

A REVISION OF THE NEOTROPICAL GENUS *LISIANTHIUS* (GENTIANACEAE)

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THE GENUS *Lisianthus* as here interpreted comprises 27 species and 2 varieties of woody or semiwoody Gentianaceae distributed throughout the Greater Antilles and continental America, from south-central Mexico to northwestern Colombia. Although the plants are frequently found on roadside banks, and the flowers are usually large and showy, the genus has been rather poorly collected.

The genus was last monographed by Perkins (1902) but that treatment is little more than a checklist with keys to only a fraction of the species now recognized. The present treatment is based upon examination of approximately 1500 specimens, nearly one third of which were especially collected for it. In addition 20 of the 27 species were studied in the field, at which time seeds and preserved material for cytological and anatomical investigation were obtained, and 10 species were grown in the greenhouse.

HISTORY OF THE GENUS

As indicated by the inordinately long list of "excluded names" at the end of this paper, *Lisianthus* has been broadly construed by many authors in the past. In addition, a number of orthographic variants of the name have been used. The genus, as *Lisianthus*, was first defined by Patrick

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Browne (1756). He described two species, both from Jamaica: *Lisianthus erectus*, *foliis lanceolatis floribus singularibus terminalibus*; and *Lisianthus foliis cordato-acuminatis, petiolis brevibus, floribus terminalibus quandoque geminatis*. Browne placed the generic description following that of the first species, as was his custom (W. T. Stearn, *in litt.*). Linnaeus (1767), in taking up Browne's genus, changed the spelling of the name to "*Lisianthus*." He assigned a binomial, *L. longifolius*, to Browne's first species, and *L. cordifolius*, to the second. Linnaeus's spelling of the name has been the one most commonly used. In fact, Rothmaler (Fedde, Repert. Sp. Nov. 53: 178. 1944.) proposed conservation of *Lisianthus* L. over *Lisianthus* P. Browne. However, the proposal was rejected (Taxon 3: 242. 1954). Only Kuntze (1891) and more recently Weaver (1969, 1970) and Robyns and Nilsson (1970) have used the correct and original spelling "*Lisianthus*."

Aublet (1775) described four species from French Guiana, using the name *Lisyanthus*. Aublet's plants are allied to but not congeneric with *Lisianthus* P. Browne, according to the present interpretation. It is difficult to believe that Aublet meant to establish a new genus, in view of the close relationship of his plants to *Lisianthus* P. Browne and the nearly identical spelling of the names. Yet, according to W. T. Stearn (*in litt.*), when Aublet (*loc. cit.*) furnished a detailed generic description, as he did in the case of *Lisyanthus*, his intent was to establish a new genus. For previously established genera, he merely cited the generic name.

If *Lisyanthus* Aubl. is indeed to be interpreted as a genus distinct from *Lisianthus* P. Browne, under the present International Code the name must be treated as an orthographic variant of *Lisianthus* P. Browne and therefore a later homonym (Art. 75) to be rejected (Art. 64).

The younger Linnaeus (1781) added two species to his father's *Lisianthus*: *L. chelonoides* and *L. glaber*, neither of which are referable to *Lisianthus* P. Browne. He cited "*Lisianthus alatus* Aubl." as a synonym of *L. chelonoides*, evidently considering *Lisyanthus* Aubl. as merely an orthographic variant of *Lisianthus* L.

Sprengel (1825) included, in what he called "*Lisianthus* P. Browne," species described by Linnaeus (1767), Aublet (1775), Linnaeus filius (1781), Swartz (1788), Kunth (1818), and others. Most of these are not referable to *Lisianthus* P. Browne as interpreted here.

Grisebach (1839) gave to *Lisianthus* P. Browne the new but nomenclaturally superfluous name *Leianthus* and divided the genus into two sections, LISIANTHIUS (P. Browne) Griseb. and OMPHALOSTIGMA. In addition he accepted *Lisyanthus* Aubl., which he divided into five sections: MACROCARPAEA, CHORIOPHYLLUM, CHELONANTHUS, HELIA (Mart.) Griseb., and CALOLISYANTHUS. Later Grisebach (1845), while maintaining *Leianthus*, elevated *Leianthus* sect. OMPHALOSTIGMA to generic rank as *Petasostylis*. At the same time he used the name *Lisianthus*, attributed to Aublet (1775), for his earlier *Lisyanthus*, but left the content of the genus essentially unchanged.

Bentham (1876) maintained *Leianthus* in the sense of Grisebach

(1839), including *Petasostylis* as a synonym, and *Lisianthus*, which he attributed to Aublet (1775). While accepting the sections of Grisebach (*loc. cit.*) he added three new sections to the latter genus: SYMBOLANTHUS (G. Don) Benth. & Hook. including *Leiothamnus* Griseb., ADENOLISIANTHUS (Progel) Benth. & Hook., and IRLBACHIA (Mart.) Benth. & Hook.

Kuntze (1891) correctly applied *Lisianthus* P. Browne and treated *Lisianthus* L. and *Leianthus* Griseb. as synonyms. Doubting that Aublet (1775) meant *Lisyanthus* to be a new genus, Kuntze adopted the name *Helia* Mart. for *Lisyanthus* (*Lisianthus*) Aubl. *sensu* Grisebach (1839, 1845) and Bentham (1876).

Gilg (1895), whose system has been employed by most recent authors, continued the taxonomic separation made by his immediate predecessors, but used the name *Lisianthus* L. for the plants here referred to *Lisianthus* P. Browne. Gilg employed a rather narrow generic concept based for the most part on pollen morphology. He elevated to generic status all of the groups which Bentham (1876) had previously treated as sections of "*Lisianthus* Aubl."

INTERGENERIC RELATIONSHIPS

In Gilg's (1895) treatment of the family *Lisianthus* (as *Lisianthus*) was associated with seven other genera, most of them small, and all but one, *Tachiadenus* Griseb., restricted to the New World, in the tribe Gentianeae subtribe Tachiinae. Gilg's fundamental taxonomy of the family was based almost entirely on the morphology of the pollen grain. As previously pointed out (Weaver, 1969), Gilg's treatment is unsatisfactory in a number of respects.

Anatomically the Tachiinae resemble the plants in Gilg's tribe Helieae more than they do those in other subtribes of the Gentianeae. Perrot (1898) reported that only the Helieae and Gentianeae-Tachiinae are characterized by having mechanical elements in the cortical area of the stem. Lindsey (1937, 1940) reported that the anatomical features of the Helieae are strikingly similar to those of the Tachiinae, but are more advanced. The two groups of genera are characterized by the nearly constant occurrence of glandular tissue at the base of the ovary, a character found only sporadically in other groups of the family. *Lisianthus* is similar to the Helieae in having fused calyx-lateral traces, found in none of the other generic groups. *Macrocarpaea glabra* (L.f.) Gilg and *Zonanthus cubensis* Griseb., both placed by Gilg in the Tachiinae, do not have fused calyx-laterals, but in other respects the flowers of these species are anatomically identical to those of the Helieae (Lindsey, 1937). Lindsey, in fact suggested, that although the Helieae and the Tachiinae are sufficiently different to be placed in distinct groups "of some grade," the similarities are such that the Helieae be best reduced to subtribal status in the Gentianeae.

According to Gilg (1895) the Helieae are unique in the family in possessing pollen that is held in tetrads or polyads. Since *Macrocarpaea*

glabra and *Zonanthus cubensis* have single pollen grains but are anatomically nearly identical to Gilg's *Helieae*, the value of pollen in tetrads as a character for delimiting a group as large as a tribe seems questionable here.

As explained earlier, *Lisianthus* has been broadly construed in the past, and the name, usually as *Lisianthus* or *Lisyanthus*, has been applied to a rather diverse group of plants. Nilsson (1970) recently surveyed the pollen morphology of these lisianthioid gentians, and his results are at variance with those of Gilg. He reported that, while the pollen types in *Lisianthus* (as delimited in this study), *Macrocarpaea* (Griseb.) Gilg, *Rusbyanthus* Gilg, and several anomalous species are distinctive, the pollen grains of *Adenolisianthus* (Prog.) Gilg, *Calolisianthus* (Griseb.) Gilg, *Chelonanthus* (Griseb.) Gilg, *Helia* Mart., *Irlbachia* Mart., *Lehmaniella* Gilg, *Pagaea* Griseb., *Purdieanthus* Gilg, and *Symbolanthus* G. Don all have approximately "the same basic morphology and some even have features which are transitional within the range of variation of pollen types in the genera."

The taxonomy of these lisianthioid gentians is in a state of chaos. *Macrocarpaea* is the only genus of any size monographed during this century. The genus, as treated by Ewan (1948) is apparently heterogeneous and hence unnatural. Nilsson (1968) found three pollen types in *Macrocarpaea*: a distinctive one; a type identical to that of *Rusbyanthus*, a monotypic genus placed by Gilg in a separate tribe between the *Gentianeae* and the *Helieae*; and a final type, with pollen in tetrads, similar to that found in *Chelonanthus*, a genus placed by Gilg in the *Helieae*. Those species of *Macrocarpaea* with *Rusbyanthus*-type pollen do not deviate significantly in other respects from others in the genus. Neither for that matter does *Rusbyanthus cinchonifolius* Gilg, and the two genera should probably be combined. Those species of *Macrocarpaea* with pollen in tetrads resemble *Chelonanthus* morphologically, and probably should be combined with it.

The remaining lisianthioid genera, all placed by Gilg in the tribe *Helieae*, are in general difficult to characterize morphologically. *Lagenanthus* Gilg, *Lehmaniella*, and *Purdieanthus* differ from the remaining genera in having tubular corollas, but, contrary to Ewan's (1948b, 1952) findings, I have been unable to recognize reliable morphological criteria for separating them. *Helia* is distinctive in having a salverform corolla, but in other respects it closely resembles *Chelonanthus*. Intergradation between *Adenolisianthus*, *Calolisianthus*, *Chelonanthus*, *Irlbachia*, and *Pagaea* completely obscures generic boundaries.

Several species are anomalous in both pollen and gross morphology and appear not to fit into any of the existing genera. These include *Irlbachia caerulescens* (Aubl.) Gilg, *Calolisianthus imthurnianus* (Oliver) Gleason, *Lisianthus chimantensis* Steyerl. & Maguire, and *Calolisianthus frigidus*. The last species, however, according to Nilsson (1970) has pollen approaching that of *Symbolanthus*.

