (Ny); without locality, Bernoulli © Cario 1804 (s); San Martín, Johnston s.n. (f). El Progresso: Sierra de las Minas, Finca el Bucaral, 14 km . from the highway from Salamá to El Rancho, Hawkes, Hjerting \& Lester 1968 (F, S) ; between Calera and middle slopes of quebradas on Volcán Siglo, Steyermark 43001 (f, ny). Guatemala: in the Sapoie barranca near Guatemala, Hayes s.n. (GH); San Juan Sacatepéquez, Lewis 895 (F). Quiché: without locality, Aguilar 1400 (F).

Lisianthius cuspidatus is a poorly collected species; only eleven specimens were available for study. It is quite similar to L. nigrescens var. chiapensis, especially in its black corollas.

I have not seen Bertoloni's type, or any authentic material known to have been in his possession when the original description was made. However, his diagnosis and the plate accompanying it are perfectly adequate and leave no doubt as to the plant he had at hand.

The relationship of Lisianthius cuspidatus to L. nigrescens, the other black-flowered species, has been the subject of considerable debate since L. cuspidatus was originally described. Grisebach (1845) and Robinson (1910) considered the two as distinct species. In fact Grisebach even placed them in different genera, cuspidatus in Leianthus and nigrescens in Petasostylis. Hemsley (1882), Kuntze (1891), and Perkins (1902) reduced L. cuspidatus to synonymy under L. nigrescens. Williams (1968, 1969) treated L. cuspidatus as a variety of L. nigrescens. His L. nigrescens var. cuspidatus, as discussed later, included plants here treated as $L$. nigrescens var. chiapensis and L. cuspidatus.

Williams (1968) felt that the characters used by Robinson (1910) to separate Lisianthius cuspidatus from L. nigrescens, i.e. the subcuneate leaf bases, the more deeply lobed corolla, and the corolla lobes distinctly surpassing the style "begin to lose their significance with more adequate collections." My observations would lead me to disagree with Williams; although there is a small overlap in lobe/tube ratio between L. cuspidatus and L. nigrescens (var. chiapensis), the other characters hold quite well. In addition the 3 -flowered dichasia, serrulate stem angles, dull-textured, papillose leaves, and especially the fusiform capsules clearly set L. cuspi-


Maps 1-3. Distribution of Lisianthius species. Map 1, L. meianthus (dots), L. saponarioides (triangles). MaP 2, L. cuspidatus (triangles), L. nigrescens var. nigrescens (dots), L. nigrescens var. chiapensis (half-circles). Map 3, L. brevidentatus var. brevidentatus (dots), L. brevidentatus var. collinus (half-circle), L. oreopolus (squares), L. quichensis (triangles).
datus apart from L. nigrescens. I think that the differences between the two taxa are of sufficient magnitude to warrant maintaining L. cuspidatus as a distinct species.

## 4. Lisianthius nigrescens Cham. \& Schlecht. Linnaea 6: 388. 1831 (as Lisianthus).

Coarse, perennial herbs. Stems $0.5-2 \mathrm{~m}$. tall and to 2 cm . in diameter, erect or ascending, green except at base, terete below but indistinctly 4 -angled above. Leaves firmly membranaceous, the lateral veins prominent, the principal foliage leaves $3-19 \mathrm{~cm}$. long and $1-6.4 \mathrm{~cm}$. broad, ovate-lanceolate or elliptic or sometimes rather oblong or even somewhat pandurate, gradually or abruptly acuminate, the bases truncate and auriculate, distinctly clasping, much broader than the stem, the upper leaves and those on the secondary branches smaller, lanceolate or ovate, rounded at the base, short-petiolate or sessile but not clasping. Inflorescences of long-pedunculate dichasia, these 1 to 4 times compound, the lateral branches often scorpioid, or sometimes reduced and appearing simple; inflorescence branches terete or indistinctly 4 -angled, elongate with the dichasia appearing loose and open. Flowers horizontal or nodding, the pedicels ( 0.3 ) $0.6-3.0(4.0) \mathrm{cm}$. long; bracteoles subulate, scarious. Calyx (6) 7.5-13.5 mm. long, fused for $1 / 8-1 / 4$ its length; the lobes (4.5)7-11 mm . long, and $1.5-2.5 \mathrm{~mm}$. broad, lanceolate, long-acuminate, scariousmargined, carinate or at least ridged abaxially. Corolla funnelform, uniformly black, glossy outside and dull within, $3.2-5.4 \mathrm{~cm}$. long; the tube $2.7-3.9 \mathrm{~cm}$. long and $4-7 \mathrm{~mm}$. in diameter at the apex; the lobes $0.5-$ $1.6(2.0) \mathrm{cm}$. long and $2-4 \mathrm{~mm}$. broad, $1 / 6-1 / 2(3 / 5)$ as long as the tube, lanceolate or ovate-lanceolate, gradually short-acuminate or rather long cuspidate-acuminate, spreading, recurved only at the tips if at all. Stamens inserted on the corolla tube ca. $1 / 3$ of the distance from the base to the apex; filaments $2.1-3.4 \mathrm{~cm}$. long, exceeding the corolla tube and frequently the lobes, the longest ones equalling the style or not; anthers $2-3.5 \mathrm{~mm}$. long and $1-2 \mathrm{~mm}$. broad, broadly oblong, truncate or obtuse at the apex, the connective very slightly if at all exserted. Ovary ovoid; style $2.1-4.5 \mathrm{~cm}$. long, exserted, not at all to conspicuously exceeding the corolla lobes. Capsules ovoid and frequently broadly so, $7-13 \mathrm{~mm}$. long and $3-6 \mathrm{~mm}$. broad; the marcescent corolla strongly persisting until after the seeds are shed.

## Key to the Varieties

Corolla lobes 9 mm . or less in length, gradually short-acuminate; filaments, at least the longest ones, usually surpassing the corolla lobes; styles always surpassing the corolla lobes, and often conspicuously so.

4a. L. nigrescens var. nigrescens.
Corolla lobes $9-20 \mathrm{~mm}$. long, but usually more than 11 mm ., long cuspidateacuminate; filaments never surpassing the corolla lobes; styles at most equal-
ling or barely surpassing the corolla lobes.
4b. L. nigrescens var. chiapensis.
4a. Lisianthius nigrescens Cham. \& Schlecht. var. nigrescens.
Lisianthius nigrescens Cham. \& Schlecht. Linnaea 6: 388. 1831 (as Lisianthus). $\checkmark$ Type. Mexico. Veracruz: in sylvis Papantla, Schiede (hal!).
Leianthus nigrescens (Cham. \& Schlecht.) Griseb. Gen. \& Sp. Gent. 199. 1839 [1838].
Petasostylis nigrescens (Cham. \& Schlecht.) Griseb. in DC. Prodr. 9: 71. 1845.

Corolla 3.2-4.6 cm. long, the lobes lanceolate, gradually short-acuminate, $5-8(9) \mathrm{mm}$. long and $2-3 \mathrm{~mm}$. broad, $1 / 6-1 / 4$ as long as the tube. Filaments $2.1-3.3 \mathrm{~cm}$. long, at least the longest ones in each flower equalling or surpassing the corolla lobes. Styles $2.7-3.5(4.2) \mathrm{cm}$. long, exceeding the corolla lobes (often conspicuously), always surpassing the styles. Flowering: Jan.-Aug. Chromosome number: $n=18$.

Distribution: From 800 to 1400 meters on dry rocky hillsides and on roadside banks in Veracruz, Hidalgo, and Oaxaca, Mexico (Map 2).

## Representative collections

Mexico: without exact locality, Sessé, Mocino, et al. 5097 (f). Hidalgo: alrededores de Huejutla, Maury 6013 (mexu). Oaxaca: I km. e. of Tonaguilla, Schultes 591 (GH); vicinity of Choapan, Nelson 893 (GH, US). Veracruz: Yotoa, Galeotti 1473 (F, GH, NY, US); Orizaba, Purpus 1182 (F, GH, MO, NY, uc); Cerro de Escamela, on road to Ojo de Agua, just e. of Orizaba, Weaver 2134 (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); Papantla, Liebmann 10787 (GH, F, MO, S, UC, US); Zacuapan, Purpus 5994 (GH, MO, UC); from El Rancho de Sacalica to El Municipio de Zongolica, Santos 2075 (Місн); Córdoba, Miranda 632 (mexu).

Williams (1969) considered Cook 65 (US) the only known Guatemalan specimen that represents the typical variety. This specimen is intermediate in character between var. nigrescens and var. chiapensis, but is closer to the latter especially in the shape of the corolla lobes and the fact that the style does not exceed the corolla lobes.

4b. Lisianthius nigrescens Cham. \& Schlecht. var. chiapensis Weaver, var. nov. Type. Mexico. Chiapas: 7.8 mi . e. of Chiapa de Corzo on Highway 190, Weaver 2168 (duke!).
Habitu et foliis varietati typicae similis, differt lobis corollae longioribus, longe cuspidato-acuminatis, longitudine vulgo $1 / 2$ tubi aequantibus, et stylum vix vel paulo superantibus.

Corolla $3.7-5.4 \mathrm{~cm}$. long, the lobes lanceolate or ovate-lanceolate, rather long cuspidate-acuminate (9) $11-16(20) \mathrm{mm}$. long and $3-4 \mathrm{~mm}$. broad, $3 / 10-1 / 2(3 / 5)$ as long as the tube. Filaments $2.3-3.4 \mathrm{~cm}$. long, never surpassing the corolla lobes, sometimes equalling the style. Styles 2.5-4.5 cm . long, at most equalling or very slightly surpassing the corolla lobes. Flowering: Apr.-Oct. Chromosome number: $n=18$.

Distribution: From 500-1800 meters in pine and/or oak forests, secondary scrub, and along roadsides in Chiapas, Mexico, and Huehuetenango, Guatemala (MAP 2).

## Representative Collections

Mexico. Chiapas: without exact locality, Ghiesbreght 702 (вм, GH, mo, ny) ; 7.8 mi . e. of Chiapa de Corzo on Highway 190,'Weaver 2168 (A, BM, DS, F, iJ, ll, mich, mo, ny, s, uc, us; isotypes); along Mexican Highway 190 in the Zinacantán paraje of Muctajoc, Municipio de Ixtapa, Breedlove 11839 (ds, mexu) ; at junction of Mexican Highway 190 and road to Bochil \& Simojovel, Municipio de Ixtapa, Breedlove 9600 (Ds, F) ; ca. 30 mi . e. of Tuxtla Gutiérrez, Webster, Miller \& Miller 11699 (duke, mich, mexu); $17 \mathrm{~km} . \mathrm{n}$. of Tuxtla Gutiérrez along road to El Sumidero, Municipio de Tuxtla Gutiérrez, Breedlove 14006 (DS, LL, MICH); along Mexico 190 at paraje Granadilla, Municipio de Zinacantán, Laughlin 1074 (Ds, LL); in paraje 'Apas, Municipio de Zinacantán, Laughlin 1213 (DS, LL, MEXU); 2 mi. sw. of Aguacatenango junction on road to Las Rosas, Weaver 2183 (A, BM, DS, duke, F, IJ, LL, MICH, MO, NY, S, UC, us); at the junction of the Pan American Highway and the road to Soyala, Breedlove 6571 (ds, MIcH); between San Ricardo \& Ocozucuantla, Nelson 2986 (us) ; along Mexican Highway 190, 7 mi. s. of La Trinitaria, Municipio de La Trinitaria, Breedlove 10038 (ds, ll, mexu). Guatemala. Huehuetenango: Finca Candelaria, Cook 65 (US); between San Ildefonso Ixtahuacan and Cuilco, Steyermark 50682 ( $\mathrm{F}, \mathrm{US}$ ).

