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A REVISION OF THE GENUS LOPHOSTOMA (THYMELAEACEAE)

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THIS STUDY OF LOPHOSTOMA is the last of three revisions treating the three genera which are currently recognized as comprising the subtribe Linostomatinae. Although a revision, as such, of *Lophostoma* has not previously appeared, Ducke (1915) in conjunction with the description of a new species of the genus, included a key which delimited the species as they were known at that time. His paper did not, however, include a full descriptive account or distribution of each species.

This genus of the Thymelaeaceae was chosen for study because it appeared to have what is considered the largest aggregation of primitive features found in the New World genera of the family. Some authors have included the species of this genus incorrectly with the Asiatic genus *Linostoma* Wall. ex Endl., even as recently as 1954 (Lemée). To be able to judge this relationship accurately, the two Asian members of the sub-tribe Linostomatinae were revised in preparation for the present study. As a result, I am convinced that while *Lophostoma* may be described as primitive it is at the same time unquestionably one of the most specialized of the eleven American genera. All three genera of the subtribe Linostomatinae occupy a rather specialized ecological niche, in that they tend to be scrambling shrubs which eventually become large lianas; while the other members of the family are generally trees or shrubs.

SPECIAL MORPHOLOGY

A few of the interesting morphological and anatomical features found within the genus *Lophostoma* are presented in this section. No attempt to include a complete anatomical survey of plant parts has been made; the emphasis being placed on paralleling information already published for the genera *Linostoma* and *Enkleia* Griff. (Nevling, 1961a, b). Although studies containing considerable anatomical information concerning members of the family have been published, the finest contribution most recently by Hamaya (1959), relatively little information is available concerning the New World genera. Additional gross morphological information can be found in the descriptions and discussion dealing with the individual species. In all instances, the materials examined were from herbarium specimens.

Mature stem and inflorescence axes were studied by means of free-hand sections which were stained with either safranin or phloroglucin and hydrochloric acid. This technique was employed also with young shoots.

Gross and microscopic structure of leaf blade and petiole was studied by clearing and staining gross specimens and thin sections. Staining was with safranin or with ferric chloride and tannic acid, in the case of cleared material, or with safranin and fast green, in the case of thin sections. Leaf material was tested also with phloroglucin and hydrochloric acid, as well as with potassium iodide and sulphuric acid, to estimate chemically the lignification or lack of it in certain tissues. As a supplementary test, leaf sections were stained with 0.5% Sudan IV in a solution of 80% ethyl alcohol to determine the presence or absence of cutin or fatty substances in epidermal walls. All specimens were examined with normal and polarized light.

Flower structure, including vascular pattern, was studied from cleared and stained whole mounts. The details of these techniques can be found in the first paper of this series (Nevling, 1961a).

Vegetative Morphology. The vegetative axis is monopodial with the leaves oppositely to alternately arranged upon it. The opposite leaf position is superficial and is the result of drastic condensation of the internode between two adjacent nodes. Alternate internodes seem to be affected in this manner. The degree of condensation is rather variable, accounting for the variation in leaf position from opposite to subopposite or alternate. Free-hand sections of the stem clearly show the initiation of the leaf traces to be on two separate levels, i.e., one usually departing from the stele of the stem prior to or simultaneously with the initiation of the second. The alternate leaf position appears to be restricted to shoots which are extremely vigorous, particularly those immediately subtending the floriferous region. This position is due to nondifferential elongation of all internodes. In every case, a single leaf trace per node is formed and the resultant gap is unilacunar.

Bifurcate and trifurcate branching of the vegetative shoots is found regularly in all species. In some instances, branching is induced by damage to the apical bud but generally it is spontaneous. The branches, which may be equal or unequal, are the result of the coordinate development of one or more axillary buds with the apical bud. The apical bud usually retains its dominance. On one sheet, *Huber 8103 (Lophostoma calophylloides)*, the opposite axillary buds of the "nodal pair" have developed coordinately with the apical bud at five separate "nodes." Each branch is gracefully curved and bears inflorescences at its terminus. In the same collection, one specimen (BM) also has axillary branch development in which the buds do not occur in "pairs" but in an alternate position. The resulting branches, therefore, are alternately arranged. In L. dinizii Huber ex Ducke, the leaves subtending the developing axillary branches are found in the normal position, i.e., on the main axis immediately below the developing branch. In L. calophylloides (Meissn.) Meissn., L. amoenum Nevl., and L. ovatum Meissn., however, this leaf usually, but not always, is displaced and is borne upon the developing branch which it actually subtends. This type of displacement, which may be as much as three centimeters in Huber 8103, has been discussed previously in other papers (Nevling, 1961a, b).

Supernumerary axillary buds can be demonstrated for all species but appear to be most common in *Lophostoma calophylloides*. The result of the development of supernumerary buds can be seen in *Ducke 413* in which three branches have developed from a single leaf axil. The occurrence of such extra buds is important when interpreting the inflorescence forms found within the family.

All four species of the genus are known to be climbers or scramblers. Unciform branches are quite conspicuous in *Lophostoma ovatum* (see *Spruce 1461* and *Ule 8953*) where they are well developed, tapering very rapidly from the much enlarged base to the slender apex. Several reduced leaves are borne at the apex. Modified axillary branches, to facilitate climbing, are rarely encountered in *L. calophylloides* and *L. dinizii*. The single specimen of *L. amoenum* has several hooked branches. It is possible that, in these latter three species, the modified branches are formed regularly only on more mature shoots which are poorly represented in the herbarium material.

The extraxylary fiber sheath surrounding the stele, by which the family often is identified in the field, is well developed. These fibers, as determined by chemical means, are lignified. In addition, other lignified fibers are found within the pith where they appear to compose the bulk of the tissue internal to the stele. In contrast to the situation in *Enkleia* where the fibers are scattered throughout the pith, the fibers in *Lophostoma* are compactly organized as a solid central core surrounded by parenchyma. The xylary elements of the stem are lignified to a greater extent than the corresponding elements in either *Linostoma* or *Enkleia*.