Study of this entire group of gentians has been hampered not only by the pitifully small number of existing specimens but also by the

wretched condition of many of them. Cytological studies may prove of considerable taxonomic value as indicated by the few chromosome counts reported by Weaver (1969). At any rate these plants are in need of concentrated study. Nilsson's pollen work is a good starting point. However, the study, when and if it is made, must be a more comprehensive one than that of Gilg. Gilg's work shows quite well the confusion that often results from reliance on a single character in the classification of a large group of plants. A comprehensive study of the lisianthioid gentians is beyond the scope of this paper and no formal taxonomic decisions concerning them will be made at present. Instead, the following key has been prepared as an aid in distinguishing, wherever possible, the lisianthioid gentians as they now stand (*Irlbachia caerulea*, *Lisianthus chilmantensis*, and *Calolisianthus imthurnianus* are not included; those species of *Macrocarpaea* with pollen in tetrads key out under *Chelonanthus*).

KEY TO THE GENERA OF LISIANTHIOID GENTIANS

1. Stigmas capitate or peltate, indistinctly bilobed, the lobes never linear or flattened; ovary unilocular or weakly bilocular, the placentae barely projecting into the lumen of the ovary, never inrolled; old placentae visible as whitish, erose bands along the margins of the dehisced capsules adjacent to the suture; corolla tube with usually conspicuous bundles of metaxylary fibers; main stem terete. *Lisianthus*.
1. Stigmas bifurcate, the lobes linear or flattened; ovary unilocular or bilocular, the placentae conspicuously inrolled, projecting strongly into the lumen of the ovary and nearly filling it; old placentae not visible on the mature capsules, the margins adjacent to the sutures smooth; corolla tube without bundles of metaxylary fibers; main stem usually 4-angled.
 2. Pollen grains single; inflorescences branched systems of apparently simple dichasia, the divisions subtended by conspicuous foliar bracts; foliage leaves with many pairs of principal lateral veins.
. *Macrocarpaea*, *Rusbyanthus*.
 2. Pollen grains in tetrads or polyads; inflorescence an apparently simple dichasium or much more commonly a compound dichasium, this once or twice bifurcately branched, the lateral divisions often secund or complanate and appearing racemose, the divisions never subtended by foliar bracts; foliage leaves with 2-3 pairs of principal lateral veins.
 3. Bases of the stamens joined by a carnose cylinder of tissue, with triangular teeth opposite the stamens; connectives of the anthers long exserted; inflorescences sessile or nearly so; flowers usually more than 6 cm. long, the corolla funnelform. *Symbolanthus*.
 3. Bases of the stamens connected by a carnose cylinder of tissue or not, but the cylinder never with triangular teeth; connectives of the anthers included or short-exserted; inflorescences long-pedunculate; flowers usually campanulate, or rarely tubular, salverform, or funnelform.
 4. Corolla tubular. *Lagenanthus*, *Lehmaniella*, *Purdieanthus*.
 4. Corolla campanulate, rarely salverform or funnelform.
 5. Corolla salverform; foliage leaves concentrated in the lower half of the stem. *Helia*.

5. Corolla campanulate, rarely funnelform; foliage leaves evenly distributed along the stem.
6. Leaves usually palminerved, sessile, coriaceous or subcoriaceous, rarely penninerved; lobes of the stigma much broader than the style; inflorescence an apparently simple or a compound dichasium, the lateral branches never appearing racemose, or often reduced to a single flower.
 *Calolisianthus*.
6. Leaves, at least the lower ones, penninerved and petiolate, membranaceous or very rarely coriaceous; lobes of the stigma usually but barely broader than the style; inflorescence a once or twice bifurcately branched dichasium, the ultimate branches usually secund or complanate and appearing racemose, or very rarely the inflorescences reduced to a single, terminal flower.
7. Ultimate branches of the inflorescences equal, usually secund or complanate; style conspicuously longer than the ovary; anthers longer than broad; corolla often gibbous; pollen in tetrads or polyads; coarse annuals or perennials.
Chelonanthus, *Adenolisianthus*,
Macrocarpaea arborea, *M. cerronis*,
M. quelchii, *M. salicifolia*.
7. Ultimate branches of the inflorescences often unequal, seldom secund; style usually shorter than the ovary or equalling it; anthers usually about as broad as long; corolla never gibbous; pollen in polyads; annuals.
 *Pagaea*, *Irlbachia*.

Lisianthus is easily separated from the other lisianthioid genera by the characters outlined in the key. The capitate or peltate, indistinctly lobed stigmas, the weakly projecting placentae, the presence of floral fibers, as well as the characteristic pollen morphology mentioned earlier, clearly set it apart as a distinct genus. Therefore I would disagree with Steyermark (1953) who argued for the inclusion of several of the lisianthioid genera, e.g. *Chelonanthus*, *Calolisianthus*, *Irlbachia*, and *Pagaea*, within *Lisianthus*.

MORPHOLOGY

Habit. The species of *Lisianthus* have been described as annual or perennial herbs, shrubs, or trees. *Lisianthus capitatus*, for example, is referred to as an herb by some collectors and a slender tree by others. Field observations, coupled with herbarium studies and observations of cultivated plants have led me to conclude that most of the species are perennials, although some of them may be rather short-lived.

Plants of sect. LISIANTHIUS subsect. HERBACEI appear to be mostly perennial, suffrutescent herbs. Only the primary roots and the basal 1 dm. of stem are distinctly woody. In the field, plants usually have both a green flowering shoot and a dead shoot with old empty capsules present at the same time. Cultivated plants of *L. nigrescens* die back to the base

after flowering and eventually new shoots are produced from the lower nodes. All plants of the subsection are monopodial. The branching is excurrent and generally opposite, and all of the shoots are determinate.

The species of section OMPHALOSTIGMA are similar in aspect and growth form to those of sect. LISIANTHIUS subsect. HERBACEI; they are coarse monopodial herbs with opposite, excurrent branching. *Lisianthus meianthus*, however, is definitely an annual. The only population of this species seen in the field, in eastern Guatemala, was made up of old dead individuals and young vegetative ones. Living and dead shoots were never present on the same plant.

The plants of sect. LISIANTHIUS subsect. FRUTICOSI are all perennials. Most species are subshrubs. Even though the aërial portions of these plants persist more than one season, they are not distinctly woody except at the base. Many of the species flower the first or second year from seed, when they are still predominantly herbaceous. *Lisianthus exsertus*, *L. jefensis*, *L. skinneri*, and sometimes *L. peduncularis* are true shrubs, while *L. capitatus* and *L. umbellatus* become slender trees with stems to 6 meters tall and 8 cm. in diameter.

The plants of sect. LISIANTHIUS subsect. FRUTICOSI are generally not monopodial; the branching is opposite or alternate and is not excurrent. These typically have a single main trunk which is branched above. However, in most species, certain individuals may be entirely unbranched and spindly, resembling herbs. The main shoots are indeterminate, and the inflorescences are borne on determinate, lateral shoots.

The genus may be divided into two artificial groups on the basis of habit. The species of sect. OMPHALOSTIGMA and sect. LISIANTHIUS subsect. HERBACEI are annual or perennial suffrutescent herbs with determinate main axes. The species of sect. LISIANTHIUS subsect. FRUTICOSI are subshrubs, shrubs, or slender trees with indeterminate main axes. This difference in habit is one of the primary characters used here to divide sect. LISIANTHIUS into two subsections. Unfortunately, this character is often difficult to interpret from herbarium specimens. Most species, even the herbaceous ones, are rather tall and coarse and since it may be impossible to fit an entire plant on an herbarium sheet, often only lateral branches are collected. These are determinate in both subsections of sect. LISIANTHIUS and may easily be mistaken for the main axes.

Indument. Most species of *Lisianthus* lack an indument of any sort. However, a very fine pubescence is present in *L. cordifolius* and *L. meianthus*, and in some collections of *L. glandulosus*, *L. longifolius*, and *L. saponarioides*. Although the pubescence may be rather dense, only in *L. cordifolius* and *L. longifolius* is it readily evident without magnification. The individual hairs (or excrescences) are unicellular, 1 mm. or (often considerably) less in length, and the pubescence is best described by the terms "puberulous" or "spiculate."

Stems. Decurrent from the leaf bases on opposite sides of the her-

baceous portions of the stems are pairs of raised parallel ridges, which run the length of each internode and are usually inconspicuous without magnification. The ridges of each pair are generally close together, appearing as one. In some species, however, the ridges of each pair are widely separated, the stem then appearing indistinctly 4-angled. The angles may be expanded into narrow, scarious wings, which in *L. cuspidatus* are minutely serrulate.