Lisianthius nigrescens is by far the most common of the Mexican species, rather frequently encountered on roadside banks, especially in the state of Chiapas. With its black corollas, ovoid capsules, and sessile leaves with broad, clasping bases, L. nigrescens is easily distinguishable from most of the other species of Lisianthius. The only other species with black flowers is L. cuspidatus, which differs from L. nigrescens in that its leaves, though sessile and more or less clasping, are papillose above and on the margins and the bases are usually narrowed and not auriculate; its corollas are more deeply lobed; and its capsules are fusiform. L. oreopolus resembles $L$. nigrescens strongly in aspect, vegetative characters, and capsule shape, but differs in having uniformly yellow corollas, with the tube expanding more or less abruptly above the basal constriction, and the lobes strongly recurved.

Williams $(1968,1969)$ treated L. cuspidatus Bertol. and L. oreopolus Robins. as varieties of L. nigrescens. He pointed out (1968) that var. cuspidatus differs from typical L. nigrescens in having larger and more deeply lobed corollas, but warned that, with more adequate collections, the varieties may eventually be shown to be the same. Williams (1968) considered var. oreopolus to be almost identical with var. cuspidatus except for its yellow corollas. In this treatment L. oreopolus, and L. cuspidatus, have been retained as full species.

Williams apparently misinterpreted Lisianthius cuspidatus. He relied too heavily on the degree of corolla lobing as the primary character for separating it from L. nigrescens; he thought the differences in the leaf
bases were insignificant and was apparently unaware of the difference in capsule shape as well as the other characters listed above.

Bertoloni described Lisianthius cuspidatus as having oblong capsules. However, Williams (1969) included in his var. cuspidatus plants with the oblong (or fusiform) capsule of L. cuspidatus and the broadly ovoid capsules of L. nigrescens. According to Williams (loc. cit.) his var. cuspidatus is distributed in the Mexican state of Chiapas and the Guatemalan departments of Huehuetenango, Guatemala, Chimaltenango, El Progresso, and Quiché. The plants from the last four Guatemalan departments are characterized by having fusiform capsules and therefore belong to L. cuspidatus. The Mexican plants and those from Huehuetenango are characterized by having ovoid capsules and therefore belong to L. nigrescens.

Williams' var. cuspidatus is therefore a heterogeneous taxon, including elements of both L. nigrescens and L. cuspidatus. His figure of var. cuspidatus (1969, p. 325, figure 88) represents both elements, although this fact is not particularly obvious from the drawing. Figure 88-A, drawn from Steyermark 50682 (F), represents L. nigrescens, and figure 88-C, drawn from Hawkes, Hjerting \& Lester 1968 ( F ), represents L. cuspidatus.

The specimens of Lisianthius nigrescens from Chiapas, Mexico, and Huehuetenango, Guatemala, mostly included in L. nigrescens var. cuspidatus by Williams $(1968,1969)$, differ in a number of ways from typical $L$. nigrescens from the Mexican states of Veracruz, Hidalgo, and Oaxaca. The flowers are generally larger, the corolla lobes are longer in absolute length and longer in relation to the tube, and the styles only equal or very barely exceed the corolla lobes. Although there is a small amount of overlap in these critical characters, the two forms are readily distinguishable in most cases. On the basis of available collections, it appears that their ranges are distinct. These two forms are not perfectly differentiated but the tendencies are strong indeed, and I think failure to draw a formal distinction between them would be taxonomically unsound. Therefore I have designated the large-flowered populations from Chiapas and Huehuetenango as a new variety of L. nigrescens. Since the new variety is nearly restricted to the state of Chiapas, I have named it $L$. nigrescens var. chiapensis.

Hemsley (1882) and Perkins (1902) cited an Oersted specimen (s.n.), supposedly of Lisianthius nigrescens, from Pacaca, Costa Rica. Both authors included L. cuspidatus in their concept of L. nigrescens. I have not seen the Oersted specimen, nor any other specimen of a black-flowered species from Costa Rica, and I could not make even a reasonable guess as to its true identity.
5. Lisianthius oreopolus Robins. Proc. Am. Acad. 45: 398. 1910 (as Lisianthus). Type: Mexico. Chiapas: without exact locality, Ghiesbreght 702 bis (GH!).
Lisianthus nigrescens var. oreopolus (Robins.) L.O. Wms. Fieldiana Bot. 31: 408. 1968.

Coarse, perennial herbs. Stems $1-2 \mathrm{~m}$. tall and to 2 cm . in diameter, erect, green except at the base, terete below but indistinctly 4 -angled above. Leaves firmly membranaceous, the lateral veins prominent, 2.521.4 cm . long and $0.5-4.9 \mathrm{~cm}$. broad, the principal foliage leaves sessile, lanceolate or more or less oblong, short-acuminate, the bases truncate and auriculate, broad, distinctly clasping, much broader than the stem; upper leaves and those on the secondary branches smaller and narrower, the bases narrower and less distinctly or not at all clasping. Inflorescences of long-pedunculate dichasia, these 1-4 times compound, the lateral divisions often scorpioid, or rarely appearing simple; inflorescence branches terete or indistinctly 4 -angled, elongate and with the inflorescences loose and open. Flowers horizontal or nodding, the pedicels $3-9.5 \mathrm{~mm}$. long; bracteoles subulate, scarious. Calyx $9-15 \mathrm{~mm}$. long, fused for $1 / 8-1 / 4$ its length; the lobes $6.5-12.5 \mathrm{~mm}$. long and $1.5-2.5 \mathrm{~mm}$. broad, lanceolate, long acuminate, scarious-margined, indistinctly carinate abaxially; the tube $1.5-3 \mathrm{~mm}$. long. Corolla 4-6 cm. long, tubular-funnelform, uniformly bright yellow; the tube $2.7-4.1 \mathrm{~cm}$. long and $5-9 \mathrm{~mm}$. in diameter at the apex; the lobes $11-20 \mathrm{~mm}$. long and $3-5 \mathrm{~mm}$. broad, $(1 / 3) 1 / 2-2 / 3$ as long as the tube, conspicuously recurved, lanceolate or oblong-lanceolate, long cuspidate-acuminate. Stamens inserted on the corolla tube ca. $1 / 3$ of the distance from the base to the apex. Filaments $2.5-5.1 \mathrm{~cm}$. long, at least the longest ones surpassing the corolla lobes, very rarely equalling the style; anthers $2-3.5 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, broadly oblong, the apex acutish, the connective slightly exserted. Ovary ovoid; style $3.7-6.2 \mathrm{~cm}$. long, exceeding the corolla lobes or rarely only equalling them; stigma peltate. Capsules broadly ovoid, short-beaked, $8-12 \mathrm{~mm}$. long and $5-7 \mathrm{~mm}$. broad; the marcescent corolla persisting until the seeds are shed. Flowering: May-Aug. Chromosome number: $n=18$.

Distribution: From 1000 to 1800 meters in dry or rather moist pine or mixed forests or on roadside banks in eastern and southern Chiapas, Mexico (Map 3).

## Representative collections

Mexico. Chiapas: slopes along the Ala Shashib River below Habenal, paraje of Mahben Chauk, Municipio de Tenejapa, Breedlove 6477 (Ds, F); in the paraje of Mahosik, Municipio de Tenejapa, Breedlove 14852 (Ds, DUKE); near schoolhouse of Pokolum, paraje of Sibanilhá, Municipio de Tenejapa, Breedlove 11015 (DS, F, LL, MICH); in the paraje of Kulak'tik, Municipio de Tenejapa, Breedlove 10996 (Ds, $\mathbf{F}$, LL, MICH); in the barrio of Ti Ha', paraje of Mahbenchoak, Municipio de Tenejapa, Alush Shilom Ton 2267 (Duke); near the Colonia Choro, Municipio de San Pedro Chenálho, Alush Shilom Ton 2457 (DUKE); $3.1 \mathrm{mi} . \mathrm{n}$. of Bochil on road to Simojovel, Weaver 2174 (A, BM, ds, duke, f, iJ, Ll, MiCH, MO, Ny, S, UC, US).

Lisianthius oreopolus has a rather restricted distribution, and has until recently been poorly collected. With its numerous, large yellow flowers it is a very striking and handsome plant. With its long, recurved corolla
lobes, ovoid capsules, and sessile, clasping leaves, it is not likely to be confused with any other yellow-flowered member of the genus.

In the original description of Lisianthius oreopolus, Robinson noted that the new species resembled $L$. nigrescens in habit but differed in its yellow corollas with longer and more spreading lobes. Williams (1968) reduced $L$. oreopolus to varietal status under $L$. nigrescens, stating that it is an almost exact duplicate of his L. nigrescens var. cuspidatus in corolla size and lobing. L. oreopolus is quite similar to L. nigrescens, especially var. chiapensis, but its flowers tend to be larger in all ways and the corolla is in general more deeply lobed. However, there is a complete overlap in all calyx and corolla measurements between the two species. The most striking difference between the two species is the color of the corolla. In addition the corolla tube of $L$. oreopolus is more or less abruptly expanded above the basal constriction and the lobes are conspicuously recurved, while the corolla tube of $L$. nigrescens is gradually expanded above the basal constriction and the lobes are merely spreading.

It seems possible that the breeding systems of the two taxa are quite different. The difference in corolla color is very striking and very probably has a marked effect on the type of pollinator attracted to the respective taxa. In addition, the anthers of $L$. oreopolus are longer exserted than those of $L$. nigrescens. The corolla lobes of $L$. nigrescens are merely spreading and the anthers are generally held within them. Access to the throat of the corolla is blocked by the anthers, and a bee seeking nectar would certainly brush against them in the process. The corolla lobes of $L$. oreopolus are recurved and the filaments project rather far from the throat of the corolla; access to the throat of the corolla is not blocked by the anthers. Unfortunately, nothing is known about the pollinators of these plants.
At any rate, Lisianthius oreopolus does differ consistently from $L$. nigrescens, even though the most striking difference, the color of the corolla, may be due to only a single gene difference. Until more is known of the biology of these plants, particularly their pollination systems and crossability, I prefer to treat them as distinct species.
6. Lisianthius silenifolius (Griseb.) Urb. Symb. Antill. 3: 334. 1902 (as Lisianthus). Type. Western Cuba, Wright, presumably at Göttingen (GOET) but not seen.

## Leianthus silenifolius Griseb. Cat. PI. Cub. 180. 1866.

Rather coarse, annual (?) herbs. Stems $0.5-1 \mathrm{~m}$. tall and to 1 cm . in diameter, erect, green above and gray-brown below, terete. Leaves membranaceous, the lateral veins prominent; the principal foliage leaves sessile, $3.0-13.3 \mathrm{~cm}$. long and $1.2-4.5 \mathrm{~cm}$. broad, oblong-lanceolate to lanceolate or more rarely elliptic, gradually acuminate at the apex, the base rounded or truncate, more or less auriculate, clasping; upper leaves and those on the secondary branches smaller, lanceolate or ovate-lanceolate, rounded or cuneate at the base, subsessile or short-petiolate, not clasping.