The leaves are dorsiventral. The upper epidermis is uniseriate, composed of tabular cells (except in Lophostoma ovatum and L. amoenum in which they are vertically elongate), and is uninterrupted by stomata. The upper epidermal cells are thin-walled in L. calophylloides but the outer periclinal wall is conspicuously thickened in L. dinizii, L. ovatum, and L. amoenum. The thickened walls of the latter three species when treated with Sudan IV give the characteristic staining for cutin or other waxy substances. The palisade tissue is composed of very compact columnar cells which occupy, together with the upper epidermis, one-third (L. calophylloides and L. dinizii) to one-half (L. ovatum and L. amoenum) the depth of the leaf. The spongy parenchyma is quite loosely organized except in L. ovatum in which this tissue is the most compact of any species of the subtribe. The individual parenchyma cells are irregularly shaped. The xylary tissue of the midrib in L. ovatum is arc-shaped with the phloem



FIGS. 1-4. Cross section of lower leaf epidermis of species of *Lophostoma* including the stomatal apparatus. Guard cells are shown in cross section, accessory cells (immediately adjacent to guard cells) are shown in longitudinal section. Mesophyll and other leaf tissues not illustrated. Note differences in shape of

restricted to the lower surface; in L amoenum it may encircle the midrib. In both L calophylloides and L dinizii the margins of the xylary arc have folded back on the arc itself with the phloem being carried partially around $(L \ calophylloides)$, or completely around $(L \ dinizii)$, the midrib. The xylary elements are poorly lignified as determined by chemical tests. The phloem elements are of the largest size in the latter species. The lower epidermis is uniseriate and is interrupted often by stomata. In all species the outer periclinal walls are thickened and stain with Sudan IV. Some thickening of anticlinal cell walls occurs in L calophylloides. In some instances, the inner periclinal walls also may be thickened, particularly when they overlie air chambers. The outer periclinal cell walls of the lower epidermis, in $L \ dinizii$ and $L \ ovatum$, in addition to being thickened each bear a conspicuous papilla.

The stomata of all species of this genus are of the pit-type previously described for *Linostoma decandrum* (Roxb.) Wall. ex Endl. and for all species of *Enkleia*. A rosette of awl-shaped accessory cells surrounds each stoma, the number of accessory cells being variable (generally seven, eight, or nine, but as few as five and as many as eleven). Each accessory cell extends beyond the guard cells forming an urceolate (*Lophostoma calophylloides*) or campanulate (*L. dinizii*, *L. ovatum* and *L. amoenum*) structure. Occasionally an accessory cell may be found being shared by two adjoining stomata. The guard cells are borne at the base of the accessory-cell rosette and therefore are not truly sunken. Some differences in stomatal structure, as well as epidermal structure may be found among the species (Figs. 1–4), but the amount of variation has not been determined, so their taxonomic worth cannot be evaluated at this time.

The pinnate venation is similar throughout the genus. The primary lateral veins generally are quite numerous, although the number appears to be variable. They are straight or slightly arcuate and end in a variously developed submarginal vein. The orientation of veins forms a pattern which is indistinguishable from that found in the Asiatic genus *Linostoma*. A fiber sheath is associated with all veins. The submarginal vein is better developed in *Lophostoma amoenum* than in the three other species, and in all instances it very nearly corresponds with the leaf margin.

The secondary veins after departing from the primary veins appear, for the most part, to reverse direction, i.e., toward the midrib. In addition, they are oriented parallel to the primary veins. Direct cross connections between primary veins are not formed. Extraxylary fibers are associated also with the veinlets.

Extraxylary fibers are not restricted to close proximity to vascular tissue in Lophostoma calophylloides and L. dinizii but wander aimlessly about the leaf. They are vermiform and reminiscent of those found in Enkleia malaccensis (Nevling, Fig. 9, 1961b) and Passerina filiformis L. (Thoday,

epidermal cells and differential thickening of cell walls. 1, L. calophylloides (Spruce s.n.); 2, L. dinizii (Ducke 9050); 3, L. ovatum (Fróes 2057); 4, L. amoenum (Wurdack & Adderley 43208).

1921). The situation in *L. ovatum* and *L. amoenum* is quite different, the fibers being associated only with the veins and veinlets. These fibers are replaced at the extremities of the veinlets by irregularly shaped sclereids similar to those found in the leaf of *Linostoma pauciflorum* (Nevling, *Text Fig. II*, 5, 1961a). I found it impossible to stain the fiber walls with either phloroglucin and hydrochloric acid or potassium iodide and sulphuric acid.

In all species of the genus, the xylem, at mid-petiole, is arc shaped but the precise configuration depends entirely on the position of the section, as a sequence of forms is found when progressing from the proximal (i.e., attached to the stem) to the distal end. As the trace leaves the stem and enters the petiole it is arc shaped, the edge of the arc begins to involute in a very short distance, and the lateral edges become adjacent and form a complete ring of xylem (except in Lophostoma dinizii in which the ring is not quite continuous). The center of the ring is occupied by parenchyma cells. Serial sections of the petiole of L. amoenum show that the circle of xylary tissue, formed by the involution of its lateral margins, reopens into an arc prior to entering the leaf blade. The leaf traces have their origin from the lateral margins of this arc. External to the xylem "ring" is a continuous band of phloem. The phloem is always external to the last formed xylary elements regardless of the position of the xylem. Individual xylary elements have very thickened walls similar to those previously reported for Enkleia. These cells stain with phloroglucin and hydrochloric acid indicating lignification.

Extraxylary fibers are found in the petioles of Lophostoma calophylloides, L. dinizii, and L. amoenum but are lacking in L. ovatum. They do not stain either with phloroglucin and hydrochloric acid or with potassium iodide and sulphuric acid. A considerable cortex of parenchyma cells is found in all species. Irregular crystals can be found in a few cortical cells in L. calophylloides, L. dinizii, and L. amoenum (birefringent in polarized light) but have not been found in L. ovatum. This character probably is of no taxonomic significance as indicated by work in other genera of this family (Gilg, 1894; Hamaya, 1959; Nevling, 1961).

Reproductive Morphology. The same terminology which I applied in previous papers concerning the Thymelaeaceae is used here. The inflorescence is composed of a primary peduncle, a rachis, secondary peduncles, and flowers with their pedicels. In striking contrast to the other members of the Linostomatinae, the species of *Lophostoma* lack the conspicuous pair of bracts associated with the primary peduncle. In addition, the bracteole may or may not be present.