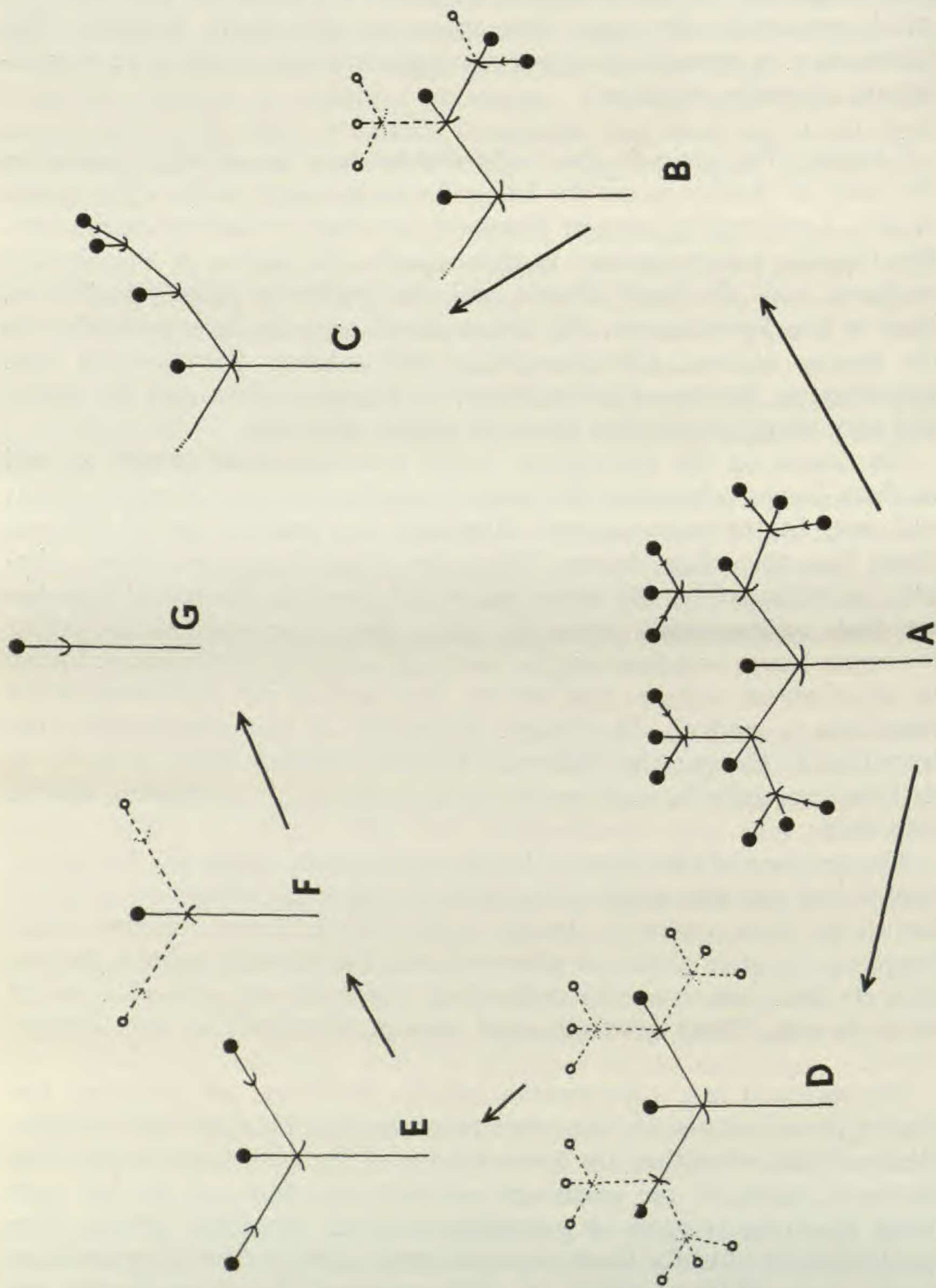
Leaves. The genus is also easily divided into two artificial groups on the basis of whether or not the foliage leaves are truly sessile. The species of sect. LISIANTHIUS subsect. HERBACEI are characterized by sessile, usually clasping foliage leaves. In these species the lamina of the blade is confluent with the basal sheath, and the petiole is entirely lacking at least in the lower leaves; the upper leaves may be short-petiolate. In the species of sect. OMPHALOSTIGMA and subsect. FRUTICOSI of sect. LISIANTHIUS, the leaves are narrowed to a petiole which may be winged and very short, causing the leaves to appear subsessile.

The leaves on the determinate lateral branches of all species, as well as those leaves subtending the lateral branches in sect. OMPHALOSTIGMA and sect. LISIANTHIUS subsect. HERBACEI, are smaller and of different shape than the foliage leaves. When the foliage leaves are elliptic, obovate, or oblanceolate, the upper leaves and those on the lateral branches are ovate or lanceolate; when the foliage leaves are ovate or lanceolate, the upper leaves and those on the lateral branches are lanceolate or linear. In sect. OMPHALOSTIGMA and subsect. HERBACEI of sect. LISIANTHIUS the transition is gradual. In subsect. FRUTICOSI of sect. LISIANTHIUS the transition is abrupt; the difference between the two types of leaves is striking, especially in such species as *L. capitatus*, *L. cordifolius*, and *L. umbellatus*.

The presence of two types of leaves on one plant makes the interpretation of leaf size and shape rather difficult, especially when only a lateral branch has been preserved. In this study "foliage leaves" refers to those leaves on the main shoots of plants of sect. LISIANTHIUS subsect. FRUTICOSI, or those leaves on the main shoot which do not subtend a lateral shoot in sect. OMPHALOSTIGMA and subsect. HERBACEI of sect. LISIANTHIUS.

The leaves of sect. LISIANTHIUS subsect. FRUTICOSI are evergreen, but after a period of one to two years they absciss. Thus, at least in older plants of this subsection, the lower portion of the stem lacks leaves. The leaves of plants in the genus are opposite, the bases of the leaf pair being joined by a green or somewhat scarious, truncated sheath. The sheaths persist after the leaves have abscissed, giving a jointed appearance to the stem. Williams (1968: p. 410) suggested that these sheaths are perhaps homologous with the interpetiolar stipules of the Rubiaceae.

Inflorescences. The inflorescences of *Lisianthus* are rather difficult to interpret, and as a result have been variously described as "cymose,"



“thyrsoid,” or “dichasial.” According to my interpretation, the inflorescences in the genus are basically compound dichasia. There have been, however, many modifications on the basic scheme. The dichasia may be 1 to 5 times compound, or they may be reduced (1) to the point where they appear simple, or (2) to single flowers. The subunits of the dichasia may be 3-flowered, or one flower in each may abort, so that the lateral branches appear scorpioid. The various modifications of the dichasium, as found in *Lisianthus*, with a possible sequence of these modifications, are illustrated in FIGURE 1.

FIGURE 1-A represents a normal (twice-) compound dichasium, the basic type found in the species of sect. OMPHALOSTIGMA and most of those in sect. LISIANTHIUS subsect. HERBACEI. This type of dichasium is found in many gentianaceous genera, including *Centaurium*, *Curtia*, *Sabatia*, and *Schultesia*, and is probably the generalized one in the family. Each of the subunits is subtended by a pair of bracts, the lowermost often foliaceous, the upper ones becoming scarious. The lateral pedicels of each of the ultimate subunits are subtended by a pair of scarious bracteoles, in the axils of which aborted buds are frequently found, indicating that the lateral flowers themselves represent reduced subunits.

From Type 1-A, the modifications have probably proceeded in two directions. FIGURE 1-C represents the type of modified compound dichasium found typically in *Lisianthus brevidentatus* and not infrequently in the remaining species, except for *L. cuspidatus*, of sect. LISIANTHIUS subsect. HERBACEI, as well as *L. seemanii* (sect. LISIANTHIUS subsect. FRUTICOSI). This type, in which the lateral branches appear scorpioid, is easily derived from Type 1-A, as shown in FIGURE 1-B, by the loss of branches or flowers on one side (often but not always the same side) of each trichotomy.

Although it may at first appear to be a simple dichasium, FIGURE 1-E actually represents a reduced compound type. The lateral axes are dichasial branches terminated by a solitary, pedicellate flower. That they are not merely simple, bracteolate pedicels is borne out by two observations: (1) aborted buds are frequently found in the axils of the bracteoles; and (2) the morphology of the axis is different above and below the bracteoles in that the raised parallel ridges mentioned before are absent above them. Type 1-E is the basic type of dichasium found in most of the species of sect. LISIANTHIUS subsect. FRUTICOSI. In addition this type is occasionally found in the other species of sect. LISIANTHIUS subsect. HERBACEI and regularly in *L. cuspidatus*. It is easily derived from Type 1-A, as shown in FIGURE 1-D, by loss of the upper subunits. In this study, Type 1-E will be referred to as an “apparently simple” dichasium.

FIGURE 1-G represents the ultimate in the reduction of the dichasium as found in *Lisianthus*. The lateral branches of Type 1-E, as shown in

FIGURE 1 (opposite). The probable sequence in the evolution of the dichasium in *Lisianthus*. See text above for explanation.

FIGURE 1-F, have been lost by reduction and a single flower remains. This type is found typically in *L. axillaris* and not infrequently in most of the other species of sect. LISIANTHIUS subsect. FRUTICOSI. Types 1-A and 1-C then, are the ones typical of most species of sect. OMPHALOSTIGMA and sect. LISIANTHIUS subsect. HERBACEI. Types 1-E and 1-G are the ones typical of most of the species of subsect. FRUTICOSI of sect. LISIANTHIUS.

The various arrangements of the inflorescences in the genus, with one possible sequence in their evolution, are shown schematically in FIGURE 2. Types 2-A, 2-B, and 2-C are similar, except for the modifications in the dichasia which were discussed earlier. In these three types, the dichasia are terminal and axillary on the primary and secondary shoots, all of which are determinate. The secondary shoots are frequently leafy below the first division and are basically similar to the upper portion of the primary shoot. In some species, such as *Lisianthus brevidentatus* (arrangement as in FIGURE 2-C) and *L. saponarioides* (arrangement as in FIGURE 2-A) the dichasia are frequently sessile or nearly so, and the upper internodes very short, so that the inflorescences appear compacted. Types 2-A to 2-C are characteristic of the species in sect. OMPHALOSTIGMA and subsect. HERBACEI of sect. LISIANTHIUS.

The remaining types shown in FIGURE 2 are characteristic of the species in sect. LISIANTHIUS subsect. FRUTICOSI. In these species the primary axes are indeterminate. The dichasia are axillary or, more commonly, terminal and axillary on determinate lateral shoots, which in this study will be referred to as "flowering branches."

Except for *Lisianthus* and a few closely related genera, the Gentianaceae are herbaceous with terminal inflorescences. The condition in sect. LISIANTHIUS subsect. FRUTICOSI, in which the plants are woody with indeterminate axes, must certainly be a derived one. Since the species of subsect. FRUTICOSI of sect. LISIANTHIUS are characterized almost entirely by having apparently simple dichasia, the evolution from determinate to indeterminate main axes has probably been through the type represented by FIGURE 2-B.

Flowering branches are probably homologous with the lower lateral shoots of Types 2-A to 2-C. The basic type is shown in FIGURE 2-D. The branching is opposite and each division is terminated by an apparently simple dichasium. One to three pairs of reduced leaves are present below the lowermost trichotomy, but rarely are any present above. Rather, the upper divisions are subtended by somewhat foliaceous or scarious bracts. This type is found occasionally in most species of sect. LISIANTHIUS subsect. FRUTICOSI and regularly in *L. latifolius* and the *L. skinneri* complex.