Inflorescences of pedunculate dichasia, these typically once-compound, but rarely 2-4 times compound, and then the lateral branches often scorpioid, or occasionally apparently simple; inflorescence branches terete or indistinctly angled. Flowers nodding, the pedicels relatively stout, $3-10 \mathrm{~mm}$. long; bracteoles subulate, scarious. Calyx $6-11.5 \mathrm{~mm}$. long, fused for $1 / 8-1 / 5$ its length; the lobes $5-10 \mathrm{~mm}$. long and $1.5-2.5 \mathrm{~mm}$. broad, lanceolate, acuminate, scarious-margined, ridged abaxially; the tube $1-1.5 \mathrm{~mm}$. long. Corolla $2.7-4.0 \mathrm{~cm}$. long, tubular-funnelform, uniformly bright yellow; the tube $2.2-3.1 \mathrm{~cm}$. long and 4-6 mm. in diameter at the apex; the lobes $5.5-9 \mathrm{~mm}$. long and $2-3 \mathrm{~mm}$. broad, $2 / 10-3 / 10$ as long as the tube, spreading, ovate-lanceolate, short-acuminate. Stamens inserted on the corolla tube ca. $1 / 3$ of the distance from the base to the apex; filaments $1.5-2.7 \mathrm{~cm}$. long, exceeding the corolla tube, the longest ones usually equalling or nearly equalling the style; anthers $1-2 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, broadly oblong, almost square, truncated at the apex. Ovary ovoid; style $1.8-3.0 \mathrm{~cm}$. long, surpassing the corolla tube; stigma peltate. Capsule ovoid, usually broadly so, short-beaked, 5-11 mm . long, not including the 1 mm . long beak, and 3-6 mm . in diameter; calyx in fruit usually equalling or surpassing the capsule, rarely only $2 / 3$ as long; marcescent corolla usually but not always persisting until the seeds are shed. Flowering: Jan.-Oct.

Distribution: On limestone or other soils, in pinelands, grassy slopes, or on cliff faces in western Cuba (Pinar del Rio) (Map 8).

## Representative collections

Cuba: without exact locality, Wright s.n. (gH; possibly an isotype). Pinar del Rio: Bahia Honda, Loma de Cajálbana, Ekman 12722 (s); pinelands, Cajálbana, Alain \& Acuña 1106 (Ny, US); base of Sierra Guane, Shafer 10548 (ny); San José de Sagua to San Marcos, Shafer 11967 (ny, us); vicinity of Sumidero, Shafer 13389 (bm, f, US, ny); Loma Pelada de Buenavista, Cayajabos, León 13204 (GH); Sierra de los Organos, hills around Arr. Rosario, w. of Cayajabos, Ekman 12970 (s).

Lisianthius silenifolius is the only member of subsect. Herbacer found in the Greater Antilles. It is easily distinguishable from L. glandulosus (sect. Lisianthius subsect. Fructicosi), the only other Cuban species, by its sessile, clasping leaves, its terminal inflorescences, and its ovoid capsules. In addition, L. silenifolius is restricted to Pinar del Rio Province in western Cuba, while L. glandulosus is found only in Oriente Province on the eastern end of the island.

No unquestionably authentic material of Lisianthius silenifolius has been seen. However, the characters described in the original diagnosis leave no doubt as to the plant Grisebach had at hand. In addition, no other species is found in western Cuba. A Wright specimen of L. silenifolius, collected between 1860 and 1864, is present in the collections at the Gray Herbarium. This specimen, which I have seen, is a possible isotype.
7. Lisianthius quichensis Donn. Sm. Bot. Gaz. 52: 51. 1911 (as Lisianthus). Type. Guatemala. Quiché: Río Negro, Heyde \& Lux 2921 (US!).

Coarse, perennial herbs. Stems $0.8-2 \mathrm{~m}$. tall and to 1 cm . in diameter, erect or ascending, green, terete or nearly so. Leaves firmly membranaceous, the lateral veins prominent; principal foliage leaves sessile, (4.2) $6.8-21.5(24) \mathrm{cm}$. long and (1.2) 2.0-5.7 cm. broad, broadest at or above the middle, narrowly elliptic or somewhat oblanceolate, long-attenuate and narrow at the base; upper leaves and those on the secondary branches smaller, $1.2-10.5 \mathrm{~cm}$. long and ( 0.6 ) $1.5-3.3 \mathrm{~cm}$. broad, lanceolate, cuneate, short-petiolate. Inflorescences of long-pedunculate dichasia, these 1 to 3 times compound and the lateral branches often scorpioid, or occasionally appearing simple; inflorescence branches terete, elongate and the inflorescences loose and open. Flowers nodding or horizontal, the pedicels $2-13$ mm . long; bracteoles subulate, scarious. Calyx (6) $7.5-13 \mathrm{~mm}$. long, fused for ca. $1 / 5$ of its length; the lobes (4.5) 6-11 mm. long and $1.5-2.5 \mathrm{~mm}$. broad, lanceolate or subulate-lanceolate, long-acuminate, scarious-margined, ridged or indistinctly carinate; the tube $1.5-3 \mathrm{~mm}$. long. Corolla (2.6) 3-4.2 cm . long, tubular, uniformly yellow; the tube (2.3)2.7-3.5 cm . long and $3-7 \mathrm{~mm}$. in diameter at the broadest point, somewhat inflated in the midparts and constricted slightly at the apex; the lobes $3-6(8) \mathrm{mm}$. long and $1.5-3 \mathrm{~mm}$. broad, more than 2 -times as long as broad, $1 / 8-1 / 4$ as long as the tube, erect, not at all spreading, ovatelanceolate to almost triangular, gradually acuminate. Stamens inserted on the corolla tube $1 / 3-2 / 5$ of the distance from the base to the apex; filaments $1.8-3.4 \mathrm{~cm}$. long, at least the longest and frequently all exceeding the corolla lobes, the longest one usually equalling or slightly exceeding the style; anthers $1.5-2.5 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, oblong, truncate or rounded at the apex, the connective sometimes very slightly exserted. Ovary ovoid; style $2.1-4 \mathrm{~cm}$. long, always surpassing the corolla lobes, often conspicuously; stigma peltate. Capsule broadly ovoid, $6-12 \mathrm{~mm}$. long and $3.5-6 \mathrm{~mm}$. broad; calyx in fruit equalling or surpassing the capsule; the marcescent corolla persisting until long after the seeds are shed. Flowering: Mar.-Sept. Chromosome number: $n=18$.

Distribution: From 900 to 1600 meters on open, rocky slopes, in secondary scrub, and on roadside banks in eastern Chiapas, Mexico, and north central Guatemala (MAP 3).

## Representative collections

Mexico. Chiapas: Los Lagos, 3 mi . nw. of Rancho San José ( 34 mi . se. of Comitán), s. shore of Lake Montebello, Carlson 1835 (F, MICH, US); La Trinitaria at Lake Tsikaw on the Guatemalan border, 30 mi . e. of La Trinitaria, Breedlove 10062 (Ds, duke, F); Ocosingo, near Laguna Ocotal Grande, ca. $25-30 \mathrm{~km}$. se. of Monte Líbano, Dressler 1626 (bM, F, GH, MEXU, Mich, ny, Uc, US); San Carlos á Santa Rita, Miranda 7130 bis (mexu). Guatemala: Alta Verapaz: along Quiché Highway about 12 km . w. of San Cristóbal, Standley 89711 (F); 7 mi. w. of San Cristóbal Verapaz on Highway 7W, Weaver

2177 (A, BM, DUKE, F, LL, MICH, MO, NY, US) ; 3.5 mi . w. of San Cristóbal Verapaz on Highway 7W, Weaver 2178 (A, BM, Ds, dUKe, f, iJ, Ll, Mich, mo, ny, s, uc, us). Huehuetenango: between Las Palmas and Chaculá, Sierra de los Cuchumatánes, Steyermark 51743 ( F ) ; vicinity of Maxbal, ca. 17 mi . n. of Barillas, Sierra de los Cuchumatánes, Steyermark 48695 (F). Quiché: Río Negro, Heyde \& Lux 2921 (GH, MO, Ny, Us; isotypes).

Lisianthius quichensis is a rather uncommon plant and until recently has been infrequently collected. Its closest relatives are probably $L$. nigrescens and L. oreopolus. It differs from both of these species by having leaves which are narrowed at the base and not clasping. It differs further from $L$. nigrescens in its yellow corollas, inflated corolla tube, and generally shorter corolla lobes. From L. oreopolus, L. quichensis differs also in its much shorter, erect corolla lobes.

Lisianthius quichensis has frequently been confused with L. saponarioides Cham. \& Schlecht., a very dissimilar plant. Perkins (1902) referred to L. saponarioides the collection (Heyde \& Lux 2921) later designated as the type of L. quichensis, a fact noted by Williams (1969), and discussed in this treatment under L. saponarioides.

## 8. Lisianthius brevidentatus (Hemsl.) O. Ktze. Rev. Gen. Pl. 2: 429. 1891.

Coarse, perennial herbs. Stems $0.5-1.5 \mathrm{~m}$. tall and to 1 cm . in diameter, terete below but 3-4-angled or -winged above, green. Leaves sessile, clasping, $3.2-20.4 \mathrm{~cm}$. long and $1.2-5.1 \mathrm{~cm}$. broad, the principal foliage leaves narrowly oblong-elliptic with a tendency to be widest slightly above the middle, broadly attenuate at the base, the apices acuminate or cus-pidate-acuminate, the upper leaves and those on the lateral branches lanceolate to ovate or more rarely elliptic, rounded or subcordate at the base, sessile but not clasping, or short petiolate. Inflorescences usually of dichasia, these 1-4 times compound, borne singly or in groups of 3 or more rarely 5 , with the terminal one often sessile or nearly so and the whole unit appearing pleiochasial, the ultimate branches monochasial and resembling secund racemes; inflorescence branches short and the dichasia or groups of dichasia consequently dense and compact, or elongate and the dichasia loose and open, terete or indistinctly angled or more commonly $2-3$-winged, if 3 -winged, 2 of the wings decidedly broader than the third, the wings to 1 mm . broad. Flowers sessile or the pedicels to 3 mm . long, the bracteoles scarious, subulate, $1-3 \mathrm{~mm}$. long and $0.5-1$ mm . broad. Calyx $6-9.5 \mathrm{~mm}$. long, fused for $1 / 5-1 / 3$ its length; the lobes $4.5-6 \mathrm{~mm}$. long and $1-2 \mathrm{~mm}$. broad, lanceolate, long acuminate, ridged abaxially, scarious-margined; the tube $1.5-3 \mathrm{~mm}$. long. Corolla tubular, somewhat fleshy, $2.4-3.4 \mathrm{~cm}$. long; the tube yellow, $2.2-3.0 \mathrm{~cm}$. long and $3-4 \mathrm{~mm}$. broad, conspicuously white-striate at base, especially with age; the lobes $2-4 \mathrm{~mm}$. long and $2-3 \mathrm{~mm}$. broad, greenish-yellow, spreading or slightly recurved at the apex, squarish to suborbicular or ovate, abruptly short-acuminate, auriculate at the base or not. Stamens
inserted on the corolla tube just below the middle, well above the apex of the calyx lobes; filaments $1.4-1.7 \mathrm{~cm}$. long, equalling or barely exceeding the corolla tube; anthers $2-3.5 \mathrm{~mm}$. long and ca. 1 mm . broad, narrowly oblong, $2-3$ times as long as broad. Style $2.3-3.3 \mathrm{~cm}$. long, surpassing the corolla lobes in mature flowers, always exceeding the stamens in relative position; stigma peltate. Capsule oblong-ellipsoid, $8-13 \mathrm{~mm}$. long and $3-5 \mathrm{~mm}$. in diameter; the persistent calyx $2 / 3$ to nearly as long as the capsule; the marcescent corolla strongly persisting.