The floriferous branches of *Lophostoma* are composed of one to several inflorescences which collectively appear to form a single terminal "inflorescence." The flowering branches generally are young shoots, either terminal or ascending branchlets. In *L. ovatum* and *L. amoenum* the "inflorescence" is simple, di- or trichotomously divided and consists of a terminal inflorescence, which is sometimes reduced to a single flower, and

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one or two lateral inflorescences. In L. calophylloides the "inflorescence" is composed of three to five individual inflorescences which are pinnately arranged. The individual inflorescences are relatively closely spaced. In L. dinizii the "inflorescence" appears dichotomously paniculate. As there is nondifferential elongation of the internodes, the inflorescences appear to alternate on a flexuose main axis. In actuality, the inflorescences terminate the shoot, but their formation is accompanied by the coordinate development of an axillary branch which assumes the role of a main axis until the succeeding node where the pattern is repeated. In all species, each individual inflorescence is simple with the flowers racemosely arranged.

The bract-like reduced leaves which are found at the base (in Lophostoma calophylloides, L. ovatum, and L. amoenum) or the summit (L. dinizii) of the primary peduncle are analogous to the paired bracts found in Linostoma and Enkleia. Their bract-like appearance is due to reduced size, thinner texture, and striking color. Their lack of homology to bracts is shown by their deciduous nature and the source of their vascular supply. The trace which supplies vascularization to this "reduced" leaf departs from the stele prior to inflorescence branching. The leaf is displaced onto the axillary branch which it subtends anatomically. This developmental pattern precisely repeats that found in the reduced and displaced leaves of both Linostoma and Enkleia. In addition to these features, in L. amoenum, several pairs of leaves subtending the inflorescence may also be colored and bract-like. It is entirely possible that if the paired bracts in Linostoma serve as insect attracting devices that the bract-like leaves in Lophostoma have assumed the same function regardless of their position. Indeed, the inflorescence structure and floral morphology indicate adaptations for insect pollination.

The bracteole, usually situated at the summit of the primary peduncle, has been seen regularly only in *Lophostoma ovatum* and *L. amoenum*. In both species it is small and somewhat ephemeral which leads me to believe that this structure may also be found in living material of the other species.

The flowers, as in all members of the Linostomatinae, are bisexual, regular, pentamerous, perigynous and pedicellate. The terminology applied to floral parts is the same as I have used in previous papers (Nevling, 1959, 1961a, b). Additional information concerning the gross morphology of the flower, beyond that presented in the following discussion, may be found in the specific descriptions.

The calyx tube, which is composed of the fused bases of calyx, corolla, and androecial members, is cylindric in all species. The size of the tube is rather constant throughout the genus, varying from 10-16 mm. in length. The exterior is glabrous (*Lophostoma dinizii*), puberulent (*L. calophylloides* and *L. amoenum*), or puberulent to tomentulose (*L. ovatum*). All species bear trichomes in the tube interior which are exclusively unicellular and unbranched with a somewhat crinkled appearance due to an undulate cell wall. This undulate wall distinguishes them immediately from the trichomes of *Linostoma* and *Enkleia* in which the wall is straight. The in-

terior is villous in the lower one-half or two-thirds, the density of trichomes varying somewhat among the species. In the upper one-half or one-third the tube is glabrous or nearly so. The trichome distribution is assumed to be associated with pollinators to encourage outcrossing. Spruce has noted that the flowers of *L. calophylloides* are perfumed, strengthening the probability that the plants are oriented toward insect pollination. The pollinating agent is unknown up to the present time but Burrows has shown in his recent work (1960) on New Zealand *Pimelea* that the pollinators tend to be nonspecific.

The calyx tube is vascularized by ten distinct veins (the anatomical observations are based on Lophostoma calophylloides, L. ovatum and L. amoenum only, due to lack of sufficient material). Five of the traces are in the antisepalous position (median traces) and five are in the alternisepalous position (commissural traces). The traces to the alternisepalous staminal whorl depart from the commissural traces only slightly below the insertion of the stamens. Shortly thereafter, the traces to the antisepalous staminal whorl depart from the median traces. Immediately after the departure of the androecial traces, both median and commissural traces undergo repeated divisions to form a complex network of vasculature which innervates the calyx lobes. A fiber sheath is associated with each vein, being more highly developed in L. ovatum than in L. calophylloides.

The shape of the calyx lobes varies among the species, and in *Lophostoma ovatum* within the species, but not significantly so. The inner surface is glabrous in all species. The lobes are vascularized by approximately a dozen veins which branch and anastomose freely. This large number of veins contrasts with the three or five trace condition in *Linostoma* and *Enkleia*. The aestivation is quincuncial.

The petals are inserted at the orifice of the calyx tube in an alternisepalous position but the median clefting of the petals is complete resulting in the formation of five petal-pairs (appearing to be 10 distinct petals). The lobes are squamelliform, erect, subexserted to exserted, and at most 1 mm. long. They are variously comose except in a few specimens of *Lophostoma calophylloides* in which they are glabrous. The trichomes are distributed on both surfaces of the petals in *L. calophylloides* (when trichomes are present) and *L. dinizii*, on the outer surface only in *L. ovatum* and, in *L. amoenum* either on the outer surface or on both surfaces. The trichomes appear nearly moniliform due to the strongly undulate cell walls. There is no vascularization of the petals in any of the specimens which I have examined.

The androecium consists of ten stamens inserted on the calyx tube. They are in two whorls, the upper whorl in the antisepalous, the lower whorl in the alternisepalous position. The traces which vascularize the stamens reflect the two-whorl pattern. The traces to the alternisepalous whorl depart from the commissural calyx traces lower in the tube than those from the median calyx traces depart to vascularize the antisepalous whorl.

The filaments are relatively short (to 3 mm. long) and filiform, with

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those of the antisepalous whorl longer than those of the alternisepalous whorl. They are glabrous exclusively. Vascularization is by a single bundle which ends blindly at the middle of the connective in *Lophostoma calophylloides* or at the apex of the connective in *L. ovatum*.

The anthers are exserted except in *Lophostoma amoenum* where the alternisepalous are sometimes included. They are 4-lobed and 4-locular in cross section. Dehiscence is longitudinal.

The pollen grains of all species are uniform and indistinguishable from those of *Linostoma* and *Enkleia*. As in the latter two genera, they are polyporate and highly sculptured.

The presence of a disc, contrary to many previous reports, is confirmed in Lophostoma calophylloides and L. ovatum but appears to be absent in L. amoenum, and is questionable in L. dinizii due to insufficient material. It is borne at the base of the calyx tube and surrounds the base of the gynoecium. It is insignificant in size, annular, minutely lobed and glabrous. The vascularization, if any, could not be determined.