Specialization has progressed from Type 2-D in two directions. Through Types 2-E (*L. longifolius*) to 2-F (*L. longifolius*) and 2-G (*L. cordifolius*) the flowering branches become more complex and freely branched, with reduced leaves found above the first division and on the secondary axes. The dichasia are mostly reduced to single flowers. The branching is op-

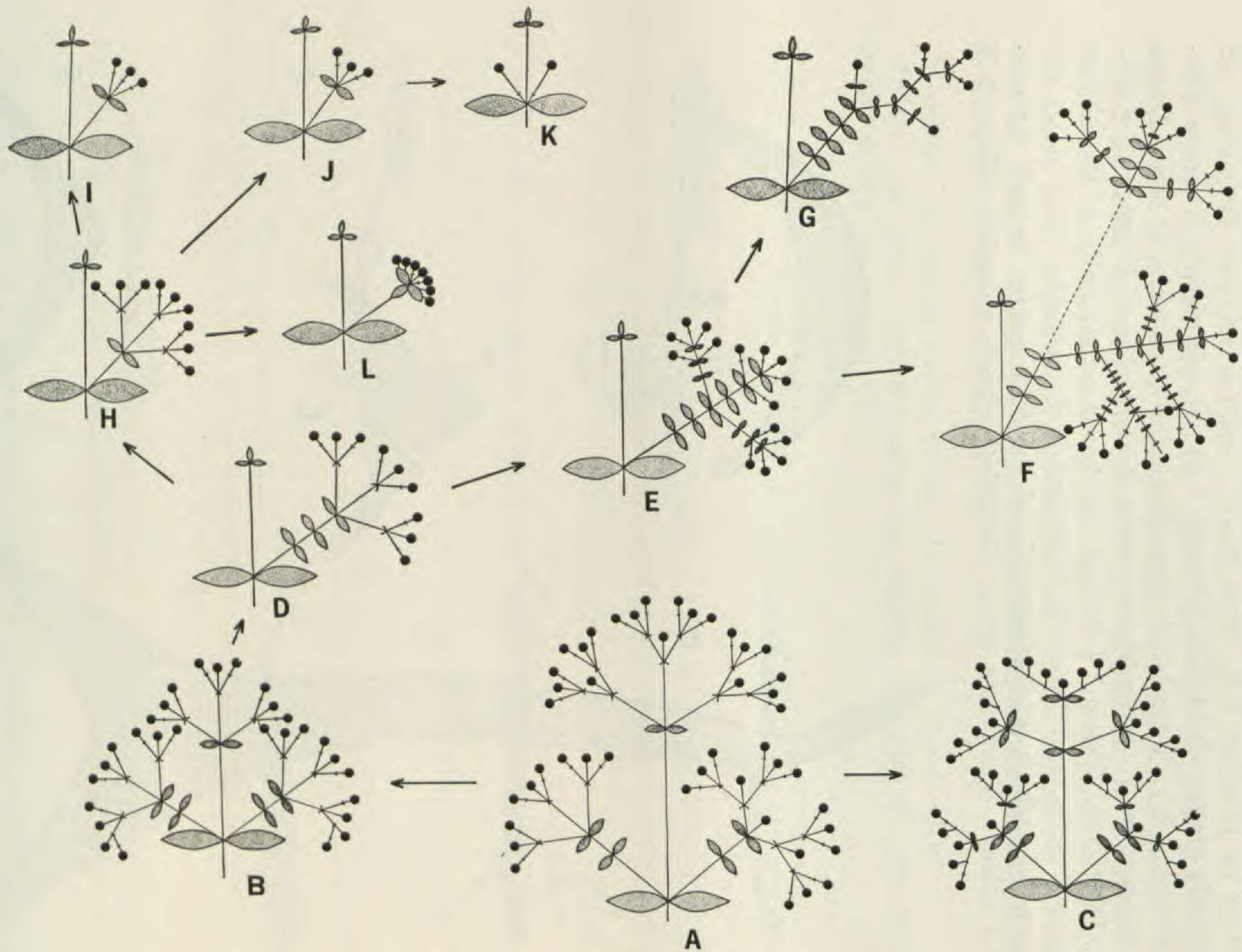


FIGURE 2. The arrangement of the inflorescences in *Lisianthus* and the probable sequence in the evolution of this arrangement. See text for explanation.

posite, alternate or bifurcate in Types 2-E and 2-F, and nearly always bifurcate in Type 2-G.

From Type 2-D through Types 2-H to 2-K, the flowering branches become simpler. The leaves are reduced in number to a single pair subtending the lowermost division, or, are lacking. The branching is reduced, resulting in (FIGURE 2-I) three flowers, each a reduced dichasium, an apparently simple dichasium (FIGURE 2-J), or, ultimately, a single flower (FIGURE 2-K). Type 2-H is typical in all of the species of series *Longifolii* (except for *L. axillaris*) and series *Exserti* of sect. LISIANTHIUS subsect. FRUTICOSI. Types 2-I to 2-K are found occasionally in the above-mentioned series, and Type 2-K is typical in *L. axillaris*.

Type 2-L, which is characteristic of the two species in sect. LISIANTHIUS subsect. FRUTICOSI series *Umbellati*, closely resembles Type 2-H

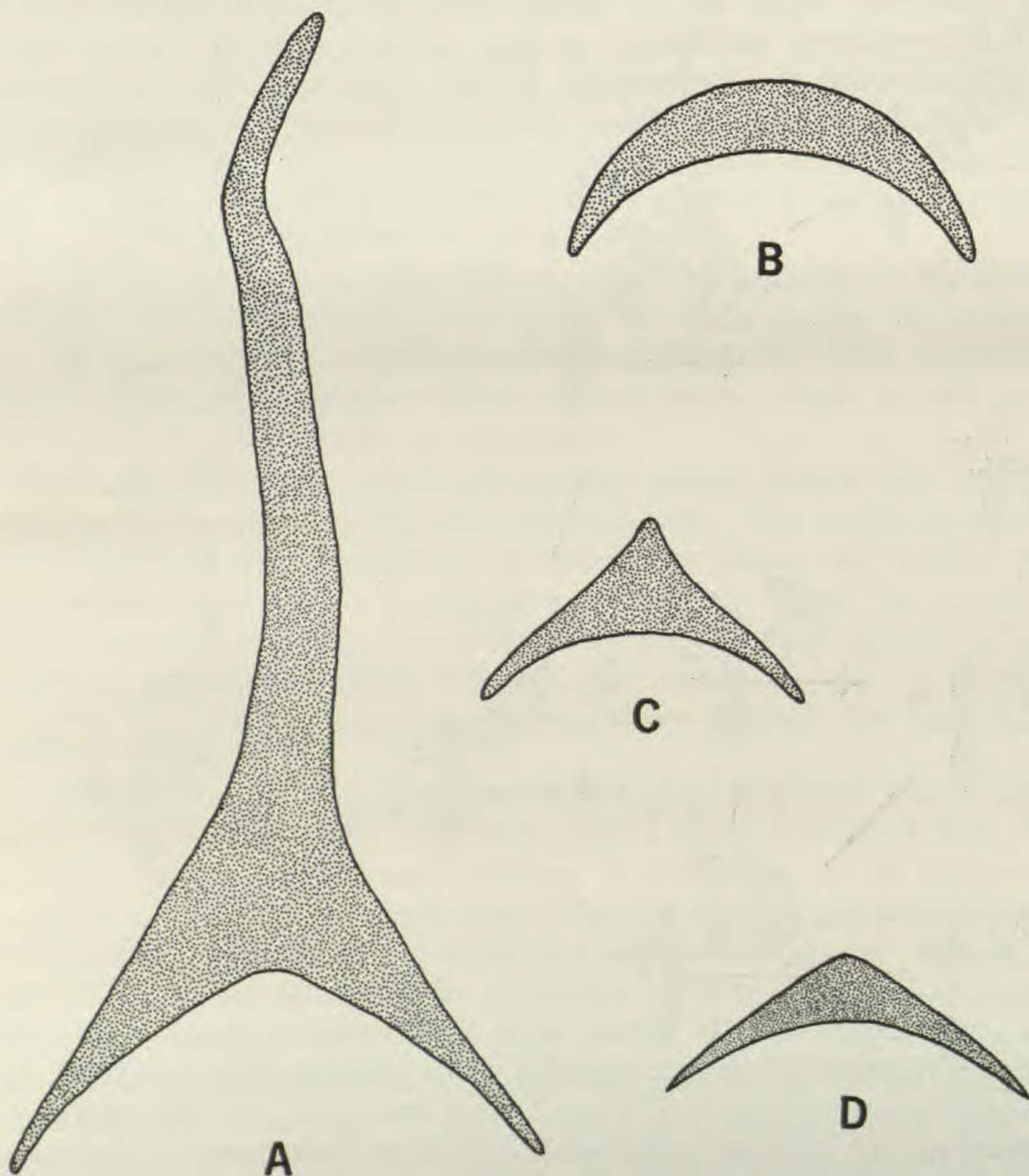


FIGURE 3. Cross-sections of the calyx lobes of representative *Lisianthus* species. A. *L. longifolius*, lobes alate; B. *L. viscidiflorus*, lobes completely ecarinate; C. *L. cordifolius*, lobes carinate; D. *L. auratus*, lobes ridged.

when dissected, and is clearly derived from it. The internodes above the lowermost division and the stalks and branches of the dichasia are greatly shortened, the whole affair resembling a capitulum or an umbel. The bracts subtending the two lowest divisions are large and foliaceous and appear involucrate.

Flowers. In most species the calyx lobes are carinate abaxially to some degree. The width of the keel varies from species to species, from a slight, almost imperceptible ridge along the midline, to a conspicuous wing 4 mm. broad. In a few species the lobes are completely ecarinate. The terms used in this study to describe the abaxial surface of the calyx lobes are defined below. Lobes, drawn in cross section, representing each of the types are shown in FIGURE 3.

Ecarinate: the abaxial surface of the lobes uniformly convex (3-B).

Ridged: the lobes thickened along the midline, the sides in cross section straight or slightly concave (3-D).