## Key to the Varieties

Inflorescence branches contracted and the dichasia or groups of dichasia appearing dense and compact; corolla lobes squarish to suborbicular, about as broad as long, auriculate at the base; calyx fused for $1 / 4-1 / 3$ its length.
a. var. brevidentatus.

Inflorescence branches elongate and the dichasia or groups of dichasia appearing loose and open; corolla lobes ovate, longer than broad, not auriculate at the base; calyx fused for ca. $1 / 5$ its length.
b. var. collinus.

8a. Lisianthius brevidentatus (Hemsl.) O. Ktze. var. brevidentatus.
Leianthus brevidentatus Hemsl. Biol. Centr. Am. Bot. 2: 344. 1882. Type. Guatemala: Sierra del Mico, Bernoulli 942, photograph (duke!), holotype (к).

Lisianthus elatus Standl. \& Steyerm. Fieldiana Bot. 22: 267, 268. 1940. Type. Guatemala. Izabal: between milla 49.5 and ridge 6 mi . from Izabal, Montaña del Mico, Steyermark 38562 ( F !).

Inflorescence branches contracted and the dichasia or groups of dichasia dense and compact. Calyx $6-9.5 \mathrm{~mm}$. long, fused for $1 / 4-1 / 3$ its length, the lobes $4.5-6 \mathrm{~mm}$. long and $1-2 \mathrm{~mm}$. broad, the tube $1.5-3 \mathrm{~mm}$. long. Corolla lobes squarish to suborbicular, about as broad as long, $2-3 \mathrm{~mm}$. long and $2-3 \mathrm{~mm}$. broad, auriculate at the base. Flowering: Feb.-Aug. Chromosome number: $n=18$.

Distribution: In pine forests, open rocky slopes, and along roadsides from near sea level to 1000 meters in the Departments of Alta Verapaz and Izabal, Guatemala (Map 3).

## Specimens examined

Guatemala. Alta Verapaz: on Guat. 4, 45 km . ne. of Cobán, Stone 2765 (A, BM, DS, DUKE, F, IJ, LL, MICH, Mo, Ny, s, UC, US); vicinity of caves, sw. of Lanquín, Steyermark 44140 ( F , US) ; sobre el paredón del camino entre San Pedro Carchá y Sacouyou, Molina \& Molina 12115 (f). Izabal: 0.8 mi . from Highway CA-9 on road to Mariscos, Weaver 2184 (A, bM, duke, f, ll, mich, mo, s, us) ; along Highway CA-9 near turnoff to Mariscos, Weaver 2186 (A, dUKe, f, Mich, Us); trail from Los Amates to Izabal, Blake 7795 (GH, US); Sierra del Mico, Bernoulli 924 (ny/ isotype); between milla 49.5 and ridge 6 mi. from Izabal, Steyermark 38562 (F; type of L. elatus).

8b. Lisianthius brevidentatus (Hemsl.) O. Ktze. var. collinus (Standl.) Weaver, comb. nov.

> Lisianthus collinus Standl. Carnegie Inst. Publ. 461: 81. 1935. Type. British Honduras: Jacinto Hills, Schipp 1205 (F!).

Inflorescence branches elongate and the dichasia or groups of dichasia appearing loose and open. Calyx $6.5-7.5 \mathrm{~mm}$. long, fused for ca. $1 / 4-1 / 3$ its length, the lobes $5-6 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, the tube ca. 1.5 mm . long. Corolla lobes ovate, $2 / 3 \mathrm{~mm}$. broad.

Distribution: Known only from the type locality on a cliff face in peaty soil at 300 ft . elevation (Map 3).

## Specimens examined

British Honduras. Toledo (?) Dist: Jacinto Hills, Schipp 1205 (GH, MICH, mo, s, Uc, isotypes).

Williams (1968, 1969) included under Lisianthius brevidentatus a rather diverse assemblage of plants, including, as I have interpreted them, L. quichensis Donn. Sm., L. calciphilus Standl. \& Steyerm., and a hybrid between L. axillaris and L. saponarioides (previously known as L. petenensis Standl. \& Steyerm.). Williams (1968, p. 407) did note that there are differences, in the inflorescence, calyx, and corolla, in the material he placed under L. brevidentatus. He remarked, however, that these differences are ones which may depend on the stage of growth of the plants, or that they are not easily defined. The following table compares Williams's treatment and mine of the same plants.

Williams (1968, 1969)
L. brevidentatus (Hemsl.) O. Ktze.
(L. elatus Standl. \& Steyerm.)
(L. collinus Standl.)
(L. quichensis Donn. Sm.)
(L. calciphilus Standl. \& Steyerm.)
(L. petenensis Standl. \& Steyerm.)

Weaver
L. brevidentatus (Hemsl.)
O. Ktze. var. brevidentatus
(L. elatus Standl. \& Steyerm.)
L. brevidentatus var. collinus (Standl.) Weaver
L. quichensis Donn. Sm.
L. calciphilus Standl. \&

Steyerm. (species non satis nota)
A hybrid (no formal designation)

Lisianthius quichensis, the range of which closely approaches that of L. brevidentatus in central Guatemala, is rather easily distinguished from that species. L. quichensis differs by corolla lobes $3-8 \mathrm{~mm}$. long, more than twice as long as broad, and long-acuminate; the corolla tube distinctly inflated in the middle; flowers distinctly pedicellate; inflorescence branches angled but not winged; dichasia never sessile and the dichasial groups never appearing pleiochasial; capsules broadly ovoid; and the
filaments, at least the longer ones, exceeding the corolla lobes; and leaves narrowed at the base and not clasping.

Lisianthius calciphilus, which is known from a single specimen from Dept. Alta Verapaz, Guatemala, also differs strikingly from L. brevidentatus in a number of characters: much longer corolla lobes, nearly twice as long as broad, gradually short acuminate; the corolla distinctly funnelform; the flowers distinctly pedicellate; and the bracteoles conspicuous, oblanceolate, to 8 mm . long, and green at least in part. This plant is here treated as a species non satis nota.

Lisianthius elatus Standl. \& Steyerm., known only from the holotype, Steyermark 38562 (F) from Dept. Izabal, Guatemala, is synonymous with L. brevidentatus. With the original description of L. elatus, Standley and Steyermark speculate that the most closely related species is $L$. collinus Standl. and note that $L$. collinus differs in having "a lax inflorescence with scattered flowers, some of which are borne on greatly elongate pedicels" (measurements of all available specimens of L. collinus, however, show that the pedicels are never more than 3 mm . long, hardly elongate).

The holotype of Lisianthius brevidentatus, Bernoulli 924 (к) from the Sierra del Mico, Guatemala, was not available for study, but I have seen a photograph of it. There is a specimen of Bernoulli 924 at the New York Botanical Garden, and it undoubtedly represents the same taxon as the holotype. Therefore I have used this specimen as typical of $L$. brevidentatus for comparison with L. elatus. Even a cursory examination leaves no doubt that the holotype of L. elatus is an entirely typical specimen of L. brevidentatus var. brevidentatus.

Actually, it is possible that at the time they described L. elatus, Standley and Steyermark were unfamiliar with typical $L$. brevidentatus. Indeed in 1940 there were no more than three specimens of $L$. brevidentatus in American herbaria, and none were at the Field Museum.

Lisianthius collinus Standl. is known from a single collection, Schipp 1205, from the Jacinto Hills in southern British Honduras. These specimens resemble $L$. brevidentatus in all respects except that the inflorescences are loose and open and the corolla lobes are slightly longer in relation to their width, distinctly ovate, and without auricles at the base. Standley, in describing it, compared L. collinus only with L. axillaris. However, it is undoubtedly closely related to L. brevidentatus, but certainly distinct. In view of its apparent distinctness and the fact that typical L. brevidentatus is absent from British Honduras, but with an eye to caution because of the extremely limited number of specimens available, I prefer to treat L. collinus as a variety of L. brevidentatus, rather than to submerge it entirely as did Williams or to treat it as a distinct species as did Standley. Perhaps more adequate collections will necessitate a change in its status.
9. Lisianthius viscidiflorus Robins. Proc. Am. Acad. 45: 398. 1910 (as Lisianthus). Type. Guatemala. Alta Verapaz: Cobán, von Tuerckheim II-1308 (GH!).

Coarse, perennial herbs. Stems $0.5-2.5 \mathrm{~m}$. tall and to 1.5 cm . in diameter, erect, green and terete above, gray-brown and somewhat quadrate below. Leaves firmly membranaceous, sessile, clasping, (3.1)4.9-18 cm . long and $1.3-7.2 \mathrm{~cm}$. broad, oblong, oblong-elliptic, or tending toward oblanceolate, more rarely ovate, the apices short-acuminate, the bases broadly rounded or subcordate or rarely narrow and tapering; upper leaves and those on the lateral branches smaller, 1.3-7.2 cm. long and $0.3-2.5 \mathrm{~cm}$. broad, narrowly ovate or lanceolate. Inflorescences of longpedunculate dichasia, these 1-5 times compound or apparently simple, the lateral branches often scorpioid and secund. Flowers horizontal, weakly ascending or weakly nodding, the pedicels stout, $2-14(21) \mathrm{mm}$. long; bracteoles scarious, subulate. Calyx 4.5-8 mm. long, fused for $1 / 3-1 / 2$ its length; the lobes $1.5-5 \mathrm{~mm}$. long and $1.5-2.5 \mathrm{~mm}$. broad, narrowly ovate to lanceolate and ovate, short-acuminate or more rarely acute, becoming somewhat blunt with age, scarious-margined, completely ecarinate; the tube $1.5-4 \mathrm{~mm}$. long. Corolla tubular, glutinous, $2.9-3.9 \mathrm{~cm}$. long; the tube $1.9-3.4 \mathrm{~cm}$. long and $4-5 \mathrm{~mm}$. in diameter at the apex, dull red; the lobes $3.5-5.5 \mathrm{~mm}$. long and $2-3.5 \mathrm{~mm}$. broad, $1 / 8-1 / 6$ as long as the tube, spreading, greenish with a dull purple base, narrowly ovate, the apex blunt and somewhat undulate and erose, very rarely the apex acute. Stamens inserted on the corolla tube $1 / 3-2 / 5$ of the distance from the base to the apex; filaments $1.5-2.9 \mathrm{~cm}$. long, the shortest sometimes barely surpassing the corolla tube, the longest ones always surpassing the corolla lobes in mature flowers and frequently equalling or exceeding the style; anthers $2-3 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, oblong, the apex truncate or retuse. Style $1.8-3.4 \mathrm{~cm}$. long, always exceeding the corolla lobes in mature flowers; stigma peltate. Capsule narrowly ovoid or oblong-ellipsoid, lustrous, glutinous, short-beaked, $9-14 \mathrm{~mm}$. long, not including the $1-2 \mathrm{~mm}$. long beak, and $3-6 \mathrm{~mm}$. in diameter; calyx in fruit $1 / 3-2 / 5(1 / 2)$ as long as the capsule; the marcescent corolla not persisting until the seeds are shed. Flowering: Mar.-Sept. Chromosome number: $n=18$.