The gynoecium is composed of a single more or less sessile pistil, presumably of the pseudomonomeric type. Vascular patterns could not be established, except in *Lophostoma ovatum* and *L. amoenum*, because of overwhelming difficulties in clearing this organ. The gynoecium was treated with a variety of clearing agents for greatly extended periods of time without satisfactory results.

The ovary is superior, ellipsoid and unilocular. It is densely sericeous. The trichomes are unicellular and erect. The trichome walls are undulate (except in Lophostoma amoenum in which the walls are nearly smooth) and quite similar to the walls of the trichomes borne on the petal lobes. The pattern of vascular supply in L. ovatum is guite similar to that illustrated for Linostoma decandrum (Nevling, Text Fig. III. 1, 1961a). There are two main veins, one of which remains unbranched into the style and the other gives rise to four or five small branches, which vascularize the ovary wall, before passing into the style. A third accessory trace ends slightly above the middle of the ovary and is unbranched. No ovular trace was observed. In Lophostoma amoenum the vascular supply is similar to that illustrated for Linostoma pauciflorum (Nevling, Text Fig. III. 3, 1961a). Two main veins are continuous from the ovary base to the base of the stigma. One of these traces gives off a few small branched traces in the upper part of the ovary wall; the other gives rise to a well-developed, hook-shaped, ovular trace.

The style is borne terminally (or somewhat eccentrically in *Lophostoma amoenum* only) and seems to be intercalated about one-quarter from the base. This trace has no connection at either end and has no cross connections with any other trace. Near the summit of the style in *L. ovatum* one of the main traces dichotomizes so that a total of four veins is found just below the stigma, whereas in *L. ovatum* the traces remain unbranched. The stigma is capitate and its position within the calyx tube is variable and dependent on the time of pollination (see Burrows, 1960). Stylar elongation must be rather rapid as the protoxylem elements are straight

and quite elongate in comparison to the much shorter and sinuous elements vascularizing the ovary wall.

Unlike Linostoma and Enkleia, the fruit preservation in Lophostoma is good. In three species of the latter genus a single fruit per inflorescence develops. The drupe is enclosed by the accrescent, papery, urceolate calyx tube. The tremendous development of the tube following anthesis is quite extraordinary. The shape and armature of the drupe varies among the species (FIGS. 5–10). The simplest drupe is found in L. calophylloides in which the eccentric apex is abruptly acuminate and somewhat hooked. The wall is smooth (although subject to considerable wrinkling on drying). In L. dinizii the drupe apex is flat with a horizontal corona of irregularly shaped spines. The drupe wall, in this species, is marked by ten



FIGS. 5-10. Illustrations of the drupes and accrescent calyces of species of Lophostoma, \times 1. FIGS. 5, 6. L. calophylloides (Spruce 1305); 5, drupe; 6, accrescent calyx (broken at apex). FIGS. 7, 8. L. dinizii (Ducke 9050); 7, drupe; 8, accrescent calyx. FIGS. 9, 10. L. ovatum (Ducke 704); 9, drupe; 10, accrescent calyx.

heavy ribs which bear mammillate projections. The ribs run from apex to base. In addition, an inconspicuous groove is found on one side which may interrupt the corona. The most complex drupe is found in L ovatum in which the apex is bicornate and the middle third of the wall is marked by ten vertical, strongly serrate wings. The wings are abruptly truncate one-third the distance from the base of the drupe, the lower third of the drupe being nearly cylindrical. What function, if any, these fancy elaborations of the drupe apex and wall serve, or may have served, is beyond my imagination.

GEOGRAPHY

As in the other genera of the Linostomatinae, the geographic distribution of species and of the genus *Lophostoma* presents no problems which could not be anticipated. The genus as presently known is restricted to the Amazon drainage system (see map for distribution of the species). *Lophostoma calophylloides* has the most extensive range but it is almost certain, even in this case, that the full range is not yet known. The disjunctions shown on the map probably will prove to be of no significance and to be due only to insufficient collection. Some 50 years hence it may be possible to delimit more precisely the range of this species.

The geographic range of the genus presents only three notable differences from that presented by Domke (*Karte 3*, 1934). The first involves the elimination of two disjunct localities: specimens marked, "Rio Janeiro" (*Glaziou 14080*) are either in error or the specimen was collected from horticulture; Spruce's "Barra" collections which are from present day



MAP 1. Distribution of the species of Lophostoma: dots, L. calophylloides; triangles, L. dinizii; star, L. ovatum; square, L. amoenum.

Manaus (see Spruce p. 200. 1908) were apparently thought to be from Barra, State of Bahia on the Rio São Francisco. The second change is due to the collection of *Lophostoma calophylloides* by Ricardo de Lemos Fróes at São Paulo de Olivença which extends the range of this species, and the genus, almost 700 miles to the west. The third and most significant change is the result of the discovery of *L. amoenum* in Venezuela by Wurdack and Adderley. Collection of this new species, the result of exploration by the New York Botanical Garden, suggests the possibility of the discovery of additional species as exploration continues.

Specimens of Lophostoma calophylloides bear notations indicating the presence of the species in ecological situations called "igapó," "restinga" and "terra firme. The igapó is defined (Ducke & Black, p. 11. 1943) as "swamp forest where the soil never dries out completely even in summer. . ." The restinga are (Ducke & Black, *ibid.*) "narrow bands of higher alluvions rarely or never flooded. . ." Lophostoma ovatum is known from "igapo" and "campina." The campina is defined (Ducke & Black, p. 10) as "small spots of open land, surrounded on all sides by the great virgin forest." Unfortunately, comparable information for L. dinizii and L. amoenum is lacking.

MATERIALS

This revision is based on specimens from the following herbaria, the abbreviations for which are taken from Lanjouw & Stafleu's *Index Herbariorum*, *Part I*. Ed. 4 (Regnum Vegetabile, **15**. 1959).