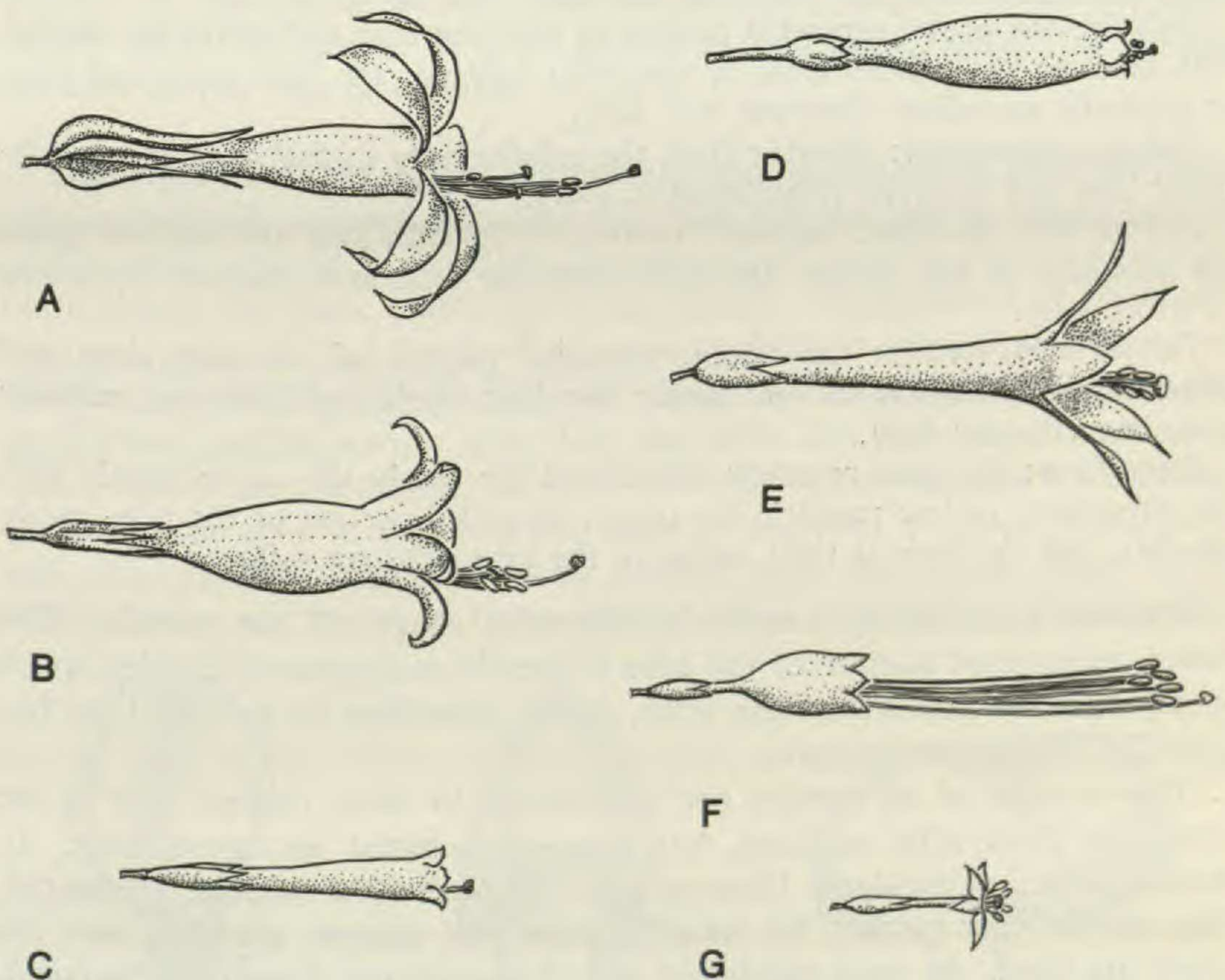


FIGURE 4. Flowers of representative species of *Lisianthus*, showing the various corolla shapes and the posture of the corolla lobes, $\times 1$. A. *L. longifolius*, corolla tubular-funnelform, lobes recurved; B. *L. adamsii*, corolla tubular-funnelform, inflated, lobes somewhat recurved; C. *L. brevidentatus*, corolla tubular, lobes spreading; D. *L. skinneri*, corolla tubular, inflated, lobes recurved at the tips; E. *L. nigrescens*, corolla funnelform, lobes spreading; F. *L. exsertus*, corolla tubular-campanulate, lobes erect; G. *L. saponarioides*, corolla salverform, lobes flaring.

Carinate: the lobes strongly thickened along the midline, the thickened portion slightly projecting; in cross section the sides strongly concave (3-C).

Alate: the thickened portion along the midline of the lobes expanded into a thin, flat, membranous and strongly projecting wing (3-A).

Although the last three calyx-lobe types intergrade from species to species, they are generally constant in a given species.

The structure of the corolla of all the species is basically the same. However, the proportions of the sectors vary, resulting sometimes in strikingly different shapes. The basal sector of the corolla tube, usually the lower third or sometimes the lower half, that portion enclosing the ovary and in turn enclosed by the calyx, is constricted into a narrow tube with parallel sides. The stamens are inserted near the distal end of this constriction. Above the insertion of the stamens, the corolla tube expands, often abruptly but sometimes gradually, into a somewhat broader tube which is terminated in the limb. The terms used in this study to describe the various corolla shapes are defined below.

Tubular: the upper, expanded portion of the tube long and relatively narrow, with more or less parallel sides or somewhat inflated; the limb short and erect or gradually spreading (FIGURES 4-C, 4-D).

Tubular-funnelform: differing from the tubular only in that the limb is relatively long and recurved (FIGURES 4-A, 4-B).

Funnelform: the upper expanded portion of the tube long and narrow, tapering gradually to the throat; the limb relatively long and gradually spreading (FIGURE 4-E).

Tubular-campanulate: the upper, expanded portion of the tube short and broad, tapering slightly to the throat; the limb short and erect or gradually spreading (FIGURE 4-F).

Salverform: the tube narrowly constricted for nearly the entire length, with the sides more or less parallel; the upper, expanded portion of the tube nearly obsolete, and the limb at right angles to the tube (FIGURE 4-G).

Pressing and drying frequently alter the shape of the corolla. The lower, constricted portion of the tube is greatly exaggerated in dried specimens, and the posture of the limb, erect, spreading or recurved, is frequently difficult to interpret.

The corollas of all species are marcescent to some degree, that is the corolla withers after anthesis but does not absciss for some time. In some species, particularly those of sect. LISIANTHIUS subsect. HERBACEI, the corolla may persist for months after the capsule matures and the seeds are shed. In most species of sect. LISIANTHIUS, however, the corolla does absciss before the capsule matures. The degree to which the corolla persists appears to be correlated with the amount of sclerification of the vascular traces to the corolla. Those species in which the fibrous bundles are most conspicuous and best developed are the species in which the corolla persists on the mature capsules.

The stamens are inserted on the corolla tube ca. $1/2$ – $1/3$ of the distance

from the base to the apex in sect. LISIANTHIUS or just below the apex in sect. OMPHALOSTIGMA. In dried flowers, the point at which the filaments become free from the corolla is usually visible externally as a slight swelling on the lower constricted portion of the corolla tube.

In sect. OMPHALOSTIGMA the filaments are of equal length in a given flower; in sect. LISIANTHIUS the filaments are of unequal length in a given flower, usually two short, two of intermediate length, and one long. From observations of greenhouse plants, it appears that the filaments are at their full length when the flower is open and the anthers have dehisced. The filaments are exerted in all species; they protrude from the throat of the corolla tube but do not necessarily surpass the lobes.

The style is filiform and always exerted, in some species surpassing the corolla lobes in pressed flowers. As is the case with the filaments, the style appears to elongate little after the flower is mature and the anthers have dehisced. In the majority of species the style always surpasses the filaments, the anthers never coming into direct contact with the stigma; in the species of sect. OMPHALOSTIGMA, the style is always overtopped by the filaments; in a few species of sect. LISIANTHIUS, the relative position of the two is variable.

The stigma is either capitate or peltate, and in contrast to most gentians, only indistinctly bilobed (FIGURE 5). The peltate type is more common in the genus, and it is probably the generalized type in that it resembles more closely the basic condition in the family. Most genera of Gentianeae are characterized by having a deeply bilobed stigma with linear or lamellar lobes. The peltate type of stigma in *Lisianthus* resembles this generalized gentianaceous type, but the lobes are very small and somewhat connate on the adaxial surface. In addition the margins are reflexed, obscuring the apex of the style and causing the lobes to appear hemispherical. The capitate stigma is easily derived from the peltate type. In its extreme form, as found in *L. longifolius* and *L. cordifolius*, the stigmatic

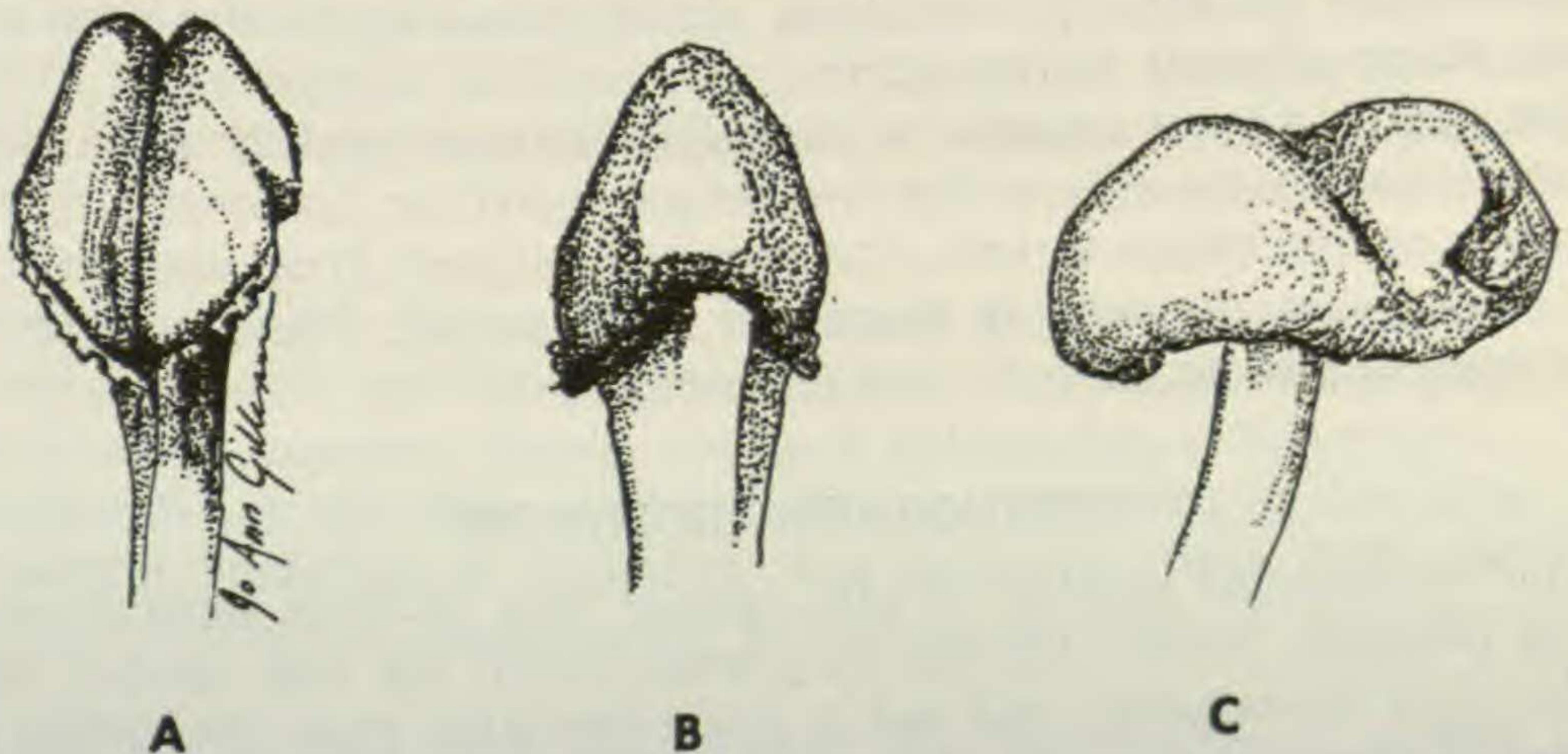


FIGURE 5. Stigmas of *Lisianthus*, $\times 15$. A. *L. longifolius*, stigma capitate, showing the lobes; B. The same, another view; C. *L. nigrescens*, stigma peltate.