Distribution: From 150-1300 meters, along roadsides and in secondary scrub in central Guatemala and Chiapas, Mexico (Map 4).

## Specimens examined

Mexico. Chiapas: Laguna Ocotal Grande, ca. $25-30 \mathrm{~km}$. se. of Cerro Líbano, Dressler 1448 (mexu, mich, ny, us). Guatemala. Alta Verapaz: 3.5 mi . w. of San Cristóbal Verapaz on Highway 7W, Weaver 2179 (A, dUke); Cobán, Johnson 718 (F, US) ; 1.5-2 mi. s. of Gubilguitz, Steyermark 44431 ( F , nY, us) ; Cobán Road, between km. 284-285, between Chiracté and Chapultepec Farm, Contreras 4725 (LL); along road, between San Cristóbal Verapaz and Chixoy, Steyermark 43885 (F) ; Cerro Chinajá, between Finca Yalpemech and Chinajá, above source of Río San Diego, Steyermark 45672 (f); Cóban, von Tuerckheim 1308 (F, MO, US; isotypes). Quiché: 24.1 mi . e. of Cunén on Highway 7W, Weaver 2182 (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, s, UC, US).

Although Lisianthius viscidiforus is a rather poorly collected species,
it is quite common along roadsides in the vicinity of Cobán, Dept. Alta Verapaz, Guatemala. The flowers are predominantly red but the plant is not particularly conspicuous even when in full flower. L. viscidiflorus is unique in the genus in having mostly obtuse corolla lobes and purple anthers. It is easily distinguishable by these characters and the red corolla tube from the other species of sect. Lisianthius subsect. Herbacei. Of these species it most closely resembles L. brevidentatus in corolla and leaf form. L. axillaris (sect. Lisianthius subsect. Fruticosi), the only other species in the genus with red corolla tubes, differs strongly from L. viscidiflorus in having acuminate corolla lobes, yellow anthers, and solitary axillary flowers.

As the specific epithet implies, and as pointed out by Robinson in the original description, the flowers of Lisianthius viscidiflorus are sticky, both in the fresh state and during the drying process. L. viscidiflorus, however, is not unique in this respect. The corolla of several species, particularly L. longifolius, and the young buds and capsules of most of the species are viscid to some degree.

Lisianthius viscidiflorus is a very distinct species, not particularly variable in most of its characters. However, the single known population from Chiapas, Mexico (Dressler 1448), differs from the Guatemalan populations in having acute rather than obtuse corolla lobes. This is the only consistent difference between the populations and is, I think, not of sufficient magnitude to warrant the recognition of the two as formal varieties.

Lisianthius sect. Lisianthius subsect. Fruticosi Weaver, subsect. nov.
Suffrutices, frutices vel arbores graciles, glabrae vel puberulae. Plantae ramosae, ramis indeterminatis. Folia petiolata vel raro subsessilia. Inflorescentiae axillares vel in ramulis determinatis dispositis, raro flores solitarii, axillares. Capsulae oblongo ellipsoideae. $\checkmark$ Species typica: $L$. longifolius L.

## Key to the Series

A. Inflorescences not densely compacted, obviously dichasioid, or reduced to single flowers and subtended by foliaceous or scarious bracts, but these not involucrate.
B. Filaments and styles shortly exserted, the exserted portion much less than the total length of the corolla; pollen grains reticulate.
a. Longifolii.
B. Filaments and styles greatly exserted, the exserted portion at least equal to the total length of the corolla; pollen grains appearing smooth or nearly so with the light microscope. .................... b. Exserti.
A. Inflorescences densely compacted, appearing umbellate or capitate and subtended by 2 pairs of foliaceous involucral bracts.
c. Umbellati.
a. Lisianthius sect. Lisianthius subsect. Fruticosi ser. Longifolii Weaver, ser. nov.

Suffrutices vel frutices, omnino glabri vel puberuli. Inflorescentiae dichasiales, diffusae, bracteis foliaceis vel scariosis non involucratis subtentae, ramulis elongatis, flores raro solitarii. Lobi calycis saepe carinati vel alati. Styli filamentaque breviter exserta. Pollinis grana exinio reticulato. -Species typica: L. longifolius L.

With its 15 species, series Longifolii is the largest species group in the genus. Seven of the species are distributed in Mexico and Central America, with one species ranging barely into northwestern Colombia. The remainder are distributed throughout the Greater Antilles, with a majority in Jamaica (five species) and one species on each of the other three islands. The group is rather diverse morphologically, but all of the species are shrubs or subshrubs with inflorescences arranged diffusely on determinate, lateral flowering branches or rarely reduced to solitary, axillary flowers.

## Key to the Spectes of Series Longifolii

A. Corolla tube red; flowers typically borne singly in the axils of the foliage leaves.
21. L. axillaris.
A. Corolla tube yellow; flowers borne in dichasia, these axillary or on determinate, lateral flowering branches, very rarely the flowers borne singly in the axils of the foliage leaves.
B. Corolla tube distinctly inflated, widest above the middle but constricted at the apex; corolla lobes and the apex of the tube often dark green; leaves coriaceous or membranaceous, broadest at or above the middle.
C. Corolla lobes $1.2-2.0 \mathrm{~cm}$. long, ca. $1 / 2$ as long as the tube; leaves coriaceous; corolla lobes greenish-yellow; calyx lobes completely ecarinate; corolla strongly persistent on the mature capsules; plants of Jamaica.
13. L. adamsii.
C. Corolla lobes 1 cm . or less in length, less than $1 / 4$ as long as the tube; leaves coriaceous or membranaceous; corolla lobes greenishyellow or dark green; calyx lobes carinate or at least ridged abaxially; corolla not persisting on the mature capsules; plants of Central America.
D. Stamens inserted well above the apex of the calyx lobes; calyx in fruit $1 / 5-2 / 5$ as long as the capsule; corolla lobes less than 2 times as long as broad, usually less than $1 / 8$ as long as the tube; calyx $5-8 \mathrm{~mm}$. long, the lobes narrowly ovate and abruptly short-acuminate, more rarely ovate-lanceolate and longer acuminate.
10. L. skinneri.
D. Stamens inserted at or just above the apex of the calyx lobes; calyx in fruit $1 / 2$ as long to nearly as long as the capsule; corolla lobes 2 times as long as broad or longer, more than $1 / 6$ as long as the tube; calyx $7-13.5 \mathrm{~mm}$. long, the lobes lanceolate and long-acuminate.
E. Leaves membranaceous; corolla (4.2)4.7-5.9 cm. long, the lobes $7-10 \mathrm{~mm}$. long, the tube $4-5$ times as long as the calyx; styles barely surpassing the corolla lobes, the filaments never surpassing the corolla lobes.
11. L. peduncularis.
E. Leaves more or less coriaceous; corolla $2.5-4.2 \mathrm{~cm}$. long,
the lobes $4-6.5 \mathrm{~mm}$. long, the tube less than 4 times as long as the calyx; the longer filaments and the styles surpassing the corolla lobes, the latter conspicuously so.
B. Corolla tube not inflated, widest at the apex; corolla 12. L. jefensis. greenish-yellow; leaves membranaceous or very rarely coriaceous, usually broadest at or below the middle.
F. Plants glabrous, or very rarely minutely spiculate; calyx lobes never alate; flowering branches very rarely with leaves above the first division and never on the secondary axes; corolla seldom persisting until the seeds are shed.
G. Inflorescences congested, of compound dichasia, the lateral branches scorpioid or helicoid; corolla paler inside than out; flowering branches with 3 to many pairs of leaves below the lowermost division. ........................22. L. seemannii.
G. Inflorescences diffuse, mostly of apparently simple dichasia, the lateral branches not scorpioid or helicoid; corolla the same color inside as out; flowering branches rarely with more than 1 pair, and never more than 3 pairs of leaves below the lowermost division.
H. Filaments, at least the longest ones in each flower, exceeding the corolla lobes.
I. Corolla lobes ca. $1 / 2$ as long as the tube, and acute or abruptly short-acuminate; leaves usually broadest above the middle, gray-green, thick and somewhat coriaceous, the lateral veins indistinct; plants of Jamaica.
I D..................13. L. adamsii. cuspidobes less than $1 / 3$ as long as the tube and long cuspidate-acuminate; leaves broadest at or below the middle, green, thin-membranaceous, the lateral veins prominent; plants of Central America.

## 15. L. auratus.

H. Filaments not exceeding the corolla lobes.
J. Corolla lobes $5-6$ times as long as broad, more than $3 / 5$ as long as the tube and gradually long-acuminate; calyx ca. $1 / 2$ as long as the corolla tube.

> J. Corolla lobes less than 4 times as long as broad, $1 / 2$ or less as long as the tube, acute or abruptly short-acuminate, very rarely gradually acuminate; calyx $1 / 3$ or less as long as the corolla tube. K. Corolla lobes less than $1 / 3$ as long as the tube. L. Styles surpassing the corolla lobes in mature flowers; bracteoles below the pedicels green, at least along the midline; flowers ascending; calyx fused for $2 / 10-1 / 3$ its length; stigma peltate; filaments $2.1-2.7 \mathrm{~cm}$. long, inserted on the corolla tube ca. $1 / 3$ of the distance from the base to the apex; plants of Mexico.
14. L. acuminatus.
L. Styles not surpassing the corolla lobes in mature flowers; bracteoles below the pedicels scarious;
flowers horizontal or nodding; calyx fused for $1 / 10-2 / 10$ its length, stigma capitate; filaments $1.0-2.2 \mathrm{~cm}$. long, inserted on the corolla tube just below the middle; plants of Cuba.
17. L. glandulosus.
K. Corolla lobes more than $1 / 3$ as long as the tube.
M. Inflorescence branches terete or indistinctly angled, the angles never expanded into narrow, scarious wings; dichasia, at least the terminal ones, $2-3$-flowered; leaves more than 2.5 times as long as broad, long-petiolate; plants of Jamaica.
N. Corolla tube tightly constricted in the lower third, then expanding abruptly; styles nearly always surpassing the corolla lobes; capsule short-beaked, the beak less than $1 / 4$ as long as the capsule.
16. L. troyanus.
N. Corolla tube more or less gradually expanding from the base; styles never surpassing the corolla lobes; capsule long-beaked, the beak $1 / 3-1 / 2$ as long as the capsule.
19. L. latifolius.
M. Inflorescence branches strongly angled, the angles often expanded into narrow, scarious wings; dichasia reduced to 1 or rarely 2 flowers; bracteoles below the pedicels green; leaves less than 2.5 times as long as broad, subsessile or petiolate; plants of Hispaniola.
F. Plants, especially the inflorescence, puberulous, if nearly glabrous, the calyx lobes broadly alate abaxially; flowering branches with leaves above the first division and often on the secondary axes; corolla persisting long after the seeds are shed.
O. Calyx lobes alate or very rarely merely carinate; leaves on the flowering branches obtuse or rounded or very rarely subcordate at the base; branching opposite or alternate below and usually opposite above; inflorescences, especially those at the apex of the flowering branches, 2-3-flowered. ......... 23. L. longifolius.
O. Calyx lobes carinate abaxially; leaves on the flowering branches, at least the upper ones, distinctly cordate at the base; branching alternate or bifurcate, very rarely opposite; inflorescences 2 flowered or the flowers solitary.
24. L. cordifolius.
10. Lisianthius skinneri (Hemsl.) O. Ktze. Rev. Gen. Pl. 2: 429. 1891 (as Skinneri).
Leianthus skinneri Hemsl. Biol. Centr. Am. Bot. 2: 345. 1882. 'Lectotype. Guatemala: without exact locality, Skinner (к); photo. (мо!).
Lisianthus arcuatus Perk. Bot. Jahrb. 31: 492. 1902. TType. None designated; $^{2}$ Warscewicz 9 (Costa Rica et Veragua) and Hoffmann 832 (Desengano) cited, both presumably at Berlin and destroyed during World War II.
Lisianthus scopulinus Robyns \& Elias, Ann. Mo. Bot. Gard. 55: 62. 1968.
$\checkmark$ Type. Panama. Veraguas: Mouth of the Río Concepción, Lewis, Croat \& Hawker 2799 (мо).