- A Arnold Arboretum of Harvard University, Cambridge
- BM British Museum (Natural History), London
 - c Botanical Museum and Herbarium, Copenhagen
 - F Chicago Natural History Museum, Chicago
 - G Conservatoire et Jardin botaniques, Genève
- GH Gray Herbarium of Harvard University, Cambridge
- IPA Instituto de Pesquisas Agronômicas, Dois Irmaõs
- к Herbarium, Royal Botanic Gardens, Kew
- L Rijksherbarium, Leiden
- LE Herbarium of the Department of Systematics and Plant geography of the Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad
- Mo Missouri Botanical Garden, Saint Louis
- NY New York Botanical Garden, New York
- P Muséum National d'Histoire Naturelle, Paris
- RB Jardim Botânico, Rio de Janeiro
- s Naturhistoriska Riksmuseum, Stockholm
- U Botanical Museum and Herbarium, Utrecht
- US U. S. National Museum, Smithsonian Institution, Washington
- w Naturhistorisches Museum, Wien.

I wish to take this opportunity to thank the directors and curators of the above institutions for allowing me to examine the specimens in their care.

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The illustrations of the new species and of the fruits of *Lophostoma* are the work of Miss Judith A. Kroll to whom I am most grateful.

TAXONOMY

Lophostoma (Meissn.) Meissn. in DC. Prodr. 14: 600. 1857.

Linostoma sect. Lophostoma Meissn. in Mart. Fl. Bras. 5(1): 72, t. 30. 1855 (TYPE SPECIES: Linostoma calophylloides Meissn.).

Scandent shrubs or lianas, the axillary branches sometimes modified for climbing, the bark containing many fibers. Leaves opposite (or approximate) to alternate, simple, pinnately veined, entire, petiolate, estipulate, the primary lateral veins numerous, more or less straight and parallel. Inflorescences borne from the terminal portions of young shoots, racemiform, the primary peduncle bearing a colored bract-like reduced leaf, true paired bracts absent. Flowers bisexual, pentamerous, perigynous; calyx tube cylindric, nonarticulated, inconspicuously ribbed, glabrous or variously pubescent; calyx lobes 5, quincuncial, subequal; petals 5, medially cleft to the base, alternisepalous, inserted at the calyx tube orifice, the lobes variously squamelliform, erect, glabrous to densely comose; stamens 10, inserted in 2 whorls, the upper whorl antisepalous, the lower alternisepalous, the anthers basifixed, longitudinally dehiscent; disc (when known) minute, annular, lobed, glabrous; gynoecium single, pseudomonomeric, superior, sessile or nearly so, unilocular with a single anatropous ovule, the style terminal or eccentric, the stigma (when known) capitate. Fruit drupaceous and enclosed by the persistent and accrescent calyx.

KEY TO THE SPECIES

- a. Bract-like leaves associated with the inflorescence glabrous, white, reddish or reddish purple; leaves 6-14 cm. long, 3-6.5 cm. broad, the apex short to long acuminate; calyx tube glabrous to sparsely puberulent without; drupe apex abruptly acuminate or flat with a horizontal corona of irregular spines, the wall smooth or with 10 heavy, mammillate, vertical ribs from apex to base.
 - b. Primary lateral veins slightly arcuate; primary peduncle 1-6 mm. long, the secondary peduncles obsolete or nearly so; bract-like leaf borne near the base or very rarely at the summit of the primary peduncle, white; calyx tube sparsely puberulent and glabrescent without; drupe apex eccentric, abruptly acuminate and somewhat hooked, the wall smooth.
 - b. Primary lateral veins more or less straight; primary peduncle 10-35 mm. long, the secondary peduncles 2-5 mm. long; bract-like leaf borne near the summit of the primary peduncle, reddish or reddish purple; calyx tube glabrous without; drupe apex flat with a horizontal corona of irregular spines, the wall with 10 heavy vertical ribs with mammillate projections from apex to base.
- a. Bract-like leaves associated with the inflorescence minutely woolly or

puberulent, white or rose; leaves 2-5.5 cm. long, 1-3 cm. broad, the apex acute to obtuse, sometimes mucronulate; calyx tube puberulent to tomentose without; drupe (unknown in *L. amoenum*) with 2 horns at the apex, the middle one-third of the drupe wall with 10 strongly serrate vertical wings.
c. Bract-like leaves associated with the inflorescence white; leaf apex acute and sometimes mucronulate; calyx tube white; disc minute, annular;

c. Bract-like leaves associated with the inflorescence rose; leaf apex acute to obtuse; calyx tube pink to rose; disc absent; style somewhat eccentric.
 4. L. amoenum.

1. Lophostoma calophylloides (Meissn.) Meissn. in DC. Prodr. 14: 600. 1857.

Linostoma calophylloides Meissn. in Mart. Fl. Bras. 5(1): 72, t. 30. 1855 (Type: Spruce 967!).

Shrubs, becoming large lianas; young stems sparsely puberulent and glabrescent, reddish brown, minutely lenticellate; axillary branches normal or gently curved, rarely recurved. Leaves opposite or subopposite to rarely alternate, the blade ovate to elliptic or oblong, 6-12 (-14) cm. long, 3-5 cm. broad, short to long acuminate at the apex, obtuse at the base, coriaceous, glabrous, varnished above and darker than below, the costa immersed above, elevated beneath, the primary lateral nerves very inconspicuous, parallel and slightly arcuate; petiole canaliculate, rugose, glabrous, 5-7 mm. long. Inflorescences borne terminally on young shoots, often compound, generally composed of one terminal and two or rarely four lateral inflorescences; each inflorescence 3-8 (-12)-flowered, racemiform, puberulent, the primary peduncle 1-6 mm. long, the rachis 3-12 mm. long, the secondary peduncles obsolete or nearly so; bracts and bracteole absent or the bracteole rarely present and caducous, the displaced leaf of the subtending node borne near the base of the primary peduncle or very rarely near the summit, white or cream, usually bractlike and deciduous. Calyx tube cylindric, 13-15 mm. long, about 2 mm. in diameter at the orifice, sparsely puberulent and soon glabrescent without, minutely villous within; calvx lobes obovate, glabrous within; petals cleft to the base, the lobes squamelliform, with irregular margin, usually 0.5 mm. long but rarely to 1 mm., 0.5 mm. broad, erect, exserted, glabrous to densely and irregularly comose; filaments filiform, glabrous, the antisepalous filaments ca. 3 mm. long, the alternisepalous filaments ca. 1.5 mm. long, the anthers oblong, 0.5 mm. long, 0.25 mm. broad, exserted, the connective at most minutely produced beyond the pollen sacs, the antisepalous whorl inserted just below the petals, the alternisepalous whorl inserted about an anther's length below the antisepalous one; disc minute, annular, lobed, glabrous; ovary broadly ellipsoid, ca. 1 mm. long, shortsericeous, sessile, the style terminal, filiform, 1-1.5 cm. long, glabrous, the stigma capitate, included to exserted; pedicel ca. 4 mm. long. In fruit the calyx accrescent, subampullaceous, apex generally broken prior to drupe maturation, 3 cm. long, 2 cm. in diameter, glabrescent; drupe

ellipsoid, ca. 2.5 cm. long, 1 cm. in diameter, smooth, abruptly and eccentrically acuminate at the apex, the acumen usually slightly hooked.