lobes are further reduced in size and are entirely connate along their adaxial surfaces; the margins are not at all reflexed. The stigmas of the closely interrelated *L. glandulosus*, *L. laxiflorus*, and *L. troyanus*, although capitate, are somewhat intermediate to the peltate type. In these species the lobes are small with barely reflexed margins, but they are not entirely connate.

Grisebach (1839) divided his genus *Leianthus* (= *Lisianthus*) into two sections based on their supposedly distinctive stigmatic types: sect. OMPHALOSTIGMA, with peltate stigmas, and sect. LISIANTHIUS, with capitate stigmas. Later (1845) Grisebach elevated sect. OMPHALOSTIGMA to generic rank, as *Petasostylis*, without changing its definition, and included within it *L. saponarioides* and *L. nigrescens*. At the same time he included in the genus *Leianthus* (his old section *Lisianthus*), *L. cordifolius*, *L. cuspidatus*, *L. exsertus*, *L. latifolius*, *L. longifolius*, and *L. umbellatus*. The genera were separated primarily by the type of stigma, as the sections were earlier. Actually, *L. nigrescens* and *L. saponarioides* are the species in which the form of the peltate stigma is most extreme. However, except for *L. longifolius* and *L. cordifolius*, all of the species included in *Leianthus* (*sensu* Grisebach, 1845), have definitely peltate stigmas.

Lisianthus nigrescens, according to my interpretation, is more closely related to all of the species included by Grisebach in *Leianthus* (*sensu* 1845) than it is to *L. saponarioides*. In fact it is so similar to *L. cuspidatus* that most authors have considered the two synonymous.

I have found the type of stigma to be nearly useless as a criterion in determining relationships in *Lisianthus*. The peltate and capitate types intergrade from species to species and sometimes, particularly in *L. auratus* and *L. seemannii*, within a species. Both types, in distinct form, are found in the Jamaican *L. longifolius*. *Petasostylis* has not been accepted by any authors since Grisebach, and there appears to be no reason whatever for maintaining it.

Fruits. The fruit is a semiwoody, bivalvate, loculicidal capsule. Upon dehiscence the placentae are visible as whitish, erose bands along the edge of the valves adjacent to the sutures.

The nearly mature capsule is generally flattened slightly on a plane perpendicular to the suture and is oblong-ellipsoid or fusiform in shape. However a few species in sect. LISIANTHIUS subsect. HERBACEI differ in that the capsules are ovoid in shape and not flattened. The two types are illustrated in FIGURE 6.

CHROMOSOME NUMBERS

The chromosome number of nine species was recently reported as $n = 18$ (Weaver, 1969). During the present study, the nine species listed below were investigated, and not a single deviation from the earlier reported number has been found:

L. adamsii (Weaver 2342)

- L. auratus* (Weaver & Wilbur 2253)
L. axillaris (Weaver & Wilbur 2252)
L. brevidentatus var. *brevidentatus* (Weaver 2184)
L. laxiflorus (Weaver & Howard 2349)
L. nigrescens var. *nigrescens* (Weaver 2134)
L. nigrescens var. *chiapensis* (Weaver 2168)
L. oreopolus (Weaver 2173)
L. peduncularis (Weaver & Wilbur 2247)
L. quichensis (Weaver 2178)
L. viscidiflorus (Weaver 2179)

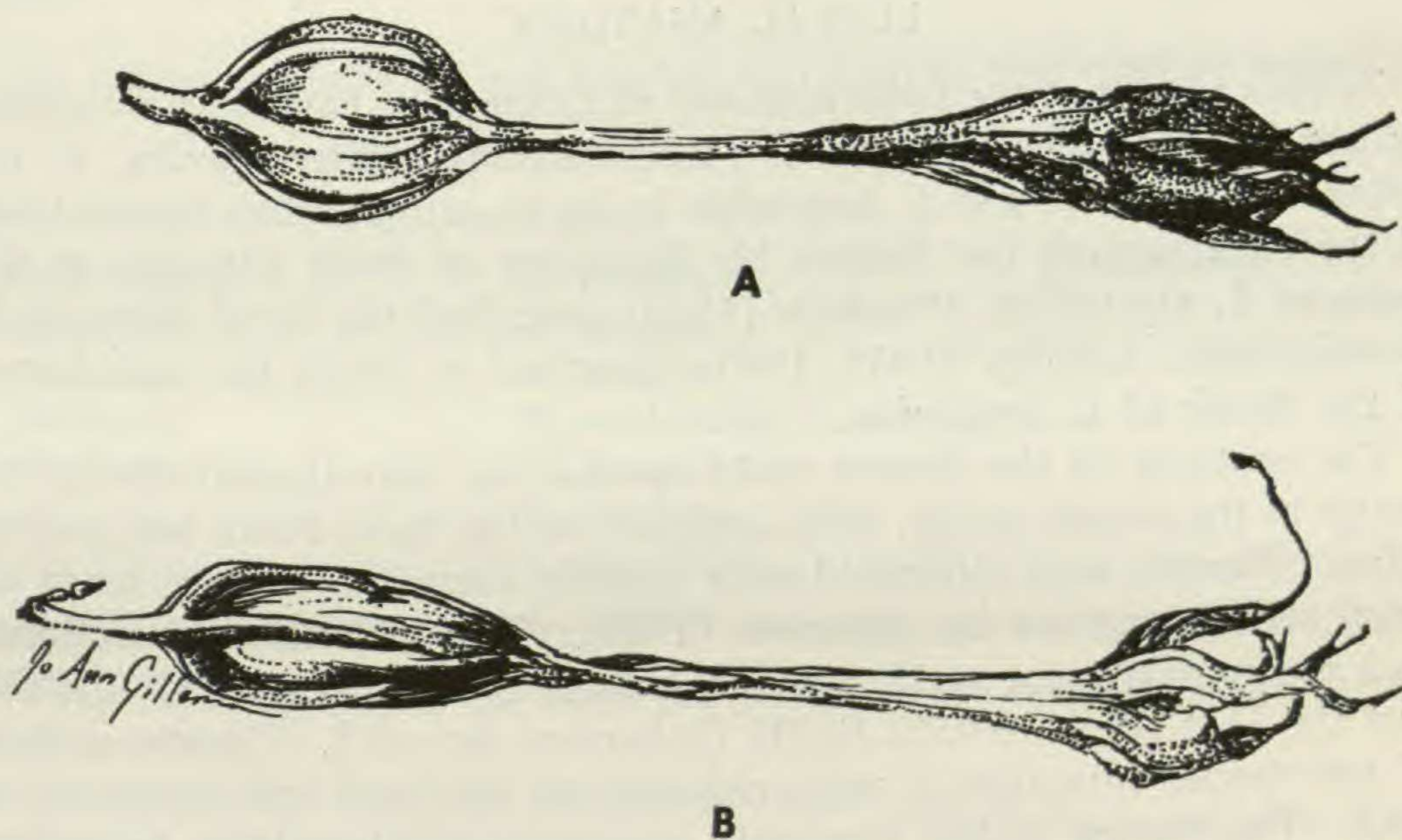


FIGURE 6. Capsules of *Lisianthus*, $\times 2$. A. *L. nigrescens*, capsule broadly ovoid; B. *L. cordifolius*, capsule oblong-ellipsoid.

Flower buds were fixed in modified Carnoy's solution and the pollen mother cells were subsequently squashed in acetocarmine. Voucher specimens have been deposited at DUKE, except for *L. laxiflorus* which is at A.

With the exception of *Gentiana* L., *Gentianella* Moench, and *Sabatia* Adans. little is known of the chromosome numbers in the Gentianaceae. However from a perusal of the summaries of chromosome numbers in the Gentianaceae (Rork, 1949, and Löve, 1953) and the chromosome indices, it appears that most of the larger genera are characterized by having more than one chromosome number. *Sabatia*, in which there is a wide array of numbers (Perry, 1967), is outstanding in this respect. *Halenia* Borkh., on the other hand is similar to *Lisianthus* in that all of the six species investigated, including representatives from both the Old and New World, are characterized by having the same chromosome number.

Although not all of the species have been investigated, a notable gap being the two species in sect. OMPHALOSTIGMA, change in chromosome number appears to have played no evolutionary role whatever within

Lisianthus. Nor has chromosome number been helpful in determining relationships within the genus. In the genera supposedly most closely related to *Lisianthus*, comprising the Gentianeae-Tachiinae of Gilg (1895), only two species, *Eustoma russellianum* G. Don, with $n = 36$ (Rork, 1949), and *Macrocarpaea thamnoides* (Griseb.) Gilg, with $n = 21$ (Weaver, 1969), have been investigated. Although these counts are too scanty to give more than a hint as to the relationships between *Lisianthus* and its supposed relatives, as previously pointed out by Weaver (*loc. cit.*), they do suggest a possible relationship between *Lisianthus* and *Eustoma*.