Shrubs or more rarely subshrubs, glabrous throughout. Stems $0.5-3 \mathrm{~m}$. tall and to 2 cm . in diameter, erect or ascending, rarely sprawling, graybrown below and green above, terete. Leaves membranaceous, glossy, dark or rather pale green above and distinctly paler beneath, the blades $3.5-20(24.5) \mathrm{cm}$. long and $1.5-5.5(7.7) \mathrm{cm}$. broad, narrowly elliptic to narrowly obovate (broadly elliptic), generally widest above the middle, abruptly acuminate, the bases long-attenuate into the winged petiole; the upper leaves essentially sessile or the petioles to 2 cm . long. Inflorescences of pedunculate, apparently simple (1-compound or rarely 3-compound) dichasia, occasionally reduced to 1 or 2 flowers; flowering branches ascending, usually ternately divided, each division terminated by a dichasium or group of dichasia; axes of the flowering branches and the dichasial branches indistinctly 4 -angled to essentially terete, elongate and the inflorescences appearing loose and open. Flowers horizontal or nodding, the pedicels $0.7-2.4 \mathrm{~cm}$. long; bracteoles subulate, scarious. Calyx 4.5-8 mm . long, united for $3 / 10-3 / 5$ of its length, $1 / 10-1 / 6(1 / 5)$ as long as the corolla tube; the lobes $2-5 \mathrm{~mm}$. long and $1.5-3 \mathrm{~mm}$. broad, narrowly ovate (lanceolate, broadly ovate, or suborbicular), abruptly short-acuminate (long-acuminate or acute), scarious-margined, ridged or carinate abaxially; tube $1.5-3.5 \mathrm{~mm}$. long. Corolla tubular, more or less fleshy or thinner, $2.7-6.3 \mathrm{~cm}$. long; tube $2.4-5.7 \mathrm{~cm}$. long and $0.4-1.1 \mathrm{~cm}$. broad at the widest point, bright yellow but with a green or yellow-green apex, constricted in the lower $1 / 4-1 / 3$, inflated in the mid-portions; lobes $2.5-6 \mathrm{~mm}$. long and $2.5-4 \mathrm{~mm}$. broad, $(1 / 6) 1 / 8-1 / 12$ as long as the tube, yellowish-green, or rather dark green with yellow green margins, spreading and with the tips often recurved, triangular-ovate and abruptly short-acuminate (ovate-lanceolate and rather long-acuminate). Stamens inserted in the lower third of the corolla tube; filaments $2-5 \mathrm{~cm}$. long, at least the longest ones equalling or surpassing the corolla lobes, the longest ones sometimes surpassing the style; anthers $1.5-3.5 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, broadly oblong, the connective slightly exserted. Style $2.3-5.3 \mathrm{~cm}$. long, exserted, usually surpassing the corolla lobes; stigma peltate. Capsules narrowly oblong-ellipsoid, conspicuously beaked, $1-2.2 \mathrm{~cm}$. long, not including the $1-6 \mathrm{~mm}$. long beak, and $4-6 \mathrm{~mm}$. in diameter; the marcescent corolla falling off before the seeds are shed. Flowering: Jan.-Sept. Chromosome number: $n=18$.

Distribution: From sea level to 1300 meters in moist forests, generally along the edge, or along roadsides, on the Atlantic Coastal Plain of southeastern Guatemala and adjacent Honduras and again in Panama, and at middle elevations in the interior of Costa Rica and Panama (MAP 4).

## Representative collections

Guatemala. IzabaL: south shore of Lake Izabal, west of the village of Izabal, Proctor, Jones \& Facey 3049 ( $\mathrm{F}, \mathrm{iJ}, \mathrm{Ll}$, mexu, Us). Honduras. Atlantida:
south of San Alejo near Río San Alejo, Standley 7829 (F); Cuyamel, Carleton 584 (f). Costa Rica. Alajuela: Villa Quesada, Smith 1884 (f, mo, ny); Cataratas de San Ramón, Brenes 13575 ( $\mathrm{F}, \mathrm{NY}$ ); ca. 13.5 mi . e. of Arenal and 6.5 mi . w. of Fortuna, Wilbur \& Stone 10257 (A, bM, duke, ds, f, iJ, LL, Mich, mo, ny, s, uc, us). Guanacaste: Tilarán, Valerio 1151 (f). Heredia: Sarapiquí, Isla Bonita, Pittier s.n. (ny, us); Finca Hnos. Vargas, Puerto Viejo de Sarapiquí, Jiménez 3577 (f). Panama. Coclé: vicinity of La Mesa, El Valle de Antón, Allen 2369 (MO); Bismarck, above Penonomé, Williams 613 (NY). Colon: roadsides $5-7 \mathrm{mi}$. se. of Portobello, Weaver \& Wilbur 2249 (A, BM, Ds, duke, f, iJ, ll, mich, mo, ny, s, UC, US); summit of Cerro Santa Rita, Allen 5104 (bm, mo). Panama: slopes of Cerro Jefe, along road from Cerro Azul, well below the turnoff to La Eneida, Weaver \& Wilbur 2244 (A, BM, DS, DUKE, F, IJ, ll, Mich, mo, ny, s, UC-US); Veraguas: mouth of the Río Concepción, Lewis, Croat \& Hawker 2799 (duke; isotype of $L$. scopulinus). Canal Zone: forest along telephone cable trail between Splice S16 \& S49, Río Indio, Steyermark \& Allen 17427 (Bm, ds, mo, s); headwaters of Río Arenal, near IWTC pump, Johnston 1502 (A, MO).

Lisianthius skinneri is the most widespread species, ranging from southeastern Guatemala to central Panama; with L. jefensis and L. peduncularis it forms a rather distinctive, closely interrelated species group. These three species differ from one another in the length of the calyx, the shape and length of the corolla lobes, and the ratio between the lengths of the corolla lobes and the corolla tube. The differences are not striking, especially in view of the variation within $L$. skinneri, but they are constant. The close sympatry of $L$. skinneri with both of the other species and the absence of intermediate forms supports the maintenance of all three as distinct.
Lisianthius skinneri is a rather variable species, but no population is sufficiently distinct to warrant recognition as a subspecies or variety. There is no perceptible pattern to the variation. The Guatemalan plants are characterized by long, narrow, thin-textured corollas; long-acuminate, relatively long and narrow calyx and corolla lobes; and styles usually longer than the filaments. Wilbur \& Stone 10257, from Volcán Arenal, Costa Rica, is characterized by long, narrow, rather fleshy corollas; merely acute calyx lobes; broad and very short-acuminate corolla lobes; and styles shorter than the filaments in a given flower. Other specimens from Costa Rica and those from Honduras and the interior of Panama resemble the Guatemalan plants but have a broader corolla, with calyx and corolla lobes broader and shorter acuminate, and styles and stamens various. The plants from the Atlantic Coastal Plain of Panama have a short, rather slender, fleshy corolla; broad, short-acuminate calyx and corolla lobes; and the styles conspicuously longer than the filaments.

Although no original material has been seen and duplicates have not been located, according to the original description $L$. arcuatus Perk. differs from L. skinneri in having arcuate rather than straight corollas and subelongate rather than short internodes. Internode length, especially in shrubs, depends largely on environmental factors and has proved of minimal taxonomic utility in this genus. Many dried specimens of $L$.
skinneri are indeed characterized by having flowers with arcuate corollas. Actually the corollas appear merely swollen on one surface and would more correctly be termed "gibbous" rather than "arcuate." This condition is almost certainly an artifact resulting from pressing and drying. The corollas of $L$. skinneri are conspicuously inflated (evenly) in the midportions, and frequently press unevenly. I have collected plants of $L$. skinneri in Panama and have observed the corollas are not gibbous in the fresh state. However, when dry my specimens frequently did have apparently gibbous corollas. There seems to be no basis whatever for maintaining L. arcuatus as distinct.

Lisianthius scopulinus Robyns \& Elias reputedly differs from L. skinneri in having narrowly ovate, long-acuminate, and longer calyx lobes. I have seen an isotype of $L$. scopulinus, and it strongly resembles typical $L$. skinneri except that the corolla lobes are generally longer than usual. The longest calyx lobes ( 5 mm .) are indeed longer than any seen in specimens of $L$. skinneri. However, the shorter lobes ( 4 mm .) on this specimen are no longer than those, for instance, on Proctor, Jones \& Facey 3049 (F, IJ, LL, MEXU, US), perfectly good L. skinneri, from Lake Izabal, Guatemala, geographically rather far removed from the type and only known locality of $L$. scopulinus at the mouth of the Río Concepción in Veraguas, Panama. In addition, L. skinneri is not infrequently characterized by having rather long-acuminate, narrowly ovate calyx lobes. Therefore, it seems that $L$. scopulinus does not really differ in any significant way from L. skinneri.

When Hemsley (1882) described Leianthus skinneri, he cited two specimens as representative of the new taxon: a Skinner specimen, without a collection number (Guatemala, without exact locality) and Fendler 137 (Panama: Chagres), both in the herbarium at Kew. I have not seen either specimen, but I have seen good photographs of both. Fendler 137 is only a scrap, consisting of a flowering branch with five flowers, while the Skinner specimen is much more complete, showing stems, leaves, flowers, and capsules. Since the Skinner specimen is far superior and the species was named for its collector, I designate it as the lectotype of Leianthus skinneri Hemsley.

## 11. Lisianthius peduncularis L.O. Williams, Fieldiana Bot. 31: 408. 1968 (as Lisianthus). Type. Panama. Coclé: El Valle de Antón, Allen 3410 (mo!).