ILLUSTRATIONS: Mart. Fl. Bras. 5(1): t. 30. 1855; Gilg in Engl. Nat. Pflanzenfam. III. 6a: 232, fig. 82f, g. 1894; Correa, Diccion. Pl. Uteis Brasil 2: 470. 1931.

DISTRIBUTION: Brazil, known only from five localities in the Amazon basin. This species has been collected in flower from August through February (May at São Paulo de Olivença) and in fruit from December through March. Ducke (1915) cites the plant as "frequent" around Belem. Spruce says that the plants are found in the forest where "the flowers are scented like the lilac, and being accompanied by young and perfectly white leaves, have a very pretty appearance." He further indicates that the perianth tube is "greenish tinged with purple; limb white." According to Ducke and Correa the plant is known locally as "cumacahy."

Brazil. AMAZONAS: Barra [Manaus] Spruce 967 (NY — lectotype), "1850– 51" (C, G, GH, W; photo. F, GH), 1305 (K, P), Fróes 20491 (F, US), Ducke 413 (A, F, MO, NY, S, US), 41311 " (US), 35690 (U); São Paulo de Olivença, Fróes 20898 (NY); without precise locality, Ducke 323 (NY). PARÁ: Rio Guamá, São Miguel do Guamá, beira do rio, Dardano & Black 48–3094 (IPA, U); Belém, Ducke 15516 (BM, G, US), Pires 2652 (NY), 3180 (US), 51807 (NY); Belém (Hort. Bot.) Huber 8103 (BM, P, U, US); Gurupá, Ducke 15942 (BM, G, US).

This genus was founded by Meissner, in 1857, in De Candolle's Prodromus. It is obvious from his writing (particularly in Mart. Fl. Bras. 5(1): 72. 1855) that the establishment of the genus had been on his mind for some time. In the latter publication he established a new section of *Linostoma* which he called sect. LOPHOSTOMA. This section, as he recognized it, was composed of a single species, *Linostoma calophylloides*. He listed as a synonym "Lophostoma Nov. Gen. Meisn. Mss. in Herb. Reg. Monac." and "Lophostoma calophylloides Meisn. Mss." Obviously at some time previous to the publication of the Flora Brasiliensis he seriously considered the publication of a new genus (Lophostoma) but changed his mind and described it as a new section instead. What facts or events led him in 1857 finally to establish the new genus are not known. Possibly the acquisition of new material which permitted him to describe the second species of the genus (Lophostoma ovatum) made him more certain of the position of the South American plant.

The typification of this species, the type species of the genus, is somewhat problematic. The basis for Meissner's *Linostoma calophylloides* (1855) is a specimen or specimens which were collected "c. Barra, oppidum prov. Rio Negro, floret m. Dec.-Mart. 1850-51 legit: R. Spruce." Elsewhere in the same publication, Meissner intimates the name is based on his manuscript name in "Herb. Acad. Monac." The question of whether or not this Spruce collection actually bore a collector's number is posed in the subsequent treatment, by Meissner (1857), of the Thymelaeaceae for De Candolle's *Prodromus*. In this publication, *Lophostoma* is given generic rank and the combination *Lophostoma calophylloides* is made. Meissn-

er cited two specimens: Spruce 967 and Spruce 1305; the citation of the former is followed by an exclamation point and the latter by a question mark. At the end of the description he said that the specimens were seen in the herbaria of "Monac. et DC." At present there are no specimens referable to the genus deposited at Munich and the photograph of the presumed type of L. calophylloides, deposited in the De Candolle herbarium is a Spruce specimen lacking a collector's number. Meissner's personal herbarium was purchased by the New York Botanical Garden and is on deposit there. In this collection are many sheets upon which one to several packets are attached which often contain fragments of classic material and are usually annotated fully by Meissner. On one such sheet I found a packet containing a number of detached leaves, a short stem and several flowers, bearing the following notation, "Barra, prov. Rio Negro, Spruce 967! Lophostoma calophylloides Dec.-Mart. 1850-51. legit R. Spruce Meisn. (26. III. 54.) in Hb. Ac. Monac." This information coincides perfectly with the citation both in the 1855 and 1857 publications and it seems clear that the New York fragment is a portion of the holotype and should therefore be designated as the lectotype until the holotype is relocated. On the same sheet is a packet containing a single fruit with the notation, "R. Spruce 1305, DC. Lophostoma calophylloides?" This specimen and information checks with Meissner's second citation of 1857.

- Lophostoma dinizii Huber ex Ducke, Arch. Jard. Bot. Rio de Janeiro 1: 51. 1915 (Type: Ducke 9050!).
 - Linostoma dinizii (Huber ex Ducke) Lemée, Fl. Guyan. Fr. 3: 108. 1954, lacking full basionym citation; Nevl. Jour. Arnold Arb. 42: 320. 1961, pro syn.