FLORAL ANATOMY

Various aspects of the floral anatomy of *Lisianthus* have been described by previous investigators. Perrot (1898) included three species, *L. exsertus*, *L. nigrescens*, and *L. longifolius* in his investigation of the anatomy of the Gentianaceae but limited his discussion of floral anatomy to the ovary of *L. nigrescens*. Woodson (1936) described the floral fibers of *L. brevidentatus*. Lindsey (1937, 1940) described in detail the vasculature of the flower of *L. longifolius*.

The anatomy of the flowers of 21 species was investigated during the course of the present study, with emphasis on the floral fibers and placentation. Flowers were infiltrated with paraffin using the tertiary butyl alcohol series suggested by Johansen (1940). The material was sectioned on a rotary microtome at 15μ and stained in 1% Safranin in 95% EtOH and 1% Fast Green in 95% EtOH (Johansen, *loc. cit.*). Flowers of most of the species investigated were collected in the field and preserved in FAA. The flowers of the remaining species were taken from herbarium specimens and boiled in water immediately before infiltration.

The vascular traces to the calyx, corolla, and androecium of *Lisianthus* are variously supplied with heavily lignified elements. These elements were described by Woodson and illustrated (1936) from what he called *L. brevidentatus*. Woodson's material was collected by W. A. Schipp in British Honduras and was almost certainly *L. brevidentatus* var. *collinus*, since the typical variety of *L. brevidentatus* is not known from that country and Schipp 1205 is the type and only collection of var. *collinus*.

According to Woodson (1936), these heavily lignified elements are primarily fibers of metaxylary origin with a few phloem or pericyclic fibers around the periphery of the bundles. They are most conspicuous in the calycine and corolline traces but are also found in the staminal traces when the stamens are still adnate to the corolla tube.

The present study has shown that there is considerable interspecific variation in the degree to which the fibers are developed, both in the same organ and among the various organs. Only in a very few species [*L. oreopolus*, *L. brevidentatus*, *L. viscidiflorus* (sect. LISIANTHIUS subsect. HERBACEI), *L. skinneri*, *L. longifolius*, *L. glandulosus* (sect. LISIANTHIUS subsect. FRUTICOSI), and *L. meianthus* (sect. OMPHALOSTIGMA)] are they well developed in the calyx, and then always more so in the tube

than in the lobes. In general, the fibers are poorly developed in the staminal traces. Only in *L. silenifolius*, *L. brevidentatus*, and *L. longifolius* are they at all conspicuous.

It is in the corolline traces that the fibers are most widespread in occurrence in the genus; they are well-developed in 15 of the 21 species investigated. In those species in which they occur, the fibers are poorly developed at the base of the corolla in fresh, newly opened flowers; however, in older flowers the fibers are well developed nearly to the base of the corolla. The development thus appears to be basipetal, as would be expected in a determinate organ. The fibers never extend into the corolla lobes.

The following species are well supplied with fibers in their corolline traces:

Sect. LISIANTHIUS		Sect. OMPHALOSTIGMA
Subsect. HERBACEI	Subsect. FRUTICOSI	
<i>L. brevidentatus</i>	<i>L. adamsii</i>	<i>L. meianthus</i>
<i>L. nigrescens</i>	<i>L. auratus</i>	
<i>L. oreopolus</i>	<i>L. axillaris</i>	
<i>L. quichensis</i>	<i>L. cordifolius</i>	
<i>L. silenifolius</i>	<i>L. glandulosus</i>	
	<i>L. laxiflorus</i>	
	<i>L. longifolius</i>	
	<i>L. skinneri</i>	

In the following species the fibers are poorly or not at all developed in the corolline traces:

Sect. LISIANTHIUS	
Subsect. HERBACEI	Subsect. FRUTICOSI
<i>L. viscidiflorus</i>	<i>L. capitatus</i>
	<i>L. exsertus</i>
	<i>L. latifolius</i>
	<i>L. troyanus</i>
	<i>L. umbellatus</i>

In all of the latter group of species, the marcescent corolla abscisses before the capsule matures and the seeds are shed. In the former group of species, except for *L. skinneri*, the corolla is more or less persistent on the mature capsule. Well developed fibers in the corolline traces obviously give support to the marcescent corolla and determine to a large extent the degree to which it persists.

Similar floral fibers were reported by Woodson (1936) to be present in *Coutoubea spicata* Aubl. (Helieae), *Canscora* Lam., *Centaurium* Gilib. (Gentianeae-Erythraeinae), and *Zygostigma* Griseb. (Gentianeae-Tachiinae) but not in those genera, e.g. *Chelonanthus* Gilg, *Macrocarpaea* Gilg, *Calolisianthus* Gilg, etc., of the Helieae and Gentianeae-Tachiinae included in *Lisianthus* by some authors.

According to Gilg, the Gentianeae-Tachiinae, of which *Lisianthus* is a member, are characterized by having unilocular ovaries. He illustrated

the ovaries of *L. nigrescens* (p. 92, Fig. 41-J) and *L. saponarioides* (p. 92, Fig. 41-E, actually *L. acuminatus* Perk., as will be explained later) as being unilocular. Perrot (1898) also described the ovary of *L. nigrescens* as being unilocular. However the present study has shown that all stages toward bilocularity, including complete bilocularity, are found in the ovaries of the various species.

The ovary of *Lisianthus* is bilocular at the base in all of the flowers examined. In most of the species, however, the septum becomes incomplete for 15 to 500 μ at the base of the placentae or below. As the placentae form, they abut and fuse and the ovaries appear bilocular again in the mid-portions. In five of the six species of sect. LISIANTHIUS subsect. HERBACEI (*L. brevidentatus* being the exception) examined, however, the placentae do not abut except in the upper portions, and the ovaries are unilocular for most of their length. Three of the species examined, *L. axillaris*, *L. skinneri*, and *L. latifolius*, in subsect. FRUTICOSI, are completely bilocular; *L. troyanus* and *L. laxiflorus* are bilocular except for a portion 15 μ in length where the septum is incomplete. In most of the species then, the ovaries are unilocular with parietal placentation but show varying tendencies toward bilocularity. A few species are bilocular with axile placentation.

Buds of *Lisianthus umbellatus*, a species characterized by having an almost completely bilocular ovary when mature, were sectioned at several stages in their development. In younger buds the septum is incomplete and the placentae completely separate. The arms of the septum and the inner surface of the placentae are covered with a distinct epidermis. In older buds the placentae abut as they enlarge; the epidermis then breaks down and the placentae fuse.

In those species where it is bilocular or nearly so, the ovary is flattened along an axis perpendicular to the septum, and the placentae are brought into close physical contact thus allowing fusion to take place. In the species of sect. LISIANTHIUS subsect. HERBACEI where it is unilocular for most of its length, the ovary is not flattened and the placentae are widely separated.

A few miscellaneous aspects of the floral anatomy of *Lisianthus* should be noted. Large crystals (druses) are found around the periphery of the basal portion of the ovary of *L. troyanus*. Crystals were not found in any other species of *Lisianthus*. Surrounding the basal portion of the ovary of all species investigated is a 5-lobed ring of densely staining, non-vascularized, glandular tissue. According to Lindsey (*loc. cit.*), ovaries glandular at the base are found in most of the genera associated with *Lisianthus* in the Gentianeae-Tachiinae by Gilg as well as those in the anatomically similar Helieae.

BREEDING SYSTEMS

The breeding systems of *Lisianthus* have not been studied in the field; the following observations were made from plants grown in the green-

houses of Duke University. All six species studied, *Lisianthus adamsii*, *L. capitatus*, *L. cordifolius*, *L. longifolius*, *L. nigrescens* (var. *chiapensis*) and *L. troyanus*, are self-compatible.

In all the species cited above, except *Lisianthus nigrescens*, the styles are considerably longer than the filaments, and the anthers do not come into physical contact with the stigmas. The flowers of these species are proterandrous and thus appear to be adapted for outcrossing. These plants, in fact, seldom set seed unless the flowers were artificially pollinated. In most populations of *L. nigrescens* var. *chiapensis*, on the other hand, at least some of the filaments in each flower are as long as the styles, and some of the anthers do come into direct contact with the stigmas. The flowers of members of this taxon are characterized by having the stigmas receptive as the anthers dehisce and thus are adapted for self-pollination. These plants invariably set seed profusely in the greenhouse without artificial pollination.

All species of *Lisianthus* have relatively showy flowers which produce copious amounts of nectar from glands at the base of the ovary, and although they are odorless, would seem to be quite attractive to animal pollinators. Little is known, however, of the pollinators of *Lisianthus*. No insects were observed on the plants in the field. Judging from the strikingly different colors of some of the flowers and the wide variation in flower form, particularly the shape and size of the corolla and the degree to which the styles and filaments are exerted, the various species are probably adapted to pollination by a wide variety of animals. In fact, specialization leading to pollination by different vectors has probably been a major evolutionary force within the genus.

Smaller bees of the genus *Bombus* were frequent visitors during the summer months to flowers of cultivated *Lisianthus adamsii*, *L. cordifolius*, *L. longifolius*, and *L. troyanus*. In all of these species the corolla tubes are relatively wide and the styles and filaments are well exerted. In addition the corolla lobes are widely spreading or even recurved, further exposing the anthers and stigmas. Bees invariably landed on the filaments and crawled into the corolla tube in search of the abundant nectar; they never came into contact with the anthers or the stigmas. Although *Bombus* is perhaps not a pollinator of the *Lisianthus* species in their native habitats, its behavior on cultivated plants strongly suggests that nectar-seeking bees are not effective pollinators of those species with well exposed anthers and stigmas.

These species are probably pollinated by various lepidopterans, pollen gathering bees, and/or hummingbirds. *Lisianthus saponarioides*, with erect flowers and short, narrow corolla tubes seems well suited to pollination by butterflies. Species in which the corolla tube is relatively broad and the anthers and stigmas held within the erect or slightly spreading corolla lobes are possibly pollinated by nectar-seeking bees. It appears that closely sympatric species of *Lisianthus* always differ strikingly in corolla and/or flower form.

POLLEN MORPHOLOGY

Nilsson (1970) has recently described the morphology of pollen grains of what he called "*Lisianthus s. lat.*" His study, based on acetolyzed grains observed both with the light microscope and scanning and transmission electron microscopes, included a large number of plants not referable to *Lisianthus* P. Browne. Only Nilsson's "*Longifolius*-type" is found in that genus; the following description is condensed from Nilsson's (*loc. cit.*, p. 4).