Slender shrubs or subshrubs, glabrous throughout. Stems $1-2.5 \mathrm{~m}$. tall and to 2 cm . in diameter, erect or ascending, terete, gray-brown and woody below, green and herbaceous above. Leaves glossy grass-green above, paler and dull beneath, the lateral veins prominent, the blades (3.2) $5.2-13.5(18.0) \mathrm{cm}$. long and (1.1) $2.0-5.4(8.4) \mathrm{cm}$. broad, narrowly obovate or oblanceolate (elliptic), widest at or above the middle, abruptly short-acuminate (acute), the bases long-attenuate into the winged, 0.4 $2.0(3.2) \mathrm{cm}$. long petiole. Inflorescences of pedunculate, apparently simple
(1-compound) dichasia, these sometimes reduced to 1 or 2 flowers; flowering branches often with several pairs of reduced leaves below the first division, once- or rarely twice-ternately divided, each division terminated by a dichasium; dichasial branches and stalks 4 -angled, elongate and with the inflorescences loose and open. Flowers nodding, the pedicels 6-14 mm. long; bracteoles subulate, scarious. Calyx $8-13.5 \mathrm{~mm}$. long, fused for $1 / 8-1 / 5(1 / 4)$ its length; the lobes $6.5-11.5 \mathrm{~mm}$. long and $1-2.5$ mm . broad, lanceolate, long-acuminate, scarious-margined, weakly carinate abaxially; the tube $1.5-3 \mathrm{~mm}$. long. Corolla tubular (4.2)4.7-5.9 cm . long; the tube (3.4)4-4.9 cm . long and $5.5-9 \mathrm{~mm}$. broad at the broadest point, bright yellow, constricted in the lower third, inflated in the midportions; the lobes (7) $8-10 \mathrm{~mm}$. long and $3-4 \mathrm{~mm}$. broad, $1 / 5-1 / 4$ as long as the tube, spreading and recurved at the tips, greenish-yellow or rather dark green, lanceolate or ovate-lanceolate, long-acuminate. Stamens inserted on the corolla tube ca. $1 / 4$ of the distance from the base to the apex; filaments (2.9) $3.5-4.2 \mathrm{~cm}$. long, the shorter ones barely surpassing the corolla tube, the longest ones not surpassing the corolla lobes; anthers $2-3 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, yellow, narrowly oblong, acutish, the connective slightly exserted. Style (3.2) $4.0-5.2 \mathrm{~cm}$. long, usually slightly exceeding the corolla lobes, always surpassing the filaments; stigma peltate. Capsule fusiform, long-beaked, $1.1-1.6 \mathrm{~cm}$. long, not including the $2-3.5$ mm . long beak, and $4-5 \mathrm{~mm}$. in diameter; the marcescent corolla not persisting until the seeds are shed. Flowering: Jan.-June. Chromosome NUMBER: $n=18$.

Distribution: Along roadsides and in dense moist forests at 1000 meters, just north of El Valle de Antón in central Panama (Map 5).

## Specimens examined

Panama. Coclé: El Valle de Antón, Allen 3410 (bм, mo; isotypes); El Valle, north rim, Allen 1793 (Gн, mo, ny); inside the crater of El Valle de Antón at La Mesa, Weaver, Wilbur \& Correa 2247 (A, duke, f, ll, mich, mo, ny, us).

Lisianthius peduncularis is known only from the type locality where it is a rather rare plant. Although the species was only described in 1968, specimens of $L$. peduncularis have been present in collections since 1939. All of the known specimens had been determined as " $L$. latifolius Sw.", a Jamaican species resembling L. peduncularis primarily in its large, broad leaves.

The affinities of Lisianthius peduncularis are clearly with L. skinneri and $L$. jefensis. From the former it may be distinguished by its longer calyx and corolla lobes, its calyx fused for $1 / 4$ its length or less, its corolla tube no more than 5 times as long as the calyx, its corolla lobes more than twice as long as broad and longer in relation to the tube, and its stamens inserted at or above the apex of the calyx lobes. L. peduncularis may be distinguished from L. jefensis by its membranaceous leaves, its longer corolla, its longer corolla lobes, and its filaments and styles not, or only barely exceeding the corolla lobes.

I have collected Lisianthius peduncularis at El Valle, where it certainly is not common. Only a single small population was found. It is entirely possible that all the known specimens are from this population, and the population is merely an aberrant one of L. skinneri. However the presence of a specimen of $L$. skinneri from El Valle [Allen 2369 (мо)], with no specimens intermediate toward L. peduncularis known from the area suggests otherwise. Although I do so with some reservation, I prefer to treat $L$. peduncularis as a species distinct from L. skinneri. Perhaps more adequate collections in the future will lead to a reconsideration.

## 12. Lisianthius jefensis Robyns \& Elias, Ann. Mo. Bot. Gard. 55: 60. 1968 (as Lisianthus). $T$ Type. Panama. Panama: Cerro Jefe, Elias \& Hayden 1798 (мо).

Slender shrubs, glabrous throughout. Stems $1.3-2.5 \mathrm{~mm}$. tall and to 2 cm . in diameter, erect or the secondary branches ascending, terete, gray-brown below and green above. Leaves glossy dark green above, paler and dull below, the lateral nerves prominent, the blades (1.5)2.7-11.8 (20.6) cm . long and $0.8-5.0(7.7) \mathrm{cm}$. broad, narrowly obovate to oblanceolate and elliptic, widest at or above the middle, abruptly acuminate, the bases long-attenuate into the winged petiole. Inflorescences of pedunculate dichasia, these apparently simple (1-compound) but sometimes reduced to 1 or 2 flowers; flowering branches ascending, the axes terete or slightly flattened, once- or more rarely twice-ternately divided, each division terminated by a dichasium; branches and the stalks of the dichasia indistinctly 4 -angled, elongate and the inflorescences loose and open. Flowers horizontal or nodding, the pedicels $0.7-2.5 \mathrm{~cm}$. long; bracteoles subulate, scarious. Calyx $7-13 \mathrm{~mm}$. long, fused for $1 / 3-2 / 5$ its length; lobes $4.5-9 \mathrm{~mm}$. long and $1.5-3 \mathrm{~mm}$. broad, lanceolate to ovate-lanceolate, long-acuminate, scarious-margined, ridged or weakly carinate abaxially; tube $3-4 \mathrm{~mm}$. long. Corolla tubular, $2.5-4.2 \mathrm{~cm}$. long; tube $2.1-3.5 \mathrm{~cm}$. long and $5-8 \mathrm{~mm}$. broad at the broadest point, bright yellow with a greenish-yellow or dark green apex, constricted in the lower third, inflated in the midparts; lobes $4-6.5 \mathrm{~mm}$. long and $1.5-3.5$ mm . broad, $1 / 5-1 / 6$ as long as the tube, spreading and recurved at the tips, greenish-yellow or dark green with paler margins, triangular-ovate to ovate-lanceolate, rather long acuminate. Stamens inserted on the corolla tube ca. $2 / 5$ of the distance of the base to the apex; filaments $1.3-3 \mathrm{~cm}$. long, exserted, the longest ones surpassing the corolla lobes; anthers $2.5-3.5 \mathrm{~mm}$. long and $1-1.5 \mathrm{~mm}$. broad, yellow, narrowly oblong, acutish, the connective slightly exserted. Style $2.2-3.6 \mathrm{~cm}$. long, conspicuously surpassing the corolla lobes, always surpassing the filaments; stigma peltate. Capsule fusiform, conspicuously beaked, $1-1.8 \mathrm{~cm}$. long, not including the $1.5-4.5 \mathrm{~mm}$. long beak; the marcescent corolla not persisting until the seeds are shed. Flowering: Jan.-Sept. Chromosome NUMBER: $n=18$.

Distribution: From 850-900 meters in cloud forest near the summit of Cerro Jefe on the Continental Divide in central Panama (Map 5).

## Representative collections

Panama. Panama: slopes of Cerro Jefe on the road to La Eneida, Weaver \& Wilbur 2250 (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); slopes of Cerro Jefe, along road from Cerro Azul, just before the turnoff to La Eneida, Weaver $\mathcal{E}$ Wilbur 2243 (A, BM, DS, DUKE, F, IJ, LL, MICH, MO, NY, S, UC, US); Cerro Jefe, Elias \& Hayden $1798^{\circ}$ (us; isotype).

Lisianthius jefensis is known from only one, low shrubby mountaintop in central Panama where it is one of the more conspicuous elements of the vegetation. It is closely related to both L. skinneri and L. peduncularis. It differs from L. skinneri in its coriaceous leaves, its longer calyx lobes, its corolla lobes more than twice as long as broad and longer in relation to the tube, its corolla tube less than 4 times as long as the calyx, its stamens inserted at or just above the apex of the calyx lobes, and its calyx in fruit more than $1 / 2$ as long as the capsule. Populations of L. jefensis and L. skinneri have been collected less than 100 meters apart on Cerro Jefe; the populations appear to be perfectly distinct. That L. jefensis is merely a cloud-forest form of $L$. skinneri is thus ruled out. Both species were grown from seed in the greenhouse at Duke University and the differences in leaf texture remained constant.

The apparent distinctness of the populations on Cerro Jefe, in spite of their close sympatry, strongly supports the separation of the two as distinct species.
13. Lisianthius adamsii Weaver, Brittonia 22: 11. 1970. Type. Jamaica. St. Ann: Douglas Castle, ca. 2 mi . n. of the Mason River Savannah, Weaver 1293 (Duke!).
Spindly shrubs or subshrubs, glabrous throughout. Stems erect, $0.2-2$ m . tall and to 1.5 cm . in diameter, terete, green and herbaceous above, gray-brown and woody below, leafy nearly to the base. Leaves dull graygreen, thickish, the venation indistinct, the blades (5.8) $8-15(17.6) \mathrm{cm}$. long and (1.9)2.5-5.5(6.6) cm . broad, broadly oblanceolate to obovate (elliptic), abruptly short-acuminate (acute), the bases attenuate into the winged, $0.5-2 \mathrm{~cm}$. long petiole. Inflorescences of pedunculate, apparently simple dichasia, these occasionally reduced to 1 or 2 flowers; flowering branches 1-2-ternately divided, each division terminated by a dichasium or group of dichasia; inflorescence branches and stalks elongate and the inflorescences loose and open. Flowers nodding, the pedicels $0.8-4.5 \mathrm{~cm}$. long; bracteoles scarious, subulate. Calyx $7-13 \mathrm{~mm}$. long, fused for $1 / 6-1 / 3$ its length; the lobes $5-9 \mathrm{~mm}$. long and $1.5-2.5 \mathrm{~mm}$. broad, lanceolate, acuminate, scarious-margined, ecarinate; the tube $1.5-4 \mathrm{~mm}$. long. Corolla tubular-funnelform, 3.9-5.6 cm . long; the tube $2.7-3.6 \mathrm{~cm}$. long and $8-11 \mathrm{~mm}$. in diameter at the broadest point, constricted in the lower third, somewhat inflated, frequently unevenly, in the midparts,


Maps 4-7. Distribution of Lisianthius species. Map 4, L. skinneri (dots), L. viscidiflorus (triangles). Map 5, L. auratus (dots), L. jefensis (half-circle), L. peduncularis (triangle). MAP 6, L. acuminatus (triangle), L. axillaris (dots). Map 7, L. seemannii.
glossy clear yellow; the lobes $1.2-2 \mathrm{~cm}$. long and $5-7 \mathrm{~mm}$. broad, greenish-yellow, spreading and conspicuously recurved, ovate-lanceolate, abruptly short-acuminate. Stamens inserted on the corolla tube ca. $1 / 3$ of the distance from the base to the apex; filaments $3-4 \mathrm{~cm}$. long, exserted, at least the longest ones conspicuously surpassing the corolla lobes; anthers $2-4 \mathrm{~mm}$. long and $1-2 \mathrm{~mm}$. broad, oblong, acute, the connective exserted. Style $3.5-5.5 \mathrm{~cm}$. long, surpassing the filaments; stigma peltate. Capsule oblong-ellipsoid, $14.5-16.5 \mathrm{~mm}$. long and $5-7 \mathrm{~mm}$. in diameter; the marcescent corolla persisting until the seeds are shed. Flowering: Feb.-Oct. Chromosome number: $n=18$.