Shrubs becoming scandent with age; young stems terete, sparsely reddish-puberulent and glabrescent, reddish brown becoming gravish, the lenticels few, horizontally elongate, whitish; axillary branches not observed. Leaves opposite or subopposite except where the shoots are extremely vigorous as in subtending the inflorescences, the blade oblongelliptic or rarely broadly elliptic, 8.5-11 cm. long, 3-4.5 (-6.5) cm. broad, long-acuminate at the apex, obtuse to truncate at the base, thick-coriaceous, glabrous, darker above than beneath, the costa plane to immersed above, elevated beneath, the primary lateral veins usually inconspicuous, parallel and more or less straight; petiole shallowly canaliculate, rugose, glabrous, ca. 5 mm. long. Inflorescences borne terminally on the young shoots, appearing dichotomously paniculiform, sparsely reddish puberulent; each inflorescence 5-12-flowered, racemiform, the primary peduncle 1-3.5 cm. long, the rachis 5-13 mm. long, the secondary peduncles 2-5 mm. long, dilated at the summit, the true bracts and bracteoles absent but the reduced leaf of the subtending node borne near the summit of the primary peduncle, bract-like, broadly ovate, 2-7 cm. long, 1.5-4(-6) cm. broad, chartaceous, glabrous, reddish or reddish-purple, not persistent. Flower description based on a single flower: calyx tube cylindric, ca. 11.5 mm. long, 1 mm. in diameter at the orifice, glabrous on the outer surface, sparsely villous within except for the glabrous upper third; calyx lobes lanceolate, ca. 3 mm. long, 0.75 mm. broad, glabrous within; petals cleft to the base, the lobes squamelliform, ca. 0.5 mm. long and broad, completely comose; stamens exserted, the filaments filiform, ca. 1.5 mm. long, glabrous, the anthers oblong, ca. 1 mm. long, 0.5 mm. broad, the antisepalous whorl inserted about an anther's length below the petals, the alternisepalous whorl inserted about an anther's length below the antisepalous whorl; disc (?); ovary ellipsoid, ca. 2 mm. long, densely sericeous, the style terminal, filiform, glabrous, the stigma not seen. In fruit the calvx accrescent, ampulliform, ca. 5 cm. long, 1.7 cm. in diameter, glabrous, the drupe ellipsoid, ca. 3 cm. long, 1.5 cm. in diameter, sparsely villous, with 10 heavy vertical ribs with irregularly-shaped, short-mammillate projections from apex to base with an inconspicuous groove on one side and with a small flat horizontal corona of irregular spines at the apex.

DISTRIBUTION: Collected only twice, both times in the state of Pará, Brazil. The collections were made either slightly before or after flowering in September and December.

Brazil. PARÁ: Oriximiná, bas Trombetas, *Ducke 10988* (BM, G, US); Rio Mapuera affl. Trombetas super cataractam Caraná, *Ducke 9050* (BM, F — photo. and fragment, G, RB — lectotype, U, US).

In the original description of this species no type was designated although two specimens, *Ducke 10988* and *9050*, were cited. I have seen three sheets of *Ducke 10988*: a specimen from Geneva with old inflorescences but lacking flowers, a specimen from the British Museum with very young flowers and a specimen from the Smithsonian Institution with a single mature flower. The collection of *Ducke 9050* is more widely distributed with the most complete sheet at Rio de Janeiro. This specimen consists of leafy shoots, old inflorescences and a single mature fruit. On this basis, I choose *Ducke 9050*, the specimen at the Jardim Botânico of Rio de Janeiro, as the lectotype.

The name Lophostoma dinizii has appeared, to my knowledge, twice before being validly published, first in Bull. Soc. Géographie 20: 105. 1909; and the following year in Bol. Mus. Goeldi 7: 163. 1910. In both instances the name appeared without description and must be considered as a nomen nudum.

3. Lophostoma ovatum Meissn. in DC. Prodr. 14: 600. 1857 (TYPE: Spruce 1461!).

Linostoma albifolium Barbosa Rodrigues, Vellosia ed. 2. 1: 67. 1891 (TYPE: Barbosa Rodrigues 63), ex char.

Lophostoma albifolium (Barbosa Rodrigues) Gilg, in Engl. Nat. Pflanzenfam. III. 6a: 232. 1894.

Lophostoma bolleanum Domke, Notizbl. 11: 350. 1932 (Type: Ducke 23469!).

Scrambling shrub becoming a climber; young stems terete, reddish brown, short puberulent and soon glabrescent, sparsely lenticellate; axillary branches normal or modified and unciform. Leaves opposite or subopposite, the blade ovate to elliptic or oblong-elliptic, 2-4.5 cm. long, 1-2.5 cm. broad, acute and sometimes minutely mucronulate at the apex, cuneate to obtuse at the base, thin-coriaceous, glabrescent above, somewhat papillate beneath, darker above than beneath, the costa plane to immersed above, slightly elevated beneath, the primary lateral veins, inconspicuous, parallel and more or less straight, the submarginal vein coinciding with the margin; petiole canaliculate, rugose, glabrous, 2-3 mm. long. Inflorescences terminal on young shoots, bi- or trifurcately compound; each inflorescence 8-15-flowered, racemiform, puberulent, the primary peduncle 2-7 mm. long, the rachis 6-30 mm. long, the secondary peduncles 0.5-1.5 mm. long, the true bracts absent, the bracteole borne at the summit of the primary peduncle, minute and ephemeral, the reduced leaf of the subtending node borne near the base of the primary peduncle, bract-like, minutely golden woolly (white in nature), caducous. Calyx tube cylindric, 12-15 mm. long, ca. 1.5 mm. in diameter at the orifice, white, tomentose to puberulent without, villous within except the glabrous upper third; calyx lobes oblong to lanceolate, 2.5-3.5 mm. long, ca. 1.5 mm. broad, glabrous within, spreading; petals cleft to the base, the lobes obtusely squamelliform, ca. 0.5 mm. long and broad, erect, subexserted, comose on outer surface, glabrous on inner surface, trichomes exserted beyond the orifice; filaments filiform, 1-2 mm. long, glabrous, the anthers oblong, 0.5-1 mm. long, 0.25-0.5 mm. broad, exserted, the antisepalous whorl inserted just below the petals, the alternisepalous whorl inserted about one-half anther's length below the antisepalous one; disc minute, annular, lobed, glabrous; ovary ellipsoid, 1.5-2.0 mm. long, short-sericeous, sessile, the style terminal, filiform, 10-15 mm. long, glabrous, the stigma capitate, included to exserted; pedicel ca. 2 mm. long, enlarging to 4 mm. in fruit. In fruit the calvx accrescent, ampulliform, ca. 7 cm. long, ca. 2.5 cm. in diameter, glabrescent except for the extreme apex; the drupe ellipsoid, ca. 4.5 cm. long, ca. 1.5 cm. in diameter at base of the wings, glabrescent, bicornate at the apex and with 10 strongly serrate vertical wings which are truncated at the lower third of the drupe, the style persistent.

ILLUSTRATION: Vellosia ed. 2. 3: pl. 20. 1891, as L. albifolium.