Pollen grains in monads, 3-colporate, subprolate to prolate, $28-50 \times 23-40 \mu$. Colpi meridional, $2/3-3/4$ of polar axis. Exine $3-5 \mu$ thick. Sexine as thick as nexine, or thicker, reticulate or occasionally \pm smooth. Lumina angular, ca. $0.5-7 \mu$ in diameter. Muri ca. $0.5-1 \mu$ wide.

According to Nilsson (1970), the plants here included in *Lisianthus* are homogeneous in their pollen type. Of the species examined, 21 are characterized by having grains with a finely reticulate sexine pattern; the coarseness of the reticulum varies intraspecifically as well as interspecifically and therefore appears to be of no taxonomic significance. Only *L. exsertus* varies significantly in its pollen morphology, and only in the sexine pattern which is nearly smooth when observed with the light microscope, but shows an intricate, very closely interwoven pattern in scanning pictures. The sexine of the grains of *L. exsertus* is basically the same as that in the other species, except that the lumina of the reticula are greatly reduced (Nilsson, *in litt.*)

According to Nilsson (1970) the pollen type found in *Lisianthus* (his *Longifolius*-type) is distinct from and not easily correlated with the pollen types of the other plants included in his study. (These plants and their relationship to *Lisianthus* has already been discussed.) It differs from the only other single-grain types in its prolate or subprolate grains with a fine reticulate pattern, relatively narrow muri, and more or less angular lumina, and in the absence of verrucoid processes (Nilsson, *loc. cit.*).

Nilsson (1970) found that *Lisyanthus loranthoides* Griseb., a Peruvian species, has pollen of his *Longifolius*-type. Grisebach (1839, 1845) placed this species in a monotypic section, CHORIOPHYLLUM, of *Lisyanthus* Aubl. (not the same as *Lisianthus* P. Browne), but suggested that perhaps it belonged in a separate genus. Macbride (1959), although not having seen any specimens of this taxon, suggested that *ex char.* it might be the same as *Macrocarpaea chlorantha* Gilg. An isotype of *L. loranthoides* (Matthews 1315, OXF) has been seen. With its conspicuously bifurcate stigmas, 4-angled stems, and calyx, with obtuse lobes, fused for nearly $2/3$ its length, this species clearly is not referable to *Lisianthus* as here interpreted. Morphologically it appears to be somewhat intermediate between it and *Macrocarpaea*, and probably should, as Grisebach suggested, be placed in a distinct genus.

INTRAGENERIC RELATIONSHIPS

Chromosome number, floral anatomy, and pollen morphology have yielded few clues for determining relationships between the species of *Lisianthus*. Therefore a reliance on gross morphological features is necessary. Since there are few morphological trends within the genus, an infrageneric classification based on them must of necessity be highly subjective.

Lisianthus longifolius, the lectotype species of the genus, and the other species also characterized by basically tubular or funnellform corollas and unequal filaments inserted in the lower half of the corolla tube, form a logical group which I am calling section LISIANTHIUS. The remaining two species, *L. meianthus* and *L. saponarioides*, which differ strikingly by their salverform corollas and their equal filaments inserted near the apex of the corolla tube, seem to form a second group of equal rank to be called section OMPHALOSTIGMA.

Section LISIANTHIUS is comprised of two subsections, the HERBACEI with 7 species, monopodial, suffrutescent herbs with determinate main axes, usually compound dichasia, and sessile leaves, and the FRUTICOSI with 18 species, subshrubs, shrubs, or even small trees with indeterminate main axes, usually apparently simple dichasia, and petiolate leaves.

Section LISIANTHIUS subsect. FRUTICOSI is rather heterogeneous in a number of respects, and three subgroups are readily recognizable. Two Jamaican species, *Lisianthus umbellatus* and *L. capitatus* differ strikingly from all other members of the subsection in that their inflorescences appear capitate or umbellate owing to extreme reduction of all the branches. These two species comprise the series *Umbellati*. The remaining species are characterized by having diffuse inflorescences which are obviously dichasioid. However, one of these, the Jamaican *L. exsertus*,

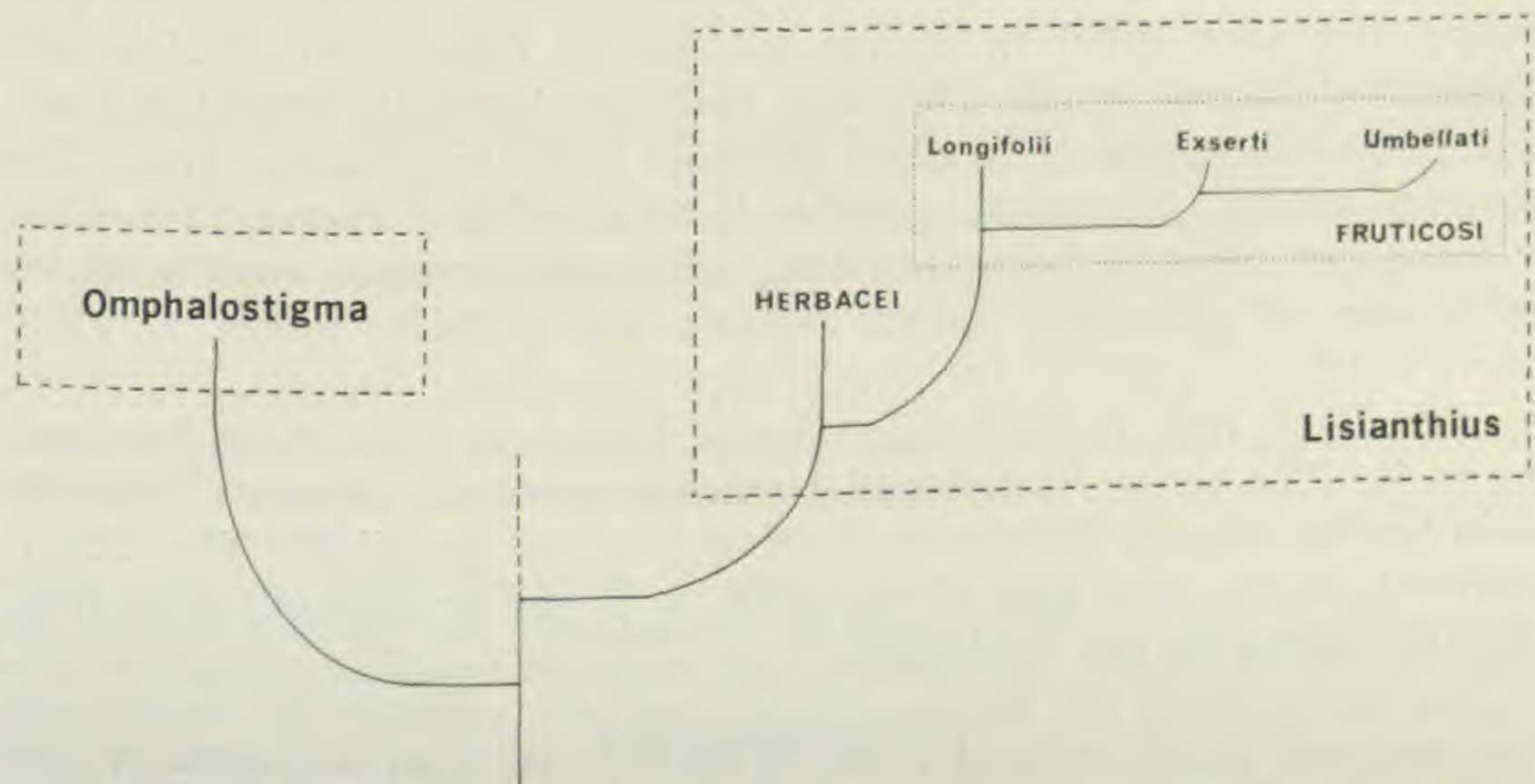


FIGURE 7. Probable relationships of the species groups in *Lisianthus*.

has flowers resembling *L. capitatus* in series *Umbellati* and is therefore intermediate between the species of that series and the remaining species in the subsection. In addition, the pollen of *L. exsertus* differs from that of all other members of the genus in having pollen with a nearly smooth rather than a distinctly reticulate sexine. On the basis of its somewhat intermediate position and its unique pollen, *L. exsertus* has been placed in a monotypic series, *Exserti*. The remaining fifteen species, still a rather heterogeneous assemblage, but all with diffuse inflorescences, tubular or funnelform corollas, and pollen with a reticulate sexine pattern, comprise the series *Longifolii*.

A suggestion as to the possible "phyletic" relationships between the various species groups is presented in FIGURE 7. This scheme is based almost entirely on gross morphological criteria and is highly conjectural. The generalized gentianaceous plant would appear to be somewhat as follows: a perennial, monopodial herb with a determinate main axis, inflorescences of compound dichasia, sessile leaves, rotate or salverform corollas, stamens of equal length in a given flower, and unilocular ovaries. If this type could be taken for the generalized one in *Lisianthus*, evolution has proceeded as follows: (1) from perennial herbs to annual herbs (rarely) in one direction and to subshrubs, shrubs or trees in the other; (2) from a determinate main axis to an indeterminate one; (3) from compound dichasia to apparently simple dichasia to solitary flowers; (4) from sessile leaves to distinctly petiolate ones; (5) from a salverform corolla to a tubular-funnelform one, with variations; (6) from stamens of equal length in a given flower to stamens of unequal length; and (7) from a unilocular to a bilocular ovary.

None of the extant species or species groups perfectly fits the hypothetical generalized type. The species in sect. *OMPHALOSTIGMA* approach it but differ in having petiolate leaves and nearly bilocular ovaries. Likewise, the plants of subsect. *HERBACEI* also approach the hypothetical prototype, but they differ in having tubular or funnelform corollas and filaments of unequal length. Therefore, both sect. *OMPHALOSTIGMA* and subsect. *HERBACEI* appear to be early offshoots from the primitive type. The plants of subsect. *FRUTICOSI* resemble those of subsect. *HERBACEI* in flower form, but differ in being fruticose, with indeterminate main axes, inflorescences of apparently simple dichasia, and petiolate leaves, all characters which deviate from the hypothetical prototype. Subsect. *FRUTICOSI* has very likely been derived from subsect. *HERBACEI* or from the line leading to it. The series *Exserti* and *Umbellati* are both offshoots from the main line in subsect. *FRUTICOSI*, leading to series *Longifolii*. The *Exserti* shares characters with both of the other series and presumably arose from the line leading to the *Umbellati*.

[To be continued]