Distribution: From 500-750 meters in thickets and on rocky, limestone hillside in the central and western parishes of Jamaica (Map 12).

## Specimens examined

Jamaica. Clarendon: upper w. slope of Croft's Mountain, Proctor 29234 (ij). Hanover: interior summit slopes of Dolphin Head, Proctor 10037 (iJ). Manchester: Somerset Woods, ca. 5 mi . nw. of Mandeville, Proctor 16182 (A, bm, IJ). St. Ann: Douglas Castle, ca. 2 mi . n. of the Mason River Savannah, Weaver 1293 (GH, UCwI; isotypes).

Lisianthius adamsii, the most recently described species in the genus, is one of the more distinct and attractive of the species. With its coriaceous, gray-green, oblanceolate or obovate leaves; rather broad, inflated corolla tube and long recurved corolla lobes; and ecarinate calyx lobes, it is not easily confused with any other.

Vegetatively Lisianthius adamsii resembles somewhat L. umbellatus and L. capitatus (Series Umbellati), also with thickish, oblanceolate leaves; but it differs strikingly from them in its loose, open inflorescences and much longer corolla lobes. Although the relationships of L. adamsii are clearly with Series Longifolii, its specific relationships within the group are obscure. Its closest relatives are possibly the Jamaican L. latifolius, or, more probably, the Central American L. skinneri.
14. Lisianthius acuminatus Perk. Bot. Jahrb. 31: 493. 1902 (as Lisianthus). Lectotype. Mexico, without exact locality, Sumichrast 1558 (us! ; a fragment).
Slender subshrubs, glabrous throughout. Lower portions of the stems unknown, the upper portions green, terete or indistinctly 4 -angled. Leaves membranaceous, papillose above, the lateral veins prominent, the margins papillose, the blades $7.7-19.6 \mathrm{~cm}$. long and $2.5-5.6 \mathrm{~cm}$. broad, elliptic, abruptly long-acuminate, shortly attenuate and tapering into the winged petiole (to 4 mm . long). Inflorescences of pedunculate, apparently simple (1-compound) dichasia; flowering branches 1-2-ternately divided, each division terminated by a dichasium; axes of the flowering branches and the stalks and branches of the dichasia 4 -angled, elongate and with the inflorescences diffuse; bracts subtending the dichasia green, linear. Flowers ascending, the pedicels $3-7 \mathrm{~mm}$. long; bracteoles linear, scarious-margined
but usually green along the midline. Calyx $6.5-7.5 \mathrm{~mm}$. long, fused for $1 / 5-1 / 3$ its length; the lobes $4-6 \mathrm{~mm}$. long and $1.5-2 \mathrm{~mm}$. broad, lanceolate, acuminate, scarious-margined, distinctly carinate; the tube 1.5-2.5 mm . long. Corolla tubular, $3.4-3.7 \mathrm{~cm}$. long; the tube $2.9-3.2 \mathrm{~cm}$. long, yellow; constricted in the lower third, the lobes $4.5-5.5 \mathrm{~mm}$. long and $2.5-3 \mathrm{~mm}$. broad, $1 / 8-1 / 6$ as long as the tube, slightly spreading, green-ish-yellow, ovate, acute or abruptly short-acuminate. Stamens inserted on the corolla tube ca. $1 / 2$ of the distance from the base to the apex; filaments $2.1-2.7 \mathrm{~cm}$. long, surpassing the corolla tube but not the lobes; anthers ca. 2.5 mm . long and 1.5 mm . broad, broadly oblong, the connective very barely exserted. Styles ca. 3 cm . long, exceeding the corolla lobes, always exceeding the filaments; stigmas peltate. Capsule not seen.

## Distribution: Near Orizaba in south-central Mexico (Map 6).

## Spectmens examined

Mexico: without exact locality, Sumichrast 1558 (k; lectotype collection), photograph (duke). Veracruz: Orizaba, Botteri (GH); Monte San Cristobal, Orizaba, Mohr \& Botteri (us).

Lisianthius acuminatus is one of the most poorly understood and rarely collected of the species. Only 2 specimens, in addition to a fragment of the lectotype and a photograph of an isolectotype, the most recent collected in 1866, were available for study. L. acuminatus appears to be most closely related to the Jamaican L. latifolius or perhaps to the alliance of West Indian species that includes L. troyanus, L. laxiflorus, and L. glandulosus. Of the Mexican and Central American species L. acuminatus might possibly be confused with L. quichensis in subsect. Herbacer. However that plant is a suffrutescent herb with a determinate main axis. In addition, the corolla tube of $L$. quichensis is somewhat inflated and broadest below the apex, the corolla lobes are erect, and the filaments exceed the corolla lobes.

In the original description of Lisianthius acuminatus, Perkins cited two specimens as representative of the new taxon. These specimens (Sumichrast 1558 and 1856), which must be treated as syntypes, were presumably at Berlin and destroyed during World War II. There is however a duplicate of Sumichrast 1558 at Kew, a photograph of which (DUKE) I have seen. In addition Perkins sent a fragment of Sumichrast 1558 to John Donnell Smith according to a letter from her dated 31 March 1910 and presently attached to Heyde \& Lux 2921 (Us), the holotype of L. quichensis. This fragment includes a leaf, a bud, and the upper portion of the corolla of a nearly mature flower. The fragment, along with the original description, serves to identify Perkins' plant; since it is all that remains of the original material, the fragment of Sumichrast 1558 (US) is designated the lectotype of $L$. acuminatus Perkins.
15. Lisianthius auratus Standl. Trop. Woods 37: 29. 1934 (as Lisianthus). Type. Honduras. Comayagua: open mountain forests, Siguatepeque, Edwards $P-556$ ( F !).

Slender subshrubs, glabrous throughout. Stems $0.5-2.5 \mathrm{~m}$. tall and to 1 cm . in diameter, erect or reputedly sprawling, green or brown at base, terete below but indistinctly 4 -angled above. Leaves thin-membranaceous, dull dark green above and paler beneath, the principal lateral veins evident on both surfaces, on drying the veinlets occasionally conspicuous, the blades $2.1-11.5 \mathrm{~cm}$. long and $0.8-3.6 \mathrm{~cm}$. broad, ovate-lanceolate or ovate or tending toward elliptic, long-acuminate, rounded, or short-attenuate at base, the upper ones and those on the secondary branches more distinctly lanceolate and rounded at base; petioles $3-8 \mathrm{~mm}$. long. Inflorescences of pedunculate, apparently simple dichasia, these frequently reduced to 1 or 2 flowers. Flowering branches with a terminal and $1-3$ pairs of axillary dichasia; axes of the flowering branch and the dichasial branches 4 -angled. Flowers nodding or almost pendent, the pedicels $0.6-1.7 \mathrm{~cm}$. long; bracteoles scarious, subulate. Calyx $5-10 \mathrm{~mm}$. long, fused for $2 / 10-3 / 10$ its length; the lobes $3.5-7.5 \mathrm{~mm}$. long and $1-2 \mathrm{~mm}$. broad, lanceolate, long-acuminate, scarious margined, weakly carinate abaxially; the tube $1.5-2.5 \mathrm{~mm}$. long. Corolla tubular-funnelform, uniformly yellow, $2.9-4.0 \mathrm{~cm}$. long; the tube $2.2-3.0 \mathrm{~cm}$. long and $4.5-7.5$ mm . broad; constricted in the lower half, the lobes $5-11 \mathrm{~mm}$. long and $3-4.5 \mathrm{~mm}$. broad, $1 / 4-3 / 8$ as long as the tube, spreading but not recurved, ovate-lanceolate, cuspidate-acuminate. Stamens inserted in the lower $1 / 4-1 / 3$ of the corolla tube; filaments $2.0-3.0 \mathrm{~cm}$. long, the longer ones exceeding the corolla lobes, and often equalling the style; anthers 2-2.5 mm . long and $1-1.5 \mathrm{~mm}$. broad, narrowly oblong, the connective slightly exserted. Style $2.4-3.6 \mathrm{~cm}$. long, surpassing the corolla lobes; stigma capitate. Capsule $8-12 \mathrm{~mm}$. long and $3-5 \mathrm{~mm}$. broad, oblong-ellipsoid, short-beaked; the marcescent corolla not persisting until the seeds are shed. Flowering: All year. Chromosome number: $n=18$.

Distribution: From near sea level to 1800 meters in pine forests or savannahs at scattered localities from western British Honduras to southeastern Guatemala, and west-central Honduras to northeastern Nicaragua (MAP 5).

## Specimens examined

British Honduras. Cayo Dist.: 3 mi . n. of Augustine on the banks of the Río No, Mountain Pine Ridge, Weaver \& Wilbur 2253 (A, duke, F, MICH, MO); Augustine, Mountain Pine Ridge, near Río Frío, Hunt 401 (BM, F, LL, US); Guatemala. Chiquimula: Cerro Tixixi, 3-5 mi. n. of Jocotán, Steyermark 31603 (F). Honduras. Comayagua: open pine forests, Siguatepeque, Edwards 556 (Us; isotype); Barranco El Soccoro, mountains about 8 km . w. of Siguatepeque, Williams \& Williams $18382(\mathrm{GH}, \mathrm{F})$; trincheras, 20 km . n. of Siguatepeque, Howard et al. 628 (a). Intibucha: paredones humedos de la Cascada de Yamaranquila, Molina 6358 (Us); Barranco Yamaranquila, cerca de Yashse, Molina 6524 (Us). Nicaragua. Comarca de el Cabo: Río Leícus 28 km . so. de Waspan, Molina 15206 (F); bosque de la Quebrada Cuyu, Molina 15037 (F); matorrales de Río Leícus cerca del campo de aviación de Tronquera, 35 km . so. de Waspan, Molina 15171 (F).

Of the Central American species of Lisianthius, L. auratus appears to be most closely related to $L$. axillaris, a fact recognized by Standley when he described L. auratus. Although they have occasionally been confused, L. axillaris differs strikingly from L. auratus in having red flowers almost invariably borne singly in the axils of the foliage leaves. L. auratus strongly resembles certain of the West Indian species especially the L. troyanus alliance, and is probably quite similar to the stock from which they evolved.

> [To be concluded]


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Weaver, Richard E. 1972. "A revision of the neotropical genus Lisianthius (Gentianaceae) [cont.]." Journal of the Arnold Arboretum 53(2), 234-272. https://doi.org/10.5962/p. 58028.

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[^0]:    * Continued from volume 53, p. 100.

[^1]:    Spectmens examined
    Guatemala. Alta Verapaz: Saquíja, 45 km . ne. of Cobán, Standley 70166 (Ny, f); between Cobán and Finca Chimoté, near Rubeltein, Steyermark 44179