DISTRIBUTION: Brazil, known with certainty only from the vicinity of Manaus. A. Glaziou collection (*Glaziou 14080*) is labelled from Rio de Janeiro but I believe this to be an error. *Index Kewensis* gives the citation "Venezuela" for this species but as previously indicated by Ducke (1915) this record is in error. The plant has been collected in flower and fruit in February and May. According to Ducke, the plants are found in swampy and periodically inundated woods (see also introduction). Barbosa Rodrigues noted that he encountered the species on the left bank of the Rio Negro.

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Brazil. AMAZONAS: Barra [Manaus] Spruce 1461 (K; LE; NY — fragment of holotype; P), Fróes 20527 (F, NY), Ule 8953 (G, GH, K, L), Ducke 704 (F, GH, NY, MO, US), 23469 (isotypes of L. bolleanum: G, U, US), 24036 (RB). Locality doubtful: "environs Rio Janeiro," Glaziou 14080 (C, K, P).

Barbosa Rodrigues, in the original description of Linostoma albifolium, admits some apprehension because he is acquainted with only one South American species (L. calophylloides) of the genus. He has not seen the other species and therefore he poses the rhetorical question whether it might not be the same as his new species. It is. I have not seen a type specimen but his very complete description and a well executed illustration leave little doubt that L. albifolium belongs in synonymy here.

Domke described Lophostoma bolleanum from a Ducke collection. As principal features to distinguish it from L. ovatum he gave larger, more oval and somewhat thicker leaves, shorter calyx tube, obtuse bud apex, multiflowered inflorescence and exserted stigma. Examination of the isotypes of this taxon shows all these statements to be true provided the specimens are contrasted solely with the types of L. ovatum. If one considers also the additional collections of L. ovatum now available it seems apparent that the characteristics which Domke mentions fall well within the total range of variation of a single species. Only the character of the exserted stigma cannot be demonstrated in other specimens positively referable to this species and this characteristic is now known to be unreliable (Nevling, 1961a, b). Domke gives the leaf position as alternate but the isotypes which I examined have opposite leaves. However, one leaf of the opposite pair often was shed giving the false impression of an alternate arrangement.

4. Lophostoma amoenum Nevl. sp. nov.

Vitis, ramis juvenibus pubescentibus usque glabrescentibus. Folia plerumque opposita coriacea glabra ovata usque elliptica 3.5–5.5 cm. longa 1–3 cm. lata apice acutis usque obtusis basi cuneatis; petiolo 2–4 mm. longo glabro. Inflorescentia compositae racemiformae pubescentes; pedunculo primario 1–5 mm. longo; rhachide 3–6 mm. longo; pedunculis secundariis usque 1 mm. longis. Bracteae roseae pubescentes. Flores hermaphroditi 10–16 per inflorescentem; pedicello ca. 3.5 mm. longo; calyce cylindrico 15–16 mm. longo 1.5–2 mm. lato roseo extus pubescente; calycis lobis subequalibus intus glabris; petalis 10 squamelliformis ca. 0.5 mm. longis dense barbatis; staminibus 10 in planis 2, antheris oblongis 0.5 mm. longis 0.25–0.5 mm. latis; disco nullo; pistillo 1, ovario ellipsoidale 1.5 mm. longo, sericeo, stigmate capitato exserto. Fructus non vidi. Holo-TYPUS: Wurdack & Adderley 43208 (A). (FIGS. 11–13.).

Vine to 2.5 m., young stems minutely puberulent and glabrescent, light brown becoming grayish; axillary branches sometimes curved or recurved. Leaves opposite or sometimes alternate on vigorous shoots, the blade ovate to elliptic, 3.5–5.5 cm. long, 1–3 cm. broad, acute to obtuse at the apex, cuneate at the base, coriaceous, glabrous, darker above than



beneath, the costa immersed above, elevated beneath, the parallel lateral nerves conspicuous and slightly arcuate beneath; petiole slightly canaliculate, rugose, glabrous, 2-4 mm. long. Inflorescences borne terminally on young shoots, compound, two or three appearing as a single inflorescence; each inflorescence 10-16-flowered, racemiform, puberulent, the primary peduncle 1-5 mm. long, the rachis 3-6 mm. long, the secondary peduncles to 1 mm. long, the bracteole minute, caducous, the displaced leaf of the subtending node near the summit of the primary peduncle, bract-like, rose-colored, minutely puberulent, the leaves of two or more subtending nodes usually similar. Calyx tube cylindric, 15-16 mm. long, 1.5-2 mm. in diameter at the orifice, minutely puberulent without, pink, the tube interior glabrous in upper half, villous in lower half; calvx lobes elliptic or lanceolate, 4-4.5 mm. long, ca. 1.5 mm. broad, glabrous within; petals 5, completely cleft to the base and appearing as 10, squamelliform, spatulate, fleshy, ca. 0.5 mm. long, 0.25-0.5 mm. broad, densely comose on outer surface, glabrous or comose on inner surface; filaments filiform, glabrous, ca. 0.5 mm. long, the anthers oblong, 0.5 mm. long, 0.25-0.5 mm. broad, the antisepalous whorl inserted immediately below the petals, exserted, the alternisepalous whorl inserted 1 or 2 anther's lengths below the antisepalous, included to exserted, sometimes slightly exceeding the petals: disc absent; ovary ellipsoid, 1.5 mm. long, sericeous, the style somewhat eccentric, filiform, glabrous, the stigma capitate, small, papillate, exserted; pedicel ca. 3.5 mm. long. Fruit unknown.

This attractive vine was collected in flower on June 27, 1959, at an elevation of 120 meters. The collectors indicate that it is "occasional" on the Caño San Miguel.

Venezuela. AMAZONAS: Caño San Miguel near Limoncito 15 km. from Río Guaiana [2° 41' N, 67° 25' W], elev. 120 m., *Wurdack & Adderley 43208* (A, NY).

This new species resembles most closely Lophostoma ovatum from which it may be distinguished in gross morphology by the following characteristics: leaf shape; more numerous bract-like leaves, rose colored and minutely puberulent beneath; pink to rose-colored calyx tube which is slightly larger than that of L. ovatum; small anthers; absence of a disc; excentric style. The fruit, unfortunately, is not known up to now, but one can scarcely help wondering whether the fruit of L. ovatum will differ as much from that of the species presently known as their fruits differ from each other.

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FIGS. 11–13. Illustration of *Lophostoma amoenum*. FIG. 11, habit \times 1.5. FIG. 12, detail of flower, \times 6. FIG. 13, detail of trichomes from petal, \times 12. All figs. from type.

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